

Early land plant developments: Global progress and Indian priorities

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ABSTRACT

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This review paper is primarily aimed to furnish a general account on the origin, evolution, radiation and the proliferation of early land plants on the earth. The story of the emergence of the plant life on the land and its subsequent development during Silurian and Devonian times has been narrated as per Edwards and Selden's (1993) theory of gradual colonization, which shows that the land plants established themselves involving four stages of continuous growth and the diversification. The paper demonstrates how the simplest land forms (*Cooksonia*, rhyniophytes) in the middle Silurian have given risen to much evolved progymnosperms (*Archaeopteris*) during the late Devonian within a span of 48 million years of time (from 423-375 ma). An account of the records of land plants from their earliest occurrences in the Ordovician to the end of Lochkovian in the Lower Devonian has been provided to show the current status of such studies on the global platform. The palaeo-phytogeography concerning spores and megafossils from Llanvirn (middle Ordovician) to Lochkovian (Lower Devonian) has also been depicted on the base maps of the globe.

Key-words—Early land plants, Ordovician, Silurian, Devonian, Cryptospores, *Cooksonia*, Rhyniophytes, Zosterophylls, Trimerophytes.

प्रारंभिक स्थलीय पादप विकास: वैश्विक प्रगति एवं भारतीय प्राथमिकताएं

कमलजीत सिंह

सारांश

यह समीक्षात्मक शोध-पत्र मुख्यतया पृथ्वी पर प्रारंभिक स्थलीय पादपों के उद्गम, विकास, विकिरण एवं क्रम प्रसरण का व्यापक विवरण देने के उद्देश्य से है। जमीन पर पादप जीवन के आविर्भाव का विवरण तथा इसके उत्तरवर्ती एडवर्ड एवं सेल्डन (1993) के क्रमिक उपनिवेशन के सिद्धांतानुसार, सिल्यूरियन एवं डिवोनी काल के दौरान विकास वर्णित है जो दर्शाता है कि स्थलीय पादपों ने स्वतः को निरंतर वृद्धि की चार प्रावस्थाओं और विविधरूपण में सम्मिलित करके स्थापना की। शोध-पत्र दर्शाता है कि मध्य में सरलतम स्थलीय पादप (*कुक्सेनिया*, *रयनियोफायट्स*) में किस प्रकार अंतिम डिवोनी के दौरान 48 मिलियन वर्षों के समय (42.3 मिलियन वर्षों से 37.5 करोड़ वर्ष) के अंतराल में सिल्यूरियन के अति विकसित प्राक अनावृतबीजी (*आर्कियोप्टेरिस*) को उत्थित किया है। वैश्विक पटल पर इस तरह के अध्ययनों की वर्तमान दशा को दर्शाने हेतु निम्न डिवोनी में ऑर्डोविशन से लॉककोवियन के अंत तक उनके प्राचीनतम प्राप्ति से भूमि पौधों के अभिलेखों का वर्णन उपलब्ध करवाया गया है। गोलक के आधार मानचित्र पर लानवर्न (मध्य ऑर्डोविशन) से लॉककोवियन (निम्न डिवोनी) तक बीजाणुओं एवं स्थूल जीवाश्मों से संबंधित पुरा-पादपभूगोल भी चित्रित किया गया है।

संकेत-शब्द—प्रारंभिक स्थलीय पादप, ऑर्डोविशन, सिल्यूरियन, डिवोनी, गूडबीजाणु, कुक्सेनिया, रयनियोफायट्स, जोस्टेरोफायट्स और ट्राइमैरोफायट्स।

INTRODUCTION

THE Earth came into existence about 4,600 million years ago by the consolidation of the accretion disc of debris orbiting the Sun. Nitrogen, hydrogen and carbon dioxide dominated the earliest atmosphere. The earliest bacteria relied on hydrogen and some carbon dioxide while extracting energy from inorganic compounds and this had a marked impact in reducing the atmospheric levels particularly of hydrogen. There are no fossils of these early life forms. The oldest known fossils date from about 3,500 million years ago, with the remains of small filamentous organisms looking like cyanobacteria. Also dating from this time are structures known as stromatolites, which are carbonaceous mounds, formed by cyanobacteria. Cyanobacteria initially used hydrogen and carbon dioxide for their metabolism, but as molecular hydrogen became depleted from atmosphere they adapted to use hydrogen present in the water. A major by-product of photosynthesis is oxygen, which was absent in the early atmosphere. Most of the oxygen being

produced by the cyanobacteria was used up as quickly as it was produced in oxidizing the soluble ferrous salts that were abundant in the primitive oceans forming banded iron formations. About 2,300 million years ago the supply of ferrous salts began to become depleted causing the ceasing of banded iron formations in the sea. The oxygen being produced by the cyanobacteria therefore started to accumulate in the oceans and then in the atmosphere. This coincided with the appearance of eukaryotes that ultimately gave rise to all multicellular organisms. At the beginning of Palaeozoic era (570 million years ago) the chemical composition of the oceans and atmosphere was broadly similar to that of present (Fig. 1). Relatively high levels of atmospheric oxygen were therefore, already available for life outside the oceans. It was not until about 430 million years ago that life, led by plants slowly started to take hold on the land. The geography of the world at that time was different from present. In the middle Silurian, there were two main land areas, separated by the Rheic Ocean, the Laurentia, which includes much of Europe and North America,

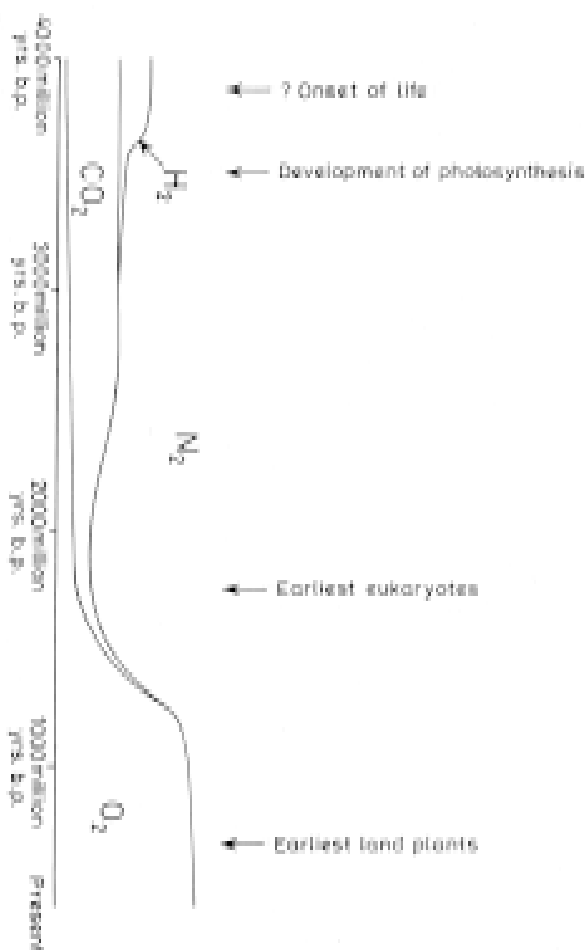


Fig. 1—Figure showing evolution of atmosphere and the main biotic changes that influenced it (after Thomas and Cleal, 2000).

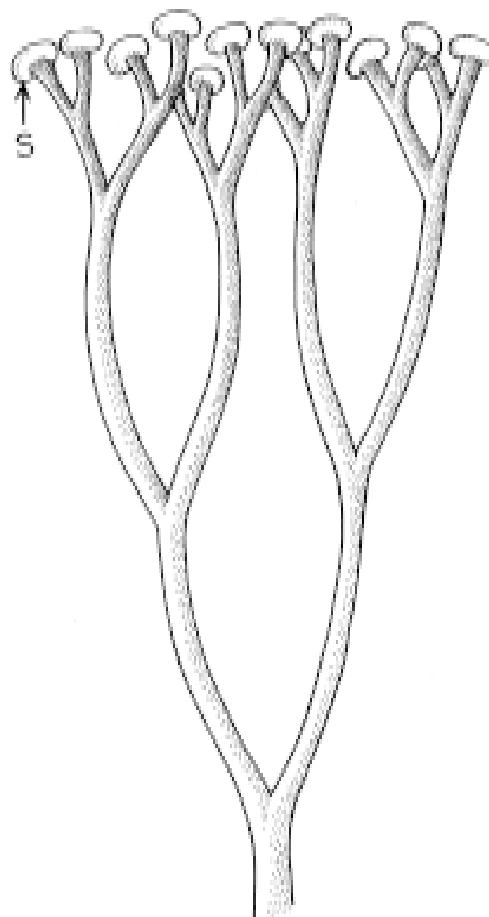


Fig. 2—Reconstruction of *Cooksonia*, showing slender, naked stems with terminal sporangia (S). They are thought to be the most primitive type of land vascular plants (after Thomas and Cleal, 2000).



Fig. 3—Photograph of Capel Horeb Quarry, mid-Wales. The middle Silurian strata here have yielded the oldest known examples of stem with vascular tissue preserved *in-situ*. They are the oldest known unequivocal examples of the land vascular plants. Prof. Dianne Edwards, F.R.S., (in black Jacket) of United Kingdom is also seen in the picture.

and the Gondwana including South America, Africa, central and east Asia and Australia. The best known early land plant fossils come from Laurentia but they have also been recorded from other parts of the world coming under Gondwana realm.

The gradual process of colonization of the land by the plants has been summarized herewith taking into consideration the views of a number of eminent workers in this field. Edwards and Selden (1993) suggested four stages of colonization. The first stage begins in the Precambrian and extends into Early Phanerozoic and later. It involved prokaryotes and photosynthesizing protists (algae) but there is no direct fossil evidence of this stage. The second stage, based on microfossils (spores and cuticles) possibly from bryophyte origin started in the Ordovician and ended in the Lower Devonian. The third one beginning early in the Silurian, consisted of small plants of axial organization with terminal sporangia, belonging to ?tracheophytes. The fourth and the final pioneering stage, responsible for the advent of taller vascular plants of varied organizations, begins around Silurian-Devonian boundary and it gave rise to the highest evolved plant groups including the extant ones.

The present paper covers the initial radiation of the embryophytes in the Ordovician; the emergence of tracheophytes, including the lycophytes in the Silurian; the proliferation of axial plants with terminal sporangia around the Silurian-Devonian boundary; the first major radiation of Zosterophylls at the end of Lochkovian and lastly the diversification and development of the trimerophytes during middle-upper Devonian. The records of early land plants (from Ordovician-Lower Devonian) including spores and megafossils have been compiled to show their age wise occurrences in different localities located across the earth (Figs 21-23). These records have also been depicted on the global maps (Figs 16, 17, 18, 19) to show the palaeo-phytogeography and the phytoprovincialism during Ordovician, Silurian and the Lower Devonian times. Sketches of a number of early land plants (Figs 2, 4-5, 7-15) have been included to strengthen the base of the paper. Similarly the photograph of a very famous plant locality (Capel Horeb, Fig. 3) and the reconstruction of the early Devonian volcanic landscape at Rhynie, Scotland (Fig. 6, commonly known as Rhynie Chert) are also given to have an idea of such important localities. Fig. 20 gives a quick glance to the geological time scale.

THE EMBRYOPHYTES AND THE DEVELOPMENT OF EARLY TERRESTRIAL ECOSYSTEM

Four stages of colonization of the land by the plants are recognized (Edwards & Selden, 1993):

Stage 1 (? Precambrian extending into Early Phanerozoic and later)

As per the current research findings, there existed a terrestrial ground cover in the Precambrian around 2,200 Ma ago (Edwards & Selden, 1993). Although the sub aerial surfaces in the Precambrian rocks were found to be carbon rich, yet no direct fossil evidence for such a covering is available with certainty (Wright, 1985; Retallack, 1990). The widespread occurrence of Cyanobacteria in the Precambrian could be a circumstantial evidence favouring the existence of such early land cover. Thus it is possible that during early phases of terrestrialization, the Cyanobacteria and other prokaryotes used to grow on the land surfaces and afterwards photosynthesizing Protists (algae) came into existence. According to Retallack (1990) the 3,000 Ma Jerico Dam and the 2,200 Ma Waterval Onder palaeosols could be examples of Precambrian soils which are produced by the interaction of organisms and sediments. These findings are based not only on the presence of the wispy trace fossils and some fabric and

structures that can be related to sediment binding in these palaeosols, but also based on the distribution of organic carbon and profiles of minerals (Phosphate) cycled by organisms in these soils. Another example of such vegetated palaeosols is one of the horizons in the 1,200 Ma Mescal Limestone of central Arizona, based on depleted $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (Beeunas & Knauth, 1985). Such surface mats might not be having good sediment binding capabilities but they could have anchored different kinds of substrates. This might have resulted in the development of thin humus layers, thereby creating microenvironments for the development of habitats for multicellular terrestrial green algae during early Palaeozoic.

Stage 2 (Llanvirn (middle-Ordovician) into Lower Devonian)

The evidences for this stage are based not on megafossils but on the sporomorphs (cryptospores) and the cuticles recovered from bulk maceration of fine grained clastic sediments belonging to a variety of Ordovician and Early Silurian environments, both continental and marine. These earliest dispersed spores are called cryptospores that comprise monads, dyads and tetrads lacking any trilete mark on their surface. The cryptospores are either naked or enclosed within a thin, laevigate or variously ornamented envelope and also impregnated with sporopollenin or sporopollenin type macromolecules as has been suggested by their preservations in the ancient deposits. Cryptospores are neither algal (having

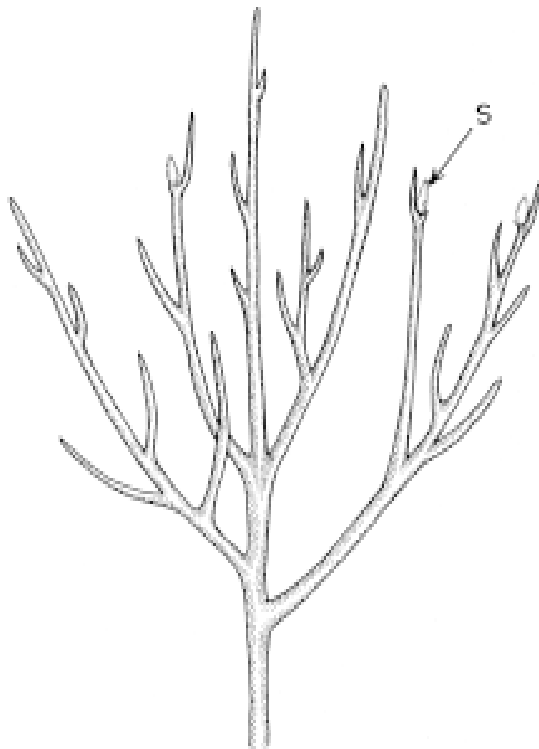


Fig. 4—A reconstruction of a plant of *Rhynia-gwynnvaughanni* Kidston and Lang. The sporangia (S) were produced at the ends of some of the axes (after Thomas and Cleal, 2000).

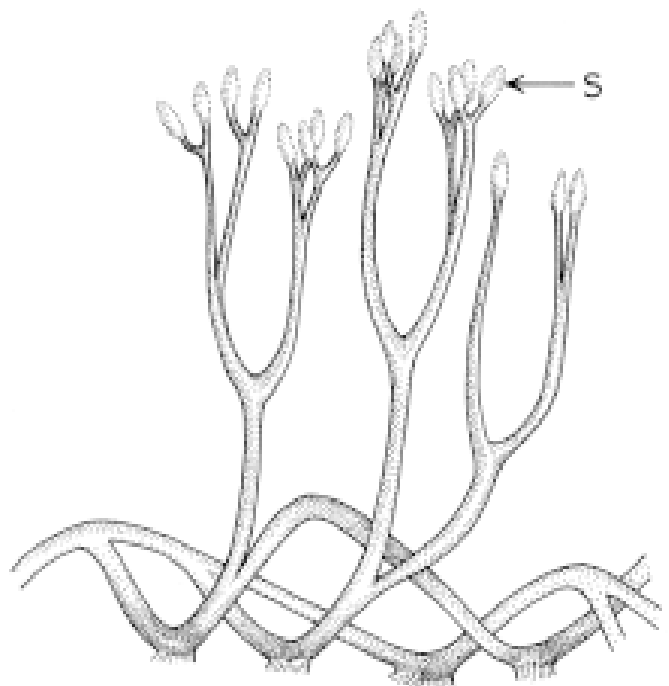


Fig. 5—A reconstruction of a plant of *Aglaophyton major*, showing terminal sporangia (S) (after Thomas and Cleal, 2000).



Fig. 6—Reconstruction of the early Devonian volcanic landscape at Rhynie, near Huntley, Scotland, United Kingdom. The hydrothermal fluids produced by the volcanic activity preserved the anatomy of the plants. The rhyniophytes are seen growing in the front and the active volcanoes can be seen in the back of the reconstruction (after Thomas and Cleal, 2000).

sporopollenin) nor belonging to a higher plant group (trilete mark absent). Gray (1985, 1991) was of the opinion that the cryptospore tetrads were derived most probably from the hepatic group of bryophytes. She noted that among free sporing extant embryophytes, only hepatics, regularly produce permanent tetrads, some of which are contained within an envelope, similar to certain enclosed cryptospores tetrads. Cryptospores thus present an indirect evidence for a land vegetation for which there is a little or no megafossil record. This suggests that the vast majority of plants during Ordovician and until Late Silurian lacked the appropriate recalcitrant biopolymers (such as lignin) in the tissues that enhance fossilization potential (Gray, 1985; Edwards *et al.*, 1999).

The earliest dyads and tetrads have been described as 'permanent', because of their inability to get separated into individual units, as a resilient membranous sac frequently surrounds them. The basis for the beginning of second stage for colonization is the records of tetrads reported from the mid-Ordovician (Llanvirn) of Saudi Arabia (Gray, 1991). The low diversity tetrads and dyads have been described from

Caradoc sediments in Welsh Border land (Richardson, 1988) and in Murzuk Basin, Libya (Gray *et al.*, 1982). In the Upper Ordovician (Ashgill Formation) they have been reported from in central Bohemia (Vavrdova, 1984), and the Appalachian region, Kentucky and Quebec in North America and possibly South Africa. The sporomorphs with bigger size and high diversity are found to occur in the early Silurian of South America (Parana Basin, Brazil; Gray *et al.*, 1985), Ghana (Bär & Riegel, 1980), North Africa (Tunisia, Morocco) as well as North America and Britain. It is presumed that this second stage of colonization was well established over a wide geographical area by the end of Ordovician. Although the diversity of the cryptospores was low as compared to the trilete spores in the Late Silurian (Prídolí), yet they were more in number than the trilete spores, suggesting that the cryptospores producing parent plants were still growing along with trilete spores producing plants (Fanning *et al.*, 1991).

Gray *et al.* (1982) described a fragment of cuticle in the Late Ordovician (Caradoc) in Libya. The cellular structures preserved in this fragment resemble very closely with the cuticles attributed to imprints similar to examples which are

attributed to *Nematothallus* Lang described in the Silurian (Lang, 1937; Edwards, 1982). Such type of cuticles certainly belong to land plants, although the nature of their internal tissues is not known. According to Lang (1937) such cuticles might be covering a plant, probably consisted of tubular structures including internally ornamented tubes. There are many records of smooth tubes in the Ordovician, but the earliest ornamented tubes have been reported in the early Silurian, Late Llandovery (Pratt *et al.*, 1978). These cuticles do not have any kind of perforation, similar to either stomata or liverwort pores. This suggests that these might not be involved in checking or reducing water evaporation as has been seen in the extant plants. According to Edwards and Selden 1993, such a superficial resilient covering (so called cuticle) could have been helpful in the absorption of ultraviolet light and in the deterring of pathogens in the pioneering land plants. Since no evidence is available regarding the vegetative parts of the spore producers, it is suggested that these plants had not evolved the homoiohydric characters of vascular plants (Raven, 1984). Gray 1985 opined that the Poikilohydric plants (Algal plants, they have little or no capacity to restrict water loss) radiated on to the land with a non-vascular grade of organization comparable with that of bryophytes. Irrespective of their affinities, it is postulated that the terrestrial vegetation comprised a low ground cover with maintenance of high humidity just above the ground.

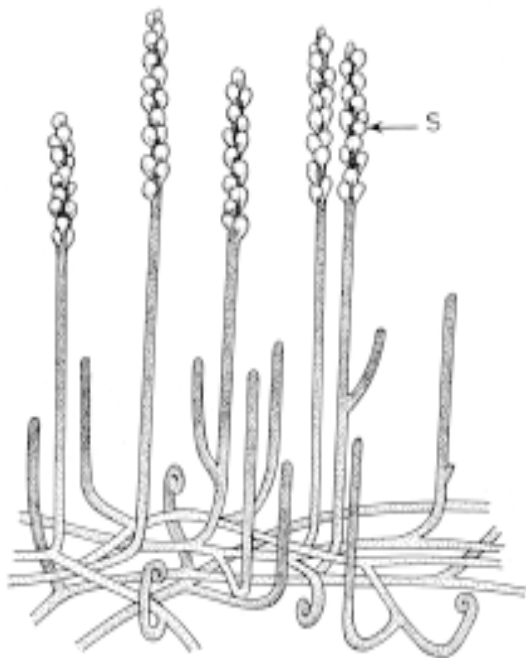


Fig. 7—Reconstruction of *Zosterophyllum*, showing vertical shoots arising from the tangled mass of axes at the base of the plant. The sporangia (S) were attached to the terminal parts of the stems (after Thomas and Cleal, 2000).

Stage-3 (Llandovery (Upper Aeronian, early Silurian) to Gedinnian (Lower Devonian))

The evidences for this stage are based on the spores in the earliest part, while the megafossils provided the basis in the late Wenlock and upto Lower Devonian. The miospores (monads) having well-defined, discrete trilete marks were the characteristic entities of this stage that appeared for the first time in Rhuddanian of Libya, North America and Ireland. From slightly younger strata, these miospores have been reported from Aeronian (Llandovery type area - Burgess, 1991; Tuscarora Formation, Pennsylvania - Strother and Traverse, 1979; Western Libya-Hoffmeister. The existence of *Ambitisporites vavrdovii* and *A. avitus* may be evidence of evolutionary progression from a separating 'Permanent' tetrad to trilete spore with discrete trilete mark (Richardson, 1988). In the late Wenlock (Homerian) there has been a great diversification in the sculpture and structure of the sporomorphs as is evidenced by the presence of sculptured spores and this trend continued into the Lower Devonian.

These evolved sculptured spores have been recorded from Southern Britain, Libya and Spain. The fertile megafossils with pteridophytic affinities also began to appear in the

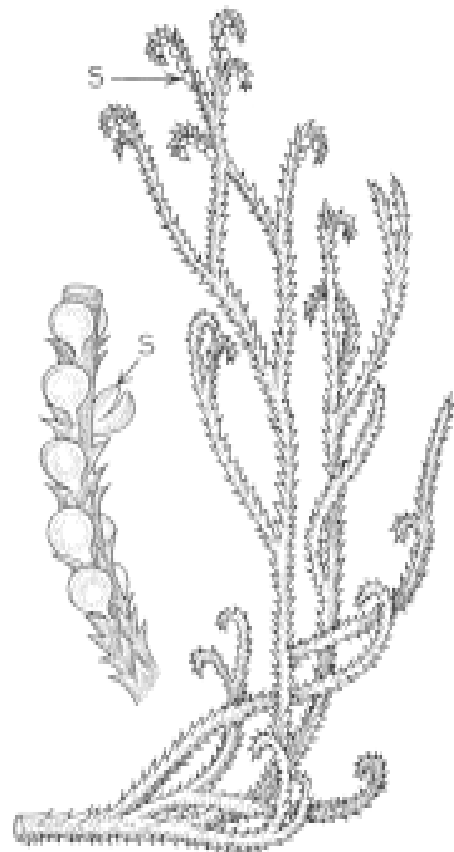


Fig. 8—Reconstruction of *Sawdonia*, showing prominent spines covering most of the aerial stems. Sporangia (S) are laterally attached to the stems and consisted of two valves (after Thomas and Cleal, 2000).

Wenlock along with sculptured spores. The axes found in the Llandovery age were sterile (Schopf *et al.*, 1966). The megafossils recorded from the Wenlock of Ireland are devoid of any anatomical details but they look very similar to *Cooksonia* plant of late Silurian and early Devonian ages. *Cooksonia* found in the Ludlow and Prídolí (Late Silurian) of North America, Britain, Bohemia, Libya and Podolia (Richardson & Edwards, 1989; Edwards, 1990) has smooth isotomously branching axes having terminal globular or discoidal sporangia. Although no complete plants have been found in the fossil record, but the small diameter and lengths of the Silurian axes suggest that these plants were of short stature (a few centimetres tall). Edwards (1990) is of the opinion that vegetation in Late Silurian Laurentia was dominated by small statured plants (Rhyniophytoids) having sporangia of different shapes and this vegetation continued into the early Devonian.

Recently Edwards *et al.* 1992 reported tracheids in Lower Devonian *Cooksonia pertoni*, confirming its vascular status, but the tracheids have never been reported in other Devonian rhyniophytoids as well as in Silurian fertile axes (Edwards & Rogerson, 1976). The recent discovery of spores, similar to dispersed taxa *Ambitisporites* from a late Silurian sporangia demonstrate that rhyniophytoids would have produced some of these dispersed spores including the oldest *Ambitisporites* (Fanning *et al.*, 1991). Although Richardson and MacGreger 1986 have established five spore assemblage zones between

Aeronian and the end of Silurian, but the presence of more or less similar type of megaplant remains during this period rules out any major change in vegetation in the present northern hemisphere.

Rhyniophytes—The group Rhyniophyta includes the simplest and the oldest known forms of vascular plants, consisting of dichotomously branched, leafless aerial stems having terminal sporangia that contain homosporous spores. A number of simple plants have been included in this group including the oldest known vascular plant, viz. *Cooksonia* whose remains are known from the Silurian and the Lower Devonian. It was first discovered and collected from several localities of the Downton Series (Prídolían, Late Silurian) in Wales, United Kingdom, in the year 1930. This was described by WH Lang in 1937 as a small, erect plant with naked, simple dichotomously branching axes and globular, terminal



Fig. 9—A reconstruction of part of *Koniora*, the most sophisticated of the known zosterophylls. The sporangia (S) were attached just below the last fork of the stems (after Thomas and Cleal, 2000).



Fig. 10—A reconstruction of a shoot of *Psilophyton forbesii* from the Devonian of North America, showing sporangial clusters (S) at the ends of ultimate branches. It shows the more complex branching pattern of the stem compared with the more primitive rhyniophytes (after Thomas and Cleal, 2000).

sporangia. The sporangia appear to have been simple sacs with no mechanism of opening and shedding their spores. The oldest known example of *Cooksonia* (Fig. 2) are from Ireland and are about 425 Million years old (Homerian, Middle Silurian). The fossils show that the plants were only a few centimeters tall (*Cooksonia hemisphaerica*- upto 6.5 cm long and 1.5 mm wide). The middle Silurian strata of Capel Horeb Quarry in Wales (Fig. 3) have yielded the oldest known examples of dichotomizing plant axes with vascular tissue (tracheids) preserved *in situ* (Edwards & Davies, 1976). In this way they are the oldest known unequivocal examples of land vascular plants. The specimens of *Cooksonia* have been described from various localities, including United States, Canada, Scotland, Libya, Wales, Czech Republic, Siberia, Bolivia, Kazakhstan, Ireland, England, Russia and Brazil.

Steganotheca, *Uskiella*, *Dutoitia*, *Hsüa*, *Hedeia*, *Yarravia*, *Salopella* and *Eogaspesia* (After Banks, 1968) are

some of the other examples of rhyniophytoids that also existed from Upper Silurian to Middle Devonian. *Steganotheca*, (Edwards, 1970) is reported from the Upper Silurian of Wales. It is similar to *Cooksonia*, approximately 5 cm tall and having larger terminal sporangia (2.5 mm) with truncated apices. *Uskiella* is reported from the Siegenian (Lower Devonian) of southern Wales as a petrified specimen that has naked, simple isotomous branching and ellipsoidal sporangia. *Dutoitia*, that resembles *Cooksonia* and *Uskiella*, has been described from the Lower Devonian (Gedinnian) of Cape Province, South Africa. *Hsüa*, from the Middle Devonian of Yunnan, China, consists of main axes, about 1.0 cm wide that divide to produce lateral branches, some of which terminate in reniform sporangium. *Hedeia corymbosa* also from Lower Devonian, consists of dichotomizing axes, each terminated by a long sporangium. Similarly, *Yarravia*, a Devonian plant, consisting of the distal ends of dichotomizing branches and has the

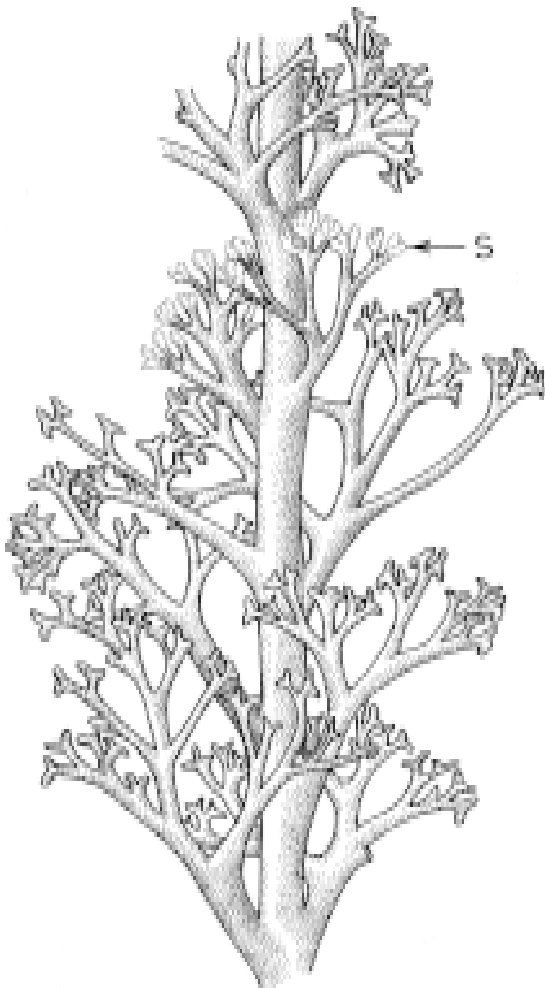


Fig. 11—A reconstruction of *Pertica* from the Lower Devonian of North America. This was the largest of the known trimerophytes, growing up to 3 metres tall, and had highly complex branching in the side shoots (after Thomas and Cleal, 2000).

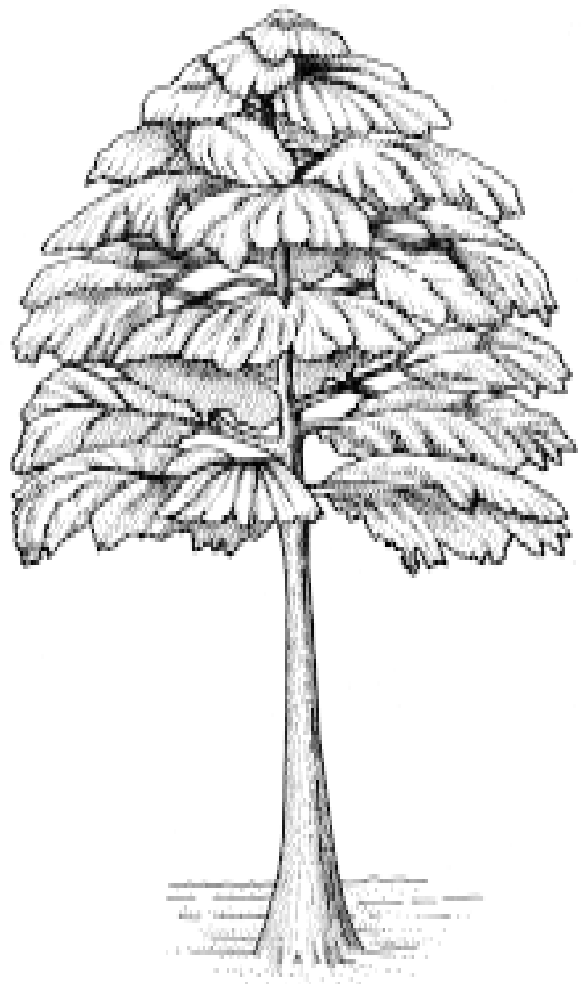


Fig. 12—A reconstruction of the *Archaeopteris/Callixylon* tree, the best known of the Devonian progymnosperms. The tree had a trunk that was upto 1.5 metres in diameter and could grow to 20 metres tall (after Thomas and Cleal, 2000).

individual sporangia aggregated to form a simple synangial cluster. Another plant described under cooksonioids is *Salopella* which consists of compressed, naked, dichotomously branched axes upto 2 mm wide, having terminal sporangia. Unfortunately, there is no report regarding the anchoring processes in all these cooksonioid taxa. How these aerial stems were interconnected? It is presumed that they were borne on some kind of basal structure like thallus or network of horizontal stems.

Kidston and Lang, 1917 described four taxa of vascular plants belonging to rhyniophytes from the early Devonian strata known as Rhynie Chert in Scotland. These taxa are slightly different and more evolved than the earlier ones (rhyniophytoides) as they are taller and have better anchoring mechanisms. *Rhynia gwynne-vaughanii* (Fig. 4) was the commonest of these simple plants that was about 20 cm tall. Its vertical photosynthesizing axes arose from creeping rhizomes, and branched both laterally and dichotomously. The stem anatomy was very simple, with central steel, surrounded by a two layered cortex and a thin epidermis with stomata. Sporangia were produced at the ends of some of the axes, producing homosporous spores produced in tetrahedral tetrads. The sporangia had stomata in their walls. Characteristic rounded protuberances, suggestive of underdeveloped lateral branches, asexual reproductive organs or hydathodes can be seen on most axes. According to Edwards (1980) *Rhynia gwynne-vaughanii* was more monopodial in appearance.

Aglaophyton major (Fig. 5, Edwards, 1986) another taxa of Rhynie Chert flora, is reconstructed to be about 18.0 cm tall and has different branching pattern than those of *Rhynia gwynne-vaughanii*. Its vertical axes undergo dichotomous

branching at wide angles of over 60° and arose from curiously arching rhizoid-bearing horizontal axes. *Aglaophyton* differed from *Rhynia* in having a central conducting strand that has numerous elongate thin-walled cells but no thick-walled conducting tracheids. In this way it is more similar to leptoids and hydroids found in certain bryophytes than to sieve cells and tracheids of vascular plants. The terminal sporangia were borne above the dichotomy and produced trilete spores.

Another member of Rhynie Chert (Fig. 6) flora is known as *Horneophyton* which is quite different from other rhyniophytes. The aerial axes of this taxa are naked and dichotomously branched but the basal portion consists of a series of bulbous, corm-like structures that bear numerous rhizoids. The sporangia of *Horneophyton* are borne terminally at the tips of some of the aerial branches and had a central column of sterile tissue around which the spores developed. The sporangia dehisce through an apical pore librating homosporous trilete spores. It is branched and consists of two to four lobes which are ellipsoidal–cylindrical in shape. The sporangial organs of *Horneophyton* have been interpreted as being intermediate between an undivided sporangia with a single sporogenous cell and a synangial organization. *Horneophyton* possesses some of the bryophytic characters which include a vascular underground corm like organ and a columellate sporangia comparable with the spore producing organ of hornwort *Anthoceros*.

Based mainly on life cycles of modern pteridophytes and on the preservation of the rhyniophytes in marine and fluvial sediments, it has been postulated that these simple land plants colonized moist habitats in coastal areas (Edwards, 1990). These rhyniophytes were probably ancestors of all the

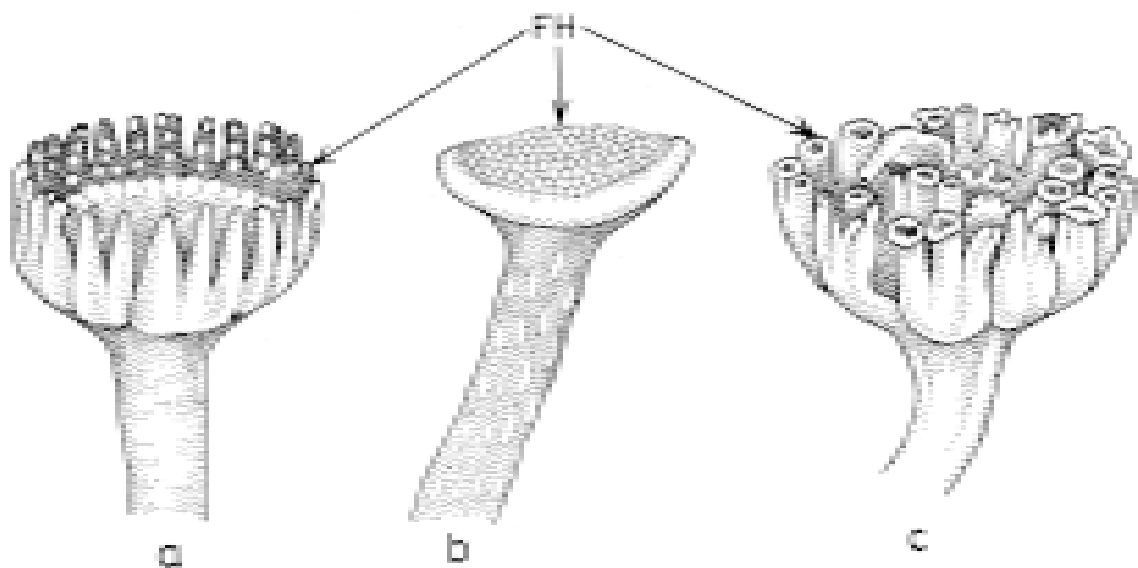


Fig. 13—Reconstruction of the fertile heads of three different types of gametophytes found at Rhynie, (a) *Lyonophyton rhyniensis* (b) *Kidstonophyton discoides* and (c) *Langiophyton mackei* (after Thomas and Cleal, 2000).

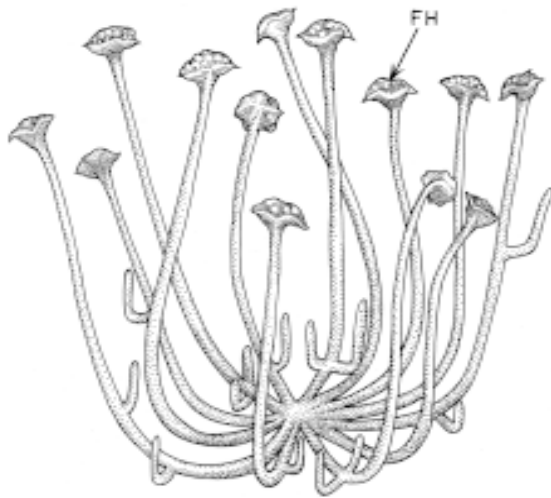


Fig. 14—Reconstruction of the gametophyte *Kidstonophyton discoides* showing fertile heads (FH) attached to vascularised stems (after Thomas and Cleal, 2000).

vascular plant groups, including the flowering plants and the gymnosperms (Thomas & Cleal, 2000). By the end of the Early Devonian there were no true rhyniophytes left.

Stage 4 (Late Ludlow (Australia)/ Early Gedinnian (Laurentia) into Frasnian (Late Devonian))

During the fourth and the final stage, the plants had undergone enormous changes. The simpler forms of second and third stages began to evolve higher plant architecture and due to this, the stunted growth patterns as seen in the rhyniophytes have been significantly changed and the plants (Zosterophylls and Trimerophytes) grew quite taller. The spore producing capacity of the plants also increased due to the development of strobili and trusses. Two major groups of tracheophyte appeared, i.e. the Zosterophyllophytina and the Drepanophycopsida (Lycophytina). The diversification of the vascular plants continued to occur throughout the Lower Devonian, firstly it was seen in Zosterophylls, and then from Siegenian onwards in Trimerophytes (Edwards & Davies, 1990). The fourth stage ended with the extinction of Zosterophyllophytina in the Frasnian, and similarly the Drepanophycopsida became extinct, although some of the lycophytes continue to persist even today (Edwards & Berry, 1991). The Emsian-Eifelian boundary has seen drastic changes, when the trimerophytes vanished and the evolutionary processes along with innovations have changed the vegetation structure and the reproductive strategies. A new era began in the Eifelian when Progymnosperms appeared and the plants grew taller with the acquisition of vascular cambium. Heterospory also evolved in many groups, the earliest ovules being recorded in the Famennian.

The reports of the genera *Baragwanathia* and *Zosterophyllum* marked the beginning of this fourth stage in



Fig. 15—A reconstruction of *Elkinsia polymorpha* Rothwell *et al.*, the best documented early pteridosperm from the upper Devonian of West Virginia (after Thomas and Cleal, 2000).

the present southern hemisphere and in the present northern hemisphere respectively. These two taxa demonstrate the two major kinds of gross morphology in the early land plants, viz. axial systems and the leafy stems. The vascular land plants that appeared and diversified soon after *Cooksonia*, are called Zosterophylls and were the important part of the Early Devonian vegetation. Zosterophylls share many features with the Lycophyta and believed to have given rises to the lycopods.

Zosterophylls—The *Zosterophyllum* (Fig. 7) was the simplest among these Zosterophylls, which had naked, erect dichotomizing stems arising from a basal tangled mass of prostrate axes, presumed to be rhizomatous system. Unlike *Cooksonia* that had delicate axes, this plant was more robust having a length upto 0.5 m and width of 1.5 mm. The circular to reniform sporangia were not simple and terminal, but attached laterally on short delicate stalks near the distal ends of the stems and released the spores by splitting apart along a well-defined line. This lateral placement of sporangia in the Zosterophylls distinguishes this group with other early vascular plants. All the Zosterophylls were homosporous.

Some Zosterophylls were leafy with the best known being *Sawdonia* from the middle Lower Devonian, having its

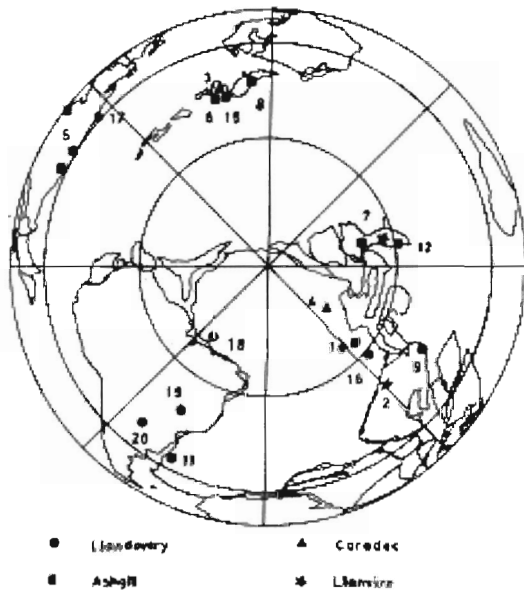


Fig. 16—Distribution of spore assemblages from the Ordovician and Llandovery on base map for Late Ordovician, 450 myr (based and redrawn from Edwards and Wellman, 2001). The figure gives a general idea of the geographical distribution of localities in the Ordovician southern Hemisphere. Numbers refer to Fig. 21. Australia (no. 13) and the Chinese Xingjian locality (no. 14) have not been shown due to positional uncertainty.

stems densely covered with leaf like spines. *Sawdonia ornata* (Fig. 8) was approximately 30 cm tall and constructed of pseudomonopodial axes that arose from a rhizome. Lateral axes branched dichotomously and were characterized by circinate tips. The sporangia were confined to the distal ends of branches and laterally attached to the stems. They are bivalved and reniform in shape producing round to sub-triangular trilete spores. Another Zosterophyll, *Discalis longistipa*, described from the Lower Devonian of Yunnan, China possesses H- and K-shaped branching, with fertile axes bearing large sporangia organized in loose spikes. All the axes and the sporangia are covered with multicellular spines. This taxon is again a homosporous.

Goslingia breconensis from Lower Devonian of Wales was approximately 50 cm tall, consisting of dichotomizing axes up to 4.0 mm wide. The aerial stems are leafless and the tips are circinately coiled. The globose to reniform sporangia are attached to the stems by slender stalks and are mostly confined to the distal regions of the plant. *Koniora andrychoviensis* (Fig. 9) believed to be the most complex Zosterophyll, is known from the Lower Devonian of Poland. The stems were covered with a number of conspicuous spines. The largest of these spines bore delicate teeth. The wing like outgrowths can be seen running along the length of the stems. The bivalved sporangia in *Koniora* are laterally attached to the stem but its mode of attachment is very exceptional. Unlike any of the other Zosterophylls, the sporangia were attached just below

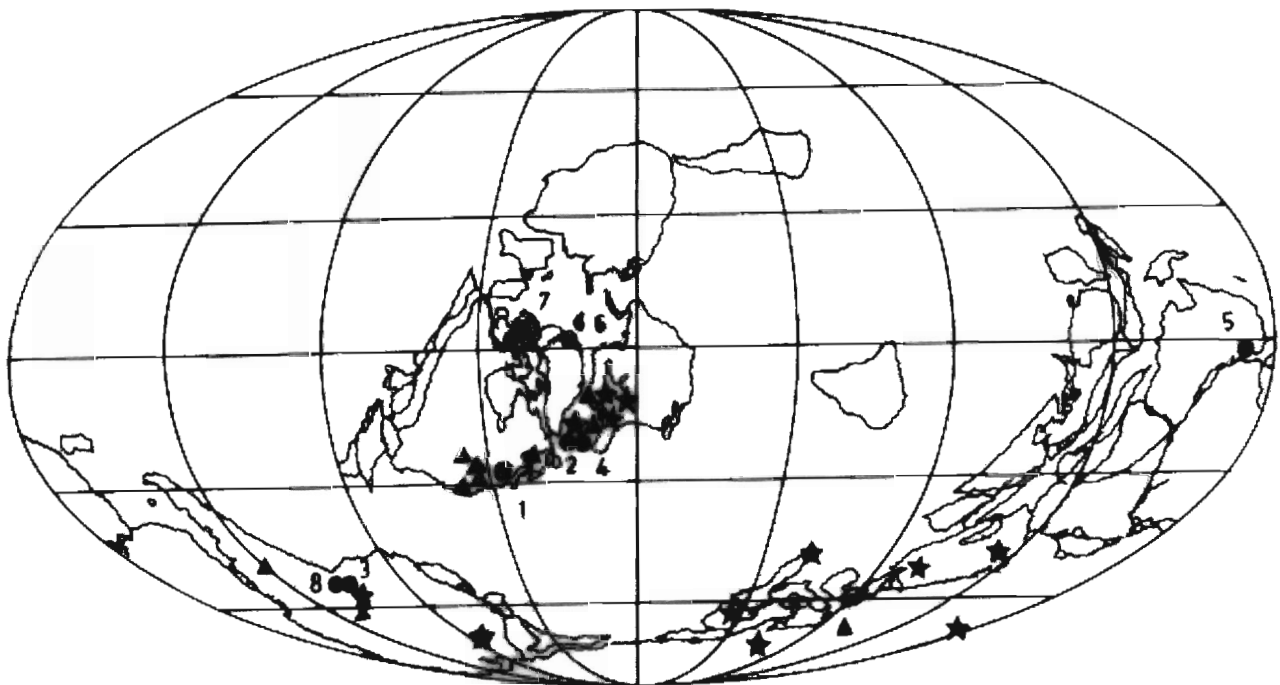


Fig. 17—Distribution of Silurian spore and megafossil assemblages (excluding Prídolí), 425 myr, (based and redrawn from Edwards & Wellman, 2001). Numbers refer to Fig. 22. Solid circles plus numbers refer to megafossil localities in Fig. 22. Stars indicate Wentlock/Ludlow microfossils; Triangles indicate Prídolí microfossils.

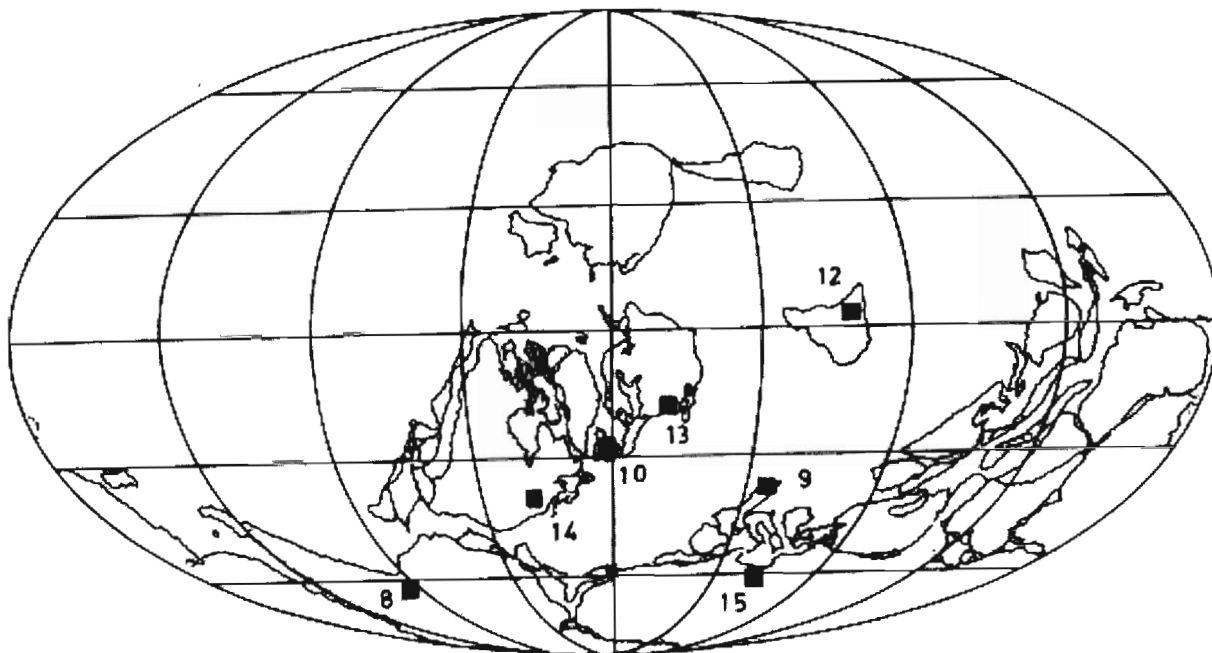


Fig. 18—Distribution of Pridoli megafossil assemblages on a base map, 408 myr (based and redrawn from Edwards & Wellman, 2001). Numbers refer to Fig. 22.

the last fork of the stems. The two ultimate branches produced by the forked stem, make a hook like structure that wraps around the sporangia to protect it. In this way these sporangia can be compared with some of the more complex sporophylls of the lycophytes and *Koniora* may be regarded as the evolutionary link between the Zosterophylls and the lycophyta.

Zosterophylls were believed to be the ancestors to the lycophytes (club mosses) as is evidenced by the fact that both groups possess exarch protosteles and the laterally produced reniform sporangia. Similarly various types of protuberances (spines and multicellular teeth), present on the stems of the Zosterophylls, would have given rise to the true leaves of Lycophytes. Zosterophylls also demonstrate various stages in the evolution and organization of the sporangia, like helically arranged sporangia over the stem surface (in *Kaulangiophyton*) and the sporangia aggregated into definite spikes, etc. They were the important component in the Early Devonian floras, but they started declining in the Middle Devonian, and became extinct during the Late Devonian.

Trimerophytes—Most early land plants had the tendency for dichotomous branching and this restricted the plants to acquire varied shapes and complex growth patterns. The first group to develop more diverse branching pattern was the trimerophytes. The plants in this group have monopodial branching of the main axes. They produced thinner lateral branches, which in turn underwent a series of dichotomies or even trichotomies. The sporangia in these plants were borne

in clusters at the ends of the stems. As far as their vascular tissue is concerned, they possessed a relatively large centrarch stele having scalariform-bordered to circular-bordered pitting. Superficially many trimerophytes would have looked like rhyniophytes or Zosterophylls. Some had naked stems (*Psilophyton dawsonii*) while others had short spines on their stems (*P. princeps*).

Psilophyton dawsonii is most completely known taxon of this group which is reconstructed to be a highly branched plant. Its fertile lateral branches are borne alternately and distichously along the main axes. Vegetative branches are smooth and dichotomize at right angles to terminate as blunt tips. Fertile branches dichotomize up to six times before terminating in clusters of approximately 32 sporangia. The vascular tissue of *P. dawsonii* consists of a centrarch protostele. *Psilophyton princeps* (Hueber & Banks, 1967) had stem surfaces covered with short spines and its sporangia were bigger than the sporangia in *P. dawsonii*. Its axes consists of a solid strand of xylem that is either mesarch or centrarch. *P. forbesii* (Andrews *et al.*, 1968, Fig. 10) was one of the largest species of *Psilophyton* (Hueber, 1968), known from the Devonian of North America, with a length of about 60 cm. Its growth habit was either monopodial or pseudomonopodial. It shows the more complex branching pattern of the stem. Ellipsoidal sporangia were produced in clusters on the fertile lateral branches.

Another Trimerophyte plant, i.e. *Pertica* (Fig. 11) from the Lower Devonian of North America was the largest of the

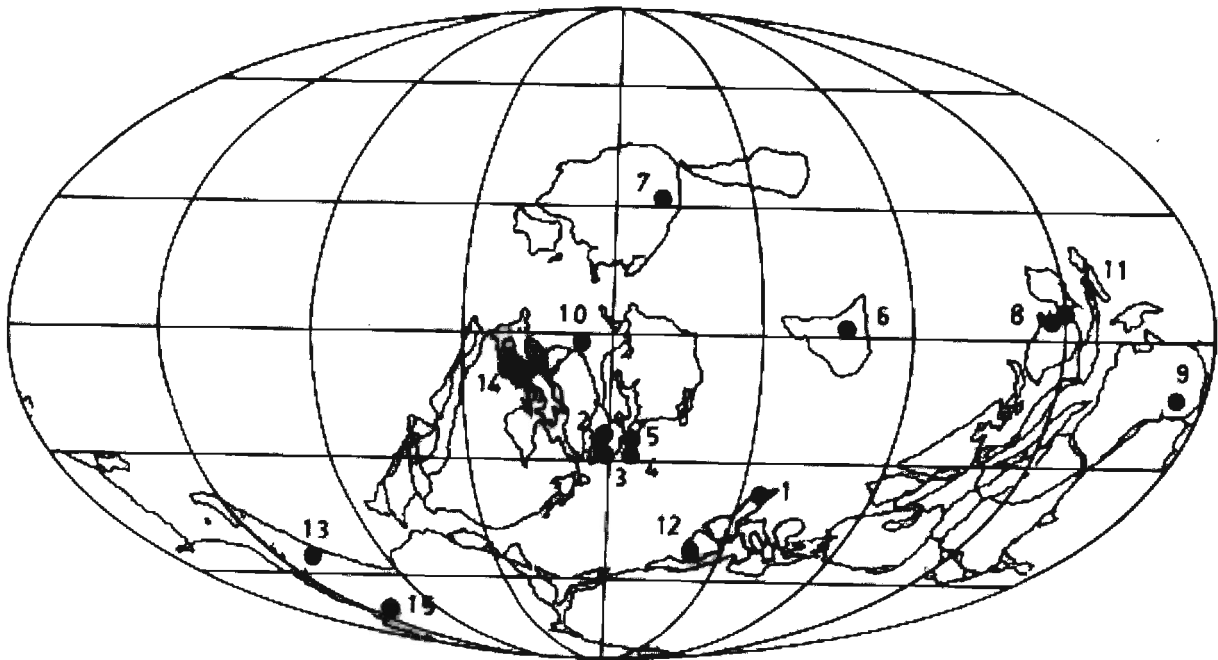


Fig. 19—Distribution of Lochkovian mega and microfossil assemblages on a base map, 408 myr (based and redrawn from Edwards & Wellman, 2001). Numbers refer to Fig. 23.

known trimerophytes, growing up to 3 metres tall, and had highly complex branching in the side shoots. Numerous, dichotomously branched laterals were borne on the main axis in an alternate, tetrastichous manner. Like all trimerophytes the lateral branches were either completely sterile or completely fertile. All branches are covered by crowded epidermal papilla. In *Trimerophyton robustius*, the type species of the division, the main stem consists of numerous helically arranged, trifurcate lateral branches. The primary and secondary branching patterns of the laterals are trichotomous. All the ultimate branches bear erect sporangia in clusters of three.

The Trimerophytes demonstrate a more complex plant body than that of rhyniophytes, having monopodial or pseudomonopodial primary axes. Lateral branches came out in a variety of patterns like helical (*Psilophyton* sterile branches), alternately and distichous (*Psilophyton* fertile branches), tristichous (*Trimerophyton*) and tetrastichous (*Pertica*). In *Pertica* the laterals tend to be produced in fours along the stem, with the ultimate branchlets consisting of slender, three dimensional dichotomizing structures. It has been suggested that the planation of these lateral branches would have developed some kind of tissue that ultimately produced recognizable leaves. Thus the taxon *Pertica* may represent an intermediate step in the evolution of a frond or leaf. This group also demonstrates how the single or paired terminal sporangia of the rhyniophytes have been modified through different stages, thereby giving way to the much evolved sporangia that grew in massive clusters (i.e., *Psilophyton depsile* and

Pertica). Some evolutionary trends can be seen in this group that include stages in the evolution of a particular type of leaf, modification of tracheid pitting towards the circular-bordered type, and possibly the early stages in the evolution of saccate pollen.

According to Gensel and Andrews (1984), *Pertica* and *Trimerophyton* in Emsian might be of 2-3 metres high. This increase in size was due to primary growth. It is practically not possible for a narrow and much branched plant to sustain such heights unless until it is well supported by some kind of a vertical or oblique underground rhizomatous system that anchored these plants. Such kind of *in-situ* vertical "rooting" structures are found preserved in the Siegenian-Emsian fluvial sediments of Rhenish Schiefergebirge (Schultka & Remy, 1990), although the original plants were not preserved.

Horizontal leafy stems of *Drepanophycus spinaeformis* produced irregularly branched smooth axes (? adventitious roots) that penetrated fluvial sediments (Schweitzer, 1983; Rayner, 1984). Such kind of vegetation, comprising herbaceous lycophytes, was widespread globally in the Middle and early Upper Devonian. Evidence for stratification in the palaeoflora is seen in the Emsian of north-eastern America, where Gensel and Andrews (1984) suggested that many Zosterophylls, *Drepanophycus* and *Kaulangiophyton*, all with rhizomes and aerial shoots, grew in dense, low mats, while trimerophytes such as *Pertica* and *Trimerophyton* formed a second taller layer. The advent of secondary thickening (xylem) in Eifelian progymnosperms (*Rellimia* and *Aneurophyton*) and the

Eonothem Eon	Erathem Era	System Period	Series Epoch	Stage Age	Age Ma	
Phanerozoic	Palaeozoic	Carboniferous	Pennsylvanian	Upper	Gzhelian	303.9 ± 0.9
					Kasimovian	306.5 ± 1.0
				Middle	Moscovian	311.7 ± 1.1
				Lower	Bashkirian	318.1 ± 1.3
			Mississippian	Upper	Serpukhovian	326.4 ± 1.6
				Middle	Visean	345.3 ± 2.1
				Lower	Tournaisian	359.2 ± 2.5
			Devonian	Upper	Famennian	374.5 ± 2.6
					Frasnian	385.3 ± 2.6
				Middle	Givetian	391.8 ± 2.7
		Eifelian			397.5 ± 2.7	
		Lower		Emsian	407.0 ± 2.8	
				Pragian / Siegenian	411.2 ± 2.8	
				Lochkovian / Gedinnian	416.0 ± 2.8	
		Silurian		Pridoli		418.7 ± 2.7
			Ludlow	Ludfordian	421.3 ± 2.6	
				Gorstian	422.9 ± 2.5	
			Wenlock	Homerian	426.2 ± 2.4	
				Sheinwoodian	428.2 ± 2.3	
			Llandovery	Telychian	436.0 ± 1.9	
				Aeronian	439.0 ± 1.8	
				Rhuddanian	443.7 ± 1.5	
			Ordovician	Upper	Hirnantian	445.6 ± 1.5
					Ashgill	455.8 ± 1.6
		Caradoc			460.9 ± 1.6	
		Darriwilian			468.1 ± 1.6	
		Middle		Llanvirn	471.8 ± 1.6	
				Areniq	478.6 ± 1.7	
		Lower		Tremadocian		

Fig. 20—A part of Geologic Time Scale 2004 (Ordovician-Carboniferous), edited by Gradstein *et al.* Cambridge University Press.

probable forerunners of the arborescent lycophytes (e.g., *Lepidosigillaria* and *Lepidodendropsis*) in the Givetian further increased the capacity for upward growth. The earliest progymnosperms (e.g., *Aneurophyton*) were bushes.

The remains of secondary wood have been known from Middle and Upper Devonian localities since the 19th Century. Earlier workers thought it to be primitive conifer wood, however no conifer cones or foliage were ever found in the rocks of this

Locator* Age	Authors	Geographic area
1. Llanvirn	Vavrdova (1984, 1990), Corna (1970)	Bohemia
2. Llanvirn	McClure(1988), Strother <i>et al.</i> (1996)	Saudi Arabia
3. Caradoc	Richardson (1988), Wellman (1996)	Southern Britain
4. Caradoc	Gray <i>et al.</i> (1982)	Libya
5. Ashgill	Gray and Boucot (1972), Gray <i>et al.</i> (1982), Gray (1985, 1988) Gray (1988) Gray (1988) Strother (1991) Gray (1988)	Kentucky, USA Tennessee, USA Georgia, USA Illinois, USA Ontario, Canada
6. Ashgill	Burgess (1991)	Southern Britain
7. Ashgill	Vavrdova (1982, 1984, 1988, 1989)	Bohemia
8. Ashgill	Reitz and Heuse (1994)	Germany
9. Ashgill	Stemans <i>et al.</i> (1996)	Turkey
10. Ashgill	Richardson (1988)	Libya
11. Ashgill	Gray <i>et al.</i> (1986)	South Africa
12. ? Ashgill	Lakova <i>et al.</i> (1992)	Bulgaria
13. ? Ashgill	Foster and Williams (1991)	Australia
14. Ashgill	Wang <i>et al.</i> (1997)	Xinjiang, China
15. Rhuddanian	Burgess (1991)	Southern Britain
16. Rhuddanian	Richardson (1988)	Libya
17. Rhuddanian Rhuddanian, ?Aeronian ?Llandovery	Miller and Eames (1982) Johnson (1985) Strother and Traverse (1979)	New York State, USA Pennsylvania, USA Pennsylvania, USA
18. Llandovery	Bar and Riegel (1980)	Ghana
19. Llandovery	Gray <i>et al.</i> (1985)	Brazil
20. Late Llandovery	Gray <i>et al.</i> (1992)	Paraguay

*Locations are noted by numbers on figure- 16

Fig. 21—Showing records of Ordovician and basal Silurian spore assemblages (after Edwards & Wellman, 2001).

age. This discrepancy was resolved in 1970s when Charles Beck, an American palaeobotanist showed that this fossil wood belong to trees that were not seed plants. They bore wedge shaped leaves that were different from the leaves of conifers. More significantly, the shoots bore clusters of sporangia that were similar in appearance to those of the trimerophytes. So this group of plants was unique to the Palaeozoic where the stems/trunks were made up of secondary woods like in the seeds plants (gymnosperms) but the reproduction was pteridophytic, i.e. through clusters of sporangia and not through seeds. These plants commonly known as progymnosperms with its representative taxon *Archaeopteris*, are believed to be ancestors of all seed-plants. The reconstruction of the *Archaeopteris* (Fig. 12, Beck, 1960, 1962) shows that its trunk (*Callixylon*) was upto 1.5 metres in diameter and the length could be up to 20 metres.

The advent of heterospory and the origin and evolution of the seed habit is one of the most significant events in the evolution of land flora. The first vascular plants had the most primitive reproductive system wherein the plants bore sporangia that contained morphologically identical spores (homospores) that might have given rise to free – living gametophytes. The nature of the sexual stages, the gametophytes, in early vascular plants was, until recently unknown. Recent discovery from the Rhynie Chert (Remy & Remy, 1980a, b) has at least revealed three different gametophyte plants. They were large and had their sexual

organs borne in terminal cup-shaped organs (gametangia) at the tips of vertical axes (gametangiophores). The three gametophytes are called *Lyonophyton rhyniensis* (Fig. 13a) which is the gametophyte of *Aglaophyton major*, *Langiophyton mackei* (Fig. 13c) which was probably the gametophyte of *Horneophyton lignieri* and *Kidstonophyton discoides* (Figs. 13b, 14), the gametophyte of *Nothia aphylla*. These Rhynie gametophytes were almost equivalent in size to the much more widely known sporophyte plants from the same locality.

After this primitive reproductive system, i.e. the homosporous, various plant groups developed a little advanced reproductive system, i.e. the heterospory, wherein two sizes of spores were produced (mega and microspores). Throughout Devonian times there is evidence for heterospory in dispersed spores (Chaloner & Sheerin, 1979). The plant taxon *Barinophyton* provides some evidence about the shift from the isospores of homosporous plants to the microspores and megaspores of free–spring heterosporous plants. Spores of two different sizes have been reported in the same sporangia of *Archaeopteris*.

The heterospory gradually gave rise to the formation of ovules and ultimately the formation of seeds. The first ovules are recorded from the United States and Belgium in the Famennian. To date, the oldest known seed plant is *Elkinsia polymorpha* (Fig. 15) a seed fern about one metre tall, described from the Late Devonian (Famennian) of West Virginia (Rothwell

Locator* Age/Strata	Authors	Geographic area	Composition
1. Llandovery (?Telychian)	Schoph <i>et al.</i> (1966)	Maine, USA	<i>Eohostimella heathana</i>
2. Homeric	Edwards <i>et al.</i> (1983)	Tipperary, Ireland	<i>Cooksonia</i> sp.
3. Late Wenlock / Ludlow	Toro <i>et al.</i> (1997)	Southern Bolivia	Sterile rhyniophytes
4. Gorstian (Pterinea Beds)	Edwards <i>et al.</i> (1979)	Cwm Graig Ddu, Powys, Wales	<i>Cooksonia pertoni</i> , cf. <i>C. cambrensis</i> , <i>C. sp.</i>
4. Ludfordian (Upper Roman Camp Fm.)	Edwards & Davies 1976 Edwards & Rogerson (1979)	Capel Horeb, Powys, Wales	<i>Cooksonia</i> sp., <i>Steganotheca striata</i>
5. ? Late Ludlow	Tims & Chambers (1984)	Victoria, Australia	<i>Baragwanathia longifolia</i> , <i>Salopella australis</i> , <i>Hedeia</i> sp., zosterophylls
6. Ludlow/ ?Ludfordian	Edwards (work in progress)	North Greenland	<i>Salopella</i> sp.
7. Ludlow	Basinger <i>et al.</i> (1996)	Bathurst Island, Arctic Canada	Cooksonioid types
8. ?Ludlow/Prídolí	Morel <i>et al.</i> (1995)	Tarjia, Bolivia	<i>Cooksonia</i> cf. <i>caledonica</i>
9. Prídolí (?ultimus)	Obrhel (1962), Schweitzer (1983)	Bohemia, Czechoslovakia	<i>Cooksonia</i> , <i>Cooksonia bohémica</i>
10. Basal Prídolí (Platyschisma Shale Member)	Edwards <i>et al.</i> (1995b) Rogerson <i>et al.</i> (2002)	Ludford Corner, Ludlow, England	<i>Cooksonia pertoni</i> , <i>Hollandophyton colliculum</i>
10. Prídolí (?ultimus) (Rushall Beds)	Lang (1937); Fanning, Edwards & Richardson (1990, 1991); Fanning, Richardson & Edwards (1990, 1991)	Perton Lane, Hereford, England	<i>Caia langii</i> <i>Cooksonia pertoni</i> , <i>C. cambrensis</i> , <i>Salopella</i> sp., <i>Pertonella dactylethra</i> ,
10. Prídolí (early) (Freshwater East Formation.)	Lang (1937) Edwards (1979)	Freshwater East Pembrokeshire, Wales	<i>Cooksonia pertoni</i> , <i>C. cambrensis</i> , <i>C. caledonica</i> , <i>C. hemisphaerica</i> , <i>Tortilicaulis transwalliensis</i> , <i>Psilophyites</i> sp.
10. Prídolí (early) (Long Quarry Formation)	Heard (1939) Edwards (1970a) Edwards & Rogerson (1979)	Capel Horeb, Powys, Wales	<i>Cooksonia</i> sp. <i>Steganotheca striata</i>
10. Prídolí (?early) (Temeside Mudstone Formation)	Rogerson <i>et al.</i> (1993)	Little Wallop Hall, Long Mountain, Shropshire, England	<i>Cooksonia pertoni</i>
11. Prídolí (bouceki)	N. Petrosyan (pers. comm.)	Kazakhstan, USSR	<i>Cooksonia</i> sp. <i>Zosterophyllum</i> sp.
12. Prídolí (late)	Senkevitch (1975)	Balkhash area, Kazakhstan	<i>Cooksonella</i> sp., ? <i>Baragwanathia</i> sp., ? <i>Taeniocrada</i> sp., <i>Jugumella burubaensis</i>
12. Prídolí (late)	Cai <i>et al.</i> (1993)	Junggar Basin, Xinjiang, China	<i>Cooksonella</i> sp., <i>Junggaria spinosa</i> , ? <i>Lycopodolica</i> , <i>Salopella xinjiangensis</i> , <i>Zosterophyllum</i> sp.
13. Prídolí (late)	Ishchenko (1975)	Podolia, USSR	<i>Cooksonia pertoni</i> , <i>C. hemisphaerica</i> , <i>Eorhynia</i> (<i>Salopella</i>), ? <i>Zosterophyllum</i> sp., <i>Lycopodolica</i>
14. Prídolí (late)	Banks (1973)	New York State, USA	<i>Cooksonia</i> sp.
15. Prídolí	Daber (1971)	Libya	? <i>Cooksonia</i> sp.

*Locations are noted by numbers on figures 17 and 18

Fig. 22—Showing Silurian localities with plant megafossils (after Edwards & Wellman, 2001; Edwards & Richardson, 2004).

et al., 1989). The foliage consisted of large, segmented leaves, looking like little fern fronds. This explains why these early gymnosperms are often called seed-ferns (or the pteridosperms). The first seed plants were gymnosperms, a group in which the ovules are borne directly on the plant. Pteridosperms formed only a small part of the Late Devonian vegetation. However, the competitive edge that seed reproduction gave them, soon started to have an effect. During the early Carboniferous, they came to dominate many land

floras. Plants could now live in all but the most inhospitable habitats, allowing the earth truly to turn green.

THE CHANGING SCENARIO

During the Silurian and Devonian, there was a drastic change in the landscape, as plants developed a number of qualities for adaptation to the drier conditions. The plants were not merely invading the land, but they were altering it

Locator* Age	Authors	Geographic area	Composition
1. <i>Uniformis</i> zone	Obrhel (1968)	Bohemia, Czechoslovakia	<i>Cooksonia downtonensis</i>
2. <i>Micromatus-newportensis</i> (lower- middle)	Lang (1937), Edwards (1975)	Forfar, Scotland	<i>Zosterophyllum myretonianum.</i> , <i>Cooksonia caledonica</i>
2. <i>Micromatus-newportensis</i> (lower-middle)	Edwards (1972)	Arbilot, Scotland	<i>Zosterophyllum fertile</i>
3. <i>Micromatus-newportensis</i> (lower) (Ditton Formation)	Lang (1937), Edwards and Fanning (1985) Fanning (1987) Fanning <i>et al.</i> (1988, 1992)	Targrove, Shropshire, England	<i>Tortilicaulis transwalliensis</i> , <i>Resilitheca</i> , <i>Uskiella reticulata</i> , <i>Tarrantia salopensis</i> , <i>Cooksonia hemisphaerica</i> , <i>C. pertoni</i> , <i>C. cambrensis</i> , cf. <i>C. caledonica</i> / <i>Renalia Salopella marcensis</i>
3. <i>Micromatus-newportensis</i> (middle) (Ditton Formation)	Fanning (1987) Fanning <i>et al.</i> (1988) Edwards <i>et al.</i> (1992, 1994) Edwards <i>et al.</i> (1995b, d) Edwards. (1996) Wellman <i>et al.</i> (1998a) Edwards <i>et al.</i> (1999) Habgood (2000a) Edwards & Richardson (2000), Edwards <i>et al.</i> (2001) Habgood <i>et al.</i> (2002)	Brown Clee Hill, Shropshire, England	<i>Salopella</i> cf. <i>marcensis</i> , <i>Tortilicaulis offaeus</i> , <i>Resilitheca salopensis</i> , <i>Cooksonia banksii</i> , <i>C. pertoni</i> , <i>Griselatheca salopensis</i> , cf. <i>Sporogonites</i> , <i>Pertonella</i> sp., <i>Fusitheca fanningiae</i> , <i>Culullitheca richardsonii</i> , <i>Tarrantia salopensis</i> , cf. <i>Hornrophyton</i> sp., <i>Sporathylacium salopence</i>
3. <i>Micromatus-newportensis</i> (middle) (Ditton Formation)	Wellman <i>et al.</i> (2000)	Brynglas Tunnels, M4 motorway, Newport, Wales	<i>Cooksonia hemisphaerica</i> , <i>Tarrantia salopensis</i> , <i>Tortilicaulis transwalliensis</i> , <i>Zosterophyllum</i> cf. <i>fertile</i>
3. <i>Micromatus-newportensis</i> (Ditton Formation)	Fanning (1987) Kenrick (1988)	Cwm Mill, Monmouthshire, Wales	<i>Zosterophyllum</i> cf. <i>fertile</i> , <i>Cooksonia</i> sp., cf. <i>Renalia</i> , <i>Salopella</i> cf. <i>marcensis</i>
3. Upper Gedinian (Ditton Formation)	Edwards & Richardson (1974), Fanning (1987)	Newton Dingle, Shropshire, England	<i>Zosterophyllum</i> sp., <i>Salopella allenii</i>
3. <i>Breconensis-zavallatus</i> Lochkovian, (Senni Formation)	Kenrick (1988) Edwards <i>et al.</i> (1989)	Allt Ddu, Brecon Beacons, Powys, Wales	cf. <i>Salopella</i> sp. cf. <i>Cooksonia</i> , <i>Deheubarthia splendens</i> , <i>Gosslingia breconensis</i> , cf. <i>Zosterophyllum fertile</i> , <i>Uskiella spargens</i> ,
3. <i>Breconensis-zavallatus</i> Lochkovian, (Cosheston Formation)	Kenrick (1988) Edwards <i>et al.</i> (1989) Wellman <i>et al.</i> (1998)	Masle Bridge Quarry, Pembrokeshire, Wales	<i>Deheubarthia splendens</i> , <i>Dawsonites</i> sp., <i>Zosterophyllum llanoveranum</i>
3. <i>Breconensis-zavallatus</i> ?Lochkovian, (Senni Formation)	Habgood (2000a)	Rhiw Wen, Black Mountains, Powys, Wales	<i>Cooksonia</i> ? <i>cambrensis</i> , <i>Salopella allenii</i> , <i>Tortilicaulis</i> sp.
3. ?Upper Gedinian/lower Siegenian, (Senni Formation)	Kenrick & Edwards (1988b)	Craig Ddu, Carmarthenshire, Wales	<i>Thrinakophyton formosum</i>
3. <i>Polygonalis-emiensis</i> Siegenian, (Cosheston Formation)	Kenrick (1988) Kenrick <i>et al.</i> (1991a) Thomas (1978)	Mill Bay, Pembrokeshire, Wales	<i>Gosslingia breconensis</i> , <i>Sennicaulis hippocrepiformis</i>
3. <i>Polygonalis-emiensis</i> Lower Siegenian, (Senni Formation)	Heard (1927, 1939); Edwards (1968, 1969a, b, 1970b, 1981); Edwards & Kenrick (1986); Kenrick (1988); Kenrick & Edwards (1988a); Shute & Edwards (1989); Edwards <i>et al.</i> (1989); Kenrick <i>et al.</i> (1991a)	Brecon Beacons Quarry, Brecon Beacons, Powys, Wales	<i>Gosslingia breconensis</i> , <i>Drepanophycus spinaeformis</i> , <i>Sennicaulis hippocrepiformis</i> , <i>Uskiella spargens</i> , <i>Zosterophyllum llanoveranum</i> , <i>Zosterophyllum</i> cf. <i>fertile</i> , <i>Zosterophyllum llanoveranum</i> , <i>Dawsonites</i> sp., <i>Deheubarthia splendens</i> , <i>Krithodeophyton croftii</i> , <i>Tarella trowenii</i>
3. <i>Polygonalis-emiensis</i> Siegenian, (Senni Formation)	Croft & Lang (1942); Edwards (1969a, b, 1970b, 1981); Edwards <i>et al.</i> (1989); Shute & Edwards (1989)	Llanover Quarry, Monmouthshire, Wales	<i>Deheubarthia splendens</i> , <i>Gosslingia breconensis</i> , <i>Sennicaulis hippocrepiformis</i> , <i>Uskiella spargens</i> , <i>Zosterophyllum llanoveranum</i> , <i>Zosterophyllum</i> cf. <i>fertile</i> , <i>Z. ?australianum</i> , <i>Drepanophycus spinaeformis</i> , <i>Dawsonites</i> sp., <i>Sporogonites exuberans</i> , <i>Sciadophyton steinmannii</i>
3. <i>Polygonalis-emiensis</i> Middle-upper Siegenian, (Cosheston Formation)	Kenrick (1988), Edwards <i>et al.</i> (1989), Wellman <i>et al.</i> (1998c)	Burton Cliff, Williamston Mountain, Pembrokeshire, Wales	<i>Deheubarthia splendens</i> , <i>Gosslingia breconensis</i> , <i>Uskiella spargens</i> , cf. <i>Zosterophyllum fertile</i> , cf. <i>Zosterophyllum</i>
4. <i>Breconensis-zavallatus</i>	Stemans & Gerrienne (1984)	Gileppe, la Vesdre, Belgium	<i>Gosslingia breconensis</i> and other abundant remains (work in progress)
4. <i>Micromatus-newportensis</i> (upper)	Leclercq (1942)	Nonceveux, Belgium	<i>Zosterophyllum fertile</i>

5. Upper Gedinnian	Schweitzer (1983)	Rhineland, Germany	<i>Drepanophycus spinaeformis</i> , <i>Taeniochrada</i> sp., <i>Zosterophyllum rhenanum</i>
6. ?Basal Gedinnian (Ainasu)	Senkevitch (1978)	Balkhash, Kazakhstan	<i>Cooksonella sphaerica</i> , <i>Taeniochrada pilosa</i> , <i>Jugumella burubaensis</i>
7. Upper Gedinnian (Kokbaital)	Senkevitch (1978)	Balkhash, Kazakhstan	<i>Tastaephyton bulakus</i> , <i>Taeniochrada pilosa</i> , <i>Mointina quadripartita</i> , <i>Jugumella jugata</i> , <i>J. burubaensis</i> , <i>Balchaschella tenera</i>
7. Gedinnian undet.	Stepanov (1975)	Kuzbass, Siberia	<i>Zosterophyllum</i> , <i>Cooksonia pertoni</i> , <i>Stolophyton acyclicus</i> , <i>Juliphyton glazkini</i> , <i>Uksunaiphyton ananievi</i> , <i>Pseudosajania pimula</i> , <i>Salairia bicostata</i> ,
8. Gedinnian	Li & Cai (1978)	E. Yunan, S.W. China	<i>Zosterophyllum</i> sp.
9. ?Lochkovian undet.	J. Tims (pers. comm.)	Tyers, Victoria, Australia	<i>Baragwanathia longifolia</i> , <i>Zosterophyllum</i> n. sp., <i>Baragwanathia</i> n. sp.
10. Gedinnian undet.	Høeg (1942)	Spitsbergen	Sterile remains only, <i>Hostinella</i> , <i>Taeniochrada</i> , <i>Zosterophyllum</i>
11. Pragian-pre-pragian ? Gedinnian	Janvier <i>et al.</i> (1987)	Viet Nam	Undet. terminal sporangia
12. Gedinnian	Alvarez-Remis (unpublished abstract), (1988)	Badajoz, Spain	<i>Sciadophyton steinmanni</i>
13. ?Lochkovian	Edwards <i>et al.</i> (work in progress)	Precordillera, Argentina	2 new rhyniophytoids, 1 plant with enations
14. Uppermost Lochkovian	Basinger <i>et al.</i> (1996)	Bathurst Island, Ar. Canada	Not specified
15. ?Uppermost Silurian, Lochkovian	Mussa <i>et al.</i> (1996), Gerrienne (1999)	Paraná Basin, Brazil	<i>Cooksonia</i> cf. <i>pertoni</i> , cf. <i>C. cambrensis</i> , <i>Pertonella</i> sp., <i>Salopella</i> sp., <i>Sporogonites</i> sp. nov.,

*Locations are noted by numbers on figure 19

Fig. 23—Showing Lower Devonian (Lochkovian/Gedinnian-Pragian/Siegenian) localities with plant megafossils after Edwards & Wellman, 2001 and Edwards & Richardson, 2004).

also. Erosion of the land became reduced as the plants covered the land surfaces and also the upland areas became more stable. In the lowlands, rivers became more sinuous as their flood plains were stabilized through plant cover. Increasing quantities of sediments became entrapped in the lower reaches of river systems, causing extensive coastal plains to develop. These plains often supported dense Swamp forests that produced large quantities of peat, ultimately forming the first significant coal deposits.

The increasing plant cover also had a significant impact on local and global climates. The massive loss of water vapour through transpiration and evaporation altered rainfall patterns. When plants became large and formed forests, they might have absorbed plenty of carbon thereby reducing the Carbon dioxide levels in the atmosphere. This resulted in the cooling of the global climate. The development of land vegetation also helped the animals to invade the land. The pre-Silurian land surfaces were just bare and unable to protect the animals from heat or dehydration. However, soon after the rhyniophytes gave the first vegetation cover, the first land animals appeared. The oldest known fossils of land animals are remains of spiders and small millipede-like creatures from the Late Silurian. In the Early Devonian, other terrestrial arthropods appeared, including mites and the flightless insects. There is no fossil evidence of flying insects until the Carboniferous. The first land vertebrates appeared in the Late Devonian. Although fossil remains of these amphibians are

scarce, they have been found in both the northern and the southern hemisphere.

After the evolutionary changes that took place in the Devonian, the subsequent Carboniferous Period was mainly a time of consolidation for the plant kingdom. Lycophytes continued to dominate many terrestrial habitats in the Early Carboniferous. They expanded in both physical size and numbers, and by the Late Carboniferous giant clubmosses dominated vast areas of lowland swamps in the tropical areas. Some of the Devonian sphenophytes (horsetails) which probably arose from the trimerophytes, rapidly proliferated in the Carboniferous and by the Late Carboniferous there were large tree-like forms growing in the tropical wetlands. True ferns also started to proliferate and diversify in the Carboniferous. The earliest recognizable fern frond occurs in Early Carboniferous flora and by the Late Carboniferous there existed the representatives of marattialean ferns. Many of the Carboniferous ferns were relatively small, herbaceous plants.

The progymnosperms were the important forest trees in the earliest Carboniferous but rapidly went into decline as they were outcompeted by the seed plants. The seed-plants proliferated and diversified in the Carboniferous. Most of our knowledge of the early seed-plants is restricted to the species growing in the lowland habitats. There existed the pteridosperms with large fern-like fronds, and trees with long strap-like leaves and conifer-like reproductive organs, known as *Cordaites*. By the early Carboniferous, land vegetation had

developed a world-wide distribution. The most diverse floras were in the lower latitudes of Europe, North America and China and here the seed-plants in particular were the most diverse group. In higher latitudes, lycophytes and progymnosperms were the dominant forms. In the Late Carboniferous, this vegetation pattern was disrupted by the onset of a major Ice Age. There was little or no vegetation in the southern high latitudes due to ice-cover and in southern mid-latitudes there was only sparse vegetation consisting of mainly lycophytes. There was a little land and thus vegetation in northern high latitudes, but in mid-latitudes there was a relatively poor vegetation of pteridosperms and progymnosperms. However, in the tropics, a broad area of tropical forests developed in the lowlands, known as the coal forests.

CONCLUSION

The aim of this paper is to document the vegetation that prevailed on the earth during the earliest stages of terrestrialization by embryophytes and its global distribution. The occurrences of early land plant fossils (micro and mega both) recorded from a number of localities across the world (Figs 21-23) show that the vegetation was cosmopolitan and very little diversified. The best-known fossils come from Laurentia, which includes much of Europe (Bohemia, Germany, Turkey, Bulgaria, Ireland, Wales, England, Scotland, Belgium, Spain, Russia and Czechoslovakia); North America (U.S.A., Canada and Arctic Canada) and Greenland (Spitsbergen). The rest of the records are from South America (Brazil, Paraguay, Bolivia and Argentina); Africa (Libya, Ghana, Tunisia, Morocco and South Africa); Asia (China, Kazakhstan, Russia, western Siberia, Saudi Arabia and Vietnam) and Australia. These data clearly depict that the early land plants grew in almost all the continents of the world. While comparing the enormous work done across the world, Indian contribution in this field is almost negligible.

The sediments of Silurian and Devonian time span are exposed at various places in India, viz. in the Tethyan Zone of Kashmir, Ladakh, Lahaul-Spiti (Himachal Pradesh) and in Kumaon-Garhwal Himalayas but the records of early plant life are meagre. There are only two doubtful records, i.e. *Taeniochrada* and *Psilophyton Princeps* from the Silurian and Lower Devonian of Spiti valley. This shows that no serious efforts were made to search the early plant life in these rocks. Now it is the high time that we should also concentrate on the investigations of early Palaeozoic rocks along with exploring Permian sediments of the late Palaeozoic times and we will definitely get the signatures of early land plant life in India too.

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REFERENCES

- Andrews HN, Kasper AE & Mencher E 1968. *Psilophyton forbessi*, a new Devonian plant from northern Maine. *Bulletin of Torrey Botanical Club* 95: 1-11.
- Banks HP 1968. The early history of land plants. *In: Drake ET (Editor)—Evolution and Environment: 73-107*. Yale University Press, New Haven.
- Beck CB 1960. 'Connection between *Archaeopteris* and *Callixylon*'. *Science* 131: 1524-1525.
- Beck CB 1962. 'Reconstruction of *Archaeopteris* and further consideration of its phylogenetic position'. *American Journal of Botany* 49: 373-382.
- Beeunas MA & Knauth LP 1985. Preserved stable isotopic signature of subaerial diagenesis in the 1.2 b.y. Mescal Limestone, central Arizona: implications for the timing and development of a terrestrial plant cover. *Geological Society of America, Bulletin* 96: 737-745.
- Burgess ND 1991. Cryptospores and miospores from the Llandovery type area, south-west Wales. *Palaeontology* 34: 575-599.
- Chaloner WG & Sheerin A 1979. Devonian macrofloras. *In: House MR, Scrutton CT & Bassett MG (Editors)—The Devonian System. Special Papers in Palaeontology* 17.
- Bär P & Riegel W 1980. Mikroflora des höchsten Ordovizium bis tiefen Silurs aus der Unteren Sekondi-Serie von Ghana (Westafrika) und ihre Beziehung zu dem Itaim-Schichten des Maranhao-Beckens in NE-Brasilien. *Neues Jahrbuch für Geologie und Paläontologie Abhandlung* 160: 42-60.
- Edwards D 1970. Fertile Rhyniophytina from the Lower Devonian of Britain. *Palaeontology* 13: 451-461.
- Edwards D 1980. Early land floras. *In: Panchen AL (Editor)—The Terrestrial Environment and the origin of Land Vertebrates: 55-85*. Systematics Association.No.15. London: Academic Press.
- Edwards D 1982. Fragmentary non-vascular plant microfossils from the late Silurian of Wales. *Botanical Journal of the Linnean Society* 84: 223-256.
- Edwards D 1990. Constraints on Silurian and Early Devonian phytogeographic analysis-based on megafossils. *In: McKerrow WS & Scotese CR (Editors)—Palaeozoic Palaeogeography and*

- Biogeography: 233-242. Geological Society Memoir No. 12. The Geological Society, London.
- Edwards D & Berry CM 1991. Silurian-Devonian. *In*: Cleal CJ (Editor)—Plant fossils in Geological investigations. The Palaeozoic: 117-153. Chichester Ellis Horwood.
- Edwards D & Davies ECW 1976. Oldest recorded *in-situ* trachieds. *Nature* 263: 494-495.
- Edwards D & Davies MS 1990. Interpretations of early land plant radiations: "facile adaptationist guesswork" or reasoned speculation? *In*: Taylor PD & Larwood GP (Editors)—Major Evolutionary Radiations: 351-376. The Systematics Association, Special Volume No. 42.
- Edwards D & Richardson JB 2004. Silurian and Lower Devonian plant assemblages from the Anglo-Welsh Basin: a palaeobotanical and palynological synthesis. *Geological Journal* 39: 375-402.
- Edwards D & Rogerson ECW 1976. Oldest recorded *in situ* tracheids. *Nature* 263: 494-495.
- Edwards D, Davies KL & Axe L 1992. A vascular conducting strand in the early land plant *Cooksonia*. *Nature* 357: 683-685.
- Edwards D & Selden PA 1993. The development of early terrestrial ecosystems. *Botanical Journal of Scotland* 46: 337-366.
- Edwards D & Wellman C 2001. Embrophytes on land: the Ordovician to Lochkovian (Lower Devonian) record. *In*: Gensel PG & Edwards D (Editors)—Plants Invade the Land: Evolutionary and Environmental Perspectives: 3-28. Columbia University Press, New York.
- Edwards D, Wellman C & Axe L 1999. Tetrads in sporangia and spore masses from the Upper Silurian and Lower Devonian of the Welsh Borderland. *Botanical Journal of the Linnean Society* 130: 111-156.
- Edwards DS 1986. '*Aglaophyton major* a non-vascular land-plant from the Devonian Rhynie Chert'. *Botanical Journal of Linnean Society* 93: 173-204.
- Fanning U, Richardson JB & Edwards D 1991. A review of *in situ* spores in Silurian land plants. *In*: Blackmore S & Barnes SH (Editors)—Systematic Association Special Volume No. 44: 25-47. Oxford Clarendon Press.
- Gensel PG & Andrews HN 1984. Plant life in the Devonian, pp. 380. New York : Praeger.
- Gray J 1985. The microfossil record of early land plants: advances in understanding early terrestrialization, 1870-1984. *Philosophical Transactions of the Royal Society of London, Series B* 309: 167-195.
- Gray J 1991. *Tetrahedraletes*, *Nodospora*, and the 'cross' tetrad: an accretion of myth. *In*: Blackmore S & Barnes SH (Editors)—Pollen and Spores: 49-87. Systematics Association Special Volume No. 44, Oxford: Clarendon press.
- Gray J, Colbath GK, de Faria A, Boucot AJ & Rohr DM 1985. Silurian age fossils from the Paleozoic Paraná Basin, southern Brazil. *Geology* 13: 521-525.
- Gray J, Massa D & Boucot AJ 1982. Caradocian land plant microfossils from Libya. *Geology* 10: 197-201.
- Hueber FM 1968. *Psilophyton*: The genus and the concept. Proceedings of International Symposium on the Devonian Systems, (D.H. Oswald, ed.) Vol. II., Alberta Soc. Petrol. Geol., Calgary, Canada: 815-822.
- Hueber FM & Banks HP 1967. *Psilophyton princeps*: The search for organic connection. *Taxon* 16: 81-85.
- Kidston R & Lang WH 1917. On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part I. *Rhynia Gwynne-Vaughanii*, Kidston and Lang. *Transactions of the Royal Society of Edinburgh*, 51: 761-784.
- Lang WH 1937. On the plant remains from the Downtonian of England and Wales. *Philosophical Transactions of the Royal Society of London, Series B* 227: 245-291.
- Pratt LM, Phillips TL & Dennison JM 1978. Evidence of non-vascular plants from the early Silurian (Llandoveryan) of Virginia, U.S.A. *Review of Palaeobotany and Palynology* 25: 121-149.
- Raven JA 1984. Physiological correlates of the morphology of early vascular plants. *Botanical Journal of the Linnean Society* 88: 105-126.
- Rayner RJ 1984. New finds of *Drepanophycus spinaeformis* Göppert from the Lower Devonian of Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 75: 353-363.
- Remy W & Remy R 1980a. Devonian gametophytes with anatomically preserved gametangia. *Science* 208: 295-296.
- Remy W & Remy R 1980b. *Lyonophyton rhyniensis* nov. gen. et nov. sp., ein Gametophyt aus dem Chert von Rhynie (Unterdevon, Schottland). *Argumenta Palaeobotanica* 6: 37-72.
- Retallack GJ 1990. *Soils of the Past. An Introduction to Paleopedology*, 520 pp. Boston: Unwin Hyman.
- Richardson JB 1988. Late Ordovician and Early Silurian cryptospores and miospores from northeast Libya. *In*: El-Armanti A *et al.* (Editors)—Subsurface Palynostratigraphy of Northeast Libya: 89-109.
- Richardson JB & Edwards D 1989. Sporomorphs and plant megafossils. *In*: Holland CH & Bassett MG (Editors)—A global Standard for the Silurian System: 216-226. National Museum of Wales, Cardiff.
- Richardson JB & MacGregor DC 1986. Silurian and Devonian spore zones of the Old Red Sandstone Continent and adjacent regions. *Geological Survey of Canada Bulletin* 364: 1-79.
- Rothwell GW, Scheckler SE & Gillespie WH 1989. *Elkinsia* gen. nov., a late Devonian gymnosperm with cupulate ovules. *Botanical Gazette* 150: 170-189.
- Schopf JM, Mencher E, Boucot AJ & Andrews HN 1966. Erect plants in the early Silurian of Maine. U.S. Geological Survey. Professional Paper 550-D: D69-D75.
- Schultka S & Remy W 1990. Ein "Flöz" – Profil im linksrheinischen Schiefergebirge als Beispiel paralischer Verhältnisse im Ems. *Neues Jahrbuch für Geologie und Paläontologie Abhandlung* 181: 41-54.
- Schweitzer HJ 1983. Die Unterdeconflora des Rheinlandes. *Palaeontographica Abteilung B* 189: 1-138.
- Strother P & Traverse A 1979. Plant microfossils from the Llandoveryan and Wenlock rocks of Pennsylvania. *Palynology* 3: 1-21.
- Thomas BA & Cleal CJ 2000. Invasion of the land. Department of Biodiversity and Systematic Biology, National Museums and Galleries of Wales: 1-32.
- Vavrdova M 1984. Some plant microfossils of possible terrestrial origin from the Ordovician of central Bohemia. *Vestník Ustredniho ustavu Geologickeho* 59: 165-170.
- Wright VP 1985. The precursor environment for vascular plant colonization. *Philosophical Transactions of the Royal Society of London, Series B* 309: 143-145.