

Palaeozoic Innovations in the Micro- and Megafossil Plant Record: From the Earliest Plant Spores to the Earliest Seeds

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Abstract

Recently, major advances have been made in understanding terrestrialization processes and the development of early vegetation. This chapter reviews the major steps in the evolution of early land plants, with focii on cryptospores, trilete spores and on the meso- and megafossil remains of Silurian and Devonian plants. The major morphological innovations of plants and their spores are described. Cryptospores are the earliest fossil record of a terrestrial vegetation cover; the oldest indisputable specimens are observed from Darriwilian (mid-Ordovician) strata in Saudi Arabia and the Czech Republic. The biological affinities of cryptospores are discussed. It is generally agreed that cryptospores were derived mainly from 'bryophytes', but some cryptospores may have arisen from early tracheophytes or their immediate ancestors. The earliest trilete spores are Ordovician in age. Most trilete spores are considered to have tracheophyte affinities; we discuss possible relationships between trilete spores and several cryptospores in dyads or monads. The earliest record of plant mesofossils comes from Middle Silurian strata. The evolution and affinities of the major groups of Late Silurian and Devonian land plants are presented within a phylogenetic and a stratigraphic framework.

Keywords

Cryptospores • Trilete spores • Meso-megafossil plants • Propagule dispersion • Tripapillate forms as biostratigraphic markers • Embryophytes • Spermatophyte adaptive radiation

For me, the most exciting events in land plant evolution were completed by end of the Devonian Period. The origin of the embryophytes (bryophytes + vascular plants) is shrouded in controversy, and represents one of the greatest palaeontological mysteries.
J.B. Richardson (1996a)

Introduction

The colonization of land by plants, fungi and animals – also known as the terrestrialization – was undoubtedly one of the most crucial advances in the history of life

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on Earth. The exact nature and timing of the early steps remain conjectural, but evidence has accumulated of the existence of complex terrestrial ecosystems in mid-Palaeozoic times. The oldest evidences of terrestrial plants are in the form of dispersed propagules (cryptospores and trilete spores) and phytodebris (tubular structures and fragmentary cuticles) in the sediments. These are at least Ordovician in age; plant megafossils are not known before the Middle Silurian. In this chapter, we review the major steps in the evolution of the early terrestrial vegetation.

The Miospores

Cambrian Palynomorphs

Ambiguous Cambrian palynomorphs from the Bright Angel Shale, Arizona, USA, have been described (Taylor and Strother 2008) as '... the desiccation-resistant spores of cryptogams belonging to the charophyte-embryophyte lineage'. They are characterized by multilaminar spore walls, characteristic of some extant liverworts and Palaeozoic cryptospores. The authors suggested such these spores could have evolved via the fusion of separate, multiple laminae, possibly of the primitive plant sporoderm type. The Cambrian palynomorphs include dyads and tetrads similar to younger cryptospores, but most differ morphologically by their much smaller size, by the presence of polyads (with a variable number of spores) and by the presence of envelopes enclosing individual spores of the polyads rather than the envelope of younger cryptospores enclosing the whole dyad or tetrad. As stated by Taylor and Strother (2008), 'Their overall morphology cannot prove their embryophytes affinity, but laminate wall ultrastructure stands out as a single character they appear to have in common with the liverworts ... For now, they might be considered as "protoembryophytes" ...'.

Cryptospores

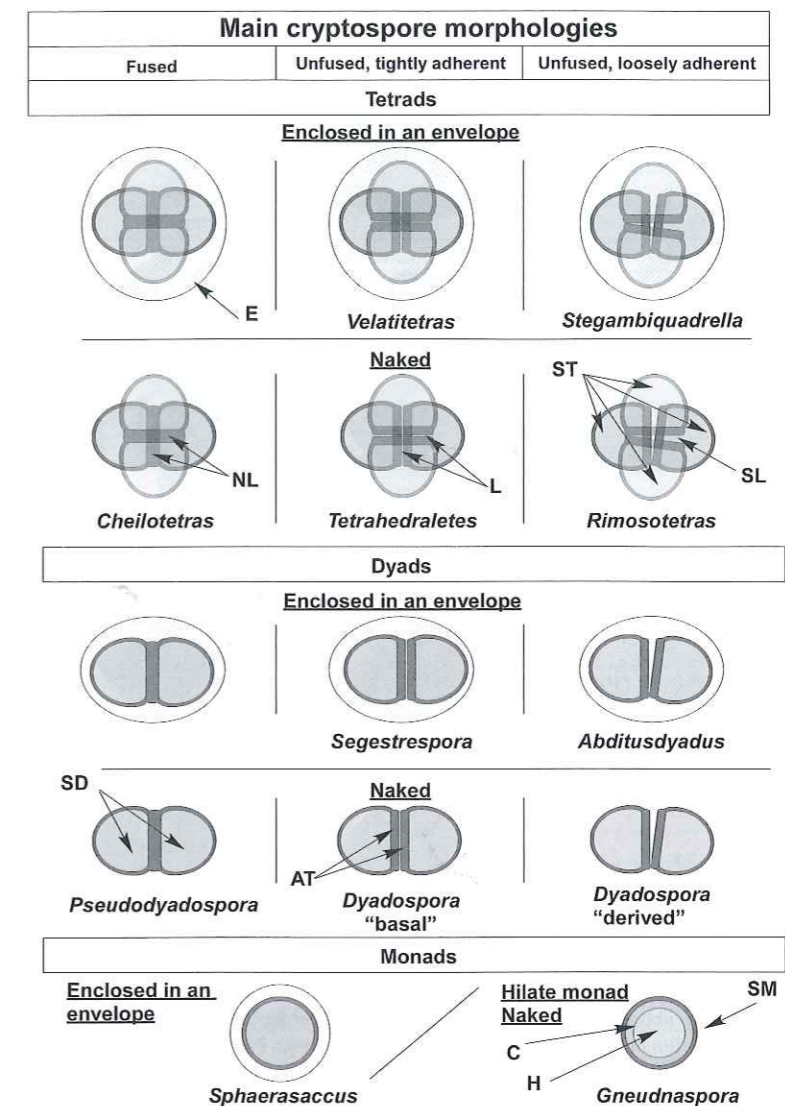
The oldest evidence for the first land plants are propagules, termed cryptospores, because of their primitive aspect, the lack of a trilete mark, and because their parent plants were previously unknown (Richardson et al. 1984). In 2000, Steemans proposed that cryptospores should be included in miospores as they

most probably are produced by embryophytes and more precisely by 'bryophytes' (Wellman et al. 2003). Cryptospores show unusual features when compared with the younger spores of tracheophytes. They are preserved either as monads or as obligate dyads or as tetrads, indicating that they remain permanently fused (Fig. 1). At the border of their contact area, each spore of a dyad or tetrad shows an annular thickening. Cryptospores are either naked or enclosed within a thin envelope, or membrane. The envelope and/or the wall of the cryptospores may be ornamented by various elements. The ornament is usually inconspicuous in the oldest species, but in Late Silurian and Early Devonian specimens, it becomes more and more similar to that of trilete spores. Dyads and tetrads are termed fused or unfused according to the respective absence or presence of a superficial area of attachment between the spores; the exact nature of the association of the spores is not clearly known (Wellman 1996). Taphonomy may also play a role in the aspect of the attachment area, presumably depending on how the specimens have been compressed during the fossilization processes. For example, the tetrads of the text fig. 5B and F in Wellman (1996) show at the same time typical sutures of *Cheilotetras caledonica* (Fig. 2.1) and of *Tetraedraletes medinensis* (Fig. 2.2-3). Note: All miospore and plant taxa and their authors are listed in Tables 1 and 2.

Evolution of the Cryptospore Assemblages Through Time

The biological affinities of the Cambrian palynomorphs remain controversial, but the embryophytic origin of the palynomorphs observed in the Darriwilian (Llanvirn) assemblages from Saudi Arabia (Strother et al. 1996) and from the Czech Republic (Vavrdová 1990a, b) is widely accepted. Llanvirnian cryptospores are very different from and much more diverse than the Cambrian palynomorphs, including tetrads, dyads and monads, naked or enclosed in an envelope, laevigate or ornamented. Assemblages from the Sandbian and Katian (Caradoc in Wellman 1996), the Katian or Hirnantian (e.g. Richardson 1988; Steemans 2001; Vavrdová 1984, 1988; Wang et al. 1997) and the early Llandovery (e.g. Burgess 1991; Mizusaki et al. 2002; Richardson 1988; Steemans et al. 2000; Steemans and Pereira 2002; Wellman et al. 2000) exhibit strong similarities. Biostratigraphic criteria based on cryptospores from the Llanvirn up to the mid-Llandovery are rare.

Fig. 1 Simplified graphic representation of the main cryptospore morphological features (modified from Richardson 1996b). *AT* annular thickening (equatorial ring bordering the area of attachment of tetrads and dyads); *C* curvaturae (line bordering the hilum); *E* envelope (inclosing tetrads, dyads or monads); *H* hilum (contact area of spores stem from dissociated dyads); *L* line of attachment (two or four spores are attached together. *L* is the line of attachment between the spores. Each *AT* of the spores are separated by the *L*); *NL* no line of attachment (no surface of attachment between the spores. Only one *AT* is visible); *SL* clear separation between the spores of tetrads or of dyads along the *L*; *SD* the two spores of the dyad; *SM* the monad spore (hilate and alete spore); *ST* the four spores of the tetrads



Strangely, the Hirnantian glaciation, causing massive extinctions in many fossil groups, did not affect the cryptospore biodiversity. The wide climatic tolerance of the parent plants demonstrated by the almost ubiquitous cryptospore distribution (from high, even from glacial sediments, to low latitudes) could explain why climatic changes did not affect their biodiversity. Lands exposed after the melting of the ice sheet could immediately be colonized by the cryptospore producing plants that had survived in refugia Steemans and Wellman (2004). From the Wenlock to the Přídolí, cryptospores assemblages diversified once more (Steemans 2000; Steemans and Wellman 2004). During the Devonian, cryptospore populations

decreased at a continuous rate. An abundant but low diversity assemblage of Middle Devonian cryptospores has recently been recorded (Breuer 2007). Contrariwise, the cryptospore biodiversity decreased dramatically below the Aeronian/Telychian boundary (Steemans 2000).

Main Morphological Events Within Cryptospores

- (1) Naked dyads and tetrads are usually unornamented and their spores are tightly attached to each other.
- (2) Morphology of the cryptospores changes greatly after the decline in biodiversity observed below the Aeronian/Telychian boundary (bioevent in Fig. 3).

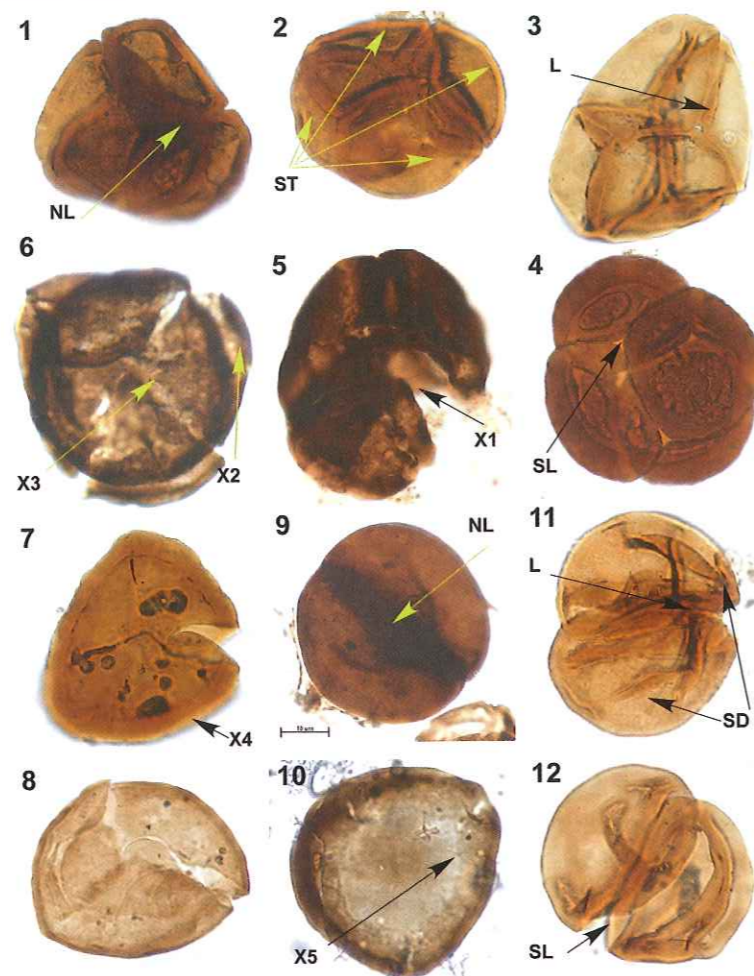


Fig. 2 For abbreviations, see Fig. 1. (1) *Cheilotetras caledonica* Wellman and Richardson 1993. Llandovery, Paraná Basin, Paraguay; diameter size: 53 μm . (2–3) *Tetraedraletes medinensis* (Strother and Traverse) Wellman and Richardson 1993. Llandovery, Paraná Basin, Paraguay. Specimen in (2) shows a thick exine; diameter size: 58 μm . Specimen in (3) has a very thin exine; diameter size: 64 μm . (4) *Rimosotetras problematica* Burgess 1991 with each spore separated from the others. The distal face is abnormally thick. Llandovery, Paraná Basin, Paraguay; diameter size: 49 μm . (5) Dissociated tetrad. Silurian of Argentina. One of the four spores is absent (X1); diameter size: 57 μm . (6–7) *Imperfectotriletes patinatus* Steemans et al. 2000. Specimen in (6), Silurian of Argentina, shows remains of the tetrad (X2). The pseudo-trilete mark is formed by tears (X3); diameter size: 30 μm . Specimen in (7), Llandovery, Paraná Basin, Paraguay, shows a thick distal face or patina (X4).

The oldest Ordovician assemblages are composed mainly of tetrads and dyads. Monads are rare (Figs. 3, 4, 5, and 6). Some monads display tears with a pseudo 'Y' shape that looks like an imperfect trilete mark

(8) *Imperfectotriletes varvdovae* (Richardson) Steemans et al. 2000. Llandovery, Saudi Arabia. The exine is thinner than that of *I. patinatus*; diameter size: 29 μm . (9) *Pseudodyadospora laevigata* Johnson 1985. Llandovery, Paraná Basin, Brasil. There is no line of separation between the two spores; diameter size: 35 μm . (10) *Gneudnaspota (Laevolancis) chibrikovae* Breuer et al. 2007. Llandovery, Paraná Basin, Paraguay. The border of the pseudohilum is torn (X5); diameter size: 38 μm . (11) *Dyadospora murusattenuata* Strother and Traverse 1979 emend. Burgess and Richardson (1991). The exine is thin and strongly folded. The line of attachment shows tendency to be separated into two monads; diameter size: 45 μm . (12) *Dyadospora murusdensa* Strother and Traverse 1979 emend. Burgess and Richardson (1991). The exine is thick. The two spores of the dyads are clearly separated and could be confused with *Gneudnaspota divellomedia* (see Fig. 7); diameter size: 40 μm .

so have been interpreted as spores resulting from the disaggregation of tetrads (Steemans et al. 2000). They are considered to be cryptospores and are named *Imperfectotriletes* (Fig. 2.6–8). Numerous dyads (e.g.

Table 1 Miospore taxa and their authors

Taxa	Authors
<i>Abditusdyadus</i>	Wellman and Richardson (1996)
<i>Acinosporites lindlarensis</i> morphon	Richardson et al. (1993)
<i>Acontotetras inconspicuis</i>	Richardson (1996c)
<i>Ambitisporites</i>	Hoffmeister (1959)
<i>Ambitisporites avitus-dilutus</i> morphon	Steemans et al. (1996)
<i>Ancyrospora</i>	Richardson emend Richardson (1996b)
<i>Apiculiretusispora</i>	(Strel) Strel (1967)
<i>Archaeozonotriletes</i>	Naumova emend. Allen (1965)
<i>Archaeozonotriletes chulusnanus</i> morphon	Steemans et al. (1996)
<i>Artemopyra</i>	Burgess and Richardson (1991)
<i>Artemopyra brevicosta</i>	Burgess and Richardson (1991)
<i>Breconisporites</i>	Richardson et al. (1982)
<i>Cheilotetras caledonica</i>	Wellman and Richardson (1993)
<i>Chelinohilates</i>	Richardson (1996c)
<i>Chelinohilates erraticus</i>	Richardson (1996c)
<i>Chelinospora</i>	Allen (1965)
<i>Chelinospora cantabrica</i>	Richardson et al. (2001)
<i>Chelinospora cassicula</i>	Richardson and Lister (1969)
<i>Chelinospora poecilomorpha</i>	(Richardson and Ioannides) Richardson et al. (2001)
<i>Clivosispora verrucata convoluta</i>	McGregor and Camfield (1976)
<i>Clivosispora verrucata verrucata</i>	McGregor and Camfield (1976)
<i>Coronaspora</i>	Rodríguez (1978)
<i>Cymbohilates</i>	Richardson (1996c)
<i>Cymbohilates baqaensis</i>	Breuer et al. (2007)
<i>Cymbohilates cymosus</i>	Richardson (1996c)
<i>Cymbohilates disponerus</i>	Richardson (1996c)
<i>Cymbosporites</i>	Allen (1965)
<i>Cymbosporites dammamensis</i>	Steemans (1995)
<i>Cymbosporites proteus</i>	McGregor and Camfield (1976)
<i>Cymbosporites stellospinosus</i>	Steemans (1989)
<i>Dibolisporites</i>	Richardson (1964)
<i>Dictyotriletes</i>	Naumova (1939) ex Ishchenko (1952)
<i>Dyadospora</i>	Strother and Traverse (1979)
<i>Dyadospora murusattenuata</i>	Strother and Traverse (1979) emend. Burgess and Richardson (1991)
<i>Dyadospora murusattenuata-murusdensa</i> morphon	Steemans et al. (1996)
<i>Dyadospora murusdensa</i>	Strother and Traverse (1979) emend. Burgess and Richardson (1991)
<i>Emphanisporites</i>	McGregor (1961)
<i>Emphanisporites protophanus</i>	Richardson and Ioannides (1973)
<i>Gneudnaspota divellomedia</i>	(Chibrikova) Balme (1988)
<i>Gneudnaspota divellomedia var minor</i>	Breuer et al. (2007)
<i>Grandispora</i>	Hoffmeister et al. emend. McGregor (1973)
<i>Hispanaediscus</i>	Cramer (1966)
<i>Hispanaediscus verrucatus</i>	(Cramer) Burgess and Richardson (1991)
<i>Hystricosporites</i>	McGregor (1960)
<i>Imperfectotriletes</i>	Steemans et al. (2000)
<i>Imperfectotriletes patinatus</i>	Steemans et al. (2000)
<i>Imperfectotriletes varvdovae</i>	(Richardson) Steemans et al. (2000)

Table 1 (continued)

Taxa	Authors
<i>Laevolancis chibrikovae</i>	Steemans et al. (2000)
<i>Perotriletes</i>	Couper emend. Evans (1970)
<i>Retusotriletes</i>	Naumova emend. Streeel (1964)
<i>Rhabdosporites</i>	Richardson emend. Marshall and Allen (1982)
<i>Rimosotetras problematica</i>	Burgess (1991)
<i>Rugosisorites</i>	Dufka (1995)
<i>Scylaspora</i>	Burgess and Richardson (1995)
<i>Segestrespora</i>	Burgess (1991)
<i>Segestrespora membranifera</i>	(Johnson) Burgess (1991)
<i>Stegambiquadrella contenta</i>	Johnson (1985)
<i>Streelispora</i>	Richardson and Lister (1969)
<i>Streelispora newportensis</i>	(Chaloner and Streeel) Richardson and Lister (1969)
<i>Synorisporites</i>	Richardson and Lister (1969)
<i>Synorisporites</i> cf. <i>S.?</i> <i>libycus</i>	in Burgess and Richardson (1991)
<i>Synorisporites maculosus</i>	Dufka (1995)
<i>Synorisporites verrucatus</i>	Richardson and Lister (1969)
<i>Tetraedraletes</i>	Strother and Traverse (1979)
<i>Tetraedraletes medinensis</i>	(Strother and Traverse) Wellman and Richardson (1993)
<i>Velatitetras</i>	Burgess (1991)
<i>Velatitetras retimembrana</i>	(Miller and Eames 1982) Wellman and Richardson (1996)
<i>Zonotriletes</i>	Luber and Walts (1938)

Segestrespora, Fig. 7.5) and tetrads (e.g. *Velatitetras*, Fig. 7.7) are enclosed by an outer laevigate or ornamented envelope. Ornament on the outer envelope is usually made up of small grana, a low reticulum or low rugulae. Dyads and tetrads may have exactly the same ornamentation; those from the early Llandovery are almost absent above this limit. The cryptospores enclosed in an outer envelope become very rare. The spores in dyads become progressively less attached, sometimes displaying a clear separation between them. Monads are more and more abundant.

The first ornamented naked dyads and monads evolved during the Llandovery becoming very abundant during the Wenlock (e.g. *Hispanaediscus verrucatus*, Fig. 7.11) evolving simultaneously with the first cryptospores with a hilum ridged by radial muri (e.g. *Artemopyra brevicosta*, Fig. 7.9). The first distal ornament consisted of verrucae, regular, irregular or merging into convoluted muri. During the Pridoli and the Lochkovian, ornamented patinate cryptospores (*Chelinohilates*, Fig. 8.1-3; *Cymbohilates*, Fig. 8.7-8, 9?) diversified and became abundant.

Trilete Spores

The Oldest Trilete Spores

The oldest known trilete spores are Llandovery specimens of Hoffmeister (1959) from Libyan sediments. Much later, rare trilete spores were isolated from Hirnantian samples from Turkey (Steemans et al. 1996). In both cases, the trilete spores belong to the simple unornamented *Ambitisporites avitus-dilutus* morph (Fig. 9.1-3).

Very recently, a diverse assemblage of trilete spores (Steemans et al. 2008a, 2009; Wellman et al. 2008) has been described from Saudi Arabian strata. These have been independently dated as being Ordovician in age (late Katian/Hirnantian boundary) by chitinozoans (Paris et al. 2008) and by acritarchs (Le Hérisse et al. 2008). The assemblage includes laevigate trilete spores (*Ambitisporites*) as well as ornamented trilete spores (mainly *Synorisporites*) and forms illustrated in Fig. 9.1-3, 6. Previously non-ornamented trilete spores had been recorded prior to the Homerian Stage (Burgess and Richardson 1991; Dufka 1995). The observation of a diverse assemblage of Ordovician

Table 2 Plant taxa and their authors

Taxa	Authors
<i>Aglaophyton</i>	D.S. Edwards (1986)
<i>Archaeopteris</i>	Dawson (1871)
<i>Asteroxylon</i>	Kidston and Lang (1920)
<i>Baragwanathia</i>	Lang and Cookson (1935)
<i>Bathurstia</i>	Hueber (1972)
<i>Calamophyton</i>	Leclercq and Andrews (1960)
<i>Chaleuria</i>	Andrews et al. (1974)
<i>Cooksonia banksii</i>	Habgood et al. (2002)
<i>Cooksonia caledonica</i>	Edwards (1970)
<i>Cooksonia parmensis</i>	Gerrienne et al. (2001)
<i>Cooksonia pertoni</i>	Lang (1937)
<i>Crossia</i>	Beck and Stein (1993)
<i>Drepanophycus</i>	Göppert (1852)
<i>Eospermatopteris</i>	Goldring (1924)
<i>Equisetum</i>	Linnaeus (1753)
<i>Estinnoophyton</i>	Fairon-Demaret (1978)
<i>Foozia</i>	Gerrienne (1992)
<i>Hollandophyton</i>	Rogerson et al. (2002)
<i>Huvenia</i>	Hass and Remy (1991)
<i>Ibyka</i>	Skog and Banks (1973)
<i>Junggaria</i>	Dou and Sun (1983)
<i>Leclercqia</i>	Banks et al. (1972)
<i>Lyonophyton</i>	Remy and Remy (1980)
<i>Metacladophyton</i>	Wang and Geng (1997)
<i>Moresnetia</i>	Stockmans (1948)
<i>Oocampsa</i>	Andrews et al. (1975)
<i>Pertica</i>	Kasper and Andrews (1972)
<i>Pseudosporochnus</i>	Leclercq and Banks (1962)
<i>Psilophyton</i>	Dawson (1859)
<i>Rellimia</i>	Leclercq and Bonamo (1973)
<i>Remyophyton</i>	Kerp et al. (2004)
<i>Rhacophyton</i>	Crépin (1875)
<i>Rhynia</i>	Kidston and Lang (1917)
<i>Runcaria</i>	Stockmans (1968)
<i>Salopella</i>	Edwards and Richardson (1974)
<i>Sciadophyton</i>	Steinmann (1929)
<i>Sennicaulis</i>	Kenrick et al. (1991)
<i>Sphenophyllum</i>	Brongniart (1822)
<i>Stockmansella</i>	Fairon-Demaret (1986)
<i>Taeniocrada dubia</i>	In Hueber (1982)
<i>Tortilicaulis</i>	Edwards (1979)
<i>Zosterophyllum</i>	Penhallow (1892)

trilete spores raises the question of their biological affinities: Were they produced by 'bryophytes' or by tracheophytes (refer to material online in Steemans et al. 2009)?

There is a clear relationship between tracheophytes and trilete spores, but not with cryptospores. The diversity of trilete spores is very low up to the Aeronian/Telychian transition, coincidental approximately with the radical modification in the cryptospore assemblages. After this bioevent (Fig. 3), the diversity trilete of spores increases strongly. The earliest plant megafossils are of Homerian age: they are *Cooksonia*-type 'rhyniophytoids' (Edwards and Feehan 1980). The earliest demonstrated tracheophytes are of Pridoli and Lochkovian ages (Edwards 2003), a period of time during which the trilete spore biodiversity explodes. During Devonian times, trilete spores and tracheophytes diversify simultaneously, whereas there is a strong decrease in the diversity of cryptospores.

Trilete spores have been observed in situ from 'rhyniophytoids', i.e. plants resembling the simplest vascular plants but lack evidence of vascular tissue (Edwards et al. 1994), and in tracheophytes. Rare trilete marks have been observed in extant 'bryophyte' spores (Gray et al. 1985). In many cases, the trilete mark is merely a scar formed during ontogeny by contact with the other members of the tetrad and is not a functional germination suture: such spores are termed cryptotrilete. Gray et al. (1985) estimates that only some 2.5% of extant 'bryophyte' genera produce trilete spores. Many of these are cryptotrilete forms. True trilete marks are characterized by a suture or a suture with associated lips; the latter are usually discernible in fossil trilete spores. Many of those observed in the Ordovician from Saudi Arabia display such a true trilete mark, and therefore suggest tracheophyte affinities for their parent plants.

Ambitisporites and *Synorisporites* with irregular 'thickenings' similar to those seen on Ordovician specimens have also been observed in sporangia from several Late Silurian and Early Devonian specimens of *Cooksonia pertoni*. The following laevigate and ornamented spores have been identified: *Aneurospora* (Fig. 9.4-5), *Retusotriletes* (Fig. 9.7-8), *Streelispora newportensis* (Fig. 10.5) and *Synorisporites verrucatus* (Edwards and Richardson 1996; Edwards et al. 1999; Fanning et al. 1988; Habgood et al. 2002; Rogerson et al. 1993). *Synorisporites* with irregular 'thickening' is very close to *Synorisporites maculosus* in Dufka (1995) and to *Synorisporites* cf. *S.?* *libycus* in Burgess and Richardson (1991). Interestingly, it seems that a progressive

Devonian	Late	
	Middle	◀ Seed megaspore and seed ▶ Megaspore > 1 mm ◀ Camerate (trilayered) ▶ punctate
	Early	◀ Hystricoid ▶ Megaspore ▶ gula
Silurian	Early	◀ Monolete ▶ Interradial structure
	Pridoli	◀ Zonate ▶ Biform ▶ Camerate (bilayered)
	Ludlow	◀ Tripapillate ▶ Annulus ▶ Kyrptome ▶ foveoreticulate
	Wenlock	◀ Retusoid ▶ Emphanoid ▶ Apiculate ornament
Ordovician	Late	◀ Verrucate & convolute ornament ▶ Trilete ▶ Alete monad
	Middle	◀ Cingulate ▶ Patinate ▶ Tetrad ▶ Dyad
	Early	

Fig. 3 Approximate time of appearance of the main morphological features and sculpturing types among cryptospores, monolete and trilete spores. For bioevent (see Section 'Main Morphological Events Within Cryptospores' and Steemans 2000)

morphological transition exists from the laevigate *Ambitisporites* to the ornamented *Synorisporites* in the Ordovician material (Steemans et al. 2009). This suggests that they may have been produced by the same plant and reinforces the possibility that the oldest trilete spores of the Ordovician were produced by tracheophytes similar to *Cooksonia* or by their ancestors.

The 'bryophyte' or tracheophyte affinities of the Ordovician trilete spores reported from Saudi Arabia will probably remain conjectural for a long time. Alternatively, the Saudi Arabian spores may have been produced by plants with a grade of organization transitional between 'bryophytes' and tracheophytes.

Main Morphological Events Within Trilete Spores

The earliest trilete spores are simple (Figs. 3, 4, 5, and 6), cingulate (with an equatorial thickening), laevigate (*Ambitisporites*) or ornamented with verrucae (*Synorisporites*). As stated earlier, these types of ornamented Ordovician trilete spores have recently been discovered from a single locality at the late Katian/Hirnantian boundary in Saudi

Arabia (Steemans et al. 2008a; Wellman et al. 2008). *Ambitisporites* has also been observed in Hirnantian strata from Turkey (Steemans et al. 1996), and from a Rhuddanian (Silurian) Saudi Arabian locality (Steemans et al. 2000). The earliest occurrences of the genus are diachronous from east to west as shown in Steemans (2000).

The first patinate (i.e. with a thin proximal face and a thick distal face) forms are laevigate and called *Archaeozonotriletes* (Fig. 8.5-6). They have been observed from several localities of Telychian age, for example, in Saudi Arabia (Wellman et al. 2000), Libya (Richardson 1988), Paraguay (Steemans and Pereira 2002) and the United Kingdom (Burgess 1991).

The first large-scale diversification of trilete spores occurs during the Homeric. It is interesting to note that the earliest *Cooksonia*-like mesofossils (tracheophytes?) are contemporaneous. Laevigate (*Retusotriletes*, Fig. 9.7-8) or ornamented (*Apiculiretusispora*, Fig. 9.9-11) retusoid forms appear. Radial muri (*Emphanisporites*, Figs. 7.10 and 10.4, 6) or irregular rugulate muri *Rugosisporites* (in Dufka 1995) or *Scylaspora* (in Burgess and Richardson 1995) on the proximal face are observed for the first

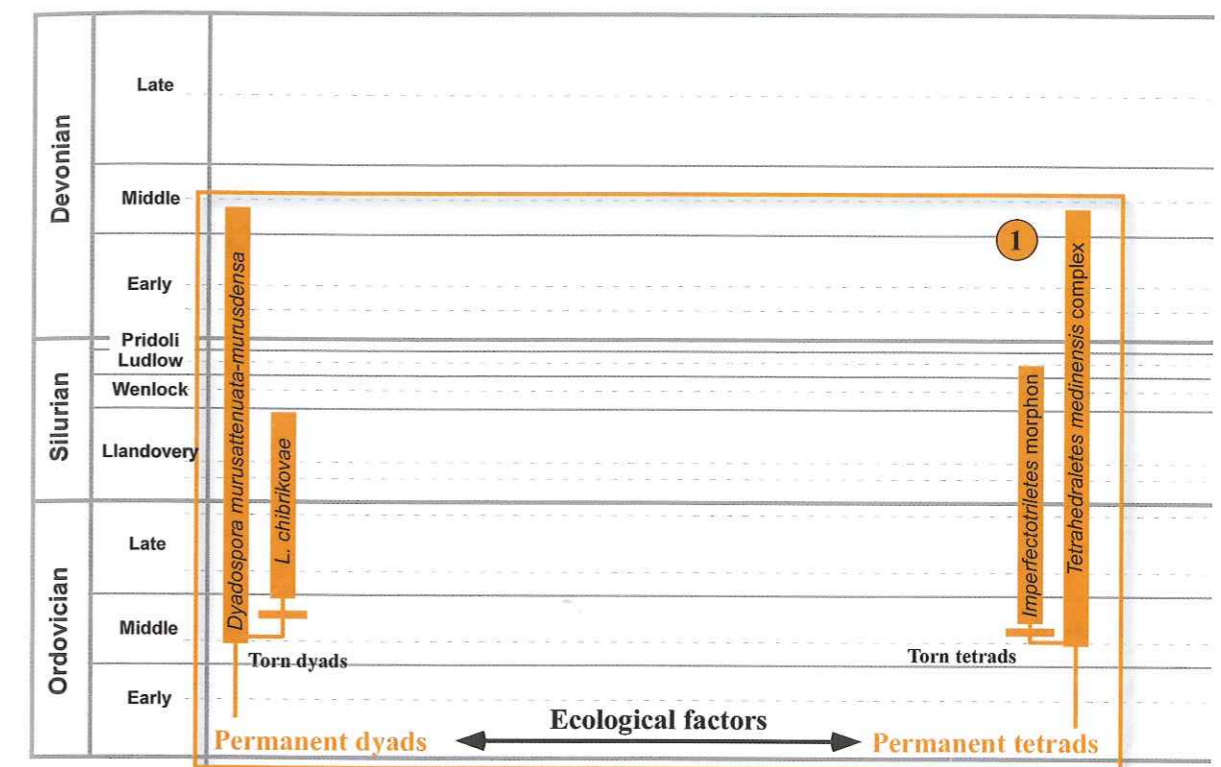


Fig. 4 Figures 4, 5 and 6 show the four successive layers illustrating approximate stratigraphic range (the vertical rectangles) of the main taxa of cryptospores and trilete spores. Lines linking rectangles symbolize possible morphological relationships between taxa. Horizontal small rectangles intersecting the lines explain the event responsible of the morphological modification between the taxa. The four layers symbolize steps of the

morphological evolutions through time for same group of morphologies and their direct descendant. Links exist between the layers. Layer 1 shows the approximate stratigraphic range of the two main simplest taxa of permanent tetrad and dyad cryptospores. They can be torn to release artificial monads with a pseudotrilete mark (Imperfectotriletes)

time. Very rare foveolate Homeric specimens have also been observed (Richardson and Ioannides 1973).

Tripapillate forms, such as in *Synorisporites papillensis* (Fig. 9.6), have long been an important biostratigraphic marker of the Ludfordian/Přídolí boundary. It has now been demonstrated that this proximal structure (see above paragraph) is present during the Ludlow (Rubinstein and Steemans 2002). That kyrtoles on the proximal surface, as in *Coronaspora cromatica* (Fig. 10.2), seem to have appeared during the Přídolí (Richardson et al. 2001) needs further consideration. The distal ring (annulus), as in *Amicosporites* (Fig. 10.3), is another important structure first appearing during the Přídolí (Richardson and Ioannides 1973). Although a possible *Aneurospora*, cingulate and ornamented (Fig. 9.4-5), has been observed in Ordovician sediments from Saudi Arabia, it suggests

that the actual diversification of the genus must have occurred during the late Ludlow. The patinate spores ornamented with coni and spines, as in *Cymbosporites* (Figs. 8.9, 10 and 10.1), or with verrucae, as in *Chelinospora* (Fig. 8.4), first appeared in the Ludlow. The late Ludlow and Přídolí interval is characterized by very similar species ornamented with coarse verrucae or convolute coarse muri, as in *Chelinospora poecilomorpha*, *Clivosispora verrucata* var. *verrucata* or *C. verrucata* var. *convoluta*. It is difficult to separate the latter species as they most probably all belong to a single morphon. The reticulate structure on the distal patina, as in *Chelinospora cantabrica*, first occurred during the Přídolí.

The Lochkovian age is marked by two important innovations: the zonate and the camerate trilete spores. The zonate spores as in *Zonotriletes* spp. (Fig. 10.10)

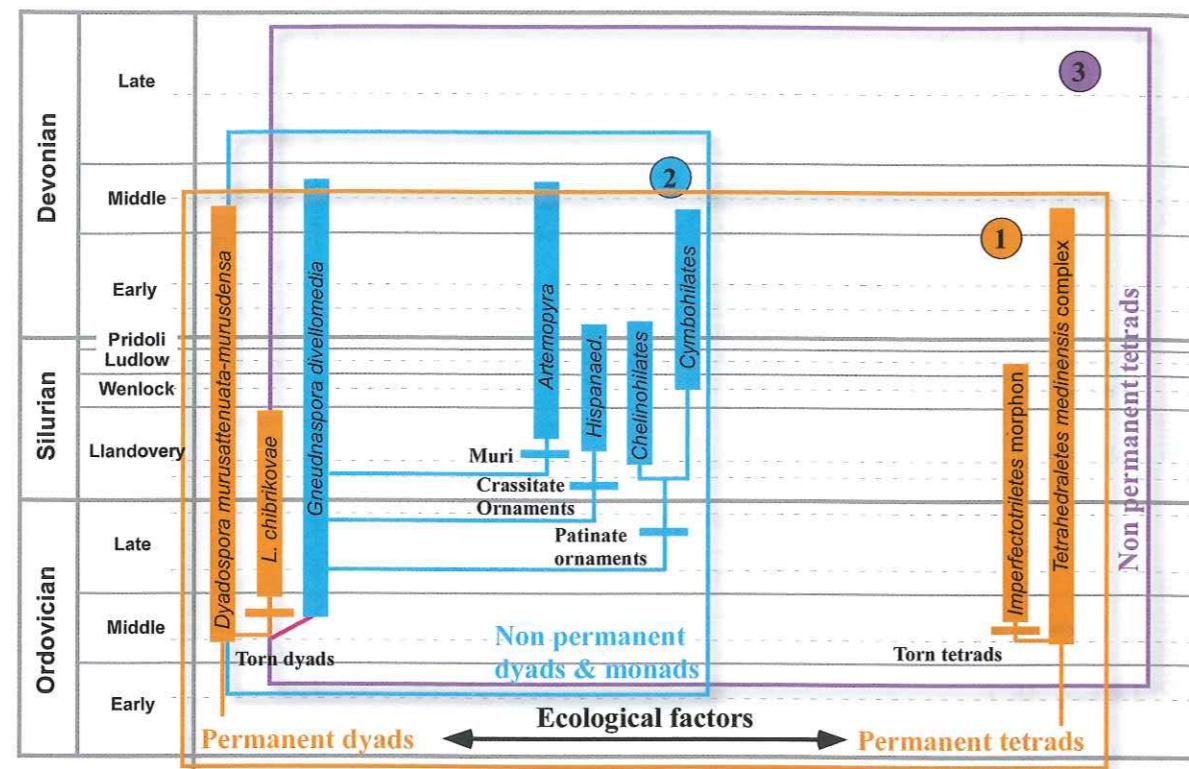


Fig. 5 (See also Fig. 4 caption) Layer 2 shows the approximate stratigraphic range of the taxa of non-permanent dyads and the monads stem from them. The definition of the different taxa relates to presence of patina or equatorial crassitude or ornament. Layer 3 contains no taxa. It symbolizes a putative stage in which

seem to appear first in Gondwanan localities during the early Lochkovian (Jardiné and Yapudjian 1968) and later in the Lochkovian on Euramerica as exemplified by *Cirratiradites diaphanus* (Fig. 10.9). Camerate spores appeared very early in the Lochkovian with *Perotriletes* (Fig. 10.11) and with the good biostratigraphic marker *S. newportensis* (Fig. 10.5) on the Old Red Sandstone area (Richardson and Lister 1969; Strel et al. 1987). On the Gondwanan continent, rare camerate specimens of *Grandispora* (Fig. 10.12) are known from the early Lochkovian of Brasil (Stemans et al. 2008b) and Saudi Arabia (Stemans et al. 2007). *Dictyotriletes* (Fig. 10.8) became very abundant from the Lochkovian onwards. No retusoid spores ornamented with bifurcate ornament such as *Dibolisporites* (Fig. 9.12) have been observed prior to mid-Lochkovian times (Stemans 1989).

The earliest monolete spores, for example, *Latosporites* (Fig. 11.1), are known from more or less

all plant producing cryptospores illustrated on the layers 1 and 2 shift from permanent to non-permanent tetrads. Non-permanent tetrads are preserved in the sporangia. When they are at maturity, tetrads split and isolated trilete spores are dispersed

coeval localities near the Pragian/Emsian transition from Saudi Arabia (Breuer et al. 2007), the United Kingdom (Wellman 2006) and Brazil (Mendlowicz Mauller et al. 2007).

Well-marked differentiation of the spore into sexine and nexine was common during mid-Emsian times, initially with *Rhabdosporites* and, shortly after, by large forms such as *Grandispora* (Fig. 11.8).

The late Emsian is characterized by the incoming of bifurcate ornament in species of the genera *Ancyrospora* (Fig. 11.4-5) and *Hystricosporites*.

From the Silurian to the Emsian, all spores increase in size. The Emsian is marked by a very important step in the evolution of the vegetation: the advent of heterospory (Andrews et al. 1974; Gerrienne 1996; Meyer-Berthaud and Gerrienne 2001). Apart from the megaspores mentioned by Richardson and McGregor (1986) from sediments now regarded as being of early Pragian to earliest Emsian in age, the earliest

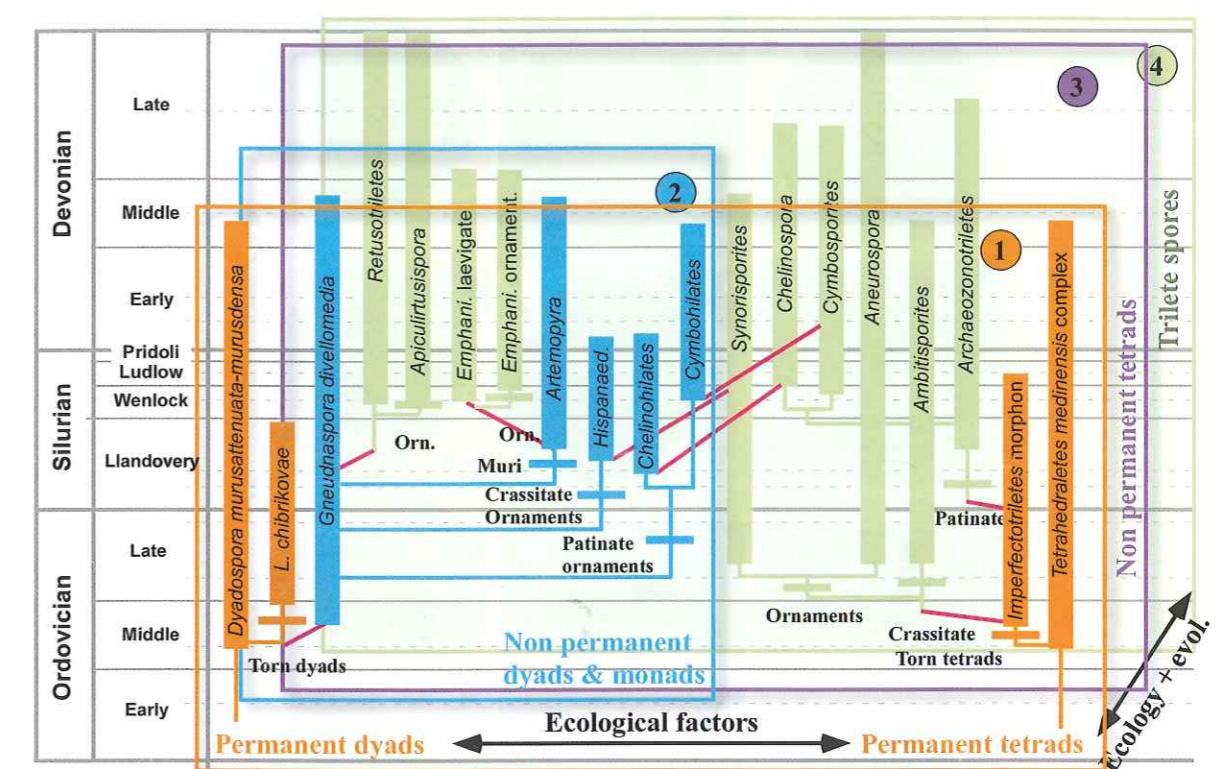


Fig. 6 (See also Fig. 4 caption). The layer 4 contains the trilete spores resulting from the dissociation of non-permanent tetrads

unequivocal incoming of dispersed megaspores (>200 μm) occurred at the end of the Emsian (Traverse 2007). Whilst the functional definition of a megaspore is clear, recognition on morphological basis only of a dispersed fossil spore as a true megaspore is difficult. The diameter size of 200 μm defining a megaspore is arbitrary, and it is not a definitive proof of heterospory. It is also widely accepted that large dispersed spores smaller than 200 μm could be small megaspores. It has been suggested (Hemsley et al. 1999) that 115 μm in diameter size could be a more realistic limit. In some cases, spores of very similar morphologies show a bimodal diameter size curve as shown in Poland (Turnau and Jakubowska 1989). The 1 mm diameter size boundary (Fig. 11.11) is crossed during the Givetian (Ville de Goyet et al. 2007).

Several Middle Devonian camerate species clearly show differentiation of the nexine, into two outer layers (Breuer 2007, Fig. 11.10). During the Middle Devonian, different patinate/crassitate taxa show for the first time a clear punctuation of their exine (Breuer 2007).

A further step in the heterospory evolution is the seed-megaspore, where three aborted spores stay attached to the megaspore (Marshall and Hemsley 2003).

From Cryptospores to Trilete Spores: A Possible Scenario

Dyads or Tetrads: Could They Be Produced by the Same Plant?

The oldest assemblages of cryptospores are composed mainly of tetrads and dyads, naked or enclosed in an envelope. The most common and morphologically simple cryptospores belong to *T. medinensis* and the *Dyadospora murusattenuata-murusdensa* morphon. They are composed of four and two cells, respectively, both laevigate and naked, and display wide morphological variation as expressed by their large range of both of their diameter and wall thickness. The lack of distinctive morphological characters and as all intermediate forms exist between the different

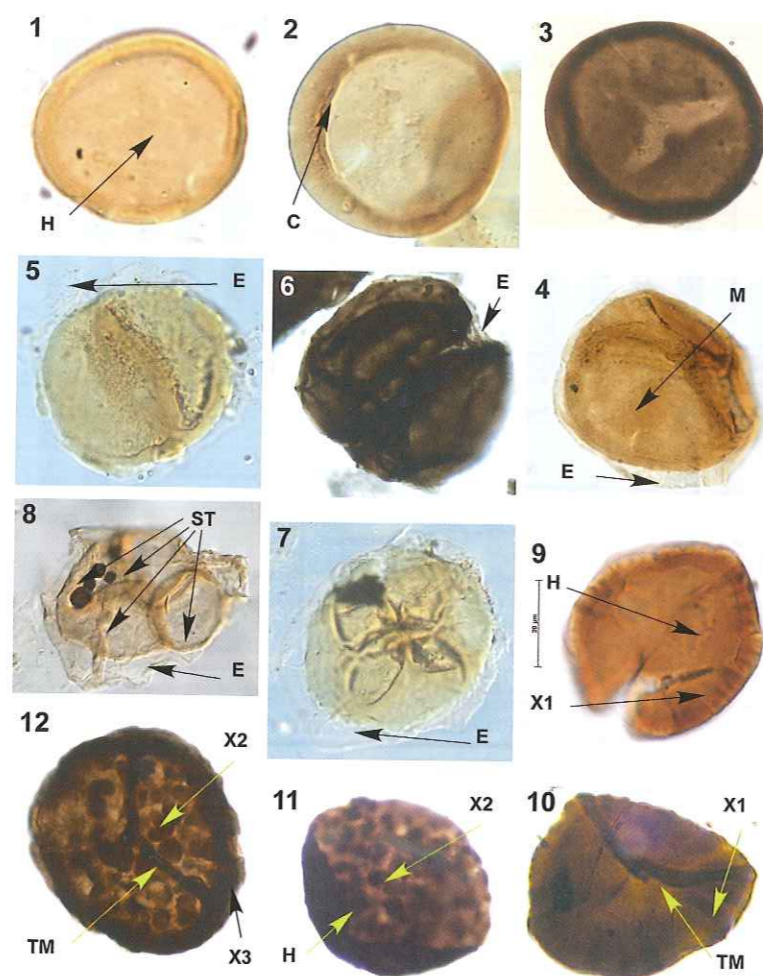


Fig. 7 For abbreviations, see Fig. 1. (1–3) *Gneudnaspora (Laevolancis) divellomedia* var. minor Breuer et al. 2007 showing different exine thickness. (1, 2) Emsian, Saudi Arabia; diameter sizes: 27 and 29 μm . (3) Lochkovian, Brittany; diameter size: 35 μm . (4) *Sphaerasaccus glabellus* Steemans et al. 2000. Llandovery, Paraná Basin, Paraguay; diameter size: 47 μm . (5) *Segestrespora laevigata* Burgess 1991 Hirnantian, Chad; diameter size: 40 μm . (6) *Abditusdyadus laevigatus* Wellman and Richardson 1996. Lochkovian, Saudi Arabia. The two cells of the dyad are separated; diameter size: 40 μm . (7) *Velatitetras laevigata* Burgess 1991. Hirnantian, Chad; diameter size: 48 μm . (8) *Stegambiquadrella contenta* Johnson 1985. Hirnantian, Chad. The four spores of the tetrad are clearly dissociated inside of the envelope; diameter size: 52 μm . (9) *Artemopyra*

brevicosta Burgess and Richardson 1991. Ludlow/Přídolí, Saudi Arabia. Short radial muri are visible at the internal limit of the hilum (X1); diameter size: 22 μm . (10) *Emphanisporites protophanus* Richardson and Ioannides 1973. Late Silurian/Early Devonian, Argentina. The trilete mark is visible (TM), the contact area is ornamented by radial muri similar to those of *A. brevicosta* in (9); diameter size: 34 μm . (11) *Hispanaediscus verrucatus* Cramer 1966. Lochkovian, Brittany. The distal face is ornamented by rounded verrucae (X2); diameter size: 18 μm . (12) *Synorisporites verrucatus* Richardson and Ioannides 1973. Lochkovian, Saudi Arabia. The trilete mark is well visible (TM), the verrucae on the distal face (X2) are similar to those of *H. verrucatus*, the equatorial crassitude here is thicker (X3); diameter size: 30 μm

morphologies, the only distinguishing character is the tetrad or dyad configuration. Considering the long stratigraphic range of the two taxa from the Middle Ordovician to the Middle Devonian, and their worldwide palaeogeographic distribution, it seems clear they

have been produced by different plants. This has been confirmed by the high variability of their ultrastructure wall (Edwards et al. 1996; Taylor 1995, 1996, 1997, 2002, 2003; Wellman et al. 1998b).

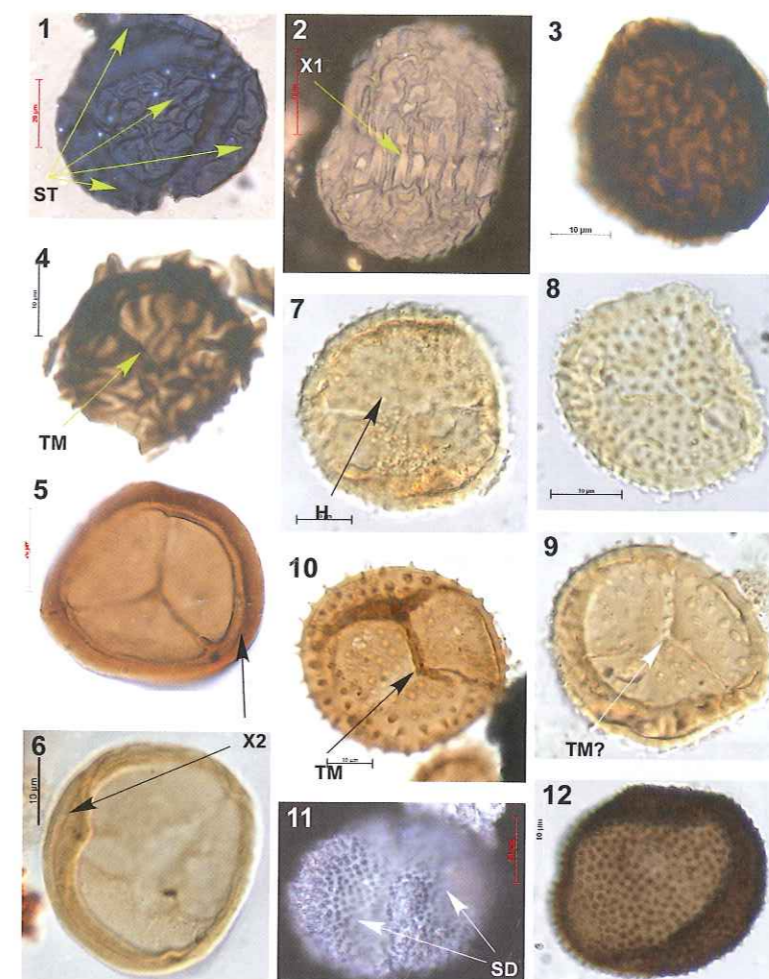


Fig. 8 For abbreviations, see Fig. 1. (1–3) *Chelinohilates erraticus* Richardson 1996c. Lochkovian, Saudi Arabia. Specimen in (1) is in tetrad configuration (image in reflected light); diameter size: 53 μm . Specimen in (2) is in dyad configuration, the envelope is ornamented by convolute muri which become parallel over the area of contact between the two spores (X1); diameter size: 58 μm . Specimen in (3) is in monad configuration; diameter size: 40 μm . (4) *Chelinospora cassicula* Richardson and Lister 1969, the specimen shows the same convolute muri on the distal face than those of *C. erraticus*. The trilete mark (TM) is clearly visible on the proximal face; diameter size: 30 μm . (5–6) *Archaeozonotriletes chulusnanus* morphon Steemans et al. 1996. Emsian, Saudi Arabia. Specimens showing a strong patina (X2) and a thin proximal face; diameter size: 52 μm (5) and 35 μm (6). (7–8) *Cymbohilates baqaensis* Breuer et al. 2007. Pragian/Emsian, Saudi Arabia. Specimens showing tears

on the hilum; diameter size: 38 μm (7) and 31 μm (8). (9) *Cymbosporites dammamensis* Steemans 1995. Pragian/Emsian, Saudi Arabia. The tears on the proximal face looks like a trilete mark, but the curvaturae are perfectly circular and do not show the typical invagination at the end of the rays of the trilete mark (X3); diameter size: 35 μm . (10) *Cymbosporites dammamensis* Steemans 1995. Pragian/Emsian, Saudi Arabia. The trilete mark and the curvaturae are well visible. Invaginations at the end of the rays of the trilete mark are present; diameter size: 36 μm . (11–12) *Cymbohilates disponerus* Richardson 1996c. Lochkovian, Brittany, France. Specimen in (11) is in dyad configuration; diameter size: 55 μm . Specimen in (12) is a monad closely similar to *Cymbosporites proteus* McGregor and Camfield 1976 (Fig. 10.1); diameter size: 27 μm

Hemsley (1994) suggested ontogenetic pathways to explain how a given sporangium might produce a great variety of cryptospores, depending on the timing of sporopollen in deposition during meiosis. It can even be hypothesized that monads, dyads or tetrads,

naked or enclosed in an envelope may be formed in the same sporangium. Ultrastructural studies, however, give conflicting results. In some cases, dyads and tetrads with identical morphologies exhibit ultrastructural differences suggesting that they were produced

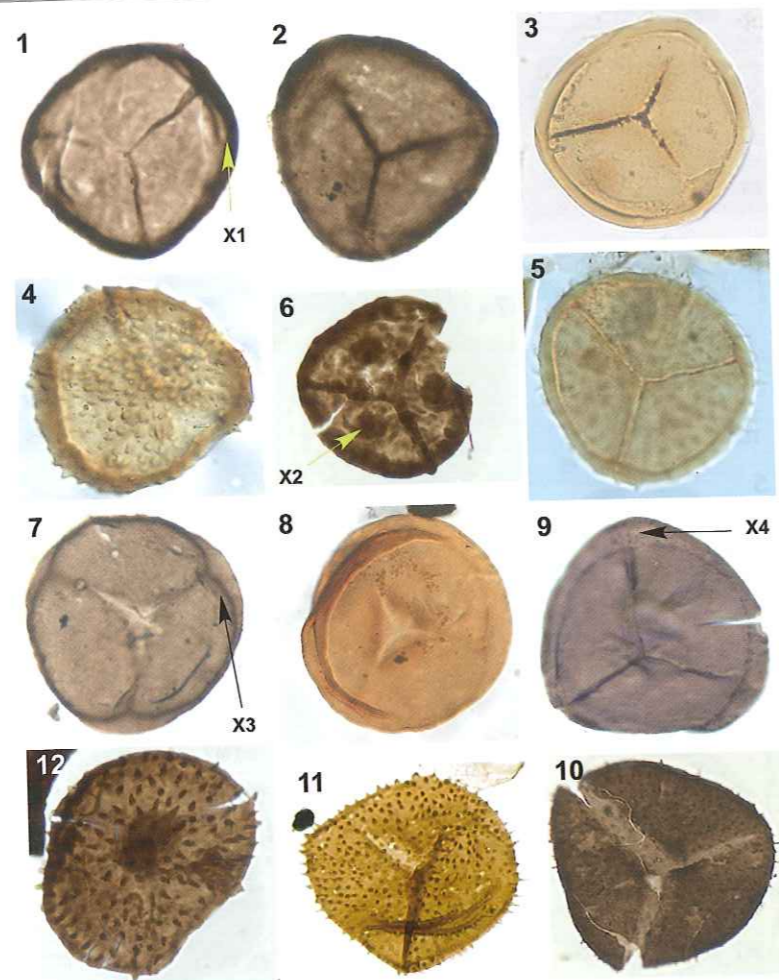


Fig. 9 For abbreviations, see Fig. 1. (1–3) Various aspects of *Ambitisporites avitusdilutus* morphon Steemans et al. 1996. Lochkovian, Brittany, France (1–2); diameter size: 28 and 33 μm . Pragian, Saudi Arabia (3); diameter size: 54 μm . The equatorial crassitude displays variable thicknesses. The lightest specimens are close to the morphological aspect of Retusotriletes. The darker specimens may more easily be confused with Archaeozonotriletes. (4) *Aneurospora* cf. *A. bollandensis* in Steemans et al. 2008a. Lochkovian, Amazon Basin, Brasil; diameter size: 35 μm . (5) *Aneurospora richardsonii* Richardson et al. 2001. Lochkovian, Amazon Basin, Brasil; diameter size: 31 μm . (6) *Synorisporites papillensis* McGregor 1973. Lochkovian/Pragian, Saudi Arabia. A papilla is present on each contact area; diameter size: 37 μm . (7–8) Various aspects

of *Retusotriletes* spp. Lochkovian, Brittany, France (7); diameter size: 38 μm . Pragian/Emsian, Saudi Arabia (8); diameter size: 40 μm . The darkest specimens (7) are close to *Ambitisporites* as their curvaturae appear thicker, appearing as an equatorial crassitude. (9–11) Various aspects of *Apiculiretusispora* spp. Lochkovian, Brittany, France (9, 10). Pragian/Emsian, Saudi Arabia (11). The ornaments (X4) are clearly situated outside the contact areas (photographed in reflected light in 9); diameter size: 47 μm . Specimens in (10) have longer spines; diameter size: 35 μm . Specimen in (11) is ornamented by spines with a slightly bulbous base close to that of some species of *Dibolisporites*; diameter size: 40 μm . (12) *Dibolisporites eifeliensis* McGregor 1973. Pragian, Saudi Arabia; diameter size: 50 μm

by distinct mother plants (Taylor 2002). Other tetrads and dyads with similar morphologies, for example, the dyad *Segestrespora membranifera* and the tetrad *Velatitetras retimembrana*, show striking ultrastructural similarities (Taylor 1996), strongly suggesting that a same plant or group of plants, possibly because

of variable ecological factors, could produce either mainly tetrads or mainly dyads.

The Tetrahedraletes Complex

The tetrad is the most common spore association produced in embryophyte sporangia. Except for obligate

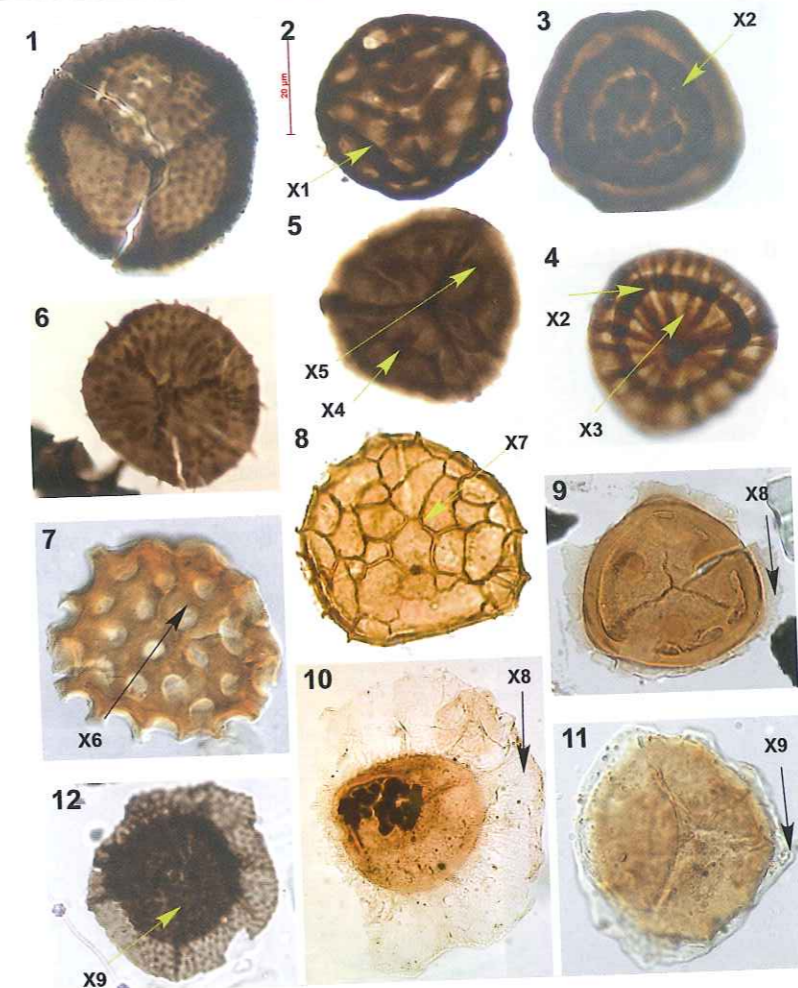


Fig. 10 For abbreviations, see Fig. 1. (1) *Cymbosporites proteus* McGregor and Camfield 1976. Lochkovian, Brittany, France. Specimen displaying a aspect similar to *Cymbosporites disponeris* Richardson (1996) (Fig. 8.12); diameter size: 32 μm . (2) *Coronaspora cromatica* Jansonius and Hills 1979. Lochkovian, Saudi Arabia. Three kyrtomes are visible on the proximal and distal areas. Similar specimens that may belong to the same species have been erroneously published in Steemans 1995 as *Chelinospora arabiensis*; diameter size: 37 μm . (3) *Amicosporites streeii* Steemans 1989. Lochkovian, Ardenne, Belgium. Presence of a distal annulus (X2) and verrucae inside it; diameter size: 42 μm . (4) *Emphanisporites annulatus* McGregor 1961. Emsian, Saudi Arabia. The annulus (X2) is on the distal face and the radial muri (X3) on the proximal face; diameter size: 46 μm . (5) *Streeispora newportensis* Richardson and Lister 1969. Lochkovian, Ardenne, Belgium. Three papillae (X4) are visible on the proximal face. The outer exine of this camerate species is folded. The folds (X5) link the papillae

and the trilete mark. Ornamentation is not clearly visible on this specimen; diameter size: 26 μm . (6) *Emphanisporites zavallatus* Richardson et al. 1982 var. *gedimniensis* Steemans and Gerrienne 1984. Lochkovian, Ardenne Belgium; diameter size: 37 μm . (7) *Brochotriletes foveolatus* Naumova 1953. Pragian/Emsian, Saudi Arabia. The foveolate structure (X6) is on the distal face; diameter size: 54 μm . (8) *Dictyotriletes subgranifer* McGregor 1973. Pragian/Emsian, Saudi Arabia. The reticulum is on the distal face (X7); diameter size: 62 μm . (9) *Cirratiradites diaphanus* Steemans 1989. Pragian/Emsian, Saudi Arabia. There are three papillae on the contact surfaces and an equatorial zona (X8); diameter size: 43 μm . (10) *Zonotriletes* sp. Emsian, Brasil. This specimen is characterized by a large equatorial zona; diameter size: 72 μm . (11) *Perotriletes laevigatus* Steemans 1989. Lochkovian, Amazon Basin, Brasil. The outer sexine (X9) is visible at the equator; diameter size: 40 μm . (12) *Grandispora* sp. A in Steemans et al. 2008a. Lochkovian, Saudi Arabia. The outer sexine is folded (X9) and ornamented by coni; diameter size: 29 μm

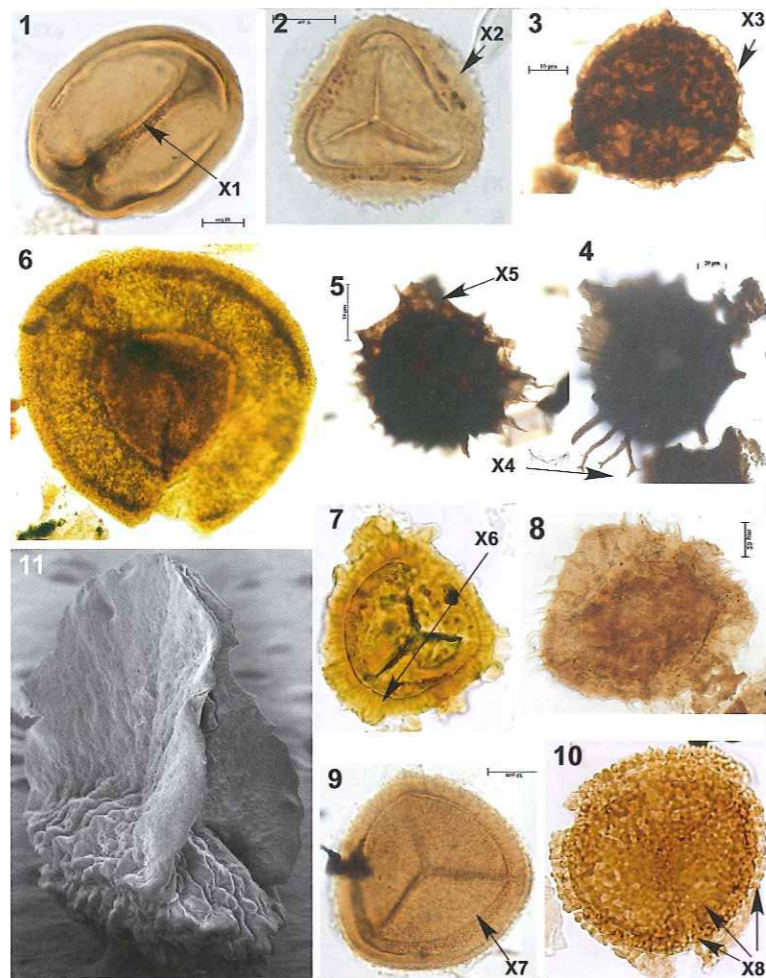


Fig. 11 For abbreviations, see Fig. 1. (1) *Latosporites ovalis* Breuer et al. 2007. Emsian, Paraná Basin, Brasil. The proximal face is characterized by a monolete mark (X1); diameter size: 56 μm . (2) *Camarozonotriletes sextantii* McGregor and Camfield 1976. Eifelian, Namur Basin, Belgium. The equatorial interradial areas (X2) are ornamented by long spines; diameter size: 33 μm . (3) *Samarisporites triangulatus* Allen 1965. Givetian, Namur Basin, Belgium. The equatorial zone is narrower in the interradial equatorial areas (X3) in the interradial area; diameter size: 52 μm . (4–5) *Ancyrospora ancyrea* Richardson 1964. Givetian, Namur Basin, Belgium. The top of the elements is clearly bifurcate (X4) in (4); diameter size: 47 μm . The gula (X5) is developed above the trilete mark; diameter size: 45 μm . (6) *Contagisporites optivus*

cryptospore tetrads, the spores at maturity are usually liberated from the sporangium as trilete or monolete isolated spores. Permanent tetrads are produced by a limited number of extant 'bryophytes'.

Even if it cannot be demonstrated, there might be a link between obligate tetrads and true trilete spores.

Owens 1971. Givetian, Saudi Arabia. Megaspore; diameter size: 220 μm . (7) *Lophozonotriletes media* Taugourdeau-Lantz 1967. Givetian, Ghadames Basin, Tunisia. The punctuatae (thin canals) are clearly visible in the thick equatorial crassitude (X6); diameter size: 80 μm . (8) *Grandispora douglstownense* McGregor 1973. Middle Devonian, Bolivia; diameter size: 92 μm . (9) *Geminospira lemurata* Balme emend. Playford 1983. Givetian, Ronquières, Belgium. The inner exine (X7) is thinner than the outer exine; diameter size: 40 μm . (10) *Acinosporites* sp. 1 in Breuer et al. 2007. Eifelian, Saudi Arabia. The specimen is camerate and is characterized by three exine layers (X8); diameter size: 84 μm . (11) *Lagenicula* sp. Givetian, Ghadames Basin, Libya. Megaspore larger than 1 mm in equatorial diameter with a very high gula; diameter size: 1861 μm

The spores from Tetrahedraletes sometimes show a tendency to become detached. Another example is *Rimosotetras problematica* (Fig. 2.4), an obligate tetrad with loosely attached spores. Sometimes, the tetrad is physically destroyed, releasing individual monads with a torn proximal face. The tears may

mimic a trilete mark: the resemblance is at times so close that it is impossible to distinguish a pseudo trilete mark from a true functional trilete mark. Those spores were first attributed to ?*Ambitisporites* (Richardson 1988). Later, the new genus *Imperfectotriletes* was established (Steemans et al. 2000) to accommodate such spores.

Tetrads are heavier and larger than monads and are statistically dispersed closer to the parent plant than isolated spores. Gray et al. (1985) suggested that the reproductive advantage of cryptospore obligate tetrads was the juxtaposition of male and female gametophytes in the propagules, conferring advantage for founder populations in stressed environments (see also Section 'From Alete Monads to Trilete Spores'). The colonization of new areas, in more favourable conditions, could presumably be improved by the production of individual spores, which disperse further because they are lighter and smaller than tetrads. This reproductive strategy allows genetic exchanges with individuals dispersed from other areas.

Imperfectotriletes patinatus (Fig. 2.6-7) is patinate (having a thick distal face), and *Imperfectotriletes varvdovae* (Fig. 2.8) is crassitate (with an equatorial crassitude). There is no clear separation between both species as all intermediate wall thickenings exist. Optically, there are obvious similarities between the cryptospore *I. patinatus* and the trilete spore *Archaeozonotriletes chulusnanus* morphon (patinate trilete spores Fig. 8.5-6) and between the cryptospore *I. varvdovae* and trilete spore *A. avitus-dilutus* morphon (equatorially crassitate trilete spores Fig. 9.1-3).

For all taxa, the laevigate trilete spore appears before its ornamented morphologic equivalent. For example, the laevigate *Archaeozonotriletes* first occurs during the Telychian and when it becomes ornamented with muri or similar structures, it is named *Chelinospira*; this event first occurs during the Ludlow. If the ornament is spines or coni, the specimens are called *Cymbosporites*. Ornamented *Ambitisporites* are either *Synorisporites* or *Aneurospora* according to the type of ornament present on the distal face.

The Dyadospora Complex

It was shown by Gray (1993) that no living plant produces dyads, except as a result of meiotic irregularities. According to Hemsley (1994), theoretically

it is possible for plants to produce dyads if they favoured meiotic dispersion strategy of their propagules. The two more abundant dyads are *D. murusatenuata* (Fig. 2.11) and *D. murusdensa* (Fig. 2.12), characterized by a thin and a thick wall respectively. Between both, all variation of thickness exists and a morphon has been created to accommodate the two species (Steemans et al. 1996).

As mentioned above for tetrads, the production of dyads as propagules might be disadvantageous for dispersion and reproduction, and the production of monads possesses important advantages. This could explain why spores in dyads show a progressive tendency to be less and less attached, to be finally completely separated in two alete monads. In Ordovician samples, some monads with a torn proximal face have clearly produced by the physical separation of dyads. It can be hypothesized that tetrads were modified in isolated *Imperfectotriletes* monads by the same process. The monads physically isolated from tightly attached dyads are called *Gneudnaspora (Laevolancis) chibrikovae* (Fig. 2.10). In younger sediments, spores from dyads are clearly separated and, when they are found as monads, they are called *Gneudnaspora (Laevolancis) divellomedia* or *plicata* (Fig. 7.1-3), according to their wall thickness (Breuer et al. 2007). Once more, there is a continuous, progressive, morphological variation of their wall thickness.

From Alete Monads to Trilete Spores

Monads are rare during the Llandovery: some were ornamented (Wellman et al. 2000). Monads become abundant during the Wenlock and later. Four genera have been created according to the type of sculpture and the wall thickness. *Artemopyra* has radial muri on the proximal face, *Hispanaediscus* is equatorially crassitate and distally ornamented by verrucae, *Chelinohilates* and *Cymbohilates* are patinate: the former ornamented by muri or similar elements and the latter by spines and cones.

There are clear morphological relationships between several hilate monads and trilete spores: some ornamented monads are very similar to trilete spore species, for example, *Artemopyra brevicosta* (Fig. 7.9) is the cryptospore equivalent to the trilete spore *Emphanisporites protophanus* (Fig. 7.10), while the cryptospore *H. verrucatus* (Fig. 7.11) corresponds to the trilete spore *S. verrucatus* (Fig. 7.12). Sometimes, a progressive transition is observable between the

hilate monad and the trilete spore, for example, the Lochkovian and Pragian *Cymbohilates baqaensis* (Fig. 8.7-8, 9?) and *Cymbosporites dammamensis* (Fig. 8.9?, 10). Some specimens of *Cymbohilates* display a torn hilum mimicking a pseudotrilete mark, thus making identification of the specimens difficult. In all cases, the cryptospore appears first, rapidly followed by the corresponding trilete spore. However, the presence of a trilete mark on spores having a cryptospore equivalent organized in a dyad is puzzling. As the necessary condition for the presence of a trilete mark is the tetrad configuration, it seems impossible that a monad isolated from a dyad could display a trilete mark. Therefore, it is inferred that plants that produced dyads dispersed as isolated alete monads (e.g. *H. verrucatus*) were also able to produce tetrads. The reason as to how the shift from dyads to tetrads occurred remains conjectural, but, tentatively, it again appears to relate to variation of ecological conditions. As the released tetrads have not been observed in the palynological record, they were presumably not obligate, and the spores were dispersed as monads. Although obligate tetrads become rare in the Early Devonian, an unusual abundance of obligate tetrads was noticed in Lochkovian samples from the Arbutnott Group in Scotland (Lavender and Wellman 2002). The authors noticed that '... perhaps land plants of Lochkovian age were rather flexible in terms of the state in which their spores were released'. We suggest that, presumably under harsh conditions, the basal obligate tetrad configuration could be superior to the derived monad configuration. Indeed, the obligate tetrad configuration of mature spores has a genetic basis. Two genes are required for the spore separation during the normal development (Rhee and Sommerville 1998). The occurrence of abnormal permanent tetrad configuration in living plants is the most common mutation due to modification by atmospheric air composition (e.g. presence of volcanic ash and gases) or increasing radiation (UV) caused by less effective protection by the ozone layer. Several observations support this suggestion. Specimens similar to *Cymbohilates cymosus* are known under three different configurations (Richardson 1996b): tetrad, alete monad and a trilete monad (then called *Cymbosporites stellospinosus*). *Chelinohilates erraticus* (Fig. 8.1-3) is known as alete monad, dyad, tetrad and a trilete monad (then called *Chelinospora cassicula*, Fig. 8.4). *Cymbohilates disporus* (Fig. 8.11-12) is known as

an alete monad and dyad; it is also very similar to the tetrad *Acontotetras inconspicuis* and to the trilete spore *Cymbosporites proteus* (Fig. 10.1).

Synthetic Diagram

The scenario leading from cryptospores to trilete spores is summarized in Figs. 4, 5, and 6. We emphasize that this figure has no strict phylogenetic implications. The palynological work is based on morphotaxa and not on Linnean species. The diagram shows the evolution of the spore morphologies through time; it does not imply any ancestor/descendant relationship. The figure is comprised of four superposed and related transparent layers. The first layer contains the permanent tetrads and dyads and is the result of their physical separation. The second layer includes the loose dyads transformed into monads and their various morphologies. The third layer symbolizes the theoretical phase when all sporangia, probably because of ecological factors, produce mainly non-permanent tetrads (and no more non-permanent dyads) however; as the tetrads are not permanent, they cannot be observed, and accordingly, layer 3 contains no taxa. The fourth layer contains only trilete spores.

The diagram shows that several morphotaxa of trilete spores (*Cymbosporites*, *Chelinospora* and *Synorisporites*) may be derived in two ways, either directly from tetrad-producing plants or indirectly from dyad-producing plants. Ecological factors most probably determine the type of propagules produced by the sporangia. In a given genus, the species may be different according to the strategy followed by the mother plant. In contrast, retusoid and emphanoid spores seem to be produced only by a plant lineage that originally produced only permanent dyads. Similarly, *Archaeozonotriletes*, *Ambitisporites* and *Aneurospora* seem to be produced only by a plant lineage that originally released only permanent tetrads.

It is sometimes very difficult, especially with coalified palynomorphs, to estimate the nature and the thickness of the spore wall. Retusoid forms may be confused with equatorially crassitate forms, which in turn may be confused with patinate forms. Therefore, the Synthetic diagram (Figs. 4, 5, and 6) tries to reflect all possibilities.

From Permanent to Non-permanent Dyads and Tetrads

Layers 2 and 3 in Figs. 5 and 6 raise the question of how permanent dyads or tetrads might be transformed

into non-permanent ones. The oldest dyads and tetrads seem to be tightly attached over the whole contact area between the spores, making it difficult to isolate one of them without tearing the contact area(s) of the isolated spore or of but the other spores in the tetrads or the dyads. On some isolated *Imperfectotriletes*, the remains the tetrad or of dyad wall have been observed. The development of haptotypic elements on the proximal surface has possibly been made easier by the division of the spores from tetrads and dyads by decreasing the area of the surfaces in contact (Fig. 12). Indeed, labra and curvaturae are raised in relief above the proximal face: this presumably decreases the surface of contact and therefore decreases also the strength of attraction between spores in the dyads and tetrads.

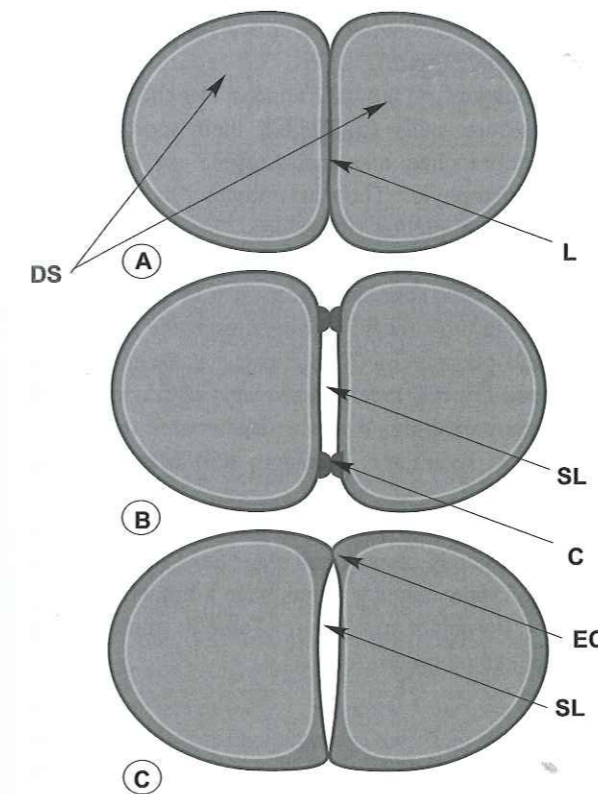


Fig. 12 (See Fig. 1 for abbreviations) **a** A dyad with a line of attachment; **b** The surface of attachment between the spores could be reduced by the presence of, for example, curvaturae slightly raised in relief on the surface of attachment; **c** The presence of a proximo-equatorial crassitude (EC) could also result in a separation between the spores

What Happens with the Cryptospores Enclosed in a Membrane?

There appears to be no place in Synopsis diagram (Figs. 4, 5, and 6) for cryptospores enclosed in an envelope. According to the hypothesis expressed above, all the morphologies displayed by the most basal trilete spores could be obtained from the sole naked *Dyadospora* and *Tetraedraletes*. Nevertheless, some taxa enclosed in an envelope seem to have followed the same evolutionary strategy, the dyads and tetrads progressively separating as monads. Indeed, *Abditusdyadus laevigata* (Fig. 7.6) and *Stegambiquadrella contenta* (Fig. 7.8) are respectively dyads and tetrads formed by spores slightly separated and enclosed in an envelope. The presence of the envelope may be interpreted as having prevented the development of a trilete mark. The abundance of cryptospores enclosed in envelopes declined drastically near the Aeronian/Telychian boundary, when trilete spores were rapidly diversifying (Steemans 2000). On the contrary, the naked *Tetraedraletes* and *Dyadospora* remained common at least up to the Lochkovian, suggesting that the presence of an envelope was disadvantageous, maybe in preventing a rapid germination of the spore. Plants producing cryptospores enclosed in an envelope were thus not able to compete with plant producing alete and trilete spores, and finally became extinct. Some could have found temporary refuge around lakes or swamps as in the Lochkovian Lorne area, Scotland, where primitive cryptospores have been observed (Wellman and Richardson 1996).

Considerations of In Situ Cryptospores and Trilete Spores

The cryptospore *H. verrucatus* (Fig. 7.11) is very similar to the trilete spore *S. verrucatus* (Fig. 7.12). As *S. verrucatus* has been observed in situ from *C. per-toni* sporangia (Fanning et al. 1988), it is clear that this trilete spore is produced by tracheophytes. What is then the real biological relationship between *H. verrucatus* and *S. verrucatus*? Are they the result of simple morphological convergence between cryptospores and trilete spores? Are some Ordovician and Silurian alete

spores produced by tracheophytes or their immediate ancestors rather than by 'bryophytes'? Wellman (1996) suggested that cryptospores could derive from two sources: bryophytes and 'rhyniophytoid' plants. It has been demonstrated that the alete spore *Gneudnaspora divellomedia* var minor (Fig. 7.1-3) is produced by Lochkovian 'rhyniophytoids' *Laevolancis divellomedia* (Wellman et al. 1998a). As *G. divellomedia* var minor has recently been observed in the Ordovician (Steeemans et al. 2008a; Wellman et al. 2008), does this mean that 'rhyniophytoids' evolved during the Ordovician, while plant meso- or mega-fossil remains are unknown below the Homerian? In fact, *G. divellomedia* var minor is a very simple laevigate monad suggesting that different taxa could possibly have been given the same name even though they derive from plants that are not necessarily closely related. Wellman et al. (1998b) have shown that detailed morphological, anatomical and ultrastructural analysis reveals subtle differences between the Lochkovian specimens of *G. divellomedia* allow them to be grouped into five distinct types. This could reflect their intraspecific variability. *G. divellomedia* var. minor are monads that are the separated products of dyads (*D. murusdensa-murusattenuata* morphon) and are occasionally seen as loosely attached dyads. The dyads *D. murusdensa* (Fig. 2.12) have also been observed in sporangia from 'rhyniophytoids' (Wellman et al. 1998a). One of the plant specimens has a bifurcating sporophytic axis, evidence against an affinity with extant 'bryophytes'.

This conflicting information supports Wellman's (1996) earlier suggestion that cryptospores are most probably produced by a polyphyletic group of embryophytes, and that they are not only restricted to 'bryophytes'. It seems that, at least during the Late Ordovician, the vegetation had reached a level of evolution allowing for wider diversification than previously believed. The kind of propagules produced by the basal embryophytes are controlled by ecological factors and probably do not reflect their biological affinities alone.

Concluding their study of Early Devonian spore assemblages from the Scottish Midlands, Lavender and Wellman (2002) said 'perhaps land plants of Lochkovian age were rather flexible in terms of the state in which their spores were released...'. This seems equally applicable to Ordovician and Silurian land plants; perhaps views of the development of earlier vegetation need further consideration.

Early Evolution of Land Plants

Land plants (embryophytes; Fig. 13) are distinguished from their green algal ancestors by several characters, most of them being related to terrestrial habitats. These characters are a multicellular sporophyte (diploid generation), pluricellular sexual organs, a pluricellular sporangium, the cuticle and the sporopollenin (Kenrick and Crane 1997a and references therein). The name of the clade derives from 'embryo' (Table 3, trait 1), the name given to the young sporophyte growing within the archegonium (female sexual organ). Land plants are also characterized by diplobiontic life cycles, i.e. an alternation of multicellular gametophytic and sporophytic generations. Extant land plants include the paraphyletic 'bryophytes' and monophyletic polysporangiophytes (plants having sporophytes producing more than one sporangium).

'Bryophytes' do not have annular or helically thickened vascular cells (tracheids); their sporophyte is small, unbranched and matrotrophic on the dominant gametophyte. The 'bryophytes' include three clades: Hepatophytes (liverworts), bryophytes sensu stricto (mosses) and Anthocerotophytes (hornworts). Liverworts lack stomata (Table 3, trait 2); these are identified in most recent phylogenies as the first divergent land plants (Qiu 2008). This has been recently confirmed by the recent discovery of fragments of sporangia containing liverwort-like spores from Late Ordovician sediments (Caradoc, 450 Ma; Wellman et al. 2003).

Polysporangiophytes are comprised of the tracheophytes (vascular plants) and their non-vascular precursors. Extant vascular plants have a branched, independent, dominant sporophyte (Table 3, trait 3) and a reduced gametophyte.

'Rhyniophytoids'

The oldest fertile axial land plant fossils are reported from the Middle Silurian (Edwards and Feehan 1980). They are extremely small consisting of isotomously branched axes terminating in cup-shaped *Cooksonia*-type sporangia. Abundant plant remains are known from younger horizons (Late Silurian–Early Devonian). All those earliest land plants are informally called 'rhyniophytoids' (plants that resemble

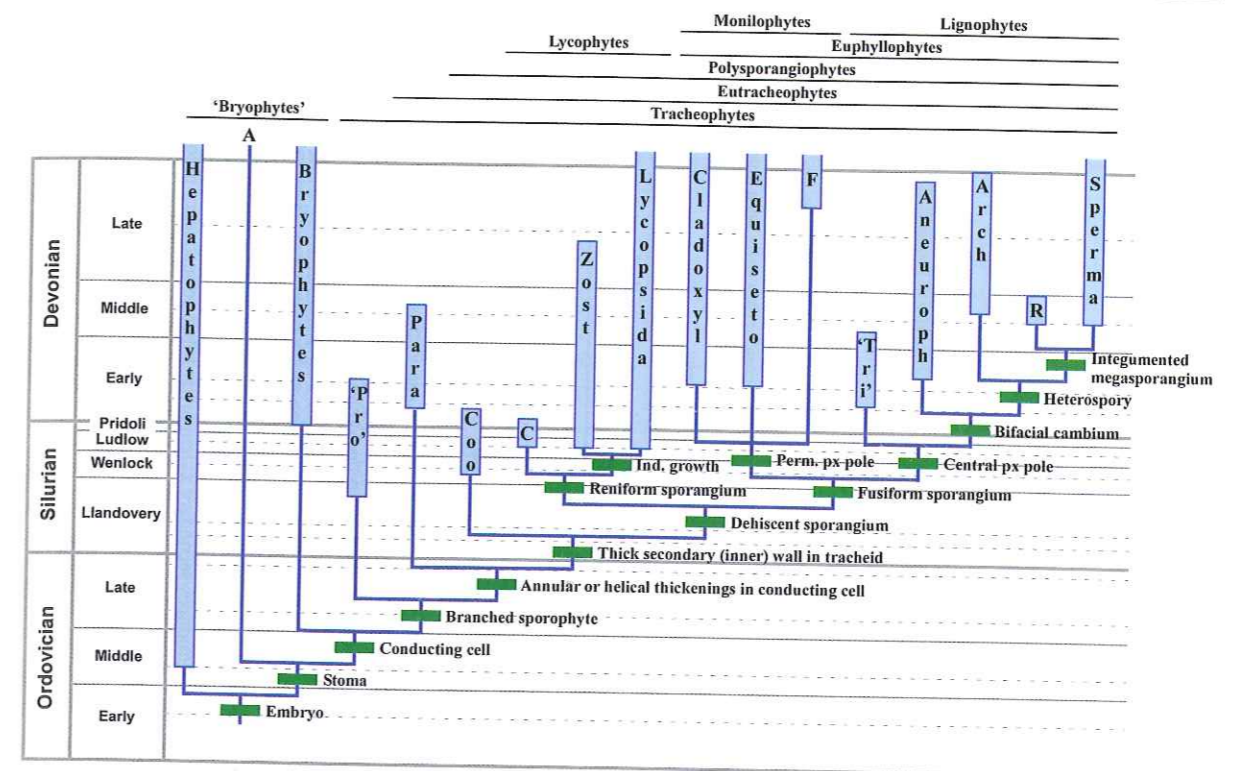


Fig. 13 (Based principally on Kenrick and Crane 1997a). Suggested phylogenetic relationships and stratigraphic distribution of early embryophytes. Taxa in quotes are para- or polyphyletic. A Anthocerotophytes; *Aneuroph* Aneurophytales; *Arch* Archaeopteridales; *R* *Rumcaria*; *C* *Cooksonia caledonica* (new genus name required); *Cladoxyl* Cladoxylopsida; *Coo* *Cooksonia pertoni* and close species; *Equiseto* Equisetophytes; *F* ferns; *Para* Paratracheophytes; 'Pro' 'Protracheophytes'; *Sperma* Spermatophytes (seed plants); 'Tri' Trimerophytina; *Zost* Zosterophyllophytes. *Ind.* indeterminate; *Perm.* permanent; *px* protaxylem

the simplest vascular plants but lack evidence of vascular tissue). As an example, the Early Devonian (early Lochkovian; 415 Ma) Brown Clee Hill locality (Shropshire, England; see Glasspool et al. 2006 and references therein) has yielded a large number of 'rhyniophytoids' exquisitely preserved as charcoal. 'Rhyniophytoids' are difficult to describe accurately, as they are often very fragmentary and because the number of useful characters is low. The two following genera are 'rhyniophytoids'. *Tortilicaulis* Edwards is a plant characterized by branched axes terminating in spiralling, branched or unbranched, elongated sporangia. *Salopella* Edwards and Richardson has dichotomous axes bearing terminal fusiform, branched or unbranched sporangia opening into two equal valves. *Sporangia* of *Salopella* may be borne by pairs. 'Rhyniophytoids' most probably comprise the precursors of many younger lineages.

As most 'rhyniophytoids' consist of an unbranched axis with a terminal sporangium, it is impossible to tell

if they are 'bryophytes' or polysporangiophytes. The liverwort affinities of the in situ cryptospores similar to *Tetrahedraletes* described by Wellman et al. (2003) have been inferred from their ultrastructure, but, generally, the presence of in situ cryptospores has long been considered as indicating affinities with 'bryophytes'. Cryptospores have also been described from sporangia of 'rhyniophytoids' with bifurcating axes (Edwards et al. 1999; Wellman et al. 1998b). Sporophytes of 'bryophytes' are typically unbranched, indicating that some non-'bryophyte' plants were also cryptospore producers.

Aglaophyton

Aglaophyton major (Kidston and Lang) described by DS Edwards (1986 and Fig. 14a) is a polysporangiophyte devoid of annular or helically thickened conducting cells; hence it is not yet a tracheophyte. It has been

Table 3 First occurrence of key traits of the embryophytes described in this chapter

Trait no.	Trait	Earliest occurrence	Comments
1	Embryo	Ordovician (Wellman et al. 2003), possibly Cambrian (Taylor and Strother 2008)	Synapomorphy of embryophytes.
2	Stoma	Late Silurian (Pridoli) In <i>Hollandophyton</i> (Rogerson et al. 2002)	First ontogenetic stages of the sporophyte, occurring within the gametophytic tissues. Synapomorphy of stomatophytes. Epidermal pore associated with a pair of guard cells
3	Branched sporophyte	Middle Silurian (Wenlock)	Synapomorphy of polysporangiophytes. Branching of the sporophyte axis implies the presence of more than one sporangium per sporophyte
4	S-type conducting cell	In <i>Cooksonia</i> (Edwards and Feehan 1980) Early Devonian (Pragian) In <i>Sennicaulis</i> (Kenrick and Crane 1997a)	Typical of paratracheophytes. Annular and helically thickened conducting cells with a very thin decay-resistant inner wall and a thick 'spongy' outer wall Synapomorphy of eutracheophytes.
5	Thick lignified inner layer in conducting cell	Early Devonian (Lochkovian) In <i>Zosterophylls</i> (Edwards 2003)	Various types exist (all have in common a thick inner wall, not demonstrated in <i>Cooksonia</i>) Synapomorphy of lycophytes.
6	Exarch primary xylem maturation in stem	Early Devonian (Lochkovian) In <i>Zosterophylls</i> (Edwards 2003)	Occurs also in lignophyte roots, and in <i>Sphenophyllum</i> (Carboniferous-Permian) Synapomorphy of lycophytes.
7	Two-valved ovoid-reniform sporangium	Late Silurian (late Ludlow) In cf. <i>Bathurstia</i> (Koyuk et al. 2002) Late Silurian (Ludlow)	Also characterized by a specialized dehiscence mechanism Synapomorphy of <i>Lycopsidea</i> .
8	Microphyll	In <i>Baragwanathia</i> (Rickards 2000) Late Silurian (Pridoli)	Leaf resulting from the vascularization of an epidermal outgrowth Occurs in lycophytes and euphyllophytes
9	Anisotomous branching	In <i>Junggaria</i> (Cai et al. 1993) Middle Devonian (Givetian)	Allows indeterminate growth Occurs in lycophytes and monilophytes.
10	Unifacial vascular cambium	In <i>Metacaladophyton</i> (Wang and Geng 1997) Late Early Devonian (Late Emsian) In <i>Chaleuria</i> (Andrews et al. 1975)	Produces secondary xylem inwards but no secondary phloem Occurs in almost all lineages of eutracheophytes. Production of micro and megaspores

Table 3 (continued)

Trait no.	Trait	Earliest occurrence	Comments
12	Dichotomous lateral appendage with determined growth	Early Devonian (Pragian) In <i>Psilophyton</i> (Edwards 2003)	Probable synapomorphy of basal euphyllophytes. Precursor of megaphyll
13	Megaphyll	Late Devonian (Frasnian) In <i>Archaeopteris</i> (Gensel and Andrews 1984)	Probable synapomorphy of euphyllophytes. Leaf resulting from planation and webbing of lateral dichotomous branches Characteristic of basal euphyllophytes.
14	Elongate sporangia borne in pairs	Early Devonian (Pragian) In <i>Psilophyton</i> (Edwards 2003)	Sporangium with dehiscence slit occurring along one side only. Sporangium C-shaped in transverse section. Sporangia often borne in pairs
15	Differentiation of exine in sexine and nexine	Late Early Devonian (Late Emsian) In <i>Oocampsa</i> (Wellman and Gensel 2004)	Probable synapomorphy of lignophytes Synapomorphy of monilophytes
16	Mesarch protoxylem confined to the lobes of the xylem strand	Middle Devonian (Givetian) In <i>Ibyka</i> (Gensel and Andrews 1984)	Synapomorphy of lignophytes.
17	Bifacial vascular cambium	Probable in <i>Crossia</i> (Beck and Stein 1993) Early Devonian (Emsian)	Produces secondary xylem inwards but secondary phloem outwards Synapomorphy of basal lignophytes
18	Central protoxylem (other strands along the midplanes of xylem ribs)		
19	Monomegaspory	In the unnamed plant of Gensel (1984) Middle Devonian (Givetian) In <i>Runcaria?</i> (Gerrienne et al. 2004)	Occurs in lycophytes; in equisetophytes and in spermatophytes. Meiosis results in four cells, but only one is functional Occurs in spermatophytes.
20	Indehiscent mega-sporangium	Middle Devonian (Givetian) In <i>Runcaria</i> (Gerrienne et al. 2004)	The megasporangium of heterosporous lycophytes is dehiscent Occurs in lycophytes and in spermatophytes.
21	Integumented meg-asporangium	Middle Devonian (Givetian) In <i>Runcaria</i> (Gerrienne et al. 2004)	The 'integument' of the lycophyte megasporangium is a lateral expansion of the megasporophyll. The origin of the spermatophyte integument is controversial

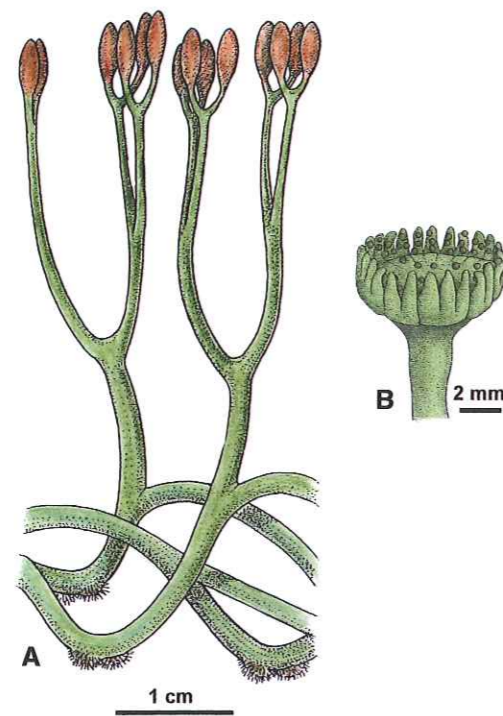


Fig. 14 a (modified from DS Edwards 1986). Reconstruction of *Aglaophyton* (sporophyte); b (modified from Remy et al. 1993). Reconstruction of *Lyonophyton* (gametophyte)

informally placed in a group called 'protetracheophytes' (Kenrick and Crane 1997a, b; Kenrick and Crane 1991). *Aglaophyton* is a monospecific genus described on the basis of exceptionally well-preserved permineralized specimens from the Rhynie Chert (Edwards et al. 1994; Kenrick and Crane 1997a; Taylor et al. 2005). The age of the Rhynie outlier is latest Pragian or earliest Emsian (Wellman 2006). The complex history of this species, previously referred to the genus *Rhynia* is summarized by Kenrick and Crane (1997a).

Simple early land plants such as *Aglaophyton*, mostly characterized by terminal sporangia were previously grouped in the *Rhyniophyt(in)a* (Banks 1975) and presented as the simplest vascular plants. We now know that *Rhyniophyt(in)a* in its various definitions is an unnatural assemblage (Kenrick and Crane 1997a) that includes precursors of vascular plants (protetracheophytes) and vascular plants. We believe that the terms *Rhyniophyta*, *Rhyniophytina* or *Rhyniophytes* are ambiguous and should be abandoned.

The sporophyte of *A. major* is comprised of naked isotomously branched axes. A prostrate rhizome with non-septate rhizoids has been described (Edwards

1986). A terminal sporangium is present on all distal axis segments. The sporangium is fusiform and radially symmetrical. No obvious dehiscence line is visible. Exceptionally well-preserved spores have been found in the sporangium of *Aglaophyton*. They are trilete, laevigate and show a distinctive thinning associated with the trilete mark; they can be accommodated in the dispersed spore genus *Retusotriletes* (Wellman et al. 2006). Interestingly, the genus *Retusotriletes* is morphologically close to the monad *Laevolancis* and the dyad *Dyadospora*, both found in situ in 'rhyniophytoid' sporangia, including a specimen with a branched axis (Wellman et al. 1998a) suggestive of polysporangiophyte affinities.

A. major plays an important role in our understanding of the evolution of land plants for two reasons:

- (1) It has features unique to vascular plants (branched, independent sporophyte) and characters that recall 'bryophytes' (terminal sporangium, absence of annular or helically thickened conducting cells).
- (2) The sporophyte and the gametophyte of the plant are known. The gametophyte has been called *Lyonophyton rhyniensis* Remy and Remy 1980 (Fig. 14b). Male and female gametophytes are distinct (Taylor et al. 2005). Male gametophytes (antheridiophores) are upright, unbranched and approximately 20 mm high. Female gametophytes (archegoniophores) are of the same size but they are dichotomously branched. The corresponding *Aglaophyton/Lyonophyton* is based on similarities in epidermal cells, stomatal structure, internal anatomy and wall structure of conducting cells.

Paratracheophytes

Paratracheophytes have been recently defined by Gerrienne et al. (2006). The division includes the plants that were previously called Rhyniaceae (Kenrick and Crane 1991) or Rhyniopsida (Kenrick and Crane 1997a). Paratracheophytes are a small distinctive group of vascular plants; they are a sister group of the eutracheophytes. Paratracheophytes include sporophytes (*Rhynia* [Fig. 15], *Stockmansella*, *Huvenia*), gametophytes (*Remyophyton* – gametophyte of *Rhynia*, *Sciadophyton*) and morphotypes (*Sennicaulis hippocrepiformis*, *Taeniocrada dubia*) (Gerrienne et al. 2006). Based on current evidence, paratracheophytes evolved during the Early Devonian

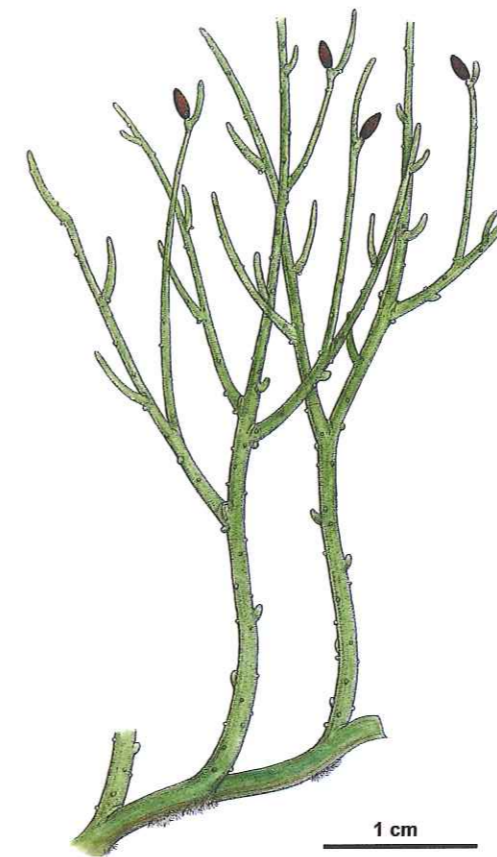


Fig. 15 (Modified from Edwards 1980) Reconstruction of *Rhynia*

and became extinct during the Late Devonian. Their synapomorphies include the following characters: (1) distinctive adventitious branching (*Rhynia*-type) (Kenrick and Crane 1997a); (2) abscission or isolation layer at base of sporangium (Kenrick and Crane 1997a); (3) sporangium attached to a 'pad' of tissue (Kenrick and Crane 1997a); (4) alternation of more or less isomorphic, independent sporophytic and gametophytic generations (Gerrienne et al. 2006). S-type conducting cell (Kenrick and Crane 1991) are obviously also an important character of the clade. S-type conducting cells (Table 3, trait 4) are annular or helically thickened cells characterized by a two-layered cell wall comprising a very thin decay-resistant inner layer and a thick, spongy outer layer. They differ from the tracheids in eutracheophytes characterized by a thick decay-resistant (lignified) inner layer (Table 3, trait 5). Whether the conducting cells in paratracheophytes and eutracheophytes are homologous or analogous characters is not known.

The gametophyte of *Rhynia* was recently described from the Rhynie Chert (Kerp et al. 2004) as 'remarkably small in comparison to those of other Rhynie chert plants'. The gametophyte consists of a dense stand of erect or prostrate antheridia- or archegonia-bearing axes.

On the basis of axial gametophyte/sporophyte combinations in *Aglaophyton* and in paratracheophytes, it is currently accepted that the alternation of isomorphic generations is the plesiomorphic condition among all early land plants, including basal eutracheophytes (Kenrick 2000). The reduction of the gametophyte would have occurred later, in more derived eutracheophytes (Kenrick 2000; Kenrick and Crane 1997a).

Cooksonia

The genus *Cooksonia* Lang (1937) (Fig. 16) includes leafless plants, a few centimetres high, with isotomously branched axes, and terminal sporangia. In the type species, *C. pertoni*, a gradual transition between the subtending axis/sporangium is visible;

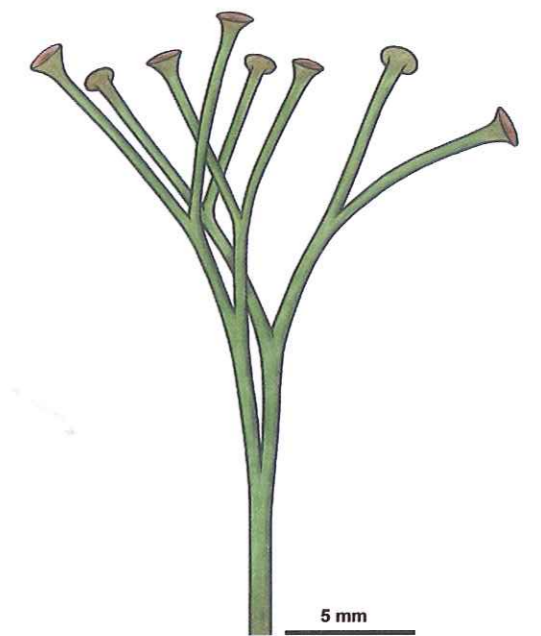


Fig. 16 (Modified from Gerrienne et al. 2001) Reconstruction of *Cooksonia paranensis*. The sporophyte is presented attached to a thalloid gametophyte

the sporangium is terminal and trumpet-shaped. Some in situ conducting cells (C-type tracheids) have been described from three specimens (Edwards et al. 1992; Edwards 2003). The stratigraphic range of the genus is Middle Silurian–Early Devonian. *Cooksonia* is currently considered as the earliest known simplest eutracheophyte.

According to the type of in situ spores, four subspecies of *C. pertoni* have been created (Habgood et al. 2002):

C. pertoni ssp. *pertoni* (in situ spores: *Ambitisporites* sp.),

C. pertoni ssp. *synorispora* (in situ spores: *S. verrucatus*),

C. pertoni ssp. *apiculispora* (in situ spores: *S. newportensis* and *Aneurospora* sp.) (Fanning et al. 1988) and

C. pertoni ssp. *reticulispora* (in situ spores: *Synorisporites* sp.).

The gametophyte of *Cooksonia* is unknown, but Gerrienne et al. (2006) have recently illustrated an exceptionally large specimen of *Cooksonia paranensis* consisting of five dichotomous axes attached at their base to a small thalloid(?) structure. A possible interpretation of this fossil would be a cluster of five individual sporophytes still attached to the remains of a small female or bisexual, prothallium-like, gametophyte. The presence of such a thalloid gametophyte is illustrated in Fig. 16.

Lycophytes

The name lycophytes is here used in a broad sense, as defined by Gensel and Berry (2001). It includes *Zosterophyllopsida*, prelycophytes such as *Baragwanathia* and *Drepanophycus*, and *Lycopsida* (*Lycopodiales*, *Selaginellales* and *Isoetales*). The lycophytes have a long geologic history extending back to the Late Silurian (Kotyk et al. 2002). Some lycophytes were arborescent and extremely abundant during most of the Carboniferous, when they were the dominant group in the extensive equatorial swamps covering Euramerica and North China. Today lycophytes are cosmopolitan, divided into seven herbaceous genera and basal within vascular plants. Their synapomorphies are the ex-arch primary xylem maturation in the stem (Table 3, trait 6), an ovoid-reniform sporangium opening into two valves (Table 3, trait 7) and, for the

most advanced members of the group, the microphyll (Table 3, trait 8). Microphylls are leaves with a single vein that do not alter the shape of the stele when it is produced. Sporangia of typical lycophytes are borne singly on adaxial surface of fertile microphylls.

A Possible Precursor: *C. caledonica* Edwards

C. caledonica (Fig. 17) is a small plant with dichotomous axes terminated in a reniform sporangium opening into two valves. It is known from the Lochkovian of Britain (Edwards 1970) and Brasil (Gerrienne et al. 2001).

A range of plants with terminal sporangia have been named *Cooksonia*. Some of them such as *C. paranensis* Gerrienne et al. and *C. banksii* Habgood et al. show the same sporangial construction as the type species *C. pertoni*, i.e. a trumpet-like sporangium resulting from the subtending axis widening. On the contrary, the sporangium of *C. caledonica* Edwards is strikingly different, being reniform and showing a distal dehiscence line that opens the sporangium into two equal valves; *C. caledonica*, therefore, should be attributed to another genus. On the basis of the presence of this reniform sporangium, it is here tentatively presented as a precursor of the lycophytes.

Zosterophyllopsida

Zosterophylls (*Zosterophyllopsida*) are a well-known group of early vascular plants, with a subcosmopolitan distribution. They range in age from the late Ludlow (Ludfordian; Kotyk et al. 2002) to the Late Devonian (Frasnian; Hueber and Grierson 1961). Zosterophylls were an important component of the Early Devonian vegetation. More than 15 *Zosterophyll* genera are

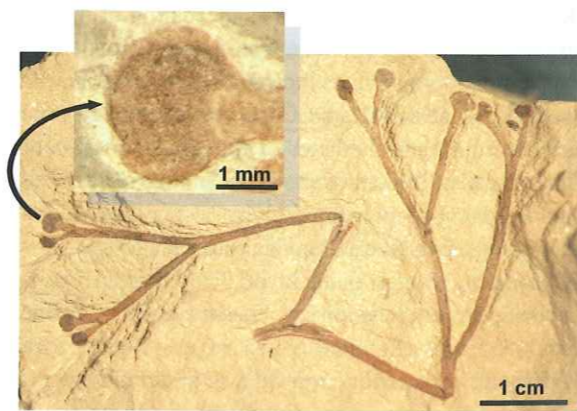


Fig. 17 *Cooksonia caledonica* (Early Devonian of Brasil)



Fig. 18 (Modified from Kenrick and Crane 1997a) Reconstruction of *Zosterophyllum*

known. The most typical representative genus is *Zosterophyllum* Penhallow (Fig. 18). *Zosterophylls* were medium-sized herbaceous plants 10–30 cm high (generally 20 cm). They are characterized by predominantly isotomous axis branching, although some genera exhibit anisotomous branching (Table 3, trait 9). Other characteristics are exarch maturation of xylem, and reniform lateral sporangia. Axes are smooth or covered with enations of various shapes; distal segments often exhibit circinate vernation. Sporangia are distributed along the distal parts of the stem or more or less densely aggregated in terminal spikes. All zosterophylls are homosporous. Simple in situ spores have been recovered several times and are generally attributed to the *Retusotriletes/Calamospora* genera of spores dispersae. Nothing is known about the gametophytes of these plants.

Lycopsida

The oldest members of this class appeared from latest Silurian to early Devonian (Gensel and Berry 2001; Kotyk et al. 2002). They are not 'true' lycopsids as they lack some typical lycopsid characters. *Asteroxylon* Kidston and Lang (1920) (Fig. 19), from the Rhynie Chert, has an exarch xylem, but its microphyll-like enations are not vascularized, as the vascular trace extends only to their base. *Drepanophycus* and *Baragwanathia* have an exarch xylem and microphylls, but their sporangia are borne directly on the stem and

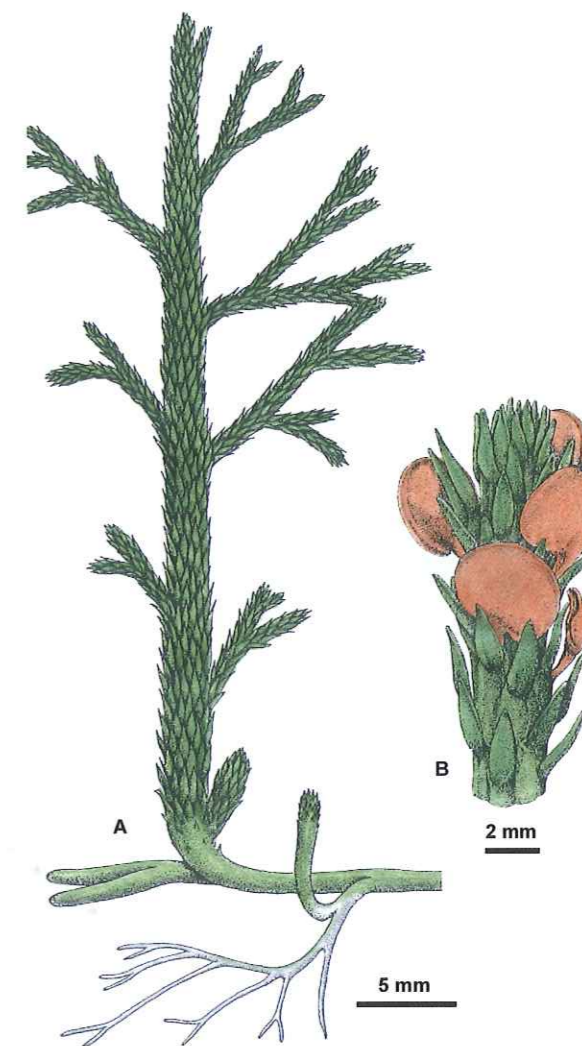


Fig. 19 (Modified from Kidston and Lang 1920) Reconstruction of *Asteroxylon*. (a) Gross view; (b) detail of a fertile axis

are not associated with a leaf. Those basal lycopsids are sometimes included in the Drepanophycales (Taylor et al. 2009). All are homosporous; their gametophytes are unknown.

Baragwanathia is known from several localities from Australia and Canada (Hueber 1983). Its stratigraphic distribution has long been controversial (Rickards 2000). It extends from the Gorstian (early Ludlow, Silurian) to the Pragian (Early Devonian). The Silurian age has been indirectly confirmed by the recent discovery of a rich and diversified Late Silurian flora at Bathurst Island (Arctic Canada; Kotyk et al. 2002). According to Raymond et al. (2006), during Late Silurian times, Australia and Canada were located in two equatorial phytogeographic units. These authors suggested that the presence of advanced early floras there could be explained by the climatic conditions.

The earliest lycopsids sensu stricto appeared at the end of the Early Devonian and were distributed world-wide during the Middle Devonian, when they were probably the major component of the herbaceous vegetation. Most of them are classified in the Protolpidodendrales; they can be distinguished from their microphyll morphology. As far as is known, the Protolpidodendrales were all homosporous; their gametophytes are unknown. *Leclercqia* Banks et al. 1972 (Fig. 20) is the best known genus. It occurs from the Early Devonian (Emsian) into the late Middle Devonian (Givetian; Meyer-Berthaud et al. 2003). The

microphylls of *Leclercqia* are easily identifiable as they have five forks: the long, central segment bears two lateral dichotomizing projections. The central segment is vascularized and abaxially recurved. The in situ spores are referable to the *Acinosporites lindlarensis* morphon sensu (Richardson et al. 1993).

During late Devonian times, several arborescent lycopsid genera evolved. Arborescent lycopsids were by far the most conspicuous elements in the Carboniferous swampy landscapes. They are responsible for the production of the extensive amount of biomass that was trapped in coal. Most of those genera belong to the Isoetales, an order that is still represented today. Among other features, those plants are characterized by (1) the presence of a unifacial vascular cambium (Table 3, trait 10), responsible for the production of some secondary xylem, (2) a pseudobipolar growth involving rhizomorphic root system (Kenrick and Crane 1997a). The arborescent lycopsids illustrate one of the many ways to make a tree: the production of large amount of periderm (external tissues of the stem, including cork cambium and its internal and external derivatives). During the Carboniferous, in parallel to the development of the tree habit, the number of heterosporous lycopsid taxa increased. All arborescent lycopsids are characteristically heterosporous (Table 3, trait 11); the number of functional megaspores is reduced to a single one in several genera. The development of their gametophytes was also endosporic (Kenrick and Crane 1997a; Taylor et al. 2009).

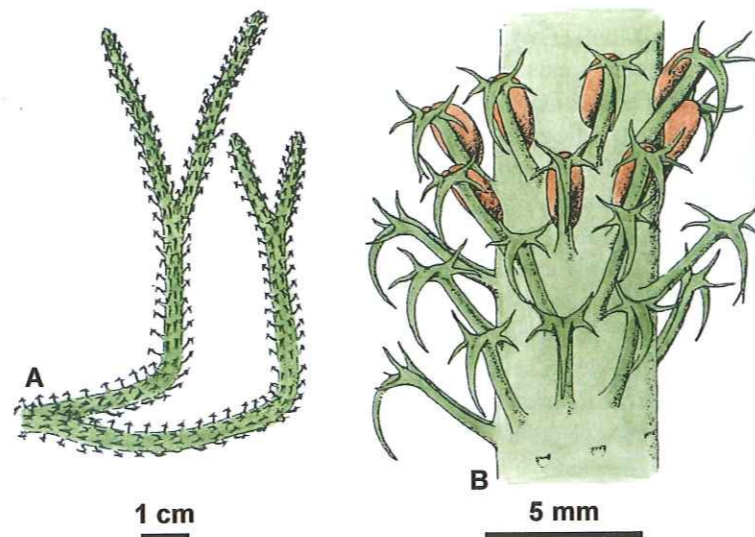


Fig. 20 (Modified from Gensel 1992) Reconstruction of *Leclercqia*. (a) Gross view; (b) detail of a fertile axis

Euphyllophytes

Within the tracheophytes, euphyllophytes are the sister group to the lycophytes. It is an extremely important group of vascular plants, representing more than 270,000 living species. Euphyllophytes are characterized by a large number of apomorphies (Kenrick and Crane 1997a), including the presence of megaphylls (leaf with multiple or branched veins; Table 3, trait 13), and pairs of elongate sporangia, each sporangium having a dehiscence slit along one side only (Table 3, trait 14). Euphyllophytes include two clades, the monilophytes (ferns sensu lato) and the lignophytes (seed plants and precursors). Both groups are discussed below. The earliest euphyllophytes evolved during Early Devonian times and belong to the 'Trimerophytina'. Those plants did not possess megaphylls, but vegetative or fertile iso- and anisotomous lateral appendages spirally inserted on their stems. Those appendages had a determinate growth (Table 3, trait 12) and are here considered as homologous to megaphylls.

'Trimerophytina' and Derivatives

Plants included in the 'Trimerophytina' are known worldwide from a large number of Early Devonian localities. Although the subdivision has been demonstrated to be paraphyletic (Kenrick and Crane 1997a), all the 'Trimerophytina' share many features. Most are medium-sized plants, ranging from several tens of centimeters to more than 1 m high. Their axes branch isotomously and anisotomously and bear lateral isotomous and anisotomous lateral appendages with determined growth. Fertile lateral branching systems terminate in clusters of fusiform sporangia borne in pairs. *Psilophyton* (Fig. 21) is the best known genus. Its stem comprises a large centrach protosteles with P-type tracheids (tracheids with scalariform pitting, the pit aperture being covered with a perforate sheet; Kenrick and Crane 1997a). The main axis of *Pertica* also bears dichotomously branched laterals: some are vegetative; others are fertile and terminate in ellipsoidal sporangia borne in pairs. The anatomy of the genus is unknown. *Psilophyton* and *Pertica* were homosporous and produced spores of the *Apiculiretusispora* type.

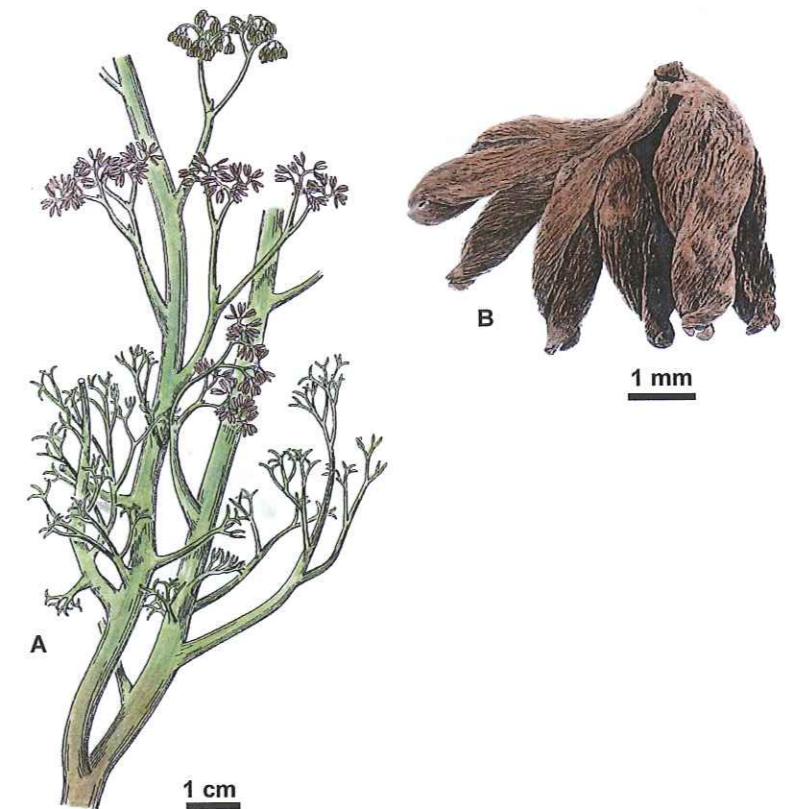


Fig. 21 (Modified from Banks 1975) Reconstruction of *Psilophyton*. (a) Gross view; (b) detail of a fertile axis

The late Emsian (late Early Devonian) plant *Oocampsa* Andrews et al. 1975 is morphologically close to *Pertica* and generally considered as an advanced 'trimerophyte'. The plant is of great interest because its spores, attributed to the genus *Grandispora*, are bilayered (differentiation between an external sexine and in internal body covered by exine) (Table 3, trait 15), a condition comparable to what is found in younger plants of the lignophyte lineage (Andrews et al. 1975; Wellman and Gensel 2004).

Chaleuria Andrews et al. is another plant that might be a 'trimerophyte' derivative. It was described from the late Early Devonian strata. Its main axis bears at least two orders of branches, the second order bearing dichotomous sterile or fertile ultimate appendages. *Chaleuria* produced spores of variable size that fall into two intergrading size classes, considered by Andrews et al. (1974) to represent 'incipient heterospority'. The large spores of *Chaleuria* have been compared to *Apiculiretusispora* or *Cyclogranisporites*, the small ones to *Streelispora* (Andrews et al. 1974).

An unnamed, well-preserved plant axis was described by Gensel in 1984 from a late Early Devonian outcrop in Gaspé, Quebec, Canada. Although poorly known, the plant is noted for its well-preserved anatomy indicating 'a level of stem-leaf differentiation more advanced than any known for trimerophytes or other taxa of this age' (Gensel 1984, *Nature* 309, 785). It has a triradiate stele with four protoxylem strands, including a central one. Traces supplying the lateral appendages show some bilateral symmetry and were interpreted as precursors of megaphylls (Gensel 1984).

Traditionally, plants grouped within the paraphyletic 'Trimerophytina' are considered the earliest euphyllophytes, and hence to have given rise to both monilophytes and lignophytes. On the basis of the presence of a central protoxylem pole (see Section 'Lignophytes'), we have chosen another evolutionary history, with the 'Trimerophytina' complex basal to the lignophytes only (Fig. 13). This implies that the last common ancestor of the monilophytes and the lignophytes has still to be identified.

Monilophytes

Monilophytes are a major clade that unites most extant vascular plants without seeds, apart from the lycophytes. The clade has one clear synapomorphy, mesarch protoxylem confined to the lobes of the

xylem strand (Table 3, trait 16). It was first recognized in a cladistic analysis of extinct and living taxa (Kenrick and Crane 1997a). Strong support for the results of the analysis came from other phylogenetic studies (Pryer et al. 2001; Qiu et al. 2007). Extant monilophytes includes equisetophytes (horsetails), psilotophytes (whisk ferns) and all eusporangiate and leptosporangiate ferns (Pryer et al. 2001). Two major monilophyte groups existed during the Devonian, the Cladoxylopsida and the Iridopteridales. Both are extinct.

Cladoxylopsida

Cladoxylopsida range from Early Devonian (Emsian; Gerrienne 1992) to the Mississippian (Meyer-Berthaud et al. 2007). They are characterized by a dissected vascular system consisting of a variable number of xylem plates. Those xylem segments are disposed in a variety of ways but are generally radially elongate. Generally, permanent protoxylem strands are positioned at the end of the xylem segments. The presence of secondary xylem has been proposed by Hilton et al. (2003), but most genera produce only primary vascular tissues. The last-order axes of the cladoxylopsids bear variously branched lateral appendages that can be vegetative and/or fertile; in this case, the ultimate segments of the appendages terminate in pairs of ellipsoidal sporangia. In most genera, lateral appendages are distributed in irregular helices. They are whorled in the proximal orders of axes in two genera: *Pietzschia* and *Polyxylon* (Meyer-Berthaud et al. 2007). Pseudosporochnalean cladoxylopsids such as *Calamophyton* (Fig. 22) or *Pseudosporochnus* (Fig. 23) share a similar body plan consisting of an upright trunk bearing densely inserted branches (Meyer-Berthaud et al. 2007). These branches divide characteristically in a digitate manner, a pattern resulting from very close dichotomies.

Cladoxylopsids were major contributors to terrestrial floras worldwide during the second half of the Devonian Period. *Eospermatopteris*, the Gilboa tree from the Middle Devonian of New York State (USA), has been recently demonstrated to belong to pseudosporochnalean cladoxylopsids (Stein et al. 2007). The plant was at least 8 m tall, with a long trunk that produced a crown of short, erect branches. It is considered as the earliest tree (Meyer-Berthaud and Decombeix 2007). *Pseudosporochnus* Leclercq and Banks (Fig. 23), although smaller, had a similar arborescent habit (Berry and Fairon-Demaret 2002).



Fig. 22 A branch of *Calamophyton* (Middle Devonian of Belgium)

The internal anatomy of the trunk of *Eospermatopteris* is unknown, but on the basis of the absence of secondary vascular tissue in *Pseudosporochnus* (Stein and Hueber 1989), it is suggested that both plants illustrate another way to make a tree: the multiplication of primary vascular strands combined with the presence of abundant sclerenchyma.

In situ spores attributed to the genus *Dibolisporites* have been isolated from *Fozzia* (Gerrienne 1992 and *Calamophyton* (Leclercq and Andrews 1960) sporangia. All cladoxylopsids are thought to have been homosporous; their gametophytes are unknown.

Iridopteridales

Iridopteridales range from the Middle to Late Devonian, possibly Mississippian (Meyer-Berthaud

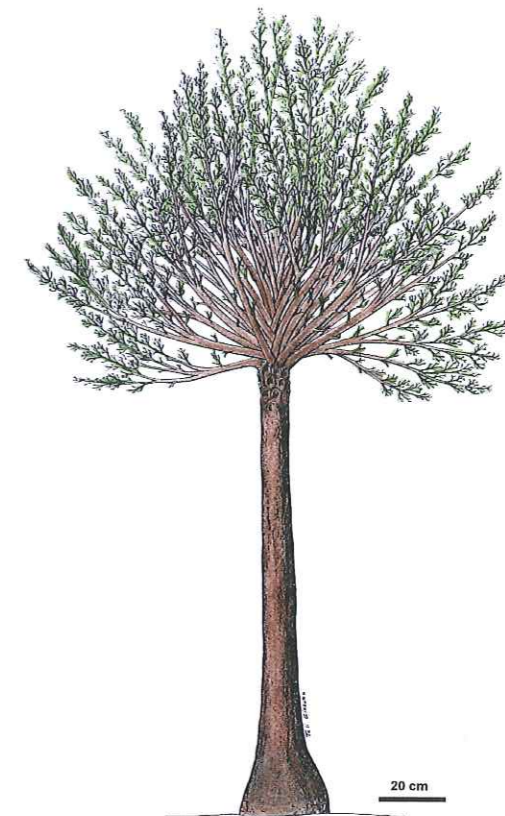


Fig. 23 (Modified from Berry and Fairon-Demaret 2002) Reconstruction of *Pseudosporochnus*

et al. 2007). They share a number of characters with the cladoxylopsids, including the possession of whorled lateral appendages and of a highly dissected, ribbed protostele containing peripheral permanent protoxylem strands. They were widespread medium-sized plants. When known, the fertile appendages were shown to terminate in pairs of ellipsoidal sporangia (Berry and Stein 2000). Another important feature of the order is the iterative branching (Cordi and Stein 2005). Iridopteridales are apparently close to the Cladoxylopsida, but both groups can be distinguished from each other by a number of characters including the iterative versus hierarchical architecture (Meyer-Berthaud et al. 2007).

The phylogenetic position of Cladoxylopsida and Iridopteridales remains questionable; their precise placement is hampered by the difficulty of identifying phylogenetically significant characters and by the fragmentary nature of fossil material (Taylor et al. 2009). It has been suggested that Iridopteridales may

be closely related to horsetails (equisetophytes) (Stein et al. 1984).

Equisetophytes (Sphenophytes; Horsetails)

Equisetophytes are characterized by a number of synapomorphies, including the presence of whorled appendages (branches and leaves) and of a sporangiophore with distinctive morphology. They first appeared in the Devonian, a possible precursor being *Estinnophyton* Fairon-Demaret, from the Early Devonian of Belgium. Equisetophytes were rather abundant during the Carboniferous and have since then experienced a gradual decline. *Equisetum* is the only extant genus. The record of Devonian equisetophytes is scarce in comparison with that of cladoxylopsids and Iridopteridales.

Other Devonian Monilophytes (= Early Fern-Like Plants Ssensu Taylor et al. 2009)

As for equisetophytes, the Devonian record of other monilophytes is generally scarce. *Rhacophyton* Crépin 1875 (Fig. 24) is a notable exception: it has been described from world-wide numerous Late Devonian localities, where it is sometimes the dominant element. Its taxonomic position is still under debate, but most authors consider it as a basal fern. It was a bushy plant, 1–2 m tall, with stems bearing large fronds

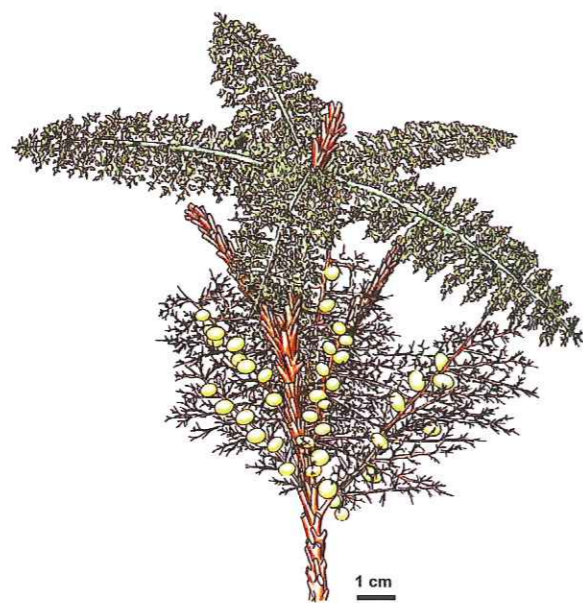


Fig. 24 (Modified from Mauseth 2003) Reconstruction of *Rhacophyton*

and numerous pinnule-like structures. The main axis of the frond comprises a central, clepsydroid-shaped strand of primary xylem that was sometimes surrounded by secondary xylem (Taylor et al. 2009). The *Rhacophyton* isospores are attributed to the *Diducites plicabilis*–*Auroraspora varia sporae dispersae* complex, characteristic of downstream or upstream ‘coal’ swamps (Maziane et al. 2002). The gametophyte of *Rhacophyton* is unknown.

Lignophytes

The lignophytes are the plants that possess a bifacial vascular cambium (Table 3, trait 17), producing secondary phloem (inner bark) towards the outside and secondary xylem (wood) towards the inside (Crane 1985). Another important character is the presence of a central protoxylem strand and of other strands along the midplanes of xylem ribs, derived by branching from the central one (Beck and Stein 1993) (Table 3, trait 18). Important also is the one-to-one correspondence of the peripheral protoxylem strands and the lateral appendages borne by the shoot (Beck and Stein 1993). The clade includes all seed plants and some of their free-sporing precursors. Today, with more than 260,000 living species (and probably much more), the spermatophytes are the most diverse and the most important group of living plants. Extant seed plants (spermatophytes) include five lineages: coniferophytes, cycadophytes, ginkgophytes, gnetophytes and angiosperms (flowering plants). All evolved later than the Devonian and will not be considered here.

The earliest lignophytes evolved during the Middle and Late Devonian. They had a gymnospermous-type of secondary xylem, but they did not produce seeds. They are collectively known as ‘progymnosperms’, an informal taxon that gathers several orders, among which are the Aneurophytales and the Archaeopteridales that are discussed here.

Aneurophytales

Aneurophytales range in age from the late Emsian to the Frasnian (Gerrienne et al. 2010). Members of the order are characterized by three-dimensional branching systems with lateral dichotomous appendages in helical or decussate arrangement (Fig. 25; the illustrated specimen belongs to the genus *Rellimia*). The primary vascular system consists of a deeply lobed mesarch protosteles, with a central protoxylem strand and others occurring along the mid-planes of the



Fig. 25 Fertile (upper left) and vegetative (lower right) specimens of *Rellimia* (Middle Devonian of Belgium)

lobes and near their tip. The sporangia are located on ultimate divisions of the much-branched, highly distinctive, lateral fertile appendages. Aneurophytales are homosporous, and produce bilayered spores attributed to *Rhabdosporites*; their gametophytes are unknown. Their phylogenetic position remains controversial, but on the basis of their homosporous status, they are often considered as sister to a group including the heterosporous Archaeopteridales and the spermatophytes.

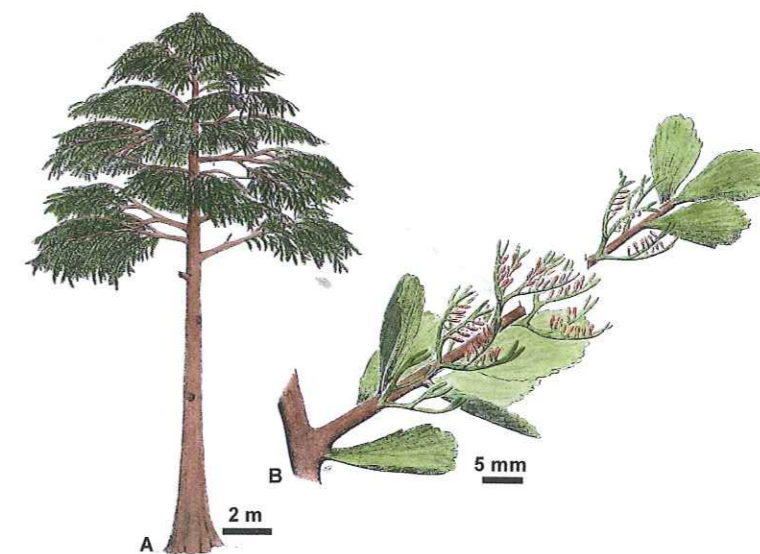


Fig. 26 (Modified from Stewart and Rothwell 1993) Reconstruction of *Archaeopteris*

The Stenokoleales are anatomically close to the Aneurophytales known exclusively from permineralizations and range in age from Middle Devonian to Early Carboniferous (Beck and Stein 1993). They are characterized by a three-ribbed protosteles, numerous protoxylem strands including a central one and others arranged along the mid-planes of the arms of the protosteles, pairs of traces to lateral appendages, and a helical phyllotaxis of those pairs of appendages. Secondary xylem is sometimes present in small amounts (Matten 1992; Beck and Stein 1993), but has not been so far described in detail. In the absence of morphological data, especially on reproductive parts, the Stenokoleales are currently left as incertae sedis. They are not represented in Fig. 13.

Archaeopteridales

The earliest arborescent representatives of the lignophytes belong to the Archaeopteridales, an order reported from the late Middle Devonian to the earliest Carboniferous. The advent of *Archaeopteris* (Fig. 26) was an important breakthrough in the evolution of plants. *Archaeopteris* experienced an extraordinary success during the Late Devonian, dominating the forest ecosystems and having a cosmopolitan distribution (Edwards et al. 2000). *Archaeopteris* was a large tree. Its trunk included a significant amount of secondary xylem that was in many respects comparable to that of extant gymnosperms. *Archaeopteris* illustrate

a third way to make a tree: the production of secondary vascular tissue, mainly xylem. The tree habit was accompanied by the acquisition of long-lived roots (Meyer-Berthaud and Decombeix 2007), which had major implications on the elaboration of early soils and complex microbial communities (Algeo et al. 2001). Vegetative leaves of *Archaeopteris* exhibit extensive interspecific variation, their margins ranging from highly dissected to nearly entire. *Archaeopteris* was heterosporous and free-sporing. Fertile leaves were generally non-laminate and bear up to 40 fusiform micro- and/or megasporangia. The microspores belong to the genera *Cyclogranisporites* or *Geminispora*; the megaspores are 16–32 per sporangium and conform to those of the genera *Contagisporites* or *Biharisporites* (Taylor et al. 2009). The presence of endosporic megagametophytes has been described but not illustrated (Scheckler et al. 1997).

Spermatophytes (Seed Plants)

There are obviously strong selecting forces in favour of heterospory, as it evolved several times, in fact in almost all tracheophyte lineages (Bateman and DiMichele 1994). In the spermatophyte lineage, heterospory is accompanied by a series of modifications involving the megasporangium and the part of the sporophyte immediately surrounding it. The number of functional megaspores drops to one (Table 3, trait 19), and the indehiscent megasporangium (Table 3, trait 20) is enclosed in sporophytic tissues called integument (Table 3, trait 21). The resulting structure is called an ovule (or a seed, after fertilization) or preovule if the integument is dissected. The ovule is the characteristic element of the spermatophyte lineage. In the earliest representatives of the group, the ovule or preovule is borne in a further external envelope called the cupule, and the megasporangium exhibits an apical modification probably related to the capture of microspores.

Runcaria, a Precursor of Seed Plants

The Middle Devonian (mid-Givetian, 390 Ma) *Runcaria* (Fig. 27) is a small, radially symmetrical megasporangium. The integument is dissected into 16–20 spiralling lobes. The structure is surrounded by a segmented cupule. The megasporangium bears an unopened distal extension protruding above the integument (Gerrienne et al. 2004). This suggests that the early evolution of the integument was related to

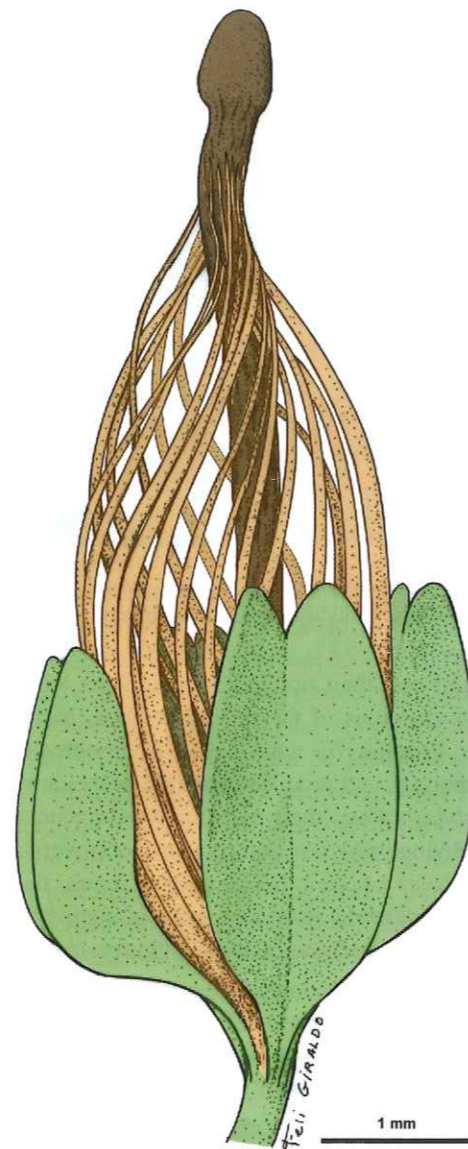


Fig. 27 (Modified from Gerrienne et al. 2004) Reconstruction of *Runcaria*

megasporangium protection rather than to pollination. *Runcaria* has been termed a 'proto-ovule' because it does not show the typical apical modification of the megasporangium shown by most of the younger pre-ovules (see below). *Runcaria* evolved during the Middle Devonian and may be considered as a precursor of those younger plants with pre-ovules. Its already complex structure also suggests that the spermatophyte lineage originated earlier than mid-Givetian times.

Late Devonian Pre-spermatophytes

A number of pre-ovules are known from Late Devonian strata distributed worldwide. They show a variety of morphologies, but they all share the hydrasperman modification (Rothwell 1986) of the megasporangium, also called a nucellus. The apex of the nucellus is transformed into a lagenostome, consisting of a pollen chamber surmounted by a cylindrical structure called the salpinx. The pollen chamber contains a central parenchymatous dome (Prestianni 2005). Late Devonian pre-ovules show various degrees of fusion of the integumentary lobes and/or various types of cupules, and have been classified into five distinctive morphological types (Prestianni 2005). *Moresnetia* Stockmans (Fig. 28) has highly dissected cupules borne at the tip of large branching systems; each cupule contains up to four pre-ovules. The diversity of the Late Devonian pre-ovules most probably

illustrates the earliest adaptive radiation of spermatophytes.

Brief Summation of Early Evolution of Land Plants

From the Late Silurian (Prídolí, 418 Ma) onwards, land plant populations evolved from patchy stands of *Cooksonia*-type plants (a few centimeters high, isotomously branched, with terminal sporangia) to worldwide distributed forests dominated by *Archaeopteris* trees at the end of the Devonian (Famennian, 360 Ma) or gigantic lycophytes and equisetophytes during the Carboniferous (359–299 Ma). On their way to the greening of the continents, plants evolved indeterminate growth, secondary tissues including wood and bark, long-lived roots, leaves, heterospory and seeds. All those innovations allowed them to increase size, to enhance propagule dispersion and efficiency and to colonize almost all terrestrial habitats. This had a global-scale impact on geophysical and geochemical cycles that peaked during the late Devonian, when Earth experienced one of the five major extinction events.

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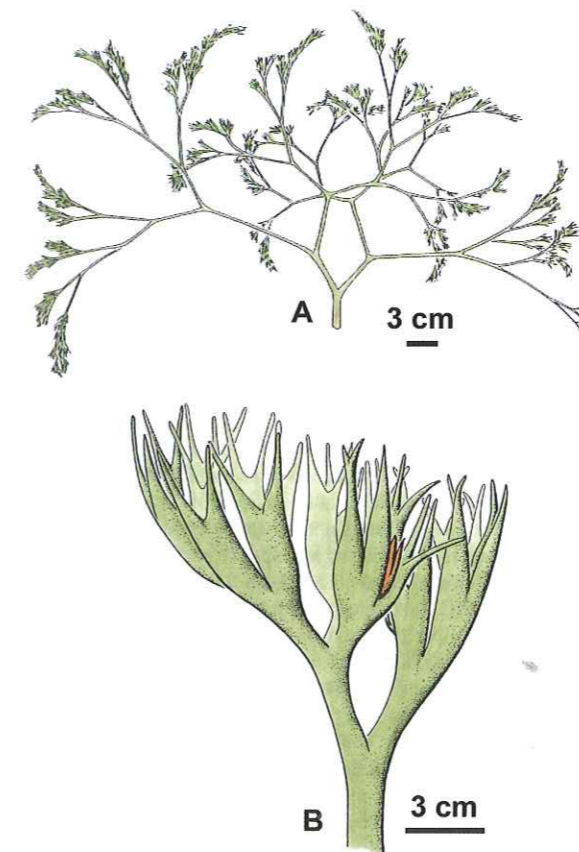


Fig. 28 (Modified from Fairon-Demaret and Scheckler 1987) Reconstruction of *Moresnetia*

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