



This is a repository copy of *A key for the identification of cryptospores.*

White Rose Research Online URL for this paper:
<http://eprints.whiterose.ac.uk/127683/>

Version: Accepted Version

Article:

Steemans, P. and Wellman, C.H. (2018) A key for the identification of cryptospores. *Palynology*, 42 (4). pp. 492-503. ISSN 0191-6122

<https://doi.org/10.1080/01916122.2017.1411844>

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



eprints@whiterose.ac.uk
<https://eprints.whiterose.ac.uk/>

A key for the identification of cryptospores

P. Steemans^{a*} and C.H. Wellman^b

^aDépt. de Géologie, Unité de recherche PPP, Université de Liège, Campus du Sart Tilman, Quartier Agora, Allée du 6 Août, 14, Bât. B-18, B-4000 Liège 1, Belgium; +3243665333; p.steemans@ulg.ac.be; ^bDept. of Animal & Plant Sciences, University of Sheffield, Alfred

Denny Building, Western Bank, Sheffield S10 2TN, UK; +441142223689 ;

c.wellman@sheffield.ac.uk

*Corresponding author. Email: p.steemans@ulg.ac.be

Funding Acknowledgment

PS is a Senior Researcher of the Belgium National Fund for Scientific Research (NFSR).

CHW's research is funded by NERC grant NE/N002067/1

Abstract

Dispersed spores interpreted as deriving from the earliest land plants have complex configurations (e.g. permanent dyads and permanent tetrads) and are readily distinguished from the more familiar trilete spores that often dominate post-late Silurian dispersed spore assemblages. These forms occur mainly from the Middle Ordovician to Early Devonian.

They were first recognised in 1971, but it was not until 1979 that the process of formal description commenced. In 1984 they were included in a newly created higher taxonomic grouping called “cryptospores”, the term reflecting their complex morphology and then the ongoing debate regarding their affinities. Subsequently the exact definition of the term cryptospore has been debated, with some preferring a wide definition encompassing all non-

marine palynomorphs produced by algae and early land plants, but others confining inclusion to spores deriving from early embryophytes. Since their recognition, numerous 'cryptospore' taxa have been described. However, their complex morphologies are difficult to interpret and numerous taxonomic debates have confused the delineation of genera and their classification into higher ranks. Here we present a key for the identification of 'cryptospore' taxa with the aim of clarifying some of this confusion.

Keywords: Ordovician; Silurian; Devonian; taxonomy; cryptospores

1. Introduction

Research into the dispersed spores produced by the earliest known land plants has been controversial because of: (i) debates concerning their biological affinities; (ii) since they were first discovered in 1971 numerous publications have documented their spatial and temporal distribution, spore/pollen morphologists have wrestled with understanding their complex morphologies, and taxonomists have attempted to adequately classify them. In this contribution we review the history of their research and then attempt to clarify their taxonomy by presenting a utilitarian hierarchal species determination key.

2. A brief history of cryptospore research

In a ground-breaking paper Gray & Boucot (1971) described permanent spore tetrads that they interpreted as the dispersed spores of early land plants from strata then considered to be of early Silurian age from New York State, USA. Such palynomorphs had previously been reported in the literature, but only rarely as they had often been overlooked and when identified they had usually been interpreted as marine green algal remains (e.g. Cramer & Diez 1972). By the early 1970s the benchmark for the earliest land plants had been established as late Silurian (Pridoli) based on the first occurrence of plant megafossils (reviewed in Wellman 2010). However, dispersed trilete spores, considered most probably to be derived from land plants, were known from the early Silurian of Libya (Hoffmeister 1959). A fierce debate ensued over the course of the 1970s and early 1980s as Jane Gray and her supporters argued for an early land plant origin based on the occurrence of dispersed permanent spore tetrads but her detractors arguing against such an interpretation of these palynomorphs (Banks 1975a, 1975b; Chaloner 1985, 1988; Edwards et al. 1979; Gray & Boucot 1977, 1980). At the time much of the debate focussed on the origin of vascular plants.

Strother & Traverse (1979) added considerably to the debate when they described an assemblage of spore-like palynomorphs, which included permanent dyads, from the Silurian of Pennsylvania, USA. It soon became apparent that such permanent dyads were an important element of these palynomorph assemblages. Richardson et al. (1984) introduced the term ‘cryptospore’ to distinguish these spore-like palynomorphs from dispersed trilete spores. They (p.116) proposed the following definition for cryptospores: “Non-marine sporomorphs (non-pollen grains) with no visible haptotypic features such as contact areas or tetrad marks. Single grains or monads, “permanent” dyads and tetrads are included.” Subsequently Richardson (1988) extended this definition to include single spores, naturally separated from dyads, which possess a circular contact area.

During the debate regarding cryptospore affinities Gray and colleagues had argued for a land plant origin based on: (i) the occurrence in tetrads suggesting meiotic origins; (ii) the dimensions of the tetrads being of a similar size to land plant spores; (iii) the presence of a resistant (presumably sporopollenin) wall; (iv) the occurrence of the tetrads in non-marine deposits and with declining abundances offshore, interpreted as an indication of transport into marine depositional settings. In another ground-breaking paper Gray (1985) recognized that permanent cryptospore tetrads are similar to the spores of certain extant liverworts and suggested they derived from basal bryophyte-like plants that evolved before the advent of vascular plants. This was an important observation as it coincided with some of the first cladistic analyses of land plants that, based on analysis of morphological characters, identified the liverworts as the most basal land plants and sister group to all other plants including vascular plants (Mishler & Churchill 1984, 1985). This directed the argument away from the origin of vascular plants with the realization that land plant origins involved stem-group embryophytes that may have been related to the most basal of the extant

embryophytes: the liverworts. Later Gray (1991) consolidated her arguments for cryptospores deriving from land plants at a bryophyte-like grade of organisation.

There followed a number of debates regarding the structure of different type of cryptospores. Two different types of permanent tetrads had been recognised: tetrahedral tetrads and cross-tetrads (Strother & Traverse 1979). Gray (1991) argued that the latter were simply taphonomical (compressional) variants of tetrahedral tetrads. Johnson (1985) recognised that some dyads constituted two discrete units (true dyads) but other shared a common crosswall (pseudodyads). Richardson (1988) recognised that single spores with a circular contact area (termed a hilum) were the dispersed products of the dissociation of true dyads (in a similar manner that trilete spores are the dispersed product of the dissociation of meiotically produced spore tetrads). Wellman & Richardson (1993) clarified the distinction between both tetrads and dyads that were 'fused' or 'unfused.' A number of workers also emphasized the distinction between true trilete and hilate spores, which were naturally dissociated from tetrads and dyads respectively, and similar forms that were artificially produced by mechanical removal from permanent tetrads and dyads (e.g. Richardson 1988; Steemans et al. 2000). For more details on the morphology of the cryptospores see Richardson (1996a) and Steemans et al. (2012).

During this time and subsequently cryptospore assemblages from the Middle Ordovician to Early Devonian were documented from around the world: Australia (Foster & Williams 1991); Avalonia (Beck & Strother 2001; Burgess 1991; Burgess & Richardson 1991, 1995; Steemans 2001; Wellman 1996); Baltica (Smelror 1987; Hagström 1997; Mehlqvist et al. 2012; Vecoli et al. 2011); Gondwana (e.g. Breuer & Steemans 2013; Breuer et al. 2007, Kermadji 2007; Mizusaki et al. 2002; Richardson 1988; Rubinstein & Steemans

2002; Rubinstein & Vaccari 2004; Spina 2015; Spina & Vecoli 2009; Steemans et al. 2000; Strother et al. 1996; Tekbali & Wood 1991; Vavrdová 1988; Wellman et al. 2000); Laurentia (Beck & Strother 2008; Gray & Boucot 1971; Johnson 1985; Miller & Eames 1982; Pratt et al. 1978; Strother & Traverse 1979); Siberia (Raevskaya et al. 2016); North China (Wang et al. 1997); Peri-Gondwana (Dufka 1995); South China (Wang et al. 1996). The wealth of data generated enabled establishment of biostratigraphical schemes (e.g. Richardson 1996b; Steemans et al. 2000) and analysis of paleogeographical distribution (e.g. Wellman et al. 2013). Of particular significance here was the work of Richardson and his students on various cryptospore-yielding type sections of the Ordovician and Silurian (e.g. Burgess 1991; Burgess & Richardson 1991; Wellman 1996). Paleobiological analyses of cryptospore diversity and other evolutionary patterns were also undertaken (e.g. Richardson & Burgess 1999; Wellman & Gray 2000; Richardson 2007; Steemans 1999, 2000; Strother 2000; Wellman et al. 2013).

In an important development Taylor (1995) reported on the first Transmission Electron Microscope (TEM) analysis of wall ultrastructure of dispersed cryptospores. He discovered a layer of multiple continuous laminae in the walls of a dyad. Such a situation is only known among extant plants in certain liverworts, and thus his findings supported Gray's interpretation of cryptospores representing basal land plants at a bryophyte-like grade of organization. Subsequently Taylor undertook in depth analysis of wall ultrastructure in the various cryptospore morphotypes (e.g. Taylor 1995, 1996, 1997, 2000, 2001, 2002) helping to clarify their structure and shed light on their wall ultrastructure. This led Taylor (2001) to suggest that cryptospores possessed two types of wall ultrastructure.

Following the discovery of the late Silurian (Pridoli) Ludford Lane and Early Devonian (Lochkovian) Hudwick Dingle early land plant Lagerstätte Dianne Edwards and colleagues began a comprehensive analysis of in situ spores of late Silurian-Early Devonian

land plants (Wellman 2014). Mostly these were trilete spores from (in the main) early vascular plants (e.g. Fanning et al. 1988). However, rare cryptospore morphotypes were also discovered in situ including permanent tetrads (Edwards et al. 1999, 2012; Habgood 2000), permanent dyads (Habgood 2000; Morris et al. 2012; Wellman et al. 1998a) and hilate spores (Edwards et al. 2012b; Morris et al. 2011; Wellman et al. 1998b). Rather frustratingly it is often difficult to ascertain the affinities of the parent plants and they seemed to possess a combination of bryophyte-like and tracheophyte-like characters (e.g. some cryptospores derived from plants that had bifurcating sporophytic axes). Ultimately the concept of cryptophyte plants was proposed (Edwards et al. 2014) that “encompass a pool of diversity from which modern bryophytes and vascular plants emerged”.

Starting in 2000 Strother and colleagues began reporting on some highly unusual palynomorphs of Cambrian age, characterised by irregularly configured polyads, that they interpreted as the reproductive propagules of a pre-vascular terrestrial flora (Baldwin et al. 2004; Strother & Beck 2000; Strother et al. 2004; Taylor and Strother 2008, 2009). However, others considered that they more likely represented remains of multicellular algae (resting cysts or even actual body cells) rather than subaerially dispersed spores of land plants (e.g. Wellman 2003, 2010; Wellman et al. 2013). These Cambrian findings led Strother & Beck (2000) to suggest that the definition of the term cryptospore be expanded to accommodate these forms, “...to include all spore-like remains of non-marine origin from the Lower Paleozoic.” At the same time Steemans (2000) proposed a very different emendation to the term cryptospore as, “Alete miospores (non-pollen grains) produced by primitive embryophytes. Single grains or monads, “permanent” dyads and tetrads, and sporomorphs from polyads which may or may not preserve contact area, are included.” In essence Strother and colleagues expanded the definition to include any non-marine spore-like remains, including those deriving from algae and potentially including green algal embryophyte

ancestors, whereas Steemans confined the definition to encompass only subaerially dispersed spores derived from embryophyte land plants. The definition of cryptospores remains controversial as does the classification of these spores with at least two very different ‘turma’ classification systems proposed (Strother 1991; Richardson 1996a).

Further evidence regarding cryptospore affinities was provided by Wellman et al. (2003) who reported sporangial contents, containing cryptospores, recovered from Late Ordovician (Katian) non-marine rocks from Oman. More than a dozen spore masses, many enclosed within a sac believed to represent the sporangial wall or lining, were described. The in situ spores included specimens with permanent dyads and others with permanent tetrads. Analysis of spore wall ultrastructure revealed a laminated wall for the dyads and a homogeneous wall for the tetrads. This finding of in situ cryptospores was important as it demonstrated that older Ordovician cryptospores were also formed in vast numbers within sporangia.

More recently, other new techniques have been utilised in the study of cryptospores. Steemans et al. (2010) undertook micro-FTIR spectroscopy analysis of the chemical composition of the walls of Silurian trilete spores and cryptospores. They demonstrated similar spectra for the walls of trilete spores and cryptospores providing further evidence for embryophyte affinities for cryptospores. Guizar-Sicairos et al. (2015) reported on the first synchrotron analysis of individually picked dispersed cryptospores which provides another technique for analysing structure and wall ultrastructure.

3. Characters used in the classification of cryptospores

Initial attempts to erect cryptospore taxa defined genera based primarily on the number of constituent units (i.e. monad, dyad or tetrad) and polyad configuration (e.g. tetrahedral- or cross-tetrads) (Strother & Traverse 1979). The presence/absence of an enclosing envelope was mentioned but not specifically used to differentiate genera. Ornament (largely of the envelope) and wall thickness was used to define species. Subsequently, Johnson (1985) recognised the difference between fused (pseudodyads) and unfused (true dyads) and separated the genera *Pseudodyadospora* and *Dyadospora*. Richardson (1988) recognised that single spores with a circular contact area (hilum) were the dispersed products of the dissociation of true dyads and Burgess (1991) and Burgess & Richardson (1991) began to assemble a taxonomy for these hilate cryptospores based largely on ornament. As discussed above, Gray (1991) demonstrated that tetrahedral- and cross-tetrads were simply taphonomical (compressional) variants of tetrahedral tetrads. Wellman & Richardson (1993) clarified the distinction between both tetrads and dyads that were ‘fused’ or ‘unfused’ and distinguished between the fused tetrad taxon *Cheilotetras* and unfused tetrad genus *Tetrahedraletes*. A number of workers also emphasized the distinction between true trilete and hilate spores, which were naturally dissociated from tetrads and dyads respectively, and similar forms that were artefacts formed by physical removal from permanent tetrads and dyads (e.g. Richardson 1988; Steemans et al. 2000).

Strother (1991) was the first attempt to establish an artificial morphology-based classification scheme for cryptospores. The highest level (Turma) classification was based on number of units (tetrads, dyads, monads). The next tier down (Subturma) divided the tetrads based on configuration (tetrahedral or cross) and the dyads depending on whether they were fused (pseudodyads) or unfused (true dyads and spores separated from these that we now call hilate cryptospores). Richardson (1996a) proposed an entirely different scheme. In this classification the highest tier (Turma) divided cryptospores into naked and envelope-enclosed

forms. The next tier down (Suprasubturma) subdivided these categories into monads, hilate cryptospores, unfused polyads (dyads and tetrads) and fused polyads. A third tier (Infraturma) utilised ornament. Strother (2000) provides a comprehensive account of the development of these two schemes and includes a key to the polyad genera assigned to cryptospores.

The stark differences between these two classification schemes proposed for cryptospores serves to emphasize just how difficult it is to ascertain which morphological characters of cryptospores are biologically informative. Clearly related to the fundamental process of sporogenesis is: (i) the number of units present in polyad cryptospores; (ii) whether they are dispersed as permanent polyads or dissociated prior to dispersal (e.g. true dyads **versus** hilate cryptospores). The nature of the junction between polyad cryptospores (fused versus unfused) also relates to the process of sporogenesis and spore wall development. More perplexing is the biological relationships of envelopes. Do they represent remnant spore mother cell or products of a tapetum? These biological interpretations have been long debated with little consensus (details of the debates may be found in the papers referenced herein). The consequence of these uncertainties is that the vital question of which characters should have most weighting in cryptospore classification remains unresolved.

4. A key for the identification of cryptospores (fig. 1)

4.1. Definition of the term cryptospore

We prefer the Steemans (2000) definition of cryptospores that explicitly considers them to be the dispersed spores of the earliest land plants (embryophytes). Since they were first described numerous lines of evidence have demonstrated that most cryptospore taxa are land plant dispersed spores (reviewed above). We believe that those that cannot be linked with

land plant dispersed spores should be excluded from the cryptospores to prevent forming a ‘dustbin’ group that includes various protists, some of which may not even be meiotically produced dispersed spores that are unrelated to the earliest land plants. For example, Tetraletes/Quadrisporites was for a long time considered as a cryptospore by many workers. However, Bock et al (2013), Le Hérissé (2002) and Wellman et al. (2015) demonstrated that it has escape structures and is almost certainly an algal resting cyst rather than a dispersed spore. We suspect that other forms such as Qualiaspora may represent euglenids but this is as yet unproven. We interpret the Cambrian forms described by Strother and colleagues as resting cysts or desiccation-resistant body cells of some form of green alga. However, we do appreciate that recognition of the earliest stages of early land plant spore evolution may be challenging (see Wellman 2003, 2004): obviously the origin of the land plants (embryophytes) from a green algal ancestor involved the origin of numerous sporopollenin-coated, meiotically produced spores, presumably from a sporopollenin coated zygote or algal resting cyst, and recognition of transitional forms may not be easy. We have included all of the above taxa in the key but indicate those taxa we suspect may not represent subaerially dispersed spores of land plants (cryptospores sensu Steemans 2000) with an asterisk.

4.2. Comment on fused versus unfused polyads

In permanent polyad cryptospores the individual spores may be fused or unfused (see discussion in Wellman & Richardson 1993 who introduced this terminology). As discussed in detail by Wellman (1996) it may be difficult to distinguish between the two, particularly in material that is poorly preserved or of high thermal maturity, and indeed the exact structure of these cryptospores is difficult to ascertain. TEM analysis has gone some way toward clarifying the precise nature of the junctions between spores in polyads and it is clear that some appear to share a common wall (i.e. fused) and others possess their own separate walls

(i.e. unfused) (e.g. Taylor 1995). Unfortunately, however, even using TEM it is often difficult to distinguish whether some polyads are fused or unfused.

4.3. Comment on the nature of envelopes

Many cryptospores are enclosed with an envelope that may be loose or tight fitting and may be laevigate or variously ornamented. These envelopes can obscure the cryptospore beneath, particularly in material that is poorly preserved or of high thermal maturity, making it difficult to observe the nature of the junctions in polyad cryptospores (i.e. fused or unfused) and the nature of any ornament on the spores (see discussion in Wellman 1996). It is also possible that loose fitting envelopes may be stripped from some specimens during transport and diagenesis. Thus envelope absence/presence may be an unreliable character for taxonomic designation.

4.4. The Key

Table 1 below represents a key for the identification of cryptospore taxa. It has been subdivided in three main parts according the principal morphological characters: Firstly, number of constituent units (monad, dyad, tetrad); Secondly, naked or envelope-enclosed; thirdly, several different criteria are taken in account including type of ornament and wall thickness and folding. Only validly described species are included in Table 1; species in open nomenclature are excluded.

5. Conclusions

We have presented a key designed to facilitate the identification of early land plant spores (Cryptospores sensu Steemans 2000). However, we recognise that controversy exists regarding: (i) what should be included in the cryptospores; (ii) which characters should have

highest weighting in cryptospore taxonomy. Regarding the former, we take a very conservative view and include only forms where we believe the weight of evidence points to the palynomorph representing the dispersed spore of an early land plants (embryophyte). Regarding the latter, we accept that only further evidence will allow us to agree on polarity and weighting of characters used in cryptospore taxonomy.

Acknowledgments

This paper is dedicated to our friend and colleague Gordon Wood. We would like to thank T. Servais (Lille, France), M. Miller (Tulsa, Oklahoma), and J. Riding (Nottingham, UK) for their invaluable help in the writing of this paper.

References

- Baldwin CT, Strother PK, Beck JH, Rose E. 2004. Palaeoecology of the Bright Angel Shale in the eastern Grand Canyon, Arizona, USA, incorporating sedimentological, ichnological and palynological data. In: McIlroy D, editor. The application of ichnology to palaeoenvironmental and stratigraphic analysis. London, UK: Geological Society; Special Publications 228; p. 213–236.
- Banks HP. 1975a. Early Vascular Land Plants: Proof and Conjecture. *BioScience* 25:730–737.
- Banks HP. 1975b. The oldest vascular land plants: A note of caution. *Review of Palaeobotany and Palynology* 20:13–25.
- Beck JH, Strother PK. 2001. Silurian spores and cryptospores from the Arisaig Group, Nova Scotia, Canada. *Palynology* 25:127–177.

- Beck JH, Strother PK. 2008. Miospores and cryptospores from the Silurian section at Allenport, Pennsylvania, USA. *Journal of Paleontology* 82:857–883.
- Bock C, Luo W, Kusber W-H, Hegewald E, Pažoutová M, Krienitz L. 2013. Classification of crucigenoid algae: phylogenetic position of the reinstated genus *Lemmermannia*, *Tetrastrum* spp. *Crucigenia tetrapedia*, and *C. lauterbornii* (Trebouxiophyceae, Chlorophyta). *Journal of Phycology* 49:329–339.
- Breuer P, Al-Ghazi A, Al-Ruwaili M, Higgs KT, Steemans P, Wellman CH. 2007. Early to Middle Devonian miospores from northern Saudi Arabia. *Revue de micropaléontologie* 50:27–57.
- Breuer P, Steemans P. 2013. Devonian spore assemblages from northwestern Gondwana: taxonomy and biostratigraphy London: The Palaeontological Association. 89:163
- Breuer P, Miller MA, Leszczyński S, Steemans P. 2015. Climate-controlled palynofacies and miospore stratigraphy of the Jauf Formation, Lower Devonian, northern Saudi Arabia. *Review of Palaeobotany and Palynology* 212:187–213.
- Burgess ND. 1991. Silurian cryptospores and miospores from the type Llandovery area, southwest Wales. *Palaeontology* 34:575–599.
- Burgess ND, Richardson JB. 1991. Silurian cryptospores and miospores from the type Wenlock area, Shropshire, England. *Palaeontology* 34:601–628.
- Burgess ND, Richardson JB. 1995. Late Wenlock to early Pridoli cryptospores and miospores from south and southwest Wales, Great Britain. *Palaeontographica Abt. B* 236:1–44.
- Chaloner WG. 1985. Discussion. *Philosophical Transactions of the Royal Society of London B* 309:192.
- Chaloner WG. 1988. Early land plants - the saga of a great conquest Koeltz, Königstein/Taunus. Greuter W, Zimmer B, editors. *Proceedings of the XIV International Botanical Congress* p. 301–316.

- Combaz A. 1967. Un microbios du Trémadocien dans un sondage d'Hassi-Messaoud. Actes Actes de la Société Linnéenne de Bordeaux.104:1-26.
- Cramer FH, Díez MDCR. 1972. North American Silurian palynofacies and their spatial arrangement: Acritarchs. *Palaeontographica*, Abt. B 138:107–180.
- Dufka P. 1995. Upper Wenlock miospores and cryptospores derived from a Silurian volcanic island in the Prague Basin (Barrandian area, Bohemia). *Journal of Micropalaeontology* 14:67–79.
- Edwards D, Bassett MG, Rogerson CW. 1979. The earliest vascular land plants: continuing the search for proof. *Lethaia* 12:313–324.
- Edwards D, Morris JL, Richardson JB, Axe L, Davies KL. 2012. Notes on sporangia and spore masses containing tetrads or monads from the Lower Devonian (Lochkovian) of the Welsh Borderland, U.K. *Review of Palaeobotany and Palynology* 179:56–85.
- Edwards D, Morris JL, Richardson JB, Kenrick P. 2014. Cryptospores and cryptophytes reveal hidden diversity in early land floras. *New Phytologist* 202:50–78.
- Edwards D, Richardson JB, Axe L, Davies KL. 2012b. A new group of Early Devonian plants with valvate sporangia containing sculptured permanent dyads. *Botanical Journal of the Linnean Society* 168:229–257.
- Edwards D, Wellman CH, Axe L. 1999. Tetrads in sporangia and spore masses from the Upper Silurian and Lower Devonian of the Welsh Borderland. *Botanical Journal of the Linnean Society* 130:111–156.
- Fanning U, Richardson JB, Edwards D. 1988. Cryptic evolution in early land plant. *Evolutionary Trends in Plants* 2:13–24.
- Foster CB, Williams GE. 1991. Late Ordovician-Early Silurian age for the Mallowa Salt of the Carribuddy Group, Canning Basin, Australia, based on occurrences of *Tetraedraletes medinensis* Strother & Traverse 1979. *Australian Journal of Earth Sciences* 38:223-228.

- Ghavidel-syooki M. 2016. Miospore assemblages from Late Ordovician (Katian-Hirnantian), Ghelli Formation, Alborz Mountain Range North-eastern Iran: Palaeophytogeographic and palaeoclimatic implications. *Journal of Sciences, Islamic Republic of Iran* 27:135–159.
- Gray J. 1985. The microfossil record of early land plants; advances in understanding of early terrestrialization, 1970-1984. In: Chaloner WG, Lawson JD, editors. *Evolution and environment in the Late Silurian and Early Devonian*. *Philosophical Transactions of the Royal Society of London B* 309:167–195.
- Gray J. 1991. Tetrahedraletes, Nodospora and the 'cross' tetrad: an accretion of myth. In: Blackmore S, Barnes S, editors. *Patterns of diversification. The Systematics Association Special Volume. Pollen et Spores* 44:49–87.
- Gray J, Boucot AJ. 1971. Early Silurian spore tetrads from New York: Earliest New World evidence for vascular plants. *Science* 173:918–921.
- Gray J, Boucot AJ. 1977. Early vascular land plants: proof and conjecture. *Lethaia* 10:145–157.
- Gray J, Boucot AJ. 1980. Microfossils and evidence of land plant evolution. *Lethaia* 13:174.
- Guizar-Sicairos, M, Holler M, Diaz A, Da Silva JC, EHR Tsai, Bank O, Martines-Perez C, Donoghue PCJ, Wellman CH, Menzel A. 2015. Ptychographic nanotomography at the Swiss Light Source. In: Lai B, editor. *X-Ray Nanoimaging: Instruments and Methods II. Proceedings of Society of Photo-Optical Instrumentation Engineers (SPIE) Volume: 9592. Article Number: UNSP 95920A*
- Habgood KS. 2000. Two cryptospore-bearing land plants from the Lower Devonian (Lochkovian) of the Welsh Borderland. *Botanical Journal of the Linnean Society* 33:203–227.
- Hagström J. 1997. Land-derived palynomorphs from the Silurian of Gotland, Sweden. *GFF* 119:301–316.

- Hennelly JPF. 1959. Spores and pollen from a Permian-Triassic transition, N.S.W. . Proc Linn Soc New South Wales.363-369.
- Hoffmeister WS. 1959. Lower Silurian plant spores from Libya. *Micropaleontology* 5:331–334.
- Higgs KT. 2004. An Early Devonian (Lochkovian) microflora from the Freshwater West Formation, Lower Old Red Sandstone, southwest Wales. *Geological Journal*.39:359-374.
- Johnson NG. 1985. Early Silurian palynomorphs from the Tuscarora Formation in central Pennsylvania and their paleobotanical and geological significance. *Review of Palaeobotany and Palynology* 45:307–360.
- Kenrick P, Wellman CH, Schneider H, Edgecombe GD. 2012. A timeline for Terrestrialization: consequences for the Carbon Cycle in the Palaeozoic. *Philosophical Transactions of the Royal Society of Edinburgh B*.367:519-536.
- Kermandji AMH. 2007. Silurian-Devonian miospores from the western and central Algeria. *Revue de micropaléontologie* 50:109–128.
- Le Hérisse A. 2002. Paleoecology, biostratigraphy and biogeography of late Silurian to early Devonian acritarchs and prasinophycean phycomata in well A1-61, Western Libya, North Africa. In: Steemans P, Servais T, Streeel M, editors. *Palaeozoic Palynology: A special issue in honour of Dr Stanislas Loboziak*. *Review of Palaeobotany and Palynology*; p. 359–395.
- Mehlqvist K, Vajda V, Steemans P. 2012. Early land plant spore assemblages from the Late Silurian of Skåne, Sweden. *GFF* 134:133–144.
- Miller MA, Eames LE. 1982. Palynomorphs from the Silurian Medina Group (Lower Llandovery) of the Niagara Gorge, Lewiston, New York, U.S.A. *Palynology* 6:221–254.

- Miller MA, Melvin J. 2005. Significant new biostratigraphic horizons in the Qusaiba Member of the Silurian Qalibah Formation of central Saudi Arabia, and their sedimentologic expression in a sequence stratigraphic context. *GeoArabia*.10:49-92.
- Mishler BD, Churchill SP. 1984. A cladistic approach to the phylogeny of the “Bryophytes.” *Brittonia* 36:406–424.
- Mishler BD, Churchill SP. 1985. Transition to a land flora: phylogenetic relationships of the green algae and bryophytes. *Cladistics* 1:305–328.
- Mizusaki AM, Melo JHG, Lelarge ML, Steemans P. 2002. Vila Maria Formation, Paraná Basin, Brazil - An example of integrated geochronological and palynological datings. *Geological Magazine* 139:453–463.
- Morris JL, Edwards D, Richardson JB, Axe L. 2012. New dyad-producing plants from the Lower Devonian (Lochkovian) of the Welsh Borderland. *Botanical Journal of the Linnean Society* 169:569–595.
- Morris JL, Richardson JB, Edwards D. 2011. Lower Devonian plant and spore assemblages from Lower Old Red Sandstone strata of Tredomen Quarry, South Wales. *Review of Palaeobotany Palynology* 165:183–208.
- Pratt LM, Phillips TL, Dennison JM. 1978. Evidence of non-vascular land plants from the early Silurian (Llandoveryan) of Virginia, U.S.A. *Review of Palaeobotany and Palynology* 25:121–149.
- Raevskaya E, Dronov A, Servais T, Wellman CH. 2016. Cryptospores from the Katian (Upper Ordovician) of the Tungus basin: The first evidence for early land plants from the Siberian paleocontinent. *Review of Palaeobotany and Palynology* 224:4–13.
- Richardson JB. 1988. Late Ordovician and Early Silurian cryptospores and miospores from northeast Libya. In: El-Arnauti A, Owens B, Thusu B, editors. *Subsurface*

- palynostratigraphy of northeast Libya. Benghazi, Libya: Garyounis University Publications; p. 89–109.
- Richardson JB. 1996a. Taxonomy and classification of some new Early Devonian cryptospores from England. In: Cleal CJ, editor. Studies on early land plant spores from Britain. Great Britain: Special Papers in Palaeontology 55: 7–40.
- Richardson JB. 1996b. Chapter 18A - Lower to middle Palaeozoic records of terrestrial palynomorphs. In: Jansonius J, McGregor DC, editors. Palynology: principles and applications. Salt Lake City, UT: American Association of Stratigraphic Palynologists Foundation; p. 391–407.
- Richardson JB. 2007. Cryptospores and miospores, their distribution patterns in the Lower Old Red Sandstone of the Anglo-Welsh Basin, and the habitat of their parent plants. *Bulletin of Geosciences* 82:355–364.
- Richardson JB, Burgess ND. 1999. Sporomorph evolution in the Anglo-Welsh Basin: tempo and parallelism. In: Kurmann MH, Hemsley AR, editors. The evolution of plant architecture. Royal Botanic Gardens, Kew; p. 35–49.
- Richardson JB, Ford JH, Parker F. 1984. Miospores, correlation and age of some Scottish Lower Old Red Sandstone sediments from the Strathmore region (Fife and Angus). *Journal of Micropalaeontology* 3:109–124.
- Rubinstein CV, Steemans P. 2002. Miospore assemblages from the Silurian-Devonian boundary, in borehole A1-61, Ghadamis Basin, Libya. In: Steemans P, Servais T, Streefling M, editors. Paleozoic Palynology: A special issue in honour of Dr Stanislas Loboziak. *Review of Palaeobotany and Palynology* 118:397–421.
- Rubinstein CV, Vaccari NE. 2004. Cryptospore assemblages from the Ordovician/Silurian boundary in the Puna region, North-west Argentina. *Palaeontology* 47:1037–1061.

- Smelror M. 1987. Llandovery and Wenlock miospores and spore-like microfossils from the Ringerike district, Norway. *Norsk Geologisk Tidsskrift* 67:143–150.
- Spina A. 2015. Latest Ordovician (Hirnantian) miospores from the NI-2 well, Algeria, North Africa, and their evolutionary significance. *Palynology* 39:205–219.
- Spina A, Vecoli M. 2009. Palynostratigraphy and vegetational changes in the Siluro-Devonian of the Ghadamis Basin, North Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 282:1–18.
- Stemans P. 1999. Paléodiversification des spores et des cryptospores de l'Ordovicien au Dévonien inférieur. *Géobios* 32:341–352.
- Stemans P. 2000. Miospore evolution from the Ordovician to the Silurian. *Review of Palaeobotany and Palynology* 113:189–196.
- Stemans P. 2001. Ordovician cryptospores from the Oostduinkerke borehole, Brabant Massif, Belgium. *Géobios* 34:3–12.
- Stemans P, Higgs KT, Wellman CH. 2000. Cryptospores and trilete spores from the Llandovery, Nuayyim-2 Borehole, Saudi Arabia. In: Al-Hajri S, Owens B, editors. *Stratigraphic palynology of the Palaeozoic of Saudi Arabia*. Manama, Bahrain: Gulf Petrolink; p. 92–115.
- Stemans P, Le Hérisse A, Bozdogan N. 1996. Ordovician and Silurian cryptospores and miospores from Southeastern Turkey. *Review of Palaeobotany and Palynology* 93:35–76.
- Stemans P, Lepot K, Marshall CP, Le Hérisse A, Javaux EJ. 2010. FTIR characterisation of the chemical composition of Silurian miospores (cryptospores and trilete spores) from Gotland, Sweden. *Review of Palaeobotany and Palynology* 162:577–590.
- Stemans P, Petus E, Breuer P, Mauller-Mendlowicz P, Gerrienne P. 2012. Palaeozoic innovations in the micro- and megafossil plant record: from the earliest plant spores to the

- earliest seeds. In: *Extinction intervals and biogeographic perturbations through time – Earth and Life*. Springer. p. 437-477.
- Stemans P, Rubinstein CV, Melo JHG. 2008. Siluro-Devonian miospore biostratigraphy of the Urubu River area, western Amazon Basin, northern Brazil. *Geobios* 41:263–282.
- Strother PK. 1991. A classification schema for the Cryptospores. *Palynology* 15:219–236.
- Strother PK, Al-Hajri S, Traverse A. 1996. New evidence for land plants from the lower Middle Ordovician of Saudi Arabia. *Geology* 24:55–59.
- Strother PK. 2000. Cryptospores: The origin and early evolution of the Terrestrial Flora. In: Gastaldo RA, DiMichele WA, editors. *Phanerozoic Terrestrial Ecosystems*. Columbus, OH: The Paleontological Society Papers 6:3–19.
- Strother PK. 2016. Systematics and evolutionary significance of some new cryptospores from the Cambrian of eastern Tennessee, USA. *Review of Palaeobotany and Palynology* 227 : 28-41.
- Strother PK, Beck JH. 2000. Spore-like microfossils from Middle Cambrian strata: expanding the meaning of the term cryptospore. In: Harley MM, Morton CM, Blackmore S, editors. *Pollen and spores: morphology and biology*. Royal Botanic Gardens, Kew; p. 413–424.
- Strother PK, Traverse A. 1979. Plant microfossils from the Llandoveryian and Wenlockian rocks of Pennsylvania. *Palynology* 3:1–21.
- Strother PK, Traverse A, Vecoli M. 2015. Cryptospores from the Hanadir Shale Member of the Qasim Formation, Ordovician (Darriwilian) of Saudi Arabia: taxonomy and systematics. *Review of Palaeobotany and Palynology* 212: 97–110.
- Strother PK, Wood GD, Taylor W, Beck J. 2004. Middle Cambrian cryptospores and the origin of land plants. *Association of Australasian Palaeontologists Memoir* 29:99–113.

- Taylor WA. 1995. Ultrastructure of *Tetraedraletes medinensis* (Strother and Traverse) Wellman and Richardson, from the Upper Ordovician of Southern Ohio. *Review of Palaeobotany and Palynology* 85:183–187.
- Taylor WA. 1996. Ultrastructure of Lower Paleozoic dyads from Southern Ohio. *Review of Palaeobotany and Palynology* 92:269–279.
- Taylor WA. 1997. Ultrastructure of Lower Paleozoic dyads from southern Ohio II: *Dyadospora murusattenuata*, functional and evolutionary considerations. *Review of Palaeobotany and Palynology* 97:1–8.
- Taylor WA. 2000. Spore wall development in the earliest land plants. In: Harley MM, Morton C.M, Blackmore S, editors. *Pollen and spores: morphology and biology*. Royal Botanic Gardens, Kew; p. 425–434.
- Taylor WA. 2001. Evolutionary hypothesis of cryptospore producing plants based on wall ultrastructure. In: Goodman DK, Clarke RP, editors. *Proceedings of the IX International palynological Congress, Houston, Texas, USA 1996*: American Association of Stratigraphic palynologists Foundation; p. 11–15
- Taylor WA. 2002. Studies in cryptospore ultrastructure: variability in the tetrad genus *Tetraedraletes* and type material of the dyad *Dyadospora murusattenuata*. *Review of Palaeobotany and Palynology* 119: 325–334.
- Taylor WA, Strother PK. 2008. Ultrastructure of some Cambrian palynomorphs from the Bright Angel Shale, Arizona, USA. *Review of Palaeobotany and Palynology* 151:41–50.
- Taylor WA, Strother PK. 2009 Ultrastructure, morphology, and topology of Cambrian palynomorphs from the Lone Rock Formation, Wisconsin, USA. *Review of Palaeobotany and Palynology* 153: 296–309.

Tekbali AO, Wood GD. 1991. Silurian spores, acritarchs and chitinozoans from the Baní Walíd Borehole of the Ghadámis Basin, Northwest Libya. In: Salem MJ, Hammuda OS, Eliagoubi BA, editors. *Geology of Libya IV*. Amsterdam, NL: Elsevier;p. 1243–1273.

Turnau E, Fijakowska-Mader A, Filipiak P, Stempień-Salek M. 2003. Miospory. In: *Budowa geologiczna Polski, Atlas skamieniałości przewodnich i charakterystycznych*. Warszawa. p. 623-678

Turnau E, Milaczewski L, Wood GD. 2005. Spore stratigraphy of Lower Devonian and Eifelian (?), alluvial and marginal marine deposits of the Radom-Lublin area (central Poland). *Ann Soc Geol Poloniae*.75:121-137.

.

Vavrdová M. 1988. Further acritarchs and terrestrial plant remains from the Late Ordovician at Hlasna Treban (Czechoslovakia). *Casopis Mineralogii Geologii* 33: 1–10.

Vavrdová M. 1990. Early Ordovician acritarchs from the locality Myto near Rokycany (late Arenig, Czechoslovakia). *Cas Mineral Geol.*35:239-250.

Vecoli M, Delabroye A, Spina A, Hints O. 2011. Cryptospore assemblages from Upper Ordovician (Katian-Hirnantian) strata of Anticosti Island, Quebec, Canada, and Estonia: Palaeophytogeographic and palaeoclimatic implications. *Review of Palaeobotany and Palynology* 166: 76–93.

Wang Y, Li J, Wang R. 1997. Latest Ordovician cryptospores from southern Xinjiang, China. *Review of Palaeobotany and Palynology*. 99:61–74.

Wang Y, Ouyang S, Cai CY. 1996. Early Silurian microfossil plants from the Xiushan Formation in Guizhou Province, China and their paleobotanical significance. *Palaeobotanist* 44:191–193.

Wellman CH. 1993. A Lower Devonian sporomorph assemblage from the Midland Valley of Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 84:117-136.

- Wellman CH. 1996. Cryptospores from the type area for the Caradoc Series (Ordovician) in southern Britain. *Palaeontology* 55:103–136.
- Wellman, CH. 2003. Dating the origin of land plants. In: Donoghue PCJ, Smith MP, editors. *Telling the evolutionary time: molecular clocks and the fossil record. Systematic Association Special Volumes 66*, Taylor & Francis, London, 288 pp.
- Wellman, CH. 2004. Origin, function and development of the spore wall in early land plants. In: Hemsley AR, Poole I, editors. *The evolution of plant physiology. Royal Botanic Gardens, Kew*; p. 43–63.
- Wellman CH. 2010. The invasion of the land by plants: when and where? *New Phytologist* 188:306–309.
- Wellman CH. 2014. The nature and evolutionary relationships of the earliest land plants. *New Phytologist*.202:1–3.
- Wellman CH, Edwards D, Axe L. 1998a. Permanent dyads in sporangia and spore masses from the Lower Devonian of the Welsh Borderland. *Botanical Journal of the Linnean Society* 127:117–147.
- Wellman CH, Edwards D, Axe L. 1998b. Ultrastructure of laevigate hilate cryptospores in sporangia and spore masses from the Upper Silurian and Lower Devonian of the Welsh Borderland. *Philosophical Transactions of the Royal Society of London B* 53:1983–2004.
- Wellman CH, Gray J. 2000. The microfossil record of early land plants. *Philosophical Transactions of the Royal Society of London B* 355:717–732.
- Wellman CH, Higgs K, Steemans P. 2000. Spore assemblages from a Silurian sequence in borehole Hawiyat from Saudi Arabia. In: *Stratigraphic palynology of the Palaeozoic of Saudi Arabia. Manama, Bahrain: Geoarabia. p. 116-133.*
- Wellman CH, Osterloff PL, Mohiuddin U. 2003. Fragments of the earliest land plants. *Nature* 425:282–285.

- Wellman CH, Richardson JB. 1993. Terrestrial plant microfossils from Silurian inliers of the Midland Valley of Scotland. *Palaeontology* 36:155–193.
- Wellman CH, Richardson JB. 1996. Sporomorph assemblages from the 'Lower Old Red Sandstone' of Lorne Scotland. In: Cleal CJ, editor. *Studies on early land plant spores from Britain* Special Papers in Palaeontology 55: 41–101.
- Wellman CH, Steemans P, Vecoli M. 2013. Palaeophytogeography of Ordovician–Silurian land plants. In: Harper D, Servais T, editors. *Early Palaeozoic Biogeography and Palaeogeography*. London, UK: Geological Society, Memoirs 38:461–476.
- Wellman CH, Steemans P, Miller MA. 2015. Spore assemblages from Upper Ordovician and lowermost Silurian sediments recovered from the Qusaiba-1 shallow core hole, Qasim region, central Saudi Arabia. *Review of Palaeobotany and Palynology* 212:111–126.