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Further observations on the spores of the Rhynie chert plant *Horneophyton lignieri* (Kidston & Lang) Barghoorn & Darrah, 1938: Implications for palaeodiversity studies

B. Cascales-Miñana^{a,*}, T. Servais^a, E. Capel^b, P. Steemans^c

^a CNRS, Univ. Lille, UMR 8198 - Evo-Eco-Paleo, F-59000 Lille, France

^b Univ. Lille, CNRS, UMR 8198 - Evo-Eco-Paleo, F-59000 Lille, France

^c EDDy Lab/Palaeobotany and Palaeopalynology, Univ. Liège, 4000 Liège, Belgium

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ABSTRACT

The Rhynie chert (Aberdeenshire, Scotland, UK) plant *Horneophyton lignieri* is likely one of the most studied elements of Lower Devonian floras considering both macro and microremains. Intriguingly, while larger plant fragments are exceptionally fossilized, *in situ* spores are not necessarily well-preserved in the chert: they are dark brown and intensively torn overall. However, spore masses are often dominated by single spores, which can be taxonomically attributed. Mainly, *Horneophyton* spores have been described as belonging to *Apiculiretusispora* type and *Emphanisporites* cf. *decoratus*, this last one being currently accepted in general. Here, we document new *Horneophyton* spore morphologies, that are sometimes quite different. Such morphologies include, but are not restricted to, *Ambitisporites*, *Dibolisporites* or *Retusotriletes*. All these observed spore morphotypes belong to the same palaeobiological entity, as they have been found in the same parent plant. These findings show that the sporangia of a same plant species may deliver diverse taxa of coeval isolated spores. But most importantly, if these spores are found in sediments, they would most probably be identified as different dispersed miospore taxa. This highlights that caution is needed when comparing plant diversity with the dispersed spore fossil record. Moreover, we confirm the presence of *Emphanisporites decoratus* inside most of the sporangia of *Horneophyton lignieri*, and its high morphological variability. We further discuss the role of the different states of maturation and preservation, as well as taphonomy-induced features, on observed spore diversity.

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1. Introduction

The exceptionally preserved biota of the Early Devonian Rhynie chert (Aberdeenshire, Scotland, UK) provides a unique window to study the early evolution of terrestrial ecosystems (e.g., Trewin, 1996, 2004; Taylor et al., 2005; Edwards et al., 2017; Strullu-Derrien et al., 2019; Strullu-Derrien et al., 2021). The Rhynie chert represents a silicified preserved ecosystem initially deposited as sinters in a hot-spring environment (Rice et al., 2002; Channing and Edwards, 2004, 2009; Channing, 2017). This preserved ecosystem captures outstanding details of fossil plants preserved therein (see Kidston and Lang, 1917, 1920a, 1920b, 1921; Lyon, 1964; Lyon and Edwards, 1991; Powell et al., 2000a, for original descriptions). Such details include anatomical information on both fertile and vegetative parts (Edwards, 2004; Kerp et al., 2013; Kerp, 2017), as well as different phase of the life cycle,

like gametophytes (Remy and Remy, 1980a, 1980b; Remy and Hass, 1991a, 1991b, 1996; Remy et al., 1993; Gerrienne et al., 2006; Kerp et al., 2004) and *in situ* spores (Wellman, 2004, 2006, 2017; Wellman et al., 2004, 2006). In addition, copious evidence of plant-fungal interactions has been described (Krings et al., 2016, 2017, 2021). As a result, the Rhynie chert flora (e.g., Powell et al., 2000b; Edwards, 2004) is central to our knowledge of basal steps of land plant evolution and terrestrial palaeoenvironments (Crane et al., 2004; Crepet and Niklas, 2018, 2019; Krings and Kerp, 2019; Niklas and Crepet, 2020), with *Horneophyton lignieri* (Kidston & Lang) Barghoorn and Darrah, 1938 being especially relevant. Indeed, *H. lignieri* and related plants (i.e., Horneophytosida), formerly considered as protracheophytes (i.e., an intermediate lineage between bryophytes and vascular polysporangiophytes (see e.g., Kenrick and Crane, 1997; Gerrienne and Genez, 2011; Cascales-Miñana and Gerrienne, 2017), have been recently resolved as a sister clade to eutracheophytes (i.e., true vascular plants), so they could be considered as evolutionary precursors of all extant vascular plant biodiversity (Cascales-Miñana et al., 2019a).

* Corresponding author.

E-mail address: borja.cascales-minana@univ-lille.fr (B. Cascales-Miñana).

Since its discovery, *Horneophyton lignieri*, first described as *Hornea lignieri*, (Kidston and Lang, 1920a; Barghoorn and Darrah, 1938), has focused the attention of many researchers during the last century (see below). In fact, *H. lignieri* is likely one of the best studied early land plants. Morphologically, *Horneophyton* is a leafless plant about 20 cm high, characterized by the presence of a basal tuberous rhizome, aerial dichotomous branching, and terminal columellate sporangia (see Bhutta, 1972, fig. 1; Edwards, 2004, figs. 1d, d'; Kerp, 2017, fig. 1g, for details), from which an intriguing spore diversity can be observed. Kidston and Lang (1920a, pl. X, 71–72) already illustrated many specimens of spores inside *H. lignieri* sporangia, but without a detailed description, although they noted spores often appear in tetrads and some of them being isolated. Some years later, Bhutta (1973a) tried to compare *in situ* spores of *H. lignieri* to coeval dispersed taxa. He concluded that *Horneophyton* spores are not attributable to any single genus, but they can be referred as belonging to *Apiculiretusispora* Streele, 1967 and *Emphanisporites* McGregor, 1961. This author also added that observed *in situ* spores mainly resemble *Apiculiretusispora plicata* (Allen, 1965) Streele, 1967 (Bhutta, 1973a, figs. 1–2), and to a lesser extent *Emphanisporites decoratus* Allen, 1965 (Bhutta, 1973a, figs. 3–4).

Further evidence of *H. lignieri* sporangia and *in situ* spores was documented by Eggert (1974, figs. 1–7, 18–21). This author made a key observation, by indicating that sporangia contain either tetrad or post-tetrad stages, showing several steps of spore development. Eggert also noted that *H. lignieri* tetrads can be found in tetrahedral or isobilateral (decussate) forms. Moreover, he commented that the post-tetrad stages closely compare to *Retusotriletes* (Naumova) Richardson, 1969 and *Apiculiretusispora*. Afterwards, Allen (1980) increased the number of observed morphologies from *Horneophyton* sporangia by commenting that some specimens seem to have a crassitude, by tentatively assigning them to *Aneurospora* Streele emend. Richardson et al., 1982. Moreover, Gensel (1980) re-examined Kidston and Lang's (1920a) original preparations and suggested that *H. lignieri* spores are generally comparable to *Apiculiretusispora*, although some specimens resemble the dispersed spore genus *Emphanisporites*. The exquisite work performed by Wellman et al. (2004) needs a special mention. These authors undertook a highly detailed study about the observed morphological variability within the sporangia of *H. lignieri*. Wellman et al. (2004) highlighted that mature *Horneophyton* spores are identical to *Emphanisporites decoratus*, which is also a common element of dispersed spore assemblages from the Rhynie chert stratigraphical sequence (see e.g., Wellman et al., 2004, fig. 4 for details).

In the present work, we aim to provide new insights into the spore diversity of *H. lignieri*. We attempt to revise the spore morphologies within *Horneophyton* sporangia and compare them to coeval dispersed taxa. From this, we intend to obtain first-hand information to discuss the implications of using palynological data in plant palaeodiversity studies.

2. Materials and methods

Studied evidence comes from the petrographic thin sections from the historical W. Hemingway collection of the Natural History Museum of Lille (NHML). These slides belong to Kidston and Lang's (1917, 1920a, 1920b, 1921) original collection of the Rhynie chert. From this, we examined the slides 357–61 (MGLame-17), 359–2 (MGLame-18), 359–5 (MGLame-19), 359–6 (MGLame-20), 379–29 (MGLame-21), 379–31 (MGLame-22), 379–34 (MGLame-23), 439–63 (MGLame-24) and 439–65 (MGLame-25), which provide comprehensive evidence of *H. lignieri* (Cascales-Miñana et al., 2019a, Table 1). Special attention was put on samples MGLame-23–24–25 from which thirty-five sporangia containing numerous *in situ* preserved spores were studied. Details of examined material are shown in Table 1. Photographs were taken using a Nikon Df camera coupled to a Zeiss Stemi 2000–C stereomicroscope and with a Zeiss Axioskop camera coupled a Zeiss AxioCam microscope, from which the digital x/y coordinates were used to locate the

palynomorphs on the slides. Because of the thickness of the slides it has been necessary to work with a long focal objective, of no more than 40x of magnification, making the observations or photographs sometimes difficult. Captured images are shown arranged by slide (see Plates I–V for details).

3. Results

All observed spores are *in situ*, still confined inside of 35 different sporangia of *H. lignieri* preserved in chert slices (Table 1). Most of the spores are poorly preserved. This aspect has been widely detailed by many authors (Bhutta, 1973a, 1973b; Eggert, 1974; Wellman, 2004, 2017; Wellman et al., 2004). Usually, spores are dark brown to dark, strongly “corroded” and with one of their faces torn. The distal or proximal face is indifferently torn. We did not observe that one of the two faces is preferentially torn (but we did no statistic measures), contrary to Bhutta (1973a) who considered that the proximal face was mainly destroyed, suggesting that this face was probably thinner than the distal one and therefore less durable. This observation should not be neglected because it artificially affects the observation in giving the impression that spores may be patinate. The preservation of the spores is somewhat interesting when we compare them with the perfect taphonomical quality of the plant tissues. Authors cited above have put different hypothesis forward. Overall, spores are very abundant and from the huge mass of specimens, it has been possible to select well-preserved ones. Results presented here are based on those specimens only, neglecting the unreliable morphologic characteristics of the poorly preserved spores.

Different kind of spores (described below as morphotypes, i.e., as taxa illustrating an intraspecific morphological variation) have been observed (Plates I–V). Morphotypes vary by their diameter size (albeit relatively constant), their shape (usually circular), their ornaments (mainly coni and spines), their exine thickness (thin or thick), the morphology of the trilete mark (mainly straight, with or without labra), the characteristic of the contact areas (ornamented or without ornamentation), and by their organization (in tetrads or isolated). They are (alphabetically) as follows:

Morphotype 1: ***Ambitisporites* sp.**

Plate IV. 4.

Description: Laevigate trilete spore with a circular shape. A cingulum of 2–4 µm width is present at the equator.

Diameter: 42–45 µm.

Comments: This kind of spore may easily be related to *Ambitisporites*, if this one may be considered as mature.

Morphotype 2: ***Apiculiretusispora* cf. *plicata*** (Allen, 1965) Streele, 1967

Plate I. 3, 6; Plate II. 4–7; Plate III. 6, 7, 12; Plate V. 5

Description: Trilete spores with a circular to subtriangular shape. The trilete mark is straight, thin, and reaching the equator. The proximal face is laevigate and bordered at the equator by thin curvaturae. The exine is 1–2 µm thick all around the spore in lateral view. The equator and the distal face are ornamented by small sharp coni/spines of 1 µm width at the base, up to 1–2 µm high and 0 (some ornaments are interconnected) to 1.5 µm apart. Several specimens are still preserved in tetrads. One specimen shows a dyad configuration. Possibly this last one is the consequence of a torn tetrad.

Diameter: 36–58 µm.

Comments: The difference between *Apiculiretusispora* and *Anapiculiretusispora* is mainly a question of ornament size, below or above 1 µm in height (Streele, 1967). We think that this limit between both genera is too artificial and we prefer the genus *Apiculiretusispora* that is more widely used in literature. Interestingly, spores isolated from a single sporangium had been referred to both *Apiculiretusispora* and *Emphanisporites* (Bhutta, 1973a, 1973b).

Comparison: These specimens are remarkably close to *Dibolisporites* sp. but they have a uniform ornamentation. They may represent

Table 1
List of examined sporangia and observed spore diversity from *Horneophyton lignieri*.

Slide code	Sporangium position (x/y)	Spore taxa	Brief description
MGLame-23	592/772	<i>Emphanisporites rotatus</i> , <i>Dibolisporites</i> sp. and Genus A sp. A	Spores are badly preserved. No evidence of <i>Emphanisporites decoratus</i>
MGLame-23	651/313	Undetermined spores	Spores are very badly preserved
MGLame-23	803/1355	<i>Ambitisporites</i> sp., <i>Apiculiretusispora</i> cf. <i>plicata</i> or <i>Dibolisporites</i> sp. and <i>Retusotriletes</i> sp.	Spores are badly preserved. Most of the spores are ornamented by coni. The <i>Retusotriletes</i> has a gaping trilete mark. No evidence of <i>Emphanisporites</i>
MGLame-23	883/1054	cf. <i>Cymbosporites</i> sp. and <i>Dibolisporites</i> sp.	The preservation and the optic observation quality are not good.
MGLame-23	856/1304	<i>Apiculiretusispora</i> cf. <i>plicata</i>	Spores are badly preserved. Most of them are tetrads (isolated specimens are mainly concentrated in the lower part of the section in the sporangia). Most of them show a small ornamentation
MGLame-23	888/1370	? <i>Apiculiretusispora</i> cf. <i>plicata</i>	Mainly spores badly preserved with thin hair-like ornaments
MGLame-23	949/1352	? <i>Apiculiretusispora</i> cf. <i>plicata</i>	Mainly spores badly preserved with thin hair-like ornaments
MGLame-23	967/1139	? <i>Apiculiretusispora</i> cf. <i>plicata</i> and cf. <i>Cymbosporites</i> sp.	Mainly spores badly preserved with thin hair-like ornaments
MGLame-23	1118/1421	? <i>Apiculiretusispora</i> cf. <i>plicata</i>	Mainly spores badly preserved with thin hair-like ornaments
MGLame-23	1170/1300	? <i>Apiculiretusispora</i> cf. <i>plicata</i>	Mainly spores badly preserved with thin hair-like ornaments
MGLame-23	1127/1081	<i>Ambitisporites</i> sp., <i>Dibolisporites</i> sp. and Genus A sp. A	Mainly spores with thin hair-like ornaments
MGLame-23	1224/758	? <i>Emphanisporites decoratus</i> and cf. <i>Cymbosporites</i> sp.	Most of the spores are similar to <i>Cymbosporites</i> . But possibly that some of them are to be related to <i>Emphanisporites</i>
MGLame-23	1220/1282	<i>Archaeozonotriletes chulus/nanus</i> and other undetermined spores	Mainly spores badly preserved and ornamented by spines
MGLame-23	1574/826	cf. <i>Cymbosporites</i> sp. and other undetermined spores	All spores are similar but some of them seem to be not patinate
MGLame-24	566/1299	Ornamented spores in tetrads and isolated. Taxa similar to <i>Apiculiretusispora</i> cf. <i>plicata</i> or <i>Dibolisporites</i> sp.	All specimens are similar. No prove of different species in the same sporangium
MGLame-24	538/1406	Ornamented spores in tetrads and isolated. Taxa similar to <i>Apiculiretusispora</i> cf. <i>plicata</i> or <i>Dibolisporites</i> sp.	Sporangium with very badly preserved spores
MGLame-24	973/1166	<i>Emphanisporites decoratus</i> with or without a gaping trilete mark. <i>Emphanisporites rotatus</i> could be present but the absence of ornamentation is questionable. Rare specimens of Genus B sp. A have been also observed.	Most of the specimens seem to belong to the genus <i>Emphanisporites</i> . All specimens do not show the same ornamentation (variable sizes). Some specimens could be laevigate. All specimens do not show the same thickness (from thin to thick exine). Some specimens show high labra. Some specimens have an open trilete mark
MGLame-24	1226/1047	<i>Apiculiretusispora</i> cf. <i>plicata</i>	All specimens belong most probably to the same taxa. There are a lot of tetrads and isolated forms
MGLame-24	1289/1610	<i>Emphanisporites decoratus</i>	The spores in the sporangium are very poorly preserved. The rare specimens with a preserved proximal face display radial muri. The presence of ornaments is visible on all the specimens. There is no evidence of other taxa in the sporangia
MGLame-24	1293/1537	<i>Emphanisporites decoratus</i> and <i>Emphanisporites rotatus</i>	Many spores are very badly preserved. All the identified specimens belong to <i>E. decoratus</i> with small intraspecific variations, except the presence of one specimen of <i>Emphanisporites rotatus</i>
MGLame-24	1294/1601	<i>Emphanisporites decoratus</i>	Many spores are very badly preserved. All the identified specimens belong to <i>E. decoratus</i> with small intraspecific variations
MGLame-24	1386/1495	Undetermined spores	Only badly preserved and unidentified tetrads
MGLame-24	1488/1360	<i>Apiculiretusispora</i> sp. and <i>Dibolisporites</i> sp.	Spores are badly preserved. There is no evidence of the presence of <i>Emphanisporites</i> .
MGLame-25	671/1579	Undetermined badly preserved spores of large sizes	All spores are similar but they are very large by comparison with spores from other sporangia. On the reverse, there is one tetrad of a normal size
MGLame-25	706/771	Undetermined spores	All spores are badly preserved and ornamented by spines
MGLame-25	942/1224	Strong <i>Emphanisporites decoratus</i> and specimens with a gaping trilete mark. Genus A sp. A, cf. <i>Cymbosporites</i> sp. and ?zonate trilete spore	Some specimens are clearly <i>Emphanisporites</i> some others are doubtful. The sporangium seems to contain several taxa
MGLame-25	917/1465	<i>Apiculiretusispora</i> cf. <i>plicata</i>	Spores are badly preserved. All specimens have a very small ornamentation
MGLame-25	919/463	<i>Cymbosporites raistrickiaeformis</i>	All spores are very similar. There are also some tetrads. It is really difficult to decide if there is a patina or not. One of the specimen observed in dispersed sediments would be probably described as patinate. Some specimens are clearly not patinate
MGLame-25	941/366	Undetermined spores	Only ornamented tetrads by small coni
MGLame-25	1040/1309	cf. <i>Cymbosporites</i> sp. and other undetermined spores	Badly preserved spores. Possibly presence of one <i>Emphanisporites</i>
MGLame-25	1092/1375	Undetermined spores	Badly preserved spores
MGLame-25	1071/1238	<i>Emphanisporites decoratus</i>	All specimens displaying the proximal face are ornamented by radial muri. The ornamentation is usually thin and small. All could be <i>E. decoratus</i>
MGLame-25	1168/1018	Undetermined spores	Very badly preserved specimens. They are all ornamented by spines. One specimen could show possible radial muri
MGLame-25	1217/654	Genus A sp. A	Except this specimen determined as Genus sp. A sp. A, all the other spores are too badly preserved but ornamented
MGLame-25	1290/636	cf. <i>Cymbosporites</i> sp., and other undetermined spores	Very badly preserved specimens

end members of a continuous morphological variation. Similar specimens have been observed by [Bhutta \(1973a\)](#) and determined as *Apiculiretusispora plicata*. However, *A. plicata*, observed in dispersed sediments, is slightly different by a more proximal curvaturae, the recurrent presence of a dark triangular area bordering the trilete mark and a less strong aspect. However, it is possible that the taphonomy

has played a role in the state of preservation and appearance of the specimens. For instance, the specimens illustrated in [Plate III, 6–7](#) could be considered as *A. plicata*.

Distribution: Specimens of *A. plicata* are cosmopolitan and well-known from the Lochkovian to Middle Devonian (e.g., [McGregor, 1973](#); [Stemans, 1989](#); [Breuer and Stemans, 2013](#)).

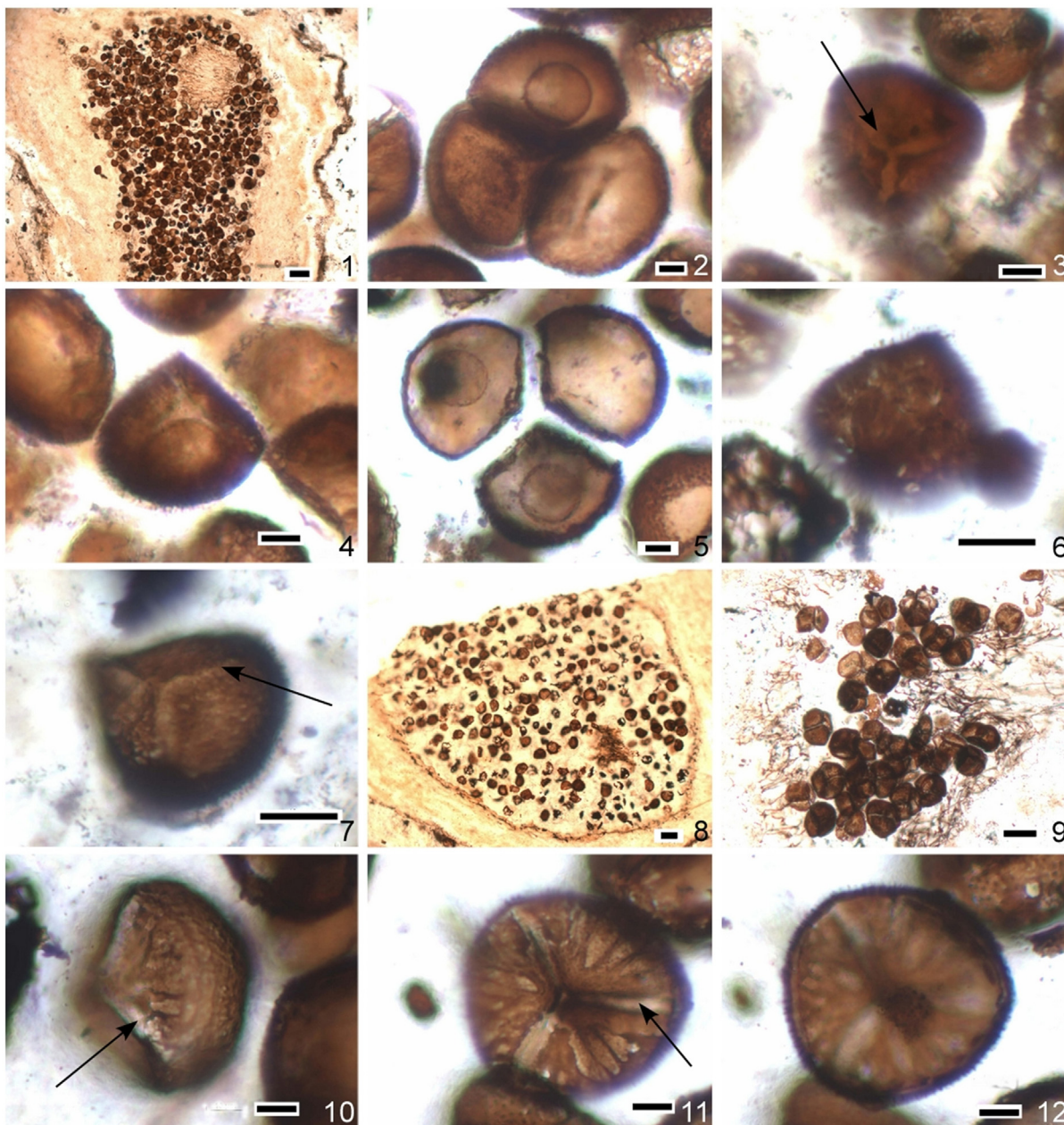


Plate I. Light microscope images of the observed morphological diversity from the *in situ* spores of *Horneophyton lignieri* (Part 1). 1. Longitudinal view of a sporangium showing *in situ* spores (555x/1305y). 2. Tetrad having lost one spore. The proximal face displays any kind of radial muri. Spores laevigate or finely ornamented (564x/1298y). 3. Finely ornamented spore with an open trilete mark (black arrow). The proximal face does not display any kind of radial muri. *Apiculiretusispora* cf. *plicata* (567x/1275y). 4. Spore ornamented by irregular thin spines. The trilete mark is open. cf. *Cymbosporites* sp. (572x/1277y). 5. Disrupted tetrad of slightly ornamented spores. The thickness of the exine is similar proximally and distally (576x/1307y). 6. Spore ornamented by thin spines with torn distal face. *Apiculiretusispora* cf. *plicata* (572x/1277y). 7. Spore ornamented by thin irregular spines. The trilete mark is prominent (black arrow). The aspect is like a patina, and it seems that it is not due to an artefact (535x/1418y). 8. Example of a sporangia with poorly preserved spores. Most of them are finely ornamented and some looks laevigate (834x/1224y). 9. Detail of spore mass inside sporangia (834x/1224y). 10. Lateral view of *Emphanisporites decoratus* with an open trilete mark (black arrow). The muri are clearly present on the proximal face. The distal face and equatorial area are ornamented by grana. Presence of curvaturae (980x/1170y). 11. Proximal view showing an open trilete mark and radial muri (black arrow). *Emphanisporites decoratus* (965x/1169y). 12. Equatorial view of the same specimen showing the ornamentation. *Emphanisporites decoratus* (960x/1181y). NHML slide MGLame-24. Scale bars = (1, 8) 50 μ m; (2–7, 9–12) = 10 μ m.

Morphotype 3: *Cymbosporites raistrickiaeformis* (Schultz, 1968) Steemans, 1981

Plate V. 1, 2, 4

Description: trilete spore with a subtriangular to subcircular shape. Trilete mark thin, difficult to observe, reaching the equator. The proximal face seems to be laevigate. The distal face and the equatorial area ornamented by densely packed thin bacula. Specimen's ornaments appear to be irregular in shape, with bifurcated and/or expanded tips. They are less than 1 μ m at their base and less than 2 μ m at their top.

Diameter: 42–45 μ m.

Comments: This taxon has been described in the literature of dispersed spores showing ornaments with an expanded tip. Most of them are left in open nomenclature. The bacula observed herein seem to be also present on other specimens but their ornaments are so thin that it is difficult to decide, the aspect may be due to the taphonomy.

Morphotype 4: cf. *Cymbosporites* sp.

Plate I. 4, 7; Plate IV. 3, 5

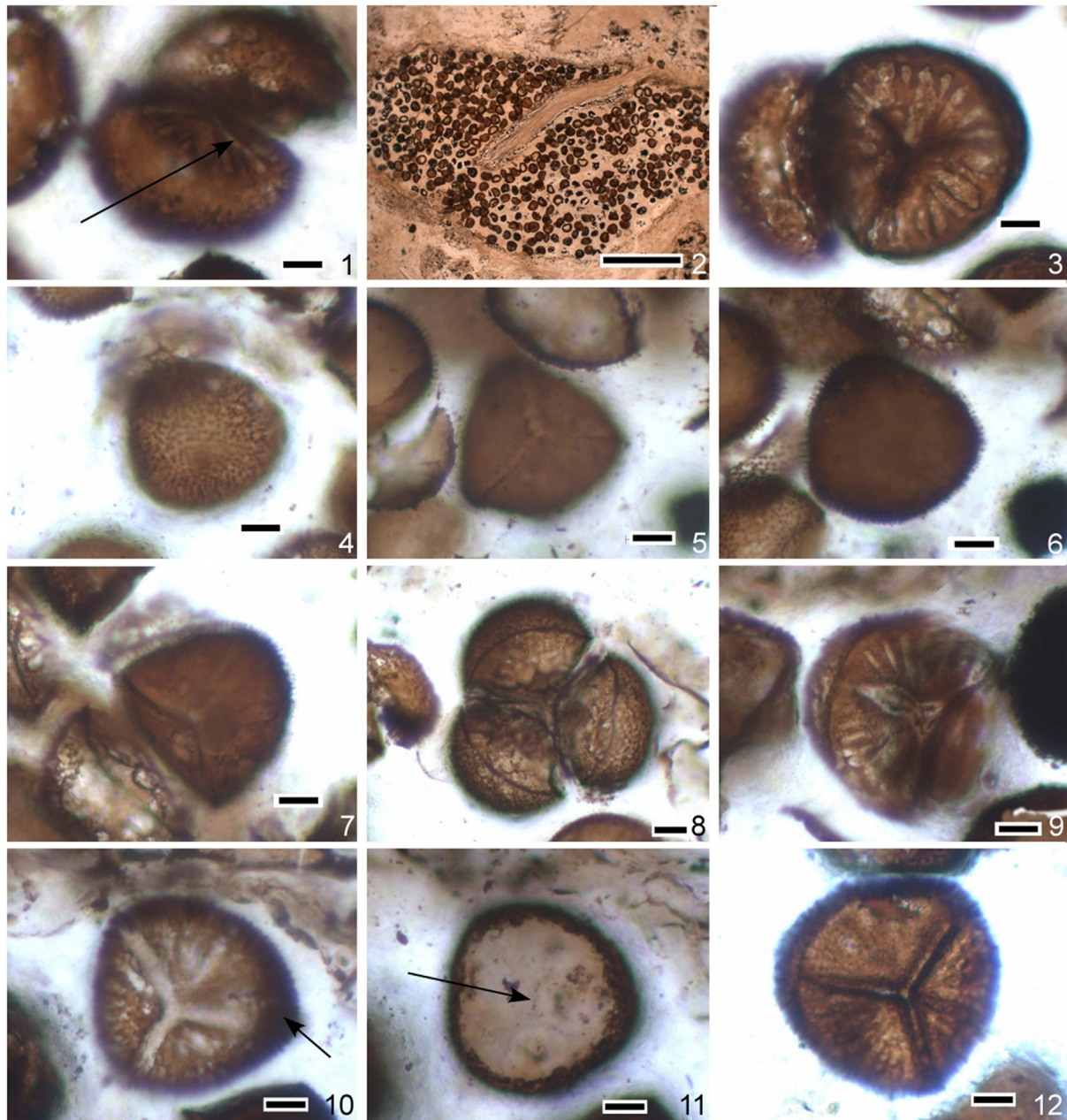


Plate II. Light microscope images of the observed morphological diversity from the *in situ* spores of *Horneophyton lignieri* (Part 2). 1. Lateral view of a disrupted tetrad showing the proximal face with radial muri and the distal face with ornaments (black arrow). *Emphanisporites decoratus* (965x/1169y). 2. Transversal view of a columellate sporangium showing *in situ* spores (965x/1169y). 3. Trilete spore characterised by radial muri on the proximal face. The equatorial area is laevigate. No ornaments are observed on distal face. *Emphanisporites rotatus* (965x/1169y). 4. Ornamented distal face. Thin exine. The proximal face is not visible. *Apiculiretusispora* cf. *plicata* (1220x/1033y). 5–7. Trilete spore ornamented by thin spines on the distal face and the equatorial area. *Apiculiretusispora* cf. *plicata* (1222x/1025y; 1222x/1025y; 1223x/10285y). 8. Disrupted tetrad. The proximal face is strongly damaged. The distal face is ornamented by grana (1238x/1018y). 9. Trilete spore with radial muri and an ornamented distal face. *Emphanisporites decoratus* (1287x/1597y). 10. Trilete spore with an open trilete mark and radial muri on the proximal face. Equatorial area is ornamented (black arrow). *Emphanisporites decoratus* (1287x/1597y). 11. Spore showing a torn distal face giving the impression that the spore is thick equatorially (black arrow, 1313x/1595y). 12. Well-preserved specimen of *Emphanisporites decoratus* (1284x/1515y). NHML slide MGLame-24. Scale bars = (2) 50 μm ; (1, 3–12) = 10 μm .

Description: Trilete spore with a subtriangular shape. The general form is patinate. The trilete mark is straight, with slightly elevated lips that reach the patina. The proximal face is laevigate. The patina is strongly ornamented by densely packed spines. They are 3 to 5 μm long and around 1–1,5 μm wide at their base.

Diameter: 42–45 μm .

Comments: Such a spore found dispersed in sediments would be considered as a *Cymbosporites*. It is difficult to find a morphological variation between *Emphanisporites decoratus* (see below) and this morphotype.

Morphotype 5: *Dibolisporites* sp.

Plate IV. 7

Description: Trilete spores with a circular to subcircular shape or more rarely a subtriangular shape. The trilete mark is straight, thin, and reaching the equator. The proximal face is laevigate and bordered at the equator by thin curvaturae. The exine is thin to thick, 1–6 μm width all around the spore in lateral view. The ornamentation is highly variable, constituted by thin hair like ornaments, thin to large coni, with a sharp to round tip. Sometimes an enlarged small ball surmounts the top. The base of the ornaments varies from 0.5–2 μm in width. They

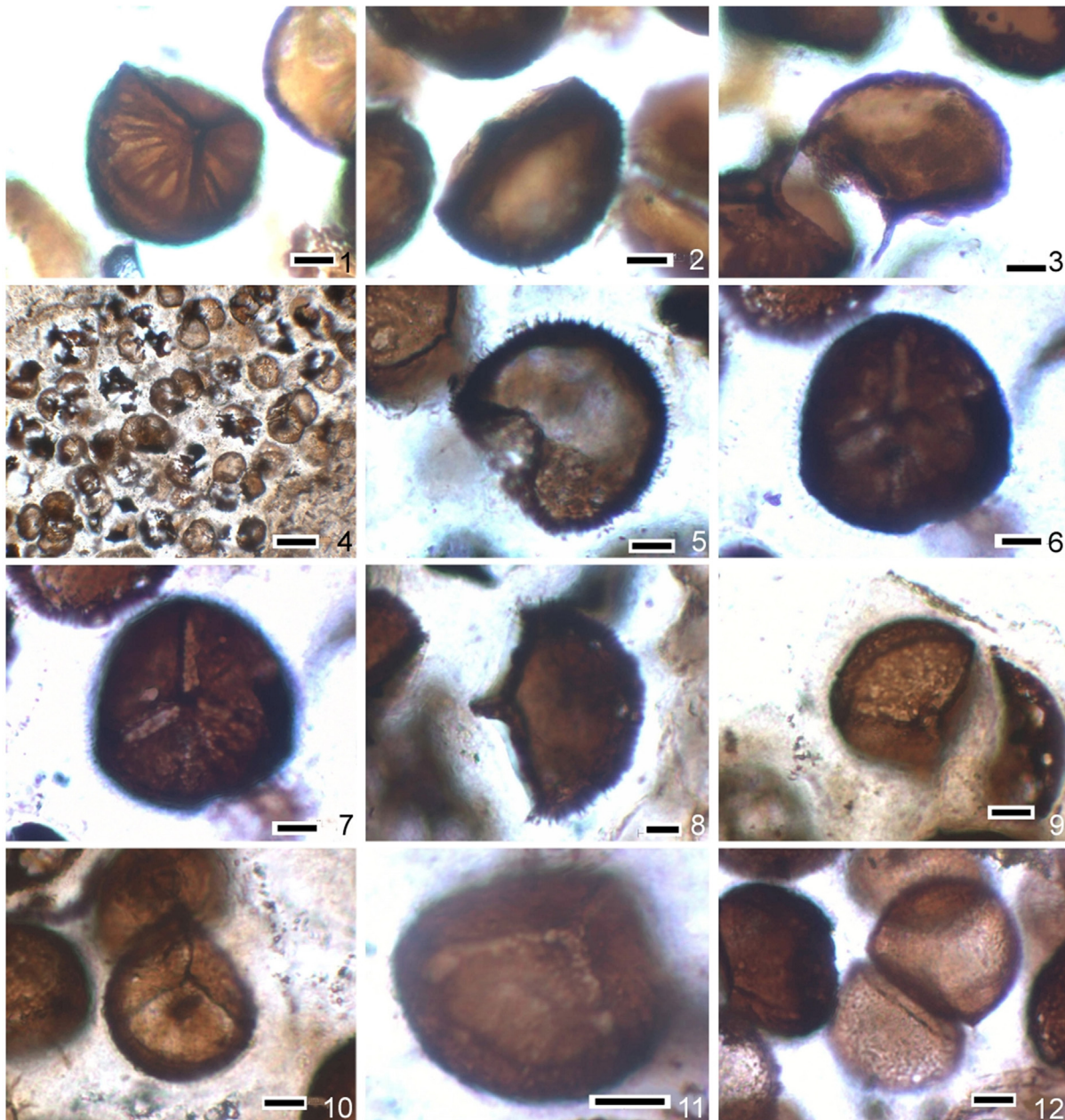


Plate III. Light microscope images of the observed morphological diversity from the *in situ* spores of *Horneophyton lignieri* (Part 3). 1. Well-preserved specimen of *Emphanisporites decoratus* (1295x/1520y). 2. Laterally preserved specimen showing elevated lips. Small spines on the distal face. Genus A sp. A (1298x/1518y). 3. Laterally preserved specimen showing a remarkably high labra. The distal face seems to be laevigate. Genus A sp. A (1298x/1532y). 4. Sporangium showing poorly preserved spores (1342x/1498y). 5. Poorly preserved spore showing long and strong spines (1482x/1363y). 6, 7. Spore with an open trilete mark. Proximal face laevigate. 7. Image of equatorial area showing a small ornamentation. *Apiculiretusispora* cf. *plicata* (1489x/1358y). 8. Lateral view of a specimen showing high labra, a thin distal ornamentation and equatorial lateral expansion. Genus A sp. A (592x/765y). 9. Proximal view of a laevigate spore with an open trilete mark and curvaturae. *Retusotrites* sp. (778x/1356y). 10. Artefact of an *Archaeozonotrites*-type spore because the distal face is partially torn (789x/1358y). 11. Trilete spore entirely laevigate and with curvaturae. *Retusotrites* sp. (777x/1369y). 12. Pseudo dyad due to the destruction of a tetrad. The spores are finely ornamented. No radial muri are visible on the proximal face. *Apiculiretusispora* cf. *plicata* (847x/1302y). NHML slides MGLame-24 (1–7) and MGLame-23 (8–12). Scale bars = (4) 50 µm; (1–3, 5–12) = 10 µm.

are typically densely distributed (0.5–1 µm apart). They can touch each other at their base, forming small, convoluted walls. They are 1–3 µm high (typically 1.5 µm). Many specimens are preserved in tetrahedral tetrad configuration.

Diameter: 45–50 µm.

Comments: Such morphologies have been found dispersed in sediments, with different species, and even genera, having been created because of the extremely high morphologic variability. In fact, during a routine scanning of slides many specimens may be confused with *Cymbosporites* or *Aneurospora* because of the thickness of the exine.

But the lateral view displays a uniform thickness of the exine of the distal, and proximal faces and at the equator. In addition, the very variable kind of ornamentation would suggest different species.

Comparison: The general aspect is like that of *Emphanisporites decoratus* but lacking the radial proximal muri. Badly preserved specimens can be confused with either genus. No similar *Dibolisporites* are known dispersed in sediments.

Morphotype 6: *Emphanisporites decoratus* Allen, 1965

Plate I. 10–12; Plate II. 1, 9, 10, 12; Plate III. 1; Plate IV. 9, 11; Plate V. 6, 7

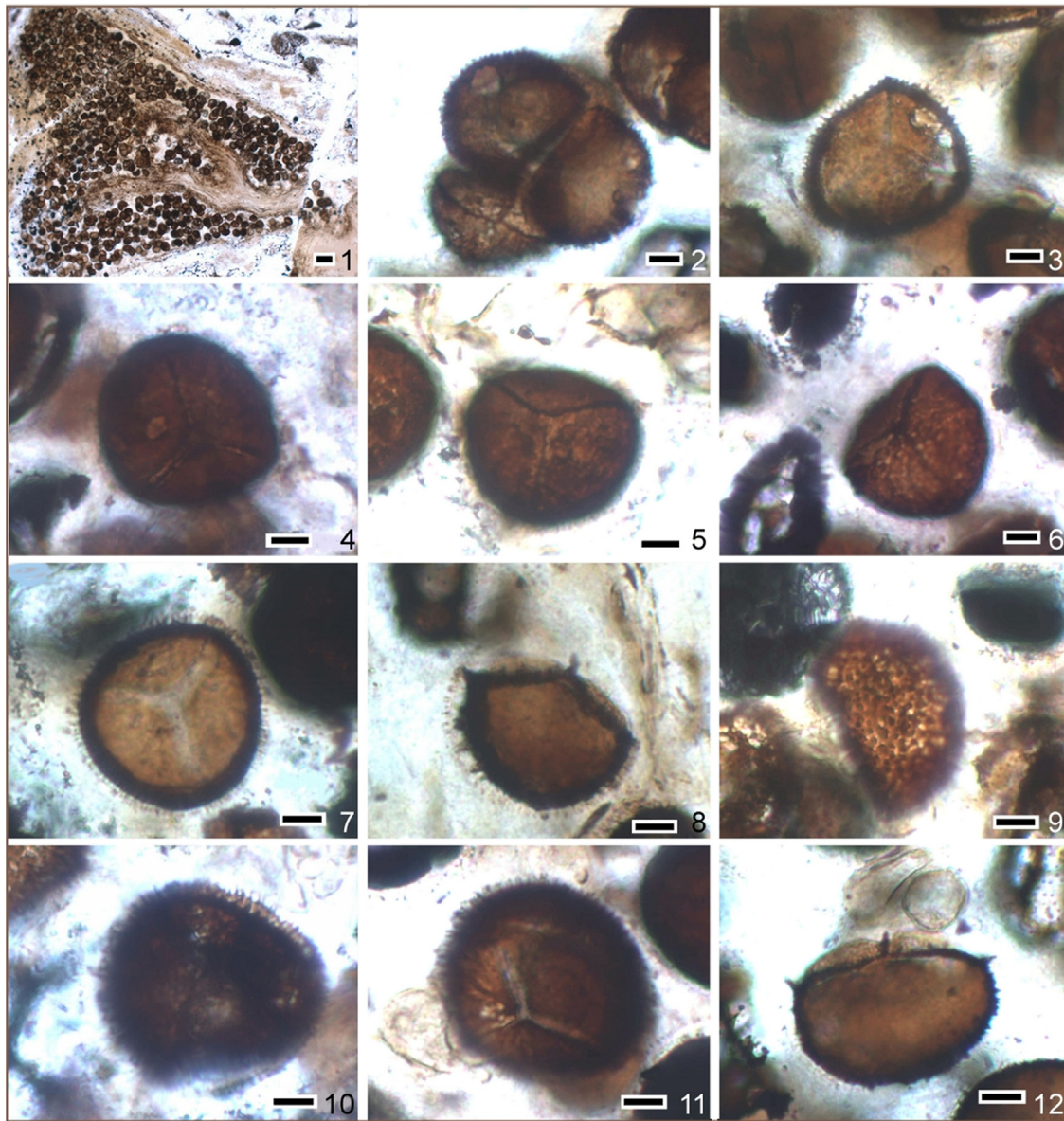


Plate IV. Light microscope images of the observed morphological diversity from the *in situ* spores of *Horneophyton lignieri* (Part 4). 1. Transversal view of a sporangium showing a bifurcate columella and *in situ* spores (853x/1314y). 2. Tetrad of ornamented spores (861x/1310y). 3. Sporangium 853x/1314y. Trilete spore proximally laevigate. Equatorially and distally thick and ornamented by various kind of spines. cf. *Cymbosporites* sp. (1107x/1093y). 4. Laevigate trilete spore looking cingulate. *Ambitisporites* sp. (1113x/1069y). 5. Ornamented trilete spore by thin spines. The spore looks patinate. cf. *Cymbosporites* sp. (1210x/797y). 6. Laevigate trilete spore. *Retusotriletes* sp. (1219x/779y). 7. Artefact due to the torn distal face. Spore showing torn distal face and a laevigate proximal face. Equatorial area ornamented by spines. *Dibolisporites* sp. (1565x/886y). 8, 12. Lateral view of a spore ornamented distally and equatorially by spines. The labra of the trilete mark are elevated. There is an equatorial expansion looking like a zona. The distal face is slightly thicker than the proximal one. Genus A sp. A (1573x/883y, 944x/1212y). 9. Distal view of *Emphanisporites decoratus* showing typical ornamentation (928x/1216y). 10. Proximal view of a spore densely ornamented by slender spined and equatorial expansion. Genus B sp. A (923x/1216y). 11. Robust trilete spore with radial muri on the proximal face. The trilete mark is open. The distal face is ornamented by spines. *Emphanisporites decoratus* (939x/1246y). NHML slides MGLame-23 (1–8) and MGLame-25 (9–12). Scale bars = (1) 50 μm ; (2–12) = 10 μm .

1981 *Emphanisporites* sp. K, in Steemans, p. 53, pl. 2, fig. 3
 2006 *Emphanisporites* cf. *decoratus* Allen; in Wellman, p. 186, pl. 15, figs. g–i.
 2009 *Emphanisporites decoratus* Allen; in Amenábar, fig. 4, aa.

Description: Trilete spores with usually a subcircular to circular shape. The trilete mark is generally straight, thin, and reaching the equator or the thin curvaturae when those ones are visible (mainly on specimens obliquely preserved), meaning that in all specimens curvaturae are equatorial. The contact areas are ornamented by radial muri corresponding to the length of the radius of the spore, reaching the curvaturae. There are in between 5 and 8 radial muri by contact areas. The number of muri is sometimes difficult to count. Those ones may

be ghostly up to clearly visible. Their width is around 2 μm . The equatorial border seems usually to be thick from 2 to 6 μm in width. The distal face and the equatorial area, outwards of the curvaturae, are ornamented by hair-like spines or by conical spines. The mean size of the ornaments is around 1–1.5 μm in width, 2 μm in length and they are 0.5–1 μm apart. Some specimens show ornaments connected by their base mimicking small convolute muri.

Diameter: 46–59 μm .

Comments: *In situ* specimens from sporangia of *H. lignieri* have been described in detail by Wellman et al. (2004). Most specimens would be identified when observed dispersed in sediments as *Emphanisporites decoratus*, according to the expanded diagnosis of McGregor and

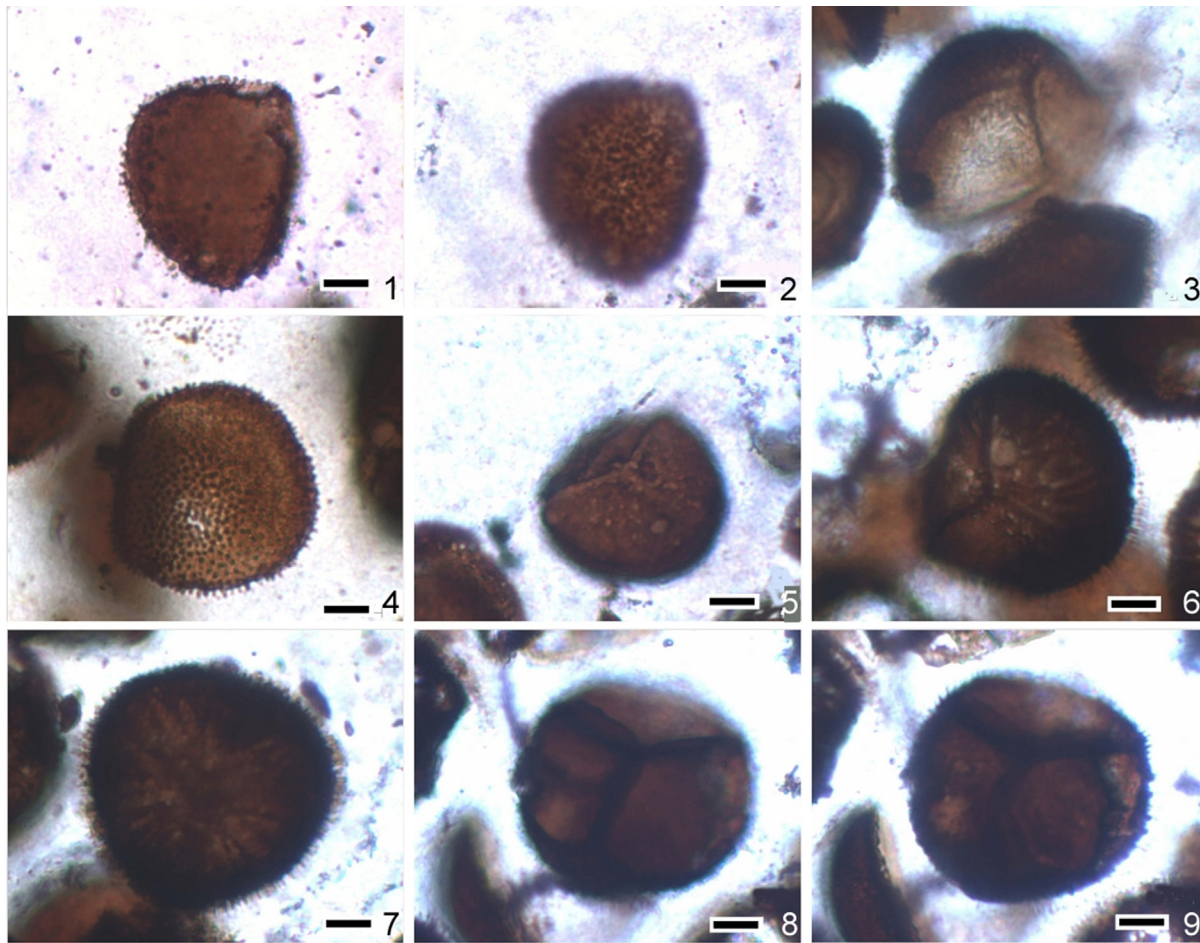


Plate V. Light microscope images of the observed morphological diversity from the *in situ* spores of *Horneophyton lignieri* (Part 5). 1, 2. Equatorial view of a trilete spore showing an ornamentation of pila. 2. Same ornamentation on the distal face. *Cymbosporites raistrickiaeformis* (914x/465y). 3. Lateral view of a spore ornamented on the distal face and at the equator by small spines. The proximal face is limited by curvaturae. The contact areas are characterised by convolute thin ridges (933x/497y). 4. Distal face of a spore ornamented by spines and pila. *Cymbosporites raistrickiaeformis* (939x/561y). 5. Proximal face of a spore without radial muri and a thin ornamentation of grana at the equator. *Apiculiretusispora* cf. *plicata* (905x/1495y). 6, 7. Proximal face ornamented by radial muri. Equatorial area ornamented by slender spines. *Emphanisporites decoratus* (1071x/1241y, 1081x/1216y). 8, 9. Proximal view of a trilete spore with elevated labra. The proximal face is laevigate and the distal face is ornamented by irregular spines. Genus A sp. A (1221x/659y). NHML slide MGLame-25. Scale bars = 10 µm for all images.

Camfield (1976). Published pictures of that species show a particularly important morphological variation of ornamentation (Allen, 1965; McGregor and Camfield, 1976; Wellman, 2004; Wellman et al., 2004). *Emphanisporites decoratus* is much more abundant than *Emphanisporites rotatus* in the sporangia of *H. lignieri*. Rare specimens show a gaping trilete mark. It is difficult to estimate if the spores displaying this proximal feature are abundant or not because of the bad preservation but also because, strangely, spores are usually preserved with the distal face turned up to the top. However, they are not uncommon.

Comparison: *Emphanisporites decoratus* resembles *E. rotatus* but ornamented on its distal face. Badly preserved specimens could be misidentified and classified in one or the other species. *Emphanisporites* cf. *decoratus* in Rubinstein and Steemans (2002) is ornamented by uniform conical spines with a polygonal base in planar view. *Emphanisporites novellus* McGregor and Camfield, 1976 bears grana or conical tips. *Emphanisporites* sp. A in Wellman and Richardson (1996) has shorter proximal ribs and rounded ornamentation in planar view on the distal face. *Emphanisporites* sp. K in Steemans (1981) is identical to *E. decoratus*. *Emphanisporites microratus* var. *microratus* Steemans and Gerrienne 1984 is smaller and is ornamented by regular small conical spines. *Emphanisporites decoratus* in Amenábar (2009) has few very thick radial muri, its ornamentation is not described and poorly preserved according to the picture. Those specimens are here considered as doubtfully identified.

Distribution: Lochkovian-Pragian of the Armorican Massif, France (Moreau-Benoît, 1976). Lochkovian-Pragian of Belgium (Stemans, 1981, 1989); Lochkovian to Pragian/Emsian of Falkland (Marshall, 2016). Siegenian (~Pragian) of Spitsbergen (Allen, 1965, 1980); late Siegenian (~Pragian/Emsian transition) of Brittany, France (Le Hérisse, 1983); middle-late Pragian, *in situ* from *H. lignieri* sporangia, Rhynie Chert, UK (Wellman, 2004, 2017; Wellman et al., 2004, 2006); Pragian-Emsian of Ontario (McGregor et al., 1970; McGregor, 1979; McGregor and Camfield, 1976); Pragian-Emsian of Saudi Arabia (Breuer and Steemans, 2013); Pragian-Emsian of Algeria (Kermandji et al., 2008, 2009); Pragian-Emsian of Argentina (Di Pasquo, 2003); Pragian-Emsian of Saudi Arabia (Breuer et al., 2015); Pragian-Emsian of the Holy Cross Mountains of Poland (Fijałkowska-Mader and Malec, 2011); Eifelian of Argentina (Di Pasquo et al., 2009).

Morphotype 7: ***Emphanisporites rotatus*** McGregor, 1961 emend. McGregor, 1973

Plate II. 3

Description: Trilete spores with usually a subcircular to circular shape. The trilete mark may be bordered by thick labra of 2 µm width. The contact areas are ornamented by radial muri corresponding to the length of the radius of the spore. Curvaturae are rarely visible because they are located at the equator. The equatorial border appears usually thick from 2 to 4 µm width. There are between 6 and 12 radial muri by contact areas. The number of muri are sometimes difficult to count.

Those ones may be ghostly up to clearly visible. Their width is around 2 μm .

Diameter: 43–59 μm .

Comments: The radial muri of this morphotype have a high variation of quantity of radial muri, from a few (~4) to numerous (~12), and a morphology from thin to large, from low to high, simple, or divided. This morphotype is remarkably like *Emphanisporites rotatus* McGregor 1961 emend. McGregor, 1973. That species has been tentatively subdivided in varieties (Stemans, 1981; Streel et al., 1981). But, after the study of many specimens, Stemans (1989) adopted the opinion of McGregor and Camfield (1982, p. 39) considering that all intermediate forms exist, they most probably constitute a morphon sensu Van der Zwan (1979), and it is difficult to fix limits characterizing varieties. It is difficult to estimate if the spores displaying this proximal feature are abundant or not because of the bad preservation but also because, strangely, spores are usually preserved with the distal face turn up to the top. However, they are not uncommon.

Distribution: *Emphanisporites rotatus* is very well-known all around the world from the late Silurian (Richardson and Ioannides, 1973) to the Devonian/Carboniferous transition (Liu et al., 2018). More data are available in i.e. McGregor (1973), Stemans (1989) and Breuer and Stemans (2013).

Morphotype 8: *Retusotriletes* sp.

Plate III. 9, 11; Plate IV. 6

Description: Subcircular trilete spore. The trilete mark is thin and reaches the proximo-equatorial curvaturae. The exine is thin, around 1–1.5 μm thick. The spore is entirely laevigate. No other distinct morphological characters are visible.

Diameter: 40–44 μm .

Comments: Such a spore resembles *Retusotriletes*. Many species of *Retusotriletes* have been described in the literature (see e.g., Breuer and Stemans, 2013, and references therein) often based on very weak criteria. Specimens of this taxon are rare and may belong to different *Retusotriletes* species.

Morphotype 9: Genus A sp. A

Plate III. 2, 3, 8; Plate IV. 8, 12; Plate V. 8, 9

Description: Trilete spore with a circular shape. The trilete mark is formed by elevated lips (gula) of 3 μm (measures done on specimens preserved in polar view) up to 9 μm height (measures done on specimens preserved laterally). It reaches the thick equatorial curvaturae of at least 3 μm width. Outside of the contact area, the exine is ornamented by hair-like ornaments of maximum 2 μm in height and being 0.5 μm apart. Laterally preserved specimens show a proximal exine (1.5–2 μm) thinner than the distal part (3–4 μm thick). Three specimens show an external proximo-equatorial expansion being in maximum 7 μm large, which has not been seen on polar preservation. It is not possible to decide if it is an external zona or not.

Diameter: 52–59 μm .

Comments: This taxon is unknown dispersed in sediments. It is possible that it represents two different taxa: with and without an equatorial zona. However, the rest of morphological characters (i.e., ornaments, size, and thickness) are similar.

Morphotype 10: Genus B sp. A

Plate IV. 10

Description: Trilete spore preserved laterally. The distal face is rounded and the proximal face slightly pyramidal. The trilete mark shows elevated labra, 5.5 μm high. The proximal face is laevigate and 2.7 μm thick. The distal face is thicker (4.2 μm thick) and is ornamented by thin spines of 3–5 μm length. The exine is probably composed of two layers.

Diameter: 55–57 μm .

Comments: This taxon is unknown dispersed in sediments. The pseudo-ornamentation could be an artefact. In that case, this taxon must be considered as laevigate.

4. Discussion

4.1. Intraspecific variation of *H. lignieri* spore morphology

During the last 50 years, several studies have shown different interpretations about the spore morphologies observed from *H. lignieri* sporangia. Classically, the spores from *H. lignieri* have been identified as belonging to *Apiculiretusispora* and *Emphanisporites*. Bhutta (1973a) described the observed morphologies as trilete spores ornamented by highly variable cones and showing a laevigate proximal surface but differing on the presence or absence of a proximal radial ribbing. However, Eggert (1974) suggested that the isolated spores from *H. lignieri* closely resemble *Retusotriletes* and *Apiculiretusispora*. He further added that both types are azonate, radial, trilete, circular, with a very irregular ornamentation over all the spore body but differing in that *Retusotriletes* is smooth and *Apiculiretusispora* shows a surface ornamentation that is reduced on contact areas. We have also observed several morphologies of spores, sometimes quite different (Table 1, Plates I–V).

Interpreting the affinities of the preserved spores in the Rhynie chert is controversial. Firstly, the spores are at different levels of ontogeny depending on when the sporangium was silicified. Roughly, the different maturation states (from more immature to mature) would be: (i) adpressed spores in tetrad (Plate I. 2, Plate IV. 2), (ii) tetrad with detached spores (Plate III. 12), (iii) isolated spores with a closed trilete mark (Plate I. 7), and (iv) isolated spores with an open trilete mark (Plate IV. 11). Secondly, the spores are preserved three-dimensionally. However, in chert slices it is rather difficult to compare these with the observed dispersed spores that are usually completely compressed (Allen, 1980; Wellman, pers. comm.). Thirdly, unlike most other plant tissues, sporopollenin spore walls are highly variably preserved in the chert. Sometimes they are perfect, but they are generally corroded at variable degrees (see Wellman et al., 2006). In addition, preservation also differs between tetrads and isolated spores, being better in the first ones due to the wall degradation observed in post-tetrad stages (Eggert, 1974).

Wellman et al. (2004) attributed the *H. lignieri* spores to *Emphanisporites decoratus* only, although they also identified some specimens ranging into *E. microratus*. Wellman et al. (2004) argued that this observed intraspecific variation is mainly due to variability in spore maturation and taphonomy-induced changes. From this, three independent continua in morphology can be observed. They are as follows: (i) the proximal surface is continuously variable between smooth to having distinct proximal radial ribs, (ii) the distal ornament is continuously variable between grana to coni to distinct spines, (iii) the distal surface is continuously and variably ornamented through smooth with patches of ornament to completely ornamented (Wellman, pers. comm.).

Importantly, Wellman et al. (2004) also described that the radial muri characterizing the *Emphanisporites* genus appears particularly early in the state of the development of spores. In fact, we see these forms already present in tetrads with slightly loosely spores (e.g., Plate I. 2). Furthermore, the distal face of these spores is also early ornamented, even in tetrads with closely attached spores. Bhutta (1973a) also showed specimens of *Apiculiretusispora plicata* as isolated spores in the sporangia, and dispersed in sediments germinating specimens, with the same morphology. Wellman et al. (2004) further commented that an open trilete mark is due to the beginning of the germination of spores. We have observed several isolated *in situ* specimens that have gaping triletes, showing that they are ready to be dispersed (Plate I. 3, 4, 10; Plate II. 10, 11). Open trilete marks further indicate that the lack of radial muri on the proximal face of some spores (e.g., Plate III. 9, 11) are not due to a maturation issue. These observations support the idea that the observed spores herein are morphologically mature, except perhaps specimens in tetrads with tightly

Table 2

List of Silurian-Devonian plant taxa from which have been documented, at least, two different spores.

Plant macrofossil species	Temporal distribution		Spore content	References
	Age	References		
<i>Cooksonia pertoni</i>	Pridoli to mid-Lochkovian	Edwards and Richardson, 2004 Morris and Edwards, 2014	<i>Ambitisporites</i> sp., <i>Synorisporites verrucatus</i> <i>Ambitisporites</i> sp., <i>Aneurospora</i> spp., <i>Streelispora newportensis</i> , ? <i>Synorisporites</i> sp.	Fanning et al., 1988; Habgood et al., 2002 Fanning et al., 1988; Habgood et al., 2002; Morris et al., 2012
<i>Paracooksonia apiculispota</i>	Mid-Lochkovian	Morris and Edwards, 2014	<i>Aneurospora</i> cf. <i>trilabiata</i> , <i>Aneurospora</i> sp., <i>Streelispora newportensis</i>	Morris et al., 2011
<i>Zosterophyllum</i> cf. <i>fertile</i>	Early Pragian	Edwards and Richardson, 2004	<i>Retusotriletes</i> cf. <i>dubius</i> , <i>Retusotriletes</i> sp.	Edwards, 1969; Edwards and Richardson, 1996
<i>Horneophyton lignieri</i>	Mid- to late Pragian	Wellman, 2006	cf. <i>Apiculiretusispora</i> , ? <i>Emphanisporites decoratus</i> ? <i>Aneurospora</i> sp., <i>Apiculiretusispora</i> sp., ? <i>Emphanisporites decoratus</i> <i>Apiculiretusispora</i> sp., <i>Retusotriletes</i> sp. <i>Emphanisporites</i> cf. <i>decoratus</i> <i>Ambitisporites</i> sp., <i>Apiculiretusispora</i> cf. <i>plicata</i> , <i>Cymbosporites raistrickiaeformis</i> , cf. <i>Cymbosporites</i> sp., <i>Dibolisporites</i> sp., <i>Emphanisporites decoratus</i> , <i>E. rotatus</i> , <i>Retusotriletes</i> sp.	Bhutta, 1973a; Gensel, 1980 Bhutta, 1973a; Allen, 1980 Eggert, 1974 Wellman, 2017 This study
<i>Rhynia gwynne-vaughanii</i>	Mid- to late Pragian	Wellman, 2006	<i>Apiculiretusispora</i> sp., <i>Granulatisporites</i> cf. <i>muninensis</i> <i>Apiculiretusispora plicata</i> , <i>Granulatisporites muninensis</i> <i>Apiculiretusispora plicata</i>	Bhutta, 1969; Allen, 1980 Bhutta, 1987; Edwards and Richardson, 1996 Wellman, 2017
<i>Pertica varia</i>	Emsian	Hotton et al., 2001	<i>Apiculiretusispora arenorugosa/plicata</i> <i>Apiculiretusispora plicata</i> , A. cf. <i>arenorugosa</i>	Granoff et al., 1976; Gensel, 1980 Granoff et al., 1976; Edwards and Richardson, 1996
<i>Renalia hueberi</i>	Emsian	Hotton et al., 2001	<i>Apiculiretusispora</i> sp., <i>Retusotriletes</i> sp.	Gensel, 1976; Allen, 1980; Edwards and Richardson, 1996
<i>Psilophyton parvulum</i>	Early Emsian	Gerrienne, 1995	<i>Apiculiretusispora</i> sp., <i>Retusotriletes</i> sp.	Gerrienne, 1995
<i>Trimerophyton robustius</i>	Mid- to late Emsian	Kennedy et al., 2012	<i>Calamospora atava/pannucea</i> <i>Apiculiretusispora</i> sp., <i>Retusotriletes</i> sp. <i>Apiculiretusispora arenorugosa</i>	McGregor, 1973; Gensel, 1980 Hopping, 1956; Allen, 1980 Hotton et al., 2001
<i>Chaleuria cirrosa</i>	Mid- to late Emsian	Kennedy et al., 2012	(microspores) <i>Camarozonotriletes sextantus</i> (megaspores) <i>Apiculiretusispora gaspiensis</i> , <i>A. microconus</i> (microspores) <i>Aneurospora</i> cf. <i>goensis</i> , cf. <i>Procoronaspora</i> sp. (megaspores) <i>Apiculiretusispora</i> sp., <i>Cyclogranisporites</i> cf. <i>flexuosus</i>	Andrews et al., 1974; Gensel, 1980 Andrews et al., 1974; Allen, 1980
<i>Oocampsa catheca</i>	Mid- to late Emsian	Kennedy et al., 2012	<i>Grandispora macrotuberculatus</i> or <i>Samarisporites praetervisus</i> cf. <i>Perotriletes eximius</i> , cf. <i>Samarisporites praetervisus</i> <i>Grandispora douglstownensis</i> /G.? <i>macrotuberculata</i>	Andrews et al., 1975; Allen, 1980 Andrews et al., 1975; Gensel, 1980 Wellman, 2018; Wellman and Gensel, 2004
<i>Pertica dalhousii</i>	Mid- to late Emsian	Kennedy et al., 2012	<i>Apiculiretusispora brandtii</i> , <i>Apiculiretusispora plicata</i> <i>Apiculiretusispora</i> sp. <i>Apiculiretusispora brandtii</i>	Doran et al., 1978; Gensel, 1980; Edwards and Richardson, 1996 Wellman, 2018
<i>Psilophyton charientos</i>	Mid- to late Emsian	Kennedy et al., 2012	<i>Apiculiretusispora brandtii</i> , <i>Calamospora</i> sp./ <i>Punctatisporites</i> sp., <i>Retusotriletes</i> sp. <i>Apiculiretusispora</i> sp.	Gensel, 1980 Balme, 1995 Wellman, 2018
<i>Psilophyton dawsonii</i>	Mid- to late Emsian	Kennedy et al., 2012	<i>Phyllothecotriletes</i> spp., <i>Retusotriletes triangulatus</i> <i>Retusotriletes</i> cf. <i>triangulatus</i> <i>Apiculiretusispora</i> sp., <i>Retusotriletes</i> cf. <i>rotundus</i>	Banks et al., 1975 Banks et al., 1975; Gensel, 1980 Banks et al., 1975; Allen, 1980
<i>Psilophyton princeps</i>	Mid- to late Emsian	Kennedy et al., 2012	<i>Apiculiretusispora</i> sp./ <i>Phyllothecotriletes</i> sp., <i>Retusotriletes</i> sp. <i>Apiculiretusispora</i> spp., <i>Retusotriletes</i> spp. <i>Apiculiretusispora</i> cf. <i>brandtii</i> , <i>Calamospora</i> cf. <i>atava</i> , <i>Retusotriletes</i> sp.	Noetinger et al., 2018 Gensel, 1980; Noetinger et al., 2018 Hueber, 1968; Allen, 1980; Edwards and Richardson, 1996
<i>Sawdonia acanthotheca</i>	Mid- to late Emsian	Kennedy et al., 2012	<i>Apiculiretusispora</i> sp. <i>Calamospora pannucea</i> , cf. <i>Calamospora atava</i> , <i>Retusotriletes rotundus</i> <i>Calamospora</i> cf. <i>atava</i> , ? <i>Apiculiretusispora</i> , <i>Retusotriletes</i> cf. <i>rotundus</i>	Wellman, 2018 Gensel et al., 1975; McGregor and Camfield, 1976; Gensel, 1980 Gensel et al., 1975; Allen, 1980
<i>Orestovia devonica</i>	Eifelian	Krassilov, 1981	<i>Retusotriletes</i> sp. <i>Acinosporites acanthomammillatus</i> , <i>Retusotriletes</i> sp.	Wellman, 2018 Krassilov, 1981; Balme, 1995
<i>Barrandeina dusliana</i>	Givetian	Jurina et al., 2009	<i>Densosporites</i> sp., <i>Samarisporites</i> sp.	Obrhel, 1961; Allen, 1980

Table 2 (continued)

Plant macrofossil species	Temporal distribution		Spore content	References
	Age	References		
<i>Mixostrobus givetensis</i>	Givetian	Senkevitch et al., 1993	(microspores) <i>Acinosporites</i> sp., <i>Dictyotrilletes</i> sp. (megaspores) <i>Archaeozonotrilletes macrodictus</i> , <i>Lagenicula devonica</i>	Senkevitch et al., 1993; Bek, 2017
<i>Svalbardia polymorpha</i>	Mid- to late Givetian	Schweitzer, 1999	<i>Aneurospora</i> cf. <i>greggsii</i> , <i>Geminospora svalbardiae</i>	Høeg, 1942; Vigran, 1964; Allen, 1980
<i>Enigmophyton superbum</i>	Late Givetian	Schweitzer, 1999	(microspores) <i>Calamospora</i> cf. <i>pannucea</i> , <i>Retusotrilletes rotundus</i>	Vigran, 1964; Allen, 1980; Edwards and Richardson, 1996
			(microspores) <i>Phyllothecotrilletes microgranulatus</i>	Vigran, 1964; Gensel, 1980; Balme, 1995
<i>Svalbardia furcihastata</i>	Late Givetian	Jurina and Raskatova, 2014	(megaspores) <i>Biharisporites</i> sp. (megaspores) <i>Contagisporites optivus</i> , <i>Biharisporites macromanifestus</i>	Krassilov et al., 1987; Balme, 1995 Jurina and Raskatova, 2014; Jurina et al., 2020
<i>Gutzetia timanica</i>	Late Frasnian	Orlova et al., 2016	(microspores) <i>Stenozonotrilletes formosus</i> , <i>S. recognitus</i>	Tschibrikova et al., 1999; Snigirevsky et al., 2007
<i>Svalbardia fissilis</i>	Late Frasnian	Orlova et al., 2016	(microspores) <i>Geminospora lemurata</i> , <i>G. rugosa</i> (megaspores) <i>Biharisporites macromanifestus</i> , <i>Contagisporites optivus</i>	Jurina et al., 2020
<i>Tauritheca gracilis</i>	Late Frasnian	Orlova et al., 2016	(microspores) <i>Leiotrilletes microrugosus</i> , <i>Cyclogranisporites</i> sp. (megaspores) <i>Stenozonotrilletes rugosus</i> , <i>S. extensus</i> var. <i>major</i> , <i>S. laevigatus</i> (microspores) <i>Cyclogranisporites solidus</i> , <i>C. medius</i> , <i>Leiotrilletes microrugosus</i> (megaspores) <i>Stenozonotrilletes rugosus</i> , <i>S. extensus</i> var. <i>major</i> , <i>S. laevigatus</i> <i>Perotrilletes</i> cf. <i>conatus</i> or <i>P. cf. perinatus</i>	Tschibrikova et al., 1999; Schweitzer and Giesen, 2008 Snigirevsky et al., 2007
<i>Rhacophyton ceratangium</i>	Famennian	Andrews and Phillips, 1968	? <i>Grandispora</i> ?/ <i>Diaphanospora</i>	Andrews and Phillips, 1968 Allen, 1980 Andrews and Phillips, 1968; Balme, 1995

addressed spores where it is impossible to observe the proximal surface (Plate II. 8), and that these spores may be classified in different taxa.

On the other hand, among many *Emphanisporites*, some rare *E. rotatus* have been observed (Plate II. 3). This fact could be explained by arguing that they come from immature forms as they lack ornamentation. Several intermediate forms likely exist between *E. rotatus* and *E. decoratus* with small ornamentation. In addition, it is well-documented that *Emphanisporites rotatus* presents a high morphological variation (Breuer et al., 2005; Taylor et al., 2011). So, evidence suggests that *E. rotatus* would be a “box”, with a high morphological variability (compare pictures from various publications, e.g., McGregor, 1973; Steemans, 1989; Breuer and Steemans, 2013), in which would be included the *in situ* specimens observed herein (Plate I, 10–12; Plate II. 1, 3, 9, 10; Plate IV. 9, 11; Plate V. 6, 7).

Furthermore, we have observed that distal ornamentation is appearing exceedingly early as it has been observed on spores in addressed tetrad. This indicates that an isolate trilete spore that is distally laevigate, without radial muri, is most probably a *Retusotrilletes* (*Ambitisporites* if presence of an equatorial thickening or *Archaeozonotrilletes* if presence of a patina; Plate III. 10; Plate IV. 4). It is also important to note that all intermediate forms exist between those “three” genera. Likewise, ornamented isolated spores without radial muri cannot be a morphological variation of *Emphanisporites*, and are classified as apiculate forms, cf. *Cymbosporites* (patinate; Plate I. 4, 7) or *Cymbosporites raistrickiaeformis* (bacula; Plate V, 1–2, 4); again, all intermediate forms exist between those three genera. Of course, we also cannot exclude the fact that those variations are very subtle and may be due to the poor state of preservation of the spores and the difficulties of observation. However, a clear exception to this scenario comes from the presence of a high gula on some specimens. This cannot be explained by a morphological variation of an *Emphanisporites* or an *Apiculiretusispora*.

In summary, results have shown that different spore morphologies can be observed inside *H. lignieri* sporangia. Results further show that some sporangia may contain more than one morphotype. Most of the sporangia are dominated by, or contain exclusively, the *Apiculiretusispora plicata*/*Dibolisporites* sp. complex (Plate II. 4; Plate III. 6, 7, 12; Plate IV. 7; Plate V. 5) and *Emphanisporites decoratus* (Plate I. 10–12). Significantly, all these trilete spores should belong to the

same species, as they are observed in sporangia of the same biological entity (i.e., *H. lignieri*). They are, therefore, biologically related one to each other. However, if all these spores had been found dispersed in sediments, they would most probably be identified as different taxa instead of an intraspecific variation of a single entity.

4.2. Spores, *in situ* spores and plant palaeodiversity

It is well-known that spores recovered from sediments are a powerful tool for the reconstruction of ancient vegetations (e.g., Wellman et al., 2013; Gibson and Wellman, 2021), as well as for biostratigraphy and phytogeography (e.g., Wellman et al., 2012, 2013; Cascales-Miñana et al., 2019b, and references therein). Moreover, *in situ* spores are a key to understand past plant palaeodiversity. They are the only evidence to link such dispersed spores and plant macrofossils. For instance, this is particularly relevant for the earliest, basalmost plant remains for which we only have palynological evidence (i.e., cryptospores; Rubinstein et al., 2010; Strother et al., 2017). For the entire Cambrian–Ordovician interval, the palynological record and few biogeochemical data are the only indication of the history of early plants, except for a few plant macrofossils in the Late Ordovician (see Wellman et al., 2003; Salamon et al., 2018; Servais et al., 2019, fig. 2 for details). There are no *in situ* records of earliest cryptospores of the Ordovician and the early Silurian, but cryptospore producers are well-documented from latest Silurian–earliest Devonian deposits (Edwards et al., 2014), which provide evidence of the plant origin of such palynomorphs.

Observations of *in situ* spores from Silurian–Early Devonian land plants are rare, but they are more common in younger sediments (Wellman and Gray, 2000; Kenrick et al., 2012; Bek, 2017, 2021). This is because early plant macrofossils are mainly preserved as coalified compressions where *in situ* spores are often absent or badly preserved (Wellman and Gray, 2000). This situation makes highly difficult any comparison to dispersed spore records that are usually better preserved. Fortunately, some exceptionally preserved assemblages show cellular details, like the Rhynie chert material studied herein. This allows characterizing *in situ* spores from small fragments of early land plants. Further uncompressed coalifications with coeval *in situ* spores are also

Table 3
List of Silurian-Devonian spores that have been documented from, at least, two different plant taxa.

Spore species	Temporal distribution		Parent plants	References
	Age	References		
<i>Retusotriletes</i> cf. <i>triangulatus</i>	Ludlow-Pragian	Liu et al., 2016; Richardson, 1967	<i>Asteroxylon mackiei</i> <i>Psilophyton dawsonii</i> <i>Tricherothyton teuchansii</i>	Wellman, 2006, 2017 Gensel, 1980 Wellman, 2006, 2017
<i>Apiculiretusispora plicata</i>	Pridoli-Famennian	Prestianni et al., 2016; Shen et al., 2020	<i>Pertica dalhousii</i> <i>Pertica varia</i> <i>Rhynia gwynne-vaughanii</i> <i>Crenaticaulis verruculosus</i>	Doran et al., 1978; Edwards and Richardson, 1996 Granoff et al., 1976; Edwards and Richardson, 1996 Wellman, 2017 Hotton et al., 2001
<i>Retusotriletes rotundus</i>	Early Devonian	Streel, 1967; McGregor and Camfield, 1982; Neregato and Hilton, 2019	<i>Enigmophyton superbum</i> <i>Sawdonia acanthotheca</i> <i>Zosterophyllum</i> sp. <i>Cooksonia pertoni</i>	Vigran, 1964; Allen, 1980 Gensel et al., 1975; McGregor and Camfield, 1976; Gensel, 1980 Hotton et al., 2001 Fanning et al., 1988; Habgood et al., 2002; Morris et al., 2012 Morris et al., 2011; Morris et al., 2012
<i>Streelispora newportensis</i>	Lochkovian-Early Emsian	Stemans, 1989; Moreau-Benoît and Boureau, 1989; Brocke et al., 2017	<i>Paracooksonia apiculisporea</i> <i>Pertica dalhousii</i>	Doran et al., 1978; Edwards and Richardson, 1996 Gensel, 1980
<i>Apiculiretusispora brandtii</i>	Late Pragian-Givetian	Breuer and Stemans, 2013; Muro et al., 2020; Streel, 1972	<i>Psilophyton charientos</i> <i>Psilophyton forbesii</i> <i>Leclercqia complexa</i> <i>Leclercqia uncinata</i> <i>Leclercqia</i> sp.	Richardson et al., 1993; Bek, 2017 Xu et al., 2011; Bek, 2017 Richardson et al., 1993; Bek, 2017 Xu et al., 2012; Bek, 2017
<i>Acinosporites lindlarensis</i>	Late Pragian-Frasnian	Xu et al., 2020	<i>Hoxtolegaya robusta</i> <i>Orestovia devonica</i> <i>Rellimia thomsonii</i>	Xu et al., 2012; Bek, 2017 Krassilov, 1981; Balme, 1995 Leclercq and Bonamo, 1971; Wellman, 2009
<i>Acinosporites acanthomammillatus</i> <i>Rhabdosporites langii</i>	Eifelian-Middle Givetian Eifelian-Frasnian	Richardson and McGregor, 1986; Balme, 1995 Wellman, 2009	<i>Tetraxylopteris schmidtii</i>	Bonamo and Banks, 1967; Wellman, 2009
<i>Aneurospora greggsi</i> (microspore)	Givetian-Famennian	Turnau and Racki, 1999; Streel, 1999	<i>Archaeopteris halliana</i> <i>Archaeopteris latifolia</i> , <i>A. cf. jacksonii</i> <i>Archaeopteris macilenta</i>	Phillips et al., 1972; Fairon-Demaret et al., 2001 Pettitt, 1965; Fairon-Demaret et al., 2001 Phillips et al., 1972; Fairon-Demaret et al., 2001
<i>Contagisporites optivus</i> (megaspore)	Givetian-Frasnian	Marshall, 1996; Kondas et al., 2018	<i>Archaeopteris cf. macilenta</i> <i>Archaeopteris halliana</i> <i>Archaeopteris</i> sp. <i>Svalbardia furcuhasta</i>	Phillips et al., 1972; Balme, 1995; Fairon-Demaret et al., 2001 Phillips et al., 1972; Edwards and Richardson, 1996 Tel'nova, 2002; Marshall et al., 2019 Jurina and Raskatova, 2014; Jurina et al., 2020
<i>Geminospora lemurata</i> (microspore)	Givetian-Famennian	Marshall, 1996; Loboziak and Streel, 1981	<i>Svalbardia fissilis</i> <i>Archaeopteris</i> sp. <i>Bisporangiostrobos harrisii</i> <i>Svalbardia fissilis</i> , <i>S. furcuhasta</i> <i>Svalbardia osmanica</i> , <i>S. polymorpha</i>	Jurina et al., 2020 Tel'nova, 2002; Marshall et al., 2019 Chitaley and McGregor, 1988; Bek, 2017 Jurina and Raskatova, 2014; Jurina et al., 2020 Marshall, 1996; Jurina et al., 2020
<i>Biharisporites macromanifestus</i> (megaspore)	Givetian-Famennian	Jurina et al., 2020	<i>Svalbardia fissilis</i> , <i>S. furcuhasta</i>	Jurina and Raskatova, 2014; Jurina et al., 2020

documented, e.g., from Early Devonian deposits of South Wales (Morris et al., 2011, 2012; Morris and Edwards, 2014).

In situ spores are documented from all Rhynie chert plants (see Wellman, 2017, table 1). From this, we see that the known Rhynie chert diversity of *in situ* spores belong to *Apiculiretusispora*, *Emphanisporites* and *Retusotriletes* types (Wellman, 2004, 2017). Results exposed herein show that all these types are present within the sporangia of *H. lignieri* (Plate II. 4–7, 9–12; Plate III. 9, 11). Interestingly, Wellman et al. (2004, p. 430) already noted that, after re-examination of Lyon's (1957) sections, Bhutta (1973a) suggested that observed spores resemble to the *Apiculiretusispora plicata* type of *H. lignieri*. Likewise, *Retusotriletes* type spores are already shared by other Rhynie chert plants such as *Trichopherophyton* and *Asteroxylon* (Wellman, 2004,

2006, 2017; Kerp et al., 2013). In contrast, *Emphanisporites* is unusual from *in situ* records (see Table 2), despite being abundant in the dispersed fossil record. Taylor et al. (2011) noted that *Emphanisporites* is known *in situ* from *H. lignieri* (*Emphanisporites* cf. *decoratus*, Wellman et al., 2004), cf. *Horneophyton* sp. (*Emphanisporites* cf. *micromnatus*, Edwards and Richardson, 2000) and from uncertain plant remains (*Emphanisporites* sp. A, Edwards and Richardson, 2000). Subsequently, Morris et al. (2012) also documented *Emphanisporites*-type spores from a discoidal spore mass, which is relevant considering that the sporangia of *H. lignieri* are elongate.

We have documented a series of spore morphotypes from *H. lignieri* (Table 1). However, this should not be surprising. Several isolated spores have already been documented from a single taxon of plant

macrofossils in and beyond the Rhynie chert (Table 2). For instance, the record of early land plants shows that the *Ambitisporites*, *Streelispora* and *Synorisporites* types have been described from the sporangia of *Cooksonia* (Fanning et al., 1988; Morris et al., 2012; Table 2). Similarly, different spore morphologies have been also observed in *Paracooksonia* (Morris et al., 2011; Morris and Edwards, 2014; Table 2). It also occurs in *Rhynia gwynne-vaughanii*, where several authors have described *in situ* spores belonging to *Apiculiretusispora* and *Granulatisporites* types (Bhutta, 1969, 1987; Edwards and Richardson, 1996; Wellman, 2006, 2017). The fact that different spore types are produced by the same plant macrofossil could be showing a case of mosaic evolution. Knoll et al. (1984) described this phenomenon in early land plants, by which some organs of a given taxa (usually reproductive structures) show more morpho-anatomical diversification than other parts (typically vegetative). Fanning et al. (1988) also advocated by this idea arguing that the evolution of the spore morphology of early land plants was quicker than the corresponding evolution of parent plant morphologies. Wellman and Gray (2000) further argued that, as early land plant spores are morphologically simple, it is highly likely that different plants could have produced similar spore forms by homoplasy. However, we have documented this phenomenon in practically all main Silurian-Devonian plant groups, i.e., rhyniophytes, basal eutracheophytes, zosterophylloids, trimerophytes, fern-like plants, even from heterosporous lycopsids and progymnosperms, where multiple spore taxa have been identified from both micro and megaspores (e.g., *Mixostrobus* and *Svalbardia*, Table 2).

On the other hand, Rhynie chert *in situ* spores have been also described elsewhere. For instance, the *in situ* spore of *Asteroxylon*, i.e., *Retusotriletes cf. triangulatus*, is also documented from *Psilophyton* (Table 3). Similarly, the *in situ* spore of *Rhynia*, i.e., *Apiculiretusispora plicata*, has also been observed in *Pertica* (Table 3). This suggests that lycopsids and paratracheophytes could produce similar spores to trimerophytes (and vice versa). This is not the unique case. Other spore morphologies, such as *Retusotriletes rotundus*, have also been identified from different zosterophylls and barinophytes. Furthermore, *Geminispora lemurata* is considered to be the *in situ* spore of *Bisporangiostrobus* and *Archaeopteris*, i.e., of a lycopsid and a progymnosperm (Table 3), respectively. This suggests that a same spore morphology can be produced by different evolutionary lineages of vascular plants, independently of its morphological complexity.

Compiled evidence further reveals that dispersed spores can have a longer temporal distribution than their parent plants (Tables 2, 3). This can be observed when comparing the known temporal distribution of spore taxa and the distribution of the spore producers. For instance, it is obvious that the temporal and spatial distribution of *Emphanisporites decoratus* goes beyond the *H. lignieri* occurrences (Taylor et al., 2011, table 1; Breuer and Steemans, 2013, p. 84). Unfortunately, we just know a few cases from which such comparisons can be done. For example, *Rhabdosporites langii*, which is the spore that goes across the aneurophytalean progymnosperms, has been documented in *Rellimia* and *Tetraxylopteris* (Wellman, 2009; Table 3). Another case, for example, is that of *Acinosporites lindlarensis*, which is a highly variable spore (see Richardson et al., 1993 for further details), that has been observed from different *Leclercqia* species (Bek, 2017; Table 3). Potential distorting effects increase when there is no possibility to test the spore-plant relationships. In fact, there are inherent constraints on both the plant macrofossil and the spore fossil records. While the dispersed microfossil record has a better preservation potential and mainly a much larger number of specimens, which might in part explain the different stratigraphical ranges, the *in situ* spore fossil record is limited by a strong preservation bias and few observations by comparison with dispersed spores. Likewise, the macrofossil record is also biased because of organ morphogenesis and mosaic evolution, which makes comparative diversity studies difficult. In that context, we cannot be fully confident whether the observed spore diversity changes through time are driven by plant diversity fluctuations or not. This likely explains the apparently

decoupled patterns between spore and plant diversity of early land plants (Knoll et al., 1984; Xiong et al., 2013; Cascales-Miñana, 2016).

5. Conclusions

Observations of *in situ* spores document a wide spectrum of spore morphologies within the sporangia of *Horneophyton* including some morphotypes that are rather different. The observed morphologies include a significative diversity of previously described dispersed spore 'genera', such as *Apiculiretusispora*, *Dibolisporites*, *Emphanisporites* or *Retusotriletes*, among others. Some morphologies never observed before from the dispersed record have also been documented. All these observed spore morphotypes are found in the sporangia of a single parent plant. Consequently, they belong to a same palaeobiological entity. Our findings clearly demonstrate that the sporangia of a same species may deliver diverse spore morphologies, previously attributed to different spore taxa, of coeval isolated palynofloras. However, found in Lower Devonian sediments, these morphologies would most probably be identified as different dispersed taxa. Therefore, extreme caution is necessary when comparing the macrofossil-based patterns of plant diversity with that of the microfossil records.

Declaration of Competing Interest

The authors declare no competing interests that could have appeared to influence the present paper.

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