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To cite this article: Milan Libertín, Jiří Kvaček, Jiří Bek & Stephen McLoughlin (2023) The early land plant Cooksonia bohemica from the Pridoli, late Silurian, Barrandian area, the Czech Republic, Central Europe, Historical Biology, 35:12, 2504-2514, DOI: 10.1080/08912963.2022.2144286

To link to this article: https://doi.org/10.1080/08912963.2022.2144286

Published online: 04 Dec 2022.

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The early land plant Cooksonia bohemica from the Pridoli, late Silurian, Barrandian area, the Czech Republic, Central Europe

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ABSTRACT

Cooksonia bohemica Schweitzer (= Aberlemnia bohemica (Schweitzer) Sakala, Pšenička et Kraft) from Přídolí strata of the Barrandian area in the Czech Republic is revised, and its morphology is documented in detail. The holotype bears sporangia that, although reniform, do not possess a slit that would allow valvate opening as assumed in earlier studies. Its axes do not show consistent shortening of segments towards the distal portion of the plant as is typical for Aberlemnia Gonez et Gerrienne. The axes contain tubular structures interpreted here as cells of conducting tissues. Masses of subtriangular tritele spores with equatorial crassitudo and finely microgranulate sculpture are of the Ambitisporites type. Cooksonia bohemica is compared with all species of Cooksonia Lang described previously. Additionally, comparisons are made with the related genus Aberlemnia. Based on studies of the type material of both taxa, we suggest retaining the species in Cooksonia. Cooksonia bohemica is differentiated from other taxa based on a combination of branching pattern, sporangial shape, and spore morphology. The remains are interpreted to be the sporophyte of an early land plant referable to tracheophytes based on the presence of vascular strands in its axes. A general radiation of cooksonioids away from a core region around the Rheic Ocean is proposed for the Silurian–Devonian transition.

Introduction

Cooksonia Lang is one of the most iconic genera in the plant fossil record; it contains the earliest known polysporangiophytes (Libertín et al. 2018a, 2018b), i.e. that clade including all plants with sporophytes having branched axes bearing sporangia. Cooksonia has a cosmopolitan distribution and ranges from middle-Silurian (Wenlock) to upper Lower Devonian (Pragian–Emsian) strata (Edwards and Feehan 1980; Edwards et al. 2004; Gonez and Gerrienne 2010a; McSweeney et al. 2021). Recent studies of Cooksonia and other early land plants have provided numerous new insights into this enigmatic and highly heterogeneous group (Morris 2014; Edwards et al. 2021; McSweeney et al. 2021). In particular, well-preserved specimens in the form of mesofossils have provided more detailed morphological information than previously available, elucidating the diversity and systematics of the early land plants (Edwards 2021 et al.). Re-investigation and revision of taxa described previously has also provided valuable new information on early land plant architecture. For example, the type material of Cooksonia caledonica Edwards (Edwards 1970) was restudied by Gonez and Gerrienne (2010b) and transferred to a new genus Aberlemnia Gonez et Gerrienne. The discovery of in situ conducting cells in Cooksonia pertoni Lang also provided new anatomical information (Edwards et al. 1992) for a taxon described many decades earlier by Lang (1937). In some cases, a re-analysis of old collections can yield surprising discoveries about plant architecture (Libertín 2018a, 2018b). However, if such revisions are carried out superficially, they can introduce even more ambiguous anatomical or morphological interpretations into the literature regarding the studied plant. Such a circumstance resulted from a paper by Kraft et al. (2018) who studied plant diversification in the late Silurian of the Barrandian area in the Czech Republic. Their report briefly mentioned Cooksonia bohemica and they transferred this species to Aberlemnia. As far as we know, their evaluation of the species was based on indirect observation of the holotype itself. Here, we question their interpretation based on detailed studies of the holotype of C. bohemica stored in the Swedish Museum of Natural History, Stockholm, and the type of Aberlemnia housed in the National Museum of Scotland. Equipped with studies of the type material of both taxa, we suggest retaining the species in Cooksonia.

Cooksonia bohemica has attracted the attention of Czech palaeobotanists for many decades. It was formally named and briefly described by Schweitzer (1980). However, it was Obrhel (1962) who figured and described the taxon in open nomenclature for the first time as Cooksonia sp. The holotype of C. bohemica was not available for study during earlier investigations of the genus since it was held in H.-J. Schweitzer’s private collection. However, in 2007, shortly before his death, the specimen was donated, together with other specimens in the collections of Hans-Joachim Schweitzer, to the Swedish Museum of Natural History (Naturhistoriska Riksmuseet), Stockholm (see Material and methods). Conditions for study of the material were complicated by Schweitzer’s testament indicating his wish that the specimens should not be moved from Stockholm. The present authors have now analysed the holotype (represented by part and counterpart) during several investigations in Stockholm. The present study aims to clarify the morphology, anatomy and reproductive features of C. bohemica based on re-analysis of the holotype from the Prague Basin, the Czech Republic.
Additionally, it integrates the new information with past results to provide a broader concept of the genus.

Material and methods

All the studied material of *Cooksonia bohemica*, including the holotype, derives from the Požáry Formation, Přídolí, upper Silurian, exposed at the locality Dlouhá hora (part of Kosov Quarry), situated 3 km southwest of Beroun, in the Barrandian area, Prague Basin, the Czech Republic (Figure 1). The holotype is preserved as a compression in graptolitic siltstone with some admixture of volcanic material. The precise stratigraphic position of the *C. bohemica* holotype is defined by the graptolite *Pristiograptus ultimus*, which is preserved on the same bedding plane as the plant fossil and is referable to the *P. ultimus-paraulitimus* Zone, which clearly denotes the Přídolí age.

The specimen was collected by Dr Jiří Kříž (oral communication 2018) from the Czech Geological Survey, Prague, in 1970s and donated to Hans-Joachim Schweitzer, who at that time studied early Palaeozoic land plants. Before he died, Hans-Joachim Schweitzer, professor of palaeobotany at Bonn University, Germany, indicated that his large collection of plant fossils should be kept intact in a palaeobotanical research environment. Schweitzer’s collection was originally submitted to the Institut für Systematische Botanik at the Friedrich-Schiller University in Jena, Germany, based on their intention to establish a palaeobotanical department, and the material was transported to Jena where it was stored in the herbarium. However, circumstances changed and the material could not be curated adequately in Jena, hence the collection was offered to the Swedish Museum of Natural History in Stockholm. The bulk of the material was transferred to Stockholm in April 2007 where it now resides on the basis of a permanent loan from the Friedrich-Schiller University.

Despite Schweitzer’s meticulous studies of the material, the lack of a permanent home for the specimens meant that no formal institutional reference numbers were given to any of the fossils whether published or not. Between mid-2007 and the end of 2008, the entire Schweitzer collection was unpacked from its transportation boxes, re-packed in individual trays, sorted according to age, locality and publication details and given formal catalogue numbers (prefixed JE for Jena and Sch for Schweitzer) registered in the Swedish Museum of Natural History’s palaeobotanical database.

The holotype, when first seen in the collection, was covered by remnants of ammonium chloride – material used for increasing the contrast of fossils during photography. This material was carefully removed using water and a brush.

The other material of *C. bohemica*, recovered from the same horizon and rock type, is housed in the collection of the National Museum Prague. The specimen No. D 479 from the type collection mentioned by Schweitzer (1980) and studied by Obrhel (1962, pl. 1, Figures 1,2) was collected by B. Bouček in 1942. The other specimen collected also by Bouček in 1942 (part and counterpart Nos D 476 and D 477) was figured by Obrhel (1962, pl. 1, Figures 4–5, pl. 2, Figure 5) as *Cooksonia* sp. The newly gathered fertile specimen (No. D 554) was found by Lenka Váchová in 2016. All specimens come from the same locality and the same rock unit as the holotype. The latter specimen was specifically from the Kosov, Obalovna Quarry.

The type material of *Aberlemnia caledonica* (Edwards) Gómez et Gerrienne studied by Edwards (1970) derives from Aberlemno Quarry in Aberlemno near Angus in Scotland, UK. It was collected and donated to the National Museum of Scotland, Edinburgh, by Dr Charles D. Waterston, a keeper of the Geology Department at this museum, in 1967. This species is represented only by the holotype (consisting of the part and counterpart: No. NMS G.1967.30.2P+C).

The material was studied and documented using an Olympus SZX 12 equipped with an Olympus DP71 digital camera at the National Museum, Prague, and at the Swedish Museum of Natural History, Stockholm. Several attempts were made to extract *in situ* spores from sporangia of the holotype of *Cooksonia bohemica*, but these were only partly successful probably due to the relatively immature character of the sporangia. However, small portions of sporangia and axis segments were removed from the holotype using a scalpel, mounted on aluminium stubs and imaged at low voltage with a Philips FEI Quanta Field Emission Gun 650 scanning electron microscope at the Swedish Museum of Natural History (Naturhistoriska riksmuseet). These yielded few spores and limited anatomical data on the sporangia and conducting tissue. Megascopic details were obtained by immersing the holotype in ethanol and imaging with a Canon EOS 5D digital camera attached to a Cognisys Stackshot 3X auto-stacking system that merges up to 30 photographs into a composite image. Photo-micrographs of JE-Sch0260 using incident-ultraviolet light (fluorescence: blue light excitation at c. 460–490 nm) were taken with an Olympus BX51 microscope with an Olympus DP71 digital camera. Photo-micrographs of JE-Sch0260 using incident white light were taken with an Olympus SZX10 stereomicroscope equipped with a Sony Exmoor E3CMOS digital camera. The final images were obtained by merging up to 30 photographs taken at different focal depths using Adobe Photoshop CC software using the ‘auto-align’ and ‘auto-stack’ functions.

Systematic palaeobotany

Phylum: Tracheophyta

Genus: *Cooksonia* Lang 1937

Type: *Cooksonia pertoni*, (1937), p. 250, pl. 8, Figures 4–19, pl. 9, figs 20–27.

*Cooksonia bohemica* Schweitzer 1980

Figures 2–7
Figure 2. *Cooksonia bohemica* Schweitzer, holotype, JE-Sch0260A, B. (A) Complete specimen. (B) Counterpart. Scale bar: 10 mm. (C, D) Details of spherical and reniform sporangia, scale bar: 1 mm. (E) Reniform sporangium borne on a short expanded terminal axis, scale bar: 1 mm. (F, G) Spherical and reniform sporangia, scale bar: 1 mm. (H) Sporangia borne on short expanded axes, scale bar: 1 mm. (I) Detail of axis containing centrally placed conducting tissues, scale bar: 1 mm. (J) Detail showing branched conducting tissues, scale bar: 1 mm. (K) Detail showing expansion of axes immediately below branching, scale bar: 1 mm. (L) Details of axes showing spots, trichomes and trichome bases. Scale bar: 1 mm.
1962 *Cooksonia* sp., Obrhel, p. 85, pl. 1, Figs 4, 5.
1962 *Cooksonia* sp., Obrhel, p. 85, text-fig. p. 85, pl. 2, Figs 1, 2.
1980 *Cooksonia bohemica* Schweitzer, p. 10, Text-fig. 11.
2004 *Cooksonia bohemica* Schweitzer; Edwards et al., p. 407, Fig. 32.
2018 *Aberlemnia bohemica* (Schweitzer) Sakala, Pšenička et Kraft in Kraft et al., p. 148, Fig. 4E.

**Holotype**

**Type locality**
Dlouhá hora, Kosov, Barrandian, the Czech Republic.

**Type unit**
Požáry Formation, Přídolí, Silurian.

**Studied material**

Emended diagnosis. Axes branched isotomously, covered by trichomes. Axis segment length variable with tendency to shortening of segments towards base; segments expanded below dichotomies. Axes containing a central vascular trace incorporating tubular structures. Ultimate axial segments each bearing a single terminal sporangium. Terminal axes conspicuously widened at the base of the sporangium. Sporangia spherical (0.9–1.2 mm in diameter), hemispherical (1–1.4 mm in diameter) or reniform (0.8–2.0 × 1.3–2.0 mm), with a wall about 0.2 mm thick. Some sporangia have a simple prominent rim (Figures 2D,E); this feature is particularly pronounced in specimen No. D 479 figured by Obrhel (1962), pl. II, Figures 1, 2), refugured here (Figs 5A–G). At the junction between the sporangium and the broadened axis, the rim is characterised by only a single thick dark line. However, there is no slit-like structure obvious in the sporangium wall indicating a definitive line of dehiscence (compare Figs 6A–F and G–J).

The axes, particularly proximal segments, contain a centrally positioned elongated strand of tubular structures (Figures 2I, J, 3 B, E, F, 4A-I). Those numerous robust longitudinal cells form a dense column along the centre of the axis segments. The individual cells are around 20–25 µm wide and reach in excess of 1 mm long, have tapered or transverse end walls, and appear to have regular thickening/pitting under UV-fluorescence (Fig. 4H, I). Cells are infilled by amorphous silica aggregates; adjacent lumen fillings are separated by gaps of 1–2 µm that likely represent the cell wall thickness. Based on these observations, we consider that these cells probably represent...
Figure 4. Cooksonia bohemica Schweitzer, holotype, JE-Sch0260A, details of vasculature. (A) SEM of central strand represented by silica infillings of elongate cell lumina (JE-Sch0260B). (B) SEM of elongate cells with transverse end wall (arrowed), JE-Sch0260B. (C) SEM enlargement of single cell filling consisting of amorphous silica aggregates (JE-Sch0260B). (D) Forking of apparent vasculature at axis dichotomy (reflected light: JE-Sch0260B). (E) Elongate, tracheid-like cells reaching 1 mm in length (reflected light: JE-Sch0260A). (F) Robust, iron-stained, elongate cells of the central strand (reflected light: JE-Sch0260B). (G) Longitudinal section of axis showing dark (iron-stained) central strand of tracheid-like cells (JE-Sch0260A). (H) UV-fluorescence image of central tracheid-like cells (JE-Sch0260A). (I) UV-fluorescence image of tracheid like cells showing possible annular thickenings (arrows on left) and pitting (arrows on right), JE-Sch0260A. Scale bars = 1 mm for D–G, 100 µm for A, B, H, I, 10 µm for C.
tracheids rather than thin-walled hydroids of a bryophyte-grade plant or a cylindrical sheath of sclerenchymatous cells.

Trilete crassitate in situ spores found in sporangia of the holotype are 35–45 µm in diameter. They have a subtriangular amb with smooth margin (Fig. 3C). Rays of the trilete mark reach to the equator (Figs 3C, D). Crassitudo is up to 4 µm wide (Fig. 3C). The sculpture is finely microgranulate (Fig. 3C).

Specimen No. D 479 figured by Obrhel (1962) and mentioned by Schweitzer (1980) is a three-times isotomously branched fragment of a sporophyte (Fig. 5A). It is 12 mm long and 0.3–1.8 mm thick. Its axes expand below each dichotomy. In several places, a centrally placed bundle of conducting tissue that is visibly branched, each trace division following the axis branches (Fig. 5A). Sporangia are borne on short expanded terminal axes (Figs B–G). Sporangia are spherical to reniform. Six are borne on axes, and three appear to be isolated. The sporangia have dimensions of 1–1.8 × 0.6–1 mm.

The other specimen figured by Obrhel (1962), represented by part and counterpart (Nos D 476 and D 477), is rather longer (24 mm) (Fig. 4H). Only one terminally borne spherical sporangium 1.2 × 1 mm is preserved (Fig. 5H).
Specimen No. D 554 is a twice isotomously branched terminal portion of a sporophyte, 10.1 mm long and 0.4–1.4 mm wide (Fig. 5I). Its axes are expanded immediately below dichotomies (Figs 5J, L). A centrally placed bundle of probable conducting tissues is preserved (Fig. 5I). Two well-preserved sporangia are borne terminally on short and clearly expanded ultimate axes. They are spherical to reniform: 1.1–1.5 × 1–1.1 mm. In the apical part of one sporangium (Fig. 5J, K), a line is evident following the shape of the sporangium, but it lacks preserved coalified matter. This line probably marks the original margin of the sporangium and, because it is indistinct, it was probably generated secondarily by erosion of coaly matter (Fig. 5L, M).

**Interpretation**

*C. bohemica* is interpreted to represent a nearly complete portion of the sporophyte generation of an early land plant. The longitudinally aligned aggregations of tubular structures in the central part of the axis segments are considered probable conducting tissues. Therefore, *C. bohemica* is interpreted here as a representative of *Cooksonia* referable to tracheophytes. Its commonly reniform sporangia represent an advanced character that was probably the precursor of the more derived valvate sporangial structures of *Aberlemnia*. In contrast to *Aberlemnia*, the sporangia
of *C. bohemica* lack an opening slit, a condition similar to that in *Tichavekia* Pšenička, Sakala et Kraft. The axes of *C. bohemica* have a branching pattern that is more similar to other representatives of *Cooksonia* than to *Aberlemnia* or *Tichavekia*. Moreover, the masses of spores are trilette with finely microgranulate sculpture and well-defined equatorial crassitudo typical for *Ambitisporites* spores, which have been isolated from several other *Cooksonia* species previously (Table 1). In summary, the absence of a sporangial dehiscence slit, lack of a consistent pattern of distally shortening axial segments and the production of trilette spores of *Ambitisporites* type have been described only from species of *Cooksonia* rather than *Aberlemnia*. Therefore, we do not agree with the interpretation by Kraft (et al. 2018) and consider *C. bohemica* to be referable to *Cooksonia*.

### Discussion

Based on the morphology of their *in situ* spores, it is possible to divide *Cooksonia* into two groups (Fanning et al. 1992). Generally, *Cooksonia* spores are separable into crassitate and non-crassitate forms (Table 1). Crassitate spores can be laevigate (*Ambitisporites* Hoffmeister) or sculptured (*Aneurospora* Přídolí and Lister or *Streelispora* Richardson and Lister). Because 7 of the 11 palynologically studied *Cooksonia* species (including the type species of the genus) produced crassitate spores, from a palynological point of view, this group can be termed the *Cooksonia sensu stricto* Group. This group includes *Cooksonia barrandi* Libertin et al., *C. cambrensis* Edwards, *C. pertoni* Lang (including all subspecies) and *C. bohemica*.

The second palynologically distinguishable group of *Cooksonia* yields non-crassitate spores referable to *Apiculiretusispora* (Streel) and is here termed the *Cooksonia sensu lato* Group, which includes *Cooksonia cassisparietis* Yurina (Yurina 1969), *C. hemisphaerica* Lang and cf. *Aberlemnia caledonica/Renalia* sp. sensu Fanning et al. (1992).

It needs to be emphasised that *Cooksonia* is the only *Ambitisporites*-producer but *Apiculiretusispora* spores were produced by some other rhyniophyoids including *Horneophyton ligieri* (Kidston and Lang) Barghoorn and Darrah (Gensel 1980), *Huia recurvata* Geng (Geng 1985), *Pertonella dactylethra* Fanning et al. (Fanning et al. 1991a), *Renalia huebneri* Gensel (Gensel 1980) and *Tortilicaulis transwalliensis* Edwards (Fanning et al. 1991a) and even by some trimerophytes and zosterophylls (Balme 1995).

Examples of another common rhyniophyloid spore genus *Retusotrilites* Naumova were produced by, e.g. *Caia langii* Fanning et al. (Fanning et al. 1991a) and *Salopella alleni* Edwards and Richardson (Allen 1980).

The simple rim around the sporangia and production of *Ambitisporites* spores indicates that *C. bohemica* is affiliated with other species of the *Cooksonia sensu stricto* Group. It is particularly similar to *C. pertoni* (Lang 1937) from which it differs in having reniform sporangia (at least in some cases), larger spores, axes with more numerous dichotomies and distinct, centrally positioned strands of probable conducting tissues. *Cooksonia barrandi* from Sheinwoodian, Silurian strata of Bohemia (Libertin et al. 2018a) differs from *C. bohemica* in that its subtending branches gradually broaden, it has lenticular sporangia and it bears trilette crassitate differently sculptured and smaller *in situ* spores of the *Aneurospora* type. *Cooksonia cambrensis* Edwards from the Přídolí (lower old Red Sandstone) of the United Kingdom (Edwards 1979) differs from *C. bohemica* in lacking any broadening of the terminal axes, in having globular to ellipsoidal sporangia, and in its smaller crassitate *in situ* spores (Fig. 6). *Cooksonia paranesis* Gerrienne et al., from the Early Devonian of Brazil (Gerrienne et al. 2001), and *Cooksonia* sp. cf. *C. paranensis* of McSweeney et al. (2021), from the Pragian–Emsian of southeastern Australia, both differ from *C. bohemica* in having terminal axes that expand gradually and ultimately bear circular to lenticular sporangia that are rather sunken, giving the complete structure a trumpet shape (Gerrienne et al. 2006). *Cooksonia hemisphaerica* Lang from the Přídolí of the United Kingdom (Lang 1937) differs from *C. bohemica* in the consistently hemispherical to spherical shape of the sporangia, in the absence of centrally located strands of conducting tissues and by having a different type of non-crassitate *in situ* spores (*Apiculiretusispora* type). *Cooksonia cassisparietis* Yurina from Lower Devonian strata of Kazakhstan, as far as it is possible to

### Table 1. List of in situ spores of *Cooksonia* species and other crassitate spore-producing early land plants.

<table>
<thead>
<tr>
<th>Parent plant</th>
<th>Age</th>
<th>Diameter of in situ spores (µm)</th>
<th>Classification of in situ spores</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cooksonia barrandi</em></td>
<td>Sheinwoodian</td>
<td>10–16</td>
<td><em>Aneurospora</em></td>
<td>Libertin et al. 2018a</td>
</tr>
<tr>
<td><em>C. cambrensis</em></td>
<td>Přídolí</td>
<td>9–22</td>
<td>A new crassitate taxon</td>
<td>Fanning et al. 1991a</td>
</tr>
<tr>
<td><em>C. crassiparietialis</em></td>
<td>Emsian</td>
<td>50–65</td>
<td><em>Apiculiretusispora pictata</em></td>
<td>Yurina 1965, 1969, McGregor 1973</td>
</tr>
<tr>
<td><em>C. hemisphaerica</em></td>
<td>Přídolí</td>
<td>22–44</td>
<td><em>Apiculiretusispora</em></td>
<td>Edwards 1979, Fanning et al. 1992</td>
</tr>
<tr>
<td><em>C. sp. sensu Croft and Lang</em></td>
<td>Breconian</td>
<td>20–35</td>
<td>Not determined</td>
<td>Hoeg in Boureau et al. 1967</td>
</tr>
<tr>
<td><em>C. bohemica</em></td>
<td>Přídolí</td>
<td>35–45</td>
<td><em>Ambitisporites</em></td>
<td>Herein</td>
</tr>
<tr>
<td><em>Salopella cf. marcellis</em></td>
<td>Lochkovan</td>
<td>15–26</td>
<td><em>Aneurospora</em></td>
<td>Edwards et al. 1994</td>
</tr>
<tr>
<td><em>Sporophyllum salopense</em></td>
<td>Lochkovan</td>
<td>23–30</td>
<td>Crassitate curvaturate undetermined spores</td>
<td>Edwards et al. 2001</td>
</tr>
</tbody>
</table>

References:

- Fanning et al. (1991a)
- Yurina 1965, 1969
- McGregor 1973
- Gensel 1980
- Gerrienne et al. 2001
- Fanning et al. 1992
- Habgood et al. 2002
- Morris et al. 2012
- Edwards et al. 1994
determine from the publication by Yurina (1965), is represented only by fragmentary axes bearing sporangia. Its terminal sporangi-ate axes are not expanded, and the sporangia appear to have a valvate architecture as described for Aberlemnia. This important character, noted earlier by Edwards (1979), should be confirmed directly in the type material of C. crassiparietilis, which was not available to us. Additionally, its in situ sporangia differ from those of C. bohemica in being significantly larger and non-crassitate.

The absence of any structure reminiscent of the capsulate opening so characteristic of Aberlemnia is the most important feature distinguishing C. bohemica from A. caledonica. The terminal sporangia of A. caledonica bear a distinct dehiscence slit lined by thickenings of both margins of the valves (Figs 6A–F). Interestingly, this key character was not mentioned in the emended diagnosis of that species by Gonez and Gerrienne (2010a). Apart from the valvate sporangia and size of the organs, the only differentiating character mentioned is that branch lengths decrease distally. This is another character in which A. caledonica differs from C. bohemica. Branches of C. bohemica are of equal length or, in some cases, more distal branches are even longer than the proximal examples (compare Figs 6A–F and G–J).

The recently described Tichavekia (Uhlířová et al. 2022) is characterised by having distally decreasing branch segment lengths – a feature shared with Aberlemnia. However, the sporangia of Tichavekia bear no dehiscence line and the terminal sporangiate segments are extremely short (Uhlířová et al. 2022). Tichavekia grandis Pšenička, Sakala et Kraft differs from Cooksonia bohemica in having distally decreasing branch segment lengths and domed rather than reniform sporangia.

Renalia hueberi is superficially similar to C. bohemica, but differs in having pseudomonopodial branching, valvate sporangia (Gensel 1976) and in the curvaturate spores of Retusotriletes type macerated from its sporangia (Gensel et al. 2013).

Cooksonia bohemica resembles Monnowella Morris et Edwards from the Lochkovian of England, particularly in having terminal ellipsoidal sporangia. However, the sporangia of C. bohemica are frequently also reniform (Morris and Edwards 2014). Additionally, Monnowella, in contrast to C. bohemica, has gradual proximo-distal tapering axes, and its systematic placement is unresolved (Morris et Edwards 2014).

Cooksonia bohemica is in some respects, particularly in its in situ spore morphology (presence of equatorial thickenings), similar to Concavatheca banksii (Habgood, Edwards and Axe) Morris, Edwards, Richardson, Axe et Davies from the Early Devonian of the UK (Morris et al. 2012). However, the terminal subtending axes of C. banksii are expanded with a cup-shaped sporangial cavity, whereas the subtending axes of C. bohemica, although expanded, never accommodate a cup-shaped sporangial cavity. Moreover, the sporangia of C. bohemica are reniform, strongly domed but never flattened like the sporangia of C. banksii. Comparisons of macro-morphology are limited, because C. banksii is preserved as a fragment of a simple axis bearing one sporangium.

In isolation, the sporangia of C. bohemica are similar in some respects to those of Sporathylacium salopense Edwards, Axe et Mendes from the Early Devonian of the UK (Edwards et al. 2001). Despite the better preservation of the British material, the sporangia of C. bohemica show no evidence of a valvate structure. Additionally, the in situ spores of S. salopense, although being trilete and crassitate with a prominent labrum, are differentially sculptured as those described from sporangia of C. bohemica.

The tubular structures interpreted here as conducting elements are reminiscent of the tubular units described by Edwards et al. (1992) and Edwards (2003) that were interpreted as conducting tissues. We agree with this interpretation and consider the features in C. bohemica to also represent conducting cells although there appear to be some differences in morphology, notably (owing to the cast-like preservation) that we do not find clear evidence of cell-wall thickenings. Thickenings may be present but inadequate preservational quality makes these features difficult to detect in the studied material.

Reconstructions

Cooksonia bohemica is reconstructed as forming diminutive thickets of dichotomising axes that are branched leaving shorter axial segments basally, longer in medial part and shorter proximally. Its sporangia do not show an opening slit (Fig. 7). Although

Figure 8. Reconstruction of Aberlemnia caledonica (Edwards) Gonez et Gerriene by Jiří Svoboda. Scale bar: 10 mm.
Aberlemnia caledonica has more ascending axes that dichotomise showing gradual shortening of axial segments proximally. Its sporangia clearly bear opening slits (Fig. 8).

**Distribution of Cooksonia**

Although Cooksonia seems to be, as indicated above, a strongly polyphyletic genus (Kenrick and Crane 1997; Gonez and Gerrienne 2010a), we treated it as a distinct clade of early land plants and plotted all the species on a palaeogeographic map of the late Silurian/Early Devonian (Fig. 9). The distribution map indicates occurrences of the genus in coastal areas of the Rheic Ocean. Multiple occurrences of Cooksonia (of several species) indicate its higher diversity in the Bohemian Massif, which is consistent with the hypothesis that the group’s origin is associated with peri-Gondwanan terranes (Libertín et al. 2018b). However, this distribution might be biased by the availability of suitable depositional environments and lithologies, and uneven collecting activities in the discussed regions. However, the rapid spread of cooksonioids to the northern coast of the Rheic Ocean is documented by the occurrence of Cooksonia in the late Wenlock (Homerian) of Ireland and its further diversification along the western coast of Laurussia in the Welsh Borderland (Fig. 9). Late Silurian and Early Devonian occurrences document the spread of cooksonioids to the north (Kazakhstan) and south (Bolivia and Australia) to reach essentially a cosmopolitan distribution by that time interval.

**Disclosure statement**

No potential conflict of interest was reported by the author(s).

**Funding**

This work was supported by the Czech Science Foundation [21-10799s], and the research plan of the Institute of Geology of the Czech Academy of Sciences, v.v.i., [RVO67985831]. SM is funded by a grant from the Centrum for Idrottsforskning [2018-04527]. We thank three anonymous reviewers for their constructive comments on the manuscript.

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