Coprolites of Late Triassic carnivorous vertebrates from Poland: an integrative approach

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Abstract

Vertebrate coprolites derived from Upper Triassic terrestrial deposits of southern Poland have been subjected to various analytical methods in order to retrieve information about their composition, producer's diet and nature of the microscopic structures preserved in the groundmass. Morphologically, the coprolites have been classified into four morphotypes, of which only three were further analysed due to their good state of preservation. Their groundmass are composed of francolite, a carbonate-rich apatite, in which abundant coccoid structures are preserved. Based on various microscopic and organic geochemical techniques, they are interpreted as fossilized bacteria which could have mediated the phosphatization of the faeces. The thin sectioning revealed that the coprolites consist of those containing exclusively bone remains, and those preserving both bone and plant remains. Those coprolites preserving only vertebrate remains are suggestive for exclusive carnivorous diet of the producers. However, the interpretation of coprolites consisting of both vertebrate and plant remains is more debatable. Although they may attest to omnivory, it cannot be excluded that potential producers were carnivorous and occasionally ingested plants, or accidentally swallowed plant material during feeding. The latter may involve predation or scavenging upon other herbivorous animals. The potential producers may have been animals that foraged in or near aquatic habitats, such as semi-aquatic archosaurs and/or temnospondyls. This is supported by the presence of ostracode and other aquatic arthropod remains, and fish scales within the coprolites, as well as by the presence of specific biomarkers such as phytanic and pristanic acids, which are characteristic constituents of fish oil. The preservation of such labile organic compounds as sterols, palmitin, stearin or levoglucosan attests for rapid, microbially-mediated mineralization of the faeces at very early stages of diagenesis.

Key words: Coprolites, vertebrates, carnivores, bacteria, biomarkers, Triassic

1. Introduction

Coprolites are fossilized faeces preserved in sedimentary rocks throughout the Phanerozoic.

Such trace fossils (e.g., Hunt and Lucas, 2005a, b; Hunt et al., 1998, 2007) are known from both terrestrial (e.g., Mancuso et al., 2004; Northwood, 2005; Smith and Botha-Brink, 2011; Owocki et al., 2012; Fiorelli et al., 2013; Bajdek et al., 2014; Khosla et al., 2015) and marine settings (e.g., Eriksson et al., 2011; Zatoń and Rakociński, 2014; Shen et al., 2014; Nakajima and Izumi, 2014). Although they are indirect traces of the producers, coprolites serve as a valuable source of information on the diet and physiology of extinct animals (e.g., Chin and Kirkland, 1998; Hollocher et al., 2005; Chin, 2007; Gill et al., 2009; Smith and Botha-Brink, 2011; Bajdek et al., 2014; Khosla et al., 2015), trophic chain structure and predator-prey interactions in the fossil record (e.g., Chin, 2002; Northwood, 2005; Aldridge et al., 2006; Zatoń and Rakociński, 2014; Nakajima and Izumi, 2014). Moreover, as lithified structures, they also provide important data on sedimentary environments and early diagenetic processes leading to their formation, as well as on microbial and invertebrate communities operating within the faeces during their residence in the given palaeoenvironmental setting (e.g., Lamboy et al., 1994; Hollocher et al., 2001, 2005, 2010; Chin et al., 2009; Eriksson et al. 2011; Owocki et al., 2012; Mahaney et al., 2013; Cosmidis et al., 2013).

Even though coprolites are not directly associated with their producers, several indicators are used to decipher the potential culprits. Coprolite size, shape and fossil content (inclusions) may depend on whether the producer was invertebrate or vertebrate, and whether it was a herbivore, omnivore, insectivore or carnivore animal (e.g., Chin and Kirkland, 1998; Chin et al., 1998; Edwards et al., 2012; Wood and Wilmshurst, 2014; Khosla et al., 2015). Moreover, on the basis of the degree of food degradation and preservation of specific biomarkers, the kind of metabolism of a producer may also be untangled (e.g. Gill et al., 2009, 2010; Owocki et al., 2012). All these data, together with information on animal fossils preserved in the same deposits may provide a coherent

knowledge on the nature of possible producers. Sometimes, in very favourable diagenetic microenvironments, the food remains may be exceptionally well-preserved, providing additional coprolite 'taphonomic windows' into past life and victim identity (e.g., Meng and Wyss, 1997; Chin et al., 2003; Northwood, 2005; Yates et al., 2012; Dentzien-Dias et al., 2013; Zatoń and Rakociński, 2014).

In the present work, we focus on Late Triassic phosphatic coprolites derived from terrestrial palaeoenvironments of two localities in southern territories of Poland, where a number of different vertebrate assemblages have been recently discovered (Dzik and Sulej, 2007; Dzik et al., 2008; Budziszewska-Karwowska et al., 2010; Sulej et al., 2011, 2012; Niedźwiedzki et al., 2012, 2014). The late Triassic was a critical time in the evolution of land vertebrates (e.g., Sues and Fraser, 2010; Brusatte et al., 2010). Important groups of tetrapods, such as crocodiles, pterosaurs, dinosaurs and mammals, evolved to flourish later on in the Mesozoic era. Therefore, coprolites from that period are important for documenting the source of diet, interactions, as well as local community structures. Recently, plant-rich coprolites putatively produced by dicynodonts have been described from the Late Triassic deposits of southern Poland by Bajdek et al. (2014). In the present paper, we focus on coprolites produced by carnivore animals. We used various analytical methods in order to retrieve information about their geochemical composition, the diet of the potential producers and preserved microbial structures.

2. Geology, stratigraphy and palaeocommunity structure

The latest Triassic (late Norian-Rhaetian) was an interval of abrupt evolutionary changes in terrestrial ecosystems (Sues and Fraser, 2010). The end of the Rhaetian was evidently also a time of widespread igneous activity in the rift basins of the Atlantic margins (e.g., Schoene et al., 2010) and extinction of many typical Triassic groups of land tetrapods (e.g., Olsen et al., 2002). The record of this extinction event is also visible in the Triassic of Poland (Pieńkowski et al., 2014). In the Late

105 Triassic times, the Silesia area (southern Poland) was located at the western margin of a large
106 Laurasian landmass, at approximately 40° N palaeo-latitude and was the part of the north-east
107 margin of the Germanic Basin (Golonka, 2007). This part of the basin is still poorly understood and
108 contains floral and faunal elements unknown from other areas of the Germanic Basin (e.g. Dzik and
109 Sulej, 2007; Dzik et al., 2008; Niedźwiedzki et al., 2014).

110

111 **Figure 1 near here**

112

113 2.1. *Poręba site*

114 A short overview of the geology and stratigraphy of the Poręba site was recently presented by
115 Sulej et al. (2012) and Niedźwiedzki et al. (2014). The site is located in the northern part of Poręba
116 city, about four kilometres from Zawiercie, southern Poland (Fig. 1). The strata exposed at Poręba
117 belong to the upper part of the Middle Keuper sequence in southern Poland. In the Polish
118 lithostratigraphic scheme (see Polish Stratigraphical Table, 2008), they are referred to as the
119 Zbąszynek beds (Woźniki Limestone or Woźniki Formation in local lithostratigraphical schemes;
120 see Szulc et al., 2006). The Zbąszynek beds exposed at Poręba contain conglomerates (with rare
121 magmatic rocks and quartzitic pebbles), grey to yellowish sandstones, grey to greenish mudstone
122 and siltstone, ‘bone-breccia’ horizons (horizons termed as the ‘Lisów Breccia’ by geologists) and
123 horizons with carbonaceous nodules (probably pedogenic in origin), as well as pyrite nests (Fig. 2).
124 The Zbąszynek beds are correlated with the upper part of the Middle Keuper–lowermost part of the
125 Upper Keuper formations (middle–upper Stubensandstein–Steinmergelkeuper or upper Arnstadt
126 Formation and lowermost Exter Formation) from the Germanic Basin (see Franz et al., 2007a, b;
127 Franz, 2008). This lithostratigraphic position of the Poręba exposures is essentially equivalent to
128 that of mid–upper Middle Keuper strata detected in the Niwki and Poręba boreholes, both located
129 close to the fossil-bearing site (Szulc et al., 2006).

130 The coprolite-bearing strata exposed at Poreba are yellowish, bone-rich, carbonated
131 conglomerates with bone-breccia (high-energy environment) and grey fluvial, calcareous, organic-
132 rich mudstones and siltstones (low-energy environment) with large fragments of fossil wood (trunks
133 fragments), charcoals (Marynowski et al., 2014), bivalves, ostracods, conchostracans, plant
134 remains, plant roots, microbial oncoids and small carbonate nodules. The entire observed
135 stratigraphic section in this locality is at least 8 m thick and contains four distinct horizons (a-d)
136 with vertebrate bones (Fig. 2).

137

138 **Figure 2 near here**

139

140 Palynological studies suggest a middle–late Norian age for the Poreba site (Niedzwiedzki et
141 al., 2014). More than 50 palynomorphs were identified in one organic-rich sample from the layer
142 located above the uppermost bone bed. This palynoassemblage is characteristic for subzone b of the
143 *Corollina meyeriani* Zone (see Orłowska-Zwolińska, 1983, 1985) in the Polish part of the Germanic
144 Basin and is characteristic of the lower–middle part of the Zbąszynek beds and the underlying
145 Jarkowo beds. The subzone IVb of the *Corollina meyeriana* Zone probably corresponds to the
146 *Corollina-Porcellispora* Subzone, the lower part of the *Corollina-Enzonalasporites* Zone of Lund
147 (1977), zones GTr 16–17 of Heunisch (1999) and the *Granuloperculatipollis rudis* Zone of
148 Kürschner and Herngreen (2010). The IVb Subzone assemblages are similar to those of the
149 Steinmergelkeuper (Orłowska-Zwolińska, 1985).

150 The tetrapod record in Poreba (Fig. 3) is dominated by skeletal remains of turtles, which are
151 represented mainly as isolated plates (or fragments of plates) from carapace or plastron, vertebrae
152 and fragments of long bones (Sulej et al., 2012). These remains represent possibly a single species
153 of terrestrial turtle, which is a new taxon similar to *Proterochersis robusta*. Several isolated
154 dinosauriform specimens were collected from Poreba (Niedzwiedzki et al., 2014). This assemblage
155 includes a silesaurid, specimens of herrerasaurid, and remains of another type of theropod

156 (potentially a neotheropod). The Poręba herrerasaurid is the first record of this rare group of
157 primitive saurischia or basal theropod from Europe and one of the youngest records worldwide,
158 whereas the silesaurid is the youngest record from Europe. Other vertebrate remains are rare, but
159 include vertebra and dermal elements of aetosaurs, dipnoan teeth plates, hybodont shark fin spines
160 and teeth, as well as actinopterygian fish skull elements and scales. Preserved fragments of bones
161 and teeth of a large carnivorous archosaur (possibly a 'rauisuchian' or a mid-sized theropod
162 dinosaur) were also found in this locality. A few isolated teeth and a small part of the shaft of a large
163 long bone collected from the organic-rich mudstone and claystone intervals belong to large
164 temnospondyls.

165 Besides the mentioned and in part published material, there are still many undescribed plant
166 macrofossils, unrecognizable bones and a collection of bivalves. The plant fossils in the Poręba
167 outcrop are very abundant and well preserved, but not characterized in detail. The dominant plant
168 species is a conifer similar to *Brachyphyllum*. Fragments of branches with leaves and numerous
169 fragments of charcoalified or mineralized wood trunks, sometimes of large size, also occur in the
170 organic-rich mudstone and claystone (Sulej et al. 2012). *Brachyphyllum* is characterized by
171 xeromorphic leaves and pollen cones, which suggests a drier/sunny habitat or a dry season during
172 this time. The occurrence of the reddish mudstones in the Poręba section also suggests the
173 appearance of dry conditions. The Middle Keuper basin was situated between 20° and 30°N and
174 was strongly influenced by Pangaeian, monsoon-like atmospheric circulation with dry and wet
175 periods (Vollmer et al., 2008). More than 25 species of palynomorphs were identified in one
176 organic-rich sample (Niedźwiedzki et al., 2014). This palynoassemblage contains spores and pollen
177 grains belonging mainly to gymnosperms and ferns.

178 The Poręba fossil assemblage, as currently known, is composed of more than six tetrapod
179 taxa. More than half of the collected fossils are represented by the new taxon of turtles. This taxon
180 was arguably one of the most abundant animals inhabiting the Poręba ecosystem. Another
181 remarkable aspect of the assemblage is the diversity of the dinosauriforms, which is greater than

182 that of the other archosauromorphs combined. Large aquatic archosauromorph taxa such as
183 phytosaurs and large dicynodonts, which are typical elements of the Late Triassic freshwater
184 ecosystems are conspicuously absent from the assemblage.

185

186 **Figure 3 near here**

187

188 2.2. *Lisowice site (Lipie Śląskie clay-pit)*

189 According to Dzik et al. (2008), Niedźwiedzki et al. (2012), Pieńkowski et al. (2014) and
190 Niedźwiedzki (2015), strata exposed in the Lipie Śląskie clay-pit at Lisowice (Fig. 1) correspond to
191 the uppermost part of the Middle and lower part of the Upper Keuper deposits of the Germanic
192 Basin (see also Franz et al., 2007a, b; Franz, 2008). In the geological literature, the
193 lithostratigraphic unit represented at the Lipie Śląskie clay-pit (Fig. 4) has been referred to as
194 Norian (see Szulc *et al.* 2006) or Rhaetian “*sensu polonico*” (see Franz et al., 2007a, b; Franz,
195 2008).

196 The identification of a palynomorph assemblage, which represent the Subzone IVc of the
197 *Corollina meyeriana* and *Ricciisporites tuberculatus* zones, with characteristic forms such as
198 *Rhaetipollis germanicus* Schulz, *Ricciisporites tuberculatus* Lundblad, *Corollina meyeriana*
199 (Klaus) Venkatachala *et* Góczán, *Granuloperculatipollis rudis* Venkatachala *et* Góczán (see Świło
200 et al., 2014) in the dark-grey and organic-rich strata at the Lipie Śląskie clay-pit suggest correlation
201 of this unit with the uppermost Zbąszynek beds and lower Wielichowo beds (uppermost Norian-
202 lower Rhaetian) from the northern part of Poland (Orłowska-Zwolińska, 1983; Franz, 2008).

203 The coprolite-bearing strata exposed at Lisowice consist of grey, fluvial, calcareous, organic-
204 rich mudstones and siltstones (low-energy environment) with bones of large tetrapods, bivalves and
205 numerous fragments of fossil wood (fragmentary trunks). Poorly preserved fragments of possible
206 coprolites were also found in conglomerates (high-energy environment). The entire observed

207 stratigraphic section in this locality is at least 12 m thick and contains two intervals with vertebrate
208 bones (Fig. 4).

209 The Lipie Śląskie clay-pit at Lisowice contains a larger number of fossils (Fig. 5) than the
210 Poręba exposure and it is one of the most diverse vertebrate assemblages of Late Triassic age in
211 Poland, representing up to 15 taxa (Niedźwiedzki, 2015). Most of the vertebrates occur in the grey
212 carbonate mudstones and siltstones in the middle part and at the top of the exposed section (Fig. 4).
213 The vertebrate assemblage is dominated by bones of a gigantic dicynodont and isolated remains of
214 actinopterygian fishes. The Lisowice fauna is composed of terrestrial rather than amphibious or
215 aquatic tetrapods. In two layers with large wood fragments, remains of dicynodonts are associated
216 with remains of *Smok wawelski* (an early predatory dinosaur), small to medium-size archosaurs
217 (pterosaur, dinosauriform, small predatory dinosaur and poposaurid), and other non-archosaur
218 archosauromorphs (e.g. a choristodere-like animal) and small diapsids. Identification of many of the
219 disarticulated, often fragmentary bones of other tetrapods is difficult (Dzik et al., 2008;
220 Niedźwiedzki et al., 2012; Niedźwiedzki, 2015). The temnospondyls (*Cyclotosaurus* sp. and
221 *Gerrothorax* sp.) are known from an isolated, partially preserved skull, skull bones, jaw bones, and
222 numerous long bones collected in a layer less than one meter above the principal bone-bearing bed
223 of the clay-pit exposure. A few isolated long bones of capitosaur and plagiosaurs were also found
224 in the main bone-bearing horizon. Such ‘amphibian assemblages’ are typical of a frequently flooded
225 alluvial floodplain. Numerous macroremains of coelacanth and dipnoan fishes and spines of
226 hybodont sharks (Świło, 2010a, b, c; Świło and Kowalski, 2011) were also found. A single
227 mammaliaform or mammal tooth (*Morganucodontidae* indet.) was also recorded (e.g., Świło et al.,
228 2014).

229

230 **Figure 4 near here**

231

232 The mudstone and siltstone intervals contained a rich assemblage of ostracods,
233 conchostracans, bivalves, and rare insect remains (Dzik et al., 2008; Kozur and Weems, 2010;
234 Skawina and Dzik, 2011). The most common are ostracods (*Darwinula* sp. and *Rhombocythere* sp.)
235 and occur only in few horizons and, if present, form massive accumulations. The conchostracans
236 *Gregoriusella polonica* Kozur and Weems, 2010 and *Euestheria* sp. of a very small size (1.5-3.5
237 mm in length) are rare and occur in two horizons in association with small vertebrate bones. In the
238 lowermost part of the grey unit, numerous carapaces of much larger species *Shipingia* sp. (3-6 mm
239 in length) were collected. Numerous bivalves collected from the mudstone facies strata represent
240 the large unionoid *Tihkia silesiaca* Skawina and Dzik, 2011. Insect remains are very rare in this site.
241 Until now only five specimens of isolated beetle elytra were collected from grey mudstone and
242 siltstone of the lower part of bone-bearing deposits.

243 In the bone-bearing strata, numerous well-preserved macrofloral remains were found
244 (Staneczko, 2007; Dzik et al., 2008; Wawrzyniak, 2010a, b, c, 2011; Wawrzyniak and Ziaja, 2009).
245 The dominant plant species in this site is a conifer similar to species of the genera *Brachyphyllum*,
246 *Pagiophyllum* or *Hirmeriella*, but other plants, probably representing the cycadophytes *Nilssonia*
247 and *Beania* are also present (Wawrzyniak, 2010a). Other plant fossils are represented by
248 representatives of cycadophytes, ginkgophytes, coniferophytes or pteridosperms, among which
249 isolated cuticles of *Lepidopteris ottonis*, confirming the Rhaetian age of the plant beds occur
250 (Staneczko, 2007; Ociepa et al., 2008; Wawrzyniak, 2010a, 2011; Pacyna, 2014).

251 The Poręba and Lisowice sites contain two distinct and different faunas, supposedly with only
252 a few overlapping vertebrate taxa (Figs. 3, 5). Taxonomically, the Poręba tetrapod fauna is
253 dominated in numbers by dinosauriforms (Silesauridae and basal theropods or saurischia) with
254 turtles, aetosaurs and temnospondyls as additional elements. The Lisowice site contains a record of
255 gigantic dicynodont and large early predatory dinosaur. Temnospondyl remains are relatively
256 abundant in the Lisowice fauna and are represented by two or even three species. The diversity of
257 small reptilians is relatively high as indicated by the presence of pterosaur, dinosauriform, small

258 predatory dinosaur, poposaurid, choristodere-like animal and other small diapsids (Niedźwiedzki,
259 2015). Moreover, the presence of basal mammaliaform or early mammal in the Lisowice fauna
260 further points to the different nature of both faunas (Świło et al., 2014).

261

262 **Figure 5 near here**

263

264 **3. Material and methods**

265

266 In total, 39 coprolite specimens have been collected for the present study. However, due to the
267 overall state of preservation, only 18 coprolites have been considered for the present study (Table
268 1). Sixteen coprolites were collected in Lisowice from siltstones and mudstones (Fig. 4), relatively
269 rich in organic remains (reaching up to 2.5% TOC; Marynowski and Wyszomirski, 2008), and two
270 specimens were collected in the Poręba site within mudstone and siltstones (coprolite COP01) and a
271 conglomerate layer (coprolite COP16, Fig. 2). For the present study, a wide array of methods and
272 analytical techniques has been used in order to retrieve information about the coprolite composition,
273 diet of potential producers, palaeoenvironment and diagenesis. The methods and techniques
274 include: inorganic and organic geochemistry, X-ray diffraction, electron microprobe analysis, total
275 organic carbon and total sulphur determination, organic geochemistry, petrography, scanning and
276 transmission electron microscopy (SEM, TEM, and STXM), and palynomorph analysis. The raw
277 samples are housed at the Institute of Paleobiology, Polish Academy of Sciences, Warsaw,
278 abbreviated ZPAL V.39/372 (for Poręba) and ZPAL V.33/1270 (for Lisowice). The thin sections, as
279 well as residues from palynological preparations are deposited at the Faculty of Earth Sciences,
280 University of Silesia, Sosnowiec, abbreviated GIUS 7-3653.

281

282 **Table 1 near here**

283

3.1. *Inorganic geochemistry and X-ray diffraction (XRD)*

For bulk geochemical data, nine coprolite samples and an additional one (enclosing sediment, COP04b) have been analysed using fusion-inductively coupled plasma (FUS-ICP) at the Actlab laboratory in Canada. For bulk mineralogical data, nine coprolites and one sample of enclosing sediment (COP04b) were analysed with a PANalytical X'Pert Pro MPD-PW 3040/60 X-ray diffractometer housed at the Faculty of Earth Sciences, Sosnowiec, Poland. The samples were ground manually using an agate mortar for c. 5 min. A standard metal sample holder in the X'Pert Pro systems was filled with powder. To calibrate the peak line position, the following internal standard was used: Respirable α -Quartz for Quantitative XRD, Standard Reference Material, NIST, 1878a. XRD data were collected using the diffractometer equipped with a Theta-Theta geometry and X'Celerator – 1D silicon strip detector. Generator settings were 45kV and 30mA. All X-ray diffraction experiments were performed using a CoK_{α} radiation ($\lambda=1,78901\text{\AA}$) and a Fe-filter to reduce the K_{β} radiation. Data were collected in the range of $3-75^{\circ}2\Theta$ with a $0.01^{\circ}2\Theta$ step size and 300sec counting time. The interpretation and quantitative analysis of the collected data were carried out by means of the HighScore+ Software using the ICSD database, version 2007. The quantitative content was calculated using the Rietveld Method. Reference carbonate-apatite patterns of Perdikatsis (1991) were used as a starting model for the refinement. The CO_3^{2-} content of carbonate-fluorapatite was determined from measurements of the $\Delta 2\Theta$ for the 004-410 reflections pair. The relationship given by Schuffert et al. (1990) was used for our calculations: $y = 10.643 \cdot x^2 - 52.512x + 56.986$, where y is the CO_3^{2-} amount [wt%] and $x = \Delta 2\Theta$ (004-410). The HighScore+ profile fit algorithm was used to determine the exact position of the 004 and 410 reflection. Shape parameter of the Pseudo-Voigt profile function and the background was refined.

3.2. *Electron microprobe (EMP) analysis*

Apatite analyses (major/minor elements) were carried out on one sample (COP04a) in the Inter-Institution Laboratory of Microanalyses of Minerals and Synthetic Substances, Warsaw,

310 Poland, using a CAMECA SX-100 electron microprobe (15 kV, 20 nA). The apatite analyses have
311 been normalized to the sum of 50 negative charges including 24 oxygen ions and two monovalent
312 anions (fluorine site) according to the ideal chemical formula of apatite: $A_{10}(BO_4)_6(X)_2$, where the
313 A site is occupied by Ca, Fe, Mn, Mg, Th, REE, Y and Na. The B site is occupied by P (substituted
314 by S, Si) and the X site by F, Cl and OH^- ions. The hydroxyl content was calculated by
315 normalization assuming ideal stoichiometry (i.e., no vacancies in the X site so that $F+Cl+OH^- = 2$).
316

317 3.3. *Total organic carbon (TOC) and total sulphur (TS) determination*

318 Abundances of total carbon (TC), total inorganic carbon (TIC) and total sulphur (TS) were
319 performed for eight coprolite samples using an Eltra CS-500 IR-analyzer with a TIC module at the
320 Faculty of Earth Sciences, Sosnowiec, Poland. TC, TS and TIC contents were measured using an
321 infrared cell detector of CO_2 and SO_2 gas, which was evolved by combustion under an oxygen
322 atmosphere for TC and TS respectively, and was obtained from reaction with 10% hydrochloric
323 acid for TIC. Total organic carbon (TOC) was calculated as the difference between TC and TIC.
324 Calibration was made by means of Eltra standards. Calcium carbonate content was calculated as
325 $CaCO_3 = 8.333 \times TIC$, assuming that all carbonate is present as calcite.
326

327 3.4. *Extraction, separation and derivatization.*

328 Six finely ground coprolite samples were extracted under 60°C and 150 bars using
329 dichloromethane/methanol mixture (5:1, v:v) with an accelerated solvent extractor Dionex ASE
330 350. Extracts were separated into aliphatic, aromatic and polar fractions by modified column
331 chromatography (Bastow et al., 2007). Silica-gel was first activated at 110°C for 24 h and then put
332 into Pasteur pipettes. The eluents for collection of the fractions were: *n*-pentane (aliphatic), *n*-
333 pentane and DCM (7:3 - aromatic), and DCM and methanol (1:1 - polar). An aliquot of the polar
334 fraction was converted to the trimethylsilyl (TMS) derivatives by reaction with *N,O*-bis-
335 (trimethylsilyl)trifluoroacetamide (BSTFA) and pyridine for 3 h at 70 °C. A blank sample was

336 analysed using the same procedure. In the blank sample, trace amounts of phthalates, fatty acids
337 (FAs) and *n*-alkanols were detected.

338

339 3.5. *Gas chromatography – mass spectrometry (GC-MS).*

340 The GC-MS analyses were carried out with an Agilent Technologies 7890A gas
341 chromatograph and Agilent 5975C Network mass spectrometer with Triple-Axis Detector at the
342 Faculty of Earth Sciences, Sosnowiec, Poland. The J&W DB35-MS (60 m × 0.25 mm × 0.25 µm)
343 capillary column with 35% polymethylsiloxane and 65% diphenylsiloxane was used. The GC was
344 programmed from 50°C after 1 min to 120°C at 20°C/min, and then to 300°C at 3°C/min, with final
345 temperature maintained for 90 min. The GC column outlet was connected directly to the ion source
346 of the mass spectrometer. Mass spectra were recorded from *m/z* 45–550 (0–40 min) and *m/z* 50–700
347 (above 40 min). The MS was operated in the electron impact mode (ionization energy 70 eV). An
348 Agilent Technologies Enhanced ChemStation (G1701CA ver. C.00.00) and the Wiley Registry of
349 Mass Spectral Data (8th edition) software were used for data collection and MS processing.

350

351 3.6. *Thin sections.*

352 In order to retrieve the information about fossil inclusions and petrography, 15 samples,
353 including two possible pyritized coprolites, have been sectioned longitudinally and transversely to
354 the longest axis at the Faculty of Earth Sciences, Sosnowiec, Poland. Thin sections were then
355 inspected using an Olympus transmitted light microscope and a Philips XL30 environmental
356 scanning electron microscope (ESEM) at the Faculty of Earth Sciences, Sosnowiec, Poland.

357

358 3.7. *Investigation of the coccoid structures.*

359 In order to check and verify the nature of the coccoid structures present in the coprolites, one
360 coprolite sample (COP04a) was further analysed by scanning electron microscopy (SEM),
361 transmission electron microscopy (TEM) and scanning transmission x-ray microscopy (STXM).

362 General SEM observations were conducted at the Faculty of Earth Sciences, University of
363 Silesia, Sosnowiec, using an ESEM Philips XL 30. The samples were investigated in uncoated state
364 using back-scattered imaging (BSE). The detailed investigations were performed at the Institut de
365 Minéralogie, de Physique des Matériaux et de Cosmochimie, Paris, France, using a Zeiss Ultra 55
366 SEM equipped with a field emission gun. COP04a was freshly broken and polished using Al_2O_3 .
367 The surface was then platinum-coated. Images were acquired with the microscope operating at 15
368 kV, and a working distance of 7.5 mm in secondary electron mode using the SE2 detector, or in
369 backscattered electron mode using the AsB detector. Energy dispersive x-ray spectrometry (EDXS)
370 analyses were performed at 15 kV at a working distance of 7.5 mm using a Bruker Quantax
371 spectrometer.

372 For TEM and STXM analyses, two electron- and x-ray-transparent foils were prepared. The
373 foils were extracted by focused ion beam (FIB) milling from the non-embedded polished COP04a
374 sample using a FEI strata DualBeam 235 FIB at the Institut d'Electronique, de Microelectronique et
375 de Nanotechnologies (IEMN), Lille, France. The FIB foils were lifted out and welded on one side
376 onto a copper grid (without carbon membrane) *in situ* before final polishing. The final foils
377 measured ~18 μm long, ~8 μm wide and 100-200 nm in thickness for FIB foil#1 and ~22 μm long,
378 ~12 μm wide and 100-200 nm in thickness for FIB foil #2. Rationale for the use of FIB milling and
379 recent applications in geobiology can be found in Benzerara et al. (2005) and Bernard et al. (2010).

380 The FIB foils were first analysed by STXM at the carbon K-edge and the Ca $\text{L}_{2,3}$ -edges.
381 STXM and X-ray absorption near edge structure (XANES) analyses were performed on beamline
382 11.0.2.2. at the Advanced Light Source (Lawrence Berkeley National Laboratory, Berkeley, USA)
383 (Bluhm et al., 2006). Energy calibration was achieved using the well-resolved 3p Rydberg peak of
384 gaseous CO_2 at 294.96 eV (Ma et al., 1991). A 25 nm zone plate was used. Data included images
385 and image stacks, from which XANES spectra and maps were retrieved. Data were processed using
386 the aXis2000 software (Hitchcock, 2012). Rationale for the use of STXM to study biominerals,

387 including Ca-phosphates can be found in Benzerara et al. (2004) and Cosmidis and Benzerara
388 (2014).

389 FIB foils were then analysed by TEM. Observations were performed on a LaB6 JEOL JEM
390 2100 TEM operating at 200 kV. Images were acquired using an ultrascan 2k CCD camera in bright
391 field mode. Compositional maps were acquired by EDXS analysis in the STEM mode.

392
393 3.8. *Preparation of palynomorphs and other organic remains.*

394 In order to better recognize the organic remains, ten samples were selected for palynological
395 investigation. Generally, c. 10 g of each coprolite were processed using standard palynological
396 procedures HCl-HF-HCl (Wood et al., 1996). Finally, residues were sieved through an 18 µm nylon
397 sieve. Four slides were prepared from each residue. Generally, the organic remains were segregated
398 into six types: miospores (pollen grains and spores), higher plant cuticles, higher plant tracheids,
399 translucent organic particles, black organic particles and animal remains (mostly cuticles). Then, the
400 cuticles were identified to the lowest possible taxonomic level. Two hundred palynomorphs were
401 counted for each coprolite sample for statistical purpose. The observation and documentation was
402 completed using a transmitted light microscope (Olympus BX51 with DS-U3 controller and Nikon's
403 NIS-Elements imaging software suite) and an ESEM Philips XL30. The palynological slides and
404 residues are housed at the Faculty of Earth Sciences, Sosnowiec, Poland.

405 406 **4. Results**

407 408 4.1. *Morphology, size and composition*

409 Most of the coprolites from Lisowice collected were found as loose fragments on the surface
410 of the freshly exposed deposits, but in some cases they were found *in situ* within the host rock.
411 Many of the collected specimens are fragmentarily preserved or lack any distinctive features and
412 thus are referred to as possible coprolites. Those from Lisowice are also usually pyritized so that

413 both their external morphology and primary composition is obliterated. Better or completely
414 preserved specimens are represented by four distinct morphotypes.

415

416 **Figure 6 near here**

417

418 **Morphotype 1** is represented by six specimens characterized by both ends similarly rounded
419 (isopolar of Thulborn, 1991). Some of these coprolites are elongated, rod-like shaped (see Eriksson
420 et al., 2011) with circular to semi-circular cross-section (Fig. 6B, D, G, J). They measure 53–160
421 mm in length and 16–70 mm in width. Others are ovoidal, measuring 46–73 mm in length and 18–
422 25 mm in width. Detailed description of the largest and cylindrical coprolites (60–160 mm long)
423 from the Lisowice site is presented by Niedźwiedzki (2015) and interpreted as faecal mass
424 produced by the large early predatory dinosaur *Smok wawelski* (Niedźwiedzki et al., 2012;
425 Niedźwiedzki, 2015).

426 **Morphotype 2** comprises 14 coprolites having one end wider than the other (anisopolar of
427 Thulborn, 1991). To that group belong those having a smooth exterior but having one end much
428 narrower than the other or even pointed (Fig. 6A, C, F, H); other specimens of that morphotype are
429 ovoidal with both ends differing, but not as much as the previous case (e.g., Fig. 6C, I). Two
430 specimens have a distinct, circular cavity inside the wider end (Fig. 6A, C). The coprolites are 14–
431 45 mm in length and 7–46 mm in width.

432 **Morphotype 3** includes ten coprolites with irregular (ellipsoidal to ovoidal) shapes. Eight
433 specimens, however, are strongly pyritized and thus considered here as possible coprolites. They
434 may be up to 100 mm in length (Fig. 6K).

435 **Morphotype 4** contains nine, tiny, 9–32 mm long, thin and curved specimens. Due to their
436 pyritization (Fig. 10D), they are considered as possible coprolites and were not furthered analysed.
437 Two cylindrical specimens are a little bit flattened and are more regular in shape and surface
438 morphology.

439 When viewed in cross-section, some coprolites are composed of more or less visible
440 concentric layers (Fig. 6J). These features were probably generated when the faecal material was
441 squeezed along the producer's intestine and extruded from the cloaca. The mass of the coprolites is
442 beige or brown in colour. Most of the coprolites have a sharp outer contact with a clear separation
443 from the adhered host sediment. The exterior surface of the coprolites is usually irregular, although
444 it can be smooth in some cases. It is sometimes covered by adherent clay with carbonaceous matter
445 and also sediment grains.

446

447 **Table 2 near here**

448

449 As evidenced from thin sections, the coprolites have a very fine-grained, micro-crystalline
450 and apatitic groundmass. Bulk chemical analyses showed that the coprolites are primarily composed
451 of Ca and P with low amount of SiO₂. The phosphate content is variable and ranges from 9.1 wt. %
452 to 20.3 wt. % (Table 2). The XRD analyses are in agreement, showing that the main minerals
453 building the coprolites are apatite and calcite (Table 3). However, their mass percentages obtained
454 by FUS-ICP and XRD may vary either due to measurement errors, and quite significant content of
455 different elements in the apatite structure. Also the content of OH⁻-groups, as well as a porosity of
456 the coprolites may result in such differences. Calcite and apatite are associated with admixture of
457 other minerals such as quartz, pyrite and barite. Traces of clay minerals, iron oxides (goethite) and
458 dolomite are also possible (Table 3).

459

460 **Table 3 near here**

461 **Figure 7 near here**

462

463 The XRD analyses showed that phosphate occurs in the form of francolite, a carbonate-rich
464 variety of the mineral fluorapatite, which is consistent with EMP analysis and SEM-EDXS

465 mapping. In the SEM backscattered electron mode, fragments of francolite (rich in Ca and P)
466 appear in light grey in a matrix of Ca-carbonates, which appears in darker grey (Fig. 7).

467

468 **Figure 8 near here**

469

470 TEM-EDXS were also consistent with SEM analyses (Fig. 8). Francolite is composed of Ca
471 and P in a ratio of ~1.6. Moreover, F, Na and S were systematically detected in association with
472 francolite. As the XRD analysis showed, phosphate-rich coprolites clearly differ from the enclosing
473 sediment (Fig. 9), which mainly contains quartz (45 wt. %) and calcite (40 wt. %); clay minerals are
474 represented by dioctahedric smectite, kaolinite, chlorite and illite (Σ ~8 wt. %). Small admixtures of
475 dolomite (~3 wt. %), feldspars (~3 wt. %) and pyrite (~1 wt. %) were also detected. Generally, the
476 composition of the coprolites, especially the presence of francolite and calcite, is similar to other
477 described examples (e.g., Hollocher et al, 2005, 2010; Eriksson et al., 2011).

478

479 **Figure 9 near here**

480

481 Thin sections of the coprolites reveal fragmented bones and other animal or plant tissues. The
482 coprofabric may either differ between particular coprolite morphotypes, or may be similar. For
483 example, some coprolites of the morphotype 2 (e.g., samples COP01 and COP14) may possess
484 characteristic mucosal folds (e.g., Jain, 1983; Eriksson et al., 2011), composed of very fine-grained
485 apatitic mass, interfingering with sparry calcite (Fig. 10A-B), which do not occur in those of the
486 morphotype 1 and 3. However, the coprofabric consisting of micro-crystalline phosphatic
487 groundmass (Fig. 10C) with some sparry calcite and pyrite grains, without any mucosal folds and
488 large areas occupied by calcite crystals, may occur in morphotypes 1, 2 and 3. The pyritized
489 putative coprolites instead, have completely obliterated coprofabric (Fig. 10D).

490

Figure 10 near here

4.2. *Bulk and molecular composition of coprolites*

The total organic carbon (TOC) content in the coprolites varied significantly between 0.4 to 1.5% (Table 4). In almost all samples, very low concentrations of total sulphur were detected, which is characteristic for terrestrial sedimentary environments and organic matter (OM) originated from such deposits. One exception, where TS >1%, occurred in one sample that was showing secondary pyritization.

Table 4 near here

Coprolite samples were characterized by very similar molecular composition, with prominence of the polar fraction and a very low percent amount of aromatic compounds.

The aliphatic fraction was characterized by a preponderance of low-molecular weight *n*-alkanes with maximum in *n*-C₁₇ and *n*-C₁₈. High molecular weight *n*-alkanes were present in low concentration but predominance of odd over even high-molecular weight *n*-alkanes was detected in most of the samples. The aliphatic fraction of coprolites contained series of mid-chain methyl-alkanes and cycloalkanes and two common isoprenoids: pristane and phytane, which were present in comparable amounts (Fig. 11). Low relative concentrations of $\alpha\alpha\alpha$ -steranes with small predomination of C₂₇ over C₂₉ compounds were detected in two samples (COP09 and COP18).

Figure 11 near here

Aromatic compounds were present in very low abundance in the samples. Only few compounds were identified including phenanthrene and its methyl- and dimethyl- derivatives,

516 fluoranthene, pyrene and phenylanthracenes (1- and 2-PhN). Among aromatic nitrogen
517 compounds, benzocarbazole isomers were identified.

518 In the polar fraction, homologue series of *n*-alkanoic acids and *n*-alkanols clearly dominated
519 with preponderance of *n*-hexadecanoic acid (Table 5, Fig. 12). Even-carbon homologues
520 predominated the distribution of *n*-alkanols, while in case of *n*-alkanoic acids such domination was
521 clearly visible starting from C_{15:0} fatty acids. Beside saturated *n*-alkanoic acids and *n*-alkanols, C_{16:1}
522 and C_{18:1} fatty acids and alcohols were detected at high relative concentration (Table 5) in all
523 coprolite samples. Sterols were a quantitatively significant group of compounds. More specifically,
524 sitosterol was the main sterol compound and cholesterol was the second most important.
525 Degradation products of sterols (cholesta-3,5-dien-7-one and stigmasta-3,5-dien-7-one) were also
526 detected. Fats such as palmitin and stearin (both 1- and 2- glyceryl esters) were present in
527 significant amount as well (Table 5, Figure 12). Other polars detected in coprolite samples as minor
528 compounds were isoprenoid acids (pristanic and phytanic acid), urea, levoglucosan and β - and α -
529 amylin (Table 5).

530

531 **Table 5 near here**

532 **Figure 12 near here**

533

534 4.3. *Coccoid structures within apatite groundmass*

535 The ESEM investigation of both broken coprolites and thin sections revealed that the apatitic
536 groundmass (including mucosal folds) is composed of abundant spherical objects measuring up to 3
537 μm in diameter (Fig. 7). These structures, forming dense aggregations, were systematically
538 observed in the francolite fragments of the coprolites (Fig. 8). Two 100-200 nm thick electron
539 transparent foils were cut within these francolite fragments. TEM observations confirmed that
540 francolite fragments are composed of packed micrometer-sized spheres. These spheres are outlined
541 by a dense wall of francolite, ~120-150 nm thick. Some spheres appear as empty shells while other

are filled by francolite laths measuring ~300 by ~50 nm wide and are radially elongate (Fig. 8). Hexagonal sections were occasionally observed, consistently with francolite habits.

STXM analyses were performed on the same foils at the C K-edge and the Ca L_{2,3}-edges. Spectra at the Ca L_{2,3} edges were very similar all over the examined areas, suggesting that only one Ca-containing phase, i.e., francolite is detected on the FIB foils. Spectra showed major peaks at 349.3 and 352.6 eV which correspond to the L₃ and L₂ edges of Ca respectively, as well as smaller features at 347.2, 347.8, 348.3, 348.7 and 351.6 eV (Fig. 8I). Such spectra are typical of apatitic minerals including francolite (Benzerara et al., 2004). A prominent narrow peak was observed at 290.3 eV at the C K-edge as well as a broader peak at 300.9 eV (Fig. 8J). They are interpreted as 1s→π* and 1s→σ* electronic transitions in carbonates respectively. Based on the ratio between the height of the peak at 290.3eV and the edge step between 340 and 360 eV at the Ca L_{2,3}-edges, the CO₃ content of francolite was mapped using the approach developed by Cosmidis et al. (2015). The ratio was relatively homogenous over the explored area and estimated between 4 and 6% of CO₃ in wt. Some organics was also detected as indicated by peaks at 285 eV, interpreted as 1s→π* in aromatic groups, and at 288.5 eV, interpreted as 1s→π* in carboxylic groups. Mapping showed that organic-rich areas appear on edges of the FIB foil and/or lining holes inside the spheres. TEM-EDXS analyses on the same areas showed a systematic enrichment in gallium (Fig. 8G). Although some organic carbon might be originally associated with these structures, areas rich in organic carbon are interpreted as re-deposition of contaminating carbon during FIB milling by the gallium beam. The origin of contaminating carbon might be, at least partly, contamination from the decomposition of the organometallic precursor used for platinum deposition, which is rich in aromatic groups (Carlut et al., 2010). This is consistent with the observation that re-deposition is higher where porosity is higher.

In some cases, spheres are completely filled by fine-grained francolite. In these cases, one or two concentric <100 nm wide, darker layers delimited the spheres as observed in the TEM bright field mode (Fig. 8B). Since Ca, P, S, F and Na, as well as CO₃ groups as shown by TEM-EDXS and

STXM analyses are all higher in these darker layers, they are interpreted as layers with less nanoporosity, hence higher density of francolite grains. As evidenced from the EMP analyses, the francolite containing the coccoid structures does not show zoning with respect to chemical composition (see ESM Fig. 1C).

572

4.4. *Fossil inclusions and their preservation*

Different inclusions were identified on the external surface of the specimens, as well as in the interior of broken samples. Most of the elements, however, were identified inside the coprolites using thin sections. They were embedded in a microcrystalline apatitic matrix and represent a variety of fossils, including bone fragments and scales (Figs 13-15), plant remains and palynomorphs (Figs 17-18), and arthropod cuticles (Fig. 19).

579

Figure 13 near here

581

4.4.1. *Scales, teeth and bones*

Nearly all identified bone fragments originated from small prey animals and were evenly scattered within the individual coprolites. In two coprolites, long fragments of dicynodont bones were identified (Niedźwiedzki, 2015), whereas in another one, a large isolated tooth of the large early predatory dinosaur *Smok wawelski* with signs of digestions was also found. Most of the bone fragments in the coprolites were white or brownish (Figs 13-15); the darker colour was due to humic acids produced by the biodegradation of the organic matter or mineral filling (e.g., pyrite or manganese oxides) the pores in observed bone elements. Some bone fragments showed external and internal damages such as deformed or missing tissues (e.g., Fig. 13E), suggesting pockets of decay. Cross-section of two specimens evidenced that most of the elongate bone fragments were oriented perpendicular to the long axis of the coprolite (e.g., Figs 13D, 15A).

593

Figure 14 near here

Two coprolites contained fish scales (Fig. 13F). The transverse section of one of the best preserved scale showed an amorphous, thick enamel layer, dentine with numerous dentinal tubules, Sharpey's fibers, and several lines of von Ebner (Fig. 13E). The scale was secondarily penetrated by straight and branching canals, probably of microbial (fungal?) origin. Several smaller unidentified bone fragments were also preserved (Figs 13A-C, 15A), including a fragment that was oval-shaped in cross-section; probably, it was a long bone of a small tetrapod with calcified cartilage of the bony trabeculae (Fig. 15C). In other coprolites, several sections of slowly formed and poorly vascularized bone (fish or amphibian bones) were also observed (e.g., Fig. 13A-B). The dentine of another preserved tooth fragment (Fig. 14C) showed dentinal tubules oriented perpendicularly to the pulp cavity. Enamel was preserved only in some margins of this tooth.

Different degrees of digestive corrosion of skeletal remains were observed in the coprolites. Some elements (e.g., scales) were complete in cross-section and others were represented by highly degraded bone fragments (Figs 14A-B, 15B). The coprolites also contained small bone splinters showing such signs of corrosion as markedly rounded and polished edges, suggesting rather strong digestive processes. Some bone fragments displayed characteristic fracture surfaces indicating breakage whilst the bone was still fresh (Fig. 13E). Some skeletal elements were perforated by tunnels, chambers and networks of microborings (Fig. 15C-F). This was the result of microbial attack (bacteria or fungi) of bony and probably collagen-rich elements. One of the sectioned coprolite contains packed fibrous elements (Figs 14D, 15A). Whether they are digested remains of hairs is currently unclear as we did not obtain any clear evidence using SEM. However, they are intriguing fossils the nature of which maybe is possible to decipher using other methods.

Figure 15 near here

The XRD data indicate, that the fossil bone fragments are similar based on their crystallographic parameters to the francolite composition of the coccooid structures and the coprolite groundmass. Overlapping peaks indicating a second generation of apatite on the XRD spectra were not observed. The EMP analyses in the micro-area, however, showed the occurrence of three different populations of apatite forming the bone fragments scattered within the coprolite groundmass. The first type of apatite occurs in the central part of the bone fragment (ESM Fig. 1A) and is characterized by higher content of SO₂ in the structure, ranging between 2.5 – 3.0 wt. %. The second type of apatite occurs in marginal part of the bones (ESM Fig. 1A) and contains stable quantity of SO₂ (2.25 – 2.5 wt. %). The phosphate content in marginal part is higher (32.6 – 33.8 P₂O₅ wt. %) than in the central part (ESM Fig. 1). The third type is represented by apatite composing the bone fragments, but does not show any zonation in the BSE images (ESM Fig. 1B); its chemical composition is similar to the first type (ESM Fig. 1). However, these relatively small changes in chemical composition within the particular apatite generations do not need to significantly influence the structural parameters of the apatite types distinguished. The data may indicate that the chemical composition of bone apatite changed slowly during diagenesis. Depending on the rate and scale of the replacement of OH⁻ and phosphate ions by flourite and carbonate ions in the original bone structure (dahllite or hydroxylapatite), the fossil bone material preserves for a while the mosaic mineral composition with the simultaneous presence of two apatite phases (Nemliher et al., 2004). The described skeletal remains are formed only by francolite, which indicates a long time of diagenetic changes, started already during the Late Triassic period.

Figure 16 near here

4.4.2. Organic remains

No correlation between the coprolite morphotype, its locality and organic residue content has been found. For example, in the coprolites COP05 and 10 (morphotype 1, Lisowice), COP08 and 16

646 (morphotype 2, Lisowice and Poręba, respectively), the organic residue was rich and differentiated
647 in categories and taxa. In other coprolites, however, as COP02 and 06 (morphotype 1, Lisowice), as
648 well as COP09 and 18 (morphotype 2, Lisowice), the organic content was poor. In the remainder,
649 only black and translucent organic particles were preserved, similar to plant or animal cuticles.

650 The organic remains were grouped into six main types: plant cuticles, plant tracheids,
651 miospores (spores and pollen grains), animal cuticles, brown, translucent organic particles and
652 black, opaque organic particles (Fig. 16). The identification of the recognizable cuticles revealed
653 the presence of four cuticle types:

654 **Cuticle type A** (Fig. 17A-D). The cuticles of this type are very robust and survived digestion
655 and diagenesis almost completely. Their epidermal cells are rectangular, occasionally polygonal,
656 and isodiametric but elongate over veins. In most cases, epidermal cells are characterized by thick
657 and straight anticlinal walls; the periclinal walls are smooth except for a central hollow papilla
658 extending above the surface of the epidermis. Stomata are arranged in loose rows between the
659 veins. From four to five subsidiary cells encircle a deeply sunken stoma; each subsidiary cell bears
660 a solid papilla that together cover the pit almost entirely. The ventral anticlinal walls of the
661 subsidiary cells are strongly cutinized, as are the dorsal anticlinal walls occasionally, too.
662 Subsidiaries are surrounded by one complete and occasionally another incomplete ring of additional
663 subsidiary cells.

664 Cuticles of this type are almost identical with those published as *Lepidopteris ottonis* from
665 the Rhaetian of Greenland (Harris, 1932), Scania (Lundblad, 1950) and Poland (Barbacka, 1991).
666 Given the fact that these cuticles derived from coprolites and thus passed the digestive tract of the
667 parent animal, a degradation of the cuticles and different preservation types are to be expected.
668 Despite this, cuticles have apparently not been so heavily attacked by digestion as they looked
669 rather “fresh” (cf. Harris, 1935; Lundblad, 1950).

670

671 **Figure 17 near here**

672

673 **Cuticle type B** (Fig. 17E-F). This cuticle is very delicate and anticlinal cell walls are almost
674 invisible, but the guard cells of the stomata have survived digestion and maceration quite properly.
675 Epidermal cells are elongate over veins, but are more polygonal in intercostal fields; anticlinal cell
676 walls are straight and thin, producing distinct corners. Periclinal walls are smooth and papillae are
677 absent. Stomata are regularly scattered between the veins, are orientated longitudinally, and flanked
678 by large and strongly cutinized lateral subsidiary cells that create a sunken stomata. Polar cells are
679 less strongly cutinized. Subsidiary cells have no papillae but strongly cutinized ventral and dorsal
680 periclinal walls. The sunken guard cells apparently did not survive maceration.

681 This type of cuticle is very similar to different cuticles of *Podozamites* leaves, described
682 from the Rhaetian of East Greenland (Harris, 1935). Of these, *Podozamites stewartensis* appeared
683 as the most similar one. Certain identification could not be made because the preserved portions in
684 the coprolites were too fragmentary.

685 **Cuticle type C** (Fig. 17G-I). This moderately delicate cuticle is characterized by elongate
686 polygonal cells with acute short ends in many cases. Each cell is characterized by three to five
687 roundish markings, which could either be papillae or other surface structures. However, the latter is
688 not easy to depict. In one specimen, a stoma with two sunken, strongly cutinized guard cells is
689 visible; further characteristics, however, are difficult to be obtained. Due to the poor preservation of
690 these cuticles, further identification is almost impossible. The cuticles might be interpreted as
691 bryophyte cuticles (cf. Reissinger, 1950; Hübers and Kerp, 2012), such as those reported by Harris
692 (1931) from the Rhaetian of Jameson Land, Greenland.

693

694 **Figure 18 near here**

695

696 **Cuticle type D** (Fig. 18M). From one coprolite, a strongly “granulate” cuticle was obtained
697 that has no signs of cells. The “granulae” could be interpreted as the densely spaced papillae of the

698 small epidermal cells of the megaspore membrane or the cupulate disc of *Peltaspermum rotula* (cf.
699 Harris, 1935; Lundblad, 1950; Barbacka, 1991). However, as no further details were visible, the
700 identification remained ambiguous.

701 A considerable amount of woody elements found in the coprolites could be identified as
702 tracheids with either bordered pits or with spirally, or helically, or even network-like arranged wall
703 thickenings (Fig. 18A-K). Most of these elements were quite intact but a further identification
704 towards generic or specific level is impossible as no references are known to us from this time
705 interval. Although rarely observed, some cuticles also show distinct signs of infestation by fungi
706 (Fig. 18L).

707

708 4.4.3. *Arthropod remains*

709 Tiny arthropod remains are occasionally present in different coprolites (e.g., Northwood,
710 2005). Here, arthropods are represented by cuticle (Fig. 19) and a single ostracod valve (Fig. 13B).
711 The cuticle features indicative for arthropod affinity consist of characteristic pores (Fig. 19A, D),
712 cuticle folding (Fig. 19B) and setae (Fig. 19B-C). The arthropod cuticles were very scarce in the
713 investigated samples. Their highest frequency was close to 0.5-1% (COP01, 10 and 16), while in
714 the rest of the samples (e.g. COP08), their frequency was much below 0.5% (Fig. 16). Their
715 identification is hampered due to their small size, high degree of fragmentation and absence of
716 preserved more diagnostic parts. However, the presence of a few distinct cuticle types (Fig. 19)
717 point to the presence of different taxa. It is not excluded that they belonged to aquatic arthropods.
718 The arthropod cuticle occurs in the coprolites of the morphotype 1 (COP10, Lisowice) and
719 morphotype 2 (COP01 and 16, Poręba).

720

721 **Figure 19 near here**

722

A single ostracod valve was recognized in one specimen (Fig. 13B). The presence of ostracods in archosaur coprolites is common (Souto, 2010), especially in crocodilian scats, probably because most of the archosaur coprolites were produced by animals living close to water environments or even in the shallow pools and swamps, usually full of small crustaceans. Recently, Khosla et al. (2015) reported numerous ostracods within putative titanosaurid coprolites from the Upper Cretaceous of India. Other small-sized aquatic crustaceans like conchostracans were also identified in coprolites from the Upper Permian of Russia (Owcocki et al., 2012) and Early Triassic coprolites from Australia (Northwood, 2005).

5. Discussion

5.1. Molecular indicators

Molecular studies of Mesozoic vertebrate coprolites are rare. To our knowledge, the only detailed study on coprolite organic matter (OM) including OM pyrolysis was performed on two organic-poor coprolites from the Cretaceous Two Medicine Formation of NW Montana, USA (Hollocher et al., 2001). Biomarker data of Mesozoic coprolites have been presented on International Meeting of Organic Geochemistry in 1993 and described by Chin and Brassell (1993). Lack of data from Palaeozoic to Mesozoic coprolites is probably due to the scarcity of well preserved, non-weathered material containing immature OM. More information comes from younger, excellently preserved Pleistocene to Holocene coprolites (e.g. van Geel et al., 2008; Gill et al., 2009; 2010; Carr et al., 2010), providing data about the nutritional habits and digestive processes of ancient animals.

The analysed Upper Triassic coprolite samples are unique due to very low thermal maturation of the rock sequence (not exceeding 0.35% of vitrinite reflectance; Marynowski et al., 2014) and their good preservation in a clay complex, without signs of weathering.

748 *n*-Alkane distribution with short chain homologues predomination is characteristic for bacterial
749 organic matter type (Peters et al., 2005). However, dominance of odd-over-even homologues was
750 observed in less abundant high molecular weight *n*-alkanes (Fig. 11), which is typical for terrestrial
751 OM input. Series of mid-chain methyl-alkanes and cycloalkanes are most probably genetically
752 connected with bacteria activity.

753 Distribution of short chain *n*-alkanoic acids and *n*-alkanols with even-carbon homologues
754 predomination is characteristic for OM derived from bacteria (e.g. Hollocher et al., 2001), while
755 even/odd dominance for long chain homologues suggests input from higher plants (e.g. Van Geelt
756 et al., 2008). Distinctive dominance of C_{16:0} and C_{18:0} as well as high abundances of C_{16:1} and C_{18:1}
757 FAs and alcohols can be genetically connected with bacteria and cyanobacteria (Fulco, 1983; Heath
758 et al., 2002; Summons et al., 2013), but other sources, like higher animals and fishes (e.g. Thiel et
759 al., 2014), or cutin from land plants (e.g. Hedges et al., 1997; Otto and Simoneit, 2001; Marynowski
760 et al., 2007), cannot be definitely ruled out. In addition, two isoprenoidal FAs: 3,7,11,15-
761 tetramethylhexadecanoic acid (phytanic acid) and 2,6,10,14-tetramethylpentadecanoic acid
762 (pristanic acid) were also detected in low abundance (Table 5). They are most possibly degradation
763 products of chlorophyll (e.g. Rontani and Volkmann, 2003), but what is noteworthy, both these
764 compounds are constituents of marine and fresh-water fish oils (Corr et al., 2008).

765 Surprisingly, despite their old age, the coprolites contain sterols. Sitosterol is the major steroid
766 compound in all samples, but cholesterol is also present in considerable amount. Two other sterols
767 (campesterol and stigmasterol) are of low significance (Table 5). Coprostanol and other stanols,
768 formed as biohydrogenation products of sterols in the gut of most higher animals and birds, and
769 considered as biomarkers of faecal material (e.g. Sistiaga et al., 2014), have not been found in the
770 samples analysed. However, gut formation of stanols is typical mainly for mammals and even in
771 this case varies a lot in intensity. For instance, the cholesterol-to-coprostanol conversion in human
772 intestine can be almost complete or totally absent (Veiga et al., 2005). Moreover, the composition
773 of faeces from herbivorous animals is more diverse than feces from carnivores and contains a much

774 wider range of lipids (Gill and Bull, 2012). Sterols and steradienones distribution detected in Upper
775 Triassic samples suggests diverse, plant-animal diets of the coprolite producers. Domination of
776 sitosterol derived from higher plants over cholesterol genetically connected with higher animals
777 does not necessarily mean that higher plants dominate in animal diet. It is well know that the decay
778 rate of terrestrial OM is slower than for any other OM type and that land-derived material is,
779 therefore, preferentially preserved in sediments (e.g. Prah et al., 1997).

780 Glyceryl esters (palmitin and stearin isomers) are identified for the first time in coprolite
781 samples (Table 5; Fig. 12). These compounds can be constituents of both plant and animal fats (e.g.
782 Hilditch and Shrivastava, 1948; Shimi et al., 1959; Bosque-Sendra et al., 2012), and seem to be
783 primary constituents of coprolite OM.

784 In all samples, relatively low amount of urea was detected (Table 5). This finding suggests
785 very fast mineralization of coprolites by apatite and preservation of OM from future
786 decay/oxidation. Also occurrence of levoglucosan, an anhydrosugar formed by biomass burning,
787 suggests very fast mineralization, especially since this compound is unstable and undergoes
788 degradation in soils in thousands of years (Elias et al., 2001). The appearance of levoglucosan in
789 coprolites is consistent with evidences of widespread wildfires detected in the Late Triassic bone-
790 bearing clays (Marynowski and Simoneit, 2009; Marynowski et al., 2014). The other explanation of
791 the presence of such compounds in investigated samples is contamination by rainwaters with
792 dissolved urine and levoglucosan. However, it seems unlikely that all coprolite samples were
793 contaminated by these compounds.

794

795 5.2. *Coccoid structures*

796

797 The origin of the abundant, micrometre-sized, coccoid structures observed in the coprolites is
798 under current debate. In the last decades, many studies have proposed a microbial origin for such
799 cocci-like objects (e.g., Lamboy et al., 1994; Soudry, 1992; Cosmidis et al., 2013). Recently, it was

800 shown experimentally that calcification induced by microorganisms could fossilize very delicate
801 cell structures, including organic molecules and help preserving these structures against aging at
802 relatively high temperature (Li et al., 2014). However, several authors have questioned the
803 biogenicity of such biomorphic particles (e.g. Baturin and Titov, 2006) and it has been shown that
804 hollow apatite spheres can be produced by abiotic processes (e.g., Gan et al., 2010; Perez et al.,
805 2011). Recently, Cosmidis et al. (2013) interpreted similar coccoid structures in Eocene coprolites
806 from the Ouled Abdoun phosphorites (Morocco), as Gram-negative bacteria fossilized by francolite.
807 This was based on several lines of evidence: (1) The coccoid structures had a wall appearing as a
808 dense francolite layer measuring between 20 and 40 nm in thickness, which corresponds to the
809 thickness of a mineralized periplasm in Gram-negative bacteria (Benzerara et al., 2004). (2)
810 Organically-rich layers were observed around the periplasm and were interpreted as fossil
811 membranes similar to what was previously observed in experimental fossils (Miot et al., 2011). (3)
812 Finally, they noted that the high density of coccoid structures in the Ouled Abdoun coprolites ($\sim 10^9$
813 per cm^3) was similar to typical bacterial cell densities in modern reptilian scats.

814 The coccoid structures observed here in Late Triassic coprolites have a similar size, show a
815 dense francolite wall and are sometimes filled or empty similarly to the coccoid structures in the
816 Ouled Abdoun coprolites. In contrast, their walls seem a little thicker than periplasms and organic-
817 rich layers were not observed as in Ouled Abdoun coprolites. The coarser size of francolite crystals
818 in Late Triassic coprolites is consistent with the older age of the sample and a possible greater
819 diagenetic alteration. Therefore, the differences between Late Triassic and Ouled Abdoun Eocene
820 coccoid structures (disruption/disappearance of organic-rich layers and thicker wall) could be due to
821 a more advanced aging and/or different early taphonomic processes. In any case, the high density of
822 these structures in coprolites which originally contained a high density of coccoid Gram-negative
823 bacteria holds as a strong support for an interpretation of such structures as phosphatized bacteria.
824 Other types than just Gram-negative bacteria may have fossilized but more specific characterization
825 of the identity of the fossils is difficult to obtain at that scale (Cosmidis et al., 2013).

826 Another, independent support for the bacterial nature of the preserved coccoid structures is
827 provided by the presence of specific biomarkers, like mid-chain methyl-alkanes and cycloalkanes,
828 or short chain *n*-alkanoic acids and *n*-alkanols with even-carbon homologues predomination, as well
829 as distinct dominance of C_{16:0} and C_{18:0} and high abundances of C_{16:1} and C_{18:1} FAs and alcohols.

830

831 5.3. *Coprolite producers*

832 Deciphering which animal is responsible for coprolite production is always speculative, as by
833 definition the coprolites are preserved outside the producer's body (e.g., Thulborn, 1991; Hunt et
834 al., 1994; Chin, 2002; Bajdek et al., 2014). Thus, the animal remains associated with coprolites in
835 the same deposits are very often used as an indication of potential coprolite producers. Association
836 of coprolites with only one or two kinds of animal groups offers an easier task. In contrast,
837 assemblages consisting of several different vertebrate groups may pose a serious problem for
838 interpreting potential animals responsible for defecation of digested remains. Sometimes, the
839 morphology of the coprolites does not allow for their easy linking with associated animals, leading
840 to the conclusions that coprolites may have been produced by as yet undiscovered animals (e.g.,
841 Jain, 1983). In other cases, the characteristic features of coprolites, e.g., exceptionally large size
842 (e.g., Chin et al., 1998, for tyrannosaurid coprolites) or characteristic composition and association
843 (e.g., Fiorelli et al., 2013, for dicynodont coprolites), may intuitively point to the likely producer.

844 From the size, morphology, and phosphatic composition of the specimens, it can be inferred
845 that all coprolites described here were produced by carnivores (e.g., Chin, 2002). However, taking
846 the coprolite size into account when interpreting the size of a potential producer may be very
847 problematic. For example, the Upper Triassic coprolites from Argentina studied by Hollocher et al.
848 (2005) were interpreted as being produced by an animal having 5-15 kg, as based on the coprolite
849 diameter (20 and 21 mm). This may equally indicate that the coprolites were produced by a single
850 species at various growth stages, or by a variety of different-sized species. Also the general shape of

851 the coprolites is not helpful, since a high intraspecific variation in morphology has been shown. For
852 example, distinguishing scats of modern crocodilian species is impossible (see Milàn, 2012).

853

854 Table 6 near here

855

856 What is evident, there is no apparent correlation between morphology, fossil content and other
857 mineralogical/geochemical parameters of the coprolites studied (Table 6). Some of the studied
858 coprolites representing morphotype 1 (04a and 06), morphotype 2 (COP01 and 14) and morphotype
859 3 (COP12) contain only bone material (plant remains are very scarce, see Fig. 15, Table 6)
860 suggesting that the producers were strictly carnivorous. Some small-sized specimens (COP01)
861 could have originated from some small to medium-sized archosaurs or temnospondyl amphibians,
862 like *Cyclotosaurus* sp. or *Gerrothorax* sp. known from the deposits sampled. The larger, elongated
863 coprolites (COP04a, 06, 14) may have been produced by medium to large-sized archosaurs. When
864 compared with the recent crocodilian scats (Milàn, 2012) the resemblance is strong. In addition,
865 comparative studies show that modern animals with a carnivorous diet such as crocodilians or big
866 cats tend to produce faecal masses with a cylindrical structure (Stuart and Stuart, 1998; Chame,
867 2003; Souto, 2010; Milàn, 2012). The studied coprolites occur in bone-bearing deposits rich in
868 remains of various vertebrate groups, which already were characterized above (see the section 2).
869 Thus, the described coprolites fall inside the size-range of medium to large archosaurs from the
870 mentioned faunistic elements. However, we cannot exclude that capitosauroid temnospondyls
871 produced the large and medium-sized coprolites from Poręba and Lisowice, especially since some
872 coprolites contain fish scales, perhaps suggesting for at least a periodical aquatic life-style of some
873 of the producers.

874 One characteristic feature of many coprolites studied is the presence of not only bone
875 fragments inside, but also abundant plant remains in the form of cuticles, tracheids/wood remains,
876 megaspores and pollen grains, as well as unrecognizable black and brown organic particles (Fig. 16,

877 Table 6). Recently, phosphatic coprolites containing plant debris have also been described from the
878 Late Cretaceous of India by Khosla et al. (2015). As coprolites putatively produced by herbivores
879 contain only plant inclusions and lack phosphate mineralization (e.g., Chin and Kirkland, 1998;
880 Chin, 2007; Fiorelli et al., 2013; Bajdek et al., 2014), the presence of various plant debris preserved
881 within the phosphatic coprolites, which are usually characteristic for carnivores, is interesting and
882 worth of discussion. Moreover, plant remains not only occur in small-sized (20 mm in diameter)
883 coprolites, but also in the largest specimens (30–50 mm in diameter) investigated here. Their
884 accidental occurrence in the coprolites, e.g., due to adhesion to deposited faeces, is unlikely as all
885 were derived from inside the coprolites. The good preservation of woody elements and cuticles
886 would suggest that the animals were feeding on living plants, mainly foliage but also swallowed
887 some wood, and were not able to degrade down lignin and cutin/cutan, both of which are complex
888 polymers usually degraded by specialized fungi. In only one instance, the cuticle bears a distinct
889 sign of fungal infestation (Fig. 18L) but it is unclear whether it happened before the plant was
890 swallowed by the animal, or after the remains were defecated.

891 The association of animal and plant remains in the phosphatic coprolites suggests that
892 potential coprolite producers were 1) omnivorous, feeding on both animals and plants, or 2)
893 carnivorous, ingesting occasionally plants, or 3) strictly carnivorous, swallowing accidentally plant
894 material during feeding. The majority of terrestrial vertebrates from investigated sites consist of
895 carnivores, mainly archosaurs. Indeed, a tooth of a predatory archosaur found in one of the
896 coprolites (Niedzwiedzki, 2015), or the presence of only arthropod cuticles, teeth and bone
897 fragments in the other one (COP01, see Table 6), strongly attests for the carnivore nature of some of
898 the producers. The only candidates, which could feed on both animals and incidentally (or
899 accidentally) plants were temnospondyls, turtles, poposaurids and other aquatic archosaurs.
900 Temnospondyls, spending much time in an aquatic habitat, could have incidentally, as well as
901 accidentally, swallowed plant remains when hunting on animal preys (including fish). Turtles more
902 likely could have swallowed both animal (fish) prey and plant remains (e.g., Northwood, 2005).

903 The poposaurids from Lisowice, when hunting close to the aquatic environment, could also have
904 accidentally swallowed some plant fragments. The presence of an ostracod and arthropod cuticles
905 (some of which could belonged to aquatic species) in some of the coprolites (COP06, see Table 6)
906 may suggest such a possibility (e.g., Northwood, 2005). It is known that during feeding, wild
907 alligators sometimes swallow plant material (see Platt et al., 1990; Elsey et al., 1992; Keenan et al.,
908 2013). Finally, it is highly possible that some coprolite producers were strictly carnivorous and
909 plant material might have been swallowed together with other animals in the form of the
910 gastrointestinal content of the latter (e.g., Thulborn, 1991). This may be supported by the presence
911 of a single type of cuticle in some of the coprolites (e.g., *Lepidopteris* in coprolites COP05, 08-10
912 and *Podozamites* in coprolites COP06-07 and 16), suggesting that prey animals would preferentially
913 feed on specific plants growing in the area. Predation on herbivorous animals are also documented
914 by the presence of dicynodont bone fragments in two coprolites studied by Niedźwiedzki (2015), as
915 well as the presence of dicynodont bones with preserved bite-marks (Niedźwiedzki et al., 2011).
916 Recently, putative dicynodont coprolites full of plant debris have also been documented from the
917 Lisowice site (Bajdek et al., 2014). Thus, such accidental swallowing of plant remains by strictly
918 carnivorous vertebrates during predation or scavenging may have occurred. As shown above, the
919 mixed animal-plant remains are well-expressed in the biomarker composition of the studied
920 coprolites. However, the phytanic and pristanic acids, which are possible degradation products of
921 chlorophyll, also occur in fish oils. Apart of fish scales preserved, it may be additional geochemical
922 evidence that the diet of at least some of the coprolite producers relied on fish. Thus, their foraging
923 in or near the aquatic habitat could have resulted in accidental swallowing of plant material as well.
924 In that case, some semi-aquatic archosaurs and/or temnospondyls could have been probable
925 culprits.

926 Vertebrate inclusions (scales, teeth and bones) can be well-preserved or show breakage and
927 some degree of digestion by stomach acids (Fig. 13C, 15B, F). Some components also show
928 degradation by microbes (Fig. 13F, 15C-E), which most probably attacked the bony material for

929 organic residues after the feces were deposited. The survival of bony material suggests that the
930 coprolite producers did not digest bones completely as extant crocodilians do (e.g., Milàn, 2012). It
931 suggests that such total bone digestion were not universal among archosauromorphs in the past
932 (Chin et al., 1998).

933

934 **6. Conclusions**

935

936 Vertebrate coprolites derived from the Upper Triassic terrestrial bone-bearing deposits have
937 been investigated using various analytical methods in order to decipher their composition, potential
938 producers' diet and nature of the preserved microbial-like structures. The coprolite groundmass is
939 composed of carbonate-rich fluorapatite (francolite) preserving abundant, micrometre-sized coccoid
940 structures interpreted as fossilized bacteria, which may have mediated the phosphatization of the
941 original faeces. The bacterial nature of the preserved coccoid structures may be supported by
942 specific biomarkers, such as *n*-alkanes with predomination of short chain homologues and
943 dominance of C_{16:0} and C_{18:0} fatty acids and alcohols as well as high abundances of C_{16:1} and C_{18:1}
944 fatty acids.

945 There is no apparent relationship between coprolite morphology and fossil inclusions
946 preserved. The coprolites include specimens, which exclusively contain vertebrate material and
947 those, which contain both vertebrate fragments and plant remains. The vertebrate material, in the
948 form of bones, scales and teeth fragments are preserved in different conditions, ranging from well-
949 preserved to those being at different stages of digestion. Those coprolites with only vertebrate
950 remains are suggestive for exclusive carnivorous diet of the producers. The interpretation of
951 coprolites consisting of both vertebrate and plant remains is more debatable. Although the
952 producers of such coprolites may have been omnivorous animals, it is highly probable that they
953 were carnivorous which only occasionally ingested plants, or swallowed them accidentally during
954 predation or scavenging upon other herbivorous animals which previously fed on plants.

955 The probable culprits swallowing animal prey and occasionally plants may have been animals
956 that foraged in or near aquatic habitats, such as some semi-aquatic archosaurs and/or
957 temnospondyls. This is supported by the presence of fish scales, ostracodes and other probable
958 aquatic arthropod remains in some of the coprolites, and also may be partly supported by the
959 presence of such specific biomarkers as phytanic and pristanic acids, which are constituents of fish
960 oil. The coprolites were quickly mineralized due to microbial activity on very early stages of
961 diagenesis, which is supported by the preservation of labile organic compounds, such as sterols,
962 palmitin, stearin, urea and levoglucosan.

963 The multidisciplinary approach performed on these coprolites during the present study
964 provides valuable data on diverse specific problems. Yet the question about the identity of the exact
965 producer remains challenging, especially when the coprolites were associated together with remains
966 belonging to a variety of vertebrate species as in the present case.

967

968

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970

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1342 Figure and table captions:

1343

1344 **Figure 1.** Geological sketch-map showing the location of the bone- and coprolite-bearing sites at
1345 Poręba and Lisowice (adopted from Niedźwiedzki et al. 2014).

1346

1347 **Figure 2.** Lithostratigraphic section of deposits exposed at the Poręba clay-pit (adopted from
1348 Niedźwiedzki et al. 2014).

1349

1350 **Figure 3.** Sketch-drawing of the faunal assemblage of the Poręba site. A - Large predatory
1351 archosaur (rauisuchian or predatory dinosaur), b - neotheropod dinosaur, c - theropod dinosaur
1352 Herrerasauridae indet., d - large temnospondyl amphibian, e - hybodont shark, f - dipnoan fish
1353 *Ptychoceratodus* sp., g - actinopterygian fish, h - aetosaur, i - turtle *Proterochersis* sp., j -
1354 dinosauriform Silesauridae indet.

1355

1356 **Figure 4.** Lithostratigraphic section of deposits exposed at the Lisowice clay-pit (adopted from
1357 Pieńkowski et al. 2014).

1358

1359 **Figure 5.** Sketch-drawing of the faunal assemblage of the Lisowice site. A - large, early predatory
1360 dinosaur *Smok wawelski*, b - large temnospondyl amphibian *Cyclotosaurus* sp., c – small theropod
1361 dinosaur Theropoda indet., d - temnospondyl amphibian *Gerrothorax* sp., e - small ‘rauisuchian’
1362 Poposauridae indet., f - small diapsid Choristodera indet., g - hybodont shark, h - coelacanth fish, i -
1363 dipnoan fish *Ptychoceratodus* sp., j - actinopterygian fish, k - large dicynodont
1364 Kannemeyeriiformes indet., l - small archosauromorph Rhynchosauria indet., m - dinosauriform
1365 Silesauridae indet., n - small lepidosaur Sphenodontia indet., o - pterosaur, p - mammaliaform
1366 *Hallautherium* sp.

1367

Figure 6. Examples of Upper Triassic coprolites from Poland studied. A-D. Coprolites of the morphotype 1. E-J. Coprolites of the morphotype 2. K. Coprolite of the morphotype 3. A-D, F-K. Coprolites from Lisowice. E. Coprolite from Poręba. Scale bars equal 1 cm.

Figure 7. ESEM photomicrographs of coccoid microstructures composing the phosphatic groundmass of the coprolites investigated. A. COP01, Poręba. B. COP04a, Lisowice. C. COP05, Lisowice. D. COP14, Lisowice.

Figure 8. TEM and STXM analyses of the coccoid structures in the FIB foils obtained from the Late Triassic coprolite from Lisowice (sample COP04a). A. General view of FIB foil 1 in TEM bright field mode. Numerous coccoid structures are observed as empty or filled spheres. B-D. Close-up of coccoid structures (FIB foil #1 and 2) showing a completely filled, small-grained coccoid structure (B) with a denser wall (arrows); an empty structure with a thick wall (C), and a structure with francolite crystals inside (D). E-G. Energy dispersive X-ray spectrometry (EDXS) maps of Ca, P and Ga. Ca and P are homogeneously distributed. Ga is preferentially located in holes. H. Typical EDXS spectrum of francolite. A Ca/P ratio of ~1.6 is derived from EDXS analyses. I. X-ray absorption near edge structure (XANES) spectrum at the Ca L_{2,3} edges obtained by STXM on francolite. Peaks at 347.2, 348.3, 348.7, 349.3, 351.6 and 352.6 are consistent with francolite. J. XANES spectrum at the C K-edge obtained by STXM on francolite. Peaks at 290.3 and 300.8 eV are characteristics of carbonate functional groups.

Figure 9. XRD patterns of nine coprolite samples (a) and host rock sample (b). A - apatite, C – calcite, D – dolomite, I-illite and mica, K – kaolinite, Q – quartz, Sm - smectite. The angular distance between the 410-00 apatite peaks is used to determine the carbonate content.

1393 **Figure 10.** Examples of coprofabrics in thin-sections of the coprolites investigated. A-B.
1394 Transmitted-light microscope views of coprofabrics consisting of microcrystalline apatitic mucosal
1395 folding and sparry calcite between the folds, morphotype 2, specimens COP01 (Poręba) and COP14
1396 (Lisowice), respectively. C. Transmitted-light microscope view of microcrystalline apatite
1397 groundmass with sparry calcitic grains and dispersed plant tissues, morphotype 2, specimen COP16
1398 (Poręba). D. Reflected-light microscope view of strongly pyritized (light areas) coprolite of the
1399 morphotype 3, specimen COP11 (Lisowice).

1401 **Figure 11.** Total ion current (TIC) of the saturated hydrocarbons fraction of two Upper Triassic
1402 coprolites from Lisowice. Numbers over the peaks identify individual carbon number homologues.
1403 Pr - pristane, Ph - phytane, NPr - nor-pristane.

1405 **Figure 12.** Total ion current (TIC) of the polar fraction (as TMS derivatives) of the sample COP09
1406 (Lisowice).

1408 **Figure 13.** Transmitted-light microscope photographs of thin-sections showing the bone and scale
1409 remains preserved in Upper Triassic coprolites. A-B. Flat and poorly vascularized long bones
1410 showing the characteristic rounded ends. C. Highly vascularized bone element with digested outer
1411 surface. D. Positions of bone elements inside the fecal groundmass. E. Bone fragments showing
1412 damages. F. Fish scale showing amorphous, thick enamel layer and dentine with numerous dentinal
1413 tubules. A. COP14, Lisowice, B, D, F. COP06, Lisowice, C. COP16, Poręba, E. COP18, Lisowice.

1415 **Figure 14.** Transmitted-light microscope photographs of thin-sections showing the bone, tooth and
1416 fibrous remains preserved in Upper Triassic coprolites. A-B. Highly degraded bone fragments. C.
1417 Transverse section of a tooth showing a thin layer of dentine surrounding a large pulp cavity. D.

1418 Poorly preserved fibrous elements. A-B. COP12, Lisowice, C. COP01, Poręba, D. COP14,
1419 Lisowice.

1420

1421 **Figure 15.** Transmitted-light microscope photographs of thin-sections showing the bone and
1422 fibrous remains preserved in Upper Triassic coprolites. A. Association of bone fragments and
1423 tightly packed fibrous elements. B. Highly degraded bone fragments. C. Small bone with calcified
1424 cartilage of the bony trabeculae. D-F. Skeletal elements showing microbial attack (bacteria or
1425 fungi). A, D-E. COP06, Lisowice, B-C, F. COP14, Lisowice.

1426

1427 **Figure 16.** Types and percentage contribution of particular organic remains present in the coprolites
1428 studied.

1429

1430 **Figure 17.** Plant cuticles found in the coprolites studied. A-D. Cuticle type A, very similar to
1431 *Lepidopteris ottonis*, COP05, Lisowice. E-F. Cuticle type B, similar to *Podozamites*, COP16,
1432 Poręba. G-I. closely unidentifiable cuticle type C, COP16, Poręba.

1433

1434 **Figure 18.** Plant tracheids and cuticle found in the coprolites studied. A-K. Various types and
1435 differently preserved woody tracheids. A, C, E-K, COP16, Poręba; B, D. COP10, Lisowice. L. A
1436 tissue infested by fungi, COP16, Poręba. M. Closely unidentified cuticle type D, COP08, Lisowice.

1437

1438 **Figure 19.** Various types of arthropod cuticle derived from coprolites. A-B. COP16, Poręba, C.
1439 COP01, Poręba, D. COP08, Lisowice.

1440

1441 **ESM Fig. 1.** Plot showing correlation of chemical elements present in apatite using the data
1442 obtained by EMP analysis. The geochemical trends for apatites in bone remains (A and B) and

1443 apatite groundmass (C) are: increase of the SO₂ content inside apatite building the interior of bone
1444 fragments (black points, A), increase in the P₂O₅ content of apatite building the marginal zones of
1445 bone fragments (grey and violet points, A-B), relatively low content of P₂O₅ in the apatite
1446 groundmass (yellow points, C).

1447
1448 **Table 1.** Data on sample number, provenance, kind of morphotype and methodologies used for the
1449 study of the Upper Triassic coprolites from Poland.

1450
1451 **Table 2.** Results of major elemental analysis using FUS-ICP of selected Upper Triassic coprolites
1452 and host rock (shaded area).

1453
1454 **Table 3.** Results of XRD analysis of selected Upper Triassic coprolites and host rock (shaded area).

1455
1456 **Table 4.** Total organic carbon (TOC), total sulphur (TS) and carbonate content (CC) in the selected
1457 Upper Triassic coprolites.

1458
1459 **Table 5.** Polar compounds detected in selected Upper Triassic coprolites as an TMS derivatives.
1460 Abundances normalized to C_{16:0} fatty acid, the most abundant lipid.

1461
1462 **Table 6.** Summarizing data on coprolite morphology, P content, TOC, biomarkers and fossil
1463 inclusions. Those coprolites which are pyritized or insufficiently studied are excluded.

1464 na - not analyzed; * - relative intensity of peaks in parentheses.

1465

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Sample/COP-		01	02	05	06	07	08	09	10	16	18
Plant cuticles	%	0	0	22,5	0,5	3,5	18	8,5	22	7,5	2
Plant tracheids		0	1	15	0	4	14	8	12	34	10
Miospores		0	0	6,5	1	14	8,5	0	3,5	16,5	1
Animal cuticles		1	0	0	0	0	0	0	0,5	0,5	0
Brown debris		34	51,5	36,5	55	72,5	33	42,5	58,5	37	59
Black debris		65	47,5	19,5	43,5	6	26,5	41	4,5	4,5	27,5

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Figure 19

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Table 1
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sample number/locality	morphotype	analyses applied
ZPAL V.39/372 COP01/Poreba	morphotype 2	transmitted-light microscopy, SEM, palynology, TOC and TS,
ZPAL V.33/1270 COP02/Lisowice	morphotype 1 (fragmentary)	palynology
ZPAL V.33/1270 COP03/Lisowice	morphotype 2	SEM, TOC and TS
ZPAL V.33/1270 COP04a/Lisowice	morphotype 1	transmitted-light microscopy, SEM, TEM, STXM, inorganic geochemistry, XRD, TOC and TS
ZPAL V.33/1270 COP05/Lisowice	morphotype 1	transmitted-light microscopy, SEM, palynology, inorganic geochemistry, XRD, TOC and TS, biomarkers
ZPAL V.33/1270 COP06/Lisowice	morphotype 1	transmitted-light microscopy, palynology, inorganic geochemistry, XRD, TOC and TS, biomarkers
ZPAL V.33/1270 COP07/Lisowice	morphotype 1	transmitted-light microscopy, palynology, inorganic geochemistry, XRD, TOC and TS
ZPAL V.33/1270 COP08/Lisowice	morphotype 2	transmitted-light microscopy, SEM, palynology, inorganic geochemistry, XRD
ZPAL V.33/1270 COP09/Lisowice	morphotype 2	SEM, palynology, inorganic geochemistry, XRD, biomarkers
ZPAL V.33/1270 COP10/Lisowice	morphotype 1	transmitted-light microscopy, SEM, palynology, inorganic geochemistry, XRD
ZPAL V.33/1270 COP11/Lisowice	morphotype 3 (pyritized)	transmitted-light microscopy
ZPAL V.33/1270 COP12/Lisowice	morphotype 3	transmitted-light microscopy
ZPAL V.33/1270 COP13/Lisowice	morphotype 1	transmitted-light microscopy
ZPAL V.33/1270 COP14/Lisowice	morphotype 2	transmitted-light microscopy, SEM, TOC and TS, biomarkers
ZPAL V.33/1270 COP15/Lisowice	morphotype 3 (pyritized)	transmitted-light microscopy
ZPAL V.39/372 COP16/Poreba	morphotype 2	transmitted-light microscopy, SEM, palynology, inorganic geochemistry, XRD, TOC and TS, biomarkers
ZPAL V.33/1270 COP18/Lisowice	morphotype 2	transmitted-light microscopy, SEM, palynology, inorganic geochemistry, XRD, biomarkers
ZPAL V.33/1270 COP19/Lisowice	morphotype 2	transmitted-light microscopy

Table 2
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Analyte Symbol	SiO ₂	Al ₂ O ₃	Fe ₂ O ₃	MnO	MgO	CaO	Na ₂ O	K ₂ O	P ₂ O ₅	TiO ₂	Sum
Unit Symbol	wt. %	wt. %	wt. %	wt. %	wt. %	wt. %	wt. %	wt. %	wt. %	wt. %	wt. %
Detection Limit	0.01	0.01	0.01	0.001	0.01	0.01	0.01	0.01	0.01	0.001	0.01
Analysis Method	FUS-ICP	FUS-ICP	FUS-ICP	FUS-ICP	FUS-ICP	FUS-ICP	FUS-ICP	FUS-ICP	FUS-ICP	FUS-ICP	FUS-ICP
COP 04a	1,17	0,19	0,41	0,143	0,24	48,73	1,14	0,04	20,3	0,012	91,7
COP 04b	49,03	4,23	1,3	0,119	1,28	23,13	0,33	0,83	0,11	0,366	100,2
COP 05	6,91	1,73	0,95	0,12	0,52	43,19	1	0,26	19,58	0,07	87,47
COP 06	3,04	0,9	0,8	0,511	0,64	50,47	0,13	0,18	9,1	0,045	93,75
COP 07	2,41	0,56	2,48	1,017	0,43	49,99	0,32	0,11	11,73	0,043	96,36
COP 08	1,92	0,62	1,13	0,214	0,38	49,15	0,86	0,13	17,97	0,033	93,17
COP 09	7,16	1,06	0,55	0,15	0,47	44,99	0,91	0,2	20,21	0,089	92,96
COP 10	0,71	0,24	0,21	0,208	0,36	49,7	0,84	0,04	17,91	0,011	87,95
COP 16	3,01	0,68	0,79	0,438	0,77	49,23	0,13	0,14	10,24	0,042	95,2
COP 18	1,91	0,45	1,54	0,214	0,32	46,81	0,53	0,15	18,5	0,026	89,08

Table 3
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sample	apatite [wt. %]	calcite [wt. %]	barite [wt. %]	quartz [wt. %]	pyrite [wt. %]	dolomite [wt. %]	clay min. [wt. %]	goethite [wt. %]	feldspars [wt. %]
COP04a	48	44	4	2	2	-	-	-	-
COP04b	-	40	-	45	tr	3	8	-	3
COP05	60	25	7	6	2	-	-	-	-
COP06	19	79	-	tr	-	tr	tr	-	-
COP07	32	65	-	2	-	-	-	tr	-
COP08	54	45	-	tr	tr	-	tr	-	-
COP09	68	28	-	4	tr	-	tr	-	-
COP10	55	45	-	tr	-	-	-	-	-
COP16	29	68	-	2	tr	-	tr	-	-
COP18	57	40	-	tr	2	-	-	-	-

Samples	TS	TOC	CC
COP1	0,06	1,16	58,1
COP3	0,00	1,31	30,7
COP04a	0,00	0,68	45,5
COP05	1,03	0,99	25,1
COP06	0,00	0,55	78,2
COP07	0,00	0,42	69,6
COP14	0,00	1,49	37,3
COP16	0,15	0,86	68,3

Table 5
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Compound	M+	COP09	COP06	COP05	COP14	COP16	COP18
Octanoic acid-TMS	216	2	3	3	2	3	4
Urea- bis-TMS	204	2	5	4	4	1	1
Benzoic acid-TMS	194	5	7	7	6	8	11
Nonanoic acid-TMS	230	9	10	10	6	8	11
Decanoic acid-TMS	244	6	10	11	12	12	13
1-Dodecanol-TMS	258	10	3	5	6	3	11
1-Tridecanol-TMS	314	4	2	3	3	1	3
1-Tetradecanol-TMS	328	15	8	14	10	8	14
Tetradecan-1-ol?	214	32	12	14	13	13	53
Levogluconan-TMS	378	2	2	2	1	1	0
Tridecanoic acid-TMS	286	2	1	4	2	2	4
1,4-Benzenedicarboxylic acid-TMS	310	16	8	8	14	19	25
1-Hexadecanol-TMS	314	57	44	45	36	69	54
Pentadecanoic acid-TMS	314	9	10	10	10	10	11
9H-Fluoren-9-one	180	8	3	4	4	3	4
Hexadecanoic acid-TMS	328	100	100	100	100	100	100
Octadec-9Z-enol-TMS	340	68	37	44	24	77	89
1-Octadecanol-TMS	342	77	40	52	42	83	80
2,6,10,14-tetramethylpentadecanoic acid (pristanic acid)-TMS	370	3	4	3	3	2	3
3,7,11,15-tetramethylhexadecanoic acid (phytanic acid)-TMS	384	2	2	2	2	1	2
Trans-9-Octadecenoic acid-TMS	354	14	7	9	9	16	16
Octadecanoic acid-TMS	356	33	32	34	29	34	38
1-Eicosanol-TMS	370	7	5	5	5	5	5
Unknown C18-Unsaturated Fatty Acid	354	9	7	8	8	11	11
1-Docosanol-TMS	398	17	14	14	16	14	22
Heneicosanoic acid-TMS	398	3	2	3	2	2	2
2-Palmitin-TMS	474	7	8	5	7	11	14
1-Palmitin-TMS	474	20	12	14	16	21	23
Docosanoic acid-TMS	412	19	17	17	17	19	18
Tetracosanol-TMS	424	4	3	3	3	3	4

2-Stearin	502	7	5	4	4	9	15
1-Stearin	502	17	10	12	11	18	25
Tetracosanoic acid-TMS	440	7	7	7	7	7	6
1-Hexacosanol-TMS	452	4	3	2	0	5	2
Pentacosanoic acid-TMS	454	4	4	4	4	5	4
1-Heptacosanol-TMS	466	5	5	2	3	6	0
Hexacosanoic acid-TMS	468	5	6	4	5	5	8
1-Octacosanol-TMS	480	39	31	32	28	30	33
1-Nonacosanol-TMS	494	2	2	2	1	2	2
Octacosanoic acid-TMS	496	18	15	14	12	12	15
Cholesterol-TMS	458	14	15	21	18	17	14
1-Triacontanol-TMS	508	23	19	21	18	19	18
Campesterol-TMS?	472	7	9	6	5	7	7
Stigmasterol-TMS?	484	2	1	2	1	2	1
Triacontanoic acid-TMS	524	9	7	9	5	6	6
Sitosterol-TMS	486	55	46	45	39	57	52
1-Dotriacontanol-TMS	536	7	0	5	0	0	6
Cholesta-3,5-dien-7-one	382	6	5	3	5	5	6
beta-Amyrin-TMS?	498	5	3	3	4	3	2
alpha-Amyrin-TMS?	498	4	4	4	4	6	4
alpha-Amyrone	424	3	3	4	5	5	4
Stigmasta-3,5-dien-7-one	410	10	9	9	16	19	18

Table 6
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Sample number/ locality	Morphotype	P content [wt. %]	TOC [%]	Important biomarkers*		Fossil inclusions
				Higher plants	Other	
COP01/Poręba	morphotype 2	na	1.16	na	na	arthropod cuticle, teeth and bone fragments
COP04a/Lisowice	morphotype 1	20.3	0.68	na	na	bone fragments
COP05/Lisowice	morphotype 1	19.58	0.99	sitosterol (45), <i>n</i> -hexadecanoic acid (100), benzoic acid (7), stigmasta-3,5-dien-7-one (9)	cholesterol (21), 1-+2-palmitin (19), 1-+2-stearin (16)	plant remains, arthropod cuticle, degraded bone fragments
COP06/Lisowice	morphotype 1	9.1	0.55	sitosterol (46), <i>n</i> -hexadecanoic acid (100), benzoic acid (7), stigmasta-3,5-dien-7-one (9)	cholesterol (15), 1-+2-palmitin (20), 1-+2-stearin (15)	rare plant remains, ostracode carapace, bone fragments, fish scales
COP07/Lisowice	morphotype 1	11.73	0.42	na	na	plant remains, degraded bone fragments
COP08/Lisowice	morphotype 2	17.97	na	na	na	plant remains, bone fragments
COP09/Lisowice	morphotype 2	20.21	na	sitosterol (55), <i>n</i> -hexadecanoic acid (100), benzoic acid (5), stigmasta-3,5-dien-7-one (10)	cholesterol (14), 1-+2-palmitin (27), 1-+2-stearin (24)	plant remains, bone fragments
COP10/Lisowice	morphotype 1	17.91	na	na	na	plant remains, arthropod cuticle, degraded bone fragments
COP12/Lisowice	morphotype 3	na	na	na	na	rare plant remains, bone fragments
COP13/Lisowice	morphotype 1	na	na	na	na	plant remains, degraded bone fragments
COP14/Lisowice	morphotype 2	na	1.49	sitosterol (39), <i>n</i> -hexadecanoic acid (100), benzoic acid (6), stigmasta-3,5-dien-7-one (16)	cholesterol (18), 1-+2-palmitin (23), 1-+2-stearin (15)	bone fragments
COP16/Poręba	morphotype 2	10.24	0.86	sitosterol (57), <i>n</i> -hexadecanoic acid (100), benzoic acid (8), stigmasta-3,5-dien-7-one (19)	cholesterol (17), 1-+2-palmitin (33), 1-+2-stearin (27)	plant remains, arthropod cuticle, bone fragments
COP18/Lisowice	morphotype 2	18.5	na	sitosterol (52), <i>n</i> -hexadecanoic acid (100), benzoic acid (11), stigmasta-3,5-dien-7-one (18)	cholesterol (14), 1-+2-palmitin (37), 1-+2-stearin (40)	plant remains, bone fragments