

Putative dicynodont coprolites from the Upper Triassic of Poland



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ABSTRACT

A significant number (more than 100) of brown to dark and silty, carbonate or pyrite-mineralized, in part organic carbon-rich, spherical or oval-shaped structures have been collected from the Upper Triassic (uppermost Norian-lower Rhaetian) sediments of the Lipie Śląskie clay-pit at Lisowice near Lubliniec town, Poland. Their geological context, morphology, content, geochemistry and association with skeletal remains suggest they are fecal masses of a sizable herbivorous tetrapod. The only large herbivore known from the site is a giant 5 meter-long dicynodont (Synapsida: Anomodontia), represented by numerous bones and also by large, oval-shaped footprints. The putative dicynodont coprolites were collected from mudstone and siltstone with numerous organic remains that were deposited in anoxic conditions. In addition, REEs and other trace element concentrations suggest that the burial environment and diagenesis of these coprolites were under anoxic conditions. SEM and thin section images of the coprolite matrix show numerous nests with pyrite (probably bacterial in origin) and large amount of mineral particles. The putative dicynodont coprolites contain also amorphous, dark organic matter, poorly preserved palynomorphs, small fragments of plant cuticle. Detailed characteristic of these coprolites reveals possible implications for the ecology and physiology of the source animal species. The $\delta^{13}\text{C}$ values of the gymnosperm cuticle and dark organic matter measured in three coprolites are -23.4% , -21.2% and -20.3% , all average. The evidence from these coprolites suggests that dicynodonts processed plant soft elements into very small pieces, but wood fragments were found also in a mass accumulation in two coprolites.

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1. Introduction

Fossil feces, formally known as coprolites, may reveal interesting and unique data about the diet of extinct animals (Chin and Kirkland, 1998; Dutta and Ambwani, 2007; Smith and Botha-Brink, 2011; Owocki et al., 2012), the food web in ancient ecosystems (Chin and Gill, 1996; Chin, 2007; Chin et al., 2009), behavior (Fiorelli et al., 2013; Niedźwiedzki, in press) and physiology of the source animals (Chin et al., 2003). However, relatively small numbers of coprolites from herbivorous tetrapods older than Pliocene in age have been described and their significance for the source animals' ecology well discussed.

Coprolites of plant eating tetrapods from the Mesozoic and Permian deposits are of great importance, since several lineages of herbivorous tetrapods appeared at that time. Coprolites of these animals can be a source of valuable data about their biology and the origin of adaptations to herbivore physiology.

The best known Mesozoic coprolites of herbivores include Upper Jurassic herbivorous dinosaur coprolites from the Morrison Formation (Chin and Kirkland, 1998), Upper Cretaceous (Campanian) hadrosaur *Maiasaura peeblesorum* coprolites from the Two Medicine Formation, Montana (Chin and Gill, 1996; Chin, 2007; Chin et al., 2009), and Upper Cretaceous (Maastrichtian) herbivorous dinosaur coprolites from the Lameta Formation, India (Ghosh et al., 2003; Kar et al., 2004; Ambwani and Dutta, 2005; Prasad et al., 2005; Dutta and Ambwani, 2007). Recently, several massive coprolite associations were reported from the Middle–Upper Triassic of the Chañares Formation, Argentina, which appear to represent fossil communal latrines of kannemeyeriiform dicynodonts (Fiorelli et al., 2013).

Here we report on a new occurrence of putative dicynodont coprolite accumulations which were discovered in the Upper Triassic strata in the Lipie Śląskie clay-pit at Lisowice, Upper Silesia (Fig. 1). The fecal nature of these specimens was originally suggested by the sedimentological context, comminuted plant contents, and associated tetrapod fossils. We provide the first description of such fossils with food residues collected in the Keuper deposits of Germanic Basin. Their morphology, content, similarity to other described dicynodont coprolites (Hunt et al., 1998; Souto, 2001; Fiorelli et al., 2013; Hunt et al., 2013) and association with the skeletal remains of large dicynodonts suggest that they are fecal masses of this large herbivorous therapsid (Fig. 2). In the same

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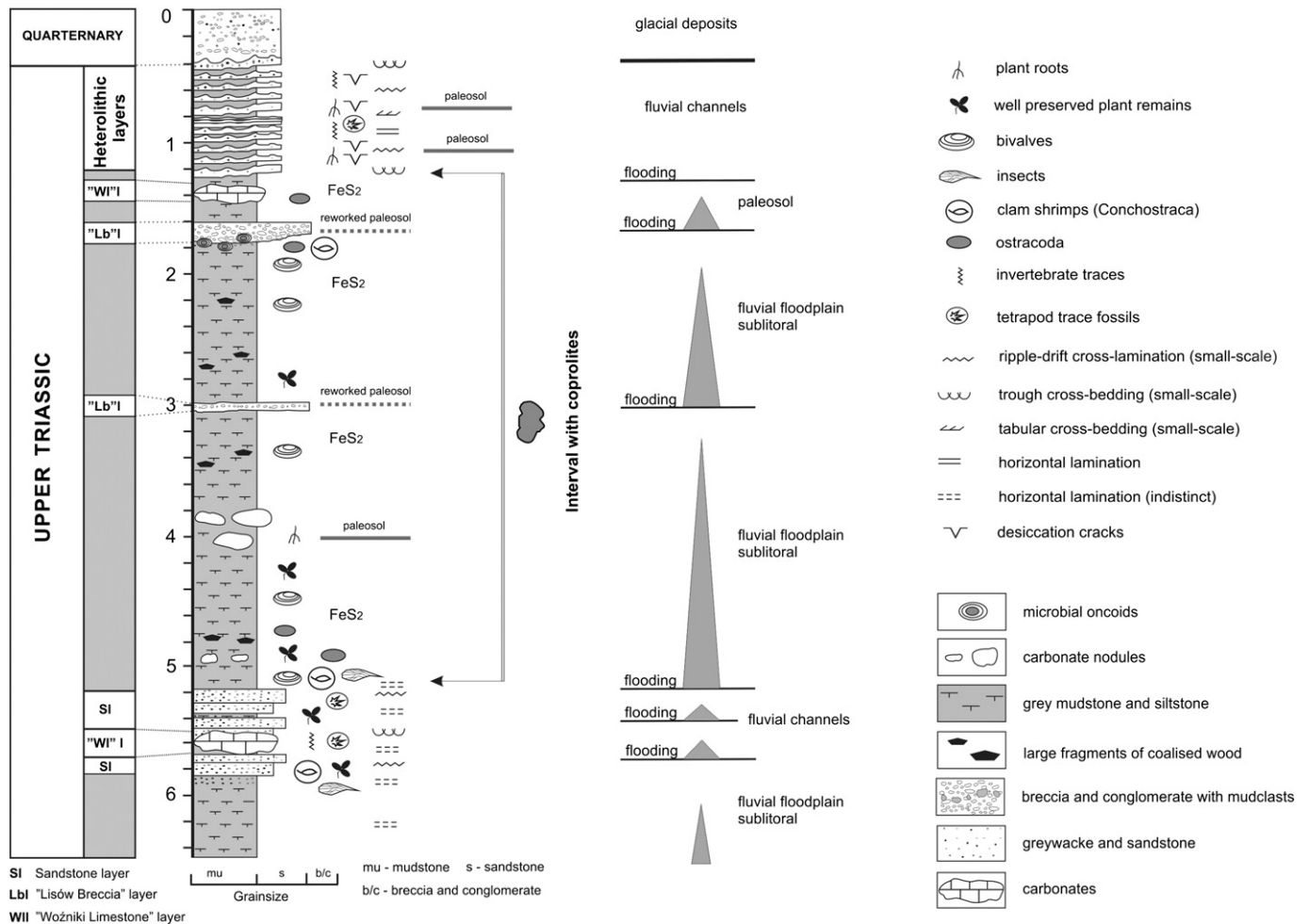


Fig. 1. Schematic rock column from the main exposure in the Lipie Śląskie clay-pit at Lisowice with position of the putative dicynodont coprolite-rich interval. Modified from Niedźwiedzki (in press).

layers numerous phosphatic coprolites (containing dicynodont bone fragments) of a large carnivore were also found (Niedźwiedzki, in press). Therefore, new specimens described in this paper offer a new view on the characteristics of dicynodont feces as well as possibly on some aspects of the dicynodont ecology and physiology. We also describe the geological and sedimentological characteristics of the putative dicynodont coprolite accumulations from the Lipie Śląskie clay-pit, which may be comparable to communal latrine-bearing areas described from other Triassic sites (Fiorelli et al., 2013).

Stable carbon and nitrogen isotopes in coprolites provide unique trophic perspectives on ancient ecosystems (Ghosh et al., 2003; Prasad

et al., 2005) as they represent residues from the digestive tract of the extinct tetrapod. According to Vogel (1978) and Lee-Thorp et al. (1989) the stable isotope ratio of organic carbon in excrements represents the average composition of food sources. Stable isotopes of carbon and nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) are powerful tools for tracing nutrient flow within ancient ecosystems (Schweizer et al., 2006). Two factors such as preservation and microbial processes sometimes change C/N ratios in organisms (DeNiro, 1985), stable isotopic compositions of C and N components tend to be preserved in fossilized remains (Masters, 1987).

Usually, it is very hard or impossible to link fossil dung with its producer species (Chin, 1997; Owocki et al., 2012; Bajdek, 2013). Some rare exceptions of very likely source-species-assigned coprolites from the tetrapod Mesozoic record include the Upper Cretaceous (Maastrichtian) theropod *Tyrannosaurus rex* coprolite from the Frenchman Formation, Canada (Chin et al., 1998), another theropod *Allosaurus fragilis* coprolite from the Upper Jurassic Morrison Formation, USA (Stone et al., 2000), previously mentioned hadrosaur *Maiaasaura peeblesorum* coprolites and predatory archosaur *Smok wawelski* coprolites (Niedźwiedzki, in press) from the Upper Triassic of Poland.

Possible dicynodont coprolites previously have been assigned to the ichnotaxon *Dicynodontocoprois maximus* by Hunt et al. (1998), who also summarized the history of their examination in review papers on vertebrate coprolites (2007, 2013). However, *D. maximus* coprolites are phosphatic in composition (anonymous journal reviewer, 2014). According to Hunt et al. (2007) possible dicynodont coprolites were initially described by Case (1922) from the Upper Triassic Tecovas Formation,



Fig. 2. Skeletal reconstruction of dicynodont species from the Lipie Śląskie clay-pit at Lisowice. Modified from Dzik et al. (2008a,b).

Texas. They were 5–18 cm long, smooth surfaced and lacking vertebrate bone inclusions. The holotype of *D. maximus* UMMP 7255, stored in the Museum of Paleontology, University of Michigan, is based on one of those specimens. Large, amorphous forms up to 12 cm in length and nearly 6 cm in width were also described by Rusconi (1949) from the Middle Triassic of Argentina. Ochev (1974) described Middle Triassic coprolites including 2–10 cm long specimens with possible plant impressions from localities in Russia (Karagachka, Donguz I and Bukobay V) and Kazakhstan (Mollo-Khara-Bala-Kantemir) and compared them with those described by Case (1922). Hunt (1992) and Hunt et al. (1998) discussed the occurrence of *D. maximus* in the Upper Triassic (Carnian) of the Chinle Group, including the Bluewater Creek Formation of Arizona. Souto (2001) described ovoid and cylindrical coprolite morphotypes from the Middle Triassic Santa Maria Formation, Brazil, suggesting that the ovoid forms might have been produced by dicynodonts. Northwood (2005) described a possible coprolite of a herbivore from the Lower Triassic Arcadia Formation, Australia. The source animal may have been a dicynodont, however Northwood noticed that this blocky, elongate specimen was morphologically different from coprolites previously assigned to dicynodonts. Recently, Fiorelli et al. (2013) reported the first non-mammal megaherbivore communal latrines from eight massive coprolite accumulations in the Middle–Upper Triassic of northwestern Argentina. Defecation of dicynodonts in so-called communal latrines reveals that this gregarious behavior is not unique to mammals. In the newest review paper on Triassic vertebrate coprolites (Hunt et al., 2013) a new ichnogenus of dicynodont coprolite (*Santamariacopros elongatus*) was introduced, based on one of the coprolite morphotypes described by Souto (2001) from the Santa Maria Formation.

2. Geological setting

The Lipie Śląskie clay-pit at Lisowice (Fig. 1) displays an approximately 12 m thick stratigraphical section composed of gray and greenish to reddish fluvial mudstone, siltstone interbedded with cross- or horizontally-stratified sandstone. The strata exposed in the Lipie Śląskie clay-pit correspond to the uppermost part of the Middle and lower part of the Upper Keuper deposits of the Germanic Basin (Aigner and Bachmann, 1992; Szulc et al., 2006; Franz et al., 2007a,b; Dzik et al., 2008a,b; Franz, 2008).

The material described in this paper was collected from the bone-bearing interval of gray mudstone and siltstone interpreted as a low energy fluvial environment (Dzik et al., 2008a,b). The dark color of the mudstone, which is rich in well-preserved plant fossils and high pyrite content, suggests anoxic conditions during the formation of the coprolite-bearing deposit. The age of the deposit of the Lipie Śląskie clay-pit is interpreted as the latest Norian–early Rhaetian, based on paleobotanical data as well as on conchostracans and tetrapods (Dzik et al., 2008a,b; Niedźwiedzki et al., 2012; Świło et al., in press).

3. Paleobiological context

Lipie Śląskie clay-pit is rich in body and trace fossils. Plant cuticles, larger plant fragments, spores and pollen tend to be well-preserved in the gray mudstone–siltstone layers and also inside of inorganic in origin calcareous nodules and septarian concretions. Charred trunks are also common in these sediments and were likely transported by stream water from drier areas. The dominant plant species at this site is a conifer similar to species of genera *Brachyphyllum*, *Pagiophyllum* or *Hirmeriella*, as is the case for other Norian, Rhaetian, and Jurassic fossil plant assemblages of the region (Clement-Westerhof and Van Konijnenburg-Van Cittert, 1991). Its pollen of *Corollina* morphology is also very common in palynomorph samples from the site. The second most common plant species is represented by branched twigs similar to *Stachyotaxus* from the Rhaetian of Greenland and Scania, Sweden (Arndt, 2002). Ginkgoales are represented by leaves similar to the genera *Schmeissneria* and pollen similar to *Monosulcites*. Ferns are represented by abundant cuticle

fragments of typical late Norian–Rhaetian seed-fern *Lepidopteris* (Staneczko, 2007). Other plant fossils include representatives of Cycadophyta, Coniferophyta and Pteridospermophyta (Wawrzyniak and Ziaja, 2009; Wawrzyniak, 2010a,b, 2011). Wawrzyniak (2010b) described from this site such as cf. *Nilsonia* sp., cf. *Androstrobus* sp., and cf. *Beania* sp. Other, but rather rare fossils are remains of cf. *Elatocladus* sp., a representative of the Coniferales. In the opinion of Wawrzyniak (2010b) these species are characteristic elements of Early–Mid Jurassic floras. Probable isoëtalean macrospores include *Trileites* cf. *pinguis* and *Horstisporites bertelseni* (Fuglewicz, 1977) and in some, organic-rich layers form mass accumulations. The most abundant pollen type is wingless pollen *Enzonasporites* sp. div., which co-occurs with abundant pollen of *Corollina meyeriana* and *Granuloperculipollis rudis* (Staneczko, 2007; Dzik et al., 2008a,b).

Among invertebrate fossils there are common freshwater bivalves *Tihkia silesiaca* (Skawina and Dzik, 2011), but the most common are ostracods (*Darwinula* sp. and *Rhombocythere* sp.) which occur only in few horizons in the lower part of the gray-unit and can form massive accumulations if present.

The conchostracans *Gregoriusella polonica* and *Euestheria* sp. are small (1.5–3.5 mm in length), being morphologically close to *Euestheria brodieana* from the Rhaetian of England and the United States (Kozur and Weems, 2005, 2007, 2010). Numerous carapaces of much larger species *Shipingia* sp. (3–6 mm in length) were also collected in the lowermost part of the gray-unit.

Vertebrates are represented by hybodont sharks (genera *Polyacrodus* and *Hybodus*) and dipnoan and actinopterygian fishes as well as numerous tetrapods (Dzik et al., 2008a,b; Świło, 2010a,b,c; Świło and Kowalski, 2011; Niedźwiedzki et al., 2012; Niedźwiedzki, in press; Świło et al., in press). Bone remains of temnospondyls are represented by a plagiosaurid and a large cyclotosaur. Reptile bone material includes remains of small dinosauriforms, dinosaurs, poposaurids, pterosaur wing bones and teeth, and a mammaliaform tooth (Świło et al., in press). The cranial–postcranial elements of small archosauromorphs and diapsids are known from the site (Niedźwiedzki, in press). A large 5–6 meter-long predatory dinosaur *Smok wawelski* Niedźwiedzki, Sulej et Dzik, 2012 is being intensively studied (Dzik et al., 2008a,b; Niedźwiedzki et al., 2012; Niedźwiedzki, in press). The only large herbivorous tetrapod known from the site is a giant 5 meter-long dicynodont (Fig. 2), which is the largest dicynodont described to date (Dzik et al., 2008a,b; Niedźwiedzki et al., 2011). Bite traces on dicynodont bones and possible predator–prey interactions of *Smok wawelski* and this dicynodont were described and discussed by Niedźwiedzki et al. (2011) as well. Varied types of tetrapod footprints (including dicynodont large and oval-shaped footprints) are also known from the site (Dzik et al., 2008a,b; Niedźwiedzki, in press).

4. Material and methods

All studied specimens were found in organic-rich, gray mudstone and siltstone exposed in the middle and upper part of the section (Fig. 1). Sixteen putative dicynodont coprolite specimens (ZPAL V.33/1101–1116) are housed in the collection of the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland (Figs. 3 and 4; Table 1).

Most of the collected specimens are fragmented and incomplete; some specimens have been partially reconstructed by fitting broken pieces together (Fig. 3B). Therefore, the measurement of the volume as suggested by some researchers (Thulborn, 1991; Chin, 2002) was not possible. Instead their total length and width were measured and the general external morphology was described (Table 1). The seven specimens subjected to destructive analysis were first photographed and measured. Four thin sections from partially preserved and organic-rich specimens were made for study of internal structures and possible food remains.

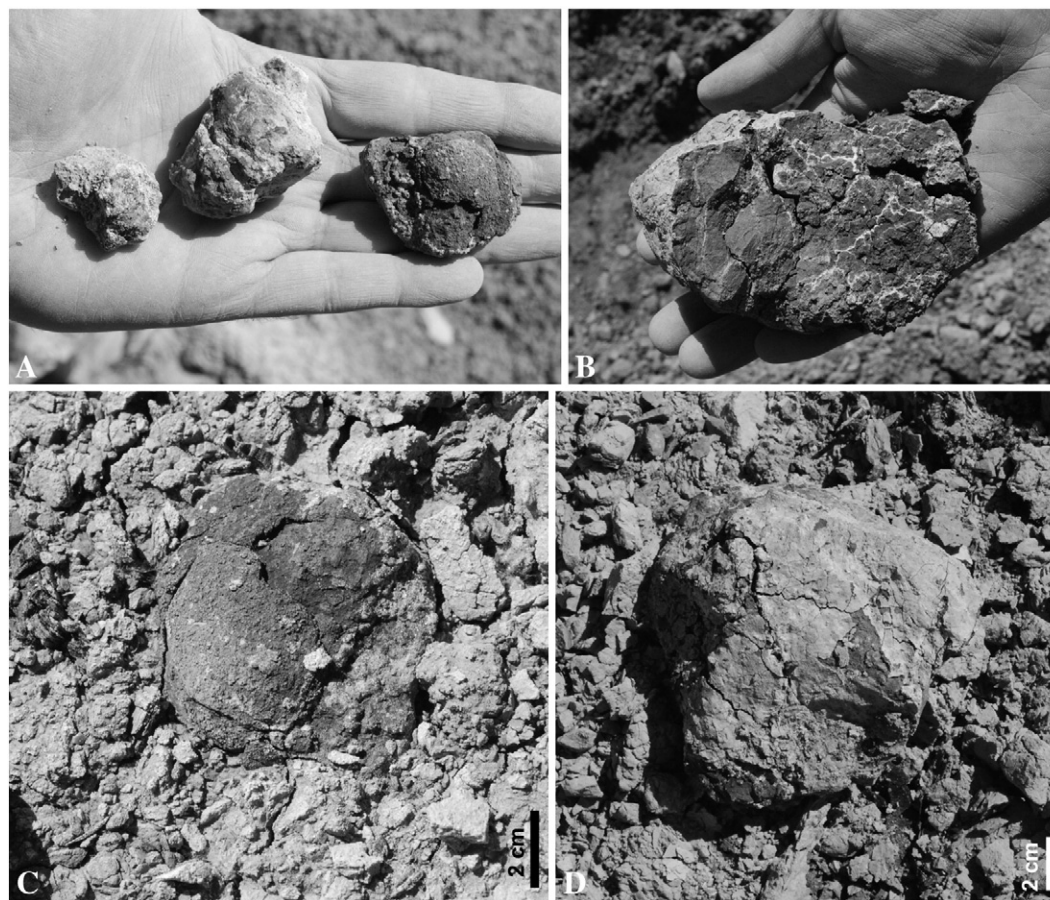


Fig. 3. Field photographs of putative dicynodont coprolites from the Lipie Śląskie clay-pit at Lisowice. (A) Small spherical and small elongated forms. (B–D) Large sphere-shaped forms.

4.1. Microscope and SEM observations

Standard polished thin sections of matrix from two coprolites were examined petrographically using a compound light microscope (Leica DM5500B at the Uppsala University), in normal and polarized light with an attached Leica microsystem camera (Figs. 7, 8). The coprolite matrices and surfaces were subjected to binocular microscope observations (Nikon Eclipse LV 100 POL at the University of Warsaw) and freshly broken surfaces were imaged and analyzed with a scanning electron microscope (SEM) equipped with an EDS detector at the University of Uppsala (Figs. 7, 8, 9).

4.2. REEs analysis

Rare earth elements (REEs) and other trace elements were analyzed using an inductively coupled plasma-mass spectrometer (Acme Analytical Laboratories Ltd., Vancouver, Canada). The 4 samples from 2 specimens were pulverized by ceramic box (Table 2). The 4-acid digestion on 0.25 g split was made on the obtained mesh. The splits were heated in $\text{HNO}_3\text{--HClO}_4\text{--HF}$ to fuming and taken to dryness. The residues were dissolved in HCl. Solutions were analyzed by ICP-MS. The detection limits were between 0.02 and 0.1 ppm varying for different trace elements. The Rare Earth Elements (REE) data were normalized (indicated

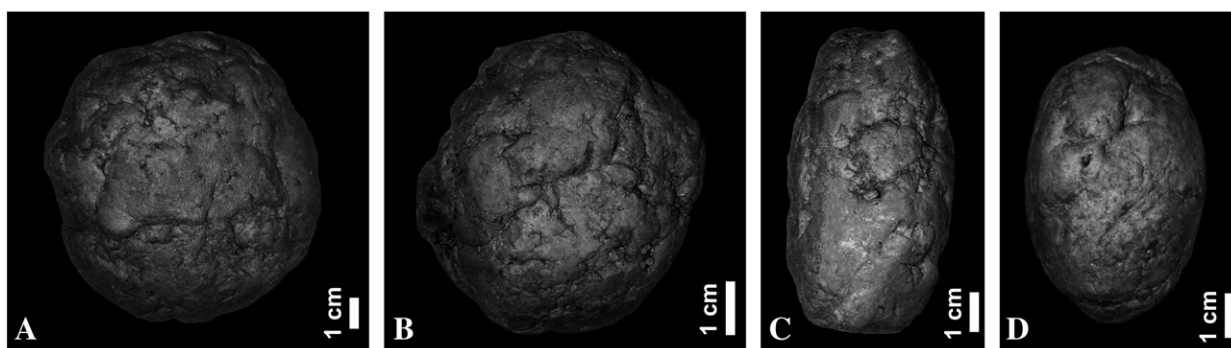


Fig. 4. The putative dicynodont coprolites from the Lipie Śląskie clay-pit at Lisowice. (A–B) Spherical forms. (C–D) Elongated forms.

Table 1

List of the collected putative dicynodont coprolite specimens from the Lipie Śląskie clay-pit at Lisowice, Poland.

ZPAL V.33/1101	Dark (black-brown) coprolite	–
ZPAL V.33/1102	Dark (black) coprolite with pyrite	Specimen for thin sections
ZPAL V.33/1103	Dark (brown) coprolite	Specimen for geochemical analysis
ZPAL V.33/1104	Dark (black) coprolite	Specimen for thin sections
ZPAL V.33/1105	Dark (black) coprolite with pyrite veins	Specimen for geochemical analysis
ZPAL V.33/1106	Dark (black) coprolite	–
ZPAL V.33/1107	Dark (black-brown) coprolite with pyrite nests	Specimen for thin sections
ZPAL V.33/1108	Dark (black) coprolite with pyrite	–
ZPAL V.33/1109	Dark (black) coprolite	–
ZPAL V.33/1110	Dark (black-brown) coprolite	–
ZPAL V.33/1111	Dark (black) coprolite with pyrite	–
ZPAL V.33/1112	Dark (black) coprolite with rare plant remains	Specimen for thin sections
ZPAL V.33/1113	Dark (brown) coprolite	–
ZPAL V.33/1114	Dark (brown) coprolite	–
ZPAL V.33/1115	Dark (black) coprolite with rare plant remains	Specimen for geochemical analysis
ZPAL V.33/1116	Dark (black) coprolite with plant remains	–

by subscript N) to the Post-Archean Australian Shale (PAAS) (Taylor and McLennan, 1985) to remove abundance effect.

4.3. TOC analysis

Concentrations of total organic carbon (TOC) were determined using a Leco Carbon Analyzer CR-12 (Uppsala University, Sweden). For determination of TOC, carbonates from the coprolite and rock samples were removed by treatment with 20% HCl and subsequent rinsing. Eight samples were analyzed (Table 3), six of them were taken from coprolites and another two from fossilized wood and host sediment.

4.4. Stable carbon and nitrogen analysis

The stable carbon and nitrogen isotope analysis of organic carbon in the coprolites was performed using stable-isotope-ratio mass spectrometry and procedure presented by Schweizer et al. (2006). Three coprolite samples were analyzed for their stable carbon and nitrogen isotopic compositions (Table 4). Soft organic material was scraped from the broken surface of the coprolites as a fine powder; a small amount (up to 15–20 mg) of macroscopically representative organic material was loosened with clear needles under a binocular microscope and placed in aluminum-foil bags with tweezers. All samples were refrigerated to minimize alteration and microbial contamination of the organic-rich material. Samples were combusted with ultra pure oxygen at 1000 °C. The resulting gases (CO₂ and N₂) were separated. Isotope ratios of the combustion gases were analyzed using continuous flow, stable-isotope-ratio mass spectrometry, Finnigan MAT, Delta^{plus}XL (Uppsala University, Sweden).

4.5. Analysis of HCl-resistant minerals

Six samples from three distinct coprolites (with a large amount of pyrite, organic matter and visible plant remains) were dissolved with 5% HCl acid and the undissolved fraction was examined. The samples weighed about 100 g (see Table 5) and were taken from the central part of the coprolites. Material after dissolution was sieved with a 2 mm mesh. The insoluble deposit was then dried and weighed. The results of the analysis of the undissolved fraction are summarized in Table 5.

5. Coprolites description and content

5.1. General shape

Numerous (about 100 specimens) more or less irregular, spherical or oval-shaped coprolites (range from 3 to 17 cm in diameter) were collected or observed in the field and sixteen of the most complete

specimens were measured (Figs. 4 and 5) and are housed in the collection. The original sizes of the largest individual coprolites are difficult to determine. Coprolite morphology is variable; some of them have original, not eroded surfaces and clear cut edges. All specimens are distinctly different (are ovoid to spheroidal in shape, usually dark gray and organic rich) from the mudstone and siltstone deposits and also bones, phosphatic coprolites of predatory tetrapods, oncoids, inorganic carbonate nodules and septarian concretions or plant remains from the same site. These coprolites vary from grayish-brown to dark gray. All sampled coprolites lack bone remains and other animal macrofossils (Figs. 6 and 7). Most of the collected coprolites comprise small mineral particles, mainly quartz grains and inorganic clasts (Fig. 8A, C, D). Coprolites are in places highly mineralized by pyrite (Fig. 8B, E, F), but the main diagenetic alteration is represented by calcite microsparity replacement. Two analyzed coprolites contain highly fragmented and macroscopically visible plant material (Fig. 6A, B). The HCl-resistant minerals and particles (including authigenic mineralization of pyrite) and organic carbon of one of the studied carbonate-rich coprolites comprise about 30–50% of the mass of the coprolites (Table 5). The vast majority of clasts are represented by very small quartz grains (between 0.5 and 0.05 mm based on SEM observations; Figs. 8, 9) and also very large grains of sand-sized particles which are not quartz grains or pyrite crystals. A few specimens contain visible but rare plant tissues (cuticle fragments and wood fragments), palynomorphs (pollen and spores) and other accumulations of amorphous and dark organic carbon (Fig. 7A–D). Two types of organic carbon remains (cuticle fragments and amorphous and dark organic matter) were examined to characterize the carbon and nitrogen isotopic composition of residue and to identify the diet of the coprolite producers. All the investigated samples are phosphate-free and contain a large amount of authigenic sulfide minerals (mainly pyrite), sometimes in the form of characteristic crystal nests (Figs. 6C and 8B), sphere-like objects or are disposed concentrically. In a few coprolites mineral particles are concentrated in the form of small spherical structures (secondary grains; Fig. 8D) and some pyrite minerals moreover show pseudomorphs after microbials, probably coccoid bacteria (Fig. 7E, F).

5.2. Plant cuticle fragments

Plant cuticle was found in two of the examined coprolites (Fig. 7B). It is probably of a gymnosperm and resembles the cuticle of the Cheirolapideae (Clement-Westerhof and Van Konijnenburg-Van Cittert, 1991). Plant cuticle can be resistant to decomposition and these are probably remains of undigested plant fragments. At the Lisowice site, several kinds of plant cuticles were described (Wawrzyniak, 2010a,b,c). Preliminary analysis of cuticle fragments recognized in the coprolites suggests that only one type of cuticle appears to be present in the coprolite material.

Table 2
REEs and other trace elements concentrations (ppm) in the putative dicynodont coprolites from the Lipie Śląskie clay-pit at Lisowice, Poland.

	La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Tm	Yb	Lu	Y
Specimen 1	2690.1	12,009.2	834.45	4889.2	992.82	306.34	1118.92	159.64	159.13	137.85	303.52	32.46	197.96	31.43	3256.2
Specimen 2	2739.3	11,834.1	837.13	4928.3	892.65	274.04	1128.59	156.49	784.79	189.58	312.98	31.39	167.93	28.94	2897.5
Specimen 3	2567.8	11,982.5	898.92	4561.2	803.23	247.47	962.53	145.41	690.53	145.00	284.63	26.85	173.75	21.42	2783.3
Specimen 4	2590.2	10,987.4	846.38	4629.7	936.30	273.67	1136.19	159.28	159.60	142.20	238.24	32.29	186.62	19.62	3126.7
NASC	32.0	70.0	7.90	31.0	5.70	1.24	5.20	0.85	5.00	1.04	3.40	–	3.10	–	–
PAAS	38.0	80.0	8.90	32.0	5.60	1.10	4.70	0.77	4.40	1.00	2.90	0.5	2.80	0.50	28.0
PAAS	La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Tm	Yb	Lu	Y
Specimen 1	70,792,105	150,115	93,758,427	152,7875	177,28929	278,49091	238,06809	207,32468	36,165909	137,85	104,66207	64,92	70,7	62,86	116,29286
Specimen 2	72,086,842	147,92625	94,059551	154,00938	159,40179	249,12727	240,12553	203,23377	178,36136	189,58	107,92414	62,78	59,975	57,88	103,48214
Specimen 3	67,573,684	149,78125	101,00225	142,5375	143,43393	224,97273	204,79362	188,84416	156,93864	145	98,148276	53,7	62,053571	42,84	99,403571
Specimen 4	68,163,158	137,3425	95,098876	144,67813	167,19643	248,79091	241,74255	206,85714	36,272727	142,2	82,151724	64,58	66,65	39,24	111,66786

5.3. Palynomorphs

Palynomorphs were found in one of the analyzed samples of the coprolites (Fig. 7A). Recognized palynotaxa include *Corollina meyeriana*, *Corollina* sp., *Monosulcites minimus* and *Porcellispora* sp. They could have been ingested by the feces producer with forage (host plant), or digested accidentally, e.g. with drinking water. If they represent the consumed plant species, the diet of this dicynodont species included gymnosperm plants. Remains of fungi were not detected in the material.

5.4. Amorphous and dark organic matter

A great part of the dark matter in two analyzed coprolites is an amorphous organic matter (Figs. 7D, 9B, C). This may represent residues of well-digested plant tissues. No remains of wood, plant fiber or cuticle were found and hence, it might be a carbon residue of a strongly disintegrated plant tissue.

5.5. Concentrations of plant remains

In two specimens a significant content of plant remains has been preserved. They compose about 40% of the coprolite volume (Fig. 6A, B). These are mainly wood fragments; which are highly carbonized in the present-day state of preservation. They are mostly elongate and do not exceed 2 cm in length in the max dimension. These are residues of highly-fibrous woody elements of gymnosperm plants. Some of them are broken, worn or sharp-edged.

5.6. Other observations

A few of the thin sections of the sampled coprolites revealed that the coprolites are massive and rather structureless. Some of the specimens possess internal small cavities that are probably an effect of microbial processes (Fig. 8C). The coprolites have also considerable diagenetic alteration represented by pyrite, gypsum and calcite veins (Figs. 6D and 7F), which probably represent secondary infill of the internal desiccation fractures or are related to septarian cracks. Another possibility is that the cracks have been made by gases, mainly methane and ammonia. Harrell and Schwimmer (2010) concluded that in large fecal masses, as opposed to the smaller ones, the gases produce rather radial fissures than more typical small vesicles, because they are confined by the large size of the coprolite matrix. The fissures in crocodylian coprolites described by Harrell and Schwimmer (2010) are generally open, rather than filled with calcite crystals, as in typical septarian concretions. Nevertheless, Thulborn (1991) illustrated similar concentric and radial fissures infilled with gypsum.

6. Discussion

6.1. Origin of the structures

Several lines of evidence suggest that the specimens are fossil feces. Firstly, the structures could not be transported as clasts of pre-existing rocks, because they are collected from mudstone sediments formed in a low energy environment. Formation of such noticeably pyrite-mineralized and in part organic rich structures is difficult to explain by hydrodynamic processes or sediment-burrowing organisms' activity, because: (a) the structures lack larger plant remains and in only two specimens the plant fragments size is constrained by the upper limit of 2 cm, (b) they reveal no internal lamination. Even if specific chemical conditions had caused decomposition of soft plant debris, we can still notice the rare occurrence of wood fragments, which are everywhere-present in the sediments, as well as the absolute lack of bone fragments or invertebrate remains in the structures. Moreover, the presence of open cavities suggests that the structures were lithified through replacement rather than as simple concretionary growth (Chin, 2007).

Table 3

Total organic carbon (TOC) data of the organic matter residue from the putative dicynodont coprolites from the Lipie Śląskie clay-pit at Lisowice, Poland.

Sample	TOC		
	%		
Lis1a cop	2.56	2.62	2.79
Lis1b cop	2.51	2.04	2.38
Lis2 cop	1.91	2.62	2.96
Lis3 cop	0.07	0.05	0.12
Lis4a cop	6.95	7.36	6.41
Lis4b cop	7.74	7.92	8.27
Lis wood 1	61.57	60.45	60.94
Lis wood 2	59.62	61.32	58.50
Lis mud	1.92	1.98	2.05
Lis sand	0.63	0.53	0.68

Table 4

Carbon and nitrogen isotopic composition of the putative dicynodont coprolites from the Lipie Śląskie clay-pit at Lisowice, Poland.

Sample	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Copro 1A	−22.49	7.8
Copro 1B	−23.37	6.9
Copro 1C	−23.79	7.2
Copro 2A	−22.25	4.9
Copro 2B	−21.52	4.7
Copro 2C	−21.12	4.9
Copro 3A	−20.81	5.5
Copro 3B	−20.72	5.2
Copro 3C	−19.94	5.5

Table 5

The HCl-resistant minerals, pyrite crystals and carbon organic remains of the studied carbonate-rich coprolites comprise about 30–50% of the mass of the specimens.

Sample	Type of coprolite	Weight	> 2 mm	< 2 mm	Dissolved part
Cop 1a	Pyrite-rich coprolite	106 g	26 g	23 g	57 g
Cop 1b	Pyrite-rich coprolite	102 g	28 g	19 g	55 g
Cop 2	Coprolite with plant remains	104 g	11 g	10 g	83 g (and organic)
Cop 3	Dark coprolite	98 g	27 g	38 g	33 g
Cop 4	Dark coprolite	106 g	15 g	32 g	59 g
Cop 5	Dark coprolite	102 g	27 g	24 g	51 g

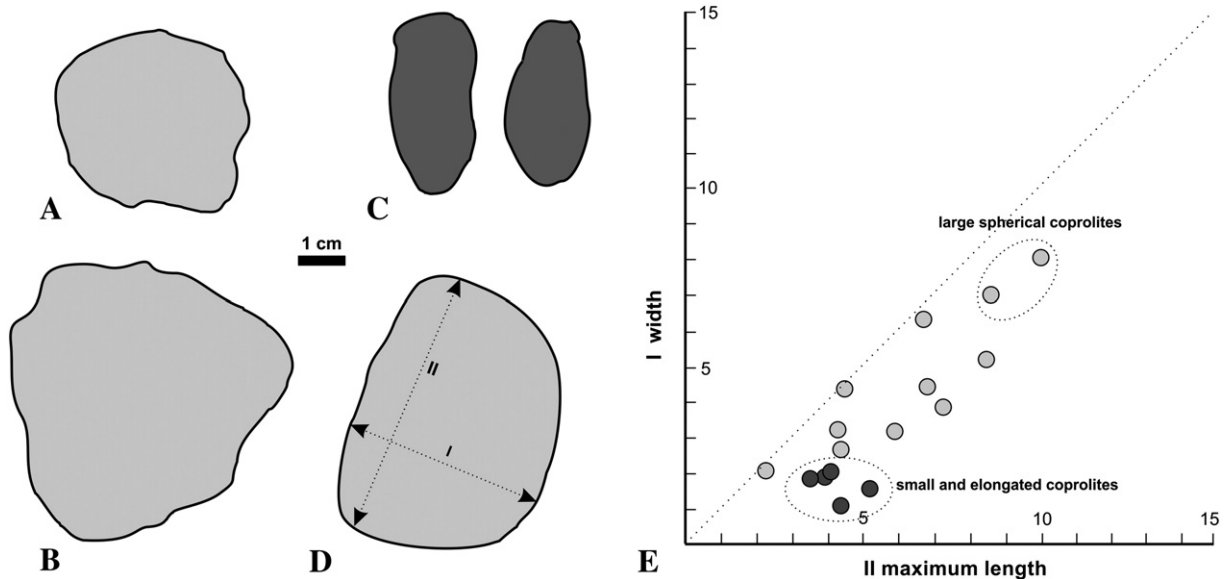


Fig. 5. Morphotypes of the putative dicynodont coprolite from the Lipie Śląskie clay-pit at Lisowice. (A) Small spherical form. (B) Large spherical form. (C) Small elongated forms. (D) Measurements used to distinguish morphotypes. (E) Plot showing the range of coprolite sizes and suggested division into two groups (based on specimens ZPAL V.33/1101–1116).

Thus, the most probable interpretation is that the structures are of fecal origin. This hypothesis is supported also by the fact that the size of the structures is constrained by an upper limit.

Few collected specimens are elongate in shape (Fig. 5), nevertheless in contrast to excrements produced by carnivorous and omnivorous animals of characteristic elongate morphologies, those produced by herbivores are usually roughly spherical or amorphous blocks (Chin and Gill, 1996; Chame, 2003). Because the specimens are not phosphatic (contain mineral particles, macroscopically visible plant material, palynomorphs, and amorphous and dark organic carbon and are mineralized by calcite and pyrite), they might indeed have been produced by a herbivore. The only herbivorous species known from the site is a giant dicynodont. Possible coprolites previously assigned to dicynodonts by other authors (Hunt et al., 1998; Souto, 2001; Hunt et al., 2007; Fiorelli et al., 2013) are of similar sizes and morphologies. Phosphatic coprolites of carnivorous animals, including specimens of sizable tetrapods, are also known from the site (Niedźwiedzki, in press). Thus, the most parsimonious and probable explanation of the origin of the structures is that they are fossilized feces of a giant 5 m long dicynodont, whose bone remains are associated with the host sediments.

Two specimens have a significant content of plant remains. They include wood fragments up to 2 cm in length and a total plant remains content of about 40% of the fecal mass volume. The spectrum in the content and mineral composition of the coprolites is interesting and includes: (1) highly mineralized specimens with pyrite and a low content of amorphous dark organic matter, (2) specimens with pockets of pyrite crystals, amorphous dark organic matter and single plant elements, (3) specimens with a great amount of organic matter in the form of wood fragments. This probably reflects the variability of ingested food

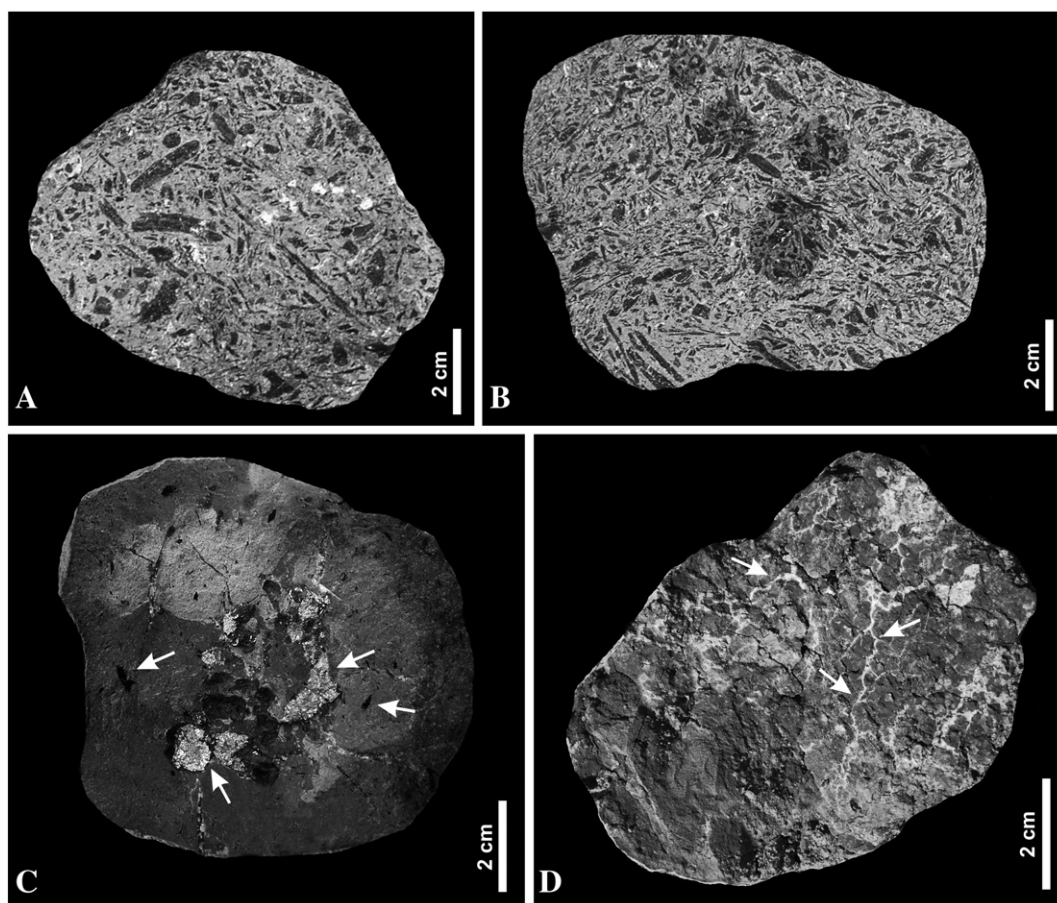


Fig. 6. Cross section (surfaces after breaking) of four spherical putative dicynodont coprolites from the Lipie Śląskie clay-pit at Lisowice. (A–B) Coprolites very rich in organic remains, mainly plant remains (wood elements and cuticle fragments). (C) Coprolite with rare plant remains and rich in dark amorphous organic matter. (D) Coprolite without visible plant remains and with rare dark amorphous organic matter and rich in pyrite and microscopic scale mineral particles. Arrows in C show pyrite nests (light areas) and plant remains (black elements). Arrows in D show cracks filled by clay.

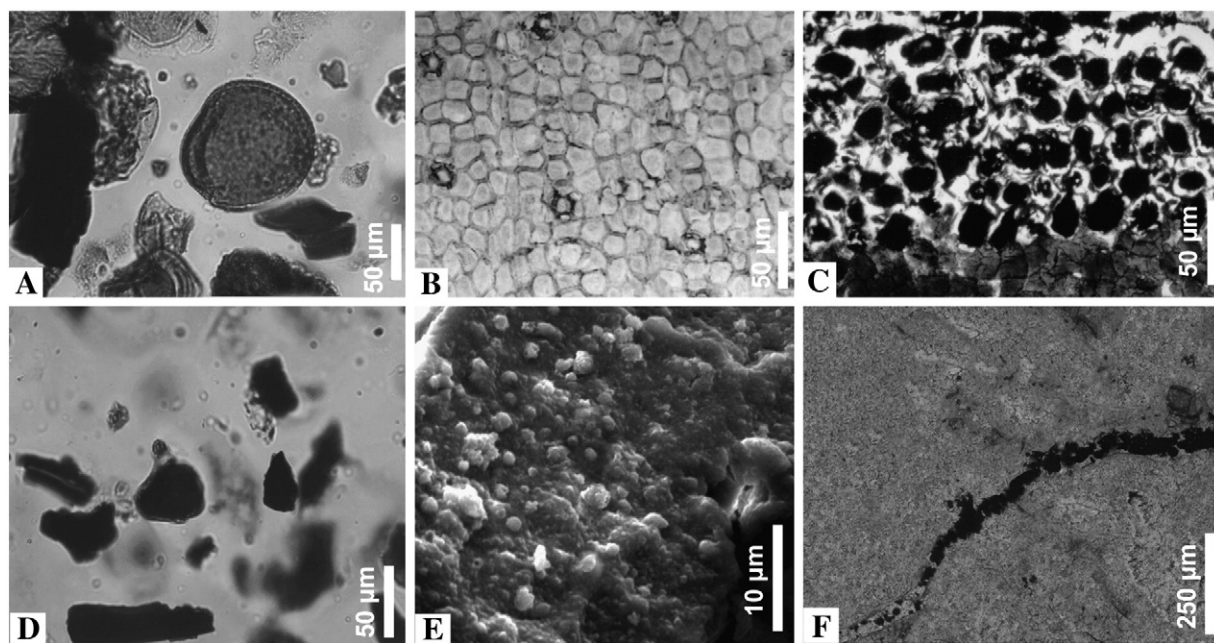


Fig. 7. Thin sections of the putative dicynodont coprolites from the Lipie Śląskie clay-pit at Lisowice. (A) Palynomorphs. (B) Plant cuticle fragment. (C) Wood tissue. (D) Dark organic carbon matter. (E) Probable microbial structures (pyrite pseudomorphs after bacteria). (F) Pyrite veins with sphere-like structures. Both cuticle fragments and palynomorphs are commonly observed in the coprolite matrix which is very rich in macroscopic organic remains.

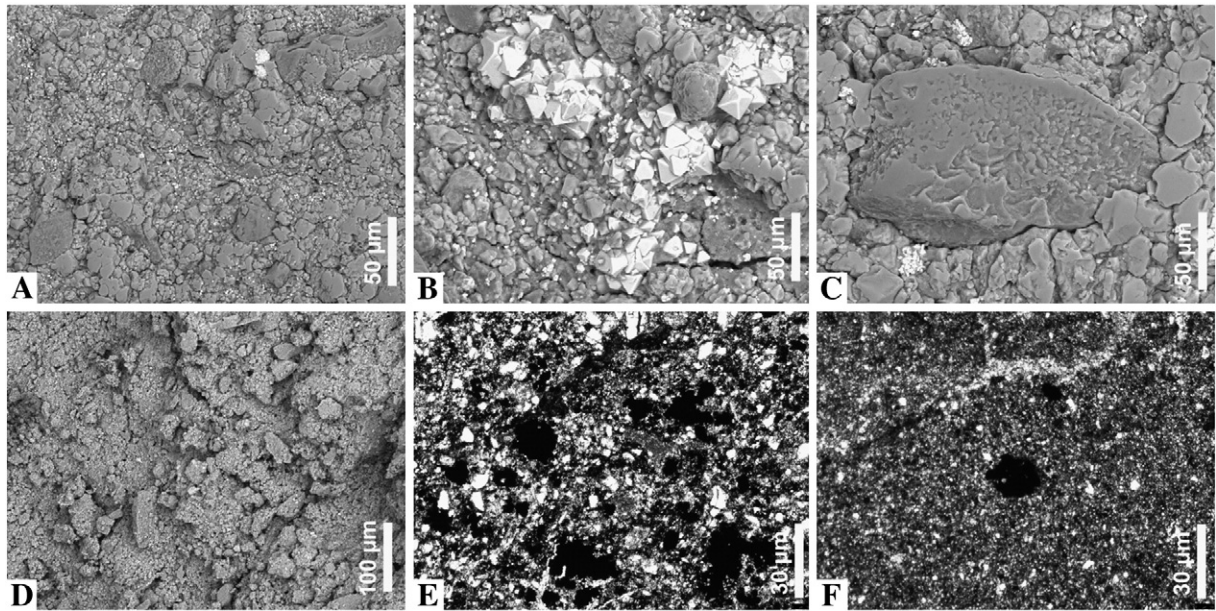


Fig. 8. SEM photos (A–D) and photomicrographs in polarized light (E–F) of the putative dicynodont coprolite matrix from the Lipie Śląskie clay-pit at Lisowice. (A) Mineral grain fabric in the coprolite matrix (note tightly packed grain fabric). (B) Pyrite nest with crystals in the coprolite matrix. (C) Mineral grain. (D) Sand grains and pyrite crystals exposed on the surface of the pyrite-rich coprolite matrix. (E) Sand grains and pyrite distribution within pyrite-rich coprolite matrix. (F) Pyrite nest in the amorphous organic matter rich coprolite matrix.

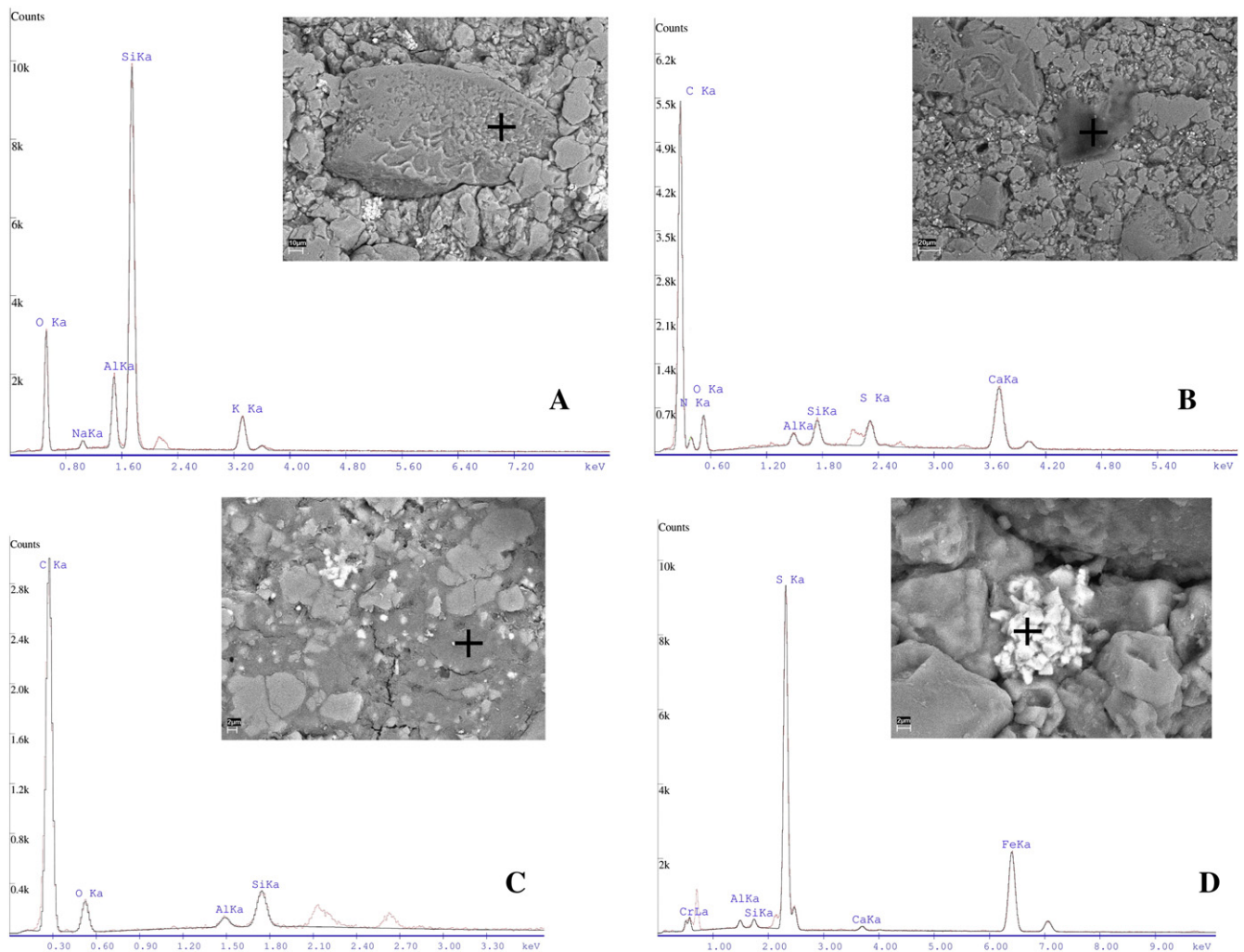


Fig. 9. Profiles of the EDS analysis from the putative dicynodont coprolites from the Lipie Śląskie clay-pit at Lisowice. (A) Mineral grain from the pyrite-rich coprolite matrix. (B) Organic element from the pyrite-rich coprolite matrix. (C) Matrix of the coprolite with rare plant remains and dark amorphous organic matter, small pyrite nests. (D) Pyrite crystals from the pyrite-rich coprolite matrix.

ingredients and could be also influenced by diagenetic processes. They could alter the geochemical conditions in the microenvironment of the fecal mass and the organic matter could influence the mineralization processes, including formation of the pockets of pyrite. Organic matter from the coprolite matrix was probably important for early diagenetic pyrite production; it can be considered a favorable ‘culture’ medium for sulfate reducing bacteria in anoxic conditions. Nevertheless, it seems that merely the diagenetic processes are not a sufficient explanation for the variability of the preserved specimens’ content and the coprolites can be classified in at least two distinct groups: wood-less and wood-rich types.

Because there is only one known species of a herbivore at the site, both specimens with and without wood fragments are parsimoniously assigned to a single producer species and most likely indicate variability in the diet, e.g. seasonal. It seems not likely that the coprolites would have been produced by multiple herbivore species. Although dicynodonts are known from various Upper Triassic sites in Poland (Dzik et al., 2008a,b; Budziszewska-Karwowska et al., 2010; Sulej et al., 2011), bones of sauropods, the other group of sizeable herbivores of the Late Triassic, remain unknown up to date.

6.2. Results from REEs studies

Geochemistry of lanthanides has been studied in marine waters, rivers, lakes and groundwater (Elderfield et al., 1990; Johannesson et al., 1993; Möller and Bau, 1993; Johannesson et al., 1996; Johannesson and Xiaoping, 1997; Johannesson and Zhou, 1999; Dia et al., 2000; Johannesson et al., 2000). Signatures of lanthanides are dependent on pH, redox state, the concentration of ligands forming complexes with rare earth elements (carbonates and dissolved organic compounds), sorption on iron oxides and hydroxides, and the composition of the source rock minerals, which provided REEs to pore waters (Johannesson and Xiaoping, 1997; Hannigan and Sholkovitz, 2001; Tang and Johannesson, 2003). Sea water and alkaline lakes are usually enriched in heavy lanthanides (HREEs; Johannesson et al., 1993; Möller and Bau, 1993) as carbonate complexes prefer HREE than light rare earth elements (LREEs). Inland waters and groundwater, and silico-clastic sediments usually have a flat (shale) pattern or the signature enriched in LREEs and middle rare earth elements (MREEs). They may also inherit the signature enriched in HREEs from the dissolved carbonate rocks present in the drainage area (Johannesson and Zhou, 1999; Hannigan and Sholkovitz, 2001). Non-carbonate coastal marine sediments and aeolian deposits are usually enriched in light lanthanides (Elderfield et al., 1990; Sholkovitz, 1992).

The reduction of iron oxides/oxy-hydroxides or phosphate precipitation (Kreamer et al., 1996; Dia et al., 2000; Johannesson et al., 2000; Kocsis et al., 2009) by binding of dissolved organic compounds (Tang and Johannesson, 2010) can lead to enrichment in medium lanthanides. Numerous works have successfully used REEs in paleoenvironmental studies (Patrick et al., 2004; Martin et al., 2005), paleoceanographic research (Elderfield and Pagett, 1986; Wright et al., 1987), taphonomy and provenance studies (Trueman, 1999; Trueman et al., 2006; Grandstaff and Terry, 2009; Rogers et al., 2010) and coprolite analyses (Kemp and Trueman, 2003; Owoc et al., 2012).

Coprolite samples have 50–250 PAAS values at the spider diagram with a distinct MREE-enriched pattern and a positive cerium anomaly. The geochemical signatures of the samples overlap each other both on spider diagram and ternary plot (Fig. 10). The so called “MREE bulge” or “bell-shaped” pattern was attributed by Reynard et al. (1999) as the pattern indicative for substitution mechanism of REE scavenging in phosphatic fossils during the diagenesis. However, the analyzed coprolite samples are depleted in phosphate phases and hence the characteristic signatures may have been inherited from the original diagenetic pore fluid. The REE model for pore waters in the marine sediments (Haley et al., 2004) presents an explanation of the “MREE bulge” in the studied coprolites. It is widely acknowledged that MREEs are preferentially scavenged by iron oxides both in the water column and oxidized sediment (Johannesson and Zhou, 1999). However, when the iron oxides are reduced, they release the previously accumulated MREEs, enriching the pore fluids in the sediment.

The plot of Bau and Dulski (1996) was used to distinguish “true” cerium anomalies from the non-redox ones induced by the lanthanum anomalies, commonly present in the aquatic environments. All coprolite samples have redox related positive anomalies paired with negative lanthanum anomalies (Fig. 11B) suggesting anoxic conditions in the sediment during the feces diagenesis. Cerium and europium are the only lanthanides that have more than one oxidation state. Cerium is susceptible to complexation by carbonate groups and dissolved organic compounds but it is most notably fractionated from the other lanthanides in oxidizing conditions (Akagi and Masuda, 1998; Haley et al., 2004; Seto and Akagi, 2008). Cerium oxidation and fractionation in natural waters is widely used to study redox characteristics of the sediment and pore waters (Elderfield et al., 1990; Dia et al., 2000). Positive cerium anomalies usually indicate reducing environments, whereas negative anomalies indicate oxidizing environments (Wright et al., 1987; DeBaar et al., 1988). Seto and Akagi (2008) argue that the cerium anomalies in groundwater are an indicator of redox, provided that these

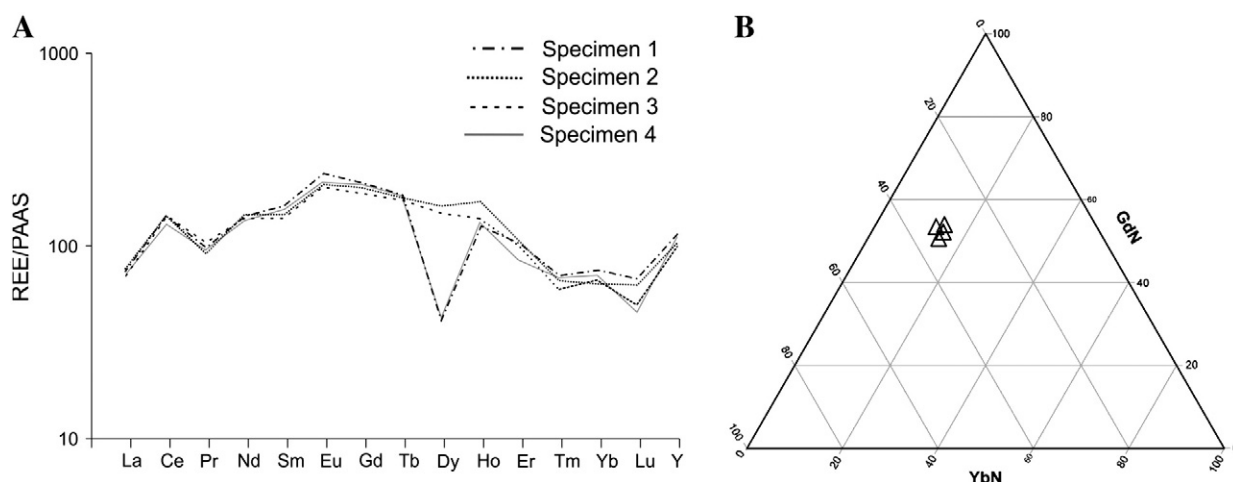


Fig. 10. Results of REEs analysis from the putative dicynodont coprolites from the Lipie Śląskie clay-pit at Lisowice. (A) Spider diagrams of the Rare Earth Elements (REEs) in four putative dicynodont coprolites from the Lipie Śląskie clay-pit at Lisowice. REEs signatures of coprolites are similar in each of the coprolites. (B) Ternary diagram of NASC-normalized REEs in coprolites. All samples have similar REEs ratios, with overlap, suggesting that coprolites were fossilized at the same place or time and were not reworked from other deposits; GdN = Gadolinium, YbN = Ytterbium, NdN = Neodymium.

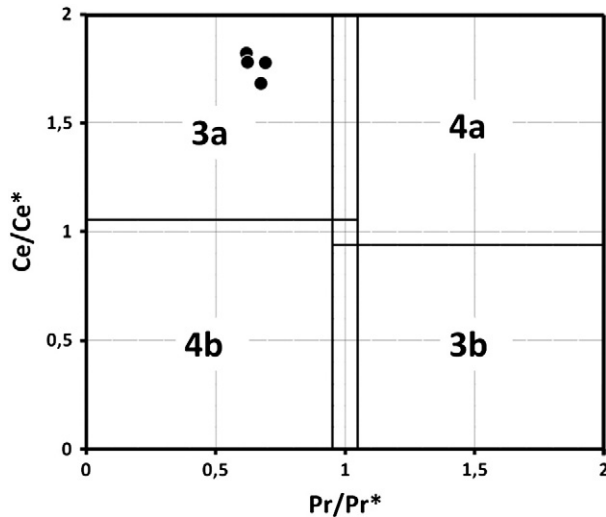


Fig. 11. Results of REEs analysis from the putative dicynodont coprolites from the Lipie Śląskie clay-pit at Lisowice. Modified plot of Bau and Dulski (1996) used for distinguishing La and Ce anomalies. Samples taken from coprolites group in the distinct field 3a-positive Ce and negative La anomalies.

waters have a low content of organic compounds that can complex cerium. In such conditions, a negative cerium anomaly may appear in shallow groundwater when cerium is captured by precipitating iron oxides (Akagi and Masuda, 1998), or bound by complexes of carbonates in alkaline waters (Pourret et al., 2008).

In the case of the dicynodont coprolites the positive anomaly in the analyzed samples may result both from the preferential scavenging of Ce (IV) by humic acids and iron oxide particles in the water column. Then, in the anoxic sediment the iron oxide reduction to pyrite and decomposition of the organic particles would have released the previously accumulated Ce (IV) to the pore waters and imprint the anomaly in the fossilizing feces.

6.3. Inference from isotopic studies

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of organic matter (dark and amorphous organic matter) from three coprolites are presented in Table 4. A plot of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ average ratios of dicynodont coprolites from Lisowice is given in Fig. 12.

The majority of present day terrestrial plants fall into two categories based on photosynthetic pathways, namely types C3 and C4, which are

characterized by distinct carbon isotopic signatures (Ehleringer, 1989). Type C3 plants have a unimodal distribution around a mean of -26% while C4 plants are enriched, having a mean $\delta^{13}\text{C}$ value around -12% . The carbon isotopic ratio of the organic matter within the coprolite falls under the category of C3-type vegetation. This result is not surprising, because Triassic ecosystems likely only had type C3 plants.

The nitrogen in the coprolites is probably derived from the undigested organic tissue (plant remains, collagen or bones etc.) from food, consumed water and bacteria from the gastrointestinal tract (Hollocher et al., 2001). In the case of the examined coprolites, direct evidence for bone or organic bacterial components was not found.

We compared the nitrogen isotopic ratio of putative dicynodont coprolite organic matter (mixture of plant tissues, palynomorphs and dark organic carbon) with feces of present day different species of birds and mammals (Ghosh et al., 2003). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are significantly different for herbivores and carnivores. There is a decrease in ^{13}C and an increase in ^{15}N with a progressive rise in the trophic level (Schweizer et al., 2006) and the $\delta^{13}\text{C}$ values are lower for herbivore feces such as the deer, supposed sauropod dinosaur, and plant eating birds, compared to carnivores. The putative dicynodont coprolite samples from Lisowice fall between the data on bird feces and large carnivorous (tiger and leopard) and occupy the middle level in the plot. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compositions of the coprolite samples suggest that the main food of the producer was plants and if the interpretation of these structures is correct, our analysis provides biogeochemical evidence of herbivorous diet in this species.

6.4. Ecology of dicynodonts

Dicynodont coprolites described herein seem to be quite common at the Lisowice site (more than 100 specimens were collected or observed in the field) and thanks to their black or dark-brown color are easy to find and recognize on weathered surfaces of the exposed mudstones. Recently, Fiorelli et al. (2013) reported so-called communal latrines of dicynodonts from eight massive coprolite accumulations in the Middle–Upper Triassic Chañares Formation, Argentina. Although Fiorelli et al. (2013) for the first time explicitly interpreted coprolite accumulation as possible non-mammal communal latrines, in fact various accumulations of coprolites of non-mammalian herbivores had already been described from numerous localities, as for example from the Upper Cretaceous Two Medicine Formation, USA associated with a nesting ground of hadrosaurs (Chin, 2007; Chin et al., 2009), or the Lameta Formation, India (Ghosh et al., 2003; Ambwani and Dutta, 2005; Sharma et al., 2005) and the Cerro del Pueblo Formation, Mexico (Rodríguez de la Rosa et al., 1998). Triassic deposits also present interesting localities abundant with coprolites of herbivores, as for example the Middle Triassic Santa Maria Formation, Brazil (Souto, 2001) and the Upper Triassic (Norian–Rhaetian) Maleri Formation, India (Vijaya et al., 2009). Defecation of dicynodonts in communal latrines reveals that this gregarious behavior is not unique to mammals (Fiorelli et al., 2013). Therefore, it might be more common in the fossil record. However, herbivore dungs simply tend to be common around sources of drinking water and hence mass occurrences of coprolites in the fossil record do not necessarily represent defecation in communal latrines. Dung counts are a reliable method in estimations of animal population sizes in modern ecosystems (Barnes, 2001). Social lifestyle, significant time spent in the water and favorable fossilization conditions may also be responsible for accumulations of coprolites. In consequence, fossil feces are among the most common fossils in many sedimentary rocks (Hunt and Lucas, 2005b). Coprolites from carnivorous animals can be common in sediments deposited in aquatic environments, but coprolites from herbivores and fully terrestrial animals are generally quite rare or rarely described (Chin and Kirkland, 1998; Chin, 2007).

In modern ecosystems, accumulations of feces produced by hippopotamuses are common in water pools. Onyeonusi (1999) discussed

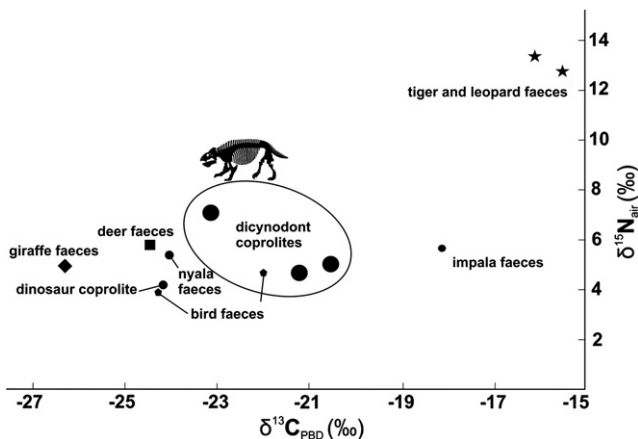


Fig. 12. Plot showing the range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition of fossil tissue, coprolites of different animals (taken from Bocherens et al., 1999; Ghosh et al., 2003; Codron and Codron, 2009) and the putative dicynodont coprolite specimens from the Lipie Śląskie clay-pit at Lisowice.

some aspects of the ecological role of *Hippopotamus amphibius* in African ecosystems. Because hippopotamuses commonly defecate in water, their excrements enrich the water in nutrients. Their feces are also fed on by detritus consumers, as some herbivorous fishes, and hence play a role in water food chains. The swampy environment habit of dicynodonts has already been suggested by Hunt et al. (1998, 2007) based on the fact that dicynodont coprolites are known from dark mudstones formed in alternating wet and dry conditions including periods of standing water. Dicynodont coprolites described herein come from deposits of a low energy environment as well. Everglades-like environment record in the Lipie Śląskie site seems to be confirmed by geochemical data (Niedźwiedzki, in press). It is noteworthy that several massive coprolite associations, determined as a latrine deposit produced by dicynodonts, described by Fiorelli et al. (2013) represent autochthonous biogenic accumulations buried in a short-term fluvial deposition event.

A social life style of the dicynodont is also possible due to the significant amount of coprolites in the sediments. For example, hippopotamus individuals require relatively little space (Onyeonusi, 1999) and congregate together in groups averaging five members, and occasionally up to 45 members (Martin, 2005). This is in accordance with conclusions of other researchers, such as Fiorelli et al. (2013). Moreover, among modern mammals to form herds is one of the most common protective strategies. Niedźwiedzki et al. (2011) described bite marks on bones of juvenile dicynodonts from Lisowice revealing predator–prey interactions between a large theropod *Smok wawelski* and the dicynodont. Because coprolites of this theropod in addition to remains similar in histology to therapsid bones contain fish scales and bones (Niedźwiedzki, in press), these data on its habit highlight interactions between the theropod and dicynodont due to the co-occupied environment.

However, there are obvious differences between the dicynodonts' ecosystem and the ecosystem of hippopotamuses. At night hippopotamuses leave the water pools to graze on grasses which compose their main food source (Onyeonusi, 1999; Martin, 2005). It is clear that grasses were absent in the Triassic ecosystems. Chin (2007) suggested that a Late Cretaceous hadrosaurid *Maiaasaura peeblesorum* intentionally fed on rotting wood consuming considerable amounts of it, which might be justified by the absence of grasses in the Mesozoic ecosystems. Wood fragments have been reported a few times in coprolites of herbivorous dinosaurs and could also be ingested unintentionally while feeding on tree branches (Chin and Kirkland, 1998). Nevertheless, most of the dicynodont coprolites at hand from the Lisowice site, contain no remains of woody plants, which might suggest a high quality diet composed of few fibrous plants, possibly expected in swampy environments and perhaps including aquatic plants.

Again, as in the case of modern hippopotamuses, it may be difficult to satisfy such a sizable animal's nutritional requirements only by feeding on aquatic plants, especially with a social life style. Recognized palynomorphs and cuticle suggest that the diet of the dicynodont was complemented with gymnosperms. However, because it seems that all the cuticle fragments found in two coprolites represent a single type of gymnosperm plant, it might reveal a selectivity in the feeding habit. Nevertheless, it may be caused by poor sampling. Another possibility would be a restricted variability of available plant species as a source of forage. A degree of selectivity in feeding habit and a high-quality diet are supported by the absence of wood fragments in nearly all of the coprolite specimens. Remains of different diet components may vary between each other in resistance to decomposition by stomach acids or diagenesis and moreover could have been transported in the gastrointestinal tract far from the place where the tissues were originally consumed (Bajdek, 2013). However, because wood tissues seem relatively well-resistant for decomposition and diagenesis their absence in most of the coprolite specimens is conspicuous. Only two collected coprolite specimens are characterized by the high content of wood fragments up to 2 cm in length with rounded terminations (Fig. 6A, B). Their

dimensions, total content (around 40% in comparison to 13%–85% of total wood content in the coprolites of *Maiaasaura*) and general appearance are similar to those from *Maiaasaura peeblesorum* hadrosaurid coprolites described by Chin (2007). The digestion of wood is extremely hard in a bacteria-dominated digestive tract of tetrapods (Chin, 2007) without previous activity of fungi (i.e., rotting wood), the Late Triassic dicynodont had no teeth (in contrast to hadrosaurids) and as it seems no functional gastroliths (see Physiology of dicynodonts below) were detected in the coprolites. Thus, it is intriguing if dicynodonts – at least occasionally – indeed complemented the diet with such a high fibrous woody forage. Rotted, initially decomposed wood might be however well-accessible in this Everglades-like swampy environment. It might also indicate general implications for feeding strategies in pre-Cenozoic ecosystems, before grasses evolved and spread. Chin (2007) described also a second, less common type of herbivore coprolite from the Two Medicine Formation. Some specimens with a so-called *gray coprofabric* differ from those of the *woody coprofabric* in being smaller and in a low content of wood. Because they were found in a close proximity to *Maiaasaura* nests and sometimes contain eggshell fragments, Chin (2007) suggested that if they were from *Maiaasaura* as well, they might possibly have been produced by juvenile individuals which required higher quality diet. However, this seems not the case of dicynodont coprolites from Lisowice, because there is, for instance, no obvious difference in size between the more common dark gray coprolites and the specimens of high woody content, although the two woody specimens indeed seem to be of adult individuals. Thus, the most probable explication seems to be temporal differences in access to diet components.

6.5. Physiology of dicynodonts

Stool form reflects the gastrointestinal transit time and can be easily used to monitor changes (as sickness) in the intestinal function in clinical practice or research (Lewis and Heaton, 1997). Because the collected dicynodont coprolite specimens appear to represent feces that were likely comparable in consistency, they are all equally interpreted as feces of healthy animals, in spite of differences in content or the state of preservation. Interestingly, Chin (2007) described the morphological variety of *Maiaasaura peeblesorum* coprolites that apparently reflected different consistencies, ranging from compact blocks to some that had a fluid morphology.

For understanding the physiology of therapsids and consequently for better understanding of the Permo-Triassic ecological events and evolutionary trends, it is crucial to investigate the food-processing mechanisms and efficiency. Interestingly, due to the high degree of decomposition of the ingested plant remains, the dicynodont coprolites at hand seem to reveal effective digestive processes.

About 30–50% of the mass of the coprolites consists of the HCl-resistant particles, including clastic mineral material of sand-sized particles. Following the terminology reviewed by Wings (2007) all of those mineral clasts with a diameter larger than 0.063 mm and that formerly retained in the digestive tract are classified as gastroliths. Gastroliths, when present, can be excreted with feces and have already been described in coprolites (Wings, 2012). However, gastroliths may be ingested intentionally as well as accidentally and do not always play a role e.g. in trituration or mixing of foodstuff. Wings et al. (2008) described a stomach content of a captive pygmy hippopotamus (*Hexaprotodon liberiensis*) containing a large amount of gravel of the mean particle diameter of 2–10 mm. It was however deduced that the hippopotamus stomach structures acted as simple sedimentation traps with no gastric mill function. Because (a) the diet of the dicynodont species at hand seems to be basically composed of very soft tissues, (b) mineral clasts present in its coprolites are of very minute sizes and (c) such particles could be easily swallowed while foraging in a swampy environment, there is a lack of trustworthy evidence for a gastric mill in dicynodonts. Most of the species of ruminants and also other animals (amphibians, reptiles, birds) consume considerable amounts of soil

while feeding. For example, bison (*Bison bison*) consumes sediments at a rate of 7%, while sandpipers (*Calidris* sp.), which feed on invertebrates in mud or shallow water, consume sediments at a rate of 7–30% of their diet (Beyer et al., 1994).

It is commonly known that digestive efficiency depends in part on the food mean retention time (Fritz et al., 2010, 2011). In herbivores, an increase in food intake causes an acceleration of ingesta passage through the digestive tract and when in excess may paradoxically decrease digestive efficiency. Clauss et al. (2007) compared feeding strategies and food retention mechanisms in two modern megaherbivore groups. In elephants, an increase in food intake is only slightly correlated to a decrease in mean food retention time which allows elephants spend a significant amount of time (75% of the day) on feeding, optimizing the gain of energy. Meanwhile, hippopotamuses are limited by an upper daily intake of theoretically 45–50 kg above which the excess of food intake drastically reduces mean food retention time and the energy gain. Therefore, hippopotamuses are known to spend only 30% of the day foraging.

In spite of the huge producer size, the dicynodont coprolites from the Lipie Śląskie clay-pit suggest a significant degree of selectivity while feeding, restricted to high quality non-fibrous diet and when not sufficient, occasionally complementing the diet with woody ingredients, meanwhile eating more generally implies eating lower-quality more fibrous and hard to process forage. The coprolites of the dicynodont described here supposedly also reveal very effective digestive processes (degree of the food ingredients decomposition). Therefore, it seems reasonable that the metabolism of the source dicynodont species was much more modern hippopotamus-like than elephant-like. This feeding strategy would allow the dicynodont to maximize the energy gain while feeding on limited amounts of higher-quality forage, rather than consuming large amounts of lower-quality ingredients. The long forage gastrointestinal pass and limited amounts of consumed food in the dicynodont are also supported by the fact that the dicynodont had no teeth. Schwarm et al. (2009) have shown that the pygmy hippopotamus (*Hexaprotodon liberiensis*) has longer food retention time than the more effectively forage-chewing bateng (*Bos javanicus*) and that in mammals more effective mastication allows increased food intake. The capacity of food retention depends on the gut volume (Fritz et al., 2009). Herbivory requires greater complexity of the gastrointestinal tract and often favors evolution of larger body size in both mammals and reptiles (Fritz et al., 2010, 2011), as exemplified by herbivorous liolaemid lizards which are larger relative to their omnivorous and insectivorous congeners (O'Grady et al., 2005). Niedźwiedzki et al. (2011) suggested that the increase of body size of dicynodonts across the Middle–Late Triassic was caused by pressure from early predatory dinosaurs. Not excluding explanations of this kind, it seems that the gigantism of the source dicynodont species was a metabolic adaptation that allowed increased retention time of limited forage amounts as it is in the case of modern hippopotamuses. This interpretation seems to support the analogies to hippopotamuses. Such highly effective food-processing would be much more expected in mammalian herbivores than in herbivorous reptiles (Fritz et al., 2010); there are however no huge extant plant-eating reptiles. On the other hand, the supposed long food retention time in the gastrointestinal tract seems to be a strategy more typical for reptiles, as opposed to its initial chewing and fast metabolism in mammals (Fritz et al., 2010). Although mastication mechanisms were not yet well-developed in therapsid herbivores and hence a long food digestion was required in recompense, apparently the digestive mechanisms were already highly effective and advanced, as supported by the $\delta^{15}\text{N}$ values similar to those from feces of modern mammals (Ghosh et al., 2003). Later on, development of the mechanism of chewing in mammals, would allow the acceleration in metabolism.

6.6. Binomial nomenclature of coprolites

One parataxonomical concept of coprotaxonomy has been developed by several researchers who state that it would be useful to apply

binomial nomenclature to coprolites with the same type of system commonly used to name other types of trace fossils (e.g. fossil footprints; Hunt et al., 2007). Binomial nomenclature has been applied to vertebrate coprolites a number of times (Hunt et al., 1998; Hunt and Lucas, 2005a,c; Hunt et al., 2005a,b, 2007, 2013) and at least 29 ichnotaxa of Paleozoic and Mesozoic vertebrate feces have been established (Hunt et al., 2012, 2013) as well as some Cenozoic coprotaxa (Aceñolaza, 2012). Some suggest that applying binomials to coprolites would make scientific communication easier and that the lack of classification limits the utility of coprolites in paleobiology (Hunt et al., 1994). The use of coprolites in biostratigraphy and correlation has also been discussed and experimented for the Permian (Hunt et al., 2005b) and Triassic (Hunt et al., 1993, 1998, 2007).

Nevertheless, this approach to coprotaxonomy is a controversial concept and there is disagreement in paleoscatology about applying the Linnaean binomial nomenclature to fossil feces' morphotypes (Hunt et al., 1994; Verde and Ubilla, 2002). Whereas most authors do not name coprolites (Owcocki et al., 2012), others suggest that development of a binomial system of coprotaxonomy is one of the basic tasks in paleoscatology (Hunt and Lucas, 2005a; Hunt et al., 2012). A. Hunt and M. Lockley in Hunt et al. (1994) argued that vertebrate coprolites have distinctive and recurring morphologies and that similar morphotypes have been recognized from different Triassic formations. Meanwhile K. Chin (in Hunt et al., 1994) was skeptical pointing out that feces can vary depending on their quality of preservation or changes in diet of their producer. She concluded that application of a Linnaean system of classification to coprolites would imply unsubstantiated taxonomic differences (Hunt et al., 1994).

For a useful and justifiable application of coprotaxonomy and coprostratigraphy, two criteria are important: (a) recognition of similar and recurring coprolite morphotypes from different formations and (b) the existence of a trustworthy link between morphology of the feces and its source animal species. Ichnotaxonomy is, for instance, commonly applied to fossil footprints thanks to the morphological restrictions imposed on them by the foot morphology of the given tracemaker (Olsen et al., 1998).

For example, because the scroll valvular intestine implies spiral morphology of feces and the spiral valve is absent in teleost fish and tetrapods, spirally coiled coprolites have been assigned to certain types of fishes, as for example sharks or lungfish (Jain, 1983; Gilmore, 1992; Dentzien-Dias et al., 2012). Moreover, Jain (1983) noted that modern lungfish spiral feces tend to uncoil after a period in the water. However, it may be difficult to distinguish non-spiral fish coprolites from those produced by tetrapods (Hunt et al., 1994).

Northwood (2005) described longitudinally striated coprolites from the Lower Triassic of the Arcadia Formation, Australia. She suggested that they were possibly produced by archosauromorphs, because (a) such a coprolite morphology is known back to the Early Triassic, (b) longitudinal striations have been observed in some extant crocodile feces, and (c) some extant reptiles have longitudinal rugae in their intestine. Such longitudinally striated coprolites are well known from various Mesozoic formations (Ghosh et al., 2003; Northwood, 2005; Hunt et al., 2007). Small, typically 2 cm long Triassic longitudinally striated coprolites were named by Hunt et al. (2007) as *Alococoprois triassicus*, meanwhile typically more than four times as long specimens from the Late Cretaceous of Lameta Formation, India, were named *A. indicus*. However, such longitudinal striations do not seem to be requisite for feces of Archosauromorpha, since they may be absent in some coprolites (Niedźwiedzki, in press).

The identification of the coprolite producer based on feces characteristics may be a subject of further research. It must be however noticed that these few examples listed above are applicable only for high level taxa. As for now, cases of identification of the exact producer genera or species of pre-Quaternary feces are very few. Usually, it is obtainable only if there was just one large enough carnivore or herbivore species to produce such sizable fecal masses in a given geological context (Chin

et al., 1998), or putatively on the preservation of a swallowed tooth fragment in the coprolite (Stone et al., 2000).

There are numerous factors that limit or completely exclude the utility of the application of binomial nomenclature to classifying coprolites:

- (1) Distinct animal taxa can produce very similar feces. For example, feces produced by herbivores are frequently pelletoid, or blocky and amorphous (Chin and Gill, 1996; Chin and Kirkland, 1998; Ambwani and Dutta, 2005; Chin, 2007). Also, the feces from many different carnivores have comparable shape and size.
- (2) The same individual or species can produce a large diversity of dung morphologies and/or dung contents depending on changes in the food habit, e.g. seasonal, in age or health (Chin, 2007).
- (3) Feces are easily fragmented, deformed or decomposed. Feces are also a subject of invertebrate activity (Chin and Gill, 1996; Wahl et al., 1998; Chin et al., 2009; Milàn et al., 2012). Moreover, the state of preservation of fossil feces depends largely on taphonomic and diagenetic processes (Hunt et al., 1994; Chin and Kirkland, 1998).

Indeed, fresh vertebrate feces can provide some taxonomic information (Chame, 2003), since (a) modern faunas can be studied, (b) direct observations linking feces' morphotypes to their producers can be made, (c) fresh feces are intact and undamaged and (d) interpretations are not skewed by the highly incomplete and complex fossil record and geological time. However, even modern mammalian feces' morphotypes can be generalized as representing rather higher taxonomic levels, such as Orders (Chame, 2003). Moreover, the DNA analyses of modern feces (Wasser et al., 1997), are more credible than morphology in identification of the producer. For example, DNA analyses made by Davison et al. (2002) have shown that naturalists commonly mistake pine marten (*Martes martes*) feces for those of foxes (*Vulpes vulpes*). The taxon of the source animal of fossil feces can be extremely difficult to identify (Chin, 1997; Chin and Kirkland, 1998; Bajdek, 2013). It is also not easy to estimate the size of the producer. Although there is a slight correlation between the total fecal mass volume and its producer body mass (Flessa et al., 2012), some large animals produce large quantities of small pelletoid feces. Thus, as suggested Chin (1997) coprolite volume should be primarily used to infer the minimum size of the producer.

The chemical composition of a coprolite, as well as, animal or plant inclusions are useful in the identification of the source animal (Hunt et al., 1994; Chin, 1997). Nevertheless, most often the producer can only be defined as a herbivore/carnivore, possibly with several potential producers known from the paleobiological context (Owociki et al., 2012). Moreover, recognizable dietary residues can be easily destroyed by digestion (Bajdek, 2013) and diagenesis, and the chemical composition can be altered during diagenesis (Chin and Kirkland, 1998). All of these difficulties can be exemplified by established coprotaxa of dicynodonts. Hunt et al. (1998) established *Dicynodontocopros maximus* based on specimens from the Late Triassic Chinle Group, USA, with the holotype UMMP 7255 (Hunt et al., 1998, fig. 2A–B, 2007, fig. 2J–K), which was incorrectly listed as UMMP 7253. The diagnosis of *Dicynodontocopros* ichnogenus (Hunt et al., 1998, page 228) was described, as: "Differs from other Triassic terrestrial vertebrate coprolites in: being large (up to 10 cm long) and dark gray in color; preserving up to 4 loose coils; containing large (up to 4 mm in diameter) blebs of carbonaceous material; having a slightly arcuate long axis with one end being broadly rounded and the other coming to an acute tip; and having a maximum width to length ratio of about 45–50% in complete specimens."...

However, Hunt et al. (2007) admitted that some dicynodont coprolites from the Carnian of the Tecovas Formation, Chinle Group, Texas (which also yielded the ichnogenus type) lack a distinct morphology. Hunt et al. (2007) also suggested that some coprolites described by Rusconi (1947, 1949) from the Triassic of Mendoza area, Argentina are likely of dicynodonts, but they are more amorphous and differ in having more rounded terminations and more consistent widths. It was

supposed that those differences are of taphonomic origin (Hunt et al., 2007). Northwood (2005) also described a possible blocky and elongate herbivore coprolite QMF39701–47 (Northwood, 2005, fig. 2J) from the Lower Triassic Arcadia Formation, Australia. She noticed, that the specimen bears little resemblance to dicynodont coprolites described by Hunt (1992). Fiorelli et al. (2013) described dicynodont coprolites from the Chañares Formation, Argentina, with a variety of morphologies, generally blocky and in some degree amorphous. Hunt et al. (2013) introduced a new ichnogenus of dicynodont coprolite (*Santamariacopros elongatus*) for a slightly elongate morphotype from the Middle Triassic Santa Maria Formation, Brasil, which was initially described by Souto (2001). Finally, the dicynodont coprolites described herein from the Late Triassic of the Lisowice site, Poland, are mostly blocky, or oval forms.

In summary, possible dicynodont coprolites known from the fossil record of various formations are generally blocky, oval, slightly elongate or amorphous forms. These characteristics obviously do not exhibit any morphological criteria that allow them to be distinguished from e.g. many dinosaurian (Chin and Kirkland, 1998) or even modern mammalian droppings. Interestingly, Hunt et al. (1998, 2007) states that *Dicynodontocopros maximus* is restricted to the Late Triassic (late Carnian) and emphasize its utility in biochronology, among other coproichnogenes. In conclusion, feces – especially if fossilized – do not have the same morphological constraints imposed on them that e.g. footprints do and provide little taxonomic information about the source animal. Therefore, the binomial nomenclature should not be applied to coprolites, since it implies unjustified taxonomic differences. This renders most coprolites unsuitable for biostratigraphic purposes.

7. Conclusions

The enigmatic structures presented here show several similarities with coprolites of herbivorous tetrapods (mainly herbivorous dinosaur and dicynodont coprolites) and contemporary feces: (1) the overall forms and composition (organic remains, microbial structures), (2) the presence of micro- and macro-plant remains, and (3) the presence of mineral particles (clasts). These coprolites from Lisowice provide rare fossil evidence for physiology of large Late Triassic therapsids. It is possible that the gigantism of the source dicynodont species was a metabolic adaptation that allowed these animals to maximize food retention time and consequently the energy gain. Like some of the present-day mammalian herbivores, the dicynodont left rather medium in size and oval-shaped fecal residues. A wide variety of plant materials, such as pollen and spores, cuticles, woody tissues of gymnosperms were observed inside the coprolites. The diet of this dicynodont was probably of high quality, it was however complemented also with poor-quality fibrous food components. This discovery also calls attention to oval-shaped, dark, organic-rich herbivore coprolites in the Triassic terrestrial rocks, such fossils may be recognized in other sites containing dicynodont bones. The described specimens were not assigned in binomial nomenclature. Morphology, composition and size of coprolites can vary depending on their quality of preservation or changes in the diet of their producer. The use of the Linnaean nomenclature for coprolites is in our opinion a rather controversial concept.

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