

The four dimensions of terrestrial plants

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The four dimensions of terrestrial plants: reproduction, structure, evolution and ecology

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1 Introduction

One of the most spectacular and important evolutionary processes on Earth was the conquest of the terrestrial environment by plants. Terrestrial plants are all embryophytes and for the purposes of this book they include plants that grow on soil (land plants), on other plants (epiphytes), on rock (lithophytes) and even in some cases are permanently submerged, but such aquatic plants are derived from land plant ancestors. Most convert carbon dioxide into more complex carbon compounds using chemical energy derived from the electromagnetic energy of visible light and produce oxygen as a byproduct. The plant photosynthetic cells need to be moist and plants are either poikilohydric and function only during humid conditions or are able to control water loss to a greater or lesser extent (homoiohydric) and can photosynthesise even under dry atmospheric conditions. Plants grow more or less successfully in all terrestrial ecosystems and nearly all ecological niches today, from swamps to deserts and some have even returned to the aquatic habitat. To accomplish the transition from the aquatic to terrestrial habitat numerous important structural, chemical, physiological and reproductive evolutionary innovations and adaptations were needed to enable plants to function in the terrestrial environmental conditions. From the time the earliest land plants appeared about 465 million years ago (Ma hereafter), there were a number of innovations in plant structure and reproduction that appeared through geological time. Many of the groups that appeared at different times in the past still have descendants present now but other groups became extinct and are now known only from fossils. The Palaeozoic seed ferns, the pteridosperms, that had fern-like foliage and also seeds, are a good example of a lineage that went extinct by the late Cretaceous (60 Ma) but are still an important group in relation to seed plant evolution. The early land plants were not highly specialised cormophytes with elaborate organs but did have a two-phased life cycle. Life cycles can be classified in terms of the relative importance of the gametophytic and the sporophytic generation which depends on the prominence of the haplo- and diplophase. Over time and with the evolution of new forms there has been a tran-

sition from dominance of the haploid (gametophyte) phase to that of the diploid (sporophyte) phase, that now characterises the later-evolved, modern land plants.

The ancestral condition of land plants was probably poikilohydry but homoiohydric developed in the sporophyte generation enabling greater control for the sporophyte over water relations. Important structural evolutionary innovations related to homoiohydric were the development of a thick cuticle reducing water loss, stomata to control gas exchange, vascular tissue in the stems for efficient fluid transport, wood as structural tissue and various kinds of roots, stems and leaves. It is postulated the first land plants were thallophytes with a simply structured body, called a thallus, as can still be found within the thallose liverworts today; they are considered to have evolved from algae that were aquatic or grew on damp soil.

These early thallophytes would likely have occurred in at least seasonally wet environments which is when sexual reproduction could take place. Thus, the ancestral type of fertilisation via motile, flagellate spermatozooids was still possible. In aquatic non-vascular plants the assignment of gender is arbitrarily related to the size of the sex cells, large female cells and smaller, mostly motile, male cells with flagella. This is a zygotic life cycle where only one cell, the zygote, is diploid and organisms with this life cycle are called haplonts. The opposite type of life cycle to this is the gametic life cycle where the only haploid cells are the gametes. Organisms in this group are called diplonts and are mainly animals. Intermediate between these life cycles is the heterophasic system where both the haplo- and diplophase have several to many mitotic cell divisions. These are haplo-diplonts and encompass all the extant land plants. The haplo- and diplophases of organisms can show similar morpho-anatomical structure and would be considered isomorphic but such life cycles do not exist at present in terrestrial plants. Now all land plants have a distinct heterophasic and heteromorphic life cycle (Fig. 1).

One of the first important evolutionary innovations in the life cycles of early land plants was

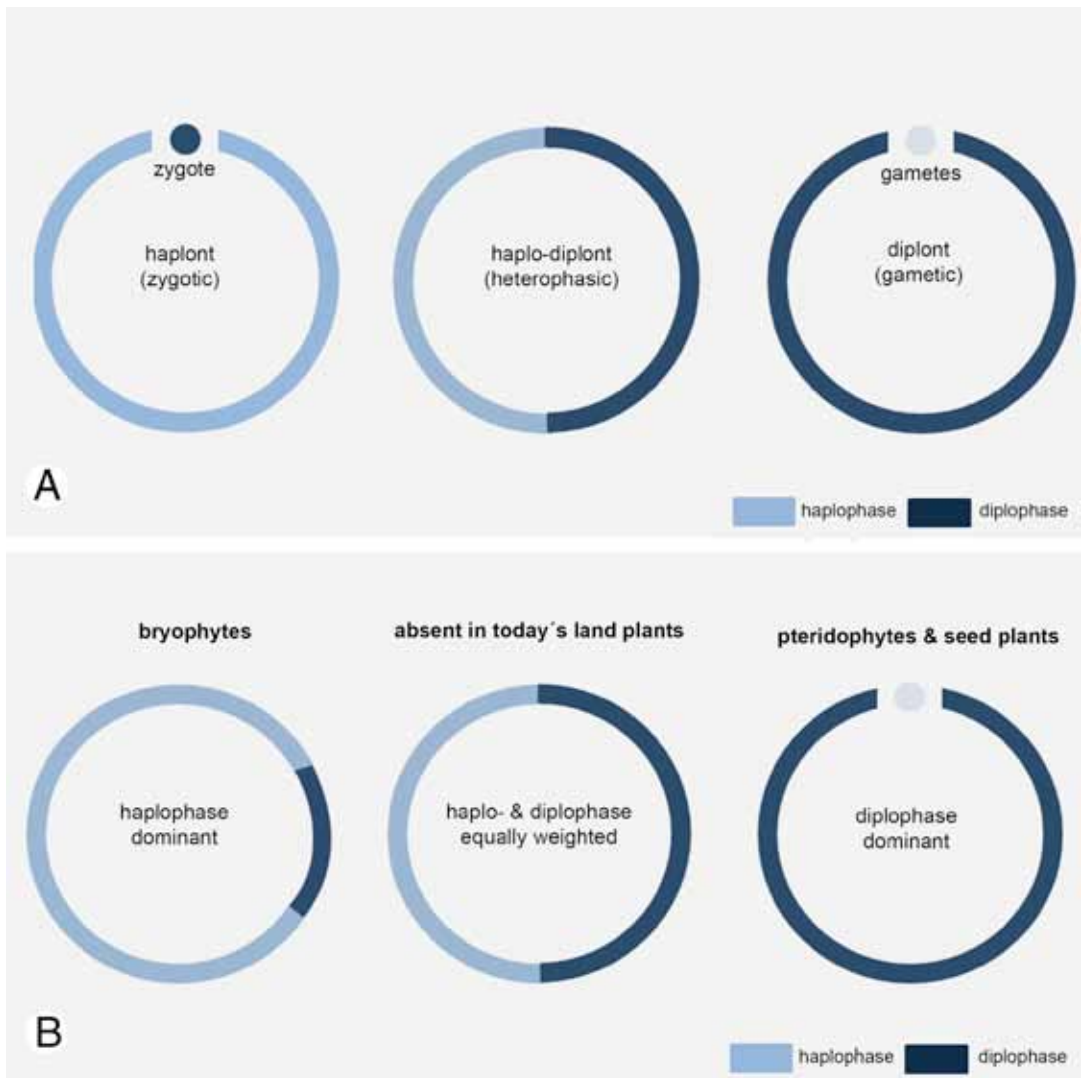


Fig. 1: Overview of the different types of life cycles; **A:** Life cycles can be classified based on the different emphasis of the haploid and diploid phase; from left to right: Zygotic life cycle, the only diploid cell is the zygote (haplont); heterophasic life cycle, haplo- and diplophase both with several mitotic divisions (haplo-diplont); gametic life cycle, the only haploid cells are the gametes (diplont); **B:** All land plants are haplo-diplonts, however with different emphasis of the diplophase; only bryophytes have a dominant haploid phase, in all other land plants the diploid phase is dominant.

the formation on the gametophytes of multicellular male and female gametangia. Inside the male ones, called antheridia, spermatozoids are formed while the female ones, called archegonia (= oogonia), each produces an egg cell. This protection of the egg cell is found throughout the land plants. The multicellular wall of the game-

tangium represents an important autapomorphy of all land plants (bryophytes, lycopods, horse-tails, ferns and seed plants). The gametophytes arise from the spores formed by meiosis that are produced by the sporophyte and in the free-sporing land plant groups there are some that are heterosporous with large spores (female),

and small spores (male), that produce female and male gametophytes respectively. Today, in addition to all seed plants only the water ferns and some lycopods (*Isoetes* and *Selaginella*) are heterosporous.

The fossil record shows that heterospory was much more widespread in the past but most of the heterosporous fern-, lycopod- and horsetail-lineages became extinct. While it may seem heterospory is an important step towards seed formation, it actually plays a more important role in the fertilisation process, because as unisexual prothalli develop from the spores, self-fertilisation is very much reduced. However, most ferns and lycopods are homosporous and produce spores of only one size. For homosporous organisms in this text with free-living gametophytes, gender of an individual is determined in the earliest ontogenetic stages by environmental signals in the haploid generation (haploid development) or by developmental and genetic influences in the diploid one (diploid development).

The exact morphological nature of the earliest land plants in the Ordovician is unknown because they are recorded only as dispersed spores comprising two or four permanently fused spores termed cryptospores. These have been found in sporangia, special spore-containing structures, that terminate smooth, forking stems in very small millimetre high plants. Their food conducting tissues most closely resemble those of mosses leading to the erection of a new pioneering group of early land plants, the eophytes, that combine features of vascular plants and bryophytes and coexisted with them. Very limited evidence suggests that the gametophytes were thalloid. The earliest unequivocal bryophyte is a liverwort recorded in the Upper Devonian.

Gametangia have not been identified in fossil liverworts. In most extant thalloid liverworts the gametangia are on the upper side of the thallus, but it is not clear if this arrangement of gametangia is ancestral. However this position would still have been useful for early land plants growing in wet habitats, because it facilitates dispersal of spermatozoids by water. Further evolutionary steps acted to reduce this strong dependence of the life cycle on the presence of free external water. Groups evolved in which spermatozoids were no longer released into the environment but were delivered in a package called pollen that placed the spermatozoids at the entrance to the

archegonia. The evolutionary changes to plant reproduction seem to have lagged behind those of the structural parts of the plant body. In the fossil record the sporophytes of the ancestors of species that are now only herbaceous plants, in many cases were immense trees, e.g. *Lepidodendron* and *Sigillaria*, (Lycopodiopsida) and *Calamites* (Equisetales), but they would probably still have had small gametophytes similar to those of their present day descendants. Across all groups there is a progressive reduction in the size and dominance of the haploid generation of the life cycle and an increase in the importance and longevity of the diploid generation. In numerous groups of land plants, the gametophyte became so strongly reduced that it is no longer a free-living generation, being developed entirely within the micro- or megaspore (= endospory). In bryophytes, the haploid generation is still dominant and the short-lived sporophyte develops on the gametophyte and is nutritionally dependent on it. In ferns, both generations are free-living, but the sporophyte is dominant and can produce spores over a long time (Fig. 2). The gametophyte is short-lived and dies soon after the first roots of the young sporophyte appear and reach the soil. In seed plants (= gymnosperms, the naked seed plants and angiosperms, the flowering plants), the sporophyte is also dominant, and the gametophytes are no longer a free-living generation throughout the entire group. They are nutritionally dependent on the sporophyte. Thus, the situation in seed plants represents exactly the opposite of that in bryophytes.

The conquest of dry terrestrial habitats also required another important innovation, the evolution of haploid spores as dispersal units (= diaspores) that are resistant to desiccation. This became necessary because a free release of gametes into the surrounding environment, as is possible in aquatic media, is impossible in dry terrestrial habitats. Each spore, which originated by meiosis of a spore mother cell, represents the starting point for a new haploid gametophytic generation. These spores are produced in special structures, called sporangia, which are part of the diploid sporophyte throughout all groups of land plants. The sporangia have a cellular wall, as is also the case for the gametangia. Due to all these innovations, the life cycles of land plants became continuously more and more complex, but the alternation of the haploid and diploid

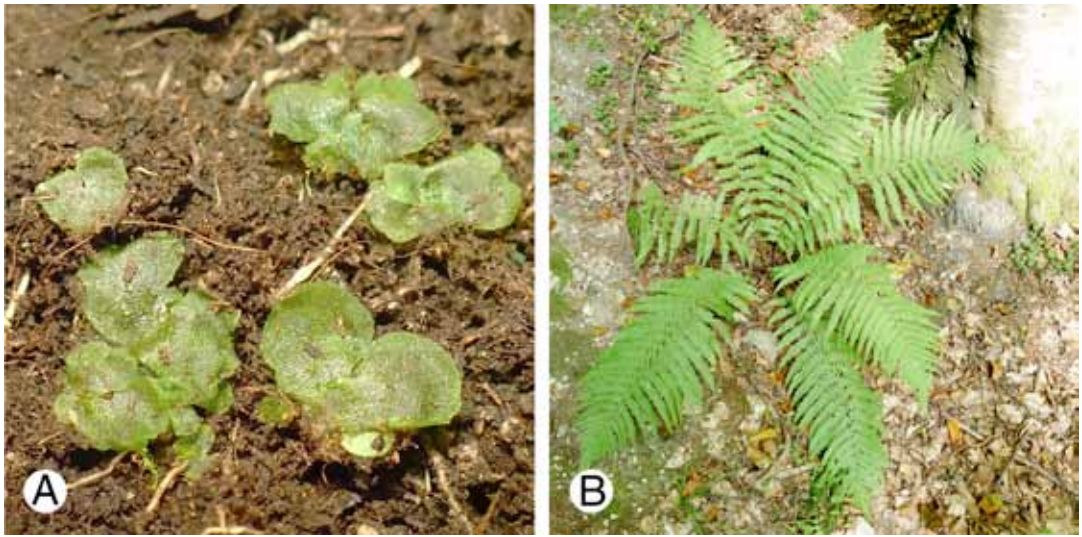


Fig. 2: All land plants have a heteromorphic life cycle showing an alternation of a haploid and a diploid phase, each with a markedly different morpho-anatomical structure; **A & B:** *Dryopteris filix-mas* (Dryopteridaceae, Polypodiopsida); **A:** The haploid gametophyte is short-lived and thallose; **B:** The diploid sporophyte is a long living cormophyte, which can produce spores over many years.

generation facilitates the important genetic recombination.

The diaspore of algae is the diploid zygote, which is released into the surrounding aquatic medium. In non-seed plants, the dispersal unit is the spore, from which the gametophyte, here called the prothallus, develops after spore germination. However, in the most recently evolved groups of land plants, the seed plants, the young sporophyte (= embryo) becomes part of the dispersal unit called the diaspore. This, in most cases, is not released without resources, but is

embedded in a more or less well-developed nutritional tissue (= nucellus or endosperm), which is surrounded by a distinct protective coat. This structure is called the seed and represents an important innovation. In times of unfavorable environmental conditions (e.g. times of drought) seeds can be dormant so that they only germinate under optimal conditions (cued by moisture, temperature, smoke, day length etc.). However, seed germination is not controlled exclusively by external factors, but also by features of the seed itself.

Tab. 1: Overview of different terms used to describe the same structures in pteridophytes and seed plants (gymnosperms and angiosperms).

pteridophytes	=	seed plants
macrosporophyll (megasporephyll)	=	carpel (in angiosperms)
macrosporangium (megasporangium)	=	nucellus
macroprothallus (megaprothallus)	=	embryo sac
microsporophyll	=	stamen
microsporangium	=	pollen sac
microspore	=	pollen grain

Previously, the life cycles of seed plants had been regarded as having evolved independently from those of mosses and pteridophytes. The extent to which the three groups are related had not been clearly understood. However, today it is widely accepted that the two-phase life cycles occurring in the different groups of land plants represent an evolutionary sequence. It is characterised by strong reductions of the gametophytic and an increased dominance of the sporophytic generation, reduced dependence on free external water, and reduced investment in non-fertilised prothalli. A number of different terms for the homologous reproductive structures for pteridophytes and seed plants has developed. This is perhaps mainly due to the organs that were obviously associated with spore production being called sporophylls or sporangia, while gametophytes with simple structure were labelled prothalli. More specialised terms were coined for the much-reduced seed plant reproductive structures (Tab. 1).

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2 Life cycles in pioneering land plants

2.1 Alternation of generations

The recognition of the alternation of generations in the life cycle of plants as well as in animals led to a paradigm shift in botanical activity towards the end of the 19th century. HOFMEISTER'S comprehensive survey of the comparative morphology of land plants which ranged from mosses through free-sporing and seed-producing coniferous plants allowed the development of his now generally accepted concept of the plant life cycle, where an asexual free-sporing phase (subsequently termed the sporophyte by Czech botanist CELAKOVSKY) alternated with a sexual gamete producing phase (the gametophyte). This conclusion was further substantiated by STRASBURGER'S discovery in Bonn, where his laboratory became a place of pilgrimage for botanists, that there were twice the number of recently described chromosomes (termed diploid) in the sporophyte generation than in the gametophyte (haploid).

Accompanying these empirical observations was much discussion on the nature of the life cycle in the ancestral green algae and the subsequent evolution of the two generations in early land plants. Two scenarios were explored. In the homologous theory (the term coined by CELAKOVSKY) in the ancestral algae and the earliest land plants the two generations were similar (isomorphic). In the antithetic theory, the ancestral alga was a photosynthetic gametophyte with, initially, the sporophyte manifested in the fertilised egg (the zygote) and, subsequently, the development of a multicellular free-sporing plant, adapted for survival in a water-stressed sub-aerial environment (the latter promoted by the English botanist, BOWER). The discussion continues today with evidence mounting for the antithetic theory based on (1) comprehensive surveys of extant plants, (2) the confirmation of the green algae as closest to higher plants on the basis of morphological, anatomical, developmental and metabolic similarities and, more precisely, to the Charophyceae based on details of a relatively complex thallus, multicellular antheridia (the sperm with flagella) and oogonia (Figs. 3A-D), with more recent molecular evidence pointing to the Zygnemataceae as the sister group to

the embryophytes, despite their lower degree of structural complexity (Fig. 3E) compared to the much more complex Characeae, (3) the phylogenetic position of the bryophytes as basal to the tracheophytes (vascular plants) and finally (4), molecular studies e.g. comparative genomics relating to features evolved in the gametophyte being co-opted in the sporophyte with potential new roles, retention of genes for organs and tissues (e.g. rhizoids, xylem) and regulatory networks from gametophytes in the sporophyte (e.g. universal polar auxin transport).

Acquisition of embryophyte characters was not instantaneous and it seems likely that the *de novo* genes would have evolved over a long period of time with the first fossil evidence of land plants being in the form of spores. Unequivocal examples comprising tetrads and dyads and named cryptospores appeared in abundance in the Middle Ordovician, but similar, although not identical, aggregations/packets are recorded in Cambrian and basal Ordovician rocks and assigned, *inter alia*, to charophytes. This evidence, combined with that from molecular clocks, suggests a long history of emerging embryophytes alongside their charophyte ancestors in the early Phanerozoic before the appearance of the vascular plants in the Silurian.

So, what can the fossil record contribute to this debate and particularly to the subsequent evolution of life cycles of vascular plants as they diversified and exploited wider ranges of habitat on land, as opposed to mere demonstration of first occurrences?

2.2 Major caveats

Initial perusal of the fossil record from the distant past, here the Lower Devonian, to the near present, shows it to be dominated by the aerial sporophytes of free-sporing and seed plants. This is because the various adaptations that resulted in successful colonisation in diverse, water-stressed habitats result from a combination of both chemical and anatomical innovations that also survive the vicissitudes of fossilisation. Most important was the evolution of the complex polymers that contribute to the formation of cuticle

(cutin) and wood (lignin), the former a waterproof covering and the latter, in xylem, essential to the functioning (preventing collapse under tension) of water conducting cells in vascular plants and, when integrated into cell walls, providing structural support. By contrast, soft (parenchymatous) tissues e.g. the flesh of an apple or the moss gametophyte, decay rapidly and might disappear except under usually aqueous anaerobic conditions and pressure when they are converted into a film of carbonaceous material. However even these might contain traces of lignified cells such as in the veins of a leaf.

Thus, considering bryophytes (mosses and liverworts) today that possess only traces of cuticle and probable precursors of lignin, their gametophyte generation, be it filamentous, thalloid or leafy, would be predicted to show low fossilisation potential, with only their spores preserved. These, like those of free-sporing plants and the pollen of seed plants, are coated by the resilient polymer, sporopollenin, and are likely to persist as fossils. This low fossilization potential severely hinders the search for bryophytic plants, particularly in Ordovician-Silurian rocks, at the time of diversification of land plants. Nevertheless spores originally considered as being of hepatic origin, because of their clustering in pairs or groups of four and their ultrastructure, might be considered as demonstrating the existence of bryophytes in the Ordovician about 460 Ma. Some of these spores are now known to be produced by a new group of minute land plants, the eophytes, whose branching sporophytes with terminal sporangia discovered in the Lower Devonian combined the features of bryophytes and tracheophytes. Gametophytes remain conjectural. The earliest unequivocal liverwort is the Upper Devonian thalloid gametophyte, *Metzgeriothallus*.

2.3 Lower Devonian gametophytes

Having been so far somewhat pessimistic over the role of fossils as outlined above, amazing preservation in a Lower Devonian chert has transformed our understanding. 407 Ma volcanic activity, to the west of Aberdeen in Scotland near a village called Rhynie, produced siliceous springs, similar to those in Yellowstone National

Park, U.S.A., today. This spring water flooded surrounding vegetation where precipitation of silica turned all the elements in the ecosystem into stone (chert) and thus produced excellent cellular preservation of the vascular plants.

Other permineralised fossils from the Rhynie chert include numerous invertebrates (e.g. spiders, Crustacea, nematodes, myriapods), fungi and algae, the latter ranging from coccoid filamentous forms of uncertain affinity and most importantly, the charophyte *Palaeonitella*. The Figures 10A-C & E show reconstructions of the leafless, axial nature of some of the vascular plant sporophytes, and their terminal sporangia. These have been known for more than one hundred years, but quite recently certain axial fossils that possess xylem, stomata and rhizoids, have been shown to possess beautifully preserved gametangia allowing their identification as gametophytes. The presence of xylem is particularly important as their tracheidal anatomy allows confirmation of affinity with four of the sporophyte vascular plants in the assemblage (see Tab. 2). Because they are fossils it was not possible to definitively link them to the co-occurring sporophyte species so they were given separate names that commemorate the pioneers of important research studies of the Rhynie chert (RC) plants, viz. KIDSTON, LANG, LYON and REMY but their anatomical similarities support their relationship to the sporophytes as listed in the table below.

All the gametophytes are much smaller than their sporophytes. Branching is rare (but most are fragmentary) and gametangia are borne on gametangiophores, except for *Remyophyton* where they are borne directly on axes (Fig. 11A). *Remyophyton* is the most completely known gametophyte in the chert and is considered the alternate life stage of *Rhynia gwynne-vaughanii*. The reconstruction (here shown as a line drawing, Fig. 11A, amongst those of other Rhynie chert gametophytes) and a chert section show part of a stand of gametophytes growing on a siliceous surface comprising at least a hundred upright axes about 10-20 mm tall and a few millimetres wide (Fig. 7B). Each arises from a bulbous structure bearing rhizoids penetrating the substrate on its lower surface with stomata on its upper surface. The latter were also found on the upright axes where a central strand composed of tracheids with the broad, helical thickenings allows linking with *Rhynia*. Twenty-seven of the

Tab. 2: Sporophytes and their identified gametophytes from the Rhynie chert (see Figs. 10 & 11 for line drawings). Unlike in extant taxa the diploid sporophytic and the haploid gametophytic generation of the same taxon have been assigned different scientific names, despite the belief that, based on their anatomy, they seem to be different parts of the life cycle of the same species.

Sporophytes	Affinity*	Gametophytes
<i>Rhynia gwynne-vaughanii</i>	R	<i>Remyophyton delicatum</i> male, female
<i>Aglaophyton majus</i>	R	<i>Lyonophyton rhyniense</i> male, female
<i>Horneophyton lignieri</i>	?	<i>Langiophyton mackiei</i> male, female
<i>Nothia aphylla</i>	?	<i>Kidstonophyton discooides</i> male ?
<i>Asteroxylon mackiei</i>	L	? ?
<i>Trichopherophyton teuchansii</i>	Z	? ?
<i>Ventarura lyonii</i>	Z	? ?

* L = lycophyte, R = rhyniophyte, Z = zosterophyll.

axes bear scattered embedded archegonia, with protruding necks, while on sixty-nine, antheridia are borne on short stalks (Figs. 8A & B), either on sides of the axis or grouped on the surface of a terminal saucer-shaped expansion.

Evidence for the beginnings of the gametophyte generation is derived from germinating spores in the *Aglaophyton* life cycle (Figs. 4B-D) leading to the formation of the gametophytic generation called *Lyonophyton*; the generations united in their possession of unusual tracheids. Remaining gametophytes are more fragmentary, essentially gametangiophores terminal on short axes; indeed *Kidstonophyton* (name for the gametophyte of *Nothia aphylla*) is known only from a swollen axis containing numerous stalked antheridia (Figs. 9B & C, 10G). The axis has surface features that are also present on *Nothia aphylla* (Fig. 10E). However, *Nothia* is of uncertain affinity, but possibly linked to a zosterophyll.

On tracheidal anatomy, *Lyonophyton* (Figs. 5, 6 & 10F), which represents the male and female gametophyte of *Aglaophyton majus* (Fig. 4), has a basic construction similar to that in *Kidstono-*

phyton (Figs. 9B, 10G), but the male antheridiophore is an entire or deeply lobed cup-shaped structure terminating a short unbranched axis (<20mm) arising from a fleshy bulbous base (protocorm) (Figs. 5A & B). Spherical, elliptical to pear-shaped antheridia occur on the inner face of the lobes or base of the cup. One of the most remarkable images from the chert shows a cloud of male gametes (spermatozoids) emerging from an antheridium of *Remyophyton delicatum* (Fig. 8C). These were curled, 20-30 μ m long and 2 μ m wide. Archegoniophores are also preserved with archegonia isolated on lateral surfaces close to the tip as well as on its flattened apex.

Finally, the gametophyte *Langiophyton* (Fig. 10H), linked anatomically to the sporophyte *Horneophyton* (Figs. 10C & D), one of the most unusual plants in the chert with columellate sporangia and again of uncertain affinity, has the most complex cup-shaped archegoniophores comprising a number of finger-shaped projections which bear the archegonia (Figs. 9D, 10H). Antheridiophores are simpler and cup-shaped with antheridia on the base of a central depression.

In the Rhynie ecosystem, where gametophytes possess axial morphology and accompanying adaptations that result in control of water relations, it can be concluded that the generations were isomorphic and thus provide evidence to support the homologous theory of alternation of generations in early land plants. However it should be emphasised that these plants existed about 60 million years after the land was first colonised, and that the pioneers might have been quite different. Further support for an independent gametophyte generation comes from slightly younger, axial, coalified compression fossils of two types, in which gametangiophores are cup-shaped; although poor preservation in coal precludes detail of construction and gametangia. In *Sciadophyton* (Figs. 11B & C), bedding planes are covered by clusters of up to 35 axes that radiate from a central point. Some of these develop into infrequently branched gametangiophores that grew upwards and terminate in a shallow cup/saucer structure with lobed margins and bearing oval to circular dark areas interpreted as gametangia (Figs. 11B, D, E). Tracheids in the axes possess broad spiralling bands similar to those in *Rhynia gwynne-vaughanii*, but also occur in a group of Lower Devonian plants that are characterised by abscission of sporangia (as also occurred in *Rhynia*!). By contrast, in *Caliculiphyton* (Fig. 11F), similar shallow structures, with entire or slightly lobed margins, terminate gametangiophores inserted at irregular intervals on short, lateral branches borne on a presumed upright axis. In cup-shaped structures with entire margins that curve inwards, numerous dark spots (probably antheridia or archegonia but lacking anatomical details) cover the inside surface, whereas in the lobed examples (3-5 lobes), flask-shaped, columnar or spherical entities are attached to a central area at its base. These were interpreted as possible antheridia, but again this cannot be substantiated by cellular detail. Nor can any details of a vascular strand, although the fossils are concluded to be gametophytic based on similarities between its gametangiophores and those in *Kidstonophyton*.

In summary, there are broad similarities of the gametangiophores in both the permineralised and compression axial fossil gametophytes and, particularly in the former, in their associated sporophytes. Thus the fossil record supports life cycles where the two independent generations

were isomorphic (and presumably with similar physiology - homoiohydric) indicating there were free-sporing plants at that time. Unfortunately with one exception (lycophytes), these free-sporing vascular plant clades became extinct, and so we have no information on similar gametophyte generations in the rapidly evolving plants of the Middle Devonian. Tantalisingly, the exception is *Asteroxylon*, a lycophyte in the Rhynie chert, but for which we have no evidence of the gametophyte generation.

2.4 The evolution of the seed

The next major transformative event in plant life cycles was the appearance of the ovule (Fig. 11H) and the seed, here defined as a fertilized, integumented ovule. The seed habit excluded the free-living gametophyte with its requirement for water fertilisation from the life cycle and thus allowed plants to colonise habitats previously unavailable to them. The transition involved the delivery of the male gametophyte-containing sperm to the female gametophyte that was retained on the parent plant. Stages in the process have long been hypothesised based on comparative reproduction in a wide range of free-sporing living plants, beginning with the evolution of two sizes of spores (heterospory) within the same sporangium followed by appearance of two separate sporangia, microsporangia with large numbers of small spores and megasporangia with fewer large spores. The latter would develop into female gametophytes and the former into male. Initially each spore would have germinated (exosporic development) to produce free-living male and female gametophytes (e.g. the living fern, *Platyzoma*). In the postulated next stage (endosporic development), gametophytes would have developed within the spores (e.g. the living lycophyte, *Selaginella*). The following stage, reduction to a megaspore and its retention on the parent plant, is hypothetical. From such a survey of living plants, it is obvious that heterospory occurred more than once. In which lineage did it result in the seed? Can the fossil record provide evidence for stages in the process and the nature of the ancestral plant?

First clues come from the dispersed spore record in which, towards the end of the Lower Devonian, there was a general increase in size and in the emergence of bimodality in their diame-

ters. This heralds the beginnings of heterospory but is unhelpful as to the affinities of the producers or if the heterospory was intrasporangial (two sizes in the same sporangium) or intersporangial involving microsporangia and megasporangia. In the former, there is the possibility that the smaller spores were aborted types, but there are unequivocal fossil examples, e.g. in the barinophyte, *Barinophyton citrulliforme*, and possibly in the zosterophylls and basal lycophytes in the Upper Devonian. So, the condition has existed in the past and probably produced free-living male and female gametophytes, but its record is in the Upper Devonian and, as so often in palaeobotany, the chronology of occurrences does not fit the theory. There is, however, a Middle Devonian plant, *Chaleuria*, again of uncertain affinity, which produced sporangia containing numerous small spores, some with fewer larger spores and in a few, a mixture of both. Such spores when liberated probably developed free-living gametophytes, endospory being the succeeding anticipated evolutionary stage. This requires anatomical evidence of the contents of the spores, data that are not available until the end of the Devonian. Nevertheless, it is noteworthy that intersporangial heterospory is recorded in a number of lineages including ferns, equisetaleans, and lycopods. It is present in the very familiar, arborescent *Archaeopteris*, a plant with fern-like foliage, heterospory and conifer-like wood, a representative of a major group of Middle–Upper Devonian plants – the progymnosperms, the complex from which the seed plants emerged. However, as in previously described Devonian plants, it possessed hundreds of microspores in each microsporangium and in this taxon up to 16 megaspores in a megasporangium, the sporangia being borne on the divisions of “leaflets” (actually the leaves) in the frond. However about this time, the dispersed spore records contain very large megaspores, which on first glance appear single, but associated with the trilete mark, a characteristic of all spores produced by meiosis, is a cluster of three very small aborted spores. These megaspores have been named seed megaspores and a similar aggregation has been isolated from one of the earliest seeds, *Archaeosperma*, as well as in the cones of Carboniferous arborescent lycophytes.

In our hypothetical progression towards the seed, a major step would be the retention of the

indehiscent megasporangium containing just one functional megaspore on the parent plant, with fertilisation by delivery of microspores which ultimately would produce sperm. These microspores are named pollen and contain a much-reduced gametophyte. Fertilisation *in situ* would allow a continuing supply of nutrients from the parent plant to the protected developing embryos, thus assisting their successful growth and survival on release.

Such intermediates are absent from the fossil record; the earliest unequivocal representative, coalified *Elkinsia polymorpha*, conforms to our definition of an ovule as an indehiscent megasporangium (nucellus) that is surrounded by an integument (eventually the seed coat) (Fig. 11G). The nucellus surrounds one functional megaspore, containing abundant nutrients and distally a number of archegonia. Above them, is a pollen chamber, sometimes extended into a short tube. Later Carboniferous examples preserved in calcium carbonate show that the pollen was captured in a drop of fluid, named the pollen drop mechanism that still exists today in conifers (Fig. 78B). When the liquid dries up, the pollen is sucked into the vicinity of the archegonia (termed hydrasperman reproduction). *Elkinsia*, being a typical member of the pteridosperms by having fern-like morphology, has fronds that branch and ultimately bear cupules – concentrations of branches – and, in this case, a cluster with four ovules (Fig. 11G). Variation in a number of Upper Devonian pteridosperms relates to the nature of the cupule (\pm branching) and number of ovules, the number and degree of fusion of lobes of the integument and its fusion to the nucellus and the nature of the pollen chamber. After fertilisation in hydrosperman reproduction, the nucellus enlarged in size and became sealed off to form the seed. A second group, characterised by absence of the cupule and presence of bilaterally symmetrical ovules on stalks, but other vegetative parts unknown, is exemplified by *Pseudosporogonites* from the Belgian Upper Devonian.

To conclude, fossils admirably record the explosive evolution of early ovules (Fig. 11H) and ovule-bearing structures, but intermediates in their origin, apart from indicating one potential ancestral form in the progymnosperms can only be inferred from traditional systematic and cladistic analyses.

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Fig. 3: Morphology of vegetative and reproductive structures of streptophytic algae using the examples of *Chara* spp. (stoneworts), Charophyceae (**A-D**) and *Spirogyra* spp. (water silk), Zygnemataceae (**E**); **A:** Natural habit in a freshwater body; **B:** Fertile branching system with numerous egg cell-producing female oogonia (= nucules) and sperm-producing male antheridia (= globules); due to the quite complex structure, the morphology resembles that of a shoot axis of a cormophyte showing segmentation into “nodes” and “internodes”; **C:** Cross section of a stem showing the single large stem cell surrounded by several cortical cells that mimic cortical tissue but are only a ring of smaller cells; **D:** Reproductive structures; the gametangia are unisexual and well exposed; the oogonium is green and several cells form a basal stalk; the wall is single-layered and consists of numerous tube cells that form a spiral structure; at the apex several coronal cells form a single-layered crown (= corona); the antheridia are smaller, globose and bright orange; **E:** Filamentous, multicellular form; despite the lower degree of structural complexity, molecular phylogenies suggest Zygnemataceae is closer to the embryophytes/land plants than the much more complex Characeae.

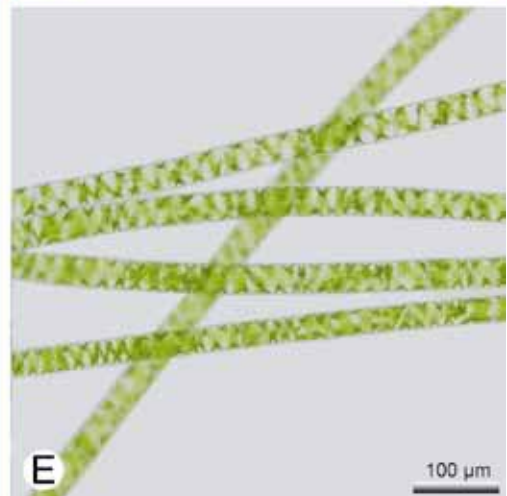
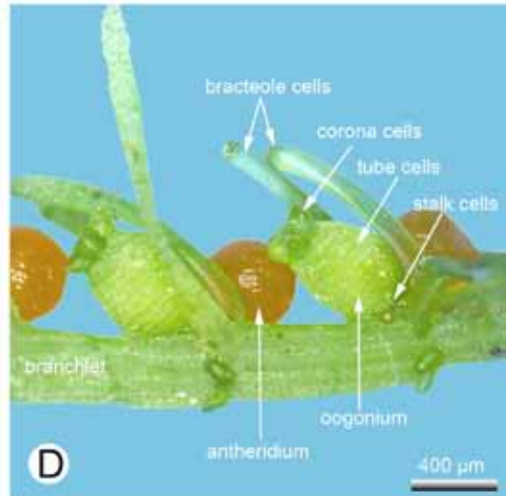
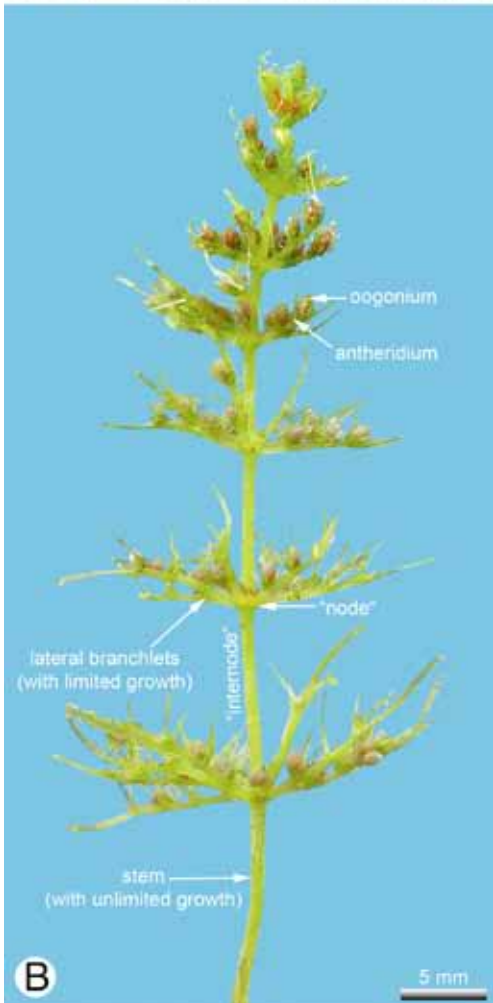
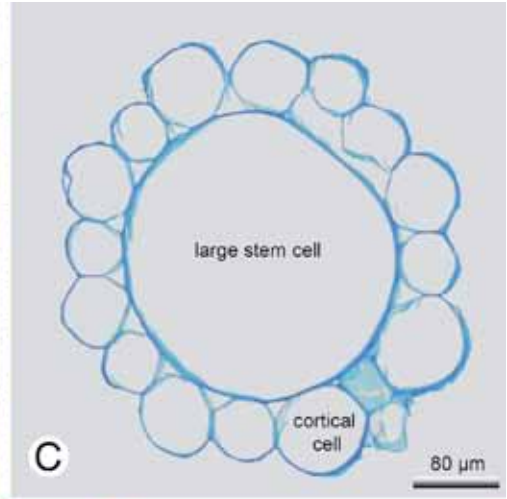
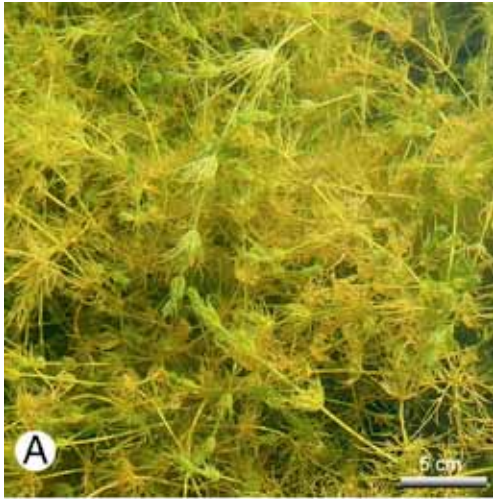


Fig. 4: Sections through silicified early terrestrial plants from the Devonian Rhynie chert (Aberdeenshire, Scotland), about 407 Ma; **A:** Transverse section through aerial stem of *Aglaophyton majus*; central dark area is water conducting tissue; darker area in cortex results from mycorrhizal colonisation; **B:** Section through tetrads of spores (three visible) produced by meiosis in the sporangium of *Aglaophyton*; **C & D:** Germinating spores of *Aglaophyton*: the beginnings of the haploid gametophyte generation.

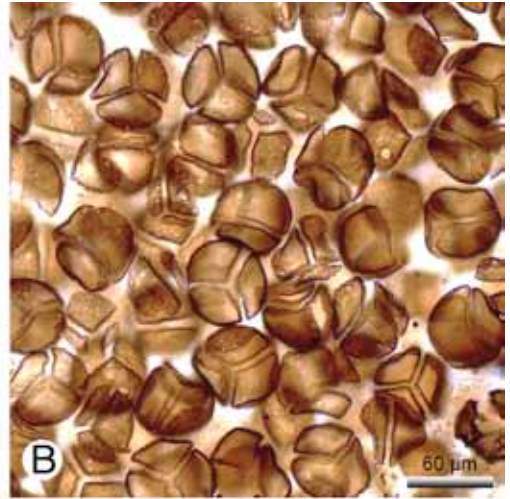
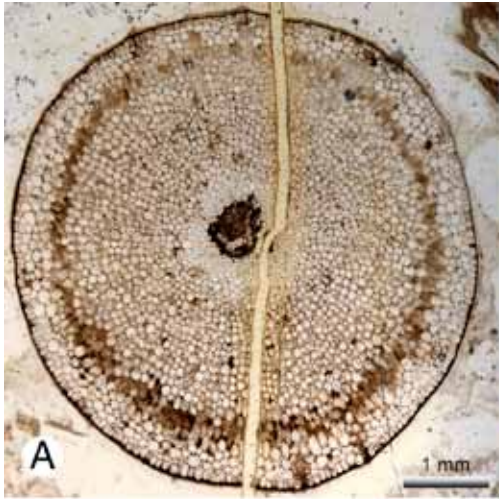


Fig. 5: Reproductive structures of early terrestrial plants from the Devonian Rhynie chert (Aberdeenshire, Scotland), about 407 Ma; **A & B:** Longitudinal sections through the free-living, male gametophyte generation of *Aglaophyton* named *Lyonophyton rhyniense*. The dark antheridia containing the male gametes are borne on the inside of a shallow bowl-shaped structure. There are central water-conducting cells whose construction is identical to those in the sporophyte *Aglaophyton*; **C:** Longitudinal section through mature antheridium of *Lyonophyton*; **D:** Longitudinal section of an antheridium of *Lyonophyton* with cloud of liberated male gametes at tip.

