Comparative actualistic study hints at origins of alleged Miocene "coprolites" of Poland

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Comment [GM1]: Here and atsome other places in the text, the format is "*coprolites*". Elsewhere, the term is *coprolites.* I question the stylistic ethics of this format evolution, since the authors appear to be declaring the authenticity of the specimens before offering evidence to support this interpretation. For example, the material and metods declares the specimens to be coprolites long before and data is presented.

Abstract

Excrement-shaped siderite masses have been the subject of much controversy. They have been variously interpreted either as being coprolites, cololithes or pseudofossils created by mechanical deformation of plastic sediment. Here we reportexcrement-shaped ferruginous masses recovered from the Miocene of Turów mine in south-western Poland.

Results of mineralogical, geochemical, petrographic and microtomographical analyses indicate that these masses consist of siderite and iron oxide rather than phosphate, and rarely contain recognizable food residues, which may suggest abiotic origins of these structures. On the other hand, evidence in support of a fecal origin include: (i) the presence of two distinct morphotypes differing in size and shape, (ii) the limited quantity of specimens, (iii) the presence of rare hair-like structures or coalified inclusions and (iv) the presence of rare fine striations on the surface. Importantly, comparative actualistic study of Recent vertebrate feces shows overall resemblance of the first morphotype (sausage-shaped with rare coalified debris) to excrements of testudinoid turtles (Testudinoidea), whose shell fragment was found in the investigated locality. The second morphotype (rounded to oval-shaped with hair-like

structures), in turn, is similar to the feces of some snakes (Serpentes), the remains of which were noted in the Miocene of the neighborhood areas.

Introduction

Incontrovertible examples of the Miocene coprolites are known from only a few localities in Europe, North and South America (Amstutz, 1958; Roberts, 1958; Hunt & Lucas, 2007, 2012, 2021; Dvořák et al., 2010; Godfrey & Smith, 2010; Hunt et al., 2012; Pesquero et al., 2014; Broughton, 2017; Dietzien-Dias, 2018; Tomassini et al., 2019; Farlow et al., 2020). Rodents, notoungulates, hathliacynid and borhyaenoid marsupials, indeterminate carnivorans, sirenians, crocodilians, were commonly invoked as potential producers of these coprolites (Godfrey & Smith, 2010; Dietzien-Dias, 2018; Tomassini et al., 2019). The majority of described Miocene vertebrate coprolites were produced by carnivores. This is not surprising because faeces of herbivorous tetrapods are commonly composed of a large quantity of undigested plant residues attracting microbial decomposition. On the other hand, the calcium phosphate derived from undigested bones in the faeces of carnivores acts as important permineralizing agent (e.g., Hunt et al., 1994; Pesquero et al., 2011; Dentzien-Dias, 2018). Excrement-shaped ferruginous masses have been considered (based on morphological grounds) by some authors as being coprolites (Amstutz, 1958; Broughton et al., 1977, 1978) or cololites (Seilacher et al., 2001; Broughton, 2017; intestinal casts - evisceralites; see e.g., Hunt & Lucas, 2021). Notably, Broughton (2017) has recently described multi-decimetre-long intestine-like elongated objects revealing bilateral symmetry in cross-section and surface features consisting of fine longitudinal parallel striations, which were ascribed to gut casts of a previously unrecognized giant terrestrial earthworm.

Excrement-shaped masses are commonly reported from clay-rich sediments ranging in age from Permian to Holocene. However, given their ferruginous composition, significant variation in size, lack of internal inclusions, and scarcity of associated vertebrate remains, most authors rejected a zoological origin (Dake, 1939, 1960; Danner 1968, 1994, 1997; Major, 1939; Roberts, 1958; Spencer & Tuttle, 1980; Love & Boyd, 1991; Spencer, 1993, 1997; Hardie, 1994; Mustoe, 2001). Different non-zoological hypotheses have been invoked to explain the origins of these objects (such as soft sediment extrusion triggered by coseismic liquefaction(reference?), sediment intrusion into hollow logs(Spencer & Tuttle 1980, Spencer 1993) or squeezed between plant stems (Roberts 1958) , expulsion of sediment in response to

Comment [GM2]: Incontrovertible? Amstutz (1958) described purported ferruginous coprolites from the Miocene Wilkes Formation in Washington State, USA, Roberts (1958) suggested the possibility that the objects were created when soft sediments were squeezed through plant stems. Later researchers (e.g., Danner, Spencer, Mustoe) all describe the specimens as being abiogenic. Seilacher (who only saw a few specimens that were purchased from a rock shop) described them as intenstinal casts, a description that has been repeated by Broughton (another instance of an author who never visited the locality, and only examined a few specimens. After years of conflicting interpretations, it is certainly not correct to describe the 1958 report of Amstutz as incontrovertible.

Comment [GM3]: One of the most abundant occurrences of ferruginous "coprolites is the Cretaceous White Mud Formation of Saskatchewan, Canada, a locality that deserves to be mentioned.

Comment [GM4]: Here's a story that relates to the Cretaceous White Mud Formation "coprolites" from Sakatchewan, Canada. In a 1977 and 1978 papers Broughton et al. declared that the trace makers were most likely big fish, e.g., sturgeon and bowfin. In 2014, Broughton proposed that the ferruginous masses included intestinal casts of a herbivorous reptilian tetrapod. In 2017, Broughton decided that these trace fossils were instead made by giant earthworms. This calls into question the wisdom of declaring reported coprolite occurrences as "incontrovertible".

Comment [GM5]: Doesn't this conflict with the valid comment that plant materials are susceptible to microbial decomposition? Earthworm guts presumably contain no calcium phosphate.

gravity (Love and Boyd 1991), and extrusion of siderite related to methanogenesis(Mustoe 2001).

Until recently, a detailed study on excrement-shaped ferruginous masses from the Miocene of Poland has been lacking. In this paper we analyse the Miocene excrement-shaped specimens collectedfrom the coal mine of Turów for the first time. According to our results, we favour the hypothesis that the specimens from Poland may represent true coprolites and more particularly pertaining to two different reptile groups.

Geological setting

The Turów lignite mine is located in the south-eastern part of the Lower Silesia Voivodeship (SW Poland) and covers the former village of Turów. It is located in the central part of themesoregion Żytawa-Zgorzelec Depression located between the state borders of Germany and the Czech Republic (Fig. 1A). Turów lignite deposits are part of the Upper Lusatian Brown Coal Basin. This basin comprises a few tectonic sinkholes (Piątkowska et al., 2000) that developed in Paleogene at the junction of two regional zones of strong activity: Ore Mts. Graben (Ohrza rift) and the Lusatian-Elbe Tectono-Volcanic Zone (Jęczmyk & Sztromwasser, 1998). The most southern of these is the Zittau basin (Fig. 1A, B), which was filledmainly by limno-fluvial or limnic clays,silts, sands and thick layers of lignites exploited in the Turów mine (Kasiński, 2000; Kasiński et al., 2015). Furthermore, there are numerous vulcanite rocks of late Eocene, Oligocene and early Miocene age (Kasiński et al., 2015). The basal part of sedimentary section of the Zittau basin is not older than the early Oligocene, however most sediments were formed in the Miocene (Kasiński et al., 2015). At the base of the Zittau Basin, Precambrian and Palaeozoic metamorphic and igneous rocks are present (Marcinkowski, 1985).

The lithological profile of the Turów mine is ca. 250 m thick and consists of 7 lithostratigraphic units of sedimentary rocks. Apart from the two youngest units (Gozdnica Fm. and glacial tills), all of them are mainly composed of clays and/ormuds. Additionally, there are coal seams, especially in Opolno and Biedrzychowice formations, which are the deposits mined at the Turów mine. The oldest Cenozoic sediments of the profile are Oligocene sediments (Egger age), forming the lower part of the Turoszów Fm. (Kasiński et al., 2015). The youngest in the profile are Gozdnica Fm. and Pleistocene deposits, mainly represented by Pannonian tills (Marcinkowski, 1985).

Comment [GM6]: References should be cited for these hypotheses

Love, J.D. and Boyd, D.W., 1991. Pseudocoprolites in the Mowry Shale, (Upper Cretaceous), northwest Wyoming. University of Wyoming Contribtions to Geology, v.28, 130-144.

Comment [GM7]: A stratigraphic section, even a generalized one, would by a great asset

The Turoszów Fm. was formed in fluvial and limnofluvial conditions, while the Opolno and Biedrzychowice Fms have been formed in limnotelmatic environments, and Porajów Fm. represents limnofluvial environment. Sediments of the upper part of Miocene profile (Rybarzowice and Gozdnica Fms) have alluvial origin (Kasiński et al., 2003). Biedrzychowice Fm., within which excrement-shaped ferruginous masses and a turtle remain have been documented, was formed in vast swamps and rushmarshes (Kasiński et al., 2010). Especially in the upper part of this formation, there are numerous palaeosols levels with plant roots and trunks preserved in situ (Kasiński & Wiśniewski, 2003). Marsh forests mainly composed of *Cupressaceae* and *Taxaceae* (Sadowska, 1995; Kasiński & Wiśniewski, 2003). Based on palaeobotanical analysis of the coal seam it was concluded that there was a humid warm temperate climate similar to that of south-eastern China today (Durska, 2008; Kasiński et al., 2010). The excrement-shaped ferruginous masses and the turtle shell fragment documentedin this article were collected in an inactive part of the excavation, within the clays of the higher part of Biedrzychowice Fm. in the uppermost part of early Miocene (Burdigalian; see Fig. 1C). Two distinct morphotypes randomly distributed within clay and mudstone on the flat surface of the excavation were noted.

Figure 1 around here

Fossil content in the Turów area and adjacent areas

No animal fossil remains have been documented so far from the Oligocene–Miocene of the Zittau Basinwith exception of burrows of sediment eating fauna (Kasiński et al., 2015). In the course of the present research in the clays of Biedrzychowice Fm, apart from the excrement-shaped ferruginous masses, a fragment of aturtle shell was found. This shell fragment (see Fig. 3N) can only be identified as an indeterminate testudinoid. This turtle lineage is otherwise abundant in Oligocene and early Miocene localities in Germany and Czech Republic (Reinach, 1900; Młynarski & Roček, 1985), but had not so far been documented from coeval localities in Poland. In older, Eocene and Oligocene localities in the neighbouring north-western Czech Republic and south-eastern Germany (Saxony and southeastern Saxony-Anhalt), rich assemblages of terrestrial-aquatic tetrapod fauna have been documented, comprising frogs, salamanders, choristoderans, crocodiles (also crocodile coprolites, see Kasiński et al., 2015, and literature cited therein), turtles, lizards, and snakes (Table 1).

Comment [GM8]: This can hardly be considered a terrestrial environment. Note that the "coprolites" are reportd to have come from clay beds, not coal seams. As I note later, the decision to consider only excrements from modern terrestrial animals does not match the taphonomy.

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Comment [GM9]: A problem here is that discovery of fossils provides important information about the presence of ancient life forms, but there may be many other creatures whose fossilized remains have not yet been found. "Absence of evidence is not proof of absence"

135 Table 1. Oligocene vertebrates (amphibians and reptiles) collected in adjacent areas (north-
136 western Czech Republic and south-eastern Germany [Saxony, south-eastern Saxony-Anhalt]);
137 after Laube, 1901; Obrhelová, 1971; Špinar, 1972; Obrhelová & Obrhel, 1987; Szyndlar,
138 1994; Böhme, 1996, 1998, 2007; Gaudant, 1996, 1997; Micklich & Böhme, 1997; Bellon et
139 al., 1998; Kvaček & Walther, 2003; Mikuláš et al., 2003; Fejfar & Kaiser, 2005; Karl, 2007;
140 Čerňanský & Augé, 2012, 2013; Čerňanský et al., 2016; Georgalis & Joyce, 2017; Chroust et
141 al., 2019.
142

Age	Locality	Amphibians	Reptiles
late Oligocene	Lužice-Žichov (Czech Republic)	*Triturus opalinus* *Rana luschitzana* *Asphaerion reussi*	
	Suletice (Czech Republic)	*Archaeotriton basalticus* *Palaeobatrachus grandipes* *Palaeobatrachus laubei*	
	Bechlejovice (Czech Republic)	*Archaeotriton basalticus* *Palaeobatrachus diluvianus* *Palaeobatrachus luedeckei* *Palaeobatrachus robustus* *Palaeobatrachus grandipes* *Palaeobatrachus novotnyi* *Eopelobates bayeri*	*'Diplocynodon'* sp.
early Oligocene	Espenhain, Saxony (Germany)		Trionychidae indet. *Pelorochelon* sp. *Diplocynodon* sp.
	Kundratice (Czech Republic)	*Palaeobatrachus* sp. cf. *Eopelobates* sp.	cf. *Diplocynodon* sp.
	Lukavice (Czech Republic)		*'Diplocynodon'* sp.
	Markvartice (Czech Republic)	*Chelotriton laticeps* *Palaeobatrachus diluvianus* *Palaeobatrachus luedeckei* *Palaeobatrachus* sp.	
	Dětaň (Czech Republic)	Salamandridae indet. Palaeobatrachidae indet. Pelobatidae indet.	Lacertidae indet. Anguidae indet. Testudinidae indet.

		Discoglossidae indet.	Serpentes indet. Crocodylia indet.

From the other hand, in the lower Miocene clays and sands of North Bohemian Brown Coal Basin, a very rich fauna assemblage was reported (Klembara, 1979, 1981; Roček, 1984; Szyndlar, 1991a, b; Szyndlar & Schleich, 1993; Szyndlar & Rage, 2003; Čerňanský, 2010a, b; Dvořák et al., 2010). The latter mentioned and illustrated numerous invertebrate sand vertebrates represented by osteichthyan fish, amphibians, reptiles, birds, and mammals. The reptile taxaare shown in the table below (Table 2).

Table 2. Reptiles recorded in the lower Miocene deposits of North Bohemia, Czech Republic (taken from Klembara, 1981, 2008, 2012, 2015; Młynarski et al., 1985; Ivanow, 2002; Čerňanský & Joniak, 2009; Čerňanský, 2010, 2012; Čerňanský & Bauer, 2010; Čerňanský et al., 2015; Dvořák et al., 2010; Joyce, 2016; Georgalis & Joyce, 2017; Klembara & Rummel, 2018; Chroust et al., 2021).

turtles	**crocodiles**	**lizards**	**snakes**	**choristoderans**
			Scolecophidia indet.	
			Bavarioboa hermi	
	Diplocynodon cf. *ratelii*	*Merkurosaurus ornatus*	*Bavarioboa* sp.	*Lazarussuchus dvoraki*
			Constrictores indet.	
			Falseryx petersbuchi	
		Pseudopus ahnikoviensis	"*Coluber*" *dolnicensis*	
		Pseudopus confertus	*Texasophis bohemiacus*	
		Pseudopus sp.		
		Ophisaurus fejfari		
Rafetus bohemicus		*Ophisaurus holeci*	"*Coluber*" *suevicus*	
		Ophisaurus robustus		
		Ophisaurus spinari		
		Ophisaurus aff. *spinari*		
		Ophisaurus sp. (two		

		morphotypes)		
		Anguinae indet. (several morphotypes)		
		Palaeocordylus bohemicus		
Trionychinae indet.		aff. *Palaeocordylus bohemicus*	"*Coluber*" *caspioides*	
			"Colubrinae" indet.	
Ptychogaster laubei		*Euleptes gallica*	*Elaphe* sp.	
Ptychogaster cf. *emydoides*		*Chamaeleo andrusovi*		
Ptychogaster sp.		Chamaeleonidae indet.	*Natrix sansaniensis*	
		Amblyolacerta dolnicensis		
Chelydropsis sp.		*Lacerta* sp.	*Natrix merkurensis*	
		Miolacerta tenuis	*Neonatrix nova*	
		Lacertidae indet.	*Palaeonatrix lehmani*	
		cf. Scincidae indet.		
		Blanus gracilis	Natricinae indet.	
		Squamata indet.	Elapidae indet.	
			Macrovipera platyspondyla	
			Vipera antiqua	
Testudinidae indet.			*Vipera* sp.	
			Viperidae indet.	

Material and methods

Among 29 coprolites obtained from the investigated locality, 10 representative coprolites were selected for detailed investigation. A tortoise shell fragment, documented macroscopically in the field and found on a flat surface of upper part of the Biedrzychowice Fm., was also subjected to further observations. All specimens are housed in the Institute of Earth Sciences of the University of Silesia in Katowice, Poland, and catalogued under registration number GIUS 10-3739.

A clay sample weighing ca. 40 kg was also collected from Biedrzychowice Fm. and transported to the Laboratory of the Institute of Earth Sciences of the University of Silesia in Katowice. It was washed using running hot tap water, screened on a sieve column (Ø1.0, 0.315 and 0.1 mm-mesh respectively), and finally dried at 180˚C. This washed and dried residue was observed under a Leica WildM10 microscope for vertebrate remains; unfortunately, nothing was found in the residue.

Coprolites recorded herein have been investigated with a number of different analytical tools.

Optical microscopy

Optical observation of thin sections were carried out using Leica SZ-630T dissecting microscope and Nikon Eclipse E100 light microscopy,while the microphotographs were collected using Olympus BX51 polarizing microscope equipped with an Olympus SC30 camera and a halogen light source, installed Faculty of Natural Sciences at the University of Silesia in Katowice (Poland).

Scanning Electron Microscopy

The chemical composition, morphology of coprolite matrix and microstructures topography were investigated using the desktop scanning electron microscopy (SEM) Phenom XL, Phenom World (Thermo Fisher Scientific, Eindhoven, Netherlands) equipped with a fully integrated energy-dispersive X-ray spectroscopy (EDS) detector and secondary electron detector (SED) located in the Faculty of Natural Sciences at the University of Silesia in Katowice (Poland). Measurements were performed with low-vacuum settings with accelerating voltage 15kV.

Microtomography

Virtual sections of a selected specimen(GIUS 10-3739/23) were made in the Faculty X-ray Microtomography Laboratory at Faculty of Computer Science and Material Science, University of Silesia in Katowice, Chorzów, Poland using the General Electric Phoenix v|tome|x micro-CT equipment at 160 kV, 70µA and scanning time of 20 min. Projection images were captured using a 1000 × 2024 pxs scintillator/CCD with an exposure time of 250

ms and processed using Volume Graphics® VGSTUDIO Max software and analysed using Volume Graphics® myVGL viewer.

Thin-sectioning

Thin sections from two specimens representing two morphotypes were made in the Grindery at the Faculty of Natural Sciences, University of Silesia in Katowice, Sosnowiec, Poland. Specimens were embedded in Araldite epoxy resin, sectioned, mounted on the microscope slides and polished with silicon carbide and aluminium oxide powders to about 30 μm thick.

Confocal Raman spectroscopy

To determine the mineralogical composition, the WITec confocal Raman microscope CRM alpha 300M equipped with an air-cooled solid state laser (λ = 532 nm and λ = 457 nm) and an electron multiplying CCD (EMCCD) detector was used. The calibration of the instrument was verified by checking the Si position. The Raman scattered light was focused onto a multi-mode fiber and monochromator with a 600 line/mm grating. To collect spectra of the coprolite matrix phases, the 50x/0.76NA and 100x/0.9NA air Olympus MPLAN objectives were used. All spectra were collected in the 200-4000 cm^{-1} range with 3 cm^{-1} spectral resolution. A surface Raman imaging map was collected in a 140 x 25 μm area using 140 x 20 pixels with an integration time of 0.5 s per spectrum, and precision of moving the sample during the measurements of ± 0.5 μm. The cluster analysis was performed to group spectra into clusters. K-means analysis with the Manhattan distance for Raman imaging maps was carried out. The data obtained was manipulated by WITec Project FIVE Software (cosmic rays removal procedure and cluster analysis) and GRAMS software package (baseline correction).

XRD

Bulk mineral composition of two powdered specimens representing each morphotypes was determined by Debye-Sherrer X-ray method using Rigaku SmartLab diffractometer equipped with Cu Kα1 source radiation. Measurement parameters were: acceleration voltage: 45 kV; filament current: 200 mA; step size: 0.05° 2Θ. Analyses of the collected data were carried out by means of XRAYAN Software using the newest ICSD database.

Observations of extant excrements

Faeces of Recent animals (private farms and from animals raised at the Silesian Zoological Garden in Chorzów, Poland) were observed. Over the course of two months, a total of 787 excrements belonging to modern fish, amphibians, reptiles, birds and mammals were collected. Lineages that had their representatives in the early Miocene sediments of North Bohemia, Czech Republic (see Tables 3-6) were selected for a more detailed observation. Additionally, the animals had to be large enough to produce excrements with dimensions comparable to those currently documented in the fossil state. Thus, the faeces of small fish, the remains of which are known from the Miocene sediments of North Bohemia, such as *Chalcaburnus* or *Nemacheilus*, toads and frogs (*Rana*, *Pelobates*), birds (*Upupa*, *Coturnix*) and mammals (*Chiroptera*, *Dryomys*, *Sciurus*, *Martes*), were not taken into account.

Those taxa that left their excrement in the aquatic environment were also rejected; the exception was fish. The same remark applies to crocodile and some lizard excrements, which, based on the observations in the Silesian Zoological Garden, left their faeces in the aquatic environment. Only those that left at least part of their faeces in the terrestrial environment were selected for subsequent observations. These were snakes [the king python (*Pythonregius*), the tiger python (*Pythonmolurus*), the reticulated python (*Malayopython reticulatus*), the common boa (*Boa constrictor*), the king cobra (*Ophiophagus hannah*), the Korean rat snake (*Elaphe anomala*), the common European viper (*Vipera berus*)], lizards [the komodo dragon (*Varanus komodoensis*)], and turtles [the Mediterranean tortoise (*Testudo hermanni*), the steppe tortoise (*Testudo horsfieldii*), the Indian star tortoise (*Geochelone elegans*), the Spanish pond turtle (*Mauremys leprosa*), and the Nile soft shell turtle (*Trionyx triunguis*)].

Comment [GM10]: This is a doubtful argument, because the sediments that contain the coprolites were deposited in fluvial or lacustrine environments. Except for tortoises, most turtles dwell in aquatic habitats. Very few snakes are aquatic, and the excrements from extant snakes cited in this report all come from terrestrial forms. Tortoises and snakes are poor analogs for coprolites that are preserved in fluvial or lacustrine sediments, unless the coprolites are assumed to have been transported. I can see no reason to exclude creatures such as crocodiles or large fish as possible coprolite producers, or mammals equivalent to modern beaver, otter, or muskrat..

Table 3. List of taxa of observed fish excrements. Fossil representatives taken from Hunt & Lucas, 2007.

modern fish	**fossil representative**
Aspius sp.	*Aspius* sp., *Aspius laubei*, *Barbus* sp., *Barbus bohemicus*
Leuciscus sp.	*Palaeoleuciscus* sp., *Palaeoleuciscus chartacerus*

Tinca sp.	*Palaeotinca* sp., *Palaeotinca egeriana*, *Palaeotinca obtruncata*

Table 4. List of taxa of observed amphibian excrements. Fossil representatives taken from Hunt & Lucas, 2007.

modern amphibians	**fossil representative**
Andrias sp.	*Andrias bohemicus, Andrias* cf. *scheuchzeri, Chelotriton* cf. *paradoxus*

Table 5. List of taxa of observed bird excrements. Fossil representatives taken from Hunt & Lucas, 2007.

modern birds	**fossil representative**
Phalacrocorax sp.	*Nectornis* sp., *Phalacrocorax littoraris*
Strigiformes indet.	*Prosybris antiqua*, *Mioglaux debellatrix*, *Intulula tinnipara*
Aquila sp.	*Polemaetus* sp.
*Accipiter*sp.	Accipitridae indet.

Table 6. List of taxa of observed mammals excrements. Fossil representatives taken from Hunt & Lucas, 2007.

modern mammals	**fossil representative**
Ursus sp.	*Ursavus elmensis, Ursavus isorei, Tomocyon* sp., *Hemicyon* cf. *stehlini*, *Amphicyon bohemicus*, *Amphicyon major*, *Megamphicyon giganteus*, *Cynelos schlosseri*
Rhinocerotidae indet.	*Mesaceratherium* aff. *paulhiacense*, *Prosantorhinus laubei*, *Protaceratherium minutum*

Cervus sp.	*Procervulus* cf. *praelucidus*
Equidae indet.	*Anchitherium aurelianense*

Results

"Coprolite" morphotypes

29 specimens of excrement-shaped ferruginous masseswere collected. Among these specimens two different shapes and sizes were identified. More specifically, morphotype 1 (M1) is represented by small (up to 40 mm long, see Table 7) sausage-shaped specimens with smooth or rough surface and flared lower part (Fig. 2A, B). Morphotype 2 (M2), in turn, is represented by large (up to 63 mm long) and more rounded to oval, massive specimens with rough surface (Fig. 2E-G). Rare specimens (Fig. 2F, G) included into M2, bear prominent pointed end covered by striate pattern (herein interpreted as a trace produced after closing anus, see Discussion below). Color of both morphotypes varies from pale orange, through greenish red, to burgundy-colored.

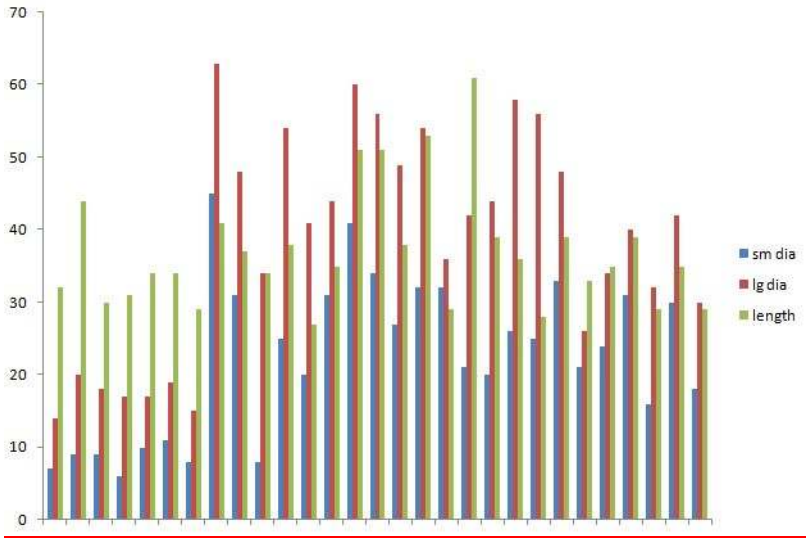

Figure 2 around here

Table 7. Summary for excrement-shaped ferruginous masses.

Comment [GM11]: The morphological characteristics are not well presented in this data table. I suggest that a bar graph would provide more clarity. I am attaching an Excel graph that I made using the data from figure 7. I am including it here as an example, not as an actual addition to the manuscript. The graph shows that the mophotype divisions are rather complex.

Length is a questionable parameter for establishing morphoptypes: the text describes M1 lengths as being up 40mm, but "M1" specimen 2 has a 43mm length. The descriptions of shape (e.g. "more rounded" are not quantifiable, making the morphotype designations rather subjective. Perhaps specimen mass (weight) is a useful parameter. Or volume, which could be measured by hydrostatic displacement.

Comment [GM12]: The morphotype division is an important observation, as is the scarcity of specimens. The situation is very different in the Miocene "coprolites" of the Wilkes Formation of Washington State. Thousands of specimens have been collected, and they are highly varied in size, ranging in length from tiny to very large, I believe this is also true of the Whitemud Formation in Saskatchewan, where a vast number of specimens have been collected from Late Cretaceous clay beds. Broughton (2017) divides the Whitemud specimens into two morphotypes based on shape, noting that lengths can vary from 1-2cm to more than 1m. In both deposits, size alone does not provide a basis for morphotype division.

One of the virtues of this manuscript is that it describes an occurrence of ferruginous "coprolites" that has distinctive differences from deposits like Wilkes Fm. and Whitemud Fm. It supports my belief that there is not a single geologic and paleoenvironmental model that explains all occurrences. It is a reason why this research has scientific importance.

specimen no.	morphotype	dimensions (diameter at its narrowest point*diameter at its widest point*lenght); all are given in mm	inferred producer
GIUS 10-3739/1	M1 (see Fig. 2B, C)	7*14*32	Testudinoidea
GIUS 10-3739/2	M1 (see Fig. 2A)	9*20*44	Testudinoidea
GIUS 10-3739/3	M1	9*18*30	Testudinoidea
GIUS 10-3739/4	M1	6*17*31	Testudinoidea
GIUS 10-3739/5	M1	10*17*34	Testudinoidea
GIUS 10-3739/6	M1	11*19*34	Testudinoidea
GIUS 10-3739/7	M1	8*15*29	Testudinoidea
GIUS 10-3739/8	M2 (see Fig. 2F)	45*63*41	Serpentes
GIUS 10-3739/9	M2 (see Fig. 2G)	31*48*37	Serpentes
GIUS 10-3739/10	M2 (see Fig. 2I, J)	8*34*34	Serpentes
GIUS 10-3739/11	M2 (see Fig. 2K)	25*54*38	Serpentes
GIUS 10-3739/12	M2 (see Fig. 2M)	20*41*27	Serpentes
GIUS 10-3739/13	M2	31*44*35	Serpentes
GIUS 10-3739/14	M2	41*60*51	Serpentes
GIUS 10-3739/15	M2	34*56*51	Serpentes
GIUS 10-3739/16	M2	27*49*38	Serpentes
GIUS 10-3739/17	M2	32*54*53	Serpentes
GIUS 10-3739/18	M2	32*36*29	Serpentes
GIUS 10-3739/19	M2	21*42*61	Serpentes
GIUS 10-3739/20	M2	20*44*39	Serpentes
GIUS 10-3739/21	M2	26*58*36	Serpentes
GIUS 10-3739/22	M2	25*56*28	Serpentes
GIUS 10-3739/23	M2	33*48*39	Serpentes

GIUS 10-3739/24	M2	21*26*33	Serpentes
GIUS 10-3739/25	M2	24*34*35	Serpentes
GIUS 10-3739/26	M2	31*40*39	Serpentes
GIUS 10-3739/27	M2	16*32*29	Serpentes
GIUS 10-3739/28	M2	30*42*35	Serpentes
GIUS 10-3739/29	M2	18*30*29	Serpentes

Thin sections made from specimens no. GIUS 10-3739/28, 29 are acronymed GIUS 10-3739/TS.

Optical microscopy, microtomographic and palaeontological studies

Comment [GM13]: The authors miss an important reference where the mineralogy of ferruginous "coprolites" is discusses in detail, including optical microscopy and SEM:

Yancey, T.E., Mustoe, G.E., Leopold, E.B., and Heizler, M.T. 2013. Mudflow disturbance in latest Miocene forests in Lewis County, Washington. Palaios, v. 28, p. 343-350.

The thin sections from two specimens representing two morphotypes were studied both under transmitted and reflected light optical microscopy. The sections from both morphotypes look very similar. They are dominated by darker matrix almost not translucent making transmitting light observations difficult. The mineral matrix seems to be rather homogenous. Within the matrix of M2-type more translucent elongated straight or curly structures (up to about few mm long and 10-99 µm thick; mean: 52 µm) are visible (Fig. 3). The structures sometimes form arcs or are twisted. In the reflected light, they seem to be areas of light reduction, while surrounding matrix is oxidized. The dark (rusty-colored, brown to almost black), poorly translucent coloring of a matrix suggests iron-rich mineral which form the matrix. Therefore both mineral matrix as well as thin elongated straight to curly structures were studied in-depth under SEM and Raman imaging (see below). No other distinguishable micro remains were noticed in thin sections. However, at the broken surfaces of some specimens of the first morphotype (M1) some tiny coalified debris were occasionally noticed (Fig. 2A, B).

Figure 3 around here

Microtomographical studies of selected specimen (GIUS 10-3739/23; Supplementary Movie 1) did not reveal any internal structures, which could have been eventually interpreted as undigested food remains.

Mineralogical, geochemical and structural analyses

XRD analyses of powdered fragments of two specimens from each morphotypes indicated that they both are composed of siderite with small admixture of geothite, and hematite (Fig.4).

Figure 4 around here

The more detailed data on microstructure and elemental composition were collected by utilizing SEM/EDS. We found that the matrix is composed of irregular forms organized in net-system structures (Fig. 5). These forms are bound by thin walls that often consist of several layers (Fig. 5G, H). The chemical analyses showed that the walls consist of iron oxides and the interioris likely filled with iron carbonate. Two types of matrix occurring in both morphotypes (M1 and M2) were distinguished. The first one includes smaller (up to 10 μm in diameter) forms with a broad wall of iron oxides and an empty inner part (Fig. 5A-F). Occasionally, larger forms with carbonate centers (up to 100 μm in diameter) can also be found in the vicinity of the large voids (Fig. 5G). Due to the presence of unfilled forms in the matrix, a distinct porosity pattern can be visible (Fig. 5A1-F1). In this matrix type, within specimen of M2-type straight or curly elongated structures, which were also observed under optical microscopy, can be found (Fig. 3, 5A-F). They can occur as thin (10-99 μm) lines with significantly limited porosity (Fig. 3, 5A-B1, C-F1). In the widest cross sections, some cellular structure is observed (Fig. 3H, 5A-B1), while in the narrowest cross sections (Fig. 5C-F1), characteristic scale-like pattern in observed (Fig. 3F, G, 5C-F1). The second type of matrix consists of larger (up to 30 μm in diameter) forms characterized by thinner walls (Fig. 5I, J). Their center is always filled with iron carbonate, so there is no distinct porosity, as well as no elongated structures to be found.

Figure 5 around here

To extend the observations and elemental analysis based on SEM, Raman spectra were collected. The data obtained from Raman spectroscopy allows to differentiate two iron oxides within the walls (Fig. 6A,B). The spectrum of the first one has bands at 1322, 662, 407, 296, and 227 cm^{-1} (Fig. 6A), which are characteristic for the hematite (Hanesch, 2009). The second mineral forms only very thin (<1 μm) layers in the hematite. The main bands of its spectrum are 684, 553, 397, 299, and 242 cm^{-1} (Fig. 5B), which allow identifying this mineral as goethite. The 1322 cm^{-1} band at the goethite spectrum originated from the admixture of the

353 hematite. The spectrum of the carbonate mineral contains bands connected to the typical
354 vibrations of the CO_3 group (Fig. 5C), and it can be recognized as siderite.
355
356 Figure 6 around here
357
358 The Raman spectroscopy was also used to investigate the thin elongated structures in
359 the matrix. There was no variation in the mineralogical composition of these forms in
360 comparison to the matrix. However, during experiments with the 532 nm laser (green), we
361 observed increased fluorescence in the area of the elongated structures with reduced porosity
362 (Fig. 7). This may indicate that although these structures are composed of the same minerals
363 as the matrix, their original chemical composition was different.
364
365 Figure 7 around here
366
367 ***Comparative actualistic studies***
368
369 For comparative purposes we investigated modern faeces (789 in total) produced by a number
370 of vertebrates, comprising all major groups (i.e., fish, amphibians, reptiles, birds, and
371 mammals) (for details see Tables 3-6). We compared our fossil specimens with excrements of
372 extant fish, amphibians, birds and mammals, but they differ in size and shape, and therefore
373 were not subject to further observations. We noticed, however, that our excrement-shaped
374 ferruginous masses ascribed to the morphotype 1 are very similar to sausage-shaped
375 excrements produced by two testudinid turtle taxa [i.e., the Mediterranean tortoise (*Testudo*
376 *hermanni*) and the steppe tortoise (*Testudo horsfieldii*)]. Their surfaces are mainly smooth and
377 rarely covered with cracks (e.g., Fig. 3C, D) ;the digested plant debris are sometimes visible
378 on their surfaces (Fig. 3C, D). We also compared these fossil excrements with excrements of
379 other extant turtles [another testudinid, i.e., the Indian star tortoise (*Geochelone elegans*), a
380 geoemydid, i.e., the Spanish pond turtle (*Mauremys leprosa*), and a trionychid, i.e., the Nile
381 softshell turtle (*Trionyx triunguis*)], but the feaces of the *Trionyx triunguis* differ in size and
382 shape. On the other hand, our excrement-shaped ferruginous masses ascribed to the
383 morphotype 2 are very similar to more or less rounded to oval, massive excrements produced
384 by three snake taxa [the king python (*Python regius*), the common boa (*Boa constrictor*), and
385 the king cobra (*Ophiophagus hannah*)]. Their surfaces are rough, and often contain some
386 remnants of etched hair and feathers (e.g., Fig. 3H, I). Moreover, the faeces of the Korean rat

snake (*Elaphe anomala*) are also similar to the fossil morphotype 1; however, they differ in size (they are smaller, cf. Fig. 3L). The excrement surfaces of the latter species are covered by some hairs. We also observed three excrements of the common European viper (*Vipera berus*). They are different in shape and size one from another, their surfaces are covered by etched hair (Fig. 3M).

Discussion

Although in the Biedrzychowice Fm there are numerous inorganic siliceous and siderite concretions (Kasiński et al., 2010; personal observations), they have a different external morphology (i.e., they do not reveal a characteristic excrement-like shape) and internal structure (i.e., they typically have a concentric zoning). On the one hand, results of our geochemical, mineralogical, petrographic and microtomographical analyses indicate that excrement-shaped masses from Poland mainly consist of siderite and iron oxide rather than phosphate, and rarely contain recognizable food residues, which may indicate abiotic origins of these structures. However, evidence in support of a fecal origin include: (i) the presence of two distinct morphotypes differing in size and shape, (ii) the limited quantity of specimens, (iii) the presence of rare fine striations on the surface of some specimens, and (iv) the presence of hair-like elongated structures or coalified inclusions.

Spencer (1993) argued that parallel striations in the pseudocoprolites from the Miocene of southwestern Washington State might have resulted from passage of the material over the grain of the wood. However, fine striations visible on the surface of two specimens from Poland are more reminiscent of marks left by the anal sphincter because they are not randomly distributed but are located in the pointed end of the specimens (Fig. 3F, G). Likewise, they differ from longitudinal parallel striations observed in the specimens ascribed to gut casts of giant terrestrial earthworms (Broughton, 2017).

Although mineralogy of the excrement-shaped masses from Poland is not indicative of coprolites, it might have been a result of diagenesis (Broughton et al., 1977, 1978; Broughton, 2017). Indeed, Seilacher et al. (2001) noted that similar excrement-shaped ferruginous masses from the Miocene of southwestern Washington State might have been alternated by secondary processes referred to as the 'roll-fronts' of oxidized groundwater (Goldhaberet, 1979; Harris & King, 1993), which dissolves calcite and phosphates bones and precipitates ferroan carbonates. The presence of numerous voids and lack of clay minerals within excrement-shaped ferruginous masses from Poland is consistent with this scenario. Furthermore, lack of

Comment [GM14]: A problem with the roll-front model is that it requires flow of groundwater through the sediment, but ferruginous "coprolites" commonly occur in clay beds that have low permeability. There are many studies of role-front deposits because f their economic importance for the origin of minerals like uranium or silver (e.g., Silver Reef, Utah). These deposits typically occur in ancient channel deposits that contain coarse clastic sediment with high permeability.
Roll front mineralization may involve replacement of organic matter, but this is problematic for ferruginous "coprolites" As an example in the Wilkes Formation of Washington, the "coprolites" occur in strata that contain large amounts of wood. The surrounding clay has so thoroughly protected the wood that it was not subject to decay or mineralization. It is hard to imagine a geochemical process where fecal or intestinal remains would become completely replaced by iron minerals while the adjacent wood remains unaltered.
The reference to Seilacher et al. hypothesis of roll-front mineralization perpetuates an unsubstantiated claim. There is a fundamental enigma regarding the origin of these ferruginous extrusions.
Paleontologists note the striking excremental form of these objects, but they rarely report detailed stratigraphic and taphonmic characteristics, or geochemical processes that could have produced the mineralization.

Comment [GM15]: Seilacher based his observations on some specimens that had been purchased at a mineral fair in Connecticut. He never visited the site, and had little if any knowledge of the geologic setting.
Broughton (2021) asserts that the iron mineralization was a result of microbial biofilms that resulted in precipitation of ferrihydrate/ goethite, and that siderite is a diagenetic alteration product, not a primary precipitate. I am not supporting this hypothesis, but it is a topic tha that deserves mention in the geologic overview:

Reference: Brougton, P.A. 2021. Ferruginous casts in kaolin beds: microbial ferrihydrate-goethite transformation as early stage taphonomy in lacustrine and riparian sediments: Lethaia. This is available online at DOI 10.111/let.12455

421 phosphates in the coprolites may be additionally explained by the fact they were produced by
422 predominantly herbivorous animals (Chin & Kirkland, 1998; Fiorelli et al., 2013; Bajdek et
423 al., 2016). Notably, within the morphotype 1 some tiny coalified debris were noted. The
424 morphotype 2, in turn, contains only some elongated thin structures. They are reminiscent of
425 hairs. Their mean size (52 μm) falls well within the range of the hair diameter (4-160 μm) of
426 extant animals (Mayer, 1952; Schneider & Buramuge, 2006; Kshirsagar et al., 2009).
427 Furthermore, their morphologies, i.e., some cellular structure observed in the widest
428 longitudinal sections (Fig. 2H, 5A-B1) and characteristic scale-like pattern observed in the
429 narrowest longitudinal sections (Fig. 5C-F1), are similar to the inner cellular structure of
430 medulla (wide medulla lattice type *sensu* Schneider & Buramuge, 2006, fig. 2) and outer
431 scale-like layers (regular wave pattern *sensu* Schneider & Buramuge, 2006, fig. 4) of the
432 extant and fossil hairs (e.g., fig. 2b, d in Meng & Wyss, 1997; figs. 3-9 in Taru & Backwell,
433 2013). If these excrement-shaped masses indeed represent true coprolites, this may indicate
434 that the digestive system of the producer was highly efficient, i.e., it dissolved and absorbed
435 everything but the prey's hair, which were excreted along with faeces.
436 The presence of two distinct morphotypes, differing in size and shape suggests that
437 they might have been expelled from the two different producers. Indeed, comparative
438 actualistic study of Recent vertebrate faeces showsoverall resemblance of the first
439 morphotype (sausage-shaped with rare coalified debris) to excrements of turtles of the group
440 Testudinoidea. This is further supported by the fact that a testudinoid shell fragment was also
441 recovered in the Turów mine, that being also the sole so far found vertebrate fossil from that
442 locality. Within Testudinoidea, tortoises (Testudinidae) are terrestrial, while the other two
443 groups that inhabited and still inhabit Europe (Emydidae and Geoemydidae) are aquatic or at
444 least semiaquatic – as such, it seems most probable that the Polish excrements were produced
445 by a terrestrial testudinid. Testudinoids have been already known in the Polish fossil record,
446 however, their earliest occurrence so far was documented in younger strata, i.e., the middle
447 Miocene (MN 6) locality of Nowa Wieś Królewska near Opole (Wegner, 1913). That being
448 said, the single shell fragment from Turów represents the earliest testudinoid occurrence from
449 Poland. Nevertheless, testudinoids are already known from early Miocene localities in the
450 vicinity area of northwestern Czech Republic and southeastern Germany (see Table 2). Other
451 turtle lineages, such as chelydrids and trionychids are found in the same vicinity area – among
452 them, the former group is also found in the middle Miocene of Poland (Joyce, 2016), while
453 the latter has never been so far identified from that country (Georgalis & Joyce, 2017). On the
454 other hand, the second coprolite morphotype from the Turów mine (morphotype M2)

approaches more in its overall morphology the excrements of extant species of snakes. More particularly, there is a high degree of resemblance with large snake species of *Constrictores* (*sensu* Georgalis & Smith, 2020; i.e., booids and pythonoids). Nevertheless, an overall resemblance of M2 is also apparent with excrements of large caenophidians, such as the elapid *Ophiophagus* and the colubrid *Elaphe*, while, conversely, smaller caenophidian taxa, such as the viperid *Vipera berus* and the colubrid *Pantherophis*, seem to produce very differently-shaped excrements, which are relatively thin and tightly curled. As such, it is probable that the excrement shape within snake taxa could be somehow size-constrained and does not have a clear taxonomic/phylogenetic value as per its exact affinities. In addition, lizards can be excluded as possible candidate producers for morphotype M2, as excrements of extant large lizard taxa, such as anguids and varanids (which have also an abundant fossil record in the early Miocene of Central Europe) were much differently-shaped. This being said, on the absence of any accompanying skeletal fossil specimen from Turów, we can only infer that the coprolite morphotype M2 was produced by large, but still indeterminate, snakes. Afterall, large snakes were rather abundant in the Burdigalian of Central Europe, being also rather diverse, pertaining to a number of different lineages (Booidea, Pythonoidea, Colubridae, Natricidae, Elapidae, Viperidae) (see Table 2). It is noteworthy that snakes are known to maintain of a very acidic pH during digestion and dissolve and absorb everything but the prey's hair (or feathers) and claws, which are excreted along with waste (Pope et al., 2007; Nørgaard et al., 2016).

Conclusions

The excrement-shaped ferruginous massesand the turtle shell fragment from the early Miocene of Turów mine in Poland have been described for the first time. Although different hypotheses were invoked to explain the origins of similar excrement-shaped ferruginous masses, we favour the hypothesis that at least the specimens from Poland represent true coprolites. Evidence in support of a fecal origin of these structures include: (i) the presence of two distinct morphotypes differing in size and shape, (ii) the limited quantity of specimens, (iii) the presence of hair-like structures or coalified inclusions and (iv) the presence of rare fine striations on the surface. If zoological in origin, the first morphotype (sausage-shaped with rare coalified debris) might have been produced by tortoises (Testudinoidea), whereas the second morphotype (rounded to oval-shaped with hair-like structures) might represent fossilfaeces of snakes (Serpentes).

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Captions to figures and movie:

Fig. 1. A. Map of central Europe with mentioned in the text areas marked as red rectangles. **B.** Geology of Zittau Basin. **C.** Synthetic lithostratigraphic section of Paleogene and Neogene sediments of the Polish part of the Zittau Basin (slightly modified after Paszcza, 2021).

Fig. 2. Miocene turtle and snake coprolites from the Turów lignite mine, Poland **(A, B, E-G)**, compared with modern turtle and snake excrements **(C, D, H-M)** and fossil remain from the Turów lignite mine, Poland **(N)**. Scale bar equals 10 mm. **A, B.** coprolites, morphotype M1. **C, D.** modern excrements of *Testudo horsfieldii* (C), and *Testudo hermanni* (D). **E-G.** coprolites, morphotype M2. **H, I.** modern excrements of *Python regius*. **J.** modern excrement of *Boa constrictor*. **K.** modern excrement of *Ophiophagus hannah*. **L.** modern excrement of *Elaphe anomala.* **M.** modern excrement of *Vipera berus*. **N**. Shell fragment of Testudinoidea indet. from the Turów lignite mine, Poland **(N)**.
Red arrows in A and B = coalified inclusions, yellow arrows in F and G = fine striations.

Fig. 3. Hair-like structure identified in coprolites (morphotype 2). A-C. Optical microscopy. D-H. SEM images. F, G. Magnification of scale-like pattern. H. Magnification of internal hair-like cellular structure.

Fig. 4. XRD diffractograms for two coprolite morphotypes. Green line – morphotype 1, red line – morphotype 2.

Fig. 5. (A-F) BSE image of the coprolite matrix with preserved structures. The red frame indicates the area of the Raman image from Fig. 5. **(A1-F1)** topographic pictures of the area from the A-F images. **(G,H)** BSE image of multi-layered iron oxides form with siderite center. **(I,J)** BSE image of the non-porous type of coprolite matrix. Mineral abbreviations: Gth - goethite, Hem - hematite, Sd - siderite.

Fig. 6. Raman spectrum of **(A)** hematite, **(B)** goethite, **(C)** siderite from coprolite matrix.

Fig. 7. The difference in the fluorescence level in the Raman spectrum of hematitefrom the structures. **(A)** Reflected light image of the elongated structure. **(B)** Cluster analysis of the structure and matrix Raman mapping. **(C)** Raman spectrum of hematite from structure area (1) and coprolite matrix (2).

Supplementary Movie 1. Tomographic animation of Miocene coprolite from Turów.