

A Silurian volcanic island slope as an archive of mixed terrestrial and marine biota from the Prague Basin, Czech Republic: an integrated biochemostratigraphy and multiproxy analysis

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ABSTRACT

The Sheinwoodian represents a critical interval in the early colonisation of terrestrial environments by vascular plants and associated cryptogamic assemblages. The Prague Basin is a historically important region, having yielded the first formally described cooksonioid plant remains. A multidisciplinary re-examination of one of Barrande's original localities, the Sedlec, Stydlé Vody Section, integrating petrography, clay mineralogy, stable-isotope and trace-element geochemistry, and macro- and microfossil data is presented herein.

The studied interval consists of tuffaceous limestones and volcaniclastic interbeds of the Motol Formation, deposited on a distal volcaniclastic slope, where episodic sediment-gravity flows transported biotic material from shallower settings. The unique integration of conodont, chitinozoan, and graptolite biostratigraphic data constrains the section to the mid-Sheinwoodian. This interval encompasses the *Monograptus belophorus* and *Cyrtograptus rigidus* graptolite biozones, the middle part of the *Jeppsonia sagitta rhenana* Conodont Superzone, and the *Cingulochitina cingulata* chitinozoan Biozone. Carbonate $\delta^{13}\text{C}$ values further confirm deposition after the early Sheinwoodian positive carbon isotope excursion (ESCIE).

Both marine and terrestrial biotic signals are preserved within the Stydlé Vody slope deposits. The high diversity of dispersed spores together with associated plant remains indicates a diverse vegetation in the source area on adjacent emergent volcanic peaks, including rhyniophytes, zosterophylls, and eophytes. Jawed polychaetes (scolecodonts) are documented in detail for the first time from this stratigraphic interval and region, extending the spatial distribution of this group. Chitinozoan, conodont, and scolecodont assemblages further support palaeobiogeographic links between the Prague Basin (peri-Gondwana) and coeval successions of Baltica.

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1. Introduction

The mid-Silurian represents a pivotal interval in Earth's history, marked by the adaptation of plants to life on land, paving the way for more complex life forms (and the initial establishment of terrestrial ecosystem). The early evolution of land plants profoundly transformed the Earth system. Rooting structures stabilised soils and reduced erosion, enhanced biogeochemical weathering and soil formation, influenced the terrestrial hydrological cycle and the transport and accumulation of terrigenous material, and drove major changes in biogeochemical cycling and carbon burial (Algeo and Scheckler, 1998; Gibling and Davies, 2012; Xue et al., 2016, 2018; Dahl and Arens, 2020). Photosynthetic activity of early land plants also contributed to the progressive oxygenation of the atmosphere.

Despite this significance, the fossil record of the earliest terrestrial ecosystems remains fragmentary. The Sedlec, Stydlé Vody Section in the Prague Basin, Czech Republic, has been recognised as an early land-plant locality since the 19th century, when extensive excavations led by a French geologist, Joachim Barrande, yielded the oldest described cooksonioid representatives (Libertín et al., 2003, 2018a, 2018b). The section comprises a volcanoclastic slope succession of the Motol Formation deposited adjacent to a volcanic peak that likely became emergent by mid-Sheinwoodian time, providing a source of terrestrial plant remains and spores (Libertín et al., 2003, 2018a, 2018b). Marine fauna and terrestrial plant remains, including dispersed spores and plant macroremains, co-occur throughout the succession.

In this study, this classic locality has been re-examined to place the biotic record within a robust stratigraphic and environmental framework by integrating petrographic observations, stable isotope and trace-element geochemistry, and clay mineralogy with detailed palaeontological datasets. Chitinozoans and scolecodonts have not previously been reported from the mid-Sheinwoodian interval of the Prague Basin; representative assemblages are documented herein to strengthen stratigraphic control and palaeoenvironmental interpretation. Importantly, the succession is constrained by three independent biostratigraphic schemes: graptolites, conodonts, and chitinozoans. This biostratigraphic control, together with a $\delta^{13}\text{C}$ record, forms a unique integrated biogeostratigraphic framework that provides unusually strong temporal resolution for a single section and enables correlation with global Sheinwoodian carbon-cycle perturbations. High-resolution studies integrating all above-mentioned groups are rare owing to their contrasting facies distributions but are critically needed (Cramer et al., 2010a, 2010b).

Given that the succession accumulated on a volcanoclastic slope adjacent to a likely emergent volcanic peak, it provides an opportunity to place the co-occurring terrestrial and marine signals within a well-constrained depositional and diagenetic framework. Volcanic island settings have been proposed as favourable substrates for early terrestrial colonisation (Gopal et al., 2020); this concept is therefore applied to the Sedlec, Stydlé Vody record, considering its volcanically influenced source area and oxygen-restricted depositional environment.

2. Geological settings

The Prague Basin, representing the central part of Teplá-Barrandian Unit (TBU, Bohemian Massif), presumably originated as a narrow, fault-bounded graben and has been interpreted as part of the extensive peri-Gondwana passive margin in the southern realms of the Rheic Ocean (e.g., Patočka et al., 2003; Patočka and Storch, 2004; Aifa et al., 2007; Žák et al., 2013), situated at the periphery of the main Gondwanan shelf, that is, far from the Gondwanan craton, in the outer margin of a marginal sea. Similar to other areas of peri-Gondwana or northern Gondwana, this unit drifted from high southern to northern equatorial latitudes during the Paleozoic. During the early Silurian, the position is estimated to have been situated at high latitudes on the northwestern peri-Gondwana shelf (Patočka et al., 2003). Havlíček et al. (1994) proposed the existence of

an independent palaeo-plate named Perunica based on the study of brachiopods, trilobites, and other largely benthic faunas. In this concept, the TBU, within which the Prague Basin was formed, forms the crustal core of Perunica. The rather isolated, though debated, position of the Perunica microplate is also suggested by palaeomagnetic data (Tasáryová et al., 2014, and references therein). However, Servais and Sintubin (2009) argued that the Perunica microplate was simply a part of the northern Gondwanan terrane assemblage (the Armorican terrane assemblage). The palaeogeographic position of the outer Gondwanan shelf is widely accepted at approximately 30° south latitude (e.g., Scotese, 2001; Servais and Sintubin, 2009; Stampfli et al., 2013).

The stratigraphic record of the Prague Basin, preserved between Prague and Pilsen, comprises Ordovician to Middle Devonian marine sediments and syn-sedimentary volcanics. The current geometry of the basin was shaped during the Variscan orogeny, which substantially modified the sedimentary infill of the former marine domain. Silurian strata are primarily confined to the central part of the synform, where sedimentation was influenced by mid-Wenlock to mid-Ludlow syn-sedimentary volcanic activity. This volcanism generated volcanic islands or archipelago surrounded by shallow-water settings (Bouček, 1934; Horný, 1962; Kríž, 1991).

The largest volcanic peak, the Svatý Jan volcanic centre, likely emerged above sea level during the middle Sheinwoodian, as indicated by the presence of land plant fossils and spores in marine sediments deposited in the adjacent area (Libertín et al., 2003, 2018a, 2018b; Bek et al., 2022). This volcanic island remained emergent until the early Přídolí, as documented by subaerial basalt lavas of the latest Wenlock–early Ludlow age, overlain by middle Přídolí crinoidal limestones with a prominent erosional unconformity (Havlíček et al., 1987). A continuous transition from shallow water biotrital limestones to offshore, laminated tuffaceous shales, associated with specific depth-related benthic faunal communities (Havlíček and Storch, 1990), indicates that the basin reached a maximum depth of approximately 200 m in offshore settings, characterised by black shale-dominated facies rich in graptolites (see Turek, 1983; Storch and Pašava, 1989; Manda et al., 2019).

The Motol Formation of the Prague Basin spans the uppermost Telychian to Homerian and comprises predominantly calcareous clayey shales that become progressively marly and carbonate-rich upward, with an increasing contribution of volcanoclastic material. Progressive environmental differentiation of the basin during the Sheinwoodian–Homerian is linked to synsedimentary basaltic volcanism, which generated volcanic peaks and associated volcano-sedimentary facies including tuffites, hyaloclastites, subordinate effusive basalts, and biotrital limestones. Distal offshore facies are characterised by laminated calcareous shales with tuffitic admixture, limestone nodules and local slump deposits, which provide high-resolution graptolite biostratigraphic records in parts of the formation (Storch, 2023). Two major Silurian carbon-isotope excursions have been documented within the Motol Formation, including the early Sheinwoodian positive excursion in its basal part (Frýda et al., 2015). A typical double-peak Homerian carbonate carbon isotope excursion occurs in several sections of the Kozel Limestone Member (Frýda and Frýdová, 2014, 2016). The Homerian organic carbon isotope excursion and associated *Lundgreni* bioevent are well documented from the offshore setting of the Prague Basin (Manda et al., 2019; Vodička and Manda, 2019; Frýda and Frýdová, 2025).

The Sedlec, Stydlé Vody Section (herein referred to as Stydlé Vody Section; NE of Beroun; 49°58'44.460"N, 14°9'2.760"E, Fig. 1) corresponds to the “Svatý Jan-Sedlec rock” of Storch (2023) and belongs to the mid-Sheinwoodian *Monograptus belophorus* and *Cyrtograptus rigidus* biozones (Figs. 2, 3). Whereas these biozones are typically represented by calcareous graptolitic black shales across most of the Prague Basin, a local *Miraspis* limestone facies, comprising alternating tuffitic calcareous shales and thin-bedded limestones with mixed graptolite, trilobite, and shelly fauna, is developed within the *belophorus* Biozone near the Svatý

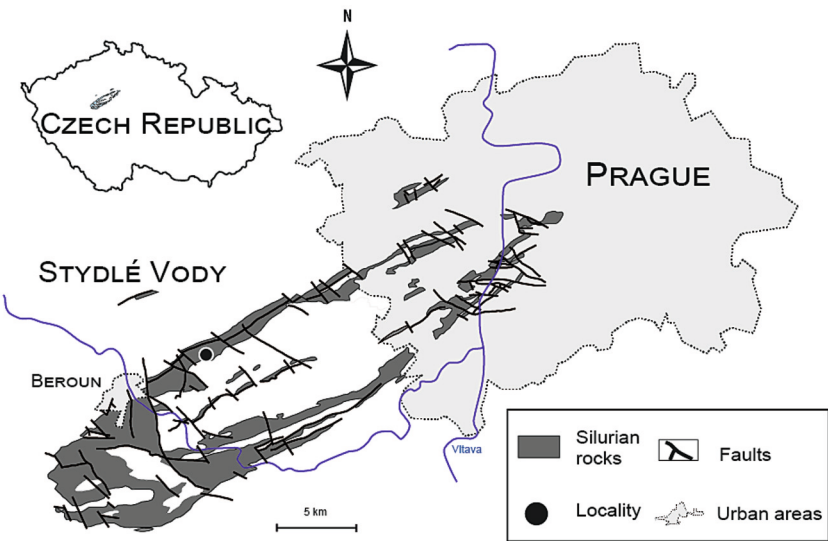


Fig. 1. Map of the studied region, position of the Prague Basin in the Czech Republic, and the position of the locality Stydlé Vody Section in the Prague Basin. The extension of the Silurian rocks is depicted.

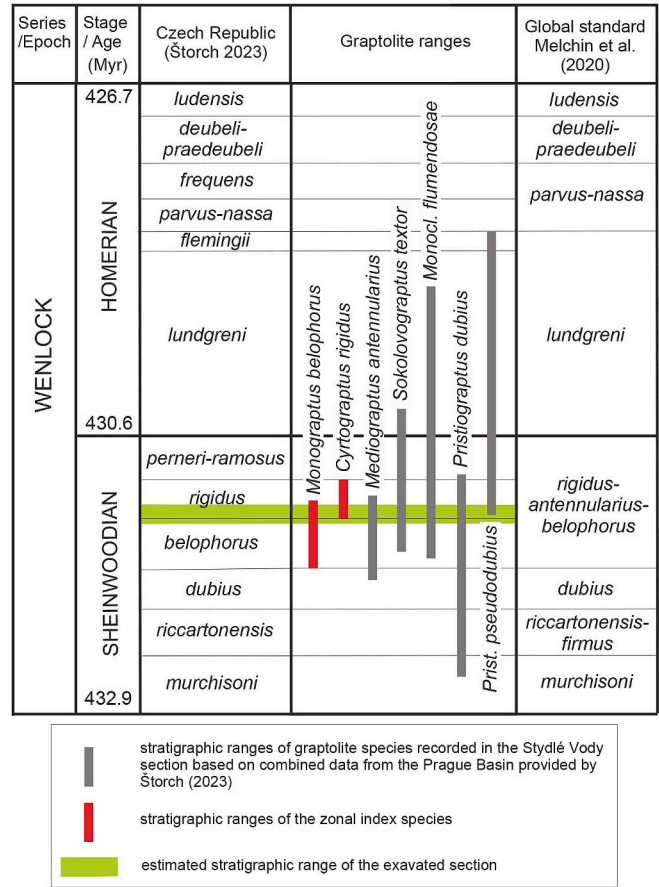


Fig. 2. Stratigraphic chart modified from publications by Slavík (2014) and Štorch (2023). The chart includes the range of graptolite species in the Stydlé Vody Section.

Jan volcanic centre (Bouček, 1941; Libertín et al., 2018a; Bek et al., 2022; Štorch, 2023; Mergl, 2024).

Renewed fieldwork in 2023 re-exposed part of Barrande's historic excavation, enabling stratigraphically constrained, high-resolution sampling of the succession. The studied interval consists of massive to

thinly laminated limestones interbedded with tuffites, consistent with deposition on a volcanoclastic slope adjacent to a volcanic peak. The associated macrofauna of the *Miraspis-Mezounia* Community (Havlíček and Štorch, 1990) comprises trilobites, brachiopods, and other shelly elements, together with dendroid graptolites (Fig. 4). This community has been interpreted to reflect quiet-water conditions with slight oxygen depletion (Havlíček and Štorch, 1999), consistent with the laminated character of the host deposits.

3. Material and methods

3.1. Fossils

Twenty-seven stratigraphic levels, represented by 52 samples from the upper part of the Motol Formation of the Stydlé Vody Section, were processed using the standard palynological techniques, including dissolution in 6% acetic acid (Jeppsson et al., 1999) and the HCl-HF-HCl protocol of Riding (2021) in the Palynological laboratory of the Czech Geological Survey, Prague. Primary treatment involved acetic acid, and, if necessary, samples were subsequently treated with HCl and HF. The wet insoluble residue was sieved using 50 and 10 µm meshes. The >50 µm fraction was hand-picked from Petri dishes under a stereomicroscope using a micropipette or an eyelash, following the wet technique introduced by Kielan-Jaworowska (1966). Picked microfossils were stored in glycerine in small plastic boxes.

The organic residue yielded scolecodonts, chitinozoans, conodonts, brachiopods, gastropods, bivalves, ostracods, sponge spicules, and, more rarely, the mollusc *Jinonicella* Pokorný. Preservation ranged from moderate to poor, with many specimens flattened and deformed. Chitinozoans and scolecodonts were mainly flattened; however, several levels yielded three-dimensionally preserved specimens. The organic matter forming the microfossil walls is notably fragile, and specimens tend to disintegrate during manipulation. Conodonts were poorly preserved, and most elements were fragmented.

Eleven levels were productive for conodonts, yielding a total of 340 specimens, with sample counts ranging from 3 (SV19) to 65 (SV16), equivalent to 7–210 specimens per kilogram of rock. Forty samples from 23 lithologic levels yielded 680 specimens of chitinozoans, with the richest assemblages occurring in the lowermost part of the section, where the abundance exceeded 500 specimens per kg (average is 20 specimens per kg). Except for four samples, all levels contained scolecodonts. In total, at least 830 specimens were present, with an average

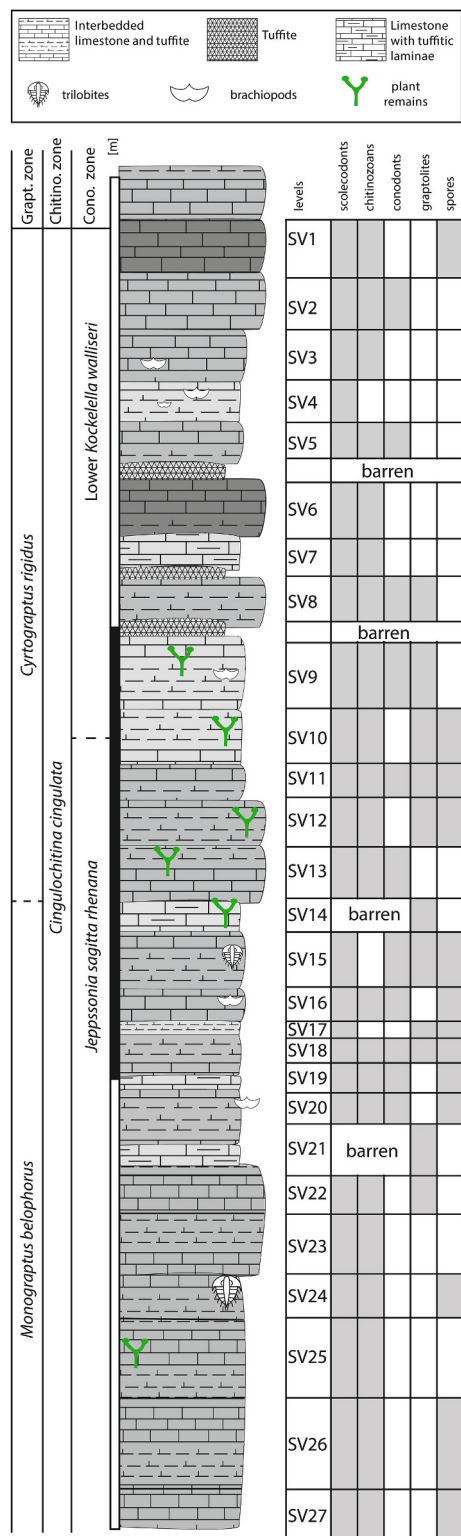


Fig. 3. Schematic illustration of the lithology of the Stydlé Vody Section, with graptolite biozones (= grapt. zone), chitinozoan zone (= chitino. zone), and conodont zones (= cono. zone). Occurrences of microfossils (scolecodonts, spores, chitinozoans, and conodonts) and graptolites are depicted in the table. The barren samples are barren for organic-walled microfossils and conodonts.

abundance of 50 specimens per kilogram of rock. The maximum abundance was in the lowermost samples, over 400 specimens per kg.

The microfossils were mounted on aluminium stubs using a water-soluble glue for microfossils (Kreativika), coated with a

gold-palladium (Au/Pd) alloy under vacuum, and imaged using a Scanning Electron Microscope (SEM) FEG-SEM Tescan Mira 3GMU at the Czech Geological Survey, Prague. Graptolites and associated fauna were photographed either dry or immersed in ethanol, using Olympus SZX 16 and Olympus SZX 10 stereomicroscopes fitted with a Canon EOS 2000D camera at the Institute of Geology of the Academy of Sciences and at the Depository of the National Museum. All specimens are housed in the collections of the National Museum under numbers L69234–L69246 and D581NM–D589NM, and in the collections of the Czech Geological Survey, Prague, under numbers PŠ4842–PŠ4862, and PT177–PT216.

3.2. Isotope chemostratigraphy, and petrography methods

For $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{18}\text{O}_{\text{carb}}$ isotope chemostratigraphy, 27 samples were analysed. A few milligrams of powder from ‘bulk’ carbonate samples, targeting (where possible) micritic mudstones or wackestones, were sampled. Powder sampling was performed using a micro-drill tool from cut rock fragments or polished slabs. The powders for $\delta^{13}\text{C}_{\text{carb}}$ analyses were first heated and dried at 100 °C for one hour to remove water and any possible volatile organic contaminants. Then, 2 mg of carbonate powder was reacted with 103% phosphoric acid at 25 °C for approximately 24 h. The carbon and oxygen isotope compositions of the released CO_2 were measured using a Thermo Delta 5 mass spectrometer in a dual-inlet configuration. All isotope values are reported in ‰ relative to the V-PDB by assigning a $\delta^{13}\text{C}$ value of +1.95‰, and a $\delta^{18}\text{O}$ value of +2.20‰ to IAEA-NBS-19. The IAEA-NBS-18 and in-house standards were used as reference standards. Replicate measurements of laboratory standard controlled accuracy and precision were better than $\pm 0.1\text{‰}$ for both carbon and oxygen isotope values.

Sampled sedimentary rocks from the Stydlé Vody Section were lithologically variable, ranging from fine-grained volcanoclastics to tuffaceous limestones. To minimise the effects of carbonate dilution and to enable a more robust comparison of the trace-element compositions, enrichment factors (EFs) were used as Al-normalised element concentrations relative to the average upper continental crust (AUCC) standard of Rudnick and Gao (2003). The enrichment factors of the selected elements were calculated as $X_{\text{EF}} = (X/\text{Al})_{\text{SAMPLE}} / (X/\text{Al})_{\text{AUCC}}$. $\text{EF} > 3$ is considered to indicate an element enrichment above average crustal values, whereas $\text{EF} > 10$ denotes moderate to strong enrichment of elements such as Mo and U (Algeo and Tribouillard, 2009). It should be noted that enrichment factors should be used with caution for marine sediments with very low terrigenous-detrital input, as the calculated enrichment factors may be subject to higher error.

Concentrations of selected major and trace elements were analysed using X-Ray Fluorescence (XRF; Rigaku WD-XRF Primus 4) and inductively coupled plasma mass spectrometry (ICP-MS; Agilent 7900). Several international carbonate or shale standards (GeoPT 40, GeoPT 40A, GeoPT 44, GeoPT 44A, GeoPT 42-Q1, GeoPT 6A-CAL-S, DC73302, DC73306) were used as reference standards. Accuracy and precision were controlled by replicate measurements of laboratory standards and were better than $\pm 5\%$.

A petrographic study was carried out on 13 regular petrographic thin sections and six polished thin sections. Transmitted-light microscopy was performed using a Zeiss Axio Imager A2m. For SEM, half of the three polished thin sections underwent acid etching with 5% CH_3COOH for 20 s; the remaining half was kept unetched. SEM analyses were conducted using a Tescan Mira 3GMU FEG-SEM (Czech Geological Survey, Prague) equipped with two Oxford Instruments Ultim Max 100 energy-dispersive spectrometers (active area 100 mm^2). Operating conditions included an accelerating voltage of 15 kV, a beam current of 1.8 nA, and a working distance of 15 mm. The imaging was performed using a BSE (back-scattered electron) detector. The samples were coated with a 15 nm amorphous carbon layer to prevent charging.

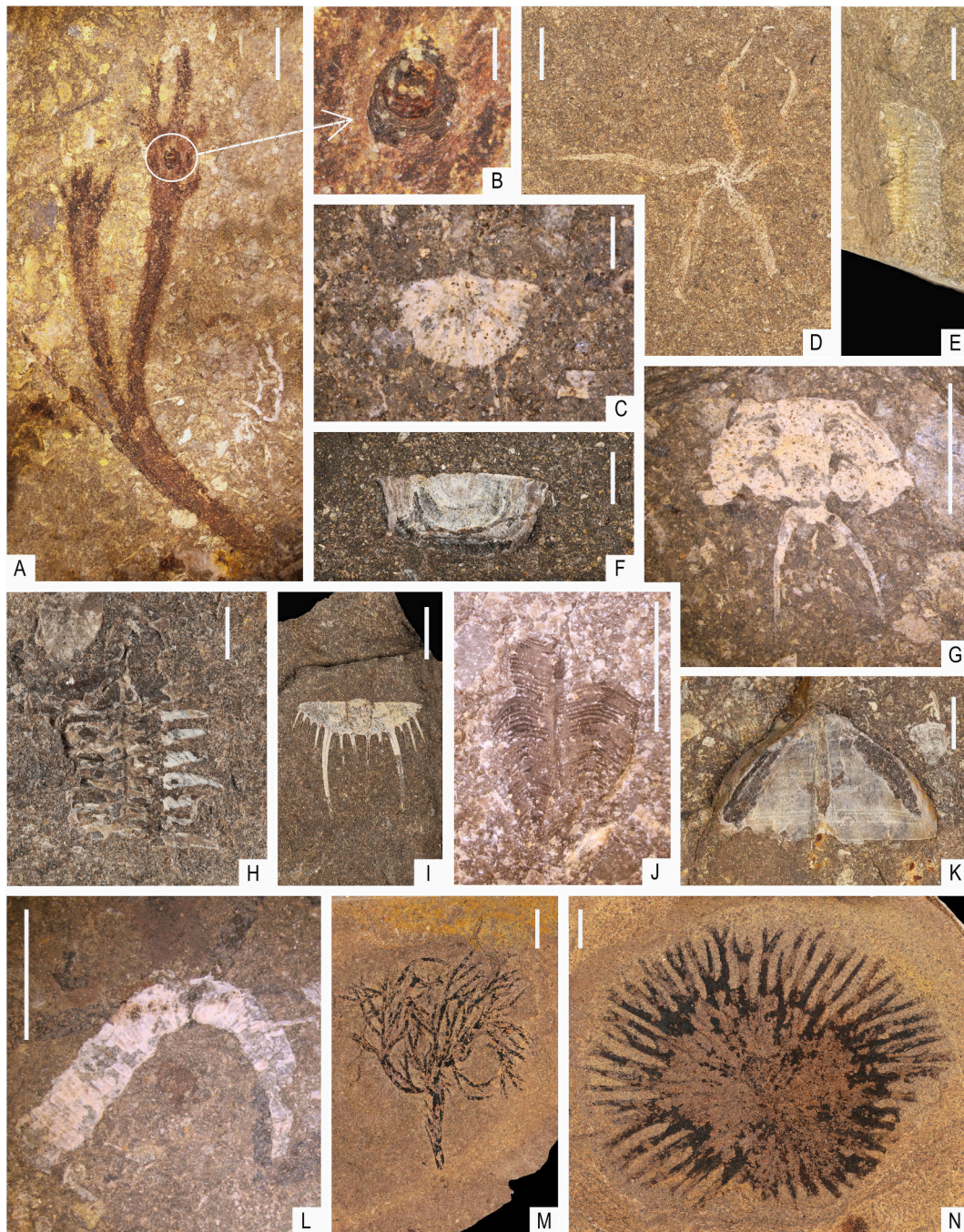


Fig. 4. Accompanying fossils found in the Stydlé Vody Section. The scale bars represent 5 mm, except for figures B and C where they represent 1 mm.

A. Algae with sessile brachiopod, specimen No. L 69234 B. Inarticulate brachiopod, specimen No. L 69234C. Brachiopod *Leptaena*?, specimen No. L69235 D. Ophiuroidea gen et sp. indet., specimen No. L69236 E. Trilobite *Odontopleura* cf. *ovata*, specimen No. L69246 F. Brachiopod *Orhoria amelia* (Havlíček), specimen No. L69237 G. *Odontopleura siemangi* Hawle & Corda, specimen No. L69238 H. *Cheirurus insignis* Beyrich, specimen No. L69239 I. *Odontopleura siemangi* Hawle & Corda, specimen No. L69240 J. Conulariid theca, specimen No. L69241 K. Brachiopod *Cyrtia maior* Bouček, specimen No. L69242 L. The epiplanktic worm or solitary coral *Kolihaia eremita* Prantl, specimen No. L69243 M. Dendroid taxon with erect growth, probably belongs to the family Dendrograptidae or the Callograptidae, specimen No. L69246 N. *Cyclograptus scharyanus* (Goeppert), specimen No. L69245.

3.3. X-ray diffraction (XRD)

The mineralogy of bulk samples, before and after carbonate removal, was analysed using X-ray diffraction (XRD) analysis of random powder mounts. The bulk samples were milled using a McCrone mill, and the mounts were prepared by the side-loading method (PMMA holder). The separated clay fraction, after carbonate removal, was also studied using XRD on random powder mounts prepared on a Si holder with a gap. The semi-quantitative phase analysis was performed using the Rietveld

method (Snyder and Bish, 1989), using the Profex programme (Döbelin and Kleeberg, 2015).

The detailed mineralogy of phyllosilicates was determined by XRD analysis of oriented specimens of the separated clay fraction before and after different treatments (Supplementary Material, Appendix B). The XRD patterns of oriented specimens were modelled using Sybilla Version 2.2 software (Chevron ETC proprietary, Aplin et al., 2006). Parameter R (Reichweite) indicates the extent of layers ordering in the mixed-layered minerals (Jagodzinski, 1949), with R0 corresponding to the random

stacking of layers and R1 to ordered stacking. Parameter N represents the average number of coherent scattering domain sizes (CSDs; Drits et al., 1997). The components of I/S2g/S1g/C mixed-layer minerals (MLMs) modelled from XRD patterns of Ca-saturated and ethylene-glycol solvated clay fraction, represent illite (I), smectite with two and one ethylene glycol layers in the interlayer (S2g and S1g, respectively), and non-expandable 14.1 Å layers (C), including the non-expandable vermiculite layers with hydrated interlayer cations and chlorite layers. The detailed methodology of clay fraction separation, cation-saturations

and X-ray diffraction is provided in the Supplementary Material (Appendix B).

4. Results

4.1. Petrography

4.1.1. Macroscopic and transmitted-light observations

The studied interval consists of thin-bedded, planar-laminated strata

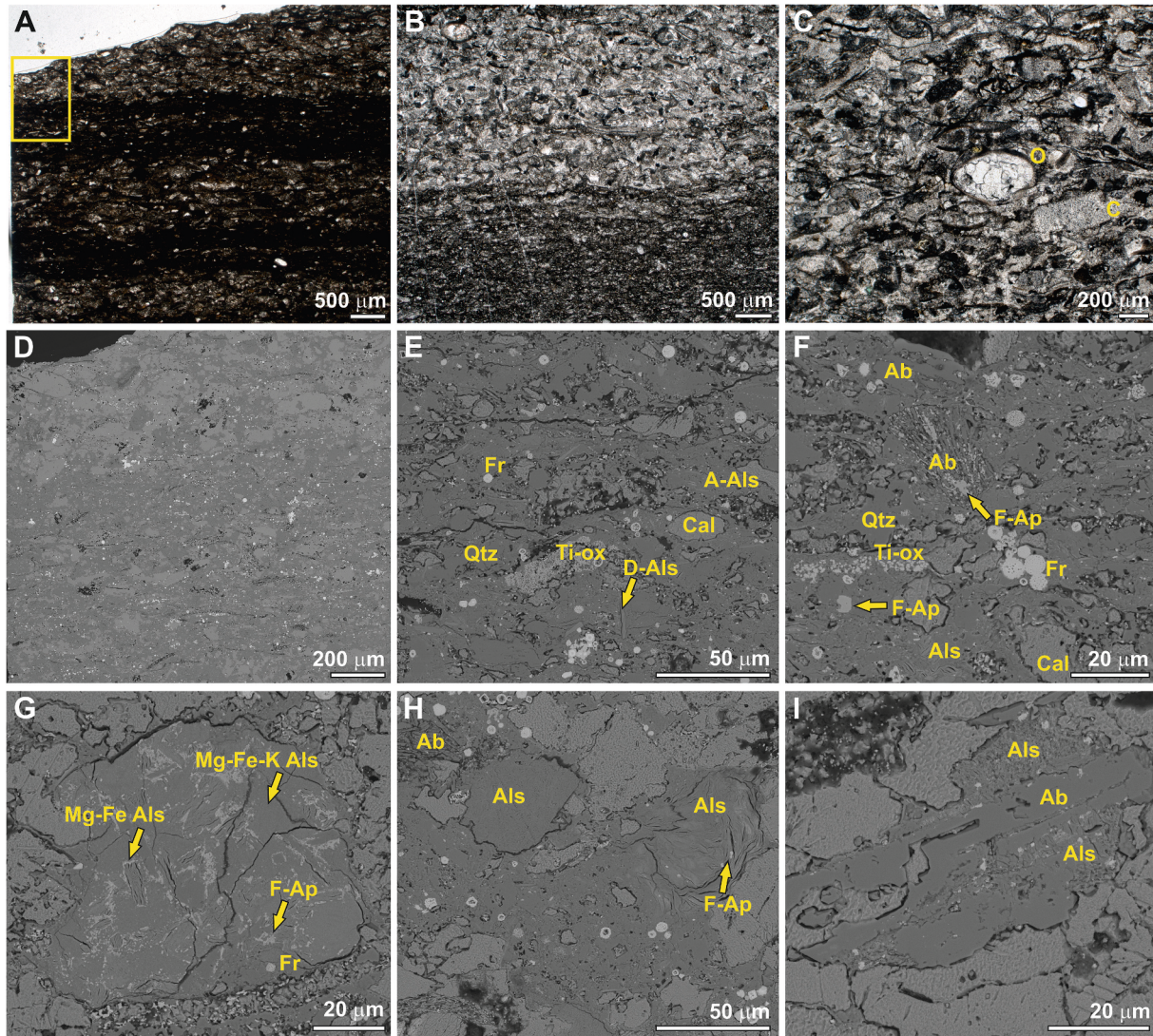


Fig. 5. Transmitted-light (A–C) and SEM-BSE (D–I) images showing microfacies and mineralogical characteristics of alternating tuffitic and skeletal carbonate layers. A. Transmitted-light image showing alternation of lighter, tuffaceous skeletal carbonate layers and darker, tuffitic layers. The yellow rectangle marks the area shown in (D). B. Transmitted-light image showing the sharp contact between a fine-grained skeletal, tuffaceous grainstone (upper part) and the underlying darker, tuffitic layer. The grainstone is composed mainly of fragmented crinoid ossicles and ostracod shells. C. Detail of the fine-grained skeletal grainstone composed mainly of fragmented ostracod shells (O) and crinoid ossicles (C). Dark, rounded to irregular micritic patches represent organic matter-rich microaggregates of uncertain origin. D. BSE image of the silicified tuffitic layer, composed of fine-grained quartz and aluminosilicates with disseminated Fe-oxide pseudomorphs after framboidal pyrite (bright spots). Dark shells (ostracods) are locally enriched in carbonaceous matter. E. BSE image of argillitised tuffite showing a silicified matrix composed of quartz (Qtz) and authigenic aluminosilicates (A-Als) with filamentous to flaky texture. Minor detrital lath-shaped aluminosilicate grain (D-Als), calcite (Cal), Fe-oxide pseudomorph after framboidal pyrite (Fr), and Ti-oxide micrograins (Ti-ox) are also present. F. BSE image showing the fine-grained silicified matrix composed of intergrown quartz (Qtz) and aluminosilicates (Als). Altered albite (Ab) occurs both as individual grains and as aggregates associated with fluorapatite (F-Ap). Ti-oxide micrograins (Ti-ox) and Fe-oxide pseudomorphs after framboidal pyrite (Fr) are dispersed within the matrix. G. SEM–BSE image of an altered volcaniclastic grain in a tuffaceous limestone layer, showing pronounced internal textural and compositional heterogeneity. Fe–Mg-rich and Fe–Mg–K-bearing aluminosilicate domains occur within a single grain and are locally associated with bright F-apatite patches. H. SEM–BSE image showing compositional variability within adjacent aluminosilicate domains (Als) in a tuffaceous limestone. The grains display heterogeneous Fe–Mg–K compositions and internal alteration textures, locally accompanied by bright F-apatite patches. The transition into a dense silicified mass indicates progressive alteration and silica redistribution during diagenesis. I. SEM–BSE image of an albite grain (Ab) partially replaced by Fe–Mg–K aluminosilicate phases (Als). In the upper left, a recrystallised shell fragment, associated with carbonaceous matter. Panels A–C = sample SV13, panels D–I=SV6. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

characterised by millimetre- to centimetre-scale alternation of dark brown mudstone laminae and light brown to yellowish skeletal carbonate laminae. Lamination is continuous and undisturbed across exposed surfaces. In thin sections, carbonate and mudstone intervals are separated by sharp, planar boundaries (Fig. 5A–B). Grading is not evident, and compaction features are common. Carbonate laminae comprise fine-grained, well-sorted skeletal grainstones containing abundant ostracod debris (articulated and fragmented), fragmentary articulate brachiopods, rare linguliform phosphatic brachiopods, crinoid ossicles, and trilobite fragments; hexactinellid sponge spicules occur sporadically (Fig. 5C). Small micritised grains (peloid-like particles, <100 µm) occur locally. Skeletal elements and cement commonly show cloudy alteration and partial silicification; microborings were not observed. Framboids were ubiquitous in both carbonate and mudstone laminae. Detrital quartz is notably rare, whereas small feldspar grains and yellowish grains with a palagonitic appearance are common.

4.1.2. SEM–BSE observations

Under SEM–BSE, the mudstone matrix forms a dense, silicified mass composed of an intergrown mosaic of fine-grained phases in which individual grain boundaries are locally difficult to distinguish (Fig. 5D–F, Appendix A). The matrix comprises SiO₂ rich phases (locally Al-bearing), 2:1 aluminosilicates (Fig. 5G–H), Ti-oxide micrograins, abundant iron-oxide pseudomorphs after euhedral-anhedronal and framboidal pyrite, and altered Na-feldspar (albite) grains, locally associated with apatite and exhibiting compositional transitions to a fine-grained mosaic of Fe–Mg–K aluminosilicate phases (Fig. 5I).

SEM–EDS analyses, in addition to dominant SiO₂-rich phases, distinguished Mg-, Fe-, and K- aluminosilicates with Si/Al atomic ratios commonly close to ~2, consistent with 2:1-type phyllosilicate compositions and with illite-rich, chlorite-rich, and smectite-bearing clay assemblages identified independently by clay-fraction XRD analysis and modelling. These aluminosilicate phases occur predominantly as irregular, non-lath-shaped grains and commonly exhibit pronounced compositional heterogeneity (variable Si, Al, Fe, Mg, and K contents within single grains) and correspond to the yellowish grains with a palagonitic appearance observed under transmitted light. Textural and compositional transitions from Na-feldspar (albite) grains to these fine-grained aluminosilicate domains were also observed. Lath-shaped aluminosilicate grains with compositions consistent with mica/illite were only sporadically observed, although their apparent scarcity may reflect the massive and intergrown character of the silicified matrix.

Fossil shells within the carbonate beds are variably silicified and recrystallised and are commonly associated with carbonaceous matter, whereas dispersed carbonaceous patches occur within the surrounding matrix. Iron-oxide pseudomorphs after framboidal pyrite are ubiquitous throughout the laminated succession.

4.1.3. Interpretation

The alternation of skeletal carbonate laminae and dark fine-grained laminae, together with the consistently fragmentary nature of skeletal debris, indicates episodic deposition by sediment-gravity flows in a distal setting. The fine-grained non-carbonate intervals are largely devoid of skeletal material and are dominated by Al-bearing SiO₂ and 2:1 aluminosilicate phases, along with altered Na-feldspar (albite). SEM–EDS shows that the yellowish grains with a palagonitic appearance observed under transmitted light are compositionally heterogeneous aluminosilicates with variable Si, Al, Fe, Mg, and K contents, and that these aluminosilicates locally develop transitional contacts with altered Na-feldspar. Together with the clay-fraction XRD data, these micro-textures and compositions support a volcanoclastic source for the non-carbonate fraction, followed by diagenetic alteration (argillised tuffitic material). The dominance of authigenic microcrystalline SiO₂ within the fine-grained matrix further supports this interpretation: SiO₂ phase most likely represents authigenic precipitation resulting from the release of silica during the transformation of volcanic ash and feldspars

into aluminosilicates. This process created the dense, intergrown mosaic observed in BSE images, in which individual grain boundaries are obscured by a silicified mass (Appendix A). The lath-shaped aluminosilicates of mica/illite composition are interpreted as terrigenous clastic components. The observed shell recrystallisation may be related to localised porewater chemistry changes during organic matter degradation within confined microenvironments.

The fossil assemblage indicates significant transport from the shelf environment. Trilobites, crinoids, brachiopods, and polychaetes (represented by scolecodonts) are typical components of the shelf benthic communities. Conodonts, although nektonic to nekto-benthic, likely inhabited shallower shelf environments and were likewise transported, as indicated by their fragmentary preservation. Fragmentary preservation affects all skeletal elements, including thin-shelled pelagic ostracods, suggesting that even these pelagic forms underwent reworking rather than representing autochthonous fallout. Chitinozoans, being planktonic, may reflect either transported or local water-column fallout. The pervasive preservation of fine lamination, dispersed organic matter, and widespread pyrite framboid pseudomorphs is consistent with oxygen-restricted bottom-water conditions during deposition.

In summary, the studied succession reflects alternating ash-derived volcanoclastic input and sediment-gravity-flow deposition on a distal slope under persistently oxygen-restricted bottom-water conditions.

4.2. Bulk mineralogy and clay mineral assemblages (XRD)

The XRD analysis of bulk samples revealed that the studied samples were calcite-dominated, with subordinate quartz, plagioclase (modelled as an An₁₆), and mica (muscovite + illite), together with mixed-layer minerals, and trace amounts of goethite, anatase, and rutile (Appendix B, Table S1a). Fluorapatite was probably present in trace amounts below the limit of quantification. After carbonate removal, muscovite (about 22 wt%) and smectite (about 8 wt% in SV19 and SV6) were more easily distinguished (Appendix B, Table S1b). Muscovite was modelled mainly as a 1Md polytype (Appendix B, Fig. S1), also including illite and illite-rich R1 mixed-layered minerals (Rafiei et al., 2020).

In the clay fraction of all samples, a) illite; b) illite-rich (I-rich) R1 mixed-layered minerals (MLMs), with approximately 90% and 70% of illite layers; and c) R0 smectite-rich (S-rich) and R0 chlorite-rich (C-rich) chlorite/smectite (C/S) MLMs of about 75:25, in which chlorite layers (C) represented especially vermiculite with hydrated cations in the interlayer, were modelled (Fig. 6, Appendix B, Table S2, Figs. S2–3). However, the smectite-rich and chlorite-rich MLMs could contain an essential “illite-like” layers ratio prior to the Ca-saturation treatment, which may cause exchange of K⁺ for Ca²⁺ in the interlayer and liberation of collapsed “illite-like” layers. The illite and I-rich R1 MLMs revealed high N and low octahedral Fe (Fe(oct)) content, up to 0.5 Fe (oct) per unit cell (UC). The R0 MLMs were modelled with low N and high Fe(oct) content in the range 2.5–3 Fe(oct)/UC. Based on Ca-saturation and heating at 550 °C, a minor content of non-defected chlorite-rich MLM was detected (Fig. 6).

4.2.1. Interpretation

The clay-mineral assemblages identified by XRD are consistent with the petrographic and SEM observations. The clay-mineral association identified in the Stydlé Vody Section included illite, illite-rich, smectite-rich, and chlorite-rich MLMs, found in Stydlé Vody Section, indicating multiple alteration pathways for the original volcanoclastic material. In general, all volcanics, irrespective of their chemical composition, contain varying proportions of i) mafic and ii) felsic minerals and iii) volcanic glass. The volcanic glass in soils provides the initial distinctive weathering products such as allophane, halloysite, smectite, and ferrihydrite (Neall, 2009). The secondary weathering products of mafic minerals (e.g., olivine, pyroxene, amphibole) and felsic minerals (plagioclases, K-feldspars, minor muscovite) include, according to Locati et al. (2022), three alteration stages associated with Fe-(oxo)

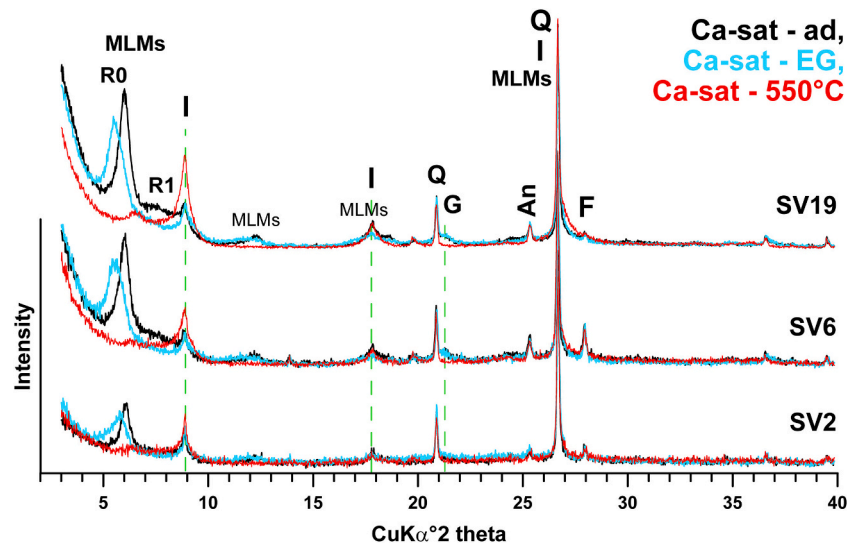


Fig. 6. XRD patterns of clay fraction after carbonate removal and Ca-saturation, oriented preparations in air-dried state (black), after ethylene glycol solvation (blue), and after heating to 550 °C for 1.5 h (red), I - illite, MLMs - mixed-layer minerals, Q - quartz, G - goethite, F - feldspars, An - anatase. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hydroxide formation: a) the alteration of pyroxene to form saponite (Mg, trioctahedral smectite); b) alteration of plagioclase to form Al-saponite; and c) formation of beidellite/montmorillonite (Al, dioctahedral smectite) with Fe-beidellite formed by in situ replacement of Fe-rich pyroxenes. The last stages include calcite, microcrystalline, and cryptocrystalline silica formation. The above-mentioned phyllosilicates transform into (Fe-rich) chlorite in a reducing environment (Beaufort et al., 2015; Patrier et al., 2023) and illite-rich mixed-layered minerals (Aplin et al., 2006; McCarty et al., 2009, and references therein), during early-burial diagenesis. The chlorite/smectite mixed-layered mineral could mainly result from incomplete Fe-smectite to chlorite transformation during diagenesis or, less likely, from the chlorite weathering on outcrop (Środoń et al., 2013).

4.3. Geochemistry

The samples studied from the Stydlé Vody Section are geochemically very diverse and range from non-carbonate, clastic fraction to tuffaceous limestones (Fig. 7). Although the samples contain very different amounts of aluminosilicate components (Fig. 7C–D), the $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{18}\text{O}_{\text{carb}}$ records are very monotonous (Fig. 7A–B). On the other hand, the $V/(V + \text{Ni})$ values show a monotonous decrease from the base of the studied interval to the youngest studied level (Fig. 7F). The U_{EF} and Mo_{EF} values show a similar trend (Fig. 7G–H).

4.3.1. Interpretation

The $\delta^{18}\text{O}_{\text{carb}}$ records are monotonic, but the $\delta^{18}\text{O}_{\text{carb}}$ values are very low (Fig. 7B). This clearly suggests diagenetic and/or post-diagenetic overprinting of this isotopic signal. The evaluation of diagenetic and/or post-diagenetic overprints of marine carbonates, marls, and calcareous shales is crucial for the reconstruction of the primary $\delta^{13}\text{C}$ signal of dissolved inorganic carbon. The $\delta^{18}\text{O}$ composition of marine carbonates, together with selected trace-element ratios such as Sr/Mn, is commonly used as an indicator of the intensity of diagenetic overprint (Brand and Veizer, 1980, 1981; Veizer, 1983; Banner and Hanson, 1990; Swart, 2015). On the other hand, $\delta^{18}\text{O}$ of modern, non-altered and biogenic marine carbonates is highly variable, ranging from -8‰ to 4‰ (Swart, 2015).

Crossplot of $\delta^{13}\text{C}_{\text{carb}}$ versus $\delta^{18}\text{O}_{\text{carb}}$ values does not show a statistically significant correlation ($N = 27$, $r_s = 0.10$; $p = 0.61$; Fig. 7I). The lack of a statistically significant correlation between $\delta^{13}\text{C}_{\text{carb}}$ and

$\delta^{18}\text{O}_{\text{carb}}$ values is often interpreted as evidence for a low degree of alteration of $^{13}\text{C}_{\text{carb}}$ values. However, this is not a sufficient argument, because the lack of correlation in diagenetically altered limestones may suggest that (1) $\delta^{13}\text{C}_{\text{carb}}$ values are unchanged (primary) and only $\delta^{18}\text{O}_{\text{carb}}$ values are altered, or that (2) $\delta^{18}\text{O}_{\text{carb}}$ values are altered and reached some equilibrium with diagenetic fluids while the $\delta^{13}\text{C}_{\text{carb}}$ values are partly altered (see models and discussion in Frýda et al., 2021). Crossplots of $\delta^{18}\text{O}_{\text{carb}}$ versus Mn/Sr, and CaCO_3 versus Mn/Sr do not indicate statistically significant correlations (Fig. 7K–L). On the other hand, the crossplot of $\delta^{13}\text{C}_{\text{carb}}$ versus Mn/Sr showed a significant correlation ($N = 27$, $r_s = -0.45$; $p = 0.02$; Fig. 7J). However, if two outliers are excluded from the dataset (Fig. 7J), no significant correlation remains between the $\delta^{13}\text{C}_{\text{carb}}$ and Mn/Sr values ($N = 25$, $r_s = -0.31$; $p = 0.13$). In addition, carbon isotopes are significantly less prone to diagenetic alteration than oxygen isotopes in marine carbonates because pore waters in sediments generally contain much more oxygen than carbon (Hudson, 1977; Anderson and Arthur, 1983; Banner and Hanson, 1990; Marshall, 1992). All these observations suggest that the $\delta^{13}\text{C}_{\text{carb}}$ record of samples from the Stydlé Vody Section probably represents primary values or values close to primary marine carbonate values.

A strong positive and statistically significant correlation between elements hosted predominantly in the non-carbonate aluminosilicate fraction (Fig. 7M–N) indicates a similar source of clastic material throughout the entire stratigraphic interval. This is in agreement with petrographic and SEM-EDS observations showing similar compositional characteristics of the ash-derived aluminosilicate grains in the tuffitic interbeds across the section. The decline in $V/(V + \text{Ni})$ values (Fig. 7F) indicates a gradual shift from suboxic/anoxic to dysoxic conditions. Similarly, U_{EF} and Mo_{EF} values indicate suboxic/anoxic conditions and sedimentation in an environment with unrestricted water exchange with the open ocean (Fig. 7G–H, O). Taken together, these redox proxies support oxygen-restricted bottom-water conditions, in agreement with petrographic observations (persistent undisturbed lamination, absence of bioturbation, dispersed organic matter, and abundant framboidal pyrite pseudomorphs).

Carbonate $\delta^{13}\text{C}$ values also provide chemostratigraphic context for the studied interval relative to the early Sheinwoodian positive carbon-isotope excursion (ESCIE). Biostratigraphic data based on graptolite record from the studied section indicate that the lower part can be assigned to the *Monograptus belophorus* Biozone and the upper part of the section to *Cyrtograptus rigidus* Biozone (see discussion in Section 5), and

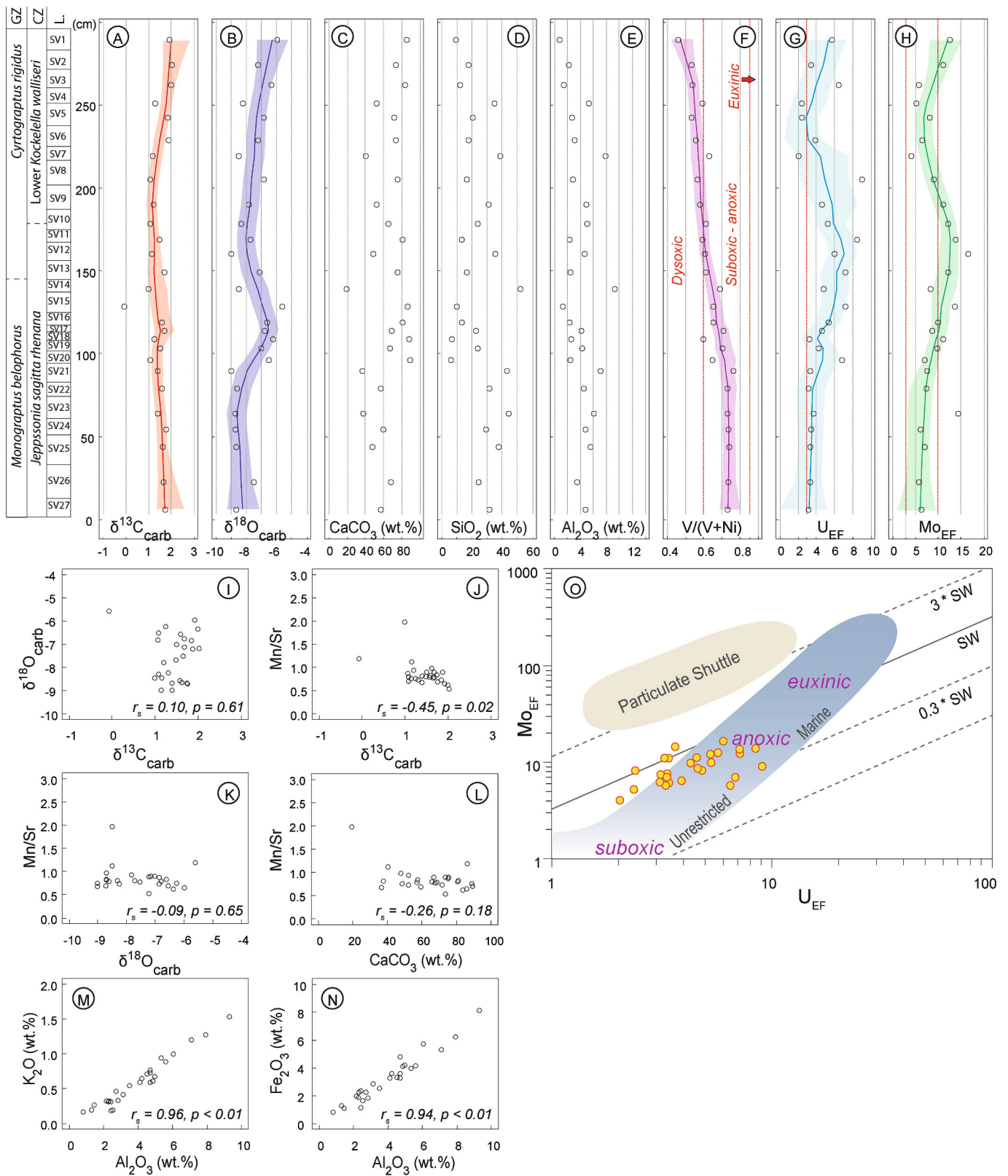


Fig. 7. Stratigraphic distribution of (A) $\delta^{13}\text{C}_{\text{carb}}$, (B) $\delta^{18}\text{O}_{\text{carb}}$, (C) CaCO_3 , (D) SiO_2 , (E) Al_2O_3 , (F) $\text{V}/\text{V} + \text{Ni}$, (G) U_{EF} , and (H) Mo_{EF} values. Crossplots of concentration of (I) $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{18}\text{O}_{\text{carb}}$, (J) $\delta^{13}\text{C}_{\text{carb}}$ and Mn/Sr , (K) $\delta^{18}\text{O}_{\text{carb}}$ and Mn/Sr , (L) CaCO_3 and Mn/Sr , (M) Al_2O_3 and K_2O , and (N) Al_2O_3 and Fe_2O_3 . (O) Crossplot of U_{EF} and Mo_{EF} values presented in a modified diagram by [Algeo and Tribouillard \(2009\)](#).

thus the data indicate assignment to the Sheinwoodian Stage.

The Sheinwoodian is characterised by the early Sheinwoodian positive carbon-isotope excursion (ESCIE). The onset of the ESCIE occurs just above its lower boundary and extends well into the Sheinwoodian Stage. As shown by Loydell (1998, 2007a, 2007b), the onset of the ESCIE occurs in the upper *Cyrtograptus purchisoni* graptolite Biozone. High $\delta^{13}\text{C}$ values are maintained through the *Monograptus riccartonensis* Biozone until the end of the excursion, which is dated by *Monograptus flexilis* (now *Monograptus belophorus*; Loydell and Frýda, 2007). The $\delta^{13}\text{C}_{\text{carb}}$ values from the Stydlé Vody Section are rather low (Fig. 7A). Therefore, the $\delta^{13}\text{C}_{\text{carb}}$ record indicates a stratigraphic position after the early Sheinwoodian carbon isotope excursion (ESCIE).

4.4. Graptolite biostratigraphy

Identifiable planktic graptolites collected from the section represent a typical mid-Sheinwoodian graptolite fauna, widely recorded from

black shale facies distal to the volcanic-carbonate facies developed on the north-western periphery of the Svatý Jan volcanic centre (Havlíček and Štorch, 1990; Štorch, 2023). This assemblage evolved in the aftermath of a major graptolite crisis following the early Sheinwoodian *Murchisoni* mass extinction event (Štorch, 1995, 2023; Melchin et al., 1998).

The most common specimens are robust, S-shaped rhabdosomes of the zonal index species *Monograptus belophorus* (Meneghini), which occur throughout all samples and occasionally form clusters in distinct laminae, likely resulting from mass mortality events and/or post-mortem transport (Fig. 8J–K). Less common taxa include *Monoclimacis flumendosae* (Gortani) (Fig. 8G, I), *Mediograptus antennularius* (Meneghini) (Fig. 8L–M), *Sokolovograptus textor* (Bouček and Münch) (Fig. 8E–F), *Pristiograptus dubius* (Suess) (Fig. 8C–D), and *Pristiograptus pseudodubius* (Bouček) (Fig. 8B). Distal fragments tentatively assigned to *Monograptus flemingii* (Salter) were also recorded. The lower part of the section can be assigned to the *M. belophorus* Biozone. *Cyrtograptus rigidus*

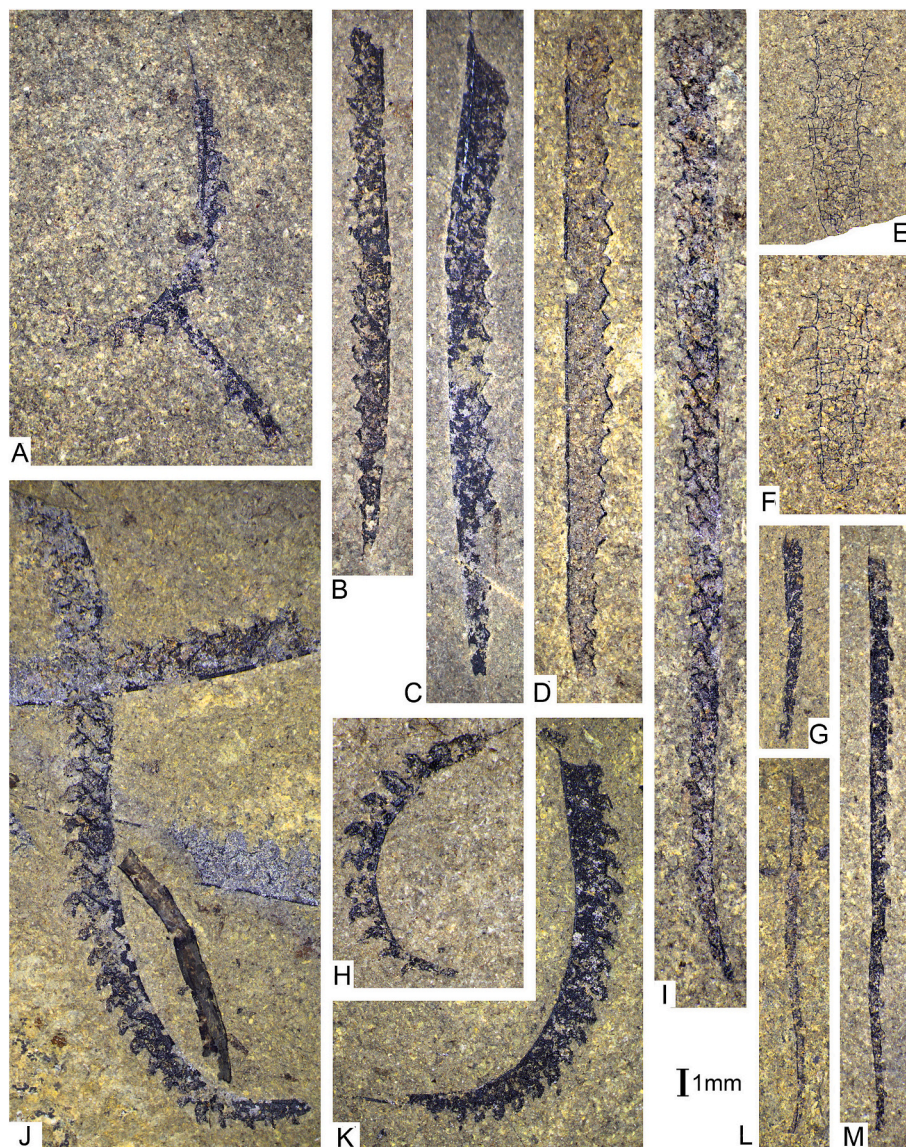


Fig. 8. The representatives of graptolites from the Stydlé Vody Section. The scale bar represents 1 mm.

A, H. *Cyrtograptus rigidus* Tullberg, A. immature specimen showing cladial development, PŠ4859a H. juvenile specimen with initial phase of the stipe twisting, PŠ4847 B. *Pristiograptus pseudodubius* (Bouček), PŠ4861 C, D. *Pristiograptus dubius* (Suess) s.l. C. PŠ4850, D. PŠ4845 E, F. *Sokolovograptus textor* (Bouček and Münch) E. PŠ4851, F. PŠ4851b G, I. *Monoclimacis flumendosae* (Gortani) G. PŠ4855 I. PŠ4857 J, K. *Monograptus belophorus* (Meneghini) J. s-shaped specimen preserved along with plant fragment, PŠ4846 K. juvenile specimen showing large sicula and robust virgella, PŠ4862 L, M. *Mediograptus antennularius* (Meneghini) L. PŠ4842 M. PŠ4854.

Tullberg (Fig. 8A, H), the zonal index species of the succeeding *Cyrt. rigidus* Biozone, first appears at SV13 (Fig. 3).

Bouček (1957) described a moderately diverse dendroid graptolite fauna from this stratigraphic level, based largely on material collected from the nearby road-cut section at Loděnice–Spicaty vrch. In the present section, a similar but less diverse assemblage has been recorded, with frequent occurrences of *Cyclograptus scharyanus* (Goeppert), and rare specimens of *Cyclograptus irregularis* Bouček, *Cyclograptus multi-theatus* Bouček, *Dictyonema* (*Dictyonema*) *gracile* Hall, and an erect

taxon probably belonging to the family Callograptidae or the Dendrograptidae (Fig. 4M–N).

The *Monograptus belophorus* graptolite Biozone is defined as the interval bounded by the first appearance of its index species at the base and the lowest occurrence of *Cyrtograptus rigidus* at the top. Species diversity remains relatively low in the *belophorus* Biozone, although it is higher than in the underlying *dubius–latus* Biozone interregnum. Across much of the Prague Basin, the *belophorus* Biozone is represented by calcareous black to dark-grey graptolitic shales. The base of the

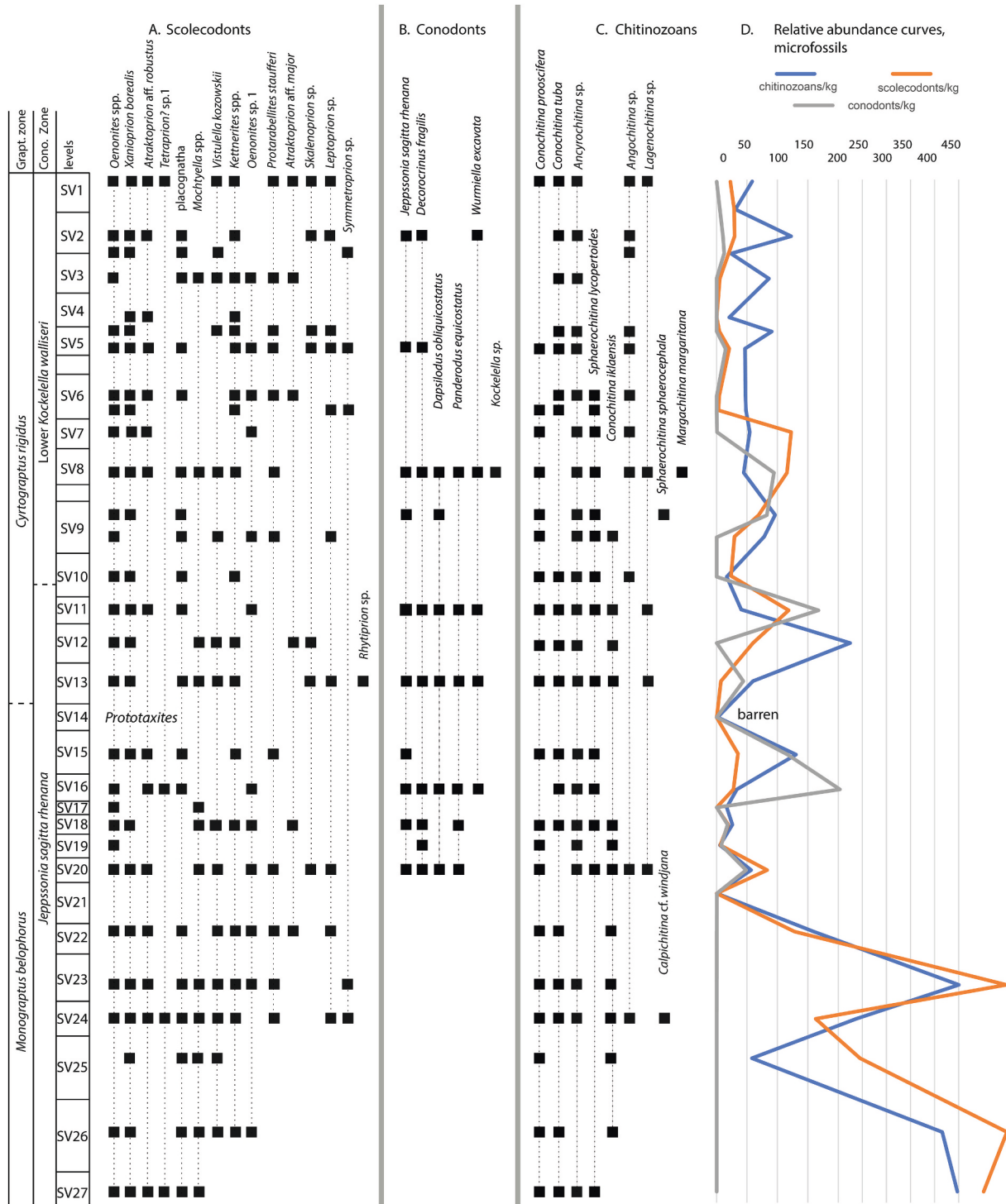


Fig. 9. A distribution of: A. scolecodont species B. conodont species C. chitinozoan species D. relative abundance of chitinozoans, conodonts and scolecodonta (per kg of rock) throughout the Stydlé Vody Section. Grapt. zone = graptolite biozone, Cono. zone = conodont zone.

succeeding *Cyrtograptus rigidus* Biozone is defined by the first occurrence of the zonal species, whereas the top is marked by the lowest occurrence of *C. ramosus*, without overlap of the index taxa. Slightly calcareous graptolitic black shale is the typical lithology of the *rigidus* Biozone in the Prague Basin (Storch, 2023). The significant overlap in the stratigraphic ranges of *M. belophorus* and *Cyrt. rigidus* has been discussed by Barca and Jaeger (1990), Zalasiewicz and Williams (1999), Zalasiewicz et al. (2009), and Storch (2023).

4.5. Conodonts

The conodont fauna in the Stydlé Vody Section (Figs. 3, 9, 10) is dominated by simple cones: *Dapsilodus obliquicostatus* (Branson and Mehl) (Fig. 10J, M, Q), *Decoriconus fragilis* (Branson and Mehl) (Fig. 10H, K–L, N–P), and *Panderodus equicostatus* (Rhodes). Present in all samples are *Dec. fragilis* and *Jeppsonia sagitta rhenana* (Fig. 10A–D); other taxa occur sporadically. *W. excavata* (Fig. 10E–G, I) was found in two samples, and two poorly preserved specimens of *Kockella* sp. were

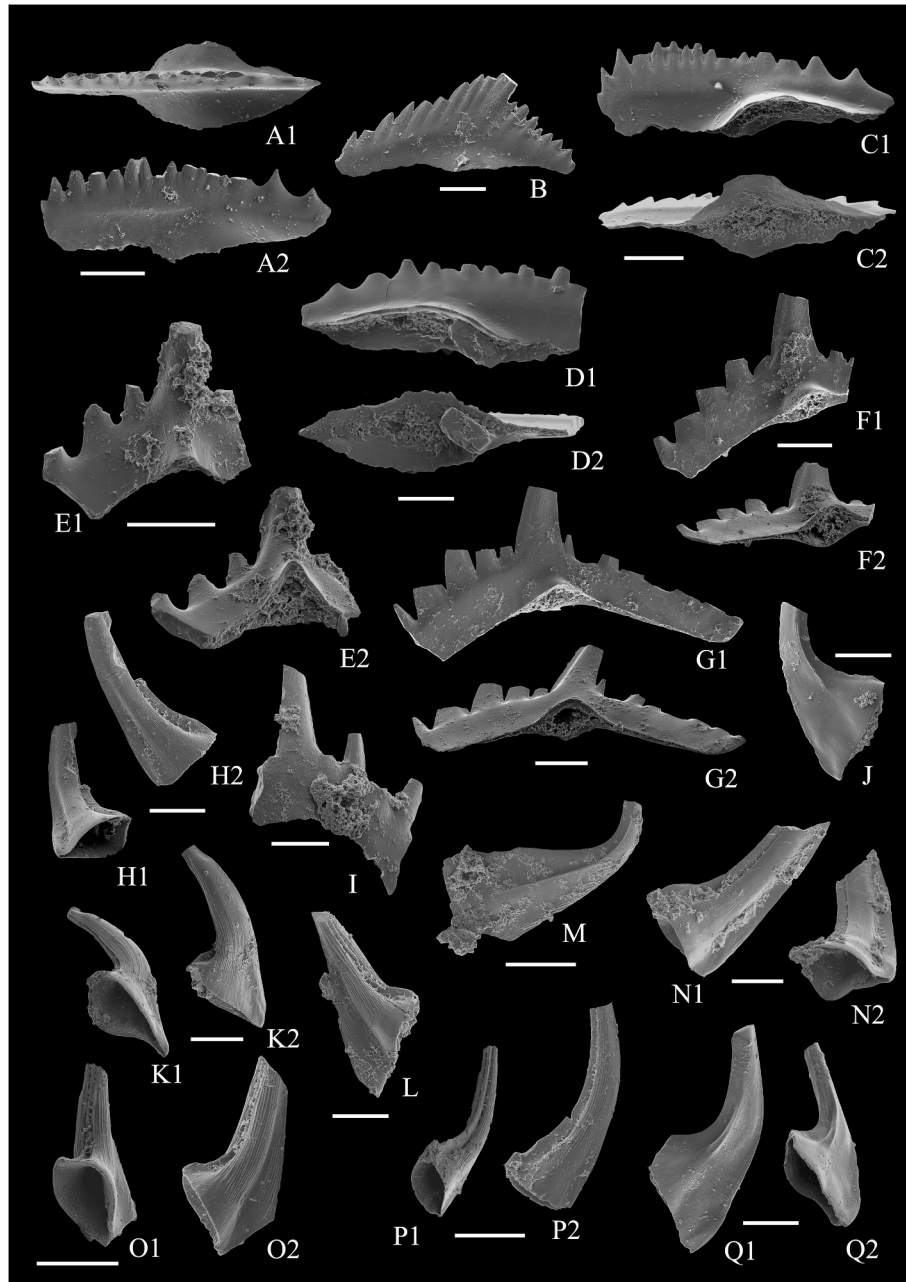


Fig. 10. A figure with selected conodonts. All scale bars, excluding that of specimen 3, which is 200 μm, represent 100 μm. Acronym with SV denotes a layer in the Stydlé Vody Section.

A–D. *Jeppsonia sagitta rhenana* (Walliser). A. PT189_1, SV15, C. PT184_2, SV20, D. PT184_3, SV20, Pa elements, lateral (A2, C1, D1), upper (A1) and lower (C2, D2) views; B. Pb element, lateral view, PT184_1, SV20. E–G, I. *Wurmiella excavata* (Branson and Mehl). E. Sa element, posterior (E1) and lower (E2) views, PT191_1, SV13; F. PT191_2, SV13, G. PT191_3, SV13, Pb elements, lateral (F1, G1) and lower (F2, G2) views; I. PT191.5, SV13, Sb(?) element, anterior view. H, K–L, N–P. *Decoriconus fragilis* (Branson and Mehl). H. PT191.4, SV13, N. PT184.6, SV20, paltodontiform elements, lateral (H2, N1) and lower (H1, N2) views; K. PT191.6, SV13, O. PT191.8, SV13, drepanodontiform(?) elements, lower (K1, O1) and lateral (K2, O2) views; L. drepanodontiform element, lateral view, PT191.7, SV13, P. acontodontiform(?) element, lower (P1) and lateral (P2) views, PT191.9, SV13 J, M, Q *Dapsilodus obliquicostatus* (Branson and Mehl). J. PT184.4, SV20, Q. PT184.7, SV20, acodontiform elements, lateral (J, Q1) and lower (Q2) views; M. distacodontiform element, lateral view, PT184.5, SV20_18.

found only in level SV8.

The occurrence of *J. s. rhenana* correlates the studied section with the *J. s. rhenana* Conodont Superzone (sensu Jeppsson, 1997), which corresponds to the total range interval of *J. s. rhenana*. *J. sagitta* (originally “*Spathognathodus sagitta*”) was described by Walliser (1964), who recognised three subspecies in it: “*S. s. rhenanus*”, “*S. s. sagitta*”, and “*S. s. bohemicus*”. Although described from different sections and not found together, these subspecies were indicated to have the same distribution interval, corresponding to the “*S. s. sagitta*” Zone. Later, “*S. sagitta*” was recognised as the Pa element of *Ozarkodina sagitta*, and its subspecies were redescribed as multielement taxa (Aldridge, 1975a). It was also demonstrated that the subspecies of *O. sagitta* are of different ages, following each other chronologically, and are therefore useful for dating strata (Aldridge, 1975b, 1985; Aldridge and Schönlaub, 1989).

The *J. s. rhenana* Conodont Zone (=Superzone according to Jeppsson, 1997) has been recognised worldwide, but its interpretation and dating in terms of graptolite succession have varied considerably among different authors (e.g., Corradini et al., 2015, and references therein). Detailed studies of extensive collections from Gotland allowed the *J. s. rhenana* Conodont Superzone to be dated as corresponding to the *M. antennularius* and the lower *M. belophorus* graptolite Biozone and also led to the definition of two zones within this superzone. The *J. s. rhenana* Conodont Zone (CZ) corresponds to the interval from the FAD of *J. s. rhenana* to the FAD of *Kockelella walliseri* (Helfrich) above. The lower part of the *J. s. rhenana* CZ is characterised by the occurrence of *K. ranuliformis*, which is absent in the upper part. *K. walliseri* appears, and *K. ranuliformis* reappears in the upper part of the *J. s. rhenana* range, following an interval in which *Kockelella* is missing. According to Jeppsson (1997), the co-occurrence interval of *J. s. rhenana* and *K. walliseri* corresponds to the Lower *K. walliseri* CZ.

The probable specimens of *Kockelella* in the Stydlé Vody Section are too poorly preserved to allow species-level identification and precise dating of the sample. However, if the unidentifiable specimens of *Kockelella* in layer SV8 belong to *K. walliseri*, then from this level upwards, the upper part of the section corresponds to the Lower *K. walliseri* CZ and the strata below it to the *S. s. rhenana* CZ. This interpretation is supported by the absence of *Kockelella* in the samples below this level, although they (particularly levels SV13 and SV20) are relatively rich in conodonts.

4.6. Early terrestrial association

Fragments of early terrestrial plants were found at several levels, as indicated in Fig. 3 and Table 1. The plant fossils are sorted by size. The remains of early land plants can be characterised as axial forms, representing sporophyte remains of eutracheophytes and thalloid forms belonging mainly to nematophytes and terrestrial algae; alternatively, they may represent gametophytes of some embryophytes (Tomescu and Rothwell, 2006; Strother, 2010). Thalloid remains dominate, whereas axial fragments occur less frequently but are present throughout the entire section (Table 1). An exception is the level SV13, where thalloid forms are rare and axial forms of eutracheophytes prevail, including the best-preserved specimen of *Cooksonia barrandei* (Fig. 11A), together with numerous fragments bearing sporangia. The SV14 horizon is distinct, consisting mainly of elongated, flattened, sharp-edged fragments of carbonaceous matter, likely derived from the cryptogamous organism tentatively comparable to the genus *Prototaxites*. In the remaining plant-bearing levels, thalloid material, probably originating from nematophytes of the genus *Nematothallus* sp., predominates, with subordinate cooksonioid axes occurring sporadically. Plant remains are commonly associated with graptolite and brachiopod fauna, and at level SV25, graptolites and cooksonioid axis fragments locally exhibit preferred orientation (Fig. 11C). No plant remains were recorded in the basal SV26 and SV27 layers.

Table 1
Distribution of plant remains in the Stydlé Vody Section. Abbreviations: t. = type of fragments T = thalloid A = axial.

Layer	t.	Size of debris	Allochthonous macrofossil association	Dispersal spore association	Graptolite biozone
SV9	T	5–15	<i>Nematothallus</i> /	<i>Retusotritiles</i> cf.	<i>rigidus</i>
	A	mm	<i>abundo</i>		
SV13	A	3–53	<i>Cosmochlaina</i> , <i>Cooksonia</i> sp.	<i>Retusotritiles</i> cf.	
		mm	<i>barrandei</i>	<i>niger</i>	
SV14		10–70	<i>Prototaxites</i> like	<i>Retusotritiles</i> sp.	<i>belophorus</i>
		mm	fossil	<i>Apiculiretusispora</i> cf. <i>plicata</i>	
SV15	T	10–30	<i>Nematothallus</i> /	<i>Apiculiretusispora</i> sp.	
		mm	<i>Cosmochlaina</i>		
SV19	T	5–35	<i>Nematothallus</i> /	<i>Scylaspora</i> cf.	
SV20	A	mm	<i>Cosmochlaina</i>	<i>downei</i>	
			<i>Cooksonia</i> sp.	<i>Scylaspora</i> cf.	
SV23	T	10–40	<i>Nematothallus</i> /	<i>vetusta</i>	
SV24	A	mm	<i>Cosmochlaina</i> , <i>Cooksonia</i> sp.	<i>Vermiverruspora</i> <i>rumneyi</i>	
SV25	T	2–25	<i>Nematothallus</i> /	<i>Cymbosporites</i> sp.	
	A	mm	<i>Cosmochlaina</i> <i>Cooksonia</i> sp.	<i>Synorisporites</i> <i>libycus</i>	
				<i>Synorisporites</i> cf. <i>libycus</i>	
				<i>Stellatispora</i>	
				<i>inframurinata</i>	
				<i>Ambitisporites</i> <i>dilutus</i>	
				<i>Ambitisporites</i> <i>avitus</i>	

4.6.1. Axial plant fragments

The assemblage consists mainly of sporophytic remains of eutracheophytes (Fig. 11C). The most abundant taxon is *Cooksonia barrandei* Libertin et al., represented by repeatedly isotomically branched axes ending in lenticular to discoid sporangia abutting on a strongly expanding terminal axis (Fig. 11A–C, E). The second eutracheophyte, *Cooksonia* sp., is less common and contains repeatedly isotomically branched axes bearing small discoid sporangia, not abutting on a very slowly expanding axis (Fig. 11D). Rare fragments of probably anisotomously branched axes were also recorded. They may represent early zosterophyll-like plants, although diagnostic sporangia could not be confirmed, and some specimens may reflect overlap with thalloid remains (Fig. 11F).

4.6.2. Thalloid fragments

Thalloid remains occur as flattened carbonised fragments composed of interlacing tubular tissues with two size classes and an outer cellular layer (Fig. 11G–H). The organisation includes a layer of larger, vertically oriented filaments beneath the surface and a basal zone of smaller (Fig. 12D, F), irregularly arranged filaments, consistent with thalloid cryptogamic organisms comparable to *Nematothallus*–*Cosmochlaina*-type structures (Strother, 1993; Edwards et al., 2013). Macerated material is locally poorly preserved but retains the characteristic outer layer with inward flanges and surface perforations attributable to *Cosmochlaina* (Fig. 12A–C, E).

4.7. Organic-walled microfossils: spores

Spores were observed throughout the profile at 13 levels (Fig. 3). The highest abundance of palynomorphs was found in levels SV11 and SV27, which also contained cryptospores. In total, eight trilete spore genera, comprising 14 species, were recorded. Among these were more than ten damaged or poorly preserved undetermined trilete spore specimens (Figs. 13R–Y), one hilate cryptospore monad of the *Artemopyra urubense* type (Fig. 13Z), and three permanent cryptospore tetrads (Fig. 13AA–AC). Some undetermined palynomorphs were also observed

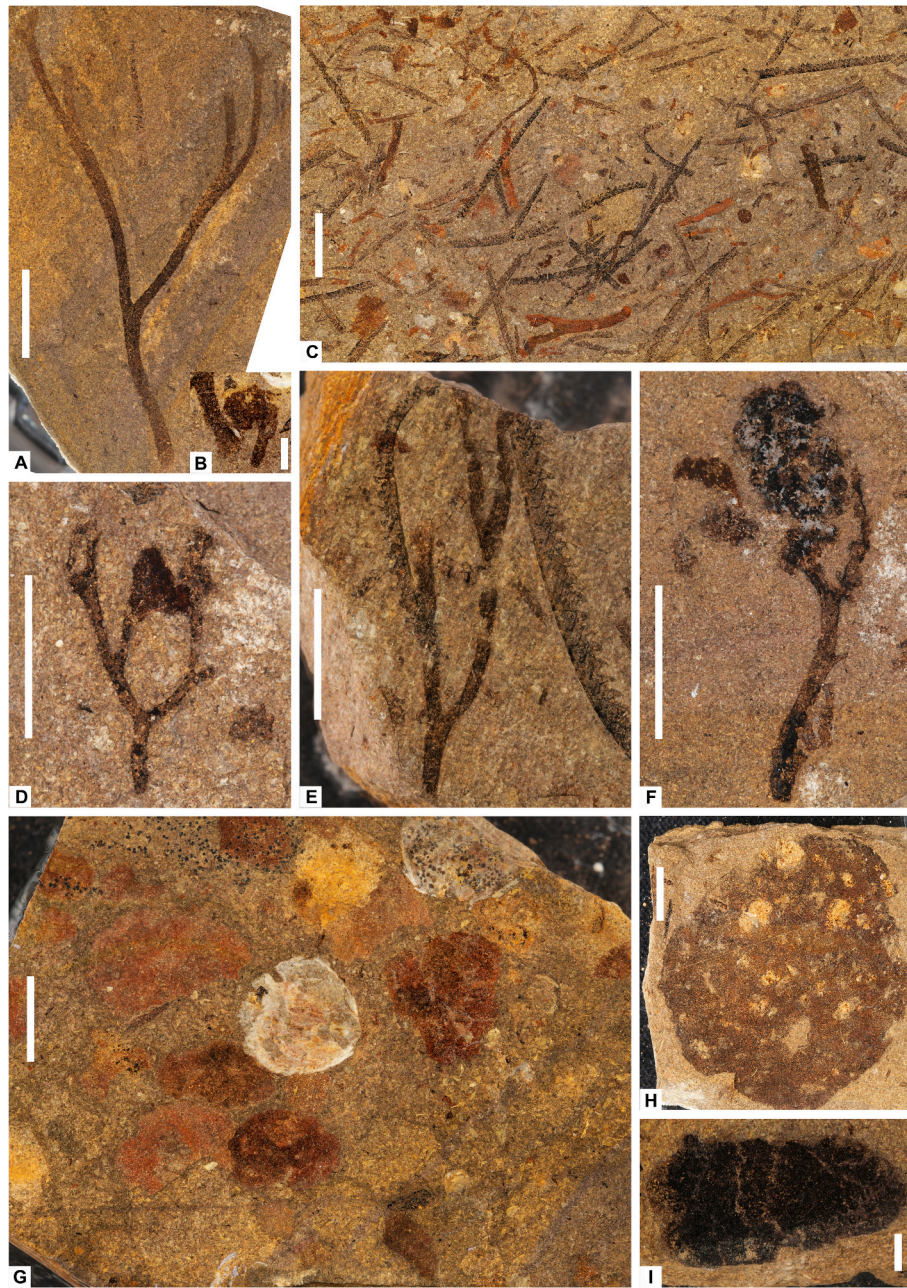


Fig. 11. Figure with early terrestrial association. A. Eutracheophyte, *Cooksonia barrandei*, (D 581aNM), scale bar = 10 mm B. Isolated sporangium probably of *C. barrandei*, (D 591NM), scale bar = 3 mm C. Fragments of terrestrial plants together with graptolite fauna, (D 582NM), scale bar = 10 mm D. Eutracheophyte, *Cooksonia* sp., (D 583NM), scale bar = 10 mm E. Eutracheophyte, *Cooksonia barrandei*, (D 584NM), scale bar = 10 mm F. Unidentified representative of early embryophyte, (D 588NM), scale bar = 10 mm G. Fragments of terrestrial thaloid organism (*Nematothallus* sp.) together with brachiopods, (D 586NM), scale bar = 10 mm H. Terrestrial thaloid organism with lichenized fungi affinity, *Nematothallus* sp., (D 585NM), scale bar = 10 mm I. *Prototaxites*-like carbonaceous matter, (D 592NM), scale bar = 5 mm.

(Fig. 13AD–AH), including three that may be of chitinozoan affinity (Fig. 13AI–AK).

Almost all trilete spores belong to the crassitate genera, including *Retusotriletes* Naumova (Fig. 13A–C), *Vermiverruspora* Beck and Strother (Fig. 13K), *Synorisporites* Richardson and Lister (Fig. 13M–N), *Ambitisporites* Hoffmeister (Fig. 13P–Q) and *Scylaspora* Burgess and Richardson (Fig. 13F–J). Only the genus *Apiculiretusispora* (Streel) Streel (Fig. 13D–E) represents non-crassitate spores. The majority of spores have a subtriangular amb, and the rays of the trilete mark extend close to the spore margin. Spores with a circular amb are less common (Fig. 13B–C, J, L, P, R, T). In some cases, a labrum (i.e. thickened rays of the trilete mark) is developed (Fig. 13A, D, H, I, L). The diameter of all

spores is up to 31 μm (size range between 14 and 31 μm). Of particular interest is the occurrence of reticulate spores of the *Scylaspora downeyi* type (Fig. 13F–I).

Spores of the *Synorisporites* type are known to have been produced only by *Cooksonia pertoni* subsp. *synorispora* Fanning et al. *Scylaspora* has not been macerated from sporangia of a complete plant, but only from dispersed sporangia, leaving its precise affinity uncertain. It is supposed that the parent plant was probably vascular (based on TEM of the spores), but in the absence of evidence for vascular tissue, it must be classified as rhyniophytoid (Wellman, 1999). *Retusotriletes* spores were produced by several parent-plant taxa of different affinities; however, within the Silurian, their producers were rhyniophytoid plants of the

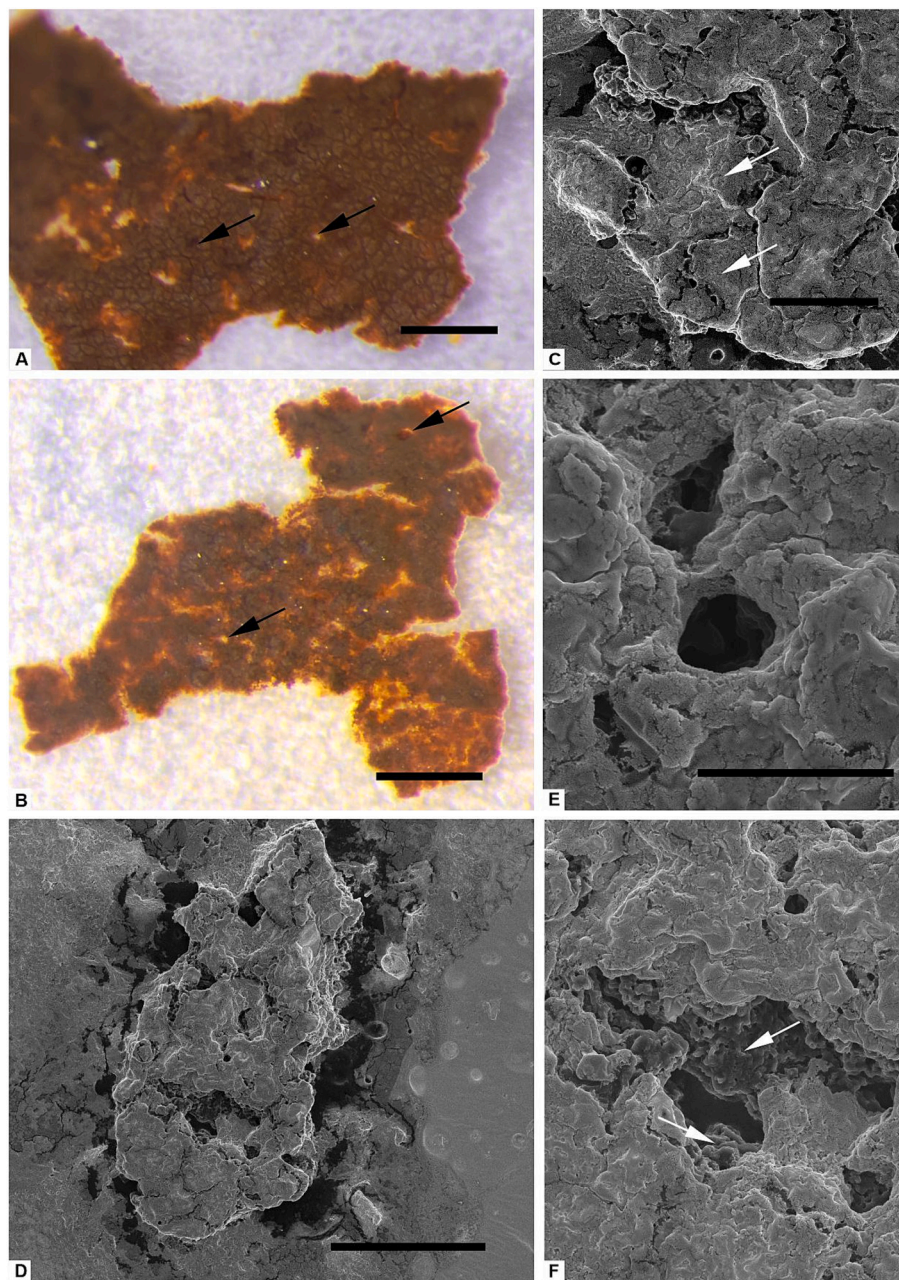


Fig. 12. Figure with plant tissues. A, B. Fragment of intact cortex *Cosmochlaina* sp., arrow indicates perforations, scale bar = 200 μ m C. Detail of the surface with a typical discoidal structure, SEM photo, scale bar = 100 μ m D. Fragment of intact cortex *Cosmochlaina* sp., SEM photo, scale bar = 200 μ m E. Detail of perforation, SEM photo, scale bar = 20 μ m F. Detail of a crack in the cortex, where two layers with hyphae are visible (arrows), scale bar = 50 μ m.

Salopella Group and some zosterophylls, including the genera *Bracteophyton* Wang and Hao, *Gumuia* Hao, *Nothia* Lyon, and *Zosterophyllum* Banks (Balme). Spores of the *Ambitisporites* type are well-known (Balme, 1995) from several plants of rhyniophytoid affinity, mainly of the genus *Cooksonia* Lang (*C. pertonii* subs. *pertonii* Lang, *C. bohémica* Schweitzer, *Concavatheca banksii* Habgood et al., *C. hemisphaerica* Lang) but also from *Paracooksonia* Morris et al. (*P. ambitispora* Morris et al.). Its dispersed spores are known from Ordovician to Devonian strata. Spores of the *Apiculiretusispora* type were produced mainly by several trimerophytalean taxa (Balme, 1995), but trimerophytes are known from the Devonian, therefore the dispersed *Apiculiretusispora* (as several morphologically simple spore types) was probably produced by an unknown parent plant, hypothetically of rhyniophytalean(?) affinity. The parent plants of *Stellatispora inframurinata* and *Vermiverruspora rumneyi* are still unknown.

These findings suggest that rhyniophytes and zosterophylls coexisted at the source area, together with some eophytes (cryptospore producers).

4.8. Organic-walled microfossils: chitinozoans

The chitinozoan assemblage is characterised by low diversity, comprising seven genera and ten species. A total of 680 specimens were recovered, with the highest concentrations found in the lower part of the section, reaching over 550 specimens per kilogram of rock. The composition of the assemblage closely resembles the post-Ireviken fauna of Baltica, including taxa such as *Conochitina proboscifera* Eisenack, *Conochitina iklaensis* Nestor, *Conochitina tuba* Eisenack, *Sphaerochitina lycoperdoides* Laufeld, and *Ancyrochitina* spp.

The most common genera occurring throughout the studied interval

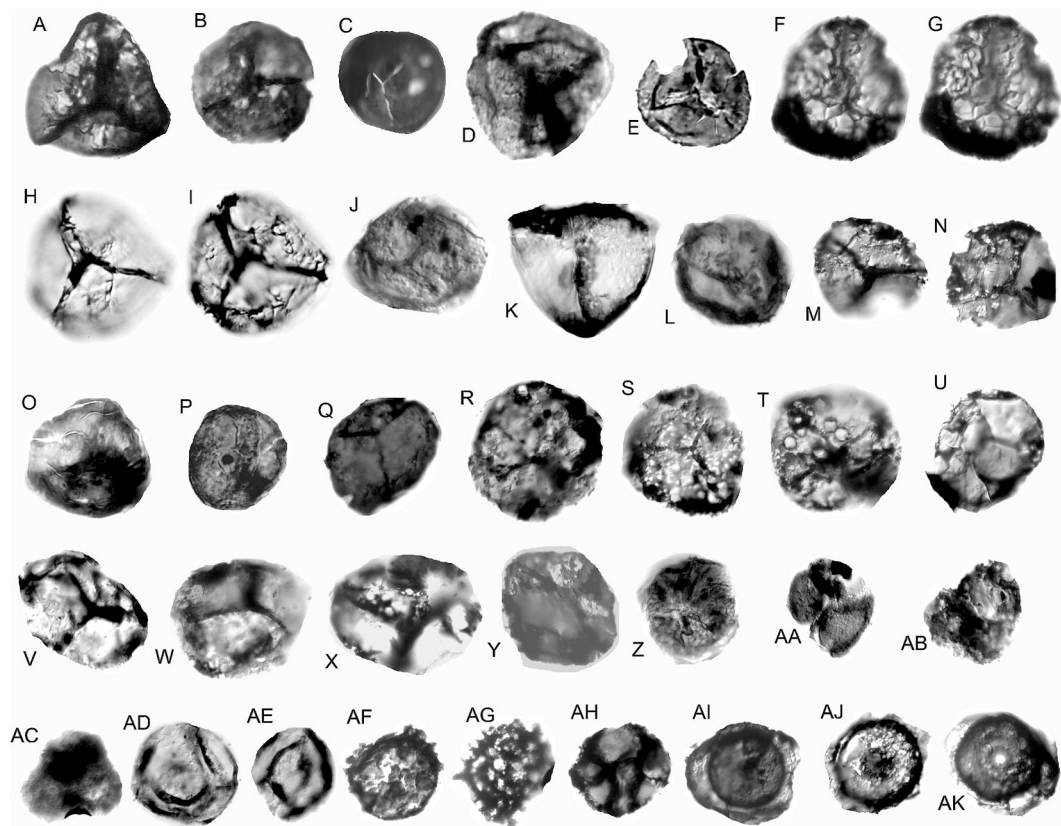


Fig. 13. Figure with selected palynomorphs. All images are under magnification x1000. Acronym SV denotes a layer number in the Stydlé Vody Section.

A. *Retusotriletes* cf. *abundo*; SV11 B. *Retusotriletes* sp.; SV16 C. *Retusotriletes* cf. *niger*; SV26 D. *Apiculiretusispora* sp.; SV15 E. *Apiculiretusispora* cf. *plicata*; SV11 F–I. *Scylaspora* cf. *downei* Burgess and Richardson; F–G. SV10; H–I. SV11 J. *Scylaspora* cf. *vetusta*; SV27 K. *Vermiverruspora runneyi* (Burgess and Richardson) Beck and Strother; SV10 L. *Synorisporites* sp.; SV27 M. *Synorisporites libycus* Richardson and Ioannides; SV11 N. *Synorisporites* cf. *libycus*; SV26 O. *Stellatispora inframurinata* (Richardson and Lister) Burgess and Richardson; SV16 P. *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister; SV19 Q. *Ambitisporites avitus* Hoffmeister; SV20 R–Y. Damaged/poorly preserved trilete spores; R–T, V–W. SV27; U. SV11; X. SV1; Y. SV16 Z. *Artemopyra urubuense* Steemans et al.; SV27 AA–AC. Cryptospores - permanent tetrads; AA, AB. SV27; AC. SV 11 AD–AH. Undetermined palynomorphs; AD. SV18; AE SV17; AF, AG. SV13; AH. SV24 AI–AK. ?Chitinozoans; AI. SV15; AJ, AK. SV12.

are *Conochitina* and *Sphaerochitina*, although several specimens tentatively assigned to the genus *Ancyrochitina* are also relatively abundant (see Fig. 14 for the most common species). A similar taxonomic pattern is observed in coeval strata from Baltica, where *Conochitina* predominates in the Raikküla Regional Stage, while *Ancyrochitina* is more prevalent in the Adavere and Jaani stages. Similar specimens were found by Bek et al. (2022) from the coeval Lodenice locality, where approximately 40 specimens could only be confidently assigned to *Conochitina* spp. and *Ancyrochitina* spp. Other species recognised in the Stydlé Vody Section include *Angochitina* spp. (Fig. 14P–S), *Calpichitina* cf. *windjana* Winchester-Seeto et al. (Fig. 14Z), *Lagenochitina*? spp. (Fig. 11X, Y), *Margachitina margaritana* (Eisenack) (Fig. 14AG), and *Sphaerochitina* cf. *sphaerocephala* (Eisenack) (Fig. 14AA). Based on its taxonomic composition, the assemblage from this section is assignable to the *Cingulochitina cingulata* global chitinozoan Biozone (Verniers et al., 1995) and may also be assigned to the *Conochitina tuba*/*Cingulochitina cingulata* East Baltic chitinozoan biozones (Nestor, 2012).

4.9. Organic-walled microfossils: scolecodonts

The Stydlé Vody Section yields a diverse assemblage of jawed polychaetes (represented by their jaws, scolecodonts), expanding the record of this group for the mid-Sheinwoodian interval of the Prague Basin. At least 20 species representing ten families are present, including Polychaetaspidae, Xanioprionidae, Mochtyellidae, Paulinitidae, Atraktoprionidae, Kalloprionidae, Rhytiprionidae, Skalenoprionidae,

Ramphoprionidae, and Tetraprionidae (Figs. 9, 15, 16). The highest within-sample richness occurs in level SV24, which contains eleven species.

Polychaetaspids are the most diverse and occur in nearly all productive samples, represented by the genus *Oenonites* with at least three species left in open nomenclature, treated as *Oenonites* sp. 1 to 3 (Fig. 15A–O). Paulinitids are the second most common group, represented throughout the section. Two species of the genus *Kettnerites* Žebera (Fig. 15P–U), *K. aff. sisyphe* and *K. aff. kosoviensis*, are distinguished by the number of pre-cuspidal denticles on the right second maxilla (=MII). The species-level assignment was limited by corrosion of diagnostic denticles. Atraktoprionids and skalenoprionids are also common and include three species, *Skalenoprion* sp. (Fig. 16J–K), *Atraktoprion* aff. *robustus* (Fig. 16S–T, W), and *Atraktoprion* aff. *major* (Fig. 15AB, AC), which likely represents an as-yet undescribed genus, but it is known from other sections (Tonarová et al., 2023, 2025). Ramphoprionids constitute less than 10% of the assemblage and are represented by *Protarabellites staufferi* Eriksson (Fig. 15V–Y), a taxon previously reported widely from Silurian successions (Eriksson, 2001; Tonarová et al., 2019, 2025).

The less abundant are kalloprionids, *Leptoprion* sp. (Fig. 16R), and an undetermined kalloprionid (Fig. 16U). Only a patchy occurrence is observed for a symmetropionid *Symmetropion* sp. (Fig. 15AA), and a yet formally undescribed tetraprionid species, *Tetraprion*? sp. 1 (Fig. 16L), which is relatively widely distributed in the Ordovician and Silurian (e.g., Hints, 2000; Tonarová et al., 2025). Placognath-type



Fig. 14. Plate with selected chitinozoans. Scale bar represents 100 μm for figures A to O, and 50 μm for figures P to AG. Acronym with SV denotes a layer in the Stydlé Vody Section. The figures with a letter and a number are details of the aboral part.

A–F. *Conochitina proboscifera* Eisenack, A. PT178.1, SV26 B. PT181.1, SV23 C. PT184.8, SV20 D. PT184.9, SV20 E. PT185.1, 19 F. PT184.10, SV20 G–L. *Conochitina tuba* Eisenack G. PT182.1, SV22 H. PT182.2, SV22 I. PT192.1, SV12 J. PT179.1, SV25 K. PT179.2, SV25 L. PT181.2, SV23 M–O. *Conochitina iklensis* Nestor M. PT182.3, SV22 N. PT178.2, SV26 O. PT179.3, SV25 P–S. *Angochitina* spp. P. PT197.1, SV8 Q. PT180.1, SV24 R. PT198.1, SV7 S. PT198.2, SV7 T–W. *Ancyrochitina* spp. T. PT177.1, SV27 U. PT197.2, SV8 V. PT197.3, SV8 W. PT215.1, SV1 X–Y. *Lagenochitina?* spp. X. PT184.11, SV20, note the pyrite coating Y. PT215.2, SV1 Z. *Calpichitina* cf. *windjana* Winchester-Seeto et al., PT180.2, SV24 AA. *Sphaerochitina* cf. *sphaerocephala* (Eisenack), PT195.1, SV9 AB–AF. *Sphaerochitina lycoperdoides* Laufeld AB. PT197.4, SV8 AC. PT195.2, SV9 AD. PT191.10, SV13, note the pyrite coating AE. PT197.5, SV8 AF. PT184.12, SV20 AG. PT197.6, *Margachitina margaritana* (Eisenack), SV8.

apparatus elements are present but are commonly incomplete; nevertheless, *Mochtyella* sp. from *fragilis* group and *Mochtyella* aff. *trapezoidea* (Fig. 16E, V), *Vistulella kozłowski* Kielan-Jaworowska (Fig. 16A–C), *Rhytiprion* sp. Kielan-Jaworowska (Fig. 16Q), and *Xanioprion borealis* Kielan-Jaworowska (Fig. 16D, F, G) were identified. *Rhytiprion* sp. occurs only at level SV13 and represents the oldest record of the genus in the Prague Basin.

5. Discussion

The Sheinwoodian was marked by major perturbations of the global carbon cycle and climate, including the early Sheinwoodian positive carbon isotope excursion (ESCIE), which coincided with pronounced cooling and biotic restructuring of marine ecosystems, with subtropical sea-surface temperatures decreasing by more than 6 °C (Loydell, 2007a,

2007b; Lehnert et al., 2010; Grossman and Joachimski, 2022). In the Prague Basin, the ESCIE was also recorded in limestone from *C. muchisoni* to the lower *M. riccartonensis* biozones at the Lištice locality with $\delta^{13}\text{C}$ values up to 4.10‰ (Frýda et al., 2015).

Integrated graptolite, conodont, chitinozoan, and carbonate $\delta^{13}\text{C}$ data indicate that the Stydlé Vody Section post-dates the ESCIE and records deposition during the mid-Sheinwoodian interval. This integrated biochemostratigraphic framework offers robust temporal control, constrains the deposition during the mid-Sheinwoodian post-ESCIE interval, and brings together a unique dataset from a single locality. According to current graptolite taxon definitions, the studied succession belongs to the *Monograptus belophorus*–*Cyrtograptus rigidus* biozones (Štorch, 2023), while conodont assemblages place it within the middle part of the *Jeppsonia sagitta rhenana* Superzone and correlate with parts of the *J. s. rhenana* and Lower *Kockelella walliseri* Conodont zones.

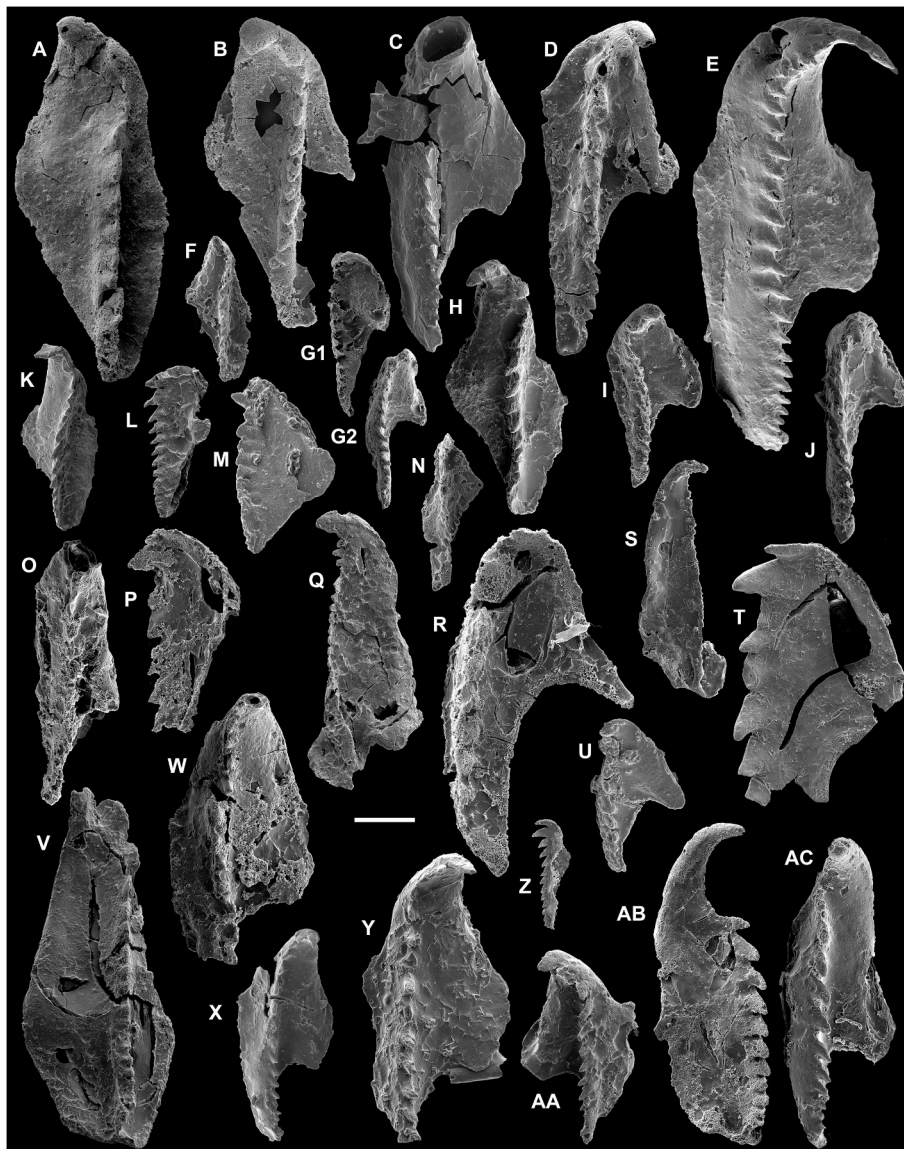


Fig. 15. Plate with selected scolecodonts. All specimens are in dorsal view unless stated otherwise. The scale bar represents 100 μm , 150 μm for figures AB and AC, and 200 μm for Figure T. Acronyms with SV denotes a layer in the Stydlé Vody Section.

A.–C., E. *Oenonites* sp. 1, A. left MI, PT178.3, SV26 B. left MI, PT181.3, SV23 C. right MI, PT185.2, SV19 E. right MI, PT178.4, SV26 D. *Oenonites* sp., right MI, PT182.4, SV22 F. *Oenonites* sp., left MI, PT197.7, SV8 G. *Oenonites* sp. 3, right MI (short), PT184.13, SV20 G1. dorsolateral view, G2. dorsal view H. *Oenonites* sp., right MI, PT182.5, SV22 I. *Oenonites* sp., right MI, PT181.4, SV23 J. *Oenonites* sp. 2, right MI, PT197.8, SV8 K. *Oenonites* sp., left MI, PT184.14, SV20 L. *Oenonites* sp. 3, right MI, PT182.6, SV22, lateral view M. *Oenonites*? sp., basal plate, PT181.5, SV23 N. *Oenonites* sp., right MI, partly broken, PT191.11, SV13 O. *Oenonites* sp., PT193.1, SV11 P–U. paulinitids from the genus *Kettnerites* Zebera P. *Kettnerites* aff. *sisyphi*, right MII, PT215.3, SV 1, dorsolateral view Q. *Kettnerites* sp., right MI, PT178.5, SV26 R. *Kettnerites* aff. *sisyphi*, right MII, PT197.9, SV8 S. *Kettnerites* sp., left MI, PT215.4, SV1 T. *Kettnerites* aff. *kosoviensis*, right MII, PT205.1, SV5 U. *Kettnerites* aff. *sisyphi*, right MII, PT181.6, SV23 V–Y. *Protarabellites staufferi* Eriksson V. left MI, PT182.7, SV22 W. right MI, PT182.8, SV22 X. right MI, PT 192.2, SV12 Y. right MI, PT184.15, SV20 Z. *Tetraprion*?, PT191.12, SV13, lateral view AA. *Symmetropion* sp., left MI, PT205.2, SV5 AB, AC. *Atraktoprion* aff. *major*, AB. left MI PT193.2, SV11 AC. right MI, PT193.3, SV 22.

Chitinozoan assemblages correspond to the *Cingulochitina cingulata* global Biozone.

The integrated petrographic, mineralogical, and geochemical datasets indicate that the studied succession accumulated on a distal slope adjacent to an emergent volcanic elevation. Sedimentation reflects alternating ash-derived input and sediment-gravity flow deposition, with gravity flows transporting skeletal debris and terrestrial material from shallower environments downslope. A volcanoclastic origin of the fine-grained fraction is supported by the dominance of ash-derived aluminosilicates, altered feldspars, and authigenic silica, together with only minor detrital contribution. Clay mineral assemblages dominated by mixed-layer illite-smectite and chlorite-smectite phases are

consistent with alteration of volcanic ash followed by early diagenetic modification under reducing conditions. Redox-sensitive geochemical proxies (V/(V + Ni), UEF, and MoEF), together with persistent fine lamination and abundant framboidal pyrite pseudomorphs, indicate deposition under oxygen-restricted bottom waters, ranging from suboxic to anoxic.

Together, the temporal constraints from integrated biogeostratigraphy and the environmental reconstruction based on petrography, mineralogy, and geochemistry provide the framework for interpreting the mixed marine and terrestrial signals archived in the section and the fossil groups discussed in chapters 5.1 and 5.2.

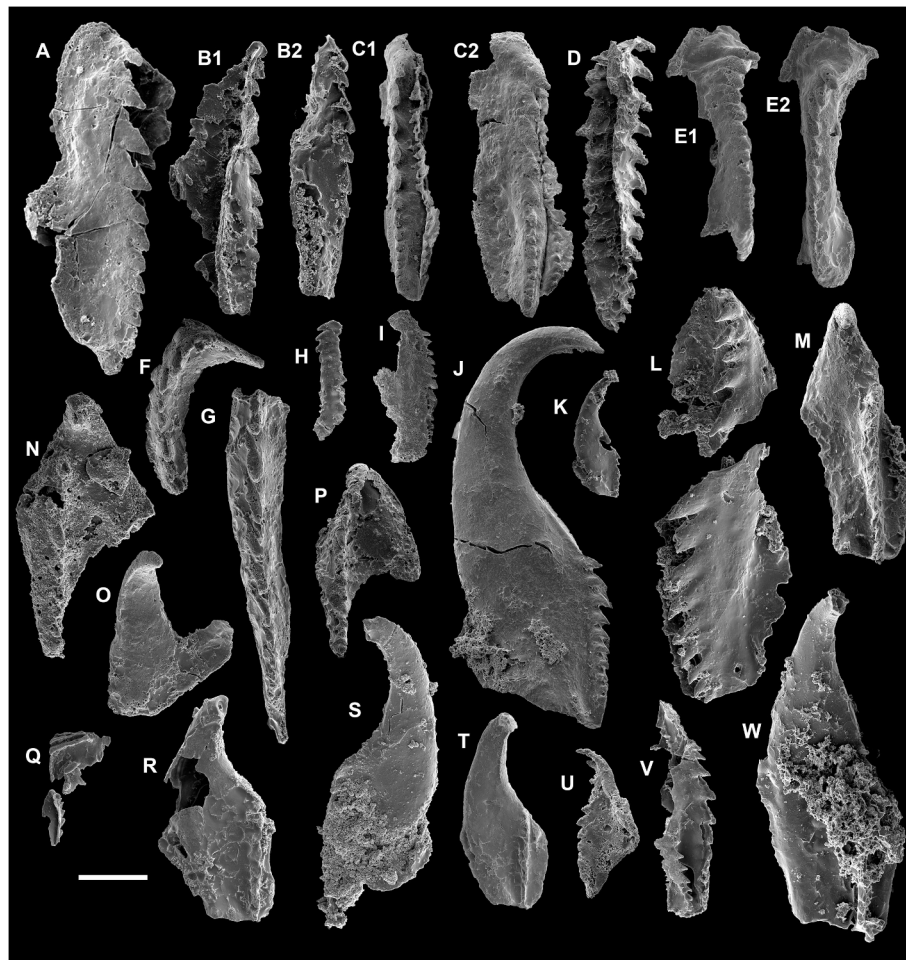


Fig. 16. Microphotographs of selected scolecodonts. All specimens are in dorsal view unless stated otherwise. The scale bar represents 100 μm and 200 μm for Fig. 10. An acronym with SV denotes a layer in the Stydlé Vody Section.

A. *Vistulella? kozlowskii*, right MI, PT181.7, SV 23 B, C. *Vistulella kozlowskii* Kielan-Jaworowska, left MI, PT182.9, SV22 B1. ventrolateral view B2. lateral view C. right MI, PT178.6, SV26 C1. dorsal view, C2. dorsolateral view D. *Xanioprion?* sp., lateral view, PT182.10, SV22 E. *Mochtyella* sp., from *fragilis* group, right MI, PT191.13, SV13 E1. dorsolateral view E2. dorsal view F. *Xanioprion borealis* Kielan-Jaworowska, PT184.16, SV20 G. *Xanioprion borealis* Kielan-Jaworowska, PT184.17, SV20 H. placognath maxilla, PT179.4, SV25 I. *Mochtyella* sp., PT184.18, SV20 J. *Skalenoprion* sp. left MI, PT184.19, SV20 K. *Skalenoprion* sp. left MI, PT205.3, SV5 L. *Tetraprion?* sp. 1, PT215.5, SV1 M, N, P. *Leptoprion* sp. M. left MI, PT184.20, SV20 N. right MI, PT182.11, SV22 P. right MI, PT182.12, SV22 O. atraktoprionid basal plate, PT191.14, SV13 Q. *Rhytiprion* sp., broken right first maxilla, PT191.15, SV13 R. *Leptoprion?* sp., left MI, PT197.10, SV8 S, T, W. *Atraktoprion* aff. *robustus*, S. right MI, PT189.2, SV15 T. left MI, PT191.16, SV13 W. left MI, PT215.6, SV1_1 U. kalloprionid? basal plate, PT180.3, SV24 V. *Mochtyella* aff. *trapezoidea*, left MI, PT177.2, SV27.

5.1. Spores and early land plants

Relatively high diversity of early land-plant remains is indicated by macrofossils and dispersed spore assemblages from several localities in the Prague Basin (Dufka, 1995a; Psenička et al., 2021; Bek et al., 2022). Abundant *Cooksonia* representatives have been reported from the road-cut section at Loděnice-Špičatý vrch, where they occur in lowermost tuffitic and limestone layers overlying tuffite and basaltic effusions (Libertín et al., 2018a, 2018b). In contrast, basalt was not recorded in the re-exposed Stydlé Vody Section, consistent with a slightly younger stratigraphic position relative to the Špičatý vrch succession.

The assemblage of early land plants at Stydlé Vody consists of the polysporangiate eutracheophytes *Cooksonia barrandei* and *Cooksonia* sp. They occur together with fragmentary cryptogamous organisms with an affinity to lichenized fungi determined as *Nematothallus* sp. and *Cosmochlaina* sp. (Edwards et al., 2018), and another representative of probably lichenized fungi or more likely an unknown organism, like *Prototaxites* sp. (Vajda et al., 2023; Loron et al., 2026). Eophytes have not been identified in the macrofossil record; however, rare cryptospore specimens were recognised (including a monad of the *Artemopyra*

urubuense type, and three permanent tetrads), indicating their presence in the source vegetation.

Because spores have a substantially higher fossilisation potential than macroremains, the dispersed palynological record provides a more complete proxy for source-area vegetation. At least 12 early vascular plant taxa and two to three eophyte taxa are inferred from the spore assemblage, exceeding estimates from the slightly older Špičatý vrch, where approximately six early land plants and two to three eophytes were inferred from palynomorphs (Bek et al., 2022). This difference may reflect a more mature stage of island colonisation. However, it could also be influenced by differences in sampling intensity, taphonomic filtering, and facies-dependent preservation differences between the two sites. Globally, Sheinwoodian dispersed-spore records remain limited, with only six trilete-spore species and nine cryptospore species reported so far (Wellman et al., 2013, suppl.). A marked decline in cryptospore diversity occurred from the Aeronian (14 genera and 28 species) to the Sheinwoodian (four genera and five species). Overall, the Stydlé Vody palynological record (Table 2) yields an unusually high diversity estimate for a single Sheinwoodian locality and suggests representation of the principal early vascular-plant lineages (rhyniophytes and zosterophylls).

Table 2

Comparison of all Sheinwoodian trilete spore taxa recorded globally (left column, from Wellman et al., 2013, Supplementary Material) and those documented from the Stydlé Vody Section (right column). Taxa shown in bold represent species identified from the Sheinwoodian for the first time.

Sheinwoodian trilete spores globally	Trilete spores herein
<i>Ambitisporites</i> avitus, <i>A. dilutus</i> , <i>Synorisporites</i> libycus, <i>Archaeozonotrites</i> chulus, <i>A. nanus</i> , <i>Retusotrites</i> warringtonii	<i>Retusotrites</i> cf. <i>abundo</i> , <i>R. cf. niger</i> , <i>R. sp.</i> <i>Apiculiretusispora</i> cf. <i>plicata</i> , <i>A. sp.</i> , <i>Scylaspora</i> cf. <i>downei</i> , <i>S. cf. vetusta</i> , <i>Vermiverruspora</i> rumneyi, <i>Cymbosporites</i> sp., <i>Synorisporites</i> libycus, <i>S. cf. libycus</i> , <i>Stellatispora</i> inframurinata, <i>Ambitisporites</i> dilutus, <i>A. avitus</i>

The comparatively diverse land-plant assemblage at Stydlé Vody Section may reflect the favourable character of the substrate at the adjacent volcanic elevation. The presence of emergent volcanic islands in the Prague Basin during the Silurian and their significance as potential early plant habitats have been documented previously (Kraft et al., 2019). In particular, Pšenička et al. (2021) proposed that nutrient-rich volcanic islands associated with the Kosov and Svatý Jan volcanic centres provided suitable substrates for early terrestrialisation. Weathering of volcanic glass and primary minerals such as olivine, pyroxene, and feldspar generates nutrient-rich soils (Dahlgren et al., 2004). Volcanic substrates supply macronutrients (P, K, Ca, Mg) and essential trace elements (Fe, Zn, Si, Cu) required for plant growth (Tulp et al., 2023). Even in the absence of fully developed soils, these highly reactive lithologies may have provided favourable conditions for early land plants. Experimental studies demonstrate that primary silicate minerals can release plant-essential nutrients directly from rock during early stages of weathering (e.g., Burghlelea et al., 2015), supporting the plausibility of such substrate-controlled nutrient availability in early terrestrial settings. The easy weathering of glass or Fe-rich mafic minerals and the resulting higher smectite content in volcanic soils (regolith) ensure slow and continuous nutrient release, as well as high soil cation exchange capacity, soil aggregation, water retention, and porosity (Peng et al., 2021). On the other hand, nutrients on volcanic islands (particularly phosphorus) are often bound in mineral forms, from which microorganisms, including bacterial and fungal communities, can more effectively mobilise nutrients, for example by increasing the physical absorption area and chemically releasing nutrients from minerals, thereby facilitating their availability to plants (Osborne et al., 2018).

Within the depositional model outlined above, terrestrial plant macroremains were delivered primarily by sediment-gravity flows, whereas dispersed spores may have reached the marine environment through a combination of atmospheric and water-mediated transport, runoff, and sedimentary reworking before incorporation into slope deposits. The sparsely covered land surface facilitated spore dispersal. The preservation was likely governed by dysoxic-anoxic conditions, which were characteristic throughout the section, with the fine-grained character of the deposits and silicification of the tuffitic matrix further enhancing the preservation potential of organic-walled microfossils. Together, these processes provided an efficient mechanism for concentrating and preserving a diverse record of early land vegetation alongside marine components in a single, stratigraphically well-constrained section.

In summary, Sheinwoodian dispersed-spore records remain sparse globally (Wellman et al., 2013), and the comparatively diverse spore assemblage at Stydlé Vody provides an important peri-Gondwana dataset for this interval, suggesting representation of all major early vascular plant lineages (rhyniophytes and zosterophylls).

5.2. Marine microfossils discussion

Lower Silurian conodonts are poorly studied in the Prague Basin. Walmsley et al. (1974) reported elements of the multi-element species

Wurmiella excavata (Branson and Mehl), *Ozarkodina sagitta rhenana* (Walliser), the genus recently redescribed as *Jeppssonina* (Barrick et al., 2024), and *Oulodus* sp. from the upper Liteň Formation at Svatý Jan pod Skalou, Bohemia. Schönlaub (in Krřz et al., 1993) documented several taxa, including *J. s. rhenana*, *J. s. sagitta* (Walliser), and *J. bohémica* (Walliser) from the Homerian–lowermost Gorstian strata of the region. Later, Slavík (2014) revised the Wenlock–Ludlow boundary assemblages, starting with the *J. s. sagitta* Zone, and provided a summary of previous conodont research in the region. More recently, Aeronian conodonts were identified from the section in the vicinity of the Hýskov Volcanic centre (Tonarová et al., 2019). All conodonts reported from the Prague Basin are also common in the Baltic region (e.g. Männik, 2003, and references therein), suggesting close connections between these regions in the Sheinwoodian.

The palaeogeographic affinities of middle and upper Wenlock chitinozoans from the Prague Basin (Dufka, 1995b; Dufka et al., 1995; Bek et al., 2022), much like to those of Llandovery chitinozoans (Dufka, 1992; Dufka and Fatka, 1993), Wenlock scolecodonts (Bek et al., 2022) and acritarchs (e.g. Dufka, 1990, pp. 88–93), support the interpretation of the basin as occupying an intermediate position between the Gondwana and Baltica palaeocontinents (see also Paris, 1993; Paris et al., 1995). Evidence for free exchange of palaeoplankton between the Prague Basin and Baltica's shelf seas is indicated by the comparable stratigraphic ranges of several species, as well as the presence of shared genera such as *Cingulochitina*. Dufka, in Krřz et al. (1993), discussed the distribution, abundance, and diversity of chitinozoans across the basin, particularly in younger Wenlock–Ludlow boundary sediments, concluding that chitinozoan distribution is strongly influenced by facies development within individual basin segments. In shallow-water volcano-carbonate facies surrounding the Svatý Jan Volcanic Centre (Central Segment), chitinozoans are rare or absent in bioterritic limestones and tuffitic shales of the *T. testis* Biozone. They are also absent in all samples from the Kozel Limestone Member facies (spanning the *M. dubius parvus* to *M. vulgaris* Biozones), which are dominated by sporomorphs of terrestrial plants (Dufka in Krřz et al., 1993; Dufka, 1995a). In contrast, in the Nová Ves Volcanic Centre and the eastern part of the Central Segment, well-preserved but sparse chitinozoans (approximately five specimens per gram of rock) were recovered from micritic limestone lenses enclosed within tuffitic shales. The most recent detailed summary of Silurian chitinozoan research in the Prague Basin was provided by Vodička and Manda (2019). Comparable assemblages have been described by Hints et al. (2006) from coeval strata in Baltica, specifically in the Paatsalu drill core (Estonia), where *Conochitina proboscifera* and *Margachitina margaritana* were recorded.

Verniers et al. (1995) defined three global chitinozoan biozones for the Sheinwoodian: *Margachitina margaritana*, *Cingulochitina cingulata*, and the base of the *Conochitina pachycephala* Biozone. The *M. margaritana* Biozone is marked by the first appearance of the nominal species, with *Conochitina proboscifera* as a characteristic taxon; *Conochitina tuba* appears near its top. The succeeding *C. cingulata* Biozone is defined by the first occurrence of *C. cingulata* and is characterised by the continued presence of *M. margaritana*, *C. proboscifera*, and *C. tuba*. In contrast, *C. proboscifera* is absent from the overlying *C. pachycephala* Biozone. This chitinozoa species distribution places the Stydlé Vody assemblage confidently within the global *C. cingulata* Biozone.

Nestor (2012) revised the East Baltic chitinozoan biozonation, restricting the *M. margaritana* Biozone to the very early Sheinwoodian and introducing a subsequent Interzone, followed by the *Conochitina mamilla* and *Conochitina tuba* biozones, broadly correlatable with the global *M. margaritana* Biozone. For the upper Sheinwoodian, she recognised a *Cingulochitina cingulata* Biozone consistent with the global scheme. However, *Sphaerochitina lycoperdoides*, which first appears in the upper Homerian in the East Baltic, occurs already in Sheinwoodian strata at the Stydlé Vody Section, complicating direct correlation. Nevertheless, the co-occurrence of *M. margaritana*, *C. proboscifera*, and *C. tuba* in the Stydlé Vody assemblage may indicate equivalence to the

Conochitina tuba/*Cingulochitina cingulata* East Baltic Biozone (sensu Nestor, 2012), corresponding to the middle to late Sheinwoodian.

Scolecodonts from the Stydlé Vody Section provide the first detailed mid-Sheinwoodian record of jawed polychaetes from the Prague Basin and represent one of the few datasets from peri-Gondwana successions of this age (research history in Bek et al., 2022). The assemblage is dominated by long-ranging taxa (e.g., *Vistulella* Kielan-Jaworowska, *Oenonites* sp. 2 ex gr. *wyszogrodensis*, *Protarabellites staufferi*) and is less diverse than well-studied coeval successions in Baltica, where sampling intensity and taxonomic resolution are considerably higher (Eriksson et al., 2004; Eriksson, 2006a, 2006b; Hints et al., 2006; Tonarová et al., 2014). A notable element is *Rhytiprion* sp., recorded here as the oldest occurrence in the Prague Basin, consistent with broader Wenlock trends toward increasing cosmopolitanisation of marine microfaunas.

In the Prague Basin, scolecodont assemblages show an increase in the relative abundance of paulinitids toward younger Silurian strata, as indicated by comparisons among the Aeronian Hýskov assemblage, the Sheinwoodian Stydlé Vody Section, and the Ludlow Kosov Quarry record (Tonarová et al., 2012, 2019, 2025). The Stydlé Vody assemblage is less diverse than both stratigraphically older and younger Prague Basin faunas, as well as intensively studied coeval successions from Baltica; this pattern likely reflects a combination of taphonomic and facies-related filtering within the slope archive and differences in sampling intensity.

6. Conclusions

- The Stydlé Vody Section records deposition on a distal volcanoclastic slope adjacent to an emergent Silurian volcanic island. Sedimentation was controlled by alternating ash-derived volcanoclastic input and sediment-gravity flows under oxygen-restricted bottom-water conditions ranging from anoxic to dysoxic, as indicated by redox-sensitive trace-element proxies, (V/(V + Ni), UEF, and MoEF), together with persistent lamination and abundant pyrite framboid pseudomorphs.
- The unique integration of graptolite–conodont–chitinozoan biostratigraphy, complemented by $\delta^{13}\text{C}$ chemostratigraphy, provides a robust biochemostratigraphic framework that constrains the section to the mid-Sheinwoodian, after the early Sheinwoodian carbon isotope excursion (post-ESCIIE). This interval encompasses parts of the *Jeppsonia s. rhenana* and Lower *K. walliseri* conodont zones, *Monograptus belophorus* and *Cyrtograptus rigidus* graptolite biozones, and the *Cingulochitina cingulata* chitinozoan Biozone. Carbon isotope values of approximately +1 to +2‰ ($\delta^{13}\text{C}$) and oxygen isotope values −10 to −5‰ ($\delta^{18}\text{O}$) further support deposition after the ESCIE.
- The comparatively high diversity of mid-Sheinwoodian plant taxa inferred from palynological data, together with the volcanoclastic nature of the source terrain, supports the hypothesis that nutrient-rich volcanic substrates promoted early terrestrial colonisation in peri-Gondwanan settings. The spore assemblage indicates that rhyniophytes and zosterophylls grew along with some eophytes (cryptospore-producers) that inhabited the adjacent volcanic elevation.
- Previously unreported mid-Sheinwoodian chitinozoans and the first detailed scolecodont record from the Prague Basin fill a key gap in the regional fossil record and, together with conodont data, support palaeobiogeographic connectivity with Baltica during the mid-Sheinwoodian.
- Overall, the Stydlé Vody Section represents a unique, stratigraphically well-constrained archive integrating marine and terrestrial signals, providing key insights into early land-sea interactions during the mid-Sheinwoodian.

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CRediT authorship contribution statement

Petra Tonarová: Writing – review & editing, Writing – original draft, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Stanislava Vodrážková:** Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Jiří Bek:** Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Jiří Frýda:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Milan Libertín:** Conceptualization, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Sonia Clara Camina:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Peep Männik:** Formal analysis, Writing – original draft, Writing – review & editing. **Zuzana Strossová:** Formal analysis, Writing – original draft, Writing – review & editing. **Petr Štorch:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Michal Kubajko:** Formal analysis, Investigation, Methodology, Writing – original draft. **Magdaléna Koubová:** Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Jana Drábková:** Formal analysis, Methodology, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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