

REVIEW
SILURIAN-DEVONIAN ORIGINS OF FERNS AND LYCOPHYTES -
WHAT WE KNOW, WHAT WE NEED TO FIND OUT

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ABSTRACT

This represents a synopsis of current knowledge of the Siluro-Devonian fossil record concerning evolution of lycophytes and ferns. This is the time period when several taxa or lineages at different grades of organisation existed that may be informative about the origins of these groups or structures typical of these groups. Considerable new data, including earlier first appearances of lineages and plant structures, new data about Siluro-Devonian lycopsids or basal euphyllophytes, and new whole plant reconstructions of small to tree-size plants in both lineages, have been published in recent years. It is not possible to be completely comprehensive, but the taxa discussed are either central to established ideas, or provide new information in relation to phylogenetic relationships and evolutionary trends. It remains difficult to trace the phylogenetic relationships of early plants relative to extant lineages. New data are reviewed which may be important in reassessing homology of characters and/or hypotheses of such relationships or in determining which taxa to exclude. Including fossils in estimates of relationships of these major lineages of plants will provide a more accurate and comprehensive understanding of the past history of seedless vascular plants.

INTRODUCTION

A consensus classification of extant seedless vascular plants by PPG1 (2016), reflecting molecular and some morphological phylogenies (Smith et al., 2006b; Kenrick & Crane, 1997; Pryer et al., 2001; 2009; Schneider et al., 2009; and others) recognises Lycopodiopsida (with three families and collectively referred to as lycophytes) and a grade “euphyllophytes” which consists of two clades - seed plants and Polypodiopsida (Figure 1). The latter includes four subclasses, Equisetidae, Ophioglossidae, Marattiidae and Polypodiidae- all referred to as ferns.

Lycopodiopsida appears to represent a monophyletic group defined by both molecular and morphological characters that diverged at least in the mid-Silurian if not earlier (Kenrick & Crane, 1997; Nickrent et al., 2000; Renzaglia et al. 2000; Pryer et al., 2001; 2004; Qiu et al., 2007; Li et al., 2014) but see Hao and Xue (2013) for a different interpretation. Relationships of several putative stem lycophytes such as some *Cooksonia pertoni*, *Aberlemnia* (formerly *Cooksonia*) *caledonica*, *Renalia* and several others, some within more derived extinct clades where critical characters are missing, are poorly resolved (Kenrick & Crane, 1997; Gensel & Berry, 2001; Hao & Xue, 2013). Additional data and more whole plant reconstructions of several Upper Silurian or Lower Devonian polysporangiophytes are needed to address these issues.

The term “fern” or “fern-like” now encompasses the majority of extant and extinct non-lycophytic seed-free vascular plants and several extinct “stem” euphyllophytes (trimerophytes), those with “peripheral permanent protoxylems” such as cladoxyloids, iridopterids, and in some cases, rhacophytes and stauropterids (Kenrick & Crane, 1997; Rothwell & Stockey, 2008; Rothwell & Nixon, 2006; Berry & Stein 2000; Berry & Wang 2006). This results in a broad view of what represents a “fern”. This is tied up in considerations of evolution of the so-called megaphyllous leaf via modification of branch systems. However it is clear such leaves evolved many times and possibly from different parts of lateral branch systems. Furthermore, using criteria such as presence/absence of a leaf gap and simple *vs* branched venation to distinguish microphyll *vs* megaphyll is not clear-cut. For a more complete discussion of these issues, see Tomescu (2009) and later sections of this paper. The term megaphyll is intentionally not used in this paper.

Fossils were intentionally excluded from the PPG1 classification, because “the phylogenetic affinities of most extinct plants are rather unclear” (p.565). While a practical starting point for names, it, along with molecular- derived phylogenies of only extant forms, implies misleading relationships by ignoring some of the major discoveries in the fossil record of the past several decades. For example, stating that ferns are the closest living relative to seed plants is correct when only living plants are considered, but ignores the existence of extinct plants with unique combinations of characters representing one or more now-extinct lineages, notably progymnosperms, but also others, indicating a more distant relationship between seed plants and ferns. While molecular-based phylogenies may suggest a close relationship among the extant subclasses, incorporation of fossil and morphological data (Figure 2) suggest they are not monophyletic (Rothwell & Nixon, 2006).

The fossil record, while still incomplete, presently suggests each Polypodiopsida subclass (PPG1 2016) differs in time of first appearance and possibly in origin. First appearances of undoubted extinct members of each clade are as follows: equisetophytes -the Late Devonian, filicaleans (extinct Polypodiidae) - Early Carboniferous, Marattiidae -Late Carboniferous, and Ophioglossidae -Cenozoic. Thus time gaps exist between the later appearing taxa/lineages and putative early representatives of those clades. Finding morphologically based synapomorphies to unite extant and extinct putative progenitor

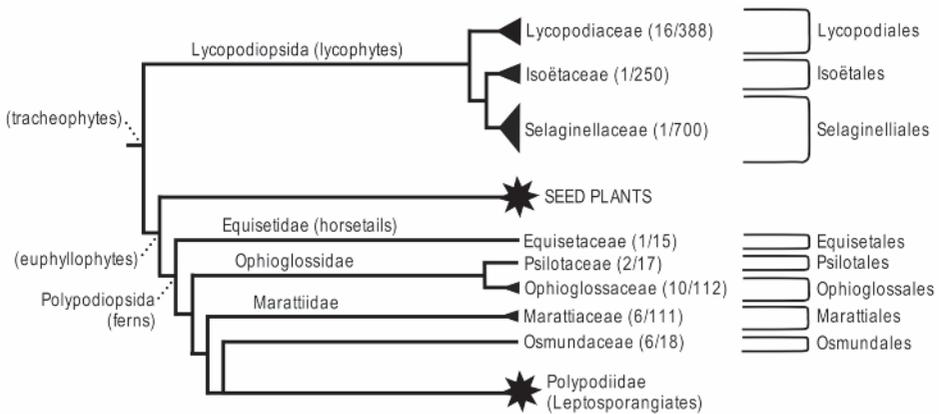


Figure 1. A simplified phylogeny of ferns and lycophytes, showing only the major lineages, modified from Figure 1 of the Pteridophyte Phylogeny Group I (PPG1) study.

or sister lineages is difficult. Characters that have been commonly employed among the Devonian age euphyllophytes are 1) branching systems, from which leaves are believed to have evolved and part or all of which are often interpreted as “leaf-equivalents”, 2) stelar anatomy and 3) protoxylem location. Sometimes interpretations are retrospective, with extant leaf morphologies influencing ideas of what constitutes a leaf-equivalent. Not everyone agrees on which part or parts of a branching system constitutes a leaf-equivalent in each lineage, and lastly, for some, all leaves are considered homologous (ignoring the fossil record) rather than evaluating the fossil plants within the context of their time and environment (Berry & Stein, 2000) and taking a more “bottom-up outlook” (Rothwell & Stockey, 2008) of extinct plants relative to extant ones. Recently acquired fossil data and whole-plant reconstructions, coupled with new developmental information or tests of certain character distributions, may improve assessment of homology of structures and character state transformations and ultimately phylogenetic relationships (Tomescu, 2009; Corvez et al., 2012 and authors cited therein). Additional work on understanding variation in anatomy also is needed. As our understanding of certain plant types improve, the fossil record may also indicate which possible progenitor candidates to preclude.

WHAT DOES THE FOSSIL RECORD CURRENTLY TELL US?

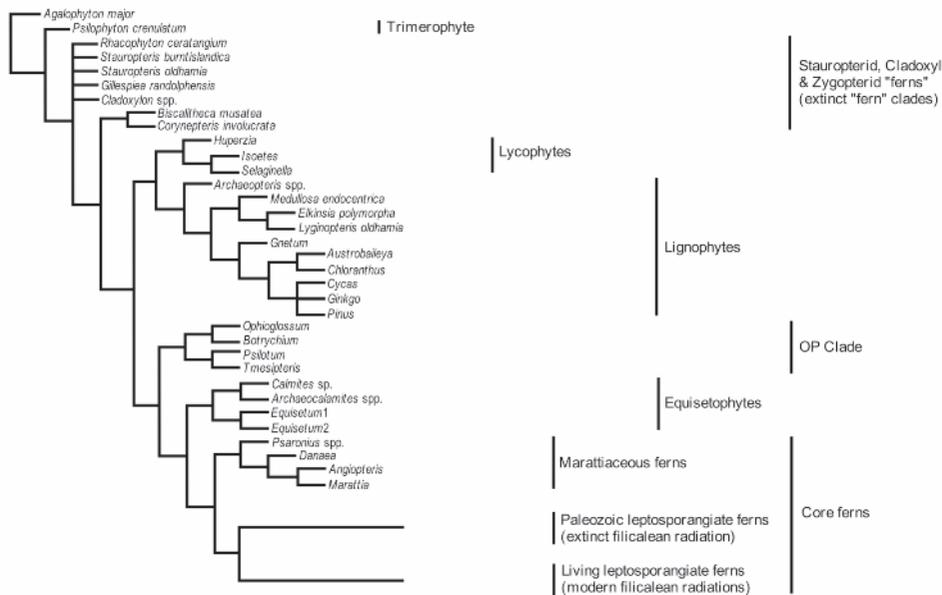


Figure 2. From Rothwell and Nixon, 2006 showing a tree based on a combination of fossil and extant plant morphological and molecular characters. Inclusion of fossils causes changes in postulated relationships of so-called “fern-like plants” relative to filicalean (=Polypodiidae) ferns. Terminology is that used by Rothwell and Nixon (2006). Lignophytes refer to progymnosperms and seed plants. OP= ophioglossid ferns and psilotophytes. Palaeozoic leptosporangiate ferns include taxa such as *Metaclepsydropsis*, *Ankyropteris*, *Psalixochlaena*, *Botryopteris*, and others.

Lower Carboniferous	Tournaisian	← Earliest polypodiids, ex: <i>Metaclepsydropsis</i>
		359
Upper Devonian	Famennian	← Earliest equisetids, ex: <i>Archaeocalamites</i>
		← Pre-ovules
		← Larger lycopsid trees
	Frasnian	← <i>Archaeopteris</i>
		372
Middle Devonian	Givetian	← Small lycopod trees; forests
		383
	Eifelian	← Arborescent cladoxyloids
		388
Early Devonian	Emsian	← Diverse basal euphyllophytes; protolepidodendrids
		408
	Pragian	← Rhynie chert
		← 2° xylem, laminate leaves, China (?megaphylls)
	Lochkovian	← Earliest pre-lycopod <i>Drepanophycus</i>
		411
Silurian		← Rhyniophytoids abundant
	Pridoli	419
	Ludlow	← Early Zosterophylls; <i>Baragwanathia</i> (lycophylls) - Lycopsidea
		423
	Wenlock	← Earliest <i>Cooksonia</i>
		427
	Llandovery	← Earliest commonly occurring trilete spores
		433
Upper Ordovician	Hirnantian	444
		445
	Katian	← Earliest sporangia; earliest trilete spores
		453
	Sandbian	458
Middle Ordovician	Darriwilian	468
	Dapingian	← Earliest cryptospores
		472

Figure 3. A stratigraphic chart showing major events in plant evolution or first appearances of certain plant groups or plant structures, spanning Ordovician to Tournaisian.

GENERALITIES

1) Everything happened earlier (Figure 3): Dispersed cryptospores and trilete spores provide evidence for Kingdom Plantae in the early Middle Ordovician to late Middle Ordovician respectively (Rubenstein et al., 2014; Steemans et al., 2009; 2010; Wellman et al., 2008; 2015; Kenrick et al., 2012; Edwards et al., 2014, Edwards & Kenrick, 2015, and references cited therein). Cryptospore types and diversity increase until the earliest Devonian, trilete spores diversify from Silurian on. Earliest forms occur in Gondwanan regions, suggesting radiation of cryptospore producers and basal polysporangiates from Gondwanan microcontinents towards Laurussia (Wellman et al., 2015; Steemans et al., 2010). The absence of megafossils during this time span may partly reflect the lack of known terrestrial sediments in the Ordovician and Silurian (Kenrick et al., 2012; Wellman et al., 2015). Some tiny Upper Silurian to Lower Devonian plants produce cryptospores, termed cryptophytes (Edwards et al., 2014), and others produce trilete spores, some possibly representing precursors of a bryophyte or polysporangiophyte grade (Edwards et al., 2014). Unfortunately, only some dispersed spores can be tied to parent plants, which limits establishing evolutionary/phylogenetic links between cryptophyte, bryophyte or polysporangiate lineages, and thus to either lycophytes or fern-like precursors (Edwards et al., 2014).

2) Innovations: The Silurian to Middle Devonian vascular plant diversification demonstrates a greater increase in plant diversity, size and complexity than previously known. Silurian to Early Carboniferous taxa exhibit a trend from considerable morphological/anatomical plasticity to more predictable body plans or architecture in younger, more derived forms (Bateman et al., 1998). Recent research suggests a transition from apparently rhizomatous forms to upright trees by the Middle to Late Devonian among lycopsids and euphylllophytes (Figure 3), tree size ranging from 3 to at least 8m tall and of varying trunk diameters (4 to ~20 cm wide). Some formed new vegetation associations, most notably early forests. In euphylllophytes, no laminate leaves and no, or limited, secondary tissues exist (thus having alternative means of mechanical support) (Stein et al., 2007; 2012; Giesen & Berry, 2013; Berry & Marshall, 2015). Archaeopteridalean forests of large trees with abundant secondary tissues dominated some regions in the Late Devonian. Evidence of early evolution of leaves and roots occurs from Late Silurian on, as discussed in greater detail later.

Another major innovation, aligned xylem meeting criteria for secondary xylem and interpreted as an early type of vascular cambium, is demonstrated by the Pragian *Amoricaphyton* (Gerrienne et al., 2011; Strullu-Derrien et al., 2013; 2014; Gerrienne & Gensel, 2015) and Emsian plants from eastern Canada (Gerrienne et al., 2011; Hoffman & Tomescu, 2013; Gensel in prep.). It is unknown if these possessed uni- or bifacial cambia. That, and lack of fertile remains, renders affinities and potential relevance as to how vascular cambia evolved or to fern and lycophyte vs. lignophyte evolution unclear. Uni- and bifacial vascular cambia originated more than once, as they are known in several extinct lineages from Middle Devonian on, including lycopsids (uni), progymnosperms (bi), early seed plants (bi), and possibly cladoxyls (unclear if secondary xylem or primary, aligned metaxylem).

Heterospory is established by the Middle Devonian in lycopsids and some euphylllophytes (the incipiently heterosporous Lower Devonian *Chaleuria*; the Upper Devonian archaeopterids and some Lower Carboniferous stauropterids). The Middle Devonian putative ovule precursor, *Runcaria* (Gerrienne et al., 2004) and numerous pre-

ovules of Late Devonian (Famennian) age indicate an initial radiation of early seed plants at nearly the same time as heterosporous euphyllophytes occurred (Prestianni & Gerrienne, 2010), but prior to appearance of all fern clades except Equisitidae.

LYCOPHYTE EVOLUTION

The presence of Late Wenlock *Cooksonia* sp. from Avalonia (Edwards & Feehan, 1980), and the Upper Silurian (Ludlow) occurrences of several zosterophylls, putative stem lycophytes, and the lycopsid *Baragwanathia* from Bathurst Island, Canada and/or Australia (Kotyk et al., 2004; Rickards, 2000) indicate several grades and clades of rhizomatous, homosporous lycophytes at that time and an early origin for lycophytes. Zosterophylls, stem lycopsids, pre-lycopsids and lycopsids occur widely in the Early Devonian. Strobilate probable zosterophylls such as *Distichophytum* and plants similar to *Bathurstia* first appear in the Late Silurian and similar forms are diverse in the Early Devonian.

Zosterophylloids are leafless but exhibit similar anatomy and sporangial morphology and dehiscence as lycopsids. *Kaulangiophyton*, lacking vascularized leaves, *Asteroxylon* with transfusion tissue in “leaves” (Hueber, 1992), and fertile *Drepanophycus* spp. all lack association of sporangia with leaves, and sometimes are considered pre-lycopsids (Gensel & Andrews, 1984; Gensel & Berry, 2001). Leaves of differing morphology occur in the Siluro-Devonian *Baragwanathia*, in the pre-lycopsid *Drepanophycus*, the putative lycopsid *Zhenglia* (Hao et al., 2006) and in some Pragian taxa of uncertain affinity from China such as *Adoketophyton* (Li & Edwards, 1992; Hao et al., 2003). Mid-Upper Devonian and younger lycopsids exhibit mostly laminate univeined lycophylls, some of which are much-divided (Protolepidodendrales) or have lacinate to fimbriate margins (e.g. *Longostachys*, *Wuxia*). Ideas about how lycophylls may have evolved vary but are unresolved, ranging from change via progressive vascularization of enations, sterilization of sporangia (Crane & Kenrick, 1997), or by reduction of branch systems (reviewed in Tomescu, 2009).

Growth habit among these basal groups (stem taxa, zosterophylls, pre-lycophytes, early lycopsids) is either rhizomatous or tufted (Gensel et al., 2001; Raven & Edwards, 2001; Gensel & Berry, 2001; Hao et al., 2010). Rooting structures appear to have arisen more than once, ranging from downward trending axes (some *Zosterophyllum* spp. of earliest to early Devonian age), to part of a bifurcation of a rhizome (H or K branching), with one half being stem-like and bearing enations or leaves, the other portion lacking those structures and appearing root-like (*Bathurstia*, *Drepanophycus* - Gensel et al., 2001). An un-named lycopsid from the Lower Devonian of Wyoming differs in that the initial K-branch produces a “root-bearing axis”, from which dichotomizing root-like structures depart (Matsunaga & Tomescu, 2016). These authors suggest rooting structures in lycophytes are *de novo* structures rather than modified stems. Hetherington and Dolan (2017) note commonalities among lycopsid root morphology as well as disparities, recognizing multiple types of structures that bear the branched roots. None of the early forms are anatomically preserved, thus features that distinguish roots from stems (root cap, root hairs, etc) in younger plants are lacking (Raven & Edwards, 2001; Gensel et al., 2001; Kenrick & Strullu-Derrien, 2014).

The order Protolepidodendrales, plants characterized by much divided or hastate leaves, epiphyllous oval to possibly round sporangia, and faintly to deeply lobed protosteles, is established by the Emsian (*Leclercqia* spp.) and taxa are much more diverse and widespread in the Middle and early Late Devonian (Gensel & Berry, 2001).

Most specimens may represent more distal or aerial branches and presumably were rhizomatous or in one case, climbing (*L. uncinata* Xu et al., 2011). Oval to elongate sporangia attach to the upper surface of sporophylls identical to vegetative leaves. *Leclercqia complexa* from the Middle Devonian Gilboa, NY locality is known to be ligulate; *L. complexa*, *L. cf. complexa* and *L. uncinata* yield spores showing them to be homosporous (Grierson & Bonamo, 1979; Richardson et al., 1993; Gensel & Kasper, 2005; Gensel & Albright, 2006; Wellman et al., 2009; Xu et al., 2011). Spores and ligules are unknown for other genera. Rooting structures, which might aid in better understanding of relationships, are unknown in all taxa. These plants are often considered to be putative precursors to the ligulate heterosporous clades Selaginellales and Isoetales, but better understanding of all plant parts would allow a more precise assessment of their relationship to other extinct and extant clades. As noted below, additional putatively transitional forms exist, although many are incompletely preserved.

A major change in growth habit and reproduction occurred in the late Mid Devonian, as shown by the bipolar/pseudobipolar, approximately half metre tall tree-like taxa *Longostachys* and *Chamaedendron* (Cai & Chen, 1996; Schweitzer & Li, 1996), both of uncertain affinity, in China. *In situ* (and some isolated) lycopsid stems from the upper Middle/lower Upper Devonian of Svalbard, consisting of approximately 1m tall, incomplete trunk pieces, and identified as *Protolepidodendropsis pulchra*, are interpreted as a paleotropical forest (present in a low paleolatitude) by Berry and Marshall (2015). *Sublepidodendron*, especially *S. songziense* Wang et al. 2003, from the Late Devonian of China, was at least a metre tall. A smaller, very slender, upright and unbranched Late Devonian lycopsid, *Clevelandodendron ohioensis* (Chitaly & Pigg, 1996), exhibits a lobed/branched base and a bisporangiate strobilus reminiscent of some lepidodendrids. Wider stemmed lycopsids such as *Cyclostigma*, *Lepidosigillaria*, and the unidentified tree lycopsid from Gilboa, NY (Haughton, 1859; Chaloner, 1968; Kräusel & Weyland, 1949; Stein et al., 2012) also occur in late Mid to early Late Devonian in Laurussia. These taxa not only differ in size (length, width), but also in branching (presence/absence, type), leaf base patterns, leaves, rooting and reproductive structures. They also clearly demonstrate the existence of upright lycopsids of varying heights, diameters, and branching architecture by Middle to Late Devonian time, coexisting with the presumably rhizomatous protolepidodendrids and presaging growth habits and reproductive strategies present among the abundant Carboniferous and younger lycopsid lineages. Various isolated anatomically preserved stem remains, when viewed in comparison to anatomy in more extensively preserved plants, also show differences in some features, not yet well understood. Secondary tissues occur in lycopsids from the Middle Devonian. Tracheid wall pitting among different taxa varies from one or more of the following pitting types: scalariform, pitted, circular bordered pitted, scalariform with fibrils connecting the bars or pitlet sheets. Much remains to be learned about its possible taxonomic implications.

Different types of stem bases with rooting structures occur among these taxa. *Longostachys* and *Chamaedendron* stems (and possibly *Clevelandodendron*) terminate in a series of downward trending, bifurcating root-like structures, but details are poorly understood. The two major rooting structures of arborescent isoetalean lycopsids dominant in the Carboniferous occur by the Middle Devonian. The earliest records of cormose lycopsid bases may be those recorded by Xu and Wang (2016) from the late Middle-Late Devonian Hujiersite Fm, China and the bases of the more extensively preserved *Protolepidodendropsis pulchra*, of similar age from Svalbard (Berry &

Marshall, 2015). Late Devonian *Leptophloem* and *Otzinachsonia* also exhibit cormose bases. A more branched, stigmarian type rooting system (Wang et al., 2003) occurs in *Sublepidodendron* spp from China. Laurussian forms are less easy to interpret. Pigg (2001) suggests that cormose and stigmarian forms represent variations of a single rooting type, perhaps being influenced by ecological factors.

Some of these Devonian lycopsid stems or branches bear sporangia aggregated into strobili, ranging from mono- to bisporangiate (*Longostachys*, *Chamaedendron*, *Sublepidodendron*, *Cyclostigma*), while others apparently have alternating fertile and vegetative zones (*Monilostrobos* Wang & Berry, 2003; *Wuxia* Berry et al., 2003), as also occurs in younger tree lycopsids. The Upper Devonian *Wuxia* is interesting in that megasporangiate “cones/fertile zones” occur just below branching points of axes but presumed microsporangiate ones are terminal (Berry et al., 2003). *Hoxtolgaya robusta* Xu et al. (2012), Middle Devonian of China, is interpreted as arborescent based on 9cm wide stems of unknown length, and exhibits sporangia yielding spores of one size, interpreted as homospory, but preservation is too incomplete to determine with certainty. In strobili or fertile zones, sporophylls are either identical to vegetative leaves, or modified with a broad fimbriate to spiny base and distal lamina, as in the Middle to Upper Devonian small tree-like lycopsids such as *Longostachys* (Cai & Chen, 1996), *Chamaedendron* (Schweitzer & Li, 1996) or *Wuxia* (and others) (Berry et al., 2003).

Berry et al. (2003) note that variation in fertile regions/structures and in stem anatomical features occurs earlier and more broadly in China than Laurussia, suggesting that perhaps China may have been an important area of early evolutionary innovation in clade(s) from which the major lineages of arborescent, heterosporous lycopsids of the Carboniferous and later arose. More whole plant reconstructions of several of these lycopsids are needed, and particularly, clarification of the organisation of basal regions, presence/absence of branching, anatomical features, and type of reproductive structures among individual plants, in order to better understand their relationships to both earlier and later occurring lineages to resolve relationships of these several plants and other taxa all considered as part of the isoetalean clade.

The record of herbaceous, homosporous lycopsids (e.g. Lycopodiaceae) is far less well known in the Devonian and Carboniferous. *Lycopodites oosensis* from the Late Devonian of Germany (Kräusel & Weyland, 1937) may represent one, but should be restudied. The Lower Carboniferous herbaceous form *Hestia* possesses too few characters to assess affinities (Bateman et al., 2007) but might represent an eligulate form. Younger fossils have been assigned to the genus *Lycopodites* but it is difficult to determine the affinities of these leafy stems; one has been found to represent conifer twigs, others exhibit a mix of lycopodiacean and sellaginellacean characters but are usually allied to Selaginellaceae (Skog & Hill, 1992; Thomas, 1992). Rowe (1988) identified a rhizomatous plant from the late Early Carboniferous Drybrook Sandstone as an early Selaginallalean, *Selaginellites resimus*, but little is known about early evolution of Selaginellales.

Several questions concerning early lycophyte evolution remain or are only partially answered by recent data. The paraphyly of some *Zosterophyllum* species and stem lycophytes remains unresolved despite new data. Much remains to be clarified about overall construction and relationships of the numerous Middle-Late Devonian protolepidodendraleans and small tree lycopsids, as discussed above, including how many times have structures such as strobili, ligules, rooting structures, and leaf abscission arisen and in what combinations? How do they relate to later-occurring lineages? And

again, questions remain about the early history of herbaceous, eligulate, homosporous Lycopodiaceae and ligulate, heterosporous Selaginellaceae through much of the Devonian and Carboniferous and even early Mesozoic.

EUPHYLLOPHYTE EVOLUTION

Extinct Devonian plants included in the Euphyllophyta mostly exhibit much branched aerial axes, some terminated by mostly fusiform sporangia. Anatomy consists of various protosteles (haplo-, actino-, dissected). Pertinent to fern evolution are stem euphyllophytes, such as *Psilophyton* and *Pertica*, the predominantly Mid-Upper Devonian Cladoxylopsida (=Pseudosporochnales [or Cladoxylales] + Iridopteridales), the enigmatic, but putative iridopterid *Rhacophyton*, and possibly Stauropteridaleans. The latter groups have been considered by many authors to be derived from a trimerophyte ancestor, and possible fern-like or fern precursors. Reasons vary; some derive from cladistic studies, others from older comparative studies. While lacking laminate leaves, either the whole or part of their lateral branch systems (LBS) are interpreted as showing possible stage(s) in the evolution of a leaf, as mentioned earlier (Kenrick & Crane, 1997; Gensel et al., 2001; Boyce & Knoll, 2002; Sanders et al., 2007; Tomescu, 2008; Galtier, 2010; Corvez et al., 2012). These occurred simultaneously but at different rates in different lineages (Galtier, 2010), and are not homologous within ferns or between “ferns” and seed plants. Secondly, some of the above taxa exhibit peripherally located protoxylem in various types of actino- or dissected protosteles (where anatomy is known) that differs from that present in aneurophytealean progymnosperms and early seed plants. The latter, and some basal euphyllophytes, exhibit radiate protoxylem (Beck & Stein, 1993), in which actinosteles or variants thereof have a central protoxylem, which appears to extend out each arm of the stele to produce lateral traces. These are considered mesarch but this depends on whether the protoxylem at the tips of arms persist, a feature presently not well understood. Anatomy of this type is typical of aneurophytealean progymnosperms, possibly some of the larger (*Pertica*-grade) trimerophytes, stenokolealeans, and other plants of uncertain affinity. However, it remains unclear if these two protoxylem patterns represent a good indicator of phylogenetic relationships. For example, Scheckler et al. (2006), in a re-study of *Langoxylon* Stockmans, a taxon of uncertain affinity, point out that *Langoxylon* stems possess a mixture of these two characters. *Pseudosporochnus hueberi* lacks a central protoxylem, but exhibits peripheral protoxylems plus several separate protoxylems along the midplane of an arm (Stein & Hueber, 1989), thus not all early euphyllophytes can be so easily categorized.

The term “peripheral loop”, initially referring to an anatomical feature of Carboniferous zygopteridalean petioles, has been used to describe protoxylem features in many Devonian plants. As originally defined, a peripheral loop consists of a central rod of parenchyma surrounded by protoxylem (Leclercq, 1970) located near the margin of an elongated vascular bundle. Similar structures are termed the same in stems of Devonian taxa. Several studies show that most of the latter represent protoxylem lacunae, resulting from break-down of thinner walled protoxylem during development or represent a different organisation of protoxylem with associated parenchyma (Scheckler, 1974; Scheckler et al., 2006; Stein, 1982). This suggests that the presence of a so-called peripheral loop should be carefully evaluated in any Devonian plant, and is not phylogenetically useful. Furthermore, care should be taken in use of the term “clepsydroid” and in any phylogenetic implications that might follow, because strap-

shaped strands in main axes or lateral branch traces in Devonian plants expand at their ends in preparation for producing the next higher order traces, thus appearing similar to the dumbbell-shaped petiole trace so termed among some early ferns.

The earliest putative euphyllophyte laminate leaf may date from the Pragian *Eophyllophyton* (Hao, 1988; Hao & Beck, 1993), considered basal and sister to other euphyllophytes by Hao and Xue (2013) but considered of uncertain affinity by this author. While laminate leaves are absent in most other coeval taxa, they occur in the Early to late Devonian *Platyphyllum* (= *Flabellifolium*?) and the Late Devonian *Ellesmeris* (Hill et al., 1997), enigmatic *Shougangia bella* (Wang DM et al., 2015), archaeopteridaleans and early seed plants, appearing earlier in time in lignophytes than in filicales (Galtier, 2010). Clearly, resolution of what constitutes homologous structures in LBSs among these different much-branched plants, and more documentation of the first appearance of laminae, would address remaining questions concerning number of times and modes of leaf evolution in these groups and non-homology of so-called megaphylls in these groups.

CLADOXYLS, IRIDOPTERIDS AND RHACOPHYTES- CALLED “FERN-LIKE” BUT?

Starting in the Mid-Eifelian and extending through the late Devonian, several taxa referable to Cladoxylopsids s.l. (e.g. including iridopterids, Berry & Stein, 2000) and rhacophytes are part of a more complex vegetation, some of the former representing small to large trees recently described as major components of in situ Middle to early Upper Devonian forests in the USA and Germany (Stein et al., 2007; 2012). Concomitantly, major revision of taxon concepts for *Pseudosporochnus* (Berry & Fairon-Demaret, 1997; 2002), *Calamophyton* (now includes *Duisbergia*, *Cladoxylon*, and most species of *Hyenia* - Fairon-Demaret & Berry, 2000; Berry, 2005; Giesen & Berry, 2013) and *Eospermatopteris/Wattieza* (Stein et al., 2007; 2012) has resulted in critical new information about the architecture of these leafless trees.

Pseudosporochnaleans

Pseudosporochnus trees (Figure 4) produce rows of branches that abscise at their base; the branches are digitately divided and produce higher-order, divided laterals that are three-dimensional to subopposite and alternate, final divisions being vegetative and non-laminate or fertile (Berry & Fairon-Demaret, 2002). *Calamophyton* is a smaller tree, with a swollen base, stems enlarging near apex and bearing vertical rows of lateral branch systems that then divide digitately (Figure 5), and produce higher order helically arranged dichotomizing vegetative or fertile non-laminate units. Older branch systems break off above their base, leaving the *Duisbergia* type morphology (Giesen & Berry, 2013). *Eospermatopteris* is larger, with a swollen base, a wide stem, and crown of digitately divided branch systems of the *Wattieza* type (Stein et al., 2007; 2012), abscising at their base. Terminal fusiform sporangia are known for all of these, being either recurved (*Calamophyton*, *Wattieza*) or erect (*Pseudosporochnus*). These apparently represent the earliest tree architectural types among euphyllophytes, being similar to some palms, cycads and tree ferns (Stein et al., 2007) in stem and root structure.

Where anatomy is known in the pseudosporochnaleans, it varies from being a multistranded, anastomosing stele, producing similar but smaller multi-stranded steles in lateral branches, as in *Calamophyton* or *Pseudosporochnus* (Figure 6), to being comprised of individual radially oriented strands near the periphery of the stem adjacent

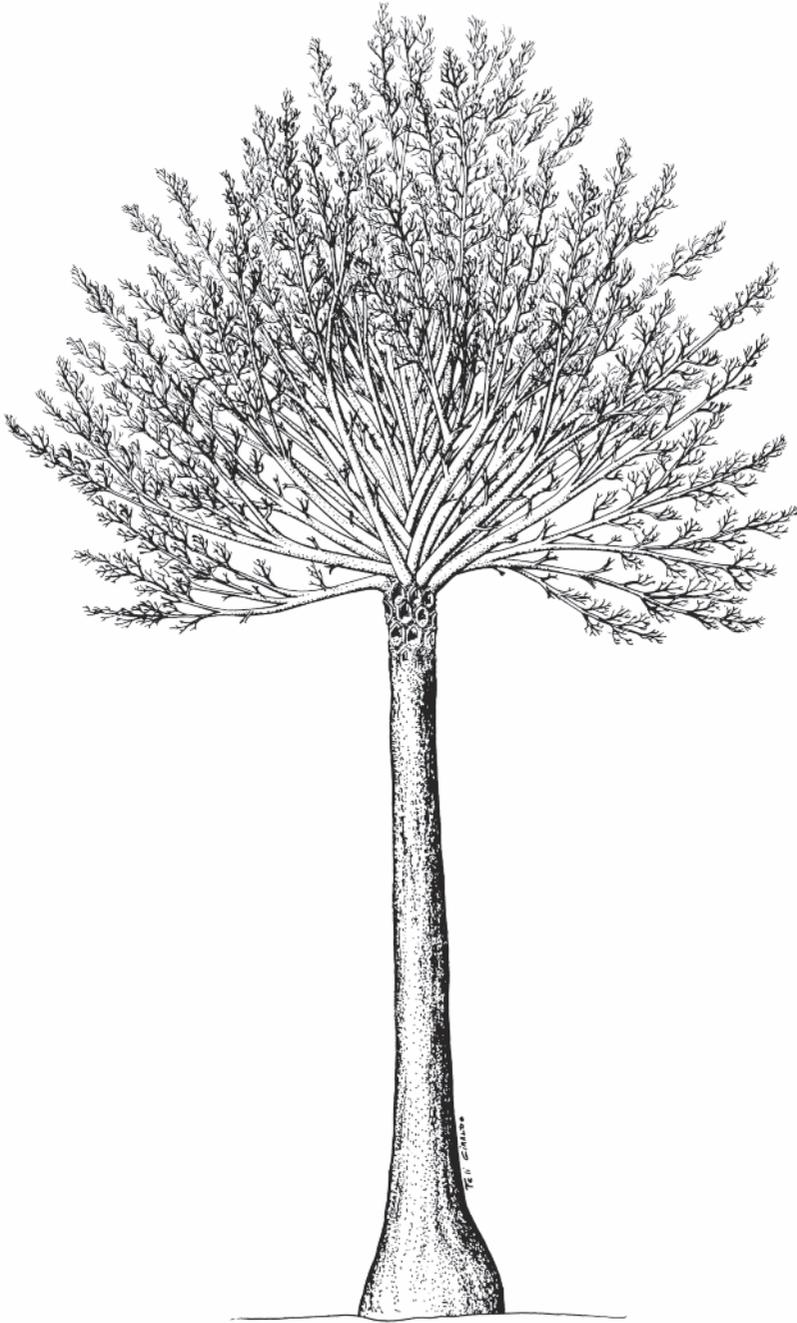


Figure 4. A recent reconstruction of the cladoxylopid *Pseudosporochnus*, showing its crown of relatively large branch systems, each of which is closely dichotomous so as to appear digitately divided. Reproduced from Berry and Fairon-Demaret, 2002, Figure 9, *Int. J. Plant Sci.* 163(5) 699-713. © 2002 by The University of Chicago.

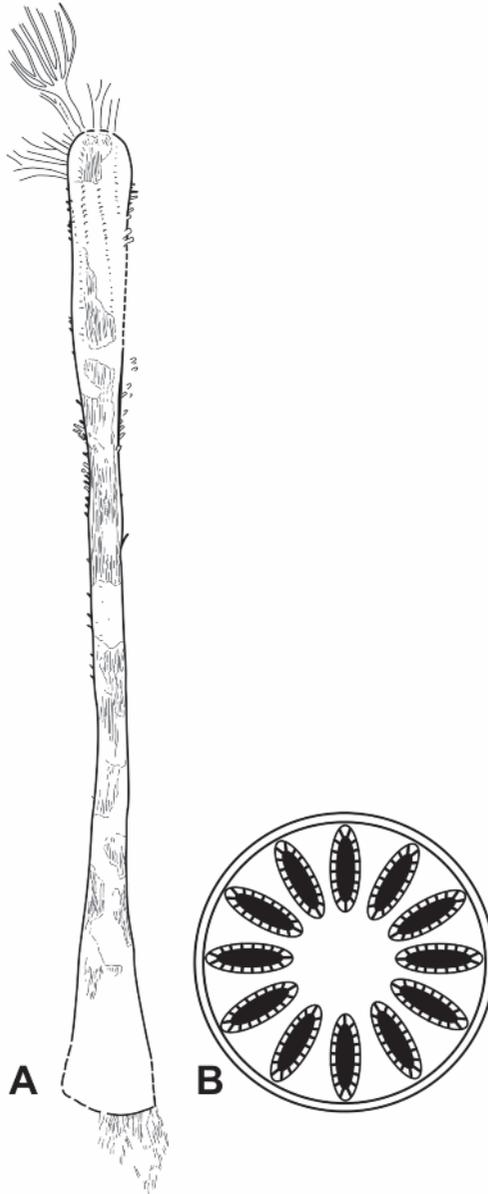


Figure 5. *Calamophyton primaevum*. Drawing of a stem showing two features- the remnant bases of branches along the stem and parts of the attached, digitately arranged branches at the crown. B. Suggested anatomy of *Calamophyton (Duisburgia)* based on Mustafa (1978) showing primary xylem in black, surrounded by aligned, possibly secondary xylem (lines). Redrawn from Giesen and Berry, 2013; stem is from Figure 5a (in part), anatomy redrawn from Figure 17d.

to a large pith in main trunk (Figure 5) as in the presumed base of *Calamophyton* stem (Giesen & Berry, 2013) and *Eospermatopteris/Wattieza* (Boyer & Matten, 1996). Opinion differs as to whether some of these plants exhibit a limited amount of aligned metaxylem or secondary tissues. Coeval progymnosperms possess a eustele and bifacial vascular cambium. Habit, branching, aspects of rooting and internal construction of the large pseudosporochnalean cladoxyloids might mean they already had diverged to the extent that they have little relationship with extant polypodiid or equisetid lineages, but instead represent a distinct lineage that flourished globally, then went extinct without any survivors (see Rothwell & Stewart, 1993).

Iridopteridaleans

Numerous Middle Devonian plants from Laurussia, Gondwana, and China comprise another lineage of Middle to Upper Devonian euphyllphytes, the Iridopteridales (Stein, 1982; Fu et al., 2011) based on anatomy, morphology, or a combination of these preservation forms (Figure 7). These plants as presently known are smaller than cladoxyloids, consisting of stems with a deeply ribbed mesarch actinostele comprised of two to three centrally united arms, each arm dividing one or more times to form six to twenty arms/ribs depending on the taxon. A single protoxylem region exists near the end of each arm (Figure 7 A-C). Branching pattern is essentially whorled, each protoxylem pole emitting a trace that supplies either a lateral branch or a smaller dichotomous appendage, the two types occurring in the same whorl (Figure 7D). Sometimes branching occurs in only part of a whorl, with successive partial whorls offset (Stein, 1982). Sporangia terminate ultimate dichotomizing appendages borne from second order branches- some upright and some recurved (Berry & Stein, 2000, *Compsocradus*). Other, often less extensively preserved, taxa attributed to the Cladoxyloids are not treated here. Relationship to Polypodiidae is unclear; depending

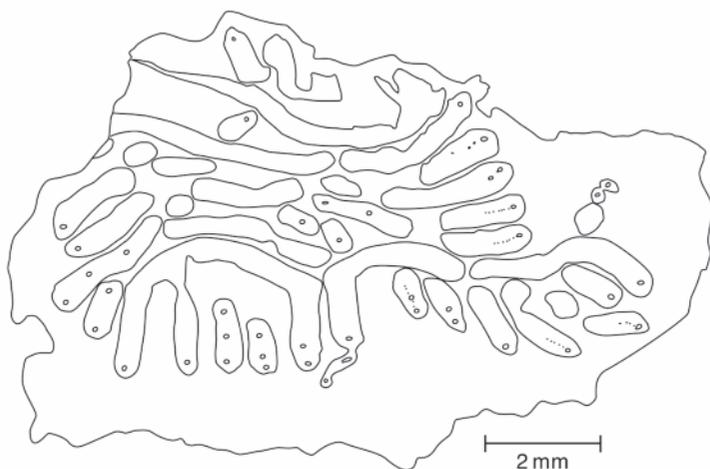


Figure 6. Anatomy of a lateral branch system of *Pseudosporochnus*, which is characteristic of many cladoxyloids; the vascular bundles are arrayed in a manner interpreted as representing the beginning of a dichotomy. Redrawn from Stein and Hueber, 1989.

on what combination of characters are selected, they may be closer to Equisetidae; if others, of uncertain affinity (Stein et al., 1984; Berry & Stein, 2000).

Rhacophyton and putative relatives

Rhacophyton (several spp) exhibits some characters that presage a fern type of organisation, but also possesses secondary tissues and some morphology reminiscent of progymnosperms or iridopteridaleans. Somewhat rhizomatous to upright axes (?stems) bearing adventitious roots in *R. ceratangium* (Cornet et al., 1976) produce single or paired much divided lateral branch systems which overall appear three dimensional, with more two-dimensional second order axes. The secondary axes depart oppositely, and range from dichotomous to slightly pseudomonopodial. Fertile lateral branch systems are more complex, each pair with one vegetative and one fertile unit. The vegetative segments are elongate and bear divided higher order non-laminate ultimates. The fertile units are much divided and recurved, forming rounded masses of dividing axes terminating in fusiform sporangia with elongate tips. Anatomy of less extensively preserved, more upright appearing stems of *R. zygopteroides* was described by Leclercq (1951) from poorly preserved specimens, and interpreted as an actinostele with unequally sized arms, although these sections have deteriorated so this cannot be confirmed. Similarly arranged lateral branches produce clepsydroid shaped steles. Both were described as surrounded by secondary xylem. In *R. ceratangium*, both main axis and lateral branches are considered to have produced an elongated clepsydroid-shaped primary xylem, surrounded by secondary xylem with rays (Cornet et al., 1976; Dittrich et al., 1983). Traces to higher order axes also are known. *R. condrusorum* Schultka (1978) is similar. *Ellesmeris* Hill et al. (1997) exhibits a simpler, but similar overall architecture, although the ultimate units are laminate, and fertile structures unknown. Anatomy is not intact, but the authors suggest main axis and lateral branch produce an elongate haplostele, with protoxylems near the tips of the arms. Knowing if all orders of branching possessed the same type of stele, or alternatively that stelar configuration changed from radial to

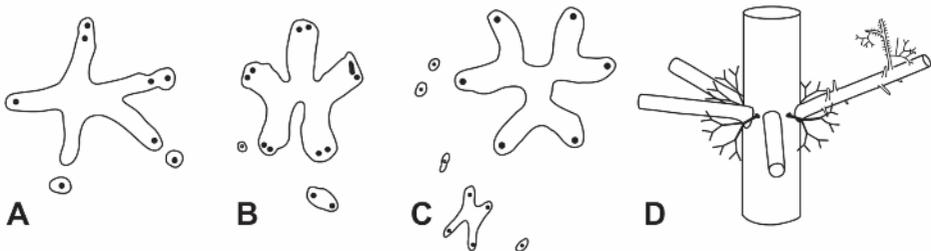


Figure 7. Line drawings of anatomy and stem portion of taxa included in Iridopteridalean cladoxylopsids. A. *Ibyka amphikoma*; B. *Iridopteris eriensis*; C. *Arachnoxylon kopfii*; D. Portion of stem and branching structure of *Anapaulia moodyi*; whorls of branches alternate with dichotomizing structures similar to ultimate branchlets; each lateral branch bears second and ultimate order branches. A-C redrawn from Stein, 1982. D redrawn from Berry and Edwards, 1996.

bilateral from main axis to lateral branch is of some significance in considering relationships and what to interpret as stem vs. leaf in these plants. For the present they usually are considered a separate lineage, Rhacophytaceae, although some authors previously placed them as a basal member of the zygopteridaleans and others consider them more allied to progymnosperms. Berry and Wang (2006) suggest, intriguingly, that *Rhacophyton* shares some characteristics of iridopteridaleans.

STEM EUPHYLLOPHYTES AND RELEVANCE TO EVOLUTION OF LATER FORMS

Trimerophyte grade euphyllophytes exhibit either dichotomous, anisotomous or strongly pseudomonopodial branching of varying degrees of predictable cladotaxy. Some of these terminate in fusiform sporangia, ranging from loosely (*Psilophyton*-grade plants) to densely (*Pertica*) clustered. Anatomy is known from parts of aerial systems of some *Psilophyton* species, while anatomy is unknown in published *Pertica* species. However, *Gothanophyton* and some undescribed plants at the *Pertica*-grade provide data about possible anatomical variation in these entities, showing some differentiation between ribbed main axes and lateral branches, and possibly indicating evolutionary trajectories different from *Pertica*, although affinities of most of these are poorly understood.

Psilophyton-grade basal euphyllophytes

Psilophyton Dawson (Banks et al.) Doran (1980), initially based on dichotomous to slightly pseudomonopodially branched axes, where anatomically preserved, exhibits a haplostele with centrally located protoxylem (centrarch) with little or no differentiation between main axis and lateral branch traces (Figure 8A). It thus appears the least specialized of stem euphyllophytes, but that may be deceptive. At the same time, plants of this type may be more closely related to polypodiids, or lineages leading to polypodiids and equisetids, than many later-appearing taxa.

Over 14 species of *Psilophyton* are now recognized, some based on morphology, one from anatomy only (*P. coniculum*) and others with both, although anatomy so far is not extensively known in most species. Based on current knowledge, preservation ranges from nearly complete plants (*P. crenulatum*) to more fragmentary remains. Phylogenetic analyses involving more than one species of *Psilophyton* indicate the genus is not monophyletic (Kenrick & Crane, 1997; Hao & Xue, 2013) and comparative evaluation of known species further suggests the possibility that these species might represent more than one taxon.

Psilophyton crenulatum Doran (1980), an apparently rhizomatous plant with upright branch systems, exhibits dense regions of mostly vegetative branching, some of which appear immature (apices present) while more distally, spacing of vegetative and fertile lateral branches varies. *Psilophyton dawsonii*, based mainly on anatomy of a 2.5 cm long specimen (Banks et al., 1975), possesses regions of closely spaced vegetative lateral branches. The more distally located fertile lateral branches exhibit a trace suggested to differ in shape from vegetative ones (Banks et al., 1975). Some short dichotomously divided lateral appendages are considered possible aphanophytes or roots. These features are not known for any other *Psilophyton* species, including *P. coniculum* (Trant & Gensel 1985), known only from anatomy (no sporangia attached). In this species, more closely spaced branching occurs mainly in lateral branches.

Comparison of the many other *Psilophyton* species indicates that relative distribution of vegetative vs fertile regions is unknown, partly because the genus is best recognized

morphologically from fertile specimens. In many instances the number of specimens available or mode of preservation limits information. Where numerous specimens are available, study shows branching is variously spaced. Frequently, lateral branches are incomplete and finding completely vegetative branch systems is difficult.

It was previously questioned whether certain previously described species of *Psilophyton* conform sufficiently to the concept of the genus. *P. kräuselii*, from the Middle Devonian of Bohemia (Obrhel, 1959) is too poorly preserved to determine affinity, being based on fragmentary fertile and sterile remains (Hao & Xue, 2013; this paper). Hao and Xue (2008) also question the generic identity of *P. saferi*, *P. striatum* (Wang & Berry, 2001) and *P. dapsile* (Kasper et al. 1974) because they are either too poorly known or lack twisted sporangia. Examination of *P. dapsile* sporangia in the author's collection suggest that while small, they do show some torsion. *Psilophyton saferi*, described by Zdebska (1986) from the Lower Devonian of Poland, consists of a portion of a lateral branch system with upright sporangia borne in loose clusters more similar to those in *Pertica* and should be restudied. *Psilophyton microspinosum* from the Early Devonian of Maine (Kasper et al., 1974) exhibits a more rigid pattern of lateral branches and erect, untwisted sporangia, suggesting its affinity should be re-evaluated.

The few morphologically preserved Pragian *Armoricaphyton* and the Emsian unnamed plant from Canada (Gerrienne et al., 2011; Strullu-Derrien et al., 2014; Gerrienne & Gensel, 2015) with an early type of secondary tissue are similar in stem

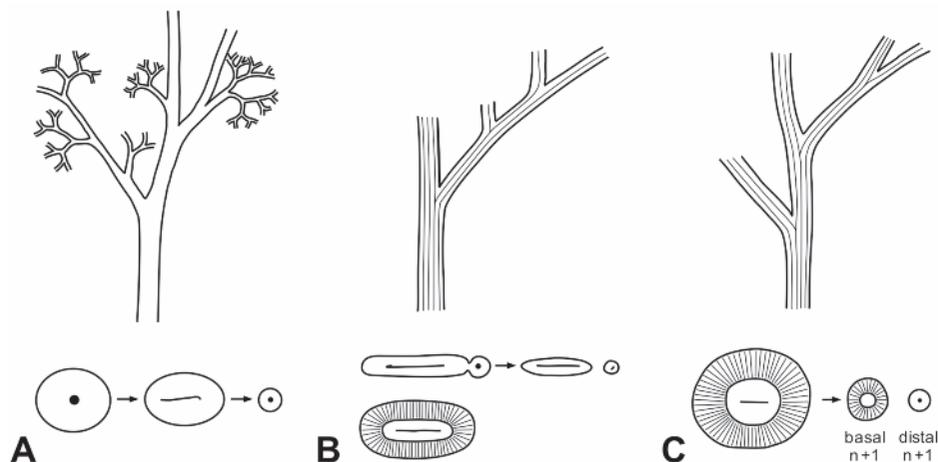


Figure 8. Diagrammatic drawings of small basal euphyllphytes; predominant mode of branching shown above, anatomy below. Axes approx. 2-5 mm. A. a generalized drawing of branch system of *Psilophyton*. Anatomy a centrarch haplostele, producing circular (or possibly square, if fertile) lateral branches. B. Unnamed plant from Emsian, New Brunswick (Gensel in prep). Ribbed, twice branched axes known. Some stems with elongate haplostele producing lateral trace, others indicate same type of haplostele surrounded by secondary xylem. C. *Armoricaphyton chateaupannense*, Pragian, France (Gerrienne et al., 2011; Gerrienne and Gensel, 2016). Ribbed, twice branched axes. Primary xylem a round haplostele, surrounded by secondary xylem. Basal part of lateral branch with secondary xylem, more distal region without. Dark circles or lines in center of steles indicate protoxylem, white area primary xylem, lines = secondary xylem.

diameter and branching, to *Psilophyton* (Figure 8 B, C). No fertile remains are known. All of these taxa, along with *Pertica* type trimerophytes showing preserved anatomy, exhibit P-type tracheid wall patterning *sensu* Kenrick and Crane, 1997 (Gensel, unpublished data). This character may be less useful at lower taxonomic levels, as the combination of characters evident in these plants suggest broader disparity among these early simpler plants than previously realised.

Morphologically preserved Middle Devonian plants such as *Planatophyton* (Gerrienne et al., 2014), *Pauthecophyton* (Xue et al., 2012), and *Tsaia* (Wang & Berry, 2001) are similar to *Psilophyton* in size and some aspects of branching but differ either in specifics of branching, sporangial orientation and/or dehiscence mode. These may represent distal regions of much larger plants or, alternatively, fragments of plants similar to *Psilophyton* in size. Additional study of these plants may reveal features useful in determining if they represent one, or several, Lower to Middle Devonian genera and/or lineages and clarify their postulated phylogenetic relationships.

Larger basal euphyllophytes similar to *Pertica*

Pertica and similar-appearing plants (Figure 9A-C) are taller and more robust in width, with a dominant main axis and variously arranged lateral branches. *Pertica* spp. exhibit mostly isotomously divided lateral branches with terminally borne, closely spaced, erect fusiform sporangia. Anatomy is unknown in published *Pertica* species.

A new genus, initially considered *Pertica*-like but definitely an unrelated taxon (Figure 9A), has a dominant main axis, helically arranged lateral branches that are single or paired, and, in contrast to *Pertica*, dichotomously- divided ultimate units located along their length, some sterile and some terminating in fusiform sporangia. Main axis anatomy is an actinostele (usually) with a single central protoxylem and a protoxylem near the end of each arm (Gensel, 1984). The lateral branch trace(s) are ovoid. There is no evidence of secondary xylem.

An undescribed plant from the Lower Devonian of New Brunswick is similar to *Pertica* spp. in morphology (Figure 9B), with a dominant main axis, helical lateral branches, and dichotomous laterals terminating in tight clusters of fusiform sporangia (Gensel, in prep.). Anatomy is unusual, consisting of a “winged” stele in which four major arms emanate from an elongate central region, but with one arm dividing further (Figure 9B). At least two types of lateral branch traces are formed, differing from main axis stelar configuration, but preservation is incomplete. Do other *perticas* have similar anatomy or might there be variation?

Gothanophyton Remy et Hass (Figure 9 C), with a 1cm wide main axis and single or paired lateral branches, exhibits a “winged” stele, consisting of an elongated central region with two major arms extending from either end (Remy & Hass, 1986a). One or more of the arms divide again, so that 4-7 armed steles are known. Protoxylems are located at either end of the central region near departure of major arms and near the end of each arm (Figure 9C). Shape and/or lobing of lateral branch traces differ from the main axis configuration. Morphology is poorly preserved, but the authors suggest lateral branches departed singly, in pairs or in threes. Much more needs to be learned about this complex Lower Devonian plant.

In all of these plant types, protoxylems emanate from one or more of the main axis arms to supply lateral branches and only primary xylem is present. Architecture of these plants is morphologically and anatomically plastic, although with some common patterns, but evidence is building that these taxa exhibit enough differences to not be closely

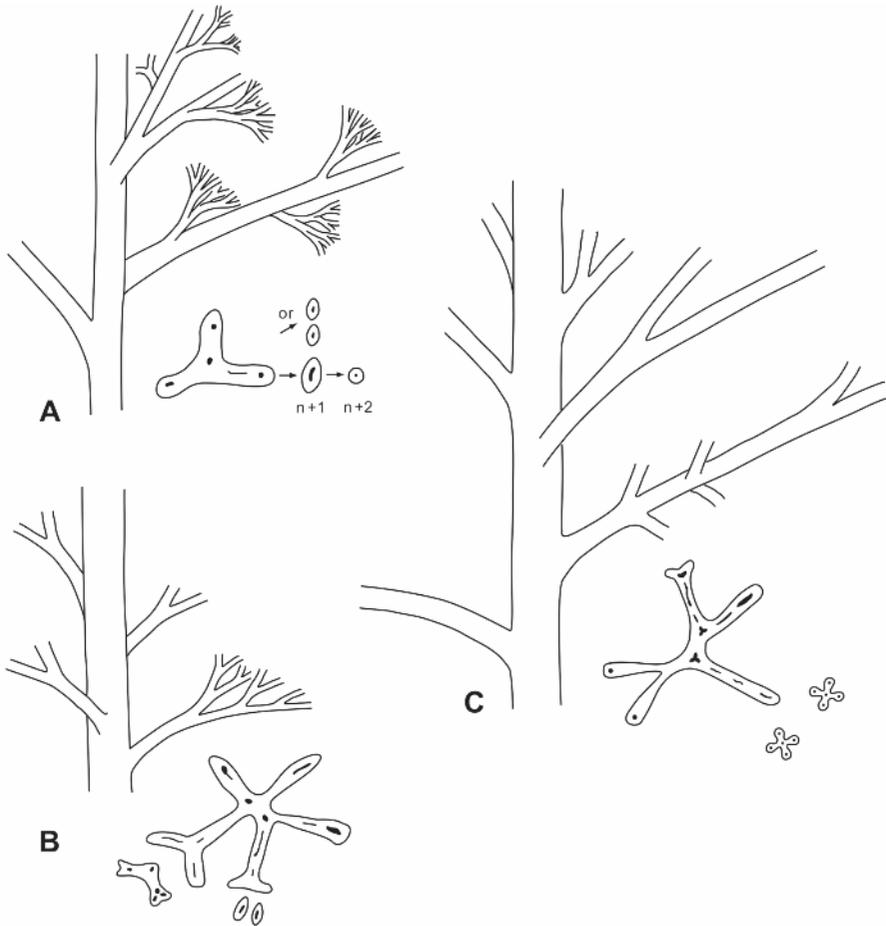


Figure 9. Diagrammatic drawings of larger basal euphylllophytes, similar in size to *Pertica* (main axes approx. 1 cm) - note that none show evidence of secondary xylem. A. Plant described by Gensel (1984), with large main axis, single or paired lateral branches, dichotomously divided ultimates arranged along lateral branches. Anatomy a three-lobed stele with central protoxylem and protoxylem at end of each arm. First order lateral trace (or pair of traces) oval, second order trace circular. (Gensel, in prep) B. A *Pertica*-like plant with large main axis, helically arranged predominantly dichotomously divided lateral branch, terminating in bunched sporangia (not shown). Anatomy consists of slightly elongate central region from which four arms emanate, one of these divides again to produce five arms total. Protoxylem located at each end of central area, and ends of arms. First order traces are elongate to v-shaped or oval and in pairs as shown. Gensel (in prep). C. *Gothanophyton zimmermanni* Remy and Hass. Large main axis with single or paired lateral branches (poorly preserved), bearing at least second order ones. Main axis stele consists of an elongate central region from which 4-7 arms emanate. Protoxylem located at each end of central region, along and at ends of arms. Lateral traces change shape after departure to become 4-lobed. Protoxylem in black. Clear area in stele is primary xylem. C. redrawn from Remy and Hass, 1986.

related. They are similar in showing a change in shape between main axis and first-order lateral branches which conforms more closely to that seen in many ferns or extinct fern-like plants than anything known in progymnosperms, despite apparently comparing more closely to the radiate protoxylem group.

Basal regions or rooting structures for *Psilophyton* and the taller euphyllophytes mentioned above are unknown. The fossils appear to represent aerial shoots extending from a rhizome, but it also is possible that some represent the main part of a non-rhizomatous plant that may have had a basal rooting system. Fairly wide, branched but detached rooting structures running perpendicular to bedding surfaces occur in sediments near some of the larger taxa in northern New Brunswick, while one long, downward extending axis was discovered by Elick (1998) in Gaspé which may represent a rooting structure.

Basal euphyllophytes *incertae sedis*

Several upper Lower Devonian plants (late Emsian) have been excluded from phylogenetic studies, largely because their anatomy is unknown and branching pattern and other features are unique. These include *Oocampsa catheta*, interpreted as a trimerophyte-progymnosperm intermediate (Andrews et al., 1975), *Chaleuria cirrosa* (Andrews et al., 1974) and an undescribed plant with similar branching architecture from northern Maine (Gensel, in prep). They all exhibit a robust, fairly long, greater than 1 cm wide dominant main axis with densely spiraled lateral branches. In *Oocampsa*, higher order branches are several times irregularly dichotomous, bearing clusters of ovoid sporangia. *Chaleuria* and the new plant from Maine exhibit isotomous second-order branches, some terminating in fusiform to ovoid sporangia. Basal regions and thus growth habit(s) are unknown. One might expect either a multilobed or cladoxyl- like stelar configuration based on the major branching patterns. *Oocampsa* differs from the other two in higher order branching and sporangial morphology, while the other two represent one or more as yet unrecognized lineages, or may be early members of one of the later-occurring lineages such as cladoxyls or iridopterids.

Stenokolealeans are still poorly known, but recent studies indicate a possible affinity to early seed plants (Moment et al., 2016).

SUMMARY

Significant new data now exist concerning the time of appearance of plants and morphology and anatomy of some taxa. Exceptionally preserved plant remains have indicated an earlier advent of plants, plant structures and habit, including transitions to upright, even arboreal types by the Middle Devonian. Limited evidence indicates a wider array of growth strategies among these. Although the euphyllophyte and lycophyte lineages separate very early in time, with each demonstrating acquisition of major plant structures, gaps in preservation preclude establishing evolutionary trends or clear phylogenetic relationships within each lineage, especially early vs later Devonian plant types, and between Devonian and Carboniferous or younger lineages that appear more directly related to extant ferns or lycophytes (similar situation for seed plants). As whole plant reconstructions are made and new approaches employed, with new discoveries or re-investigation of earlier material, assessment of character homology will be more possible.

Several putative candidate lineages leading to equisetids or polypodiids remain, but it is clear that some, such as cladoxyls, are already highly specialized in development

and construction by the Middle Devonian. Were more basal taxa similar, as suggested by *Lorophyton* Fairon-Demaret et Li (1993), *Foozia minuta* Gerrienne (1992) or perhaps as yet unrecognized taxa? Basal euphyllophytes at the *Psilophyton*, *Pertica*, and *Gothanophyton* grade are increasingly interesting in that it is among plants of this type that early differentiation of anatomical configurations of main axis- lateral branch is established. Within this group one might possibly be able to discern early divergence of the fern *sensu lato* vs seed plant lineages. Further examination of anatomy and organisation of lateral branch architecture, incorporating signals of developmental differences, may aid in recognizing early stages in evolution of leaves- these clearly will be different in various lineages. Similarly, the questions of transitions between predominantly rhizomatous and upright habit, and between types of rooting and of organisation of reproductive structures in both major lineages may become clearer with future discoveries or new approaches.

REFERENCES

- ANDREWS, H.N., GENSEL, P.G., & FORBES, W.H. 1974. An apparently heterosporous plant from the Middle Devonian of New Brunswick. *Palaeontol.* 17: 387-408.
- ANDREWS, H.N., GENSEL, P.G. & KASPER, A.E. 1975. A new fossil plant of probable intermediate affinities (Trimerophyte-Progymnosperm). *Can. J. Bot.* 53: 11719-1728.
- BANKS, H.P., LECLERCQ S., & HUEBER, F.M. 1975. Anatomy and morphology of *Psilophyton dawsoni*, sp. n. from the late Lower Devonian of Quebec (Gaspé) and Ontario, Canada. *Paleontographica Americana* 8 (48): 77-127.
- BATEMAN, R.M., CRANE, P.R., DIMICHELE, W.A., KENRICK, P., ROWE, N.P., SPECK, T., STEIN, W.E. 1998. Early Evolution of land plants: Phylogeny, physiology, and ecology of the primary terrestrial radiation. *Ann. Rev. Ecol. Syst.* 29: 263-92.
- BATEMAN, R. M., KENRICK, P. & ROTHWELL, G.W. 2007. Do eligulate herbaceous lycopsids occur in Carboniferous strata? *Hestia eremosa* gen. et sp. nov. from the Mississippian of Oxroad Bay, East Lothian, Scotland. *Rev. Palaeobot. Palynol.* 144 (3): 323-335.
- BECK, C.B. & STEIN, W.E. 1993. *Crossia virginiana* gen. et sp. nov., a new member of the Stenokoleales from the Middle Devonian of southwestern Virginia. *Palaeontographica* B229: 115-134.
- BERRY, C.M. 2005. '*Hyenia*' *vogtii* Hoeg from the Middle Devonian of Spitsbergen- its morphology and systematic position. *Rev. Palaeobot. Palynol.* 135(1-2), pp. 109-116.
- BERRY, C. M. & FAIRON-DEMARET, M. 1997. Reinvestigation of the cladoxylopsid *Pseudosporochnus nodosus* Leclercq et Banks from the Middle Devonian of Goe, Belgium. *Int. J. Plant Sci.* 158(3), pp. 350-372
- BERRY, C. M. & STEIN, W.E. 2000. A new iridopteridalean from the Devonian of Venezuela. *Int. J. Plant Sci.* 161(5), pp. 807-827.
- BERRY, C. M. & FAIRON-DEMARET, M. 2002. The architecture of *Pseudosporochnus nodosus* Leclercq et Banks: a Middle Devonian cladoxylopsid from Belgium. *Int. J. Plant Sci.* 163(5), pp. 699-713.
- BERRY, C. M. & WANG, Y. 2006. *Eocladoxylon* (*Protopteridium*) *minutum* (Halle) Koidzumi from the Middle Devonian of Yunnan, China: an early *Rhacophyton*-like

- plant? *Int. J. Plant Sci.* 167(3), pp. 551-566.
- BERRY, C. M. & MARSHALL, J.E.A. 2015. Lycopoid forests in the early Late Devonian paleoequatorial zone of Svalbard. *Geology* 43(12): 1043-1046.
- BERRY, C. M., WANG, Y. & CHONGYANG, C. 2003. A lycopoid with novel reproductive structures from the Upper Devonian of Jiangsu, China. *Int. J. Plant Sci.* 164(2), pp. 263-273.
- BOYCE, C.K. & KNOLL, A.H. 2002. Evolution of developmental potential and the multiple independent origins of leaves in Paleozoic vascular plants. *Paleobiology* 28(1): 70-100.
- BOYER, J. S. & MATTEN, L.C. 1996. Anatomy of *Eospermatopteris eriana* from the Upper Middle Devonian (Givetian) of New York. *Int. Org. Palaeobot.* 5, 13 (1996).
- CAI C-Y & CHEN, L-Z. 1996. On a Chinese Givetian lycopod, *Longostachys latisporophyllus* Zhu, Hu and Feng, emend.: its morphology, anatomy and reconstruction. *Palaeontogr. Abt B.* 1996; 238: 1-43.
- CHALONER, W. G. 1968. The cone of *Cyclostigma kiltorkense* Haughton, from the Upper Devonian of Ireland. *J. Linn. Soc. London (Botany)* 61: 25-36.
- CHITALY, S. & PIGG, K.B. 1996. *Clevelandodendron ohioensis*, Gen. et sp. Nov., A slender upright lycopoid from the Late Devonian Cleveland Shale of Ohio. *Am. J. Bot.* 83(6): 781-789.
- CORNET, B., PHILLIPS, T.L. & ANDREWS, H.N. 1976. The morphology and variation in *Rhacophyton ceratangium* from the Upper Devonian and its bearing on frond evolution. *Palaeontographica B* 158: 105-129.
- CORVEZ, A., BARIEL, B. & DUBUISSON, J-Y. 2012. Diversity and evolution of the megaphyll in Euphyllophytes: phylogenetic hypotheses and the problem of foliar organ definition. *Comptes Rend. Palevol.* 11: 403-418.
- CRANE, P.R. AND KENRICK, P. 1997. Diverted development of reproductive organs: a source of morphological innovation in land plants. *Plant Syst. & Evol.* 206 (1997): 161-174.
- DITTRICH, H.S., MATTEN, L.C. & PHILLIPS, T.L. 1983. Anatomy of *Rhacophyton ceratangium* from the Upper Devonian (Famennian) of West Virginia. *Rev. Palaeobot. Palynol.* 40: 127-147.
- DORAN, J.B. 1980. A new species of *Psilophyton* from the Lower Devonian of northern New Brunswick, Canada. *Can. J. Bot.* 58: 2241-2262.
- EDWARDS, D. & FEEHAN, J. 1980. Records of *Cooksonia*-type sporangia from the Late Wenlock strata of Ireland. *Nature* 287: 41-42.
- EDWARDS, D. & KENRICK, P. 2015. The early evolution of land plants, from fossils to genomics: a commentary on Lang (1937) 'On plant remains from the Downtonian of England and Wales'. *Phil. Trans. R. Soc. B* 370: 20140343.
- EDWARDS, D., MORRIS, J. L., RICHARDSON, J.B. & KENRICK, P. 2014. Cryptospores and cryptophytes reveal hidden diversity in early land floras. *New Phytol.* 202: 50-78.
- ELICK, J. M., DRIESE, S.G. & MORA, C.I. 1998. Very large plant and root traces from Early to Middle Devonian: Implications for early terrestrial ecosystems and atmospheric p (CO₂) estimations. *Geology* 26: 143-146.
- FAIRON-DEMARET, M. & LI, C-S. 1993. *Lorophyton goense* gen. et sp. nov. from the Lower Givetian of Belgium and a discussion of the Middle Devonian Cladoxylopsida. *Rev. Palaeobot. Palynol.* 77(1-2): 1-22.
- FAIRON-DEMARET, M. & BERRY, C.M. 2000. A reconsideration of *Hyenia elegans*

- Krausel et Weyland and *Hyania 'complexa'* Leclercq: Two Middle Devonian Cladoxylopsida from western Europe. *Int. J. Pl. Sci.* 161(3): 473-494.
- FU, Q., WANG, Y., BERRY, C.M. & XU, H-H.. 2011. Complex branching patterns in a newly recognized species of *Compsocradus* Berry et Stein (Iridopteridales) from the Middle Devonian of North Xinjiang, China. *Int. J. Pl. Sci.* 172(5): 707-724.
- GALTIER, J. 2010. The origins and early evolution of the megaphyllous leaf. *Int. J. Plant Sci.* 171(6):641-661.
- GENSEL, P.G. & ANDREWS, H.N. 1984. *Plant life in the Devonian*. New York: Praeger Press, 379 pp.
- GENSEL, P.G. & KASPER, A.E. 2005. A new species of the Devonian lycopod genus, *Leclercqia*, from New Brunswick, Canada. *Rev. Palaeobot. Palynol.* 136, 105–123.
- GENSEL, P.G. & ALBRIGHT, V.M. 2006. *Leclercqia complexa* from the Early Devonian (Emsian) of northern New Brunswick, Canada. *Rev. Palaeobot. Palynol.* 142: 103-121.
- GENSEL, P.G. & BERRY, C.M. 2001. Early lycophyte evolution. *Am. Fern J.* 91: 74-98.
- GENSEL P.G., KOTYK, M.E. & BASINGER, J.F. 2001. Morphology of above- and below-ground structures in Early Devonian (Pragian-Emsian) plants In GENSEL P.G. & D. EDWARDS, eds, *Plants Invade the Land: Evolutionary and Environmental Perspectives*. Columbia University Press, New York, pp. 83–102.
- GERRIENNE, P. 1992. The Emsian plants from Fooz-Wépion (Belgium). III. *Foozia minuta* gen. et spec. nov., a new taxon with probable cladoxylolean affinities. *Rev. Palaeobot. Palynol.* 74: 139-157.
- GERRIENNE, P.M. & GENSEL, P.G. 2016. New data about anatomy, branching, and inferred growth patterns in the Early Devonian plant *Armoricaephyton chateaupannense*, Montjean-sur-Loire, France. *Rev. Palaeobot. Palynol.* 224: 38-53.
- GERRIENNE, P., MEYER-BERTHAUD, B., FAIRON-DEMARET, M., STREEL, M. & STEEMANS, P. 2004. *Runcaria*, a Middle Devonian seed plant precursor. *Science* 306: 856-858.
- GERRIENNE, P., MEYER-BERTHAUD, B., YANG, N., STEEMANS, P., & Li, C-S. 2014. *Planatophyton* gen. nov., a late Early or Middle Devonian euphyllphyte from Xinjiang, North-west China. *Rev. Palaeobot. Palynol.* 208:55-64.
- GERRIENNE, P., GENSEL, P.G., STRULLU-DERRIEN, C. LARDEUX, H., STEEMANS, P., & PRESTIANNI, C. 2011. A simple type of wood in two Early Devonian plants. 2011. *Science* 333(6044):837.
- GIESEN, P. & BERRY, C.M. 2013. Reconstruction and growth of the early tree *Calamophyton* (Pseudosporochnales, Cladoxylopsida) based on exceptionally complete specimens from Lindlar, Germany (Mid-Devonian): Organic connection of *Calamophyton* branches and *Duisbergia* trunks. *Int. J. Plant Sci.* 174 (4): 665-686.
- GRIERSON, J.D. & BONAMO, P.M. 1979. *Leclercqia complexa*: Earliest ligulate lycopod (Middle Devonian). *Am. J. Bot.* 474-476.
- HAO, S-G. 1988. A new Lower Devonian genus from Yunnan, with notes on the origin of leaves (in Chinese). *Acta Bot. Sin.* 30: 441-448.
- HAO, S G. & BECK, C. B. 1993. Further observations on *Eophyllophyton bellum* from the Lower Devonian (Siegenian of Yunnan, China. *Palaeontogr. B* 230: 27-41
- HAO, S-G, & XUE, J. 2013. The Early Devonian Posongchong flora of Yunnan- a contribution to an understanding of the evolution and early diversification of vascular plants. *Science Press*, 366 pp.
- HAO S, XUE, J., GUO, D, & WANG, D-M.. (2010) Earliest rooting system and

- root:shoot ratio from a new *Zosterophyllum* plant. *New Phytol* 185: 217–225
- HAO, S., WANG, D., WANG, Q. & XUE, J. 2006. A New Lycopid, *Zhenglia radiata* gen. et sp. nov., from the Lower Devonian Posongchong Formation of Southeastern Yunnan, China, and Its Evolutionary Significance. *Acta Geol. Sin.* 80(1): 11-19.
- HAUGHTON, S. 1859. On *Cyclostigma*, a new genus of fossil plants from the Old Red Sandstone of Kiltorcan Co Kilkenny. *J. Roy. Soc. Dublin* 2:407-420.
- HETHERINGTON, A.J. & DOLAN, L. 2017. The evolution of lycopsid rooting structures: conservatism and disparity. *New Phytologist* 215 (2): 538-544.
- HILL, S.A., SCHECKLER, S.E. & BASINGER, J.F. 1997. *Ellesmeris sphenopteroides*, gen. et sp. nov., a new zygopterid fern from the Upper Devonian (Frasnian) of Ellesmere, N.W.T., Arctic Canada. *Am. J. Bot.* 84: 85-93.
- HOFFMAN, L.A. & TOMESCU, A.M. F. 2013. An early origin of secondary growth: *Franhueberia gerriennei* gen. et sp. nov. from the Lower Devonian of Gaspé (Quebec, Canada). *Amer. J. Bot.* 100, 754-763.
- HUEBER, F.M. 1983. A new species of *Baragwanathia* from the Sextant Formation (Emsian) Northern Ontario, Canada. *Bot. J. Linn. Soc.* 86:57-79.
- HUEBER, F.M. 1992. Thoughts on the early lycopsids and zosterophylls. *Ann. Mo. Bot. Gdn.* 79:474-499.
- JOHNSON, T. 1913. On *Bothrodendron (Cyclostigma) kiltorkense* Haughton, sp. Roy. Soc. Dublin, *Sci. Proceed.* 13 (n.s.): 500-528.
- KASPER, A.E, ANDREWS, H.N. & FORBES, W.H. 1974. New fertile species of *Psilophyton* from the Devonian of Maine. *Am. J. Bot.* 61: 339-359.
- KENRICK P. 2013. The origin of roots. In: Eshel A, Beeckamn T, eds. *Plant roots: the hidden half*. London, UK: Taylor & Francis, 1–14.
- KENRICK P. & CRANE, P. R. 1997. The origin and early diversification of land plants: A cladistic study. Washington: Smithsonian.
- KENRICK P. & STRULLU-DERRIEN, C. 2014. The Origin and early evolution of roots. *Plant Phys.* 166: 570-580.
- KENRICK, P., WELLMAN, C.H., SCHNEIDER, H. & EDGECOMBE, G.D. 2012. A timeline for terrestrialization: consequences for the carbon cycle in the Palaeozoic. *Phil. Trans. Roy. Soc. B* 367: 519-536.
- KOTYK, M. E., BASINGER, J.F., GENSEL, P. G. & DE FREITAS, T. A. 2004. Morphologically complex plant macrofossils from the Late Silurian of Arctic Canada. *Am. J. Bot.* 89: 1004-1013.
- KRÄUSEL, R. & WEYLAND, H. 1937. Pflanzenreste aus dem Devon. X. Zwei Pflanzenfunde im Oberdevon der Eifel. *Senckenbergiana* 19: 338-355.
- KRÄUSEL, R. & WEYLAND, H. 1949. *Gilboaphyton* und die Protolépidoxytales. *Senckenbergiana* 30: 129-152.
- LECLERCQ, S. 1951. Étude morphologique et anatomique d'une Fougère du Dévonien Supérieur. *Ann. Soc. Geol. Belg.* Mem. Vol. XIV (3): 39 pp.
- LECLERCQ, S. 1970. Classe des Cladoxylopsida Pichi-Sermolli, 1959. In: Boureau, E> (Ed.). *Traité de Paléobotanique*. IV. Fasc. I. Filicophyta. Masson, Paris, pp. 119-165.
- LI, F-W., VILLARREAL, J.C., KELLY, S., ROTHFELS, C.J., MELKONIAN, M., FRANGEDAKIS, E., RUHSAM, M., SIGEL, E.M., DER, J.P., PITTERMANN, J., BURGE, D.O., POKORNY, L., LARSSON, A., CHEN, T., WESTSTRAND, S., THOMAS, P., CARPENTER, E., ZHANG, Y., TIAN, Z., CHEN, L., YAN, Z., ZHU, Y., SUN, X., WANG, J., STEVENSON, D.W., CRANDALL-STOTLER, B.J.,

- SHAW, A. J., DEYHOLOS, M.K. SOLTIS, D.E. ,GRAHAM, S.W., WINDHAM, M.D., LANGDALE, J.A., WONG, G.K-S. MATHEWS, S. & PRYER, K.M. 2014. Horizontal transfer of an adaptive chimeric photoreceptor from bryophytes to ferns. PNAS, 111:6672-6677
- MATSUNAGA, K.K.S. & TOMESCU, A.M.F. 2016. Root evolution at the base of the lycophyte clade: insights from an Early Devonian lycophyte. Ann. Bot 117(4):585-598.
- MOMENT, N., GERRIENNE, P. & PRESTIANNI, C. 2015. *Brabantophyton*, a new genus of stenokolealean affinities from the Middle to earliest Upper Devonian locality from Belgium. Rev. Palaeobot. Palynol. 227: 77-96.
- MUSTAFA, H. 1978. Beiträge zur Devonflora III. Argum. Palaeobot. 5: 91-132.
- NICKRENT, D. L., PARKINSON, C. L., PALMER, J. D. & DUFF, R. J. 2000. Multigene phylogeny of land plants with special reference to bryophytes and the earliest land plants. Mol. Biol. Evol. 17:1885–1895.
- OBRHEL, J. 1959. Neue pflanzenfunde in den Sbrsko-Schichten (Mitteldevon). Vestn. Ustred. Ustavu Geol. 34: 384-388.
- PPG1. 2016. A community-derived classification for extant lycophytes and ferns. J. Syst. Evol. 54 (6): 563–603.
- PRESTIANNI, C. & GERRIENNE, P.M. 2010. Early seed plant radiation: an ecological hypothesis pp. 71-80 in Vecoli, M., Clement, G. & Meyer-Berthaud, B. (eds). The Terrestrialization Process: Modelling Complex Interactions at the Biosphere-Geosphere Interface. Geol. Soc. Lond. Spec. Pub., 339.
- PRYER, K.M., SMITH, A.R., & ROTHFELS, C. 2009. Polypodiopsida (14 January 2009) [online]. In: Tree of Life Web Project: <http://tolweb.org/Polypodiopsida/20615/2009.01.14> [accessed 7 October 2016].
- PRYER K.M., SCHNEIDER H., SMITH A.R., CRANFILL R., WOLF P.G., HUNT J.S. 2001. Horsetails and ferns are a monophyletic group and the closest living relatives to seed plants. Nature 409: 618–621.
- PRYER, K.M., SCHUETTPELZ, E., WOLF, P.G., SCHNEIDER H., SMITH A.R., & CRANFILL, R. 2004. Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences. Amer. J. Bot. 91: 1582–1598
- QIU Y-L, LI, L., WANG, B., CHEN, Z., DOMBROVSKA, O., LEE, J., KENT, L., LI, R., JOBSON, R.W., HENDRY, T.A., TAYLOR, D.W. 2007. A nonflowering land plant phylogeny inferred from nucleotide sequences of seven chloroplast, mitochondrial, and nuclear genes. Int. J. Plant Sci. 168: 691–708.
- RAVEN J.A. & EDWARDS, D. (2001) Roots: evolutionary origins and biogeochemical significance. J. Exp. Bot. 52: 381–401
- REMY, W. & HASS, H. 1986. *Gothanophyton zimmermanni* nov.gen., nov. spec., eine Pflanze mit komplexem Stelar-Körper aus dem Emsian. Arg. Palaeobotanica 7 (9): 9-69.
- RENZAGLIA, K. S., DUFF, R. J. T, NICKRENT, D. L. & GARBARY, D. J. 2000. Vegetative and reproductive innovations of early land plants: implications for a unified phylogeny. Phil. Trans. R. Soc. Lond. B 355:769–793
- RICHARDSON, J.B., BONAMO, P. M. & MCGREGOR, D.C. 1993. The spores of *Leclercqia* and the dispersed spore morphon *Acinosporites lindlarensis* Riegel: a case of gradualistic evolution. Bull. Nat. Hist. Mus., Lond. (Geol.) 49, 121–155.
- RICKARDS, R. B. 2000. The age of the earliest club mosses: the Silurian *Baragwanathia* flora in Victoria, Australia. Geol. Mag. 137(2): 207-209.

- ROTHWELL, G.W. & NIXON, K. C. 2006. How does inclusion of fossil data change our conclusions about the phylogenetic history of euphyllophytes? *Int. J. Plant Sci.* 167(3): 737-749.
- ROTHWELL, G. W. & STOCKEY, R. A. 2008. Phylogeny and evolution of ferns: a paleontological perspective. Pp. 332-364, Ranker, T.A. & Haufler, C. H. (eds) *Biology and Evolution of Ferns and Lycophytes*. Cambridge University Press.
- ROWE, N. 1988. A herbaceous lycophyte from the Lower Carboniferous Drybrook Sandstone of the Forest of Dean, Gloucestershire. *Palaeontol.* 31 (1): 69-83.
- RUBINSTEIN, C.V.; GERRIENNE, P. DE LA PUENTE, G.S., ASTINI, R.A. & STEEMANS, P. (2010). Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). *New Phytologist*. **188** (2): 365–369
- SANDERS, H., ROTHWELL, G.W. & WYATT, S. 2007. Paleontological context for the developmental mechanisms of evolution. *Int. J. Plant Sci.* 168: 719-728.
- SCHECKLER, S.E., 1974. Systematic characters of Devonian ferns. *An. Mo. Bot. Gard.* 61:462-473.
- SCHECKLER, S.E., SKOG, J.E. & BANKS, H.P.. 2006 *Langoxylon asterochlaenoideum* Stockmans: Anatomy and relationships of a fern-like plant from the Middle Devonian of Belgium. *Rev. Palaeobot Palynol.* 142: 193-217.
- SCHNEIDER H, SMITH, A. R. & PRYER, K. M. 2009. Is morphology really at odds with molecules in estimating fern phylogeny? *Sys. Bot.* **34**: 455–475.
- SCHULTKA, S. 1978. Beiträge zur Anatomie von *Rhacophyton condrusorum* Crepin. *Arg. Palaeobot.* 5: 11-22.
- SCHWEITZER H-J & LI, C-S. 1996 *Chamaeodendron* nov. gen., eine multisporangiate lycopsid aus dem Frasnium Sudchinas. *Palaeontogr B* 238:45–69.
- SKOG, J. & HILL, C. 1992. The Mesozoic herbaceous lycopsids. *Ann. Mo. Bot. Gard.* 79: 648-675.
- SMITH A.R., PRYER, K.M., SCHUETTPELZ, E. KORALL, P., SCHNEIDER, H. & WOLF. P.G. 2006b. A classification for extant ferns. *Taxon* **55**: 705–731.
- STEEMANS, P., WELLMAN, C.H. & GERRIENNE, P. 2010. "Paleogeographic and paleoclimatic considerations based on Ordovician to Lochkovian vegetation". *Geological Society, London, Special Publications*. **339** (1): 49–58. doi:10.1144/SP339.5
- STEEMANS, P., LE HÉRISSE, A., MELVIN, J., MILLER, M.A., PARIS, F., VERNIERS, J., WELLMAN, C.H.. 2009. Origin and radiation of the earliest vascular plants. *Science* 324: 353.
- STEIN, W. 1982. *Iridopteris eriensis* from the Middle Devonian of North America, with systematics of apparently related taxa. *Bot. Gaz.* 143(3): 401-416.
- STEIN, W. & HUEBER, F. M. 1989. The anatomy of *Pseudosporochnus: P. hueberi* from the Devonian of New York. *Rev. Palaeobot. Palynol.* 60: 311-359.
- STEIN, W., Wight, D. C. & Beck, C. B. 1984. Possible alternatives for the origin of Sphenopsida. *Syst. Bot.* 9: 102-118.
- STEIN, W., MANNOLINI, F., HERNICK, L V-A., LANDING, E., & BERRY, C.M.. 2007. Giant cladoxylipsoid trees resolve the enigma of the Earth's earliest forest stumps at Gilboa. *Nature* 446: 904-907.
- STEIN, W., BERRY, C.M., HERNICK, L V-A. & MANNOLINI, F. 2012. Surprisingly complex community discovered in the mid-Devonian fossil forest at Gilboa. *Nature* 483(7387), pp. 78-81.
- STRULLU-DERRIEN, C., KENRICK, P., TAFFOREAU, P., COCHARD, H., JEAN-

- LOUIS BONNEMAIN, J-L, LE HÉRISSE, A., LARDEUX, H. & BADEL, E. 2014. The earliest wood and its hydraulic properties documented in c. 407-million-year-old fossils using synchrotron microtomography. *Bot. J. Linn. Soc.* 175: 423-437.
- THOMAS, B. 1992. Paleozoic herbaceous lycopsids and the beginnings of extant *Lycopodium* sens. lat. and *Selaginella* sens. lat. *Ann. Mo. Bot. Gdn* 79: 623-631.
- TOMESCU, A.M.F. 2009. Megaphylls, microphylls and the evolution of leaf development. *Trends Plant Sci.* 14:5-12.
- TRANT, C. & GENSEL, P.G. 1985. Branching in *Psilophyton*: a new species from the Lower Devonian of New Brunswick, Canada. *Am. J. Bot.* 72(8): 1256-1273.
- WANG, DM, XU, H-H., XUE, J-Z., WANG, Q., LIU, L. 2015. Leaf evolution in early-diverging ferns: insights from a new fern-like plant from the Late Devonian of China. *Ann. Bot.* 115: 1133-1148.
- WANG, QI, HAO, S-G., WANG, D-M., WANG, Y. & DENK, T. 2003. A Late Devonian arborescent lycopsid *Sublepidodendron songziense* Chen emend. (Sublepidodendraceae Krausel et Weyland 1949) from China, with a revision of the genus *Sublepidodendron* (Nathorst) Hirmer 1927. *Rev. Palaeobot. Palynol.* 127: 269-305.
- WANG, Y. & BERRY, C.M. 2001. A new plant from the Xichong Formation (Middle Devonian) South China. *Rev. Palaeobot. Palynol.* 116:63-85.
- WANG, Y. & BERRY, C.M. 2003. A novel lycopsid from the Upper Devonian of Jiangsu, China. *Palaeontology* 46(6): 1297-1311.
- WELLMAN, C.H., STEEMANS, P., MILLER, M.A. 2008. Trilete spores from the Ordovician of Saudi Arabia: earliest evidence for vascular plants and their immediate predecessors (“protracheophytes”). *Terra Nostra* 2, 304.
- WELLMAN, C.H., STEEMANS, P., MILLER, M.A. 2015. Spore assemblages from Upper Ordovician and lowermost Silurian sediments recovered from the Qusaiba-1 shallow core hole, Qasim region, central Saudi Arabia. *Rev. Palaeobot. Palynol.* 212: 111-126.
- XU, H.H. & WANG, Y. 2016. The earliest cormose rhizomorph of putative lycopsid affinity from the Middle Devonian of West Junggar, Xinjiang, China. *Rev. Palaeobot. Palynol.* 226: 54-57.
- XU, H-H, BERRY, C.M., WANG, Y., MARSHALL, J.E.A. 2011. A new species of *Leclercqia* Banks, Bonamo et Grierson (Lycopsida) from the Middle Devonian of North Xinjiang, China, with a possible climbing habit. *Int. J. Plant Sci.* 172 (6): 836-846.
- XUE, J.Z., HAO, S-G, ZHU, X., WANG, D-M. 2012. A new basal euphyllphyte, *Pauthecophyton* gen. nov., from the Lower Devonian (Pragian) of Yunnan, China. *Rev. Palaeobot. Palynol.* 183(1): 9-20.
- ZDEBSKA, D. 1986. *Psilophyton szaferi* sp. nov., from the Lower Devonian of the Holy cross Mountains, Poland. *Acta Soc. Bot. Poland* 55: 315-324.