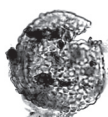# Early Silurian (mid-Sheinwoodian) palynomorphs from the Loděnice-Špičatý vrch, Prague Basin, Czech Republic

Jiří Bek, Petr Štorch, Petra Tonarová & Milan Libertín

Dispersed spores, cryptospores, scolecodonts, acritarchs, prasinophytes and chitinozoans, dated by graptolites as being middle Sheinwoodian (early Wenlock, *ca* 432 Ma), are described from the Loděnice-Špičatý vrch locality, Prague Basin, Czech Republic. Palynomorphs were macerated from a specimen (stored in the National Museum, Prague), with fragments of *Cooksonia* sp. and the zonal index graptolite *Monograptus belophorus* giving precise stratigraphic position within *Monograptus belophorus* Biozone. Important is the oldest occurrence of monolete spores. The number of spore taxa indicate that minimally six types of early vascular plants and probably two to three types of cryptosporophytes grew on the Svatý Jan Volcanic Island in the Prague Basin. The ecology of the first cryptospore and trilete spore producers within Sheinwoodian–Přídolí interval is discussed with special focus on first two globally important key events (after Homerian glaciation and during Přídolí) for earliest vascular land plants. The combination of palynological and palaeobotanical records confirms important role of volcanic islands of the Prague Basin for the evolution of early land plants. • Key words: palynology, earliest plants, spores and cryptospores, plant events.

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The origin of land plants is one of the most important events in the Earth's history, having influenced continental and marine ecology as well as the global climate system (Berner *et al*. 2007, Wellman 2010). Many authors have hypothesized that land plants, *i.e.* embryophytes, originated from charophycean green algae and that the earliest land plants were "bryophyte-like" (*e.g.* Steemans *et al*. 2009). Most plants naturally shed their sterile and fertile organs during their lives. Upon death, plants become disarticulated and only rarely it is possible to find large fragments, which provide direct evidence of their existence. Indirect evidence includes phytodebris (or palynodebris or nematoclasts) like tubes, tissues, cuticles and sporangia together with both dispersed or *in situ* spores and/or cryptospores. Spores are much more abundant than plant fossils because they are smaller and consist of resistant material (sporopollenin). It is generally considered that the spore record is several times greater than that of plant macrofossils (Beck & Strother 2001). Another advantage is the often enormous production of spores by their plant producers.

The oldest palynological evidence for the first land plants are cryptospores (*sensu* Strother 1991) preserved either as monads, obligate dyads, or tetrads which lacked trilete marks. Cryptospores are a non-phylogenetic group of spores with cell walls consisting of sporopollenin. They are distinct from trilete and monolete spores and pollen but resemble land plant spores (Strother 1991). The oldest cryptospores are described from lower to middle Cambrian strata (Strother 2016) and are last seen during the Middle Devonian rocks (Steemans *et al*. 2012, Breuer & Steemans 2013, Wellman *et al*. 2015). Cryptosporophytes (cryptospore producers) are generally considered to represent the earliest terrestrial flora (Steemans 1999, Steemans *et al*. 2009). Trilete spores are generally considered to represent vascular plants and their immediate ancestors (Wellman & Gray 2000, Wellman *et al*. 2013, Edwards *et al*. 2014), with the oldest trilete spores being described from the Ordovician (Steemans *et al.* 2009).

The Ordovician–Silurian interval is generally considered to be the crucial period for the evolution of the earliest vascular land plants. The oldest known sporophyte
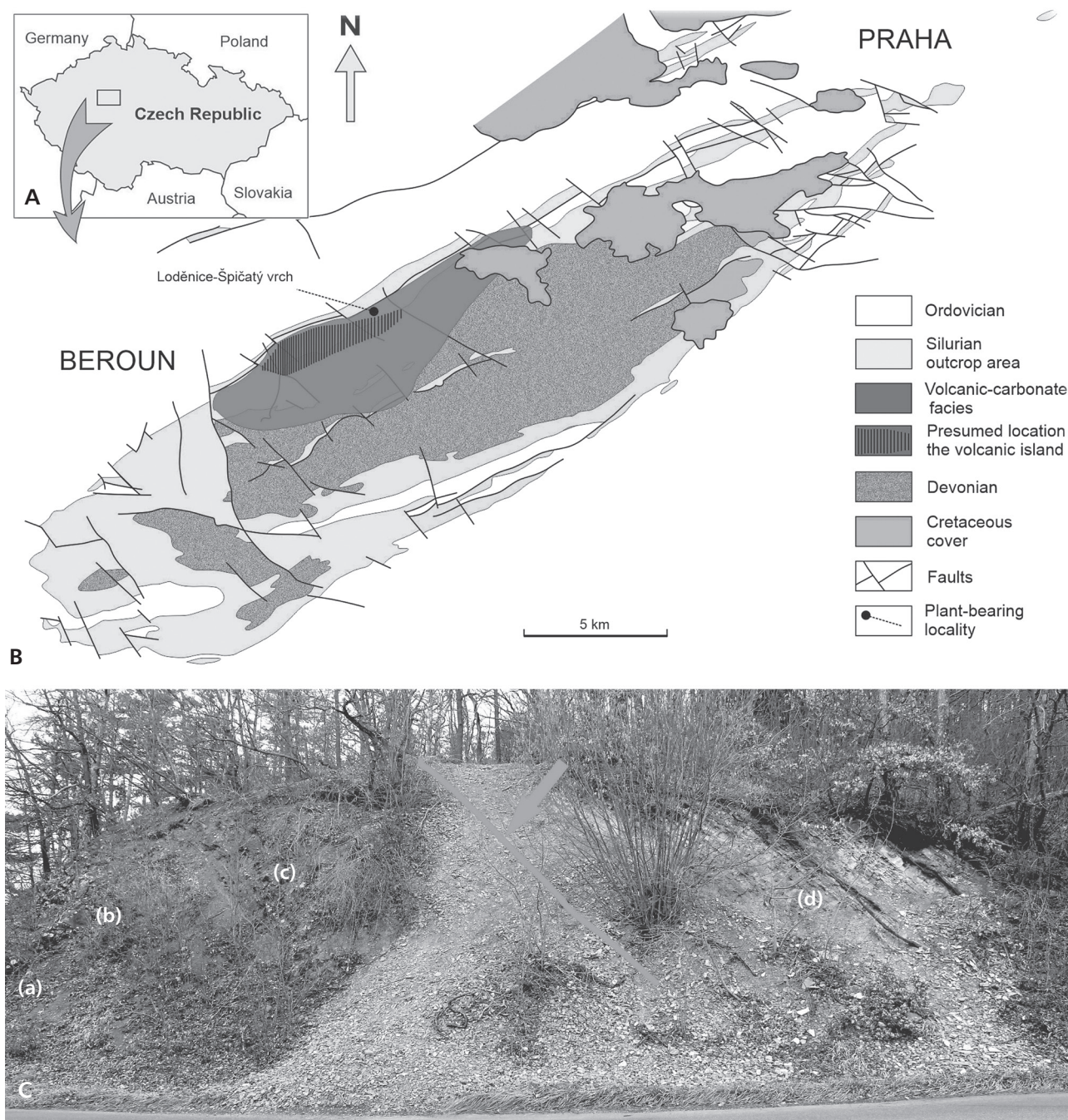
Figure 1. A– schematic map of the Czech Republic with the Prague Synform area indicated. • B – simplified map of the Silurian outcrop area of the Prague Synform with position of the Loděnice-Špičatý vrch locality and presumed location of the volcanic island(s). • C – general view of the road-cut exposure. Legend: (a) – basalt pillow lava; (b) – alkaline basalt lava flow; (c) – thick bedded yellow-brown tuffs and tuffites with further transition through brown tuffitic shales into (d) – laminated calcareous and tuffaceous shales interchanging with increasing proportion of grey platy limestones. Red line exhibits position of the sampled fossiliferous layer with *Cooksonia* plants and spores, largely covered by a debree cone.

of a vascular land plant is *Cooksonia barrandei* Libertín *et al.* 2018a from the middle Sheinwoodian (432 Ma; Libertín *et al.* 2018a) of the Czech Republic.

The dispersed palynomorphs and graptolites described herein come from the type collection of *Cooksonia barrandei* (Libertín *et al.* 2018a, b), *i.e.* the Loděnice-

Špičatý vrch locality in the Prague Basin (Fig. 1B, black dot). As the fossil plant record is several times smaller than the palynological record, the main goal of the current study was to document the biodiversity of plants, using dispersed spores and cryptospores described from this important locality.
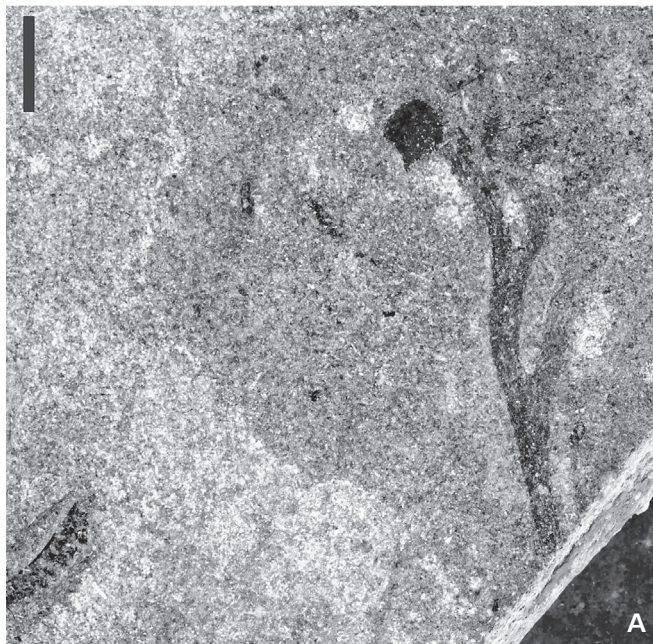
Material and methods

Three specimens (Nos NM-D 554, NM-D 557a and NM-D 550, National Museum, Prague) with fragments of *Cooksonia* sp. (Libertín *et al.* 2018b) have been sampled from the brown-grey calcareous and tuffaceous shale that well corresponds with lithological character of strata examined in the Loděnice-Špičatý vrch roadcut section and belong to the *Monograptus belophorus* graptolite Biozone. The only spore-bearing sample, No. D 550 with remains of *Cooksonia* sp. (Fig. 2A) and the zonal index graptolite *Monograptus belophorus* Meneghini, 1857 (on the other side of the rock slab), comes from Barrande's original collection from the Lodenitz locality (Barrandian area, Czech Republic; Fig. 1B, C) and is a part of the type collection of *Cooksonia barrandei* (Libertín *et al.* 2018b), *i.e.* from the Špičatý vrch locality. Another three samples of identical lithology have been taken from *belophorus* Biozone at the locality but all of them were barren.

Rock was macerated using HCl (24 hours), HF (seven days) and warm HCl (20 minutes) for the spores in the Geological Institute v.v.i., Academy of Sciences of the Czech Republic. The specimens of prasinophytes and scolecodonts were documented using a Hitachi S-3700N scanning electron microscope in the National Museum in Prague, a NIKON Eclipse 80i microscope was used for the study of the spores in the Institute of Geology v.v.i. AS CR in Prague.

Specimens of chitinozoans, prasinophytes and scolecodonts are stored in the Czech Geological Survey, Prague, Czech Republic (Nos PT98–PT101) and palynological slides (Nos. BA1-21) in the Institute of Geology v.v.i., Academy of Sciences of the Czech Republic, Prague, Czech Republic.

Geological setting

The Teplá-Barrandian Unit of the central Bohemian Massif encompasses sedimentary and volcanic infill of the classic Prague Basin recognised in the Barrandian area of Central Bohemia by Havlíček (1981). It is situated in the middle of the highly metamorphosed and deformed Moldanubian Zone of the Variscan Belt (Verniers *et al.* 2008). The Barrandian area is only mildly deformed and displays one of the most complete Silurian successions in the world. Comparable to other areas of peri-Gondwana or northern Gondwana, this unit drifted from high southern to northern equatorial latitudes during the Palaeozoic. Havlíček *et al.* (1994) argued for the existence of an independent palaeo-plate named Perunica on the basis of brachiopod, trilobite and other, largely benthic faunas. Rather isolated, though questionable position of the Perunica microplate may be assumed also from palaeomagnetic data (Tasáryová *et al.* 2014 and reference therein). However, this concept was challenged by Servais & Lehnert (2006) who claimed

Figure 2. A – *Cooksonia* sp. (Libertín *et al.* 2018b). Scale bar represents 10 mm. B – stratigraphic position of the plant spores and the earliest *Cooksonia barrandei* Libertín *et al.* 2018a macrofossils (marked by black asterisk) from Loděnice-Špičatý vrch dated by graptolites. Graptolite biozonation of the Prague Synform plotted with stratigraphical ranges of the associated graptolites. Right column exhibits correlative graptolite zones applied in the British Isles. Time scale calibration after Melchin *et al.* (2020).

Figure 3. Palaeogeographic map for the Wenlock Epoch. Modified from Cocks & Torsvik (2002). Presumed position of the locality marked by asterisk.

that the Perunica microplate was only a part of northern Gondwanan terrane assemblage (Fig. 3).

Un-metamorphosed Ordovician, Silurian and Lower and Middle Devonian marine sediments and synsedimentary volcanics preserved in the central part of the Teplá-Barrandian unit belong to a large erosional remnant of the Prague Basin located between the eastern periphery of Prague and the NE periphery of Pilsen. The Prague Synform was formed during the Variscan orogeny that substantially modified the sedimentary infill of the former marine basin.

Silurian rocks largely confined to the central part of the synform account for extremely limited continental siliciclastic input in this part of the basin, apparently located away from the substantial land mass. However, mid-Wenlock to mid-Ludlow synsedimentary volcanic activity formed a volcanic island or archipelago surrounded by shallow-water domains (Bouček 1934, Horný 1962, Kříž 1991). The largest volcanic high, the Svatý Jan volcanic centre (Fig. 1B), presumably extended above sea level as soon as middle Sheinwoodian times, as indicated by the presence of land plant fossils and spores in marine sediments deposited close to the island shore (Libertín *et al.* 2003, 2018a, b). Svatý Jan Volcanic Island, the presumed source of the plant remains and spores, remained above sea level until early Přídolí times, 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 continual transition from shallow water biodetrital limestones through off-shore, laminated tuffaceous shales associated with specific depth-related benthic faunal communities (Havlíček & Štorch 1998) suggest the basin reached a maximum depth

of about 200 metres in the most-offshore black shale dominated facies rich in graptolites (see Turek 1983, Štorch & Pašava 1989, Brett *et al.* 1993, Manda *et al.* 2019).

A complex facies suite of upper Telychian, Shein-woodian and Homerian black shales, and various limestones and basaltic volcaniclastics make up the 40–250 m thick Motol Formation (see Kříž 1975, 1998). The proximal volcanic-sedimentary facies of the Motol Formation developed in the vicinity of Svatý Jan pod Skalou village, between Tetín near Beroun and Mezouň, and consists of effusive basalts, agglomerates, hyaloclastics, coarse-grained pyroclastics and tuffites (for summary see Kříž 1991, 1998). Skeletal limestones, restricted to periods of ceased volcanic activity, form thin local beds and lenses. Land plant remains and dispersed palynomorphs, described herein, have been preserved in a relatively distal facies of laminated brown-grey calcareous and tuff-aceous shale with a rich and diversified marine fauna. A number of sterile cooksonioids, newly collected in the test pit above the local road from Loděnice to Bubovice (GPS coordinates 49° 58′ 53.48″ N, 14° 9′ 25.14″ E), immediately next to the original Barrande's locality, were briefly discussed by Libertín *et al.* (2018b). The entire section was described by Bouček (1941) and Kříž (1992).

Mid-Sheinwoodian succession exposed in a sharp left curve of the local road (Fig. 1C) is separated from the underlying Homerian shales by the southern branch of the Tachlovice thrust Fault. Plant-bearing section starts with 5 m thick basalt pillow lava (a) overlain by 2.5 m thick alkaline basalt lava flow (b) and 4.60 m thick bedded yellow-brown tuffs and tuffites (c) with further transition through brown tuffitic shales into at least 4 m thick succession of laminated calcareous and tuffaceous shales interchanging with increasing proportion of grey platy limestones (d). Land plant fossils are relatively common in the lowermost 0.5–1 m of interchanging tuffaceous shales and laminated limestones.

Associated with land plant fossils and dispersed spores are brachiopod shelly fauna (*Miraspis–Mezounia* benthic Community of Havlíček & Štorch (1990, 1998), trilobites assigned by Chlupáč (1987) to the *Miraspis* Community, relatively uncommon but significant graptolites of *Monograptus belophorus* Biozone, chitinozoans, prasinophytes and scolecodonts. Benthic fauna indicate sedimentation occurred in a moderately shallow, well-oxygenated but quiet-water environment, in a Benthic Assemblage 4–5 life zone *sensu* Boucot (1975). Plant-bearing facies, widely known as the "*Miraspis* Limestone" is confined to the NW periphery of the Svatý Jan Volcanic Island from which both cooksonioid land plants and dispersed palynomorphs disseminated. The shore line must have been situated a few kilometres at maximum from the studied outcrop although direct evidence of middle Sheinwoodian emergence of the island is still missing.

Results

Biostratigraphic dating

As the highly distinctive *Monograptus belophorus* is present on many slabs of Barrande's original samples with fossil plant remains (Libertín *et al*. 2018a, b), and spores and cryptospores, recognizing the stratigraphical level is very straightforward. This graptolite species is confined to the *Monograptus belophorus* Biozone in peri-Gondwanan Europe (Prague Synform in Bohemia, Štorch 1994; Sardinia, Italy, Štorch & Piras 2009; Carnic Alps, Italy, Piras *et al*. 2012) with slight overlap into the succeeding *Cyrtograptus rigidus* Biozone (*e.g.* eastern Taurus, Turkey, Sachanski *et al*. 2015 and western Yunnan, China, Zhang *et al*. 2014). *Monograptus belophorus* is a senior name of *Monograptus flexilis* Elles 1900 which is widely reported from the lower *rigidus* Biozone in the British isles (Zalasiewicz & Williams 1999, Zalasiewicz *et al*. 2009). In the peri-Gondwanan Europe, a separate *belophorus* Biozone is recognized below the *rigidus* Biozone (Fig. 2B).

Mature rhabdosomes of *M. belophorus* are moderately S-shaped with pronounced dorsal curvature that comprise 10–18 proximal thecae. In the plant-bearing samples, only immature and/or incomplete rhabdosomes with characteristic long sicula, and a robust and long virgella have been documented. In addition to *M. belophorus*, other characteristic graptolites were found, including: *Monograptus flemingii* (Salter, 1852), *Monoclimacis meneghinii* Gortani, 1922, *Mediograptus antennularius* (Meneghini, 1857), *Pristiograptus dubius* (Suess, 1851) and *Sokolovograptus textor*? (Bouček & Münch, 1952).

Monograptus flemingii is a long-ranging species that is present and common in the middle Sheinwoodian *belophorus* Biozone up to the mid-Homerian *lundgreni* Extinction event (top of *Cyrtograptus lundgreni* Biozone). *Pristiograptus dubius* is a Sheinwoodian species ranging approximately from the upper *Cyrtograptus murchisoni* to the *rigidus* Biozone. *Monoclimacis meneghinii* was reported from the *Pristiograptus dubius* and *belophorus* biozones by Štorch (1994); a closely similar range was recorded in the Sardinian type section at Goni by Barca & Jaeger (1990). *Mediograptus antennularius* is particularly common in the *belophorus* Biozone but its total range is from the upper (most) *dubius* to the lower *rigidus* Biozone. *Sokolovograptus textor* is a typical retiolitid of the *belophorus* and lower–middle *rigidus* biozones. The same range of the latter species was reported by Zalasiewicz *et al*. (2009) from the U.K.

The full stratigraphical ranges of the graptolites recorded in the *Cooksonia* Lang 1937 and spore-bearing interval are shown in Fig. 2B with zonal index species illustrated in Fig. 4. The presence of the *M. belophorus* graptolite Biozone indicates a middle Sheinwoodian age (~ 332 Ma; see Melchin *et al*. 2020) for the *Cooksonia* macrofossils and associated spores recovered from laminated calcareous and tuffaceous shale at Loděnice-Špičatý vrch locality.

Palynology

Spores and cryptospores. – Cryptospores and monolete and trilete spores were identified from the palynological slides, with the latter being more prevalent. The overall number of both is exceedingly small and palynomorph preservation is poor, probably due to the marine origin of sediments. Generally, cryptospores and trilete spores are small, with the largest Sheinwoodian miospores being up to 22 μm in diameter that is comparable with average diameter (20.5 μm) of trilete spores and cryptospores described by Dufka (1995a) from the Wenlock of the Prague Basin a few kilometres far from the Loděnice-Špičatý vrch locality. Average diameter of Silurian *in situ* trilete spores 21.3 μm (Gonez & Gerrienne 2010) is also comparable.

Cryptospores included laevigate monads of the forms that resemble those of the *Gneudnaspora* cf. *divellomedia* type (Fig. 5R) and undetermined tetrads (Fig. 5P, Q).
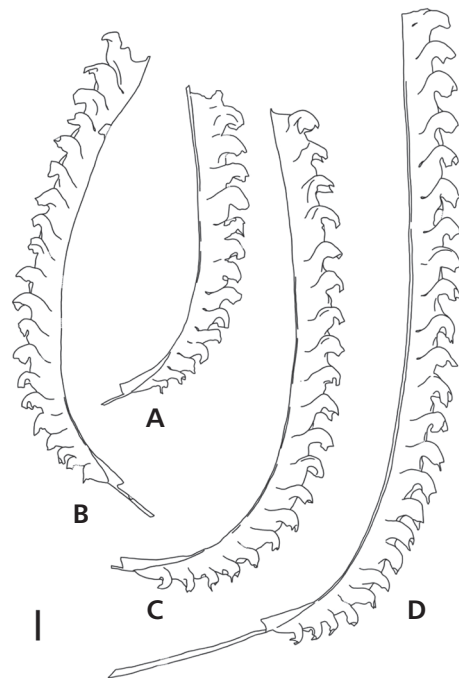
Figure 4. Middle Sheinwoodian zonal index graptolite *Monograptus belophorus* Menenghini, 1857 from Loděnice-Špičatý vrch plant-bearing samples: A – specimen from the reverse side of slab No. D550; B – specimen from slab No. D 550. C – specimen from from slab No. D 553. D – specimen No. PŠ 1356 from graptolite-rich black-shale reference section in Kosov quarry near Beroun. Black bar represents 1 mm.
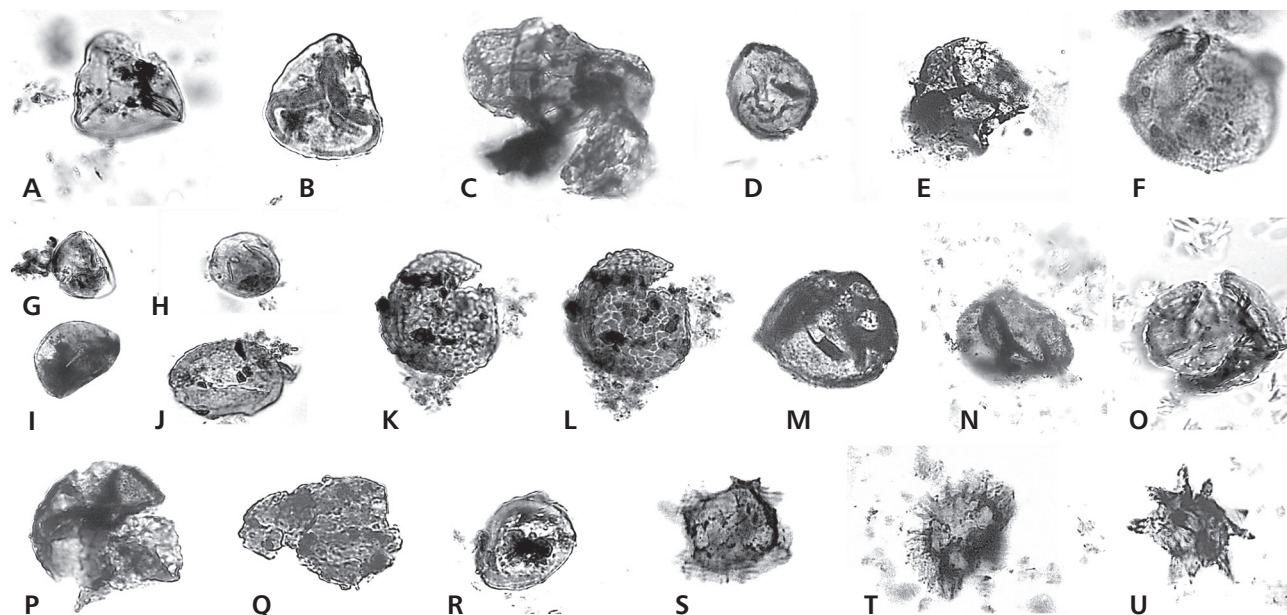
Figure 5. Spores, cryptospores, algae and acritarchs. All ×1500. • A – *Ambitisporites parvus* Burgess & Richardson 1995. • B – *Ambitisporites* spp. • C – tetrad of trilete sculptured spores of the *Aneurospora* type. • D – probably trilete spore of the *Ambitisporites* type. • E – poorly preserved and partly damaged probably trilete spore. • F – circular microspinate to microgranulate palynomorph resembles trilete spore. Note possible trilete mark in the centre. • G – oval laevigate monolete spore. Note monolete laesurae along right margin. • H – probably laevigate monolete spore. Possible monolete laesurae is close to right margin. • I – oval laevigate monolete miospore. Note short monolete laesurae in the centre. • J – oval sculptured palynomorph roughly resembles some monolete spore(?). • K, L – reticulate undetermined algae. • M, N – undetermined algae. • O – tetrad of undetermined algae. • P – tetrad of cryptospores of the *Aconthotetras* type(?). • Q – sculptured tetrad, possibly cryptospores. • R – cryptospores of the *Gneudnaspora* cf. *divellomedia* type. • S – acritarch of the *Cymatiosphaera* type. • T – acritarch of the *Fimbiaglomerella* type. • U – acritarch of the *Cordobesia* type(?).

Some palynomorphs closely resembling trilete spores are poorly preserved and their precise classification is questionable or even not possible (Fig. 5D–F). Sometimes only the rays of the trilete mark, the most important characteristic, are visible with the surface being damaged and poorly preserved (Fig. 5E).

Spores can be divided into trilete and monolete forms. Trilete spores are of *Ambitisporites* (Fig. 5A, B) and *Ambitisporites*-like types (Fig. 5D). Another form is tetrad of spores of the *Aneurospora* type (Fig. 5C) which are the same as those being macerated from a sporangium of *Cooksonia barrandei* from the same stratigraphical horizon and locality (Libertín *et al*. 2018a).

The occurrence of laevigate monolete (Fig. 5G–I) and possibly sculptured laevigate (Fig. 5J) monolete spores is surprising and novel.

Associated marine palynomorphs. – There are several studies published on Sheinwoodian microfossils from the Prague Basin, including acritarchs (Dufka 1992), leiosphaerids, chitinozoans (*e.g.* Dufka 1990, 1992, 1995b;

Morávek 2009; Vodička & Manda 2019), and scolecodonts (Šnajdr 1951). A detailed summary on previous research of organic walled microfossils from the Prague Basin was published by Morávek (2004). The present sampling has revealed that preservation of organic walled microfossils is poor. The original organic matter is corroded, and specimens are flattened and deformed probably due to marine origin of sediments. The state of preservation influenced the determination/classification of chitinozoans and scolecodonts, with the majority being indeterminate. Prasinophytes (Fig. 6U–X) were not studied in detail, though they may be the subject of future research.

The chitinozoan assemblage is not diverse, with two determined taxa and two questionable genera present. Approximately a half of specimens were assigned to *Conochitina* spp. (Fig. 6A–D) and remaining specimens to *Ancyrochyitina* spp. (Fig. 6E–N). Approximately forty specimens were found in sample D 550.

Šnajdr (1951) determined that scolecodonts from the Motol Formation were paulinitids, belonging to the genus *Kettnerites* Žebera, 1935. He studied only poorly preserved

Figure 6. Chitinozoans (A–N), scolecodonts (O–T) and prasinophytes (U–X). All scale bars are 100 μm, except for V where it is 200 μm. • A–D –*Conochitina* spp.; A – specimen collection number (SCN) PT101.22; B – SCN PT101.26; C – SCN PT101.28; D – SCN PT101.1. • E–N – *Ancyrochitina* spp.; E – SCN PT98.3; F – SCN PT101.4; G – SCN PT101.23; H – SCN PT101.9; I – SCN PT99.6; J – SCN PT101.14; K – SCN PT99.10; L – SCN PT98.23; M – SCN PT98.8; N – SCN PT101.16. • O, P – Polychaetaspidae, *Oenonites* sp.; O – first left maxilla, lateral view,
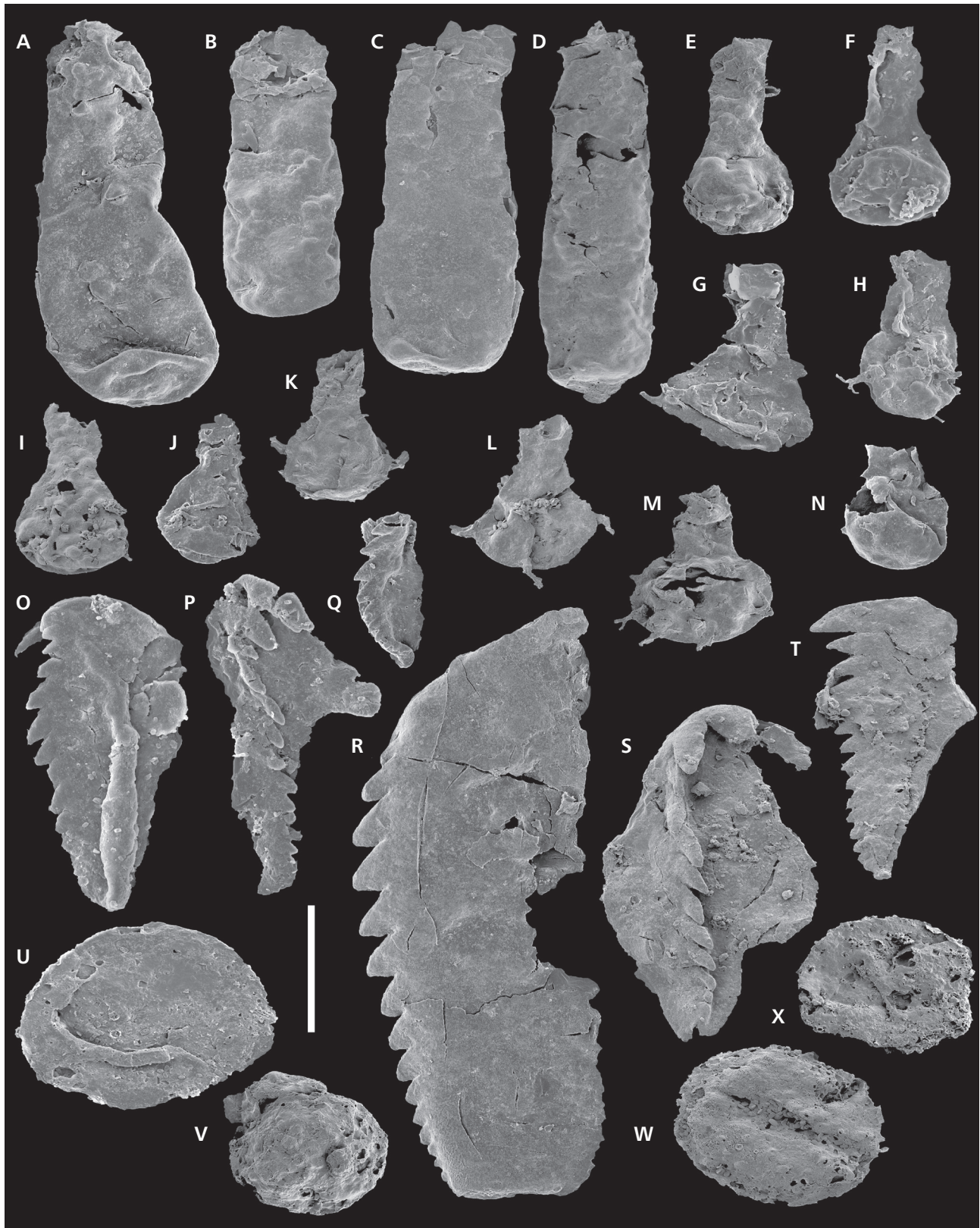
SCN PT100.19; P – first right maxilla, dorsal view, SCN PT100.9. • Q – family Xanioprionidae, dorso-lateral view, SCN PT100.6. • R – family Mochtyellidae, *Vistulella* sp. left first maxilla, lateral view, SCN PT100.22. • S – Ramphoprionidae, *Protarabellites* cf. *staufferi*, first right maxilla, dorsal view, SCN PT100.10. • T – family Tetraprionidae, lateral view, SCN PT99.9. • U–X – Prasinophytes; U – SCN PT101.11; V – SCN PT98.2; W – SCN PT98.14; X – SCN PT99.17.

specimens from the rock surface and unfortunately did not illustrate them. The restudy of original Šnajdr's collection has shown that maxillae of scolecodonts from the Loděnice locality belong to placognaths and their poor preservation was confirmed again. Our sampling has shown that the diversity of jawed polychaete forms was higher than previously reported. The rock yielded approximately 20 posterior maxillae. Nevertheless, such a small number does not allow a detailed analysis of the assemblage. At least five families are present: Polychaetaspidae (Fig. 6O, P), Xanioprionidae (Fig. 6Q), Mochtyellidae (Fig. 6R), Ramphoprionidae (Fig. 6S) and Tetraprionidae (Fig. 6T).

Some undetermined algae (Fig. 5K–O) were recognised including reticulate (Fig. 5K, L) forms and tetrad (Fig. 5O).

The number of acritarchs is very small and they are represented by specimens probably of the *Cymatiosphaera* type (Fig. 5S), *Fimbiaglomerella* type (Fig. 5T) and *Cordobesia* type (Fig. 5U).

Discussion

Affinity of spores

Critical to understanding the early land plant record is integrating the plant macrofossils and dispersed spores. This is achieved primarily through studies of *in situ* spores that enable identification of spore-parent plant relationships. *In situ* spores isolated from one parent plant species can often be assigned to one or more dispersed spore species of one genus or different species of two or more genera (Balme 1995, Bek 2017). Spores isolated from Silurian and Devonian plants have minimal morphological variations (usually only in diameter) and all of them usually belong to the only one dispersed species (Allen 1980, Gensel 1980, Balme 1995, Gonez & Gerrienne 2010). This was confirmed by *in situ* spores isolated from *Cooksonia barrandei* (Libertín *et al.* 2018a) from the same locality.

Spores of the genus *Ambitisporites* Hoffmeister 1959 were produced by only two plant genera; *Cooksonia* and *Concavatheca* Morris *et al.* 2011 [*Concavatheca banksii* (Habgood *et al.* 2002) Morris *et al.* 2012, formerly *Cooksonia banksii* (Habgood *et al.* 2002)]. The diversity of *Ambitisporites* at the locality together with minimal morphological variations of the *in situ* spores of this age (Balme 1995) suggest that at least two or three different *Ambitisporites*-cooksonioid producers were growing at this volcanic island during the middle Sheinwoodian. Spores of the *Aneurospora* type were produced by *Cooksonia barrandei*, the oldest vascular land plant described at the locality (Libertín *et al.* 2018a). About two unknown plants might produced two probably trilete undetermined spores (Fig. 5G–I).

As such, about six parent plants probably grew at the locality together with *Cooksonia* spp. and *C. barrandei*.

We can recognise two types of cryptospores so, it is probable that two different cryptospore producers (cryptosporophytes) grew at the locality.

Palynological comparison

Palynological studies from the Silurian interval are not very numerous (*e.g.* Richardson & Ioannides 1973, Burgess 1991, Wellmann 1993, Dufka 1995a, Burgess & Richardson 1995, Wang & Li 2000, Beck & Strother 2001, Steemans *et al.* 2012, Wellman *et al.* 2013, *etc.*). The only palynological paper about cryptospores and trilete spores from the Silurian of the Prague Basin was published by Dufka (1995a), who described six genera of cryptospores and seven genera of trilete spores (plus four undetermined types) from the late Wenlock (Homerian). This assemblage is from the same basin, but from a different locality and stratigraphic level, and represents a different plant association and only one spore genus *Ambitisporites* is described from both localities. Dufka's (1995a) assemblage belongs to the *Artemopyra brevicosta–Hispanaediscus verrucatus* Palynozone whereas our assemblage is a part of the *Archaeozonotriletes chulus* var. *chulus–Archaeozonotriletes chulus* var. *nanus* Palynozone (Richardson & McGregor 1986).

Silurian spore and cryptospore diversity

Similarities with the dispersed spore assemblages from the Dapingian to the Llandovery suggest the occurrence of very uniform, cosmopolitan, and simple vegetation (interpreted as "liverwort-like" plants) for some 30 million years. During this time similar spore assemblages have been reported globally from the equator to high latitudes, suggesting that the parent plants were palaeogeographically widespread (Steemans *et al.* 2009) with minimal floristic provincialism. Some dispersed spore assemblages reported from high latitudes are intimately related to glacial deposits of the Hirnantian glaciations, *e.g.* from the Czech Republic (Vavrdová 1988).

There is a dramatic exponential increase in diversity of trilete spores from small numbers in the Late Ordovician–early Silurian, through the remainder of the Silurian (from the Homerian) and into the Devonian (Wellman *et al.* 2013, Pšenička *et al.* 2021). Many cryptospores disappear in the Rhuddanian to Sheinwoodian, and almost no new taxa appear during the Aeronian and the Telychian (Steemans 1999). This extinction represents an important fall in plant biodiversity during the Telychian and the Sheinwoodian (Steemans 2000, fig. 3; Wellman

et al. 2013; Pšenička *et al.* 2021, fig. 8). As trilete spore-producers were progressively freed from aquatic habitats, they colonized regions of newly exposed land area after Homerian glaciation and came to dominate all vegetation. However, cryptosporophytes become extinct in the Early Devonian (Steemans 2000).

It is possible to recognise two key global plant events during the Silurian as demonstrated mainly by palynological data, *e.g.* Steemans (2000), Wellman *et al.* (2013) and Pšenička *et al.* (2021). Wellman *et al.* (2013) used more than 1500 occurrences of cryptospores and trilete spores from all palaeocontinents for qualitative and quantitative analysis. The number of trilete spores (not cryptospores) is extremely low (only a few genera on average are recognised) and constant from the Sandbian to the Sheinwoodian (Pšenička *et al.* 2021, fig. 8). Cryptospores reach their maximum during the late Katian and Rhuddanian, but their number rapidly decreases towards a Sheinwoodian minimum. Numbers of both cryptospores and trilete spores significantly increase from the Homerian and reach a first global high key diversity event after Homerian glaciation (Wellman *et al.* 2013, Pšenička *et al.* 2021).

The same feature is reported by *e.g.* Wellman *et al.* (2013) and Pšenička *et al.* (2021, fig. 8).

Cryptospores reached their maximum within Rhuddanian (17 genera with 33 species) and minimum in Sheinwoodian (9 genera with 9 species). The number of cryptospore taxa is stable (14 genera with 25 species on average) till Přídolí (Pšenička *et al.* 2021). The number of trilete spore taxa is constant from Hirnantian to Sheinwoodian (3 genera with 4 species on average) but they reached the peak after Homerian glaciation (13 genera with 29 species) that represents first global event for diversification of early land plants (Pšenička *et al.* 2021). After decrease within Gorstian (10 genera with 20 species) the number of trilete spore taxa grows significantly from Ludlow (20 genera with 48 species) to Přídolí (35 genera with 129 species).

Collectively, these data indicate that the first global, key event in the geological history for trilete spore-plant producers was after Homerian glaciation, with a second event in the Přídolí as demonstrated by Steemans (2000), Wellman *et al.* (2013), Kraft *et al.* (2018) and Pšenička *et al.* (2021).

Kraft *et al.* (2018) proposed a new genus and species of an early land plant, *Tichavekia grandis* Pšenička *et al.* 2018, from the Prague Basin, but from stratigraphically younger strata of Přídolí age. They recognised only the latter (Přídolí) event and interpreted it as being the first one (called Initial Plant Diversification and Dispersal Event – IPDDE) because they did not include previous palynological data from the stratigraphically older Homerian strata where the first global key event is documented (Steemans 2000, figs 1–3; Wellman *et al.* 2013, fig. 1; Pšenička *et al.* 2021,

fig. 8). However, the Přídolí event has much higher numbers of both new spores as well as plant taxa than is seen during the Homerian event. In addition, the Homerian event, although documented mainly by palynological data, must also reflect high diversification among the parent plant associations (although plant macrofossils are rare here). As such, the Homerian event represents the first globally significant key event (IPDDE *sensu* Kraft *et al.* 2018) in land vascular plant phylogeny (Steemans 2000, Wellman *et al.* 2013, Pšenička *et al.* 2021).

The importance of volcanic islands for plant evolution in the Prague Basin during the Silurian was stressed by Kraft *et al.* (2018). The islands were of a low altitude with a broad shore plain which, through constant erosion, provided places with suitable substrates for the proliferation of plants. Furthermore, the local environment on the islands was stable for sufficient lengths of time to accommodate land plants permanently or periodically (Kraft *et al.* 2018). It is confirmed by absolute (not average) number of trilete spores from all Sheinwoodian localities counted from Wellman *et al.* (2013).

Conclusions

Palynomorphs and mainly graptolites confirm a middle Sheinwoodian age (432 Ma) for the Loděnice-Špičatý vrch locality. Dispersed spores and cryptospores (macerated directly from rocks with *Cooksonia*) reflect the biodiversity of plant associations that developed concurrently with the first until recorded vascular land plants, *Cooksonia barrandei* and *Cooksonia* sp. from the same locality. Recovered palynomorphs can be divided into trilete and monolete spores. Especially surprising occurrence of monolete spores represents the stratigraphically oldest monoletes described. Based on our knowledge about Silurian *in situ* spores it is possible to hypothetically estimate that about six different vascular land plants and two types of cryptosporophytes might have grown on a volcanic island that was adjacent to sea. Although only two species of *Cooksonia* were previously recognized at the locality, some still unpublished probably lycophyte, cooksonioid, zosterophyll-like and cryptosporophyte specimens were found and the palynological record provides evidence of more diversified vegetation that existed on this volcanic island 432 Ma ago.

Although the described assemblage falls into the interval with a minimum number of cryptospore and spore taxa during the Sheinwoodian, the assemblage appears to be relatively well diversified. Subsequent younger Homerian assemblages from the Prague Basin (Dufka 1995a) yielded higher numbers of cryptospore and spore taxa, which corresponds well with an increased average number (11) globally at this younger stratigraphical level.

It is apparent that the Sheinwoodian volcanic islands of present Bohemian Massif were important for plant colonization. Spores of early Silurian plants were small, usually only 15–25 μm, which would have been optimal for wind dispersal (25 μm or less). It is probable that plants spread to neighbouring islands and coastal zones mainly via wind dispersal of their spores. The palynological record (the oldest known monolete spores) together with the specimens of the oldest sporophytes of vascular land plant *Cooksonia barrandei* and other cooksonioids stress the importance of the Loděnice-Špičatý vrch locality, and the significant role of volcanic islands for the early evolution of land plants before the Homerian first global key event.

Acknowledgements

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