

Back to the Beginnings: The Silurian-Devonian as a Time of Major Innovation in Plants and Their Communities

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Abstract

Massive changes in terrestrial paleoecology occurred during the Devonian. This period saw the evolution of both seed plants (e.g., *Elkinsia* and *Moresnetia*), fully laminate* leaves and wood. Wood evolved independently in different plant groups during the Middle Devonian (arborescent lycopsids, cladoxylopsids, and progymnosperms) resulting in the evolution of the tree habit at this time (Givetian, Gilboa forest, USA) and of various growth and architectural configurations. By the end of the Devonian, 30-m-tall trees were distributed worldwide. Prior to the appearance of a tree canopy habit, other early plant groups (trimerophytes) that colonized the planet's landscapes were of smaller stature attaining heights of a few meters with a dense, three-dimensional array of thin lateral branches functioning as "leaves". Laminate leaves, as we now know them today, appeared, independently, at different times in the Devonian. In the Lower Devonian, trees were not present and plants were shrubby (e.g., *Aglaophyton major*), preserved in a fossilized community at the Rhynie chert locality in Scotland and other places. Many of these stem-group plants (i.e., preceding the differentiation of most modern lineages) were leafless and rootless, anchored to the substrate by rhizoids. The earliest land plant macrofossil remains date back to the

Silurian, with the Early Silurian *Cooksonia barrandei* from central Europe representing the earliest vascular plant known, to date. This plant had minute bifurcating aerial axes terminating in expanded sporangia. Dispersed microfossils (spores and phytodebris) in continental and coastal marine sediments provide the earliest evidence for land plants, which are first reported from the Early Ordovician.

15.1 Introduction

Patricia G. Gensel and Milan Libertin

We are now approaching the end of our journey to vegetated landscapes that certainly are unfamiliar even to paleontologists. As we delve deeper and deeper in time, we will visit a succession of some of the earliest plant life to cover Earth. Until this point, our time has been spent in various woodland settings and, without a doubt, there were wooded topographies where we begin our "hike" [U1501]. But, unlike the past 390 million years, trees will not remain a part of the countryside as we step back further and further in time. Trees and tree-like architectures will disappear from the fossil record. We will see a significant decrease in the heights of the plants anchored to more primitive soils, and we will pass through the oldest shrub- or meadow-like areas where the tallest forms may have been only head high. As we continue further, plants become diminutive, barely brushing against our ankles but appearing, seemingly, like a carpet covering all available moist surfaces. And, finally, we reach a point where we no longer encounter evidence of the very earliest plants in sediments of a continental nature. Rather, minute and scattered remains attributed to land plants, including their microscopic parts, are now found preserved in ocean basins along with members of the Paleozoic fauna (see Chap. 14). Before

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Fig. 15.1 *Archaeopteris* has been described as the earliest known “modern tree”, having a woody trunk, growing to heights in excess of 30 m and bearing near-horizontal, helically arranged deciduous branches. (a) Artist reconstruction. Despite this, *Archaeopteris* has many features far removed from those of trees today. This progymnosperm had a pteridophytic method of reproduction and bore some of the earliest planate leaves, though they are remarkably fern-like in appearance. (b) Lateral branch with alternately arranged ultimate branches bearing spirally arranged, planar leaves. (a) © The Field Museum, GEO86500_125d and Karen Carr, Artist. With permission. (b) Image courtesy of Walter Cressler

[AU5]

63 we enter the unknown, let us begin with an overview of what
64 is familiar and what is unfamiliar.

65 Traveling up or down any major Late Devonian river by
66 “dugout” canoe, we first encounter the riparian forests lining
67 the riverside in which the major tree, *Archaeopteris*, is known
68 (Fig. 15.1). The name of this woody tree is a misnomer
69 because it implies that the plant is an “early (archaeo) fern
70 (pteris)”. Rather, this canopy-forming tree possessed a weird
71 combination, or mosaic, of gymnosperm and fern features,
72 and is placed in a plant group distinctive from the others
73 we’ve encountered thus far (see Sect. 15.1.1). When
74 *Archaeopteris* colonized the landscape, the land’s surface
75 was covered by a well-established tiered community. Gallery
76 forests grew adjacent to swampy areas populated by sprawling
77 shrubs (*Rhacophyton*) and smaller groundcover plants,
78 such as *Protobarinophyton*. Other low-lying environments
79 were colonized by the earliest tree lycopsids, including
80 *Lepidosigillaria* or *Cyclostigma*, similar to those that domi-
81 nated wetland settings in the Carboniferous (see Chap. 13).
82 By the latest Devonian, plants had evolved reproductive
83 strategies to conquer seasonally dry regions outside of the
84 wetlands. Here, several types of early seed plants, such as
85 *Elkinsia*, were abundant. These forests that might seem
86 familiar, in a general sense, become less familiar as we
87 approach the Middle Devonian.

88 Middle Devonian forests can be separated into two
89 types [U1502]. The forest structure that retains a familiar
90 feeling is dominated by tree lycopsids such as

Protolepidodendropsis, which were persistent into the lat- 91
est Paleozoic. The second forest is stranger. These puzz- 92
ling forests were comprised of medium to very tall trees 93
that bore no leaves. Each tree had a sort of crown made up 94
of branches that branched and branched and branched and 95 [AU6]
terminated in a branch. These plants, the cladoxyloids 96
Calamophyton or *Eospermatopteris*, first appear in the 97
Middle Devonian and are successful cohabitants until the 98
early Late Devonian. Lianescent (vines) and herbaceous 99
plants are known to occur in some of these early forests, as 100
well as ancestors to the lycopsids, the zosterophylls (see 101
Box 15.1), comparable to Early Devonian taxa. Plants get 102
smaller the further we regress in time, with short-stature 103
riparian and coastal marsh-like vegetation expanding in 104
the late Early Devonian. These replaced open areas cov- 105
ered by a “green fuzz” of the earliest vegetation in moist 106
settings adjacent to river or ocean margins (Silurian to ear- 107
liest Devonian) [U1503]. Descendants of the early colo- 108
nizers are still found in the mosses and liverworts. Yet, we 109
have no evidence that any other earliest plant group 110
remained relatively static and survived until today. 111

112 Fossils representing the earliest evidence of plants, con- 112
sisting of small to “large” macrofossils (large being a relative 113
term of only several centimeters in length) and dispersed 114
spores, take us into an even stranger world. While most of 115
these fossils are found in Silurian and Devonian rocks, the 116
earliest evidence of plants is known from the Ordovician 117
(Katian or possibly earlier; Wellman 2010). Marine rocks 118

119 preserve small sporangia with spore tetrads, an evolutionary
 120 feature ascribed to all higher plants (Steenmans et al. 2009),
 121 as well as a myriad of dispersed spore assemblages contain-
 122 ing similar types of spores from various parts of the globe.
 123 Before we machete our way through these unknown terranes,
 124 we need to gain an appreciation for the plant groups that
 125 occupied Silurian-Devonian landscapes.

126 15.1.1 Relationships

127 When fossil plants first were recognized as more than just a
 128 carbon smudge on a rock surface, all Early Devonian plants
 129 were collectively referred to as the “psilophyte flora” due to
 130 a similarity in growth architecture to a living plant (Arber
 131 1921; Axelrod 1959). Living *Psilotum*, the whisk fern, grows
 132 in subtropical and tropical parts of the Americas, Africa,
 133 Asia, and Australasia. This plant does not have the appear-
 134 ance of any fern you may know. The plant body dichoto-
 135 mizes (evenly forks) as it grows from its flat-lying stem
 136 (rhizome), but it lacks both roots and leaves. The reproduc-
 137 tive sporangia develop in the axils of a small “spine” called
 138 an enation, and this suite of characters was thought to be
 139 primitive and similar to all early land plants. Hence, the idea
 140 of a group of “psilophytes” first conquering land. We now
 141 recognize a number of unique plant groups during the
 142 Devonian-Silurian thanks, in large part, to the paleobotanist
 143 Harlan Banks. Today, *Psilotum* is no more recognized as a
 144 close relative of early land plants; it is rather considered a
 145 basal eusporangiate fern (see Chap. 11). With the addition of
 146 newly discovered plant fossils in the past 50 years and the
 147 advent of phylogenetic techniques since his classification,
 148 we now understand that early plant life was a bit more com-
 149 plex than initially proposed.

150 Banks (1968) presented a major reclassification of these
 151 plants in which he recognized at least four definable lin-
 152 eages, plus others of less well understood affinity [U1504].
 153 His four categories of earliest vascular plants are the
 154 Rhyniophytina [U1505], Zosterophyllophytina [U1506],
 155 Trimerophytina [U1507], and Lycopytina [U1508]. At the
 156 same time, he also provided a more rigorous framework in
 157 which to consider the characteristics and affinities of these
 158 earliest land plants. With the discovery by Beck (1962) that
 159 *Archaeopteris* and other plants possessed a combination of
 160 woody stems and fern-like leaves with fern-like reproduc-
 161 tion, Banks also recognized two more advanced groups, the
 162 aneurophytalean and archaeopteridalean progymnosperms
 163 [U1509]. Kenrick and Crane (1997) undertook a cladistic
 164 analysis focusing on Silurian-Early Devonian plants, but
 165 with inclusion of some of the younger groups, to better
 166 understand evolutionary relationships (Box 15.1). This
 167 resulted in several, sometimes major, changes in their clas-
 168 sification (Fig. 15.2) [U1510]. For greater ease of description

in our site visits to the Siluro-Devonian, however, the terms
 rhyniophytoid, rhyniophyte, zosterophyll, trimerophyte, and
 progymnosperm, accompanied by diagnostic characters, will
 be used in the postcard descriptions to follow.

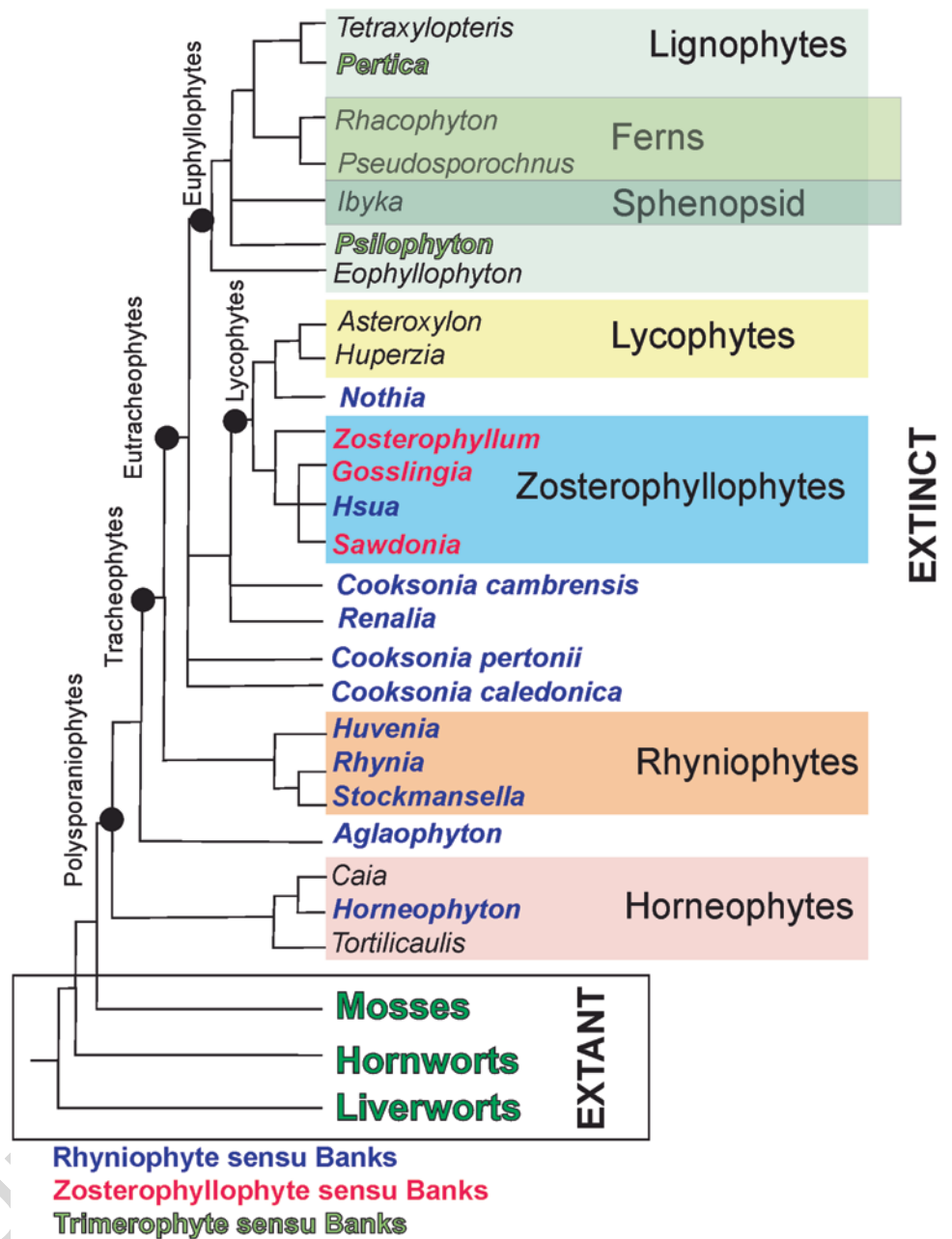
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Box 15.1: Relationships of Siluro-Devonian Plants: Banks (1968) to Kenrick and Crane (1997) to Now

Banks (1968) subdivided the Early Devonian “psilophytes” into several distinct lineages, which were recognized as subdivisions. These were the Rhyniophytina, Zosterophyllophytina, and Trimerophytina, and he clarified lineages such as Lycopytina, the cladoxylopsids, and the progymnosperms. The cladistic study of Kenrick and Crane (KC; 1997) reorganized and clarified many of these groups and updated ideas about relationships of some Middle-Late Devonian plants.

In the KC analysis, the Rhyniophytina of Banks is dismembered such that some taxa represent stem lineages possibly more related to lycopsids, whereas other taxa are now included in a redefined *Rhyniopsida* (e.g., *Rhynia*, *Stockmansella*). The Zosterophyllophytina are considered polyphyletic, with several stem* lineages and two more well-defined zosterophyllaceous clades, called *Zosterophyllopsida* by KC. They consist of basal (e.g., most *Zosterophyllum* spp., *Distichophytum*) and core (e.g., *Z. divaricatum*, *Oricilla*, *Barinophyton*, *Sawdonia*, *Serrulacaulis*, *Crenaticaulis*) groups. Some (or all?) of these plants are a possible sister group* or basal to Lycopsidea. Lycopytina, according to KC, consists of plants ranging from stem taxa, including *Cooksonia* and *Renalia*, plus the Zosterophyllopsida and Lycopsidea. Their *Lycopsidea* include the “pre-lycophytes” (e.g., *Asteroxylon*, *Drepanophycus*) where sporangia originate from the stems, to true lycophytes including the Middle-Late Devonian Protolopododendrales and (now) small tree lycophytes. It also is clear from several lines of evidence, but not shown in the cladogram (Fig. 15.2), that lycophytes diverged in the Late Silurian and have been a separate lineage (consisting of several clades) since then (Gensel and Berry 2001). The Trimerophytina (e.g., *Psilophyton*, *Pertica*, *Trimerophyton*) are split into several lineages. In fact, the trimerophyte genus *Psilophyton* alone now is known to encompass several different taxa, each representing a distinct evolutionary line of plants. At least 12 species of *Psilophyton*, of varying degrees of preservation, are described, and these vary in size, branching pattern, and presence/absence of emergences. Trimerophytina are considered to be basal members of

Fig. 15.2 Phylogenetic relationships of Devonian plant groups modified from Kenrick and Crane (1997, *The Origin and early Diversification of land plants*, Smithsonian Press



the euphyllophyte clade, or *Euphyllophytina*. This lineage includes ferns and their relatives and lignophytes (including seed plants). The *progymnosperms*, consisting of leafless, shrubby Aneurophytales and arborescent, leafy Archaeopteriales, form two clades basal to seed plants. They differ from the latter in being free-sporing, while sharing the presence of secondary xylem and phloem with seed plants. These, plus seed plants, are the *lignophyte clade*.

Some plants are difficult to place in any established lineage and are considered to be “of uncertain affinity” or some reference is made to possible affinities. For example, certain tiny plants with branched stems bearing sporangia, but in which vascular tissue is unknown, are termed *rhyniophytoids* (Gensel 2008). More recently, some cryptospore-bearing plants are called *cryptophytes* (Edwards et al. 2014), and, finally, another example is the *nematophytes*.

15.2 The Oldest Woodlands

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Wood evolved independently in several different plant groups during the Devonian (arborescent lycopsids, cladoxyloids, some trimerophytes, and progymnosperms) resulting in the evolution of the tree habit first seen in the Middle Devonian. A virtual walk in tropical wet terrains stretching across the latest Devonian coastal plains would allow us to see groves and stands of *Archaeopteris*, one of the first woody trees to attain an impressive 30-m height (Fig. 15.1). These forests were distributed worldwide. From first glance, these plants would appear to be the analog of many Neogene landscapes [U1511]. These forests had a towering branched canopy on which individual leaves grew from twigs, providing the understory with a cool, moist shade. Yet, although the wood of any fallen tree might not appear exactly the same as modern conifer woods, what was even more different was the way in which they reproduced. *Archaeopteris* was free-sporing, like ferns, and upon closer inspection, even the leaves looked “fern-like” in a number of their features [U1512].

15.2.1 *Archaeopteris* Coastal Woodlands/Forests

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Coastal zones and floodplains that spread across Late Devonian continents hosted a vegetation that was ecologically partitioned into different paleoenvironments when compared to similar settings a bit deeper in time. Sediments in the area around Elkins, West Virginia, USA, and adjacent areas preserve Mid-Late Famennian (c. 368–359 Ma) plants [U1509]. These plants grew on soils developed on a southwestward developing delta and floodplain complex, now called the Hampshire Formation. In addition to normal fluvial sandstone and mudstone deposits, these rocks contain at least two, about 1-m-thick coals (see Chap. 12). Detailed mapping of the coal and associated rocks and a paleoecological census of the plant remains show that the setting represents a low-lying deltaic shoreline, which was subjected to coastal storm events (Scheckler 1986). Plants preserved near the base of the lower coal include the enigmatic *Barinophyton sibiricum*, a core-zosterophyll. Overlying the peat swamp are planar laminated beds in which abundant *Sphenopteris* foliage, ovules, and other seed plant remains are often preserved as “leaf mats,” which may have accumulated under tidal influence. These laminated beds terminate up section in a rooted zone indicating the development of an immature

paleosol, most likely populated by *Rhacophyton* because considerable branching biomass of the plant occurs atop the rooting zone. These foliar axes are indicative of a scrambling growth habit for, what some authors consider to be, a “pre-fern” or an aneurophyte progymnosperm. There is some evidence to support the idea that tips of “fronds”/branch systems could root to propagate new plants such that vegetative production dominated the plant life cycle. If this is true, such a strategy could account for the high proportion of biomass in these coals.

The peat swamp, which now is a Late Devonian coal, was dominated by *Rhacophyton* biomass (Fig. 15.3). Although most of the biomass degraded to amorphous organic matter, pyrite concretions in the coal preserve their anatomy. The same proportion of *Rhacophyton* biomass is found in the second, or upper, coal. Sandwiched in between these peat swamps are deltaic sand and mud deposits in which abundant *Rhacophyton* [U1513] and *Archaeopteris* foliage and some stems, along with a tree lycopod similar to *Protolpidodendropsis pulchra*, are preserved. Other plant remains in deltaic deposits include cupules and seeds. The occurrence of this aneurophyte or “pre-fern” in wetland (peat) and better-drained soils supports the idea that *Rhacophyton* was broadly tolerant of soil differences (Scheckler 1986).

Non-peat-accumulating swamps, in general, are muddy because of a high water table in these immature soils of low relief. If we were to slog our way through these floodplains—we would not actually easily walk—we would want to keep our feet on top of the plant cover rather than stepping in the mud between them. Late Devonian swampy areas were dominated by the shrubby, scrambling *Rhacophyton*, making it easier for our trek, with possible rare occurrences of *Barinophyton*, the scrambling horsetail *Sphenophyllum*, and the plants that bore *Eviostachya* reproductive cones (strobili). We would encounter early seed plants, such as *Elkinsia* (Fig. 15.4) on slightly higher ground and growing on better-drained soils of the stream margins. Lining the rivers, growing a kilometer or so into the floodplain, or on slightly higher topographies, back of the coastal area, were stands of *Archaeopteris*. Tree lycopsids, the systematic affinities of which are not yet known, grew somewhere between the wettest peat and muddy *Rhacophyton* swamps and the gallery progymnosperm forests. These forms may be precursors to the giant scale trees of the Carboniferous (see Chaps. 12 and 13), but the most unique aspect of these landscapes is the appearance of the earliest seed-bearing plants, the gymnosperms. *Elkinsia* is the early seed plant that is most extensively known in the plant fossil record, to date (Rothwell et al. 1989; Serbet and Rothwell 1992). It has been reconstructed (Box 15.2) with a main stem with a rather unique anatomy [U1514]. In Late Devonian, seed-bearing plants



Fig. 15.3 *Rhacophyton*, a fern-like plant. (a) Charcoalified remains of *Rhacophyton*, with a pinnate branching pattern (image courtesy of Walter Cressler). (b) Anatomy of central axis showing secondary, woody tissues (from Dittrich et al. (1983) *Anatomy of Rhacophyton ceratangium* from the Upper Devonian (Famennian) of West Virginia. *Rev. Palaeobot. Palynol.* 40:127–147 with permission from Elsevier); (c) Reconstruction of vegetative and fertile parts of the plant (from Andrews and Phillips (1968), *Rhacophyton* from the Upper Devonian of West Virginia, *Bot. J. Linn. Soc.* 61 (284): 37–64, with permission from Oxford U. Press)

Box 15.2: The Early Seed Plant *Elkinsia*

The plant *Elkinsia* has a three-lobed vascular conducting strand usually consisting of only primary xylem. This is surrounded by a “sparganum” cortex, a feature seen in the lyginopterid seed ferns (see McLoughlin and Bamford in Chap. 12), characterized by a distinctive outer cortex of reinforced cells forming a pattern like Roman numerals on a clock face in cross section. When leaves emerged from the stem, a lobed leaf trace divided into two C-shaped bundles in the leaf and then divided up to four times more. Vegetative leaves are *Sphenopteris*-like in their leaf architecture. Cupulate organs (seeds) and synangia (pre-pollen organs) terminated fertile axes that divided in a cross-shaped organization and lacked leaves (Serbet and Rothwell 1992). Scheckler (1986) suggested that *Elkinsia* was a pioneering plant and Prestianni and Gerrienne (2010) concur. We could walk through similar Late Devonian landscapes in other parts of the world and witness similar vegetation and community organization. These include: Red Hill in Pennsylvania, USA; Taff’s Well

and Avon Gorge, Great Britain; Kerry Head, Ireland; the Condroz sandstones, Belgium; and Oese, Germany (Prestianni and Gerrienne 2010). Many of these sites contain Late Devonian plants that are preserved away from their site of growth, often in marginal marine or lagoonal sediments. Here, plants may be associated with other biotic components of the Late Devonian biosphere. We’ll stop first at Red Hill near North Bend, less than a kilometer north of highway 120 in Gleasonston, Pennsylvania, USA.

diversified [U1515] and spread across the landscape, beginning to alter the planet’s vegetation. 271
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15.2.2 Red Hill, Pennsylvania 273

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As the name implies, the Red Hill locality exposed a Late Devonian succession of red, primarily, mudrock (Fig. 15.5). 275
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Fig. 15.4 The earliest known seed-bearing *Elkinsia*. (a) A reconstruction of the branching architecture on which both leaf-bearing and ovule-bearing axes occurred. (b) Laminate pinnules terminating axes. (c) Terminal cupules (ovule-bearing). (d) Thin section of ovule showing cupule (c) micropyle, and megaspore membrane (m). (modified from Serbet and Rothwell 1992)



277 What is unique about this Famennian (372–359 Ma) 297
 278 sequence is the array of arthropods, fish, and early tetrapods 298
 279 (vertebrates) with anatomical features that indicate these fish 299
 280 and fish-like amphibians could survive out of the water. 300
 281 Fossil plants, the base of this food chain, are preserved in one 301
 282 thin interval but served as the habitat for terrestrial inverte- 302
 283 brates including trigonotarbid arachnids and myriapods, 303
 284 both of which have been recovered from the site (Daeschler 304
 285 and Cressler III 2011). The succession consists of sandstone 305
 286 deposited in river channels, siltstone that filled abandoned 306
 287 freshwater channels and lakes, and floodplain paleosols adja- 307
 288 cent to these ancient bodies of water. 308

289 The Red Hill paleoenvironment was an alluvial floodplain 310
 290 with meandering rivers often overflowing their banks and 311
 291 burying the vegetation associated with Vertisols (soils with 312
 292 shrink-swell clays) and Calcisols (calcium-rich soils). 313
 293 Meandering river channels produced an ever-changing envi- 314
 294 ronment, with abandoned channels becoming quiet-water 315
 295 lakes in which a teeming vertebrate community existed. 316
 296 Remains of both plants and terrestrial arthropods are pre-

served in oxbow lake or pond deposits [U1516]. Plants 297
 include the progymnosperm *Archaeopteris*, the pre-fern 298
Rhacophyton, barinophytes, two kinds of tree size lycopsids, 299
 and seed plants (mostly represented by their cupulate ovules, 300
 and some foliage that may belong to this lineage; Cressler 301
 2006; Cressler et al. 2010). Similar to other Late Devonian 302
 landscapes, *Archaeopteris* canopies were underlain by a 303
Rhacophyton understory with various scrambling plants 304
 occupying the groundcover, most likely in light breaks. In 305
 more open sites, lycopsids grew adjacent to oxbow lakes and 306
 ponds, and seed plants colonized disturbed areas or those in 307
 which soil drainage was better. Channel deposits contain the 308
 vertebrate assemblage. 309

Fish and some of the earliest tetrapod fossils are pre- 310
 served in freshwater lenses of silty mudrock in shallow 311
 channel margin, floodplain pond, and overbank pond depos- 312
 its. Here, a stem tetrapod found outside of coeval rocks in 313
 Greenland was identified based on two shoulder bones (i.e., 314
 cleithrum* and scapulacoracoid). The shoulder-bone fea- 315
 tures in *Hynerpeton* are advanced, indicating that the animal 316



Fig. 15.5 The Famennian age, char-bearing outcrop at Red Hill, Pennsylvania, USA. (photo PG Gensel)

317 was capable of both supporting its body and powering itself
 318 on land [U1517] (Daeschler et al. 1994). *Hynerpeton* and
 319 the more complete, three-dimensionally preserved *Tiktaalik*
 320 from Ellesmere Island, Arctic Canada (Daeschler et al.
 321 2006), record the transition between fish with fins and tetra-
 322 pods with limbs and digits. In addition to the shoulder gir-
 323 dle, an unusual, isolated humerus* and jaw fragments of
 324 two different tetrapods have been collected. A single bone
 325 from the snout of a tetrapod resembles that of an Early
 326 Carboniferous tetrapod, *Pederpes*, from Scotland (Daeschler
 327 et al. 2009). These are our deep time ancestors. Without
 328 their transition from a fully aquatic to a terrestrial life strat-
 329 egy, all higher vertebrate groups we've seen would not have
 330 existed. But, because we did evolve from these stem tetra-
 331 pod groups, it's now only a short 4-h drive north from Red
 332 Hill to the town of Gilboa, New York, where our next post-
 333 card is located.

15.2.3 Gilboa Quarry, New York, USA

Patricia G. Gensel

The localities we now visit in eastern New York State dem-
 onstrate that diverse forests, where large trees of different
 affinities grew in abundance, occurred very early in time.
 Here, those trees were not only leafless but also evolved a
 very different type of rooting structure to fix themselves in a
 poorly developed soil. We will have to make our way through
 at least two plant lineages living in the understory, each of
 which grew in a slightly different mode. Undoubtedly, vari-
 ous types of arthropods and spiders, as recognized from their
 fossilized exoskeletons (cuticles), were scuttling around in
 the undergrowth (e.g., Shear et al. 1987, 1989).

Late Middle Devonian fossil-tree stumps, preserved in
 life position and bearing radiating roots, were discovered in
 the 1870s at several horizons in the Riverside Quarry at
 Gilboa, New York [U1518]. These tree stumps were named
Eospermatopteris by one of the first female paleontologists,

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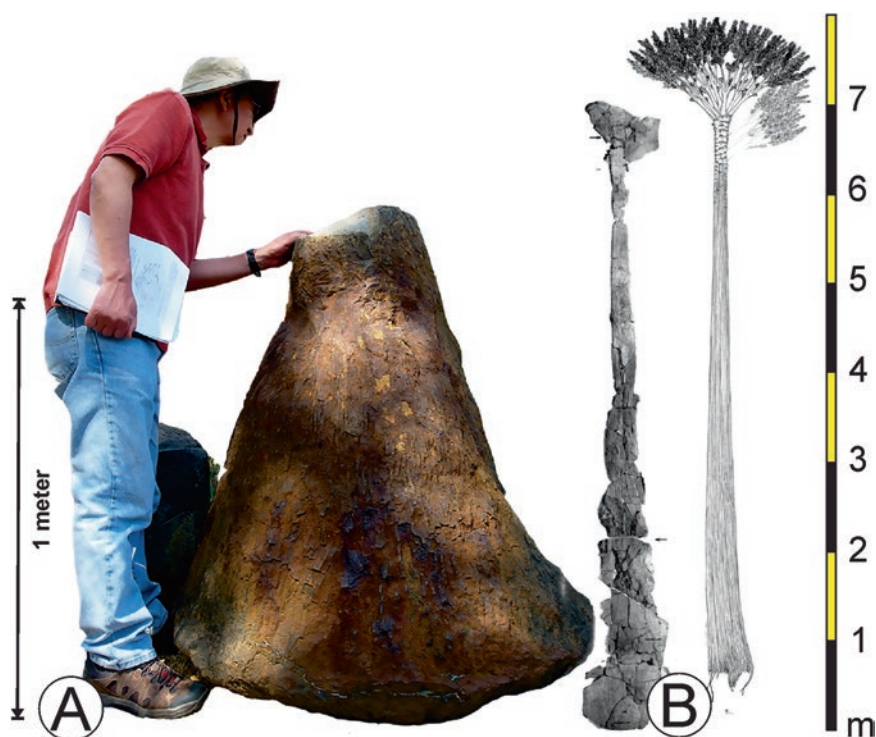
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Fig. 15.6 The Middle Devonian cladoxylalean fern, *Eospermatopteris*. (a) Stump excavated from Schoharie Reservoir, Gilboa, New York. (photo: R.A. Gastaldo) (b) Tree cast and reconstruction of cladoxylalean fern (from Stein et al. 2007, Giant cladoxylalean trees resolve the enigma of Earth's earliest forest stumps at Gilboa (Nature 446 (7138) with permission, Springer Nature)



352 Winifred Goldring (1924; Fig. 15.6), and were widely cited
 353 as evidence of the Earth's "oldest forest" (e.g., Goldring
 354 1927). These trees were not restricted to the quarried expo-
 355 sure because *Eospermatopteris* stumps also were found in
 356 nearby outcrops. In the early 2000s, impressions and flat-
 357 tened stem casts extending across a quarry floor not far from
 358 the Gilboa site, at South Mountain, showed a basal trunk
 359 comparable to *Eospermatopteris* and a crown region with
 360 attached, digitately divided, upward-extending branch sys-
 361 tems (Fig. 15.6). Each branch division bore sterile and fertile
 362 appendages that allowed their identification with plants pre-
 363 viously known from Belgium and Venezuela as the cladoxyl-
 364 oloid *Wattieza* (Pseudosporochnales) (Stein et al. 2007).
 365 *Wattieza* is a very strange plant [U1519]. It grew to a height
 366 of at least 8 m with a trunk bearing large branches in verti-
 367 cal ranks (Stein et al. 2007). The much-divided branches bore
 368 smaller divided, leafless terminal units that, in some cases,
 369 bore sporangia that shed spores. These trees belong to an
 370 extinct group, the pseudosporochnaleans, sometimes
 371 believed to be related to ferns—new data may revise that
 372 idea. It appears that the stems were fast-growing and
 373 "cheaply" constructed. The center of these trunks was hol-
 374 low and encircled by many conducting (vascular) strands in
 375 the periphery (Stein et al. 2012). The trunks were surrounded
 376 by roots near the base, with a growth strategy similar to liv-
 377 ing palms or tree ferns. The sedimentology indicates a series
 378 of burial events affected these forests which were frequently
 379 disturbed, followed by their reestablishment in new soil hori-
 380 zons. Looking at the face of a rock exposure, if lucky enough,

provides a view about the spacing of trees along a single
 plane. To understand the forest structure, though, you have to
 be able to see it from above.

Stein and others were able to access the original Riverside
 Quarry site for a limited time when the area was cleaned of
 backfill and the quarry floor exposed. That exposure revealed
 remnants of a forest at soil level. New *Eospermatopteris*
 casts were retrieved from the backfill, and the cleaned forest
 floor showed numerous root mounds with radiating axes and
 a central depression (representing the base of the plant) with
 downward growing roots. A large portion of the quarry was
 plan-mapped and displayed the spatial distribution of the
Eospermatopteris/Wattieza plants (the two named fossil-
 genera can be referred to the same reconstruction of an
 ancient "whole plant"). These trees often grew in clusters
 and were of different diameters at the time of preservation,
 suggesting an uneven aged stand (Stein et al. 2012). Roots
 extend from above the bases outward across the paleosol as
 well as downward from the basal region. Another important
 discovery was that at least two other plant types were found
 on the forest floor. One is a woody rhizome with adventitious
 roots and aerial branch systems. The branching pattern in
 aerial axes, along with the anatomy preserved in the rhizome,
 is consistent with these plants being related to the aneuro-
 phytalean progymnosperms, a group that is known from
 numerous other Middle Devonian localities. Like
Archaeopteris, aneurophytes grew woody stems and repro-
 duced by spores but were smaller in stature (as presently
 known) and presumed to have been leafless and shrubby

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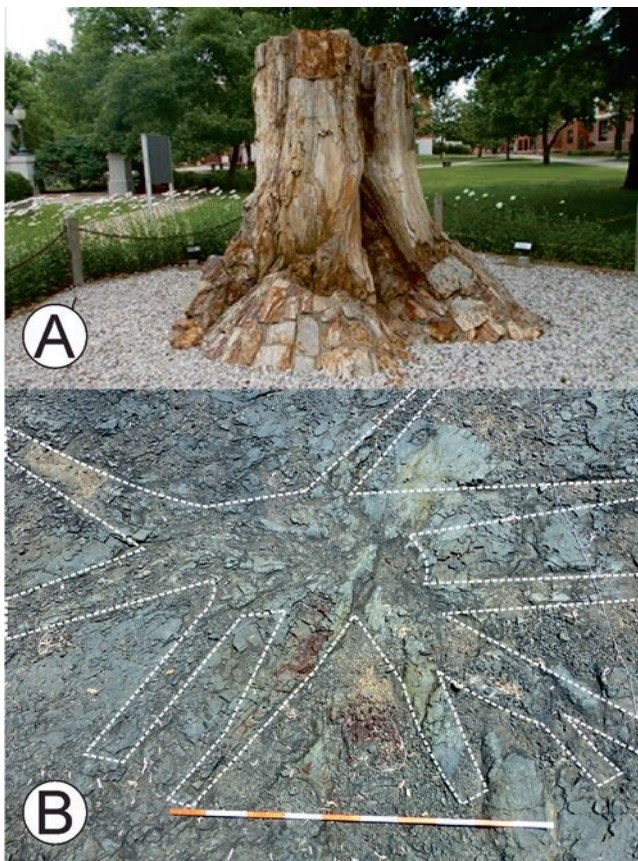


Fig. 15.7 Trunk and tree base of *Archaeopteris*. (a) Silicified stump (photo: PG Gensel). (b) The tree base and rooting structure of *Archaeopteris* outlined on a paleosol exposed in the Cairo Quarry, Town of Cairo Public Works, New York, USA. (photo: R.A. Gastaldo)

410 [U1516]. The rhizomes curve around the bases of
 411 *Eospermatopteris* (*Wattieza*) tree bases, and sometimes
 412 approach them as if, in life, they may have been vines. The
 413 anatomy and branching system of these scrambling vines are
 414 similar to the aneurophytalean *Tetraxylopteris*. A few of
 415 these are preserved up to 4 m in length, associated with distal
 416 branches of an upright tree lycopsid [U1520], indicating the
 417 heterogeneous nature of this forest.

418 The forests in Gilboa are interpreted to have grown in a
 419 coastal wetland setting, with frequent marine incursions that
 420 buried successive forests. Originally, the paleoenvironment
 421 had been interpreted as a wetland swamp, but the underlying
 422 paleosol is well-developed, as are those from other Devonian
 423 sites (Morris et al. 2015) and may indicate that these plants
 424 grew in better drained conditions. Stein et al. (2012) indi-
 425 cated that this forest type may not be too different from
 426 coeval *Archaeopteris*-dominated ones. It is, therefore, inter-
 427 esting that an exposed quarry floor in nearby Cairo,
 428 New York, provides evidence that both *Eospermatopteris*
 429 and *Archaeopteris* coexisted, the latter being more abundant
 430 (Fig. 15.7). *Archaeopteris* has a rooting system that is
 431 broadly spreading and branched and is considered to pene-

trate more deeply into the soil (Fig. 15.7). Hence, the rooting
 architecture of this plant is more modern-looking and, per-
 haps, altered soil composition and weathering patterns in the
 latest Devonian (Algeo and Scheckler 1998, 2010; Algeo
 et al. 2001; Stein 2018). There is evidence that these soils
 also supported other groundcover.

Smaller plants, of various systematic affinities, probably
 grew under or around these trees. The apparently rhizoma-
 tuous lycopsid *Leclercqia* is abundant in the Gilboa region
 (Banks et al. 1972), and the zosterophylls *Serrulacaulis* and
 cf. *Sawdonia* sp. (Hueber and Banks 1979; Hueber and
 Grierson 1961) are preserved in nearby deposits of similar
 age. Several genera of aneurophytaleans also are known,
 including *Relimmia* and *Tetraxylopteris*. Most likely we only
 know of their more distal (terminal) branch systems, rather
 than the entire plant, itself. And, several authors think that
 some of these plants were shrubby besides their interpreted
 scrambling or nearly lianous growth strategies. The pseudo-
 sporochnelean *Calamophyton* is represented in North
 America by its distal branch systems, but nearly whole plants
 were recently described from quarries in Germany [U1521]
 (Giesen and Berry 2013).

15.3 Middle Devonian Coastal Marshes

Robert A. Gastaldo

Only about 900 km geographically from the Gilboa forests
 of New York State, but nearly eight million years older in
 time, we head to Devonian rocks exposed in the conifer for-
 ests of northern Maine, USA (Fig. 15.8a, d). Here, our post-
 card is of an idyllic trout stream in Baxter State Park, where
 the air is scented by balsam fir resins, are the remnants of
 latest early (Emsian) or earliest middle (Eifelian) Devonian
 rocks [U1522]. The outcrops, exposed at the surface follow-
 ing the last glacial episode that scoured this landscape some
 12,000 years ago, are not very impressive. All of these are of
 low relief, and many are covered in a carpet of recent mosses
 and club mosses, and we do not have to go back thousands of
 years in time to understand why the fossil plants preserved in
 the Trout Valley Formation became a turning point in our
 insight into early terrestrial communities. For that, we have
 to turn our attention to the second half of the twentieth
 century.

The United States Geological Survey (USGS) began a
 national mapping program following the end of the Second
 World War, targeting rural parts of the country that had, yet,
 to be detailed. Douglas Rankin, a USGS geologist, spent part
 of his early career with the Maine Geological Survey and
 began mapping northern Maine. Here, he discovered what
 looked to be compression-impression remains of rare plant
 fossils then known as “psilophytes”. These were examined

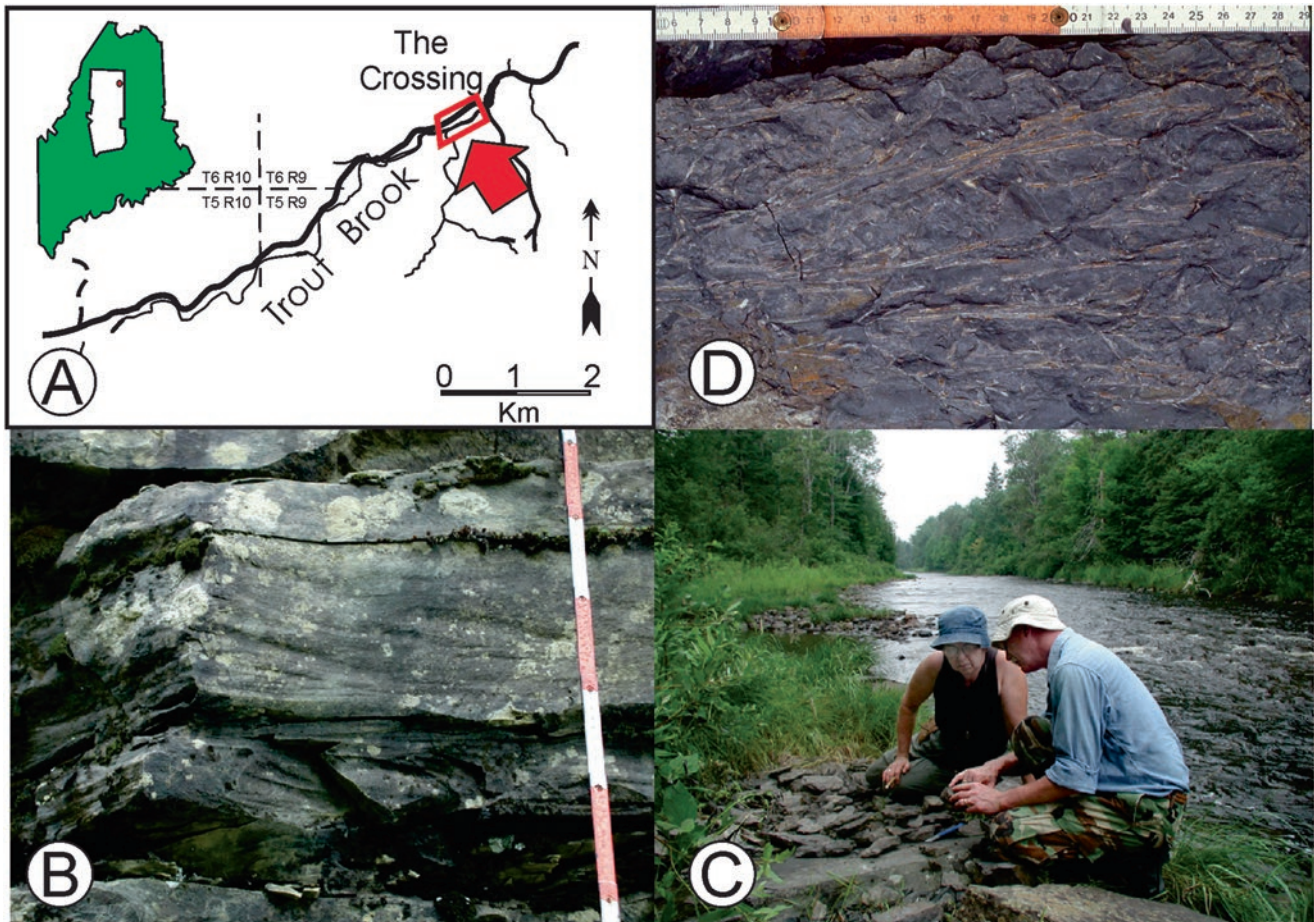


Fig. 15.8 Middle Devonian Trout Valley Formation, Maine, USA. (a) Outcrop localities along Trout Brook, Baxter State Park, Maine. (b) Low-angle trough cross-bedded siltstone of tidal origin in which the fossil flora is preserved. (c) Glacially exposed, fossiliferous bedrock along the margins of Trout Brook. P. Gensel and J. Allen. (d) Bedding surface of tidal siltstone in which biotically oriented axes of *Psilophyton* are exposed. Scales in dm and cm. (photos: RA Gastaldo)

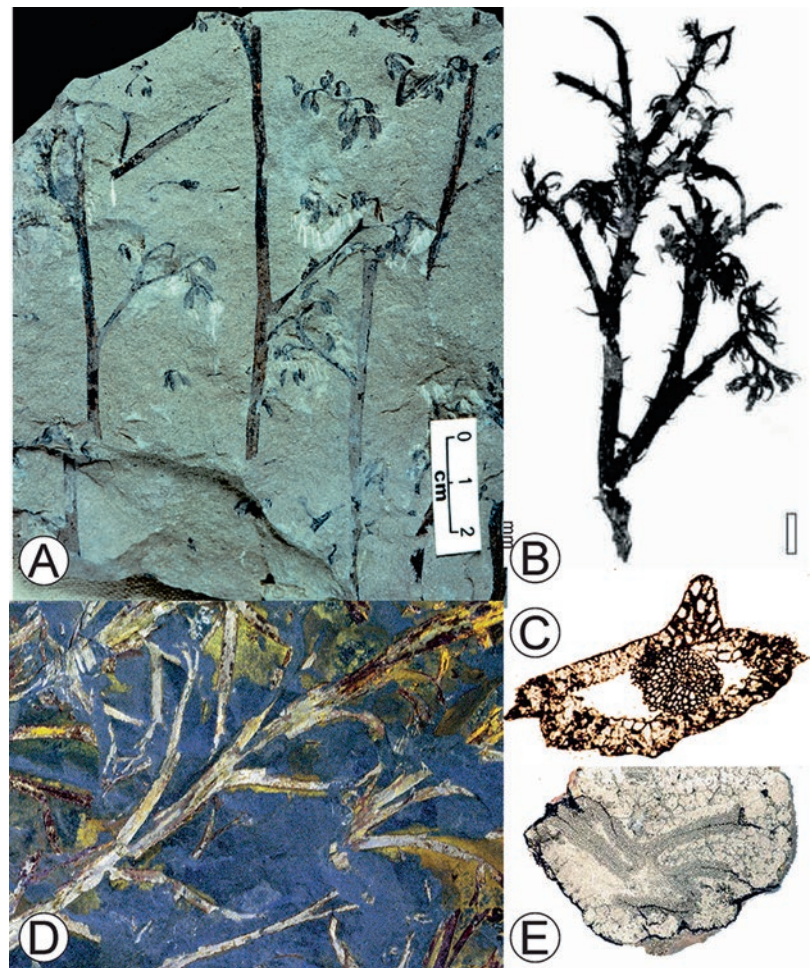
481 by Erling Dorf who recognized their significance, and one of
 482 the first reports on these plants was published shortly there-
 483 after (Dorf and Rankin 1962). With the recognition that early
 484 land plants are preserved in Maine and in coeval strata of
 485 New Brunswick, Canada, a series of studies over the past
 486 60 years have added to our understanding of their evolution-
 487 ary history and paleoecology (e.g., Kasper Jr et al. 1988;
 488 Allen and Gastaldo 2006). Both the environmental setting
 489 and the early land plants, themselves, are very different from
 490 the mosses and club mosses now covering the floor of
 491 Maine's northern balsam fir forests.

492 Rocks of the Trout Valley Formation were deposited as
 493 pebble conglomerate, fluvial and nearshore (marine) sand-
 494 stone bodies, and muddy tidal flats. These sediments repre-
 495 sent an estuarine coastal zone flanking an extinguished
 496 volcanic island, the remnants of which are now the Traveler
 497 Rhyolite against which the Trout Valley rocks lie (Allen and
 498 Gastaldo 2006). There is some evidence of in situ (autoch-
 499 thonous) preservation of the vegetation, in the form of very
 500 fine, vertically oriented rootlets, which colonized the mud-

flats [U1523]. But, the majority of fossil material is preserved
 on the bedding surfaces of tidal channels that traversed the
 mudflats (Fig. 15.8c, d). Here, aerial axes up to 50 cm in
 length, with lateral dichotomizing appendages, are aligned
 parallel to one another, (Fig. 15.8c) mimicking their original
 growth architectures in life. This "biological" orientation is
 the result of fibrous, longitudinal tissues, appearing as stria-
 tions, which developed in the walls of these thin axes to
 assist in an erect growth habit. The two most conspicuous
 plants are *Psilophyton* and *Pertica* (Fig. 15.9), true vascular
 plants assigned to the early group called trimerophytes
 [U1520]. Intermixed or interbedded with dense *Psilophyton*
 and *Pertica* mats are other vascular plants belonging to vari-
 ous early clades [U1524]. These include *Sciadophyton*
 (embryophyte of unknown affinity); *Sporogonites* (a possi-
 ble bryophyte); *Taeniocrada* (rhyniophyte); and
Drepanophycus, *Kaulangiophyton*, and *Leclercqia* (lycop-
 sids; Andrews et al. 1977; Kasper Jr et al. 1988; Allen and
 Gastaldo 2006).

Fig. 15.9 Middle Devonian “trimerophytes”.

(a) *Psilophyton forbesii* showing pseudomonopodial main axes from which laterals branched dichotomously (3×; photo PG Gensel). (b) *Psilophyton crenulatum* recovered via maceration (Yale University image). (c) *Psilophyton coniculum* stem anatomy (from Trant and Gensel 1985, *Branching in Psilophyton: a new species from the Lower Devonian of New Brunswick*, *Am. J. Bot.* 72(8): 1256–1273, with permission from Wiley Press); (d) *Pertica quadrifaria*. (photo RA Gastaldo). (e) Axial anatomy of a new taxon reminiscent of *Pertica* (photo courtesy of PG Gensel)



520 The biotically oriented assemblages in the Trout Valley
 521 Formation are unusual for several reasons. Trimerophyte,
 522 rhyniophyte, and lycophyte remains are preserved in associ-
 523 ation with molluscan bivalves of various affinities, eurypter-
 524 ids, and trace fossils (ichnofossils), all of which are
 525 interpreted from brackish water (estuarine) settings [U1525]
 526 (Selover et al. 2005; Gastaldo 2016). Hence, it seems plau-
 527 sible that these early colonizing plants were tolerant of fluc-
 528 tuating coastal salinities. If true, this interpretation may also
 529 explain two facets of their preservation. Trimerophytes grew
 530 aerial axes from a surficial or shallowly buried axis or rhi-
 531 zome. Yet, the only evidence of rooting structures is verti-
 532 cally oriented rootlets that are unattached to a rhizome.
 533 Similarly, there is no evidence that the biotically ordered
 534 axes (Fig. 15.8d) are attached to any rhizomatous organ. The
 535 axis from which these plants developed is missing. Second,
 536 most of these aerial axes rotted and filled with mud before
 537 burial, resulting in internal casts. Saltwater incursion into
 538 these marshlands in response to coastal subsidence, then,
 539 would be responsible for their death, loss of any evidence of
 540 rhizomes through rotting, and the easy transport via tidal
 541 activity of the aerial axes into tidal channels where they are

preserved. We have to dare to head farther northward into
 eastern Canada where these plant groups are best preserved
 to gain insights into coastal plains of the Devonian.

15.4 Late Early Devonian Floras of Gaspé and New Brunswick: Coastal Margins and Intermontane Rivers and Lakes

Patricia G. Gensel

Several localities in the Canadian provinces of New
 Brunswick and Quebec have been the source of information
 about Emsian (408–393 Ma) plants since the initial descrip-
 tion of the genus *Psilophyton* by Dawson (1859) from the
 Gaspé Peninsula, Quebec, and adjacent regions of northern
 New Brunswick. Dawson (e.g., 1870, 1871) described other
 plant taxa, some included in *Psilophyton* and some not.
 Additional collections and studies by paleobotanists in both
 areas, especially in past decades, have clarified various taxa
 and produced a picture of a diverse late Early Devonian flora.
 These plants are mostly smaller and simpler than those from

560 the Middle Devonian but include some that provide indica-
561 tions of the ones known mainly from the Middle Devonian.

562 **15.4.1 Gaspé Battery Point Formation (Gaspé** 563 **Sandstone Group), Emsian**

564 The Battery Point Formation, outcropping on both the north
565 and south shore of Gaspé Bay, Quebec, Canada, consists of a
566 coarsening-up clastic wedge, located at 10–20° S latitude in
567 Emsian times. This paleolatitude places it near the equator
568 with a prevailing tropical climate. Unlike Red Hill (see Sect.
569 15.2.2), there are no calcretes or other sedimentary features
570 indicative of seasonal dryness, and the plants probably grew
571 under moderate rainfall. The Cap-aux-Os Member is the
572 most plant-rich component of the Battery Point Formation
573 and has been extensively studied sedimentologically (e.g.,
574 Griffing et al. 2000). It is in this depositional context that we
575 understand these early Devonian plants.

576 The sedimentary facies in the Cap-aux-Os Member are
577 dominated by sandstones of various internal architectures,
578 and three different fluvial associations are identified. River
579 deposits at the base of the succession are large multistory
580 sandstone bodies with interbedded thinner mudstone
581 (Association 1). These rocks are overlain by gray mudstone
582 with thin sandstone sheets or single-story sandstone bodies
583 (Association 2). The uppermost interval (Association 3) con-
584 sists of relatively coarse-grained, multistory sandstone bod-
585 ies with uncommon thinner red mudstone intervals [U1526].
586 There is evidence of bedding with wave- or current-ripple
587 marks, trace fossils, and disarticulated cephalaspid fish skel-
588 etons in some intervals. Desiccation-cracked mudstones pre-
589 serve articulated lingulid brachiopods, and in dark gray shale
590 and siltstone acritarch microfossils, small bivalves, and bra-
591 chiopods can be found. The most current interpretation is
592 that these rocks represent fluvial and delta-plain deposits
593 close to the coastline, with some intervals interpreted as hav-
594 ing been close to the tidal limit of tidally influenced lowlands
595 (Griffing et al. 2000; Hotton et al. 2001). The vegetation that
596 grew across these coastal zones commonly is found at or
597 near their sites of growth.

598 Many fossil-plant assemblages, buried in situ, form
599 monospecific stands, although attached rooting structures
600 are not found. Rather, putative rhizomes and rooting struc-
601 tures are preserved in other intervals and may extend into
602 underlying beds beneath some axes (Elick et al. 1998; Gensel
603 and Berry 2001; Hotton et al. 2001). Plants preserved near
604 their sites of growth include the majority of trimerophyte and
605 rhyniophyte remains. Hotton et al. (2001) note that these
606 occur in shaley (mudstone) drapes over channel-form sand-
607 stone bodies. They suggest that the plants were growing
608 along channel margins or channel bar tops and probably
609 detached and transported a short distance prior to burial.

Others, especially zosterophylls, were established in low, 610
wet areas and buried by flood deposits. A few plants may 611
have had specific growth conditions limiting their distribu- 612
tion. For example, the zosterophylls *Sawdonia ornata* and 613
Crenaticaulus [U1527], commonly found associated with 614
brackish and marine invertebrate fossils, are interpreted as 615
being located near a coastline where washover occurred. 616
Spongiophyton and *Prototaxites* were transported, some- 617
times in a more fragmentary form, from floodplains or a 618
riparian habit, and deposited in channel-bar and channel-fill 619
deposits of main river channels. But, one genus of early plant 620
is cosmopolitan. 621

622 In our rambles, we will encounter large stands of
623 *Psilophyton*, probably along the river channel margins and
624 within stands of different zosterophylls in some of the
625 marshes (see Sect. 15.3). *Psilophyton* plants grew to a height
626 of several decimeters with slender (c. 4 mm), dichotomizing
627 stems (Fig. 15.9b). Lateral branches divided in a similar pat-
628 tern and are either the same or slightly smaller diameter than
629 the central erect axes. They terminate in pointed (acuminate)
630 tips or pairs of spindle-shaped (fusiform) sporangia, forming
631 loose clusters, and which dehisce (burst open) longitudinally
632 [U1528]. The plant's anatomy consists of an unlobed core of
633 vascular tissue in which the first developed conducting cells
634 differentiate in the center. This anatomy is seen to persist in
635 lateral branches. The anatomy of one of its species,
636 *Psilophyton dawsonii* from the south shore of Gaspé, is the
637 most completely known. As we've seen previously,
638 *Psilophyton* is a very common element in Gaspé and New
639 Brunswick and the Trout Valley Formation in Maine. It also
640 is known from the early Devonian of Wales, England,
641 Belgium, possibly the Czech Republic, and Germany. Only
642 one species is recorded in China and is of Pragian age (411–
643 408 Ma). However, some early referrals of plant remains to
644 *Psilophyton* have since been shown to be inaccurate. The
645 devil lies in the details, also in plant identification, as we will
646 see when studying some of Gaspé's plant fossils.

647 Some rooting structures, or “rhizomes,” from Gaspé,
648 attributed to *Psilophyton* by Dawson, are now known to rep-
649 resent another plant (Hotton et al. 2001). Their anatomy is
650 very different from what we know from *Psilophyton dawso-*
651 *nii*. Smooth, wide axes, bifurcating at long intervals, bear
652 rounded scars and exhibit a dark central strand. Unpublished
653 specimens show similar axes with laterally attached ovoid
654 sporangia with a thickened base (Gensel, pers. obs.), leaving
655 a round scar when detached and, thus, are similar to
656 *Stockmansella* (Fairon-Demaret 1985, 1986). That taxon,
657 along with *Rhynia*, is currently viewed as part of the
658 Rhyniopsida (Kenrick and Crane 1997). The Gaspé plant's
659 water-conducting cells also resemble *Stockmansella* in
660 exhibiting a unique wall pattern, with tiny holes perforating
661 the walls and randomly oriented thickenings (Hueber 1983;
662 Hotton et al. 2001; Gensel pers. obs.). A second taxon from

663 this clade, *Huvenia*, may also be present in the Gaspé flora
 664 (Hotton et al. 2001). Rooting structures were not the only
 665 plant remains erroneously referred to as *Psilophyton* in the
 666 past.

667 *Psilophyton princeps* var. *ornatum* was described by
 668 Dawson based on vegetative remains, and its actual affinity
 669 was questioned for many years. Ultimately, the plant's suite
 670 of characters was recognized as similar to the zosterophyl-
 671 lophytes, and the plant renamed *Sawdonia ornata* (Hueber
 672 1971). Stems are covered in tapered spine-like emergences
 673 and are similar to specimens from Abitibi River, Ontario, in
 674 which lateral sporangia occur (Hueber 1964; Hueber and
 675 Banks 1967). *Sawdonia* and other anatomically preserved
 676 zosterophylls exhibit an ovoid water-conducting central cyl-
 677 nder, which develops from the outside to the center (the
 678 opposite direction of what we know from *Psilophyton*).
 679 Recently studied fertile remains from Gaspé also reveal dif-
 680 ferences on the lateral sporangia of the plant, which are
 681 short-stalked and possess two valves of unequal size, with
 682 emergences covering the larger abaxial valve (Gensel and
 683 Berry 2016). Apart from rooting structures now referred to as
 684 rhyniopsids and vegetative remains reidentified as
 685 zosterophylls, stems initially attributed to *Psilophyton* were
 686 found to be different taxa as well.

687 Large stems up to 1 cm wide, from which regularly
 688 arranged lateral branches grew, terminating in tight clusters
 689 of fusiform* sporangia, are now attributed to the trimerophy-
 690 phytes (Banks 1968). These plants also occur at Cap-aux-Os.
 691 One taxon was based on specimens originally labeled
 692 *Psilophyton robustius* (Dawson 1871) and was redescribed,
 693 more than 80 years later, as *Trimerophyton robustius* by
 694 Hopping (1956). These large axes exhibit a lateral branching
 695 pattern that divides into three branches (trichotomous),
 696 instead of two, with some branches terminating in tight clus-
 697 ters of sporangia. Other specimens, possibly from the same
 698 sequence, were described as *Pertica varia* by Granoff et al.
 699 (1976). The plant fossils consist of up to 0.75 m-long, incom-
 700 plete main axes from which regularly arranged, clearly sec-
 701 ondary lateral branches depart. These laterals may retain a
 702 central branch or continue to subdivide dichotomously. Some
 703 of the more dichotomous branches terminate in tight clusters
 704 of sporangia. These plants may represent the tallest of known
 705 late Early Devonian vascular plants and probably attained
 706 heights of a few meters. But, trimerophytes and zosterophylls
 707 were not the only Emsian coastal zone vegetation.

708 Lycopside obtained from the Battery Point Formation
 709 include *Drepanophycus spinaeformis*, a plant with branching
 710 rhizomes, possible rooting structures and short to long, some-
 711 times curved (falcate) leaves (Grierson and Hueber 1967).
 712 Fertile remains of these plants from New Brunswick show
 713 that stalked sporangia developed along the stem and occur
 714 among the leaves (Li and Edwards 1995). *Renalia hueberi*,
 715 probably an early member of the lycophyte lineage, occurs at

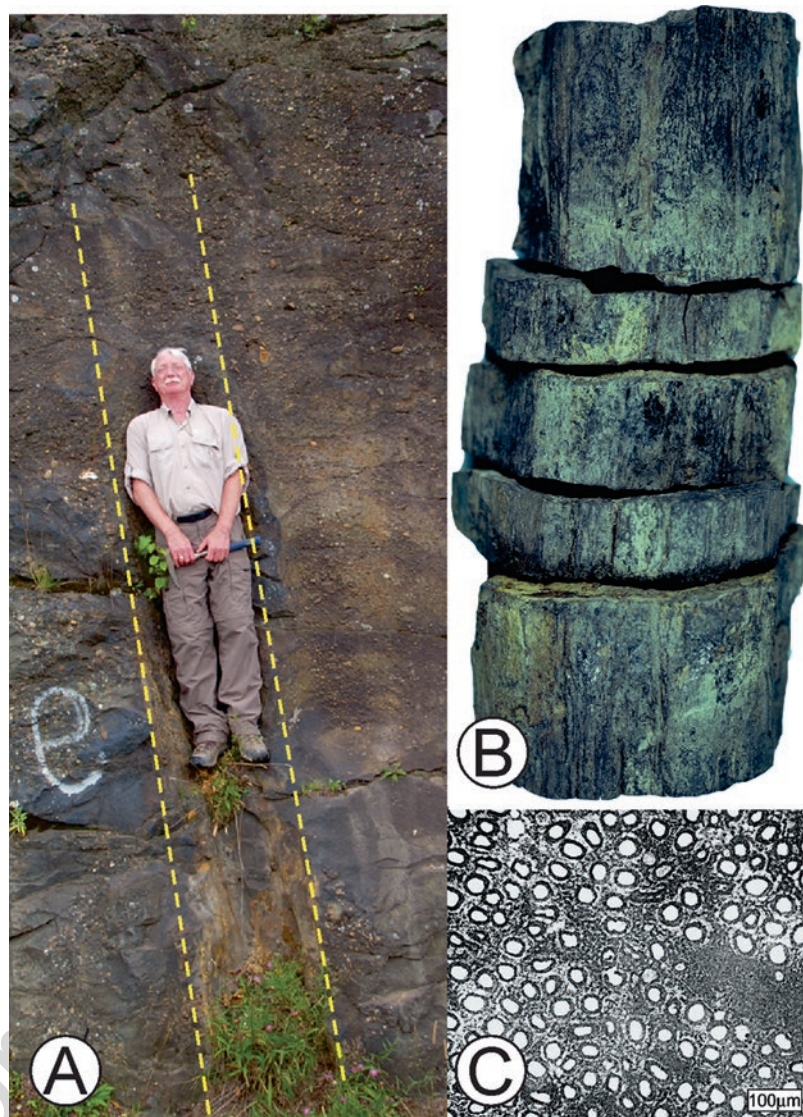
a different outcrop on the north shore of Gaspé Bay (Gensel
 1976). The main stems are tiny, the axes of approximately
 1 mm in width, and specimens are up to only a few centime-
 ters in length. Lateral branches divide unequally and may be
 terminated in kidney-shaped (reniform) sporangia. A dark
 strand evident in stems indicates the presence of vascular tis-
 sue but cellular patterns are unknown. There are other plant
 types noted and described from this locality (Andrew and
 Gensel 1984; Hotton et al. 2001), but we end our postcard
 tour of the Gaspé with mention of a most enigmatic plant.

Prototaxites is the elephant in the Emsian room. It is a
 giant (Fig. 15.10). Dawson (1859) first described the taxon
 based on silicified trunk-like structures and, now, it is known
 to occur not only in the Gaspé Bay area but also at Pointe-a-
 la-Croix, Gaspé, in northern Maine, and several other Early
 to Late Devonian localities in the United States, Europe, and
 North Africa [U1529]. The best-preserved specimens consist
 of wide "stems" that attained nearly 1 m in diameter, whereas
 Moroccan specimens are up to 8 m in length (Boyce et al.
 2007). Various ideas as to what these "logs" represent have
 been presented, ranging from a prototypical conifer (Dawson)
 to alga, rolled-up liverwort, and even fungus. Hueber (2001)
 suggested the preserved structures most closely resemble the
 fruiting body of a fungus. This, in turn, raises questions
 about a carbon source for such a large organism and has
 spurred additional research resulting in some controversial
 interpretations of this organism (Graham et al. 2010;
 Retallack and Landing 2014). However, we will not delve
 into this scientific discussion here and instead travel further
 to northern New Brunswick.

15.4.2 Campbellton Formation, Emsian, New Brunswick: Enlarging our Postcard View of an Early Devonian Landscape

Driving along the winding New Brunswick coast on Route
 132 for about 4 h, we eventually arrive in Campbellton. We
 will briefly visit another Early Devonian locality of northern
 New Brunswick contemporaneous, in part, with Gaspé.
 Here, plants are preserved in both coastal and inland settings.
 Outcrops of the Campbellton Formation extend, discontinu-
 ously, from Campbellton to Dalhousie, New Brunswick (not
 Nova Scotia). Detailed stratigraphic studies by Kennedy and
 Gibling (2011), along with a subsequent consideration of the
 depositional environments and plants preserved therein,
 were published by Kennedy et al. (2012). The western-most
 outcrops near Campbellton were deposited along a Devonian
 coastline, with one horizon burying remains of *Psilophyton*
crenulatum in volcanic ashfall. Similar to other ashfall burial
 sites (see Chap. 13), preservation is exceptional (Fig. 15.11).
 Eastern outcrops are interpreted as intermontane fluvial or
 lacustrine, inland floodplain deposits, or mass flow deposits.

Fig. 15.10 *Prototaxites*, a giant fungus. (a) Erect mold of *Prototaxites* in siltstone, Dalhousie Junction, New Brunswick, Canada. R.A. Gastaldo for scale; edges of mold marked by yellow arrows. (photo courtesy of M. Gibling). (b) Small silicified *Prototaxites* (photo courtesy of PG Gensel). (c) Transverse section of silicified specimen showing tubular nature of cells (from Retallack and Landing 2014, Affinities and architecture of Devonian trunks of *Prototaxites loganii*. (Mycologia 106(6):1143–1158, with permission, Wiley Press)



766 We've seen this vegetation before. Plants similar at the
 767 generic level to *Psilophyton*, and *Pertica* [U1530],
 768 *Drepanophycus*, and possibly *Sawdonia*, as well as new taxa
 769 of zosterophylls and lycopsids [U1531], occur. One of the
 770 earliest occurrences of the lycophyte *Leclercqia* is here, as
 771 well as two strange taxa, *Chaleuria* and *Oocampsa*, which
 772 differ from each other and from the major Devonian plant
 773 lineages [U1532]. *Chaleuria* and *Oocampsa* both exhibit
 774 broad main stems, up to 1 cm in diameter, which may have
 775 been partly rhizomatous and partly upright. In contrast to
 776 other plants we've encountered, the lateral branches of these
 777 are dense and spirally arranged. The lateral branches in
 778 *Chaleuria* have dichotomizing, spirally arranged ultimate
 779 branches with fusiform, terminal sporangia in which two
 780 sizes and two kinds of spores were produced. This condition
 781 has been interpreted as incipient heterospory, a more derived
 782 mode of reproduction in spore-producing plants (Andrews
 783 et al. 1974). In *Oocampsa*, lateral branches are more dichot-

omously to pinnately divided, terminating in clusters of
 ovoid erect sporangia. Large, zonate spores are quite different
 from spores known from other early Devonian plants
 (Wellman and Gensel 2004). Unfortunately, most plant
 assemblages were transported, to some degree, before burial
 and preservation, leaving us without any specific environ-
 mental context, although it is believed that these plants
 exhibited less niche partitioning than was suggested for
 Gaspé.

15.5 Rhynie, the Oldest Vegetated Hot Springs

Milan Libertin and Patricia G. Gensel

It is a quick trip across the Atlantic "pond" to the village of
 Rhynie in northeastern Scotland, approximately 50 km



Fig. 15.11 Lower Devonian assemblages from Campbellton, New Brunswick, Canada. (a) Typical outcrop along the shores of Chaleur Bay (photo courtesy of PG Gensel). (b) Transported assemblage of biologically ordered axes of lycopsid affinity (photo courtesy of RA Gastaldo)

798 northwest of Aberdeen. It is hard to imagine that this area
 799 hosts one of the most important and famous localities of
 800 early Paleozoic plants when we walk through the country-
 801 side (Fig. 15.12a). There is no rock exposed at the surface.
 802 Rather, it lies beneath the green pasture lands studded with
 803 livestock as pictured on our postcard. The locality, known as
 804 the Rhynie chert, first was discovered by examining loose
 805 blocks turned up in the soil during plowing or as part of the
 806 stone walls edging the fields. Around 1912, during one of his
 807 collecting trips, Dr. William Mackie (for whom geology was
 808 a hobby) found fragments of fossiliferous chert in the dry
 809 stone walls, possibly while sitting on one and eating his
 810 lunch [U1533] (Andrew and Gensel 1984). He recognized
 811 that the chert contained plants entombed in the silicates and
 812 took them to Robert Kidston. Along with W. H. Lang, the
 813 chert was sectioned and studied, and they produced a series
 814 of papers (1917–1921) providing initial descriptions of the
 815 fossilized plants. In recent decades, trenches were dug in
 816 selected areas to collect additional plant material, and later

excavations were undertaken to study the lateral and vertical
 extent of the deposits. Major drilling and mapping led by
 geologists at the University of Aberdeen, with the assistance
 of many collaborators, has resulted in a much-improved
 understanding of the geology and of the environment in
 which this earliest ecosystem is preserved (Edwards et al.
 2018a, <https://www.abdn.ac.uk/rhynie>).

The paleoenvironment in which the Rhynie chert formed
 is surrounded by sandstone and mudrock (shale) and is simi-
 lar to today's hot spring-and-geyser landscape in Yellowstone
 National Park, Wyoming, USA (Rice et al. 2003). The fos-
 siliferous cherts were deposited in a tectonic sedimentary
 basin in which volcanic activity occurred. Sandstone depos-
 its reflect deposition in a braided river system with andesitic
 (igneous lava) flows associated with the fault systems along
 the margin of the basin. Surface water penetrated through
 porous sediment in the floodplain to a depth where these
 were heated by hydrothermal activity. Hydrothermally influ-
 enced sediments were intruded by dykes of andesitic lava
 and accelerated hydrothermal reaction, pushing heated,
 silica-rich waters to the surface. Hot springs formed sinter
 layers that penetrated and enveloped everything living
 around the hot spring, preserving an intact biota in various
 stages of vegetative growth and reproduction (Fig. 15.12b).

Plants are preserved in growth position by the sinter, and
 their spatial distribution is locked into the deposit. The plant
 and invertebrate community lived around a shallow, tempo-
 rary, freshwater lake, adjacent to active geysers. The permin-
 eralization was so thorough and rapid that even the finest
 anatomical details have been preserved, providing insight
 into the life history of several early plant genera. One of the
 most thoroughly investigated groups in the Rhynie chert is
 the rhyniophytes (Kerp 2018). In addition, several types of
 algae (Taylor et al. 1997), fungi (Remy et al. 1994; Taylor
 et al. 1999), and arthropods (proto-spiders, harvestmen,
 nematodes) are found (see summary by Dunlop and
 Garwood 2018).

One of the most common plants close to the hot springs is
 the genus *Aglaophyton*, currently considered a pro-
 tracheophyte [U1534]. It grew with an equally dividing (iso-
 tomous) branched rhizome, with hair-like extensions called
 rhizoids that acted to affix the plant to the ground surface and
 facilitate mineral uptake (Fig. 15.12b). Aerial axes devel-
 oped from the rhizomes, some of which are preserved with
 terminal oval-shaped sporangia. Conducting cells in this
 plant exhibit a unique wall pattern, with anatomical affinities
 similar to some mosses (Fig. 15.12c). As with other early
 plants, *Aglaophyton* had no leaves or roots. Another taxon,
Rhynia, initially considered similar to *Aglaophyton*, bore
 sporangia on terminating lateral branches and tracheid-like
 conducting cells (Box 15.3). It is considered part of the
 Rhyniopsida clade. Gametophytes [U1535], which are mul-
 ticellular, haploid, sexual structures in plants, are known in

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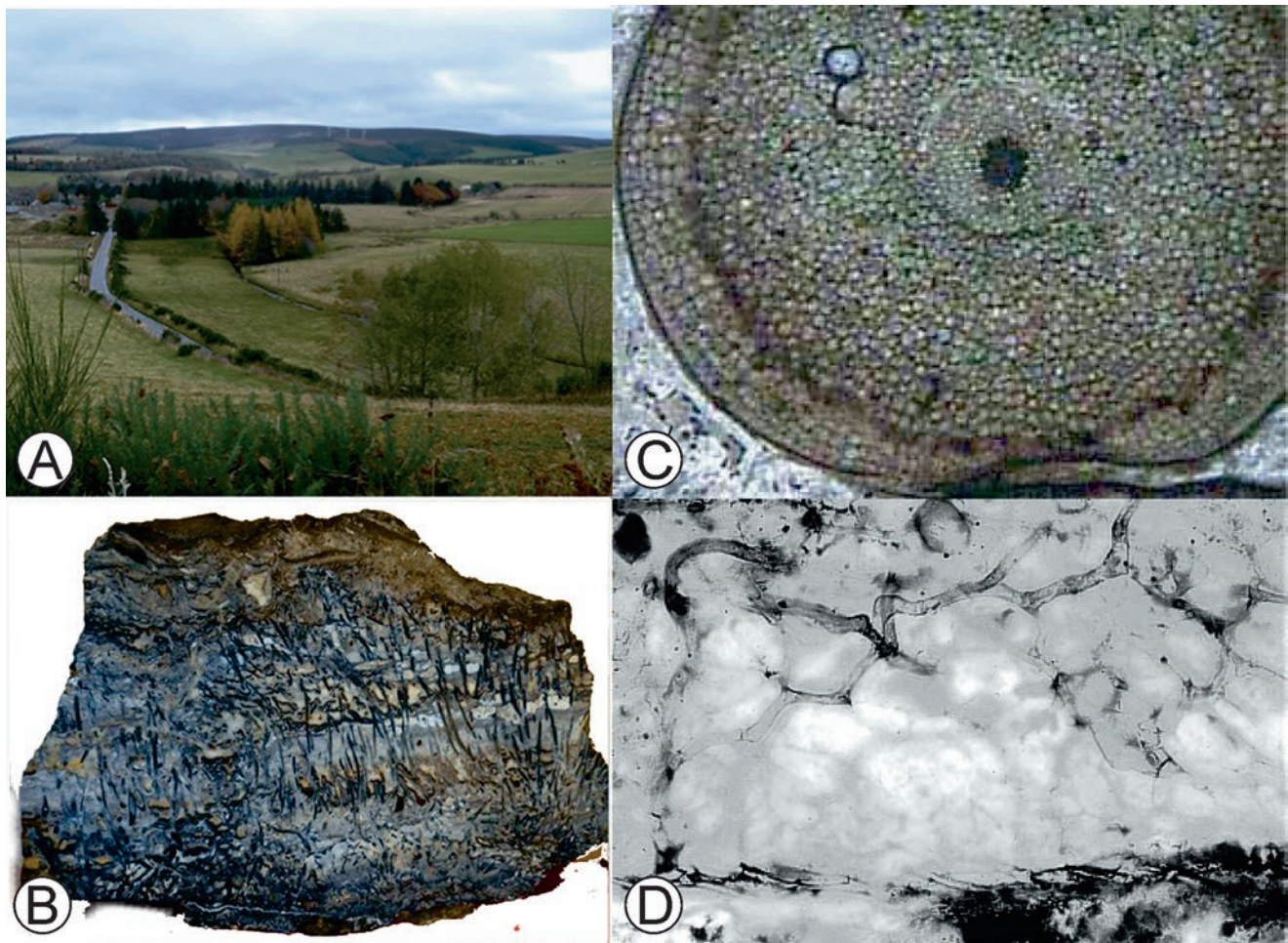


Fig. 15.12 The Early Devonian (Pragian) Rhynie chert, Aberdeenshire, preserved the oldest documented terrestrial ecosystem. (a) The Rhynie chert is not surficially exposed but, rather, is the bedrock beneath green pastures. (b) Polished specimen of the Rhynie chert showing vertically preserved stems of early land plants. (c) Transverse section of *Aglaophyton* stem showing anatomy. (With permission by the University of California-Berkeley Museum of Paleontology) (d) Fungal association preserved in cells

870 considerable detail, including the structures containing egg
 871 and sperm (Kerp et al. 2003; Taylor et al. 2005). Both of
 872 these taxa exhibit endophytic (within the plant cells) fungi
 873 that probably aided in water uptake (VA mycorrhizae). The
 874 Rhynie flora was more diverse than just rhyniophytes.

Box 15.3: Evolution of Specialized Water-Conducting Cells in Silurian-Devonian Plants

Most bryophytes (mosses) lack specialized water-conducting cells, with the exception of certain taxa, where centrally located cells exhibit either smooth or finely pitted, or otherwise ornamented walls. All of these cells apparently lack lignin (a complex organic polymer providing structural support in cell walls). Extant vascular plants are defined, in part, by the presence of specialized, dead, lignified water-conducting

cells in their xylem. These are called tracheids or, in flowering plants, tracheids and vessel elements. These cells exhibit particular patterns of lignified secondary walls—annular, helical, scalariform, or pitted—depending on whether cells differentiated early or later in stem or root or by plant group. The presence of lignin promotes preservation and has provided useful characters for distinguishing taxa or lineages and discriminating between stem and root structures.

We find several different developmental patterns when we examine the earliest plants and go back in time. For example, rhyniophytoids lack any evidence of such lignified cells, whereas others show centrally located cells that differ in wall thickness or pattern than those of the rest of the stem. These latter forms are more comparable to cells of some bryophytes. In other

early plant lineages of the Silurian to mostly Early Devonian, the following unique types of water-conducting cells, considered lignified and closer to tracheids, have been recognized:

- A late Silurian–Early Devonian *Cooksonia*, *C. per-toni*, exhibits tracheids with two wall layers and annular secondary wall thickenings facing the cell center (lumen).
- S-type cells are typical of rhyniopsid tracheids. These have a two-layered wall that consists of a thin resistant layer facing the hollow center of the cell (lumen) and an outer, less resistant spongy layer. The resistant layer is covered in minute pores. The wall is helically thickened, with the gyre of the helix at different angles.
- G-type cells are found in zosterophylls, *Asteroxylon*, and probably *Baragwanathia* (Lycopsida). This cell type exhibits tracheids with two wall layers, the inner decay-resistant one with closely spaced annular thickenings and a non-resistant outer layer. The spaces in between the inner decay-resistant layer often show a number of small openings.
- P-type tracheids are typical of *Psilophyton* and *Pertica* (basal euphyllophytes or former trimerophytes). The two-layered wall exhibits an inner decay-resistant layer that is closely spaced, parallel, and interconnected. This layer developed overarching edges (scalariform-bordered thickenings), and the decay-resistant layer in between thickenings exhibits one or more rows of round openings (pits). Less resistant material formed the outer wall and the area within the scalariform thickenings.

Recent discoveries have shown some plants, similar to *Psilophyton*, but with secondary xylem, exhibit round-oval bordered pits in primary and P-type pitting in secondary xylem (*Franhueberia*). By end of Early Devonian, secondary wall thickenings (pitting patterns) were more similar to those of extant plants, first appearing in lycopsids.

875 *Nothia aphylla* is another well-preserved plant more
876 closely related to the zosterophyll clade (Kerp et al. 2001). It
877 had spreading rhizomes, perhaps partly below ground, with
878 rhizoids, and upright axes that branched dichotomously. The
879 aerial axes were covered by elliptical emergences, many
880 topped by a stoma (a specialized gas exchange structure).
881 Sporangia producing only one type of spore developed near
882 branch tops. To release the spores, each sporangium opened
883 around the margins of the sporangium. *Nothia* was a geo-

phyte in that it grew in sandy soils and reproduced clonally. 884
Underground rhizomes survived from season to season, and 885
elevated axes grew again annually. Another geophyte, the 886
proto-lycopsids, also is part of the hot spring landscape. 887

A vascular plant, allied to the lycopsids, is the genus 888
Asteroxylon. These plants also grew in sandy substrates more 889
distant from the main sinter zone, but still were permineral- 890
ized by silica (Kerp 2018). The rhizomes of *Asteroxylon* 891
were geotropic, growing into the soil substrate [U1536]. 892
Rooting structures branched equally (isotomous) whereas 893
aerial stems, 1–2 cm wide and possibly up to 40 cm in height, 894
branched unequally (anisotomous). These are covered with 895
helically arranged, unvascularized leaf-like structures, and 896
vascular strands extend into the cortex almost, but not quite, 897
to the level of leaf-like attachment. Both aerial axes and the 898
leaf-like structures possessed stomata. The internal anatomy 899
exhibits several features not found in other groups at the 900
time. The xylem in the aerial axes consists of lignified, sim- 901
ple conducting cells (tracheids) with closely spaced thicken- 902
ings that encircle the cell (annular thickening). Their 903
arrangement forms a star-shaped pattern. Similar to lycop- 904
sids, the sporangia of *Asteroxylon* are kidney-shaped (reni- 905
form) and developed on a short stalk (pedicel). Fertile zones 906
are arranged spirally on axes interspersed among sterile ones 907
(Kerp et al. 2013). This arrangement indicates the potential 908
for periodic sexual reproduction promoted by changing envi- 909
ronmental conditions. Dispersed spores described from these 910
sediments indicate that the vegetation of the larger region 911
was more diverse than the plant association preserved in the 912
Rhynie chert (Wellman 2010). 913

Significant discoveries in this locality include another 914
part of the Rhynie ecosystem, the fungi (Fig. 15.12d) 915
[U1537]. Fungi serve several functions in an ecosystem, 916
ranging from mutualistic to saprophytic. Rhynie fungi may 917
be some of the best detailed forms, with mutualistic fungi 918
allied to Glomales found inside plants (Taylor et al. 1992; 919
Krings et al. 2017), as well as saprophytic forms degrading 920
them (Taylor et al. 2003). The relationship between the water 921
fungus *Sorodiscus*, which attacked the cells of the alga 922
Palaeonitella, is one of the first examples of parasitism in the 923
fossil record (Taylor et al. 1992). 924

The preservation of extremely minute details, which 925
allows the investigation of vascular systems, reproductive 926
organs, spores, generation of gametes, and even seasonal 927
growth of plants, allows us to recreate a picture of the entire 928
Rhynie hot spring ecosystem (Channing and Edwards 2009). 929
These fossil Lagerstätten with complex preservation poten- 930
tial are very valuable [U1538]. They are windows, frozen in 931
time, that enhance our understanding of early vascular plant 932
evolution (Trewin and Kerp 2018). It was the exquisite pres- 933
ervation of the plants in the Rhynie chert that convinced ear- 934
lier geologists and botanists that pre-Carboniferous terrestrial 935
plants existed. 936

937 **15.6 Bathurst Island, Canada:**
938 **A Counterview to the Hot Springs**

939 Patricia G. Gensel

940 We now travel from the modern conveniences found in one
941 small village in Aberdeenshire, Scotland, to a very remote
942 island setting in the high Arctic where we'll get a different
943 perspective on late Silurian and Early Devonian vegetation.
944 Back in time, this island was part of a large tectonic block
945 located around the equator. In contrast to the mostly small
946 and simple rhyniophytoids described from many Silurian
947 localities in Laurussia, Baltica, and South American assem-
948 blages, a walk through these equatorial regions brings us to
949 another worldly view. Late Silurian plants in eastern Bathurst
950 Island, Nunavut, Canada, are somewhat familiar in their
951 basic architecture and structure (Basinger et al. 1996; Kotyk
952 et al. 2002). Plants attained several centimeters in length and
953 stems were as wide as 4 mm, more closely resembling Early
954 Devonian taxa. Unlike fossil-plant assemblages we've previ-
955 ously visited, these are preserved in offshore, deep marine,
956 fly ash deposits ("Bathurst Island beds") securely dated as
957 Silurian (late Ludlow or Ludfordian, 426–423 Ma) based on
958 graptolites, conodonts, and brachiopods (see Chap. 14, for
959 more information on these early animals). The sedimento-
960 logical context of these assemblages indicates that the plants
961 were deposited by mudflows in a marine basin, where they

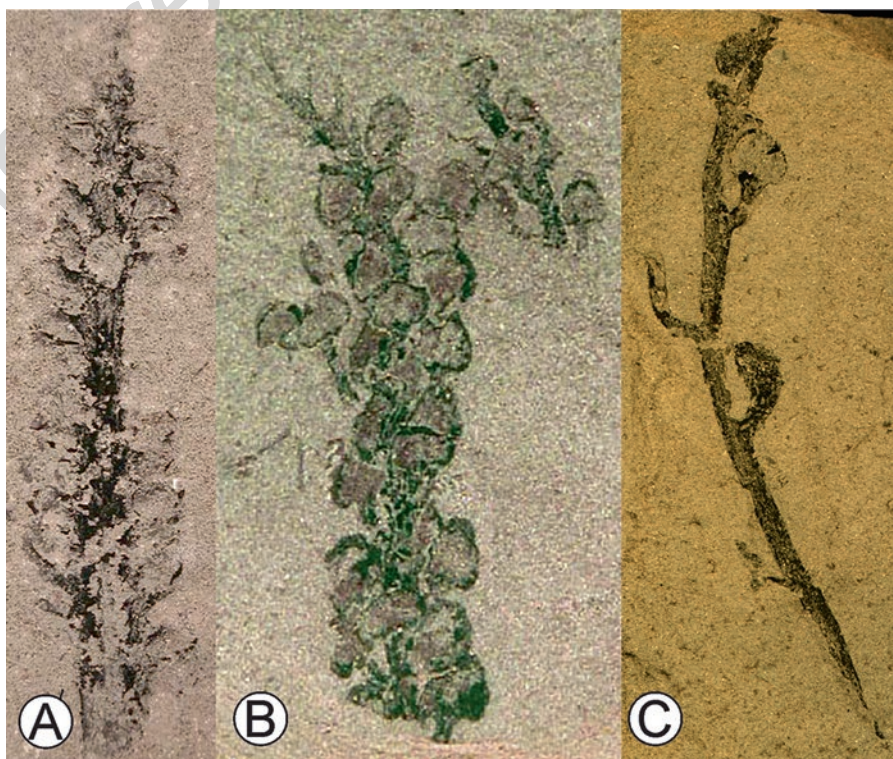
were quickly buried with little biological (bioturbation) 962
activity to alter them. These mudrocks now are exposed 963
mostly along stream margins on the island. 964

Transport of the plants to the marine realm resulted in 965
their partial deterioration and most appear as incomplete 966
portions of vegetative or fertile structures. Stem fragments, 967
some with spines, are associated with fertile specimens that 968
are referable to seven distinct taxa previously known *only* 969
from the Early Devonian. They represent members of the 970
zosterophylloids and plants bearing terminal sporangia 971
more similar to typical rhyniophytoids, although larger in 972
size. 973

The zosterophylls preserved here include taxa that vary 974
mostly in the structure and organization of their sporangia. 975
These reproductive structures can be organized in a helical or 976
subopposite arrangement (different species of 977
Zosterophyllum), or they can be borne in dense, two rowed 978
spikes oriented toward one side of the stem (*Distichophytum*). 979
A zosterophyll that had first been found on Bathurst Island, 980
Macivera gracilis, exhibits sporangia that are longer than 981
wide and located only in the distal regions of a branched 982
stem. The Silurian species of these genera are smaller in size 983
than their Devonian congeners. 984

A brief visit to the Early Devonian (Pragian, 411–408 Ma) 985
of Bathurst Island provides insight into the significance of 986
these fossils [U1539]. The assemblage (Kotyk 1998) is dom- 987
inated by zosterophylls, especially different types of the gen- 988
era *Zosterophyllum* and *Distichophytum*. These differ mainly 989

Fig. 15.13 Late Silurian to Early Devonian plants from Bathurst Island, Arctic Canada. (a) *Bathurstia* sp. (b, c) *Zosterophyllum* sp. (from Kotyk et al. 2002). Morphologically complex plant macrofossils from the Late Silurian of Arctic Canada, *Am. J. Bot.* 80(6): 1004–1013, with permission, Wiley Press), color photos PG Gensel



- in size, being considerably larger than their Silurian counterparts. Here, we also find the (pre)-lycophyte *Drepanophycus*, some with putative rooting structures (Kotyk 1998). Kotyk and Basinger (2000) published a description of another zosterophyll, *Bathurstia denticulata*, where axes are covered with emergences and one specimen is exceptionally preserved attached to its rhizome [U1540]. Parts of the K-type branching pattern of this taxon appear to be rooting structures as well as aerial fertile axes (Fig. 15.13). Other taxa also occur on Bathurst Island and can be found in localities across different present continents.
- Early Devonian and latest Silurian rhyniophyoids and zosterophlloids are reported from China, Europe, and South America. For example, the Pragian Posongchong Formation in China is very rich in zosterophylls (Hao and Xue 2013). Fossils from localities in the Přídolí (423–419 Ma) of Podolia, Czech Republic (Bohemia), and Brazil are entities larger than the tiny rhyniophytoids noted above and below. Even without consideration of controversial plant assemblages in Australia (e.g., Tims and Chambers 1984), the Bathurst Island fossils, and possibly those from Podolia and Brazil, indicate that plants more complex than rhyniophytoids existed in the late Silurian. Additionally, the occurrence of very similar zosterophylls and lycopsids over more than 25 million years tells us that these groups remained relatively static over that time span. Thus, the more complex and larger plants in these Silurian deposits indicate an earlier appearance of most vascular plant clades than the fossil record currently shows. This conclusion is supported by the dispersed spore record.
- Targrove, and Tin Mill Race, continue to be studied and are advancing our understanding of the evolution of early land plant body plans and their paleoecology, as well as offering insights into plant–arthropod interactions and latest Silurian–earliest Devonian food webs. Paleobotanically, these sites have demonstrated that *Cooksonia pertoni* had both tracheids and stomata, and that its spores varied over time (an example of cryptic evolution; Fanning et al. 1988). These localities have also yielded a far greater range of rhyniophytoids than had previously been appreciated, with *Cooksonia*-like plants such as *Hollandophyton colliculum*, *Tortilicaulis offaeus*, *Culullitheca richardsonii*, *Fusiformitheca fanningiae*, and others (Morris et al. 2011, 2018a). Much of this new evidence is not derived from the adpression fossils of *Cooksonia* that are so familiar in classic textbooks. Rather, our insights come from exquisite three-dimensional and anatomically preserved charred fossils that represent some of the earliest evidence of wildfire known on the planet (Fig. 15.14; Glasspool et al. 2006). Studied by SEM, these fossils exhibit incredible, even subcellular, anatomic details. These details reveal an early terrestrial flora characterized by “cryptogamic covers”, a soil crust comprising a complex of bacteria, cyanobacteria, algae, fungi, lichens, nematophytes (an enigmatic group that may have fungal affinities; Edwards et al. 2018b), basal tracheophytes (e.g., *Cooksonia hemisphaerica*), and cryptophytes (e.g., Edwards et al. 2014). Although these floras have been termed “Lilliputian” (Edwards 1996), their role in early terrestrialization and the evolving biogeochemical carbon cycle of the latest Silurian and earliest Devonian is anything but small.
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- 15.7 The Diminutive World of the Clee Hills of Shropshire**
- Ian Glasspool
- In 1937, William H. Lang published “On the plant-remains from the Downtonian of England and Wales”. This seminal paper focused on transitional Downtonian (uppermost Ludlow to Lochkovian; c. 425–411 Ma) successions from the Clee Hills of Shropshire in the Welsh Borderlands of the United Kingdom [U1541]. During the late Silurian, the locality was along the margin of the Laurussian continent. It’s now time to head back across the pond to see what Lang first observed, and what has subsequently been much expanded upon by Dianne Edwards (e.g., Edwards et al. 2014).
- Examining what had been thought to be unpromising fossil remains from terrestrial rocks, Lang was able to describe a highly diminutive (<10 cm tall; Edwards 1996), taxonomically simplistic, rootless, and leafless flora that included the first description of the now iconic genus *Cooksonia* [U1542]. Lang’s localities, including Ludford Lane, Perton Quarry,
- 15.8 Pre-Devonian Land Plants**
- Ian Glasspool, Jiri Kvaček, and Milan Libertin
- There are a number of small-stature plants and enigmatic plant groups that appear in the pre-Devonian fossil record. Some of these forms look like plants, while others are more amorphous in their organization. We have seen the iconic oldest truly vascular plant (Lang 1937; Edwards et al. 1992), *Cooksonia*, in Shropshire, but species assigned to it are known from several localities in Europe, North America, northern Africa, South America, and China (Taylor et al. 2009). The oldest currently known species, and one of the larger plants, is *C. barrandei* from the Czech Republic (Fig. 15.15) [U1537], and similar to many other localities from which it is described, the Czech rocks are not of continental origin. These fossils are described from the middle Silurian *Monograptus belophorus* marine Biozone of Wenlockian age (432 Ma; Libertin et al. 2018a, b). Like other members of the group, *C. barrandei* has twice-branched, relatively “robust” axes up to 1 mm in width, bear-

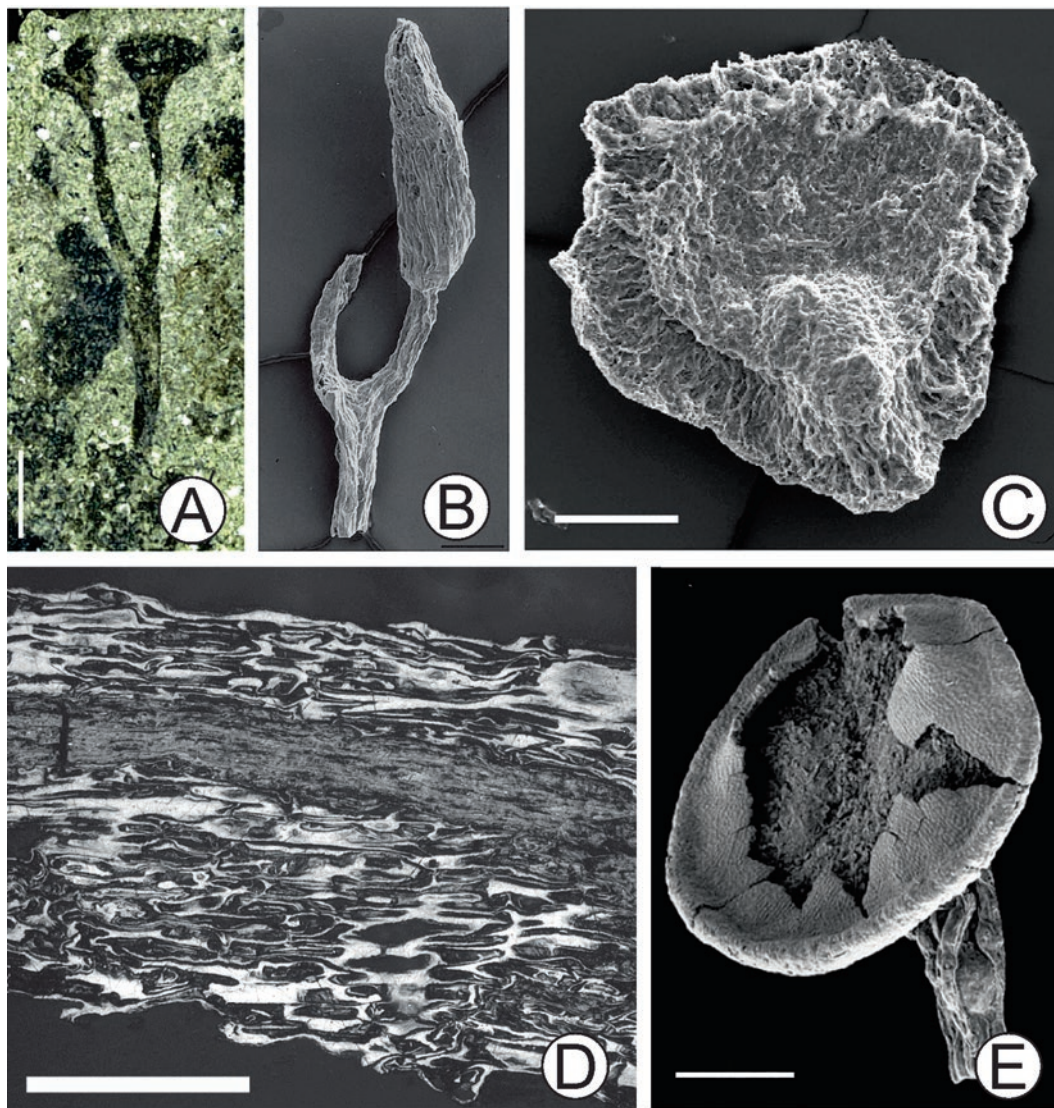


Fig. 15.14 Early Devonian plants from Shropshire, United Kingdom. (a) A compression specimen, the counterpart to the lectotype of *Cooksonia pertoni* from the Přídolí at Perton Lane, the surrounding black patches may be *Nematothallus*. NHM V58010 Scale bar = 2 mm. (from Edwards and Kenrick 2015. The 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. Roy. Soc. Lond., with permission). (b) A cryptophytic plant with a simple, fusiform sporangium from the Lochkovian of North Brown Clee Hill assignable to *Fusiformitheca fanningiae* (c) Scale bar = 500 μ m. (from Wellman et al. 1998. Permanent dyads in sporangia and spore masses from the Lower Devonian of the Welsh Borderland, Bot. J. Linn. Soc. 127(2): 117–147, with permission, Oxford Univ. Press.) (c) The lower surface of the thallus of *Nematothallus* sp., Ludlow, Upper Silurian, Downton Castle Sandstone Formation, Ludford Lane. This specimen illustrates the tripartite organization, from left to center: cortex, palisade tissue and fused basal layer. Scale bar = 200 μ m. (Edwards et al. 2013. Contributions to the diversity in cryptogamic covers in the Mid-Palaeozoic: *Nematothallus*-revisited. Bot. J. Linn. Soc. 173:505–534, with permission, Oxford Univ. Press.) (d) Differentially charred axis of *Hollandophyton colliculum* from the basal Přídolí of Ludford Lane. (from Glasspool et al. 2004. Charcoal in the Silurian as evidence of the earliest wildfires. Geology 32(5):381–383 with permission, Geol.Soc.America) (e) Charred, anatomically preserved *Cooksonia pertoni* subsp. *apiculispora* from the Lochkovian of Brown Clee Hill, Shropshire, containing *Aneurospora newportensis* spores. Scale bar = 500 μ m. (from Edwards et al. 1992. A vascular conducting strand in the early land plant *Cooksonia*. Nature 357(6380): 683, with permission, Springer Nature)

1088 ing terminal funnel-form sporangia [U1543]. Slightly
 1089 younger examples of the genus *Cooksonia* (e.g., *C. pertoni*,
 1090 *C. cambrensis*, and *C. hemisphaerica*) have been described
 1091 from Wenlockian strata in County Tipperary, Ireland
 1092 (Edwards et al. 1983). Due to many examples being excep-
 1093 tionally preserved as charcoal, the species *C. pertoni* is prob-

ably the most comprehensively studied of all *Cooksonia*
 species (see Morris et al. 2012). Whereas different examples
 of this species are morphologically and anatomically homol-
 ogous, four subspecies are recognized based on differences
 in the spores found in situ in their sporangia (Fanning et al.
 1988; Habgood et al. 2002; Morris et al. 2012).

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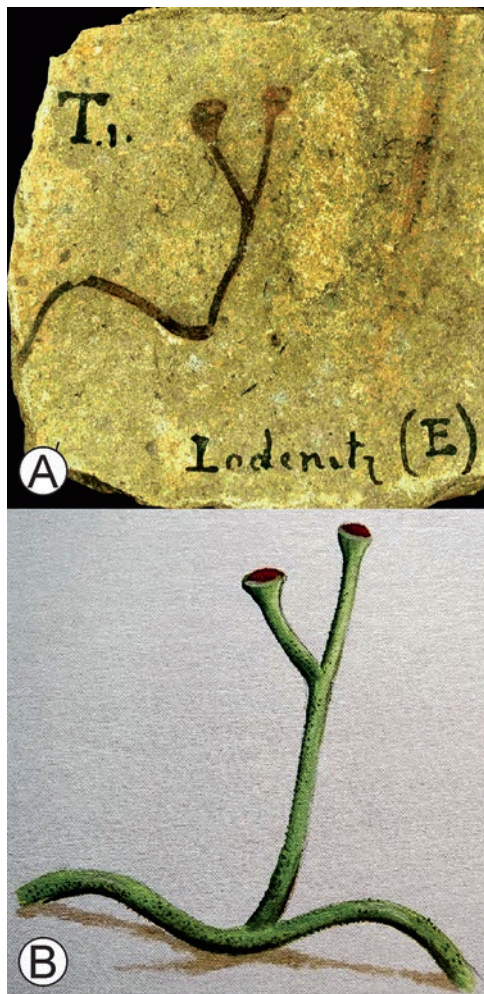


Fig. 15.15 *Cooksonia barrandei*. (a) Isotomously branched axis with sporangia, Loděnice, Špičatý vrch—Barrandovy Jámy, Czech Republic. Scale bar = 10 mm. (b) Reconstruction by Jiří Svoboda. (Both with permission Wiley Press)

1100 Cooksonias are currently placed in the polysporangio-
 1101 phytes, which are sporangia-bearing plants that may, or may
 1102 not, contain vascular tissues. The small size of many
 1103 *Cooksonia* and other rhyniophytoïd taxa has led to the ques-
 1104 tion of whether they were able to adequately photosynthe-
 1105 size, or if they may have remained attached to their
 1106 gametophyte structure for that purpose (Boyce et al. 2007).
 1107 There are a variety of *Cooksonia* forms, some of which have
 1108 been assigned to more than one lineage. For example, the
 1109 genus *Aberlemnia* is morphologically very similar to
 1110 *Cooksonia*, but its sporangia are bilobate, opening with two
 1111 flaps. Based on this character, Gonez and Gerrienne (2010)
 1112 assigned it to the stem or basal lycopsids. Perhaps the best
 1113 known, possible early lycopsid is *Baragwanathia* [U1544].
 1114 This plant gained notoriety due to its presumed late Silurian
 1115 age, large size, and relative organizational complexity that
 1116 often rendered it subject to debate (Hueber 1983; Garratt
 1117 et al. 1984). First described by Lang and Cookson (1935)

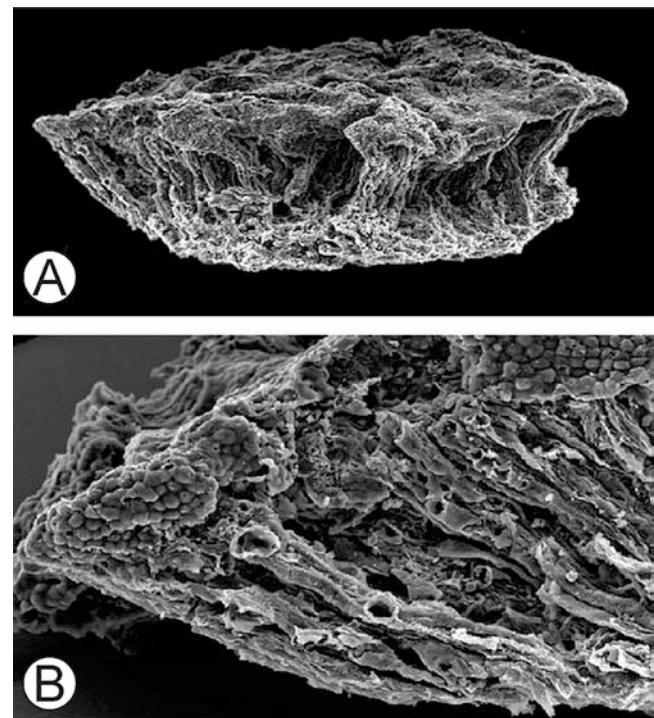


Fig. 15.16 (a, b): Fragment of *Nematothallus williamii*, Lochkovian, Shropshire in two magnifications of the same specimen showing a pattern typical for *Nematothallus* cuticle. Arrows indicate positions of lateral branches or areas. Scale bar 100 μ m. (from Edwards et al. 2013. Contributions to the diversity in cryptogamic covers in the Mid-Palaeozoic: *Nematothallus*-revisited. Bot. J. Linn. Soc. 173:505–534, with permission, Oxford Univ. Press)

1118 from the late Silurian of Yea, in Victoria, Australia, it now
 1119 has been reported from other Early Devonian localities
 1120 including Canada (Hueber 1983) and China (Hao and Xue
 1121 2013). *Baragwanathia* grew along the ground (procumbent)
 1122 and had forking, branched axes that gave rise directly to
 1123 occasional roots [U1545]. Similar to zosterophylls and other
 1124 lycopsids, the central conducting cylinder formed from a
 1125 star-shaped arrangement of tracheids. The sporangia grew in
 1126 the axils of vascularized microphylls, which were helically
 1127 arranged on the axes. Other stem group lycopsids of late
 1128 Silurian age were discussed in Sect. 15.6.

1129 Several other late Silurian plants had similar growth
 1130 architectures to *Cooksonia*. *Steganotheca* (Edwards 1970) is
 1131 somewhat more equally branched than *Cooksonia* and has
 1132 elongate, striated, and flat-topped sporangia terminally
 1133 arranged on gradually widening axes. This plant is known
 1134 from the late Silurian to earliest Devonian. Although it is
 1135 considered to be a vascular plant, there is no definitive proof,
 1136 to date, about either the presence or character of tracheids in
 1137 the axes. Recently, the genus *Tichavekia* was found in asso-
 1138 ciation with *Cooksonia* in the Prague Basin (Kraft et al.
 1139 2018). The plant axes attained lengths of at least 14 cm and
 1140 branched up to five times equally (isotomously), each branch

1141 being no wider than 1 mm [U1539]. The terminal dichoto- 1190
 1142 mies of the plant were short and tipped with oval sporangia 1191
 1143 forming groups of four. In addition to the rhyniophytoids, 1192
 1144 other pre-Devonian plants did not possess true stems, vascu- 1193
 1145 lar tissue, or sporangia, such as the nematophytes. 1194

1146 The curious group of the nematophytes have long been 1195
 1147 considered neither alga nor vascular plant, leading some to 1196
 1148 consider them transitional forms [U1546]. New data indicate 1197
 1149 otherwise. One such genus is *Nematothallus* (Lang 1937) 1198
 1150 and often is preserved as either a resistant cuticle, with “cell 1199
 1151 outlines” or on which there are openings that may have func- 1200
 1152 tioned similarly to stomata. Some specimens consist of cuti- 1201
 1153 cle with underlying wefts or aligned tubes, and occasional 1202
 1154 banded tubes may occur intermixed. It now seems that 1203
 1155 *Nematothallus* is either a fungus or lichen, and some other 1204
 1156 layered tubes with cuticle might represent lichens (Fig. 15.16;
 1157 Honegger et al. 2012; Edwards et al. 2013). Some of the
 1158 ornamented (banded) tubes may represent epibionts
 1159 (microbes living on or within these organisms). Another
 1160 intriguing type of fossil is *Parka* (Fleming 1831), a flattened
 1161 oval (thallus) with rounded bodies on it, present in the late
 1162 Silurian and continuing into the Early Devonian. Its similar-
 1163 ity to a charophycean green alga, *Coleochaete* (where
 1164 zygotes appear as round to oval bodies on the algal thallus) is
 1165 interesting because molecular phylogenies identify charo-
 1166 phyceans as the sister group of the land plants. An organism
 1167 like *Parka* can help us figure out the aspect of their possible
 1168 common ancestor.

1169 Other enigmatic plants include flattened axial structures,
 1170 up to 20 cm in length, that most probably represent cuticles
 1171 of stems. One example is *Orestovia* (Ergolskaya 1936)
 1172 occurring in the Early Devonian of the Kuznetsk basin of
 1173 Siberia. Primitive stomata, conducting cells, and spores have
 1174 been interpreted in the taxon (Kräusel and Venkatachala
 1175 1966). Details of their sunken stomata, shown in thin sec-
 1176 tions, are known from specimens that lacked any associated
 1177 spores or conducting cells (Gensel and Johnson 1994).
 1178 *Orestovia* and some related forms have extremely thick and
 1179 resistant cuticles and form thick deposits of so-called paper
 1180 coal in the Lower Devonian of Russia, which have been used
 1181 as a fuel source.

1182 15.9 The Oldest Evidence 1190 1183 for the Colonization of Land 1191

1184 Milan Libertin, Jiri Kvaček, and Ian Glasspool

1185 The oldest evidence of land being colonized by plants comes
 1186 from the dispersed spore record (Gensel 2008; Rubenstein
 1187 et al. 2010). Derived plants can be distinguished from algal
 1188 precursors by their spores, which are developed into tetrads
 1189 via meiosis, encased in a sporopollenin wall, and, subse-

quently, separated (Strother and Taylor 2018). The majority
 of the early spores (Box 15.4) are cryptospores, occurring
 in obligate tetrads, dyads (pairs), or singularly as monads.
 Ultrastructural data and in situ cryptospores suggest a bryo-
 phyte and/or basal polysporangiophyte* affinity. Trilete
 spores, ones with a Y-shaped scar delimiting site of opening
 for spore germination, are typical of vascular plants and only
 a few bryophytes. Early records of trilete spores consistently
 came from the Llandovery (basal Silurian, 444–433 Ma)
 until a recent report by Steemans et al. (2009), in which sev-
 eral types of trilete spores were reported from the upper
 Ordovician (Katian, 543–445 Ma) of Saudi Arabia. In many
 Silurian samples, cryptospores and/or trilete spores may co-
 occur with isolated cuticles or tubes of uncertain affinity,
 which could be remnants of nematophytes.

Box 15.4: Cryptospores Differ from Acritarchs and Trilete Spores

Permanent tetrahedral tetrads in which trilete marks, typical of vascular plant spores, first are detected were reported by Gray and Boucot (1971) from early-to-mid-Llandovery (444–433 Ma) rocks of New York State. They regarded permanent tetrads and permanent monads lacking a haptotypic* mark as being derived from land plants, not algae. In fact, Gray (1985) argued they exhibited features closer to liverworts. Richardson (1985) coined a term for these, plus dyads and monads lacking a haptotypic mark, namely cryptospores.

Cryptospores occur as monads (single spore), permanent dyads (two fused spores), or tetrads (four fused spores) (Figs. 15.17, 15.18, and 15.19) [U1542]. Some tetrads are enclosed in an outer envelope, whereas other examples are not. Spore assemblages containing cryptospores are found in Cambrian (but see below) to Devonian sediments, mainly from the paleotropics, and in marine to terrestrial deposits. They are different from acritarchs in that they exhibit a more robust wall and/or occur in tetrads.

The oldest fragments of a sporangium in which cryptospores, in the form of permanent tetrads, are found, comes from the Llanvirn (Ordovician; 475 Ma) of Oman. Analysis of their wall ultrastructure supports a possible liverwort affinity (Wellman et al. 2003). Other ultrastructural studies of cryptospore walls from Darriwilian-aged (467–458 Ma) material show the presence of homogeneous wall structure. This is a characteristic of living embryophytes where the layer is secreted by an active tapetum. The presence of a tapetum has been used to imply that these Ordovician cryptospores developed inside a sporangium, although

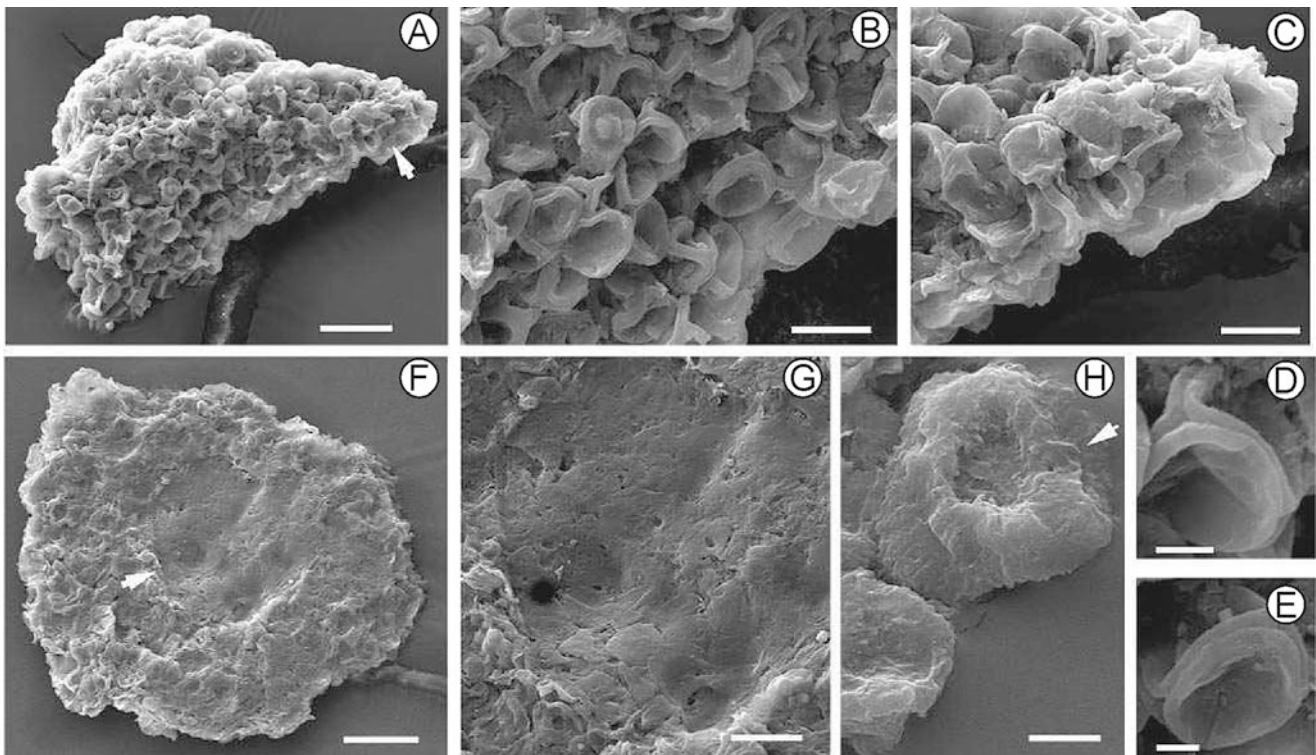


Fig. 15.17 Fossil plant fragments from the Ordovician (Llanvirn, 475 million years ago) of Oman. (a) SEM of fragment of sporangium containing naked permanent tetrads. Note the presence of sporangium covering in the bottom right-hand corner (arrow). Scale bar 50 mm. (b) Close-up of a illustrating the spore contents. Scale bar 20 mm. (c) Close-up of a illustrating spores overlying the sporangium covering. Scale bar 20 mm. (d, e) Close-up of a illustrating individual spore tetrad. Scale bar 5 mm. (f) Specimen CW47f. SEM of relatively complete sporangium, with a large patch of sporangium covering preserved (arrow). Scale bar 75 mm. (g) Close-up of illustrating the nature of the sporangium covering. Scale bar 30 mm. (h) Specimen CW47i. SEM of an envelope-enclosed permanent tetrad that is preserved in a fragmentary sporangium. Note the muri ornamenting the envelope (arrow). Scale bar 10 mm. (Wellman et al. 2003. *Nature* 425(6955):248–9 © Springer Nature with permission)

fossilized sporangia of this antiquity are not known (Taylor et al. 2017). Other cryptospores exhibit a multi-laminated wall as found in many liverwort spores. The extant liverwort *Haplomitrium gibbsiae* has also been shown to regularly produce cryptosporic permanent dyad pairs (Renzaglia et al. 2015).

The parent plant fossils from which cryptospores have been obtained were recently placed into the group cryptophytes. This is a basal group of early land plants such as those described by Edwards et al. (2014). However, this category might not encompass all types known from the dispersed spore record. More recently, Cambrian forms have been referred to as streptophytic algae (in the plant clade), rather than a taxon related to other green algae (Strother 2016). Cryptospores (Fig. 15.18) dominated spore assemblages until the late Ordovician when a few trilete forms, single spores resulting from disassociated tetrads, appeared in small numbers. These became more diverse and abundant in

the Silurian, particularly the Wenlock (Stemans et al. 2009, 2010; Wellman et al. 2013).

The oldest trilete spores are known from the mid-to Late Ordovician of Saudi Arabia based on chitinozoan and acritarch biostratigraphy (Stemans et al. 2009). These forms range from Katian (453–445 Ma) to Hirnantian (see Chap. 14) and may represent the earliest evidence of vascular plants [U1548]. However, trilete spores occur in some mosses, although many are alete (without a lete mark). It remains probable that plants producing trilete monads may have come from a broader morphological group of basal embryophyta.

To gain an impression of how the earliest land plant vegetation may have looked, we must return and visit two places in the Welsh Basin, both in Shropshire. The first locality is from the latest Silurian (Přídolí, c. 419 Ma); a second locality, a profile of the Brown Clee Hill, is about four million years younger. Very small but remarkably well-preserved mesofos-

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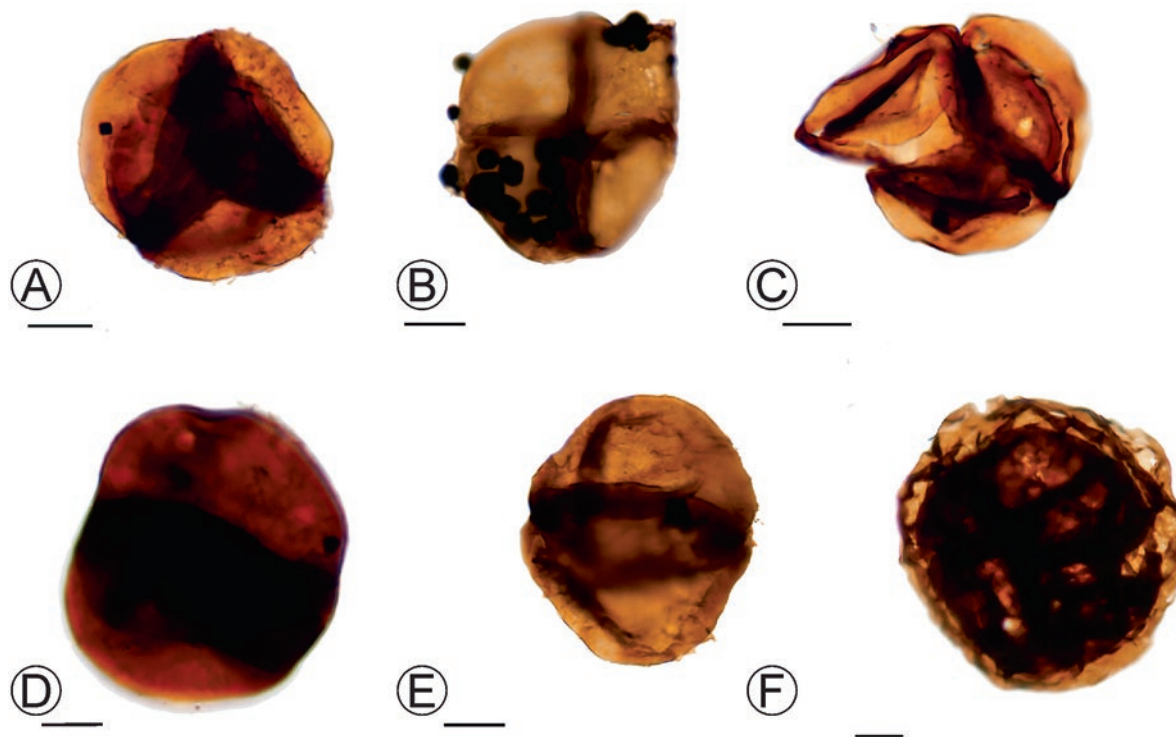


Fig. 15.18 Cryptospores. (a) Permanent spore tetrad in tightly attached tetrahedral configuration. *Tetrahedraletes* sp. of Hirnantian age. (b) Cryptospore spore tetrad in planar configuration, *Tetrplanisporites* of Hirnantian age. (c) Broken tetrahedral cryptospore tetrad of *Imperfectotrilletes vavrdovii*; spores have broken away from a permanent tetrad. (d) Permanent cryptospore dyad, *Dyadospora murusdensa*. (e) Permanent cryptospore dyad, *Dyadospora* cf. *D. murusattenuata*. (f) Permanent cryptospore tetrad enclosed in a reticulate synoocosporal wall, *Velatitetras* cf. *V. retimembrana*. All originate from the Power Glen Formation, Hirnantian age. Balls Falls Provincial Park, Ontario, Canada. (Images courtesy of P Strother)

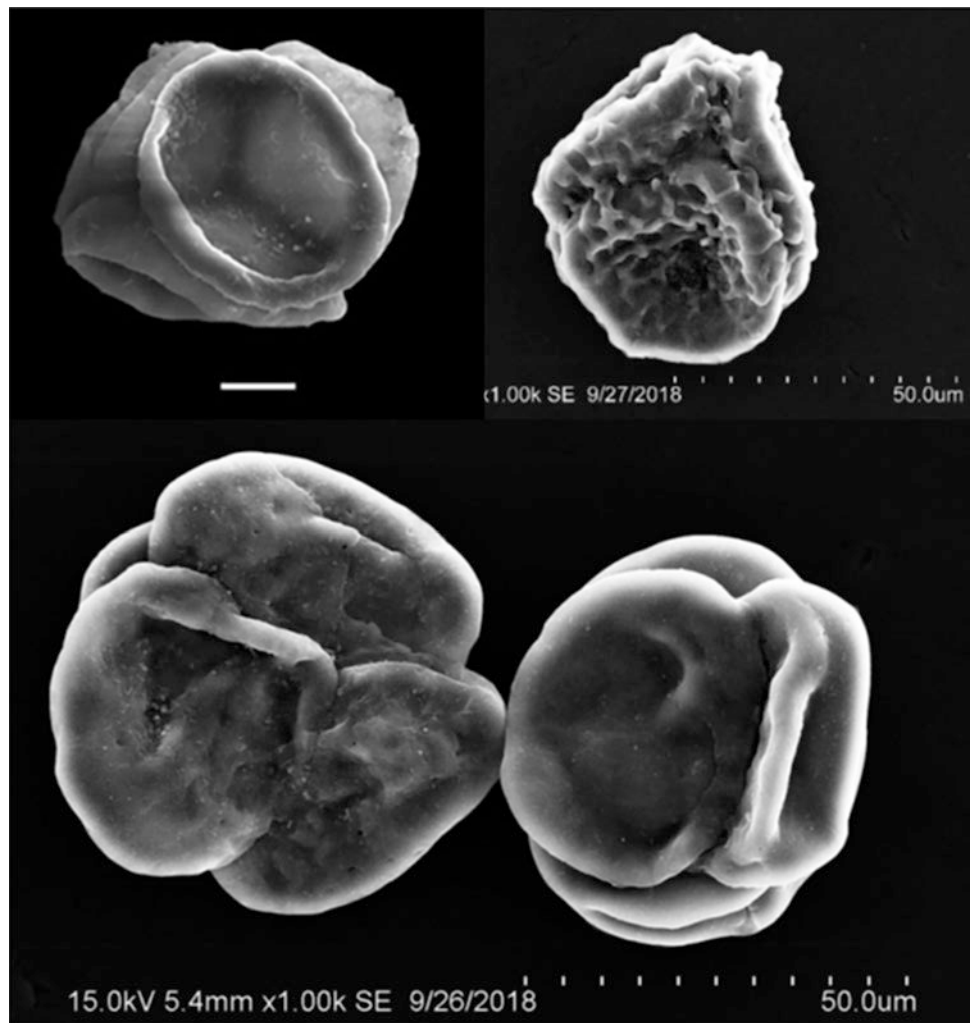
1211 sils containing cryptospores occur in both sites (e.g., Morris
1212 et al. 2018a). Based on studies from these localities, it is pos-
1213 sible to say that producers of cryptospores grew to only a few
1214 millimeters in size and probably had a stature similar to
1215 small mosses (bryophytes) (Stee mans et al. 2009; Kenrick
1216 et al. 2012). Even at these small sizes, we can discriminate
1217 several different cryptophyte groups. *Partiatheca* includes
1218 plants with dichotomously branched axes terminated by spo-
1219 rangia with stomata, which conform to a cooksonioid appear-
1220 ance. But, these plants produced permanent dyads with a
1221 laminated spore-wall structure that are assigned to the dis-
1222 persed spore genus *Cymbohilates* (Edwards et al. 2012).
1223 *Lenticulatheca*, recognized in the same assemblage, has dis-
1224 coid sporangia, containing similar dyads of the same group
1225 (*Cymbohilates*). Axes of *Grisellatheca* were terminated by
1226 short, dichotomously branched axes bearing slightly elon-
1227 gate sporangia, and these contain permanent tetrads of the
1228 *Tetrahedraletes*-type (Edwards et al. 2014). Dispersed forms
1229 of cryptospore occur earlier in southern Gondwana, and
1230 apparently radiated into Avalonia, then Euroamerica, and
1231 Baltica (Wellman et al. 2013).

15.10 Discussion

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1232
1233
1234 Colonization of land by photosynthesizing plants is one of
1235 the most important evolutionary events in the history of the
1236 biosphere and appears to have occurred in several steps,
1237 beginning in the Late Ordovician, or possibly the Cambrian,
1238 and continuing into the Devonian (Strother and Taylor 2018).
1239 There are several requirements for an organism to survive
1240 and propagate on land. One critical abiotic parameter was the
1241 presence of an ozone layer, at least a weak one, to block cos-
1242 mic (radioactive) and ultraviolet radiation, which damages
1243 cellular DNA. Only after an ozone layer was generated,
1244 could organisms colonize land! Algae were the first plants to
1245 abandon fully marine chemistries and move, initially, into
1246 the intertidal brackish zone and, later, freshwater environ-
1247 ments. Algal groups diversified during the early Paleozoic
1248 and included single-celled flagellated organisms to highly
1249 diversified thalli, measuring up to several meters in length.
1250 Some green algae, primarily brittleworts, Zygnematophyceae,
1251 and related charophycean algae achieved significant diver-
1252 sity during the Ordovician, and it seems likely that they

Fig. 15.19 Cryptospores. (a) Permanent spore tetrad in tightly attached tetrahedral configuration. *Tetraedraletes* sp. of Hirnantian age. (b) Cryptospore spore tetrad in planar configuration, *Tetraplanisporites* of Hirnantian age. (c) Broken tetrahedral cryptospore tetrad of *Imperfectotrilletes vavrdovii*; spores have broken away from a permanent tetrad. (d) Permanent cryptospore dyad, *Dyadospora murusdensa*. (e) Permanent cryptospore dyad, *Dyadospora* cf. *D. murusattenuata*. (f) Permanent cryptospore tetrad enclosed in a reticulate synoospore wall, *Velatitetras* cf. *V. retimembrana*. All originate from the Power Glen Formation, Hirnantian age. Balls Falls Provincial Park, Ontario, Canada. (Images courtesy of P. Strother)



[AU12]

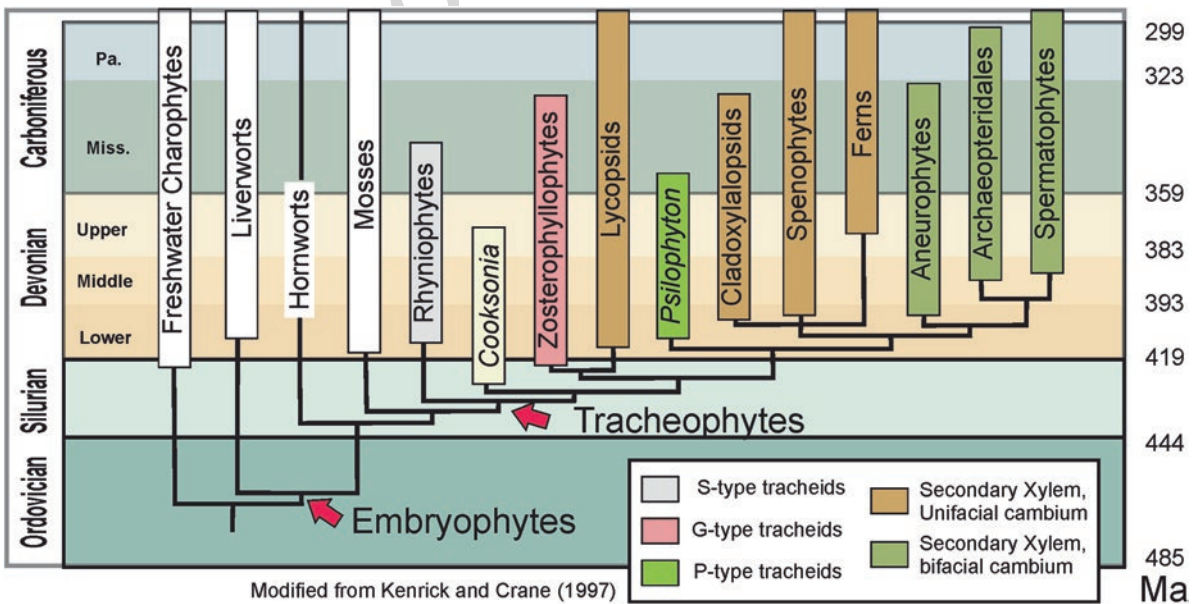


Fig. 15.20 Phylogenetic relationships between the major Paleozoic plant groups (modified from Kenrick and Crane 1997)

1253 inhabited shallow water settings and perpetually damp near-
 1254 shore environments. A move to conquer moist to dry land
 1255 followed with the advent of evolutionary innovations
 1256 [U1549]. Although the unfiltered sunlight on land facilitated
 1257 photosynthesis, heat affected internal cellular water and
 1258 nutrient relationships. To prevent desiccation, a sheathing in
 1259 a resistant compound evolved. Several lines of evidence are
 1260 used to clarify relationships of chlorophytes (green algae)
 1261 and their descendants, including photosynthetic pigments
 1262 (chlorophyll A and B), a common storage product (starch),
 1263 and molecular features. Chlorophytes, though, are not closely
 1264 related to terrestrial green plants. Rather, a separate branch
 1265 of the green algae, the charophytes are considered to be their
 1266 sister taxa (Fig. 15.20; McCourt et al. 2004). The emergence
 1267 of terrestrial plants is still not well understood, because the
 1268 soft tissue of these colonizers had a very low preservation
 1269 potential.

1270 Two primary hypotheses are put forth for the emergence
 1271 of vascular plants. The first is that vascular plants evolved
 1272 from mosses and their ancestors, plants that produced one
 1273 type of sporangium (monosporangiate plants; Graham et al.
 1274 2000). The alternative view is that they evolved from the pre-
 1275 decessors of hornworts, from plants in which more than one
 1276 type of sporangia developed (polysporangiate; Puttick et al.
 1277 2018). On the basis of the most recent phylogenetic analysis
 1278 (Morris et al. 2018b), it seems that vascular plants have a
 1279 common ancestor with hornworts.

1280 Beginning some 432 million years ago until the end of the
 1281 Devonian, approximately 75 million years in duration, we
 1282 have seen in this chapter a considerable change in plant type,
 1283 size, diversity, and complexity. We have witnessed major
 1284 innovations in plant organs such as the first appearance of
 1285 leaves and roots, changing reproductive modes, and the evolu-
 1286 tion of wood (secondary xylem; Box 15.5).

Box 15.5: Evolution of Vascular Cambium Producing Secondary Xylem and Phloem

Gerrienne et al. (2011) reported the occurrence of plant stems appearing similar in size and morphology to *Psilophyton* from the Pragian of France and the Emsian of New Brunswick. These fossils possess aligned conducting cells (tracheids) in their xylem associated with features typical of secondary xylem as is produced by the activity of newly activated stem cells referred to as a vascular cambium (VC). In extant plants, and in other groups with a VC, both secondary xylem and secondary phloem (food-conducting cells) are normally produced. But, in these plants, preservation ends outside the secondary xylem with the exception of a few squashed thin-walled cells that may be remnants of the VC. This discovery pushes back in

time the presence of secondary tissues, or wood, and suggests that perhaps attaining the type of wood prevalent in seed plants, characteristic of Devonian to recent plants, occurred in a stepwise manner.

Plants exhibiting secondary xylem include:

- *Armoricaphyton chateaupannense* (Strullu-Derrien et al. 2014); Pragian, France
- Unnamed plant (Gerrienne et al. 2011; Gensel 2018); Emsian, New Brunswick, Canada
- *Franhueberia gerriennii* (Hoffman and Tomescu 2013); Emsian of Gaspé, Canada
- As yet undescribed trimerophyte (Gensel 2018); Emsian, Gaspé, Canada

All these fossils exhibit a haplostelic primary xylem, with up to 24 rows of aligned tracheids. These tracheids also show signs of a doubling in places and spaces where presumably less resistant cells of rays (typical of secondary xylem) occurred. The earliest occurrence of a bifacial VC, producing both secondary xylem and phloem, and also periderms, is Middle Devonian. This feature is found in aneurophytalean progymnosperms.

The end of our adventurous journey is the most important event in the history of plant evolution. This is their adaptation from a fully aquatic to a fully terrestrial environment. In addition to features discussed earlier, this phenomenon is associated with the development of a two-parted life strategy, involving evolution of a longer-lived, complex sporophyte generation, along with adaptations necessary to sustain life on land. In plants other than bryophytes, an independent diploid sporophyte generation, namely the diploid roots, stems, and leaves represent an evolutionary novelty. Hypotheses as to the evolution of a dominant sporophyte-based plant include the homologous and antithetic theories.

The homologous origin of alternation of land plant generations that was originally introduced by Čelakovský (1874) supposes that land plants arose from ancestors of green algae with isomorphic (equal morphologies) haploid and diploid phases. On the other hand, the antithetic (or interpolation) hypothesis supposes a heteromorphic (two different morphologies) haploid and diploid phase, where the haploid gametophyte phase was gradually reduced. The diploid sporophyte became more complex as mitotic cell division in the zygote formed a multicellular structure as a result of delayed meiosis (Bower 1908). Ideas as to how this dominant sporophyte generation evolved over the gametophyte are still under discussion, with ideas about Early Devonian gametophytes recently presented (Kerp et al. 2003; Kenrick 2018).

1313 Land plant diversification [U1550] significantly influ-
 1314 enced the development of the lithosphere and, in turn, other
 1315 Earth systems in many different chemical and physical ways
 1316 [U1551]. Probably, the most significant of these was that of
 1317 soil development and the stabilization of continental sedi-
 1318 ments. Terrestrial plants affected weathering and erosion
 1319 and, as a consequence, fluvial systems (Gibling and Davies
 1320 2012; Gibling et al. 2014). The expansion and diversification
 1321 of land plants impacted climate, especially in incorporation
 1322 of CO₂ into organic carbon that either was held by plants,
 1323 incorporated into soil, or transported to the oceans (Berner
 1324 and Kothavala 2001). The fossil record of this time period
 1325 demonstrates that nearly every important phase of plant evo-
 1326 lution happened in the Devonian (and according to H. P.
 1327 Banks, “the rest is icing on the cake”).

1328 15.11 Conclusions

1329 As we have walked through these landscapes, it is clear that
 1330 the earliest land plants, now extinct, were very different from
 1331 those that we see around us at present and some interpreta-
 1332 tion is needed [U1552]. The earliest land plants of the latest
 1333 Silurian and Early Devonian generally lacked recognizable
 1334 roots and leaves and, in some cases, vascular tissue, giving
 1335 one the impression that these were nothing more than
 1336 branched sticks. Shortly thereafter, emergences begin to
 1337 develop along these axes, increasing the body area over
 1338 which photosynthesis could possibly occur. As internal water
 1339 and gas exchange relationships became more complex, we
 1340 find that two innovations evolve. The first is evidence of
 1341 some type of vascular tissue, ranging from lignified tracheids
 1342 similar to those in extant plants to water-conducting cells
 1343 with different wall patterns, or no wall pattern more similar
 1344 to bryophyte-grade conducting cells. The second is the
 1345 appearance of stomata, regulatory structures that provide a
 1346 means to move CO₂ from the atmosphere to photosynthesiz-
 1347 ing cells, and let the byproduct, O₂, be emitted back to the
 1348 atmosphere despite the presence of a waterproof cuticle. As
 1349 photosynthesis became more efficient and the need to uptake
 1350 water increased, root-like and true root structures, many with
 1351 mycorrhizal (fungal) associations, evolved. Propagation and
 1352 population sustainability are always needed for any species
 1353 to survive. Hence, the evolution of the sporangium, the struc-
 1354 ture in which meiosis occurs to produce haploid spores.
 1355 Sporangia were borne first terminally or laterally on stems,
 1356 singly or in groups. Sporangia vary widely in shape, pres-
 1357 ence, or absence and, if present, location on the stem, type of
 1358 dehiscence structure, and spore type. But, releasing spores
 1359 into a hostile environment also required protection from des-
 1360iccation, a problem solved by terrestrial plant ancestors that
 1361 had evolved a resistant and robust spore-wall chemical, spo-
 1362ropollenin. These innovations set the stage for the conquest

of all continental environments, the establishment of a myr- 1363
 iad of ecosystems, and an ever-changing planetary surface, 1364
 with the comings and goings of plant groups over the course 1365
 of the Phanerozoic. 1366

Questions 1367

1. What defines a forest? When do the earliest forests 1368
 occur? How are they different from extant ones? Be able 1369
 to describe two types of plants that form the canopy of 1370
 an early forest. What forms of preservation have enabled 1371
 us to recognize the existence of forests? What limita- 1372
 tions do we have in terms of characterizing early 1373
 forests? 1374
2. Where are plants preserved, and inferred to have grown, 1375
 during the Late, Middle, and Early Devonian, respec- 1376
 tively? What type of vegetation was present? 1377
3. What is an embryophyte? A cryptophyte? Alga or 1378
 fungus. 1379
4. Some plant stems, and/or sporangia, are covered with 1380
 emergences, and these frequently are used to define 1381
 taxa. What are these structures? 1382
5. Name several major innovations in plant size, anatomi- 1383
 cal organization, architecture, or reproduction that 1384
 occurred in the Silurian-Devonian. What is the signifi- 1385
 cance of each in terms of changes to Earth systems or to 1386
 the composition of vegetation types? What is the earliest 1387
 record of each? 1388
6. What features distinguish a progymnosperm, such as 1389
Tetraxylopteris or *Archaeopteris*? 1390
7. What are three characteristics of early seed plants, and 1391
 why are they significant for their survival? 1392
8. Know basic features of the four main lineages of early 1393
 vascular plants (rhyniaceans, zosterophylls, trimero- 1394
 phytes, and progymnosperms) and provide an exemplar 1395
 genus for each. Potential exemplar genera are *Cooksonia*, 1396
Sawdonia, *Zosterophyllum*, *Psilophyton*, *Pertica*, 1397
Rhynia, *Aglaophyton* 1398
9. Lycopside (zosterophylls + Lycophytes) are known to be 1399
 a distinct lineage since the late Silurian. What defines a 1400
 lycophyte versus a zosterophyll? When do lycopsids 1401
 become tree-like? Are they similar today? 1402
10. What role did the following plants play in structuring 1403
 vegetation, affecting soils or Earth processes, or in evolu- 1404
 tionary changes in lineages? *Eospermatopteris/Wattieza*, 1405
Rhacophyton, *Archaeopteris*, *Protolepidodendropsis*, 1406
Leclercqia, *Elkinsia*, and its relatives. 1407
11. What is a Fossil Lagerstätte? Why might the Rhynie 1408
 chert be considered a Fossil Lagerstätte? 1409
12. Some paleobotanists suggest that lichens, which today 1410
 are pioneer plants in establishing soils, existed during 1411
 the Devonian. What taxa may represent lichens? Fungi? 1412
 How might nematophytes address this question? 1413

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 1421 University, Blacksburg, USA; Dr. William Stein, State University of
 1422 New York-Binghamton, USA; Dr. Paul Strother, Boston College, USA.
-
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Uncorrected Proof