Late Cretaceous coprolite from the Opole area (southern Poland) suggests a more variable diet of *Ptychodus* (#83483)

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Late Cretaceous coprolite from the Opole area (southern Poland) suggests a more variable diet of *Ptychodus*

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Background. Coprolites, i. e. fossilized faeces, are an important source of knowledge on the diet and food processing mechanisms in the fossil record. Here we examine shark coprolite from Opole Cretaceous deposits to describe its producer and producer's feeding habit.

Methods. To achieve that, coprolite was scanned using micro-computed tomography to show the arrangement of the inclusions (remnants of the producer's meal). In addition, the cross-section was examined under SEM/EDS to analyze the microstructure and chemical composition of the inclusions.

Results. Analysis showed numerous inclusions in various shapes. Some of them can be described as possible brachiopod, and at least one foraminiferan shell can be determined. SEM photographs confirm that most of the inclusions are fragments of brachiopod shells.

Conclusions. The producer of the coprolite can be determined as the shark *Ptychodus*. Since there is no bivalve (inoceramid) shells in the coprolite mass, but foraminifera remains can be recognized among numerous brachiopod shells, a combination of durophagy and filter feeding can be proposed for *Ptychodus* instead of typical durophagous habit.

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Abstract

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Introduction

Coprolites, i.e. fossilized faeces, together with consumulites (intestine contents), gastroliths (stomach, or gizzard, stones), and regurgitates (orally expelled masses) make up the group of ichnofossils known as bromalites (Hunt & Lucas, 2021). These are informative for establishing the diet and food processing style. The major caveat is the uncertainty concerning the specific producer of this kind of fossils. Sometimes, the co-occurrence in the same strata of fossils and faeces, and specific features of the animal linking the coprolite and skeletal material (e.g. size, purported diet), can be used as means to pinpoint, with a certain level of certainty, the most likely producer. These were done for the Late Triassic site of Krasiejów in the Opole area, where small coprolites, containing insect remains, were identified as a product of a co-occurring dinosauromorph *Silesaurus opolensis*, with the main reasoning based on body sizes and possible diets of the skeletally identified fauna at locality (Qvarnström et al. 2017, 2019, 2021). The discussion there, however, did not take into account a range of taxa from the site identified thus far only on dental remains. Here the producer of the Late Cretaceous coprolite from Opole is identified to the genus, based on the diet preferences of co-occurring ichthyofauna.

Shark teeth and coprolites are a common find in Late Cretaceous deposits, including the Turonian-Coniacian of Opole area. Skeletal fossils consist mainly of isolated teeth, with few finds of an associated dentition or even a single vertebra. Niedźwiedzki (2005) and Niedźwiedzki & Kalina (2003) are the only authors that have studied the shark fauna of the Opole area in recent years. Niedźwiedzki & Kalina (2003) described from Opole the following taxa: *Ptychodus latissimus*, *P. mammillaris*, *P. polygyrus*, *Squalicorax* sp., *Scapanorhynchus raphiodon,* and *Paranomotodon angustidens*. Niedźwiedzki (2005) listed jointly taxa from Opole and Sudetes ~~area.~~ Apart from those mentioned above, other taxa said to be common were *Cretoxyrhina mantelli*, *Cretolamna appendiculata*, *Squalicorax falcatus,* and *Odontaspis subulate*, while rare finds included *Hexanchus microdon*, *Synechodus major* and *Hybodus dentalus*. In a popular book (Yazykova (ed.) 2017, 2019, 2022), Niedźwiedzki confirms the presence specifically in the Opole area of *Squalicorax falcatus*, *Cretolamna appendiculata*, *Cretoxyrhina mantelli,* and *Odontaspis subulata*. These works are supplemented by the collecting efforts of the current authors, whose rich collection preserves *Squalicorax falcatus* and other lamniforms, *Ptychodus* spp., as well as a single find of hexanchiform.

As for coprolites, spiral shark faeces are especially common in clayey marls. Their general presence was noted by one of us in an MSc Thesis (Mazurek, 2008), an occurrence later cited by Hunt et al. (2015). The paper presents one of such coprolites, based on the shape and size assigned as produced by a Chondrichthyan fish that was analysed under SEM-EDS and microCT to describe the infillings and to recognize the producer.

Geology

Odra II quarry is a working quarry within the city of Opole (southern Poland). The succession ~~exposed~~ starts with clayey marls (Middle Turonian *Inoceramus apicalis* Zone) and proceeds with limy marlstones (Middle Turonian *I. lamarcki* Zone to the lowermost part of Upper Turonian *I. perplexus* Zone), and ends with marly limestones (*I. perplexus* Zone). This sequence of strata forms part of a one transgression-regression megacycle (Cenomanian-Coniacian) that represents the Cretaceous strata of the so-called Opole Trough (Jagt-Yazykova et al. 2022). The biota preserved is numerous and consists of ichnofossils, sponges, inoceramids and other bivalves, brachiopods, fish remains, cephalopods, echinoderms, crustaceans, cnidarians, shark coprolites, land flora, and rare marine reptiles. The coprolites are quite common and of uniform size and shape, with spiral structure pointing to sharks as their makers. The specimen studied comes from the clayey marls (Middle Turonian: *I. apicalis* Zone).

Materials & Methods

A ~~shark~~ coprolite from the Odra II quarry was collected during the summer digging camp in 2020. It is housed at University of Opole (col. no. IBUO-DM-KOPRO1). 8.5µm resolution scan is uploaded to Morphosource database (http://n2t.net/ark:/87602/m4/514300) in the form of 2882 tiff image series. Fieldwork was possible due to the legal agreement between the quarry owner (Cement Factory "Odra" and European Centre of Palaeontology, University of Opole) from 24.05.2017.

The coprolite has a typical size (22 mm in length, however, it is incomplete, and the whole coprolite could be at least two times larger compared to other specimens in the collection ranging between ca. 20-55 mm – e. g. Fig. 1C Specimen possess heteropolar (Dentzien-Dias et al. 2012) spiral shape (Fig. 1C, 2D) of a chondrichthyan coprolite. As the specimen is broken, some dark infillings are visible within the grey phosphatic mass on the cross-section (Fig. 1). To decide what kind of infilling they are, the specimen was analysed with micro CT scanner SkyScan 1273 in Bruker Laboratory in Kontich, Belgium. Obtained data were presented using DataViewer (for multiple cross sections in three directions) and CTVox (for the presentation of the 3D orientation of infillings) software.

For chemical identification of the infilling, the surface of the broken part (cross-section) was polished with grinding powder. The obtained polished surface was examined under Scanning Electron Microscope TM 3000 with secondary electrons as well as with the use of Energy-Dispersive X-ray Spectroscopy.

Results

MicroCT scan reveals numerous infillings of density different from than phosphatic background of the coprolite mass (Fig. 2, 3). Most of the shapes are irregular, many being boat-shaped. Some of them can be recognized and assigned to certain groups of animals, specifically micromorphic brachiopods (Fig. 4) and foraminifera (Figure 2F), based on, successively, SEM observations of microstructure and cross-section visible in micro CT scan. Two unidentified shells/tests have been observed under higher magnification under SEM. Both inclusions (Fig. 4) show the walls consisting of horizontal lamellae. No vertical elements are present, which would be expected in the case of an inoceramid prismatic layer (e. g. Jiménez-Berrocoso et al., 2006). No macroscopic chunks of large bivalves are present ~~either~~. The microstructure is more reminiscent of inpuncate brachiopod shells (Griesshaber et al., 2007). Regardless, some inclusions can be firmly and identified as brachiopods and forams (Fig. 2, 3), while inoceramids (the supposed food source of *Ptychodus* – Hattin, 1975) are lacking entirely.

In the EDS analysis, the main elements are Ca, O, C, and P (Fig. 4).

Discussion

Irregular and boat-shaped infilling creates a similar pattern to the infillings in coprolites of durophagous fishes from the Middle Triassic (Antczak et al., 2020). EDS signature suggests that these are elements made of calcium carbonate (while the matrix of the coprolite possesses a phosphatic character). The spiral nature of the Opole Cretaceous coprolites points to sharks as their producers. Taking into account the above, it means that the analysed coprolite was produced not by a piscivorous shark but rather by species feeding on invertebrates with calcareous shells. The only known candidate is *Ptychodus*. The assignment of some of the infillings to brachiopods suggests that the producer was feeding at the bottom of the sea (nektobenthonic) instead of in open water (nektonic). In addition, tests of calcareous foraminifera can be recognized, similar to genera *Lenticulina* or *Gavelinella* (Kłapciński & Teisseyre, 1981) which are bottom-dwelling taxa, probably swallowed accidentally together with the sediment and a brachiopod laying on the bottom of the sea.

In the Turonian of Opole, several shark species could produce coprolites of this size. The known taxa are *Cretoxyrinha, Hexanchus, Squalicorax,* and *Ptychodus*. Among them, only the last ~~one~~ is ~~the only one~~ commonly described as durophagous based on tooth morphology (Shimada et al., 2009, 2010) (Fig. 5). Niedźwiedzki and Kalina (2003) identified at the Opole Cretaceous three taxa of *Ptychodus*. Apart from isolated teeth, the Opole Cretaceous also yielded two sets of teeth: one is deposited at the University of Wrocław, while the other is in a museum of the University of Opole. Similar finds are known for several taxa worldwide (Amadori et al., 2019; Hamm, 2017), with partial skeletons or skulls much rarer (Shimada et al., 2009, 2010).

This means that the producer of the coprolite might be specifically identified to the mentioned genus. However, the lack of inoceramid shell fragments within the coprolite is puzzling. There are several possible explanations.

First is that producer of a coprolite fed also on the common inoceramids, but was able to feed only on the soft tissue and for example regurgitate the hard shells. Modern mammal *Odobenus rosmaris* feed on benthic mollusks by sucking the soft tissue and ejecting the hard parts (Sheyer et al., 20011). However, up to date, no dentalites were recognized from Opole Cretaceous inoceramid shells (even though many microscopical epifauna remnants can be observed – e. g. Bryozoa, Serpulidae, Ostreoida). From numerous specimens described by Walaszczyk (1992) a single sublethal injury was mentioned. If sharks were efficient predators there should be evidence of failed prey subjugation. However deformations and growth iterations in inoceramid shells are known, they are rather effects of decapod predation (Harries & Ozanne, 1998).

The second possibility is that the fossils of a coprolite producer are not present (or not recognized yet) in the Quarry due to the sedimentation bias or being less common representative of the Cretaceous fauna of this area. Hunt et al. (2015) show that producers of coprolites are often not represented by body fossils. Chondrichthyan fossilized faeces are the most common, while in terms of body fossils palaeoichthyofaunas are usually much more diversified, which Hunt et al. (2015) termed the 'shark surplus paradox'.

The third option, explaining the lack of dentalites and brachiopod infillings in the described coprolite is to consider *Ptychodus* as the produce which, contrary to current opinions, was not a typical durophagous taxon, but rather a durophagous-filter feeder specialized in small prey, with bulbous teeth for crushing shells, but also with water moving between the ridges of the teeth (Fig. 1). Such elaborated ornamentation as present on the teeth of *Ptychodus* is lacking in many other durophagous taxa, including among others: fishes (e. g. Purnell and Darras, 2015; Raguin et al., 2020), placodonts (Pommery et al., 2021) and mosasaurs (Leblanc et al., 2019), the teeth are usually restricted to the outer edge of the jaws, and supposed shark dentalites on inoceramids are surprisingly rare in the literature known to us (e.g. Kauffman, 1972; Hunt & Lucas, 2021, table A.5). Also not all filter-feeders possess small, gracile, sieve-like teeth. Several species of pinnipeds have teeth modified into filter-feeding, specifically with elaborate cusps of postcanines on both the upper and lower jaw. This modification is well-seen, especially in crabeater seal *Carinophaga lobodon* (Chatterjee & Small, 1989; Bengtson, 2002; Adam, 2005).

Conclusions

MicroCT scan and EDS analysis show that coprolite collected in the Turonian deposits of Odra II quarry in Opole, southern Poland is filled with shell fragments. Inclusions can be identified as remains of small brachiopods (and occasionally foraminifers). Such content indicates the producer of the coprolite to *Ptychodus*, the only large fish that fed on shell-covered invertebrates in the Late Cretaceous deposits of this locality, although 'shark sulprus paradox' need to be considered as well (Hunt et al., 2015). A diet composed of benthonic forams and small-sized brachiopods suggests that *Ptychodus* (if considered a producer) might have been a durophagous-filter feeder and not a typical durophagous fish as there is no evidence of preying on abundant large inoceramids (in the forms of coprolite or regurgitates).

Acknowledgments

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Captions

Fig. 1. *Ptychodus* remains from Opole Cretaceous. Analyzed coprolite IBUO-DM-KOPRO1 in lateral view) and cross-section (B). Coprolite IBUO-DM-KOPRO2 in lateral view (C). Teeth IBUO-DM-ZAB1 (D).

Fig. 2. MicroCT scan of the coprolite. Infillings – 3D model (A-B). Coprolite mass with infillings – 3D model (C-D). Longitudinal cross-section (E-F). b – brachiopod shell, f – foram shell. S – spiral structure.

Gavelienella illustration from Hornibrook et al. 1989, Fig. 18.17. Brachiopod shell photograph from alexstrekeisen.it. 3D model made in CTVox. Scan resolution: 8.5µm

Fig. 3. Cross-sections of the analysed coprolite in 3 directions (A, C, D). Magnification of the example of indet. shell fragment (B). Image obtained in DataViewer

Fig. 4. EDS analysis. Brachiopod shell fragments (A, B), the surface of the EDS analysis (C), and mass percentage result (D). SEM photographs: own. Made at Faculty of Chemistry, University of Opole.

Fig. 5. *Ptychodus* reconstruction. Author: Jakub Kowalski

Figure 1

Ptychodus remains from Opole Cretaceous.

Analyzed coprolite IBUO-DM-KOPRO1 in lateral view) and cross-section (B). Coprolite IBUO-DM-KOPRO2 in lateral view (C). Teeth IBUO-DM-ZAB1 (D).

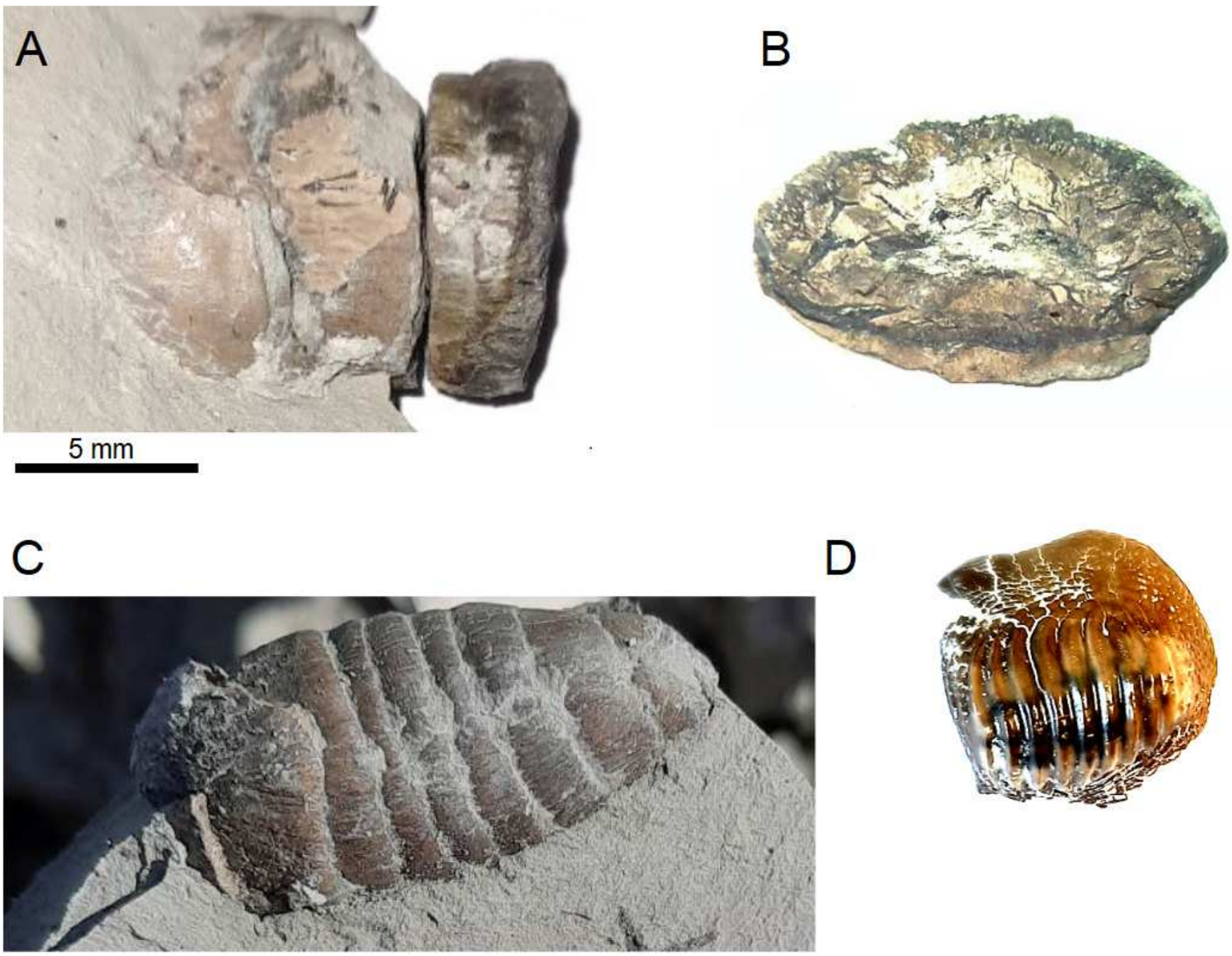

Figure 2

MicroCT scan of the coprolite.

Infillings – 3D model (A-B). Coprolite mass with infillings – 3D model (C-D). Longitudinal cross-section (E-F). b – brachiopod shell, f – foram shell. S – spiral structure.

Gavelienella illustration from Hornibrook et al. 1989, Fig. 18.17. Brachiopod shell photograph from alexstrekeisen.it. 3D model made in CTVox. Scan resolution: 8.5µm

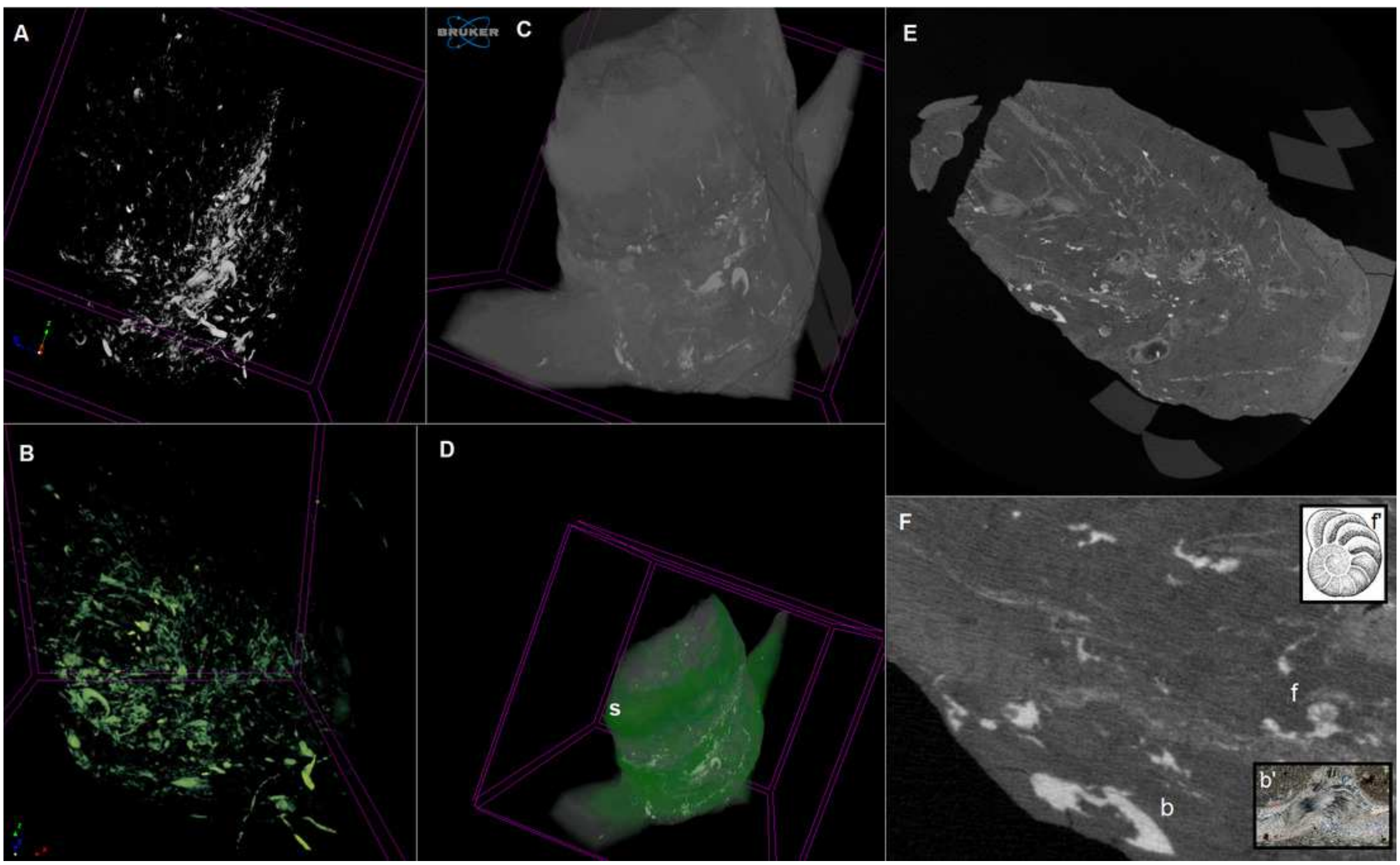

Figure 3

Cross sections of the analysed coprolite.

Cross-sections of the analysed coprolite in 3 directions (A, C, D). Magnification of the example of indet. shell fragment (B). Image obtained in DataViewer

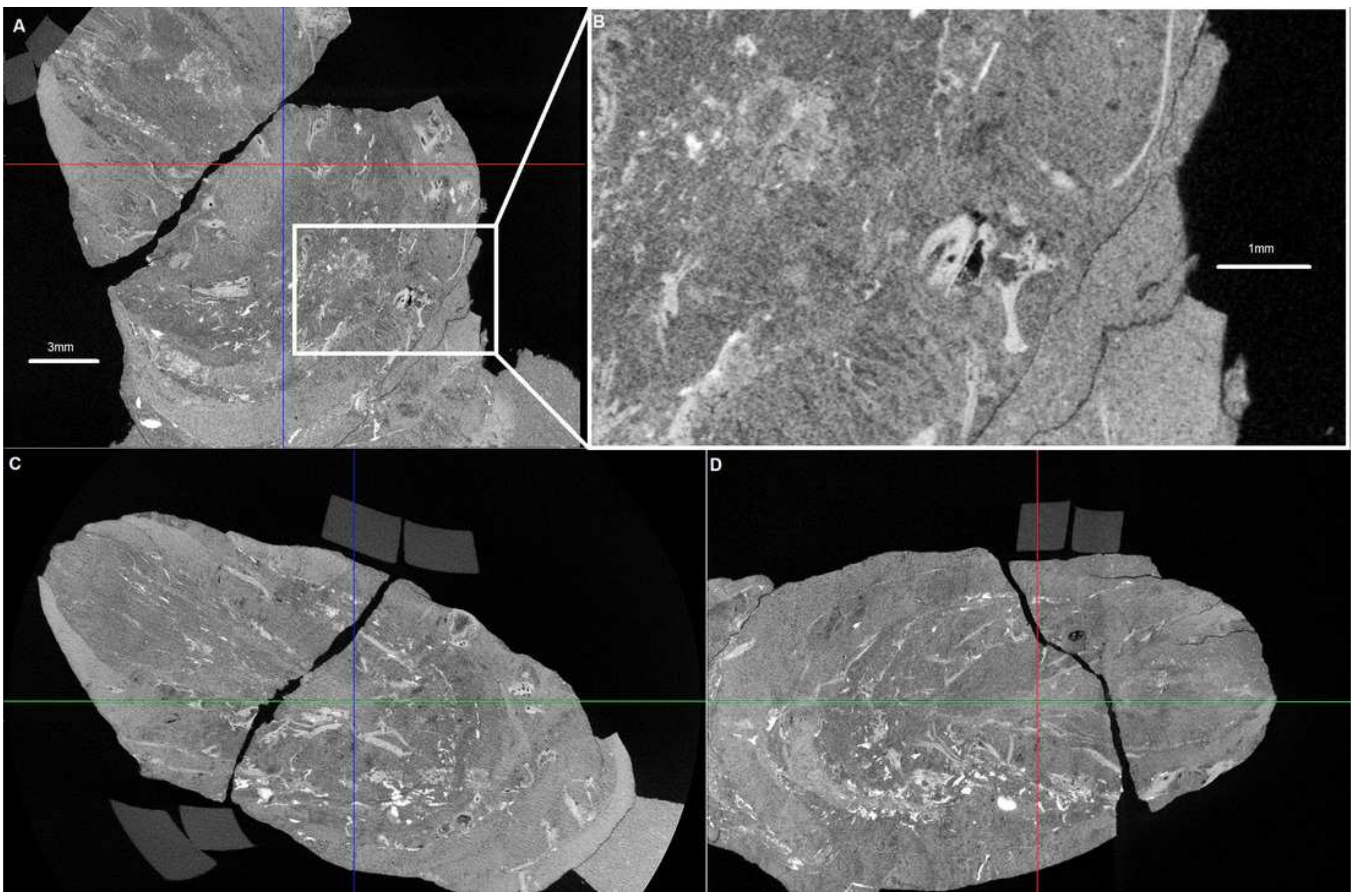

Figure 4

Fig. 4. EDS analysis.

Brachiopod shell fragments (A, B), the surface of the EDS analysis (C), and mass percentage result (D). SEM photographs: own. Made at Faculty of Chemistry, University of Opole.

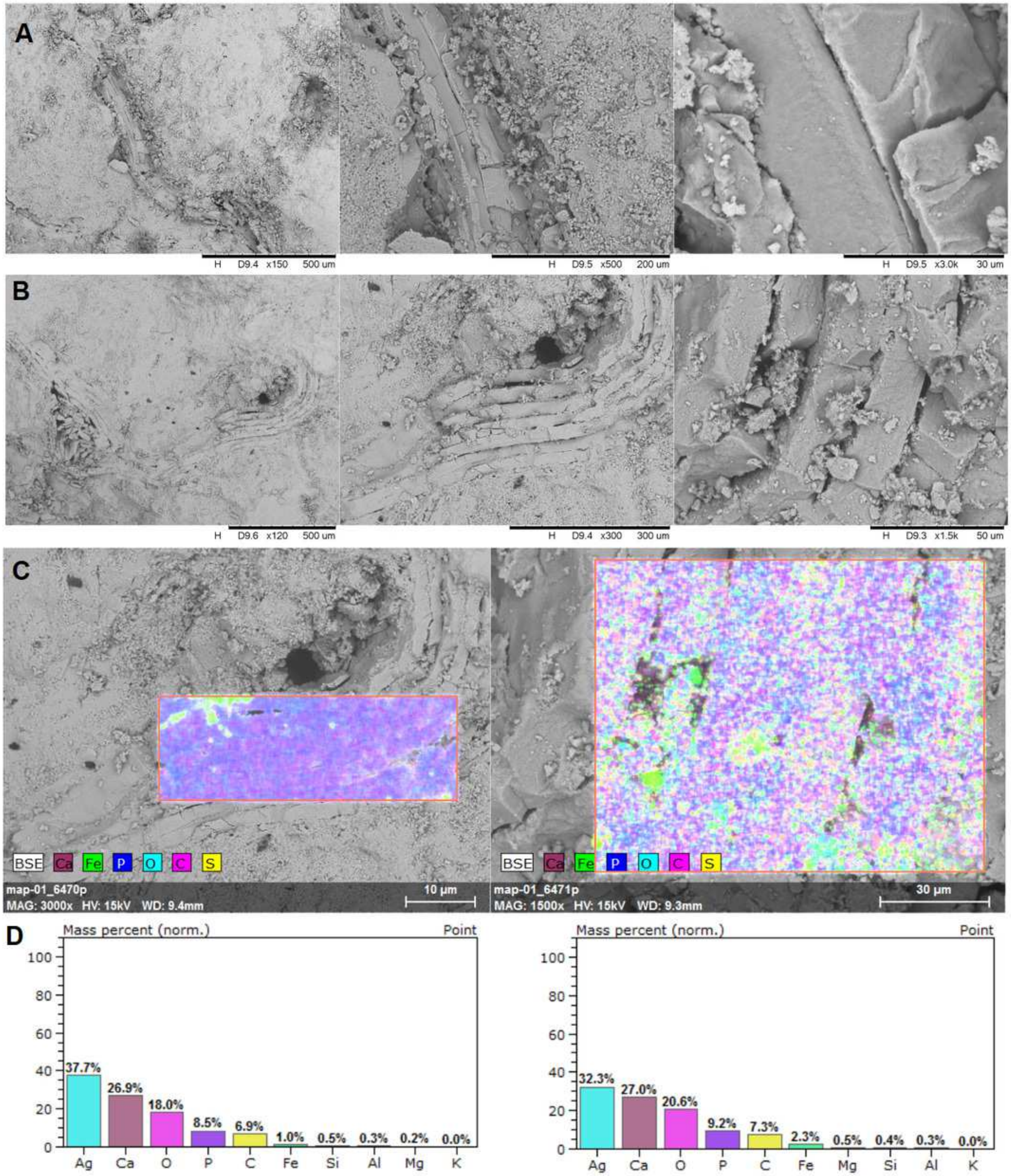
A
H D9.4 x150 500 um
H D9.5 x500 200 um
H D9.5 x3.0k 30 um
B
H D9.6 x120 500 um
H D9.4 x300 300 um
H D9.3 x1.5k 50 um
C
BSE Ca Fe P O C S
map-01_6470p
MAG: 3000x HV: 15kV WD: 9.4mm
10 µm
map-01_6471p
MAG: 1500x HV: 15kV WD: 9.3mm
30 µm
D
Mass percent (norm.)
Point
37.7% 26.9% 18.0% 8.5% 6.9% 1.0% 0.5% 0.3% 0.2% 0.0%
Ag Ca O P C Fe Si Al Mg K
32.3% 27.0% 20.6% 9.2% 7.3% 2.3% 0.5% 0.4% 0.3% 0.0%
Ag Ca O P C Fe Mg Si Al K

Figure 5

Ptychodus reconstruction

(Drawing by Jakub Kowalski)