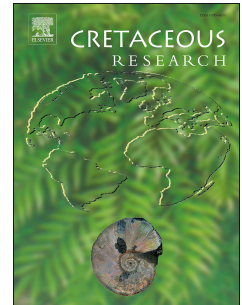


# Accepted Manuscript

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

Martin Segesdi, Gábor Botfalvai, Emese Réka Bodor, Attila Ósi, Krisztina Buczkó,  
Zsolt Dallos, Richárd Tokai, Tamás Földes



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

3 MARTIN SEGESDI<sup>1\*</sup>, GÁBOR BOTFALVAI<sup>2,3</sup>, EMESE RÉKA BODOR<sup>1,4</sup>,

4 ATTILA ÓSI<sup>1,3</sup>, KRISZTINA BUCZKÓ<sup>5</sup>, ZSOLT DALLOS<sup>6</sup>, RICHÁRD TOKAI<sup>7</sup>, TAMÁS FÖLDES<sup>8</sup>

5 <sup>1</sup> Eötvös Loránd University, Department of Paleontology, Pázmány Péter sétány 1/C, H-1117  
6 Budapest, Hungary.

7 <sup>2</sup> MTA-MTM-ELTE Research Group for Paleontology, Pázmány Péter sétány 1/C, H-1117 Budapest,  
8 Hungary.

9 <sup>3</sup> Hungarian Natural History Museum, Department of Paleontology and Geology, Baross utca. 13, H-  
10 1088 Budapest, Hungary.

11 <sup>4</sup> Geological and Geophysical Institute of Hungary, Stefánia út. 14, H-1143 Budapest, Hungary.

12 <sup>5</sup> Hungarian Natural History Museum, Department of Botany, Baross utca. 13, H-1088 Budapest,  
13 Hungary.

14 <sup>6</sup> Eötvös Loránd University, Department of Mineralogy, Pázmány Péter sétány 1/C, H-1117 Budapest,  
15 Hungary.

16 <sup>7</sup> Kaposvár Universtiy, Institute of Diagnostic Imaging and Radiation Oncology, Guba Sándor utca 40.  
17 H-7400 Kaposvár, Hungary.

18 <sup>8</sup> University of Pécs Medical School, Department of Radiology, Ifjúság út 13, H-7624 Pécs, Hungary.

19 **\*Corresponding author: Martin Segesdi, martinsegesdi@gmail.com, Eötvös Loránd University,**  
20 **Department of Paleontology, Pázmány Péter sétány 1/C, H-1117 Budapest, Hungary.**

21 *E-mail:* martinsegesdi@gmail.com (M. Segesdi); botfalvai.gabor@gmail.com (G. Botfalvai);

22 emesebodor@gmail.com (E. R. Bodor); hungaros@gmail.com (A. Ósi); krisztina@buczko.eu (K.

23 Buczkó); regnere.dallos@gmail.com (Zs. Dallos); richard.tokai@gmail.com (R. Tokai); t.foldes@t-  
24 online.hu (T. Földes)

25 Keywords: coprolites, plant and animal residues, high phosphorous content, carnivore  
26 coprolites, partially digested animal inclusions

## 27 **Abstract**

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

47 content of coprolites and the apatite might be derived from the carnivorous diet. Plant remains  
48 in the phosphatic coprolites may imply an omnivore producer or were the result of their  
49 incidental ingestion. Rapid burial and the mineral content of the animal nutriment might have  
50 been the responsible factors for the good preservation of the excrements.

51

## 52 **1. Introduction**

53 The study of coprolites (fossil feces) is an old and important part of paleontology, dating back  
54 to the 19<sup>th</sup> century (Buckland, 1829). The analysis of fossilized feces helps improve the  
55 knowledge on the biological processes and lifestyle of extinct animals (Chin et al., 1998;  
56 Chin, 2002). As in other parts of paleontology, paleoscatology also takes notice of the recent  
57 zoological observations (Fisher, 1981), but, of course, in most cases it is not easy (or  
58 practically not possible) to ascertain the real producer of the coprolites (Hunt and Lucas,  
59 2010). However, fossilized excrement could be informative not only about feeding behavior,  
60 but the embedded remains are useful for a more specific knowledge on the paleoenvironment  
61 (Prasad et al., 2005). In most cases, these remains are the evidence of the ancient food web  
62 (Zatoń and Rakociński, 2014), but coprolites often contain well-preserved incidentally  
63 swallowed (during drinking or feeding) plant or animal fragments as well.

64 Iharkút is an Upper Cretaceous (Santonian) vertebrate-bearing locality in the Bakony  
65 Mountains of western Hungary (Fig. 1), where productive and continuous excavations have  
66 been carried in the last 13 years (Ósi et al., 2012). Besides the very rich coprolite assemblage,  
67 the field work resulted in a diversified assemblage of continental and fresh water animals,  
68 including fish, amphibians, turtles, mosasaurs, lizards, pterosaurs, crocodylians and dinosaurs,  
69 comprising about 35 vertebrate species (Csiki-Sava et al., 2015). The vertebrate assemblage is  
70 dominated by bones of aquatic and semi-aquatic animals, whereas the bones of terrestrials are  
71 subordinate (Botfalvai et al., 2015). Rich and diverse fossil plant material was also discovered

72 from the same horizon with the bones and coprolites, and is dominated by Normapolles and  
73 angiosperm elements (Bodor et al., 2012; Bodor and Baranyi, 2012; Botfalvai et al., 2016).

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

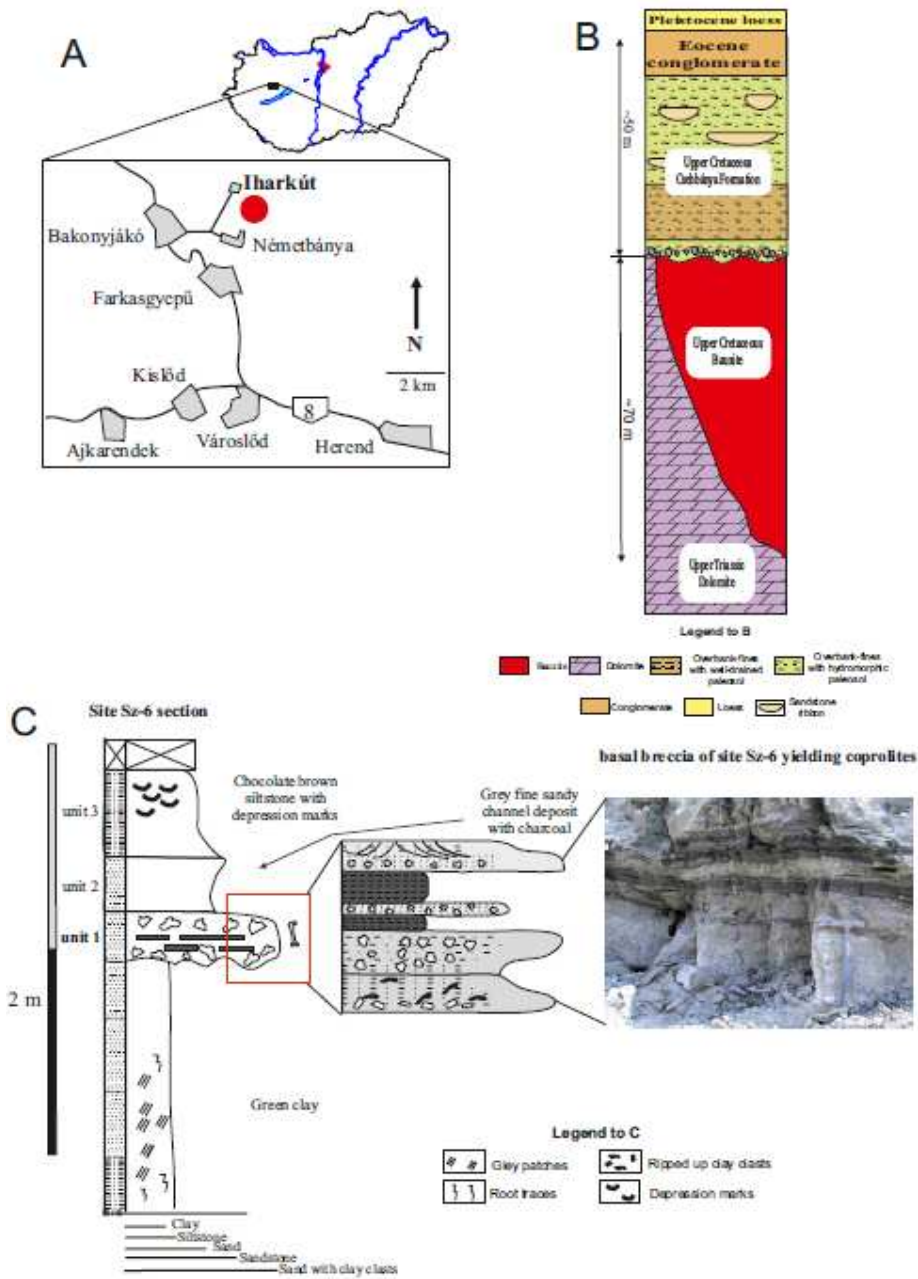
78

## 79 **2. Locality and geological settings**

80

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

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



92

93 **Figure 1.- Map and schematic stratigraphic section of the coprolite-bearing vertebrate**

94 **site: A, Location map of the Iharkút vertebrate locality; B, Schematic section of the Iharkút**

95 **open-pit mine; C, Schematic stratigraphic section of site SZ-6 after Botfalvai et al. (2016)**

96

97 All of the coprolites were discovered in the Csehbánya Formation at the Iharkút

98 vertebrate-bearing locality. The Csehbánya Formation at Iharkút locality is built up of cyclic

99 alternations of sandstone, and variegated siltstone and clay layers with sporadic intercalation  
100 of thin coal seams. The entire sequence being interpreted to have been deposited by an  
101 anastomosing fluvial system in a topographically low-level, wet, alluvial plain environment  
102 (Jochá-Edelényi, 1988; Botfalvai et al., 2016). The paleontological (subtropical floodplain  
103 forest vegetation) and sedimentological (the absence of desiccation cracks, the frequent  
104 presence of hydromorphic paleosols and the subordinate amount of secondary (pedogenic)  
105 carbonate accumulation) investigations indicate that the climate was dominantly humid, but  
106 seasonal, with flashflood-like episodes during the deposition of the Csehbánya Formation at  
107 the Iharkút open-pit (Botfalvai et al., 2016). The palynological investigation pointed out that  
108 the sedimentation took place in the *Oculopollis zaklinskaiae* - *Brecolpites globosus*  
109 palynozones, the *Oculopollis-Triatriopollenites* subzone indicating a late Santonian age of the  
110 formation in this outcrop (Bodor and Baranyi, 2012).

111 The coprolites described in this paper are from the basal part of site SZ-6 (see Fig.1C),  
112 that also yielded most of the vertebrate remains at Iharkút (Botfalvai et al., 2015), and is  
113 represented by a 10 to 50 cm thick basal breccia layer composed of grey-green sand, siltstone,  
114 clayclasts, pebbles. The poorly-sorted sandy breccia (including fine to coarse sand and  
115 pebbles) is interrupted by laminated siltstone horizons and these coarse and fine grained  
116 layers are repeated several times resulting in a stacked series of fining upward units.  
117 Sedimentological and taphonomical investigations suggest that the coprolite yielding horizons  
118 were deposited by ephemeral high density flash-flood events, probably triggered by episodic  
119 heavy rainfalls (Botfalvai et al., 2016). Furthermore, the depositional area of this unit (site Sz-  
120 6) acted as a trap where current velocity of the flood suddenly decreased and the poorly sorted  
121 sand, ripped-up clayclasts, pebbles, bones and coprolites accumulated (Botfalvai et al., 2015,  
122 2016).

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

127

### 128 **3. Materials and methods**

129

#### 130 **3.1. Material**

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

136

#### 137 **3.2. Methods**

138 In the course of the field work the potentially fossiliferous layers were opened up into  
139 meter sized blocks and were carefully broken into smaller pieces to find the remains. The  
140 covering sediment was removed from the surface of all the collected coprolites with  
141 mechanical preparation and they were carefully cleaned with wet toothbrush in a laboratory.  
142 After preparation, morphological groups were separated based on complete (or nearly  
143 complete) specimens. The intact and the fractured surfaces of the coprolite material (2600  
144 specimens) were scrupulously examined with the use of light microscope. We selected 45  
145 specimens based on visible remain content and different morphology for further investigations  
146 (CT, mineralogical composition, palynological processing, thin sectioning). Apart from these,  
147 14 specimens were dissolved in H<sub>2</sub>O<sub>2</sub> to extract microscopic residues. In addition, one more



148 coprolite specimen is discussed here, with important taphonomical features (VER 2016.1333.)  
149 (see Supplementary Data).

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

156

### 157 **3.3. Morphological groups**

158 The different morphotypes for the Iharkút coprolites were established mainly based on their  
159 external shapes but following McAllister (1985) and Coy (1995). Their internal patterns,  
160 visible on broken surfaces and by polished sections, have been used as well for the  
161 morphological grouping.

162

### 163 **3.4. Taphonomical observations**

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

167

### 168 **3.5. CT-scanning**

169 Computed Tomography scans were recorded at the Institute of Diagnostic Imaging and  
170 Radiation Oncology of the Kaposvár University by a Siemens Stomatom Definition Flash  
171 instrument. We examined eight large coprolites from different morphological groups to find  
172 their inner inclusions (VER 2016.1297.; VER 2016.1301.; VER 2016.1302.; VER

173 2016.1304.; VER 2016.1305.; VER 2016.1307.; VER 2016.1308.; VER 2016.1310.). The  
174 scans were analyzed with the RadiAnt DICOM viewer program. The analysis of the scans  
175 helped find and collect the inclusions from the coprolites, moreover the CT-scanning digitally  
176 recorded the morphology of the unique coprolites.

177

### 178 **3.6. Mineralogical components**

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

185

### 186 **3.7. Micropaleontological processing**

187 Standard palinology preparation following the Schulze Method was used, like in Bodor and  
188 Baranyi (2012). Six specimens from different morphological groups and with different  
189 macroscopic inclusion content were studied in this way. The sampled coprolites were chosen  
190 because of their content in macroscopic plant (VER 2014.119.; VER 2016.1319.; VER  
191 2014.118.) and bone remains (VER 2016.1322.) and the cylindrical (VER 2016.1304.) and  
192 roundish (VER 2016.1307.) morphology. Preparates from the inner matrix of the coprolites  
193 were examined by a Nikon Eclipse LV100Pol polarization microscope and QImaging  
194 Micropublisher 5.0 RTV digital camera. Fourteen roundish coprolites were processed by  
195 H<sub>2</sub>O<sub>2</sub> to find additional fossils. These coprolites were separated into three size groups: one  
196 specimen with 2 cm diameter, four with 1 cm diameter, and nine with less than 1 cm. The  
197 powdered coprolites were boiled in H<sub>2</sub>O<sub>2</sub> (30%) for eight hours. The remnants were washed

198 three times with distilled water, and a few drops of the suspension were poured onto  
199 coverslips and allowed to dry. Permanent slides were mounted with the aid of a hot plate and  
200 using Pleurax as the mounting medium. The permanent slides were studied with LEICA DM  
201 LB2 microscopy (100X HCX PLAN APO inner objective) and a VSI-3.0M(H) digital  
202 camera.

203

### 204 **3.8. Scanning Electron Microscopy**

205 SEM was used for the identification of small embedded remains. Coating with gold-  
206 palladium was accomplished using a XC7620 Mini Sputter Coater for 120 s at 16 mA. A  
207 Hitachi S-2600N scanning electron microscope operated at 20 kV and 5–8 mm distance was  
208 used in the Department of Botany of Hungarian Natural History Museum. In one case, the  
209 composition of the microscopic inclusions was analyzed by energy dispersive spectrometry  
210 (EDS). Measuring took place at the laboratory of Department of Petrology and Geochemistry  
211 at the Eötvös University. An AMRAY 1830 scanning electron microscopy was used for this  
212 analysis.

213

### 214 **3.9. Thin sectioning**

215 Seven coprolites with macroscopic plant (VER 2016.1311.; VER 2014.118.) and animal  
216 (VER 2016.1298.; VER 2016.1299.; VER 2016.1324.; VER 2016.1325.; VER 2016.1329.)  
217 inclusions were studied with thin sectioning. Preparations were made in the laboratory of the  
218 Department of Physical and Applied Geology at the Eötvös University. Coprolites were  
219 placed into synthetic resin (a mixture of IPOX MR 3012 and IPOX MR 3122 with the titre  
220 10: 4.). The coprolites were cut in different directions with a Buehler IsoMet 1000 Precision  
221 Saw. After impregnating the cutaway surface with synthetic resin, we polished them with SiC  
222 powder (standard grain sizes: 220, 400, 600, 800). The samples were then placed onto glass

223 plates and after that, the cutting and polishing of the other side was done. The thin sections  
224 were examined using a Nikon Eclipse LV100Pol polarization microscope and a QImaging  
225 Micropublisher 5.0 RTV digital camera.

226

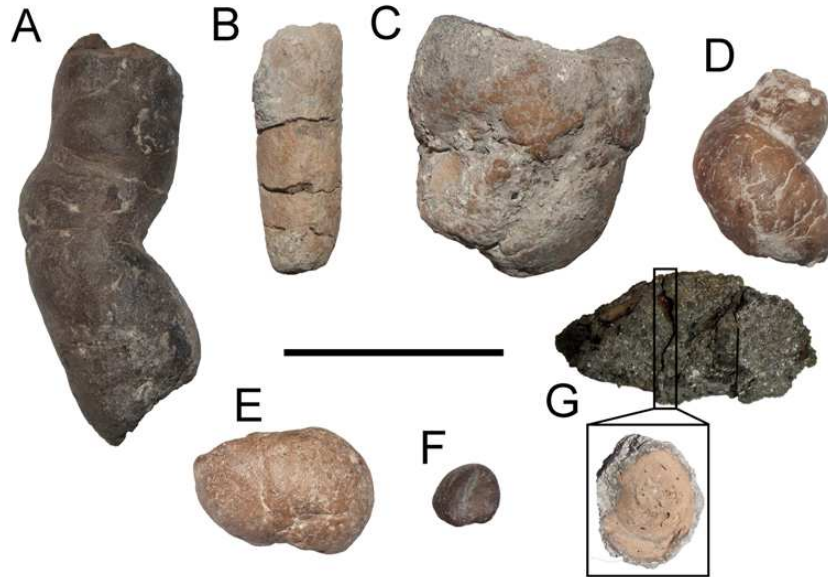
## 227 **4. Results**

228

### 229 **4.1. Morphological separation**

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

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



246

247 **Figure 2.- Morphotypes of Late Cretaceous coprolites from Iharkút:** **A**, cylindrical (VER  
 248 2016.1304.); **B**, cylindrical with tapered endings (VER 2016.1297.); **C**, amorphous (VER  
 249 2016.1310.); **D**, coiled (VER 2016.1290.); **E**, roundish (VER 2016.1307.); **F**, roundish with a  
 250 concave side (VER 2016.1294.); **G**, spiral (place of transverse section is marked) (VER  
 251 2016.1312.) [Scale bar: 5 cm]

252

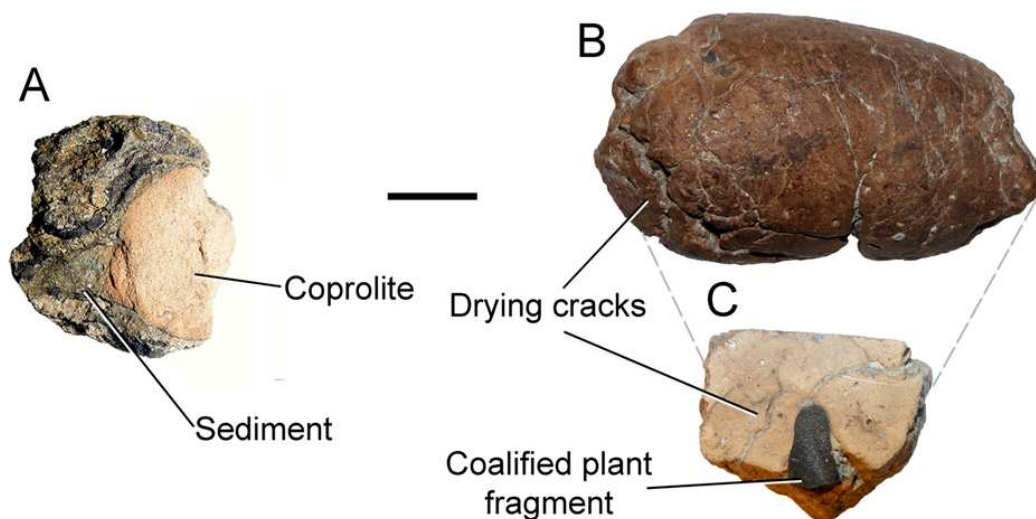
#### 253 **4.2. Taphonomical characters**

254 About 2600 more or less complete coprolites were discovered from an area of  
 255 approximately 400 m<sup>2</sup>, showing a density up to 6 specimens/m<sup>2</sup>. All of the coprolites from  
 256 Iharkút have the same general inner structure: homogeneous fine-grained matrix containing  
 257 small holes, partially digested plant and animal residues but no sedimentary particles. The  
 258 color of their inner matrix is mainly grayish, pale brown, yellowish brown, mostly unicolor  
 259 (exceptions: VER 2016.1305.; VER 2016.1308.; VER 2016.1311.; VER 2016.1321.),  
 260 whereas the outer surface is always darker.

261 The embedded plant remains are coalified (not charcoaled, but only carbonised)  
262 similarly to the plant remains frequently present in the sediment (Bodor and Baranyi, 2012).  
263 In the case of many specimens, it could have been observed that the coprolite was not  
264 transported by the covering sediment: a boundary can be separated, where the feces deposited  
265 on the surface of the underlying beds and on which the overlying sediments covered it later on  
266 (Fig. 3A). This preservational feature was mentioned as a "bird's eye pattern" by Thulborn,  
267 1991 (p.343 fig. 2).

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

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



277

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

282

### 283 4.3. Mineral components

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

287

Mineral phases (wt%)	VER 2016.1321.*	VER 2016.1322.*	VER 2014.119.*	HR-Swcc*	HR-Sst*
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	-

**Table 1.- Mineral components of Late Cretaceous coprolites from Iharkút: \*VER 2016.1321.**

– coprolite bearing a cuticle fragment; VER 2016.1322. – Coprolite bearing a ganoid fish scale ;

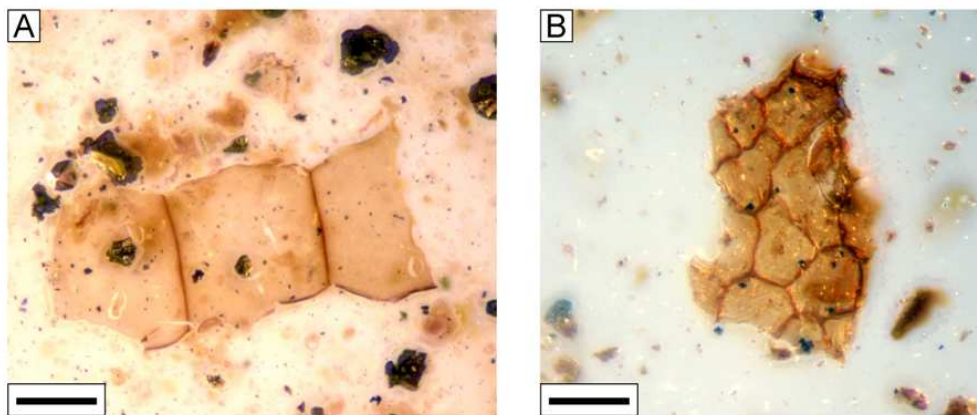
VER 2014.119. – Coprolite bearing a seed and plant fragments ; HR-Swcc – Host Rock - Silstone

with clay clasts; HR-Sst – Host Rock - Sandstone

288

#### 289 4.4. Results from the micropaleontological processing

290 The preparates from the palynological processing contained a large amount of organic  
291 material. Five out of six samples contained plant fragments, and two samples contained  
292 Normapolles pollen grains (Bodor and Baranyi, 2012). Two samples contained plant cuticle  
293 remains, which can be separated into two groups: one type (Fig. 4A) has nearly hexagonal  
294 cells (about 50  $\mu\text{m}$  width), whereas the other one has irregular cells (Fig. 4B). Both types  
295 were devoid of stomas. In the course of  $\text{H}_2\text{O}_2$  processing, besides the organic material, 14  
296 diatom fragments have been recognized by LM, but none during the SEM analysis. Because  
297 of their poor preservation, only two of them could be determined: the cylindrical diatoms are  
298 probably belonging to *Aulacoseira*, which is known from other Cretaceous localities as well  
299 (see e.g. Ambwani et al., 2003).



300

301 **Figure 4.- Plant cuticle fragments from the micropaleontological processing of coprolites**  
302 **from Iharkút: A, Plant cuticle fragment with near hexagonal cells (VER 2014.118.) [Scale**  
303 **bar: 30  $\mu\text{m}$ ]; B, Plant cuticle fragment with irregular cells (VER 2014.119.) [Scale bar: 30**  
304  **$\mu\text{m}$ ]**

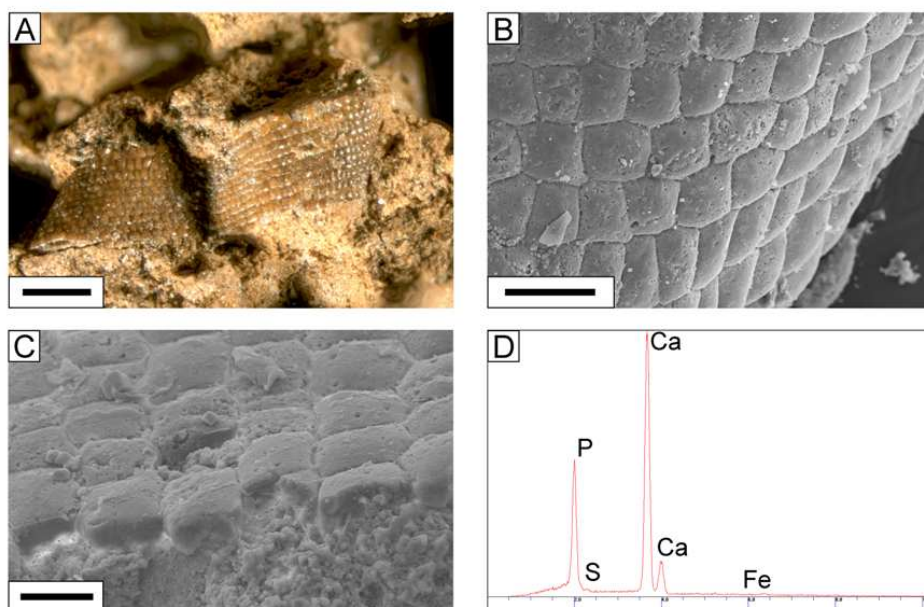
305



306 **4.5. Macroscopic food remains**

307 **4.5.1. Plant remains**

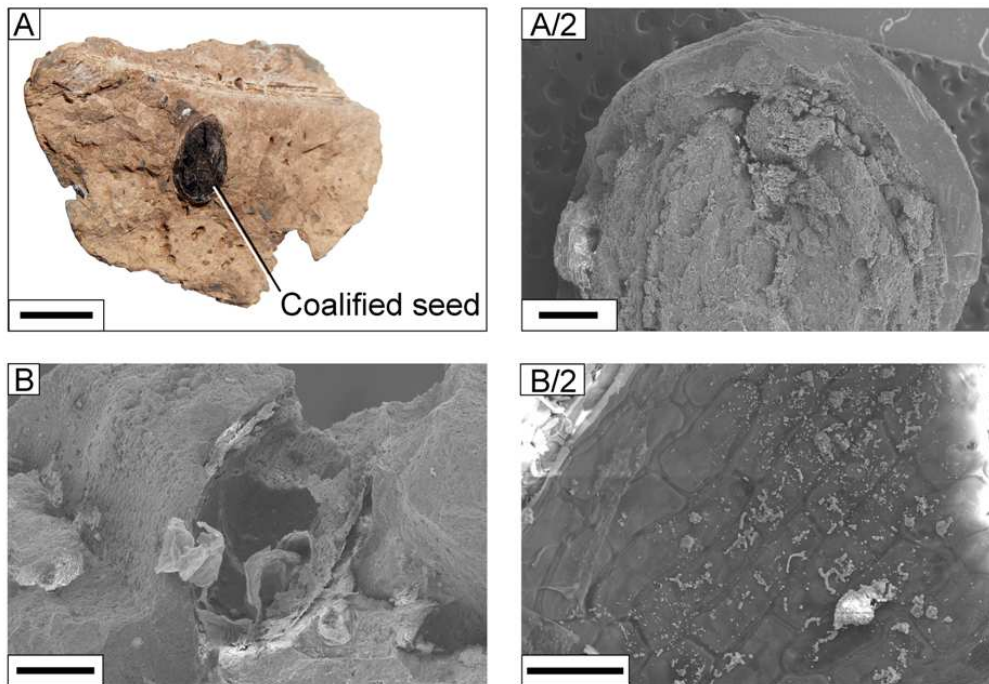
308 Thirteen coprolites from different morphological groups (roundish, spiral, cylindrical and  
309 amorphous) contained macroscopic plant remains. Among the embedded plant remains, some  
310 specimens are unidentifiable coalified fragments, but others are in better condition providing  
311 more information. The surface of seven broken coprolites preserved cuticle remains (Fig. 5A,  
312 B), being similar to the cuticle pieces with near hexagonal cell structure, also known from the  
313 palynological processing (Fig. 4A). These cuticle fragments are varying in size, but are  
314 always thinner than 1 mm: average thickness is 10  $\mu\text{m}$ , whereas the width of the cell-like  
315 structures is varying between 30-50  $\mu\text{m}$  (Fig. 5C). They are not coalified, but clearly  
316 separated from the matrix. Stomas are not recognizable on their surfaces. Analysis of these  
317 cuticle remains with energy dispersive spectrometry showed that they do not differentiate  
318 from the matrix in their chemical components (Fig. 5D). Similar to the content of the inner  
319 coprolite matrix, mainly calcium (Ca), phosphorous (P), sulphur (S) and iron (Fe) are  
320 observable.



321

322 **Figure 5.- Probable cuticle imprints in the matrix of coprolites from Iharkút: A,**  
323 Probable cuticle imprint in the matrix of a coprolite (VER 2016.1321.) [Scale bar: 300  $\mu\text{m}$ ];  
324 **B,** Scanning electron micrograph of a probable cuticle imprint on a broken surface (VER  
325 2016.1321.) [Scale bar: 50  $\mu\text{m}$ ]; **C,** Probable imprints of the cells of cuticle on the broken  
326 surface (VER 2014.118.) (SEM) [Scale bar: 25  $\mu\text{m}$ ]; **D,** Energy dispersive spectrometry  
327 (EDS) measurement of a probable cuticle imprint (VER 2014.118.)

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



331

332 **Figure 6.- Seed remains from Late Cretaceous coprolites from Iharkút: A,** Coalified,  
333 probably Rosaceae seed (VER 2014.119.) [Scale bar: 0.5 cm]; **A/2,** Scanning electron  
334 micrograph of a probable Rosaceae seed (VER 2014.119.) [Scale bar: 0.5 mm]; **B,**

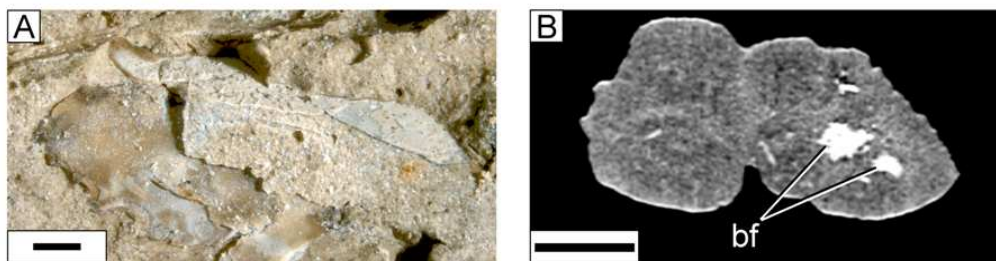
335 Magnoliaceae seed (VER 2014.118.) (SEM) [Scale bar: 0.5 mm]; **B/2**, Inner structure of a  
336 Magnoliaceae seed (VER 2014.118.) (SEM) [Scale bar: 100  $\mu$ m]

337

#### 338 **4.5.2. Animal remains**

339 Animal remains were frequent in the small (1-2 cm diameter, such as VER  
340 2016.1329.) and in the large sized (more than 5 cm in length, such as VER 2016.1301.)  
341 coprolites as well. These coprolites turned up from different morphologies, such as coiled,  
342 cylindrical and spiral.

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

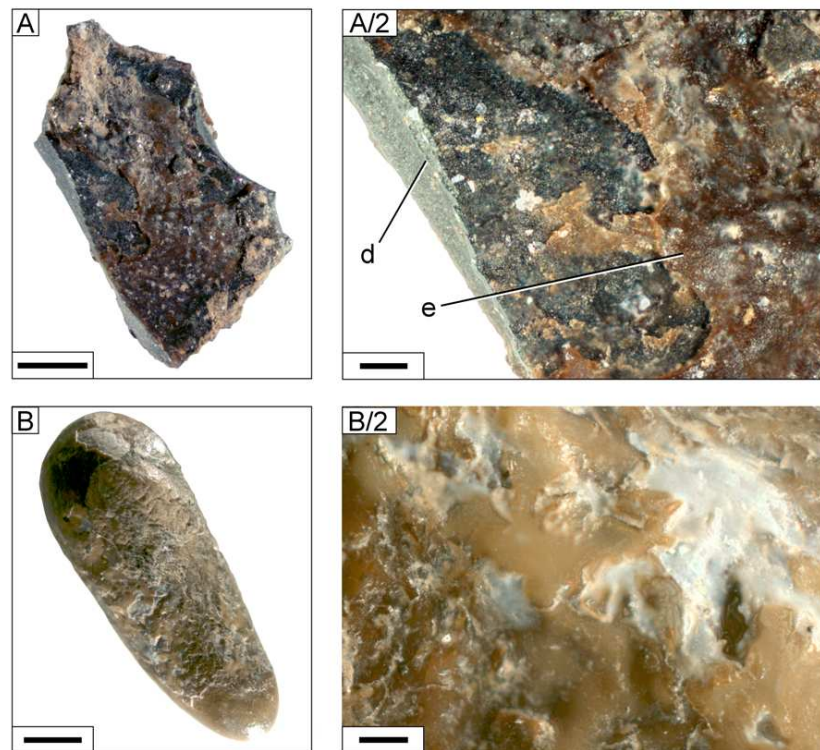


349

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

353 Two teeth were found in the coprolites: a smaller one is a 3 mm long undeterminable  
354 fragment (Fig. 8A, A/2) (VER 2016.1313.), and a larger is a 7 mm long complete

355 Pycnodontiformes fish tooth (Fig. 8B, B/2) (VER 2016.1329.). This fish tooth is rounded,  
356 bean-like in shape, similar to those Pycnodontiformes fish teeth which are well-known from  
357 Iharkút (sometimes in jaw fragments). According to previous studies these Pycnodontiformes  
358 fossils belongs to the genus *Coelodus* (Szabó et al., 2016b). Both teeth show the signs of  
359 digestion, but the fragments of the enamel is still visible on them (Fig. 8A/2, B/2). The  
360 Pycnodontiformes fish tooth was associated with small bone fragments in the coprolite (Fig.  
361 9A).

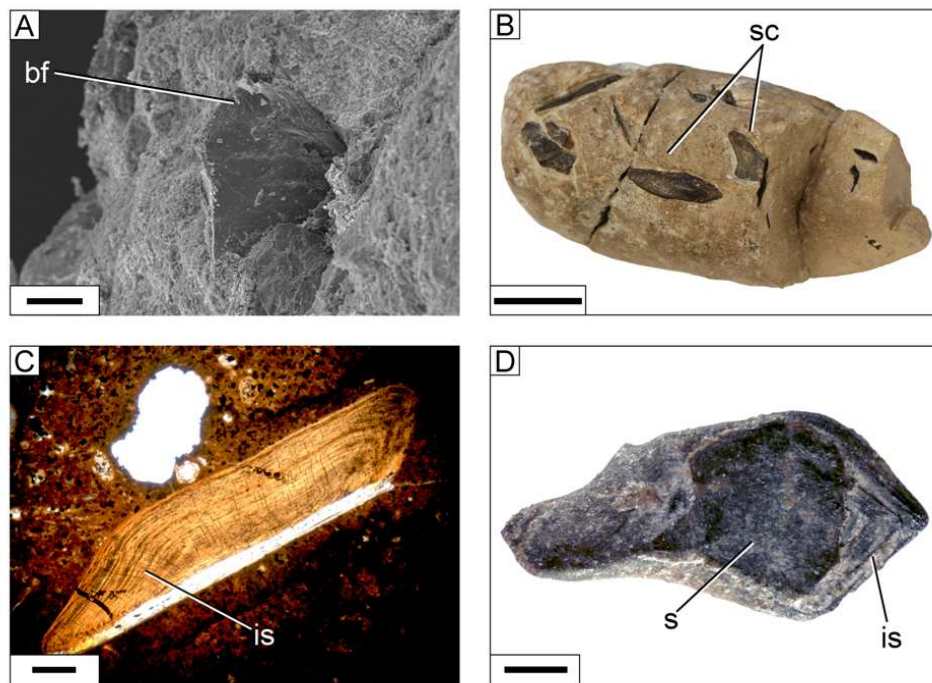


362

363 **Figure 8.- Tooth remains from Late Cretaceous coprolites from Iharkút: A,** Partially  
364 digested unidentified tooth fragment (VER 2016.1313.) [Scale bar: 0.6 mm]; **A/2,** Etched  
365 surface of the unidentified tooth fragment showing the dentine (d) and the remains of enamel  
366 (e) (VER 2016.1313.) [Scale bar: 120  $\mu$ m]; **B,** Tooth of a Pycnodontiformes fish (VER  
367 2016.1329.) [Scale bar: 1.2 mm]; **B/2,** Etched surface of the Pycnodontiformes fish tooth  
368 (VER 2016.1329.) [Scale bar: 120  $\mu$ m]

369

370 Fifteen ganoid fish scales were also collected from four coprolites (Fig. 9B) (VER  
371 2016.1299.; VER 2016.1313.; VER 2016.1317.; VER 2016.1322.). The size of these  
372 “diamond shaped” scales is varied from the 2 mm long fragment up to the 6.1 mm long  
373 almost complete scale. One of the characteristics of the ganoid scales is the enamel-like  
374 hypermineralized ganoin tissue (Sire et al., 2009) covering the surface of the scales. This  
375 ganoin layer was partially eroded from the surface of the scales from the coprolites and in  
376 several cases the inner laminar structure (Fig. 9C) was visible (Fig. 9D) next to the extant  
377 ganoin. These scales probably belong to the Lepisosteiformes carnivore fishes, which are  
378 known from Iharkút by their skull and jaw elements, teeth, vertebrae, and scale fossils (Szabó  
379 et al., 2016a).



380

381 **Figure 9.-** A, Small bone fragment (bf) from a coprolite bearing a Pycnodontiformes fish  
382 tooth (VER 2016.1329.) [scale bar: 100  $\mu$ m]; B, Small coprolite (VER 2016.1322.) with  
383 ganoid fish scale (sc) inclusions [scale bar: 0.5 cm]; C, Inner structure (is) of a ganoid fish

384 scale in the thin section of a coprolite (VER 2016.1299.) [scale bar: 0.6 mm]; **D**, Partially  
385 digested ganoid scale with visible inner structure (is) next to an extant scale surface (s) from a  
386 coprolite (VER 2016.1299.) [scale bar: 0.6 mm]

387

## 388 **5. Discussion**

389

### 390 **5.1. Morphology**

391 It is not possible to find clear connection between the coprolites and producers based  
392 on the seven recognized morphology, because often the same group of animals could produce  
393 different shaped excrement and the morphology might be varied by the different composition  
394 of the nutriment (Thulborn, 1991; Chin and Kirkland, 1998). Although there are morphologies  
395 with characteristic small size, this phenomenon does not mean that they were produced by  
396 smaller animals, since large animals could produce small sized excrement (Thulborn, 1991).

397 Only in the case of coiled and spiral coprolites is possible to find closer assumption for  
398 their origin. The shape of these coprolites suggests that they were produced by fish with spiral  
399 intestinal valves (McAllister, 1985; Thulborn, 1991). This pattern is similar to other spiral  
400 coprolites mentioned by Coy (1995). It is known from recent analogies that the function of the  
401 spiral intestinal valves is to increase the surface of nutriment absorption without the  
402 elongation of the intestines (Hassanpour and Joss, 2009). There are different types of spiral  
403 intestinal valves (differentiated on the basis of the width of the infolding tissue and the  
404 direction of the valves) and a similar type of intestine termed scroll valve (Parker, 1885;  
405 McAllister, 1985). Among spiral coprolites two main types are distinguished: heteropolar and  
406 amphipolar (Jain, 1983; Thulborn, 1991). On the heteropolar coprolites the narrow whorls are  
407 concentrated at one ending while on the amphipolar coprolites the whorls (relatively fewer  
408 than on the heteropolar ones) are extended on the whole surface of the coprolite (Thulborn,

409 1991). It is contentious that this distinction means taxonomical differences (Chin, 2002). The  
410 coiled coprolites from Iharkút (Fig. 2D) are most similar to the amphipolar type, whereas the  
411 tightly rolled spiral coprolites (Fig. 2G) resemble the heteropolar type. Unfortunately, the  
412 surface of the spiral coprolites with the best preserved inside spirally pattern is covered with  
413 hard pyritic crust, preventing us to observe the surface whorls. The matrix of the coiled and  
414 spiral coprolites contained bone fragments and fish scales. These residues and the apatite in  
415 the matrix indicate that their producers probably consumed nutriment of animal origin  
416 (Hollocher et al., 2005).

417         Spiral valve intestine is mainly present in all Chondrichthyes (like sharks, rays and  
418 skates) and in lungfish (Hassanpour and Joss, 2009; Stringer and King, 2012). There is a  
419 vestigial spiral valve intestine in some actinopterygian too. The fossilized intestinal contents  
420 in the well-preserved Pycnodontiformes fish fossils from the Fossil-Lagerstätten (Kriwet,  
421 2001) showed that these fish did not possess spiral valve intestine. Lepisosteiformes fish have  
422 a remnant spiral valve with few turns (Suttkus, 1963; Argyriou et al., 2016), but it is  
423 questionable that this structure could cause the up rolling of the excrement (Waldman, 1970).  
424 Up to the present, fossils of Chondrichthyes or lungfish are unknown from Iharkút. It is  
425 possible that these coiled and spiral coprolites were produced by the Lepisosteiformes fish,  
426 but their presence may indicate that the fish fauna of the fossil site may have also contained  
427 Chondrichthyes or lungfish.

428

## 429 **5.2. Taphonomy**

430         The fossils presented in this study are definitely coprolites and not concretions, that is  
431 further supported by the following taphonomical and sedimentological features: (1) in the host  
432 rock it is clearly visible that the excrement was deposited on a surface that was later covered  
433 by sediment (e.g. Fig. 3A); (2) in many cases coprolites were found in the siltstone layer, but

434 mostly surrounded by coarser sandy sediments and the grain size of the fossilized excrement  
435 was finer than both sediments; (3) if they are not coprolites but concretions that were growing  
436 around in the altered chemical conditions caused by the decaying material, the "bird's eye  
437 pattern" seen on many specimens could not have been observed; (4) lateral association among  
438 the coprolites was not detectable; (5) the cylindrical and the coiled shapes of the observed  
439 nodules are not consistent with those that would be expected in chemical concentrations or  
440 fluvial transported intraclasts; (6) the observed specimens have relatively high phosphorous  
441 content, while this element was completely undetectable in the embedding sediments (see  
442 Table 1).

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

455 Most of the observed coprolites have a smooth surface, without cracks, but this does  
456 not necessarily indicate that they were produced by aquatic animals, because (1) desiccation  
457 cracking is dependent on the moisture content of the original excrement (Northwood, 2005)  
458 and (2) feces of terrestrial animals can also be accumulated into the water saturated



459 environment without getting dried. Based on taphonomical evidence, the habitat of producers  
460 of the observed coprolites certainly cannot be determined. However, it can be stated that  
461 most of the coprolites were buried rapidly after the accumulation without long-term exposure.

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

471

472

### 473 **5.3. Mineralogical components**

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

484 Northwood, 2005). However, the later scenario is unlikely, because the embedded sediments  
485 do not contain phosphorus, and this element was only detectable from the coprolites, thus  
486 making it more conceivable that the phosphorous content of the studied coprolites related to  
487 the dietary of their producers.

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

507 Pyrite was traceable from the samples of coprolites, this mineral of external origin  
508 being highly present in the bone remains from the Csehbánya Formation as well (Tuba et al.,  
509 2006).

510

#### 511 **5.4. Inclusions from micropaleontological processing**

512 The recognized diatoms and pollen grains from the coprolites were not the parts of the  
513 animal's diet, but they were rather swallowed accidentally during drinking or feeding.  
514 Identical sporomorphs and pollen grains are more concentrated in the palynofacies of the  
515 sediment than in the coprolites (Bodor and Baranyi, 2012). Both the sediment and the  
516 coprolites have high dispersed organic material concentration. The few diatom fossils  
517 discovered by H<sub>2</sub>O<sub>2</sub> processing could be significant, since Cretaceous diatoms are rare  
518 (Ambwani et al., 2003; Witkowski et al. 2011). Unfortunately, however, the scarcity of these  
519 diatoms does not allow us for a more precise determination, more samples and further  
520 investigation being needed in this attempt.

521

#### 522 **5.5. Inferences from nutriment inclusions**

523 The cuticle remains, recognized on the broken coprolite surfaces (Fig. 5) are probably  
524 imprints and consistent with the cuticle fragments with near-hexagonal cells found in the  
525 palynological processing (Fig. 4A). These remains were originally parts of a large cuticle  
526 surface, but, as they were indigestible (Bajdek et al., 2014), the matrix of the soft excrement  
527 embedded them. The organic cuticles disappeared during later diagenetic processes, but their  
528 shape is still visible in the fine-grained matrix of the coprolites. This theory explains why the  
529 EDS analysis showed the same chemical compositions (Fig. 5D) on the surface of these  
530 remains, as that seen in the matrix of the coprolites (Table 1.). The other cuticle fragment type  
531 from the palynological processing, showing irregular cells (Fig. 4B), is similar to the

532 underside leaf surface of the lotus. The underside epidermis of this type of leaf, being in  
533 contact with water, has no or just a few stomas and it is wax-coated (Ensikat et al., 2011). It is  
534 possible that the cuticle fragments and cuticle imprints preserved in coprolites belonged to a  
535 cuticle of a water plant, which was indigestible due to its wax-coating.

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

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

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

557 from the excrements of herbivorous animals (Thulborn, 1991; Chin and Kirkland, 1998;  
558 Hollocher et al., 2005; Northwood, 2005).

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

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

575         According to the preserved stomach and intestinal contents of mosasaurs (Lindgren et al.,  
576 2010), theropod dinosaurs (Charig and Milner, 1997; Hone and Rauhut, 2010), and the  
577 coprolites attributed to large theropod dinosaurs (Chin et al., 1998), these animals probably  
578 did not have such acidic stomach environment or long digestion period to absolutely dissolve  
579 the inorganic parts of bones, such as enamel and ganoin (Hone and Rauhut, 2010).

580         The approximately 6 m long adult individuals of the freshwater mosasaur  
581 *Pannoniasaurus inexpectatus* (Makádi et al., 2012) from Iharkút, could have been a potential

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

588

## 589 **5.6. Depositional mode and palaeoenvironment**

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

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

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

603 The first scenario is that the coprolites were collected and transported by the high  
604 density flash floods and were deposited in a similar way to the clayclasts or other intraclasts  
605 present in the basal breccia layers (see Botfalvai et al., 2016). This is supported by the  
606 following observations: (1) many small-sized and rounded coprolites were discovered from

607 the poorly-sorted sandy breccia horizons; (2) the presence of smaller or larger intraclasts of  
608 floodplain origin in the coprolite-yielding layers indicates an efficient reworking of the  
609 material of the interfluvial areas, which processes, along with the bone and tooth material as  
610 demonstrated by Botfalvai et al. (2015), could have also collected animal excrements from the  
611 floodplain environment.

612 The second scenario is that many of the coprolites were accumulated during the  
613 standing water periods and were buried when the following flood event deposited its coarser  
614 sediments covering the siltstone layer. Between two flood events, carcasses might have been  
615 available for the carnivore animals in the evolved standing water area, since there is evidence  
616 that the flash flood collected many ankylosaur skeletons from the surrounding part of the  
617 floodplain and deposited 12 skeletons in an area of 600 m<sup>2</sup> (Botfalvai et al., 2015). The  
618 available abundant food source should have attracted the carnivore animals from the  
619 surrounding area and the depositional place was littered with their wastes. The rotten  
620 carcasses of dead animals provided a large amount of flesh and soft tissue (e.g. chitterlings)  
621 for the carnivore or scavenger animals who might have eaten rather the easier digestible part  
622 of the carcass (e.g. flesh) than the bones (e.g. Shipman, 1975; Haynes, 1988), resulting bone-  
623 less coprolites with high phosphorous content. The large amount of the decaying organic  
624 material caused reductive, oxygen-deficient environment between two flood events (Tuba et  
625 al., 2006), which was also a favorable condition for the preservation of excrements.  
626 Sedimentological investigation pointed out that the standing water periods represent short  
627 time intervals (few weeks or months) (Botfalvai et al., 2016), thus the following flood could  
628 have rapidly buried the deposited excrements. This is supported by the following experiences:  
629 (1) the relatively high coprolites concentration (6 specimens/m<sup>2</sup>) associated with the fossil  
630 bone material, (2) many times, the coprolites were found in the siltstone layer, but mostly  
631 surrounded by coarser sandy sediments, (3) the larger sized coprolites and the coiled

632 morphology probably suggest an *in situ* rapid burial after the deposition, (4) the surface  
633 modification (e.g. cracks, abrasion) are subordinate, (5) all of the observed coprolites were  
634 produced by carnivores or scavengers (based on their phosphate content) which also prefer  
635 this scenario.

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

639

## 640 **6. Conclusions**

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

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

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

654

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