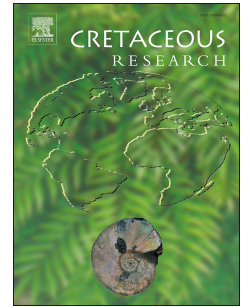# Accepted Manuscript

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

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1 **First report on vertebrate coprolites from the Upper Cretaceous (Santonian) Csehbánya**

2 **Formation of Iharkút, Hungary**

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**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 19th century (Buckland, 1829). The analisys 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 (Ősi 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, crocodilians 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 Németbánya and Bakonyjákó 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
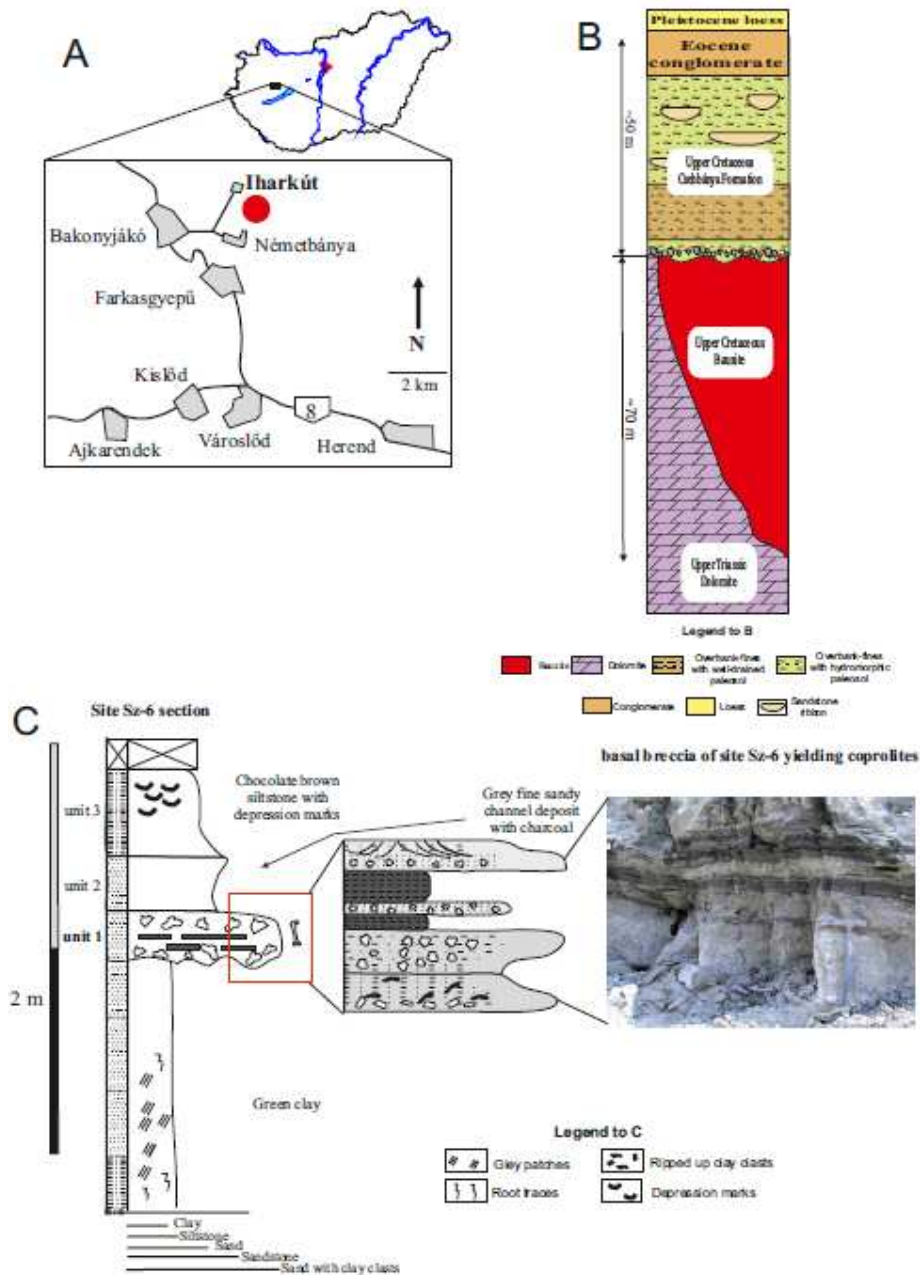
**Figure 1.- Map and schematic stratigraphic section of the coprolite-bearing vertebrate site: A**, Location map of the Iharkút vertebrate locality; **B**, Schematic section of the Iharkút open-pit mine; **C**, Schematic stratigraphic section of site SZ-6 after Botfalvai et al. (2016)

96

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

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 (Jocha-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 uncomformably 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 $H_2O_2$ to extract microscopic residues. In addition, one more

7

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

8

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-Kα

181  source, 40 kV 40mA). Measurements of 0.007° (2θ)/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  $H_2O_2$ 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 $H_2O_2$ (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
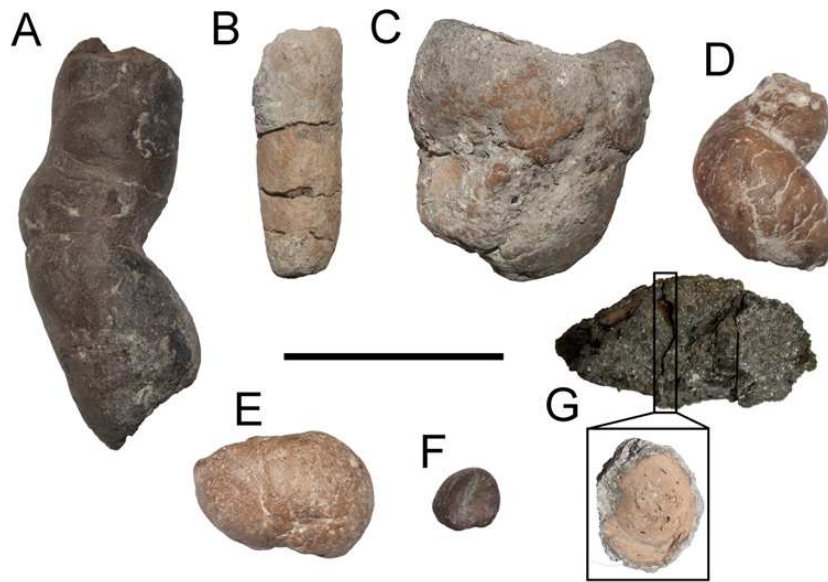
**Figure 2.- Morphotypes of Late Cretaceous coprolites from Iharkút: A,** cylindrical (VER 2016.1304.); **B,** cylindrical with tapered endings (VER 2016.1297.); **C,** amorphous (VER 2016.1310.); **D,** coiled (VER 2016.1290.); **E,** roundish (VER 2016.1307.); **F,** roundish with a concave side (VER 2016.1294.); **G,** spiral (place of transverse section is marked) (VER 2016.1312.)  [Scale bar: 5 cm]

252

### 4.2. Taphonomical characters

About 2600 more or less complete coprolites were discovered from an area of approximately 400 m$^2$, showing a density up to 6 specimens/m$^2$. 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.

261    The embedded plant remains are coalified (not charcoalified, 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).
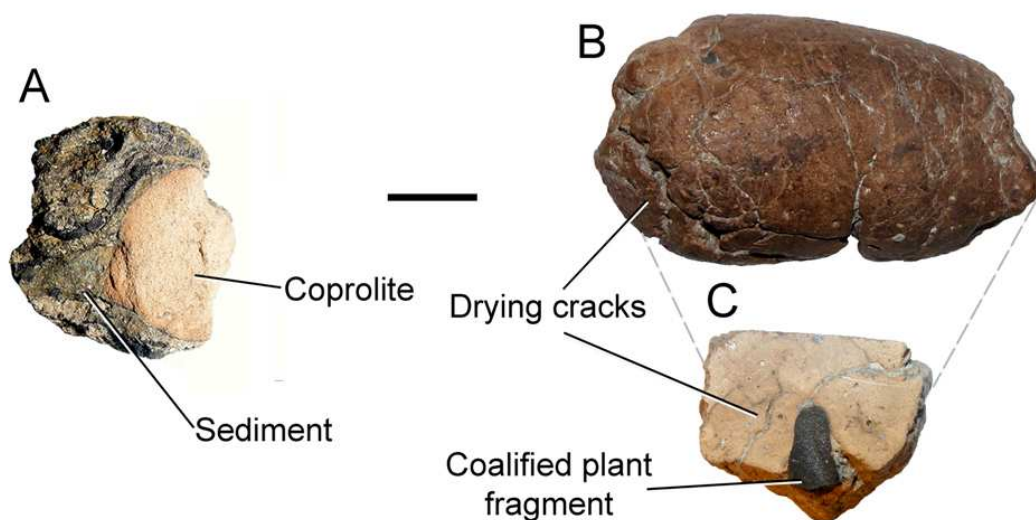


277

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

### 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 $H_2O_2$ 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).



300
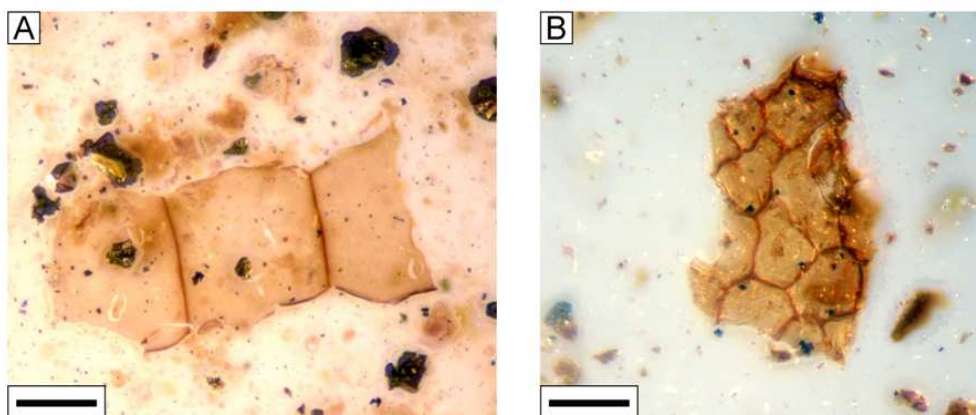
**Figure 4.- Plant cuticle fragments from the micropaleontological processing of coprolites from Iharkút: A,** Plant cuticle fragment with near hexagonal cells (VER 2014.118.) [Scale bar: 30 µm]; **B,** Plant cuticle fragment with irregular cells (VER 2014.119.) [Scale bar: 30 µm]

305

### 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 30-50 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.
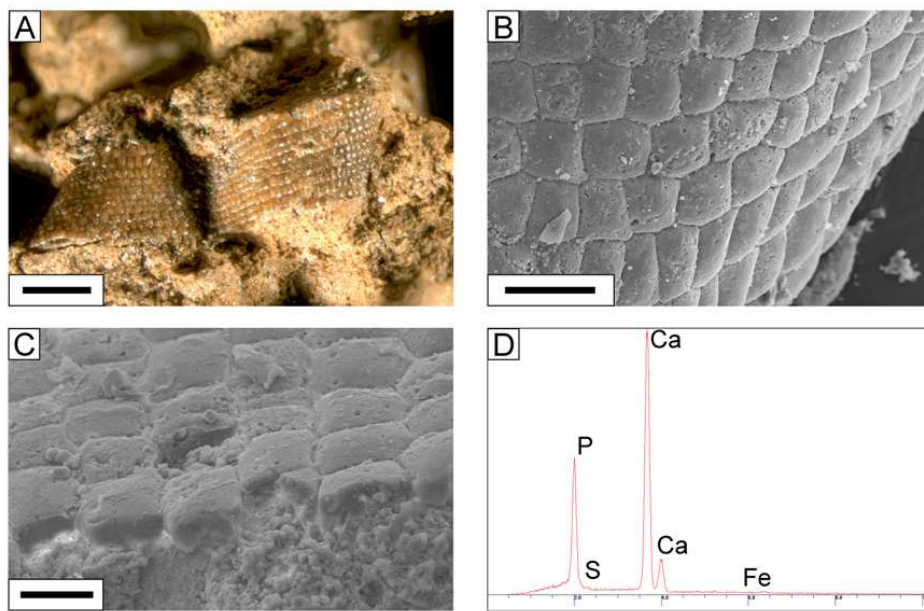
322    **Figure 5.- Probable cuticle imprints in the matrix of coprolites from Iharkút: A,**

323    Probable cuticle imprint in the matrix of a coprolite (VER 2016.1321.) [Scale bar: 300 µm];

324    **B,** Scanning electron micrograph of a probable cuticle imprint on a broken surface (VER

325    2016.1321.) [Scale bar: 50 µm]; **C,** Probable imprints of the cells of cuticle on the broken

326    surface (VER 2014.118.) (SEM) [Scale bar: 25 µm]; **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).
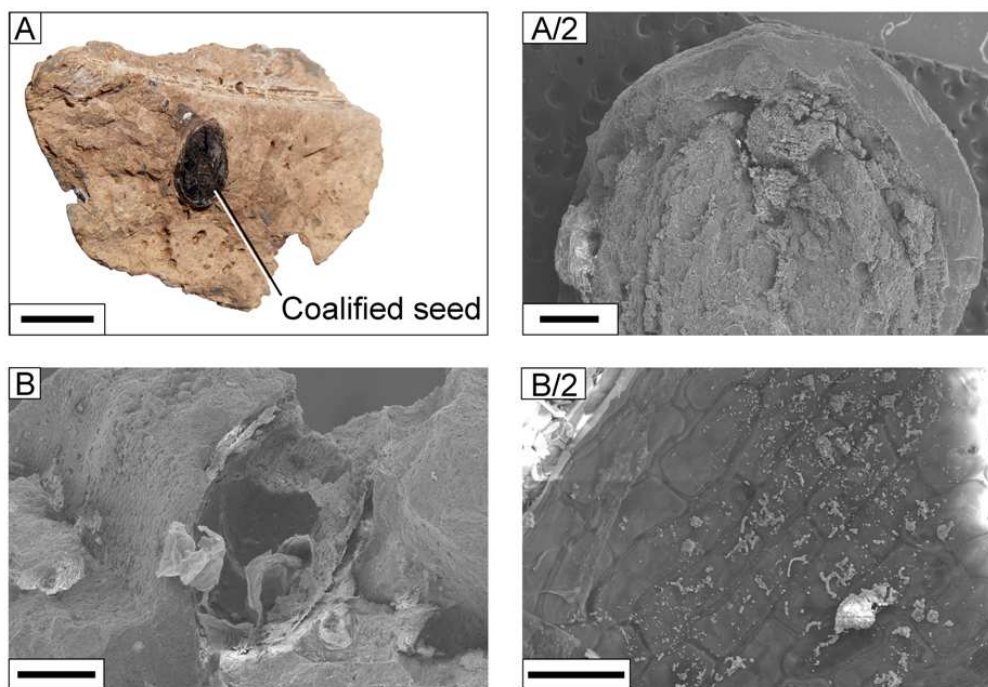


331

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 µm]

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 cristals (Fig. 7B). On the scans the inclusions differ

348 significantly from the host matrix because of their different density (Milán et al., 2012).
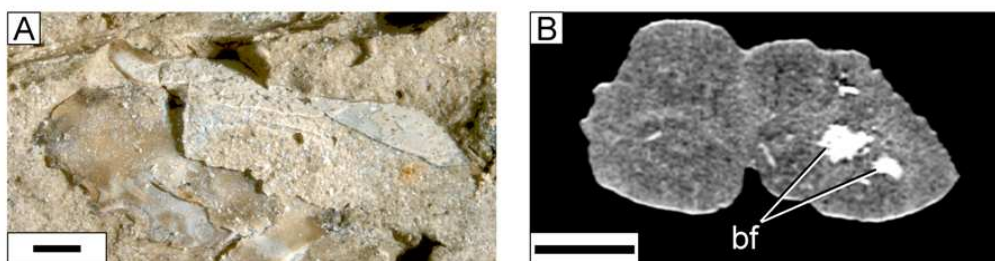


349

350 **Figure 7.- Fragmentary animal remains in Late Cretaceous coprolites from Iharkút: A,**

351 Mollusk shell fragments (VER 2016.1323.) [Scale bar: 300 µm]; **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).
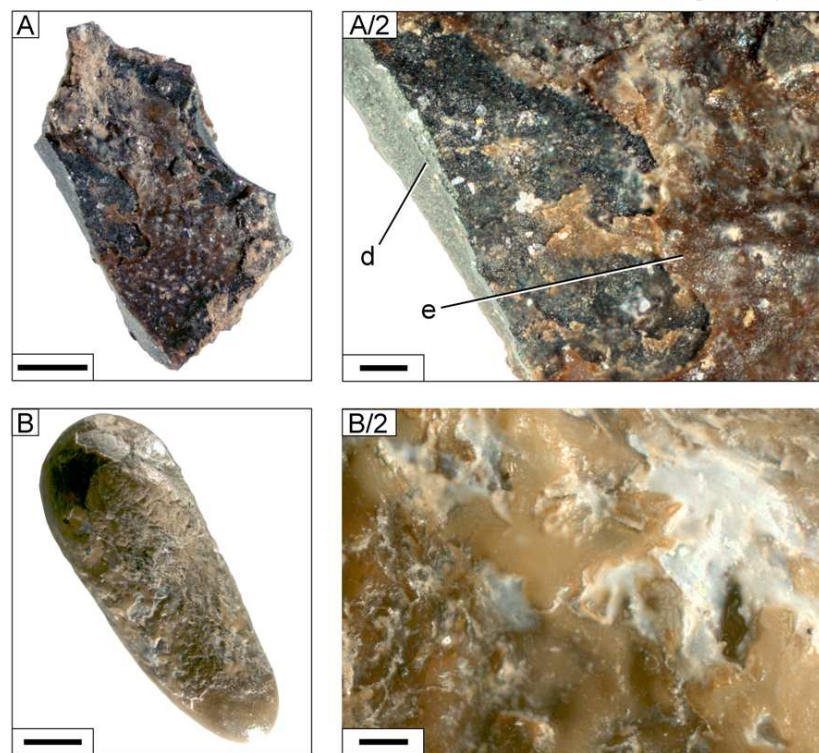


362

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 µm]; **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 µm]

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).
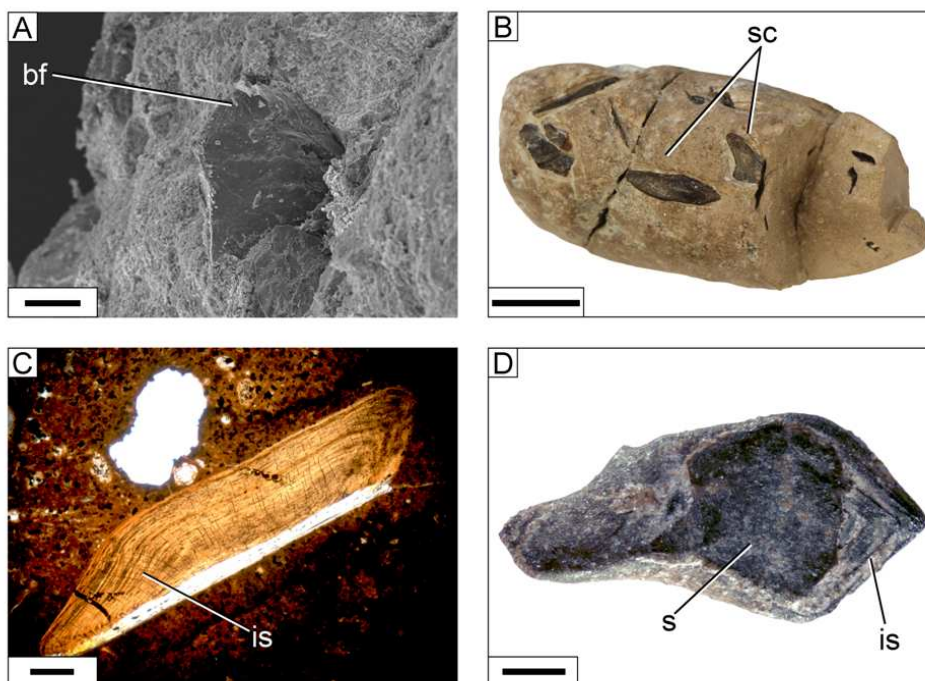


380

381    **Figure 9.- A,** Small bone fragment (bf) from a coprolite bearing a Pycnodontiformes fish

382    tooth (VER 2016.1329.) [scale bar: 100 µm]**; 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 corpolites (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 Chondrichtyes (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-Lagerstatten (Kriwet,

421    2001) showed that these fish did not posses 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 excepted 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

23

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 phospathic

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 faces 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 Fromation 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 $H_2O_2$ 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 indigestable (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

26

532    underside leaf surface of the lotus. The underside epidermis of this type of leafs, 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 µm 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 (Ősi et al., 2007),

562 which might have consumed a wide range of food resources with its peculiar heterodont

563 dentition (Ősi 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 circumastance 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 interfluve 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$^2$ (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$^2$) 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

655 **Acknowledgements**

674

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