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DOI: 10.2478/fbgp-2025-0001

PALEOZOIC *IN SITU* SPORES AND POLLEN. EARLY LAND PLANTS

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Abstract: *The paper reports records of* in situ *spores of Paleozoic early land plants totalling 44 genera with 72 species (including four subspecies). Their reproductive organs yielded* in situ *spores belonging to 3 cryptospore species and 18 spore genera with 59 species. All descriptions of* in situ *spores have been modified employing current terminology for the description of Paleozoic spores.* In situ *spores of early plants are usually small, morphologically simple and can be divided into a few morphological groups. The most abundant spore genera are* Apiculiretusispora*,* Retusotriletes *and* Ambitisporites*.*

Keywords: *In situ* spores, early land plants, reproductive organs, Paleozoic.

INTRODUCTION

This paper reviews the records of Paleozoic spores from the earliest land plants. The origin of these early plants has been discussed in many papers and books. Undoubtedly, this event is of the most importance in life history, being at least equal in significance to the appearance of vertebrates. The origin of early vascular plants may be polyphyletic (e.g., Andrews 1959, Banks 1968) or monophyletic (e.g., Stewart & Rothwell 1993, Taylor *et al.* 2009), but the majority of authors prefer the monophyletic approach. Land plants (embryophytes) probably evolved from an unknown charophycean green alga ancestor related to Zygnematophyceae or streptophyte algae (Becker & Marin 2009).

Indirect and direct evidence of the earliest plants can be recognised. The first indirect evidence (±470 Ma) comes from both marine and continental environments and is mainly represented by mesofossils and phytodetritus, including dispersed cuticles and cuticle-like material, spores, cryptospores, sporangia, tubes, and tissue fragments. Direct evidence comprises larger plant specimens. The earliest dispersed embryophyte spores have been found in the Early Llanvirn period in the Czech Republic (Vavrdová 1984) and in the Mid-Llanvirn period in Saudi Arabia (Strother *et al.* 1996).

Pioneering works concerning dispersed palynological records of early plants include e.g. Lang (1925), Thomson (1940), Eisenack (1944), Naumova (1953) and Radforth & McGregor (1954). Subsequent important papers were published e.g. by McGregor (1960, 1961), Chaloner (1963), Streel (1964), Allen (1965), Richardson (1960, 1962, 1965), Richardson & Lister (1969) and Richardson & Ioannides (1973). Important papers concerning *in situ* spores of early land plants were published e.g. by Allen (1980), Gensel (1980), Andrews *et al.* (1975), Edwards (1979, 1996), Edwards *et al.* (1994), Fanning *et al.* (1991a,b) and Gonez & Gerrienne (2010).

Pioneering works concerning earliest vascular plants were published e.g. by Kräusel & Weyland (1935), Lang (1937), Høeg (1942) and Chaloner (1970). The earliest vascular land plants (432 My) are reported by Libertín *et al.* (2018a,b) who described more than fifty specimens up to 75 mm long of the *Cooksonia* type with *in situ* isospores of the *Ambitisporites* cf. *avitus* type from the Sheinwoodian of the Barrandian area of the Czech Republic.

There is very little published data on fossil *in situ* spores, with notable exceptions including Potonié (1962, 1965), Chaloner (1967) and Boureau (1964), as well as the most recent review by Balme (1995). These publications only provide brief descriptions of *in situ* spores and utilise the currently recommended terminology for fossil spores (Punt *et al.* 2007). Another issue is that almost all papers concerning Paleozoic *in situ* spores were not prepared in collaboration with palynologists. Nowadays, information about *in situ* spores and pollen is an integral part of the diagnosis and description of all fossil fertile plant taxa (Thomas 1987). Sometimes cooperation between palynologists and palaeobotanists can result in a more consistent identification of reproductive organs, particularly using *in situ* spores in conjunction with the organs morphology, if the preservation of fossils is poor.

Palaeobotanical studies have advanced in astounding ways thanks to modern technologies and techniques, such as SEM and TEM. For example, we now have free access to SEMs and TEMs, enabling us to observe details that were previously unobservable. The internet also facilitates literature searches, ensuring that a new taxon with *in situ* spores is not erected immediately upon discovery, only to find that it is synonymous with an earlier taxon erected under a different name, or that the same *in situ* spores were previously known from different plants. Palynologists can provide palaeobotanists with information about the parent plants that produced the same or similar spores. This information is important when these taxa are closely related or synonymous, or when they represent independent, parallel phylogenetic lineages of different plants that produce similar spores.

This paper aims to provide a comprehensive description and list of fertile Paleozoic early land plants, and to emphasise the importance of palynology in classifying the reproductive organs of these plant groups. It also highlights the necessity for close collaboration between palaeobotanists and palynologists. Early land plants are a good example of how palynology can help with the classification of plants, as they are all morphologically very similar. They have small stems, which are sometimes branched, and one or a few apical sporangia. *In situ* spores are usually the only reliable criterion for their classification, as can be seen with the four subspecies of *Cooksonia pertonii* Lang, which were classified based on different *in situ* spores.

MATERIAL AND METHODS

The descriptions of *in situ* spores, which were sometimes considered 'old-fashioned', were redone using the latest recommended palynological terminology (Punt *et al.* 2007). The descriptions herein are therefore more detailed than those found in the last general, comprehensive review of all fossil *in situ* spores and pollen, which was published by Balme (1995). The spores were macerated by me and recovered by dissolving the sporangia in hydrochloric acid for about 20 hours, hydrofluoric acid for about 170 hours, and then hydrochloric acid again for about one hour, followed by KOH for less than one hour. The maceration techniques used by other authors are detailed in their papers and were usually the same (adpressions). The *in situ* spores were compared directly with the original diagnoses (type specimens), descriptions, and illustrations of dispersed spore species. Species determinations are based solely on original diagnoses and not on subsequent authors' interpretations. The stratigraphic and geographic positions of the holotypes of all the Paleozoic fertile early land plants mentioned herein were determined wherever possible. However, it was not always possible to do so precisely, particularly in the case of the pioneer publications, where such data were given only briefly, if at all. This means that the complete stratigraphic and geographic distributions of every species reported by all authors cannot be provided, as it is not possible to rely on every subsequent author's interpretation of the occurrence of the taxon. Therefore, the 'Stratigraphy and geography of the holotype' section only concerns holotypes, except for species named sp. and cf., where the stratigraphic position and locality of the specimen were described by the author who reported the taxon. Each species has a list of synonymous taxa reflecting changes in its classification. It was sometimes difficult to find all the synonyms, so it is possible that the number of synonyms for each species is incomplete.

SYSTEMATIC PALAEOBOTANY

Classification of Paleozoic early land plants follows the systems proposed by Boureau (1964) and Stewart & Rothwell (1993).

Eophytidae

Culullitheca Wellman, Edwards et Axe 1998
Fusitheca Wellman, Edwards et Axe 1998
Grisellatheca Edwards, Wellman et Axe 1999

Tracheophyta

Euphyllophytina

Polysporangiophyta

Rhyniophytopsida

Rhyniaceae

Cooksonia Lang 1937
Concavatheca Morris et al. 2012
Paracooksonia Morris et al. 2011
Rhynia Kidston et Lang 1917
Salopella Edwards et Richardson 1974
Tarrantia Fanning et al. 1992

Rhyniophytopsida of uncertain position

Cooksonia crassiparietilis Yurina 1964
cf. Cooksonia caledonica/Renalia Fanning *et al.* 1992
Pertonella Fanning et al. 1991a
Renalia Gensel 1976
Uskiella Shute et Edwards 1989

Horneophytopsida

Caia Fanning et al. 1990
Horneophyton Lang 1937
Tortilicaulis Edwards 1979

Taeniocradaceae

Huia Geng 1985

Subdivision Zosterophyllophytina

Zosterophyllopsida

Zosterophyllaceae

Discalis Hao 1989a
Gosslingia Heard 1927
Gumuia Hao 1989b
Nothia Kidston et Lang 1920
Oricilla Gensel 1982a
Rebuchia Hueber 1972
Sawdonia (Dawson) Gensel et Berry 2016
Tarella Edwards et Kenrick 1986
Zosterophyllum Penhallow 1892

Trimerophytopsida

Trimerophytaceae

Dawsonites Halle 1916
Hostinella Stur 1882
Hsüa Li 1982
Pertica Kasper et Andrews 1972
Psilophyton Dawson 1859
Trimerophyton Hopping 1956
Yunia Shou-Gang et Beck 1991

Barinophytaceae

Barinophyton (White) Brauer 1980
Krithodeophyton Edwards 1968
Protobarinophyton Ananiev 1955
Omniastrobus Bonacorsi et al. 2020

Incertae sedis

Aglaophyton Edwards 1986
Bracteophyton Wang et Hao 2004
Chauleria Andrews et al. 1974
Eocladoxylon (Koidzumi) Berry et Wang 2006
Oocampsa Andrews et al. 1975
Resilitheca Edwards, Fanning, Davies et Axe 1995
Sporathylacium Edwards, Axe et Mendes 2008
Tichavekia Pšenička, Sakala et Kraft 2018 in Kraft *et al.* 2018

Eophytidae

Genus: *Culullitheca* Wellman, Edwards et Axe 1998

Type species: *Culullitheca richardsoni* Wellman, Edwards et Axe 1998

Species: *Culullitheca richardsoni* Wellman, Edwards et Axe 1998

Stratigraphy and geography of the holotype: Lochkovian of UK.
***In situ* cryptospores** (modified from Wellman, Edwards & Axe 1998, pp. 123–133): Permanent dyads; size range 39 (42) 44 μm. Laevigate sculpture.
Remark: *In situ* cryptospores are of the *Diaspora murusdensa* type. Specimens are preserved as adpressions.
Reference: Wellman, Edwards & Axe (1998).

Genus: *Fusitheca* Wellman, Edwards et Axe 1998

Type species: *Fusitheca fanningiae* Wellman, Edwards et Axe 1998

Species: *Fusitheca fanningiae* Wellman, Edwards et Axe 1998
Stratigraphy and geography of the holotype: Lochkovian of UK.

***In situ* cryptospores** (modified from Wellman, Edwards & Axe 1998, pp. 133–137): Permanent dyads; size range 27 (30) 33 μm. Laevigate sculpture.
Remark: *In situ* cryptospores may be of the *Pseudodyadospora peltatus* type. Specimens are preserved as adpressions.
Reference: Wellman, Edwards & Axe (1998).

Genus: *Grisellatheca* Edwards, Wellman et Axe 1999
Type species: *Grisellatheca salopensis* Edwards, Wellman et Axe 1999

Species: *Grisellatheca salopensis* Edwards, Wellman et Axe 1999
Stratigraphy and geography of the holotype: Gedinian-Lochkovian of UK.
***In situ* spores** (modified from Edwards, Wellman & Axe 1999, pp. 133–137): Circular permanent tetrads of cryptospores; size range 32 (38) 43 μm. Laevigate sculpture.
Remark: *In situ* cryptospores can be of the *Cheilotetras/Velatitetras* type. Specimens are preserved as adpressions.
Reference: Edwards, Wellman & Axe (1999).

Tracheophyta

Euphyllophytina

Polysporangiophyta

Rhyniophytopsida

Rhyniaceae

Genus: *Cooksonia* Lang 1937
Type species: *Cooksonia pertoni* Lang 1937

Species: *Cooksonia barrandei* Libertín et al. 2018a
Stratigraphy and geography of the holotype: Wenlock (Sheinwoodian) of the Czech Republic.
***In situ* spores** (modified from Libertín *et al.* 2018a, pp. 269–271): Trilete circular crassitate spores; size range 10–15 μm. Microgranulate distal surface, proximal sculpture probably similar. Rays of the trilete mark equal to the radius.
Remark: *In situ* spores are of the *Ambitisporites* type. Specimens represent the oldest sporophyte (432 Myr) of vascular land plants in the global scope. Specimens are preserved as compressions.
Reference: Libertín *et al.* (2018a).

Species: *Cooksonia bohemica* Schweitzer 1980
1962 *Cooksonia* sp. – Obrhel, p. 85, pl. 1, Figs 4, 5.
1962 ? *Cooksonia* sp. – Obrhel, p. 85, text–fig. 1, p. 85, pl. 2, Figs 1, 2.
1980 *Cooksonia bohemica* Schweitzer – Schweitzer, p. 10, text–fig. 11.
2004 *Cooksonia bohemica* Schweitzer – Edwards & Richardson, p. 407, Fig. 32.
2022 *Cooksonia bohemica* Schweitzer – Libertín *et al.*, pp. 2506–2510.

Stratigraphy and geography of the holotype: Přídolí of the Czech Republic.
***In situ* spores** (modified from Libertín *et al.* 2022, p. 2509): Trilete subtriangular crassitate *in situ* spores 35–45 μm in diameter with smooth margin. Rays of the trilete mark reach to the equator. Crassitudo is up to 4 μm wide. The sculpture is finely microgranulate
Remark: Libertín *et al.* (2022) compared *in situ* spores to the miospore genus *Ambitisporites* Hoffmeister. Specimens are preserved as compressions.
References: Libertín *et al.* (2022).

Species: *Cooksonia cambrensis* Edwards 1979
1979 *Cooksonia cambrensis* Edwards, pp. 36–38.
1991a *Cooksonia cambrensis* Edwards – Fanning *et al.*, pp. 37–47.
1991b *Cooksonia cambrensis* Edwards – Fanning *et al.*, pp. 30–31.
1992 *Cooksonia cambrensis* Edwards – Fanning *et al.*, pp. 168–169.
1995 *Cooksonia cambrensis* Edwards – Balme, pp. 92–93.
2004 *Cooksonia cambrensis* Edwards – Edwards & Richardson, fig. 1h, i.
2010 *Cooksonia cambrensis* Edwards – Gonez & Gerrienne, pp. 200, 211.

Stratigraphy and geography of the holotype: (Downtown) Přídolí of UK.
***In situ* spores** (modified from Fanning *et al.* 1991a, pp. 39–44, 1991b, p. 31): Trilete circular, subcircular to subtriangular spores; size range 9 (13) 22 μm. Equatorial crassitudo developed, the sculpture microgranulate and cristate.
Remark: Edwards (1979) recognised two forms (α and ß) based on different types of sporangia but *in situ* spores were not macerated. They are described later by Fanning *et al.* (1991a). Although few authors (e.g., Balme 1995) referred *in situ* spores to the genus *Ambitisporites*, most authors (e.g., Gonez & Gerrienne 2010) mentioned that they can represent a new taxon. Specimens are preserved as compressions.
References: Edwards (1979), Fanning *et al.* (1991a, b).

Species: *Cooksonia hemisphaerica* Lang, 1937
1937 *Cooksonia hemisphaerica* Lang, pl. 37, figs. 31–36.
1947 *Cooksonia hemisphaerica* Lang – Arnold, p. 215.
1961 *Cooksonia hemisphaerica* Lang – Andrews, p. 224.
1967 *Cooksonia hemisphaerica* Lang – Hoeg in Boureau, p. 215.
1979 *Cooksonia hemisphaerica* Lang – Edwards, pp. 30–36.
1980 *Cooksonia hemisphaerica* Lang – Allen, p. 255.
1991a *Cooksonia hemisphaerica* Lang – Fanning *et al.*, pp. 200, 211.
1992 *Cooksonia hemisphaerica* Lang – Fanning *et al.*, pp. 163–168.
1995 *Cooksonia hemisphaerica* Lang – Balme, p. 93.
2004 *Cooksonia hemisphaerica* Lang – Edwards & Richardson, fig. 1j, k, o.
2010 *Cooksonia hemisphaerica* Lang – Gonez & Gerrienne, pp. 200, 211.

Stratigraphy and geography of the holotype: Downtonian of UK.
***In situ* spores** (modified from Edwards 1979, p. 30, Fanning *et al.* 1992, p. 165 and Balme 1995, p. 93): Trilete circular to subcircular spores; size range 23–44 μm (Balme 1995 and Fanning *et al.* 1992), 22.5–34.5 μm (Edwards 1979). Curvaturae and labrum developed. Contact area with very final microgranulate to microrugulate sculpture, outside the contact areas and on the distal surface the sculpture is laevigate or microgranulate to microbaculate or even microrugulate (seen only in SEM). Rays of the trilete mark with labrum, sinous from a half to 7/8 of the radius.
Remark: *In situ* spores are probably of the *Ambitisporites* type. Fanning *et al.* (1992) mentioned fragments of tapetum on the surface of spores and suggested their relatively immature character.
Reference: Fanning *et al.* (1991a, 1992).

Species: *Cooksonia pertonii* subsp. *apiculispora* Fanning et al., 1988
1986 ?*Cooksonia pertonii* Lang – Edwards, pp. 204–210.
1988 *Cooksonia pertonii* subsp. *apiculispora* Fanning et al., p. 23.
1992 *Cooksonia pertonii* Lang – Fanning et al., p. 168.
1995 *Cooksonia pertonii* subsp. *apiculispora* Fanning et al. – Edwards *et al.*, pp. 160–162.
2002 *Cooksonia pertonii* subsp. *apiculispora* Fanning et al. – Habgood *et al.*, pp. 340–348.
2012 *Cooksonia pertonii* subsp. *apiculispora* Fanning et al. – Morris *et al.*, pp. 39–43.

Stratigraphy and geography of the holotype: Lochkovian, Shropshire of UK.
***In situ* spores** (modified from Balme, 1995, p. 93 and Habgood *et al.*, 2002, pp. 340–352): Trilete circular to subcircular cingulate isospores; size range 18–30 μm (Balme 1995), 12.6–36 μm (Habgood *et al.* 2002), 16 (21) 24 μm (Morris *et al.* 2012). Labrum developed. Cingulum 0.57–1 μm wide. Laevigate and apiculate contact area, pronounced trilete apertural folds extend to cingulum. Exospore thickened distally with reticulum. Spore wall bilayered.
Remark: Habgood *et al.* (2002) recognised four types of sporangia. Type A yielded spores of the *Streelispora newportensis* type, i.e., apiculate with papillate contact area. Type B contains spores of the *Streelispora newportensis* (contact area papillate) or *Aneurospora* (laevigate contact area) types (Plate I, fig. K). Adjacent apiculae are 1.25 (1.8–2.3) 3.1 μm apart. Type C yielded spores of the *Streelispora newportensis* type [(25 (30.6) 36 μm in diameter] as well as sporangia of the Type D. No significant differences among *Aneurospora* and *Streelispora newportensis* sporangia in their measurements. Morris *et al.* (2012) recognised two types of sporangia based on gross morphology and two groups of *in situ* spores assigned to *Ambitisporites* (*Retusotriletes*) *warringtonii* Richardson et al. Edwards *et al.* (1995) described detail TEM of *Streelispora newportensis* and *Aneurospora* sp. isolated from sporangia assigned to *Cooksonia pertonii* subsp. *apiculispora*.
Specimens are preserved as compressions.
References: Fanning *et al.* (1988), Habgood *et al.* (2002), Edwards *et al.* (1995), Balme (1995).

Cooksonia pertonii subsp. *pertonii* Fanning et al., 1988
1988 *Cooksonia pertonii* subsp. *pertonii* Fanning et al., p. 23.
1991b *Cooksonia pertonii* Lang – Fanning et al., pp. 27–30 (part).
1995 *Cooksonia pertonii* subsp. *pertonii* Fanning et al. – Balme, p. 93.

2002 *Cooksonia pertonii* subsp. *pertonii* Fanning et al. – Habgood et al., p. 340.
2004 *Cooksonia pertonii* Lang – Edwards & Richardson, fig. 1a.
2010 *Cooksonia pertonii* subsp. *pertonii* Fanning et al. – Gonez & Gerrienne *et al.*, p. 211.
2012 *Cooksonia pertonii* subsp. *pertonii* Fanning et al. – Morris *et al.*, pp. 41, 43.

Stratigraphy and geography of the holotype: Upper Silurian to Lower Devonian of UK.
***In situ* spores** (modified from Fanning *et al.* 1988, p 23, 1991b:, p. 27): Trilete circular, subcircular, subtriangular to triangular spores; size range 22 (31) 43 μm. Concave sides, crassitudo up to 2 μm wide, laevigate sculpture. Morris *et al.* (2012) described TEM of these isospores.
Remark: *In situ* spores are of the *Ambitisporites* (*Retusotriletes*) *warringtonii* type. Specimens are preserved as compressions.
References: Fanning *et al.* (1988, 1991b) and Morris *et al.* (2012).

Cooksonia pertonii subsp. *reticulispora* Habgood et al. 2002
1991b *Cooksonia pertonii* Lang – Fanning *et al.*, pp. 27–30 (part).
2002 *Cooksonia pertonii* subsp. *reticulispora* Habgood et al., pp. 348–352.
2010 *Cooksonia pertonii* subsp. *reticulispora* Habgood et al. – Gonez & Gerrienne, p. 211.
2012 cf. *Cooksonia pertonii* subsp. *reticulispora* Habgood et al. – Morris *et al.*, pp. 43–49.

Stratigraphy and geography of the holotype: Lochkovian of UK.
***In situ* spores** (modified from Fanning *et al.* 1991b, p. 27, Habgood *et al.* 2002, pp. 348–352): Trilete circular to subcircular spores, laevigate contact area, reticulate distal surface. The distal reticulum with muri 0.77–1.09 μm wide and lumina 3.5–5.8 μm in diameter. The rays of the trilete mark reach to the crassitudo. Morris *et al.* (2012) recognised two groups of *in situ* spores. Group 1 consists of spores 16 (21) 24 μm in diameter (Habgood *et al.* 2002) and 15–30 μm (Fanning *et al.* 1991b) in diameter with circular to subtriangular amb and convex sides. Proximal surface is laevigate, distal reticulate with muri 0.8 μm wide and 1.8 μm high. Lumina ranges between 4.4 and 12.1 μm. Spores of the Group 2 differ mainly in the sculpture that is microgranulate and microconate.
Remark: Detail TEM of spores is given by Habgood *et al.* (2002, p. 351). *In situ* spores are of the ?*Synorisporites* type although Habgood *et al.* (2002) mentioned some similarities with spore genus *Chelinospora* Allen (Plate I, fig. F). Similarly, Morris *et al.* (2012) stressed some similarities with *Chelinospora cassicula* Richardson & Lister, *Perotrilites* sp. *sensu* Wellman *et al.* (2000), *Iberospora cantabrica* Cramer & Diaz or the *Scylaspora* type (Plate I, fig C) but the closest is the genus *Synorisporites* Richardson & Lister. Specimens are preserved as compressions.
References: Fanning *et al.* (1991b), Habgood *et al.* (2002) and Morris *et al.* (2012).

Cooksonia pertonii subsp. *synorispora* Fanning et al., 1988
1988 *Cooksonia pertonii* subsp. *synorispora* Fanning et al., p. 23.
1991b *Cooksonia pertonii* subsp. *synorispora* Fanning et al. – Fanning *et al.*, pp. 27–30.
1995 *Cooksonia pertonii* subsp. *synorispora* Fanning et al. – Balme, p. 93.
1995 *Cooksonia pertonii* subsp. *synorispora* Fanning et al. – Edwards *et al.*, pp. 150–160.
2010 *Cooksonia pertonii* subsp. *synorispora* Fanning et al. – Gonez & Gerrienne, p. 211.

Stratigraphy and geography of the holotype: Upper Silurian of UK.
***In situ* spores** (modified from Fanning *et al.*, 1988, p. 23 and Balme 1995, p. 93): Trilete circular to subtriangular spores; size range 15–30 μm. Crassitudo and labrum developed. Proximal surface laevigate, distal verrucate to microverrucate. Edwards *et al.* (1995) described detail TEM of *Synorisporites verrucatus* isolated from sporangia assigned to *Cooksonia pertonii* subsp. *synorispora*.
Remark: *In situ* spores are of the *Synorisporites verrucatus* type. Specimens are preserved as compressions.
References: Fanning *et al.* (1988), Edwards *et al.* (1995) and Balme (1995).

Species: *Cooksonia* sp. Croft et Lang, 1942
1942 *Cooksonia* sp. Croft et Lang, pl. 2, figs. 43–51.
1959 *Cooksonia* sp. Croft et Lang – Andrews p. 224.
1967 *Cooksonia* sp. Croft et Lang – Hoeg in Boureau, p. 218.

Stratigraphy and geography of the specimen: Breconian of UK.
***In situ* spores** (modified from Chaloner in Boureau 1967, p. 218): Trilete circular spores; size range 35 × 20–30 μm. Laevigate sculpture.
Remark: No detail description and classification of *in situ* spores were given but they may resemble those of the *Ambitisporites* type. Specimen is preserved as compression.
Reference: Høeg in Boureau (1967).

Genus: *Concavatheca* Morris et al. 2012
Type species: *Concavatheca banksii* (Habgood *et al.*) Morris *et al.* 2012

Species: *Concavatheca banksii* (Habgood et al.) Morris et al. 2012
2002 *Cooksonia banksii* Habgood et al., pp. 352–358.
2010 *Cooksonia banksii* Habgood et al. – Gonez & Gerrienne, pp. 211.
2012 *Concavatheca banksii* Habgood et al. – Morris *et al.* p. 51

Stratigraphy and geography of the holotype: Lochkovian of UK.
***In situ* spores** (modified from Habgood *et al.* 2002, pp. 352–356 and Morris *et al.* 2012, pp. 51–53): Trilete circular to subcircular spores; size range 13 (17.6) 23 μm (Habgood *et al.* 2002) and 13 (18) 28 μm (Morris *et al.* 2012). Crassitudo 0.6 (0.86) 1.5 μm (Habgood *et al.* 2002) and 1.1 μm (Morris *et al.* 2012) wide. Rays of the trilete mark reach equator. Laevigate sculpture. Morris *et al.* (2012) described TEM of these spores.
Remark: Some authors assigned this species to the genus *Cooksonia*, some others to a new genus *Concavatheca*. *In situ* spores are of the *Ambitisporites avitus* type. Specimens are preserved as compressions.
Reference: Habgood *et al.* (2002) and Morris *et al.* (2012).

Genus: *Paracooksonia* Morris et al. 2011
Type species: *Paracooksonia apiculispora* Morris *et al.* 2011
Species: *Paracooksonia apiculispora* Morris et al. 2011

Stratigraphy and geography of the holotype: Lochkovian of UK.
***In situ* spores** (modified from Morris *et al.* 2011, p. 54): Trilete spores proximally smooth, with simple trilete mark, interradial papillae and further radial folds developed. Distal surfaces
Remark: *In situ* spores are of the *Streelispora newportensis*/*Aneurospora trilabiata* type. Specimens are preserved as coal-balls.
Reference: Morris *et al.* (2011).

Species: *Paracooksonia ambitispora* Morris et al. 2011

Stratigraphy and geography of the holotype: Lochkovian of UK.
***In situ* spores** (modified from Morris *et al.* 2011, p. 74): Trilete crassitate subtriangular to circular spores. Size range 8 (22) 43 μm. Crassitudo 0.4 (1.9) 3.8 μm wide. The sculpture of both surfaces laevigate.
Remark: *In situ* spores are of the *Ambitisporites avitus*/*A. parvus* type. Specimens are preserved as coal-balls.
Reference: Morris *et al.* (2011).

Genus: *Rhynia* Kidston et Lang 1917
Type species: *Rhynia gwynne–vaughanii* Kidston et Lang 1917
Species: 1917 *Rhynia gwynne–vaughanii* Kidston et Lang, pp. 763–780.
1931 *Rhynia gwynne–vaughanii* Kidston et Lang – Seward, pp. 127, 129.
1937 *Rhynia gwynne–vaughanii* Kidston et Lang – Hoeg, figs. f, l.
1939 *Rhynia gwynne–vaughanii* Kidston et Lang – Darrah, pp. 35–38.
1940 *Rhynia gwynne–vaughanii* Kidston et Lang – Walton, p. 129.
1947 *Rhynia gwynne–vaughanii* Kidston et Lang – Arnold, p. 67.
1954 *Rhynia gwynne–vaughanii* Kidston et Lang – Gothan & Weyland, p. 71.
1956 *Rhynia gwynne–vaughanii* Kidston et Lang – Mägdefrau, pp. 78–81.
1959 *Rhynia gwynne–vaughanii* Kidston et Lang – Andrews, p. 220.
1961 *Rhynia gwynne–vaughanii* Kidston et Lang – Andrews, pp. 32–33.
1962 *Rhynia gwynne–vaughanii* Kidston et Lang – Potonié, pp. 29–30.
1962 *Rhynia gwynne–vaughanii* Kidston et Lang – Zimmermann, fig. 8a.
1962 *Rhynia gwynne–vaughanii* Kidston et Lang – Potonié, fig. 8a.

1967 *Rhynia gwynne–vaughanii* Kidston et Lang – Potonié, p. 38.
1968 *Rhynia gwynne–vaughanii* Kidston et Lang – Edwards, pp. 1655–1657.
1969 *Rhynia gwynne–vaughanii* Kidston et Lang – Bhutta, pp. 52–59.
1971 *Rhynia gwynne–vaughanii* Kidston et Lang – Boullard & Lemoigne, pp. 1–16.
1974 *Rhynia gwynne–vaughanii* Kidston et Lang – Edwards & Richardson, pp. 315–316.
1980 *Rhynia gwynne–vaughanii* Kidston et Lang – Edwards, pp. 177–188.
1980 *Rhynia gwynne–vaughanii* Kidston et Lang – Allen, p. 255.
1980 *Rhynia gwynne–vaughanii* Kidston et Lang – Gensel, pp. 104–105.
1987a *Rhynia gwynne–vaughanii* Kidston et Lang – Bhutta, pp. 1–16.
1987b *Rhynia gwynne–vaughanii* Kidston et Lang – Bhutta, pp. 45–48
1995 *Rhynia gwynne–vaughanii* Kidston et Lang – Balme, p. 94.
2003 *Rhynia gwynne–vaughanii* Kidston et Lang – Edwards, pp. 397–398.
2014 *Rhynia gwynne–vaughanii* Kidston et Lang – Willins & McElwain, p. 74.

Stratigraphy and geography of the holotype: Lochkovian, Shropshire of UK.
***In situ* spores** (modified from Kidston & Lang 1917, Bhutta 1969 and Allen, 1980): Trilete circular to subcircular spores; size range 65 μm (Kidston & Lang 1917), 35–50 μm (Bhutta 1969), 40 μm (Chaloner in Boureau 1967). The sculpture is described as distally finely reticulate (Potonié, 1967) and curvaturae is developed.
Remark: *In situ* spores are compared to the dispersed miospore species *Perotrilites microbaculatus* Richardson & Lister by Edwards & Richardson (1974), *Granulatisporites muniensis* type, *Apiculiretusispora plicata* type (Balme 1995). Specimens are preserved as petrifactions.
Reference: Bhutta (1969), Edwards & Richardson (1974), Allen (1980)

Genus *Salopella* Edwards et Richardson 1974
Type species: *Salopella allenii* Edwards et Richardson 1974

Species: *Salopella allenii* Edwards et Richardson 1974

1974 *Salopella allenii* Edwards et Richardson, pp. 315–318.
1980 Salopella allenii Edwards et Richardson – Allen, p. 255.
1980 Salopella allenii Edwards et Richardson – Gensel, p. 105.
1995 Salopella allenii Edwards et Richardson – Balme, p. 94.

Stratigraphy and geography of the holotype: Dittonian of UK.
***In situ* spores** (modified from Edwards & Richardson, 1974, pp. 315–316): Trilete circular to subcircular azonate spores; size range 23 (29.7) 37 μm. Exine 1 μm thick. Rays of the trilete mark not always visible. Laevigate sculpture. Secondary folds of exine sometimes present.
Remark: Edwards & Richardson (1974) mentioned possible fragments of tapetal material and suggested relatively immature character of the spores. *In situ* spores can be of the *Retusotriletes* type. Specimens are preserved as compressions.
Reference: Edwards & Richardson (1974).

Species: *Salopella* cf. *marcensis* Edwards *et al.* 1994
Stratigraphy and geography of the specimen: Lochkovian/Gedinnian of UK.
***In situ* spores** (modified from Edwards *et al.* 1994, pp. 93, 95): Trilete circular to subtriangular spores. Size range 15–26 μm. Rays of the trilete mark of variable length. Equatorial crassitudo. Proximal surface laevigate, distal irregularly granulate to conate or with baculae sometimes bearing truncated tips.
Remark: *In situ* spores are of the *Aneurospora* type. Specimens are preserved as coalified sporangia.
Reference: Edwards *et al.* (1994).

Species: *Salopella* sp. Fanning *et al.* 1991b

Stratigraphy and geography of the specimen: Přídolí of UK.
***In situ* spores** (modified from Fanning *et al.* 1991b, pp. 34, 35): Trilete circular to subcircular spores; size range 80–97 μm. Finely scabrate exine, curvaturae developed. Rays of the trilete mark slightly elevated (1–2 μm), reaching to the equator.
Remark: *In situ* spores are of the *Retusotriletes* type. Specimens are preserved as compressions.
Reference: Fanning *et al.* (1991b).

Genus *Tarrantia* Fanning et al. 1992
Type species: *Tarrantia salopensis* Fanning et al. 1992

Species: *Tarrantia salopensis* Fanning et al. 1992
1992 *Tarrantia salopensis* Fanning et al., pp. 179–183.
2004 *Tarrantia salopensis* Fanning et al. – Edwards & Richardson, pl. 1r.

Stratigraphy and geography of the holotype: early Gedinnian of UK.
***In situ* spores** (modified from Fanning *et al.* 1992, pp. 180–181): Trilete circular spores; size range 20 (23) 25 μm.
Remark: *In situ* spores are preserved three-dimensionally and are seen as small globules on the surface of ruptured sporangia. Fanning *et al.* (1992) did not give more detail description due to the preservation. Specimens are preserved as petrifaction.
Reference: Fanning *et al.* (1992).

Spores of Rhyniaceae

We mentioned six genera of Rhyniaceae but only five of them produced *in situ* spores that were compared to some dispersed spore taxa. Rhyniaceae yielded spores of two morphological types, majority of them (genera *Cooksonia*, *Concavatheca*, *Paracooksonia* and *Salopella*) are crassitate spores of the *Ambitisporites*, (Plate I, figs D, H, L), *Synorisporites* Plate I, figs B, G J), *Streelispora*, *Retusotriletes* and *Aneurospora* types (Plate I, fig. I. Only the genus *Rhynia* produced spores of the *Perotrilites*, *Apiculiretusispora* (Plate I, figs E, M) and *Granulatisporites* type. It may suggest a special taxonomic position of *Rhynia* among Rhyniaceae because its spores are morphologically different from all others, i.e., they are not crassitate. Spores isolated from *Tarrantia* were not compared to any dispersed spore taxon. The best known and the most often reported genus of Rhyniaceae is *Cooksonia*. Its spores belong to three to four dispersed

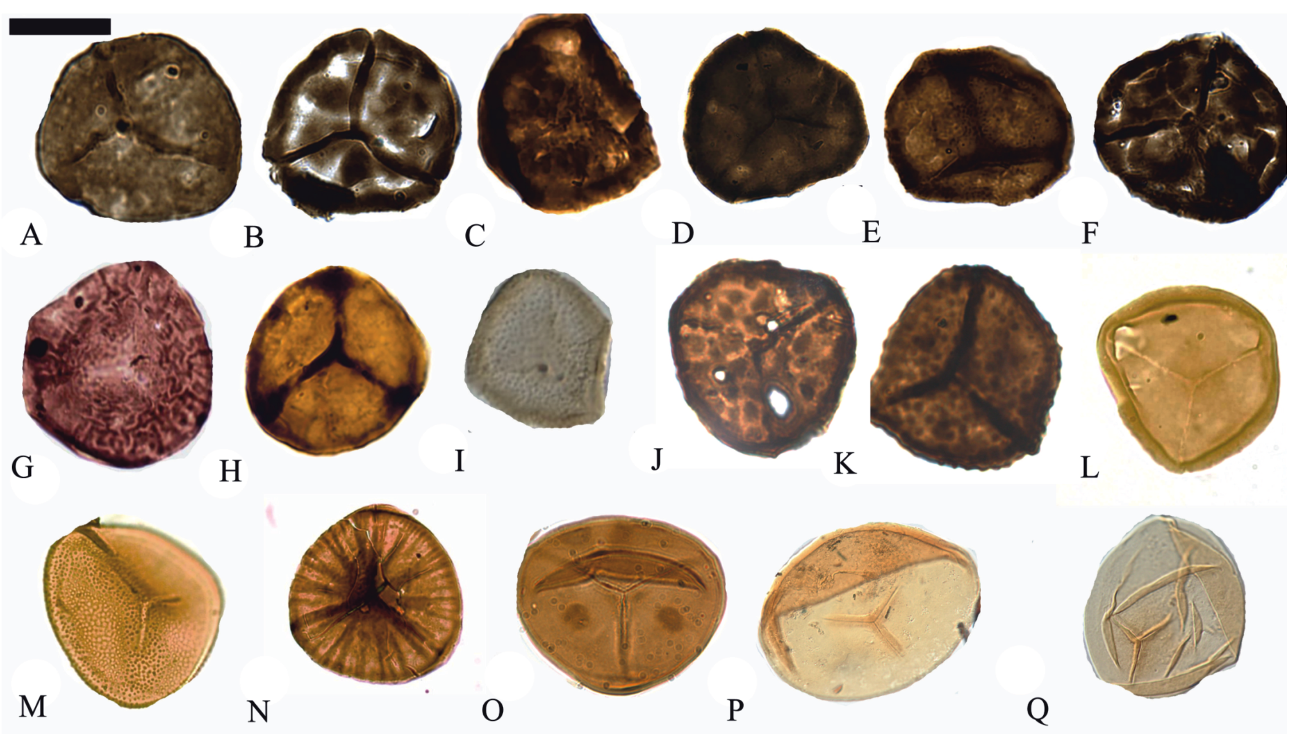

Plate I. **A** – *Retusotriletes* sp. **B** – *Synorisporites papillatus* Richardson et Lister. **C** – *Scylaspora vetusta* (Rodriguez) Rodriguez et Sutherland. **D** – *Ambitisporites avitus* Hoffmeister. E – *Apiculiretusispora* sp. F – *Chelinospora* sp. **G** – *Synorisporites verrucatus* Richardson et Lister. **H** – *Ambitisporites* cf. *avitus* Hoffmeister. **I** – *Aneurospora* sp. **J** – *Synorisporites verrucatus* Richardson et Lister. **K** – *Aneurospora isidori* (Cramer et Diéz) Richardson et al. **L** – *Ambitisporites ambitus* Hoffmeiter. **M** – *Apiculiretusispora plicata* (Allen) Streel. **N** – *Emphanisporites rotatus* McGregor. **O** – *Retusotriletes maculatus* McGregor et Camfield. **P** – **Q** – *Calamospora* sp. Scale bar 15 μm. A – G = from Muro *et al.* (2013), H – I = from Wellman (2024), J – P = courtesy P. Breuer. Q = Bek J.

genera, some *Cooksonia* species were later assigned to different genera (Bek & Votočková Frojdová 2025). Not all specimens assigned to the genus are generally accepted as vascular land plants (Gonez & Gerrienne 2010). *Cooksonia* is a good example of how *in situ* spores can be important for the classification of their parent plants in palynology. The type species of the genus, *Cooksonia pertonii*, was divided into four subspecies, mainly based on different spores, which is exceptional for Paleozoic plants. The four subspecies of *Cooksonia pertonii* Lang (*C. pertonii* subsp. *pertonii* Fanning *et al.*, *C. pertonii* subsp. *apiculispora* Fanning *et al.*, *C. pertonii* subsp. *reticulispora* Habgood *et al.*, and *C. pertonii* subsp. *synorispora* Fanning *et al.*) from the Lochkovian stage in Britain are very difficult (if not impossible) to distinguish using macrofloral characteristics. However, their division based on *in situ* spores (the morphological criteria used to establish the four subspecies) is clear. The spores of *Cooksonia* are crassitate (of the *Ambitisporites*, *Synorisporites* and *Streelispora* types), but the most common are those of the *Ambitisporites* type (recorded six times). The oldest known *Cooksonia*, and therefore the oldest known vascular land plant with *in situ* spores, dates from the lower Silurian (Wenlockian, 432 Ma) in the Czech Republic (Libertín *et al.* 2018a). The last specimens of *Cooksonia* are known from the Lower Devonian (Gonez & Gerrienne 2010).

Rhyniophytopsida of uncertain affinity

Species: *Cooksonia crassiparietalis* Yurina 1964
1964 *Cooksonia crassiparietalis* Yurina 1964, p. 109.
1967 *Cooksonia crassiparietalis* Yurina – Hoeg in Boureau, p. 217.
1973 *Cooksonia crassiparietalis* Yurina – McGregor, p. 65.
1980 *Cooksonia crassiparietalis* Yurina – Allen, p. 255.
1980 *Cooksonia crassiparietalis* Yurina – Gensel, p. 105.
1995 *Cooksonia crassiparietalis* Yurina – Balme, p. 93.
2010 *Cooksonia crassiparietalis* Yurina – Gonez & Gerrienne, pp. 200, 211.

Stratigraphy and geography of the holotype: Emsian of Russia.
***In situ* spores** (modified from McGregor 1973, p. 65 and Balme 1995, p. 93): Trilete circular to subcircular spores; partly azonate, size range 50–65 μm. Apiculate, microgranulate to granulate sculpture, sculpture elements 0.5–1 μm high.
Remark: *In situ* spores are classified as *Apiculiretusispora plicata* (Allen) Streel (Balme 1995) or *Apiculiretusispora* cf. *plicata* (Gonez & Gerrienne 2010). Specimens are preserved as compressions. *Cooksonia crassiparietalis* was excluded from the genus *Cooksonia* by Gonez & Gerrienne (2010) based on morphological differences and the fact that it possesses *in situ* spores that are much bigger (50–65 μm on average) than those of other *Cooksonia* species (20 μm on average; Bek & Votočková Frojdová 2025).
References: Yurina (1964), McGregor (1973), Balme (1995), Gonez & Gerrienne (2010).

Species: cf. *Cooksonia caledonica*/*Renalia* sp. Fanning *et al.* 1992
1992 cf. *Cooksonia caledonica*/*Renalia* sp. Fanning *et al.*, pp. 169–172.
1995 cf. *Cooksonia caledonica*/*Renalia* sp. Fanning *et al.* – Balme, p. 92.
2004 cf. *Cooksonia caledonica* – Edwards & Richardson, fig. 1c.
2010 cf. *Cooksonia caledonica*/*Renalia* sp. Fanning *et al.* – Gonez & Gerrienne, p. 211.

Stratigraphy and geography of the specimen: Lochkovian of UK.
***In situ* spores** (modified from Fanning *et al.* 1992, p. 171): Trilete subtriangular to subcircular spores; size range 12–16 μm. Proximal surface laevigate, distal sculpture microgranulate. Curvaturae developed.
Remark: *In situ* spores are of the *Apiculiretusispora* type. Specimen is preserved as compresion. Cf. *Cooksonia hemisphaerica*/*Renalia* described by Fanning *et al.* (1992) does not correspond with the generic diagnosis of *Cooksonia* and its *in situ* spores are different.
Reference: Fanning *et al.* (1992).

Genus: *Pertonella dactylethra* Fanning *et al.* 1991a
Type species: Pertonella dactylethra Fanning *et al.* 1991a

Species: *Pertonella dactylethra* Fanning et al. 1991a
1991a *Pertonella dactylethra* Fanning et al. pp. 37–47.

1991b *Pertonella dactylethra* Fanning et al. – Fanning *et al.*, pp. 31–32.
1995 *Pertonella dactylethra* Fanning et al. – Balme, p. 94.
2004 *Pertonella dactylethra* Fanning et al. – Edwards & Richardson, fig. 1e.

Stratigraphy and geography of the holotype: Přídolí of UK.
***In situ* spores** (modified from Fanning *et al.* 1991a, p. 39, 1991b, p. 31): Trilete subcircular to subtriangular spores; size range 34 (39) 45 μm. Trilete mark with tectum. Exine 2–4 μm slightly thickened equatorially. Contact areas developed well. Proximal variable band (3–4 μm wide) following the curvaturae perfectae and confluent with a broad band of grana and microconi. Curvatural band varies radially. The sculpture elements changes from low ridges separated by canaliculae, to crowded ridges surmounted by sharply pointed coni decreasing in size to grana and microconi (> 1 μm); this innermost band is confluent with the broad sculptural band (2–6 μm wide). The tectum with grana and microconi. Distal surface laevigate, "roughened" and punctate or sparsely granulate. Distal exine c. 2 μm thick.
Remark: *In situ* spores are of the *Retusotriletes coronatus* type. Specimens are preserved as compressions.
References: Fanning *et al.* (1991a, b), Balme (1995)

Genus: *Renalia* Gensel 1976
Type species: *Renalia hueberi* Gensel 1976

Species: *Renalia hueberi* Gensel 1976
1976 *Renalia hueberi* Gensel, pp. 25–34.
1980 *Renalia hueberi* Gensel – Gensel, p. 94.
1980 *Renalia hueberi* Gensel – Allen, p. 255.
2013 *Renalia hueberi* Gensel – Gensel et al., pp. 1303–1306.

Stratigraphy and geography of the holotype: Emsian of Canada.
***In situ* spores** (modified from Gensel, 1976, pp. 25, 27 and Gensel *et al.* 2013, pp. 1303–1306): Trilete circular to subcircular spores; size range 46–70 μm. Rays of the trilete mark a half to three-quarters of the radius, not always visible. The ends of the trilete marks can continue and form slightly upraised arcuate ridges. Curvaturae developed. Laevigate to finely microgranulate sculpture. Exine 0.3 μm thick. TEM studies (Gensel *et al.* 2013) show a single-layered wall mostly homogeneous, with laminae. The distal wall of some spores is thinner than the proximal one. Single isolated spores exhibit widely spaced, infrequent globules showing homogeneous structures identical to the exospore on the surfaces of both proximal and distal walls. Sections through a trilete laesura show that it is slightly raised and that the inner-wall region adjacent to and within it is loosely organized to granular. This granulate area extends less than half the thickness of the wall. There is a small break and looser organization at the site of what appears to be a suture in an early stage of formation.
Remark: *In situ* spores are of the *Retusotriletes/Apiculiretusispora* type. Specimens are preserved as compressions.
References: Gensel (1976, 1980), Balme (1995), Gensel *et al.* (2013).

Genus: *Uskiella* Shute et Edwards 1989
Type species: *Uskiella spargens* Shute et Edwards 1989

Species: Uskiella spargens Shute et Edwards 1989

Stratigraphy and geography of the specimen: Early Gedinian of UK.
***In situ* spores** (modified from Fanning *et al.* 1992, pp. 119–117): Circular spores; size range 28–42 μm in length and 20–35 μm in width. Exine two-layered, strong folding. Inner layer 1.1 μm thick laevigate, outer layer 0.8 μm thick is microgranulate, micrograna 0.13–0.36 μm large.
Remark: Shute & Edwards (1989) mentioned that *in situ* spores are alete and did not determine them. Specimens are preserved as petrifactions.
Reference: Shute & Edwards (1989).

Species: cf. *Uskiella reticulata* Fanning *et al.* 1992
Stratigraphy and geography of the specimen: Early Gedinian of UK.
***In situ* spores** (modified from Fanning *et al.* 1992, pp. 179–180): Circular spores; size range 60–68 μm. Distal exine is 4–5 μm thick, at the equator 3–5 μm. Laevigate to granulate (?) sculpture pf the distal surface.
Remark: Proximal surfaces are not clear and the specimens may have been alete derived from dyads. Specimens are preserved as petrifactions.
Reference: Fanning *et al.* (1992).

Horneophytopsida

Genus: *Caia* Fanning et al. 1990
Type species: *Caia langii* Fanning et al. 1990

Species: *Caia langii* Fanning *et al.* 1990
1990 *Caia langii* Fanning et al., pp. 725–728.
1991a *Caia langii* Fanning et al. – Fanning *et al.*, pp. 37–47.
1991b *Caia langii* Fanning et al. – Fanning *et al.*, pp. 32–34.
1995 *Caia langii* Fanning et al. – Balme, p. 92.
2004 *Caia langii* Fanning et al. – Edwards & Richardson, fig. 1g.
2010 *Caia langii* Fanning et al. – Gonez & Gerrienne, p. 211.

Stratigraphy and geography of the holotype: Silurian of UK.
***In situ* spores** (modified from Fanning *et al.* 1990, p. 726): Trilete circular to subcircular spores; size range 23–32 μm. Labrum and curvaturae developed. Exine less than 1 μm thick, often folded. The sculpture mostly laevigate, sometimes maybe microgranulate. Rays of the trilete mark not always visible.
Remark: *In situ* spores are of the *Retusotriletes* and *R.* cf. *triangulatus* types (Fanning *et al.* 1990). Fanning *et al.* 1990) suggested possible affinity to plants of the *Horneophyton* type. Specimens are preserved as compressions.
References: Fanning *et al.* (1990, 1991a).

Genus: *Horneophyton* (Kidston et Lang) Barghoorn et Darrah 1938
Type species: *Horneophyton lignierii* (Kidston et Lang) Barghoorn et Darrah 1938

Species: *Horneophyton lignierii* (Kidston et Lang 1920) Barghoorn et Darrah 1938
1920 *Hornea lignierii* Kidston et Lang, p. 616. pls. 4–10.
1930 *Hornea lignierii* Kidston et Lang – Zimmermann, pp. 107–109.
1930 *Hornea lignierii* Kidston et Lang – Jongmans, p. 932.
1938 *Horneophyton lignierii* Kidston et Lang – Barghoorn & Darrah, pp. 144–146.
1940 *Hornea lignierii* Kidston et Lang – Walton, pp. 29–33.
1947 *Horneophyton lignierii* Kidston et Lang – Arnold, pp. 68–69.
1960 *Horneophyton lignierii* Kidston et Lang – Potonié, p. 38.
1961 *Horneophyton lignierii* Kidston et Lang – Andrews, pp. 33, 36.
1962 *Hornea lignierii* Kidston et Lang – Zimmermann, pp. 355.
1967 *Horneophyton lignierii* Kidston et Lang – Hoeg in Boureau, pp. 209–213.
1971 *Horneophyton lignierii* Kidston et Lang – Chaloner & Orbell, pp. 273–294.
1973a *Horneophyton lignierii* (Kidston et Lang) Barghoorn & Darrah – Bhutta, pp. 45–55.
1974 *Horneophyton lignierii* (Kidston et Lang) Barghoorn & Darrah – Eggert, pp. 408–411.
1980 *Horneophyton lignierii* (Kidston et Lang) Barghoorn & Darrah – Allen, p. 255.
1980 *Horneophyton lignierii* (Kidston et Lang) Barghoorn & Darrah – Gensel, p. 105.
1995 *Horneophyton lignierii* (Kidston et Lang) Barghoorn & Darrah – Balme, pp. 93–94.
2004 *Horneophyton lignierii* (Kidston et Lang) Barghoorn & Darrah – Wellman et al., pp. 93–94.
2003 *Horneophyton lignierii* (Kidston et Lang) Barghoorn & Darrah – Edwards, pp. 398–399.

Stratigraphy and geography of the holotype: Lochkovian, Shropshire of UK.
***In situ* spores** (modified from Bhutta 1973a, pp. 49–51; Eggert 1974, pp. 409–410 and Wellman *et al.* 2004, pp. 430–442): Trilete subtriangular to circular spores; size range 50 μm (Kidston & Lang 1920), 45 (54) 71.4 μm (Bhutta 1973a), 42–71 μm (Balme 1995), 39–49 μm (Eggert 1974), 42 (47) 54 μm (Wellman *et al.* 2004), 57 μm (Edwards 2003). Curvaturae and narrow crassitudo developed. Some spores distally apiculate to conate, proximally laevigate, others with proximal radial ribbing.
Remark: *In situ* spores with apiculate distal and laevigate proximal sculpture are of the *Apiculiretusispora plicata* type, those with proximal ribbing belong to the *Emphanisporites decoratus* type. Specimens are preserved as petrifactions.
Reference: Bhutta (1973a), Eggert (1974), Balme (1995), Wellman *et al.* (2004).

Genus: *Tortilicaulis* Edwards 1979
Type species: *Tortilicaulis transwallensis* Edwards 1979

Species: *Tortilicaulis offaceus* Edwards et al. 1994
1984 *Tortilicaulis offaceus* Edwards et al., pp. 201–215.
2012 *Tortilicaulis offaceus* Edwards et al. – Morris *et al.*, pp. 61–62.

Stratigraphy and geography of the holotype: Lochkovian/Gedinnian of UK.
***In situ* spores** (modified from Edwards *et al.* 1994, pp. 102–106 and Morris *et al.* 2012, pp. 61–62): Trilete circular to subcircular spores; size range 15 (18) 26 μm. Labrum 0.8–1.9 μm high and wide. Sculpture of both surfaces densely granulate, microgranulate and microconate.
Remark: Authors did not determine *in situ* spores. Specimens are preserved as coalified sporangia.
Reference: Edwards *et al.* (1994).

Species: *Tortilicaulis transwallensis* Edwards 1979
1979 *Tortilicaulis transwallensis* Edwards, pp. 315–318.
1980 *Tortilicaulis transwallensis* Edwards – Allen, p. 255.
1992 *Tortilicaulis transwallensis* Edwards – Fanning *et al.*, p. 173.
1995 *Tortilicaulis transwallensis* Edwards – Balme, p. 94.
2004 *Tortilicaulis transwallensis* Edwards – Edwards & Richardson, pl. 1l.

Stratigraphy and geography of the holotype: Dittonian of UK.
***In situ* spores** (modified from Edwards & Richardson, 1974, pp. 315–316 and Fanning *et al.* 1992, p. 173): Trilete circular to subcircular azonate spores; size range 23 (29.7) 37 μm (Edwards 1979) and 43 (47) 49 μm (Fanning *et al.* 1992). Exine 1 μm thick. Rays of the trilete mark not always visible. Laevigate (Edwards 1979) and granulate (Fanning *et al.* 1992) sculpture. Secondary folds of exine sometimes present.
Remark: Edwards & Richardson (1974) mentioned possible fragments of tapetal material and suggested relatively immature character of the spores. *In situ* spores can be of the *Retusotriletes* type (Edwards 1979) and *Apiculiretusispora* type (Fanning *et al.* 1992). It is evident that *in situ* spores described by Edwards (1979) and Fanning *et al.* (1992) were isolated from different parent plants. Both sets of spores differ in diameter, sculpture as well as classification. Specimens are preserved as compressions.
Reference: Edwards (1979), (Fanning *et al.* 1992).

Spores of Horneophytopsida

We know only three taxa of Horneophytopsida that yielded *in situ* spores. Two of them (*Caia* and *Tortilicaulis*) produced crassitate spores of the *Retusotriletes* type, the second group are non-crassitate spores of the *Apiculiretusispora* and *Emphanisporites* types (Plate I, fig N), i.e., it seems that Horneophytopsida were palynologically heterogeneous group.

Taeniocradaceae

Genus: *Huia* Geng 1985
Type species: *Huia recurvata* Geng 1985

Species: *Huia recurvata* Geng 1985
1985 *Huia recurvata* Geng, pp. 419–429.
1995 *Huia recurvata* Geng – Balme, p. 94.

Stratigraphy and geography of the holotype: Early Devonian of Yunnan, China.
***In situ* spores** (modified from Balme 1995, p. 94): Trilete subtriangular spores; size range 40–53 μm. Curvaturae developed, spinate to conate sculpture.
Remark: There are some doubts about the sculpture of these *in situ* spores, because only two specimens were illustrated and it is not clear if distal or proximal surface is sculptured, or both. Specimens are preserved as compressions.
References: Balme (1995).

Spores of Taeniocradaceae

Only one species of Taeniocradaceae yielded *in situ* spores but they were not compared to any dispersed spore taxon.

Zosterophyllaceae

Genus: *Discalis* Hao 1989a
Type species: *Discalis longistipa* Hao 1989a

Species: *Discalis longistipa* Hao 1989a
Stratigraphy and geography of the holotype: Siegenian of Yunnan, China.
***In situ* spores** (modified from Hao 1989a, pp. 159, 166): Trilete circular to subcircular spores; size range 30 (42) 50 μm. Rays of the trilete mark simple, a half to three-quarters of the radius. Laevigate exine, sometimes folded.
Remark: *In situ* spores are of the *Punctatisporites*/*Calamospora* type. Specimens are preserved as compressions.
Reference: Hao (1989a).

Genus: *Gosslingia* Heard 1927
Type species: *Gosslingia breconensis* Heard 1927

Species: *Gosslingia breconensis* Heard 1927
1927 *Gosslingia breconensis* Heard, pp. 195–209.
1942 *Gosslingia breconensis* Heard – Croft & Lang, pp. 141–144.
1964 *Gosslingia breconensis* Heard – Boureau, pp. 195–209.
1970 *Gosslingia breconensis* Heard – Edwards, pp. 195–209.
1980 *Gosslingia breconensis* Heard – Allen, p. 257.
1980 *Gosslingia breconensis* Heard – Gensel, p. 110.
1995 *Gosslingia breconensis* Heard – Balme, p. 97.

Stratigraphy and geography of the holotype: Lower Devonian of UK.
***In situ* spores** (modified from Balme 1995, p. 97): Trilete (?) circular spores; size range 36–50 μm. Apiculate sculpture.
Remark: *In situ* spores described by Edwards (1970) are poorly preserved, their trilete character is even questioned and therefore, they did not compared with any dispersed spore taxon. Specimens are preserved as petrifactions.
Reference: Edwards (1970), Balme (1995).

Genus: *Gumuia* Hao 1989b
Type species: *Gumuia zyzzata* Hao 1989 b

Species: *Gumuia zyzzata* Hao 1989b
1989b *Gumuia zyzzata* Hao, pp. 956– 960.
1995 *Gumuia zyzzata* Hao – Balme, p. 99.

Stratigraphy and geography of the holotype: Devonian of China.
***In situ* spores** (modified from Hao 1989b, p. 56, Balme 1995, pp. 98): Trilete triangular to subtriangular spores; size range 50–90 μm. Exine laevigate.
Remark: *In situ* spores are of the *Retusotriletes* type. Specimens are preserved as compressions.
Reference: Hao (1989b), Balme (1995).

Genus: *Nothia* Kidston et Lang 1920
Type species: *Nothia aphylla* Kidston et Lang 1920

Species: *Nothia aphylla* Lyon ex Høeg 1967
1957 *Nothia aphylla* Lyon, p. 1219.
1967 *Nothia aphylla* Lyon ex Høeg – Høeg, p. 356.
1969 *Nothia aphylla* Lyon ex Høeg – Bhutta, pp. 65–70.
1980 *Nothia aphylla* Lyon ex Høeg – Allen, pp. 257.
1995 *Nothia aphylla* Lyon ex Høeg – Balme, p. 97.
2005 *Nothia aphylla* Lyon ex Høeg – Daviero–Gomez *et al.*, pp. 319–326.

Stratigraphy and geography of the holotype: Devonian of UK.
***In situ* spores** (modified from Balme 1995, p. 97): Trilete subcircular to subtriangular spores; size range 59–74 μm. Laevigate to finely microgranulate sculpture. Curvaturae developed.
Remark: *In situ* spores are of the *Apiculiretusispora/Retusotriletes* type. As suggested by Daviero–Gomez *et al.* (2005) *Nothia aphylla* incor porates detached sporangia originally tentatively attributed to *Asteroxylon mackiei*. Specimens are preserved as petrifacxtions.
Reference: Høeg (1967), Balme (1995), Daviero–Gomez *et al.* (2005).

Genus: *Oricilla* Gensel 1982a
Type species: *Oricilla bilinearis* Gensel 1982a

Species: *Oricilla bilinearis* Gensel 1982a
1982a *Oricilla bilinearis* Gensel, pp. 354.
1984 *Oricilla bilinearis* Gensel – Gensel & Andrews, p. 126.
1995 *Oricilla bilinearis* Gensel – Balme, p. 95.

Stratigraphy and geography of the specimen: Emsian of USA.
***In situ* spores** (modified from Gensel 1982a, p. 354): Trilete circular spores; size range 68–92 μm. Curvaturae developed. Laevigate sculpture. Exine thin with irregular secondary folds of exine. Contact area presents. The surface sometimes covers by globules, probably of tapetal origin.
Remark: *In situ* spores are of the *Calamospora* and *Retusotriletes* types (Gensel 1982a, Balme 1995). Specimens are preserved as compressions.
Reference: Gensel (1982a), Balme (1995).

Genus: *Rebuchia* Hueber 1972
Type species: *Rebuchia ovata* Hueber 1972

Species: *Rebuchia ovata* Hueber 1972
1972 *Rebuchia ovata* Hueber p. 972
1980 *Rebuchia ovata* Hueber – Allen, p. 257.
1980 *Rebuchia ovata* Hueber – Gensel, p. 110.
1995 *Rebuchia ovata* Hueber – Balme p. 97.

Stratigraphy and geography of the holotype: Gedinian–Emsian of Germany.
***In situ* spores** (modified from HUEBER 1972: 115–120): Trilete circular spores; size range 68–75 μm. Curvaturae developed. Exine laevigate.
Remark: As suggested by Balme (1995) spores might be immature and of the *Retusotriletes* type. Specimens are preserved as compressions.
Reference: Hueber (1972), Balme (1995).

Genus: *Sawdonia* (Dawson) Gensel & Berry, 2016
Type species: *Sawdonia ornata* (Dawson) Gensel & Berry, 2016

Species: *Sawdonia acanthotheca* Gensel et al. 1975
1975 *Sawdonia acanthotheca* Gensel et al., pp. 50–62.
1976 *Sawdonia acanthotheca* Gensel et al. – McGregor & Camfield, pp. 23–25.
1980 *Sawdonia acanthotheca* Gensel et al. – Allen, p. 257.
1980 *Sawdonia acanthotheca* Gensel et al. – Gensel, p. 110.

Stratigraphy and geography of the holotype: Middle Devonian of USA.
***In situ* spores** (modified from Gensel *et al.* 1975, pp. 56–59): Trilete circular to subtriangular spores; size range 40–76 μm. Curvaturae developed. Rays of the trilete mark a half of the diameter. Dark contact area sometimes visible. Secondary folds of exine of irregular size, number, shape and position occur. Laevigate to finely microgranulate to granulate sculpture of both surfaces, but the number of sculpture elements is higher on the distal surface.
Remark: *In situ* spores are of the *Calamospora atava* or *C. pannucea* types. Specimens are preserved as compresisons.
Reference: Gensel *et al.* (1975).

Species: *Sawdonia ornata* (Dawson) Gensel et Berry, 2016
1871 *Psilophyton princeps* var. *ornata* Dawson, pp. 56–59.
1964 *Psilophyton princeps* var. *ornata* Dawson – Hueber, pp. 5–9.
1967 *Sawdonia ornata* Dawson – Hueber & Banks, pp. 81–85.
1968 *Sawdonia ornata* Dawson – Ananiev & Stepanov, pp. 30–46.
1971 *Sawdonia ornata* Dawson – Hueber, pp. 618–632.
1972 *Sawdonia ornata* Dawson – Zdebska, pp. 77–97.
1975 *Sawdonia ornata* Dawson – Gensel *et al.*, pp. 618–632.
1978 *Sawdonia ornata* Dawson – Chaloner *et al.*, pp. 694–702.
1980 *Sawdonia ornata* Dawson – Allen, p. 257.
1980 *Sawdonia ornata* Dawson – Gensel, p. 110.
1983 *Sawdonia ornata* Dawson – Rayner, pp. 79–83.
1984 *Sawdonia ornata* Dawson – Gensel & Andrews, fig. 44/7.
1990 *Sawdonia ornata* Dawson – Gensel *et al.*, pp. 520–547.
1995 *Sawdonia ornata* Dawson – Balme, p. 97.
2016 *Sawdonia ornata* Dawson – Gensel & Berry, pp. 618–632.

Stratigraphy and geography of the holotype: Emsian of UK.
***In situ* spores** (modified from Balme 1995, p. 97): Trilete circular to subcircular spores; size range 54–64 μm. Laevigate sculpture. Curvaturae developed.
Remark: *In situ* Although McGregor (1973) compared spores from sporangium assigned to *Sawdonia ornata* to the genus *Calamospora* Schopf et al., they are more similar to the dispersed species *Retusotriletes actinomorphus* Chibrikova. Specimens are preserved as compressions.
Reference: Gensel & Berry (2016), Balme (1995).

Genus: *Tarella* Edwards et Kenrick 1986
Type species: *Tarella trowenii* Edwards et Kenrick 1986

Stratigraphy and geography of the holotype: Early Devonian of UK.
***In situ* spores** (modified from Edwards & Kenrick 1986, pp. 271, 278): Trilete circular to subtriangular spores; size range 31–34 μm. Rays of the trilete mark almost equal to the radius. Finely microgranulate sculpture. Cingulum developed.
Remark: Only a few specimens of *in situ* spores are preserved, all of them are illustrated only using SEM and their classification remains unclear. Specimens are preserved as compressions.
Reference: Edwards & Kenrick (1986).

Genus: *Zosterophyllum* Penhallow 1892
Type species: *Zosterophyllum myretonianum* Penhallow 1892

Species: *Zosterophyllum australianum* Lang et Cookson, 1930
1930 *Zosterophyllum australianum* Lang et Cookson, pp. 143–148, pl. 12.
1942 *Zosterophyllum australianum* Lang et Cookson – Croft & Lang, pp. 145–146.

1949 *Zosterophyllum australianum* Lang et Cookson – Cookson, pp. 120, 127.
1967 *Zosterophyllum australianum* Lang et Cookson – Hoeg in Boureau, pp. 255–256.
1977 *Zosterophyllum australianum* Lang et Cookson – Li & Cai, p. 23.
1980 *Zosterophyllum australianum* Lang et Cookson – Allen, p. 257.
1992 *Zosterophyllum australianum* Lang et Cookson – Hao, pp. 189–195.
1995 *Zosterophyllum australianum* Lang et Cookson – Balme, p. 98.

Stratigraphy and geography of the holotype: Emsian of Australia.
***In situ* spores** (modified from Hao 1992, pp. 189–195): Trilete triangular, subtriangular, rarely subcircular spores; size range 75 μm (Lang & Cookson 1930) and 20–50 μm (Hao 1992). Rays of the trilete mark a third to a quarter of the radius. Curvaturae developed. A dark thickened contact area almost equal to the length of rays of the trilete mark. Microconate sculpture of both surfaces.
Remark: *In situ* spores are of the *Apiculatisporis*/*Apiculiretusispora* type. Specimens are preserved as compressions.
Reference: Lang & Cookson (1930), Hao (1992).

Species: *Zosterophyllum divaricatum* Gensel, 1982b
1982b *Zosterophyllum divaricatum* Gensel, pp. 652–660.
1984 *Zosterophyllum divaricatum* Gensel – Gensel & Andrews, p. 75.
1995 *Zosterophyllum divaricatum* Gensel – Balme, p. 98.
2014 *Zosterophyllum divaricatum* Gensel – Willis & McElwain, p. 75.

Stratigraphy and geography of the holotype: Emsian of Canada.
***In situ* spores** (modified from Gensel 1982b, pp. 658, 660): Trilete circular to subtriangular spores; size range 55–85 μm. Rays of the trilete mark a half to a third of the radius, slightly raised or folded. Curvaturae and small dark contact area developed. Contact area laevigate, distal surface microgranulate sometimes with fragments of tapetum (ubisch bodies?).
Remark: *In situ* spores are of the *Retusotriletes* type. Specimens are preserved as compressions.
Reference: Gensel (1982b).

Species: *Zosterophyllum* cf. *fertile* Edwards 1969
1969 *Zosterophyllum* cf. *fertile* Edwards, pp. 924–929.
1980 *Zosterophyllum* cf. *fertile* Edwards – Gensel, p. 110.
1980 *Zosterophyllum* cf. *fertile* Edwards – Allen, p. 257.
1984 *Zosterophyllum* cf. *fertile* Edwards – Gensel & Andrews, pp. 98–99.
1995 *Zosterophyllum* cf. *fertile* Edwards – Balme, pp. 98–99.

Stratigraphy and geography of the specimen: Siegen-Emsian of UK.
***In situ* spores** (modified from Edwards 1969, pp. 926–927): Trilete circular to subtriangular spores; size range 59 (65) 70 μm. Rays of the trilete mark a half to two-thirds of the radius. Curvaturae developed, not always prominent. Two-layered laevigate exine.
Remark: *In situ* spores are of the *Retusotriletes dubius* type. Specimens are preserved as compressions.
Reference: Edwards (1969).

Species: *Zosterophyllum llanoveranum* Croft et Lang, 1942
1942 *Zosterophyllum llanoveranum* Croft et Lang, pp. 146–149, pl. 10.
1967 *Zosterophyllum llanoveranum* Croft et Lang – Høeg in Boureau, pp. 260–261.
1969 *Zosterophyllum llanoveranum* Croft et Lang – Edwards, pp. 201–210.
1980 *Zosterophyllum llanoveranum* Croft et Lang – Allen, p. 257.
1980 *Zosterophyllum llanoveranum* Croft et Lang – Gensel, p. 110.
1984 *Zosterophyllum llanoveranum* Croft et Lang – Gensel & Andrews, p. 146.
1995 *Zosterophyllum llanoveranum* Croft et Lang – Balme, p. 98.

Stratigraphy and geography of the holotype: Siegenian of UK.
***In situ* spores** (modified from Edwards 1969, pp. 206–207): Trilete circular, subcircular to triangular spores; size range 45–65 μm (Croft & Lang 1942) and 45–59 μm (Edwards 1969). Rays of the trilete mark a half to two-quarters of the radius. Two-layered laevigate exine. The surface is irregularly covered by probably fragments of tapetum.

Remark: Edwards (1986) did not assigned *in situ* spores to any dispersed spore taxon, but Balme (1995) compared them to the dispersed species *Leiotriletes liebigensis* Hodgson. Specimens are preserved as petrifactions.
Reference: Edwards (1969) and Balme (1995).

Species: *Zosterophyllum myretonianum* Penhallow 1892
1892 *Zosterophyllum myretonianum* Penhallow, p. 12.
1930 *Zosterophyllum myretonianum* Penhallow – Lang & Cookson, pp. 140–145.
1967 *Zosterophyllum myretonianum* Penhallow – Høeg in Boureau, pp. 253–254.
1980 *Zosterophyllum myretonianum* Penhallow – Allen, p. 257.
1995 *Zosterophyllum myretonianum* Penhallow – Balme, p. 98.

Stratigraphy and geography of the holotype: Downtonian of UK.
***In situ* spores** (modified from Balme 1995, p. 98): Trilete circular spores 30 μm in diameter.
Remark: *In situ* spores are not described in detail and were not assigned to any spore taxon. Specimen is preserved as compression.
Reference: Balme (1995).

Species: *Zosterophyllum yuannicum* Hao 1985
1985 *Zosterophyllum yuannicum* Hao, p. 12.
1995 *Zosterophyllum yuannicum* Hao – Balme, p. 98.
1967 *Zosterophyllum yuannicum* Hao – Høeg in Boureau, pp. 253–254.
1980 *Zosterophyllum yuannicum* Hao – Allen, p. 257.
1980 *Zosterophyllum yuannicum* Hao – Gensel, p. 257.
1995 *Zosterophyllum yuannicum* Hao – Balme, p. 98.

Stratigraphy and geography of the holotype: Siegenian of China.
***In situ* spores** (modified from Balme 1995, p. 98): Trilete subtriangular spores; size range 32–75 μm. Curvaturae developed.
Remark: *In situ* spores are not described in detail and are not compared to any dispersed spore taxon. Specimens are preserved as compressions.
Reference: Hao (1985), Balme (1995).

Spores of Zosterophyllaceae

Eight zosterophyllalean genera were palynologically studied. Two of them (*Gosslingia* and *Tarella*) yielded *in situ* spores that were not compared to any dispersed spore taxon. Spores of other genera are of two morphological types; crassitate (*Retusotriletes* type) and non-crassitate (*Calamospora*, *Punctatisporites*, *Apiculiretusispora* types) that means that zosterophylls are heterogeneous from palynological view.

Trimerophytaceae

Genus: *Dawsonites* Halle 1916
Type species: *Dawsonites arcuatus* Halle 1916

Species: *Dawsonites arcuatus* Halle 1916
1916 *Dawsonites arcuatus* Halle, pp. 24.
1942 *Dawsonites arcuatus* Halle – Croft & Lang, pp. 140–141.
1967 *Dawsonites arcuatus* Halle – Høeg in Chaloner *et al.*, pp. 603–604.
1980 *Dawsonites arcuatus* Halle – Allen, p. 261.
1980 *Dawsonites arcuatus* Halle – Gensel, p. 114.
1995 *Dawsonites arcuatus* Halle – Balme, p. 95.

Stratigraphy and geography of the holotype: Lower Devonian of Norway.
***In situ* spores** (modified from Chaloner *et al.* 1967, p. 705): Trilete circular spores 45 (50) 55 μm. Laevigate, micropapillate to microconate sculpture of both surfaces. Rays of the trilete mark two-thirds of the radius.
Remark: *In situ* spores are of the *Apiculiretusispora brandtii* or *Cyclogranisporites* types (Chaloner *et al.* 1967) or *Punctatisporites* type (Balme 1995). Some specimens might be degradated. Specimens are preserved as compressions.
Reference: Croft & Lang (1942), Chaloner *et al.* (1967), Balme (1995).

Species: *Dawsonites* cf. *arcuatus* Hueber, 1964
1964 *Dawsonites* cf. *arcuatus* Hueber, pp. 7–9.
1980 *Dawsonites* cf. *arcuatus* Hueber – Allen, p. 261.
1980 *Dawsonites* cf. *arcuatus* Hueber – Gensel, p. 121.

Stratigraphy and geography of the holotype: Early Devonian of Canada.
***In situ* spores** (modified from Balme 1995, p. 95): Trilete circular spores; size range 50 μm. Exine

laevigate. Curvaturae developed. Microapiculate sculpture. Rays of the trilete mark a half to two-thirds of the radius.
Remark: *In situ* spores are interpreted as the *Apiculiretusispora* type but based on the occurrence of curvaturae its determination as *Retusotriletes* is more probable. Specimen is preserved as compression.
Reference: Balme (1995).

Genus: *Hostinella* Stur 1882
Type species: *Hostinella hostimensis* (Barrande) Stur 1882

Species: *Hostinella globosa* Lang 1925
1925 *Hostinella globosa* Lang, pp. 266
1936 *Hostinella globosa* Lang – Jongmans, p. 1024.
1962 *Hostinella globosa* Lang – Potonié, p. 40.
1980 *Hostinella globosa* Lang – Allen, p. 255.
1995 *Hostinella globosa* Lang – Balme, p. 94.

Stratigraphy and geography of the holotype: Middle Devonian of UK.
***In situ* spores** (modified from Potonié 1962, p. 40 and Balme 1995, p. 94): Trilete circular spores; size range 60 μm. Laevigate sculpture.
Remark: Allen (1980) described *in situ* spores as the *Calamospora atava* and *Apiculiretusispora* types. Specimens are preserved as compressions.
References: Potonié (1962), Allen (1980) and Balme (1995).

Genus: *Hsüa* Li 1982
Type species: *Hsua robusta* Li 1982

Species: *Hsüa robusta* Li 1982
1982 *Hsüa robusta* Li, pp. 331–340
1995 *Hsüa robusta* Li – Balme, p. 99.

Stratigraphy and geography of the holotype: Early Devonian of China.
***In situ* spores** (modified from Li 1982, pp. 331–340 and Balme 1995, p. 99): Trilete circular spores; size range 18–36 μm. Exine laevigate.
Remark: *In situ* microspores are not described in detail and are not compared to any dispersed spore taxon. Specimens are preserved as compressions.
Reference: Li (1982), Balme (1995).

Genus: *Pertica* Kasper et Andrews 1972
Type species: *Pertica quadrifaria* Kasper et Andrews 1972

Species: *Pertica dalhousii* Doran et al. 1978
1978 *Pertica dalhousii* Doran et al., pp. 3052–3068.
1980 *Pertica dalhousii* Doran et al. – Gensel, p. 114.
1995 *Pertica dalhousii* Doran et al. – Balme, p. 95.

Stratigraphy and geography of the holotype: Emsian of Canada.
***In situ* spores** (modified from Doran *et al.* 1978, pp. 3057–3065): Trilete circular to subcircular spores; size range 52–85 μm. Outer sculptured layer is microgranulate to microapiculate and maybe be particularly or completely detached. Rays of the trilete mark one third to a half of the radius. Curvaturae developed, contact area laevigate.
Remark: *In situ* spores are of the *Apiculiretusispora plicata* or *A. arenorugosa* types. Specimens are preserved as compressions.
Reference: Doran *et al.* (1978).

Species: *Pertica varia* Granoff et al. 1976
1976 *Pertica varia* Granoff et al., pp. 119–128.
1980 *Pertica varia* Granoff et al. – Gensel, p. 114.
1980 *Pertica varia* Granoff et al. – Allen, p. 261.
1995 *Pertica varia* Granoff et al. – Balme, p. 95.

Stratigraphy and geography of the holotype: lower Devonian of Canada.
***In situ* spores** (modified from Balme 1995, p. 95): Trilete circular to subcircular spores; size range 59–90 μm. Curvaturae developed. Apiculate to microapiculate sculpture.
Remark: *In situ* spores are of the *Apiculiretusispora* type. Balme (1995) mentioned that forms without outer sculptured layer can remember those isolated from *Pertica dalhousii* Doran *et al.* Specimens are preserved as compressions.
Reference: Balme (1995).

Genus: *Psilophyton* Dawson, 1859
Type species: *Psilophyton princeps* Dawson 1859

Species: *Psilophyton charientos* Gensel, 1979
1979 *Psilophyton charientos* Gensel, pp. 81–99
1980 *Psilophyton charientos* Gensel, p. 114.
1983 *Psilophyton charientos* Gensel – Gensel & White, pp. 225–230.
1995 *Psilophyton charientos* Balme, p. 96.

Stratigraphy and geography of the holotype: Lower Devonian of Canada.
***In situ* spores** (modified from Gensel 1979, pp. 81–99 and Balme 1995, p. 96): Trilete circular

spores; size range 48–74 μm. Curvaturae developed. Microapiculate to apiculate sculpture. Two-layered exine; outer sculptured layer developed except for contact area.
Remark: *In situ* spores are of the *Apiculiretusispora brandtii* type. Balme (1995) mentioned that specimens without perispore can be of the *Calamospora* or *Punctatisporites* types. Specimens are preserved as compressions.
Reference: Gensel (1979), Balme (1995).

Species: *Psilophyton crenulatum* Doran, 1980
1980 *Psilophyton crenulatum* Doran, pp. 2241–2262.
1983 *Psilophyton crenulatum* Doran – Gensel & White, p. 227.
1995 *Psilophyton crenulatum* Doran – Balme, p. 96.

Stratigraphy and geography of the holotype: Middle Emsian of Canada.
***In situ* spores** (modified from Doran 1980, pp. 2246, 2248, 2250): Trilete circular spores; size range 48 (70) 102 μm. Curvaturae developed. Microapiculate to apiculate sculpture.
Remark: *In situ* spores are of the *Apiculiretusispora* type. Specimens are preserved as compressions.
Reference: Doran (1980).

Species: *Psilophyton forbesii* Andrews et al., 1968
1968 *Psilophyton forbesii* Andrews et al., pp. 1–11.
1980 *Psilophyton forbesii* Andrews et al. – Gensel, p. 114.
1983 *Psilophyton forbesii* Andrews et al. – Gensel & White, p. 228.
1995 *Psilophyton forbesii* Andrews et al. – Balme, p. 96.

Stratigraphy and geography of the holotype: lower Devonian of Canada.
***In situ* spores** (modified from Andrews *et al.* 1968, pp. 4–9 and Balme 1995, p. 96): Trilete circular spores; size range 48–80 μm. Curvaturae developed. Microapiculate to apiculate sculpture.
Remark: *In situ* spores are of the *Apiculiretusispora* type. Specimens are preserved as compressions.
Reference: Andrews *et al.* (1968), Balme (1995).

Species: *Psilophyton princeps* Dawson, 1859
1859 *Psilophyton princeps* Dawson, pp. 480–485.
1921 *Psilophyton princeps* Dawson – Arber, pp. 17–21.
1931 *Psilophyton princeps* Dawson – Lang, pp. 421–442.
1968 *Psilophyton princeps* Dawson – Banks, pp. 167–170.
1968 *Psilophyton princeps* Dawson – Hueber, pp. 815–822.
1980 *Psilophyton princeps* Dawson – Allen, p. 261.
1980 *Psilophyton princeps* Dawson – Gensel, p. 114.
1983 *Psilophyton princeps* Dawson – Gensel & White, pp. 225–230.
1995 *Psilophyton princeps* Dawson – Balme, p. 96.

Stratigraphy and geography of the holotype: Lower Devonian of Canada.
***In situ* spores** (modified from Balme 1995, p. 96): Trilete circular spores; size range 40–120 μm. Laevigate to apiculate sculpture. Rays of the trilete mark a half to a third of the radius.
Remark: *In situ* spores are of the *Apiculiretusispora* type. Specimens are preserved as compressions.
Reference: Balme (1995).

Genus: *Trimerophyton* Hopping, 1956
Type species: *Trimerophyton robustius* Dawson, 1859

Species: *Trimerophyton robustius* Dawson, 1859
1859 *Trimerophyton robustius* Dawson, pp. 477–488.
1956 *Trimerophyton robustius* Dawson – Hopping, p. 15.
1973 *Trimerophyton robustius* Dawson – McGregor, p. 125.
1980 *Trimerophyton robustius* Dawson – Gensel, p. 114.
1980 *Trimerophyton robustius* Dawson – Allen, p. 261.
1995 *Trimerophyton robustius* Dawson – Balme, p. 96.

Stratigraphy and geography of the holotype: Early Devonian of Canada.
***In situ* spores** (modified from Balme 1995, p. 96): Trilete circular spores; size range 40–63 μm. Laevigate to finely microconate and conate sculpture, curvaturae developed.
Remark: *In situ* miospores are of the *Calamospora atava*/*C. pannucea* types (McGregor 1973) or *Apiculiretusispora*/*Retusotriletes* types (Allen 1980, Gensel 1980). Specimens are preserved as compressions.
Reference: Balme (1995).

Genus: *Yunia* Shou-Gang et Beck 1991
Type species: *Yunia dichotoma* Shou-Gang et Beck 1991

Species: *Yunia dichotoma* Shou-Gang et Beck 1991

Stratigraphy and geography of the holotype: Siegen of Yunnan, China.
***In situ* spores** (modified from Shou-Gang & Beck 1991, p. 183): Trilete circular spores; size range 35.3–53.3 μm. Rays of the trilete mark more than a half of the radius. Secondary folds of exine sometimes developed. Laevigate to finely scabrate sculpture.
Remark: *In situ* microspores are poorly described and illustrated so it is not possible to compare them with dispersed miospore taxa. Specimens are preserved as coal-balls.
Reference: Shou-Gang & Beck (1991).

Spores of trimerophytes

Nine genera were studied for *in situ* spores and two of them (*Hsüa* and *Yuania*) yielded spores that were not compared to any dispersed spore taxon. Majority of trimerophytalean plants (genera *Dawsonites*, *Hostinella*, *Pertica*, *Psilophyton* and *Trimerophyton*) produced non-crassitate spores of the *Apiculiretusispora* and *Calamospora* types and from two of them (*Estinophyton* and *Gumuia*) authors described crassitate spores of the *Retusotriletes* type.

Barinophytaceae

Genus: *Barinophyton* (White) Brauer 1980
Type species: *Barinophyton richardsonii* (Dawson) White 1905

Species: *Barinophyton citrulliforme* (Arnold) Brauer 1980
1939 *Barinophyton citrulliforme* Arnold, pp. 290–293.
1967 *Barinophyton citrulliforme* Arnold – Høeg in Chaloner, p. 623.
1980 *Barinophyton citrulliforme* Arnold – Allen, p. 259.
1980 *Barinophyton citrulliforme* Arnold – Brauer, pp. 1186–1206.
1980 *Barinophyton citrulliforme* Arnold – Gensel, p. 259.
1983 *Barinophyton citrulliforme* (Arnold) Brauer – Taylor & Brauer, pp. 3–15.
1984 *Barinophyton citrulliforme* (Arnold) Brauer – Gensel & Andrews, pp. 175–176.
1995 *Barinophyton citrulliforme* (Arnold) Brauer – Balme, p. 99.

Stratigraphy and geography of the holotype: Upper Devonian of Maine, USA.
***In situ* spores** (modified from Brauer 1980, pp. 1189–1204 and Taylor & Brauer, p. 3-15): Trilete circular microspores; size range 33–48.5 μm (Brauer 1980) and 30–50 μm. Rays of the trilete mark a half to three-quarters of the radius. Curvaturae developed. Laevigate sculpture. Trilete circular to oval megaspores; size range 700–900 μm. Rays of the trilete mark simple a third of the radius. Laevigate sculpture, surface usually folded.
Remark: *In situ* microspores might be of the *Retusotriletes* type and *in situ* megaspores are of the *Calamospora* type. Specimens are preserved as petrifactions.
Reference: Brauer (1980), Taylor & Brauer (1983).

Species: *Barinophyton richardsonii* (Dawson) White 1905
1871 *Lepidostrobus richardsonii* Dawson, pp. 165–170.
1905 *Barinophyton richardsonii* Dawson – White, pp. 51–58.
1965 *Barinophyton richardsonii* Dawson – Pettitt, pp. 85–89.
1970 *Barinophyton richardsonii* Dawson – Pettitt, pp. 405–407.
1980 *Barinophyton richardsonii* Dawson – Allen, p. 259.
1980 *Barinophyton richardsonii* Dawson – Gensel, pp. 85–89.
1983 *Barinophyton richardsonii* Dawson – Taylor & Brauer, pp. 108–110.
1987 *Barinophyton richardsonii* Dawson – Meyen, pp. 85–89.
1995 *Barinophyton richardsonii* Dawson – Balme, p. 99.

Stratigraphy and geography of the holotype: Late Devonian, USA.
***In situ* spores** (modified from Balme 1995, p. 99): Trilete circular cavate microspores; size range 48–62 μm. Exine laevigate. Trilete subcircular to circular megaspores; size range 220–250 μm. Exine laevigate. Taylor & Brauer (1983) studied TEM of megaspores and mentioned alveolate character of sporoderm.

Remark: *In situ* microspores are of the *Diaphanospora* type, megaspores can be *Retusotriletes*/*Enigmophyton* type. Specimens are preserved as adpressions.
Reference: Taylor & Brauer (1983), Balme (1995).

Species: *Barinophyton* cf. *obscurum* (Dun) White 1905
1898 *Pecopteris* (?) *oscura* Dun, pp. 117–121.
1905 *Barinophyton oscurum* White, pp. 35–84.
1980 *Barinophyton* cf. *obscurum* Brauer – Brauer, p. 351.

Stratigraphy and geography of the holotype: Late Devonian, USA.
***In situ* spores** (modified from Brauer 1980, p. 351): Trilete circular to subcircular microspores; size range 47–65 μm. Laevigate exine. Rays of the trilete mark a half of the radius. Labrum sometimes developed. Trilete circular to subcircular megaspores; size range 480–600 μm. Laevigate exine with number of secondary folds.
Remark: *In situ* micro– and megaspores are of the *Calamospora* type. Specimens are preserved as adpressions.
Reference: Brauer (1980).

Genus: *Protobarinophyton* Ananiev 1955
Type species: *Protobarinophyton obrutchevii* Ananiev 1955

Species: *Protobarinophyton pennsylvanicum* Brauer 1980

Stratigraphy and geography of the holotype: Late Devonian, USA.
***In situ* spores** (modified from Brauer 1980, pp. 352, 356): Trilete circular to subcircular microspores; size range 30–42.5 μm. Rays of the trilete mark a half to two-thirds of the radius. Laevigate exine, sometimes folded. Trilete circular megaspores; size range 410–560 μm. Rays of the trilete mark about a third of the radius. Laevigate exine, often folded.
Remark: *In situ* micro– and megaspores are of the *Calamospora* type. Specimens are preserved as adpressions.
Reference: Brauer (1980).

Genus: *Krithodeophyton* Edwards 1968
Type species: *Krithodeophyton croftii* Edwards 1968

Species: *Krithodeophyton croftii* Edwards 1968

Stratigraphy and geography of the holotype: Early Devonian, UK.
***In situ* spores** (modified from Edwards 1968, pp. 684, 688, 689): Trilete circular to subcircular microspores; size range 55 (58) 68 μm. Rays of the trilete mark almost the whole radius. Microconate to microspinate sculpture except for contact area where it is strongly reduced. Sculpture elements usually less than 1μm high, exceptionally up to 3 μm. Tips of some sculpture elements truncate.
Remark: *In situ* micro– and megaspores are of the *Apiculiretusispora brandtii* type. Specimens are preserved as adpressions.
Reference: Edwards (1968).

Genus: *Omniastrobus* Bonacorsi, Gensel, Hueber et Leslie 2020
Type species: *Omniastrobus dawsonii* Bonacorsi, Gensel, Hueber et Leslie 2020

Species: *Omniastrobus dawsonii* Bonacorsi, Gensel, Hueber et Leslie 2020

Stratigraphy and geography of the holotype: Emsian of Canada.
***In situ* spores** (modified from Bonacorsi *et al.* 2020, pp. 199–205): Trilete circular to subcircular spores; size range 65 (156) 280 μm, but it is possible to recognise two size peaks; smaller spores are 70-150 μm and larger 200-280 μm. Microgranulate to granulate sculpture, rays of the trilete mark about a third of the radius, sometimes with dark contact area.
Remark: Bonacorsi *et al.* (2020) supposed that all the spores have the same degree of maturity, i.e., it is not possible to interpret their different diameters by stages of maturity. It means that their different biological function, i.e., micro- and megaspores is probable. Both sets of spores are of the *Apiculiretusispora* type.
Reference: Bonacorsi *et al.* (2020).

Spores of barinophytes

Barinophytes are palynologically different from all above-mentioned early land plants because they produced micro- and megaspores in the same sporangum, that is significant evolutionary feature. Probably the first heterosporangial plant is *Omniastrobus* from Emsian of Canada. *Omniastrobus* and some other barinophytalean genera including *Protobarinophyton* and *Krithodeophyton* represent probably early stage of heterospory when male and female spores are morphologically identical (compare to the same spore genus) and differ in diameter and biological function. A little bit later stage when micro- and megaspores are morphologically different and have different diameter is reported from two species of *Barinophyton*.

Incertae sedis

Genus: *Aglaophyton* Edwards 1986
Type species: *Aglaophyton major* (Kidston et Lang) Edwards 1986

Species: *Aglaophyton major* (Kidston et Lang) Edwards 1986
1917 *Rhynia gwynne-vaughanii* Kidston et Lang, p. 780.
1920 *Rhynia major* Kidston et Lang, pp. 603–627.
1931 *Rhynia major* Kidston et Lang – Seward, pp. 127, 130.
1940 *Rhynia major* Kidston et Lang – Walton, pp. 29–31.
1947 *Rhynia major* Kidston et Lang – Andrews, p. 98.
1956 *Rhynia major* Kidston et Lang – Mägdefrau, pp. 78–83.
1957 *Rhynia major* Kidston et Lang – Lyon, p. 1219.
1961 *Rhynia major* Kidston et Lang – Andrews, p. 222.
1962 *Rhynia major* Kidston et Lang – Zimmermann, p. 354.
1962 *Rhynia major* Kidston et Lang – Potonié, p. 38.
1967 *Rhynia major* Kidston et Lang – Høeg in Boureau, pp. 205–208.
1967 *Rhynia major* Kidston et Lang – Potonié, p. 25.
1973b *Rhynia major* Kidston et Lang – Bhutta, pp. 47–55.
1974 *Rhynia major* Kidston et Lang – Edwards & Richardson, pp. 315–320.
1978 *Rhynia major* Kidston et Lang – Remy, pp. 23–30.
1980 *Rhynia major* Kidston et Lang – Lemoigne & Zdebska, pp. 3–8.
1980 *Rhynia major* Kidston et Lang – Allen, pp. 255–256.
1980 *Rhynia major* Kidston et Lang – Gensel, pp. 104–105.
1986 *Aglaophyton major* Kidston et Lang – Edwards, pp. 173–204.
1995 *Aglaophyton major* Kidston et Lang – Balme, p. 90.
1996 *Aglaophyton major* Kidston et Lang – Remy & Hass, pp. 175–193.
2003 *Aglaophyton major* Kidston et Lang – Edwards, p. 398.
2006 *Aglaophyton major* Kidston et Lang – Wellman *et al.*, pp. 229–250.
2014 *Aglaophyton major* Kidston et Lang – Willis & McElwain, p. 73.

Stratigraphy and geography of the holotype: Siegenian/Emsian of Rhynie Chert Bed, UK
***In situ* spores** (modified from Wellman *et al.* 2006, pp. 229–250): Trilete circular retusoid spores, curvaturae perfectae developed; size range 57–65 μm (Kidston & Lang 1917), 70 μm (Kidston & Lang 1920), 53 (64) 127 μm (Bhutta 1973b) 63 (77) 85 μm (Bhutta 1973a), 65 μm (Chaloner in Boureau 1967), 64 (72) 85 μm (Wellman *et al.* 2006). Rays of trilete mark a half to three-quarters of the radius. Exine of both surfaces laevigate. Exospore (1–1.5 μm thick) sometimes corroded and it may seem that it is apiculate to even reticulate.
Remark: Several authors studied *in situ* as well as dispersed spores from *Rhynia* plants and *Rhynia* cherts (details see e. g., Wellman *et al.* 2006) including the process of germinating. Wellman *et al.* (2006) mentioned 400,000 spores in one sporangium. Bhutta (1973b) assigned these *in situ* spores to the *Geminospora tuberculata* type and *Crassispora* cf. *balteata*, Allen (1980) determined them as ?*Ambitisporites* sp., Balme (1995) classified them as *Apiculiretusispora–Aneurospora* type and Wellman *et al.* (2006) as *Retusotriletes* CW-A and B. Edwards (1986) proposed a new combination and erected a new genus and species *Aglaophyton major* for former *Rhynia major* and assigned it among non-vascular plants. Specimens are preserved as petrifactions.
References: Edwards (1986) and Wellman *et al.* (2006).

Genus: *Bracteophyton* Wang et Hao 2004
Type species: *Bracteophyton variatum* Wang et Hao 2004

Species: *Bracteophyton variatum* Wang et Hao 2004

***In situ* spores** (modified from Wang & Hao 2004, p. 339): Trilete triangular to subtriangular microspores, about 30 μm in diameter. Exine laevigate, contact area sometimes developed. Ray soft he trilete mark two-thirds to three-fourths of the radius.
Remark: *In situ* spores are of the *Retusotriletes* type. Specimens have terminal strobili, helically arranged leaves and adaxial sporangia. Some features might be similar to lycopsids, zosterophylls and barinophytes (Wang & Hao 2004). Specimens are preserved as compressions.
Reference: Wang & Hao (2004).

Genus: *Chauleria* Andrews *et al.*, 1974
Type species: *Chauleria cirrosa* Andrews *et al.*, 1974

Species: *Chauleria cirrosa* Andrews et al., 1974
1974 *Chauleria cirrosa* Andrews et al., pp. 378–408.
1980 *Chauleria cirrosa* Andrews et al. – Allen, p. 261.
1980 *Chauleria cirrosa* Andrews et al. – Gensel, p. 125.
1984 *Chauleria cirrosa* Andrews et al. – Gensel & Andrews, p. 125.
1995 *Chauleria cirrosa* Andrews et al. – Balme, p. 187.
1997 *Chauleria cirrosa* Andrews et al. – Niklas, pp. 192–194.

Stratiraphy and geography of the holotype: Middle Devonian of Canada.
***In situ* spores** (modified from Andrews *et al.* 1974, pp. 394–400): Trilete circular to subtriangular spores. Size range 30–48 μm and 60–156 μm. Large spores with circular to subcircular amb. Exine 1–6 μm thick. Contact area developed, laevigate to finely microgranulate sculpture. Distal sculpture microgranulate, granulate to microbaculate. Rays of the trilete mark a half to two-thirds of the radius, straight or sinuous, simple or with lips. Small spores with triangular to subtriangular amb. Exine 1–2 μm thick, usually thinner proximally. Proximal sculpture laevigate, contact area developed. delimited by folds or a thickening close to the equator. Distal sculpture baculate, baculae sometimes with biform coni. Sculpture elements 2–3 μm wide and 1–3 μm high. Rays of the trilete mark simple, with lips or folds extend three-quarters to seven-eighth of the radius.
Remark: Sometimes large spores occur among small spores and *vice versa*. Andrews *et al.* (1974) interpreted large spores as megaspores and small forms as microspores and *Chauleria* represents important evidence of apparently early stage in the evolution of heterospory. *In situ* small spores are of the *Apiculiretusispora* type and large spores belong to the miospore species *Cyclogranisporites flexuosus* Playford. Specimens are preserved as compressions.
Reference: Andrews *et al.* (1974).

Genus: *Eocladoxylon* (Koidzumi) Berry et Wang 2006
Type species: *Eocladoxylon minutum* (Halle) Koidzumi 1943

Species: *Eocladoxylon minutum* (Halle) Koidzumi 1943
1936 *Protopteridium minutum* Halle, pp. 16–22.
1943 *Eocladoxylon minutum* Halle – Koidzumi, p. 64.
1966 *Cathaiopteridium minutum* Halle – Hsü, pp. 56–62.
1966 *Cathaiopteridium minutum* Halle – Obrhel, pp. 442.
1973 *Cathaiopteridium minutum* Halle – McGregor, pp. 126–128.
1973 *Cathaiopteridium minutum* Halle – Gensel, pp. 140–146.
1974 *Protopteridium minutum* Halle – Gu & Zhi, p. 16.
1980 *Cathaiopteridium minutum* Halle – Gensel, p. 123.
1980 *Cathaiopteridium minutum* Halle – Allen, p. 264.
1987 *Pseudosporochnus nodosus* Leclercq et Banks – Schweitzer & Cai, fig. 17a.
1995 *Cathaiopteridium minutum* Halle – Balme, p. 187.
2006 *Eocladoxylon minutum* Halle – Berry & Wang, pp. 551–566.

Stratigraphy and geography of the holotype: Lower and Middle Devonian of Yunnan, China.
***In situ* spores** (modified from Halle 1936, pp. 7–15 and Balme 1995, p. 187): Trilete subcircular, pseudosaccate spores. Size range 30–60 μm. Central body two-thirds of the radius. Microapiculate to baculate sculpture. Rays of the trilete mark equal to the central body.
Remark: *In situ* spores are of the *Rhabdosporites* type. Specimens are preserved as compressions.
Reference: Halle (1936), Balme (1995).

Genus: *Oocampsa* Andrews et al. 1975
Type species: *Oocampsa catheta* Andrews et al. 1975

Species: *Oocampsa catheta* Andrews et al. 1975
1975 *Oocampsa catheta* Andrews et al., pp. 1719–1728.
1980 *Oocampsa catheta* Andrews et al. – Gensel, p. 123.
1980 *Oocampsa catheta* Andrews et al. – Allen, p. 266.
1984 *Oocampsa catheta* Andrews et al. – Gensel & Andrews, p. 186.
1987 *Oocampsa catheta* Andrews et al. – Meyen, p. 59.
1995 *Oocampsa catheta* Andrews et al. – Balme, pp. 187–188.
2004 *Oocampsa catheta* Andrews et al. – Wellman & Gensel, pp. 269–295.

Stratigraphy and geography of the holotype: Middle Devonian of Canada.
***In situ* spores** (modified from Andrews *et al.* 1975, pp. 1723–1726 and Wellman & Gensel 2004, pp. 271–293): Trilete triangular to subtriangular spores; size range 96–120 μm. Distal sculpture microconate, conate with biform apexes, proximal sculpture laevigate. Pseudozona and labrum developed. Rays of the trilete mark equal to the radius. Zona about a half of the spores. Exine is bilayered and partly camerate.
Remark: *In situ* spores are of the *Samarisporites* type. Wellman & Gensel (2004) suggested that dispersed miospore species *Grandispora douglastownense* McGregor and *G. macrotuberculata* McGregor can be derived from microspores of *Oocampsa catheta*. TEM of these spores was published by Wellman & Gensel (2004) who mentioned that they do not conform closely to any plant group, although they show most in common with the spores of the progymnosperms. Specimens are preserved as adpressions.
Reference: Andrews *et al.* (1975), Wellman & Gensel (2004).

Genus: *Resilitheca* Edwards, Fannning, Davies et Axe 1995
Type species: *Resilitheca salopensis* Edwards, Fannning, Davies et Axe 1995

Species: *Resilitheca salopensis* Edwards, Fannning, Davies et Axe 1995

Stratigraphy and geography of the holotype: Gedinian-Lochkovian of UK.
***In situ* spores** (modified from Edwards, Fannning, Davies & Axe 1995, pp. 237–234): Trilete circular to subtriangular spores; size range 22 (32) 39 μm. Curvaturae developed. Rays of the trilete mark a half of the radius or to the margin of curvaturae. Proximal exine up to 2.5 μm thick, distal exine about 0.5 μm thick. Distal sculpture laevigate to very finely microgranulate, microverrucate. Sculpture of contact area densely rugulate. Labrum up to 2 μm sometimes developed. The sculpture except for contact area microgranulate and microverrucate, densely than on the distal surface.
Remark: *In situ* spores are of the *Apiculiretusispora* type. Edwards, Fannning, Davies & Axe (1995) described TEM of *in situ* spores. Specimens are preserved as adpressions.
Reference: Edwards, Fannning, Davies & Axe (1995).

Genus: *Sporathylacium* Edwards, Axe et Mendes 2008
Type species: *Sporathylacium salopense* Edwards, Axe et Mendes 2008

Species: *Sporathylacium salopense* Edwards, Axe et Mendes 2008

Stratigraphy and geography of the holotype: Lochkovian of UK.
***In situ* spores** (modified from Edwards, Axe & Mendes 2008, pp. 301–306): Trilete circular spores; size range 23 (27) 30 μm. Equatorial crassitude/cingulum 1.6 μm thick. Rays of the trilete mark reach to the margin of contact area. Labrum up to 2 μm thick. Proximal sculpture finely microgranulate, distal exine with large granulae, verrucae often connected resemble very irregular rugulate pattern.
Remark: Edwards, Axe & Mendes (2008) described TEM of *in situ* spores but did not compare them with any dispersed spore taxon. Specimens are preserved as compressions.
Reference: Edwards, Axe & Mendes (2008).

Genus: *Tichavekia* Pšenička, Sakala et Kraft 2018 in Kraft *et al.* 2018
Type species: *Tichavekia grandis* Pšenička, Sakala et Kraft 2018 in Kraft *et al.* 2018

Species: *Tichavekia grandis* Pšenička, Sakala et Kraft 2018 in Kraft *et al.* 2018

2018 *Tichavekia grandis* Pšenička, Sakala et Kraft in Kraft *et al.*, 2018, pp. 144–150.
2022 *Tichavekia grandis* Pšenička, Sakala et Kraft – Uhlířová *et al.* pp. 3–9.
2024 *Tichavekia grandis* Pšenička, Sakala et Kraft – Bek *et al.* p. 302.

Stratigraphy and geography of the holotype: Přídolí of the Czech Republic.
***In situ* spores** (modified from Bek *et al.* 2024, p. 302): Trilete subcircular spores; size range 27 (28.3) 32 x 17 (19) 21 μm in diameter. Equatorial crassitude up to 2 μm wide. Rays of the trilete mark extend to a half of the radius, but are not always clearly visible. The sculpture of proximal surface varies from microspinate, to microgranulate, to microverrucate, to vermiculate, to rugulate. Microspinae are located close to the proximal pole and vermiculae and microgranulae are close to the margin
Remark: Bek *et al.* (2024) described SEM of *in situ* spores but did not compare them with any dispersed spore taxon and mentioned that spores can belong to some new genus. Specimens are preserved as compressions.
Reference: Bek *et al.* (2024).

CONCLUSION

Sometimes it is possible to recognise palynological lineages of some Paleozoic plants. In other words, there are groups of plants (taxonomic groups) comprising one or more genera that produce the same or very similar spores. This principle can be helpful for the precise classification of plants, especially if their preservation/fossilisation is imperfect (e.g., adpressions). A similar approach to that used for early land plants was published by Bek & Votočková Frojdová (2025).

Almost all of the main plant groups of early land plants are more or less palynologically heterogeneous. Almost all rhyniophytes produced crassitate spores; however, only Rhynia yielded non-crassitate spores, which may suggest its special position among rhyniophytes. Spores of hornophytes and zosterophylls exhibit a similar character, i.e. crassitate and non-crassitate taxa. Trimerophytalean spores are homogeneous as they are all non-crassitate spores of the *Apiculiretusispora* (Plate I, figs A, O) and *Calamospora* types (Plate I, figs P, Q). Barinophytes are evolutionarily distinct plants comprising heterosporous taxa. The first heterosporous plants produced spores with the same morphology, and they can all be compared to the same dispersed spore taxon; that is to say, they differ only in diameter and biological function. Some later barinophytes represent a more advanced stage of heterospory, in which the micro- and megaspores differ in morphology, as well as in diameter and biological function, and can be compared to different dispersed spore genera.

Acknowledgement

The research was supported by the Grant Agency of Czech Republic (21-10799S), and the research plan of the Institute of Geology of the Czech Academy of Sciences, v.v.i. (RVO67985831).

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