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 monolette spores and pollen but resemble land plant spores (Strother 1991). The oldest cryptospores are 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...
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–Spičatý 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 Barrandé’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 biozonalation 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).](image-url)
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 dispersed spores in marine sediments deposited close to the island shore (Libertín et al. 2003, 2018, b). Svatý Jan Volcanic Island, the presumed source of the plant remains and spores, remained above sea level until early Přídlí times, as documented by subaerial basalt lavas of the latest Wenlock–early Ludlow age overlain by middle Přídlí crinoidal limestones with a prominent erosional unconformity (Havlíček et al. 1987). A continual transition from shallow water biodetrital limestones through offshore, 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, Sheinwoodian and Homerian black shales, and various limestones and basaltic volcanics 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 Tetin 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 tuffaceous 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 4.6 m thick bedded yellow-brown tuffis 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 Havliček & 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 slab No. D553. D – specimen No. PS 1356 from graptolite-rich black-shale reference section in Kosov quarry near Beroun. Black bar represents 1 mm.
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 (Snajdr 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 Ancyrochitina spp. (Fig. 6E–N). Approximately forty specimens were found in sample D 550.

Snajdr (1951) determined that scolecodonts from the Motol Formation were paulinitids, belonging to the genus Kettnerites Žebera, 1935. He studied only poorly preserved
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 scaleodonts 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), Xaniopironidae (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 Cymatiopsphaera type (Fig. 5S), Fimbriaglomerella 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 dispersed species (Allen 1980, Gensel 1980, Balme 1995, Gonez & Gerrienne 2010). This was confirmed by in situ spores isolated from Cooksonia barrandei (Libertin 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 (Libertin 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 (cryptosporephytes) 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. namus 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 Silurian volcanics 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 neighboring 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**

We acknowledge financial support from the Czech Science Foundation, First vascular land plants and palynomorphs from the Silurian–Lower Devonian of the Barrandian area, Czech Republic (GAČR 17–10233S). Part of this contribution was also supported by the Research Program of the Institute of Geology AS CR, v.v.i. (RVO67985831). Authors are obliged to C. Eble for linguistic corrections and help and P. Steemans, University of Liege, Belgium for many helpful suggestions and remarks.

**References**

**Allen, K.C.** 1980. A review of in situ late Silurian and Devonian spores. Review of Palaeobotany and Palynology 29, 253–270. DOI 10.1016/0034-6667(80)90062-7

**Balmé, B.A.** 1995. Fossil in situ spores and pollen grains: an annotated catalogue. Review of Palaeobotany and Palynology 87, 81–323. DOI 10.1016/0034-6667(95)93235-X

**Barca, S. & Jaeger, H.** 1990. New geological and biostratigraphical data on the Silurian in SE-Sardinia. Close affinity with Thuringia. Bolletino della Società geologica Italiana 108, 101–117.

**Beck, J.H. & Strother, P.K.** 2001. Silurian spores and cryptospores from the Arisaig Group, Nova Scotia, Canada. Palynology 25, 127–177. DOI 10.2113/0250127

**Bek, J.** 2017. Paleozoic in situ spores and pollen. Lycopsida. Palaeontographica, Abteilung B 296, 1–111. DOI 10.1127/palb/296/2017/1

**Berner, R.A., Brooks, J.M. & Ward, P.D.** 2007. Oxygen and evolution. Science 316, 557–558. DOI 10.1126/science.1140273

**Boček, B.** 1934. Bemerkungen zur Stratigraphie des böhmischen Gotlanden und seinen Faziesverhältnissen. Centralblatt für Mineralogie, Geologische und Paläontologische Abteilung B 11, 477–494.

**Boček, B.** 1941. O novém odkryvu siluru u Lodenic. Zprávy Geologického ústavu pro Čechy a Moravu 17(4), 165–172.

**Boček, B. & Münch, A.** 1952. The Central European Retiolites of the Upper Wenlock and Ludlow. Sborník Ústredního ústavu geologického, Oddíl paleontologický 19, 1–151.

**Boucot, A.J.** 1975. Evolution and Extinction Rate Controls. 424pp. Elsevier, Amsterdam.

**Brett, C.E., Boucot, A.J. & Jones, S.B.** 1993. Absolute depths of Silurian benthic assemblages. Lethaia 26, 25–40. DOI 10.1111/j.1502-3931.1993.tb01507.x

**Breuer, P. & Steemans, P.** 2013. Devonian spore assemblages from northwestern Gondwana: taxonomy and biostatigraphy. Special Papers in Palaeontology 89, 1–163.

**Burgess, N.D.** 1991. Silurian cryptospores and miospores from the type Llandovery area, south-west Wales. Palaeontology 34, 575–599.

**Burgess, N.D. & Richardson, J.B.** 1995. Late Wenlock to early Pridoli cryptospores and miospores from south and SW Wales, Great Britain. Palaeontographica Abteilung B 236, 1–44.

**Chlupač, I.** 1987. Ecostratigraphy of Silurian trilobite assemblages of the Barrandian area. Newsletters on Stratigraphy 17, 169–186. DOI 10.1127/nos/17/1987/169

**Cocks, L.R.M. & Torsvik, T.H.** 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. Journal of the Geological Society London 159, 631–644. DOI 10.1144/0016-764901118

**Dufka, P.** 1990. Palynomorphs in the Llandovery black shale sequence of the Prague Basin (Barrandian area, Bohemia). *Casopis pro mineralogii a geologii* 35(1), 15–31.

**Dufka, P.** 1992. Lower Silurian chitinozoans of the Prague Basin (Barrandian, Czechoslovakia) – preliminary results. Revue de Micropaléontologie 35(2), 117–126.

**Dufka, P.** 1995a. Upper Wenlock miospores and cryptospores derived from a Silurian Volcanic island in the Prague Basin (Barrandian area, Bohemia). Journal of Micropalaeontology 14, 67–79. DOI 10.1144/jm.14.1.67

**Dufka, P.** 1995b. Chitinozoans from the Sheinwoodian/Homerian boundary beds (Wenlock) in the Prague Basin (Barrandian, Bohemia). Review of Palaeobotany and Palynology 86(1–2), 135–145. DOI 10.1016/0034-6667(94)00102-P

**Edwards, D., Morris, J.L., Richardson, J.B. & Kenrick, P.** 2014. Cryptospores and cryptophytes reveal hidden diversity in early land floras. New Phytologist 202, 50–78. DOI 10.1111/nph.12645

**Elles, G.L.** 1900. The zonal classification of the Wenlock Shales of the Welsh Borderland. Quarterly Journal of the Geological Society 56, 370–414. DOI 10.1144/GSL.JGS.1900.056.01-04.25

**Gensel, P.G.** 1980. Devonian in situ spores: a survey and discussion. Review of Palaeobotany and Palynology 30, 101–132. DOI 10.1016/0034-6667(80)90009-3

**Gomez, P. & Gerrienne, P.** 2010. A new definition and a lectotypification of the genus *Cooksonia* Lang 1937. International Journal of Plant Sciences 171, 199–215. DOI 10.1086/648988

**Gortani, M.** 1922. Fauna paleozoico della Sardegna. Graptoliti di Goni. Graptoliti della Sargena orientale 2. Palaeontographica Italica 28, 51–67, 85–111.

**Hargood, K.S., Edwards, D. & Axe, L.** 2002. New perspectives on Cooksonia from the Lower Devonian of the Welsh
Borderland. *Botanical Journal of the Linnean Society* 139, 339–359. DOI 10.1046/j.1095-8339.2002.00073.x

Havlíček, V. 1981. Development of a linear sedimentary depression exemplified by the Prague Basin (Ordovician–Middle Devonian; Barrandian area–Central Bohemia). *Sborník geologických věd. Geologie* 35, 7–48.

Havlíček, V. & Štöch, P. 1990. Silurian brachiopods and benthic communities in the Prague Basin (Czechoslovakia). *Rozpravy Ústredního ústavu geologického* 48, 1–275.

Havlíček, V. & Štöch, P. 1998. Silurian and Lochkovian communities in the Prague basin (Barrandian area, Czech Republic), 200–228. In Boucot, A.J. & Lawson, J.D. (eds) *Paleocommunities: A Case Study from the Silurian and Lower Devonian*. Cambridge University Press. Cambridge.

Havlíček, V., Brunerová, Z., Holub, V., Hrkál, Z., Cháb, J., Chlupáč, I., Kovanda, J., Rudolsky, J., Šalanský, K., Štöch, P., & Volšan, V. 1987. Vysvětlivky k základní geologické mapě ČSSR 1:25000, 1–275. Beroun.

Havlíček, V., Vaněk, J. & Fatka, O. 1994. Perunica microcontinent in the Ordovician (its position within the Mediterranean Province, series division, benthic and pelagic associations). *Sborník geologických věd. Geologie* 46, 23–56.

Hofmeister, W.S. 1959. Lower Silurian plant spores from Libya. *Micropaleontology* 5, 331–334.

Horný, R. 1962. Das Mittelböhmische Silur. *Geologie* 11, 843–916.

Kraft, P., Pseníčka, J., Sakala, J. & Frýda, J. 2018. Initial plant diversification and dispersal event. In upper Silurian of the Prague Basin. *Paleoecography, Palaeoclimatology, Palaeoecology* 514, 144–155.

DOI 10.1016/j.palaeo.2018.09.034

Kríž, J. 1975. Revision of the Lower Silurian stratigraphy in Central Bohemia. *Věstník Ústredního ústavu geologického* 50, 275–282.

Kríž, J. 1991. The Silurian of the Prague Basin (Bohemia) – tectonic, eustatic and volcanic controls on facies and faunal development. *Special Papers in Palaeontology* 44, 179–203.

Kríž, J. 1992. Silurian field excursions: Prague Basin (Barrandian area). *National Museum of Wales, Geological Series* 13, 1–111.

Kríž, J. 1998. Silurian, 79–100. In Chlupáč, I., Havlíček, V., Kríž, J., Kukal, Z. & Štöch, P. (eds) *Palaeozoic of the Barrandian (Cambrian to Devonian)*. Czech Geological Survey., Prague.

Lang, W.H. 1937. On the plant-remains from the Downtonian of England and Wales. *Philosophical Transactions of Royal Society B* 227, 245–291. DOI 10.1098/rstb.1937.0004

Libětín, M., Labušová, R. & Dašková, J. 2003. The oldest vascular plants from the Bohemian Massif. *Zprávy o geologických výzkumních v roce* 2002, 127.

Libětín, M., Kvaček, J., Bek, J., Žársky, V. & Štöch, P. 2018a. Sporophytes of polysporangiate land plants from the early Silurian period may have been photosynthetically autonomous. *Nature Plants* 4(5), 269–271.

DOI 10.1038/s41477-018-0140-y

Libětín, M., Kvaček, J., Bek, J., Žársky, V. & Štöch, P. 2018b. Plant diversity of the Mid Silurian (Lower Wenlock, Shinwoodian) terrestrial vegetation preserved in marine sediments from the Barrandian area, the Czech Republic. *Fossil Imprints* 74, 327–333. DOI 10.2478/fit-2018-0020

Manda, Š., Štöch, P., Frýda, J., Slavík, L. & Tasárůvá, Z. 2019. The mid-Homerian (Silurian) biotic crisis in offshore settings of the Prague Synform, Czech Republic: integration of the graptolite fossil record with conodonts, shelly fauna and carbon isotope data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 528, 14–34. DOI 10.1016/j.palaeo.2019.04.026

Melchin, M.J., Sadler, P.M. & Cramer, B.D. 2020. The Silurian Period, 695–732. In Gradstein, F.M., Ogg, J.G., Schmitz, M.D. & Ogg, G.M. (eds) *Geologic Time Scale 2020*. Elsevier, Amsterdam. DOI 10.1016/B978-0-12-824360-2.00021-8

Mengehini, N. 1857. Palaeontologie de l’Ile de Sardeigna. In La Marmora, A. (ed.) *Voyage en Sardaigne*. 584 pp. Imprimaire Royal, Turin, Paris.

Morávek, R. 2004. Silurian organic-walled microfossils in the Prague Basin (Barrandian area): their localities, literature and distribution. *Journal of the Czech Geological Society* 49(1), 63–73.

Morávek, R. 2009. Lower Wenlock Chitinozoa from the locality Bykoš (Silurian, Prague Basin, Barrandian area, Czech Republic). *Acta Musei Naturalis Pragae, Series B, Historia Naturalis* 65(1–2), 37–60.

Morris, J.L., Edwards, D., Richardson, J.B., Axe, L. & Davies, K.L. 2011. New plant taxa from the Lower Devonian (Lochkovian) of the Welsh Borderland, with a hypothesis on the relationship between hilate and trilette spore producers. *Review of Palaeobotany and Palynology* 167, 51–81.

DOI 10.1144/0016-76492011-072

Morris, J.L., Wright, V.P. & Edwards, D. 2012. Siluro–Devonian landscapes of southern Britain: The stability and nature of early vascularplant habitats. *Journal of the Geological Society* 169, 173–190.

Pirás, S., Corradini, C. & Simonetto, L. 2012. Wenlockian (Silurian) graptolites from “La Valute Nordsection” (Mt. Zermula, Carnic Alps, NE Italy). Gortania: Geology, Paleontology. *Gortania* 33, 5–14.

Pseníčka, J., Bek, J., Frýda, J., Žársky, V. & Uhliřová, M. 2021. Dynamics of Silurian plants as response to climatic changes. *Life* 11, art. 906. DOI 10.3390/life11090906

Richardson, J.B. & Ioannides, N. 1973. Silurian palynomorphs from the Tanezzuft and Acacus Formations, Triqoliitana, North Africa. *Micropalaeontology* 19(3), 357–407.

DOI 10.2307/1484881

Richardson, J.B. & McGregor, D.C. 1986. Silurian and Devonian spore zones of the Old Red Sandstone continent and adjacent regions. *Geological Survey of Canadian Bulletin* 364, 1–79. DOI 10.4095/120614

Sachanski, V., Kozlu, H. & Göncooglu, M.H. 2015. Thuringian affinity of the Silurian-Lower Devonian succession from the Eastern Taurus, Turkey. *Turkish journal of Earth Sciences* 24, 303–324. DOI 10.3906/yer-1411-27

Sauter, J.W. 1852. Description of some graptolites from the south of Scotland. *Quarterly Journal of the Geological Society of London* 8, 1–5. DOI 10.1144/GSL.JGS.1852.008.01-02.40
SERVAIS, T. & LEHNERT, O. 2006. Good and bad terranes: Are some methods better than others for inferring palaeogeography? In Programme: Abstracts and Field Excursion Guides of the Annual Meeting of project IGCP 503. ‘Changing palaeogeographical and palaeobiogeographical patterns in the Ordovician and Silurian’, Glasgow, 28 August to 4 September 2006.

ŠNAIDR, M. 1951. O errantních Polychaetech z českého spodního paleozoika. Sborník Ústředního ústavu geologického 18, 241–292.

STEEMANS, P. 1999. Paléodiversification des spores et des cryptospores de l’Ordovicien au Dévonien inférieur. Geobios 32, 341–352. DOI 10.1016/S0034-6667(00)00059-2

STEEMANS, P. 2000. Miospore evolution from the Ordovician to the Silurian. Review of Palaeobotany and Palynology 113, 189–196. DOI 10.1016/S0034-6667(00)00059-2

STEEMANS, P., LE HÉRISSE, A., MELVIN, J., MILLER, M.A., PARIS, F., VERNIERS, J. & WELLMAN, C.H. 2009. Origin and radiation of the earliest vascular land plants. Science 324, art. 353. DOI 10.1126/science.1169659

STEEMANS, P., PETUS, E., BREEER, P., MAUILLER-MENDLOWICZ, P. & GIERENIE, P. 2012. Palaeozoic innovations in the micro- and megafossil plant record to the earliest seeds. International Year of Plant Earth, 437–477. In TAYLOR, J.A. (ed.) Earth and Life. Springer–Science and Bussiness Media B.V.

STORCH, P. 1994. Graptolite biostratigraphy of the Lower Silurian (Llandovery and Wenlock) of Bohemia. Geological Journal 29, 137–165. DOI 10.1002/gj.3350290204

STORCH, P. & PASAVO, J. 1989. Stratigraphy, chemistry and origin of the Lower Silurian black graptolitic shales of the Prague Basin (Barrandian, Bohemia). Věstník Ústředního ústavu geologického 64, 143–162.

STORCH, P. & IRAS, S. 2009. Silurian graptolites of Sardinia: assemblages and biostratigraphy, 77–93. In CORRADIN, C., FERRETTI, A. & STORCH, P. (eds) Silurian of Sardinia. Rendiconti della Societa Paleontologica Italiana 3.

STROTHER, P.K. 1991. A classification schema for the cryptospores. Palynology 15, 219–236. DOI 10.1080/01916122.1991.9989397

STROTHER, P.K. 2015. Systematics and evolutionary significance of some new cryptospore taxa from the Cambrian of eastern Tennessee, USA. Review of Palaeobotany and Palynology 227, 28–41. DOI 10.1016/j.revpalbo.2015.10.006

SUESS, E. 1851. Über böhmische Graptolithen. Naturwissenschaftliche Abhandlungen von Haidinger, Wien 4, 87–134.

TASÁRYOVA, Z., SCHNABL, P., ČÍŽKOVA, K., PRUNER, P., JANOUŠEK, V., RAPPRICH, V., STORCH, P., MANDA, Š., FRYDA, J. & TRUBAC, J. 2014. Gorstian palaeoecosystem and geotectonic setting of Suchomasty Volcanic Centre (Silurian, Prague Basin, Teplá-Barrandian Unit, Bohemian Massif). Geologiska Föreningens Förhandlingar 136, 262–265. DOI 10.1080/11305897.2013.879735

TUREK, V. 1983. Hydrodynamic conditions and the benthic community of upper Wenlockian calcareous shales in the western part of the Barrandian (Kosov Quarry). Časopis pro mineralogii a geologii 28, 245–260.

VAVROVÁ, M. 1988. Further acritarchs and terrestrial plant remains from the Late Ordovician at Hlásná Trébáň (Czechoslovakia). Časopis pro mineralogii a geologii 33, 1–10.

VERNERS, J., MALETZ, J., KŘÍZ, J., ŽIGAJTÉ-MORO, Ž., PARIS, F., SCHONLAUB, H.P. & WRONA, R. 2008. Silurian. Geological Society of London, Special Publication 1, 249–302. DOI 10.1144/CEV1P.6

VODÍČKA, J. & MANDA, Š. 2019. A taxonomical and statistical study of chitinozoan distribution across the lundgreni Event (Wenlock, Silurian) from the Prague Basin, Czech Republic: A specific pattern driven by ecological changes. Marine Micropaleontology 149, 44–63. DOI 10.1016/j.marmicro.2019.04.002

WANG, Y. & LI, J. 2000. Late Silurian spores from northern Jiangsu, China. Review of Palaeobotany and Palynology 111, 111–125. DOI 10.1016/S0034-6667(00)00021-X

WELLMAN, C.H. 1993. A land plant microfossil assemblage of Mid Silurian age from the Stonehaven Group, Scotland. Journal of Micropaleontology 12, 47–66. DOI 10.1144/jm.12.1.47

WELLMAN, C.H. 2010. The invasion of the land by plants: when and where? New Phytologist 188, 306–309. DOI 10.1111/j.1469-8137.2010.03471.x

WELLMAN, C.H. & GRAY, J. 2000. The microfossil record of early land plants. Philosophical Transactions of Royal Society of London B 355, 717–732. DOI 10.1098/rstb.2000.0612

WELLMAN, C.H., STEEMANS, P. & VEcoli, M. 2013. Paleophyto-geography of Ordovician–Silurian land plants. Geological Society of London, Memoirs 38, 461–476. DOI 10.1144/M38.29

WELLMAN, C.H., STEEMANS, P. & MILLER, M.A. 2015. Spore assemblages from Upper Ordovician and lowermost Silurian sediments recovered from the Qusaiba-1 shallow core hole, Qasim region, central Saudi Arabia. Review of Palaeobotany and Palynology 212, 111–126. DOI 10.1016/j.revpalbo.2014.09.003

ZALASEWICZ, J.A. & WILLIAMS, M. 1999. Graptolite biobozonation of the Wenlock Series (Silurian) of the Builth Wells district, central Wales. Geological Magazine 136, 263–283. DOI 10.1017/S0016756899002599

ZALASEWICZ, J.A., TAYLOR, L., RUSHTON, W.A., LOYDELL, D.K., RICKARDS, R.B. & WILLIAMS, M. 2009. Graptolites in British stratigraphy. Geological Magazine 146, 785–850. DOI 10.1017/S0016756809900434

ŽEBERA, K. 1935. Les Conodontes et les Scolécodontes du Barrandien. Bulletin international de l’Académie des Sciences de Bohême 36, 88–96.

ZHANG, Y.D., WANG, Y., ZHAN, R.B., FAN, J.X., ZHOU, Z.Q. & FANG, X. 2014. Ordovician and Silurian Stratigraphy and Palaeontology of Yunnan, Southwest China. 138 pp. Science Press, Beijing.