

First report on vertebrate coprolites from the Upper Cretaceous (Santonian) Csehbánya Formation of Iharkút, Hungary



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ARTICLE INFO

Article history:

Received 26 September 2016

Received in revised form

5 February 2017

Accepted in revised form 10 February 2017

Available online 12 February 2017

Keywords:

Coprolites

Plant and animal residues

High phosphorous content

Carnivore coprolites

Partially digested animal inclusions

ABSTRACT

More than 2600 coprolites produced by vertebrates have been found in the fluvial lacustrine beds of the Upper Cretaceous (Santonian) Csehbánya Formation, Iharkút, western Hungary. In this study the mineral components, embedded dietary residues of these coprolites were examined and their ecological significance are discussed. The coprolite assemblage, containing mostly small-sized (length between 0.8 and 8.6 cm) specimens, can be ordered into seven different morphotypes, among which the spiral ones might have been produced by fish with spiral intestinal valves. The surface of the coprolites is mostly smooth and desiccation cracks were observed in only one case, suggesting that most of these coprolites were buried in-situ without long-term subaerial exposure. The fine-grained matrix of coprolites contains small holes, partially digested plant and animal residues but no sedimentary particles. CT-scanning was an effective method for revealing embedded dietary residues despite that the coprolites contain a large amount of pyrite. The coprolites contain cuticle remains, coalified seeds, pollen grains and diatoms. Animal residues may be the evidence of predation: mollusk shell and bone fragments, ganoid scales of Lepisosteiformes fish were frequent and one Pycnodontiformes fish tooth was found as well. It is not possible to ascertain the real producer of the coprolites, but, according to these remains, the Lepisosteiformes and Pycnodontiformes fish were included in the producer's prey. Not only the bone- but also the plant-bearing coprolites are highly phosphatic with mineral apatite in their matrix. However, the embedding fluvial sediment has significantly different chemical composition. The high phosphatic content of coprolites and the apatite might be derived from the carnivorous diet. Plant remains in the phosphatic coprolites may imply an omnivore producer or were the result of their incidental ingestion. Rapid burial and the mineral content of the animal nutriment might have been the responsible factors for the good preservation of the excrements.

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1. Introduction

The study of coprolites (fossil feces) is an old and important part of paleontology, dating back to the 19th century (Buckland, 1829). The analysis of fossilized feces helps improve the knowledge on the biological processes and lifestyle of extinct animals (Chin et al., 1998; Chin, 2002). As in other parts of paleontology, paleoscatology also takes notice of the recent zoological observations (Fisher, 1981), but, of course, in most cases it is not easy (or practically

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not possible) to ascertain the real producer of the coprolites (Hunt and Lucas, 2010). However, fossilized excrement could be informative not only about feeding behavior, but the embedded remains are useful for a more specific knowledge on the paleoenvironment (Prasad et al., 2005). In most cases, these remains are the evidence of the ancient food web (Zatoń and Rakociński, 2014), but coprolites often contain well-preserved incidentally swallowed (during drinking or feeding) plant or animal fragments as well.

Iharkút is an Upper Cretaceous (Santonian) vertebrate-bearing locality in the Bakony Mountains of western Hungary (Fig. 1), where productive and continuous excavations have been carried in the last 13 years (Ösi et al., 2012). Besides the very rich coprolite assemblage, the field work resulted in a diversified assemblage of continental and freshwater animals, including fish, amphibians, turtles, mosasaurs, lizards, pterosaurs, crocodilians and dinosaurs, comprising about 35 vertebrate species (Csiki-Sava et al., 2015). The vertebrate assemblage is dominated by bones of aquatic and semi-aquatic animals, whereas the bones of terrestrials are subordinate (Botfalvai et al., 2015). Rich and diverse fossil plant material was also discovered from the same horizon with the bones and coprolites, and is dominated by Normapolles and angiosperm elements (Bodor et al., 2012; Bodor and Baranyi, 2012; Botfalvai et al., 2016).

The aim of this preliminary study is to document the coprolites produced by vertebrates from the Santonian Csehbánya Formation of Iharkút, western Hungary. Besides grouping them into morphological categories, we describe their chemical composition, embedded remains and discuss their taphonomical aspects and paleoecological significance.

2. Locality and geological settings

The coprolite material described here was collected from the Iharkút vertebrate locality, which is situated in a recultivated open-pit bauxite mine near the villages of Némethánya and Bakonyjácó in the northern part of the Bakony Mountains (the Transdanubian Central Range), western Hungary (Fig. 1A).

The oldest rocks of the Iharkút open-pit mine are Upper Triassic shallow marine dolomites (the Main Dolomite Formation; Fig. 1B). These rocks composed the irregular karstic surface that was filled with bauxite (the Nagytárkány Bauxite Formation) during the Late Cretaceous (pre-Santonian) subaerial exposure phase (Bárdossy and Mindszenty, 2013). The bauxite and the dolomite are unconformably overlain by the Upper Cretaceous (Santonian) Csehbánya Formation, which yielded abundant coprolites, plant and vertebrate fossils.

All of the coprolites were discovered in the Csehbánya Formation at the Iharkút vertebrate-bearing locality. The Csehbánya Formation at Iharkút locality is built up of cyclic alternations of sandstone, and variegated siltstone and clay layers with sporadic intercalation of thin coal seams. The entire sequence being interpreted to have been deposited by an anastomosing fluvial system in a topographically low-level, wet, alluvial plain environment (Jochai-Edelényi, 1988; Botfalvai et al., 2016). The paleontological (sub-tropical floodplain forest vegetation) and sedimentological (the absence of desiccation cracks, the frequent presence of hydromorphic paleosols and the subordinate amount of secondary (pedogenic) carbonate accumulation) investigations indicate that the climate was dominantly humid, but seasonal, with flash flood-like episodes during the deposition of the Csehbánya Formation at the Iharkút open-pit (Botfalvai et al., 2016). The palynological investigation pointed out that the sedimentation took place in the *Oculopolis zaklinskaiae* – *Brecolpites globosus* palynozones, the *Oculopolis-Triatriopollenites* subzone indicating a late Santonian age of the formation in this outcrop (Bodor and Baranyi, 2012).

The coprolites described in this paper are from the basal part of site SZ-6 (see Fig. 1C), that also yielded most of the vertebrate remains at Iharkút (Botfalvai et al., 2015), and is represented by a 10–50 cm thick basal breccia layer composed of gray-green sand, siltstone, clayclasts, pebbles. The poorly-sorted sandy breccia (including fine to coarse sand and pebbles) is interrupted by laminated siltstone horizons and these coarse and fine grained layers are repeated several times resulting in a stacked series of fining upward units. Sedimentological and taphonomical investigations suggest that the coprolite yielding horizons were deposited by ephemeral high density flash-flood events, probably triggered by episodic heavy rainfalls (Botfalvai et al., 2016). Furthermore, the depositional area of this unit (site Sz-6) acted as a trap where current velocity of the flood suddenly decreased and the poorly sorted sand, ripped-up clayclasts, pebbles, bones and coprolites accumulated (Botfalvai et al., 2015, 2016).

The Csehbánya Formation is unconformably covered by Middle Eocene (Lutetian) conglomerates and limestones higher up in the stratigraphic sequence. The youngest deposit here is the Pleistocene loess which forms a discontinuous blanket over most of the area (Botfalvai et al., 2016).

3. Materials and methods

3.1. Material

The studied specimens were collected during the excavations of the Hungarian Dinosaur Expedition between 2000 and 2012 (2600 specimens) and were placed in the Vertebrate Collection of the Department of Paleontology and Geology of the Hungarian Natural History Museum. See [Supplementary Data](#) for the list and data of investigated coprolites.

3.2. Methods

In the course of the field work the potentially fossiliferous layers were opened up into meter sized blocks and were carefully broken into smaller pieces to find the remains. The covering sediment was removed from the surface of all the collected coprolites with mechanical preparation and they were carefully cleaned with wet toothbrush in a laboratory. After preparation, morphological groups were separated based on complete (or nearly complete) specimens. The intact and the fractured surfaces of the coprolite material (2600 specimens) were scrupulously examined with the use of light microscope. We selected 45 specimens based on visible remain content and different morphology for further investigations (CT, mineralogical composition, palynological processing, thin sectioning). Apart from these, 14 specimens were dissolved in H₂O₂ to extract microscopic residues. In addition, one more coprolite specimen is discussed here, with important taphonomical features (VER 2016.1333.) (see [Supplementary Data](#)).

Because investigating a coprolite is often destructive (Chin, 2002), photographic documentation, measurements, surface marks and color data recording (with the usage of Munsell Geological Rock-Color Chart) was first done (see [Supplementary Data](#)). During the processing of the selected ones we took care that half of the coprolite specimens be left for further analysis. The inclusions found in the coprolites were taken out by mechanical preparation.

3.3. Morphological groups

The different morphotypes for the Iharkút coprolites were established mainly based on their external shapes. However following McAllister (1985) and Coy (1995) their internal patterns

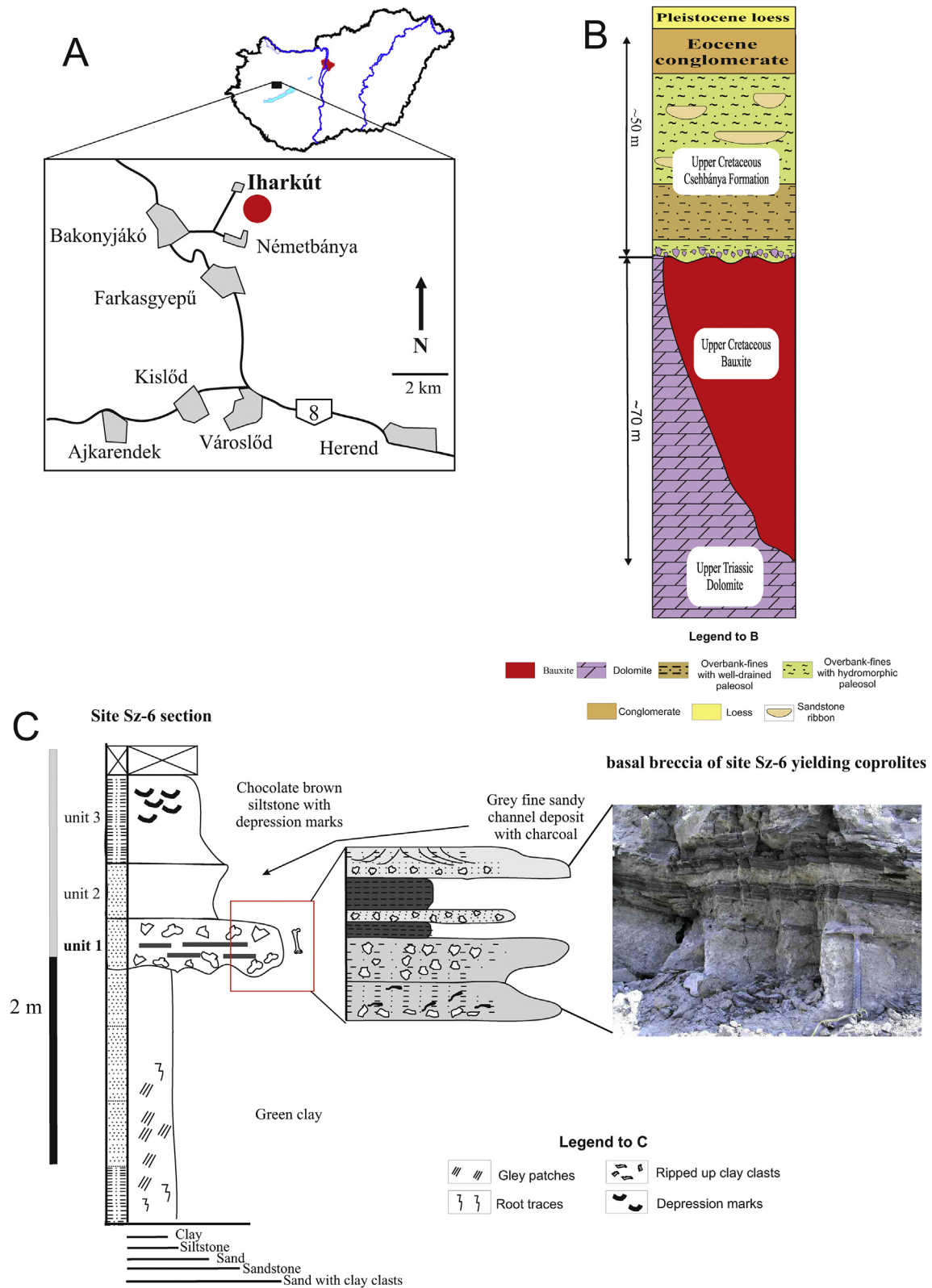


Fig. 1. Map and schematic stratigraphic section of the coprolite-bearing vertebrate site: **A**, Location map of the Iharkút vertebrate locality; **B**, Schematic section of the Iharkút open-pit mine; **C**, Schematic stratigraphic section of site SZ-6 after Botfalvai et al. (2016).

(visible on broken surfaces and by polished sections) have been used as well for the morphological grouping.

3.4. Taphonomical observations

Following Northwood (2005), the coprolite's contact with their former environment was recorded. The contact with the sediment, surface marks, desiccation cracks and mineral coatings was studied.

3.5. CT-scanning

Computed Tomography scans were recorded at the Institute of Diagnostic Imaging and Radiation Oncology of the Kaposvár University by a Siemens Stomatom Definition Flash instrument. We examined eight large coprolites from different morphological groups to find their inner inclusions (VER 2016.1297.; VER 2016.1301.; VER 2016.1302.; VER 2016.1304.; VER 2016.1305.; VER 2016.1307.; VER 2016.1308.; VER 2016.1310.). The scans were analyzed with the RadiAnt DICOM viewer program. The analysis of the scans helped find and collect the inclusions from the coprolites, moreover the CT-scanning digitally recorded the morphology of the unique coprolites.

3.6. Mineralogical components

Samples were grinded and top-loaded powder specimens (in low background silicon sample holders) were investigated with powder X-ray diffraction (Bruker D8 Advance, Cu-K α source, 40 kV 40 mA). Measurements of 0.007° (2 θ)/14 s were run in parallel beam geometry (with Göbel-mirror) and Vantec 1 position sensitive detector (1° opening). The Bruker DiffracPlus EVA software was used for the evaluation of diffractograms and TOPAS4 for quantitative and structural data obtained by Rietveld refinement.

3.7. Micropaleontological processing

Standard palynology preparation following the Schulze Method was used, like in Bodor and Baranyi (2012). Six specimens from different morphological groups and with different macroscopic inclusion content were studied in this way. The sampled coprolites were chosen because of their content in macroscopic plant (VER 2014.119.; VER 2016.1319.; VER 2014.118.) and bone remains (VER 2016.1322.) and the cylindrical (VER 2016.1304.) and roundish (VER 2016.1307.) morphology. Preparates from the inner matrix of the coprolites were examined by a Nikon Eclipse LV100Pol polarization microscope and QImaging Micropublisher 5.0 RTV digital camera. Fourteen roundish coprolites were processed by H₂O₂ to find additional fossils. These coprolites were separated into three size groups: one specimen with 2 cm diameter, four with 1 cm diameter, and nine with less than 1 cm. The powdered coprolites were boiled in H₂O₂ (30%) for eight hours. The remnants were washed three times with distilled water, and a few drops of the suspension were poured onto coverslips and allowed to dry. Permanent slides were mounted with the aid of a hot plate and using Pleurax as the mounting medium. The permanent slides were studied with LEICA DM LB2 microscopy (100X HCX PLAN APO inner objective) and a VSI-3.0M(H) digital camera.

3.8. Scanning electron microscopy

SEM was used for the identification of small embedded remains. Coating with gold–palladium was accomplished using a XC7620 Mini Sputter Coater for 120 s at 16 mA. A Hitachi S-2600N scanning electron microscope operated at 20 kV and 5–8 mm distance was used in the Department of Botany of Hungarian Natural History

Museum. In one case, the composition of the microscopic inclusions was analyzed by energy dispersive spectrometry (EDS). Measuring took place at the laboratory of Department of Petrology and Geochemistry at the Eötvös University. An AMRAY 1830 scanning electron microscopy was used for this analysis.

3.9. Thin sectioning

Seven coprolites with macroscopic plant (VER 2016.1311.; VER 2014.118.) and animal (VER 2016.1298.; VER 2016.1299.; VER 2016.1324.; VER 2016.1325.; VER 2016.1329.) inclusions were studied with thin sectioning. Preparations were made in the laboratory of the Department of Physical and Applied Geology at the Eötvös University. Coprolites were placed into synthetic resin (a mixture of IPOX MR 3012 and IPOX MR 3122 with the titre 10: 4.). The coprolites were cut in different directions with a Buehler Iso-Met 1000 Precision Saw. After impregnating the cutaway surface with synthetic resin, we polished them with SiC powder (standard grain sizes: 220, 400, 600, 800). The samples were then placed onto glass plates and after that, the cutting and polishing of the other side was done. The thin sections were examined using a Nikon Eclipse LV100Pol polarization microscope and a QImaging Micropublisher 5.0 RTV digital camera.

4. Results

4.1. Morphological separation

The coprolites from Iharkút represent more size ranges, but they are characteristically larger than 4–5 mm, which indicates that they were most probably produced by vertebrates (Thulborn, 1991). Their shape is mostly irregular; some specimens are rather roundish, others are elongated. The elongated forms are straight or curved, sometimes rolled up. Seven morphotypes could be distinguished: cylindrical; cylindrical with tapered endings; amorphous; coiled; roundish; roundish with a concave side; and spiral (Fig. 2). The diameters of the studied roundish ones are between 20 and 45 mm, whereas the diameter of the roundish coprolites having a concave side is 12.8–16.9 mm. The largest length of the coiled coprolites is between 36 and 48 mm. Cylindrical coprolites with tapered endings are 26.75–56 mm long, whereas the cylindrical ones are 19.25–86 mm long. The length of the spiral coprolites is between 17 and 50 mm.

The shape of the coiled coprolites (Fig. 2D) seems like they were twisted around a central axis. Folds that are perpendicular to the length can be observed on their outer surface. Spiral coprolites (Fig. 2G) are elongated and the spiral pattern is visible on their transverse section (on broken surface and on polished sections too). In some specimens, the inner spiral pattern was not well visible, but the contours of the transverse section implied the spiral-like origin.

4.2. Taphonomical characters

About 2600 more or less complete coprolites were discovered from an area of approximately 400 m², showing a density up to 6 specimens/m². All of the coprolites from Iharkút have the same general inner structure: homogeneous fine-grained matrix containing small holes, partially digested plant and animal residues but no sedimentary particles. The color of their inner matrix is mainly grayish, pale brown, yellowish brown, mostly unicolored (exceptions: VER 2016.1305.; VER 2016.1308.; VER 2016.1311.; VER 2016.1321.), whereas the outer surface is always darker.

The embedded plant remains are coalified (not charcoaled, but only carbonized) similarly to the plant remains frequently present in the sediment (Bodor and Baranyi, 2012). In the case of

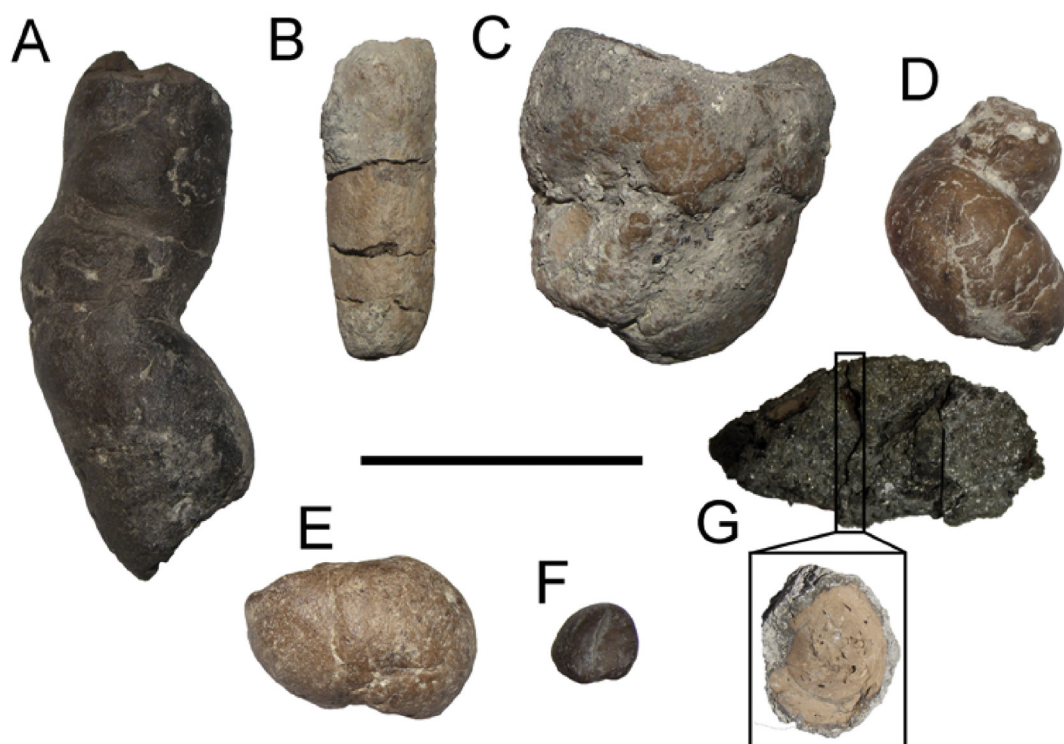


Fig. 2. Morphotypes of Late Cretaceous coprolites from Iharkút: A, cylindrical (VER 2016.1304.); B, cylindrical with tapered endings (VER 2016.1297.); C, amorphous (VER 2016.1310.); D, coiled (VER 2016.1290.); E, roundish (VER 2016.1307.); F, roundish with a concave side (VER 2016.1294.); G, spiral (place of transverse section is marked) (VER 2016.1312.) [Scale bar: 5 cm].

many specimens, it could have been observed that the coprolite was not transported by the covering sediment: a boundary can be separated, where the feces deposited on the surface of the underlying beds and on which the overlying sediments covered it later on (Fig. 3A). This preservational feature was mentioned as a “bird’s eye pattern” by Thulborn, 1991 (p.343 fig. 2).

The outer surface of the coprolites is mostly smooth, sometimes bearing a few pits. In some cases (such as: VER 2016.1312.; VER 2016.1306.) the real surface of the remains was not visible through the covering hard pyritic coating (Fig. 2G). In one case (VER 2014.119.) the visible surface cracks (Fig. 3B) continued into the body of the coprolite (Fig. 3C). These calcite and sediment filled cracks are wider on the surface and narrowing inward.

It is not easy to ascertain the pre-depositional morphology of the coprolites. For example, the roundish form could be the original excrement morphology or may be caused by the transportation in the river. However, according to their morphology, there are some coprolites which could have been more vulnerable in their soft state (Fig. 2A).

4.3. Mineral components

According to our measurements, both the plant- and bone-bearing coprolites are highly phosphatic, with mainly apatite in their matrix. However, apatite has not been detected in the host sediment (Table 1).

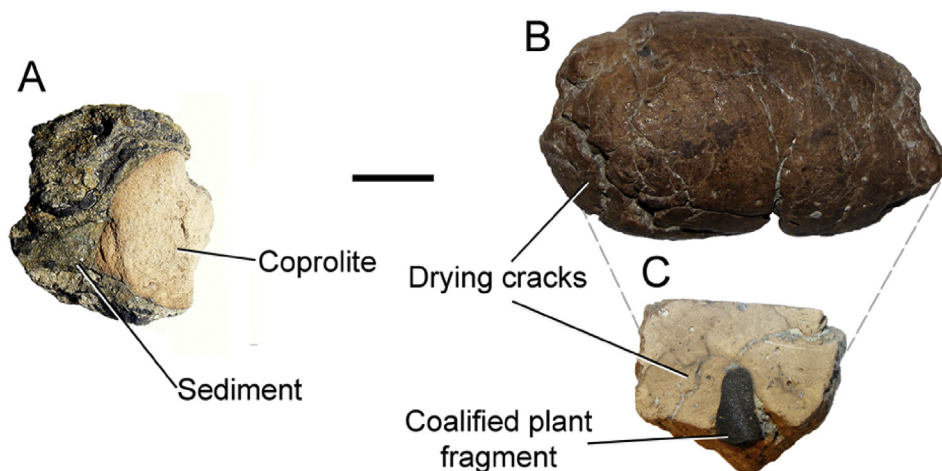


Fig. 3. Taphonomical observations on Late Cretaceous coprolites from Iharkút: A, Coprolite (VER 2016.1333.) in the host rock (‘bird’s eye pattern’); B–C, Plant-bearing coprolite (VER 2014.119.) with desiccation cracks on its surface (B) and inside (C) [Scale bar: 1 cm].

Table 1
Mineral components of Late Cretaceous coprolites from Iharkút.

Mineral phases (wt%)	VER 2016.1321. ^a	VER 2016.1322. ^a	VER 2014.119. ^a	HR-Swcc ^a	HR-Sst ^a
Apatite	94.4	87.0	84.1	—	—
Pyrite	5.6	—	1.3	—	—
Calcite	—	12.7	9.6	—	9.9
Dolomite	—	—	3.3	28.4	24.8
Quartz	—	0.3	1.7	35.1	65.3
Illite	—	—	—	19.3	—
Chlorite	—	—	—	5.9	—

^a VER 2016.1321. — coprolite bearing a cuticle fragment; VER 2016.1322. — Coprolite bearing a ganoid fish scale; VER 2014.119. — Coprolite bearing a seed and plant fragments; HR-Swcc — Host Rock — Silstone with clayclasts; HR-Sst — Host Rock — Sandstone.

4.4. Results from the micropaleontological processing

The preparates from the palynological processing contained a large amount of organic material. Five out of six samples contained plant fragments, and two samples contained Normapolles pollen grains (Bodor and Baranyi, 2012). Two samples contained plant cuticle remains, which can be separated into two groups: one type (Fig. 4A) has nearly hexagonal cells (about 50 µm width), whereas the other one has irregular cells (Fig. 4B). Both types were devoid of stomas. In the course of H₂O₂ processing, besides the organic material, 14 diatom fragments have been recognized by LM, but none during the SEM analysis. Because of their poor preservation, only two of them could be determined: the cylindrical diatoms are probably belonging to *Aulacoseira*, which is known from other Cretaceous localities as well (see e.g. Ambwani et al., 2003).

4.5. Macroscopic food remains

4.5.1. Plant remains

Thirteen coprolites from different morphological groups (roundish, spiral, cylindrical and amorphous) contained macroscopic plant remains. Among the embedded plant remains, some specimens are unidentifiable coalified fragments, but others are in better condition providing more information. The surface of seven broken coprolites preserved cuticle remains (Fig. 5A, B), being similar to the cuticle pieces with near hexagonal cell structure, also known from the palynological processing (Fig. 4A). These cuticle fragments are varying in size, but are always thinner than 1 mm: average thickness is 10 µm, whereas the width of the cell-like structures is varying between 30 and 50 µm (Fig. 5C). They are not coalified, but clearly separated from the matrix. Stomas are not

recognizable on their surfaces. Analysis of these cuticle remains with energy dispersive spectrometry showed that they do not differentiate from the matrix in their chemical components (Fig. 5D). Similar to the content of the inner coprolite matrix, mainly calcium (Ca), phosphorous (P), sulphur (S) and iron (Fe) are observable.

Two definable seeds were excavated from the coprolites. One of them is a large (6 mm long) seed (VER 2014.119.), (Fig. 6A, A/2), whereas the other (VER 2014.118.) is a small (1.55 mm long), partially digested one (Fig. 6B, B/2).

4.5.2. Animal remains

Animal remains were frequent in the small (1–2 cm diameter, such as VER 2016.1329.) and in the large sized (more than 5 cm in length, such as VER 2016.1301.) coprolites as well. These coprolites turned up from different morphologies, such as coiled, cylindrical and spiral.

Six analyzed coprolites contained mollusk shell fragments (Fig. 7A). The 60 studied coprolites contained 17 undeterminable bone fragments, the smallest being only 0.35 mm, whereas the largest is 5 mm in length. Most of the bone fragments showed the typical spongy structure of bones sometimes with pyrite crystals filling their cavities. On CT scans bone fragments are visible besides pyrite crystals (Fig. 7B). On the scans the inclusions differ significantly from the host matrix because of their different density (Milán et al., 2012).

Two teeth were found in the coprolites: a smaller one is a 3 mm long undeterminable fragment (Fig. 8A, A/2) (VER 2016.1313.), and a larger is a 7 mm long complete Pycnodontiformes fish tooth (Fig. 8B, B/2) (VER 2016.1329.). This fish tooth is rounded, bean-like in shape, similar to those Pycnodontiformes fish teeth which are

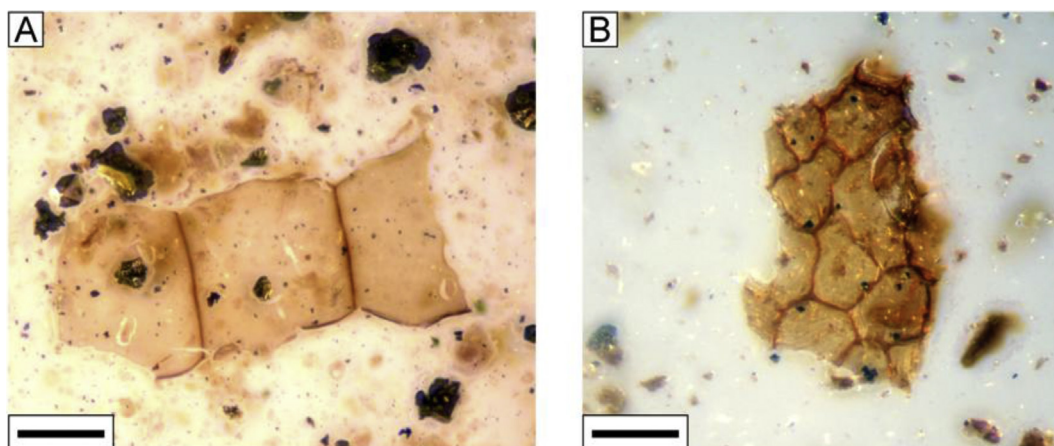


Fig. 4. Plant cuticle fragments from the micropaleontological processing of coprolites from Iharkút: **A**, Plant cuticle fragment with near hexagonal cells (VER 2014.118.) [Scale bar: 30 µm]; **B**, Plant cuticle fragment with irregular cells (VER 2014.119.) [Scale bar: 30 µm].

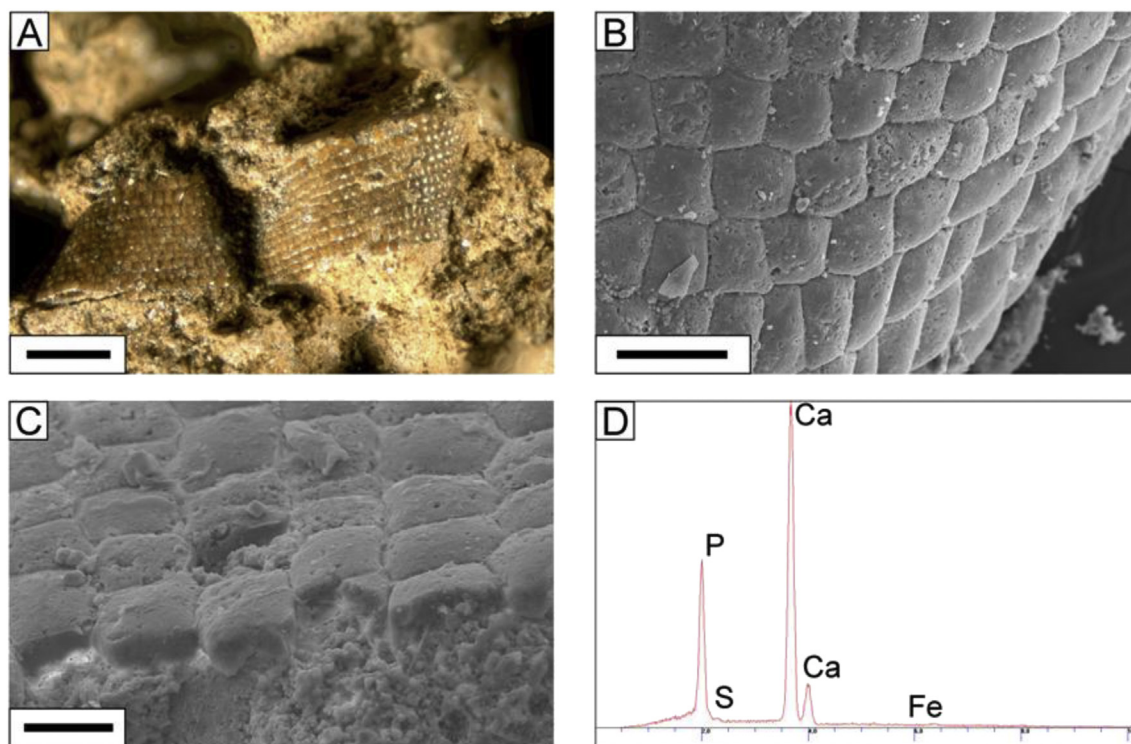


Fig. 5. Probable cuticle imprints in the matrix of coprolites from Iharkút: **A**, Probable cuticle imprint in the matrix of a coprolite (VER 2016.1321.) [Scale bar: 300 µm]; **B**, Scanning electron micrograph of a probable cuticle imprint on a broken surface (VER 2016.1321.) [Scale bar: 50 µm]; **C**, Probable imprints of the cells of cuticle on the broken surface (VER 2014.118.) (SEM) [Scale bar: 25 µm]; **D**, Energy dispersive spectrometry (EDS) measurement of a probable cuticle imprint (VER 2014.118.).

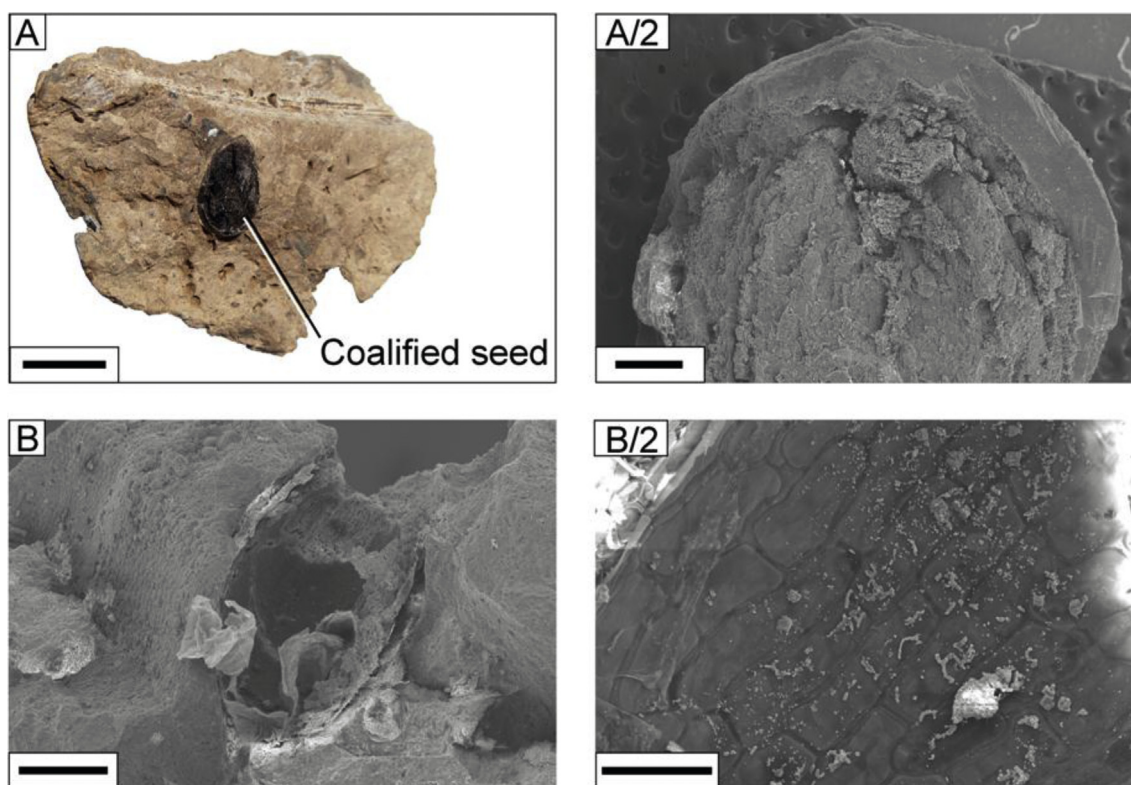


Fig. 6. Seed remains from Late Cretaceous coprolites from Iharkút: **A**, Coalified, probably Rosaceae seed (VER 2014.119.) [Scale bar: 0.5 cm]; **A/2**, Scanning electron micrograph of a probable Rosaceae seed (VER 2014.119.) [Scale bar: 0.5 mm]; **B**, Magnoliaceae seed (VER 2014.118.) (SEM) [Scale bar: 0.5 mm]; **B/2**, Inner structure of a Magnoliaceae seed (VER 2014.118.) (SEM) [Scale bar: 100 µm].

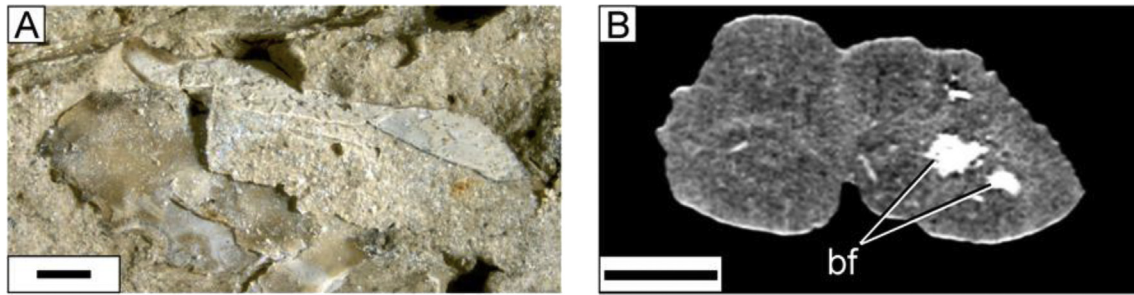


Fig. 7. Fragmentary animal remains in Late Cretaceous coprolites from Iharkút: **A**, Mollusk shell fragments (VER 2016.1323.) [Scale bar: 300 μ m]; **B**, CT-scan of a coprolite (VER 2016.1301.) showing areas with bone fragment (bf) inclusions [Scale bar: 2 cm].

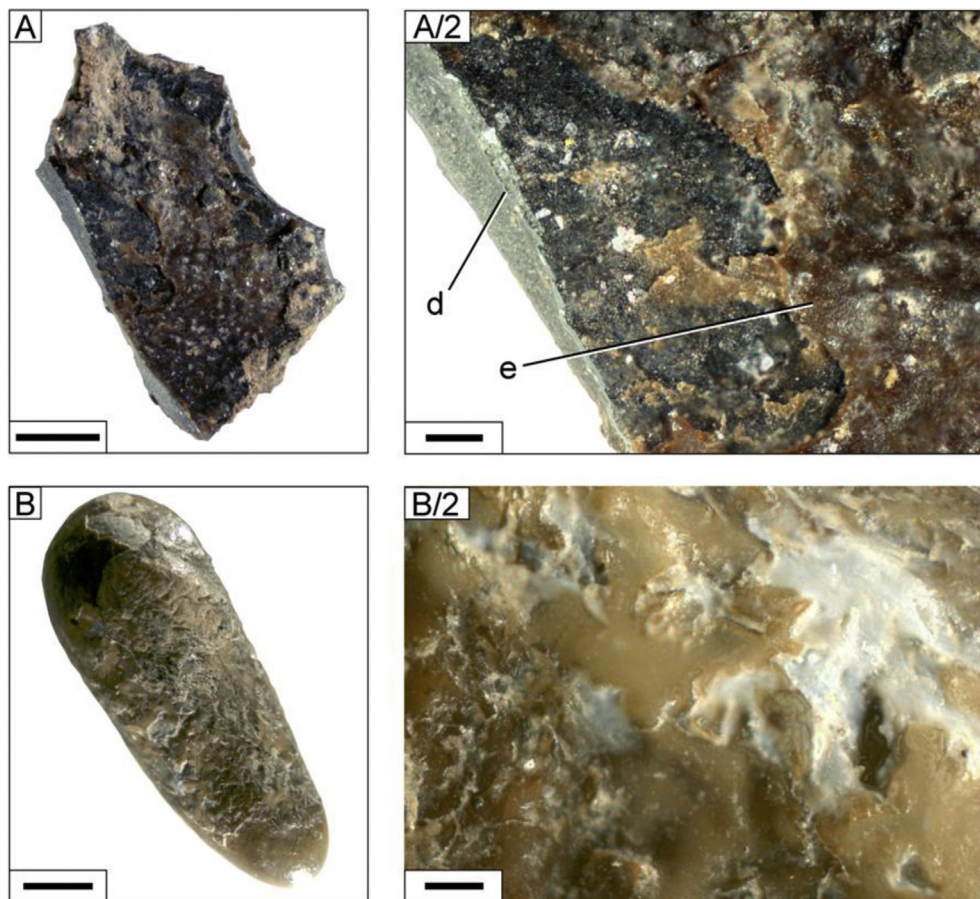


Fig. 8. Tooth remains from Late Cretaceous coprolites from Iharkút: **A**, Partially digested unidentified tooth fragment (VER 2016.1313.) [Scale bar: 0.6 mm]; **A/2**, Etched surface of the unidentified tooth fragment showing the dentine (d) and the remains of enamel (e) (VER 2016.1313.) [Scale bar: 120 μ m]; **B**, Tooth of a Pycnodontiformes fish (VER 2016.1329.) [Scale bar: 1.2 mm]; **B/2**, Etched surface of the Pycnodontiformes fish tooth (VER 2016.1329.) [Scale bar: 120 μ m].

well-known from Iharkút (sometimes in jaw fragments). According to previous studies these Pycnodontiformes fossils belongs to the genus *Coelodus* (Szabó et al., 2016b). Both teeth show the signs of digestion, but the fragments of the enamel is still visible on them (Fig. 8A/2, B/2). The Pycnodontiformes fish tooth was associated with small bone fragments in the coprolite (Fig. 9A).

Fifteen ganoid fish scales were also collected from four coprolites (Fig. 9B) (VER 2016.1299.; VER 2016.1313.; VER 2016.1317.; VER 2016.1322.). The size of these “diamond shaped” scales is varied from the 2 mm long fragment up to the 6.1 mm long almost complete scale. One of the characteristics of the ganoid scales is the enamel-like hypermineralized ganoin tissue (Sire et al., 2009) covering the surface of the scales. This ganoin layer was partially

eroded from the surface of the scales from the coprolites and in several cases the inner laminar structure (Fig. 9C) was visible (Fig. 9D) next to the extant ganoin. These scales probably belong to the Lepisosteiformes carnivore fishes, which are known from Iharkút by their skull and jaw elements, teeth, vertebrae, and scale fossils (Szabó et al., 2016a).

5. Discussion

5.1. Morphology

It is not possible to find clear connection between the coprolites and producers based on the seven recognized morphology, because

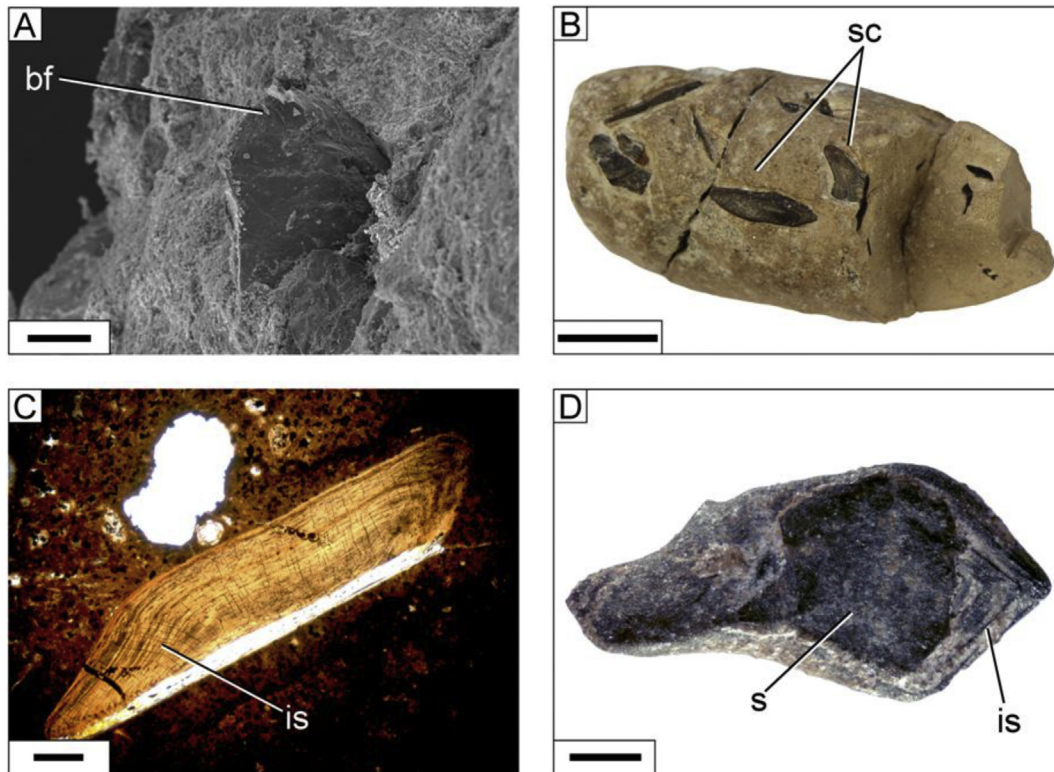


Fig. 9. A, Small bone fragment (bf) from a coprolite bearing a Pycnodontiformes fish tooth (VER 2016.1329.) [scale bar: 100 µm]; B, Small coprolite (VER 2016.1322.) with ganoid fish scale (sc) inclusions [scale bar: 0.5 cm]; C, Inner structure (is) of a ganoid fish scale in the thin section of a coprolite (VER 2016.1299.) [scale bar: 0.6 mm]; D, Partially digested ganoid scale with visible inner structure (is) next to an extant scale surface (s) from a coprolite (VER 2016.1299.) [scale bar: 0.6 mm].

often the same group of animals could produce different shaped excrement and the morphology might be varied by the different composition of the nutriment (Thulborn, 1991; Chin and Kirkland, 1998). Although there are morphologies with characteristic small size, this phenomenon does not mean that they were produced by smaller animals, since large animals could produce small sized excrement (Thulborn, 1991).

Only in the case of coiled and spiral coprolites is possible to find closer assumption for their origin. The shape of these coprolites suggests that they were produced by fish with spiral intestinal valves (McAllister, 1985; Thulborn, 1991). This pattern is similar to other spiral coprolites mentioned by Coy (1995). It is known from recent analogies that the function of the spiral intestinal valves is to increase the surface of nutriment absorption without the elongation of the intestines (Hassanpour and Joss, 2009). There are different types of spiral intestinal valves (differentiated on the basis of the width of the infolding tissue and the direction of the valves) and a similar type of intestine termed scroll valve (Parker, 1885; McAllister, 1985). Among spiral coprolites two main types are distinguished: heteropolar and amphipolar (Jain, 1983; Thulborn, 1991). On the heteropolar coprolites the narrow whorls are concentrated at one ending while on the amphipolar coprolites the whorls (relatively fewer than on the heteropolar ones) are extended on the whole surface of the coprolite (Thulborn, 1991). It is contentious that this distinction means taxonomical differences (Chin, 2002). The coiled coprolites from Iharkút (Fig. 2D) are most similar to the amphipolar type, whereas the tightly rolled spiral coprolites (Fig. 2G) resemble the heteropolar type. Unfortunately, the surface of the spiral coprolites with the best preserved inside spirally pattern is covered with hard pyritic crust, preventing us to observe the surface whorls. The matrix of the coiled and spiral coprolites contained bone fragments and fish scales. These residues

and the apatite in the matrix indicate that their producers probably consumed nutriment of animal origin (Hollocher et al., 2005).

Spiral valve intestine is mainly present in all Chondrichthyes (like sharks, rays and skates) and in lungfish (Hassanpour and Joss, 2009; Stringer and King, 2012). There is a vestigial spiral valve intestine in some actinopterygian too. The fossilized intestinal contents in the well-preserved Pycnodontiformes fish fossils from the Fossil-Lagerstätten (Kriwet, 2001) showed that these fish did not possess spiral valve intestine. Lepisosteiformes fish have a remnant spiral valve with few turns (Suttikus, 1963; Argyriou et al., 2016), but it is questionable that this structure could cause the up rolling of the excrement (Waldman, 1970). Up to the present, fossils of Chondrichthyes or lungfish are unknown from Iharkút. It is possible that these coiled and spiral coprolites were produced by the Lepisosteiformes fish, but their presence may indicate that the fish fauna of the fossil site may have also contained Chondrichthyes or lungfish.

5.2. Taphonomy

The fossils presented in this study are definitely coprolites and not concretions, that is further supported by the following taphonomical and sedimentological features: (1) in the host rock it is clearly visible that the excrement was deposited on a surface that was later covered by sediment (e.g. Fig. 3A); (2) in many cases coprolites were found in the siltstone layer, but mostly surrounded by coarser sandy sediments and the grain size of the fossilized excrement was finer than both sediments; (3) if they are not coprolites but concretions that were growing around in the altered chemical conditions caused by the decaying material, the “bird’s eye pattern” seen on many specimens could not have been observed; (4) lateral association among the coprolites was not

detectable; (5) the cylindrical and the coiled shapes of the observed nodules are not consistent with those that would be expected in chemical concentrations or fluvial transported intraclasts; (6) the observed specimens have relatively high phosphorous content, while this element was completely undetectable in the embedding sediments (see Table 1).

The cracks on the surface of the specimen VER 2014.119. probably formed by the drying of the feces (Fig. 3B,C). Their opening must have started from the surface, because they are perpendicular to it and wider outside and narrow inside the coprolite. The cracks are filled with sediment, so these feces probably dried on land and later on fell into the river where they were buried, or, alternatively, this specimen was reworked from a former accumulation during a flood event. Nevertheless, the presence of the cracks on the surface of the coprolite by itself does not necessarily indicate that the coprolite was deposited on land, because similar cracks can be developed by subaqueous shrinkage on the bedding surface, without desiccation (Pratt, 1998; Northwood, 2005). However, the syneresis cracks origin probably can be excluded in this case, because only one coprolite shows this modification and therefore the salinity changes during the deposition is a hardly tenable explanation. The cracks of specimen VER 2014.119. most probably formed by the drying of the feces.

Most of the observed coprolites have a smooth surface, without cracks, but this does not necessarily indicate that they were produced by aquatic animals, because (1) desiccation cracking is dependent on the moisture content of the original excrement (Northwood, 2005) and (2) feces of terrestrial animals can also be accumulated into the water saturated environment without getting dried. Based on taphonomical evidence, the habitat of producers of the observed coprolites certainly cannot be determined. However, it can be stated that most of the coprolites were buried rapidly after the accumulation without long-term exposure.

The morphology and size of coprolites probably provide information about the exposure and/or the transportation time prior to burial. They are built up from very fine, physically/biologically fragile and chemically reactive particles and thus their mass should have been rapidly reduced during transportation or when they were exposed on the soil surface for a long time. The presence of some larger coprolites (e.g. Fig. 2A) in the Iharkút assemblage suggests that some excrement was buried rapidly, without long transportation, whereas the smaller (1–3 cm) and the more rounded ones may have been transported for a while and/or reworked (similar to the large amounts of intraclasts; Botfalvai et al., 2016) from the former depositional area by the final, high density flash flood events.

5.3. Mineralogical components

Mineralogical composition of the coprolites shows that not only the bone- but also the plant-bearing coprolites mainly consist of apatite, whereas the host sediment is not phosphatic (Table 1). Phosphorus derived from diet is mainly present in the excrement of the carnivorous animals (Thulborn, 1991; Hollocher et al., 2005; Northwood, 2005), with the source in the apatite component, of the bone, but phosphorus attends the other parts of the body too. Most of the phosphorus is located in bones and teeth, but it is also present in the soft tissues and in the blood (Uribarri, 2007). The phosphorous content of the feces may not have changed appreciably during fossilization (e.g. Bradley, 1946), but it is conceivable that in some cases the microbial decay of the organic matter releases phosphorous into the pore water, creating a phosphorous enrichment in the coprolites during the fossilization (e.g. Northwood, 2005). However, the later scenario is unlikely, because the embedded sediments do not contain phosphorus, and this

element was only detectable from the coprolites, thus making it more conceivable that the phosphorous content of the studied coprolites related to the dietary of their producers.

Although in most terrestrial ecosystems the herbivorous animals highly exceed the number of carnivores, coprolites produced by herbivorous vertebrates are really rare (Chin and Kirkland, 1998; Chin, 2007). It is because the excrement of herbivores often contains more organic materials being a utility for smaller organisms (such as dung beetles) (Chin and Gill, 1996; Chin, 2007). Besides this, the excrement of herbivores does not contain *in situ* mineral components like calcium-phosphate in the case of carnivorous animals (Zatoń and Rakociński, 2014), that could quickly mineralize the dung. The coprolites of herbivores are mostly calcareous/siliceous nodules with concentrated plant remains, cemented with minerals from external source (Chin and Kirkland, 1998; Chin, 2007). In the case of carnivores or scavengers, the bone utilizing ability depends on the dentition and on the digestive system. The more acidic agent could dissolve more calcium-phosphate (Bergeim, 1926) which could be absorbed. It is documented in extant crocodiles that the acidic environment of their stomach (pH: 1.2) can totally decalcify the inorganic components of bones and teeth, even the resistant enamel and ganoin (Fisher, 1981). The consumed phosphorus cannot be absorbed completely: after getting through the acidic environment of the stomach, besides the absorption in the neutral or mildly alkaline intestines, the dissolved materials start to precipitate (Uribarri, 2007). After defecation, the re-precipitated phosphate will compose the matrix of the coprolite, which is a distinctive feature differentiating them from regurgitated pellets (Hattin, 1996).

Pyrite was traceable from the samples of coprolites, this mineral of external origin being highly present in the bone remains from the Csehbánya Formation as well (Tuba et al., 2006).

5.4. Inclusions from micropaleontological processing

The recognized diatoms and pollen grains from the coprolites were not the parts of the animal's diet, but they were rather swallowed accidentally during drinking or feeding. Identical sporomorphs and pollen grains are more concentrated in the palynofacies of the sediment than in the coprolites (Bodor and Baranyi, 2012). Both the sediment and the coprolites have high dispersed organic material concentration. The few diatom fossils discovered by H₂O₂ processing could be significant, since Cretaceous diatoms are rare (Ambwani et al., 2003; Witkowski et al., 2011). Unfortunately, however, the scarcity of these diatoms does not allow us for a more precise determination, more samples and further investigation being needed in this attempt.

5.5. Inferences from nutriment inclusions

The cuticle remains, recognized on the broken coprolite surfaces (Fig. 5) are probably imprints and consistent with the cuticle fragments with near-hexagonal cells found in the palynological processing (Fig. 4A). These remains were originally parts of a large cuticle surface, but, as they were indigestible (Bajdek et al., 2014), the matrix of the soft excrement embedded them. The organic cuticles disappeared during later diagenetic processes, but their shape is still visible in the fine-grained matrix of the coprolites. This theory explains why the EDS analysis showed the same chemical compositions (Fig. 5D) on the surface of these remains, as that seen in the matrix of the coprolites (Table 1). The other cuticle fragment type from the palynological processing, showing irregular cells (Fig. 4B), is similar to the underside leaf surface of the lotus. The underside epidermis of this type of leaf, being in contact with water, has no or just a few stomas and it is wax-coated (Ensikat

et al., 2011). It is possible that the cuticle fragments and cuticle imprints preserved in coprolites belonged to a cuticle of a water plant, which was indigestible due to its wax-coating.

One of the found seeds (VER 2014.119.), shows morphological similarities to Rosaceae seeds (Fig. 6A). However, there is no unequivocal Cretaceous record of Rosaceae (Friis et al., 2011). The fruit types of Rosaceae are highly diverse, from follicles, nuts and drupes to pomes (Cronquist, 1981). Based on the cross-section of the fossil (Fig. 6A/2) the inside layer of the pericarp is strong, thick and presumably wooden. These endocarps seem to be drupes, which is characteristic for the stone fruits of Rosaceae. The oldest unambiguous Rosaceae fossils are from the Eocene (*Paleorosa similkameenensis*) and show characters intermediate between subfamilies Spiraeoideae and Malvoideae, which have no drupes. Therefore, this seed from Iharkút requires a more detailed study for precise taxonomic determination.

According to the scanning photos of the other seed (VER 2014.118.) (Fig. 6B), the tegmen of its inner seed coat is single-layered, with rectangle shaped cells (20–40 µm length) on the inside surface. Fibrous lignin bundles and prismatic wall structure can be also observed (Fig. 6B/2). These features suggest an affinity to Magnoliaceae (Frumin and Friis, 1999; Friis et al., 2011), which are known from Iharkút (Bodor and Baranyi, 2012).

The mineralogical components of the coprolites from Iharkút imply that they were produced by bone and flesh consumers, based on the relatively high portion of phosphorus in the coprolites from Iharkút (e.g. Bradley, 1946; Chin et al., 1998; Northwood, 2005), even though more larger plant remains were embedded in them (seeds, cuticle fragments). The phosphorus content in the observed coprolites from Iharkút site probably suggests that they were produced by carnivores or scavengers, because the phosphorus is completely absent from the excrements of herbivorous animals (Thulborn, 1991; Chin and Kirkland, 1998; Hollocher et al., 2005; Northwood, 2005).

These plant remains might be the evidence of accidental swallowing, but they could have been part of a diet in case of omnivorous producers as well. May be these coprolites belong to *Iharkutosuchus makadii*, an omnivorous crocodile from Iharkút (Ösi et al., 2007), which might have consumed a wide range of food resources with its peculiar heterodont dentition (Ösi and Weishampel, 2009). Nevertheless, dentition not always reflects clear food preference. It was observed that the stomach of the wild crocodiles sometimes contains seeds and other plant fragments (Platt et al., 2013); furthermore, it was documented that captive caimans eats fruits (Brito et al., 2002). Knowing these facts, it is possible that animals in the ancient ecosystem with carnivorous dentition occasionally consumed plants and produced phosphatic coprolites with seeds inside.

The teeth and ganoid scales from the coprolites showed signs of degradation, but the enamel and the ganoin is still visible on their surface. In case of extant crocodiles their stomach acid can dissolve mineralized tissues including enamel during digestion, while the organic parts of dentine still exist (Fisher, 1981). Accepting this statement for extinct crocodiles (Hunt and Lucas, 2010) the pycnodontiform or the lepisosteiform fish were probably not eaten by a carnivorous crocodile.

According to the preserved stomach and intestinal contents of mosasaurs (Lindgren et al., 2010), theropod dinosaurs (Charig and Milner, 1997; Hone and Rauhut, 2010), and the coprolites attributed to large theropod dinosaurs (Chin et al., 1998), these animals probably did not have such acidic stomach environment or long digestion period to absolutely dissolve the inorganic parts of bones, such as enamel and ganoin (Hone and Rauhut, 2010).

The approximately 6 m long adult individuals of the freshwater mosasaur *Pannoniasaurus inexpectatus* (Makádi et al., 2012) from

Iharkút, could have been a potential consumer of these fish (Botfalvai et al., 2014). The chance that the fish-bearing coprolites from Iharkút were produced by ichthyophagous dinosaurs is possible, but not provable. The carnivorous Lepisosteiformes fish could be potential predators for the Pycnodontiformes too. Those coprolites without recognizable inclusions were probably produced by animals which did not consume bones or harder parts, or they are from animals with very acidic stomach environment (Fisher, 1981).

5.6. Depositional mode and palaeoenvironment

The sedimentological and paleobotanical investigations of the Csehbánya Formation in the Iharkút open-pit mine indicate that the climate was dominantly humid, but seasonal, where the shorter dry periods were followed by rainy seasons with frequent flood events (Bodor et al., 2012; Botfalvai et al., 2016). This type of palaeoenvironment is known to be an ideal preservational environment for coprolites, where rapid burial could have produced rich coprolite horizons in the alluvial sediments (e.g. Chin and Kirkland, 1998; Chin et al., 1998; Northwood, 2005; Dentzien-Dias et al., 2012).

The coprolite-yielding horizon of site Sz-6 represents a basal breccia layer, where the poorly sorted sandy breccia horizons are interrupted several times by laminated siltstone horizons (Fig. 1C) indicating that the alternation of high energy events and standing water periods was an important circumstance of sedimentation (Botfalvai et al., 2016).

There are two conceivable scenarios which might explain the high concentration of coprolites in the Iharkút site.

The first scenario is that the coprolites were collected and transported by the high density flash floods and were deposited in a similar way to the clayclasts or other intraclasts present in the basal breccia layers (see Botfalvai et al., 2016). This is supported by the following observations: (1) many small-sized and rounded coprolites were discovered from the poorly-sorted sandy breccia horizons; (2) the presence of smaller or larger intraclasts of floodplain origin in the coprolite-yielding layers indicates an efficient reworking of the material of the interfluvial areas, which processes, along with the bone and tooth material as demonstrated by Botfalvai et al. (2015), could have also collected animal excrements from the floodplain environment.

The second scenario is that many of the coprolites were accumulated during the standing water periods and were buried when the following flood event deposited its coarser sediments covering the siltstone layer. Between two flood events, carcasses might have been available for the carnivore animals in the evolved standing water area, since there is evidence that the flash flood collected many ankylosaur skeletons from the surrounding part of the floodplain and deposited 12 skeletons in an area of 600 m² (Botfalvai et al., 2015). The available abundant food source should have attracted the carnivore animals from the surrounding area and the depositional place was littered with their wastes. The rotten carcasses of dead animals provided a large amount of flesh and soft tissue (e.g. chitterlings) for the carnivore or scavenger animals who might have eaten rather the easier digestible part of the carcass (e.g. flesh) than the bones (e.g. Shipman, 1975; Haynes, 1988), resulting bone-less coprolites with high phosphorous content. The large amount of the decaying organic material caused reductive, oxygen-deficient environment between two flood events (Tuba et al., 2006), which was also a favorable condition for the preservation of excrements. Sedimentological investigation pointed out that the standing water periods represent short time intervals (few weeks or months) (Botfalvai et al., 2016), thus the following flood could have rapidly buried the deposited excrements. This is supported by the following experiences: (1) the relatively high coprolite concentration (6 specimens/m²) associated with the fossil bone

material, (2) many times, the coprolites were found in the siltstone layer, but mostly surrounded by coarser sandy sediments, (3) the larger sized coprolites and the coiled morphology probably suggest an *in situ* rapid burial after the deposition, (4) the surface modification (e.g. cracks, abrasion) are subordinate, (5) all of the observed coprolites were produced by carnivores or scavengers (based on their phosphate content) which also prefer this scenario.

The above mentioned hypotheses currently include several assumptions and thus more taphonomical observation is needed (e.g. accurate mapping work), in order to confirm one of the preferred scenarios about the depositional mode of the coprolites at Iharkút site.

6. Conclusions

Coprolites produced by vertebrates recording 2600 specimens are among the most frequent fossils in the Csehbánya Formation of the Iharkút vertebrate site. Fossilized feces of herbivorous vertebrates were not recognized from the formation yet. The found coprolites are highly phosphatic, with mainly apatite in their matrix: the chemical components from the animal nutriment (calcium-phosphate) helped to mineralize the excrement. The spiral coprolites might have been produced by fish with spiral intestinal valves. Only one of the investigated coprolites showed signs of drying, whereas the others have a smooth surface without modification, indicating a rapid burial after defecation.

The partially digested teeth and the large number of ganoid scales indicate that the Lepisosteiformes and Pycnodontiformes fish were prey in the ancient ecosystem in Iharkút.

The fine phosphatic matrix and the great number of the Iharkút coprolites give a chance to find rare fossils such as cuticles and diatoms, otherwise unknown from the Cretaceous sediments of the Iharkút locality.

Acknowledgements

We thank Stefan Vasile and the anonymous reviewer for their useful suggestions. We thank Réka Kalmár (Hungarian Natural History Museum, Budapest), Miklósné Batori (Geological and Geophysical Institute of Hungary, Budapest), Zsolt Bendő (Eötvös University, Department of Petrology and Geochemistry, Budapest) for their technical assistance. We thank the 2000–2012 field crews for their assistance in the fieldwork.

We are grateful to Edina Prondvai (Ghent University, Department of Biology, Belgium), Orsolya Sztanó, Andrea Mindszenty, Ágnes Görög, Tibor Kalapos, István Szente, István Dódon, Károly Bóka (Eötvös University, Budapest), László Makádi (Geological and Geophysical Institute of Hungary, Budapest), Márton Szabó (Hungarian Natural History Museum, Budapest), Attila Virág (MTA-MTM-ELTE Research Group of Paleontology, Budapest) and Tibor Pecsics for helpful discussions. We are especially grateful to the Bakony Bauxite Mines and to Geovolán Zrt. for their logistic help.

Field- and laboratory work was supported by the Hungarian Natural History Museum, the National Geographic Society (Grant Nos. 7228-02, 7508-03), the Hungarian Scientific Research Fund (OTKA T-38045, PD 73021, NF 84193, K 116665), and the Hungarian Oil and Gas Company (MOL). This project was also supported by MTA-ELTE Lendület Programme (Grant no. 95102), the Jurassic Foundation, the Hantken Miksa Foundation, and the Bolyai Fellowship (A.Ö.). This is MTA–MTM–ELTE Paleo contribution no. 242.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cretres.2017.02.010>.