

# Chaetognath grasping spines from the Devonian of Poland: their structure and geochemistry

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Previously unidentified small (up to 1.3 mm in length), gently curved hollow spines composed of calcium phosphate and derived from the upper Famennian (Devonian) of the Holy Cross Mountains in central Poland are described. They are similar to the type species of *Phakelodus*, but show some distinct morphological differences, therefore, have been included into *Phakeloides polonicus* gen. et sp. nov. The studied specimens of that species show relatively massive mineral structure characterized by significant porosity with well-preserved major structural features. The outer layer of the spines is, in contrary, fragmentarily preserved, and exposes distinct mosaic-like ornamentation of the surface of the middle layer, which consists of obliquely arranged, shallow furrows. Geochemical analyses of the Devonian *Phakeloides polonicus* gen. et sp. nov. spines have revealed the presence of a weaker mineralized structure, compared to conodont apatite, composed of a diagenetic phosphate phase. It is characterized by moderate cathodoluminescence intensity, elevated concentrations of iron and sulphur as well as decreased concentrations of strontium, calcium, and phosphorus. The “Orsten” type, early diagenetic phosphatization of the outer layer of the spines is not observed in studied specimens of *Phakeloides polonicus* gen. et sp. nov., contrary to the previously investigated Furongian (Cambrian) material. This points to the low rate of diagenetic phosphatization, which was likely enabled by very slow sedimentation and long residence time of the spines close to sediment-water interface at varying redox conditions and significant flux of phosphate ions.

**Key words:** Conodonta, Protoconodonta, Chaetognatha, elemental ratios, microstructure, phosphatized spines, Devonian, Holy Cross Mountains, Poland.

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## Introduction

The occurrence of phosphatic chaetognath grasping spines, previously included into protoconodonts, is generally restricted to the lower Palaeozoic (cf. Bengtson 1976, 1983; Szaniawski 1982, 1983, 2002, 2005, 2009, 2015; Andres 1988; McIlroy and Szaniawski 2000; Carlorosi et al. 2019). The spines, mostly assigned to the genera *Phakelodus* (earlier *Prooneotodus*) and *Protoherzina*, are considered a product of diagenetic phosphatization of originally organic chaetognath elements based on similarity in their architecture and microstructure, findings of the natural clusters of spines arranged in a form of chaetognath grasping apparatus (Szaniawski 1982, 2002, 2009, 2015; McIlroy and Szaniawski 2000; Vannier et al. 2007), their conserved plastic deformations

(Doguzhaeva et al. 2002; Szaniawski 2002; Wierzbowski et al. 2021) and a growing number of discoveries of preserved fossil carbonaceous spines, which sometimes co-occur with remnants of soft tissues of chaetognaths (Szaniawski 2005; Vannier et al. 2007; Briggs and Caron 2017; Shu et al. 2017; Slater et al. 2018; Slater and Willman 2019). In addition, Wierzbowski et al. (2021) have recently documented the presence of a few generations of diagenetic phosphate phases in Furongian (Cambrian) chaetognath *Phakelodus* sp. spines from the Öland Island (Sweden). A thin, outermost layer of the spines is composed of early diagenetic apatite phase, which incrustated the original cuticle integument, contributing to the preservation of fine details of their surface. Its mineralization is assigned to the “Orsten”-type phosphatization process known from the excellently preserved three-dimensional small invertebrate fossils of the early Palaeozoic age

(cf. Müller and Waloszek 1985; Waloszek 2003; Maas et al. 2006; Wierzbowski 2021).

There are, however, other Cambrian–lowermost Ordovician problematic protoconodont-like fossils that show a strong resemblance to chaetognath grasping spines. Some of the protoconodont-like cones assigned to the genera *Coelocerodontus* and *Virodus* have recently been interpreted as chaetognaths grasping spines (Szaniawski 2015). Fossils assigned to *Rhombocorniculum cancellatum* despite structural affinity to chaetognath grasping spines are included into pseudoconodonts and regarded as sclerites of *Hallucigenia*-type lobopodians or other incertae sedis (Brasier 1989; Guoxiang et al. 2003; Caron et al. 2013; Kouchinsky et al. 2015).

A relatively large number of discoveries of Cambrian–Lower Ordovician chaetognath phosphatic grasping spines may be linked to phosphorus re-mobilization and high phosphate concentrations in ancient pore waters. It was probably linked to elevated phosphorus input to the oceans and diminished sediment mixing and ventilation before the Ordovician diversification of burrowing organisms, which may have contributed to the elevated position of oxic-anoxic interface within the sediment and fluctuating redox conditions in the upper part of sediment column (Allison and Briggs 1993; Brassier and Callow 2007; Dornbos 2011; Creveling et al. 2014). Rare findings of phosphatized chaetognath grasping spines are, nevertheless, reported from upper Palaeozoic deposits (Doguzhaeva et al. 2002).

The present paper is devoted to newly found upper Palaeozoic phosphatic chaetognath grasping spines from the upper Famennian (Devonian) of the Holy Cross Mountains in central Poland. The spine assemblage is composed of numerous, almost identical, isolated elements. The spines have been investigated morphologically and microstructurally. The present study highlights disparities in the microstructure and chemical composition among the new chaetognath material, consisting of secondary phosphate, co-occurring conodont elements built of primary phosphate, and previously described phosphatized chaetognath spines of the Furongian (Cambrian) age from Sweden (cf. Wierzbowski et al. 2021). The taxonomical affinity of studied Devonian fossils to previously described Cambrian forms is also discussed. The purpose of this study is to find apparent similarities and/or differences in the morphology, construction and structure of phosphatized spines of early and late Palaeozoic chaetognaths along with the specific pathways of their diagenetic mineralization processes. This study also demonstrates the potential of upper Palaeozoic deposits for further research on the evolution and physiological functions of chaetognaths and other problematic spines of invertebrates.

*Institutional abbreviations.*—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

*Other abbreviations.*—CAI, conodont colour-alteration index.

*Nomenclatural acts.*—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:26225CF8-3682-414D-A16B-4883AC67E04B.

## Geological setting

Newly found upper Famennian (Devonian) chaetognath grasping spines come from the extensively exploited Ostrówka Quarry, which is situated on the Ostrówka Hill, near the village of Gałęzice, in the south-western part of the Holy Cross Mountains in central Poland (Fig. 1A, B). In the quarry are exposed upper Devonian limestone beds, which are covered by lower Carboniferous carbonate-mudstone strata (Fig. 1C). This lithological succession was formed as a result of drowning of a Frasnian (upper Devonian) shallow-water carbonate platform deposits, which are overlain by a discontinuity surface and condensed Famennian (upper Devonian) limestone beds. Tournaisian and Viséan (lower Carboniferous) deep water limestone-clay beds, black siliceous shale and carbonate gravity flow deposits occur higher in the section (Szulczewski et al. 1996).

Facies development and stratigraphic completeness of Famennian exposures from the northern wall of the Ostrówka Quarry is variable. The most complete Famennian section is located on the Todowa Grząba peak in the Gałęzice region (Fig. 1; Szulczewski 1978; Szulczewski et al. 1996). Currently, only a few relatively thin beds of extremely condensed crinoidal-cephalopod Famennian limestone can be found above an erosional discontinuity surface developed on the top of shallow-water Frasnian “*Amphipora* limestones” (Racki 1993; Szulczewski et al. 1996; Berkowski 2002). Stratigraphical studies of the condensed unit have revealed a standard succession of Famennian conodont zones, interrupted by several internal paraconformities (cf. Szulczewski 1971, 1978; Szulczewski et al. 1996). The oldest deposits covering the unconformity belong to the upper part of the middle Famennian *Conditolepis marginifera* Zone, while the youngest deposits represent the upper Famennian *Dasbergina trigonica* Zone (Szulczewski et al. 1996; Dzik 2006). The *D. trigonica* Zone roughly corresponds to Ziegler and Sandberg’s (1984) *Siphonodella praesulcata* Zone (cf. Szulczewski et al. 1996; Dzik 2006). The materials studied herein come from cephalopod limestone beds which were formed in neritic environment during the pelagic stage of deposition (Szulczewski 1978; Szulczewski et al. 1996).

## Material and methods

The upper Famennian (Devonian) chaetognath spines and conodont elements are derived from archival rock samples collected by Michał Szulczewski (Faculty of Geology, University of Warsaw, Poland) from the uppermost part of dark grey cephalopod limestone beds (sample Ost-5) of the

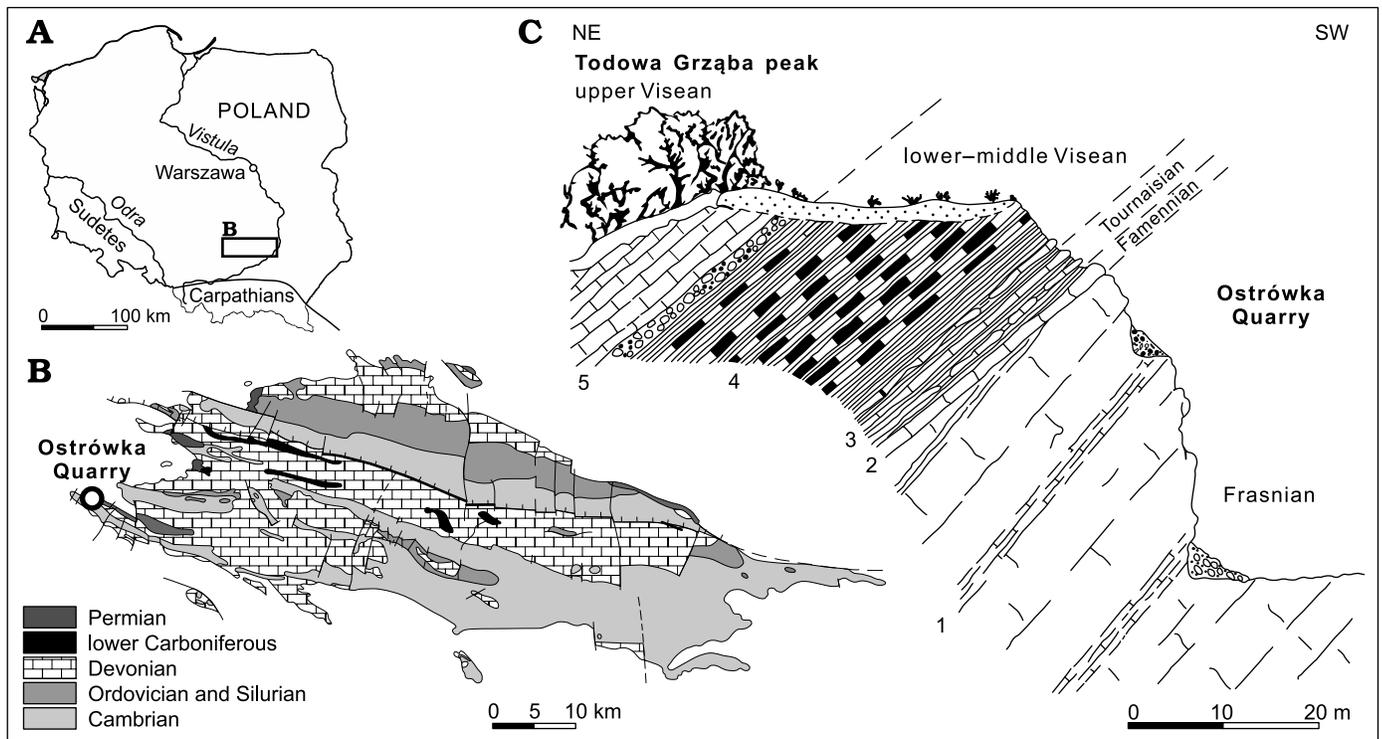


Fig. 1. Geographical location (A) and simplified geologic map (B) of the Holy Cross Mountains with location of the studied exposure. C. Cross-section through the ledge of the Ostrówka Quarry. 1, peritidal carbonates (Kowala Formation); 2, condensed crinoidal-cephalopod limestone beds; 3, clay with limestone intercalations; 4, black radiolarian shale (Zaręby Beds); 5, carbonate gravity flows (after Szulczewski et al. 1996).

northern wall of the Ostrówka Quarry (latitude 50.843667, longitude 20.400528). Several chaetognaths grasping spines of *Phakeloides polonicus* gen. et sp. nov. and co-occurring conodont elements belonging to species of *Dasbergina*, *Palmatolepis*, *Polygnathus*, and *Polynodosus* were studied for the biostratigraphy, macro- and microstructure, cathodoluminescence and chemical composition (Table 1). All specimens were separated from carbonate rocks by dissolving in 10% acetic acid, washing, drying, and picking out of the residue under a binocular microscope by Hubert Szaniawski (ZPAL). Most of the recovered specimens exhibit excellent state of preservation and different ontogenetic growth stages.

Scanning electron microscope (SEM) and cathodoluminescence imaging were conducted at the Institute of Paleobiology, Polish Academy of Sciences in Warsaw, Poland. The architecture and microstructure of specimens were investigated using Philips XL-20 SEM and Thermo Fisher Scientific Quattro S ESEM devices after coating the whole or fragmented specimens with platinum. Thin sections made from chaetognath spines and conodont elements were studied using a petrographic microscope (Zeiss, Axio Scope A1) and, after coating with carbon, using a hot cathodoluminescence microscope (HC1-LM) with a beam of 14 keV and the current density of 0.1  $\mu\text{A}/\text{mm}$ .

The electron microprobe studies were conducted at the Micro-area Analysis Laboratory of the Polish Geological Institute-National Research Institute in Warsaw, Poland. Concentrations of Ca, P, F, S, Sr, Fe, Mn, Ba, Si, Ti, Na, K, Mg, Cl, and Ce in thin sections made from different morpho-

logical parts of chaetognath grasping spines and conodont elements were measured by means of wavelength-dispersive spectrometers (WDS) of the Cameca SX100 electron microprobe analyser. The analyses were carried out using a 15 kV acceleration voltage, a 20 nA beam current, and a beam diameter of 5  $\mu\text{m}$ . Natural minerals provided by Cameca were used as analytical standards. Average detection limits of the WDS analyses were as follows: Ca (299 ppm), P (202 ppm), F (1304 ppm), S (184 ppm), Sr (999 ppm), Fe (666 ppm), Mn (653 ppm), Ba (1466 ppm), Si (117 ppm), Ti (696 ppm), Na (194 ppm), K (181 ppm), Mg (118 ppm), Cl (170 ppm), Ce (1108 ppm). Mn, Ba, Ti, K, Mg and Ce elements were excluded from the interpretation as their detection limits were close to their measured concentrations. To show mineral density of different structural zones of the fossils backscattered electron (BSE) analysis was conducted. All figured specimens are deposited at the Institute of Paleobiology, Polish Academy of Sciences (ZPAL).

## Systematic palaeontology

Phylum Chaetognatha Leuckart, 1854

Class, Order, and Family uncertain

Genus *Phakeloides* nov.

Zoobank LCID: urn:lsid:zoobank.org:act:A9F30FE6-A721-4FF8-99CE-26BC533F154A

Type species: *Phakeloides polonicus* sp. nov.; see below.

*Etymology*: A combination of the generic name *Phakelodus* and the suffix *-oides*, implying likeness and referring to the similarity of this new genus to Cambrian chaetognath grasping spines of *Phakelodus*. Gender masculine.

*Diagnosis*.—As for species, by monotypy.

*Phakeloides polonicus* sp. nov.

Fig. 2A–C.

Zoobank LCID: urn:lsid:zoobank.org:act:1E251F23-2036-4AEF-8E1F-16129CBD8C32

*Etymology*: From Latin *Polonia*, name of Poland, the country from which the specimen was collected.

*Type material*: Holotype, ZPAL Cg. 2/Ost-Ch.22 (Fig. 2A), well-preserved complete grasping spine. Paratypes: ZPAL Cg. 2/Ost-Ch.7, ZPAL Cg. 2/Ost-Ch.5 (Fig. 2B, C), almost complete grasping spines from the type locality and horizon.

*Type locality*: Ostrówka Quarry close to the Todowa Grząba peak, Gałęzice region, Holy Cross Mountains, central Poland.

*Type horizon*: *Lagovignathus styriacus* Zone, upper Famennian, Upper Devonian.

*Diagnosis*.—Small, gently curved hollow and round spines (approximate length 0.9–1.3 mm and width 0.1–0.2 mm); internal cavity long. The spine walls consisting of three layers: (i) the remainders of a thin outer layer which are fragmentarily preserved at the bottom of the spines, (ii) a thick middle layer composed of massive mineral structure with locally preserved fibril pattern and (iii) a thin, inner, microcrystalline layer. Furrows on the surface of the middle layer arranged in intersecting strips forming a mosaic-like or reticular ornamentation, most pronounced at the tip and in the central region of the spines. Ornamentation disappearing towards the spine's base; individual furrows running obliquely around the spine. The internal cavity terminating, in some specimens, with open holes at the spine's tips.

*Remarks*.—The upper Famennian (Devonian) *Phakeloides polonicus* gen. et sp. nov. is similar in architecture to the upper Cambrian and Early Ordovician species of the genus *Phakelodus* but is relatively round and devoid of longitudinal ornamentation (e.g., Müller 1959; Zhang in An et al. 1983; Szaniawski 2002; Wierzbowski et al. 2021). The characteristic feature of the *Phakeloides polonicus* gen. et sp. nov., readily distinguishing it from all previously named Palaeozoic chaetognath grasping spines, is reticular, surface ornamentation consisting of obliquely crossing furrows. In contrast, species of *Phakelodus* have longitudinal ridges and narrow oblique furrows that mark growth lines on the surface of grasping spines (see Szaniawski 2002: fig. 3A). The function of holes at the tips of some spines (Fig. 2B<sub>2</sub>) is not clear but we cannot rule out that cracking or chipping of the spine tip may have exposed its internal cavity.

The similarity in architecture of the grasping spines in species of *Phakelodus* and those of the Recent species of

*Sagitta* chaetognaths concerns several major features of their morphology mentioned by Szaniawski (2002).

*Stratigraphic and geographic range*.—Type horizon and locality only.

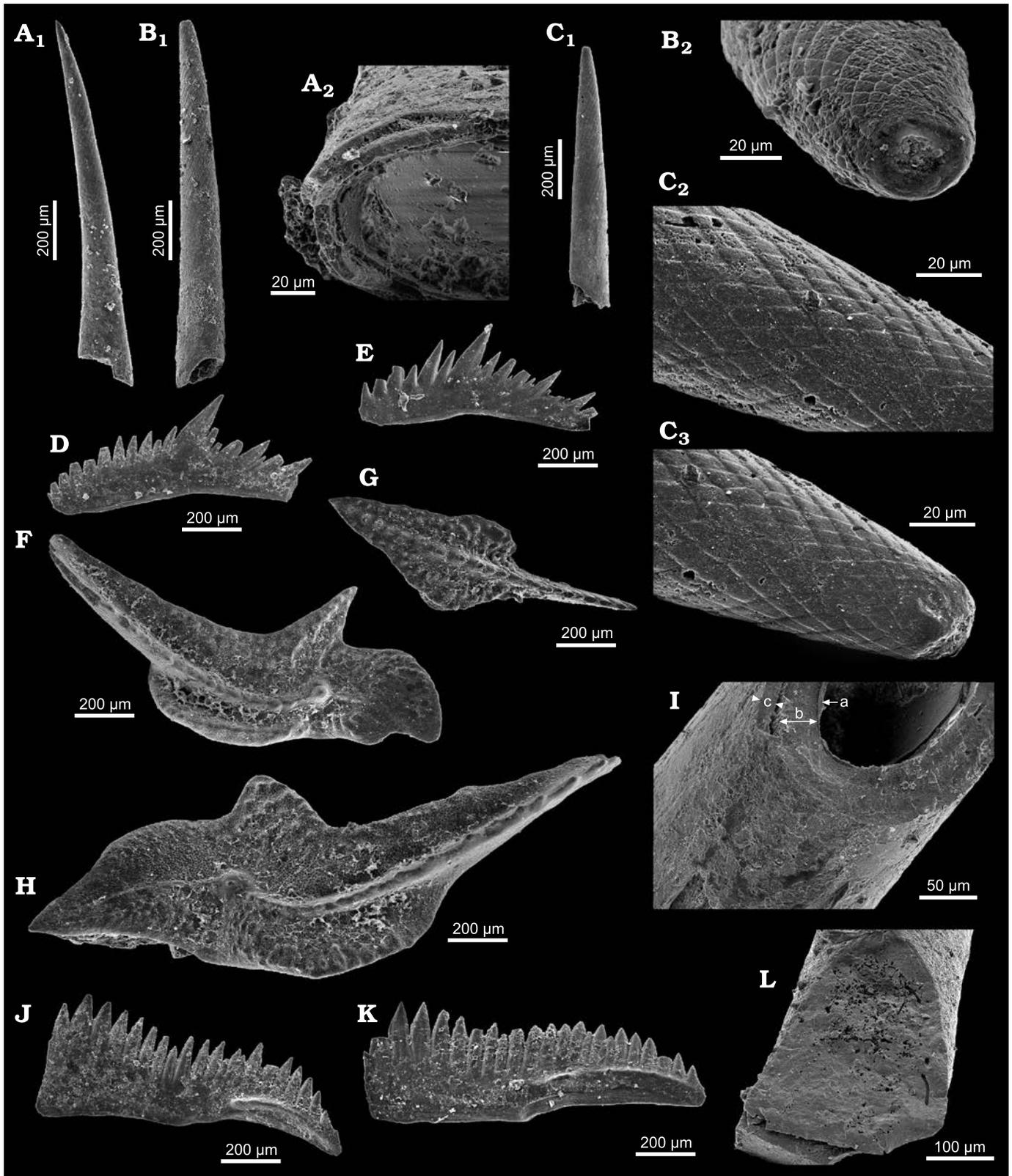
## Results

**Petrographic microscope and scanning electron microscope studies**.—The petrographic microscope studies have revealed the existence of a fragmentary, very thin, dark brown, opaque cortex of the Devonian *Phakeloides polonicus* gen. et sp. nov. spines and mostly translucent, patchy light brown to dark brown inner area, which predominantly represents the bulk middle layer (Fig. 3A; cf. Wierzbowski et al. 2021). A thin, internal layer is often visible on the surface of internal cavity of the spines, which is similar to Cambrian chaetognath grasping spines (cf. Szaniawski 1983, 2002). The phosphate crystals of all zones of the studied spines are arranged in the same optical orientation and show undulose extinction pattern. The internal cavity of the spines is mostly empty, albeit clotted, dark brown, diagenetic phosphate infillings occur in some places.

The studied conodont elements belonging to species of *Dasbergina*, *Palmatolepis*, *Polygnathus*, and *Polynodosus* show pale yellow to light brown colours, which points to their low thermal alteration demonstrated by CAI (conodont colour-alteration index) of 1 (cf. Epstein et al. 1977; Rejebian et al. 1987). The conodont elements consist of tissues distinguishable in transmitted light zones: the top, brown and opaque albid (white matter) tissue, the translucent hyaline (lamellar) tissue (Fig. 3B) and, in some cases, remainders of dark brown, opaque and porous basal body of disordered mineral structure (cf. Wright 1989; Trotter et al. 2007; Zhuravlev and Gerasimova 2015; Zhuravlev 2017).

Scanning microscope observations do not point to the presence of a distinct outer layer in the majority of studied Devonian *Phakeloides polonicus* gen. et sp. nov. grasping spines, which contrasts to Furongian (Cambrian) grasping spines of *Phakelodus* sp. (cf. Szaniawski 1982, 1983, 2002; Wierzbowski et al. 2021). A thin, cylindrical, outer zone of microcrystalline fabric, which likely represents fragments of the outer layer, is, however, visible in some specimens, especially at the base of the spines (Fig. 4D<sub>2</sub>). The major portion of the spines, belonging structurally to the middle layer, consists of fused granular grains or a massive mineral structure characterized by the perpendicular, uneven or conchoidal fracture with minor breaks forming the second-order cleavage plane (Fig. 4A, B). The surface of the spines reveals a reticular or mosaic-like texture consisting of obliquely crossing furrows, which likely represents primary

Fig. 2. Devonian chaetognath grasping spines *Phakeloides polonicus* gen. et sp. nov. (A–C, I, L) and conodonts (D–H, J, K) from the upper Famennian, Ostrówka Quarry, Holy Cross Mountains, Poland. **A**. ZPAL Cg. 2/Ost-Ch.22, A<sub>1</sub>, almost complete spines; A<sub>2</sub>, three layers in the wall observed at the base of the spines. **B**. ZPAL Cg. 2/Ost-Ch.5, B<sub>1</sub>, almost complete spines; B<sub>2</sub>, the hole at the tip of the spine. **C**. ZPAL Cg. 2/Ost-Ch.7, C<sub>1</sub>, almost complete spines; C<sub>2</sub>, C<sub>3</sub>, intersecting furrows create mosaic-like, reticular ornamentation of the surface of the middle layer close to the spine's tip. **D**, **E**. *Polygnathus* sp., →



P<sub>2</sub> element. **D**. ZPAL Cg. 2/Ost-C.14. **E**. ZPAL Cg. 2/Ost-C.26. **F**. *Palmatolepis trachytera* Ziegler, 1960, from the *Lagovignathus styriacus* Zone, ZPAL Cg. 2/Ost-C.25, P<sub>1</sub> element. **G**. Idiognathodontid *Dasbergina granulosa* (Ziegler, 1962) from the *Lagovignathus styriacus* Zone, ZPAL Cg. 2/Ost-C.4, P<sub>1</sub> element. **H**. *Palmatolepis schindewolfi* Müller, 1956, from the *Lagovignathus styriacus* Zone, ZPAL Cg. 2/Ost-C.15, P<sub>1</sub> element. **I**. ZPAL Cg. 2/Ost-Ch.10, three layers in the wall: a thin, most internal, layer (a), the middle layer (b), and the outer layer (c). **J, K**. Platform-bearing elements of *Polynodosus lauriformis* (Dreesen and Dusar, 1974), from the *Lagovignathus styriacus* Zone, P<sub>1</sub> element. **J**. ZPAL Cg. 2/Ost-C.13. **K**. ZPAL Cg. 2/Ost-C.21. **L**. ZPAL Cg. 2/Ost-Ch.9, irregular boring on the surface and inside the middle and inner layers.

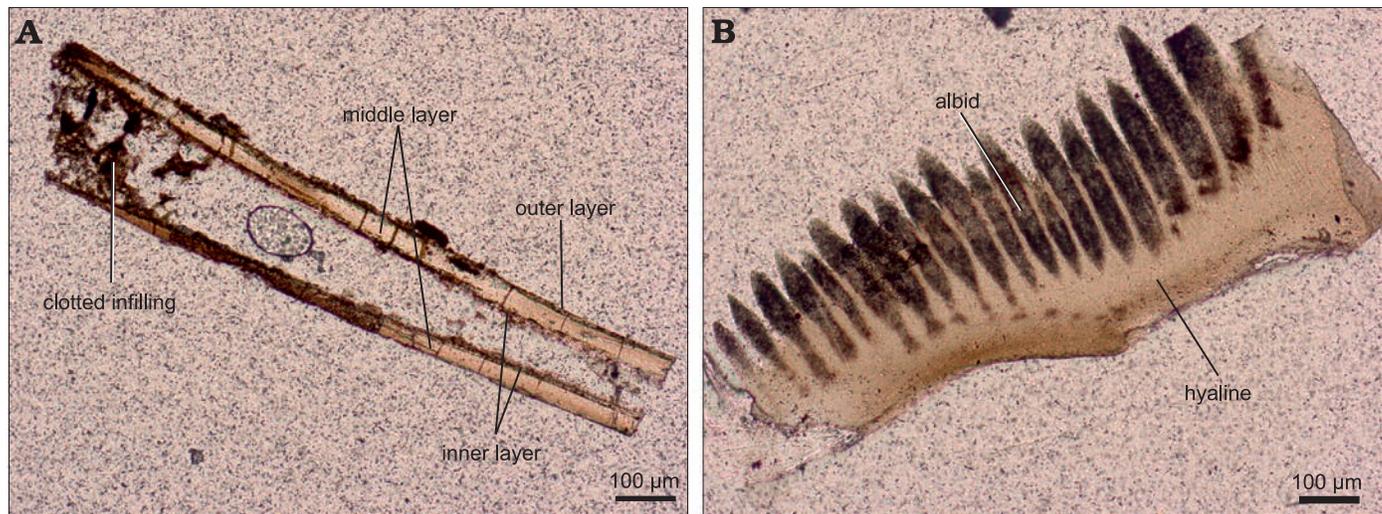


Fig. 3. Transmitted light images of thin sections of Devonian chaetognath spine and conodont element from the upper Famennian, Ostrówka Quarry, Holy Cross Mountains, Poland. **A.** Longitudinal section of *Phakeloides polonicus* gen. et sp. nov. grasping spine showing a very thin and partially preserved, dark brown, opaque cortex; a mostly translucent, light brown to dark brown, in patches, inner area representing the bulk middle layer and a thin, internal layer fragmentarily visible on the surface of internal cavity of the spine, ZPAL Cg. 2/Ost-Ch.30. **B.** Longitudinal section of *Polynodosus* sp. conodont element showing the top, brown and opaque albid (white matter) tissue and the underlying, translucent hyaline (lamellar) tissue, ZPAL Cg. 2/Ost-C.35.

ornamentation of the middle layer (Fig. 4A, C, D<sub>2</sub>). Parallel fibrils of the middle layer, arranged obliquely to the spine axis, which were reported from other fossil and modern chaetognath spines, are visible locally on broken surfaces of studied specimens of *Phakeloides polonicus* gen. et sp. nov. (Fig. 4C; cf. Szaniawski 1982, 1983, 2002; Doguzhaeva et al. 2002; Vannier et al. 2007).

The innermost portion of the spines, around the internal cavity, usually shows the presence of a thin, cylindrical internal layer of microcrystalline fabric composed of granular calcium phosphate crystals (Fig. 4B, D<sub>1</sub>). Pitting or significant internal porosity is observed within many parts of the studied *Phakeloides polonicus* gen. et sp. nov. spines. In some places, in the cross-section of the spine walls are visible narrow porous zones dividing solid well-mineralized zones (Fig. 4D<sub>1</sub>). Networks of small borings are often observed in cross sections of the spines (Fig. 4A).

In contrast, studied conodont elements consist of densely packed, weakly lamellar, albid (white matter) tissue, which is typical of the crown tips and innermost parts of conodont elements composed of the strongly lamellar, hyaline tissue (Fig. 4E). The oblique lamellae of the hyaline tissue of lower parts of conodont elements are very characteristic. They pass into more chaotic structure of lateral parts of the conodont platform, which may be assigned to the paralamellar variety of the lamellar tissue (Fig. 4E; cf. Zhuravlev 2017).

**Cathodoluminescence imaging.**—*Phakeloides polonicus* gen. et sp. nov. spines show weak to moderate red cathodoluminescence, excluding narrow fractures and fragments of outermost rim areas which show bright luminescence colours (Fig. 5A). In conodont elements, very weak yellow-red luminescence is observed in albid tissue, whereas the bulk

of hyaline tissue and remnants of basal body are non-luminescent (Fig. 5B).

**Electron microprobe and backscattered electron studies.**—Electron microprobe studies have revealed low calcium and phosphorus concentrations in the middle layer of the studied Devonian *Phakeloides polonicus* gen. et sp. nov. spines (Ca ~31.8 wt.%, P ~13.4 wt.%), which are much lower than concentrations of the same elements in co-occurring conodont elements (albid crown: Ca ~37.8 wt.%, P ~18.3 wt.%; hyaline crown: Ca ~38.6 wt.%, P ~18.0), except for their basal body (Ca ~33.9 wt. %, P ~14.4 wt.%; cf. Fig. 6A, B). It should be noted that relatively low calcium and phosphorus concentrations were previously measured from the middle layer and internal cavity infilling of Cambrian, *Phakelodus* sp. spines from Sweden, unlike to higher concentrations of the same elements in their outer layer (Wierzbowski et al. 2021).

Fluoride concentrations are relatively high in all studied Devonian fossils (middle layer of *Phakeloides polonicus* gen. et sp. nov. spines: ~3.6 wt.%; conodont albid crown: ~4.2 wt.%; conodont hyaline crown: ~4.2 wt.%; conodont basal body: ~4.1 wt.%; Fig. 6C). Comparable fluoride concentrations were previously reported from the middle layer and cavity infilling of Cambrian, *Phakelodus* sp. spines from Sweden (Wierzbowski et al. 2021). Much lower fluoride content (~2.4 wt.%) was measured from the outer layer of the latter fossils (Wierzbowski et al. 2021).

High sulphur and iron concentrations are observed in the middle layer of Devonian *Phakeloides polonicus* gen. et sp. nov. spines (S ~0.59 wt.%, Fe ~0.24 wt.%) and basal body of coeval conodont elements (S ~0.49 wt.%; Fe ~0.16 wt.%; Fig. 6D, E). Albid and hyaline tissues of conodont elements show much lower concentrations of these elements (albid

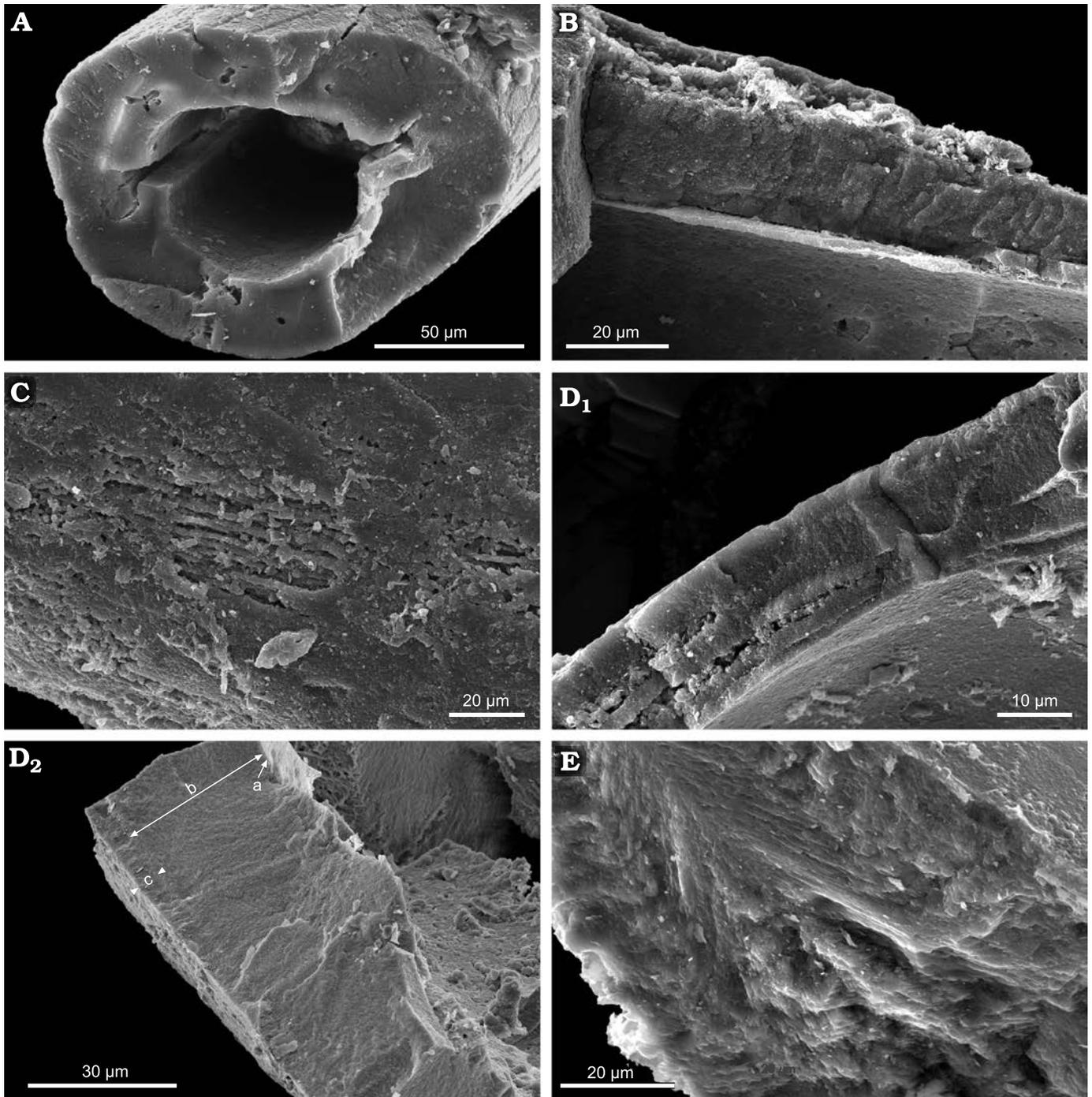


Fig. 4. Scanning electron microscope images of Devonian chaetognath grasping spines *Phakeloides polonicus* gen. et sp. nov. (A–D) and conodont elements (E) from the upper Famennian, Ostrówka Quarry, Holy Cross Mountains, Poland. A. ZPAL Cg. 2/Ost-Ch.31, cross-section throughout the spine showing massive mineral structure of the middle layer characterized by the conchoidal fracture, a reticular ornamentation of the surface of the middle layer is partially visible. B. ZPAL Cg. 2/Ost-Ch.32, longitudinal section throughout the spine showing a massive mineral structure characterized by uneven fracture, which is superimposed on minor breaks forming the second-order cleavage plane. A thin, cylindrical internal layer composed of fine-grained calcium phosphate crystals is visible in the innermost portion of the spine wall, around the internal cavity. C. ZPAL Cg. 2/Ost-Ch.33, a surface of the middle layer of the spine showing oblique to the spine axis, primary fibrils, visible at its slightly, broken part, and less noticeable surface striations of the reticular ornamentation. D. ZPAL Cg. 2/Ost-Ch.34, D<sub>1</sub>, cross-section throughout the spine showing porous internal zones of the middle layer, which are divided by solid cylindrical zones, a thin, cylindrical internal layer is visible in the innermost portion of the spine wall; D<sub>2</sub>, three layers in the wall of the basal portion of the spine: a thin, most internal, layer (a), the middle layer (b), and the outer layer (c). E. ZPAL Cg. 2/Ost-C.38, cross-section throughout *Polynodosus* sp. conodont element showing innermost pillar-like structure of densely packed, weakly lamellar, albid (white matter) tissue, and outer hyaline tissue composed of oblique apatite lamellae. The outermost portion of the conodont element consists of paralamellar variety of the hyaline tissue of more chaotic structure.

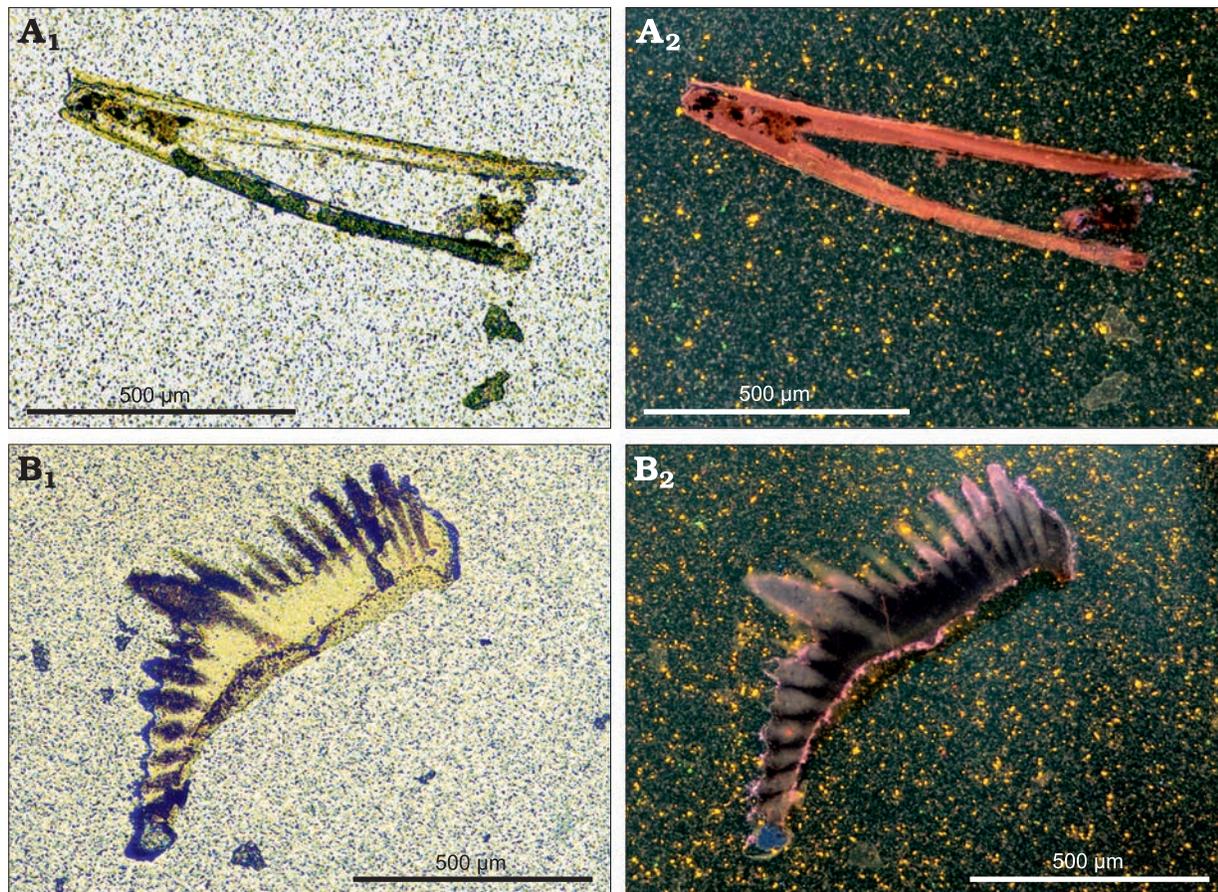


Fig. 5. Transmitted light (A<sub>1</sub>, B<sub>1</sub>) and hot cathodoluminescence images (A<sub>2</sub>, B<sub>2</sub>) of Devonian *Phakeloides polonicus* gen. et sp. nov. grasping spine (A, ZPAL Cg. 2/Ost-Ch.41) and *Polygnathus* sp. conodont element (B, ZPAL Cg. 2/Ost-C.45) from the upper Famennian, Ostrówka Quarry, Holy Cross Mountains, Poland. A<sub>2</sub>, weak to moderate red cathodoluminescence of the grasping spine and bright luminescence of some parts of its outermost rim area. B<sub>2</sub>, very weak yellow-red luminescence of conodont albid tissue and non-luminescent hyaline tissue.

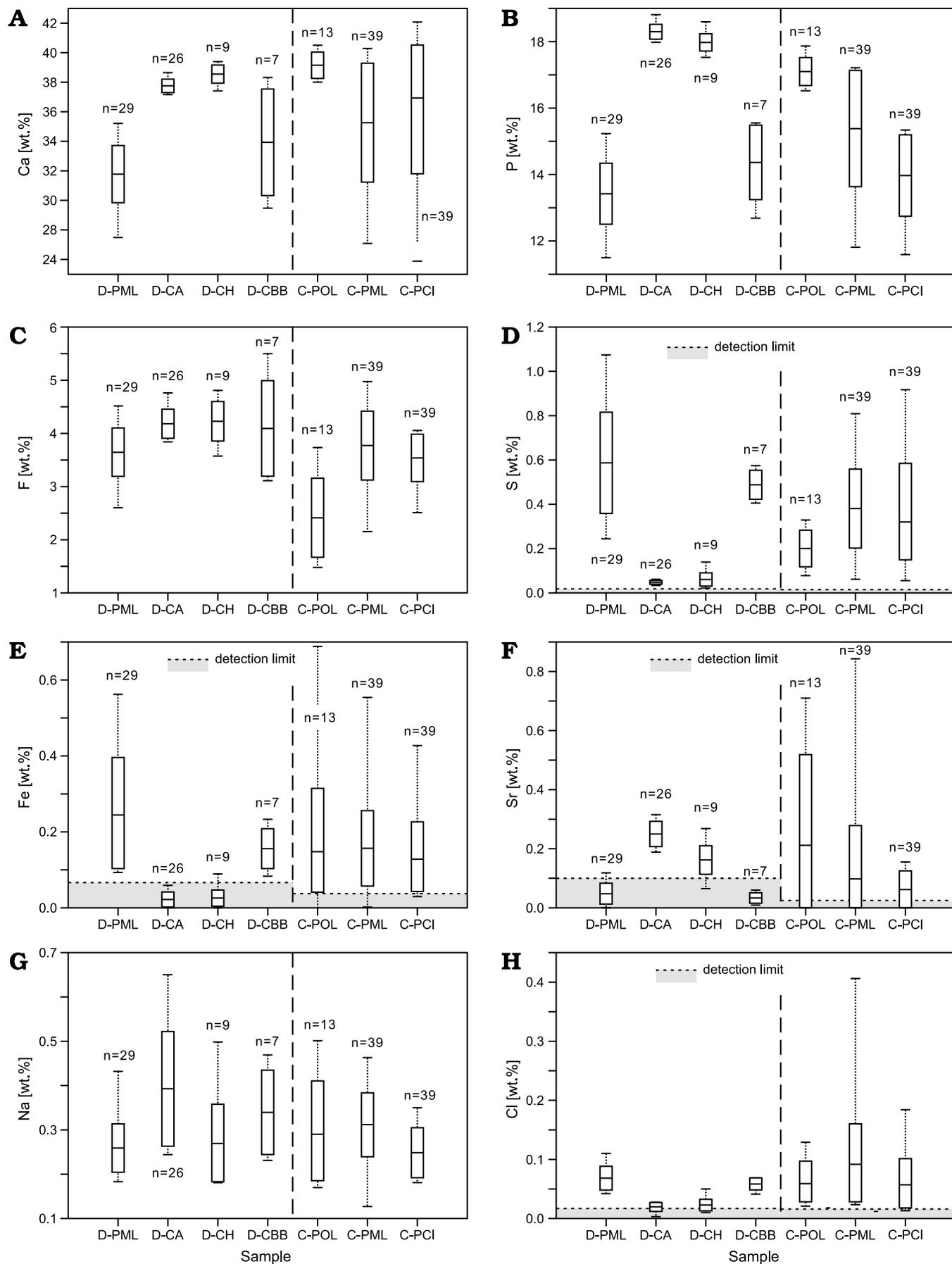
crown: S ~0.05 wt.%; Fe <0.07 wt.%; hyaline crown: S ~0.06 wt.%; Fe <0.07 wt.%). It is worth noting that elevated sulphur and iron concentrations were previously found in all parts of Cambrian, *Phakelodus* sp. spines from Sweden (Wierzbowski et al. 2021).

Studied Devonian, *Phakeloides polonicus* gen. et sp. nov. spines and basal body of conodont elements are characterized by much lower strontium content (<0.1 wt.%) than conodont albid (~0.25 wt.%) and hyaline tissues (0.16 wt.%; Fig. 6F). Relatively low strontium concentrations were also found in middle layer and internal cavity infilling of Cambrian, *Phakelodus* sp. spines from Sweden (Wierzbowski et al. 2021). Distinct differences in sodium and chlorine concentrations of various parts of chaetognath spines and conodont elements are not observed, except for slight chlorine depletion in conodont albid and hyaline tissues (Fig. 6).

BSE images have shown that the studied Devonian *Phakeloides polonicus* gen. et sp. nov. spines consist of apatite phases of similar density, which form the bulk middle and inner layers (Fig. 7). A thin cortex of slightly higher density, which may represent remainders of outer layer, is fragmentarily preserved and occurs in some specimens only (Fig. 7B). It was too thin to be studied for chemical composition using the electron microprobe. The same applies to minute grains of higher density visible in inner parts of the spine walls, which probably represent pyrite microcrystals (Fig. 7).

**Comparison of the structure of the spines of Devonian *Phakeloides polonicus* gen. et sp. nov., Cambrian *Phakelodus* sp. and *Rhombocorniculum cancellatum*.**—The investigation of Devonian *Phakeloides polonicus* gen. et sp. nov. and Cambrian spines of *Phakelodus* sp. has shown

Fig. 6. Concentrations of Ca, P, F, S, Fe, Sr, Na and Cl (A–H) in different structural parts of studied Devonian (D-) conodont elements from the upper → Famennian, Ostrówka Quarry, Holy Cross Mountains, Poland (new data) as well as previously studied Cambrian (C-) *Phakelodus* sp. spines from the Furongian of Sweden (from Wierzbowski et al. 2021). D-PML, *Phakeloides polonicus* gen. et sp. nov. middle layer; D-CA, *Polygnathus* sp. conodont albid; D-CH, *Polygnathus* sp. conodont hyaline; D-CBB, *Polygnathus* sp. conodont basal body; C-POL, *Phakelodus* sp. outer layer; C-PML, *Phakelodus* sp. middle layer; C-PCI, *Phakelodus* sp. cavity infilling. Dotted lines, a range of values; rectangles, 1 standard deviation limits; black horizontal bars, average elemental content.



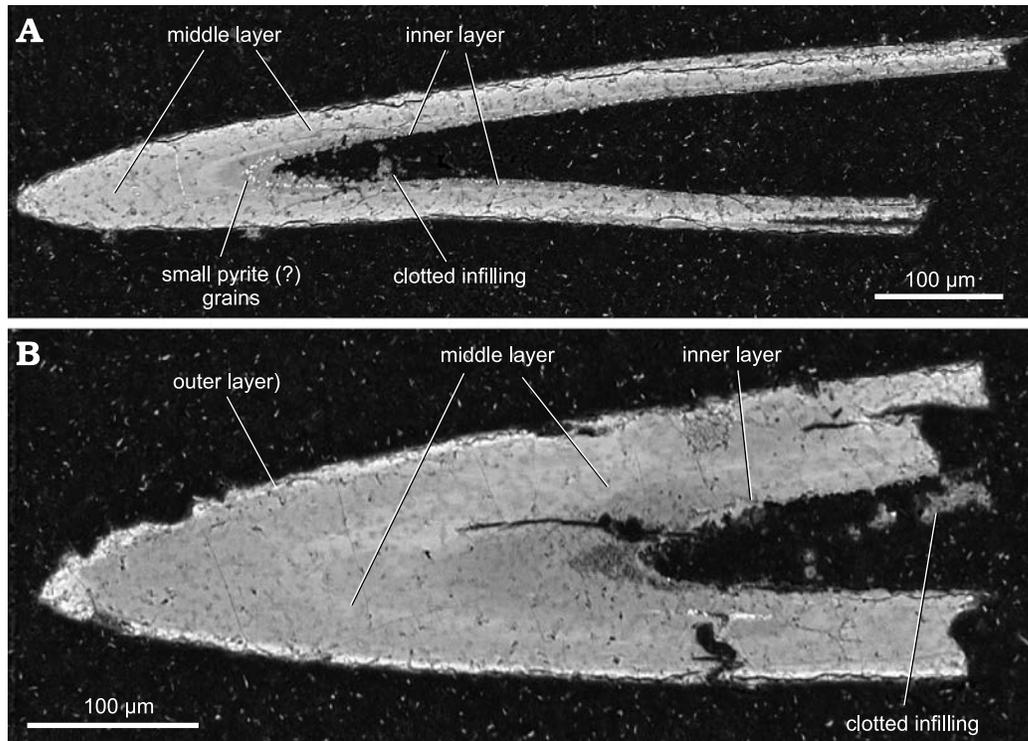


Fig. 7. Back scattered electron images of thin section made of Devonian *Phakeloides polonicus* gen. et sp. nov. spines from the upper Famennian, Ostrówka Quarry, Holy Cross Mountains, Poland. **A.** Longitudinal section of the spine showing the apatite phases of similar density of the middle and inner layers, ZPAL Cg. 2/Ost-Ch.48. **B.** Longitudinal section of the spine showing the apatite phases of similar density of the middle and inner layers as well as a thin cortex of slightly higher density, which may represent fragmentarily preserved outer layer, ZPAL Cg. 2/Ost-Ch.49.

significant similarity of these fossils in terms of their shape and morphology. They include a similar hollow and approximately round shape, layered internal structure, and the same manner of ontogenetic growth of individual elements into basal direction. Both Devonian *Phakeloides polonicus* gen. et sp. nov. and Cambrian *Phakelodus* sp. chaetognath grasping spines are gently curved. Their wall structure likely consisted of a thin, outer, and an apparently homogenous, comparatively thick and fibrous middle layer as well as a thin inner, laminated layer. The outer layer of Devonian *Phakeloides polonicus* gen. et sp. nov. is, however, fragmentarily preserved, mostly in basal areas of the spines (Fig. 2A), while relatively intact middle and inner layers of the same fossils extend around a large pulp cavity from the base to the tip of the spines. Both groups of spines show, in many places, a fibrous structure of the middle layer (Fig. 4C and Szaniawski 2002: fig. 4B).

Grasping spines of Cambrian *Phakelodus* sp. have oval or trapezoidal cross-section (Szaniawski 1983, 2002), whereas Devonian *Phakeloides polonicus* gen. et sp. nov. spines are more circular. The surfaces of both Cambrian *Phakelodus* sp. and the Devonian *Phakeloides polonicus* gen. et sp. nov. spines are ornamented but their details are different. The surface of *Phakelodus* sp. grasping spines is ornamented by longitudinal ridges and narrow oblique furrows (Szaniawski 1983, 2002: fig. 1). In contrast, the *Phakeloides polonicus* gen. et sp. nov. spines show a mosa-

ic-like, rhomboidal ornamentation consisting of obliquely crossing shallow furrows (Fig. 2A–C).

It is worth noting that ornamentation of the Devonian *Phakeloides polonicus* gen. et sp. nov. spines greatly resembles the reticular, rhomboidal sculpture developed on the surface of Cambrian (Series 2 and 3) spines of *Rhombocorniculum cancellatum* interpreted presently as sclerites of a *Hallucigenia*-like lobopodian worm (Caron et al. 2013). The *Rhombocorniculum* spines despite mostly elongated, gently curved shape, the occurrence of dextral and sinistral forms, internal cavity and three structural layers differ from the phosphatized chaetognath grasping spines due to the presence of thicker spine walls and mostly coaxial, internal hollow tubules in the internal structure of the middle layer (Guaxiong et al. 2003), although their fibrous wall structure was also reported (Landing et al. 1980). In addition, the convex shape of rhomboidal sculpture of *Rhombocorniculum* spines (cf. Brasier, 1986: fig. 5, 1989: pl. 7.2; Landing 1995: fig. 5; Guaxiong et al. 2003: fig. 1; Caron et al. 2013: figs. 1, 2; Kouchinsky et al. 2015: figs. 49–52), which actually consists of inclined triangular scales raised above the smooth surface of the spines (Caron et al. 2013), differs from concave rhomboidal surface furrows of the studied Upper Devonian *Phakeloides polonicus* gen. et sp. nov. spines.

Irregular boring networks composed of minute meandering and branching tunnels, which are visible on the surface and inside of the middle and inner layers of studied chaetognath spines (Figs. 2I, 4A) can be regarded as second-

ary phenomena. These burrows in the phosphatized spines might have been formed by some food-seeking benthic organisms during short periods of their excavation.

## Discussion

**Biostratigraphy.**—The stratigraphy and sedimentology of the Famennian limestone beds from the Ostrówka Quarry is documented by Szulczewski (1971), Szulczewski et al. (1996), and Dzik (2006). The studied samples have yielded a conodont assemblage with dominant *Dasbergina granulose*, *Palmatolepis schindewolfi*, *Palmatolepis trachytera*, *Polynodosus lauriformis*, and *Polygnathus* sp., which suggests that all studied chaetognath spines and conodonts are derived from the *Lagovignathus styriacus* Zone of the upper Famennian of the Upper Devonian (cf. Dzik 2006: fig. 3). All the previously unidentified small chaetognath grasping spines have been assigned to a new species, *Phakeloides polonicus* gen. et sp. nov.

**Microstructure, cathodoluminescence, and chemical composition of Devonian *Phakeloides polonicus* gen. et sp. nov. grasping spines.**—Weak to moderate red cathodoluminescence of the bulk interior of the studied Devonian *Phakeloides polonicus* gen. et sp. nov. spines may be related to remarkable incorporation of manganese and rare earth element (REE) into apatite crystal lattice during diagenetic processes (Fig. 5; Ségalen et al. 2008; Fischer et al. 2012, 2013; Wierzbowski 2021). In addition, low calcium and phosphorus contents, as well as elevated sulphur, iron, and fluoride concentrations of the middle layer of the *Phakeloides polonicus* gen. et sp. nov. spines (Fig. 6A–E) should be regarded, respectively, as a result of (i) its poorly mineralized, porous structure and/or the presence of significant amount of organic matter (cf. Szaniawski 1982, 1983, 2002) and (ii) the effect of supplying of certain chemical elements by pore waters in post-depositional processes (cf. Bocherens et al. 1994; Kohn et al. 1999; Wierzbowski 2021; Wierzbowski et al. 2021). This points to the re-crystallization or the secondary origin of phosphate mineral phases of the studied chaetognath spines. Their phosphatization, associated with pyrite incrustation, likely occurred in reducing pore waters, characterized by the abundance of dissolved manganese and iron and elevated REE concentrations (cf. Marshall 1992; Haley et al. 2004).

The diagenetic origin of chaetognath apatite may be substantiated by the frequent lack of the distinct incremental microstructure of the spines. The spines predominantly consist of randomly oriented, fused apatite microcrystals with pseudolamination emphasised by zones of higher porosity (Fig. 4B, D<sub>1</sub>). Such lamination pattern may arise because of the secondary phosphatization of different, morphological parts of previously organic (chitinous) spines, rather than their original biomineralization. Arranged obliquely to the spine axis and closely packed fibrils of the middle layer, which are distinctive of modern and fossil spines

(cf. Szaniawski 1982, 1983, 2002; Doguzhaeva et al. 2002; Vannier et al. 2007), are observed in certain fragments of the studied specimens only (Fig. 4C). It indicates that the phosphatization process has only partially conserved the original microstructure of the spines. Minor internal microbreaks (cleavage) of the spines (Fig. 4A, B) shows the fragility of diagenetic apatite crystals.

The diagenetic phosphate mineralization was likely a selective process as co-occurring albid and hyaline tissues of conodont elements, which have common taphonomic history with the studied chaetognath spines, do not show any signs of re-crystallization. Conodont apatite is non-luminescent or shows very weak cathodoluminescence intensity and low concentrations of secondary sulphur and iron (Figs. 5, 6). In addition, high strontium concentrations in conodont albid and hyaline may be linked to their chemical equilibration with seawater. It is also worth noting that low value of CAI contradicts significant thermal alteration of the upper Famennian (Devonian) deposits of the Holy Cross Mountains in central Poland. Therefore, such process could not have been responsible for the pervasive re-crystallization of phosphate components of the studied rocks.

A thin, outer layer of Cambrian *Phakelodus* sp. spines from Sweden characterized by a dense mineral structure, low fluoride and elevated strontium concentration, which has been assigned to the early marine “Orsten” type phosphatization (cf. Wierzbowski et al. 2021), is mostly lacking in the studied Devonian *Phakeloides polonicus* gen. et sp. nov. The formation of the bulk middle layer of the Cambrian *Phakelodus* spines is, however, related to later stages of diagenesis similarly to the middle layer of the Devonian *Phakeloides polonicus* gen. et sp. nov. spines (cf. Wierzbowski et al. 2021). This points to a difference in the pathways of phosphatization processes between Cambrian and Devonian chaetognath grasping spines, the latter of which did not undergo very early “Orsten”-like apatite impregnation of their cuticle layer.

The “Orsten” type phosphatization of small invertebrate organisms leading to preservation of their three-dimensional fossils with minor structural details and, at least, some phosphatized chaetognath spines is mostly known from the Cambrian–Lower Ordovician (cf. Müller 1979; Andres 1989; Müller and Walossek 1985; Maas and Waloszek 2001; Waloszek 2003; Maas et al. 2006; Eriksson et al. 2012, 2016; Shen et al. 2013; Wierzbowski et al. 2021; Olempska et al. 2023). It is assigned to the widespread phosphate mineralization in the earliest Palaeozoic sediments due to high load and concentrations of phosphorus in pore waters, varying redox conditions and low ventilation of deposits, before the Ordovician diversification of burrowing animals (Shen et al. 2000; Dornbos 2011; Creveling et al. 2014; Pruss et al. 2018). Less common findings of phosphatized small shelly fossils, including one discovery of chaetognath spines, are reported from the upper Palaeozoic, Mesozoic or Cenozoic deposits of various parts of the world (Dzik 1994; Duncan et al. 1998; Walossek 1999; Doguzhaeva et al. 2002; Dattilo et al. 2016; Pruss et al. 2018). It is, unfortunately, unclear if the re-

ported, younger phosphatized fossils show any differences in timing and the pathway of diagenetic mineralization processes, which might be comparable to differences noted between the previously studied Cambrian *Phakelodus* sp. spines and the newly investigated Devonian *Phakeloides polonicus* gen. et sp. nov. material.

**Specific structural features of Devonian *Phakeloides polonicus* gen. et sp. nov. grasping spines.**—A removal of the cuticle layer of the studied chaetognath spines may have unveiled the concave reticular ornamentation of the surface of the middle layer (Fig. 4D<sub>2</sub>), which is not visible in other fossil or modern chaetognath spines with preserved outer layer. It is also possible that the mosaic-like ornamentation pattern may be a characteristic feature of some late Palaeozoic chaetognath grasping spines being not present in their fossil and modern counterparts.

The rhomboidal ornamentation of the Devonian, *Phakeloides polonicus* gen. et sp. nov. chaetognath grasping spines may also point to their affinity to problematic spines of the Cambrian *Rhombocorniculum cancellatum*. In fact, one of the major structural difference of *Rhombocorniculum cancellatum* spines, compared to those of *Phakeloides* sp., i.e., their porous internal structure and the presence of internal hollow tubules, parallel to the longitudinal axis of the spines (cf. Guoxiang et al. 2003; Kouchinsky et al. 2015), can be a diagenetic feature related to incomplete apatite mineralization of the middle layer of originally organic spines. Although the middle layer of modern chaetognath spines is described as consisting of obliquely arranged fibrils or fiber bundles (cf. Szaniawski 1983; Bone et al. 1983), those structures are often arranged nearly parallel to the spine axis (see Szaniawski 2002: fig. 5; Doguzhaeva et al. 2002: fig. 6C). It is therefore possible that partial phosphatization of original, thicker and less tightly packed fiber structure of the middle layer of some Cambrian chaetognath spines might have produced hollow tubules and spongy mineral network similar to that of *Rhombocorniculum cancellatum*. On the other hand, the convex shape of rhomboidal sculpture of *Rhombocorniculum cancellatum* clearly differs from concave rhomboidal ornamentation of the studied Devonian, *Phakeloides polonicus* gen. et sp. nov. spines. Therefore, the resemblance of internal structures of both fossil groups may be related to convergent evolution. It is also possible that some Cambrian chaetognath spines of rhomboidal ornamentation are wrongly classified as belonging to *Rhombocorniculum*.

Another feature of the Devonian *Phakeloides polonicus* gen. et sp. nov. spines from the Holy Cross Mountains of central Poland is their approximately round shape, devoid of any signs of flattening and the lack of longitudinal lamination. They are different from the majority of more oval or trapezoidal fossil or modern spines showing external ridges or lamination (cf. Bone et al. 1983; cf. Doguzhaeva et al. 2002; Moreno and Kapp 2003; Szaniawski 2002, 2015). The lack of such structures can hardly be linked to the removal of the outer layer of the studied spines. In addition, the lack

of flattening of the studied Devonian chaetognath grasping spines contradicts their deep burial before phosphatization (contrary to flattening of the Cambrian carbonaceous spines; Slater et al. 2018; Slater and Willman 2019). This may point to relatively long residence time of these fossils in the upper part of sediment column, in the oxygen-depleted environment, under fluctuating redox conditions and significant flux of phosphorus, which might have led to their phosphatization. The condensed Famennian limestone beds exposed in the Ostrówka Quarry show mixed lithology and represent a transition between the crinoidal and cephalopod limestone beds. The crinoidal limestone beds are distinctive of an earlier phase of drowning of the shallow-water carbonate platform, whereas the cephalopod limestone, from which the studied material is derived, represents a later, pelagic stage of deposition (e.g., Szulczewski et al. 1996). The condensed nature of these beds may have allowed accumulation of organic skeletal elements close to the sediment-water interface and their subsequent phosphatization.

## Conclusions

Devonian chaetognath grasping spines from the upper Famennian of the Holy Cross Mountains in central Poland have been assigned to the newly established *Phakeloides polonicus* gen. et sp. nov. species. It is known from an isolated occurrence in upper Palaeozoic rocks of the Holy Cross Mountains in central Poland and shows characteristic mosaic-like ornamentation of the surface.

The studied Devonian *Phakeloides polonicus* gen. et sp. nov. chaetognath grasping spines are built of diagenetic phosphate phases and possess poorly mineralized, porous mineral structure. It is demonstrated by moderate cathodoluminescence intensity, high concentrations of diagenetic sulphur, iron and fluoride, low concentrations of strontium as well as decreased contents of major elements including calcium and phosphorus. *Phakeloides polonicus* gen. et sp. nov. spines mostly consist of secondary, fairly massive, mineral structure of the middle layer, which has preserved major structural features of the spines including primary shape and layered-architecture. Minor structural details of the spines like fibrils of the middle layer are visible only locally. In addition, the outer layer of the spines is fragmentarily preserved, which has revealed characteristic, mosaic-like ornamentation of the surface of their middle layer. The remainders of the outer layer are mostly found at the base of the spines.

The observed features of *Phakeloides polonicus* gen. et sp. nov. spines likely arose because of their slow, post-depositional phosphatization, close to the sediment-water interface, in condensed, transgressional Upper Devonian sequence. The Devonian, *Phakeloides polonicus* gen. et sp. nov. spines possess a round shape, without longitudinal lamination, contrary to many lower Palaeozoic spines and are devoid of early diagenetic “Orsten” type mineralization of the outer, cuticle layer (cf. Wierzbowski et al. 2021).

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