Comparative actualistic study hints at origins of alleged Miocene “coprolites” of Poland (#70520)

First submission

Guidance from your Editor

Please submit by **24 Feb 2022** for the benefit of the authors (and your $200 publishing discount) .

✓ **Structure and Criteria**
Please read the 'Structure and Criteria' page for general guidance.

Author notes
Have you read the author notes on the guidance page?

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files Download and review all files from the materials page.	7 Figure file(s) 1 Video file(s)

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- ✓ Clear, unambiguous, professional English language used throughout.
- ✓ Intro & background to show context. Literature well referenced & relevant.
- ✓ Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- ✓ Figures are relevant, high quality, well labelled & described.
- ✓ Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- ✓ Original primary research within Scope of the journal.
- ✓ Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- ✓ Rigorous investigation performed to a high technical & ethical standard.
- ✓ Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- ℹ Impact and novelty not assessed. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- ✓ All underlying data have been provided; they are robust, statistically sound, & controlled.
- ✓ Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	***Example***
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Comparative actualistic study hints at origins of alleged Miocene “coprolites” of Poland

Tomasz Brachaniec [1] , **Dorota Środek** [1] , **Dawid Surmik** [1] , **Niedźwiedzki Robert** [2] , **Georgios Georgalis L.** [3] , **Bartosz Płachno J.** [4] , **Piotr Duda** [1] , **Alexander Lukeneder** [5] , **Przemysław Gorzelak** [6] , **Mariusz Salamon A.** Corresp. [1]

[1] University of Silesia, Sosnowiec, Poland
[2] Wrocław University, Wrocław, Poland
[3] University of Zurich, Zurich, Switzerland
[4] Jagiellonian University Cracow, Cracow, Poland
[5] Natural History Museum, Vienna, Austria
[6] Institute of Paleobiology, Warszawa, Poland

Corresponding Author: Mariusz Salamon A.
Email address: paleo.crinoids@poczta.fm

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 report excrement-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.

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

Tomasz Brachaniec[1], Dorota Środek[1], Dawid Surmik[1], Robert Niedźwiedzki[2], Georgios L. Georgalis[3], Bartosz J. Płachno[4], Piotr Duda[5], Alexander Lukeneder[6], Przemysław Gorzelak[7], Mariusz A. Salamon[1*]

[1]University of Silesia in Katowice, Faculty of Natural Sciences, Będzińska 60, 41-200 Sosnowiec, Poland, paleo.crinoids@poczta.fm (MAS - corresponding author)

[2] Institute of Geological Sciences, Wrocław University, Borna 9, 50-204 Wrocław, Poland

[3]Palaeontological Institute and Museum, University of Zurich, Karl Schmid-Strasse 4, 8006 Zurich, Switzerland

[4]Jagiellonian University in Kraków, Faculty of Biology, Institute of Botany, Gronostajowa Street 9, 30-387 Cracow, Poland

[5]University of Silesia in Katowice, Faculty of Science and Technology, Będzińska Street 39, 41-200 Sosnowiec, Poland

[6]Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria

[7]Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warszawa, Poland

Abstract

Excrement-shaped siderite masseshave 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 tetrapodsare 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, sediment intrusion into hollow logs, expulsion of sediment in response to gravity, extrusion of sideriterelated to methanogenesis).

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).

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 massesand 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).

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

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		'*Diplocynodon*' sp.

	(Czech Republic)		
	Markvartice (Czech Republic)	*Chelotriton laticeps* *Palaeobatrachus diluvianus* *Palaeobatrachus luedeckei* *Palaeobatrachus* sp.	
	Dětaň (Czech Republic)	Salamandridae indet. Palaeobatrachidae indet. Pelobatidae indet. Discoglossidae indet.	Lacertidae indet. Anguidae indet. Testudinidae 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*)].

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.

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

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 microremains 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 hematite. The spectrum of the carbonate mineral contains bands connected to the typical vibrations of the CO_3 group (Fig. 5C), and it can be recognized as siderite.

Figure 6 around here

The Raman spectroscopy was also used to investigate the thin elongated structures in the matrix. There was no variation in the mineralogical composition of these forms in comparison to the matrix. However, during experiments with the 532 nm laser (green), we observed increased fluorescence in the area of the elongated structures with reduced porosity (Fig. 7). This may indicate that although these structures are composed of the same minerals as the matrix, their original chemical composition was different.

Figure 7 around here

Comparative actualistic studies

For comparative purposes we investigated modern faeces (789 in total) produced by a number of vertebrates, comprising all major groups (i.e., fish, amphibians, reptiles, birds, and mammals) (for details see Tables 3-6). We compared our fossil specimens with excrements of extant fish, amphibians, birds and mammals, but they differ in size and shape, and therefore were not subject to further observations. We noticed, however, that our excrement-shaped ferruginous masses ascribed to the morphotype 1 are very similar to sausage-shaped excrements produced by two testudinid turtle taxa [i.e., the Mediterranean tortoise (*Testudo hermanni*) and the steppe tortoise (*Testudo horsfieldii*)]. Their surfaces are mainly smooth and rarely covered with cracks (e.g., Fig. 3C, D);the digested plant debris are sometimes visible on their surfaces (Fig. 3C, D). We also compared these fossil excrements with excrements of other extant turtles [another testudinid, i.e., the Indian star tortoise (*Geochelone elegans*), a geoemydid, i.e., the Spanish pond turtle (*Mauremys leprosa*), and a trionychid, i.e., the Nile softshell turtle (*Trionyx triunguis*)], but the feaces of the *Trionyx triunguis* differ in size and shape. On the other hand, our excrement-shaped ferruginous masses ascribed to the morphotype 2 are very similar to more or less rounded to oval, massive excrements produced by three snake taxa [the king python (*Python regius*), the common boa (*Boa constrictor*), and the king cobra (*Ophiophagus hannah*)]. Their surfaces are rough, and often contain some 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 phosphates in the coprolites may be additionally explained by the fact they were produced by predominantly herbivorous animals (Chin & Kirkland, 1998; Fiorelli et al., 2013; Bajdek et al., 2016). Notably, within the morphotype 1 some tiny coalified debris were noted. The morphotype 2, in turn, contains only some elongated thin structures. They are reminiscent of hairs. Their mean size (52 µm) falls well within the range of the hair diameter (4-160 µm) of extant animals (Mayer, 1952; Schneider & Buramuge, 2006; Kshirsagar et al., 2009). Furthermore, their morphologies, i.e., some cellular structure observed in the widest longitudinal sections (Fig. 2H, 5A-B1) and characteristic scale-like pattern observed in the narrowest longitudinal sections (Fig. 5C-F1), are similar to the inner cellular structure of medulla (wide medulla lattice type *sensu* Schneider & Buramuge, 2006, fig. 2) and outer scale-like layers (regular wave pattern *sensu* Schneider &

Buramuge, 2006, fig. 4) of the extant and fossil hairs (e.g., fig. 2b, d in Meng & Wyss, 1997; figs. 3-9 in Taru & Backwell, 2013). If these excrement-shaped masses indeed represent true coprolites, this may indicate that the digestive system of the producer was highly efficient, i.e., it dissolved and absorbed everything but the prey's hair, which were excreted along with faeces.

The presence of two distinct morphotypes, differing in size and shape suggests that they might have been expelled from the two different producers. Indeed, comparative actualistic study of Recent vertebrate faeces showsoverall resemblance of the first morphotype (sausage-shaped with rare coalified debris) to excrements of turtles of the group Testudinoidea. This is further supported by the fact that a testudinoid shell fragment was also recovered in the Turów mine, that being also the sole so far found vertebrate fossil from that locality. Within Testudinoidea, tortoises (Testudinidae) are terrestrial, while the other two groups that inhabited and still inhabit Europe (Emydidae and Geoemydidae) are aquatic or at least semiaquatic – as such, it seems most probable that the Polish excrements were produced by a terrestrial testudinid. Testudinoids have been already known in the Polish fossil record, however, their earliest occurrence so far was documented in younger strata, i.e., the middle Miocene (MN 6) locality of Nowa Wieś Królewska near Opole (Wegner, 1913). That being said, the single shell fragment from Turów represents the earliest testudinoid occurrence from Poland. Nevertheless, testudinoids are already known from early Miocene localities in the vicinity area of northwestern Czech Republic and southeastern Germany (see Table 2). Other turtle lineages, such as chelydrids and trionychids are found in the same vicinity area – among them, the former group is also found in the middle Miocene of Poland (Joyce, 2016), while the latter has never been so far identified from that country (Georgalis & Joyce, 2017). On the 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).

Acknowledgements

We are particularly grateful to Marek Mitrenga, Director of the Silesian Zoological Garden, for making it possible for us to observe the faeces of modern reptiles. Andrzej Malec and Adriana Strzelczyk from the Silesian Zoological Garden provided help, logistic support and information on the mode of life and diet of reptiles kept in the Silesian Zoological Garden. We would also like to thank the dozens of breeders from Poland and the Czech Republic for acquiring modern research material. Our thanks are also due to the management of the Turów Brown Coal Mine for granting permission to enter the plant, and in particular to Ewa Dąbrowska, who supported us with advice and provided all logistical assistance during the field works. Eligiusz Szelęg is acknowledged for providing an access to Olympus BX51 polarizing microscope. This research Project is partially supported by the National Science Centre, Poland (www.ncn.gov.pl), Grant No. 2019/32/C/NZ4/00150. GLG acknowledges funding from Forschungskredit of the University of Zurich, Grant no. [FK-20-110].

References

Amstutz G. 1958. Coprolites: A review of the literature and a study of specimens from southern Washington. *Journal of Sedimentary Petrology* **28**:498–508.

Bajdek P, Qvarnström M, Owocki K, Sulej T, Sennikov AG, Golubev VK, Niedźwiedzki G. 2016. Microbiota and food residues including possible evidence of pre-mammalian hair in Upper Permian coprolites from Russia. *Lethaia* **49**:455–477.

Bellon H, Bůžek C, Gaudant J, Kvaček Z, Walther H. 1998. The České Středohoří magmatic complex in Northern Bohemia 40K-40Ar ages for volcanism andbiostratigraphy of the Cenozoic freshwater formations. *Newsletters on Stratigraphy* **36**:77–103.

Böhme M. 1996. *Revision der oligozänen und unter-miozänen Vertreter der Gattung Palaeoleuciscus (Teleostei, Cyprinidae) Mitteleuropas*. University Leipzig.

Böhme M. 1998. *Archaeotriton basalticus* (v. Meyer, 1859) (Urodela, Salamandridae) aus dem Unteroligozänvon Hammerunterwiesenthal (Freistaat Sachsen). *Abhandlungen des Staatlichen Museums für Mineralogieund Geologie zu Dresden* **43/44**:265–280.

Böhme M. 2007. Revision of the cyprinids from the Early Oligocene of the České Středohoří Mountains, and the phylogenetic relations-hips of Protothymallus Laube 1901 (Teleostei, Cyprinidae, Gobioninae). *Acta Musei Nationalis Pragae, Ser. B, Hist. Nat*. **63**:175–194.

Broughton PL. 2017. Enigmatic origin of massive Late Cretaceous-to-Neogene coprolite-like deposits in North America: a novel palaeobiological alternative to inorganic morphogenesis. *Lethaia* **50**:194–216.

Broughton PL, Simpson F., Whitaker SH. 1977. Late Cretaceous coprolites from southern Saskatchewan: comments on excretion, plasticity and ichnological nomenclature. *Bulletin of Canadian Petroleum Geology* **25**:1097–1099.

Broughton PL, Simpson F., Whitaker SH. 1978. Late Cretaceous coprolites from western Canada. *Palaeontology* **21**:443–453.

Čerňanský A. 2010a. A revision of chamaeleonids from the Lower Miocene of the Czech Republic with description of a new species of *Chamaeleo* (Squamata, Chamaeleonidae). *Geobios* **43**:605–613.

Čerňanský A. 2010b. Earliest world record of green lizards (Lacertilia, Lacertidae) from the Lower Miocene of Central Europe. *Biologia* **65**:737–741.

Čerňanský A. 2012. The oldest known European Neogene girdled lizard fauna (Squamata, Cordylidae), with comments on Early Miocene immigration of African taxa. *Geodiversitas* **34**:837–848.

Čerňanský A, Joniak P. 2009. Nové nálezy jašteríc (Sauria, Lacertidae) z neogénnych sedimentov Slovenskaa Českej republiky. *Acta Geologica Slovaca* **1**:57–64.

Čerňanský A, Bauer AM. 2010. *Euleptes gallica* Müller (Squamata: Gekkota: Sphaerodactylidae) from the Lower Miocene of North-West Bohemia, Czech Republic. *Folia Zoologica* **59**:323–328.

Čerňanský A, Augé M. 2012. Additions to the lizard fauna (Squamata: Lacertilia) of the Upper Oligocene (MP 28) of Herrlingen 8, Southern Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **264/1**:11–19.

Čerňanský A, Augé M. 2013. New species of the genus *Plesiolacerta* (Squamata: Lacertidae) from the upper Oligocene (MP 28) of southern Germany and a revision ofthe type species *Plesiolacerta lydekkeri*. *Palaeontology* **56**:79–94.

Čerňanský A, Rage J-C, Klembara J. 2015. The Early Miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe. *Journal of Systematic Palaeontology* **13**:97–128.

Čerňanský A, Klembara J, Müller J. 2016. The new rare record of the late Oligocene lizardsand amphisbaenians from Germany and its impacton our knowledge of the European terminal Palaeogene. *Palaeobiodiversity and Palaeoenvironments* **96**:559–587.

Chin K, Kirkland JI. 1998. Probable herbivore coprolites from the Upper Jurassic Mygatt-Moore Quarry, Western Colorado. *Modern Geology* **23**:249–275.

Chroust M, Mazuch M, Luján ÀH. 2019. New material from the Eocene–Oligocene transition of the NW Bohemia (Czech Republic): an updated fossil record in Central Europe during the Grande Coupure. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **293**:73–82.

Chroust M, Mazuch M, Ivanov M, Ekrt B, Luján ÀH. 2021. First remains of *Diplocynodon* cf. *ratelii* fromthe early Miocene sites of Ahníkov (Most Basin, Czech Republic). *Bulletin of Geosciences* **96**:123–138.

Dake HC. 1939. *Northwest gem trails: Portland, Oregon*. Mineralogist Publishing Company.

Dake HC. 1960. Washington coprolites again. *Mineralogist* **28**:2–6.

Danner WR. 1968. Origin of the siderite coprolite-like bodies of the Wilkes Formation, late Miocene, of southwestern Washington. *Canadian Mineralogist* **9**:571.

Danner WR. 1994. *The pseudocoprolites of Salmon Creek, Washington*. University of British Columbia Department of Geological Sciences Report.

Danner WR. 1997. *The pseudocoprolites of Salmon Creek, Washington*. British Columbia Paleontological Symposium.

Dentzien-Dias P, Carrillo-Briceño JD, Francischini H, Sánchez R. 2018. Paleoecological and taphonomical aspects of the Late Miocene vertebrate coprolites (Urumaco Formation) of Venezuela. *Palaeogeography, Palaeoclimatology, Palaeoecology* **490**:590–603.

Durska E. 2008. A 90 m-thick coal seam In the Lubstów lignite deposit (Central Poland) palynological analysis and sedimentary environment. *Geological Quarterly* **52**:281–290.

Dvořák Z, Mach K, Prokop J, Knor S. 2010. *Třetihorni fauna severočeské hnědouhelné pánve*. Nakladatelství Granit.

Farlow OJ, Chin K, Argast A, Poppy S. 2020. Coprolites from the Pipe Creek Sinkhole (Late Neogene, Grant Country, Indiana, U.S.A.). *Journal of Vertebrate Paleontology* **30**:959–969.

Fejfar O, Kaiser T. 2005. Insect bone-modification and paleoecology of Oligocene mammal-bearing sites in the Doupov Mountains, Northern Bohemia. *Palaeontologia Electronica* **8**:1–11.

Fiorelli LE, Ezcurra MD, Hechenleitner EM, Argañaraz E, Taborda JRA, Trotteyn MJ, Belén von Baczko M, Desojo JB. 2013. The oldest known communal latrines prove evidence of gregarism in Triassic megaherbivores. *Scientific Reports* **3**:3348.

Gaudant J. 1996. Rectifications de nomenclature relatives à l'ichthyofaune oligo-miocène dulcaquicoles de Bohême. *Journal of the Czech Geological Society* **41**:91–96.

Gaudant J. 1997. Cinq nouveaux gisements de Pelobatidae (Amphibiens anoures) dans l'Oligocène d'Europe centrale. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1997**:434–446.

Georgalis GL, Joyce WG. 2017. A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. *Bulletin of the Peabody Museum of Natural History* **58**:115–208.

Georgalis GL, Smith KT. 2020. Constrictores Oppel, 1811 – the available name for the taxonomic group uniting boas and pythons. *Vertebrate Zoology* **70**:291–304.

Godfrey JS, Smith BJ. 2010. Shark-bitten vertebrate coprolites from the Miocene of Maryland. *Naturwissenschaften* **97**:461–467.

Goldhaberet MG, Reynolds LR, Rye OR. 1979. *Relationship of modern groundwater chemistry to the origin and reduction of south Texas roll-front uranium deposits*. U.S. Geological Survey Professional Paper.

Hanesch M. 2009. Raman spectroscopy of iron oxides and (oxy) hydroxides at low laser power and possible applications in environmental magnetic studies. *Geophysical Journal International* **177**:941–948.

Hardie JK. 1994. Dolomite and siliciclastic dikes and sills in marginal-marine Cretaceous coals of central Utah. *U.S. Geological Survey Bulletin* **2087**:1–19.

Harris R, King KJ. 1993. Geological classification and origin of radioactive mineralization in Wyoming. In: Snoke AW, Steidmann JR, Roberts SM, eds. *Geology of Wyoming*. Geological Survey of Wyoming Memoir. 898-916.

Hunt AP, Lucas SG. 2007. Cenozoic vertebrate trace fossils of North America: ichnofaunas, ichnofacies and biochronology. *New Mexico Museum of Natural History and Science Bulletin* **42**:17–41.

Hunt AP, Lucas SG. 2012. Classification of vertebrate coprolites and related trace fossils. *New Mexico Museum of Natural History and Science Bulletin* **57**:137–146.

Hunt AP, Lucas SG. 2021. The ichnology of vertebrate consumption: dentalites, gastroliths and bromalites. *New Mexico Museum of Natural History and Science Bulletin* **87**:1–216.

Hunt AP, Chin K, Lockley, M. 1994. The palaeobiology of vertebrate coprolites. In: Donovan S, ed. *The palaeobiology of trace fossils*. John Wiley and Sons: London. 221–240.

Hunt AP, Lucas SG, Spielmann JA, 2012. The bromalite collection at the National Museum of Natural History (Smithsonian Institution), with descriptions of new ichnotaxa and notes on other significant coprolite collections. *New Mexico Museum of Natural History and Science Bulletin* **57**:105–114.

Ivanov M. 2002. The oldest known Miocene snake fauna from Central Europe: Merkur-North locality, Czech Republic. *Acta Palaeontologica Polonica* **47**:513–534.

Jęczmyk M, Sztromwasser E. 1998. Kominowe syderytowe dajki karbonatytowe w bazaltoidach Kopalni Węgla Brunatnego Turów (Sudety). *Przegląd Geologiczny* **46**: 87–94.

Joyce WG. 2016. A review of the fossil record of turtles of the clade *Pan-Chelydridae*. *Bulletin of the Peabody Museum of Natural History* **57**:21–56.

Karl HV. 2007. The fossil reptiles (Reptilia: Chelonii, Crocodylia) from the marine early Oligocene of the Weisselster Basin (Central Germany: Saxonia). *Studia Geologica Salmanticensia* **43**:25–66.

Kasiński JR. 2000. *Atlas geologiczny trzeciorzędowej asocjacji brunatnowęglowej w polskiej części Niecki Żytawskiej. Skala 1:50 000.* PIG.

Kasiński JR, Wiśniewski J. 2003. Stanowisko 5. Formacja biedrzychowska. In: Ciężkowski A, Wojewoda J, Żelaźniewicz A, eds. *Sudety Zachodnie od wendu do czwartorzędu.* WIND: Wrocław. 31–33.

Kasiński JR, Badura J, Przybylski B. 2003. Cenozoic depressions at the northwestern Sudetic Foreland. In: Ciężkowski A, Wojewoda J, Żelaźniewicz A, eds. *Sudety Zachodnie od wendu do czwartorzędu.* WIND: Wrocław. 183–196.

Kasiński J.R, Badura J, Pańczyk M, Pécskay Z, Saternus A, Słodkowska B, Urbański P. 2015. Osady paleogeńskie w polskiej części niecki żytawskiej – nowe światło na problem wieku zapadliska tektonicznego. *Biuletyn Państwowego Instytutu Geologicznego* **461**:295–324.

Kasiński JR, Piwocki M, Swadowska E, Ziembińska-Tworzydło M. 2010. Lignite of the Polish Lowlands Miocene: Characteristics on a base of selected profiles. *Biuletyn Państwowego Instytutu Geologicznego* **439**:99–154.

Klembara J. 1979. Neue Funde der Gattungen *Ophisaurus* und *Anguis* (Squamata, Reptilia) aus dem Untermiozan Westbohmens (CSSR). *Vestnık Ustrednıho ustavu geologickeho* **54**:163–169.

Klembara J. 1981. Beitrag zur Kenntnis der Subfamilie Anguinae (Reptilia, Anguidae). *Acta Universitatis Carolinae, Geologica* **2**:121–168.

Klembara J. 2008. A new anguimorph lizard from the Lower Miocene of North-West Bohemia, Czech Republic. *Palaeontology* **51**:81–94.

Klembara J. 2012. A new species of *Pseudopus* (Squamata, Anguidae) from the early Miocene of Northwest Bohemia (Czech Republic). *Journal of Vertebrate Paleontology* **32**:854–866.

Klembara, J. 2015. New finds of anguines (Squamata, Anguidae) from the Early Miocene of North-West Bohemia (Czech Republic). *Paläontologische Zeitschrift* **89**:171–195.

Klembara J, Rummel M. 2018. New material of *Ophisaurus*, *Anguis* and *Pseudopus* (Squamata, Anguidae, Anguinae) from the Miocene of the Czech Republic and Germany and systematic revision and palaeobiogeography of the Cenozoic Anguinae. *Geological Magazine* **155**:20–44.

Kshirsagar SV, Singh B, Fulari SP. 2009. Comparative study of human and animal hair in relation with diameter and medullary index. *Indian Journal of Forensic Medicine and Pathology* **2**:105–108.

Kvaček Z, Walther H. 2003. Reconstruction of vegetation and landscape development uring volcanic activity in the České Středohoří Mountains. *Geolines* **15**:60–64.

Laube GC. 1901. Synopsis der Wirbelthier fauna der Böhm. Braunkohlenformation. *Abhandlungen desdeutschen naturwissenschaftlich-medicinischen Verei-nes für Böhmen "Lotos"* **2**:107–186.

Love JD, Boyd DW. 1991. Pseudocoprolites in the Mowry Shale (Upper Cretaceous), northwest Wyoming. *University of Wyoming Contribution to Geology* **28**:139–144.

Major D. 1939. Origin of Washington „coprolites". *Mineralogist* **20**:387–389.

Marcinkowski B. 1985. Przejawy mineralizacji kruszcowej w kompleksie magmowo-metamorficznym okolic Bogatyni. *Kwartalnik Geologiczny* **29**:551–570.

Mayer WV. 1952. The hair of California mammals with keys to the dorsal guard hairs of California mammals. *American Midland Naturalist* **48**:480–512.

Meng J, Wyss AR. 1997. Multituberculate and other mammal hair recovered from Palaeogene excreta. *Nature* **385**:712–714.

Micklich N, Böhme M. 1997. Wolfsbarsch-Funde (Perciformes, Moronidae) aus den Süßwasser-Diato-miten von Kučlín (Böhmen) nebst Anmerkungen zur taxonomischen Stellung von *"Perca" lepidota* aus den Süßwasserkalken von Öhningen (Baden). *Paläontologische Zeitschrift* **71**:117–128.

Mikuláš R, Fejfar O, Ulrych J, Žigová A, Kadlecová E, Cajz VA. 2003. Study of the Dětaň locality (Oligocene, Doupovské hory Mts. Volcanic Complex, Czech Republic): collection of field data and starting points for interpretation. *Geolines* **15**:91–97.

Młynarski M, Roček Z. 1985. Chelonians (Reptilia, Testudines) from the Lower Miocene locality Dolnice (Bohemia, Czechoslovakia). *Časopis pro mineralogii a geologii* **30**: 397–408.

Mustoe EG. 2001. Enigmatic origin of ferruginous „coprolites": Evidence form the Miocene Wilkes Formation, southwestern Washington. *GSA Bulletin* **113**:673–681.

Nørgaard S, Andreassen K, Lind Malte C, Enok S, Wang T. 2016. Low cost of gastric acid secretion during digestion in ball pythons. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **194**:62–66.

Obrhelová N. 1971. Über einen Serranid (Pisces) ausdem nordböhmischen Süßwassertertiär. *Časopis promineralogii a geologii* **16**:371–387.

Obrhelová N, Obrhel J. 1987. Paläoichthyologie und Paläoökologie des kontinentalen Tertiärs und Quartärsin der ČSSR. *Zeitschrift für geologische Wissenschaften* **15**:709–731.

Paszcza K. 2021. Nowe znaleziska polskich tektytów z obszaru niecki żytawskiej. *Przegląd Geologiczny* **69**:244–247.

Pesquero DM, Salesa JM, Espílez E, Mampel L, Siliceo G, Alcalá L. 2011. An exceptionally rich hyaena coprolites concentration in the Late Miocene mammal fossil site of La Roma 2 (Terual, Spain): Taphonomical and palaeoenvironmental inferences. *Palaeogeography, Palaeoclimatology, Palaeoecology* **311**:30–37.

Pesquero DM, Souza-Egipsy V, Alcalá L, Ascaso C, Fernández-Jalvo Y. 2014. Calcium phosphate preservation of faecal bacterial negative moulds in hyaena coprolites. *Acta Palaeontologica Polonica* **59**:997–1005.

Piątkowska A, Kasiński J, Graniczny M. 2000. Analysis of integrated remote sensing and tectonic data in the Żytawa-Zgorzelec Depression (SW Poland). *Przegląd Geologiczny* **48**:991–999.

Pope R, Helmstetter C, Lignot JH, Secor S. 2007. Bone absorption through specialised intestinal cells in juvenile Burmese pythons. *Comparative Biochemistry and Physiology* **146A**:S174.

Reinach A von. 1900. Schildkrötenreste im Mainzer Tertiärbecken und in benachbarten ungefähr gleichaltrigen. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **28**:1–135.

Roberts AE. 1958. *Geology and coal resources of the Toledo-Castle Rock District, Cowlitz and Lewis Counties, Washington*. U.S. Geological Survey Bulletin.

Roček Z. 1984. Lizards (Reptilia, Sauria) from the lower Miocene locality Dolnice (Bohemia, Czechoslovakia). *Rozpravy Ceskoslovenské Akademie Ved, Rada Matematickych a prírodních Ved* **94**:3–69.

Sadowska A. 1995. Palynostratigraphy and paleoecology Neogene of the Sudetic Foreland. *Annales Societatis Geologorum Poloniae, Wydanie Specjalne* **33**:37–47.

Schneider MF, Buramuge VA. 2006. Atlas of the Microscopic Hair Structure of Southern African Shrews, Hadgehogs, Golden Moles and Elephant-shrews (Mammalia). *Bonner zoologische Beiträge* **54**, 103–172.

Seilacher A, Marshall C, Skinner WC, Tsuihiji T. 2001. A fresh look at sideritic “coprolites”. *Paleobiology* **27**:7–13.

Spencer PK, Tuttle FH. 1980. Coprolites or pseudo-coprolites? New evidence concerning the origin of Washington coprolites. *Geological Society of America* **12**:153.

Spencer PK. 1993. The „coprolites” that arent: The straight poop on specimens from the Miocene of southwestern Washington State, Ichnos. *An International Journal for Plant and Animal Traces* **2**:231–236.

Spencer PK. 1997. The method of multiple working hypotheses in undergraduate education with an example of its application and misapplication. *Journal of Geoscience Education* **45**:123–128.

Špinar ZV. 1972. *Tertiary frogs from Central Europe*. Academy of Science.

Szyndlar Z. 1991a. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. *Estudios Geológicos* **47**:103–126.

Szyndlar Z. 1991b. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. *Estudios Geológicos* **47**:237–266.

Szyndlar Z. 1994. Oligocene snakes of southern Germany. *Journal of Vertebrate Paleontology* **14**:24–37.

Szyndlar Z, Schleich H-H. 1993. Description of Miocene snakes from Petersbuch 2 with comments on the lower and middle Miocene ophidian faunas of southern Germany. *Stuttgarter Beiträge zur Naturkunde B* **192**:1–47.

Szyndlar Z, Rage J-C. 2003. *Non-erycine Booidea from the Oligocene and Miocene of Europe*. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences.

Taru P, Backwell L. 2013. Identification of fossil hairs in Parahyaena brunnea coprolites from Middle Pleistocene deposits at Gladysvale cave, South Africa. *Journal of Archaeological Science* **40**:3674–3685.

Tomassini LR, Montalvo IC, Bargo MS, Vizcaíno FS, Cuitiño IJ. 2019. Sparassodonta (Metatheria) coprolites from the early-mid Miocene (Santacrucian age) of Patagonia (Argentina) with evidence of exploitation by coprophagous insects. *Palaios* **34**:639–651.

Wegner RN. 1913. Tertiär und umgelagerte Kreide bei Oppeln (Oberschlesien). *Palaeontographica* **60**:3–4.

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.

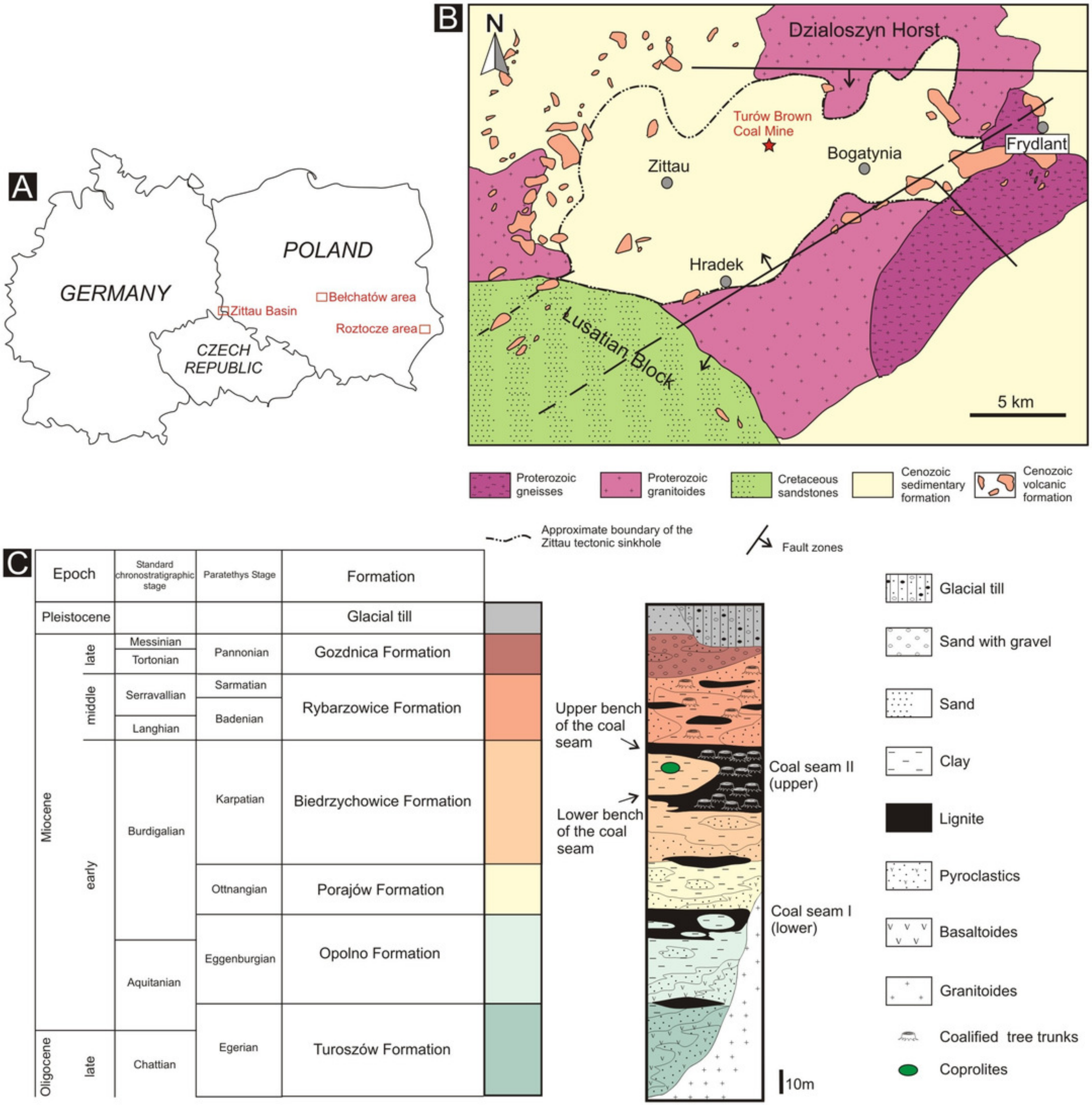
Fig. 7. The difference in the fluorescence level in the Raman spectrum of hematitefrom the structures. **(A)** Reflected light image of the elongated structure. **(B)** Cluster analysis of the structure and matrix Raman mapping. **(C)** Raman spectrum of hematite from structure area (1) and coprolite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

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

Figure 1

Figure 01

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).



Epoch		Standard chronostratigraphic stage	Paratethys Stage	Formation
Pleistocene				Glacial till
Miocene	late	Messinian	Pannonian	Gozdnica Formation
		Tortonian		
	middle	Serravallian	Sarmatian	Rybarzowice Formation
		Langhian	Badenian	
	early	Burdigalian	Karpatian	Biedrzychowice Formation
			Ottnangian	Porajów Formation
		Aquitanian	Eggenburgian	Opolno Formation
Oligocene	late	Chattian	Egerian	Turoszów Formation

Figure 2

Figure 02

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.

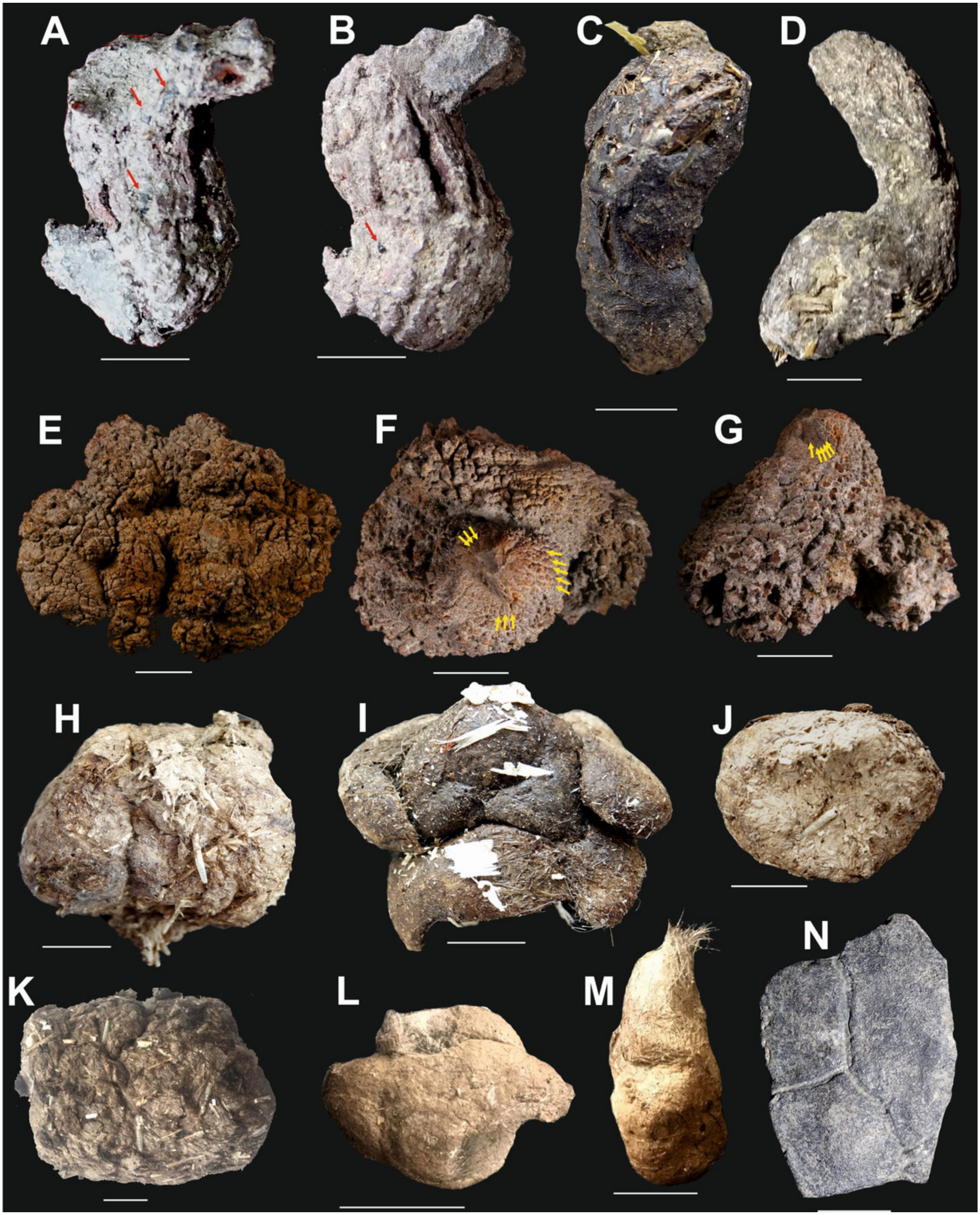

A
B
C
D
E
F
G
H
I
J
K
L
M
N

Figure 3

Figure_03

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.

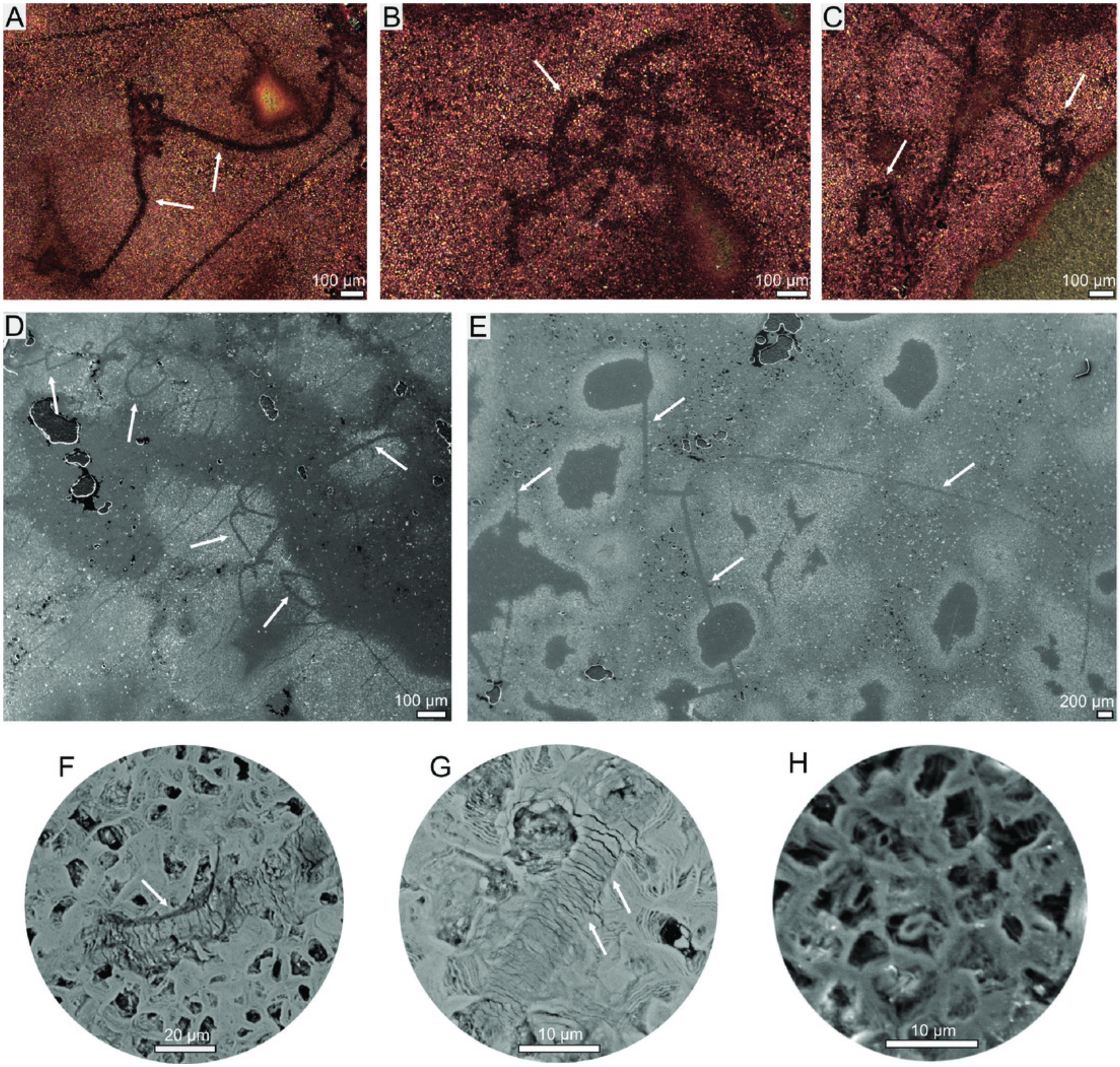

A
100 µm
B
100 µm
C
100 µm
D
100 µm
E
200 µm
F
20 µm
G
10 µm
H
10 µm

Figure 4

Figure_04

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

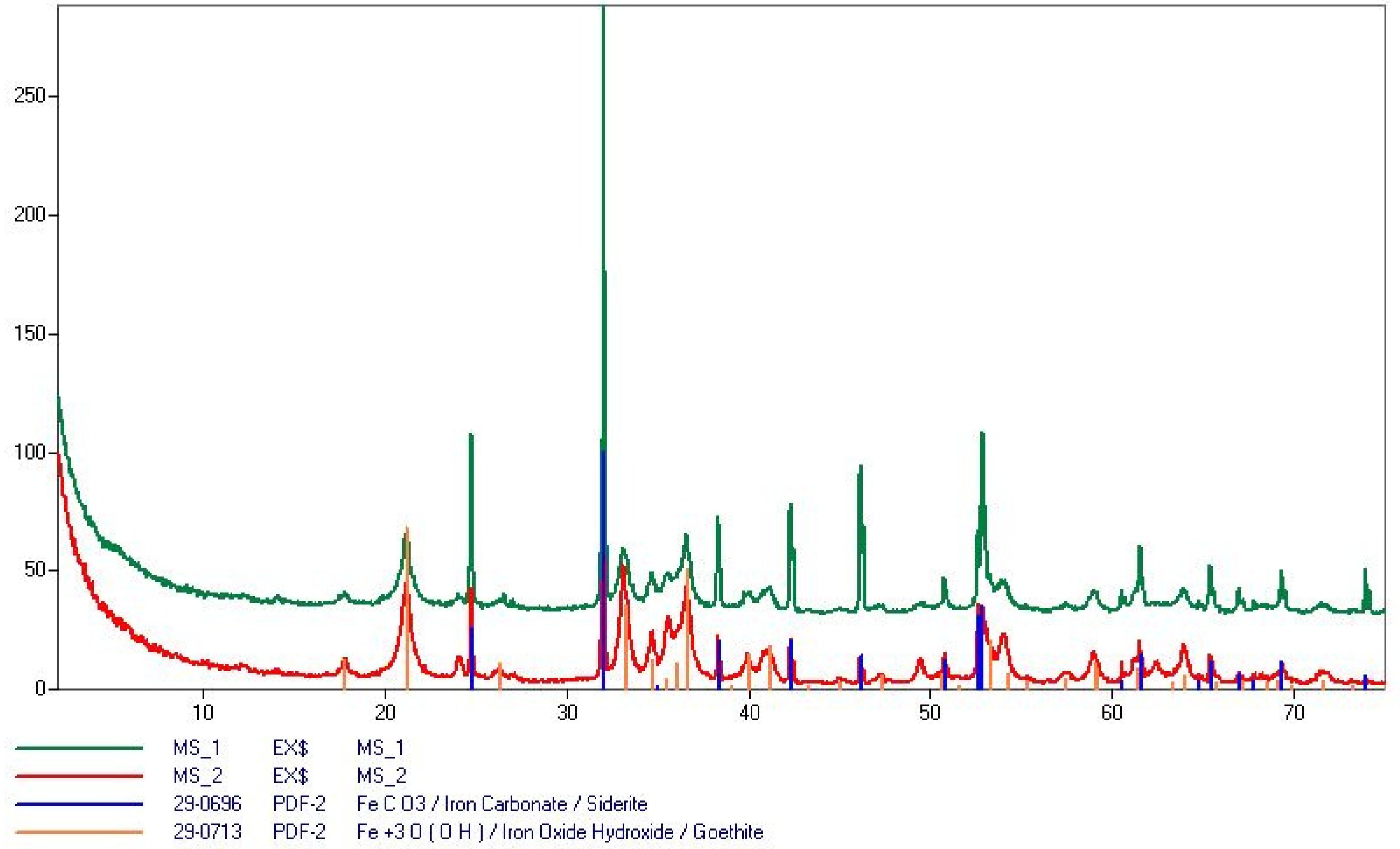


Figure 5

Figure_05

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.

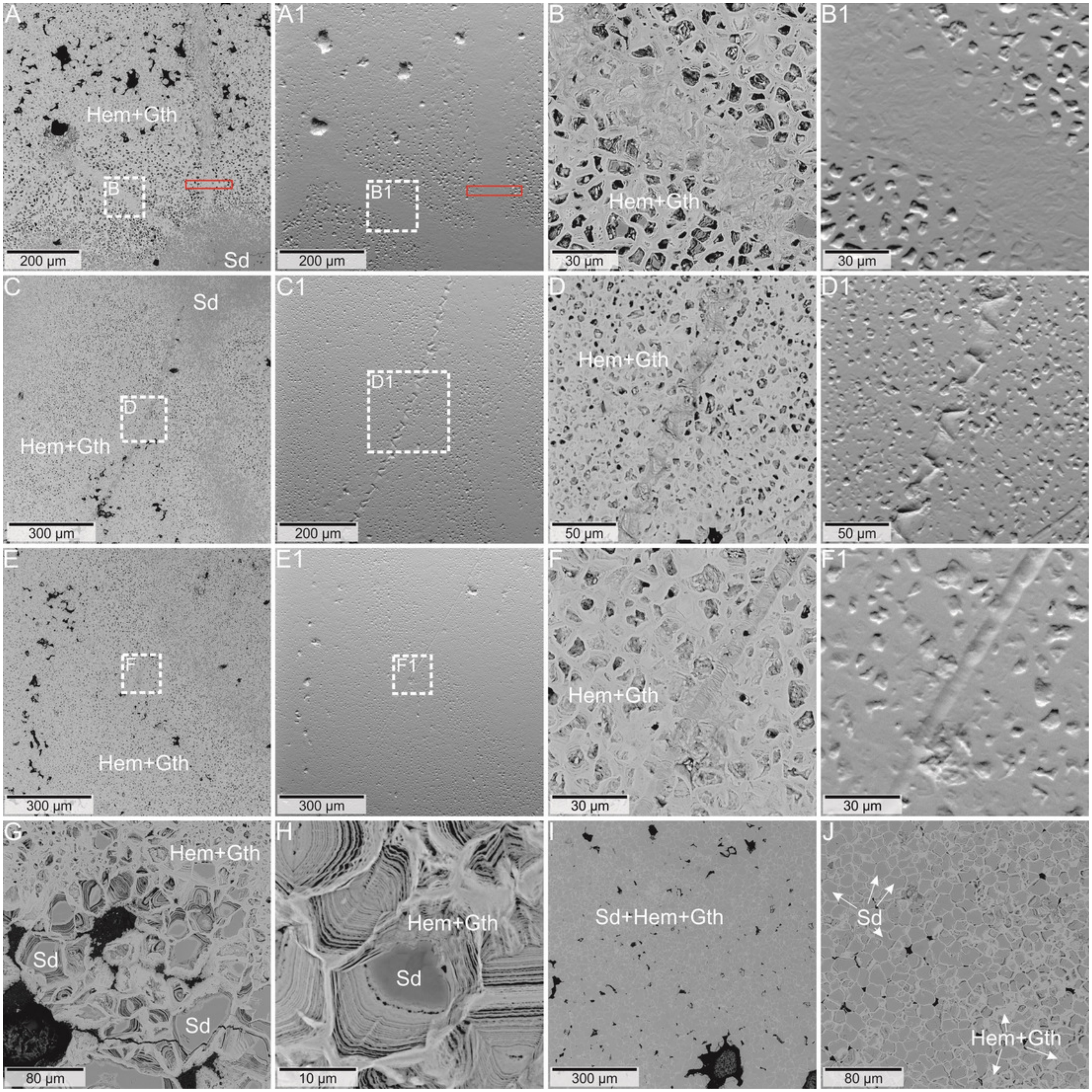

A
Hem+Gth
B
Sd
200 µm
A1
B1
200 µm
B
Hem+Gth
30 µm
B1
30 µm
C
Sd
D
Hem+Gth
300 µm
C1
D1
200 µm
D
Hem+Gth
50 µm
D1
50 µm
E
F
Hem+Gth
300 µm
E1
F1
300 µm
F
Hem+Gth
30 µm
F1
30 µm
G
Hem+Gth
Sd
Sd
80 µm
H
Hem+Gth
Sd
10 µm
I
Sd+Hem+Gth
300 µm
J
Sd
Hem+Gth
80 µm

Figure 6

Figure_06

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

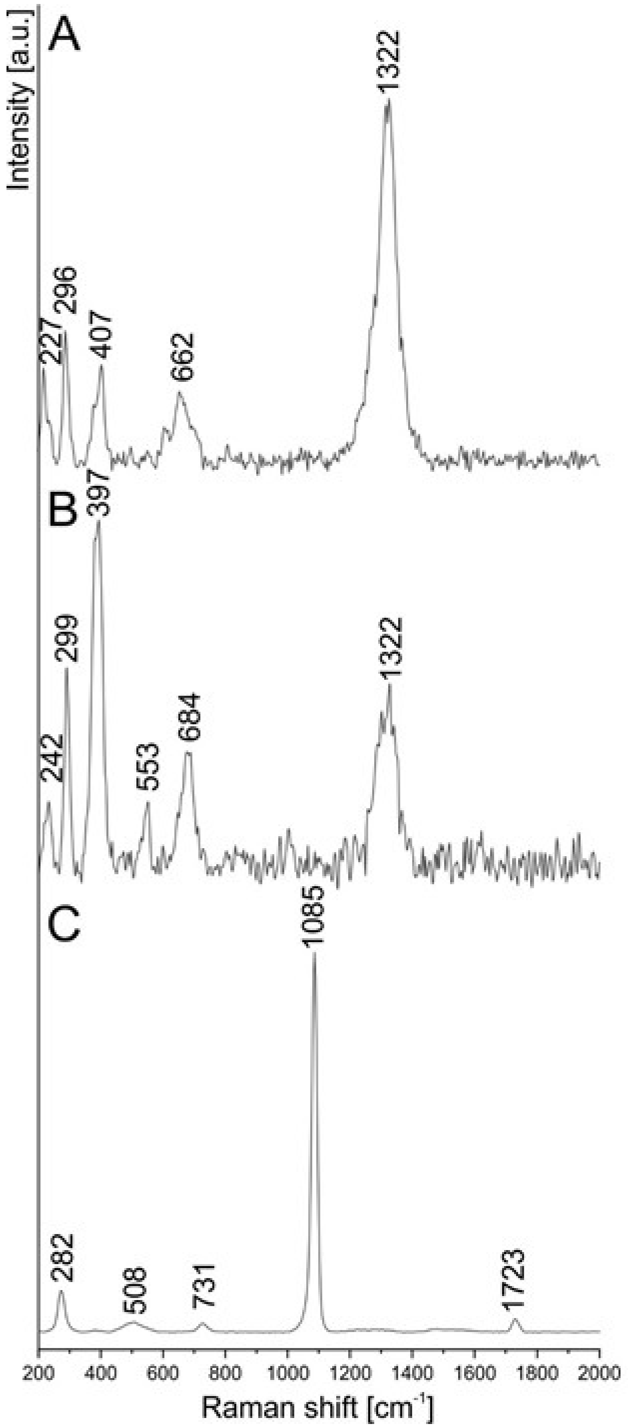


Figure 7

Figure_07

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).