Palaeophytogeography of Ordovician-Silurian land plants

Charles H. Wellman[1] Philippe Steemans[2] Marco Vecoli[3]

[1]Department of Animal and Plant Sciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, UK

[2]Paléobotanique, Paléopalynologie, Micropaléontologie (PPM), University of Liège, Batiment B-18, allée du 6-Août, 4000, Liège-1, Belgium

[3]Université Lille 1, UMR 8157 "Géosystèmes" CNRS, Villeneuve d'Ascq F-59655, France

Abstract. A database of all reported Ordovician-Silurian land plant megafossil and dispersed spore assemblages has been assembled. For each assemblage a list of taxa has been prepared and its location plotted on new palaeocontinental reconstructions. These new data compilations are analyzed with respect to palaeophytogeographical differentiation and various patterns of taxon diversity and morphological disparity that emerged during the origin, adaptive radiation and geographical spread of land plants. Our analyses include new quantitative assessments.

Introduction

The aim of this contribution is to review the palaeophytogeography of the earliest land vegetation in conjunction with newly created palaeocontinental reconstructions established for the Ordovician and Silurian. It is anticipated that this exercise will shed new light on the distribution of vegetation over this interval, in addition to providing an independent test of the new palaeocontinental reconstructions. Palaeocontinental reconstructions are mainly based on evidence from palaeomagnetism and the distribution of marine fossils. However, dispersed plant spores are by far the most common type of continental fossil, and provide an independent line of evidence useful in palaeocontinental reconstruction that is often neglected. They have the potential to provide both latitude and longitude constraints.

The Ordovician-Silurian time interval is of great interest regarding land plants as it witnessed their origin and subsequent diversification as they successfully colonized the land. The palaeophytogeography of the earliest land plants has been regularly reviewed over the years. However, the analysis presented herein differs from most previous attempts in that it: (i) integrates both the megafossil and dispersed spore fossil records of early land plants (with both at the species level); (ii) considers the adaptive radiation and dispersal of land plants quantitatively in terms of measures of dispersed spore palaeophytogeographic distribution, taxonomic diversity and morphological disparity; (iii) utilises the most comprehensive dispersed spore database hitherto contructed. Many previous reviews have been restricted to the very meagre plant megafossil record (e.g. Edwards 1990; Raymond *et al*. 2006). Reviews of the more extensive dispersed spore record have tended to be rather general in approach (e.g. Richardson 1996; Steemans 1999, 2000; Wellman and Gray 2000). Some reviews have considered both fossil records (e.g. Edwards and Wellman 2001; Gensel 2009; Steemans *et al*. 2010) but these have been little integrated and none considered both plant megafossils and dispersed spores at the species level. We hope that our new analysis, combining both fossil records at the species level and utilising new palaeocontinental reconstructions, will shed new light on the spatial/temporal (i.e. palaeophytogeographical/evolutionary) distribution of the earliest vegetation. In addition we present preliminary quantitative data on dispersed spore palaeogeographical distribution, taxonomic diversity and morphological disparity. These data are critical to our understanding of early land plant palaeophytogeography as they demonstrate the nature of the adaptive radiation and palaeogeographical dispersal of early land plants.

The early land plant fossil record

Plants leave two fossil records: a plant megafossil record and a dispersed spore fossil record. The plant megafossil record consists of fossils of a significant portion of the actual plant. For the earliest land plants it is very incomplete and is highly biased (e.g. Edwards 1990). These plants were generally diminutive and either lacked, or contained limited, recalcitrant tissues. Thus they were highly unlikely to be preserved. In fact there are only 23 localities where Ordovician-Silurian land plants have been reported (see Appendix 1). The early land plant record is also highly biased. Firstly, it favours plants that contain recalcitrant tissues (e.g. sterome). Many of the earliest land plants are believed to have been ‘bryophyte-like’ in construction and completely lacked recalcitrant tissues, while even some of the Protracheophytes contained very little recalcitrant tissue (e.g. the Rhynie chert plant *Aglaophyton*). Consequently, they are only preserved in extremely rare cases of exceptional preservation. Secondly, terrestrial strata are uncommon in the Ordovician-Silurian. In fact all of the known Silurian plant megafossil assemblages are allochthonous and from near-shore marine strata. Thus plants that lived near the sea, or alongside water courses that drained into the sea, are probably overrepresented. Thirdly, rare cases of exceptional preservation skew the megafossil record (see later the discussion concerning the charcoalified early land plants from the Pridoli of the Anglo-Welsh basin).

In contrast to the plant megafossil record, the early land plant dispersed spore fossil record is abundant (Appendix 2) and less biased. This is because Ordovician-Silurian land plants were most likely all free-sporing homosporous plants that relied on wind to distribute their spores. Free-sporing homosporous plants: (i) produce small isospores in vast numbers; (ii) have the ability to disperse these small spores long distances by the vectors of wind and water, so they commonly accumulated in freshwater and near-shore marine environments suitable for sediment preservation; (iii) have spores with high fossilization potential because they have a resistant sporopollenin wall that serves to protect them during transportation. Despite the richness of the dispersed spore record one must bear in mind that it too suffers from various biases. Thus plants that produced abundant spores (over producers) and those that lived near watercourses that readily transported their spores into sedimentary environments are over represented (summarized in Steemans *et al*. 2007).

Critical to understanding the fossil record of early land plants is integrating the plant megafossil and dispersed spore fossil records. This is achieved primarily through studies of *in situ* spores that enable identification of spore-parent plant relationships. Studies of Ordovician-Silurian *in situ* spores are reviewed in Allen (1980), Gensel (1980), Fanning *et al*. (1991); Balme (1995) and Edwards and Richardson (1996). Since these reviews records of Ordovician-Silurian *in situ* spores have burgeoned, largely due to work on the Late Silurian deposits of the Anglo-Welsh basin, including that on the exceptionally preserved charcoalified flora of Ludford Corner (e.g. Edwards *et al*. 1995, 1996, 1999; Edwards 1996; Rogerson *et al*. 1993, 2002; Wellman *et al*. 1998a) (see p. 000). However, it remains the case that many taxa of Ordovician-Silurian spores (species and higher taxa including entire morphotypes) are not known *in situ*. Whilst recent research suggests possible biological affinities at higher taxonomic levels for some groups (e.g. Emphanoid spores in Taylor *et al*. 2011) others remain totally unknown (e.g. patinate spores).

Understanding of plant spore relationships can also be gleaned from studies of spore wall ultrastructure. Spore wall development is often characteristic in different plant groups (summarized for extant homosporous plants in Brown and Lemmon 1990; Lugardon 1990) and thus can be used to infer the biological relationships of spores (e.g. Wellman 2004). Ordovician-Silurian studies of spore wall ultrastructure follow two modes of investigation. Firstly, spore wall ultrastructure has been studied in plants containing *in situ* spores. Relevant studies are from Ordovician sporangia from Oman (Wellman *et al*. 2003) and Silurian sporangia from the Anglo-Welsh Basin (Rogerson *et al*. 1993, 2002; Edwards *et al*. 1995, 1996, 1999; Wellman *et al*. 1998a), including those that are exceptionally preserved by charcoalification. Secondly, individual Ordovician-Silurian dispersed spores have been sectioned. These include various cryptospore morphotypes (Taylor 1995a, 1995b, 1996, 1997, 2002) and trilete spores (Taylor 2003; Johnson and Taylor 2005). These studies have provided some evidence for possible relationships among the different spore morphotypes, particularly when considered in conjunction with information on *in situ* occurrence (most recently summarized in Edwards and Wellman 2001; Taylor 2000, 2001; Wellman 2004). Unfortunately, however, to date these studies have provided little definitive information regarding the biological affinities of the spore producers other than that some of the cryptospores have liverwort-like spore wall ultrastructure (e.g. Taylor 1995a; Wellman *et al*. 2003) and some emphanoid spores (i.e. *Emphanisporites*) may derive from a protracheophyte-hornwort clade (Taylor *et al*. 2011).

It is extremely fortunate that the fossil record of Ordovician-Silurian land plants includes an exceptionally preserved biota. The Ludford Corner locality in the Welsh Borderland is of Pridoli age and yields an assemblage of charcoalified plant mesofossils

(Glasspool *et al*. 2004) in addition to assemblages of well preserved spores. These fossils have enabled detailed anatomical investigation of Silurian plants washed into a shoreface-shallow marine environment (Jeram *et al*. 1990; Rogerson *et al*. 1993, 2002; Edwards *et al*. 1995, 1996, 1999; Edwards 1996; Wellman *et al*. 1998a; Glasspool *et al*. 2004), including detailed studies of *in situ* spores and their wall ultrastructure, and comparison with coeval dispersed spore assemblages (Richardson and Lister 1969; Richardson and Rasul 1990).

The origin and early diversification of land plants.

Numerous lines of evidence, from extant and fossil plants, suggest that the embryophytes (land plants) are monophyletic (summarized in Graham 1993; Kenrick and Crane 1997; Qiu 2008). There is very strong evidence, based on morphological and molecular studies, that land plants evolved from some form of charophycean green algae (e.g. Graham 1993; Karol *et al*. 2001; Qiu 2008). Thus it appears that land plants evolved from a charophycean green algal ancestor as an adaptive response to the invasion of the land (i.e. as they overcame the physiological problems associated with moving from an aquatic to subaerial existence). However, phylogenies of extant land plants are in a state of flux with various scenarios presented based on evidence from both morphological and molecular studies. Most concur that liverworts are the most basal group of living plants, with either the mosses, or more likely the hornworts, sister group to the vascular plants (e.g. Qui *et al*. 2006). Analyses consistently reveal that within the extant vascular plants lycopsids form a sister group relationship with all other vascular plants (e.g. Kenrick and Crane 1997).

The ‘liverwort basal’ hypothesis has led to suggestions that the earliest land plants were ‘liverwort-like’. This has been fuelled by fossil evidence of the earliest land plant that exhibit certain characteristic liverwort characters (Taylor 1995a; Edwards *et al*. 1995b (but see Edwards *et al*. 1999); Wellman *et al*. 2003; Graham *et al*. 2004). In reality, however, it is unclear exactly how closely related to modern liverworts these earliest land plants were. A taxonomically more realistic concept of stem group embryophytes is required. In fact the earliest convincing fossil evidence for liverworts of modern aspect is from the Middle Devonian (Hernick *et al*. 2008).

The fossil record for the earliest land plants consists of dispersed spores that first appear in the early Mid Ordovician (Arenig/Dapingian) (Rubinstein *et al*. 2010; Wellman 2010). These dispersed spores occur in unusual configurations and are often called cryptospores. Similar cryptospore assemblages occur from the Dapingian to the Llandovery and are dominated by monads, dyads and tetrads that are either naked or envelope-enclosed. The envelopes may be variously ornamented. Occasionally the walls are ornamented with micrograna and/or are infrapunctate. Interestingly these latter forms appear to be confined to South Eastern Gondwana and may represent the first evidence for palaeophytogeographical differentiation. However, the hypothesis of Gray (1993), that envelope-ornamentation indicated palaeophytogeographical differentiation, has now been discredited based on observation that the distribution of ornamented envelopes is essentially global. The first appearance of cryptospores is considered to represent the earliest evidence for land plants. Palynomorphs claimed to be spore-like have also been described from older Cambrian sediments from several localities in the North America (Strother and Beck 2000; Strother et al. 2004; Taylor and Strother 2008, 2009). These authors consider that these palynomorphs belong to the cryptospore group and possibly represent evidence for the existence of primitive land plant vegetation since Cambrian times. However, at the present state of knowledge, the question as to whether these Cambrian palynomorphs represent true terrestrialy adapted land plants or were produced by freshwater or terrestrial algae remains unresolved (Wellman 2003, 2009). Thus we prefer to take the Arenig/Dapingian cryptospore assemblages as the first undisputed evidence for land plants.

Gray (1985, 1991) and references therein made a convincing case for the land plant affinities of the Arenig/Dapingian cryptospores. She also made a case for the parent plants having liverwort-like physiology and ecology but did not overstress a direct relationship with extant liverworts. Subsequent finding have strengthened the evidence for these spores deriving from land plants (e.g. Steemans *et al*. 2010—evidence for sporopollenin walls) and a liverwort-like grade of organization for the parent plants (Taylor 1995a; Edwards *et al*. 1995b (but see Edwards *et al*. 1999); Wellman *et al*. 2003).

Similar spore assemblages from the Dapingian to the Llandovery suggest that an uniform vegetation was present for some 30 million years. This vegetation is usually interpreted as consisting of ‘liverwort-like’ plants that were presumably founder populations of ecological generalists. It is often considered that they would have been confined to damp environments because a film of water would have been required for reproduction. However, it is noteworthy that some extant bryophytes: (i) successfully reproduce in extremely dry environments by utilising dew; (ii) can survive in dry environments because they are homoiohydric; (iii) can tolerate high UV-B environments due the presence of UV-B screening phenolic compounds in their cells. Perhaps the earliest vegetation was more ecologically resilient and widespread than we anticipate? However, the upshot is that the aerial continental coverage of biotas is presently unknown. Presumably areas not colonised by the earliest land plants would have retained some form of simple microbial soil crust. However, even the simple and diminutive earliest land plants would have begun to influence their environment in terms of development of a rudimentary soil (Boucot and Gray 2001).

During this time similar spore assemblages are reported globally from the equator to high latitudes suggesting that the parent plants were palaeogeographically widespread. This is exactly what might be expected of the earliest land plants, interpreted as founder populations of ecological generalists tolerant of a wide range of ecological and climatic conditions. Widespread dispersal into what were essentially empty niches would have been particularly favourable (i.e. step-by-step dispersal through continents and long distance dispersal across barriers). Such dispersal via spores would have been of prime importance, as would the ability to colonise a wide range of habitats and environments. Some dispersed spore assemblages occur at high latitudes and are intimitely related to glacial deposits of the Hirnantian glaciations (e.g. from the Czech Republic (Vavrdova 1988) and South Africa

(Gray *et al*. 1986)). This provides further evidence for cold tolerance among at least some of the parent plants. However, when interpreting parent plant palaeogeography based on dispersed spore record one should bear in mind that the similarity among the rather simple spore morphologies does not necessarily reflect similarity among the actual parent plants. The plants may have evolved differing morphology/anatomy but retained simple spores well adapted to their simple reproductive strategy.

From the Mid Ordovician hilate spores and trilete spores first appear in the dispersed spore record (Steemans *et al*. 2009). The hilate spores and trilete spores are the product of dissociation of dyads and tetrads, respectively. At first these are confined to southern Gondwana (Steemans *et al*. 2009). However, they subsequently spread into Avalonia, then into Euramerica, and finally into Baltica. Steemans *et al*. (2010) trace their dispersal around the globe. It is generally considered that trilete spores derive from vascular plants (or their immediate ancestors) (see discussion in Gray 1985 and Online Supporting Material in Steemans *et al*. 2009). Thus it would appear that vascular plants (or their immediate ancestors) may have evolved in Gondwana before subsequently migrating beyond this continent and colonizing the rest of the globe. Where they appear they initially remain a subsidiary element of spore assemblages. However, by the Late Silurian (Wenlock) they begin to increase in quantity, diversity and disparity, presumably as the vascular plants underwent an adaptive radiation (Gray 1985, 1991; Richardson 1996; Steemans 1999, 2000; Strother 2000; Wellman and Gray 2001). The same pattern is seen in hilate spores. However, their affinities are more controversial. *In situ* studies demonstrate that at least some derive from polysporangiates (Wellman *et al*. 1998b; Habgood 2000) including some that possessed stomata (Habgood 2000).

Throughout the Late Silurian trilete and hilate spores continue to proliferate in terms of abundance, taxonomic diversity and morphological disparity. At the same time envelope-enclosed cryptospores virtually disappear (although they occur sporadically and rarely until the Early Devonian). Other cryptospores morphotypes persist but are generally subsidiary components of dispersed spore assemblages, although they may dominate locally (the “Wellman effect” of Steemans (1999)). Presumably the plants that produced trilete spores (vascular plants and their immediate ancestors) and hilate spores (?polysporangiate protracheophytes) underwent an adaptive radiation and outcompeted the more primitive ‘liverwort-like’ cryptospore-producing plants that were thus relegated to the ecological ‘nooks-and-crannies’ unoccupied by the vascular plants, where they presumably have remained as bryophytes to the present day (with a later secondary diversification as epiphytes once arborescence evolved).

The change from cryptospore to hilate/trilete spore dominance is a major global event in the dispersed spore record. Increasing trilete/hilate spore diversity most likely reflects the adaptive radiation of vascular plants as they begin to expand their range and exploit new habitats. Presumably there was an increase in community species packing related to increasing diversity and evolutionary innovations (crudely measured by our preliminary measures of disparity--see later). There is evidence for the development of more complex ecology (see, for example, the contrasting models proposed by Wellman *et al*. 2000 and Edwards and Richardson 2004). During this time the first significant plant megafossil record appears (Appendix 1). The beginnings of phytogeographical differentiation become apparent in both the megafossil (e.g. Raymond *et al*. 2006) and dispersed spore (e.g. Steemans *et al*. 2010) records.

The dispersed spore fossil record clearly illustrates the nature of the adaptive radiation of vascular plants and their competitive replacement of the bryophyte-like plants. Clear patterns have been demonstrated in terms of palaeogeographic spread, taxonomic diversity and morphological disparity (see below). Unfortunately, these patterns are far less apparent in the Ordovician-Silurian land plant megafossil record due to the frustrating paucity of data. Indeed a number of mysteries remain. For example, the presence of the large lycopsid *Baragwanathia* from the Ludlow of Australia remains an enigma. The Ludlow age is now generally agreed to be secure, and consequently explanations for their anomalous size requires explanation other than incorrect age assignment. Perhaps they represent either an extreme case of endemism, or they have strongly divergent morphology due to unusual ecology (e.g. they were aquatic plants), or our fossil record of plant megafossils is simple too incomplete to represent the entire spectrum of Silurian plant life (afterall, only 23 plant megafossil assemblages are reported from the entire Silurian).

The nature of the early land plant adaptive radiation

It is evident from the previous discussion that the earliest land plants rapidly colonized the globe forming vegetation that appears to have been cosmopolitan and is considered to have comprised diminutive and simple plants at a ‘liverwort-like’ grade of organization. The presence of similar spore assemblages over the next 30 million years suggests a period of stasis dominated by this simple vegetation. This period of stasis was shattered by the competitive replacement by vascular plants and their immediate precursors that subsequently underwent an adaptive radiation. Understanding of this major event is based on patterns displayed by the dispersed spore and plant megafossil records.

There is a long history of plotting the temporal distribution of Ordovician-Silurian plant megafossils (e.g. Banks 1980; Chaloner and Sheerin 1979; Richardson and Edwards 1989) and dispersed spores (e.g. Richardson and McGregor 1986; Richardson and Edwards 1989; Richardson 1996; Gray 1998; Wellman and Gray 2000; Steemans 2000; Beck and Strother 2001, 2008). These data have biostratigraphical utility, in addition to informing us of the evolutionary sequence of events of the adaptive radiation of early land plants. Both fossil records demonstrate the displacement of the ‘bryophyte-like’ flora by vascular plants following their origin and subsequent adaptive radiation. This essentially involves the origin of polysporangiate protracheophytes and their diversification into the traditional (i.e. non-cladistic) rhyniophyte, zosterophyll, lycopsid and trimerophyte groupings. For information of recent cladistic re-evaluation of these groupings see Kenrick and Crane (1997).

A number of workers have undertaken taxon counts on Ordovician-Silurian dispersed spores to demonstrate the nature of the adaptive radiation of vascular plants (e.g. Richardson and Lister 1969; Knoll *et al*. 1984; Steemans 1999, 2000; Strother 2000; Beck and Strother 2001). Similar curves have been generated for plant megafossil data (e.g. Niklas 1977, 1978; Knoll *et al*. 1979, 1984; Niklas *et al*. 1980, 1983; Raymond and Metz 1995). Obviously far fewer and less palaeogeographically widespread records are available from the plant megafossil compared to dispersed spore database. New dispersed spore diversity curves, based on the data from Appendix 2, are presented in Fig.1. These curves demonstrate a fairly consistent low abundance of dispersed spores (dominated by obligate cryptospores) during the Ordovician and earliest Silurian. There is a dramatic exponential increase in trilete spore diversity from small numbers in the Late Ordovician-Early Silurian through the remainder of the Silurian and into the Devonian. Hilate spore diversification in general mirrors that of trilete spores. However, they appear to begin diversifying prior to the trilete spores, and their diversification is more variable. After an initial diversification, there is a temporary reduction in diversity, followed by a rediversification, before a further reduction in diversity towards the end of the Silurian. Obligate cryptospores exhibit variable, but low, diversity throughout the Silurian.

Relatively few plant megafossil taxa have been described from the Ordovician-Silurian (see Appendix 1), and these data are skewed by the exceptionally preserved charcoalified biota of the Pridoli of the Welsh Borderland, to the extent that there is little value in plotting them.

Various workers have considered disparity (i.e. morphological diversity) of Ordovician-Silurian dispersed spores (Allen 1981; Richardson and Burgess 1999) and plant megafossil (e.g. Chaloner and Sheerin 1979; Banks 1981; Knoll *et al*. 1984). However, these analyses are non-quantitative except for Knoll *et al*. (1984). They scored plant megafossil characters and developed an “anatomical and morphological advancement score”. These showed an exponential increase in early land plant “anatomical and morphological advancement score” in the Late Silurian-earliest Devonian. However, only one plant taxon was scored for the Ordovician-Silurian interval.

We have generated new diversity and disparity curves based on Silurian-Early Devonian (Lochkovian) dispersed trilete spores. We gathered data from three palaeogeographically distinct areas where there is a relatively complete succession of well preserved dispersed spore assemblages: the Anglo-Welsh basin of Avalonia, the Spanish Cantabrian Mountains of PeriGondwana and African sequences of South Eastern Gondwana. We have restricted these initial analyses to trilete spores because: (i) trilete spores represent a discrete and easily recognized group that is probably monophyletic; (ii) cryptospores are difficult to work with because their distribution appears to be fairly cosmopolitan but they are often lacking in near-shore marine deposits due to ecological/transportation effects (Steemans *et al*. 2007); (iii) cryptospores were often overlooked in early works on Silurian dispersed spore assemblages.

Spore taxon diversity data was simply measured by assembling all the publications on Silurian spores from these locations and counting all reported trilete spore species from each biozone (the Spore Assemblage Biozones of Richardson and McGregor 1986 were used). The count was then plotted in the chronological midpoint of each biozone using the timescale of Gradstein *et al*. (2004). One must, of course, be aware that the biozones are of differing duration. Spore morphological disparity was measured in a similar way but by giving each trilete spore species a disparity score based on its morphological characteristics. Table 1 outlines the numerical scoring system. Average (mean) disparity for the spores reported from each biozone was then calculated. The generated trilete spore species diversity and disparity curves are illustrated in Figs 2 and 3 respectively.

The spore taxon diversity curve (Fig. 2) exhibits a general exponential increase in trilete spore species over the course of the Silurian and into the Devonian. Apparent reductions in diversity in the Pridoli of the Anglo-Welsh Basin and Lochkovian (Early Devonian) of North Africa are almost certainly a product of a paucity of strata and described assemblages in these regions at this particular time. It is evident from our database and palaeophytogeographical analysis (see later) that although many spore taxa are common between the three areas, there are distinct differences. In fact PeriGondwana appears to be more closely associated with Southern Gondwana than with Avalonia: a not entirely unsurprising result. Interestingly, however, taxon numbers and pattern of diversification are similar in all three regions even though different taxa are involved.

The spore morphological disparity curve (Fig. 3) suggests a pattern of additive increase in trilete spore disparity over the course of the Silurian in all three regions. Again it is interesting that in all three areas disparity values and the pattern of disparity increase is similar even though different taxa are involved.

Early land plant palaeophytogeography: previous analyses

Megafossils: Ordovician-Silurian land plant megafossil assemblages were first described in the 1930s (e.g. Lang 1937). Since this time there have been many attempts to plot their spatial/temporal distribution, with the most relevant obviously those postdating the realization of continental drift. Due to the small number of reported assemblages most of these simply plot locations directly on palaeocontinental and/or palaeogeographical base maps of consecutive age. Edwards (1990) is an excellent example. More recently, as numbers of described assemblages has gradually risen, there have been attempts to use statistical techniques to analyse such data. For example, Raymond *et al*. (2006) utilized cluster analysis and correspondence analysis.

Edwards (1990) included a comprehensive review of Silurian early land plant megafossils. She reported 16 assemblages of plant megafossils and plotted their distribution on the Silurian continental reconstruction of Scotese. Edwards went on to discuss the problems of working with such a fragmentary database but stated that "the intention of this account is to emphasize the pitfalls when handling Silurian and Early Devonian megafossils, but is not meant to be critically destructive". She emphasized problems of: (i) stratigraphical accuracy and precision; (ii) recognition of facies bias; (iii) accuracy of identification and affinity. Although the number and palaeogeographic spread of described Silurian plant megafossil assemblages has increased significantly since Edwards' review, in no small part to her own labours, these inherent problems persists. This must be borne in mind when making sweeping generalizations concerning Silurian plant palaeophytogeography, particularly as the database, improved as it is, remains woefully inadequate.

Raymond *et al*. (2006) reported on a detailed quantitative analysis of Silurian plant megafossils. They used a database containing 35 macrofloral assemblages reported as megafossil genera and morphological traits. The database was analysed using cluster analysis and correspondence analysis. They recognized four phytogeographical units: (i) A North Laurussian unit (Bathurst Island); (ii) a south Laurussian unit-SouthwestGondwana unit (Great Britain, Podolia and Bolivia); (iii) a Kazakhstanian unit; (iv) a Southwest Gondwana unit (Australia).

Dispersed spores: Ordovician-Silurian dispersed spore assemblages were first described in the late 1950s (e.g. Hoffmeister 1959). Since this time a huge literature has amassed with numerous assemblages (usually containing many different spore types) described from all over the globe (reviewed in Richardson and McGregor 1986; Richardon 1996; Steemans 2000, 2001; Strother 2000; Wellman and Gray 2001). Plots of assemblage distribution are fairly common (e.g. Wellman 1996; Steemans *et al*. 2010). However, due to the magnitude of the database, attempts to plot the distribution of individual taxa in a thorough way are limited. At this point a note of caution is warranted. Historically many palynologists and their students have confined (or at least concentrated) their research on specific palaeogeographical areas. Thus taxonomies favoured by particular 'palynology schools' may be slightly different and confined to different palaeogeographical areas (see Marshall 1996). Obviously this can skew an analysis suggesting palaeogeographic differences when none exists.

Steemans *et al*. (2007) reviewed spore dispersal among early land plants. They concluded that long distance dispersal was uncommon, but rare long distance transportation events potentially could have resulted in successful establishment of populations. They also proposed that cryptospore-producers and trilete spores-producers had different dispersal potential. They suggest that cryptospore-producers ('bryophyte-like' plants) inhabited restricted habitats (such as bogs and marshes) with little access to waterways and hence transportation to the sea. They considered that they were not climatically sensitive and were cosmopolitan. On the other hand they suggested that trilete spore-producers (vascular plants) were more widespread and inhabited a variety of habitats with access to waterways and hence the sea. However, they considered that they were climatically sensitive and hence restricted in distribution. Ecological models for the Ordovician-Silurian vegetation have been proposed by Wellman *et al*. (2001) and Edwards and Richardson (2004). These vary slightly in detail. Wellman *et al*. (2001) suggest that diminutive and short-lived plants (both bryophyte-like cryptospore-producing and vascular trilete spore-producing) inhabited unstable areas prone to flooding near water bodies, but with larger and longer lived vascular plants inhabiting more stable areas away from water bodies liable to flooding. Edwards and Richardson (2004) suggest that cryptospore-producing plants became restricted to dry areas away from water bodies once vascular plants evolved and outcompeted them to colonize the more favourable damper areas near to water bodies.

Early land plant palaeophytogeography: general principles

What essentially governs the palaeogeographic distribution of the world flora at any given time is where plant taxa originate (centre of origin), and their ability to disperse and successfully colonise, counterbalanced by local, regional and ultimately total extinction. Local distribution is governed by the ability of individual species to occupy niches which is essentially controlled by their tolerance of local environmental conditions (substrate, climate, water availability etc.) and their ability to co-exist with or outcompete other plants that already inhabit these environments.

The Ordovician-Silurian situation regarding plant distribution presumably was initially rather simple. The first land plants essentially invaded an unoccupied niche (other than the microbial inhabitants of a pre-land plant world). Thus there was limited competition and suitable environments would soon have been colonized. This is particularly the case because the earliest land plants were almost certainly homosporous, producing prodigious quantities of isospores that would have easily been transported vast distances by wind and water (see Gray 1985). However, the early vegetation would soon have occupied suitable habitats and begun to modify the environment in terms of sediment stabilization and soil formation. Thereafter in order to colonize new areas plants had to invade new habitats or co-exist with/displace plants that already occupied a particular habitat.

Obviously the ecology of Ordovician-Silurian plants is critical. It is important to understand to what extent individual plant species were confined to particular habitats on the local (e.g. substrate specific) and regional (e.g. climatic tolerance) scale. This is one of the main factors governing the distribution of plants and whether they are cosmopolitan, endemic etc. There is little firm evidence regarding this issue. However, it has been discussed and various scenarios proposed by Gray (1984, 1985), Wellman *et al*. (2001), Edwards and Richardson (2004) and Steemans *et al*. (2007) among others.

At this juncture spore dispersal requires consideration. Based on the Ordovician-Silurian dispersed spore record it would appear that all plants groups of this time were homosporous with the vast majority of spores falling within the size range 20-40 μm, although some were up to 70 μm in size. Optimum size for wind dispersal is 25 μm or less according to Mogensen (1981). None-the-less, it is generally assumed that wind was the main agents of spore dispersal during the Ordovician-Silurian. In fact wind dispersal may have been easier during this time than at present because: (i) the vegetation was essentially ground hugging with no tall plants to impede transport out of the boundary layer and into wind currents at higher altitudes; (ii) average surface wind strength may have been greater due to the absence of large vegetation forming wind breaks; (iii) it has been calculated that total atmospheric pressure was higher than at present, resulting in a higher density of air (Berner 2006), and hence increased spore buoyancy. Thus although the vast majority of spores would have been deposited very close to parent plants (following the classic leptokurtic distribution), there would have been potential for long distance transport.

A number of workers have suggested that long distance transport is unusual among extant bryophytes and therefore by analogy early land plants (e.g. Van Zanten, 1978; Van Zanten and Gradstein, 1988; van Zanten and Pócs, 1981). Long distance transport requires high altitude wind currents which is damaging to spores due to problems associated with dessication, frost and UV-B. Additionally, such wind currents are usually parallel to latitudes and never cross the equator. Spores also need to settle in a suitable environment to successfully germinate, grow and reproduce to establish a new colony. To favour maximal fertility a bisexual gametophyte is required, but to prevent endemic assemblages it is important that genetic exchange between two localities occurs in both directions. Following the above arguments, basing palaeocontinental reconstructions on the shortest distances between miospore palaeogeographic distributions becomes the most parsimonious method (Steemans et al. 2007, 2010; Spina and Vecoli 2009). However, we recognize that it is not possible to completely rule out the possibility that rare events over vast periods of geologic time could permit colonization of new locations by long distance transport bisexual spores of homosporous plants.

Early land plant palaeophytogeography: a new database and quantitative analysis

In this review we treat both plant megafossils and dispersed spores. For plant megafossils we provide an up-to-date list of all described Ordovician-Silurian plant megafossil localities (Appendix 1) and plot these on the new palaegeographical plots (Fig. 4). For dispersed spores we have constructed an extensive database of all records of Ordovician-Silurian dispersed spore taxa. This database is too large to print in full in this paper and is available from the authors. A greatly condensed version of the database is presented in Appendix 2. The location of the most important reports has been plotted on the newly constructed palaeocontinental reconstructions (Figs 5-6). However, we have excluded a few brief reports where spores constitute only a small component of the palynomorph assemblage and/or are poorly age constrained and/or are too poorly preserved or thermally mature to enable accurate identification. Furthermore, due to the size of the Ordovician-Silurian dispersed spore record there are also problems concerning the quality of data in the database. Synonomy is probably rife and there are many published examples of incorrect identification. It is anticipated that over time continual re-evaluation of the dispersed spore record will eliminate much of this bad data. Our preliminary attempts are evident in the database we have erected (Table 2). Throughout this review the Geological Time Scale of Gradstein *et al.* (2004) is utilized.

The data on stratigraphical and palaeogeographical occurrences of Silurian miospore species have been treated by means of statistical analysis in order to quantitatively analyze the similarities among assemblages belonging to defined palaeogeographical areas. A total of 787 data points have been analyzed; each datapoint represents the occurrence of a miospore species in a given stratigraphic interval and in a given palaeogeographical area. The stratigraphic subdivisions used correspond to the Silurian Series: Llandovery, Wenlock, Ludlow and Pridoli. The following palaeogeographic localities have been defined: "southwestern Gondwana" (mainly North African localities); "PeriGondwanan terranes" (corresponding to Western Europe, Bohemia, etc.); Avalonia (British Isles, part of northern France); Arabian Plate (including mainly Saudi Arabia and adjacent areas such as Iran and Iraq); Laurentia (corresponding to North America); "Eastern Gondwana" (South America: Argentina, Paraguay, Bolivia); Baltica (Sweden, Norway, Batic States, northern Poland), South? China Plate (mainly localities belonging to the Yangtze Platform), and "Northern Gondwana" (South Africa).

In order to assess the similarities among the fossil assemblages, two methods have been used: cluster analysis and metric multidimensional scaling (MDS). Cluster analysis has been widely applied in the past for analysis of palaeobiogeographical patterns of different fossil groups, including palynomorphs (e.g. Fortey and Mellish 1992; Vecoli and Samuelsson 2001). However, when this method is applied to fossil biogeography using databases which might be affected by sample biases, limitations become evident because artefacts can easily arise that may result in unreliable or artificial clustering of sets of little similarity (Brayard *et al*. 2007). On the contrary, the MDS is generally used in modern ecological studies and is considered among the most reliable methods in quantitative assessment of biogeographical patterns (e.g. Edinger *et al*. 2000). In both cases, the Jaccard index was used to calculate the "similarity" (fraction of species shared) among assemblages; the Jaccard coefficient is among the most commonly used species similarity measure in extant biogeographical and ecological studies (e.g. Izsak and Price 2001; Condit *et al*. 2007). The linkage method used for cluster analysis was Ward's method. Calculations and plotting of diagrams were performed using the "R" freeware statistical package (http://www.r-project.org/) and the programming script was kindly provided by Prof. Wolfgang Kiessling (Natural History Museum, Berlin).

The MDS scatterplot of the Llandovery subset (Fig. 7) shows considerable similarities among most of the palaeocontinents, as almost all miospore localities plot very close to each other, with the exception of South China and northearn Gondwana (South Africa). The isolated position of these continents with respect to the main cluster is most probably a consequence of sampling effect, since only impoverished assemblages are known in from the Llandovery of these two localities (a monospecific assemblage in South Africa, and only nine species described from South China). The cluster plot (Fig. 7) also reflect this situation, with northen Gondwana (South Africa) and South China constituting a cluster of low similarity clearly distinct from the larger cluster formed by the rest of the localities. Note that data from

Baltica are almost non-existent, with only rare tetrads reported from around the Ordovician-Silurian boundary from Gotland, Sweden (Le Hérissé 1989).

The MDS plot for the Wenlock (Fig. 8) shows more scattering of the locality data points. However, some grouping can be recognized, with a group consisting of North Africa, PeriGondwana and Avalonia, with Arabia, Laurentian, Baltica and South America plotting separately. The cluster diagram (Fig. 8) recognizes two related groupings of North Africa and PeriGondwana and Laurentia, Arabia and Avalonia. South America and Baltica are distinct from this cluster.

The Ludlow MDS plot (Fig. 9) show a significant degree of scattering of all localities, although South America, PeriGondwana and North Africa form a cluster. Because of the large scattering of the data in the MDS plot, the cluster diagram for the Ludlow (Fig. 9) must be interpreted with care, as the resulting clustering is not highly significant (e.g. first-order grouping of Arabia with South America and Baltica with South China).

The Pridoli MDS diagram (Fig. 10) clearly highlights similarities among North Africa, PeriGondwana, South America and Avalonia. Note also that no Pridoli occurrences are available for the Arabian Plate.

Unfortunately it is very difficult to compare these analyses with those based on plant megafossils by Raymond *et al.* (2006) because dispersed spore assemblages have not been reported from two of their four phytogeographic units (Kazakhstanian and Southwestern Gondwana (Australian)). However, for both the Ludlow and Pridoli dispersed spores do not appear to support Raymond *et al.*'s South Laurussian-Southeastern Gondwana unit or the distinction between this unit and their North Laurussian unit.

As stated before, the palaeobiogeographic interpretation of the quantitative analysis of assemblage similarities must be undertaken with care because the available sample sets show high spatial heterogeneity and significant differences in sample size. It is evident that data are completely lacking for certain areas (e.g. Russia, Siberia, most of western Gondwana) and there is a concentration of data from North America, Europe, North Africa and the Middle East (especially Saudi Arabia). Baltica is also under-reported.

Interpretation of new database/analyses

In general, analysis of the newly assembled database/palaeogeographical plots confirms the general picture of early land plant origins and diversification that has emerged over the last 40 years-or-so (as outlined on p.000-000). However, its importance lies not in highlighting previously unforeseen patterns, but in quantifying and statistically analysing those patterns that were beginning to emerge from the ever increasing database.

Bearing in mind the limitations described above, the data seem to indicate that, generally, during the entire Silurian phytogeographical differentiation seems not to be very pronounced. However, more detailed scrutiny suggests that there is a tendency towards the development of some degrees of phytogeographical differentiation from Llandovery to Pridoli times between Godwanan and North American/Baltic localities. This tendency is paralleled by the progressive decline in diversity and abundance of the cryptospores and the rapid diversification of the trilete spores, especially starting from Late Silurian times (Fig. 1). This finding seems to be in contradiction to several of the palaeogeographical map reconstructions that show that the distance between these palaeocontinents is decreasing progressively during this time period. Gondwana and North America/Baltica become closer longitudinally and also, but to a lesser extent, latitudinally. It is likely that these apparent contradictions are related to trilete spore producing plants becoming less climatically tolerant than the more primitive cryptospore-producing plants (e.g. Steemans 1999; Steemans *et al.* 2007).

Conclusions

The fossil record has much to inform us regarding the origin and adaptive radiation of land plants. As always more data (i.e. more fossils increasing temporal and spatial coverage) are essential for improved interpretation. But continual re-evaluation of the database is also imperitive. This includes taxonomic revision, in addition to analysis of diversity, disparity, biogeography etc., particularly as new methods and statistical techniques become available. However, key to successful interpretation of this fossil record as always involves understanding of its incompleteness and biases.

Plants and their spores are by far the richest fossil group from the continents. Potentially they provide invaluable data for palaeogeographical reconstructions in determining acceptable distances between continents to allow spores to colonize new areas. These constraints are especially important for longitudinal proximities between continents, but also, but to a lesser extent, for latitude. The early land plant fossil record is most satisfactorily explained by palaeocontinental reconstructions showing shorter distances between the continents.

Acknowedgements

CHW’s research is supported by NERC grants. PS’s research is supported by NFSR.

References

Al-Ameri, T. K., Omer, S. F. & Khalaf, F. H. 1991. Lower Silurian palynomorphs from Western Iraqi Desert and the paleoclimate. *Journal Science and Nature*, **1**, 57-65.

Aldridge, R. J., Dorning, K. J., Hill, P. J., Richardson, J. B. & Siveter, D. J. 1979. Microfossil distribution in the Silurian of Britain and Ireland. *Geological Society, London, Special* *publications*, **8**, 433-438.

Aldridge, R. J., Jeppsson, L. & Dorning, K. J. 1979. Early Silurian oceanic episodes and events. *Journal of the Geological Society, London*, **150**, 501-513.

Allen, K. C. 1980. A review of *in situ* Late Silurian and Devonian spores. *Review of Palaeobotany and Palynology*, **29**, 253-270.

Allen, K. C. 1981. A comparison of the structure and sculpture of *in situ* and dispersed Silurian and Early Devonian spores. *Review of Palaeobotany and Palynology*, **34**, 1-9.

Aristova, K. E. & Arkhangelskaya, A. D. 1976. Microfossils from stratotype sections of Upper Silurian horizons of Estonia. *In*: Byvsheva, T. V. (ed) *Results of palynological research on Precambrian, Paleozoic and Mesozoic of the USSR*. Trudy Vsesoiuznogo Nauchno-Issledovatel'skogo Geologorazvedochnogo Neftianogo Instituta, Kama Branch, **192**, 28-38.

Balme, B. E. 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology*, **87**, 81-323.

Banks, H. P. 1980. Floral assemblages in the Siluro-Devonian. 1-24. *In*: Dilcher, D. L. & Taylor, T. N. (eds) *Biostratigraphy of fossil plants*. Dowden, Hutchinson, & Ross, Stroudsburg, Pennsylvania.

Banks, H. P. 1981. Time and appearance of some plant biocharacters during Siluro-Devonian time. *Canadian Journal of Botany*, **59**, 1292-1296.

Barron, H. F. 1989. Mid-Wenlock acritarchs from the inlier in the Cheviot Hills, NE England. *Scottish Journal of Geology*, **25**, 81-89.

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

Beck, J. H. & Strother, P. K. 2008. Miospores and cryptospores from the Silurian section at Allenport, Pennsylvania, USA. *Journal of Paleontology*, **82**, 857-883.

Berner, R. A. 2006. Geological nitrogen cycle and atmospheric N_2 over Phanerozoic time. *Geology*, **34**, 413-415.

Bodziock, A., Kozlowski, W. & Poplawska, A. 2003. A *Cooksonia*-type flora from the Upper Silurian of the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica*, **48**, 653-656.

Boucot, A. J. & Gray, J. 2001. A critique of Phanerozoic climatic models involving changes in the CO_2 content of the atmosphere. *Earth Science Reviews* 56, 1-159.

Brayard, A., Escarguel, G. & Bucher, H. 2007. The biogeography of Early Triassic ammonoid faunas: Clusters, gradients, and networks. *Geobios*, **6**, 749-765.

Brown, R. C. & Lemmon, B. E. 1990. Sporogenesis in bryophytes. 55-94. *In*: Blackmore, S. and Knox (eds). *Microspores: evolution and ontogeny*. Academic Press Limited.

Buret, M. B. & Moreau-Benoit, A. 1986. Données nouvelles apportées par la palynoplanctologie sur la formation des alternances argilo-gréseuses (Silurien supérieur de Libye, bassin de Rhadamès). *Comptes Rendus de l'Académie des Sciences de Paris*, **302**, 1009-1014.

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

Burgess, N. D. & Richardson, J. B. 1991. Silurian cryptospores and miospores from the type Wenlock area, Shropshire, England. *Palaeontology*, **34**, 601-628.

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

Cai Chong-Yang, Ya-Wei Dou & Edwards, D. 1993. New observations on a Pridoli plant assemblage from north Xinjiang, northwest China, with comments on its evolutionary and palaeogeographical significance. *Geological Magazine,* **130**, 155-170.

Chaloner, W. G. & Sheerin, A. 1979. Devonian macrofloras. *Special Papers in Palaeontology*, **23**, 145-161.

Combaz, A. 1967. Un microbios du Trémadocien dans un sondage d'Hassi-Messaoud. *Actes de la Société Linnéenne de Bordeaux*, **104**, 1-26.

Condit, R., Pitman, N., Leigh, E.G. Jr., Chave, J., Terborgh, J., Foster, R.B., Nunez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbels, S.P., 2007. Beta-diversity in tropical forest trees. *Science*, **295**, 666-669.

Cramer, F. H. 1966. Palynomorphs from the Siluro-Devonian boundary in N. W. Spain. *Notas y Comunicaciones del Instituto Geologico y Minero de Espana*, **85**, 71-82.

Cramer, F. H. 1967. Palynology of Silurian and Devonian rocks in Northwest Spain. *Boletin del Instituto Geologico y Minero de Espana*, **77**, 225-286.

Cramer, F. H. & Díez, M. D. C. R. 1975. Earliest Devonian miospores from the Province of León, Spain. *Pollen et Spores*, **XVII**, 331-344.

Cramer, F. H. & Rodríguez, R. M. 1977. Robledo and Arroyacas Formation (Arroyo de las

Arroyacas, Province of Palencia, Spain) palynologically dated as late Silurian. *Breviora Geologica Asturica*, **21**, 2-4.

Cramer, F. H. & Díez, M. D. C. R. 1977. *Ovnia*, genero nuevo de Acritarcos del Gedinniense de Arabia Saudita. *Rev. Espanola Micropal.*, **IX**, 85-88.

Daber, R. 1971. *Cooksonia* - one of the most ancient psilophytes - widely distributed, but rare. *Botanique (Nagpur)*, **2**, 35-40.

Deunff, J. & Chateauneuf, J. J. 1976. Sur la présence d'un riche microplancton siluro-dévonien à acritarches, chitinozoaires, au sommet des Schistes et Quartzites de Plougastel (Rade de Brest); son intérêt stratigraphique. *Geobios*, **9**, 337-343.

Díez, M. D. C. R. & Cramer, F. H. 1976. Acritarches et miospores du Ludlovien de Corniero, Province de León, Espagne. *Revue de Micropaléontologie*, **19**, 121-133.

Dorning, K. J. 1983. Palynology and stratigraphy of the Much Wenlock Limestone Formation of Dudley, Central England. *Mercian Geologist*, **9**, 31-40.

Douglas, J. & Holmes, F. 2006. The *Baragwanathia* story: an update. *The Fossil Collector*, **77**, 9-26.

Duffield, S. L. 1985. Land-derived microfossils from the Jupiter Formation (upper Llandoverian), Anticosti Island, Quebec. *Journal of Paleontology*, **59**, 1005-1010.

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.

Edinger, E. N., Kolasa, J. & Risk, M. J. 2000. Biogeographic variation in coral species diversity on coral reefs in three regions of Indonesia. *Diversity and distributions,* **6**, 113-127.

Edwards, D. 1979. A late Silurian flora from the Lower Old Red Sandstone of south-west Dyfed. *Palaeontology* 22, 23-52.

Edwards, D. 1990. Constraints on Silurian and Early Devonian phytogeographic analysis based on megafossils. In W.S. McKerrow. and C.R. Scotese, eds, *Palaeozoic palaeogeography and biogeography*, Memoir No.12, pp. 233-242. The Geological Society: London.

Edwards, D. 1996. New insights into early land ecosystems: a glimpse of a Lilliputian world. *Review of Palaeobotany and Palynology,* **90**, 159-174.

Edwards, D., Banks, H. P., Ciurca, J. R. & Laub, R. S. 2004. New Silurian cooksonias from dolostones of north-eastern North America. *Botanical Journal of the Linnean Society*,

146, 399-413.

Edwards, D., Bassett, M. G. & Rogerson, E.C.W. 1979. The earliest vascular land plants: continuing the search for proof. *Lethaia,* **12**, 313-324.

Edwards, D., Davies, K. L. Richardson, J. B. & Axe, L. 1995a. The ultrastructure of spores of *Cooksonia pertoni*. *Palaeontology,* **38**, 153-168.

Edwards, D., Davies, K. L., Richardson, J. B., Wellman, C. H. & Axe, L. 1996b. Ultrastructure of *Synorisporites downtonensis* and *Retusotriletes* cf. *coronadus* in spore masses from the Prídolí of the Welsh Borderland. *Palaeontology,* **39**, 783-800.

Edwards, D., Duckett, J. G. & Richardson, J. B. 1995b. Hepatic characters in the earliest land plants. *Nature* 374, 635-636.

Edwards, D., Feehan, J. and Smith, D.G. 1983. A late Wenlock flora from Co. Tipperary, Ireland. *Botanical Journal of the Linnean Society,* **86**, 19-36.

Edwards, D., Morel, E. M., Paredes, F., Ganuza, D. G. & Zuniga, A. 2001. Plant assemblages from the Silurian of southern Bolivia and their palaeogeographic significance. *Botanical Journal of the Linnean Society*, **135**, 229-250. 2001

Edwards, D. & Richardson, J. B. 1996. Review of *in situ* spores in early land plants. In J. Jansonius and D.C. McGregor eds, *Palynology: principles and applications*, *Volume 1*, *Principles*, pp. 391-407. Salt Lake City, Utah American Association of Stratigraphic Palynologists Foundation. Publishers Press.

Edwards, D. & Richardson, J. B. 2004. Silurian and Lower Devonian plant assemblages from the Anglo-Welsh Basin: A palaeobotanical and palynological synthesis. *Geological Journal*, **39**, 375-402.

Edwards, D. & Rogerson, E. C. W. 1979. New records of fertile Rhyniophytina from the late Silurian of Wales. *Geological Magazine*, **116**, 93-98.

Edwards, D., Wang, Yi, Bassett, M. G. and Li, Chen-Sen. 2007. The earliest vascular plant or a later rooting system? *Pinnatiramous qianensis* from the marine Lower Silurian Xiushan Formation, Guizhou Province, China. *Palaios*, **22**, 155-165.

Edwards, D. & Wellman, C. H. 2001. Embryophytes on land: The Ordovician to Lochkovian (Lower Devonian) record. 3-28. In: Gensel, P. G. and Edwards, D. (eds). *Plants invade the land: Evolutionary and environmental perspectives*. Columbia University Press, New York.

Edwards, D., Wellman, C. H. & 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**, 111-115.

Eley, B. E. & Legault, J. A. 1988. Palynomorphs from the Manitoulin Formation (Early Llandovery) of Southern Ontario. *Palynology*, **12**, 49-63.

Emo, G. T. & Smith, D. G. 1978. Palynological evidence for the age of the Lower Palaeozoic rocks of Slieve Aughty, Counties Clare and Galway. *Proceedings of the Royal Irish Academy*, **78**, 287-292.

Fanning, U., Edwards, D. & Richardson, J. B. 1990. Further evidence for diversity in late Silurian land vegetation. *Journal of the Geological Society London,* **147**, 725-728.

Fanning, U., Edwards, D. & Richardson, J. B. 1991. A new rhyniophytoid from the late Silurian of the Welsh Borderland. *Neues Jahrb. Geol. und Palaeontol. Abh.,* **183**, 37-47.

Fanning, U., Richardson, J.B. & Edwards, D. 1988. Cryptic evolution in an early land plant. *Evolutionary trends in plants,* **2**, 13-24.

Fanning, U., Richardson, J. B. & Edwards, D. 1991. A review of *in situ* spores in Silurian land plant. *In*: Blackmore, S. & Barnes, S. H. (eds) *Systematics Association Special Volume*. Pollen and spores, Oxford, **44**, 25-47.

Fombella, M. A. 1982. Determinacion palinologica del Tremadoc en la localidad de Verdiago, Provincai de León, NO de España. *Revista Española de Micropaleontologia*, **XIV**, 13-22.

Fortey, R. A., Mellish, C. J. T. 1992. Are some fossils better than other for inferring palaeogeography? The Early Ordovician of the North Atlantic region as a test case. *Terra Nova* 4, 210-216.

Gensel, P. G. 1980. Devonian *in situ* spores: a survey and discussion. *Review of Palaeobotany and Palynology,* **30**, 101-132.

Gensel, P. G. 2009. The earliest land plants. *Annual Review of Ecology, Evolution and Systematics*, **39**, 459-477.

Gensel, P. G., Johnson, N. G. & Strother, P. K. 1990. Early land plant debris (Hooker's 'waifs and strays'?). *Palaios*, **5**, 520-547.

Glasspool, I. J., Edwards, D. & Axe, L. 2004. Charcoal in the Silurian as evidence for the earliest wildfire. *Geology,* **32**, 381-383.

Gradstein, F., Ogg, J. & Smith, A. 2004. A geologic time scale 2004. Cambridge University

Press.

Graham, L. E. 1993. Origin of land plants. Wiley.

Graham, L. E., Wilcox, L. W., Cook, M. E. & Gensel, P. G. 2004. Resistant tissues of modern marchantioid liverworts resemble enigmatic Early Paleozoic microfossils. *Proceedings of the National Academy of Sciences*, **101**, 11025-11029.

Gray, J. 1984. Ordovician-Silurian land plants: the interdependence of ecology and evolution. *Special Papers in Palaeontology,* **32**, 281-295.

Gray, J. 1985. The microfossil record of early land plants; advances in understanding of early terrestrialization, 1970-1984. *Philosophical Transactions of the Royal Society, London*, **B 309**, 167-195.

Gray, J. 1988. Land plant spores and the Ordovician-Silurian boundary. *Bulletin of the British Museum (Natural History), Geology*, **43**, 351-358.

Gray, J. 1991. *Tetrahedraletes, Nodospora* and the 'cross' tetrad: an accretion of myth. *In*: Blackmore, S. & Barnes, S. (eds) *Pollen and spores: Patterns of diversification*. The Systematics Association Special Volume Clarendon Press, Oxford, **44**, 49-87.

Gray, J. 1993. Major Paleozoic land plant evolutionary bio-events. *Palaeogeography; Palaeoclimatology, Palaeoecology*, **104**, 153-169.

Gray, J. & Boucot, A. J. 1971. Early Silurian spore tetrads from New York: Earliest New World evidence for vascular plants. *Science*, **173**, 918-921.

Gray, J., Massa, D. & Boucot, A. J. 1982. Caradocian land plant microfossils from Libya. *Geology*, **10**, 197-201.

Gray, J., Theron, J. N. & Boucot, A. J. 1986. Age of the Cedarberg Formation, South Africa and early land plant evolution. *Geological Magazine*, **123**, 445-454.

Gray, J., Boucot, A. J., Grahn, Y. & Himes, G. 1992. A new record of early Silurian land plant spores from the Paraná Basin, Paraguay (Malvinokaffric Realm). *Geological Magazine*, **129**, 741-752.

Gray, J., Colbath, G. K., de Faria, A., Boucot, A. J. & Rohr, D. M. 1985. Silurian-age fossils from the Paleozoic Paraná Basin, southern Brazil. *Geology*, **13**, 521-525.

Grösser, J. R. & Prössl, K. F. 1991. First evidence of the Silurian in Colombia: Palynostratigraphic data from the Quetame Massif, Cordillera Oriental. *Journal of South American Earth Sciences*, **4**, 231-238.

Habgood, K. S. 2000. Two cryptospore-bearing land plants from the Lower Devonian

(Lochkovian) of the Welsh Borderland. *Botanical Journal of the Linnean Society,* **133**, 203-227.

Hagström, J. 1997. Land-derived palynomorphs from the Silurian of Gotland, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar*, **119**, 301-316.

Hao, S., Xue, J., Guo, D. & Wang, D. 2007. Earliest rooting system and root : shoot ratio from a new Zosterophyllum plant. *New Phytologist*, **185**, 217-225.

Hernick, L. V., Landing, E. & Bartowski, K. E. 2008. Earth's oldest liverworts-*Metzgeriothallus sharonae* sp. nov. from the Middle Devonian (Givetian) of eastern New York, USA. *Review of Palaeobotany and Palynology*, **148**, 154-162.

Hill, J. P., Paris, F. & Richardson, J. B. 1985. Silurian palynomorphs. *Journal of Micropaleontology*, **4**, 27-48.

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

Ishchenko, T. A. 1975. *The late Silurian flora of Podolia.* Institute of Geological Science, Academy of Science of the Ukrainian SSR., Kiev, 1-80.

Izsack, C. & Price, A. R. G. 2001. Measuring beta-diversity using a taxonomic similarity index, and its relation to spatial scale. *Marine Ecology Progress Series* 215, 69-77.

Jardiné, S. & Yapaudjian, L. 1968. Lithostratigraphie et palynologie du Dévonien-Gothlandien gréseux du Bassin de Polignac (Sahara). *Revue de l'Institut Français du Pétrole*, **23**, 439-469.

Jeram, A. J., Selden, P. A. & Edwards, D. 1990. Land animals in the Silurian: Arachnids and myriopods from Shropshire, England. *Science,* **250**, 658-661.

Johnson, N. G. 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.

Johnson, T. R. & Taylor, W. A. 2005. Single grain analysis of the Late Silurian spore *Cymbosporites echinatus* from the Welsh Borderland. *Review of Palaeobotany and Palynology*, **137**, 163-172.

Karol, K. G., McCourt, R. M., Climino, M. T. & Delwiche, C. F. 2001. The closest living relatives of land plants. *Science*, **294**, 2351-2353.

Kenrick, P. & Crane, P. R. 1997.The origin and early diversification of land plants: a cladistic study. Smithsonian Institution Press, Washington.

Kermandji, A. M. H. 2007. Silurian-Devonian miospores from the western and central

Algeria. *Revue de Micropaléontologie*, **50**, 109-128.

Knoll, A. H., Niklas, K. J., & Tiffney, B. H. 1979 Phanerozoic land-plant diversity in North America. *Science*, **206**, 1400-1402.

Knoll, A. H., Niklas, K. J., Gensel, P. G., & Tiffney, B. H. 1984. Character diversification and patterns of evolution in early vascular plants. *Paleobiology*, **10**, 34-47.

Kotyk, M. E., Basinger, J. F., Gensel, P. G., & de Freitas, T. 2002. Morphologically complex plant macrofossils from the Late Silurian of Arctic Canada. *American Journal of Botany*, **89**, 1004-1013.

Lakova, I., Gocev, P. M. & Yanev, S. 1992. Palynostratigraphy and geological setting of the Lower Paleozoic allochthon of the Dervent Heights, SE Bulgaria. *Geological Balcanica*, **22**, 71-88.

Lang, W. H. 1937. On plant-remains from the Downtonian of England and Wales. *Philosophical Transactions of the Royal Society of London*, **B227**, 245-291.

Larsen, P. –H, Edwards, D. and Escher, J. C. 1987. Late Silurian plant megafossils from the Peary Land Group, North Greenland. *Rapp. Grønlands Geol. Unders.* 133, 1-7-112.

Le Hérissé, A. 1989. Acritarches et kystes d'algues prasinophycees du Silurien de Gotland, Suede. *Palaeontographica Italica*, **76**, 57-302.

Le Hérissé, A., Melo, J. H. G., Quadros, L. P., Grahn, Y. & Steemans, P. 2001. Palynological characterization and dating of the Tiangua Formation, Serra Grande Group, northern Brazil. *In*: Melo, J. H. G. & Terra, G. J. S. (eds) *Correlaçâo de Seqüências Paleozóicas Sul-Americanas*. Ciência-Técnica-Petróleo. Seção: Exploração de Petróleo, Rio de Janeiro, **20**, 25-42.

Libertin, M., Labuta, R. & Daskova, J. 2002. The oldest vascular plants from the Bohemian Massif. *Zpravy o Geologickych Vyzkumech v Roce*, **2002**, 127

Lugardon, B. 1990. Pteridophyte sporogenesis: a survey of spore wall ontogeny and fine structure in a polyphyletic plant group. 95-120. *In*: Blackmore, S. and Knox (eds). Microspores: evolution and ontogeny. Academic Press Limited.

Marshall, J. E. A. 1991. Palynology of the Stonehaven Group, Scotland: evidence for a Mid Silurian age and its geological implications. *Geological Magazine*, **128**, 283-286.

Marshall, J. E. A. 1996. Vegetational history of Devonian spores. 1133-1141. In. Jansonius, J. & McGregor, D. C. (eds). Palynology: principles and applications. American Association of Stratigraphical Palynologists Foundation.

Martin, F. 1973. Ordovicien supérieur et Silurien inférieur à Deerlijk (Belgique). *Mémoires* *de l'Institut royal des Sciences naturelles de Belgique*, **174**, 1-71.

Maziane-Serraj, N., Bruck, P. M., Higgs, K. T. & Vanguestaine, M. 2000. Ordovician and Silurian acritarch assemblages from the west Leinster and Slievenamon areas of southeast Ireland. *Review of Palaeobotany and Palynology*, **113**, 57-71.

McClure, H. A. 1988. The Ordovician-Silurian boundary in Saudi Arabia. *Bulletin of the British Museum (Natural History), Geology Series*, **43**, 155-163.

McGregor, D. C. 1984. Late Silurian and Devonian spores from Bolivia. *Academia Nacional de Ciencias Cordoba*, **69**, 1-57.

McGregor, D. C. & Camfield, M. 1976. Upper Silurian? to Middle Devonian spores of the Moose River Basin, Ontario. *Geological Survey of Canada, Bulletin*, **263**, 1-63.

McGregor, D. C. & Narbonne, G. M. 1978. Upper Silurian trilete spores and other microfossils from the Read Bay Formation, Cornwallis Island, Canadian Arctic. *Canadian Journal of Earth Sciences*, **15**, 1292-1303.

Mendlowicz Mauller, P., Pereira, E., Grahn, Y. & Steemans, P. 2004. Análise bioestratigráfica do intervalo Llandoveriano da Bacia do Paraná no Paraguai Oriental. *Revista Brasiliera de Paleontologia*, **7**, 199-212.

Miller, M. A. & Eames, L. E. 1982. Palynomorphs from the Silurian Medina Group (Lower Llandovery) of the Niagara Gorge, Lewiston, New York, U.S.A. *Palynology*, **6**, 221-254.

Miller, M. A. & Al-Ruwaili, M. H. 2007. Preliminary palynological investigation of Saudi Arabian Upper Ordovician glacial sediments. *Revue de Micropaléontologie*, **50**, 17-26.

Mizusaki, A. M., Melo, J. H. G., Lelarge, M. L. & Steemans, P. 2002. Vila Maria Formation, Paraná Basin, Brazil - An example of integrated geochronological and palynological datings. *Geological Magazine*, **139**, 453-463.

Mogensen, G. S. 1981. The biological significance of morphological characters in bryophytes: the spore. *The Bryologist*, **84**, 187-207.

Molyneux, S. G. & Al-Hajri, S. 2000. Palynology of a problematic Lower Palaeozoic lithofacies in Central Saudi Arabia. *In*: Al-Hajri, S. & Owens, B. (eds) *Stratigraphic palynology of the Palaeozoic of Saudi Arabia*. GeoArabia, Bahrain, **special volume 1**, 18-41.

Moreau-Benoit, A. & Dubreuil, M. 1987. Confirmation et découverte du Dévonien inférieur par la palynoplanctonologie dans les schistes et grès de la terminaison orientale du bassin d'Ancenis (sud-est du Massif armoricain). *Géologie de la France*, **1**, 37-54.

Niklas, K. J. 1977. Theoretical evolutionary rates in plant groups and the fossil record. *Brittonia*, **29**, 241-254.

Niklas, K. J. 1978. Morphometric relationships and rates of evolution among Paleozoic vascular plants. *Evolutionary Biology*, **11**, 509-543.

Niklas, K. J., Tiffney, B. H. & Knoll, A. H. 1980. Apparent changes in the diversity of fossil plants. Evolutionary Biology, **12**, 1-89.

Niklas, K. J., Tiffney, B. H. & Knoll, A. H. 1983. Patterns in vascular land plant diversification. *Nature*, 303, 614-616.

Obrhel, J. 1962. Die Flora der Pridoli-Schichten (Budnany-Stufe) des mittelböhmishcen Silurs. *Geologie*, **11**, 83-97.

Pittau, P. 1985. Tremadocian (Early Ordovician) acritarchs of the Arburese Unit, Southwest Sardinia (Italy). *Bolletino della Societa Paleontologica Italiana*, **23**, 61-204.

Qiu, Y-L. 2008. Phylogeny and evolution of charophytic algae and land plants. *Journal of Systematics and Evolution*, **46**, 287-306.

Qiu, Y-L., Li, L., Bin, W., Chen, Z., Knoop, V., Groth-Malonek, M., Dombrovska, O., Lee, J., Kent, L., Rest, J., Estabrook, G. F., Hendry, T. A., Taylor, D. W., Testa, C. M., Ambros, M., Crandall-Stotler, B., Duff, R. J., Stech, M., Frey, W., Quandt, D. & Davis, C. C. 2006. The deepest divergences in land plants inferred from phylogenomic evidence. *Proceedings of the National Academy of Sciences*, **103**, 15511-15516.

Rauscher, R. & Robardet, M. 1975. Les microfossiles (acritarches, chitinozoaires et spores) des couches de passage du Silurien au Dévonien dans le Cotentin (Normandie). *Annales de la Société Géologique du Nord*, **XCV**, 81-92.

Raymond, A., Gensel, P. G. and Stein, W. E. 2006. Phytogeography of late Silurian macrofloras. *Review of Palaeobotany and Palynology*, **142**, 165-192.

Raymond, A. & Metz, C. 1995. Laurussian land-plant diversity during the Silurian and Devonian: mass extinction, sampling bias, or both? *Paleobiology*, **21**, 74-91.

Reitz, E. 1987. Silurische Sporen aus einem granatführenden Glimmerschiefer des Vor-Speesart, NW-Bayern. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte*, **11**, 699-704.

Reitz, E. & Heuse, T. 1994. Palynofazies im Oberordovizium des Saxsothringikums. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **6**, 348-360.

Richardson, J. B. 1985. Lower Paleozoic sporomorphs: their stratigraphical distribution and possible affinities. *Philosophical Transactions of the Royal Society*, **B309**, 201-205.

Richardson, J. B. 1988. Late Ordovician and Early Silurian cryptospores and miospores from northeast Libya. *In*: El-Arnauti, A., Owens, B. & Thusu, B. (eds) *Subsurface palynostratigraphy of northeast Libya*. Garyounis University Publications, Benghazi, Libya, 89-109.

Richardson, J. B. 1996. Chapter 18A. Lower and Middle Palaeozoic records of terrestrial palynomorphs. *In*: Jansonius, J. & McGregor, D. C. (eds) *Palynology: principles and applications*. American Association of Stratigraphic Palynologists Foundation, Salt Lake City, **2**, 555-574.

Richardson, J. B. & Edwards, D. 1989. Sporomorphs and plant megafossils. 216-226. In: Holland, C. H. & Bassett, M. G. (eds) *A global standard for the Silurian System*. National Museum of Wales Geological series No. 9, Cardiff.

Richardson, J. B. & Ioannides, N. S. 1973. Silurian palynomorphs from the Tanezzuft and Acacus Formations, Tripolitania, North Africa. *Micropaleontology*, **19**, 257-307.

Richardson, J. B. & Burgess, N. D. 1999. Sporomorph evolution in the Anglo-Welsh basin: tempos and parallelism. 35-49 in Kurmann, M. H. & Hemsley, A. R. (eds) *The evolution of plant architecture*. Royal Botanic Gardens, Kew.

Richardson, J. B. & Lister, T. R. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology*, **12**, 201-252.

Richardson, J. B. & McGregor, D. C. 1986. Silurian and Devonian spore zones of the Old Red Sandstone Continent and adjacent regions. *Geological Survey of Canada Bulletin,* **364**, 1-79.

Richardson, J. B. & Rasul, S. M. 1990. Palynofacies in a Late Silurian regressive sequence in the Welsh Borderland and Wales. *Journal of the Geological Society, London,* **147**, 675-686.

Richardson, J. B., Rasul, S. M. & Al-Ameri, T. 1981. Acritarchs, miospores and correlation of the Ludlovian-Downtonian and Silurian-Devonian boundaries. *Review of Palaeobotany and Palynology*, **34**, 209-224.

Richardson, J. B., Rodríguez, R. M. & Sutherland, S. J. E. 2001. Palynological zonation of Mid- Palaeozoic sequences from the Cantabrian Mountains, NW Spain: implications for inter-regional and interfacies correlation of the Ludford/Prídolí and Silurian/Devonian boundaries, and plant dispersal patterns. *Bulletin Natural History Museum London (Geology)*, **57**, 115-162.

Rodríguez, R. M. 1978a. Nuevas mioesporas de la Formación San Pedro en Geras de Gordon, Cordillera Cantabrica (Provincia de León, Noroeste de España). *Breviora Geologica Asturica*, **22**, 9-16.

Rodríguez, R. M. 1978b. Miospores de la Formation San Pedro (Silurien-Devonien) à Corniero (Province de León, Espagne). *Revue de Micropaléontologie*, **20**, 216-221.

Rodríguez, R. M. 1978c. Mioesporas de la Formación San Pedro/Furada (Silúrico Superior-Devónico Inferior), Cordillera Cantabrica, NO de España. *Palinologia*, **Número Extraordinario 1**, 407-433.

Rodríguez, R. M. 1983. Palinologia de las Formaciones del Silúrico superior - Devonico inferior de la Cordillera Cantabrica. *Servicio de Publicaciones, Universidad de Leon*, 1 - 231.

Rogerson, C., Edwards, D., Axe, L. and Davies, K. L. 2002. A new embryophyte from the Upper Silurian of Shropshire, England. *Special Papers in Palaeontology* 67, 233-249.

Rogerson, E. C. W., Edwards, D., Davies, K. L. and Richardson, J. B. 1993. Identification of *in situ* spores in a Silurian *Cooksonia* from the Welsh Borderland. *Special Papers in Palaeontology,* **49**, 17-30.

Rubinstein, C. 1992. Palinologia des Silurico superior (Formacion Los Espejos) de La Quebrada de las Aguaditas, Precordillera de San Juan, Argentina. *Ameghiniana*, **29**, 231-248.

Rubinstein, C. 1994. Palynological investigation in the Lower Paleozoic of Argentina. *Zeitschrift fur Geologische und Paläontologie*, **1/2**, 271-230.

Rubinstein, C. 1995. Acritarchs from the upper Silurian of Argentina: their relationship with Gondwana. *Journal of South American Earth Sciences*, **8**, 103-115.

Rubinstein, C. V. & Brussa, E. D. 1999. A palynomorph and graptolite biostratigraphy of the Central Precordillera Silurian Basin, Argentina. *In*: Tongiorgi, M. & Playford, G. (eds) *Studies in Palaeozoic Palynology, Selected papers from the CIMP Symposium at Pisa*. Bolletino della Società Paleontologica Italiana, Modena, **38**, 257-266.

Rubinstein, C. V., Gerrienne, P., de la Puente, G. S., Astini, R. A. & Steemans, P. 2010. Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). *New Phytologist* **188**, 365-369.

Rubinstein, C. V. & Steemans, P. 2002. Miospore assemblages from the Silurian-Devonian boundary, in borehole A1-61, Ghadamis Basin, Libya. *In*: Steemans, P., Servais, T. & Streel, M. (eds) *Paleozoïc Palynology: a special issue in honour of Dr. Stanislas Loboziak*. Review of Palaeobotany and Palynology, Amsterdam, **118**, 397-421.

Rubinstein, C. & Vaccari, N. E. 2004. Cryptospore assemblages from the Ordovician/Silurian boundary in the Puna region, North-west Argentina. *Palaeontology*, **47**, 1037-1061.

Schopf, J. M., Mencher, E., Boucot, A. J. & Andrews, H. N. 1966. Erect plants in the early Silurian of Maine. *United States Geological Survey Professional Paper,* **550-D**, 69-75.

Schweitzer, H.-J. 1983. Die Unterdevonflora des Rheinlandes. *Palaeontographica*, **B 189**, 1-138.

Senkevich, M. A. 1975. New Devonian psilophytes from Kazakhstan. *Esheg Vses Paleontol Obschestva,* **21**, 288-298 (in Russian).

Senkevich, M. A. 1986. Fossil plants in the Tokrau horizon of the Upper Silurian. In I.F. Nikitin, and S.M. Bandaletoc, eds. *The Tokrau horizon of the Upper Silurian Series: Balkhash Segment*, 236 pp. Nuka: Alma-Ata. (in Russian).

Smelror, M. 1987. Llandovery and Wenlock miospores and spore-like microfossils from the Ringerike district, Norway. *Norsk Geologisk Tidsskrift*, **67**, 143-150.

Smelror, M. 1990. Palynomorphs from the *Cyrtograptys centrifugus* graptolite zone (Early Wenlock, Silurian), Bornholm. *Bulletin of the Geological Society of Denmark*, **39**, 83-89.

Smith, D. G. 1975. Wenlock plant spores and tetrads from County Mayo Ireland. *Geological Magazine*, **112**, 411-414.

Smith, D. G. 1979. The distribution of trilete spores in Irish Silurian rocks. *In*: Harris, A. L., Holland, C. H. & Leake, B. E. (eds) *The Caledonides of the British Isles - Reviewed.* Geological Society of London, London, 423-431.

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.

Steemans, P. 1995. Silurian and Lower Emsian spores in Saudi Arabia. *Review of Palaeobotany and Palynology*, **89**, 91-104.

Steemans, P. 1999. Paléodiversification des spores et des cryptospores del'Ordovician au Dévonien Inférieur. *Geobios,* **32**, 341-352.

Steemans, P. 2000. Miospore evolution from the Ordovician to the Silurian. *Review of Palaeobotany and Palynology,* **113**, 189-196.

Steemans, P. 2001. Ordovician cryptospores from the Oostduinkerke borehole, Brabant Massif, Belgium. *Geobios*, **34**, 3-12.

Steemans, P., Higgs, K. T. & Wellman, C. H. 2000. Cryptospores and trilete spores from the Llandovery, Nuayyim-2 Borehole, Saudi Arabia. *In*: Al-Hajri, S. & Owens, B. (eds) *Stratigraphic palynology of the Palaeozoic of Saudi Arabia*. GeoArabia, Bahrain, **Special Volume 1**, 92-115.

Steemans, P., Le Hérissé, A. & Bozdogan, N. 1996. Ordovician and Silurian cryptospores and miospores from Southeastern Turkey. *Review of Palaeobotany and Palynology*, **93**, 35-76.

Steemans, P., Le Herisse, A., Melvin, J., Miller, M. A., Paris, F., Verniers, J. & Wellman, C. H. 2009. Origin and radiation of the earliest vascular land plants. *Science*, **324**, 353.

Steemans, P., Lepot, K., Marshall, C. P. & Javaux, E. J. 2010. FTIR characterisation of the chemical composition of Silurian cryptospores from Gotland, Sweden.

Steemans, P. & Pereira, E. 2002. Llandovery miospore biostratigraphy and stratigraphic evolution of the Paraná Basin, Paraguay - palaeogeographic implications. *Bulletin de la Société géologique de France*, **173**, 407-414.

Steemans, P., Rubinstein, C. & Melo, J. H. G. 2008. Siluro-Devonian miospore biostratigraphy of the Urubu River area, western Amazon Basin, northern Brazil. *Geobios*, **41**, 263-282.

Steemans, P., Wellman, C. H. & Filatoff, J. 2007. Palaeophytogeographical and palaeoecological implications of a miospore assemblage of earliest Devonian (Lochkovian) age from Saudi Arabia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **250**, 237-254.

Steemans, P., Wellman, C. H. & Gerrienne, P. 2010. Paleogeographic and paleoclimatic considerations based on Ordovician to Lochkovian vegetation. 49-58. *In*: Vecoli, M., Clement, M. and Meyer-Berthaud, B. (eds) *The terrestrialization process: modelling complex interactions at the biosphere – geosphere interface.* Geological Society, London, Special Publications, **339**.

Strother, P. K. 1991. A classification schema for the Cryptospores. *Palynology*, **15**, 219-236.

Strother, P. K. 1993. Clarification of the Genus *Nematothallus* Lang. *Journal of Paleontology*, **67**, 1090-1094.

Strother, P. K. 2000. Cryptospores: the origin and early evolution of the terrestrial flora. 3-20 in Gastaldo, R. A. & DiMichele, W. A. (eds) *Phanerozoic terrestrial ecosystems*. The Paleontological Society.

Strother, P. K., Al-Hajri, S. and Traverse, A. 1996. New evidence for land plants from the lower Middle Ordovician of Saudi Arabia. *Geology,* **24**, 55-58.

Strother, P. K. & Beck, J. H. 2000. Spore-like microfossils from Middle Cambrian strata: expanding the meaning of the term cryptospore. 413-424. In: Harley, M. M., Morton, C. M. & Blackmore, S. (eds) *Pollen and spores: morphology and biology*. Royal Botanic gardens, Kew.

Strother, P. K. & Lenk, C. 1983. *Eohostimella* is not a plant. *American Journal of Botany,* **70**, 80.

Strother, P. K. & Traverse, A. 1979. Plant microfossils from the Llandoverian and Wenlockian rocks of Pennsylvania. *Palynology*, **3**, 1-21.

Strother, P. , Wood, G., Taylor, W. & Beck, J. 2004. Middle Cambrian cryptospores and the origin of land plants. *AAP Memoir*, **29**, 99-113.

Taylor, W. A. 1995a. Spores in earliest land plants. *Nature*, **373**, 391-392.

Taylor, W. A. 1995b. Ultrastructure of *Tetrahedraletes medinensis* (Strother and Traverse) Wellman and Richardson, from the Upper Ordovician of Southern Ohio. *Review of Palaeobotany and Palynology*, **85**, 183-187.

Taylor, W. A. 1996. Ultrastructure of lower Paleozoic dyads from southern Ohio. *Review of Palaeobotany and Palynology,* **92**, 269-279.

Taylor, W. A. 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, W. A. 2000. Spore wall development in the earliest land plants. 425-434 in Harley, M. M., Morton, C. M. & Blackmore, S. (eds) *Pollen and spores: morphology and biology*. Royal Botanic gardens, Kew.

Taylor, W. A. 2001. Evolutionary hypothesis of Cryptospore producing plants based on wall ultrastructure.11-15. *In*: Goodman, D. K. & Clarke, R. T. (eds) *Proceedings of the IX International palynological Congress Houstan, Texas, U.S.A., 1996*. American Association of Stratigraphical Palynologists Foundation, Dallas, Texas.

Taylor, W. A. 2002. Studies in cryptospore ultrastructure: variability in the tetrad genus *Tetrahedraletes* and type material of the dyad *Dyadospora murusattenuata*. *Review of*

Palaeobotany and Palynology, **119**, 325-334.

Taylor, W. A. 2003. Ultrastructure of selected Silurian trilete spores and the putative Ordovician trilete spore *Virgatasporites*. *Review of Palaeobotany and Palynology,* **126**, 211-223.

Taylor, W. A., Gensel, P. G. & Wellman, C. H. In press. Wall ultrastructure in three species of the Lower Devonian spore *Emphanisporites*. *Review of Palaeobotany and Palynology*

Taylor, W. A. & Strother, P. K. 2008. Ultrastructure of some Cambrian palynomorphs from the Bright Angel Shale, Arizona, USA. *Review of Palaeobotany and Palynology*, **151**, 41-50.

Taylor, W. A. & Strother, P. K. 2009. Ultrastructure, morphology, and topology of Cambrian palynomorphs from the Lone Rock Formation, Wisconsin, USA. *Review of Palaeobotany and Palynology*, **153**, 296-309.

Tekbali, A. O. & Wood, G. D. 1991. Silurian spores, acritarchs and chitinozoans from the Baní Walíd Borehole of the Ghadámis Basin, Northwest Libya. *Geology of Libya*, **IV**, 1243-1273.

Tims, J. D. & Chambers, T. C. 1984. Rhyniophytina and Trimerophytina from the early land flora of Victoria, Australia. *Palaeontology,* **27**, 265-279.

Toro, M., Chamon, O., Salguero, R. & Vargas, C. 1997. Las plantas de la Formacion Kirusillas (Silurico) en la region de La Angostura Departamento de Cochabamba. *Mem. del XII Congreso Geol. de Bolivia - Tarija, Bolivia*, pp. 523-529.

Turner, R. E. 1984. Acritarchs from the type area of the Ordovician Caradoc Series, Shropshire, England. *Paleontographica*, **190**, 85-157.

Van Zanten, B. O. 1978. Experimental studies on trans-oceanic long-range dispersal of moss spores in the southern hemisphere. *Journal of the Hattori Botanical Laboratory*, **44**, 445-482.

Van Zanten, B. O. & Gradstein, S. R. 1988. Experimental dispersal geography of neotropical liverworts. *Beiheft zue Nova Hedwigia* 41-94.

Van Zanten, B. O. & Pocs, T. 1981. Distribution and dispersal of bryophytes. *Advances in Bryology*, **1**, 497-562.

Vanguestaine, M., Steemans, P. & Streel, M. 1986. Microfossiles végétaux. *In*: Racheboeuf, P. R. (ed) *le Groupe de Liévin. Pridoli-Lochkovien de l'Artois (N. France). Biostratigraphie du Paléozoïque*. Mém. Soc. Géol. Min. Bretagne, **3**, 47-55.

Vavrdová, M. 1982. Recycled acritarchs in the uppermost Ordovician of Bohemia. *Casopis pro Mineralogii a Geologii*, **27**, 337-345.

Vavrdová, M. 1984. Some plant microfossils of the possible terrestrial origin from the Ordovician of central Bohemia. *Vestnik Ceskeho Geologickeho Ustavu*, **59**, 165-170.

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

Vavrdová, M. 1989. New acritarchs and miospores from the Late Ordovician of Hlasna Treban, Czechoslovakia. *Casopis pro Mineralogii a Geologii*, **34**, 403-420.

Vavrdová, M. 1990a. Early Ordovician acritarchs from the locality Myto near Rokycany (late Arenig, Czechoslovakia). *Casopis pro Mineralogii a Geologii*, **35**, 239-250.

Vavrdová, M. 1990b. Coenobial acritarchs and other palynomorphs from the Arenig/Llanvirn boundary, Prague basin. *Vestnik Ceskeho Geologickeho Ustavu*, **65**, 237-242.

Vecoli, M. & Samuelsson, J., 2001. Quantitative evaluation of microplankton palaeobiogeography in the Ordovician - Early Silurian of the northern Trans European Suture Zone: implications for the timing of the Avalonia-Baltica collision. *Review of Palaeobotany and Palynology*, **115**, 43-68.

Wang, Y. & Li, J. 2000. Late Silurian trilete spores from northern Jiangsu, China. *Review of Palaeobotany and Palynology*, **111**, 111-125.

Wang, Y. & Zhang, Y. D. 2009. Llandovery sporomorphs and graptolites from the Manbo Formation, the Mojiang County, Yunnan, China. *Proceedings of the Royal Society B-Biological Sciences*, **277**, 267-275.

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

Wang, Y., Zhu, H. C. & Li, J. 2005. Late Silurian plant microfossil assemblage from Guangyuan, Sichuan, China. *Review of Palaeobotany and Palynology*, **133**, 153-168.

Wellman, C. H. 1993. A land plant microfossil assemblage of Mid Silurian age from the Stonehaven Group, Scotland. *Journal of Micropalaeontolgy*, **12**, 47-66.

Wellman, C. H. 1996. Cryptospores from the type area for the Caradoc Series (Ordovician) in southern Britain. *Palaeontology*, **55**, 103-136.

Wellman, C. H. 2003. Dating the origin of land plants. 119-141. *In*: Donoghue, P. C. J. and Smith, M. P. (eds) *Telling the evolutionary time: Molecular clocks and the fossil record*. CRC Press.

Wellman, C. H. 2004. Origin, function and development of the spore wall in early land plants. 43-63. *In*: Hemsley, A. R. and Poole, I. (eds), *The evolution of plant physiology.* Royal Botanic Gardens, Kew.

Wellman, C. H. 2010. The invasion of the land by plants: when and where? *New Phytologist* **188**, 306-309.

Wellman, C. H., Edwards, D. & Axe, L. 1998a. 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, London,* **353**, 1983-2004.

Wellman, C. H., Edwards, D. & Axe, L. 1998b. 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, C. H. & Gray, J. 2000. The microfossil record of early land plants. *Philosophical Transactions of the Royal Society London* B 355, 717-732.

Wellman, C. H., Higgs, K. T. & Steemans, P. 2000. Spore assemblages from a Silurian sequence in Borehole Hawiyah-151 from Saudi Arabia. *In*: Al-Hajri, S. & Owens, B. (eds) *Stratigraphic Palynology of the Palaeozoic of Saudi Arabia*. GeoArabia, Bahrain, **Special Volume 1**, 116-133.

Wellman, C. H., Habgood, K., Jenkins, G. & Richardson, J. B. 2000. A new plant assemblage (microfossil and megafossil) from the Lower Old Red Sandstone of the Anglo-Welsh Basin: its implications for the palaeoecology of early terrestrial ecosystems. *Review of Palaeobotany and Palynology*, 109, 161-196.

Wellman, C. H., Osterloff, P. L. & Mohiuddin, U. 2003. Fragments of the earliest land plants. *Nature,* **425**, 282-285.

Wellman, C. H. & Richardson, J. B. 1993. Terrestrial plant microfossils from Silurian inliers of the Midland Valley of Scotland. *Palaeontology*, **36**, 155-193.

Wetherall, P. M., Dorning, K. J. & Wellman, C. H. 1999. Palynology biostratigraphy, and depositional environments around the Ludlow-Pridoli boundary at Woodbury Quarry, Hereforshire, England. *Bolletino della Societa Paleontologica Italiana*, **38**, 397-404.

Williams, D. M., Harkin, J. & Higgs, K. T. 1996. Implications of new microfloral evidence from the Clew Bay Complex for Silurian relationships in the western Irish Caledonides. *Journal of the Geological Society, London*, **153**, 771-777.

Yin, L. & He, S. 2000. Palynomorphs from the transitional sequences between Ordovician and Silurian of northwestern Zhejiang, South China. *Palynofloras and Palynomophs* *of China*, 186-202.

FIGURE CAPTIONS

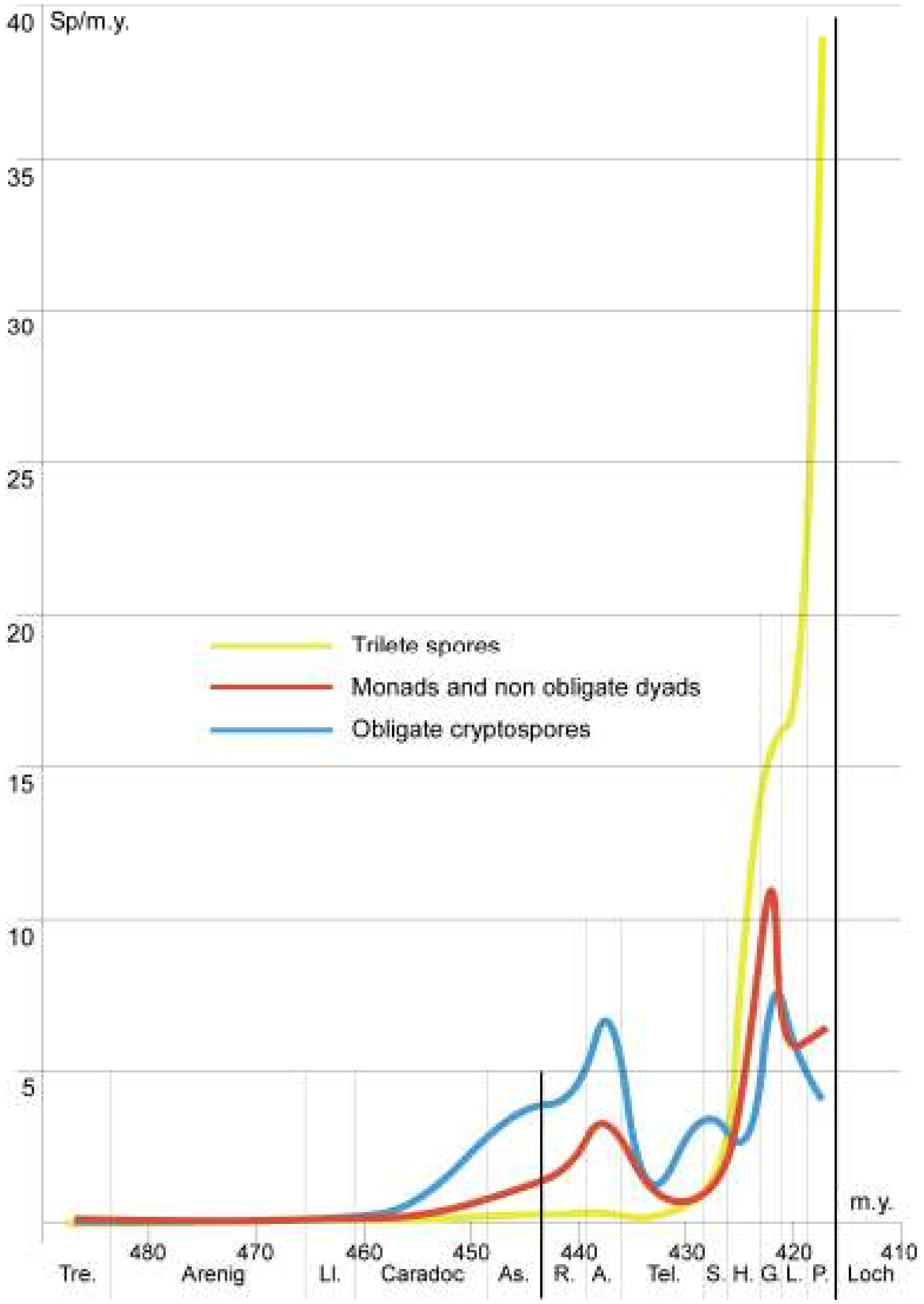


Fig. 1: Ordovician-Silurian dispersed spore diversity curve generated from the data presented in Appendix 2. Timescale is from Gradstein *et al*. (2004).

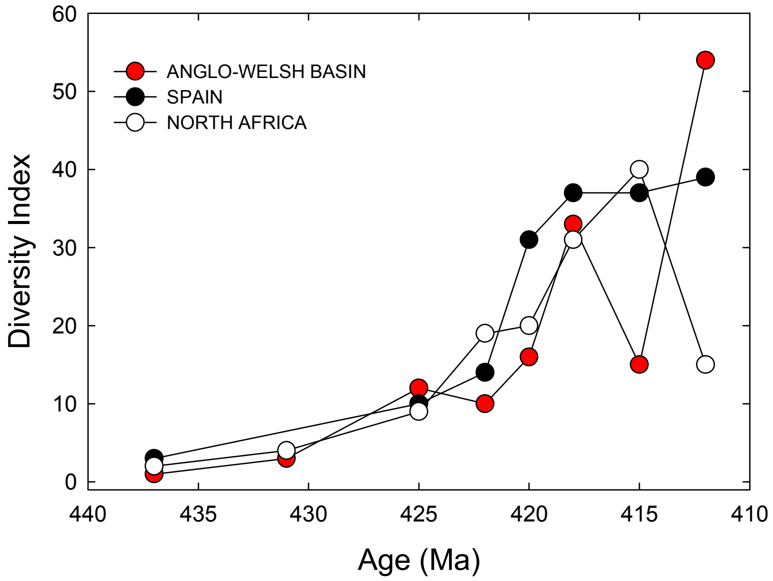


Fig. 2: Newly developed Silurian-Early Devonian (Lochkovian) trilete spore diversity curve based on sequences from Avalonia (Anglo-Welsh basin), PeriGondwana (northern Spain) and Northern Gondwana (Libya). Details of how the curve was constructed are outlined in the text.

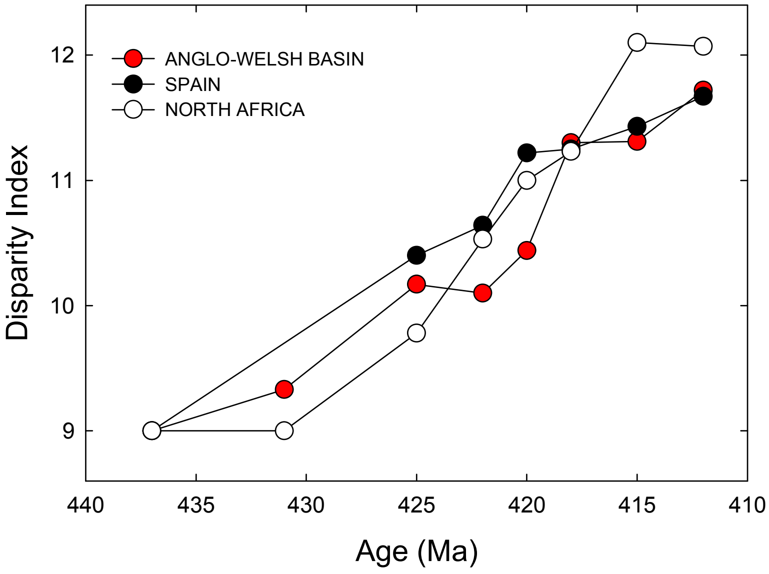
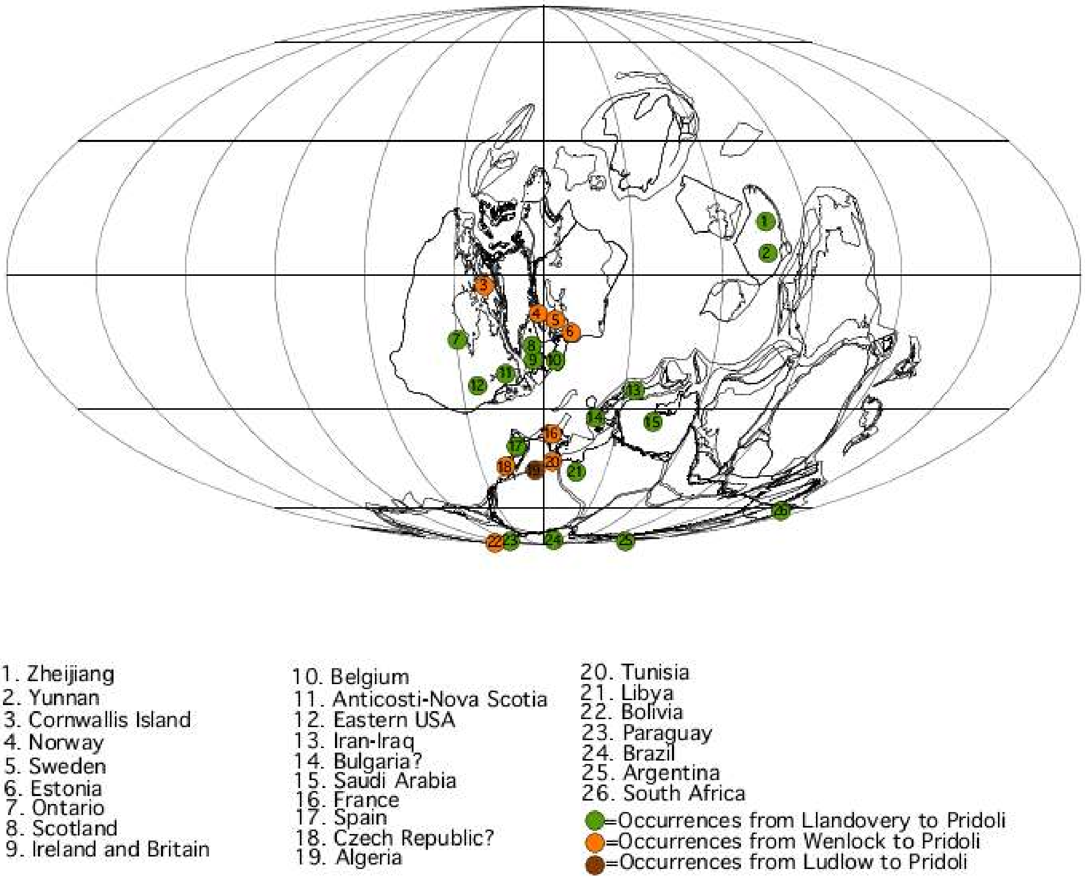
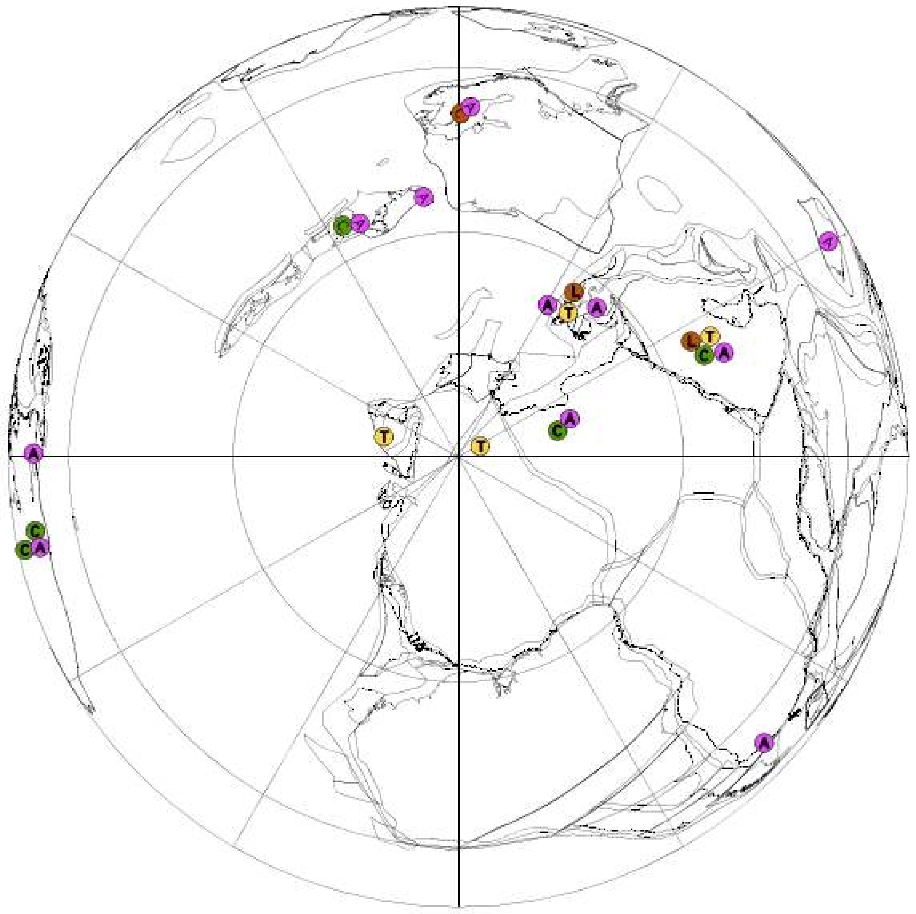


Fig. 3: Newly developed Silurian-Early Devonian (Lochkovian) trilete spore disparity curve based on sequences in Avalonia (Anglo-Welsh basin), PeriGondwana (northern Spain) and Southern Gondwana (Libya). Details of how the curve was constructed are outlined in the text and Table 1. In the figure: change North Africa by Soutern Gondwana


Distribution of Silurian (Llandovery-Pridoli) miospore assemblages on base map from plate bug software at 425 My (Wenlock)

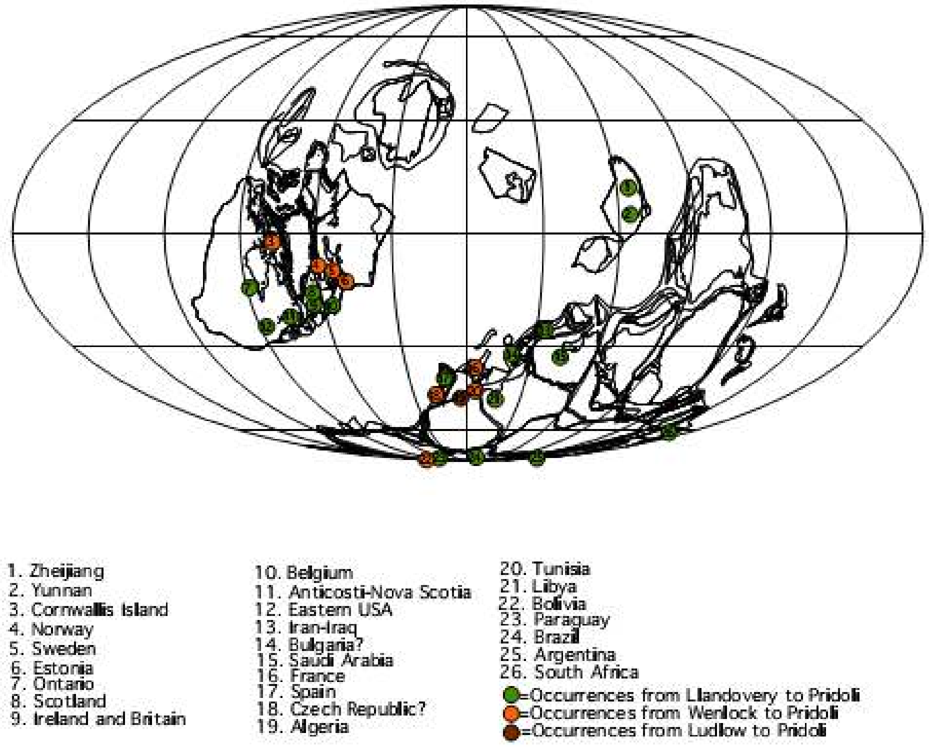
Figs 4-: Silurian palaeocontinental reconstructions plotting palaeogeographic distribution of plant megafossils. Data from Appendix I. Same remark as above



Distribution of Ordovician (Tremadoc-Ashgill: Tremadocian - Hirnantian) cryptospore assemblages on base map from plate bug software at 465 My (Darriwilian)

T = Tremadocian
L = Darriwilian (Llanvirn)
C = Sandbian - Katian (Caradoc)
A = Katian - Hirnantian (Ashgill)

Figs 5-: Ordovician palaeocontinental reconstructions plotting palaeogeographic distribution of dispersed spores. Data from Appendix II.



Figs 6-: Silurian palaeocontinental reconstructions plotting palaeogeographic distribution of dispersed spores. Data from Appendix II. (uncorrect figure)

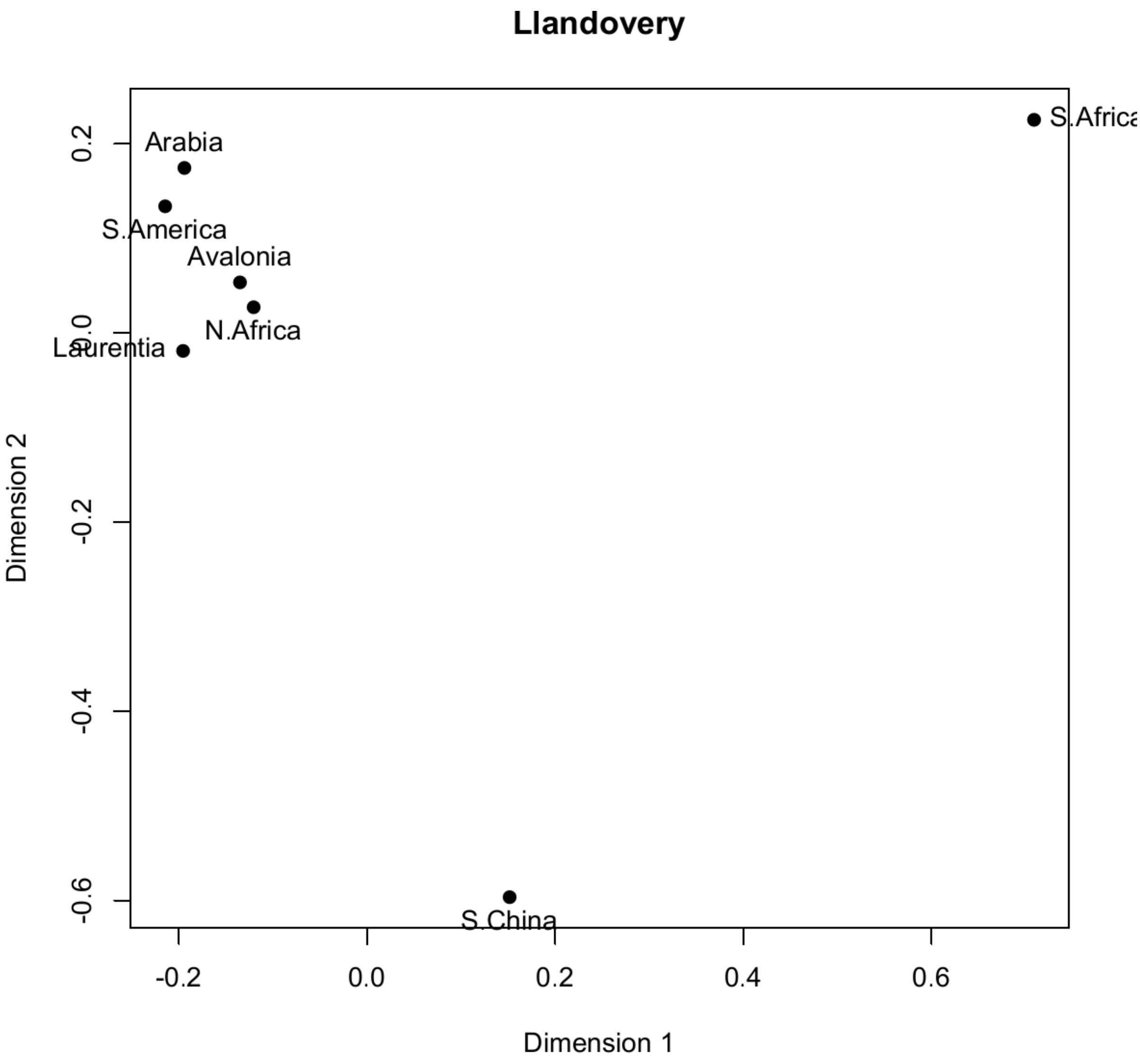


Fig. 7-MDS scatter plot and cluster diagram for Silurian (Llandovery) dispersed spores. Details of methods are in the text. All MDS need to be modified in using only palaeogeograpgic name not Arabia (SW Gondana) N Africa (S Africa)etc…

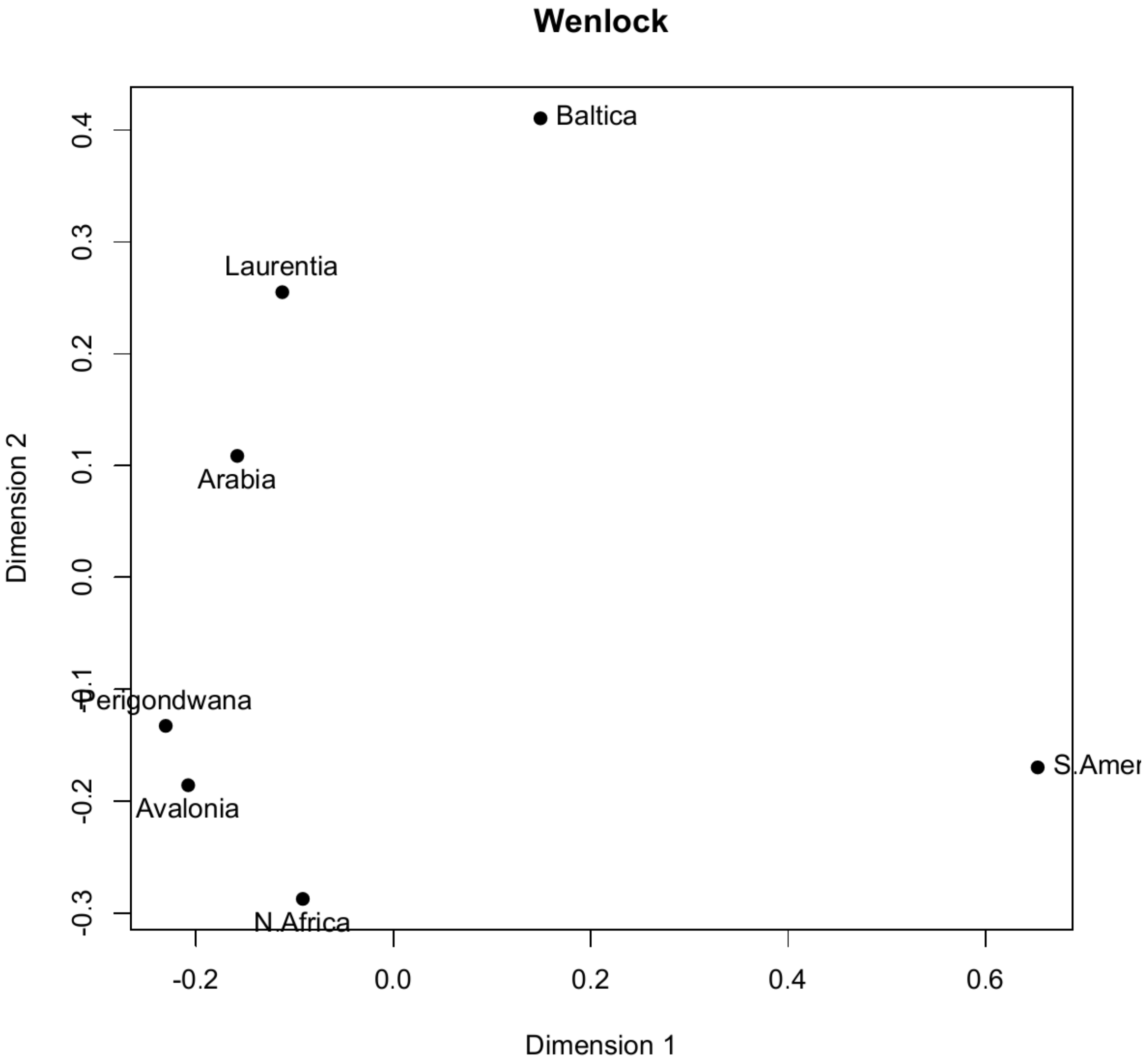


Fig. 8-MDS scatter plot and cluster diagram for Silurian (Wenlock) dispersed spores. Details of methods are in the text.

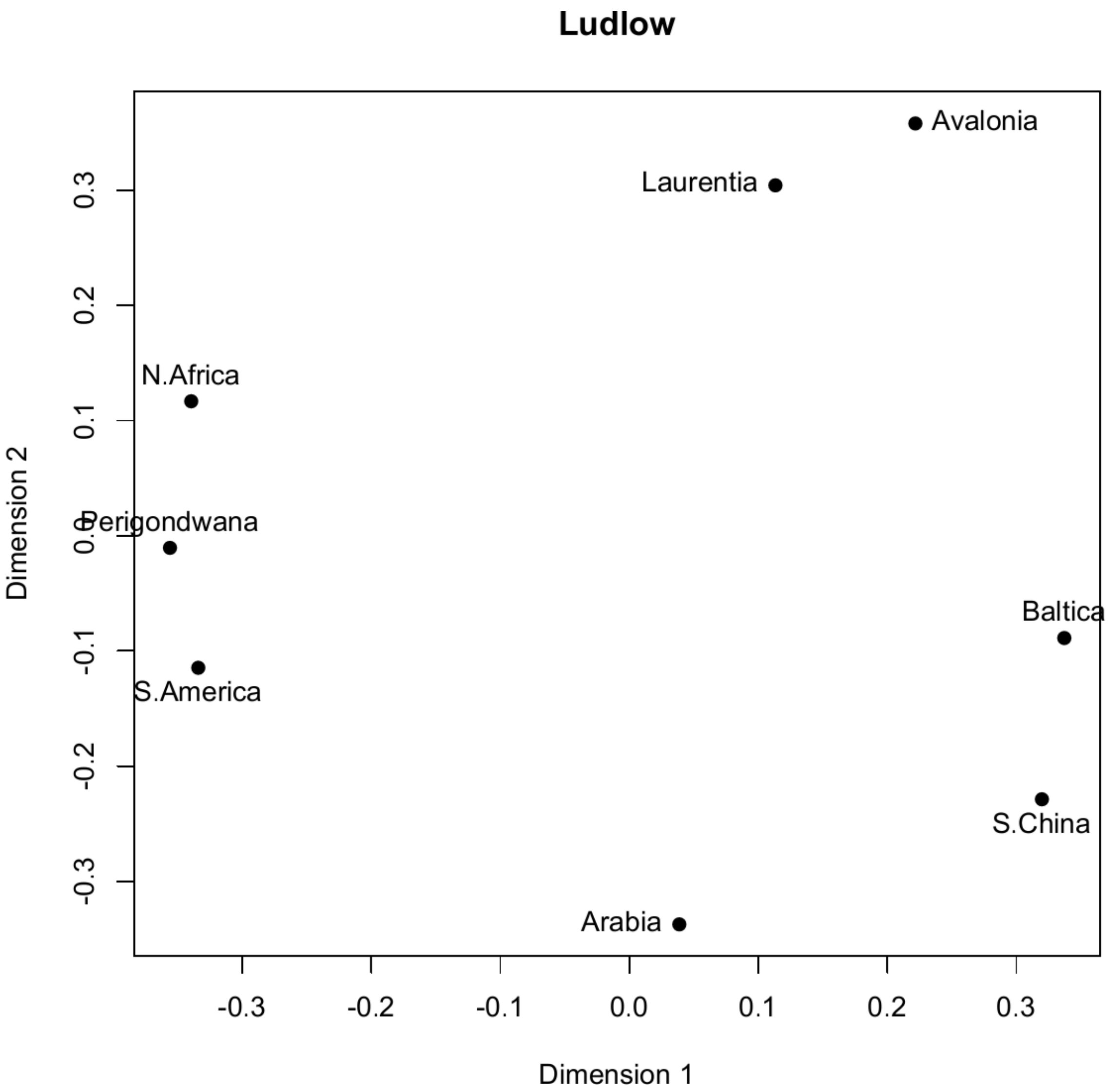


Fig. 9-MDS scatter plot and cluster diagram for Silurian (Ludlow) dispersed spores. Details of methods are in the text.

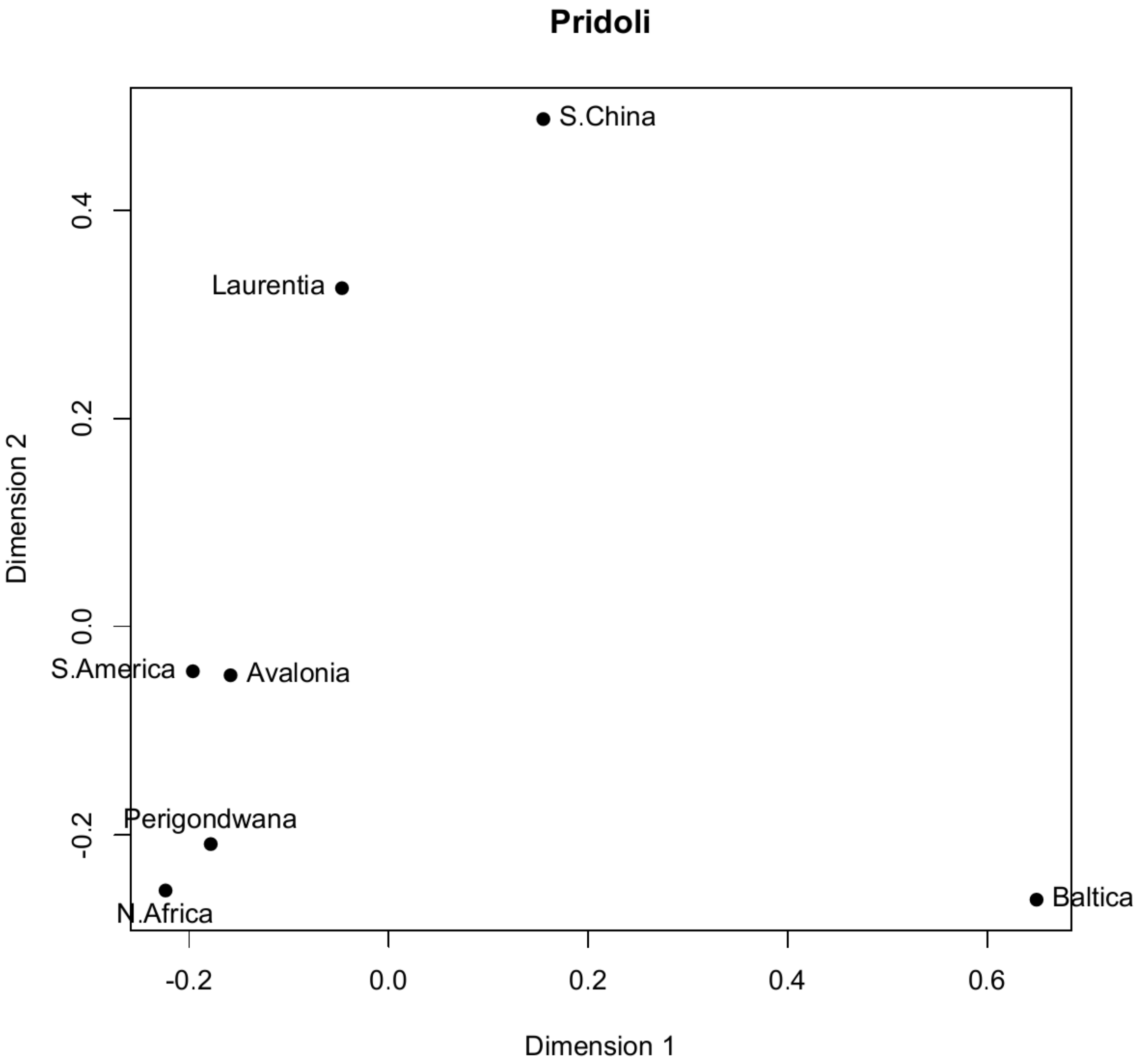


Fig. 10-MDS scatter plot and cluster diagram for Silurian (Pridoli) dispersed spores. Details of methods are in the text.

TABLES

Table 1: Character scoring for spore disparity index. Each spore is scored for each of the nine morphological components listed below. These are summed to provide the 'spore disparity index'. Scores within each of the nine morphological components are intended to reflect morphological complexity, rather than order of appearance in the fossil record. We have attempted to consider their complexity within a developmental context (i.e. how easy are they to construct in terms of exospore development).

1. Amb shape

Circular-subcircular-subtriangular (1); Ellipsoid (monolete only) (1); Triangular(2); Triangular convex(3); Triangular concave(3); Triangular truncated(3)

2. Amb size

0-50 μm (1); 50-100 μm (2); 100-200 μm (3); >200 μm (4)

3. Structure

Crassitate (1); Retusoid (2); Patinate (2); Cingulate (2); Zonate (3); Bilayered-perine or sloughing outer layer (3); Camerate (4)

4. Tetrad configuration

Trilete (1); Monolete (2)

5. Laesurae

Simple (1); Prominent lips (2)

6. Proximal structural features

None (1); Interradial papillae (2); Thickening associated with trilete mark(2); Thinning associated with trilete mark (2); Radial ribs (3); Radial ribs and thickening associated with trilete (4)

7. Proximal ornament

Laevigate (1); Irregular murornate (2); Irregular apiculate (2); Irregular fovea (2); Regular murornate (3); Regular apiculate (3); Regular reticulate (3); Regular foveolate (3); Biform (4); Complex elements (4)

8. Distal structural features

None (1); Circular thickening(2); Infrastructure (prox and/or distal) (2); Annular thickening (3)

9. Distal ornament

Laevigate (1); Irregular murornate (2); Irregular apiculate (2); Irregular fovea (2); Regular murornate (3); Regular apiculate (3); Regular reticulate (3); Regular foveolate (3); Biform elements (4); Reticulate with extended intersections (4); Complex elements(e.g. grapnel-tipped) (5)

APPENDICES

Appendix 1: Ordovician-Silurian land plant megafossil assemblages (after Edwards and Wellman (2001) and Edwards and Richardson (2004) with updates). Locality codes refer to those plotted on the palaeogeographical base maps. *Pinnatiramosus qianensis* is now considered to represent the roots of a younger, possibly Permian, plant that penetrated into Silurian strata (Edwards *et al*. 2007) and is omitted from this review.

LOCALITY	**AGE**	**DATING**	**COMPOSITION**	**REFERENCE**[1]
(K1) Oman	Katian	Palynology (acritarchs, Chitinozoans) and field relations	Isolated sporangia	Wellman et al. (2003)
(L1) Maine, USA	Llandovery (?Telychian)	Invertebrates	*Eohostimella heathana*[2]	Schopf *et al*. (1966)
(W1) Tipperary, Ireland	Wenlock (Homerian)	Graptolites	*Cooksonia* sp.	Edwards *et al.* (1983)
(W2) Czech Republic	Wenlock	Graptolites	*Cooksonia* sp.	Libertin et al. (2002)
(W3/Lu7) Southern Bolivia	Late Wenlock/Ludlow	Graptolites	Sterile rhyniophytes	Toro et al. (1997)
(Lu1) Anglo-Welsh Basin (Cwm Craig Ddu, Powys)	Ludlow (Gorstian)	Graptolites	cf. *Cooksonia cambrensis* *Cooksonia pertoni* *Cooksonia* sp.	Edwards *et al.* (1979)
(Lu2) Anglo-Welsh Basin (Capel Horeb, Powys)	Ludlow (Ludfordian)	Invertebrates; Acritarchs	*Cooksonia* sp. *Steganotheca striata*	Edwards & Rogerson (1979)
(Lu3) Northern Greenland	Ludlow (?Ludfordian)	Graptolites	*Salopella* sp.	Larsen et al. (1987)
(Lu4) Bathurst Island, Arctic Canada	Ludlow	Graptolites Conodonts Brachiopods	*Hostinella* cf. *Bathurstia* sp. *Zosterophyllum* sp. aff. *Z.* sp. A a.ff. *Zost.* sp. B *Distichophytum* sp. *Macivera gracilis* Rhyniophytoid	Kotyk et al. (2002)
(Lu5) Victoria, Australia	?late Ludlow	Graptolites	*Baragwanathia longfolia* *Salopella australis* *Hedeia* sp. Zosterophylls	Tims & Chambers (1984); Douglas & Holmes (2006)
(Lu6/P1) Tarija, southern Bolivia	Ludlow-?early Pridoli	Field relations Spores	*Cooksonia* cf. *caledonicaca* cf. *Tarrantia* cf. *Cooksonia hemisphaerica*	Edwards et al. (2001)
(P1-5) Anglo-Welsh Basin (Ludford Corner, Ludlow)	Pridoli	Invertebrates Spores	*Cooksonia pertoni* *Hollandophyton colliculum* Various isolated sporangia	Rogerson *et al.* (2002)
(P1-5) Anglo-Welsh Basin (Perton Lane, Hereford)	Pridoli	Invertebrates Spores	*Caia langii* *Cooksonia cambrensis* *Cooksonia pertoni* *Pertonella dactylethra* *Salopella* sp.	Fanning *et al.* (1990, 1991)
(P1-5) Anglo-Welsh basin (Freshwater East, Pembrokeshire)	Pridoli	Spores	*Cooksonia cambrensis* *Cooksonia hemisphaerica* *Cooksonia pertoni* *Cooksonia* sp. *Psilophytites* sp. *Tortilicaulis transwalliensis*	Edwards (1979)

(P1-5) Anglo-Welsh basin (Capel Horeb, Powys)	Pridoli	Spores	*Cooksonia* sp. *Steganotheca striata*	Edwards & Rogerson (1979)
(P1-5) Anglo-Welsh basin (Little Wallop Hall, Shropshire)	Pridoli	Invertebrates Spores	*Cooksonia pertoni*	Rogerson *et al.* (1993)
(P6) Ontario (Canada) and New York State (USA)	Pridoli	Conodonts Eurypterids	*Cooksonia* cf. *hemisphaerica* *Cooksonia* sp.	Edwards *et al.* (2004)
(P7) Poland	Pridoli	Invertebrates	*Cooksonia* sp.	Bodzioch *et al.*, (2003)
(P8) Podolia, Ukraine	Pridoli		*Cooksonia pertoni* *C. hemisphaerica* *Eorhynia* (*Salopella*) ?*Zosterophyllum* sp. *Lycopodolica*	Ishchenko (1975)
(P9) Czech Republic	Pridoli	Graptolites	*Cooksonia bohemica*	Orbhel (1962) Schweitzer (1983) Libertin et al. (2002)
(P10) Libya	Pridoli	Graptolites	?*Cooksonia* sp.	Daber (1971)
(P11) Kazakhstan	Pridoli	Graptolites	*Cooksonia* sp. *Zosterophyllum* sp.	Petrosyan (in Edwards and Wellman 2001)
(P12) Balkhash area, Kazakhstan	Pridoli	Graptolites	*Cooksonella* sp. ?*Baragwanathia* sp. ?*Taeniocrada* sp. *Jugumella burubaensis*	Senkevitch (1975)
(P13) Yunnan, China	Pridoli	Chitinozoans	*Zosterophyllum qujingense*	Hao et al. (2007)
(P14) Junggar Basin, Xinjiang, China	Pridoli	Graptolites	*Cooksonella* sp. *Junggaria spinosa* ?*Lycopodolica* *Salopella xinjiangensis* *Zosterophyllum* sp.	Cai et al. (1993)

[1] For brevity only the most recent review of the flora is referenced.

[2] Strother and Lenk (1983) suggested *Eohostimella* represents an animal burrow rather than a plant although this was refuted by Gray (1984).

Appendix 2: Ordovician-Silurian dispersed spore assemblages. Locality codes refer to those plotted on the palaeogeographical base maps. Data compiled by Philippe Steemans. Certain reported assemblages are omitted either because they are poorly age constrained or too poorly preserved/too high thermal maturity to enable accurate identification. Other assemblages are omitted where spore identification is questionable. Cited references refer to the original paper that reported on the spore assemblage plus subsequent papers that have been used in taxonomic updates of the species list. Note that Tremadoc-Arenig records report only terrestrial spore-like palynomorphs of questionable affinities and are marked with an *.

Tremadoc

S **PeriGondwana (Armorica) - Spain:** **Attritasporites messaoudi* (Fombella 1982)

S **Gondwana - Algeria:** **Abacum rudi, *A. messaoudi, *A. scabra, *A. velata* (Combaz 1967; Pittau 1985)

SW **Gondwana – Saudi Arabia:** **Virgatasporites rudii* (Molyneux & Al-Hajri 2000)

Arenig

S **PeriGondwana (Perunica) – Czech Republic:** **Attritasporites messaoudi, *A. velata,* Virgatasporites rudi, *V. baccatus* (Vavrdová 1990a, b)

Llanvirn

S **PeriGondwana (Perunica) – Czech Republic:** **Virgatasporites rudi* (Vavrdová 1990a, b)

SW **Gondwana - Saudi Arabia:** *Stegambiquadrella contenta* (McClure 1988; Gray 1988; Strother *et al.* 1996; Molyneux & Al-Hajri 2000)

Caradoc

Avalonia - UK, Shropshire: *Abditusdyadus histosus, Dyadospora murusdensa, Laevolancis chibrikovae, Moyeria cabottii, Pseudodyadospora laevigata, Rimosotetras problematica, Rugosphaera cerebra, Segestrespora laevigata, S. rugosa, Sphaerasaccus glabellus, Strophomorpha ovata, Tetrahedraletes grayae, T. medinensis, Velatitetras laevigata, V. rugosa, V. rugulata, Vestitusdyadus qalibahinus*. (Burgess 1991; Richardson 1988; Rubinstein & Vaccari 2004; Steemans *et al.* 1996; Steemans *et al.* 2000; Strother 1991; Turner 1984; Wellman 1996; Wellman & Richardson 1993)

S **Gondwana - Libya:** *Ambitisporites vavrdovii, Imperfectotriletes patinatus, Tetrahedraletes medinensis*.(Gray *et al.* 1982; Steemans *et al.* 1996; Steemans *et al.* 2000; Wellman & Richardson 1993)

SW **Gondwana - Saudi Arabia:** *Ambitisporites* sp., *Chelinospora* sp., *Leiotriletes* sp., *? Synorisporites* sp. (Steemans *et al.* 2009)

Ashgill

Laurentia - USA: *Nodospora retimembrana, Tetrahedraletes grayii, T. medinensis, T. medinensis parvus, Velatitetras laevigate, Velatitetras reticulata, V. retimembrana, V. rugosa* (Beck & Strother 2008; Burgess 1991; Gray 1985, 1988; Steemans *et al.* 1996; Strother 1991; Taylor 1995; Wellman & Richardson 1993)

Baltica - Germany: *Dyadospora murusdensa, Rugosphaera tuscarorensis* (Reitz & Heuse 1994)

Avalonia - Nova Scotia, Canada: *Tetrahedraletes medinensis* (Beck & Strother 2008)

Avalonia - Belgium: *Ambitisporites avitus*, *Dyadospora murusattenuata*, *Imperfectotriletes patinatus*, *I. vavrdovae*, *Moyeria cabottii*, *Pseudodyadospora laevigata*, *Rugosphaera cerebra*, *R. tuscarorensis, Segestrespora membranifera, S. rugosa, Stegambiquadrella contenta, Tetrahedraletes grayae, T. medinensis, Velatitetras anatoliensis, V. laevigata, V. retimembrana, V. rugosa* (Martin 1973; Steemans 2001; Steemans *et al.* 1996; Wellman & Richardson 1993).

Avalonia – southern Britain: *Ambitisporites avitus, Imperfectotriletes vavrdovae, Rimosotetras problematica, Segestrespora laevigata, S. membranifera, S. rugosa, Tetrahedraletes medinensis parvus, Velatitetras laevigata, V. retimembrana* (Burgess 1991; Steemans *et al.* 1996)

S PeriGondwana (Moesian platform) - Bulgaria: *Tetrahedraletes medinensis* (Lakova *et al.* 1992)

S PeriGondwana (Perunica) – Czech Republic: *Chaetosporites pollensimillis, Dyadospora murusattenuata, D. murusdensa, Imperfectotriletes patinatus, Laevolancis divellomedium, Pseudodyadospora laevigata, Quadrisporites horridus, Q. variabilis, Rugosphaera cerebra, R. tuscarorensis, Segestrespora membranifera, Stegambiquadrella contenta, Tetrahedraletes grayii, T. medinensis, Tritonialetes vacuolus, Vallatialetes aureolatus, Velatitetras retimembrana, V. retimembrana, V. rugosa* (Gray 1991; Steemans *et al.* 1996; Steemans *et al.* 2000; Strother 1991; Vavrdová 1982, 1984, 1988, 1989; Wellman 1996)

S PeriGondwana (Taurides) - Turkey: *Ambitisporites avitus, A. dilutus, Dyadospora murusattenuata, D. murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Pseudodyadospora laevigata, Quadrisporites granulatus, Rimosotetras problematica, Rugosphaera cerebra, Segestrespora burgessii, S laevigata, S. membranifera, S. rugosa, Tetrahedraletes medinensis, Velatitetras anatoliensis, V. laevigata, V. retimembrana, V. rugosa* (Steemans *et al.* 1996; Steemans *et al.* 2000)

SW Gondwana – Saudi Arabia : *Ambitisporites* sp., *Chelinospora* sp., *Leiotriletes* sp., ? *Synorisporites* sp (Steemans *et al.* 2009)

S Gondwana - Libya: *Dyadospora murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Pachytetras rugosa, Rimosotetras problematica, Rugosphaera cerebra, Segestrespora laevigata, S.rugosa, Tetrahedraletes grayae, T. medinensis, Velatitetras rugulata* (Burgess 1991; Gray 1991; Gray *et al.* 1982; Hill *et al.* 1985; Richardson 1988; Steemans *et al.* 1996; Steemans *et al.* 2000; Wellman 1996; Wellman & Richardson 1993)

N Gondwana - South Africa: *Tetrahedraletes medinensis, T. medinensis parvus* (Burgess 1991; Gray 1991; Gray *et al.* 1986; Strother 1991; Wellman & Richardson 1993)

TarimTerrane – Xinjiang, China: *Dyadospora murusattenuata, D. murusdensa, Laevolancis chibrikovae, Pseudodyadospora laevigata, Segestrespora rugosa, Tetrahedraletes medinensis, Velatitetras laevigata* (Rubinstein & Vaccari 2004; Steemans *et al.* 2000; Wang *et al.* 1997)

–North? China Terrane – Zhejiang, China: *Dyadospora murusattenuata, Strophomorpha ovata, Tetrahedraletes medinensis, Velatitetras retimembrana* (Yin & He 2000)

Hirnantian

Avalonia - UK: *Ambitisporites avitus, Imperfectotriletes vavrdovae, Pseudodyadospora laevigata, Rimosotetras problematica, Segestrespora laevigata, S. membranifera, S. rugosa, Velatitetras laevigata, V. retimembrana* (Burgess 1991; Steemans *et al.* 1996; Steemans *et al.* 2000)

SW Gondwana - Saudi Arabia: *Ambitisporites* sp., *Chelinospora* sp., *Imperfectotriletes vavrdovae*, *Laevolancis divellomedia*, *Leiotriletes* sp., ?*Synorisporites* sp (Miller & Al-Ruwaili 2007; Steemans *et al.* 2009)

Llandovery

Laurentia – Anticosti, Canada: *Tetrahedraletes medinensis, Velatitetras retimembrana* (Duffield 1985; Steemans *et al.* 1996; Strother 1991; Wellman & Richardson 1993)

Laurentia - USA: *Abditusdyadus laevigatus, Ambitisporites avitus, A. dilutus, Dyadospora murusattenuata, D. murusdensa, Imperfectotriletes patinatus, I. patinatus, I. vavrdovae, Nodospora oyleri, Pseudodyadospora laevigata, P. rugosa, Rimosotetras problematica, Rugosphaera tuscarorensis, Segestrespora laevigata, S. membranifera, S. rugosa, Stegambiquadrella contenta, Velatitetras retimembrana, V. rugosa* (Burgess 1991; Burgess & Richardson 1991; Gensel *et al.* 1990; Gray 1985, 1991; Gray & Boucot 1971; Gray *et al.* 1982; Gray *et al.* 1992; Johnson 1985; Miller & Eames 1982; Steemans *et al.* 1996; Steemans *et al.* 2000; Strother 1991; Strother & Traverse 1979; Wellman & Richardson 1993)

Avalonia - Belgium: *Moyeria cabottii* (Martin 1973; Wellman & Richardson 1993)

Avalonia - Ireland: *Ambitisporites avitus, A. dilutus* (Emo & Smith 1978)

SW PeriGondwana (Moesian platform) - Bulgaria: *Tetrahedraletes medinensis* (Lakova *et al.* 1992)

S PeriGondwana (Iberia) - Spain: *Ambitisporites avitus, A. dilutus* (Rodríguez 1983)

SW Gondwana - Saudi Arabia: *Tetrahedraletes medinensis* (Wellman *et al.* 2000)

N Gondwana - Libya: *Ambitisporites avitus, A. dilutus, Dyadospora murusdensa, Rimosotetras problematica* (Hill *et al.* 1985; Hoffmeister 1959; Richardson 1985; Steemans *et al.* 1996; Wellman & Richardson 1993)

E Gondwana - Brazil: *Rugosphaera rugosa, Tetrahedraletes medinensis* (Gray *et al.* 1985; Le Hérissé *et al.* 2001; Strother 1991; Wellman & Richardson 1993)

E Gondwana - Paraguay: *Laevolancis chibrikovae, L. divellomedium, Pseudodyadospora laevigata, Segestrespora rugosa, Sphaerasaccus glabellus, Vellatitetras rugosa* (Mendlowicz Mauller *et al.* 2004)

N Gondwana - South Africa: *Tetrahedraletes medinensis, T. medinensis parvus* (Burgess 1991; Gray 1991; Gray *et al.* 1986; Strother 1991; Wellman & Richardson 1993)

Llandovery: Rhuddanian

Laurentia - Canada: *Tetrahedraletes medinensis* (Eley & Legault 1988; Gray 1991)

Laurentia - USA: *Dyadospora murusattenuata, D. murusdensa, Rugosphaera cerebra, R.tuscarorensis, Segestrespora laevigata, Strophomorpha ovata, Tetrahedraletes medinensis, Velatitetras retimembrana, V. rugosa, Vermiculatisphaera obscura* (Beck & Strother 2008; Gray 1991; Miller & Eames 1982; Strother 1991; Wellman 1996; Wellman & Richardson 1993)

Avalonia - Nova Scotia, Canada: *Tetrahedraletes medinensis* (Beck & Strother 2001)

Avalonia - UK: *Ambitisporites avitus, Dyadospora murusattenuata, D. murusattenuata, Hispanaediscus lamontii, Imperfectotriletes vavrdovae, Rimosotetras problematica, Rugosphaera cerebra, Segestrespora burgessii, S. laevigata, S. membranifera, S. rugosa, Strophomorpha ovata, Tetrahedraletes medinensis, Velatitetras anatoliensis, V. laevigata, V. retimembrana, V. rugosa, V. rugulata* (Beck & Strother 2008; Burgess 1991; Richardson 1996; Steemans *et al.* 1996; Steemans *et al.* 2000; Wellman 1993, 1996; Wellman & Richardson 1993)

SW Gondwana - Saudi Arabia: *Abditusdyadus laevigatus, Ambitisporites avitus, A. dilutus, Chelinohilates maculatus, Complectitetras alhajrii, Dyadaspora murusattenuatta, D. murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Laevolancis chibrikovae, L. divellomedia, L. divellomedia, L. plicata, Pachytetras rugosa, Pseudodyadospora laevigata, P. petasus, Rimosotetras problematica, Rugosphaera tuscarorensis, Segestrespora laevigata, S. membranifera, S. rugosa, Sphaerasaccus glabellus, Tetrahedraletes medinensis, Velatitetras anatoliensis, V. laevigata, V. retimembrana, V. rugosa, Vestitusdyadus qalibahinus* (Steemans *et al.* 2000; Wellman *et al.* 2000)

S Gondwana – Libya: *Dyadospora murusattenuata, D. murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Pseudodyadospora rugosa, Rimosotetras problematica, Segestrespora laevigata, S.membranifera, S. rugosa, Tetrahedraletes grayae, T. medinensis, Velatitetras anatoliensis, V. laevigata, V. retimembrana, V. rugosa, V. rugulata* (Burgess 1991; Gray 1991; Hill *et al.* 1985; Richardson 1988; Steemans *et al.* 1996; Steemans *et al.* 2000; Strother 1991; Wellman 1996; Wellman & Richardson 1993)

E Gondwana - Argentina: *Dyadospora murusattenuata, D. murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Laevolancis chibrikovae, Pseudodyadospora petasus, Rimosotetras problematica, Segestrespora laevigata, S. membranifera, Sphaerasaccus glabellus, Tetrahedraletes medinensis, Velatitetras laevigata, V. retimembrana, V. rugosa, Vestitusdyadus qalibahinus* (Rubinstein & Vaccari 2004)

E Gondwana - Brazil: *Abditusdyadus laevigatus, Dyadospora murusattenuata, D. murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Laevolancis divellomedia, Pseudodyadospora laevigata, Rimosotetras problematica, Segestrespora laevigata, S. membranifera, S. rugosa, Sphaerasaccus glabellus, Tetrahedraletes medinensis, Velatitetras anatoliensis, V. laevigata, V. retimembrana, V. rugosa* (Mizusaki *et al.* 2002)

E Gondwana - Paraguay: *Ambitisporites avitus, A. dilutus, Dyadospora murusattenuata, D. murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Laevolancis divellomedia, Rimosotetras problematica, Segestrespora* *laevigata, Tetrahedraletes medinensis, Velatitetras anatoliensis, V. laevigata, V. retimembrana* (Mendlowicz Mauller *et al.* 2004; Steemans & Pereira 2002)

–**South? China Terrane – Zhejiang, China:** *Dyadospora murusattenuata, Strophomorpha ovata, Velatitetras retimembrana* (Yin & He 2000)

Llandovery (Aeronian)

Laurentia - USA: *Nodospora rugosa, Velatitetras rugosa* (Gray 1985)

Avalonia - Nova Scotia, Canada: *Ambitisporites avitus, Tetrahedraletes medinensis* (Beck & Strother 2001)

Avalonia - UK: *Ambitisporites dilutus, Imperfectotriletes vavrdovae, Tetrahedraletes medinensis parvus, Velatitetras retimembrana* (Burgess 1991)

W Gondwana - Iraq: *Ambitisporites avitus* (Al-Ameri *et al.* 1991)

SW Gondwana - Saudi Arabia: *Ambitisporites avitus, A. dilutus, Chelinohilates maculatus, Dyadospora murusattenuata, D. murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Laevolancis chibrikovae, L. divellomedia, L. plicata, Pseudodyadospora laevigata, P. petasus, Rimosotetras problematica, Tetrahedraletes medinensis, Velatitetras laevigata, V. rugosa* (Steemans *et al.* 2000)

N S Gondwana - Libya: *Ambitisporites avitus, A. dilutus, Dyadospora murusattenuata, D. murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Pseudodyadospora rugosa, Rimosotetras problematica, Segestrespora membranifera, S. rugosa, Tetrahedraletes medinensis, Velatitetras anatoliensis, V. laevigata, V. retimembrana, V. rugosa, V. rugulata* (Burgess 1991; Gray 1991; Hill *et al.* 1985; Richardson 1985, 1988; Steemans *et al.* 1996; Steemans *et al.* 2000; Strother 1991; Wellman 1996; Wellman & Richardson 1993)

E Gondwana - Brazil: *Abditusdyadus laevigatus, Ambitisporites avitus, A. dilutus, Dyadospora murusattenuata, D. murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Laevolancis divellomedia, Pseudodyadospora laevigata, Rimosotetras problematica, Rugosphaera cerebra, Rugosphaera rugosa, Segestrespora burgessii, S. laevigata, S. membranifera, S. rugosa, Sphaerasaccus glabellus, Tetrahedraletes medinensis, Velatitetras anatoliensis, V. laevigata, V. retimembrana, V. rugosa* (Le Hérissé *et al.* 2001; Mizusaki *et al.* 2002)

E Gondwana - Paraguay: *Ambitisporites avitus, A. dilutus, Dyadospora murusattenuata, D. murusttanuata, D. murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Laevolancis divellomedia, Pseudodyadospora petasus, Rimosotetras problematica, Rugosphaera cerebra, R. rugosa, R. tuscarorensis, Segestrespora laevigata, Tetrahedraletes medinensis, Velatitetras anatoliensis, V. laevigata, V. retimembrana, V. rugosa* (Mendlowicz Mauller *et al.* 2004)

–**South? China Terrane – Zhejiang, China:** *Dyadospora murusattenuata, Strophomorpha ovata, Velatitetras retimembrana* (Yin & He 2000)

Llandovery (Telychian)

Laurentia USA: *Ambitisporites avitus.*

Avalonia - Nova Scotia, Canada: *Ambitisporites avitus, A. dilutus, Laevolancis divellomedia, Tetrahedraletes medinensis* (Beck & Strother 2001)

Avalonia - Ireland: *Tetrahedraletes medinensis* (Maziane-Serraj *et al.* 2000)

Avalonia - UK: *Ambitisporites dilutus, Tetrahedraletes medinensis parvus* (Burgess 1991)

W Gondwana - Iraq: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus, Retusotriletes warringtonii* (Al-Ameri *et al.* 1991)

SW Gondwana- Saudi Arabia: *Ambitisporites avitus-dilutus Morphon, Archaeozonotriletes chulus, Dyadospora murusattenuata - murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Laevolancis divellomedia-plicata Morphon, Pseudodyadospora petasus, Rimosotetras problematica, R. problematica, Tetrahedraletes medinensis, Velatitetras anatoliensis, V. laevigata, V. rugosa* (Steemans *et al.* 2000)

S Gondwana - Libya: *Ambitisporites avitus, A. dilutus, A. dilutus, Dyadospora murusattenuata, D. murusattenuata, D. murusdensa, Imperfectotriletes patinatus, I. vavrdovae, Pseudodyadospora rugosa, Rimosotetras problematica, R. problematica, Segestrespora rugosa, Tetrahedraletes medinensis, T. medinensis, Velatitetras rugulata* (Burgess 1991; Gray 1991; Hill *et al.* 1985; Richardson 1988; Steemans *et al.* 1996; Steemans *et al.* 2000; Strother 1991; Wellman 1996; Wellman & Richardson 1993)

E Gondwana Argentina: *Hispanaediscus verrucatus, Laevolancis divellomedia* (Rubinstein & Brussa 1999)

E Gondwana Brazil: *Ambitisporites avitus, A. avitus-dilutus morphon, Imperfectotriletes vavrdovae, I. vavrdovae, Laevolancis divellomedia, L. divellomedia, Rimosotetras problematica, R. problematica, Rugosphaera cerebra, R. rugosa, Segestrespora burgessii, S. laevigata, S. rugosa, Tetrahedraletes medinensis, Velatitetras anatoliensis, V. laevigata, V. retimembrana, V. rugosa* (Le Hérissé *et al.* 2001)

E Gondwana Paraguay: *Ambitisporites avitus, A. avitus-dilutus Morphon, A. dilutus, Archaeozonotriletes chulus, Archaeozonotriletes chulus-nanus Morphon, Dyadospora murusattenuata, D. murusttanuata-murusdensa Morphon, Laevolancis divellomedia, Pseudodyadospora petasus, Rimosotetras problematica, R. problematica, Tetrahedraletes medinensis, T. medinensis, Velatitetras anatoliensis* (Mendlowicz Mauller *et al.* 2004; Steemans & Pereira 2002)

Indo-China Terrane – Yunnan, China: *Ambitisporites avitus-dilutus morphon, Imperfectotriletes patinatus, I. vavrdovae, Laevolancis chibrikovae, Laevolancis divellomedium, Velatitetras rugospora* (Wang & Zhang 2009)

South China? Terrane – Zheijiang, China: *Dyadaspora murusattenuata, Velatitetras retimembrana, Strophomorpha ovate* (Yin & He 2000)

Wenlock

Laurentia - USA: *Aremopyra brevicosta, Artemopyra radiata, Confossuspora reniforma, Laevolancis divellomedium, Stegambiquadrella contenta* (Burgess & Richardson 1991, 1995; Strother 1991; Strother 1993; Strother & Traverse 1979; Wellman & Richardson 1993)

Laurentia - UK - Scotland: *Ambitisporites avitus, A. dilutus, Cheilotetras caledonica, Dyadospora murusattenuata, D. murusdensa, Laevolancis divellomedium, L. plicata, Moyeria cabottii, Pseudodyadospora petasus, Rimosotetras problematica, Tetrahedraletes medinensis* (Wellman & Richardson 1993)

Avalonia - Ireland: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus nanus, Artemopyra brevicosta, Dyadospora murusattenuata, Hispanaediscus verrucata, Laevolancis divellomedia, L. plicata, Tetrahedraletes medinensis* (Aldridge *et al.* 1979; Emo & Smith 1978; Wellman & Richardson 1993; Williams *et al.* 1996)

Avalonia - UK: *Ambitisporites dilutus, Artemopyra brevicosta, Dyadospora murusattenuata, D. murusdensa, Laevolancis divellomedia, Retusotriletes warringtonii, Rimosotetras problematica, Tetrahedraletes medinensis, T. medinensis medinensis* (Burgess & Richardson 1991; Dorning 1983; Richardson & Lister 1969; Wellman & Richardson 1993)

Avalonia- UK: *Archaeozonotriletes chulus nanus* (Aldridge *et al.* 1979)

S PeriGondwana (Armorica) - France: *Ambitisporites avitus* (Deunff & Chateauneuf 1976)

S PeriGondwana (Iberia) - Spain: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus, Archaicusporites asturicus, Convolutispora sanpetrensis, Laevolancis divellomedium, Quadrisporites granulatus, Q. variabilis, Retusotriletes abundo, R. minor, R. warringtonii, Scylaspora vetusta, Synorisporites verrucatus* (Richardson *et al.* 2001; Rodríguez 1978a, b, c, 1983)

SW Gondwana - Saudi Arabia: *Ambitisporites avitus, Dyadospora murusdensa, Emphanisporites neglectus, Laevolancis divellomedium, Quadrisporites variabilis, Scylaspora chartulata, Synorisporites verrucatus, Tetrahedraletes medinensis* (Rubinstein & Steemans 2002; Steemans 1995)

S Gondwana - Libya: *Ambitisporites avitus, A. dilutus, A. tripapillatus, Apiculiretusispora spicula, A. synorea, Archaeozonotriletes chulus chulus, A. chulus nanus, Artemopyra brevicosta, A. urubuense, Coronaspora subornata, Dyadospora murusattenuata, Emphanisporites neglectus, E. protoannulatus, E. protophanus, E. rotatus, E. splendens, Hispanaediscus verrucatus, Laevolancis divellomedium, Quadrisporites variabilis, Retusotriletes abundo, R. delicatus, R. dubius, R. frivolus, R. goensis, R. minor, R. warringtonii, Scylaspora* *chartulata, S. distincta, S. vetusta, Synorisporites verrucatus, Tetrahedraletes medinensis, Tetraletes granulatus* (Beck & Strother 2008; Burgess & Richardson 1991, 1995; Kermandji 2007; Richardson & Ioannides 1973; Richardson *et al.* 2001; Rodríguez 1983; Rubinstein & Steemans 2002; Steemans *et al.* 1996; Steemans *et al.* 2008; Tekbali & Wood 1991; Wellman 1993; Wellman & Richardson 1993)

Wenlock (Sheinwoodian)

Laurentia - USA: *Abditusdyadus laevigatus, Ambitisporites avitus, Dyadospora murusattenuata, Laevolancis divellomedia, Tetrahedraletes medinensis, Velatitetras rugosa* (Beck & Strother 2008)

Laurentia - UK-Scotland: *Ambitisporites avitus, A. dilutus, Cheilotetras caledonica, Laevolancis divellomedia, Pseudodyadospora petasus, Rimosotetras problematica, Tetrahedraletes medinensis* (Wellman 1993)

Baltica - Norway: *Ambitisporites avitus, A. dilutus, A., Quadrisporites variabilis, Tetrahedraletes medinensis, Synorisporites libycus* (Smelror 1987, 1990; Steemans *et al.* 1996; Wellman & Richardson 1993)

Baltica – Sweden: *Ambitisporites dilutus, Synorisporites libycus*. (Hagström 1997)

Avalonia - Nova Scotia, Canada: *Ambitisporites avitus, A. dilutus, Laevolancis divellomedia, L. plicata, Tetrahedraletes medinensis* (Beck & Strother 2001)

Avalonia - Ireland: *Tetrahedraletes medinensis* (Maziane-Serraj *et al.* 2000; Smith 1975; Strother 1991)

Avalonia - UK: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus chulus, A. chulus nanus, Dyadospora murusattenuata, D. murusdensa, Laevolancis divellomedium, L. plicata, Tetrahedraletes medinensis* (Burgess & Richardson 1991, 1995)

W Gondwana- Iraq: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus, Retusotriletes warringtonii* (Al-Ameri *et al.* 1991)

Wenlock (Homerian)

Laurentia - UK-Scotland: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus, Artemopyra brevicosta, Cheilotetras caledonica, Dyadospora murusattenuata, D. murusdensa, Hispanaediscus lamontii, H. wenlockensis, Laevolancis divellomedium, L. plicata, Pachytetras rugosa, Pseudodyadospora petasus, Retusotriletes maculatus, Tetrahedraletes medinensis* (Burgess & Richardson 1995; Marshall 1991; Richardson 1996; Steemans *et al.* 2000; Wellman 1993)

Baltica - Sweden: *Ambitisporites dilutus, Cymbohilates variabilis, Laevolancis divellomedia, Tetrahedraletes medinensis* (Hagström 1997)

Avalonia - Nova Scotia, Canada: *Ambitisporites avitus, A. dilutus, Chelinospora textilis, Hispanaediscus verrucatus, Insolisporites bassettii, Laevolancis divellomedia, L. plicata, Quadrisporites variabilis, Tetrahedraletes medinensis, Vermiverruspora rumneyi* (Beck & Strother 2001)

Avalonia - Ireland: *Archaeozonotriletes chulus nanus* (Smith 1979)

Avalonia - UK: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus chulus, A. chulus nanus, Artemopyra brevicosta, A. radiata, A. rugaticosta, A. temericosta, Cheilotetras caledonica, Chelinospora vermoluta, Concentricosisporites saggitarius, Confossuspora reniforma, Dyadospora murusattenuata, D. murusdensa, Emphanisporites protophanus, Hispanaediscus lamontii, H. rugulatus, H. verrucatus, H. wenlockensis, Insolisporites anchistinus, I. bassettii, Laevolancis divellomedia, L. plicata, Pachytetras rugosa, Scylaspora chartulata, S. downiei, S. scipta, Tetrahedraletes medinensis, T. medinensis medinensis, Velatitetras cristata, Vermiverruspora rumneyi* (Beck & Strother 2001, 2008; Burgess & Richardson 1991, 1995; Dufka 1995; Richardson & Lister 1969; Rubinstein & Steemans 2002; Steemans *et al.* 2000; Wellman & Richardson 1993)

S PeriGondwana (Perunica) – Czech Republic: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus nanus, Artemopyra brevicosta, A. radiata, A. rugaticosta, Confossuspora reniforma, Dyadospora murusattenuata, Emphanisporites protophanus, Hispanaediscus verrucatus, Laevolancis divellomedium, L. plicata, Rugosisporites kozlicus, Scylaspora chartulata, S. vetusta, Synorisporites maculosus, Tetrahedraletes medinensis* (Dufka 1995; Richardson *et al.* 2001; Rubinstein & Steemans 2002)

W Gondwana - Iraq: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus, Retusotriletes warringtonii* (Al-Ameri *et al.* 1991)

SW Gondwana - Saudi Arabia: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus, Artemopyra rugaticosta, Dyadospora murusattenuata D. murusdensa, Hispanaediscus wenlockensis, Imperfectotriletes patinatus, I. vavrdovae, Laevolancis divellomedia, L. plicata, Pseudodyadospora petasus, Rimosotetras problemtica, Tetrahedraletes medinensis, Velatitetras rugosa* (Wellman *et al.* 2000).

S Gondwana - Libya: *Ambitisporites avitus, Archaeozonotriletes chulus chulus, Artemopyra brevicosta, Synorisporites libycus* (Richardson 1996)

S Gondwana - Algeria: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus chulus, A. chulus nanus, Emphanisporites neglectus, E. protophanus, Laevolancis divellomedia, Retusotriletes abundo, Scylaspora distincta, S. kozlica, S. vetusta* (Kermandji 2007)

E Gondwana - Argentina: *Ambitisporites avitus, A. dilustus, Emphanisporites rotates* (Rubinstein & Brussa 1999)

Ludlow

Laurentia - Cornwallis Island, Canada: *Laevolancis divellomedium, Moyeria cabottii, Tetrahedraletes medinensis* (Burgess & Richardson 1991; Gray 1991; McGregor & Narbonne 1978; Strother 1991; Wellman & Richardson 1993)

Laurentia - USA: *Tetrahedraletes medinensis* (Aldridge *et al.* 1979; Wellman & Richardson 1993)

Baltica - Estonia: *Ambitisporites avitus* (Aristova & Arkhangelskaya 1976)

Baltica - Germany: *Ambitisporites avitus , A. dilutus, Apiculiretusispora synorea, Archaeozonotriletes chulus chulus, Retusotriletes warringtonii* (Reitz 1987)

Baltica - Sweden: *Tetrahedraletes medinensis* (Gray *et al.* 1982; Wellman & Richardson 1993)

Avalonia - Ireland: *Apiculiretusispora synorea, Archaeozonotriletes chulus chulus, A. chulus nanus* (Aldridge *et al.* 1979)

Avalonia - UK: *Apiculiretusispora synorea, Archaeozonotriletes chulus nanus, Laevolancis divellomedium, Stellatispora inframurinata cambrensis* (Burgess & Richardson 1995; Richardson & Lister 1969; Wellman & Richardson 1993)

Avalonia - UK: *Apiculiretusispora synorea, Archaeozonotriletes chulus chulus, A. chulus nanus* (Aldridge *et al.* 1979)

S PeriGondwana (Armorica) - France: *Ambitisporites avitus, Synorisporites verrucatus* (Deunff & Chateauneuf 1976)

S PeriGondwana (Iberia) - Spain: *Ambitisporites avitus, A. dilutus, Amocosporites miserabilis, Anapiculatisporites isidori, Archaeozonotriletes chulus, Archaicusporites asturicus, A.torrestionensis, Brochotriletes sanpetrensis, Concentricosisporites agradabilis, C.sagittarius, Convolutispora quititae, C. sanpetrensis, Coronaspora infraornata, C. mariae, C. primordiale, C. reticulata, C. subornata, Cyclogranisporites zumbonus, Emphanisporites perfilum, E. protoannulatus, E. protophanus, E. rotatus, E. splendens, Laevolancis divellomedium, Paradominoespora maravedi, Quadrisporites granulatus, Q. variabilis, Retusotriletes abundo, R. aureoladus, R. minor, R. sanpetrensis, R. splendidus, R. warringtonii, Scylaspora vetusta, Stenozonotriletes pumillus, Streelispora granulata, Synorisporites downtonensis, S. lobatus, S. tripapillatus, S.verrucatus* (Cramer 1967; Cramer & Díez 1975; Cramer & Rodríguez 1977; Díez & Cramer 1976; Richardson *et al.* 2001; Rodríguez 1978a, b, c, 1983)

S PeriGondwana (Taurides) - Turkey: *Amicosporites splendidus, Archaeozonotriletes chulus, Artemopyra brevicosta, Convolutispora quititae, Cymbosporites catillus, Dyadospora murusattenuata, D. murusdensa, Hispanaediscus verrucatus, H. wenlockensis, Laevolancis divellomedium, Pseudodyadospora laevigata, P. petasus, Quadrisporites variabilis, Retusotriletes warringtonii, Rimosotetras problematica, Tetrahedraletes medinensis* (Steemans *et al.* 1996)

S Gondawana - Libya: *Ambitisporites avitus, A. dilutus, A. tripapillatus, Amicosporites miserabilis, Aneurospora richardsonii, Apiculiretusispora perfecta, A. spicula, A. synorea, Archaeozonotriletes chulus, A.*

chulus chulus, A. chulus nanus, Artemopyra brevicosta, A. rugaticosta, Chelinospora obscura, C. retorrida, Clivosispora verrucata convoluta, Concentricosisporites agradabilis, Coronaspora subornata, Cymbosporites multiconus, C. verrucosus, Dyadospora murusattenuata, Emphanisporites neglectus, E. protoannulatus, E. protophanus, E. rotatus, E. splendens, Hispanaediscus lamontii, H. verrucatus, Iberoespora noninspisatosa, Laevolancis divellomedium, Pseudodyadospora petasus, Punctatisporites dilutus, Quadrisporites variabilis, Retusotriletes abundo, R. delicatus, R. dubius, R. minor, R. triangulatus, R. warringtonii, Scylaspora chartulata, S. distincta, S. downiei, S. vetusta, Stellatispora inframurinata inframurinata, Synorisporites verrucatus, Tetrahedraletes medinensis, Tetraletes granulates (Beck & Strother 2001, 2008; Buret & Moreau-Benoit 1986; Burgess & Richardson 1991, 1995; Gray *et al.* 1982; Kermandji 2007; Richardson & Ioannides 1973; Richardson *et al.* 2001; Rodríguez 1983; Rubinstein & Steemans 2002; Steemans *et al.* 1996; Steemans *et al.* 2008; Tekbali & Wood 1991; Wellman 1993)

S Gondwana - Algeria: *Emphanisporites neglectus* (Jardiné & Yapaudjian 1968)

SE Gondwana - Argentina: *Ambitisporites avitus, Amicosporites splendidus, Emphanisporites neglectus, E. rotatus, Retusotriletes minor, Synorisporites verrucatus* (Grösser & Prössl 1991; Rubinstein 1994)

South China Terrane – Jiangsu and Sichuan, China: *Ambitisporites dilutus, Artemopyra brevicosta, Cymbosporites sparseus, Dyadospora murusattenuata, D. murusdensa, Hispanaediscus verrucatus, Laevolancis divellomedia, Pseudodyadospora laevigata, P. petasus, Scylaspora downiei, S. scripta, Velatitetras laevigata* (Wang & Li 2000; Wang *et al.* 2005)

Ludlow (Gorstian)

Laurentia - Scotland: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus, Artemopyra brevicosta, Cheilotetras caledonica, Dyadospora murusattenuata, Hispanaediscus lamontii, H. wenlockensis, Laevolancis divellomedium, L. plicata, Pachytetras rugosa, Pseudodyadospora petasus, Retusotriletes maculatus, Tetrahedraletes medinensis* (Burgess & Richardson 1995; Marshall 1991; Steemans *et al.* 2000; Wellman 1993)

Baltica - Sweden: *Abditusdyadus chalazus, Acontotetras gotlandica, Ambitisporites dilutus, Tetrahedraletes medinensis* (Hagström 1997)

Avalonia - Nova Scotia, Canada: *Ambitisporites avitus, A. dilutus, A. marginatus, Cheilotetras caledonica, Hispanaediscus major, H. scabiosus, Laevolancis divellomedia, L. plicata, Stellatispora inframurinata inframurinata, Tetrahedraletes medinensis, Vermiverruspora rumneyi* (Beck & Strother 2001)

Avalonia - UK: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus chulus, A. chulus nanus, Artemopyra radiata, A. temericosta, Cheilotetras caledonica, Chelinospora obscura, C. vermoluta, Concentricosisporites saggitarius, Hispanaediscus lamontii, H. rugulatus, H. verrucatus, Insolisporites anchistinus, I. bassettii, Laevolancis divellomedia, L. plicata, Scylaspora downiei, Stellatispora inframurinata cambrensis, S. inframurinata inframurinata, Tetrahedraletes medinensis medinensis, Velatitetras cristata, Vermiverruspora rumneyi* (Beck & Strother 2001; Burgess & Richardson 1995)

PeriGondwana (Iberia) - Spain: *Moyeria cabottii* (Rodríguez 1983)

S **Gondwana - Saudi Arabia:** *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus, Artemopyra rugaticosta, Dyadospora murusattenuata, D. murusdensa, Hispanaediscus wenlockensis, Imperfectotriletes patinatus, I. vavrdovae, Laevolancis divellomedia-plicata, Pseudodyadospora petasus, Rimosotetras problemtica, Tetrahedraletes medinensis, Velatitetras rugosa* (Wellman *et al.* 2000)

S **Gondwana - Libya:** *Ambitisporites avitus, Archaeozonotriletes chulus chulus, Confossuspora reniforma, Emphanisporites protophanus, Hispanaediscus verrucatus* (Richardson 1996; Rubinstein & Steemans 2002)

S **Gondwana - Tunisia:** *Ambitisporites avitus, Archaeozonotriletes chulus, Artemopyra brevicosta, Concentricosisporites sagittarius, Dyadospora murusattenuata, Emphanisporites protophanus, Hispanaediscus verrucatus, Laevolancis divellomedia, Pseudodyadospora laevigata, P. petasus, Retusotriletes abundo, R. dubius, R. minor, R. warringtonii, Scylaspora downiei, Synorisporites verrucatus, Tetrahedraletes medinensis* (Spina & Vecoli 2009)

Ludlow (Ludfordian)

Laurentia - USA: *Abditusdyadus laevigatus, Ambitisporites avitus, A. warringtonii, Archaeozonotriletes chulus, Artemopyra brevicosta, Concentricosisporites sagittarius, Confossuspora reniforma, Dyadospora murusattenuata, Empanisporites protophanus, Laevolancis divellomedia, Retusotriletes abundo, Rugosphaera falloambita, Scylaspora scipta, Tetrahedraletes medinensis, Vermiverruspora cotter* (Beck & Strother 2008)

Baltica - Sweden: *Abditusdyadus chalazus, Acontotetras gotlandica, Ambitisporites avitus, A. dilutus, A. parvus, Artemopyra brevicosta, Cheilotetras caledonica, Cymbohilates micrograngulatus, C. variabilis, Dyadospora murusattenuata, D. murusdensa, Hispanaediscus verrucatus, Laevolancis divellomedia, L. plicata, Pachytetras rugosa, P. rugosa, Pseudodyadospora laevigata, P. petasus, Rugosisporites chartulatus, Tetrahedraletes medinensis* (Hagström 1997; Steemans *et al.* 2000)

Avalonia - Nova Scotia, Canada: *Ambitisporites avitus, A. marginatus, Cheilotetras caledonica, Hispanaediscus imbricatus, H. major, H. scabiosus, Laevolancis divellomedia, L. plicata, Stellatispora inframurinata inframurinata, Tetrahedraletes medinensis* (Beck & Strother 2001)

Avalonia - UK: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus chulus, A. chulus nanus, Cheilotetras caledonica, C. obscura, C. vermoluta, Concentricosisporites saggitarius, Hispanaediscus major, Insolisporites bassettii, Laevolancis divellomedia, L. plicata, Stellatispora inframurinata cambrensis, S. inframurinata inframurinata, Tetrahedraletes medinensis medinensis, Vermiverruspora rumneyi* (Beck & Strother 2001; Burgess & Richardson 1995)

S **PeriGondwana (Iberia) - Spain:** *Chelinospora canistrata, C. cantabrica, C. poecilomorpha, C. sanpetrensis, Concentricosisporites agradabilis, C. sagittarius, Coronaspora cromatica, C. reticulata, Emphanisporites splendens, Hispanaediscus verrucatus, Laevolancis divellomedium, L. divellomedium, Moyeria cabottii,* *Quadrisporites granulatus, Q. variabilis, Q. variabilis, Scylaspora vetusta* (Burgess & Richardson 1991; Cramer 1966; Richardson *et al.* 2001; Rodríguez 1983; Steemans *et al.* 1996; Wellman & Richardson 1993)

S Gondwana - Algeria: *Ambitisporites avitus, A. dilutus, Archaeozonotriletes chulus chulus, A. chulus nanus, Chelinospora sanpetrensis, Cymbosporites triangulatus, Emphanisporites neglectus, E. protophanus, Laevolancis divellomedia, Retusotriletes abundo, Scylaspora distincta, S. kozlica, S. vetusta* (Kermandji 2007)

S Gondwana - Libya: *Apiculiretusispora synorea, Artemopyra robusta, Confossuspora reniforma, Emphanisporites neglectus, E. splendens, Hispanaediscus verrucatus, Laevolancis divellomedia, Tetraletes variabilis* (Richardson 1996; Rubinstein & Steemans 2002)

S Gondwana - Tunisia: *Ambitisporites avitus, Archaeozonotriletes chulus, Artemopyra brevicosta, Chelinospora poecilomorpha, Concentricosisporites sagittarius, Coronaspora cromatica, Cymbohilates comptulus, Dyadospora murusattenuata, Emphanisporites neglectus, E. protophanus, E. rotatus, Gneudnaspora divellomedia, Hispanaediscus verrucatus, H. wenlockensis, Pseudodyadospora laevigata, P.petasus, Retusotriletes abundo, R. dittonensis, R. dubius, R. maccullockii, R. minor, R. triangulatus, R. warringtonii, Rimosotetras problematica, Rugosphaera cerebra, Scylaspora downiei, Segestrespora membranifera, Synorisporites libycus, S. verrucatus, Tetrahedraletes medinensis, Velatitetras rugosa* (Spina & Vecoli 2009)

E Gondwana - Brazil: *Ambitisporites avitus Morphon, Archaeozonotriletes chulus, Artemopyra brevicosta, Chelinospora poecilomorpha, Emphanisporites neglectus, E. protophanus, E. rotatus, Laevolancis divellomedium, Retusotriletes abundo, R. minor, Scylaspora downiei, Sphaerasaccus glabellus, Synorisporites verrucatus, Tetrahedraletes medinensis, Velatitetras rugosa* (Steemans *et al.* 2008)

Pridoli

Laurentia - Canada: *Archaeozonotriletes chulus chulus* (McGregor & Camfield 1976)

Laurentia - USA: *Abditusdyadus laevigatus, Ambitisporites avitus, A. warringtonii, Archaeozonotriletes chulus, Artemopyra brevicosta, Concentricosisporites sagittarius, Confossuspora reniforma, Dyadospora murusattenuata, Empanisporites protophanus, Laevolancis divellomedia, Retusotriletes abundo, Rugosphaera falloambita, Scylaspora scipta, Tetrahedraletes medinensis, Vermiverruspora cotter* (Beck & Strother 2008)

Laurentia - Scotland: *Tetrahedraletes medinensis* (Barron 1989)

Baltica - Estonia: *Emphanisporites protophanus, Retusotriletes simplex* (Aristova & Arkhangelskaya 1976)

Avalonia - Nova Scotia, Canada: *Ambitisporites avitus, A. capitaneus, A. parvus, Artemopyra scalariformis, Cheilotetras caledonica, Dyadospora murusattenuata, D. murusdensa, Hispanaediscus verrucatus, Laevolancis divellomedia, L. plicata, Quadrisporites variabilis, Scylaspora asperverruca, Synorisporites verrucatus, Tetrahedraletes medinensis* (Beck & Strother 2001)

Avalonia - Ireland: *Apiculiretusispora spicula, A. synorea, Archaeozonotriletes chulus chulus, A.chulus nanus, Cymbosporites echinatus, Cymbosporites verrucosus, Synorisporites downtonensis, S. tripapillatus, S. verrucatus* (Aldridge *et al.* 1979)

Avalonia - UK: *Ambitisporites avitus, A. dilutus, A. parvus, A. tripapillatus, Amicosporites splendidus, Apiculiretusispora spicula, A. synorea, Archaeozonotriletes chulus, A. chulus chulus, A. chulus nanus, Cheilotetras caledonica, Concentricosisporites saggitarius, Cymbosporites echinatus, C. verrucosus, Laevolancis divellomedium, L. plicata, Retusotriletes charulatus, R. dubius, Stellatispora inframurinata cambrensis, Synorisporites downtonensis, S. labeonis, S. tripapillatus, S. verrucatus, Tetrahedraletes medinensis medinensis* (Aldridge *et al.* 1979; Burgess & Richardson 1995; Fanning *et al.* 1991; Johnson & Taylor 2005; Richardson 1996; Richardson & Lister 1969; Richardson *et al.* 1981; Wetherall *et al.* 1999)

Avalonia - UK: *Apiculiretusispora spicula, A. synorea, Archaeozonotriletes chulus chulus, A. chulus nanus, Cymbosporites echinatus, C. verrucosus, Synorisporites downtonensis, S. tripapillatus, S. verrucatus* (Aldridge *et al.* 1979)

Avalonia – Northern France: *Emphanisporites neglectus* (Vanguestaine *et al.* 1986)

S PeriGondwana (Armorica) - France: *Ambitisporites avitus, A. dilutus, Amocosporites miserabilis, Anapiculatisporites isidori, Apiculiretusispora microconus, A. Plicata, A. spicula, Archaeozonotriletes chulus, A. chulus chulus, Archaeozonotriletes chulus nanus, Calamospora microrugosa, Convolutispora quititae, Emphanisporites neglectus, Leiotriletes parvus, L. pyramidalis, Punctatisporites punctatus, Quadrisporites granulatus, Q. variabilis, Retialetes legionis, Retusotriletes eslae, R. rotundus, R. warringtonii, Synorisporites tripapillatus, S. verrucatus* (Deunff & Chateauneuf 1976; Moreau-Benoit & Dubreuil 1987; Rauscher & Robardet 1975; Steemans *et al.* 1996)

S PeriGondwana (Iberia) - Spain: *Ambitisporites avitus, A. dilutus, Amocosporites miserabilis, Anapiculatisporites isidori, A. terciensis, A. ventae, Apiculiretusispora arcidecus, A. toriensis, Archaeozonotriletes chulus, Archaicusporites asturicus, A. torrestionensis, Brochotriletes sanpetrensis, Chelinospora canistrata, C. cantabrica, C. hemiesferica, C. lavidensis, C. media, C. poecilomorpha, C. sanpetrensis, Concentricosisporites agradabilis, C. borbullatus, C. sagittarius, Convolutispora quititae, C. sanpetrensis, Coronaspora cromatica, C. infraornata, C. mariae, C. primordiale, C. reticulata, C. subornata, Cymbosporites dittonensis, Emphanisporites disformis, E. perfilum, E. protoannulatus, E. protophanus, E. rotatus, E. splendens, Eupoikilofusa cabottii, Hispanaediscus bernesgae, H. leonensis, H. verrucatus, Iberoespora cantabrica, Leiotriletes socorridus, L. titanicus, , Laevolancis divellomedium, Paradominoespora maravedi, Quadrisporites granulatus, Q. variabilis, Retialetes legionis, Retusotriletes abundo, R. aureoladus, R. bipellis, R. chulus, R. coronadus, R. minor, R. warringtonii, Scylaspora elegans, S. vetusta, Stenozonotriletes pumillus, Streelispora granulata, Synorisporites downtonensis, S. lobatus, S. tripapillatus, S. verrucatus, Tetraletes granulatus, T. variabilis* (Cramer 1967; Cramer & Rodríguez 1977; Cramer & Díez 1977; Richardson *et al.* 2001; Rodríguez 1978a, b, c, 1983)

S PeriGondwana (Taurides) - Turkey: *Amicosporites splendidus, Archaeozonotriletes chulus, Artemopyra brevicosta, Clivosispora reticulata, Convolutispora quititae, Cymbosporites catillus, Dyadospora* *murusattenuata, D. murusdensa, Hispanaediscus verrucatus, H. wenlockensis, Laevolancis divellomedium, Pachytetras rugosa, Pseudodyadospora laevigata, P. petasus, Quadrisporites variabilis, Retusotriletes warringtonii, Rimosotetras problematica, Tetrahedraletes medinensis* (Steemans *et al.* 1996; Steemans *et al.* 2000)

S Gondwana - Algeria: *Ambitisporites avitus, A. dilutus, Amocosporites miserabilis, Apiculiretusispora synorea, Archaeozonotriletes chulus chulus, A. chulus nanus, Chelinospora hemiesferica, C.poecilomorpha, C. sanpetrensis, Cymbosporites triangulatus, Dictyotriletes gorgoneus, Emphanisporites neglectus, E. protophanus, E. rotatus, E. splendens, Laevolancis divellomedia, Retusotriletes abundo, R. delicatus, R. minor, Scylaspora distincta, S. kozlica, S. radiata, S. vetusta, Synorisporites tripapillatus, S. verrucatus* (Kermandji 2007)

SGondwana - Libya: *Ambitisporites avitus, A. dilutus, A. tripapillatus, Amicosporites miserabilis, A.splendidus, Aneurospora geikiei, A. richardsonii, Apiculiretusispora perfecta, A. spicula, A. synorea, Archaeozonotriletes chulus nanus, Artemopyra brevicosta, A. robusta, A. rugaticosta, Breconisporites simplex, Brochotriletes foveolatus, Chelinospora cantabrica, C. poecilomorpha, C. retorrida, Clivosispora reticulata, C. verrucata convoluta, C. verrucata verrucata, Concentricosisporites agradabilis, C. sagittarius, Coronaspora cromatica, Cymbohilates comptulus, C. dittonensis, C. multiconus, C. paulus, C. verrucosus, Dyadospora murusattenuata, D. murusattenuata, Emphanisporites neglectus, E. protophanus, E. rotatus, E. splendens, Hispanaediscus lamontii, H. verrucatus, H. wenlockensis, Iberoespora cantabrica, I. noninspisatosa, Laevolancis divellomedium, Perotrilites laevigatus, Pseudodyadospora laevigata, Punctatisporites dilutus, Quadrisporites variabilis, Retusotriletes abundo, R. bipellis, R. dittonensis, R. dubius, R. maccullockii, R. maculatus, R. minor, R. pychovii, R. rotundus, R. triangulatus, R. warringtonii, Rimosotetras problematica, Rugosphaera cerebra, Scylaspora chartulatus, Segestrespora membranifera, Stellatispora inframurinata cambrensis, S. inframurinata inframurinata, Synorisporites libycus, S. papillensis, S. verrucatus, Tetrahedraletes medinensis, Velatitetras rugosa, Verrucosisporites devonicus* (Buret & Moreau-Benoit 1986; Richardson 1996; Rubinstein & Steemans 2002; Spina & Vecoli 2009; Steemans *et al.* 2008; Tekbali & Wood 1991)

E Gondwana - Argentina: *Ambitisporites avitus, Amicosporites splendidus, Emphanisporites rotatus, Synorisporites papillensis* (Rubinstein 1992, 1994, 1995)

E Gondwana - Bolivia: *Ambitisporites dilutes* (McGregor 1984)

E Gondwana - Brazil: *Ambitisporites avitus, A. dilutus, Aneurospora richardonii, Archaeozonotriletes chulus, Artemopyra urubuense, Brochotriletes foveolatus, Chelinohilates sinuosus sinuosus, C. cantabrica, C. poecilomorpha, C. sanpetrensis, C. verrucata convoluta, C. verrucata verrucata, Coronaspora cromatica, Cymbosporites verrucosus, Dyadospora murusattenuata, Emphanisporites multicostatus, E. neglectus, E. rotatus, Hispanaediscus verrucatus, Laevolancis divellomedium, Quadrisporites horridus, Q. variabilis, Retusotriletes amazonensis, R. minor, Synorisporites verrucatus, Tetrahedraletes medinensis* (Steemans *et al.* 2008)

South China? Terrane - Jiangsu and Sichuan, China: *Ambitisporites dilutus, Artemopyra brevicosta, Cymbosporites sparseus, Dyadospora murusattenuata, D. murusdensa, Hispanaediscus verrucatus, Laevolancis divellomedia, Pseudodyadospora laevigata, P. petasus, Scylaspora downiei, S. scripta, Velatitetras laevigata* (Wang & Li 2000; Wang *et al.* 2005)