



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

Patricia G. Gensel, Ian Glasspool, Robert A. Gastaldo, Milan Libertin, and Jiří Kvaček

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, cladoxyloids, 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 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 (= Embryophytes), 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

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*The asterisk designates terms explained in the Glossary.

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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 progymno-

sperm 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, laminate leaves. (a) © The Field Museum, GEO86500_125d and Karen Carr, Artist. With permission. (b) Image courtesy of Walter Cressler

with members of the Paleozoic fauna (see Chap. 14). Before we enter the unknown, let us begin with an overview of what is familiar and what is unfamiliar.

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

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

which were persistent into the latest Paleozoic. The second forest is stranger. These puzzling forests were comprised of medium to very tall trees that bore no leaves. Each tree had a sort of crown made up of branches that branched multiple times, each branch terminated in a branch. These plants, the cladoxyloids *Calamophyton* or *Eospermatopteris*, first appear in the Middle Devonian and are successful cohabitants until the early Late Devonian. Lianescent (vines) and herbaceous plants are known to occur in some of these early forests, as well as ancestors to the lycopsids, the zosterophylls (see Box 15.1), comparable to Early Devonian taxa. Plants get smaller the further we regress in time, with short-stature riparian and coastal marsh-like vegetation expanding in the late Early Devonian. These replaced open areas covered by a “green fuzz” of the earliest vegetation in moist settings adjacent to river or ocean margins (Silurian to earliest Devonian) [U1503]. Descendants of the early colonizers are still found in the mosses and liverworts. Yet, we have no evidence that any other earliest plant group remained relatively static and survived until today.

Fossils representing the earliest evidence of land plants, consisting of small to “large” macrofossils (large being a relative term of only several centimeters in length) and dispersed spores, take us into an even stranger world. While most of these fossils are found in Silurian and Devonian rocks, the earliest evidence of plants is known from the Ordovician (Katian or possibly earlier; Wellman 2010). Marine rocks preserve small sporangia with spore tetrads, an evolutionary feature ascribed to all higher plants (Steemans

et al. 2009), as well as a myriad of dispersed spore assemblages containing similar types of spores from various parts of the globe. Before we machete our way through these unknown terranes, we need to gain an appreciation for the plant groups that occupied Silurian-Devonian landscapes.

15.1.1 Relationships

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

Banks (1968) presented a major reclassification of these plants in which he recognized at least four definable lineages, plus others of less well understood affinity [U1504]. His four categories of earliest vascular plants are the Rhyniophytina [U1505], Zosterophyllophytina [U1506], Trimerophytina [U1507], and Lycophytina [U1508]. At the same time, he also provided a more rigorous framework in which to consider the characteristics and affinities of these earliest land plants. With the discovery by Beck (1962) that *Archaeopteris* and other plants possessed a combination of woody stems and fern-like leaves with fern-like reproduction, Banks also recognized two more advanced groups, the aneurophytalean and archaeopteridaean progymnosperms [U1509]. Kenrick and Crane (1997) undertook a cladistic analysis focusing on Silurian-Early Devonian plants, but with inclusion of some of the younger groups, to better understand evolutionary relationships (Box 15.1). This resulted in several, sometimes major, changes in their classification (Fig. 15.2) [U1510]. For greater ease of description in our site visits to the Siluro-Devonian, however, the terms rhyniophytoid, rhyniophyte,

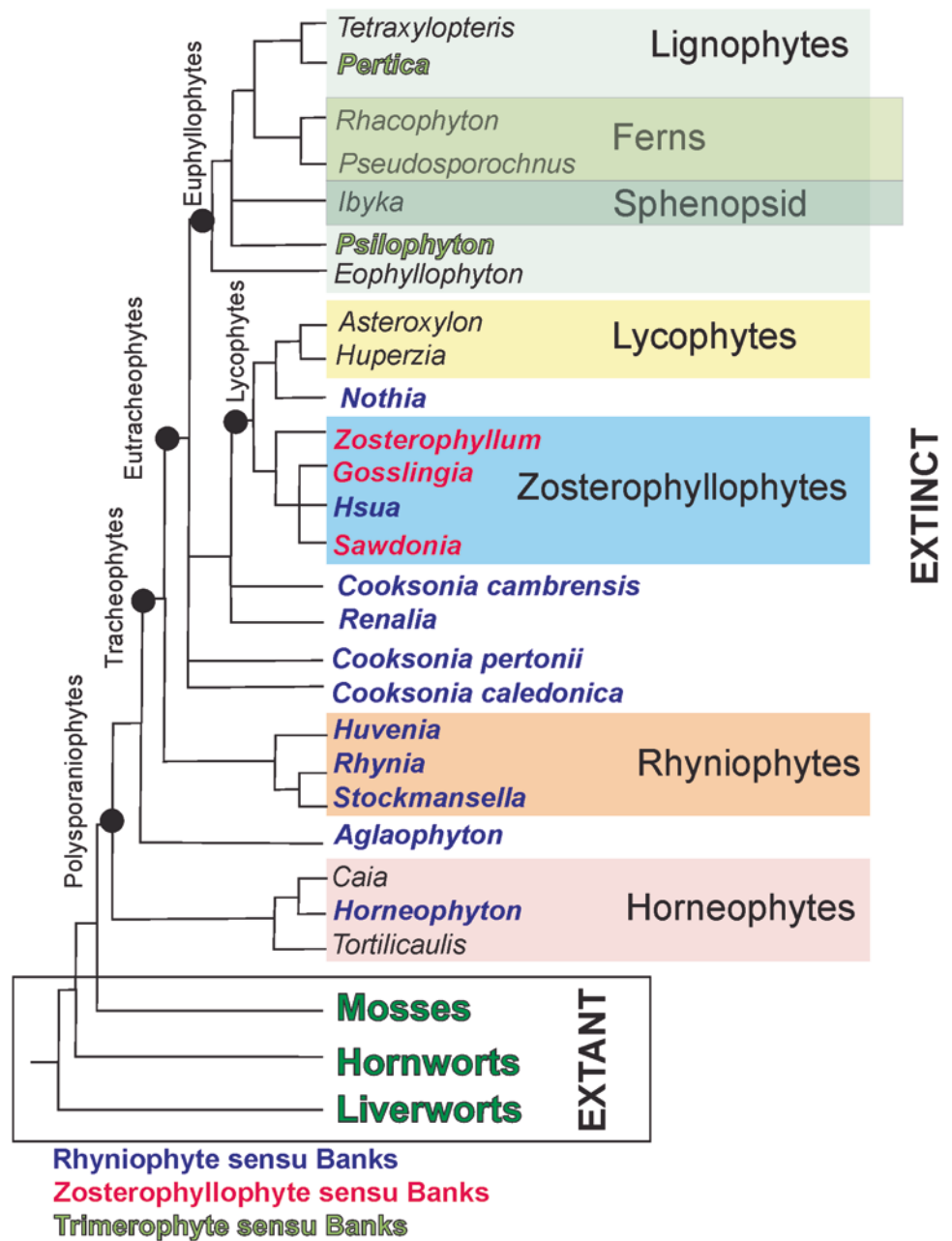
zosterophyll, trimerophyte, and progymnosperm, accompanied by diagnostic characters, will be used in the post-card descriptions to follow.

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 Lycophytina, 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 Lycopsida. Lycophytina, according to KC, consists of plants ranging from stem taxa, including *Cooksonia* and *Renalia*, plus the Zosterophyllopsida and Lycopsida. Their Lycopsida 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 land plant (= Embryophytes) 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). Other unplaced groups are the cryptospore-bearing plants (Edwards et al. 2014), and the nematophytes.

15.2 The Oldest Woodlands

Milan Libertin and Patricia G. Gensel

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

Patricia G. Gensel

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 prograding 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 diversified [U1515] and spread across the landscape, beginning to alter the planet’s vegetation. We could walk through similar Late Devonian

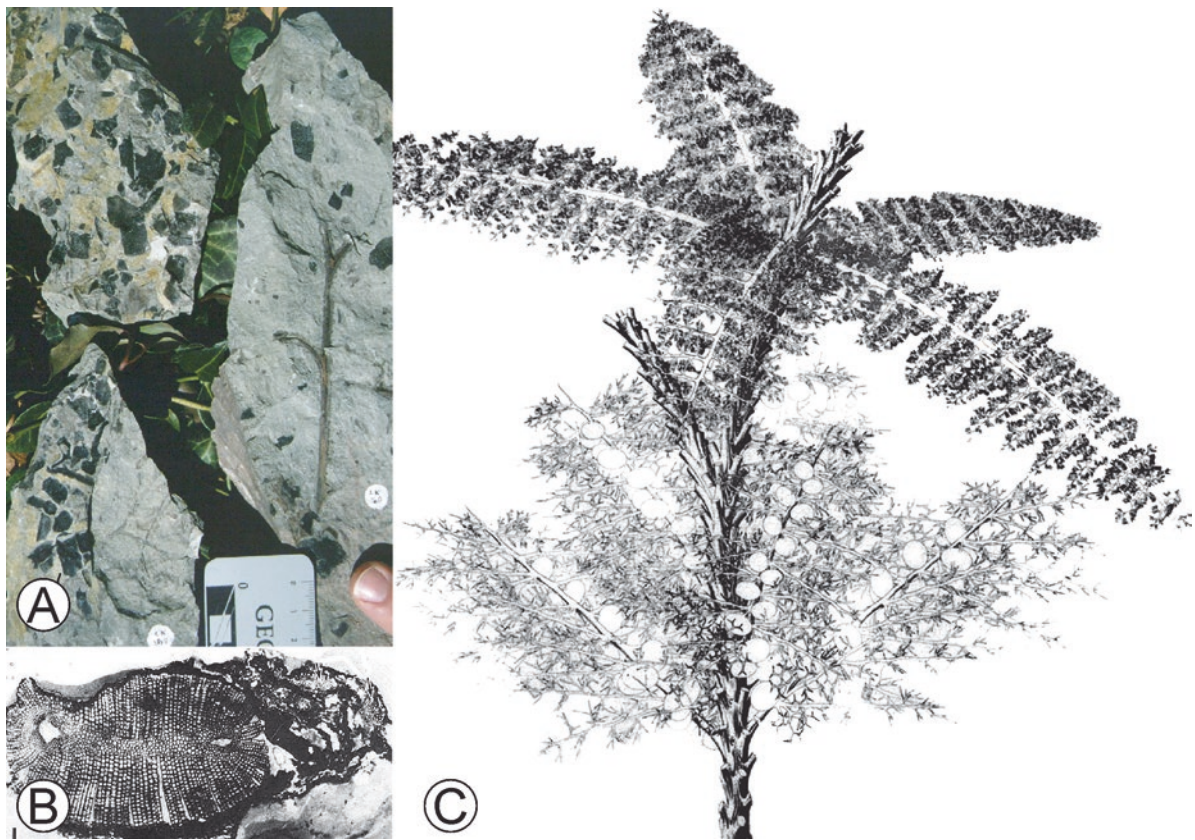


Fig. 15.3 *Rhacophyton*, a fern-like plant. (a) Charcoalified remains of *Rhacophyton*, with a pinnate branching pattern (image courtesy of Walter Cressler). (b) Anatomy of central axis showing secondary, woody tissues (from Dittrich et al. (1983) *Anatomy of Rhacophyton ceratangium* from the Upper Devonian (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 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.

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 Gleasonton, Pennsylvania, USA.

15.2.2 Red Hill, Pennsylvania

Patricia G. Gensel

As the name implies, the Red Hill locality exposed a Late Devonian succession of red, primarily, mudrock

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)



(Fig. 15.5). What is unique about this Famennian (372–359 Ma) sequence is the array of arthropods, fishes, and early tetrapods (vertebrates) with anatomical features that indicate these fishes and fish-like amphibians could survive out of the water. Fossil plants, the base of this food chain, are preserved in one thin interval but served as the habitat for terrestrial invertebrates including trigonotarbid arachnids and myriapods, both of which have been recovered from the site (Daeschler and Cressler III 2011). The succession consists of sandstone deposited in river channels, siltstone that filled abandoned freshwater channels and lakes, and floodplain paleosols adjacent to these ancient bodies of water.

The Red Hill paleoenvironment was an alluvial floodplain with meandering rivers often overflowing their banks and burying the vegetation associated with Vertisols* (soils with shrink-swell clays) and Calcisols* (calcium-rich soils). Meandering river channels produced an ever-changing environment, with abandoned channels becoming quiet-water lakes in which a teeming vertebrate

community existed. Remains of both plants and terrestrial arthropods are preserved in oxbow lake or pond deposits [U1516]. Plants include the progymnosperm *Archaeopteris*, the pre-fern *Rhacophyton*, baringophytes, two kinds of tree size lycopsids, and seed plants (mostly represented by their cupulate ovules, and some foliage that may belong to this lineage; Cressler 2006; Cressler et al. 2010). Similar to other Late Devonian landscapes, *Archaeopteris* canopies were underlain by a *Rhacophyton* understory with various scrambling plants occupying the groundcover, most likely in light breaks. In more open sites, lycopsids grew adjacent to oxbow lakes and ponds, and seed plants colonized disturbed areas or those in which soil drainage was better. Channel deposits contain the vertebrate assemblage.

Fish and some of the earliest tetrapod fossils are preserved in freshwater lenses of silty mudrock in shallow channel margin, floodplain pond, and overbank pond deposits. Here, a stem tetrapod found outside of coeval rocks in Greenland was identified based on two shoulder



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

bones (i.e., cleithrum* and scapulacoracoid*). The shoulder-bone features in *Hynerpeton* are advanced, indicating that the animal was capable of both supporting its body and powering itself on land [U1517] (Daeschler et al. 1994). *Hynerpeton* and the more complete, three-dimensionally preserved *Tiktaalik* from Ellesmere Island, Arctic Canada (Daeschler et al. 2006), record the transition between fishes with fins and tetrapods with limbs and digits. In addition to the shoulder girdle, an unusual, isolated humerus and jaw fragments of two different tetrapods have been collected. A single bone from the snout of a tetrapod resembles that of an early Carboniferous tetrapod, *Pederpes*, from Scotland (Daeschler et al. 2009). These are our deep time ancestors. Without their transition from a fully aquatic to a terrestrial life strategy, all higher vertebrate groups we've seen would not have existed. But, because we did evolve from these stem tetrapod groups, it's now only a short 4-h drive north from Red Hill to the town of Gilboa, New York, where our next postcard is located.

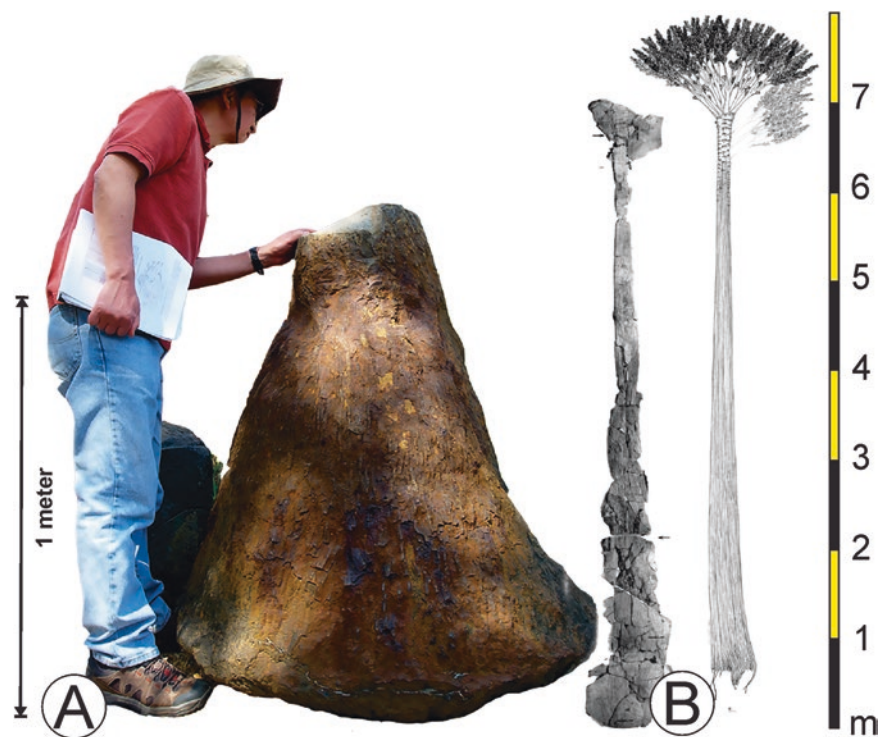
15.2.3 Gilboa Quarry, New York, USA

Patricia G. Gensel

The localities we now visit in eastern New York State demonstrate 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, various 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,

Fig. 15.6 The Middle Devonian cladoxylalean fern, *Eospermatopteris*. (a) Stump excavated from Schoharie Reservoir, Gilboa, New York. (photo: RA 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)



Winifred Goldring (1924; Fig. 15.6), and were widely cited as evidence of the Earth's "oldest forest" (e.g., Goldring 1927). These trees were not restricted to the quarried exposure because *Eospermatopteris* stumps also were found in nearby outcrops. In the early 2000s, impressions and flattened stem casts extending across a quarry floor not far from the Gilboa site, at South Mountain, showed a basal trunk comparable to *Eospermatopteris* and a crown region with attached, digitately divided, upward-extending branch systems (Fig. 15.6). Each branch division bore sterile and fertile appendages that allowed their identification with plants previously known from Belgium and Venezuela as the cladoxylalean *Wattieza* (Pseudosporochnales) (Stein et al. 2007). *Wattieza* is a very strange plant [U1519]. It grew to a height of at least 8 m with a trunk bearing large branches in vertical ranks (Stein et al. 2007). The much-divided branches bore smaller divided, leafless terminal units that, in some cases, bore sporangia that shed spores. These trees belong to an extinct group, the pseudosporochnaleans, believed to be related to ferns—new data may revise that idea. It appears that the stems were fast-growing and "cheaply" constructed. The center of these trunks was hollow and encircled by many conducting (vascular) strands in the periphery (Stein et al. 2012). The trunks were surrounded by roots near the base, with a growth strategy similar to living palms or tree ferns. The sedimentology indicates a series of burial events affected these forests which were frequently disturbed, followed by their reestablishment in new soil horizons. 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 aneurophytalean progymnosperms, a group that is known from numerous other Middle Devonian localities. Like *Archaeopteris*, aneurophytes grew woody stems and reproduced by spores, but were smaller in stature (as presently known) and presumed to have been leafless and shrubby

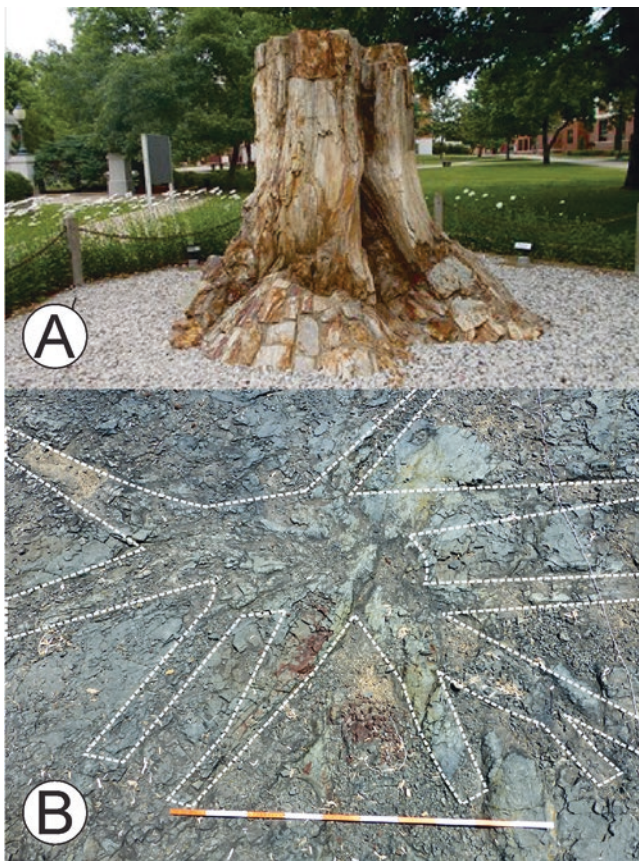


Fig. 15.7 Trunk and tree base of *Archaeopteris*. (a) Silicified stump (photo: PG Gensel). (b) The tree base and rooting structure of *Archaeopteris* outlined on a paleosol exposed in the Cairo Quarry, Town of Cairo Public Works, New York, USA. (photo: RA Gastaldo)

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

The forests in Gilboa are interpreted to have grown in a coastal wetland setting, with frequent marine incursions that buried successive forests. Originally, the paleoenvironment had been interpreted as a wetland swamp, but the underlying paleosol is well-developed, as are those from other Devonian sites (Morris et al. 2015), and may indicate that these plants grew in better drained conditions. Stein et al. (2012) indicated that this forest type may not be too different from coeval *Archaeopteris* dominated ones. It is, therefore, interesting that an exposed quarry floor in nearby Cairo, New York, provides evidence that both *Eospermatopteris* and *Archaeopteris* coexisted, the latter being more abundant (Fig. 15.7). *Archaeopteris* has a rooting system that is 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, perhaps, 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 rhizomatous 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-sporochnalean *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 Early 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 forests of northern Maine, USA (Fig. 15.8a, d). Here, our postcard is of an idyllic trout stream in Baxter State Park, where the air is scented by balsam fir resins, and remnants of latest Early (Emsian) or earliest Middle (Eifelian) Devonian rocks [U1522]. The outcrops, exposed at the surface following 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

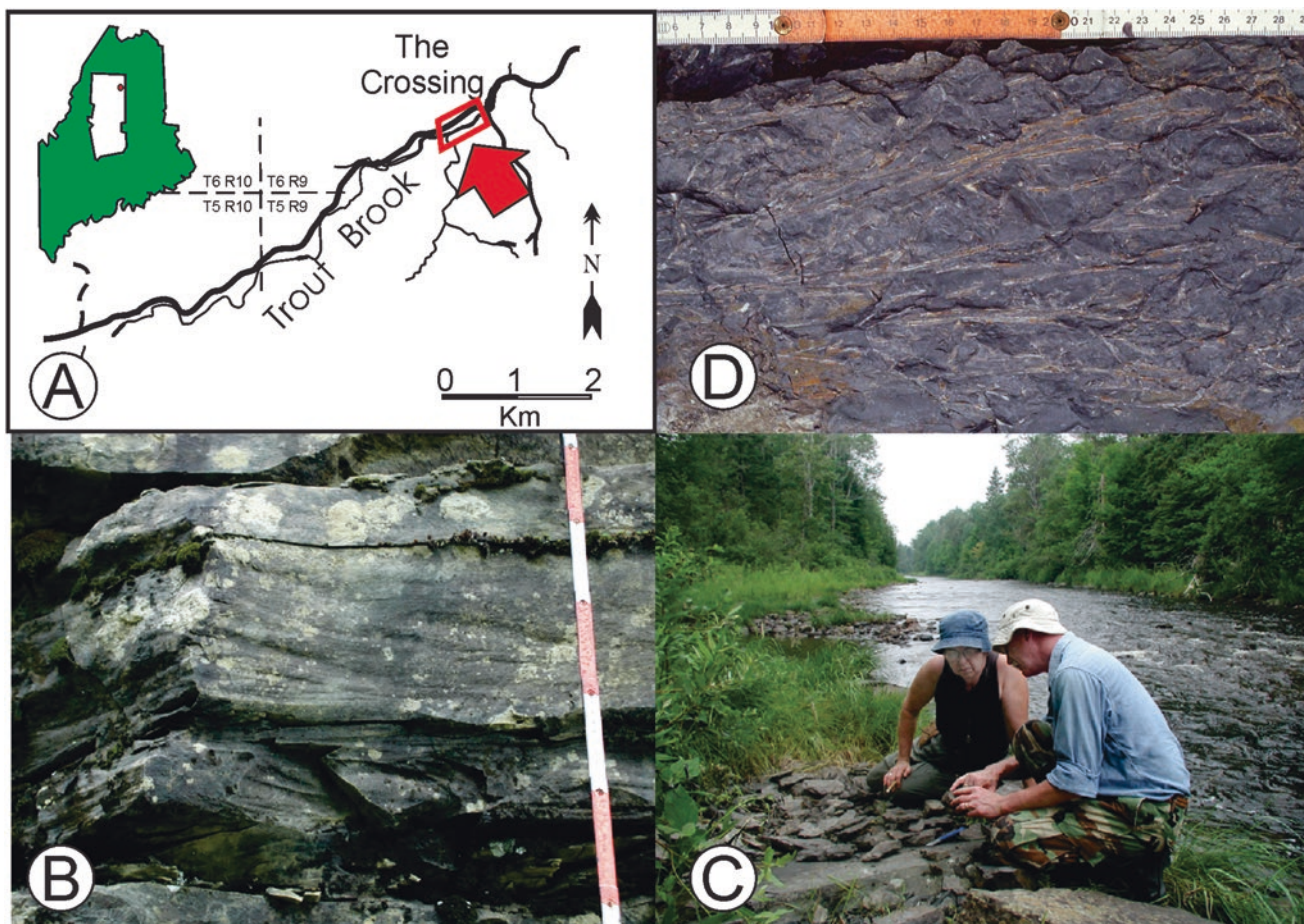


Fig. 15.8 Middle Devonian Trout Valley Formation, Maine, USA. (a) Outcrop localities along Trout Brook, Baxter State Park, Maine. (b) Low-angle trough cross-bedded siltstone of tidal origin in which the fossil flora is preserved. (c) Glacially exposed, fossiliferous bed-

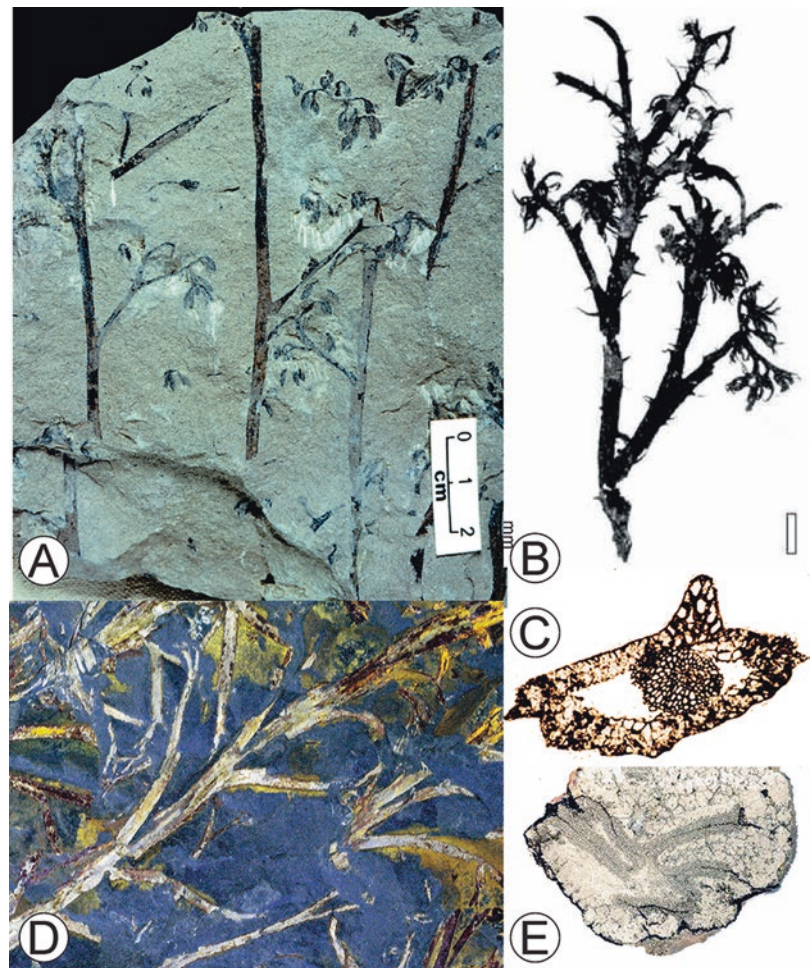
rock along the margins of Trout Brook. P. = P Gensel and RA Gastaldo. (d) Bedding surface of tidal siltstone in which biotically oriented axes of *Psilophyton* are exposed. Scales in dm and cm. (photos: RA Gastaldo)

fossils then known as “psilophytes”. These were examined by Erling Dorf who recognized their significance, and one of the first reports on these plants was published shortly thereafter (Dorf and Rankin 1962). With the recognition that early land plants are preserved in Maine and in coeval strata of New Brunswick, Canada, a series of studies over the past 60 years have added to our understanding of their evolutionary history and paleoecology (e.g., Kasper Jr et al. 1988; Allen and Gastaldo 2006). Both the environmental setting and the early land plants, themselves, are very different from the mosses and club mosses now covering the floor of Maine’s northern balsam fir forests.

Rocks of the Trout Valley Formation were deposited as pebble conglomerate, fluvial and nearshore (marine) sandstone bodies, and muddy tidal flats. These sediments represent an estuarine coastal zone flanking an extinguished volcanic island, the remnants of which are now the Traveler Rhyolite against which the Trout Valley rocks lie (Allen and Gastaldo 2006). There is some evidence of in situ (autochthonous) preservation of the vegetation, in the form of very

fine, vertically oriented rootlets, which colonized the mudflats [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 striations, 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 various early clades [U1524]. These include *Sciadophyton* (embryophyte of unknown affinity); *Sporogonites* (a possible 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 Early-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)



The biotically oriented assemblages in the Trout Valley Formation are unusual for several reasons. Trimerophyte, rhyniophyte, and lycophyte remains are preserved in association with molluscan bivalves of various affinities, eurypterids, and trace fossils (ichnofossils*), all of which are interpreted from brackish water (estuarine) settings [U1525] (Selover et al. 2005; Gastaldo 2016). Hence, it seems plausible that these early colonizing plants were tolerant of fluctuating coastal salinities. If true, this interpretation may also explain two facets of their preservation. Trimerophytes grew aerial axes from a surficial or shallowly buried axis or rhizome. Yet, the only evidence of rooting structures is vertically oriented rootlets that are unattached to a rhizome. Similarly, there is no evidence that the biotically ordered axes (Fig. 15.8d) are attached to any rhizomatous organ. The axis from which these plants developed is missing. Second, most of these aerial axes rotted and filled with mud before burial, resulting in internal casts. Saltwater incursion into these marshlands in response to coastal subsidence, then, would be responsible for their death, loss of any evidence of rhizomes through rotting, and the easy transport via tidal 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 description 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 the Middle Devonian.

15.4.1 Gaspé Battery Point Formation (Gaspé Sandstone Group), Emsian

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

The sedimentary facies in the Cap-aux-Os Member are dominated by sandstones of various internal architectures, and three different fluvial associations are identified. River deposits at the base of the succession are large multistory sandstone bodies with interbedded thinner mudstone (Association 1). These rocks are overlain by gray mudstone with thin sandstone sheets or single-story sandstone bodies (Association 2). The uppermost interval (Association 3) consists of relatively coarse-grained, multistory sandstone bodies with uncommon thinner red mudstone intervals [U1526]. There is evidence of bedding with wave- or current-ripple marks, trace fossils, and disarticulated cephalaspid fish skeletons in some intervals. Desiccation-cracked mudstones preserve articulated lingulid brachiopods, and in dark gray shale and siltstone acritarch microfossils, small bivalves, and brachiopods can be found. The most current interpretation is that these rocks represent fluvial and delta-plain deposits close to the coastline, with some intervals interpreted as having been close to the tidal limit of tidally influenced lowlands (Griffing et al. 2000; Hotton et al. 2001). The vegetation that grew across these coastal zones commonly is found at or near their sites of growth.

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

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

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

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

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

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

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

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

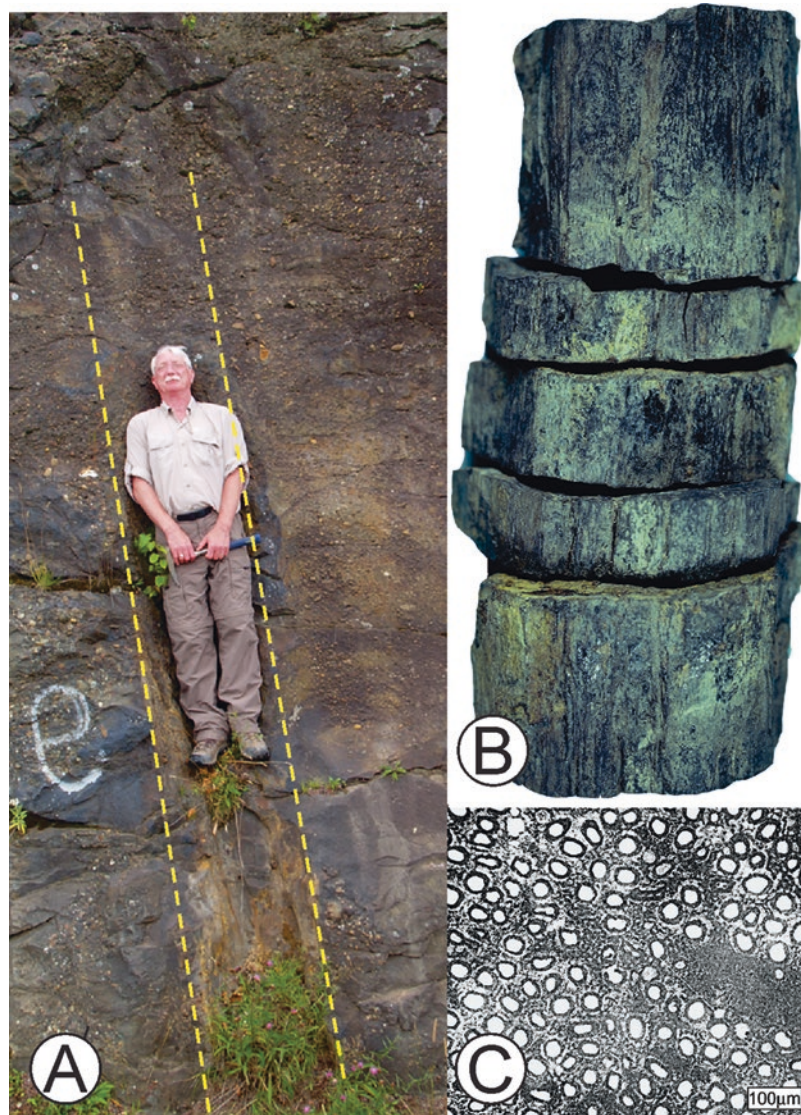
a different outcrop on the north shore of Gaspé Bay (Gensel 1976). The main stems are tiny, the axes of approximately 1 mm in width, and specimens are up to only a few centimeters in length. Lateral branches divide unequally and may be terminated in kidney-shaped (reniform) sporangia. A dark strand evident in stems indicates the presence of vascular tissue 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 (Box 15.3).

Box 15.3: 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.

Fig. 15.10 *Prototaxites*, a giant fungus. (a) Erect mold of *Prototaxites* in siltstone, Dalhousie Junction, New Brunswick, Canada. RA Gastaldo for scale; edges of mold marked by yellow dashed lines. (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)



Plants exhibiting secondary xylem include:

- *Armoricaephyton 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.

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



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)

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, discontinuously, 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.

We've seen this vegetation before. Plants similar at the generic level to *Psilophyton*, and *Pertica* [U1530], *Drepanophycus*, and possibly *Sawdonia*, as well as new taxa of zosterophylls and lycopsids [U1531], occur. One of the

earliest occurrences of the lycophyte *Leclercqia* is here, as well as two strange taxa, *Chaleuria* and *Oocampsa*, which differ from each other and from the major Devonian plant lineages [U1532]. *Chaleuria* and *Oocampsa* both exhibit broad main stems, up to 1 cm in diameter, which may have been partly rhizomatous and partly upright. In contrast to other plants we've encountered, the lateral branches of these are dense and spirally arranged. The lateral branches in *Chaleuria* have dichotomizing, spirally arranged ultimate branches with fusiform, terminal sporangia in which two sizes and two kinds of spores were produced. This condition has been interpreted as incipient heterospory, a more derived mode of reproduction in spore-producing plants (Andrews et al. 1974). In *Oocampsa*, lateral branches are more dichotomously 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 environmental 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 northwest of Aberdeen. It is hard to imagine that this area hosts one of the most important and famous localities of early Paleozoic plants when we walk through the countryside (Fig. 15.12a). There is no rock exposed at the surface. Rather, it lies beneath the green pasture lands studded with livestock as pictured on our postcard. The locality, known as the Rhynie chert, first was discovered by examining loose blocks turned up in the soil during plowing or as part of the stone walls edging the fields. Around 1912, during one of his collecting trips, Dr. William Mackie (for whom geology was a hobby) found fragments of fossiliferous chert in the dry stone walls, possibly while sitting on one and eating his lunch [U1533] (Andrew and Gensel 1984). He recognized that the chert contained plants entombed in the silicates and took them to Robert Kidston. Along with W. H. Lang, the chert was sectioned and studied, and they produced a series of papers (1917–1921) providing initial descriptions of the fossilized plants. In recent decades, trenches were dug in selected areas to collect additional plant material, and later excavations were undertaken to study the lateral and vertical extent of the deposits. Major

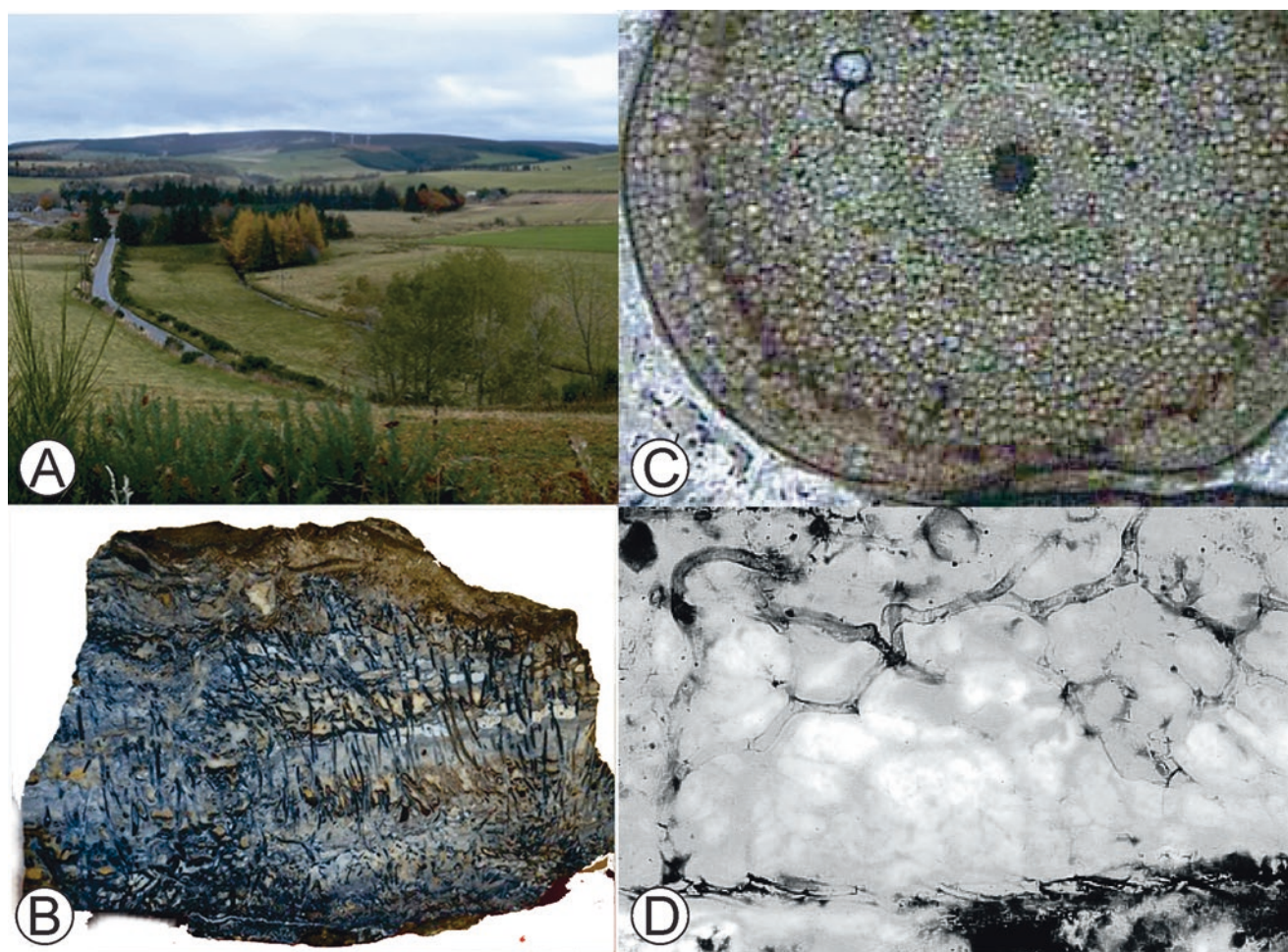


Fig. 15.12 The Early Devonian (Pragian) Rhynie chert, Aberdeenshire, preserved the oldest documented terrestrial ecosystem. (a) The Rhynie chert is not surficially exposed but, rather, is the bedrock beneath green pastures. (b) Polished specimen of the Rhynie chert showing vertically

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

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 similar to today's hot spring-and-geyser landscape in Yellowstone National Park, Wyoming, USA (Rice et al. 2003). The fossiliferous cherts were deposited in a tectonic sedimentary basin in which volcanic activity occurred. Sandstone deposits reflect deposition in a braided river system with andesitic (igneous lava rock) 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 influenced 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, temporary, freshwater lake, adjacent to active geysers. The permineralization 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 (isotomous) 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 developed 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 15.4). It is considered part of the Rhyniopsida clade. Gametophytes [U1535],

Box 15.4: 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.

which are multicellular, haploid, sexual structures in plants, are known in considerable detail, including the structures containing egg and sperm (Kerp et al. 2003; Taylor et al. 2005). Both of these taxa exhibit endophytic (within the plant cells) fungi that probably aided in water uptake (VA mycorrhizae). The Rhynie flora was more diverse than just rhyniophytes.

Nothia aphylla is another well-preserved plant more closely related to the zosterophyll clade (Kerp et al. 2001). It had spreading rhizomes, perhaps partly below ground, with rhizoids, and upright axes that branched dichotomously. The aerial axes were covered by elliptical emergences, many topped by a stoma (a specialized gas exchange structure). Sporangia producing only one type of spore developed near branch tops. To release the spores, each sporangium opened around its margins. *Nothia* was a geophyte in that it grew in sandy soils and reproduced clonally. Underground rhizomes survived from season to season, and

elevated axes grew again annually. Another geophyte, the proto-lycopsids, also is part of the hot spring landscape.

A vascular plant, allied to the lycopsids, is the genus *Asteroxylon*. These plants also grew in sandy substrates more distant from the main sinter zone, but still were permineralized by silica (Kerp 2018). The rhizomes of *Asteroxylon* were positively geotropic, growing into the soil substrate [U1536]. Rooting structures branched equally (isotomous) whereas aerial stems, 1–2 cm wide and possibly up to 40 cm in height, branched unequally (anisotomous). These are covered with helically arranged, unvascularized leaf-like structures, and vascular strands extend into the cortex almost, but not quite, to the level of leaf-like attachment. Both aerial axes and the leaf-like structures possessed stomata. The internal anatomy exhibits several features not found in other groups at the time. The xylem in the aerial axes consists of lignified, simple conducting cells (tracheids) with closely spaced thickenings that encircle the cell (annular thickening). Their arrangement forms a star-shaped pattern. Similar to lycopsids, the sporangia of *Asteroxylon* are kidney-shaped (reniform) and developed on a short stalk (pedicel). Fertile zones are arranged spirally on axes interspersed among sterile ones (Kerp et al. 2013). This arrangement indicates the potential for periodic sexual reproduction promoted by changing environmental conditions. Dispersed spores described from these sediments indicate that the vegetation of the larger region was more diverse than the plant association preserved in the Rhynie chert (Wellman 2010).

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

The preservation of extremely minute details, which allows the investigation of vascular systems, reproductive organs, spores, generation of gametes, and even seasonal growth of plants, allows us to recreate a picture of the entire Rhynie hot spring ecosystem (Channing and Edwards 2009). These fossil Lagerstätten with complex preservation potential are very valuable [U1538]. They are windows, frozen in time, that enhance our understanding of early vascular plant evolution (Trewin and Kerp 2018). It was the exquisite preservation of the plants in the Rhynie chert that convinced earlier geologists and botanists that pre-Carboniferous terrestrial plants existed.

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

Patricia G. Gensel

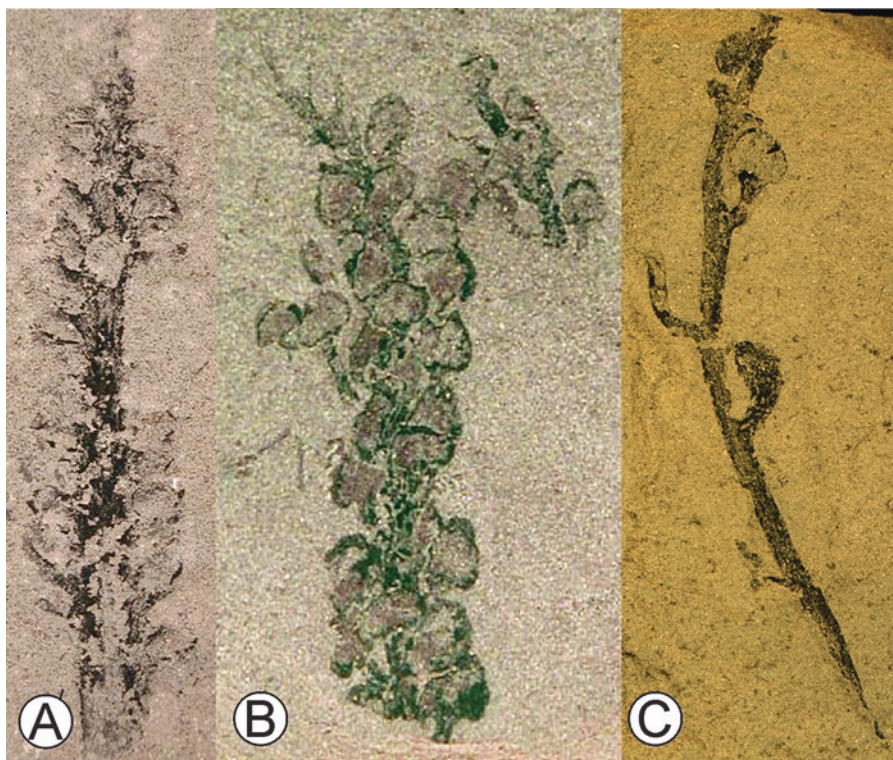
We now travel from the modern conveniences found in one small village in Aberdeenshire, Scotland, to a very remote island setting in the high Arctic where we'll get a different perspective on late Silurian and Early Devonian vegetation. Back in time, this island was part of a large tectonic block located around the equator. In contrast to the mostly small and simple rhyniophytoids described from many Silurian localities in Laurussia, Baltica, and South American assemblages, a walk through these equatorial regions brings us to another worldly view. Late Silurian plants in eastern Bathurst Island, Nunavut, Canada, are somewhat familiar in their basic architecture and structure (Basinger et al. 1996; Kotyk et al. 2002). Plants attained several centimeters in length and stems were as wide as 4 mm, more closely resembling Early Devonian taxa. Unlike fossil-plant assemblages we've previously visited, these are preserved in offshore, deep marine, fly ash deposits ("Bathurst Island beds") securely dated as Silurian (late Ludlow or Ludfordian, 426–423 Ma) based on graptolites, conodonts, and brachiopods (see Chap. 14, for more information on these early animals). The sedimentological context of these assemblages indicates that the plants were deposited by mudflows in a marine basin, where they were quickly buried with little biological (bioturbation) activity to alter them. These mudrocks now are exposed mostly along stream margins on the island.

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

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

A brief visit to the Early Devonian (Pragian, 411–408 Ma) of Bathurst Island provides insight into the signifi-

Fig. 15.13 Late Silurian 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



cance of these fossils [U1539]. The assemblage (Kotyk 1998) is dominated by zosterophylls, especially different types of the genera *Zosterophyllum* and *Distichophytum*. These differ mainly 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 zosterophylloids 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.

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,

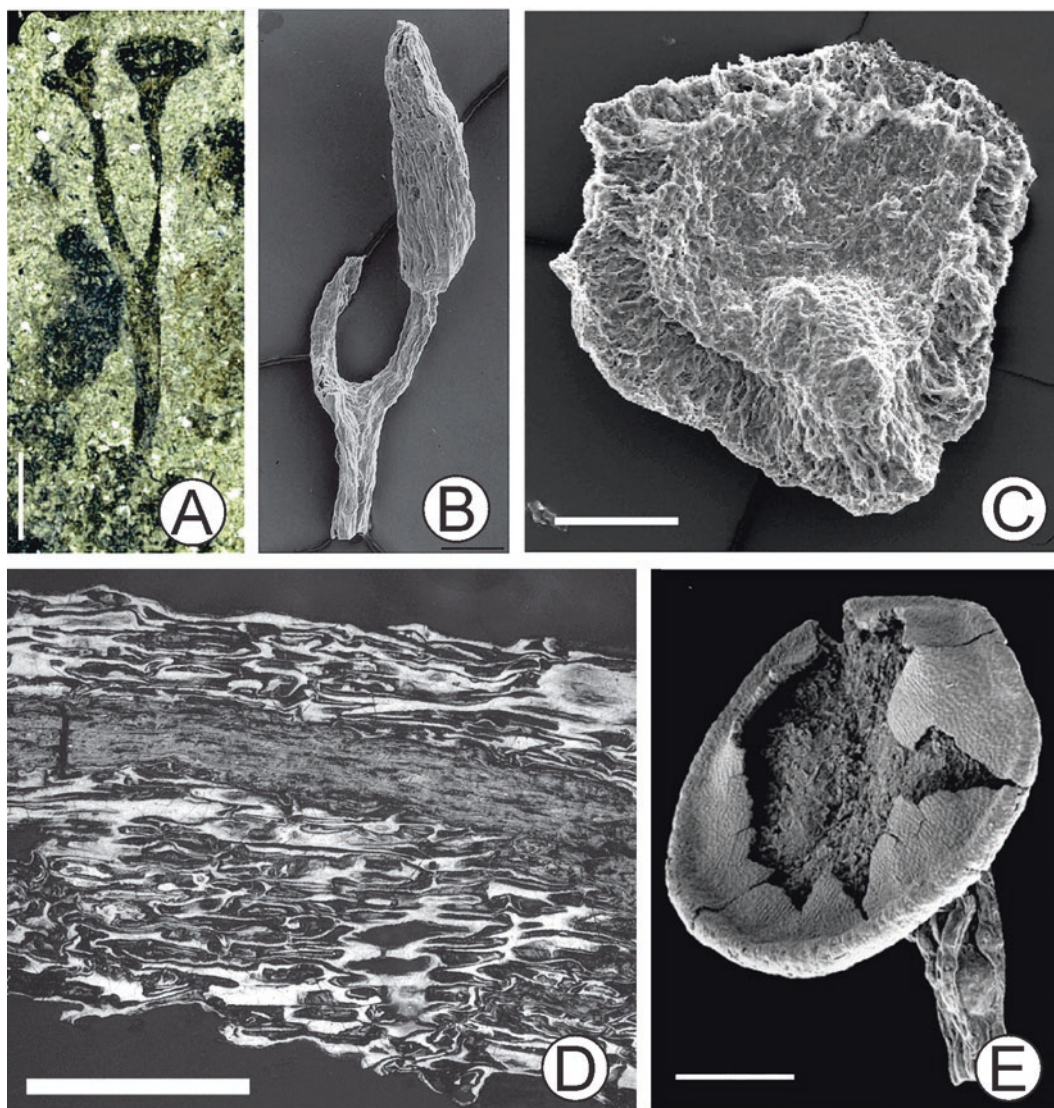


Fig. 15.14 Early Devonian plants from Shropshire, United Kingdom. (a) A compression specimen, the counterpart to the lectotype of *Cooksonia pertoni* from the Přídolí at Perton Lane, the surrounding black patches may be *Nematohallus*. NHM V58010 Scale bar = 2 mm. (from Edwards and Kenrick 2015. The 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 cryptospore-bearing plant with a simple, fusiform sporangium from the Lochkovian of North Brown Clee Hill assignable to *Fusiformitheca fanningiae*. 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 *Nematohallus* 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: *Nematohallus*-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)

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*, *Cullulitheca 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 cryptospore-bearing plants (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.

15.8 Pre-Devonian Land Plants

Ian Glasspool, Jiří 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]. 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, bearing terminal funnel-form sporangia [U1543]. Slightly younger examples of the genus *Cooksonia* (e.g., *C. pertoni*, *C. cambrensis*, and *C. hemisphaerica*) have been described from Wenlockian strata in County Tipperary, Ireland (Edwards et al. 1983). Due to many examples being exceptionally preserved as charcoal, the species *C. pertoni* is probably the most comprehensively studied of all *Cooksonia* species (see Morris et al. 2012). Whereas different examples of this species are morphologically and anatomically homologous, 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).

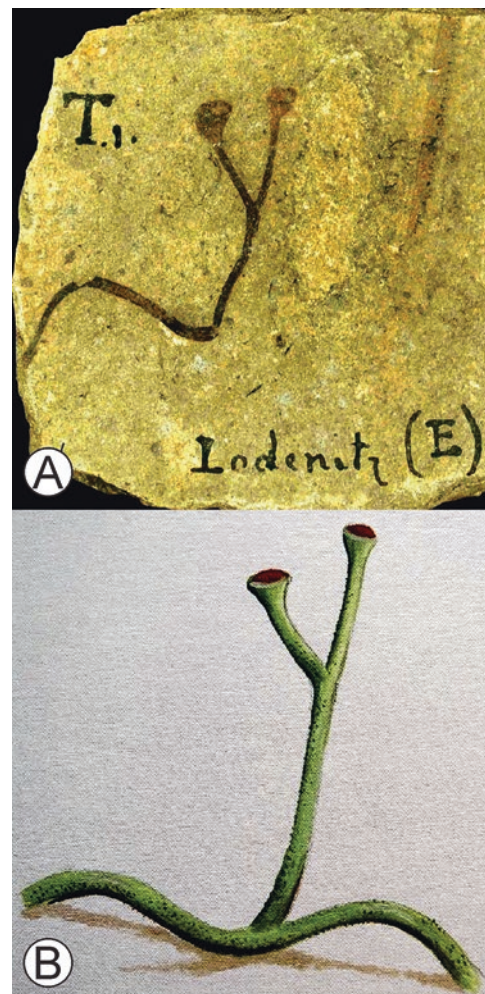


Fig. 15.15 *Cooksonia barrandei*. (a) Isotomously branched axis with sporangia, Loděnice, Špičatý vrch—Barrandovy Jámy, Czech Republic. Scale bar = 10 mm. (b) Reconstruction by Jiří Svoboda. (Both with permission Wiley Press)

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

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

Several other late Silurian plants had similar growth architectures to *Cooksonia*. *Steganotheca* (Edwards 1970) is somewhat more equally branched than *Cooksonia* and has elongate, striated, and flat-topped sporangia terminally arranged on gradually widening axes. This plant is known from the late Silurian to earliest Devonian. Although it is considered to be a vascular plant, there is no definitive proof, to date, about either the presence or character of tracheids in the axes. Recently, the genus *Tichavekia* was found in association with *Cooksonia* in the Prague Basin (Kraft et al. 2018). The plant axes attained lengths of at least 14 cm and branched up to five times equally (isotomously), each branch being no wider than 1 mm [U1539]. The terminal dichotomies of the plant were short and tipped with oval sporangia forming groups of four. In addition to the rhyniophytoids, other pre-Devonian organisms did not possess true stems, vascular tissue, or sporangia, such as the nematophytes.

The curious group of the nematophytes have long been considered neither alga nor vascular plant, leading some to consider them transitional forms [U1546]. New data indicate otherwise. One such genus is *Nematothallus* (Lang 1937) and often is preserved as either a resistant cuticle, with “cell outlines” or on which there are openings that may have functioned similarly to stomata. Some specimens consist of cuticle with underlying wefts or aligned tubes, and occasional banded tubes may occur intermixed. It now seems that *Nematothallus* is either a fungus or lichen, and some other layered tubes with cuticle might represent lichens (Fig. 15.16; Honegger et al. 2012; Edwards et al. 2013). Some of the ornamented (banded) tubes may represent epibionts (microbes living on or within these organisms). Another intriguing type of fossil is *Parka* (Fleming 1831), a flattened oval (thallus) with rounded bodies on it, present in the late Silurian and continuing into the Early Devonian. Its similarity to a charophycean green alga, *Coleochaete* (where zygotes appear as round to oval bodies on the algal thallus) is interesting because molecular phylogenies identify charophyceans as the sister group of the land plants. An organism like *Parka* can help us figure out the aspect of their possible common ancestor.

Other enigmatic plants include flattened axial structures, up to 20 cm in length, that most probably represent cuticles

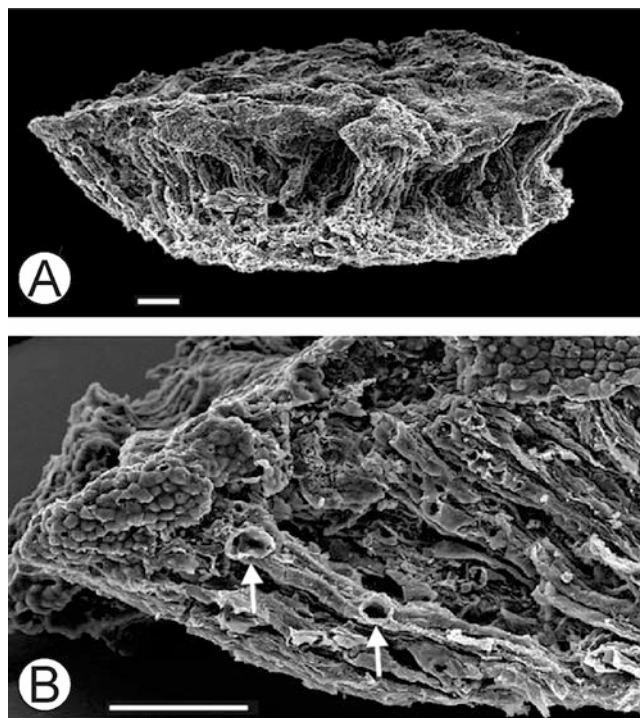


Fig. 15.16 (a, b): Fragment of *Nematothallus williamii*, Lochkovian, Shropshire in two magnifications of the same specimen showing a pattern typical for *Nematothallus* cuticle. Arrows indicate positions of lateral branches or areas. Scale bar 100 μm . (from Edwards et al. 2013. Contributions to the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

of stems. One example is *Orestovia* (Ergolskaya 1936) occurring in the Early Devonian of the Kuznetsk basin of Siberia. Primitive stomata, conducting cells, and spores have been interpreted in the taxon (Kräusel and Venkatachala 1966). Details of their sunken stomata, shown in thin sections, are known from specimens that lacked any associated spores or conducting cells (Gensel and Johnson 1994). *Orestovia* and some related forms have extremely thick and resistant cuticles and form thick deposits of so-called paper coal in the Lower Devonian of Russia, which have been used as a fuel source.

15.9 The Oldest Evidence for the Colonization of Land

Milan Libertin, Jiří Kvaček, and Ian Glasspool

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

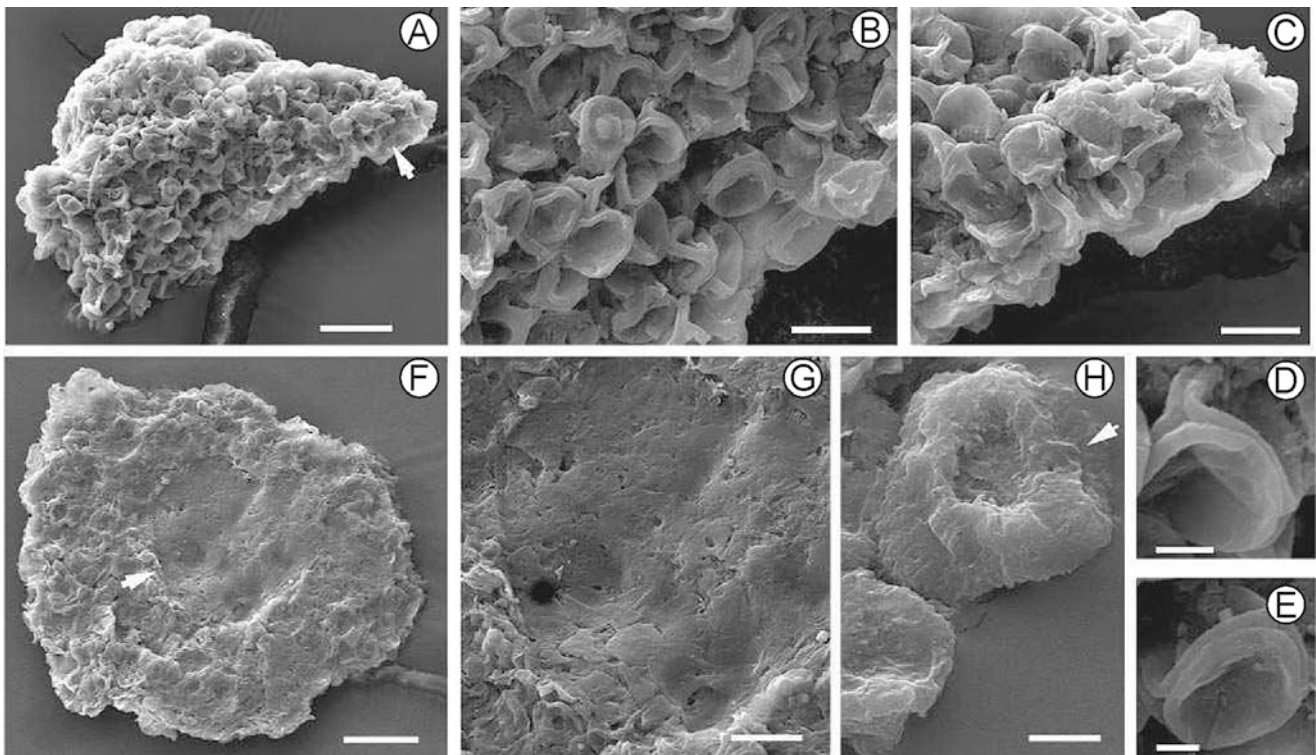


Fig. 15.17 Fossil plant fragments from the Ordovician (Llanvirn, 475 million years ago) of Oman. (A) SEM of fragment of sporangium containing naked permanent tetrads. Note the presence of sporangium covering in the bottom right-hand corner (arrow). Scale bar 50 μm . (B) Close-up of A illustrating the spore contents. Scale bar 20 μm . (C) Close-up of A illustrating spores overlying the sporangium covering. Scale bar 20 μm . (D, E) Close-up of A illustrating individual spore tet-

rads. Scale bar 5 μm . (F) Specimen CW47f. SEM of relatively complete sporangium, with a large patch of sporangium covering preserved (arrow). Scale bar 75 μm . (G) Close-up of F illustrating the nature of the sporangium covering. Scale bar 30 μm . (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 μm . (Wellman et al. 2003. *Nature* 425(6955):248–9 © Springer Nature with permission)

Box 15.5: 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 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).

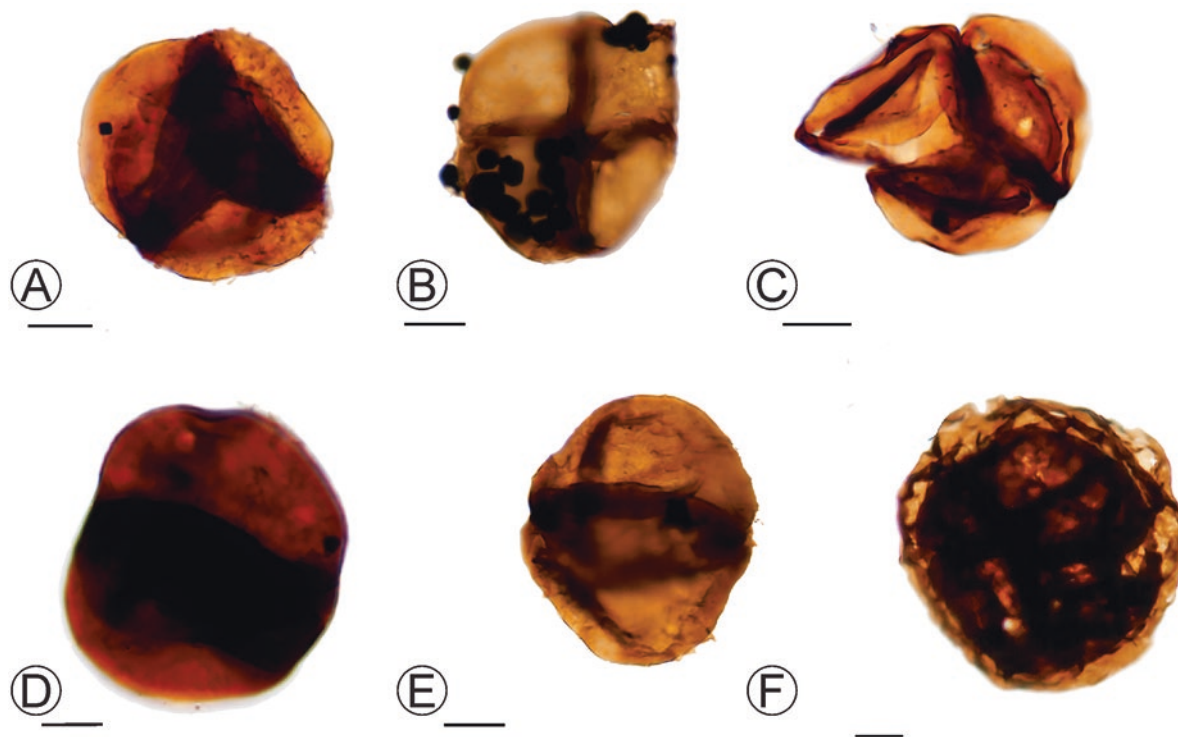


Fig. 15.18 Cryptospores. (A) Permanent spore tetrad in tightly attached tetrahedral configuration, *Tetraedraletes* sp. of Hirnantian age. (B) Cryptospore spore tetrad in planar configuration, *Tetraplanisporites* of Hirnantian age. (C) Broken tetrahedral cryptospore tetrad of *Imperfectotriletes vavrdovii*; spores have broken away from a permanent tetrad. (D) Permanent cryptospore dyad, *Dyadospora*

murusdensa. (E) Permanent cryptospore dyad, *Dyadospora* cf. *murusdensa*. (F) Permanent cryptospore tetrad enclosed in a reticulate synoecosporal wall, *Velatitetras* cf. *retimembrana*. All originate from the Power Glen Formation, Hirnantian age. Balls Falls Provincial Park, Ontario, Canada. (Images courtesy of P Strother)

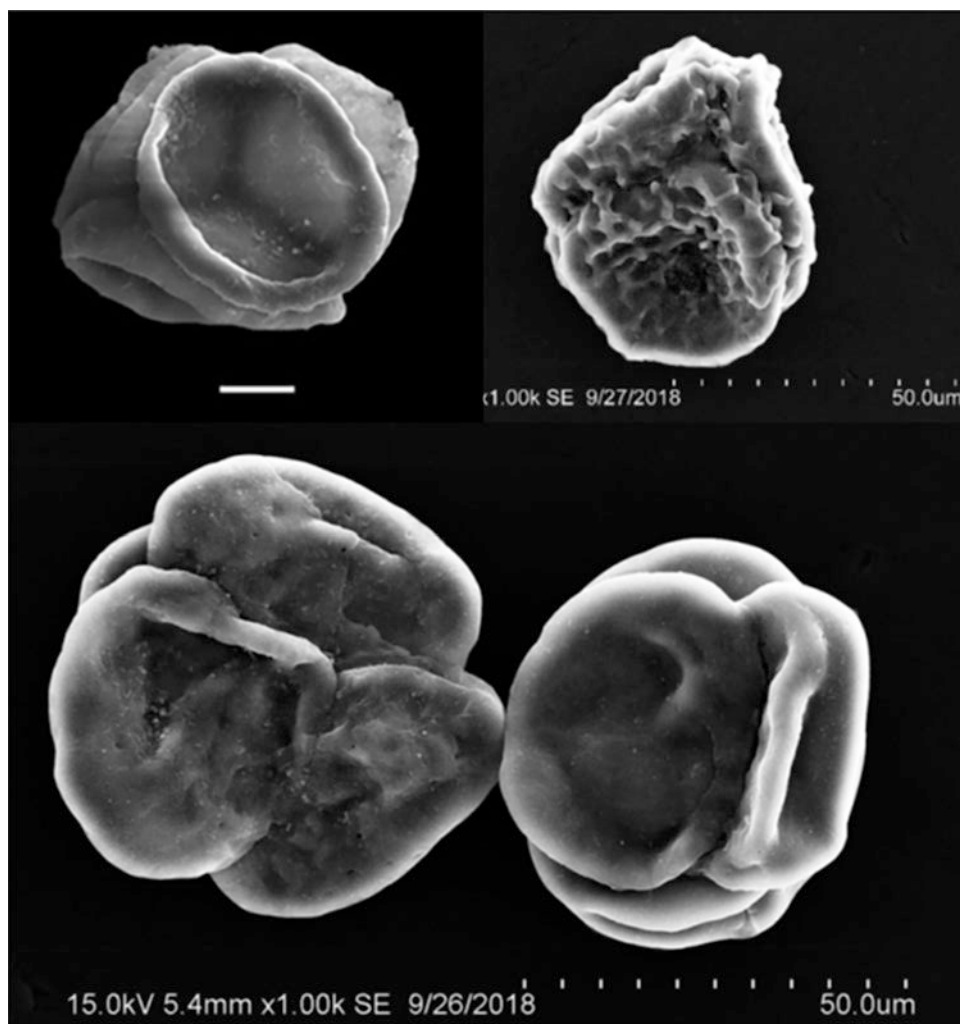
The parent plant fossils from which cryptospores have been obtained were recently placed into a basal group of early land plants described by Edwards et al. (2014). Cambrian forms have been referred to “algae” aligned with the embryophyte clade (probably extinct forms), rather than to the sister clade of the 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 (Strother 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 (Strother 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.

quently, separated (Strother and Taylor 2018). The majority of the early spores (Box 15.5) are cryptospores, occurring in obligate tetrads, dyads (pairs), or singularly as monads. Ultrastructural data and in situ cryptospores suggest a basal embryophyte affinity. Trilete spores*, ones with a Y-shaped scar delimiting site of opening for spore germination, are typical of vascular plants (tracheophytes) 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 several 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.

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 mesofossils containing cryptospores occur in both sites (e.g., Morris et al. 2018a). Based on studies

Fig. 15.19 Cryptospores. (A). Permanent cryptospore tetrad. *Tetraedraletes medinensis*. (B). Permanent cryptospore tetrad enclosed in a reticulate synoocosporal wall, *Velatitetras retimembrana*. (C). Two specimens of permanent cryptospore tetrads, one in tetrahedral configuration, the other in a cross configuration. These are considered to be taphonomic variants of the same taxon, *Tetraedraletes medinensis*. All cryptospores originate from the Tuscarora Formation, Llandoverly (Aeronian) age. Mill Hall, PA, USA. (Images courtesy of P Strother)



from these localities, it is possible to say that producers of cryptospores grew to only a few millimeters in size and probably had a stature similar to small mosses (bryophytes) (Steevens et al. 2009; Kenrick et al. 2012). Even at these small sizes, we can discriminate several different cryptospore-bearing groups. *Partitatheca* includes plants with dichotomously branched axes terminated by sporangia with stomata, which conform to the appearance of *Cooksonia*. But, these plants produced permanent dyads with a laminated spore-wall structure that are assigned to the dispersed spore genus *Cymbohilates* (Edwards et al. 2012). *Lenticulatheca*, recognized in the same assemblage, has discoid sporangia, containing similar dyads of the same group (*Cymbohilates*). Axes of *Grisellatheca* were terminated by short, dichotomously branched axes bearing slightly elongate sporangia, and these contain permanent tetrads of the *Tetraedraletes*-type (Edwards et al. 2014). Dispersed forms of cryptospore occur earlier in southern

Gondwana, and apparently radiated into Avalonia, then Euroamerica, and Baltica (Wellman et al. 2013).

15.10 Discussion

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Colonization of land by photosynthesizing plants is one of the most important evolutionary events in the history of the biosphere and appears to have occurred in several steps, beginning in the Late Ordovician, or possibly the Cambrian, and continuing into the Devonian (Strother and Taylor 2018). There are several requirements for an organism to survive and propagate on land. One critical abiotic parameter was the presence of an ozone layer, at least a weak one, to block cosmic (radioactive) and ultraviolet radiation, which damages cellular DNA. Only after an ozone layer was generated,

could organisms colonize land! Algae were the first plants to abandon fully marine chemistries and move, initially, into the intertidal brackish zone and, later, freshwater environments. Algal groups diversified during the early Paleozoic and included single-celled flagellated organisms to highly diversified thalli, measuring up to several meters in length. Some green algae, primarily brittleworts, Zygnematophyceae, and related charophycean algae achieved significant diversity during the Ordovician, and it seems likely that they inhabited shallow water settings and perpetually damp near-shore environments. A move to conquer moist to dry land followed with the advent of evolutionary innovations [U1549]. Although the unfiltered sunlight on land facilitated photosynthesis, heat affected internal cellular water and nutrient relationships. To prevent desiccation, a sheathing in a resistant compound evolved. Several lines of evidence are used to clarify relationships of chlorophytes (green algae) and their descendants, including photosynthetic pigments (chlorophyll A and B), a common storage product (starch), and molecular features. Chlorophytes, though, are not closely related to terrestrial green plants. Rather, a separate branch of the green algae, the charophytes are considered to be their sister taxa (Fig. 15.20; McCourt et al. 2004). The emergence of terrestrial plants is still not well understood, because the soft tissue of these colonizers had a very low preservation potential, which is also true for the earliest vascular plants.

Two primary hypotheses are put forth for the emergence of vascular plants. The first is that vascular plants evolved from mosses and their ancestors, plants that produced one type of sporangium (monosporangiate* plants; Graham et al. 2000). The alternative view is that they evolved from the pre-

decessors of hornworts, from plants in which more than one type of sporangia developed (polysporangiate; Puttick et al. 2018). On the basis of the most recent phylogenetic analysis (Morris et al. 2018b), it seems that vascular plants have a common ancestor with hornworts.

Beginning some 432 million years ago until the end of the Devonian, approximately 75 million years in duration, we have seen in this chapter a considerable change in plant type, size, diversity, and complexity. We have witnessed major innovations in plant organs such as the first appearance of leaves and roots, changing reproductive modes, and the evolution of wood (secondary xylem).

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

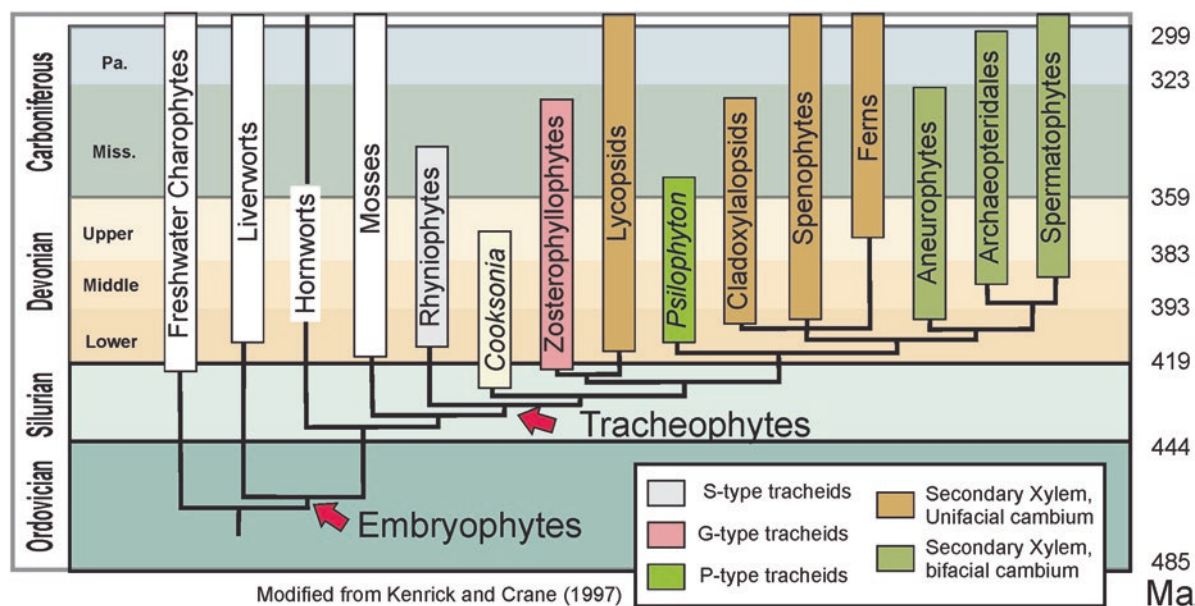


Fig. 15.20 Phylogenetic relationships between the major Paleozoic plant groups. Land plants correspond to embryophytes, and vascular plants to tracheophytes (modified from Kenrick and Crane 1997)

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).

Land plant diversification [U1550] significantly influenced the development of the lithosphere and, in turn, other Earth systems in many different chemical and physical ways [U1551]. Probably, the most significant of these was that of soil development and the stabilization of continental sediments. Terrestrial plants affected weathering and erosion and, as a consequence, river systems (Gibling and Davies 2012; Gibling et al. 2014). The expansion and diversification of land plants impacted climate, especially in incorporation of CO₂ into organic carbon that either was held by plants, incorporated into soil, or transported to the oceans (Berner and Kothavala 2001). The fossil record of this time period demonstrates that nearly every important phase of plant evolution happened in the Devonian (and according to H. P. Banks, “the rest is icing on the cake”).

15.11 Conclusions

As we have walked through these landscapes, it is clear that the earliest land plants, now extinct, were very different from those that we see around us at present and some interpretation is needed [U1552]. The earliest land plants of the latest Silurian and Early Devonian generally lacked recognizable roots and leaves and, in some cases, vascular tissue, giving one the impression that these were nothing more than branched sticks. Shortly thereafter, emergences begin to develop along these axes, increasing the body area over which photosynthesis could possibly occur. As internal water-and-gas exchange relationships became more complex, we find that two innovations evolve. The first is evidence of some type of vascular tissue, ranging from lignified tracheids similar to those in extant plants to water-conducting cells with different wall patterns, or no wall pattern more similar to bryophyte-grade conducting cells. The second is the appearance of stomata, regulatory structures that provide a means to move CO₂ from the atmosphere to photosynthesizing cells, and let the byproduct, O₂, be emitted back to the atmosphere despite the presence of a waterproof cuticle. As photosynthesis became more efficient and the need to uptake water increased, root-like and true root structures, many with mycorrhizal (fungal) associations, evolved. Propagation and population sustainability are always needed for any species to survive. Hence, the evolution of the sporangium, the structure in which meiosis

occurs to produce haploid spores. Sporangia were borne first terminally or laterally on stems, singly or in groups. Sporangia vary widely in shape, presence, or absence and, if present, location on the stem, type of dehiscence structure, and spore type. But, releasing spores into a hostile environment also required protection from desiccation, a problem solved by terrestrial plant ancestors that had evolved a resistant and robust spore-wall chemical, sporopollenin. These innovations set the stage for the conquest of all continental environments, the establishment of a myriad of ecosystems, and an ever-changing planetary surface, with the comings and goings of plant groups over the course of the Phanerozoic.

Questions

1. What defines a forest? When do the earliest forests occur? How are they different from extant ones? Be able to describe two types of plants that form the canopy of an early forest. What forms of preservation have enabled us to recognize the existence of forests? What limitations do we have in terms of characterizing early forests?
2. Where are plants preserved, and inferred to have grown, during the Late, Middle, and Early Devonian, respectively? What type of vegetation was present?
3. Which plant groups are embryophytes?
4. Some plant stems, and/or sporangia, are covered with emergences, and these frequently are used to define taxa. What are these structures?
5. Name several major innovations in plant size, anatomical organization, architecture, or reproduction that occurred in the Silurian-Devonian. What is the significance of each in terms of changes to Earth systems or to the composition of vegetation types? What is the earliest record of each?
6. What features distinguish a progymnosperm, such as *Tetraxylopteris* or *Archaeopteris*?
7. What are three characteristics of early seed plants, and why are they significant for their survival?
8. Define or characterize the basic features of the four main lineages of early vascular plants (rhyniaceans, zosterophylls, trimerophytes, and progymnosperms) and provide an exemplar genus for each. Potential exemplar genera are *Cooksonia*, *Sawdonia*, *Zosterophyllum*, *Psilophyton*, *Pertica*, *Rhynia*, *Aglaophyton*
9. Lycopside (zosterophylls + lycophytes) are known to be a distinct lineage since the late Silurian. What defines a lycophyte versus a zosterophyll? When do lycopside become tree-like? Are they similar today?
10. What role did the following plants play in structuring vegetation, affecting soils or Earth processes, or in evolutionary changes in lineages? *Eospermatopteris/Wattieza*,

Rhacophyton, *Archaeopteris*, *Protolepidodendropsis*, *Leclercqia*, *Elkinsia*, and its relatives.

11. What is a Fossil Lagerstätte? Why might the Rhynie chert be considered a Fossil Lagerstätte?
12. Some paleobotanists suggest that lichens, which today are pioneer plants in establishing soils, existed during the Devonian. What taxa may represent lichens? Fungi? How might nematophytes address this question?

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