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PLANTS | | CHLOROBIONTA

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Chlorobionta: Land Plants

```
LIFE
|--Eubacteria
`--Eukarya
   |--+--Rhodophyta
   |  `--CHLOROBIONTA
   |     |--Chlorophyta
   |     `--Charophyta
   |        |--(various green algae)
   |        `--Embryophyta
   |           |--Bryophyta
   |           `--Tracheophyta (rhyniophytes)
   |              |--Lycophyta
   |              `--Euphyllophyta
   |                 |--Monilophyta
   |                 `--Spermatophytata
   |                    |--Trimerophytes
   |                    `--Spermatopsida
   |
   `--+--Fungi
      `--Metazoa
         |--Chordata
         `--Protostomia
```

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  - Glossary
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- "The Wearing of the Green"
- Evolution of Land Plants
  - Green Algae
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  - Bryophyta
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  - Lycophyta
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  - Monilophyta
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Fern, *Blechnum nudum* from Nunniong, Australia (Tracheophyta, Euphyllophytina,Moniliformopses, Pteridophyta, Polypodiopsida, Hymenophyllidae, Aspidiales, Blechnaceae).(Wikipedia)

Lists

A. Glossary of terms and abbreviations.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

B. Taxon Index: alphabetical list of taxa.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

C. References: literature citations by author.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

Aristotle divided all living things between plants, which generally do not move, and animals, which do. In Linnaeus' system, these became the Kingdoms Vegetabilia (later Plantae) and Animalia. Since then, it has become clear that the Plantae as originally defined included several unrelated groups, and the fungi and several groups of algae were removed to new kingdoms. However, these are still often considered plants in many contexts. Indeed, any attempt to match "plant" with a single taxon is doomed to fail, because plant is a vaguely defined concept unrelated to the presumed phylogenetic concepts on which modern taxonomy is based. At the very least, there are three distinct monophyletic definitions - the descendants of the primary endosymbiosis homologous with land plants, the green photosynthetic clade (also called Chlorobionta), or the land plants only (also called Embryophyta). (modified from Wikipedia)

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Chlorobionta: Land Plants

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   |                 |--Monilophyta
   |                 `--Spermatophytata
   |                    |--trimerophytes
   |                    `--Spermatopsida
   |
   `--+--Fungi
      `--Metazoa
         |--Chordata
         `--Protostomia
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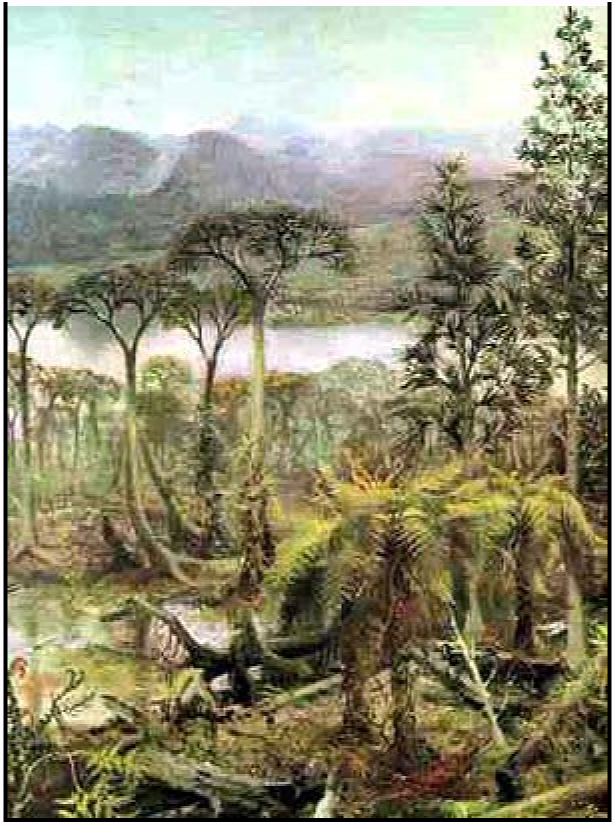
"The Wearing of the Green"

Beginning in the Archean era, Cyanobacteria evolved photosynthesis, which enabled them to use sunlight to draw carbon dioxide from the atmosphere and convert it to oxygen, water and glucose (a simple carbohydrate). These could be considered the first simple "plants" Plants therefore might be seen as any organism that is able to use sunlight, carbon dioxide, and water, to manufacture its own food, that is, as a special class of autotroph. However, that's far too broad. It would include all kinds of things like diatoms, chromists, and photosynthetic bacteria which have nothing to do with plants in a phylogenetic sense. They are, to be sure, all within the subject matter of a General Botany class. All of these groups share some essential biochemistry. However, what they *don't* share is a common ancestor to the exclusion of all other organisms. This similarity arises from (a) convergent evolution and (b) the exchange of



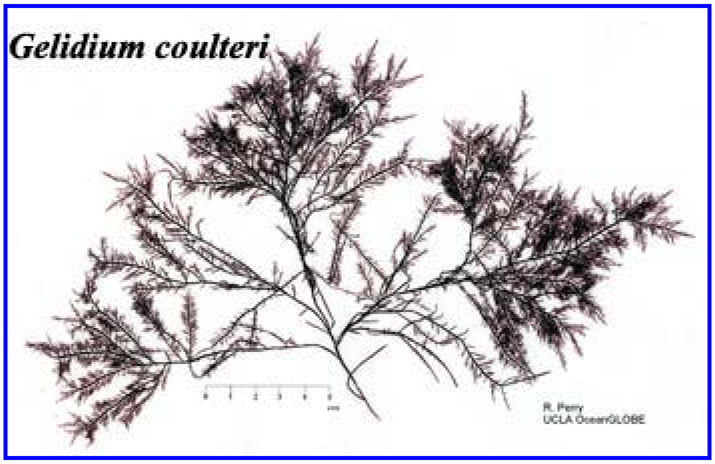
plastids.

The description above also fails because it is only partially correct, even as a general description. Plants not only breathe out (respire) oxygen, but parts of their tissues also respire carbon dioxide, just as animals (heterotrophs) do. These processes provide the plant with energy for growing and maintaining its life support systems, and go on at all times. During the sunlit day, more carbon dioxide is consumed than is released in respiration, but at night photosynthesis ceases and the plant respires only carbon dioxide, returning a portion of its carbon to the atmosphere.

One better approach to defining "plants" is the "Chlorobionta" hypothesis, as used on the Tree of Life site:

> There are two major lineages of green plants. One consists of most of what have been classically considered "green algae" -- mostly microscopic freshwater forms and large seaweeds. The other lineage contains several groups of "green algae" that are more closely related to land plants. Because these two lineages are monophyletic, they have been placed in a single monophyletic group called green plants, or, in technical parlance, the subkingdom Chlorobionta ...

This suffers only from being vague. Is there anything *else* in the box besides green algae and land plants? The ToL authors don't suggest any other content. Alternatively, this might be an attempt to suggest a crown group: "the last common ancestor of Chlorophyceae and evergreens and all of its descendants," or something like that. That sounds like a workable definition, but that can't be right, since they include the prasinophytes among the Plants. Some, but not all, prasinophytes would be excluded from the plants by a crown group definition. We think what the ToL authors actually had in mind is an even better choice: the stem group "green algae > red algae." This includes all of the prasinophytes, all other green algae and all plants, as those terms are normally used, but not much of anything else.



Why do we care about definitions? The price of admission to doing good science taking an explicit position, so that others can prove you wrong. A vague definition, such as ToL's original formulation, is not good science. Unless we know precisely what they mean by "plant" we can't really make testable statements about what are or are not plants, nor about what characteristics plants have or do not have, nor about whence they might have derived their characteristics. Without really crisp definitions, these issues quickly get bogged down in semantics and arm-waving. Arguably that is exactly what happened to the whole business of taxonomy for the better part of a century.

Of course, definitions can never be "wrong," in a logical sense. However, they can be useless, if they fail to draw lines within our area of interest. A vague definition is *always* useless because it draws no line at all. Phylogenetic definitions have revived the whole business of evolutionary systematics because they are quite precise and refer to historical events (*e.g.*, the evolution of red and green algae from a common ancestor), rather than to some man-made list of (sometimes fuzzy) characteristics. However, this precision also comes at a price. A phylogenetic definition is built around a phylogenetic hypothesis. Unlike a definition, a hypothesis *can* be wrong. If so, any definition based on that hypothesis usually must be abandoned, and a lot of good work may go down the tubes.

Suppose for example, that we interested in the evolution of birds. Our hypothesis is that birds are the sister group of dinosaurs, and that some "dinobird" was their last common ancestor. We thus define birds as *Struthio* (ostrich) > *Struthiomimus* (a theropod dinosaur which looked like an ostrich) and dinosaurs as *Struthiomimus* > *Struthio*. Sadly, after years of frustrating labor sorting out the characteristics of the supposed dinobird ancestor, we realize that birds *are* dinosaurs. Oops. Our definition of "bird" turns out to include embarrassingly unbirdlike things like therizinosaurs, while our definition of "dinosaur" includes only tyrannosaurids and ornithomimosaurs. How to explain this little *faux pas* to those notoriously humorless folk whose grants supported our research the last three years? Again, that is simply the price of doing good science.

For that reason, we should be careful, as well as explicit, in framing the definition and articulating the underlying hypothesis. Here, the hypothesis is that red algae, in a colloquial sense, are closely related to green plants, in an equally colloquial sense. This then allows us to define both rigorously in terms of that relationship. Strictly speaking, we should do so in terms of particular anchor taxa, just in case either group turns out to be polyphyletic (which is possible). By all means, then, let's do so. On the red algae side, we'll pick *Gelidium coulteri*, a randomly chosen species of a well-known and very successful genus of red algae. On the green plant side, let's use an angiosperm, a highly derived group, and *Quercus albus*, because (as any citizen of the state of Connecticut will know) it symbolizes the willingness to take risks to vindicate historical truth. Based on our phylogenetic hypothesis, our working definitions are Chlorobionta (plants) = *Q. alba* > *G. coulteri*, and Rhodophyta (red algae) = *G. coulteri* > *Q. alba*.

Was that so hard? Of course not. But then, unlike ToL, we are not subject to the temptations to waffle which come with peer review and the caprice of granting agencies. Lest we be misunderstood, we support both peer review and *post hoc* review by grantors as excellent things for science; but they are not unmixed blessings. The inducements to please everyone may become irresistable. Now, unlike ToL, the purpose of Palaeos is only to amuse those who write it. However, if we can, occasionally, counterweight the temptation for others to hide behind intentionally vague and inconsistent pronouncements made in the service of their own comfort, perhaps it may serve another purpose as well.

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Evolution of Paleozoic Land Plants

Green Algae

The Green Algae - the Chlorophyta and Charophyta - include a number of mostly aquatic forms, including some unicellauar and primitive colonial forms. and other multi-cellular types that however lack a true root system

They are very closely related to (and probably the ancestors of) the higher plants in the kingdom Plantae. Molecular and cellular similarities between green algae, particularly the charophytes, and land plants include the following:

(1) Both the green algae and plants have chlorophyll b and beta-carotene

(2) Green algae and plants both have special intracellular membranes (the thylakoid membranes) which contain the chlorophyll stacked into grana.

(3) Charophytes have a cellulose content of 20 to 25% of the cell wall, a composition similar to that of plants.

(4) Cell division in green algae is very similar to that of land plants. Both use microtubules to bring vesicles containing new material in to form the cell plate which will divide the cell into two.

(5) Nuclear genes and RNA are similar between charophytes and plants.

Plants Conquer the Land

If the great evolutionary radiation of metazoa (multicellular animals) in the earliest Cambrian oceans was the first great dramatic even of the Phanerozoic era (indeed ushering in the Phanerozoic), the conquest of land by multicellular plants was the next, and of equal importance. Indeed, without the plants no animals would ever have been able to survive on land.

But whereas the Cambrian explosion was very rapid, in the order of perhaps 3 to 5 million years for the origin of all major phyla (and many others now extinct), the colonization of the land by vegetation was a much slower and more protracted. The reason for this is not hard to understand. Cambrian animals were moving into a favorable new environment with no competitors. Plants had to brave desiccation, extremes of temperature, and harsh ultra-violet radiation.

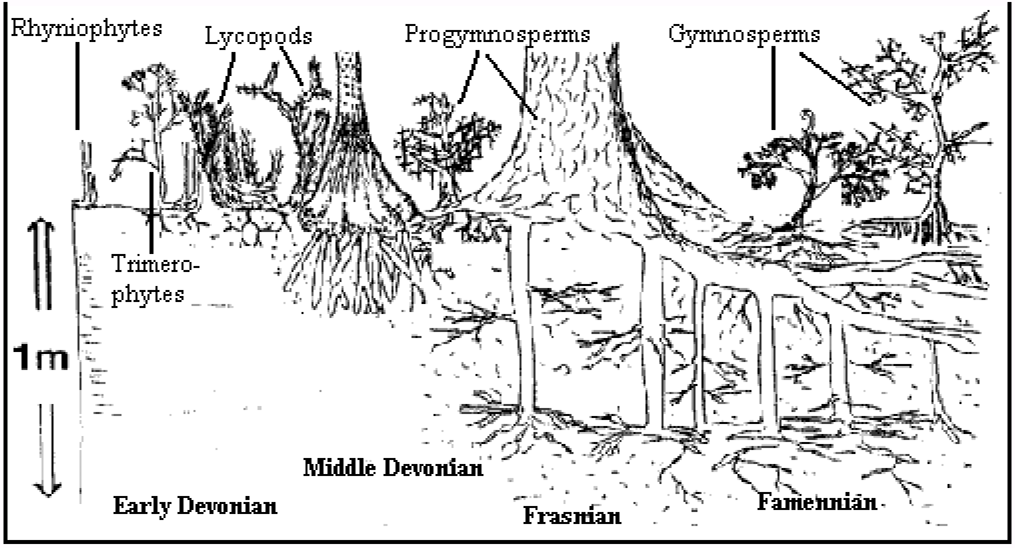
Enigmatic traces are known from the early and middle Ordovician, These are fossils of spores, cuticles, and tubes and don't reveal much about the structures or nature of these plants. All we can say is that these plants were probably of a hepatophyte grade of evolution - small, non-vascular, and lacking morphological differentiation into roots, stems, and leaves, like modern mosses and liverworts.

The first unambiguous record of land plants is from the Silurian period. They were mostly small, primitive forms, dependent on the proximity of water, and with the most rudimentary stem and leaf structure.

A common middle Silurian to early Devonian plant is *Cooksonia*, which had dichotomous branching and terminal sporangia (spore cases) at the tips of its green leafless stems. It is not known whether *Cooksonia* was a proper vascular (tracheid-bearing) plant. True vascular plants evolved and began to diversify during the Latest Silurian and Early Devonian.

The Devonian Period

The Devonian period. marked a major shift in plant evolution and terrestrial ecosystems. Early Devonian plants such as the rhyniophytes, zosterophyllophytes and lycopsids have features such as vascular tissue, stomata, a cuticle to protect against drying, rhizoids, and



sporangia at the tips of short lateral branches instead of terminal as in *Cooksonia*. These forms were small, non-rooted or shallowly rooted, lacked woody tissue and hence were unable to grow beyond the height of small bushes. These plants reproduced by means of spores, which requires a moist habitat. They were therefore confined to moist, lowland habitats, thus having little effect on their physical environment

The first shrub and tree-like plants, such as Progymnosperms and lycopsids, had evolved by the middle Devonian. By the late Devonian the first real trees, such as *Archaeopteris* ("ancient fern" - not to be confused with *Archaeopteryx*, "ancient wing", the first bird!), had appeared. Trees have special vascular systems to allow for water circulation and nutrient flow against the pull of gravity. At the very end of the Devonian seed-bearing (gymnosperm) plants appeared for the first time, breaking free of the dependence on moisture that limits spore-bearing (pteridophyte) plants. Along with these developments came the development of advanced root systems and the production of soils, increased weathering, and huge ecological feedback.

The black & white figure shows the increasing terrestrial plant root depth penetration with time during the Devonian, leading to increasing soil depth and weathering. "Rhyniophytes" are a basal radiation of land plants such as *Aglaophyton* or *Horneophyton*. Trimerophytes include such plants as *Psilophyton*. Large lycopsids arrived in the Middle Devoinian. They originally appeared as low-lying herbaceous forms, such as *Asteroxylon* or *Drepanophycus*. Tree-sized lycopsids (*e.g.*, *Lepidosigillaria* and *Cyclostigma*) appeared by the end of the Middle Devonian. Progymnosperms, such as *Tetraxylopteris*, arose in the Frasnian. By the Famennian, *Archaeopteris* forests are common. At the very end of the Devonian, *Archaeopteris* is found together with early gymnosperms, such as *Elkinsia* and *Moresnetia*, and zygopierid ferns such as *Rhacophyton*.

Image: from Prehistoric Animals, J. Augusta, illust. by Z. Burian, (Paul Hamilyn, London, 1960), pl.5, and Life Before Man by Zdenek V. Spinar, illustrated by Zdenek Burian

The Carboniferous Period

Despite the origin of the seed habit, the majority of Carboniferous plants reproduced by spores. The moist swampy environments of the time provided a nurturing environment. Lycophytes (scale trees and club mosses), which had evolved as small plants during the late Silurian? or early Devonian, and diversified greatly during the succeeding Devonian period, continued and thrived throughout the Carboniferous, but being dependent on water and moist conditions, most died out with the increasing aridity at the end of the Paleozoic, only a few small ones making it through. Calamites and ferns were other spore-bearing plants that appeared during the Devonian and flourished during the following Carboniferous period.

Image: *Psaronius*, a common Late Pennsylvanian tree fern, image from Earth History Resources (former site).

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Chlorobionta (Green Plants) - 2

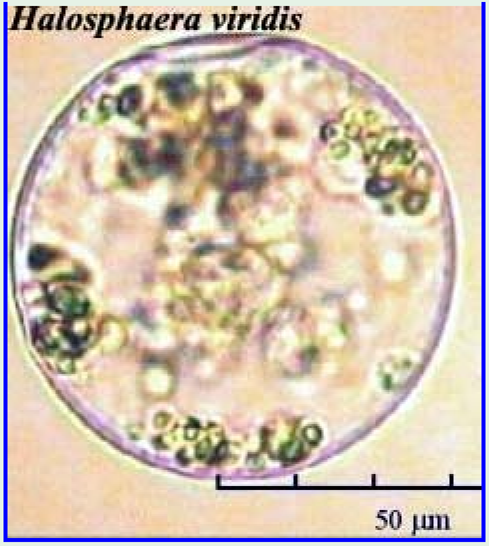
```
LIFE (=Archaea?)
|--Eubacteria
`--Eukarya
   |--+--Rhodophyta
   |  `--CHLOROBIONTA
   |     |--Chlorophyta
   |     `--Charophyta
   |        |--(various green algae)
   |        `--Embryophyta
   |           |--Bryophyta
   |           `--Tracheophyta (rhyniophytes)
   |              |--Lycophyta
   |              `--Euphyllophyta
   |                 |--Monilophyta
   |                 `--Spermatophytata
   |                    |--trimerophytes
   |                    `--Spermatopsida
   `--+--Fungi
      `--Metazoa
         |--Deuterostomia
         `--Protostomia
```

The Diversity of Plants

We will cover the higher taxa of lower plants in two blocks: Chlorobionta and Embryophyta. Theprasinophytes (basalmost chlorobionts), chlorophytes and charophytes are essentially algae, which normally impinge on our consciousness just long enough to apply a little *wasabi* and *shoyu*. *Arigato*, and next I'll have *ni unagi*, *kudasai*. Don't try that with an embryophyte. There's a differnce between *sushi* and *soba*. Embryophytes are mostly land plants, and it was the ability of plants to live on land that allowed all the other branches of life to live on land as well. In fact, only the plants can really be said to have adapted to land. With few exceptions, the rest of life simply adapted to plants.

Chlorobionta

The general characteristics of the green plants are touched on above. The purpose of this section is to introduce the prasinophytes. These are a paraphyletic group of green algae which radiate from the base of the Chlorobionta. Most are photosynthetic flagellates. In addition, the



prasinophytes are the only mixotropic plants, *i.e.*, they obtain food both by photosynthesis and phagotrophy. This is, presumably, how they obtained chloroplasts in the first place.

The *phycomate* prasinophytes (those with large, thick-walled floating stages, or "phycomata") have received special attention because of their extremely long fossil record. Phycomata are known as acritarchs well into Proterozoic time. One genus (*Tasmanites*) dates back to 600 Mya. Javaux *et al.* (2004) have turned up an entire menagerie of forms from the Mesoproterozoic, and even beyond (at least 1500 Mya), which are almost certainly eukaryotic and could well be prasinophytes, or somewhat stemward of the plants. They cannot be too distantly related, as the presence of thick organic walls, with extreme resistance to degradation, seems to be a trait of the plant-chromist lineage. One of these in particular, *Leiosphaeridia crassa*, from the c. 1460 Mya Roper Fm. of northern Australia, is being investigated as a possible green alga. Interestingly, in Recent or merely Paleozoic forms, these relatively large, thick-walled morphs are associated with moderately anoxic conditions and nutrient exhaustion during algal blooms.

Image: *Halosphaera viridis* from the **National Oceanographic Data Center**.

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Chlorophyta

Within the Chlorobionta are two large clades making up the "green algae." The green algae, as currently conceived, have no formal taxonomic name. We will define the group as *Quercus* + *Chlamydomonas*. The corresponding stem clades are Chlorophyta (*Chlamydomonas* > *Quercus*) and Charophyta (*Quercus* > *Chlamydomonas*). "Chlorophyta" is also the old name for all green algae, so this is perhaps unnecessarily confusing. Tough luck. The ambiguity is now so embedded in the literature that there's nothing anyone can do about it.

The Chlorophyta have largely been delineated by molecular techniques, so it is a bit difficult to describe their characters. We know of two possible synapomorphies of the Chlorophyta. First, chlorophyte sexual forms bear paired apical flagellae usually separated by 180°, but sometimes at the same end. Second, they retain the nuclear envelope during mitosis. Indeed, chlorophytes seem to be distinguished by a variety of bizarre variations on the usually pedestrian theme of mitosis; however those variations are not entirely consistent within the group.

Like the land plant lineage, they tend to form large aggregates, with some tissue differentiation (primarily holdfasts and reproductive structures). They are very often found in terrestrial and fresh water environments, with a distinct preference for very cold environments, such as under snow cover, or even within Antarctic ice. Various species are important in forming symbiotic relationships with fungi, *i.e.*, lichens. As with all green algae, chlorophytes tend to have a double cell wall -- an inner wall of *cellulose* and an outer gelatinous wall of protein, particularly *pectin*, known in higher plants as a marker for *parenchyma*. Starch stored in *pyrenoids*, located inside the chloroplasts.

Image: *Ulva lobata* from the **California Biota Website**.

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Chlorobionts

Charophyta (= Streptophyta)

The Charophyta are the other lineage of green algae, the group which includes the land plants. Karol *et al.* (2001). As mentioned above, our working definition is *Quercus* (oak) > *Chlamydomonas*. The Charophyta have recently been referred to as the *Streptophyta*, but the reasons given for this change in nomenclature are probably insufficient. Unfortunately, the name is also frequently, and wrongly, used in place of *Charophycea* or *Charales* to describe the stoneworts -- one of several distinct groups of charophytes.

The *synapomorphies* of the group are said to include the the dissolution of the nuclear membrane during mitosis and the presence of paired flagella (when flagella are present at all) directed perpendicularly to each other. In addition, the charophytes are strongly inclined toward growth as long filaments.

Image: *Klebsormidium* from **The Delwiche Lab** at the Univ. of Maryland.

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Charophytes

Embryophyta

The Embryophyta constitute the terrestrial or land plants, the first representatives of which appeared during the Silurian or possibly even the Middle or Late Ordovician period. The most primitive of these are nonvascular land plants, a group that classically includes liverworts (Hepatophyta / Hepaticopsida), hornworts (Anthocerotophyta / Antheroceratopsida) and mosses (Bryophyta). The majority of land plants however are included within the huge and diverse clade awkwardly named Tracheophyta, including the Vascular Pants, and a basal radiation of plants loosely called rhyniophytes.

We treat Embryophyta in a specialized sense, as *Quercus* + moss. This may be a mistake, as this definition probably excludes the liverworts (see image) and perhaps even the hornworts. Both of these groups have traditionally been thought of as embryophytes.

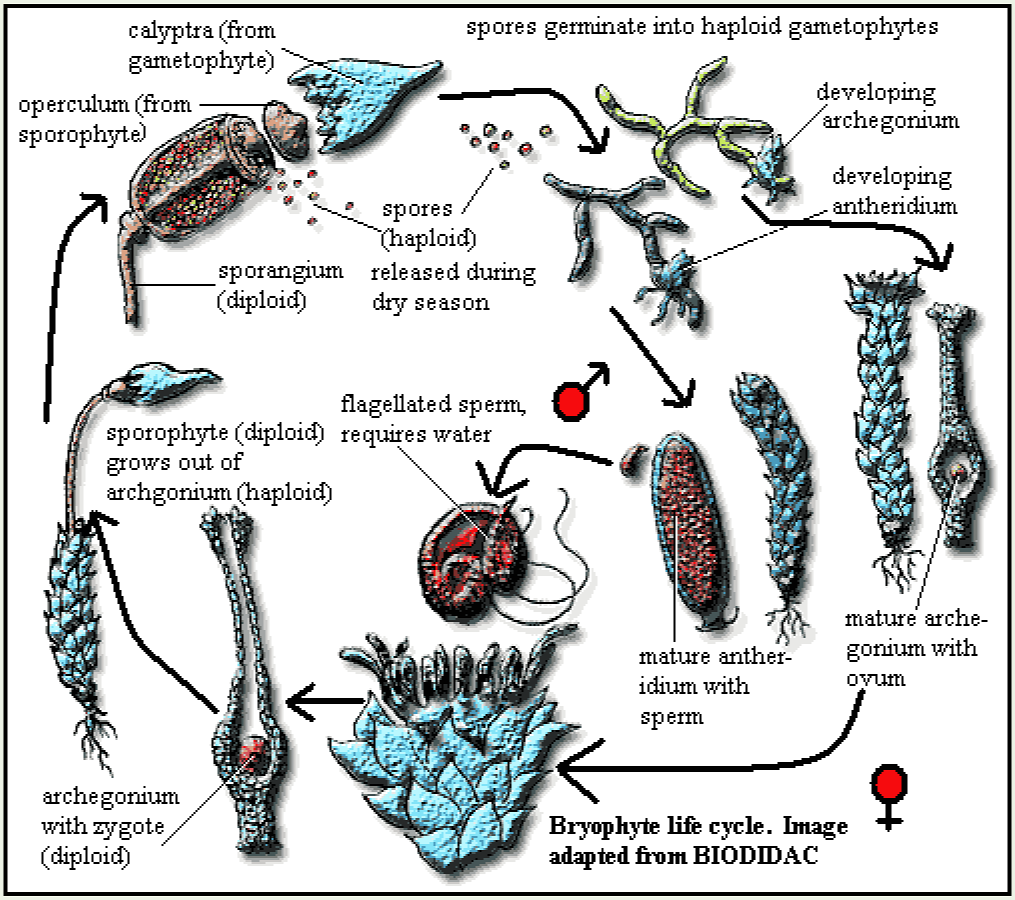
Embryophytes (including liverworts) have the following *synapomorphies*: 1) a life cycle with *alternation of generations* 2) apical cell growth (some kind of *meristem*-like growth organization), 3) *cuticle* (needed to control water loss on land), 4) antheridia (male gametophyte organs), and 5) archegonia (female *gametophyte* organs). The more derived embryophytes are *vascular* plants. Vascular plants have an elaborate system of conducting cells, consisting of *xylem* - in which water and minerals are transported) and *phloem* (in which carbohydrates are transported). This method of internal support enables them to stand and grow upright and pull up nutrients against the force of gravity. There are two developmental grades - those that reproduce by means of spores, and hence are dependent on water or extensive moisture (e.g. ferns), and those that reproduce by means of seeds (e.g. conifers and flowering plants). The most primitive forms reproduce by means of spores (haploid (1N) spores). They generally require a moist environment, because the flagellated sperm require water for fertilization.

text by MA Kazlev 2002, revised ATW041215, ATW090227.

The Embryophytes, then, are plants with an alternation of generations and some ability to live on land. The basal embryophytes were still not land plants, since they required, and still require, open water to propogate. As we define the Embryophyta, they split basally into mosses (Bryophyta) and land plants (Tracheophyta). The tracheophytes include a basal miscellany of extinct "rhyniophytes" and two important living groups: the Lycophytina (lycopsids and the extinct zosterophylls) and the Euphyllophyta (ferns and seed plants).

Embryophyta

Bryophyta



Bryophyte life cycle. Image adapted from BIODIDAC

If the mosses had not survived into the present, we would be forced to invent them as just the sort of intermediate we might expect between essentially aquatic algae and fully terrestrial plants.

Mosses do have differentiated stems. Although these are generally only a few millimeters tall, they are still designed to provide mechanical support against gravity without help from water -- the first such structure in any kingdom. Bryophytes also have leaves. These are typically one cell thick and lack veins, although they may have a central thickening for support. Mosses also have *rhizomes*. These may have some function in extracting soil nutrients, although their primary function seems to be mechanical attachment to the substrate. Thus they are not true roots, but do approach that condition.

The bottom line is that, structurally, mosses really differ from rhyniophytes in only one aspect: mosses lack specialized *vascular* tissues. That alone is sufficient to explain the lack of big leaves, long stems, and true roots. This whole complex of characters is thus probably primitive. The other distinctive character of mosses is that the plant we normally observe is the *haploid*, *gametophyte* stage. But this character is shared with liverworts (basal embryophytes) and so is also probably *plesiomorphic*.

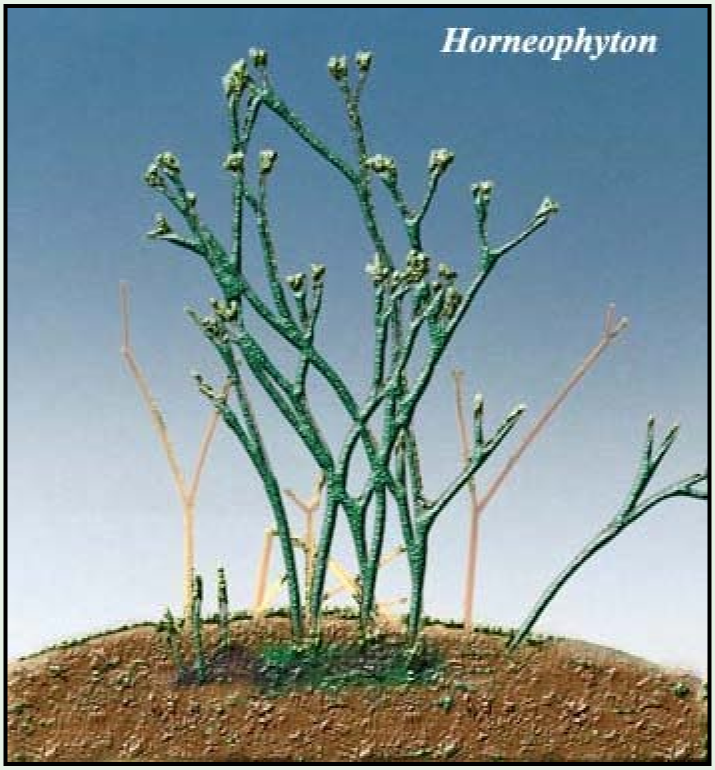
Curiously, in hornworts (also basal embryophytes) the sporophyte generation is dominant. In addition, it turns out that the leaves of moss probably evolved independently from the leaves of higher plants. So the relationships of the mosses and basal embryophytes are still uncertain. What really does seem to set mosses apart is their unique form of leaf. What really seems to unite mosses with higher plants is (a) the presence of *stomata* to control water loss and (b) *meristem* (apical growth) in the sporophyte generation. *See*, Friedman *et al.* (2004). Phylogenetically, we treat Bryophyta as Moss > *Quercus*.

Image: adapted from **BIODIDAC**.

Embryophyta

Tracheophyta

See **Tracheophyta**. That section covers the basal rhyniophytes, such as *Horneophyton*, which were the first real land plants. These probably evolved in the Ludlow and formed the stem group for all other land plants. Consequently, they are paraphyletic. The working phylogenetic definition is definition is *Quercus* > moss. Cantino *et al*. (2007).



This group is characterized by the ability to reproduce without open water. Anatomically, in all tracheophytes, the (diploid) *sporophyte* generation is dominant, and the sporophyte is branched. For this reason, these plants are often referred to as polysporangiophytes. In addition, the *archegonium* develops inside the body of the plant, rather than being superficial as in mosses and most basal embryophytes. Kenrick & Crane (1997).

Horneophyton and a few other basal forms lack *tracheids*. That is, they are avascular plants. However, almost all other tracheophytes have some development of specialized vascular tissues. The most basal tracheid type, present in most stem tracheophytes, appears to be the *S-type tracheid*.

Image: *Horneophyton* sculpture by Stephen Caine for the Rhynie Research Group, University of Aberdeen. Image substantially modified by ATW041229.

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Tracheophyta

Lycophyta

The Lycophyta include the lycopsids, zosterophylls, and related forms, including (probably) a number of plants often treated as basal rhyniophytes, such as *Baragwanathia*. Kenrick & Crane (1997). Since they are a complex group and are treated extensively elsewhere, we will defer discussion to a revision of the existing materials.

Euphyllophyta

The clade that unites oak trees and ferns is Euphyllophyta = *Quercus* + *Equisetum*. The two complementary stem clades are Monilophyta and Spermatophytata.   Euphyllophytes are characterized (Kenrick & Crane, 1997) by *monopodial* or *pseudomonopodial* branching, helical arrangement of branches, small, *pinnule*-like vegetative branches, the branch apex is recurved or coiled, paired *sporangia* which split open along one side through a single slit, and radially-alligned *xylem* in the larger axes. Only early Euphyllophytes have *P-type tracheids*. Kenrick & Crane identified this clade based entirely on morphological characters. However, Euphytophytina has also been recovered, with essentially the same structure, using *ssu rDNA*. Duff & Nickrent (1999).

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Monilophyta

The Monilophyta are the horsetails and ferns, including the Psilotidae (whisk ferns). They are closely related to the seed plants. Pryer *et al*. (2001). So, for example, they exhibit apical growth (*meristem*) in both *sporophyte* and *gametophyte* generations. They have well-developed roots *megaphyllous* leaves and the *vascular* system needed to make use of both. However, both may have been evolved independently of higher plants. Friedman *et al.* (2004). In addition, Monilophyta lack a complete *vascular cambium*, and growth of xylem is restricted to lobes of the *primary xylem* strand.

Since this is a new clade -- discovered, for all practical purposes, by Preyer's group, we have little to say about Monilophyta as a taxon, and defer discussion to a fuller consideration of its three component parts. The Psilotidae are the most basal, followed by the horsetails, then the remainder of the ferns.

We apply a crown group defiition to Monilophyta: *Equisetum* + ferns.

Image: *Psilotum nudum* from the **University of Wisconsin - Madison Plant Systematics Collection**.

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Euphyllophytes

Spermatophytata

The clade that unites oaks and lycopsids is Eutracheophyta. The two complementary stem clades are Lycophyta and Spermatophytata = *Quercus* > *Lepidodendron*. A second way to look at Spermatophytata is as the stem group leading to angiosperms. It includes Trimerophyta and the progymnosperms, in fact everything up to and including the seed plants (Spermatopsida). However, we will only be concerned with the more basal forms for now. A third way of considering Spermatophytata is as the *seed* plants. However, this applies only to living forms. The basal Trimerophyta and their immediate descendants (assuming Trimerophyta is *paraphyletic*) lacked seeds, true leaves, or even, perhaps, roots. It is quite likely that virtually *all* the important land plant adaptations were independently developed in the monilophyte and spermatophytate lineages.

What seems to have set Spermatophytata apart quite early is not, in fact, the development of seeds, but the evolution of a full *vascular cambium* which permitted *secondary growth*. Early plants with apical growth were able to use that trait to grow taller and (a) get more sunlight (b) shade their competition and (c) have a better shot at *spore* dispersal.

However, supporting a long stalk is much easier with a wider central column. Less derived groups either had no way to do this, or developed lateral lobes of the apical *meristem*. The latter worked, but required the tree to grow wide *before* it grew tall. The evolution of a complete vascular cambium permitted the tree to grow just wide enough to suit its height -- growing continuously wider as it grew tall.

The evolution of seeds follwed this innovation. Seeds are embryonic *sporophytes*, held in a sort of metabolic stasis and provided with enough food to get started once their growth has been re-stared by exposure to suitable growing conditions. Well adapted seeds combined sexual reproduction with spore-like wide dispersal and so made the alternation of generations obsolete. However, early seeds, which might lack these refinements, probably evolved on tall trees which gave any sort of *propagule* a head start in dispersal.

Image: *Psilophyton* from the **PhD project page** of Ben Sheppard at the University of Sheffield.

The Spermatophytata are the stem group for our next major division, the Spermatopsida.

Links

Introduction to the Plantae - The green kingdom

Integrative Biology 181/181L - Paleobotany - at UC Berkeley - excellent!!!!

Land Plants On-line - covers recent plants only, links to images etc

International Plant Taphonomy Meeting - The purpose of the International Plant Taphonomy Meetings is to stimulate scientific research and to promote contacts among scientists engaged in the study of plant taphonomy including living and fossil plants of all geological periods.

Botany Web Sites by Subject - excellent annotated list of links to Botany and related subjects - note, some of these links are no longer current

A BASIC BIOLOGICAL CLASSIFICATION OF PLANT-LIKE ORGANISMS

A History of Palaeozoic Forests - Hans Kerp - very informative - originally published in German. Deals with forests of the Devonian, Carboniferous, and Permian periods.

Hans' Paleobotany Pages - info on the earliest land plants and on the lycopod *Lepidodendron*

Carboniferous Forests - Ralph E. Taggart - good non-technical intro, covers main groups of Carboniferous plants, also brief mention of insects, amphibians, and reptiles

The Biota of Early Terrestrial Ecosystems: The Rhynie Chert - includes useful information on Early Devonian plants from this location

The First Land Plants - The Conquest of the Land - gives a good introduction to basic concepts regarding the transition of plants from water to land

Orto Botanico - somewhat technical but not too difficult coverage of plants and paleobotany. Includes glossary.

Integrative Biology 181/181L - Paleobotany - at UC Berkeley - includes material on Paleozoic plants. A bit technical but if you stick at it you will learn a lot.

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Taxon List A-Z

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

'*' indicates image on that page

-A-

Aglaophyton: X (Tracheophyta*) Early Devonian of Scotland. Remy *et al.* (1994).
Andreaea: (Bryophyta), *see* Bryophyta (Andreaeids)
Andreaeidae: (Bryophyta), *see* Bryophyta (Andreaeids)
Andreaeids: (Bryophyta): paraphyletic Andreaeidae + *Takakia*.
Andreaeobryum: (Bryophyta), *see* Bryophyta (Andreaeids)
Archaeopteris: X (Lignophyta). Late Devonian cosmopolitan. Osborne *et al.* (2004); Rothwell & Lev-Yadun (2005). *See* Tracheophyta.
Asteroxylon: X (Lycophyta: Drepanophycales*), *see* Tracheophyta.

-B-

Baragwanathia: (Lycophyta: Drepanophycales*): *see* Tracheophyta.*
BRYOPHYTA = moss > *Quercus*. Mosses.
Bryopsida:
Buxbaumia: *see* Bryophyta (Polytrichales).

-C-

Caia: X (Tracheophyta). Pridoli of England. Kenrick & Crane (1997).
Charophyta = *Quercus* > *Chlamydomonas*. Green algae in the land plant stem group
Chlorobionta: = *Quercus alba* > *Gelidium coulteri*. ~ Viridaeplantae.
Chlorophyta = *Chlamydomonas* > *Quercus*. Green algae in the land plant stem group.
Cooksonia: X (Tracheophyta). Wenlock to Early Devonian worldwide. Boyce (2008).

-D-

Dawsonia: *see* Bryophyta (Polytrichales).
Drepanophycales: X (Lycophyta)
Drepanophycus: X (Lycophyta: Drepanophycales). *See also*, Tracheophyta.

-E-

Embryophyta = *Quercus* + *moss*
Eophyllophyton: X (Eutracheophyta). Pragian of China. Kenrick & Crane (1997). *See* Tracheophyta.
Equisetum: (Monilophyta). *See* Tracheophyta.
Euphyllophyta = ferns + fruit. *See also* Tracheophyta.
Eutracheophyta: (Tracheophyta). Lycopsids + limes. From the Wenlock. *See also* Tracheophyta.

-F-

Funaria: *see* Bryophyta (Bryopsida)

-G-

Green Algae = *Quercus* + *Chlamydomonas*. An informal crown group.

-H-

Hedeia: X (Tracheophyta*).
Hicklingia: X (Lycophyta). *See* Tracheophyta. Middle Devonian of Scotland, possibly U.S. Kenrick & Crane (1997).
Horneophyton: X (Tracheophyta). Early Devonian of Scotland.
Huia: X (Lycophyta). *See* Tracheophyta. Early Devonian of China. Kenrick & Crane (1997).
Huperzia: (Lycopsida). *See* Tracheophyta.
Huvenia: X (Tracheophyta). Early Devonian of Germany. Kenrick & Crane (1997).

-J-

-K-

Kidstonophyton: X Pragian of Scotland. Invalid genus. This form is the male gametophyte of *Nothia*. Taylor *et al*. (2005).

-L-

Land Plants: *see* Embryophyta
Langiophyton: X Pragian of Scotland. Invalid genus. This form is the gametophyte of *Horneophyton*.

Lignophyta: fruits > ferns. See Tracheophyta.
LYCOPHYTA: *See also* Tracheophyta.
Lycophytina: lycopsids (*Huperzia*) + derived zosterophylls (*Sawdonia*). *See* Tracheophyta
Lycopsida: *Selaginella* > *Sawdonia*. See Tracheophyta.
Lyonophyton: X Pragian of Scotland. Invalid genus. This form is the gametophyte of *Aglaophyton*.

-M-

Marchantia: *see* Tracheophyta.
Monilophyta: *Equisetum* > *Quercus*. *See* Tracheophyta.

-N-

Neckera: (Bryophyta) *see* Bryophyta.
Neckeropsis: (Bryophyta) *see* Bryophyta.

-O-

Oedipodium: *see* Bryophyta (Polytrichales).

-P-

Pan-Tracheophyta: *see* Tracheophyta.
Pertica: X (Eutracheophyta). Emsian? of Canada and U.S. Kenrick & Crane (1997). *See* Tracheophyta.
Phaeoceros: *see* Tracheophyta.
Physcomitrella: (Bryophyta) *see* Bryophyta.
Pinnatiramosus: X (Tracheophyta*). Llandovery (disputed) of South China.
Pogonatum: *see* Bryophyta (Polytrichales).
Polytrichales: (Bryophyta) *Polytrichum* > Bryopsida.
Polysporangiomorpha = Tracheophyta (more or less).
Polytrichopsida: *see* Bryophyta (Polytrichales)
Polytrichum: (Bryophyta) *see* Bryophyta, Tracheophyta.
Prasinophyta = basal paraphyletic radiation of Chlorobionta.
protracheophytes: X ?paraphyletic group of Tracheophyta without apomorphic tracheids. Early Devonian of Scotland.
Psilophyton: X (Eutracheophyta). Emsian of Canada. Kenrick & Crane (1997). *See* Tracheophyta.
Psilotum: (Euphyllophyta). *See* Tracheophyta*.
pteridophytes: paraphyletic group of all Tracheophyta without seeds. From the Wenlock worldwide.

-R-

Remyophyton: X Pragian of Scotland. Invalid genus. This form is the gametophyte of *Rhynia*.
Renalia: X (Lycophyta). *See* Tracheophyta. Early Devonian of Canada, Germany & UK. Kenrick & Crane (1997).
***Rhynia*: X** (Tracheophyta). Early Devonian of Scotland. Kenrick & Crane (1997).
rhyniophytes: X paraphyletic group of probably basal Tracheophyta. Early Devonian of Scotland. Ludlow to Middle Devonian and worldwide, if *Cooksonia* is included.

-S-

Salopella: X (Tracheophyta).
Sawdonia: X (Zosterophyllopsida). *See* Tracheophyta. Pragian to Frasnian of Canada, Europe, Siberia. Kenrick & Crane (1997).
Selaginella: (Lycopsida). *See* Tracheophyta.
Spermatophytata: *Quercus* > *Equisetum*. *See also*, Tracheophyta.
Sphagnum: (Bryophyta) *see generally*, Bryophyta.
Stockmansella: X (Tracheophyta). Early Devonian of Belgium. Kenrick & Crane (1997).
Streptophyta: *see* Charophyta.

-T-

Taeniocrada: X (Tracheophyta*) Devonian of Europe and North America.
Takakia: (Bryophyta: Andreaeids) *see* Bryophyta (Andreaeids).
Tarrantia: X (?) Lochkovian of England and Brazil. Osborne *et al.* (2004); Edwards & Wellman (2001)*. *See* Tracheophyta
Tetraphidales: (Bryophyta) *see* Bryophyta (Polytrichales).
Tetraphis: *see*Bryophyta (Polytrichales).
Tortilicaulis: X (?) Lochkovian of England. Kenrick & Crane (1997). *See* Tracheophyta.
TRACHEOPHYTA = *Quercus* > moss. Land plants. From the Wenlock or earlier, cosmopolitan.
trimerophytes: paraphyletic group of Eutracheophyta forming the stem group of Euphyllophyta. Kenrick & Crane (1997). *See* Tracheophyta.

-V-

Viridaeplantae: *see* Chlorobionta

-Z-

Zea: *see* Tracheophyta.
Zosterophyllopsida: X. *Sawdonia* > *Selaginella*. Wenlock to Late Devonian, cosmopolitan. Benton & Harper (1997); Kotyk *et al.* (2002). *See also* Tracheophyta.
Zosterophyllum: X *see* Tracheophyta. Probable garbage taxon, with not all species within Lycophytina, much less Zosterophyllopsida.

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Plant Dendrograms

In a refreshing departure from recent additions to our phylogenetic sections, the basic outline of plant evolution is rather well-known and stable. Nevertheless, we will be cautious, and build slowly. Imagine the embarassment should we err in drawing the tree of life for trees. In addition, botany seems to be unusually rich in thorny problems of nomenclature, with numerous synonyms which need to be weeded out, root and branch. Thus wewill begin with a small kernel of higher level taxa and allow it to germinate slowly, as our ideas about plant taxonomy bear fruit in detailed coverage.

All tedious metaphores aside, we intend this section to be an experiment in setting up a rational scheme of taxonomy, without our usual fawning defference to definitions in the literature. To that end, we're going to vary the usual cladogram notation to explicitly state what *kind* of clade (or other taxon) is being noted. The scheme is as follows:

o : crown group
< : stem group
= : paraphyletic basal radiation
^ : apomorphy-based clade
* : similarity based classical taxon
? : basis not yet established

```
< Chlorobionta = Quercus > Gelidium
|--= Prasinophyta
`--o "Green algae" = Quercus + Chlamydomonas
   |--< Chlorophyta = Chlamydomonas > Quercus
   `--< Charophyta = Quercus > Chlamydomonas
      |--* (various algal groups)
      `--o Embryophyta = Quercus + moss
         |--< Bryophyta = moss > Quercus
         |  |--* Sphagnum
         |  `--= "Andreaeids"
         |     |--< Polytrichales
         |     `--< Bryopsida
         `--< Tracheophyta (= Pan-Tracheophyta Cantino & Donoghue 2007 = Polysporangiomorpha of
Kenrick & Crane, 1997) = Quercus > moss
                         |--= various rhyniophytes (Rhynia, Cooksonia, etc.)
                 `--+--o Lycophytina = lycopsids (Huperzia) + zosterophylls (Sawdonia)
                `--o Euphyllophyta = ferns & horsetails (Equisetum) + Quercus
                   |--< Monilophyta = Equisetum > Quercus
                   `--< Spermatophytata = Quercus > Equisetum
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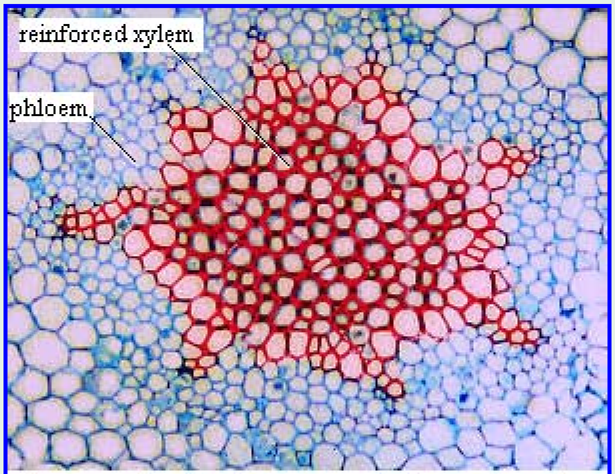
Glossary A-C

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

A really extraordinary botanical glossary can be found at **A glossary of botanical terms**. Bluntly, it is far better than our own glossary, but lacks images and hyperlinks. I can't seem to get the French version to work, but it may be even better.

-A-



Cross section of Psilotum stem showing actinostele. The heavy red staining of the central xylem is due to impregnation with lignin. The phloem surrounds the xylem.

Actinostele: a type of *protostele* that looks like a star in cross section. The walls of the *stele* are heavily reinforced with *lignin* and are relatively thick. *Xylem* occupies the center but the *phloem* occupies the indentations in the xylem. This generates the star-like pattern. Image from the **Botany 210** site of Prof. David Webb at the University of Hawaii at Manoa.

Active transport: transport across a cell membrane which requires energy generated by the hydrolysis of some energy carrier (usually ATP). The selective active transport of ions (usually sodium) out of the cell is often used as a secondary energy storage mechanism. *See* ion gradient system.

Adaxial: "on the upper surface; situated or directed toward an axis." Virtual Paleobotany Lab Glossary (Univ. Calif. Berkeley)

Alternation of generations: a life cycle in which there are two stages: (a) a *diploid*, *sporophyte* stage which produces *haploid spores* by *meiosis*, and (b) a haploid, *gametophyte* stage which produces (by mitosis) haploid gametes of two types, usually called *male* and *female* but technically *microgametes* and *megagametes*. The female gamete is fertilized to become a diploid zygote, which matures to become a diploid sporophyte, completing the cycle. Either the gametophyte or the sporophyte stage may be very small and remain attached to the other stage. According to Taylor *et al*. (2005):

> Two principal theories have been proposed to explain the evolution of the dimorphic alternation of generations that characterizes vascular plants and bryophytes. The ***antithetic***

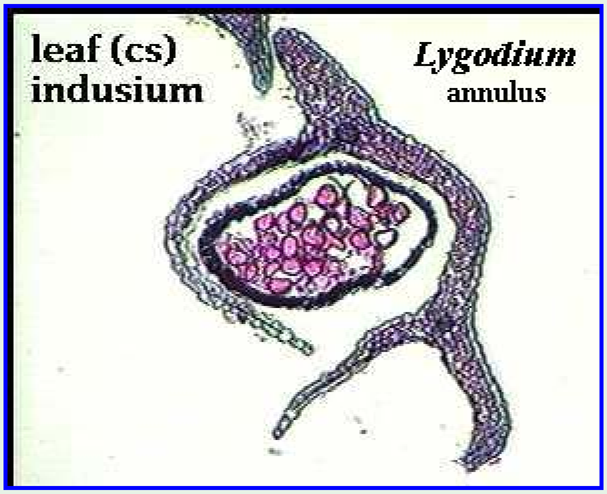
> ***theory*** suggests that the sporophyte generation evolved from a haploid green algal thallus in which repeated mitotic cell divisions of a zygote resulting in an embryo retained on the thallus gave rise to the diploid phase (sporophyte). Evidence supporting this theory can be found in the life cycle of modern bryophytes in which the sporophyte is physiologically dependent on the gametophyte. Although generally not addressed, the antithetic theory necessitates that both types of *gametangia* were probably borne on the same *thallus*. The ***homologous theory*** assumes a green algal ancestor but with two nearly identical (isomorphic) phases, one producing gametes, the other producing spores. Various stages in the evolution of the sporophyte have been postulated, leading to the sporophyte becoming the dominant phase both morphologically and physiologically. The increasing size and complexity of the sporophyte phase results in more sporangia and spores being produced, and thus with potentially greater genetic variation represented among these spores, there is a corresponding increase in the probability of successful colonization of additional habitats. The gametophytic phase, although a less conspicuous part of the life cycle and not essential in local areas of clonal growth of the sporophyte, is equally essential for the long-term success of the species. Although *hermaphroditic* (bisexual) gametophytes may turn out ultimately to be the primitive type, all of the gametophytes thus far described from the *Rhynie chert* appear to be unisexual. [citations omitted].

Amphithecium: The outer, "ectodermal" cell layer of the sporophyte in basal plants.

Anisotomous: branching pattern. Branching system in which the daughter axes are of unequal diameter. Kenrick & Crane (1997). Compare *isotomous*.

Anispory: Intersporangial heterospory. That is, segregation of male and female spores into different sporangia. Taylor *et al*. (2005). Or, to be more accurate, the segregation into different sporangia of spores which will develop into gametophytes producing male and female gametes. Taylor et al.'s point is that anispory is often thought to be the basal condition, yet it doesn't seem to apply to *Rhynie Chert* plants. All of the spores in the Rhynie sporophytes look exactly alike, yet the Rhynie gametophytes are all unisexual.

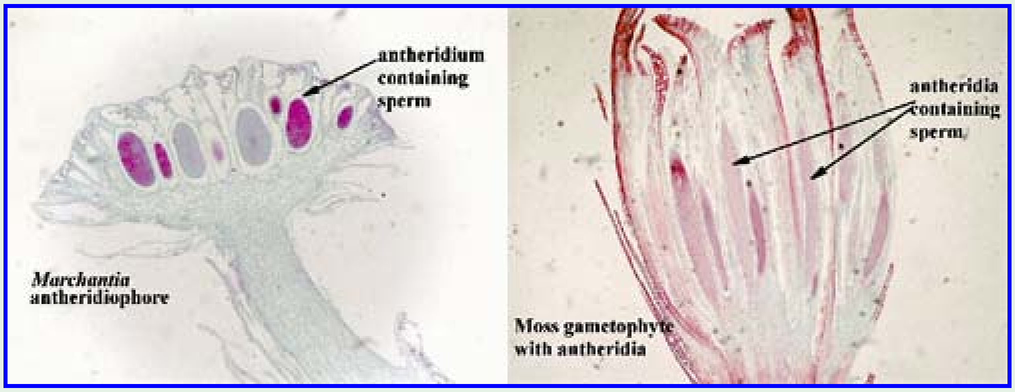
Annual: a plant with a lifespan of one year.



Annulus: specialized structure of some fern sporangia that is involved in the opening of the sporangium. In some mosses, on drying out the cells of the annulus contract and the sporangium ruptures, releasing the *spores*. In others, the annulus bears the *peristome teeth*, which perform a similar function. Image from the **Biology 3560** site of the University of Lethbridge (Alberta).

Anther: in a flower, the terminal part of the *stamen* which holds the *pollen*; an antheridium.

Antheridiophore: essentially the same as *antheridium*. If you care desperately about the distinction, see *gametangiophore* for a fuller explanation. Image from the **Biology 102 Lab** site of Brookdale Community College (New Jersey).



Antheridium: reproductive structure that produces male gametophytes (pollen).

Apical: from or towards the apex, or tip, of a plant *axis* (stem, branch, root, etc.).

Apical meristem: *see meristem*.

Apomorphy: a character state which is unique to a single, terminal taxon. Example: among primates, complex grammar is an apomorphy of human beings. It is quite diagnostic of humans, but useless in determining phylogenetic relationships because it is not a shared, derived characteristic, or synapomorphy, of any larger group.

Arborescent: of tree-like growth-habit, a tree. A *woody* plant.

Archegoniophore: essentially the same as *archegonium*. If you care desperately about the distinction, see *gametangiophore* for a fuller explanation.

Archegonium: reproductive structure that produces female gametes (egg). Image from the **Department of Botany** site of the University of Wisconsin at Madison.

Arthrodontous: of moss sporophytes, having *peristome teeth* which are formed by walls growing between the rows of cells making up the mouth of the spore capsule. See Tree of Life: Bryopsida.

Autotroph: an organism which obtains energy from inorganic sources, sunlight or the oxidation of inorganic chemicals.

Autotrophic nutrition: synthesis of organic food molecules from inorganic compounds such as carbon dioxide.

Axial: with reference to a growth habit, growing upward from the substrate (*e.g.*, trees); as opposed to *thalloid*, recumbent, spreading along the substrate (*e.g.*, mosses and liverworts).

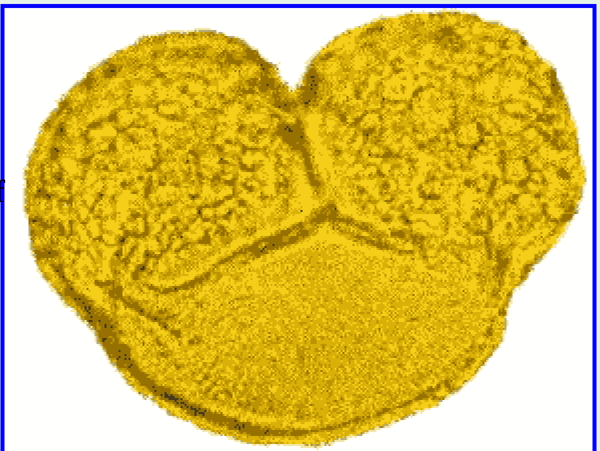
Axis: a stem, branch, root or other elongate structure conceived of as the main longitudinal structure of the plant or portion of a plant being considered.

-B-

Biennial: a plant with a lifespan of two years. Often only flowers and goes to *seed* (yes, that's the source of this phrase) during the second year.

Bifacial Cambium: *cambium* which produces tissue both towards the center (medially, periclinally, internally) and towards the surface (axially, anticlinally, externally) of a stem. Bifacial cambium builds xylem and phloem on its internal face and more cambium on the external face. Compare *unifacial cambium*.

Bisaccate: a *pollen* grain with two *sacci*. The two "sacs" or bladders are used to promote wind dispersal. Pollen of this type is known from as early as the Devonian. Image from the **Earth History Research Center**.


Bisaccate pollen of pine

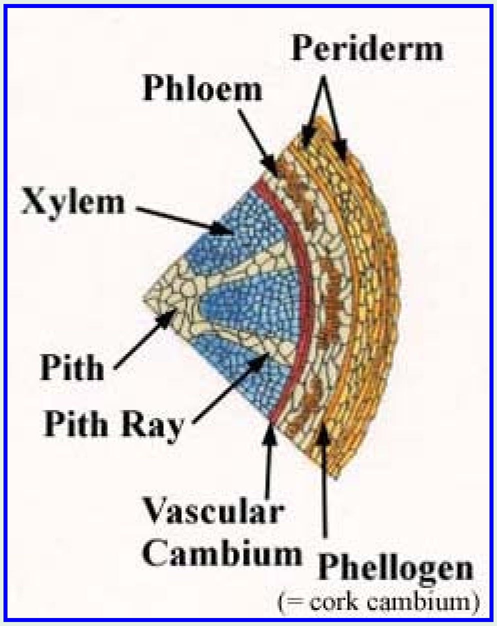
Budding: reproduction by binary fission, a characteristic form of propagation in yeasts. "The onset of the cellular events is accompanied by the nuclear events of mitosis. ... The initial events of budding can be seen as the development of a ring of chitin around the point where the bud is about to appear. This reinforces and stabilizes the cell wall. Enzymatic activity and turgor pressure the act to weaken and extrude the cell wall. New cell wall material is incorporated during this phase. Cell contents are forced into the progeny cell, and as the final phase of mitosis ends a cell plate, the point at which a new cell wall will grow inwards from, forms." Reproduction in the fungi (former http:// www-micro. msb. le. ac. uk/ 224/ mycology/ 2. html).

Bulb: an underground stem bearing modified (scalelike) leaves and fibrous basal roots; generally food storage organs.

Bulbil: a bulb produced above the ground, often on the flowering stem or on a leaf axil.

-C-

Calyptra: in mosses, a derivative of the distal *archegonium* forms a hard, protective layer around the developing sporophyte called the *epigonium*. Later the epigonium breaks up, but the sporophyte retains a conical "dunce cap" over its distal end, and sometimes a ring around the base. The cap is the calyptra. The piece retained around the base is the *vaginula*.



Cambium: a layer of actively dividing cells (lateral *meristem*), found within stems and roots, that gives rise to *secondary growth* in perennial plants, causing an increase in girth. There are two main types of cambium: **vascular cambium**, which gives rise to *secondary xylem* and *phloem* tissues, and **cork cambium** (or *phellogen*), which gives rise to secondary cortex and cork tissues, as in bark. Image from the **Population Biology** site of San Diego State University. The vascular cambium surrounds the roots, trunk, branches, and shoots, extending throughout a tree. Each year, the vascular cambium produces a new layer of phloem toward the outside of the tree and a new layer of xylem, or *wood*, toward the inside.

Carpel: the female reproductive organ of a *flower*, consisting of *stigma*, *style* and *ovary*.

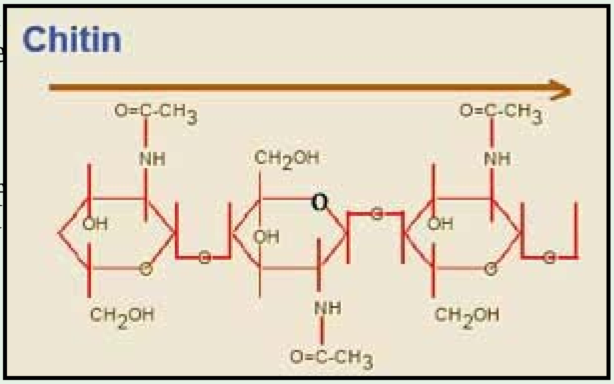
Cauline: of, related to, borne on, or growing from a plant stem.

Cauloneme: a lateral process from the *protoneme* (initial, threadlike process) which develops into the *gametophore* in mosses.

Cellulose: polysaccharide that consists of a long unbranched chain of glucose units; cellulose is the main constituent of the cell walls of most land plants.

Centrarch: used to describe a form of *xylem* development in which maturation occurs from the center of the stem to the periphery. Alternatively, a pattern of xylem maturation in which the *protoxylem* is central and is surrounded by *metaxylem*. Compare *endarch*, *exarch*, *mesarch*.

Chitin: a polymer of repeating sugar molecules (a slightly modified glucose, poly-N-acetyl-D-glucosamine). See image. Chitin is the material which makes up the exoskeleton of insects and, in more or less modified form, in almost all arthropods. In arthropods, chitin occurs in a cross-linked form, a-chitin. Significantly, it is also found in the radular "teeth" of mollusks, the setae (bristles) and jaws of annelid worms, and the cell walls of Fungi. So, this is exceedingly ancient stuff, possibly predating the split between bacteria and metazoans. [What may be of sociological interest is that the 1,5 aldose linkage was missing from the middle glucose in this diagram and no one spotted it for over a year ....]



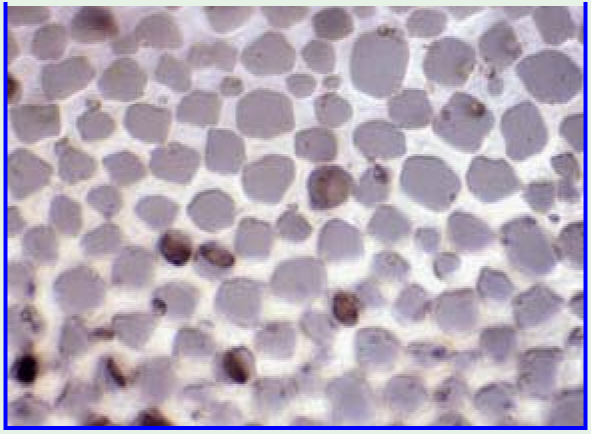
Chloroplast: the organelle in plant cells which performs photosynthesis. Chloroplasts are almost certainly descended from formerly free-living cyanobacteria.

Circinate: coiled, as in a fern *crozier*.

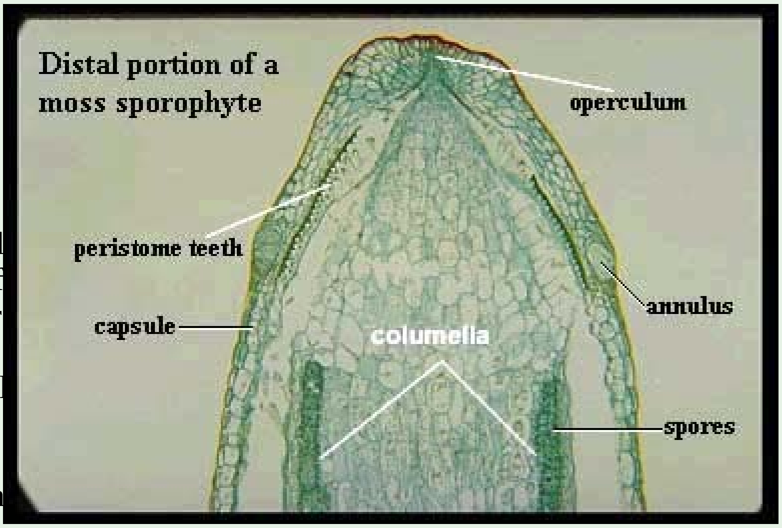
Clade: a group of organisms consisting of an organism and all of its descendants.

Climber: a soft- or non-woody-stemmed vine that clasps the stems or branches of trees and shrubs to raise its foliage and flowers above the ground; a type of growth form.

Collenchyma: Collenchyma cells, like parenchyma cells, are living at maturity. Collenchyma cells are irregularly shaped, with walls thicker



than those of parenchymal cells due to secondary layers of cellulose. These cell walls are not lignified (woody). Although they are fairly soft and pliable, they are arranged in strands and provide an elastic mechanical support for growing regions of the plant. *Compare parenchyma*, *sclerenchyma*. Image from Dr. David Lemke's **Botany 1410 Lab site** (Texas State Univ. -- San Marcos).



Columella: this is another one of those anatomical terms of almost unbelievable generality. It refers to any small rod-like structure (and some that are not rod-like in the slightest), such as the ear ossicle of reptiles, the basal column of univalves in gastropods, the sterile support of the fruiting body in fungi, and, for our purposes, either (a) a structure closely analogous to the fungal columella in the sporophyte of basal plants; or (b) the central portion of the root cap in higher plants. Kenrick & Crane (1997) define the columella essentially as in (a): a "[c]olumnar mass of sterile tissue that develops within the spore mass of the *sporangium* of horn worts, mosses, and some early fossil polysporangiophytes [= Tracheophyta]."

Complex tissue: tissue that consists of more than one cell type, e.g. *phloem*.

Compound: in leaf (*megaphyll*) classification, a leaf with multiple separate blades.

Cone: see *strobilus*.

Cork a plant tissue composed of cells whose walls are impregnated with *suberin* and are non-living at maturity; cork is produced by the *cork cambium*.

Cork cambium: a narrow cylindrical sheath of *meristematic* cells that produces cork cells to replace the epidermis during secondary growth (growth in width). A type of *cambium*, also called *phellogen*.

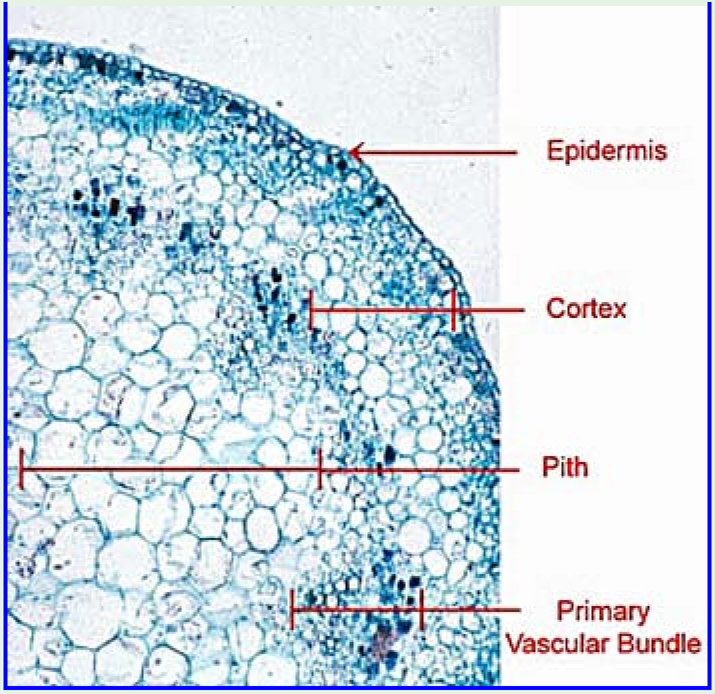
Cormose: bulb-like.

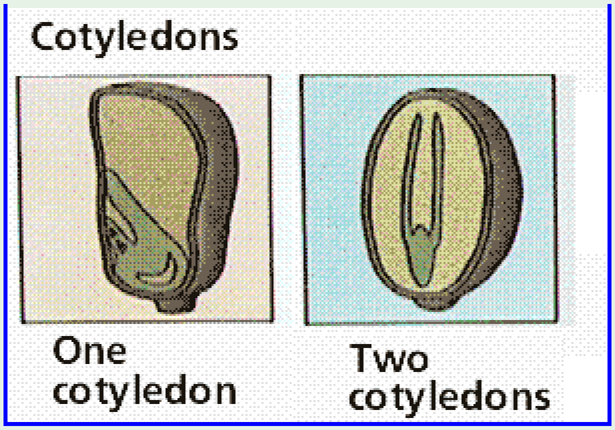
Cormus: currently used to refer to a bulb, but appears to have had one or more specialized meanings in Nineteenth Century botany which we have not been able to nail down. We mention it only in the vague hope that someone will supply us (augwhite@sbcglobal.net) with a better explanation of this term.

Cortex: a primary tissue composed mainly of *parenchyma* cells, which extends between the epidermis and the vascular tissue. Image from Nola Kinaston's **Virtual Crops Grape** site (Univ. Calif. Davis).

Costa: the midline vein, nerve or midrib of a bryophyte leaf (or *phyllid*).

Costate: having a mid-line vein or rib





Cotyledon: the embryo leaf or leaves of seed plants that absorbs nutrients packaged in the seed, until the seedling is able to produce its first true leaves and begin photosynthesis. "The number of cotyledons present in an embryo is an important character in the classification of flowering plants (angiosperms). Monocotyledons (such as grasses, palms, and lilies) have a single cotyledon, whereas dicotyledons (the majority of plant species) have two. In seeds that also contain endosperm (nutritive tissue), the cotyledons are thin, but where they are the primary food-storing tissue, as in peas and beans, they may be quite large. After germination the cotyledons either remain below ground (hypogeal) or, more commonly, spread out above soil level (epigeal) and become the first green leaves. In gymnosperms there may be up to a dozen cotyledons within each seed. Tiscali. Image from the **Online Biology Book** by Dr. Mike Farabee of Estrella Mountain Community College.

Crista: (pl. *cristae*) **(1)** of mitochondria, folds in the internal membrane of the mitochondrion which gives the organelle its characteristic appearance. This is the site of the electron transport chain in oxidative metabolism. The cristae, therefore, serve as the physical link between the tricarboxylic acid cycle and oxidative phosphorylation (ATP synthesis). *See also* Mitochondrion - Wikipedia. **(2)** more generally, a crest (its literal meaning in Latin) or ridge.

Crown Group: if A and B are two extant (living) organisms, their crown group is the clade defined as "the last common ancestor of A and B, and all of its descendants." Such a definition is often written as "A + B." The term "crown group" or "crown clade" is, strictly speaking, limited to groups defined with reference to extant organisms. If, for example, species A were extinct, then the clade A+B would be a "node-based" clade, but not a crown group. See, e.g. Cantino *et al*. (2007). Frankly, we aren't that careful most of the time. Like Bateman & DiMichele (2003), we think that this restriction only tends to overemphasize the importance of living species.

Crozier: the spirally coiled "fiddlehead" of an immature fern leaf. Image from the **New York Botanical Gardens** site.

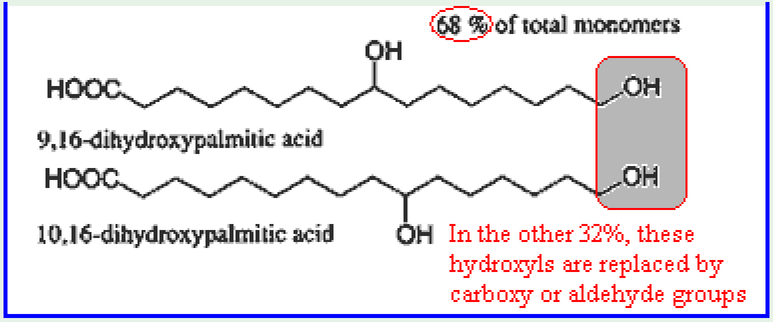

Crozier of Microsorium viellardi (Polypodiaceae)

Cuneate: wedge-shaped.

Cupule: structures that surround one or more *ovules* or *seeds*, *e.g.*, the "cap" of an acorn. The cupule lobes may be free or united.

Cuticle: an impermeable layer of *cutin* on the outer walls of epidermal cells.

Cutin: the waxy substance of which a cuticle is composed. The basic



structure of cutin is shown in the image.

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Glossary D-K

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

-D-

Deciduous: falling off; in plants: shedding leaves annually.

Decussate: branching pattern. Pattern in which successive pairs of branches (or leaves, etc.) are perpendicular to each other. Image from the Dr. Carol Brewer's (U. Montana) **ECOS Guide to the Ecology of the Northern Rockies**.

Dehiscence: any process used to expel spores, microgametes, or seeds into the environment. To be more precise, dehisence refers to the steps which the plant performs to expose the seeds, etc. to the environment. *Dispersal* is the mechanism by which they are actually distributed in the environment. So, for example, moss spores may dehisce by the opening of the operculum and retraction of the peristomal teeth. They are then dispersed by wind. However some plants, like *Sphagnum* moss, may explosively dehisce and so get involved in dispersal as well.

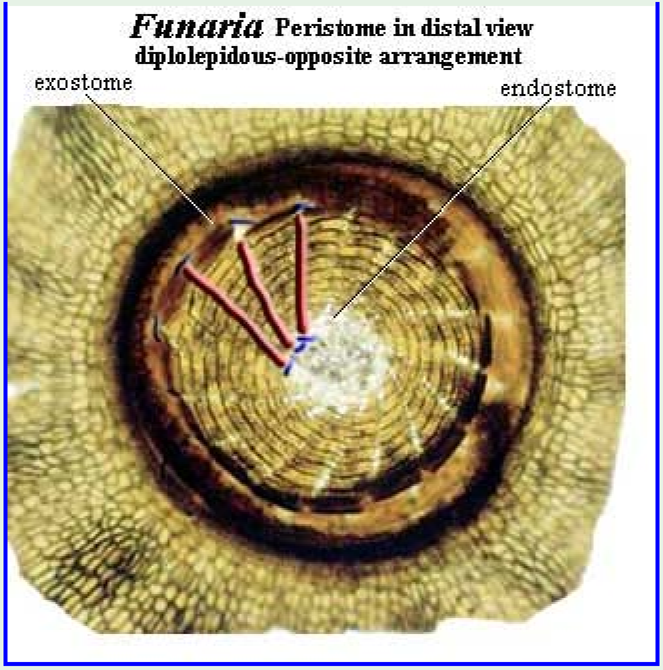
Dichotomous branching: a type of branching in which the tip divides into two more-or-less equal *apices*; by repetition of this type of branching in various planes distinctive shoot systems may be produced.

Dioecious: used to describe plant species in which male and female sex organs are borne on separate individuals.

Diplobiontic: relating to a life cycle in which the diploid and haploid generations are separate and morphologically distinct.

Diploid: a nucleus is diploid if it contains two copies of each non-redundant gene. In Fungi, it is necessary to distinguish between diploid nuclei and diploid cells. A hypha may contain several haploid nuclei (either identical or from different individuals). Technically, the cell is diploid or polyploid. However, there may be no diploid nuclei.

Diplolepidous: of moss sporophytes, having an inner (endostome) and outer (exostome) row of plates forming the *peristome teeth*. See Tree of Life: Bryopsida.


Funaria Peristome in distal view diplolepidous-opposite arrangement

Diplolepidous-opposite: of moss sporophytes, having an inner (endostome) and outer (exostome) row of plates forming the *peristome teeth* as radial elements between them. See Tree of Life: Bryopsida.

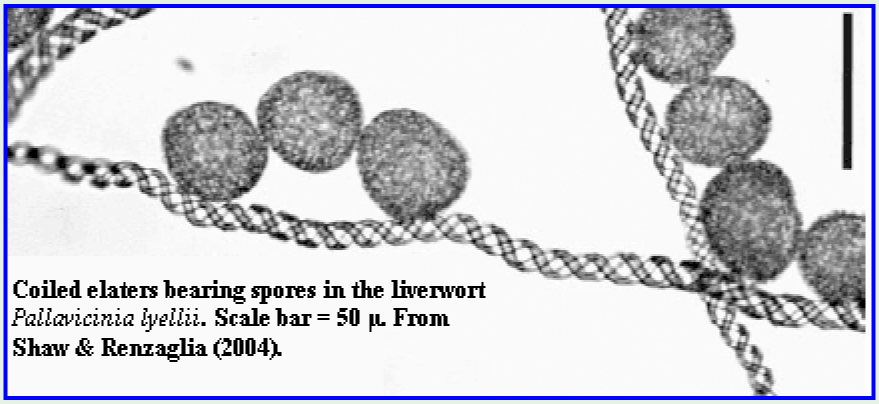
Dispersal: to disperse: to dispel or scatter; in plants dispersal refers to mechanism of dispersing reproductive propagules like seeds or pollen.

Double fertilization: in flowering plants: the more or less simultaneous union of one sperm and one egg to form a *zygote* (N=2) and another sperm with two polar nuclei to form *triploid* (N=3) endosperm in the ovule; in the Gnetales: the fusion of two sperm with two eggs to produce two zygotes, only one of which will mature into an embryo.

Double integument: the two outermost layers of an ovule in angiosperms, one of which will differentiate into the seed coat; see integument.

-E-

Elater: Coiled structures, formed from one or more non-living cells, which are associated with spore dispersal in (for example) liverworts, hornworts, and the basal fern *Equisetum*. Elaters are *hygroscopic*. When exposed to moisture, elaters uncoil, separating spore tetrads and raising the spores for dispersal. Elaters in hornworts have spiral wall thickenings which may be homologous to thickenings in early tracheids, but lack lignin. Ligrone *et al.* (2000).


Coiled elaters bearing spores in the liverwort *Pallavicinia lyellii*. Scale bar = 50 µ. From Shaw & Renzaglia (2004).

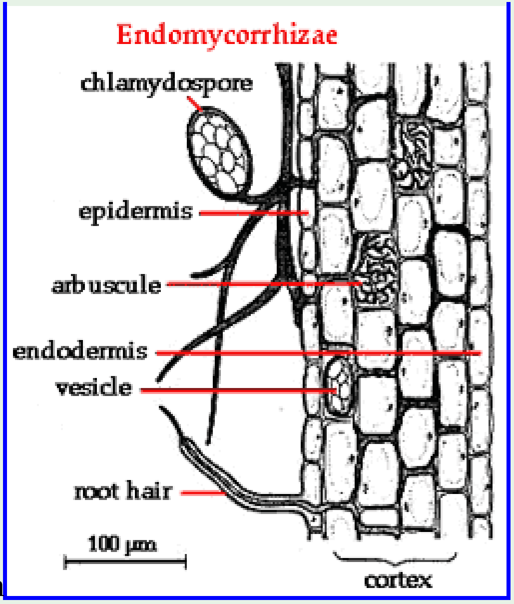
Embryo: "a stage in the life cycle during which the sporophyte is associated with and depends on the gametophyte." Ligrone *et al*. (2000).

Embryophyte: the group of all organisms that retain the zygote on the parent to form an embryo, includes Bryophyta and vascular plants.

Enation: a non-vascularized, epidermal outgrowth found in some early land plants.

Endarch: "a type of xylem maturation in which protoxylem is internal to metaxylem and development prodeeds centrifugally (from the inside out)." **Virtual Paleobotany Laboratory Glossary**. Compare *centrarch*, *exarch*, *mesarch*.

Endomycorrhizae: a general type of symbiotic fungus, also called vesicular-arbuscular mycorrhizae (VAM). Endomycorrhizal fungi do not form a sheath around the roots. Instead, the fungus penetrates the cortical cells, although it does not penetrate the cell membranes. Endomycorrhizal fungi are zygomycotes. Endomycorrhizal associations form with about 70% of extant plants in nature, including all the grasses (but not sedges, which usually lack mycorrhizae), most herbaceous plants, and some trees. Probable endomycorrhizal fungi are associated with planys of the Rhynie Chert. See Endomycorrhizae (this entry is largely quoted



from the cited page), in **The Kingdom Fungi** by Tom Volk. Image from the **Tree Structure** site of Professor Eric L. Singsaas, Univ. of Wisconsin, Stephens Point.

Endosperm: the *triploid* (N=3) product of double fertilization in angiosperms; during seed maturation the endosperm will develop into a storage tissue that will provide nutrients to the seedling as it emerges (in *monocots*) or that will be digested and stored by the cotyledons before germination (in dicots)

Endospory: a condition in which the gametophyte develops within the spore wall, rather than externally.

Endostome: of moss sporophytes, the inner row of walls forming the *peristome teeth*. See Tree of Life: Bryopsida.

Endothecium: the inner cell mass of the sporpphyte in basal plants. It usually produces both the central *columella* and the spores, which accumulate around the surface of the columella.

Entire margin: in leaves, the condition in which the margin forms a smooth line or arc without noticeable serrations; note that lobed leaves can also have entire margins; compare to lobed margin and toothed margin.

Epidermis: the exterior tissue, usually one cell thick, of leaves and young stems and roots.

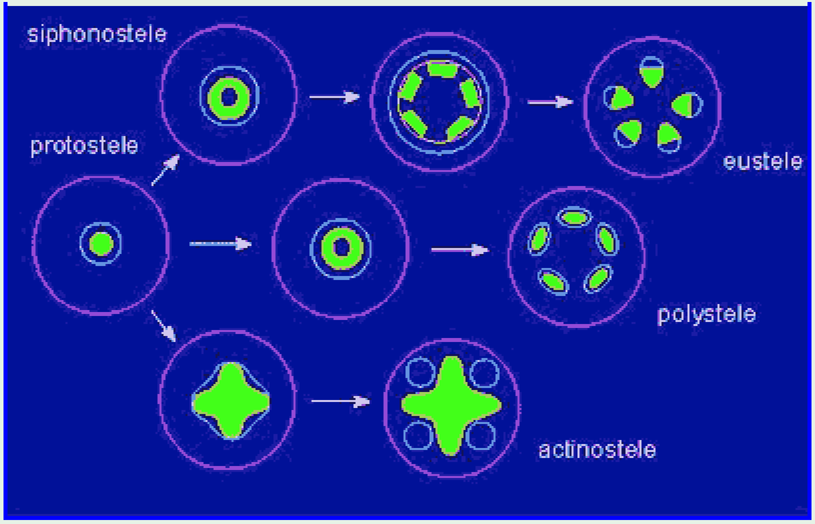
Epigonium: in mosses, a derivative of the *archegonium* which forms a hard, protective layer around the developing sporophyte. Later it breaks up, but the sporophyte retains a conical "dunce cap" or *calyptra* over its distal end. Strictly speaking, the term calyptra refers *only* to the "dunce cap," and the piece of the epigonium retained around the base (if any) is the *vaginula*.

Epiphyte: a plant that grows on another plant, or which uses a rock or host plant merely as a place of residence and obtains its moisture and nutrients directly from the air; an air plant. A type of growth form. No parasitism is involved. The epiphyte is rooted on the surface of the host. Vines rooted in the soil and climbing up on anotherplant are not epiphytes.

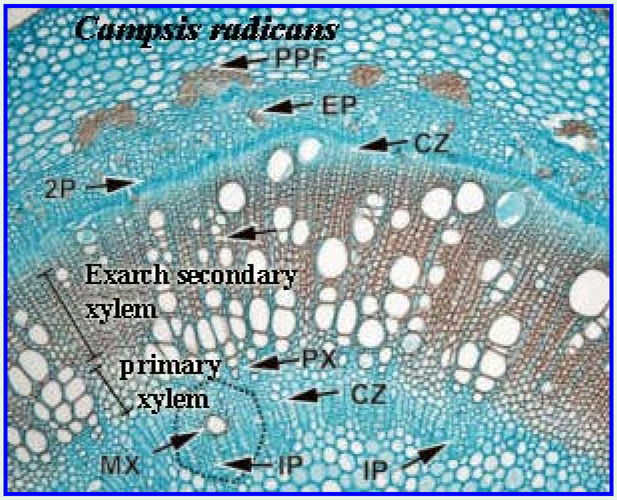
Eusporangium: *sporangia* that arise from a group of superficial cells; this is the primitive character state in vascular plants; compare to *leptosporangium*. "The eusporangium is usually large with a relatively thick wall comprising two or more cell layers, one of which may ultimately degenerate. Ontogenetically, the presence of a eusporangium is first recognized when a group of one or more rows of superficial cells begins to divide periclinally. Typical eusporangia occur in lycopsids and many other early fossil tracheophytes." Kenrick & Crane (1997).

Eustele: "eustele - the most common *stelar* arrangement in stems of living plants. Here, the vascular tissue is arranged in vascular bundles, usually in one or two rings around the central pith. In addition to being found in stems, the eustele appears in the roots of monocot flowering plants." Wikipedia: stele (biology). Image from **Botany Online**. In the image, the green regions are *xylem*, the other regions bounded in pale blue are *phloem*.

Evergreen: opposite of deciduous, *i.e.* evergreen plants do not shed all their leaves annually, but shed



and grow new leaves continually; most conifers are evergreen, but the evergreen habit is not restricted to conifers.



Exarch: *protoxylem* which is peripheral to *metaxylem*. Kenrick & Crane (1997). More generally, a directional/anatomical term describing a structure or tissue as being adjacent to, but more external, peripheral, radial, or further from a reference axis than some other structure or tissue. The word sometimes carries a slight suggestion that the inner tissue had something to do with inducing development of the exarch tissue. Opposite of *endarch*. Image adapted from **The Virtual Plant**. Compare *centrarch*, *endarch*, *mesarch*.

Exine: "the outermost architecture of pollen walls, protects male gametes from the environment by virtue of its chemical and physical stability. ... *Arabidopsis* ... pollen grains have one of the most typical surface structures, namely a reticulate sculpture with uniform mesh size .... . This structure consists of inner intine, mainly made of cellulose and pectin, and outer exine, composed of sporopollenin, presumed to be a polymer of fatty acid derivatives and phenylpropanoids (Fig. 1B) [citations omitted]. Exine is composed of inner nexine and outer sexine. Sexine has a three-dimensional structure composed of many columns called baculae and a roof-like tectum that gives a reticulate appearance to the pollen surface. Nexine is divided into outer nexine I and inner nexine II based on differences in chemical components. Nexine I is composed of sporopollenin, like sexine, whereas the components of nexine II are unknown. In addition, a pollen coat, composed of adhesive compounds containing proteins and lipids, accumulates in cavities of the exine." Suzuki *et al*. (2008). The cited figure can be seen at this direct link.

Exosporic: "Of spore germination where the first mitotic division occurs after rupture of the spore wall and outside the spore; gametophyte development outside the spore wall, i.e. the development of a free-living, multicellular gametophyte." exosporic.

Exostome: of moss sporophytes, the outer wall of plates forming the *peristome teeth*. See Tree of Life: Bryopsida.

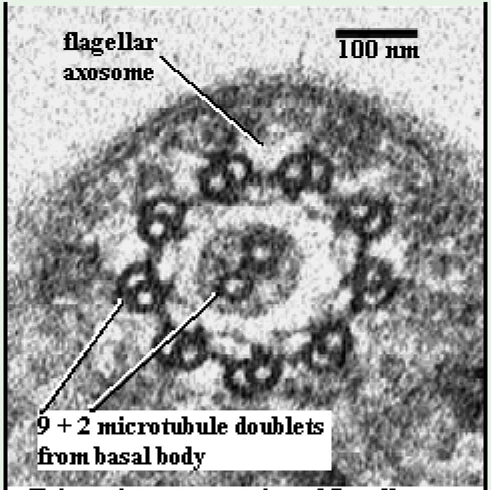
-F-

Fiber cell: a long-walled plant cell which is often dead at maturity; fibers impart elasticity, flexibility and tensile strength to plant structure

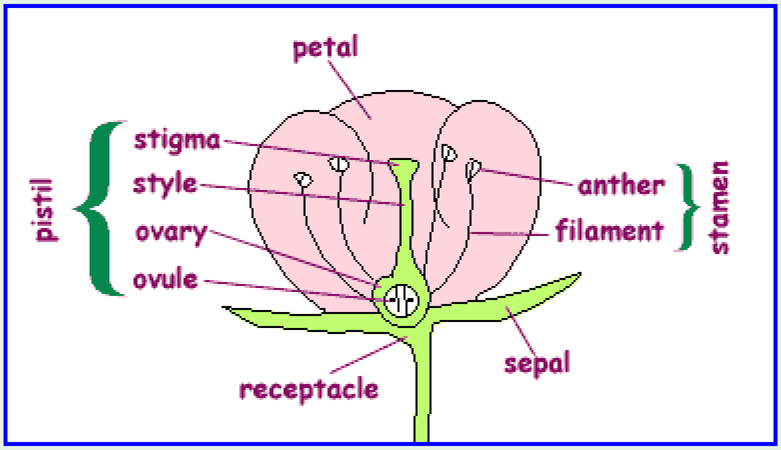
Fission: cytoplasmic division of a cell to form two cells, a form of asexual reproduction.

Flagellum: (pl. *flagella*) A eukaryotic flagellum is a bundle of nine fused pairs of microtubules called "doublets" surrounding two central single microtubules (the so-called 9+1 structure of paired microtubules; also called the "axoneme"). At the base of a eukaryotic flagellum is a microtubule organizing center about 500 nm long, called the basal body or kinetosome.

The flagellum is encased within the cell's plasma membrane, so that the interior of the flagellum is accessible to the cell's cytoplasm. This is necessary because the flagellum's flexing is driven by the protein dynein bridging the microtubules all along its length and forcing them to slide relative to each other, and ATP must be transported to them for them to function. This extension of the cytoplasm is called the *axosome*. **Important note:** The eukaryotic flagellum is completely different from the prokaryote flagellum in structure and in evolutionary origin. The only thing that the bacterial, archaean, and eukaryotic flagella have in common is that they stick outside of the cell and wiggle to produce propulsion. From Flagellum - Wikipedia. Image: O'Kelly *et al*. (1999).



Trimastix: cross section of flagellum near base. From O'Kelly et al. (1999).



Flower: condensed reproductive shoot of flowering plants, generally consisting of four whorls from the outside in: sepal, petal, stamen, and carpel; the diversity of flower form comes from variation of the general four-whorled structure. Image from the **Great Plant Escape** site of the University of Illinois.

Foot: another grossly over-used anatomical term. For botanical purposes, we use : "The foot is a specialized mass of tissue that develops early in the ontogeny of embryophytes, forms an intimate connection with the gametophytic tissues, and performs a nutritive function for the young sporophyte ... . Two distinctive types of foot form are recognized: a bulbous mass of tissue is the general condition in embryophytes, whereas an elongate tapering foot is characteristic of some mosses." Kenrick & Crane (1997).

Forb: a small, upright soft-stemmed or non-woody plant with broadleaves; the growth form of many common wildflowers.

Form genus: a genus name which does not correspond to a clade, but is used to describe a group of similar fossils. In paleobotany, form genera are used frequently. They typically refer to the fossilized remains of some part of a plant, when the actual genus of the plant is unknown. Thus, *Stigmaria* refers to fossil "root" (actually basal branch) systems from tree-like lycopsids of no particular genus. Other form genera are maintained for one generation (*i.e*. sporophyte or gemetophyte) of a plant or group of plants.

Frond: leaf of a fern

Fusiform: tapering towards each end; football-shaped

-G-

G-Type Tracheid: *See tracheid types.*

Gametangiophore: "An upright structure that bears the female gametes (see archegoniophore) or male gametes (see antheridiophore) in certain liverworts [and in some very basal tracheophytes]. Gametangiophores are extensions of the *thallus*... ." **Dictionary of Botany**. Image from **de.wikipedia**. The various *gamet__* terms are not always used rigorously.

However, as best we can tell, the *gametophyte* is the entire *haploid* organism, *i.e.* thallus plus gametangiophore plus any other attachments. The *gametangiophore* refers to the entire gamete-producing structure, including the stalk growing out of the thallus. The *gametangium* is the organ at the end of the gametangiophore which produces individual *gametes*. The *gametes* are equivalent to the eggs or sperm of animals. The term *gametophore* is generally used only when discussing higher plants (Tracheophyta). In tracheophytes, the gametophyte is not an independent organism. It is a simplified appendage of the *sporophyte* generation. Thus, the careful distinctions we have just made between gametophyte, gametangiophore, and gametangium are essentially meaningless in the context of higher plants. Hence the use of the vague term *gametophore*. In lower plants (mosses, liverworts and relatives), the case is frequently reversed. That is, the sporophyte is usually a simplified appendage which develops from a fertilized gamete but remains attached to the gametophyte. Finally, note that each of the *gamet__* terms has some equivalent *archegon__* term for the female and an *antherid__* term for the male. For example, since the gametangiophore labelled in the image bears female gametes, it might be referred to as an *archegoniophore*.

Gametangium: the sexual organ of the *gametophyte* generation -- either an *antheridium* ("male") or *archegonium* ("female"). See *alternation of generations*.

Gametophore: the structure in tracheophytes which produces the gamete. In tracheophytes, it is usually pointless to distinguish between the gametangiophore (the structure which bears the sex organs) and the gametangium (the sex organ which produces gametes) because the whole gametophyte generation is not a separate organism from the sporophyte. The gametophyte in tracheophytes has no separate structures for vegetative growth. Consequently, the whole gametophyte is regarded as an organ of the sporophyte, the gametophore.

Gametophyte: the haploid phase (n = 1) of the life cycle, during which gametes (reproductive cells) are produced.

Gemma: (pl. *gemmae*) a bud (or simply a group of cells) from which plants vegetatively reproduce.

Growth form: the overall morphology of a plant species, including its stature, leaf type, and habit. The general description of the type of growth exhibited by a plant, such as herbaceous, shrubby (bush-like) and arborescent (tree-like). The most basic grow forms are trees, shrubs, forbs, and graminoids; but there are many more specialized growth forms such as epiphytes, lianas, and stem succulents.

-H-

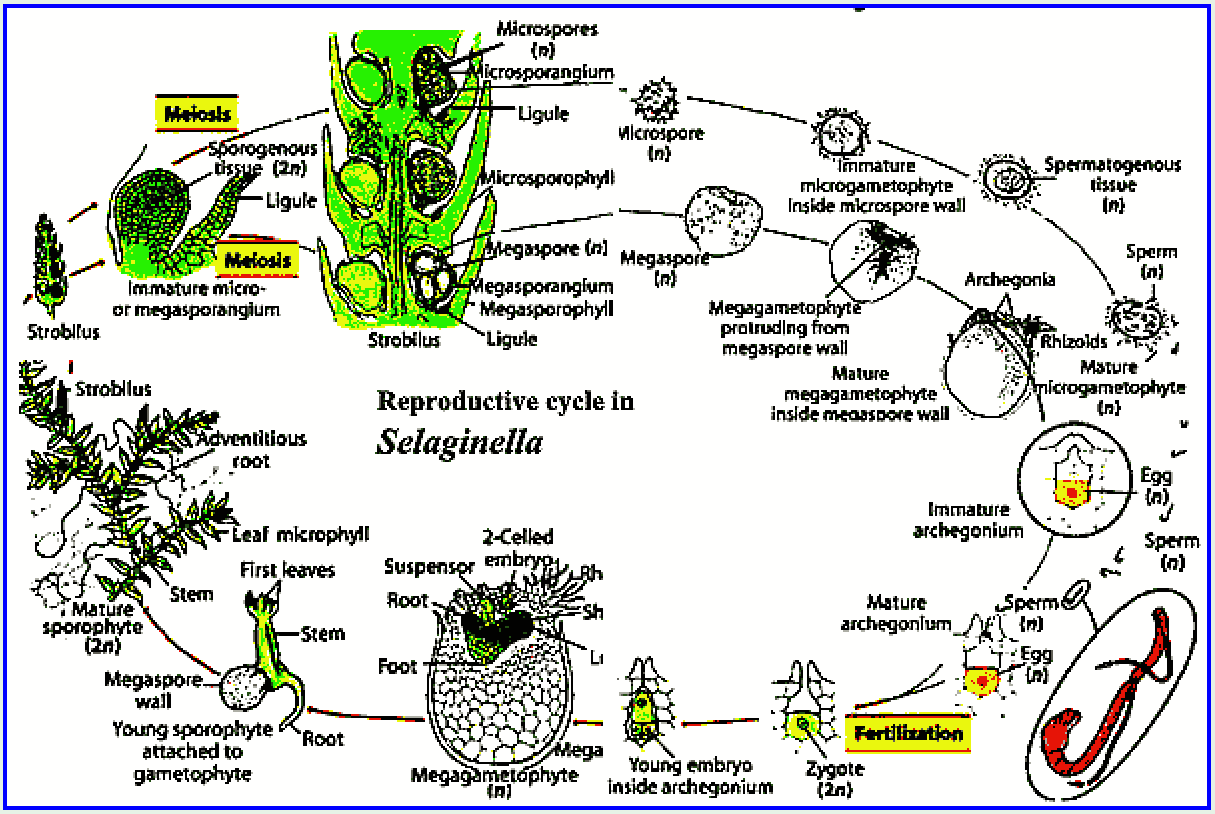
Haploid: a nucleus is haploid if it contains only one copy of each non-redundant gene. The great majority of animals, and higher plants, are diploid. That is, the form we usually observe has two copies of each gene, one from each parent. In lower plants there are numerous exceptions to the rule. Furthermore, the gametophyte generation (see alternation of generations) is always haploid.

Herb: any non-woody vascular plant; a category of plants including both forbs and graminoids (grasses). Hence the term "herbaceous" layer. **Herbaceous**: having this sort of growth form.

Hermaphroditic: displaying sex organs of both sexes in a single organism.

Heterogametes: male and female gametes that are morphologically distinguishable.

Heterosporous: having two types of spores: megaspores and microspores.



Heterospory: a condition in which an organism produces two different types and sizes of spores, viz. microspores and megaspores. As a reproductive strategy, heterospory involves the following steps: (1) The mature diploid plant (sporophyte*)* produces "male" and "female" spores. Typically, the plant produces numerous small "male" spores (*microspores*) and fewer, but larger "female" spores (*megaspores*). (2) The megaspores are usually retained on the sporophyte, where a haploid female gametophyte develops inside the spore. (3) The microspores may or may not be retained on the sporophyte. They develop into sperm-producing, haploid gametophytes. (4) The sperm are released into the environment, and dispersed between plants. (5) The sperm fertilize female gametophytes grown from megaspores, producing a diploid *zygote* (fertilized cell). (6) The zygote develops into an embryo and finally a new diploid sporophyte. Heterospory evolved a number of times among different ancient plants. Lycopsids, ferns, sphenopsids and progymnosperms all developed heterospory. Many of these plants also evolved into large trees. The obvious advantage for heterosporous trees is that their great height would enhance the dispersal of windborne microspores. Competition for light in the shady *Archaeopteris* forests, may have also have encouraged heterospory, since the macrospores, like seeds, included food reserves to assist early plant growth. Heterospory is generally regarded as the precursor to the evolution of seeds. Microspore dispersal and macrospore viability in pteridosperms thus become pollen dispersal and ovule viability in seed-bearing plants. The change in sexual reproduction from moisture-bound gametophytes to seedsbearing sporophytes enable vascular plants to colonize drier habitats and upland environments, and also provided the embryo with a protective case against hungry invertebrate herbivores.

Heterotrichous: (filament) a growth pattern of algae with prostrate filaments for attachment and erect, spreading filaments for photosynthesis.

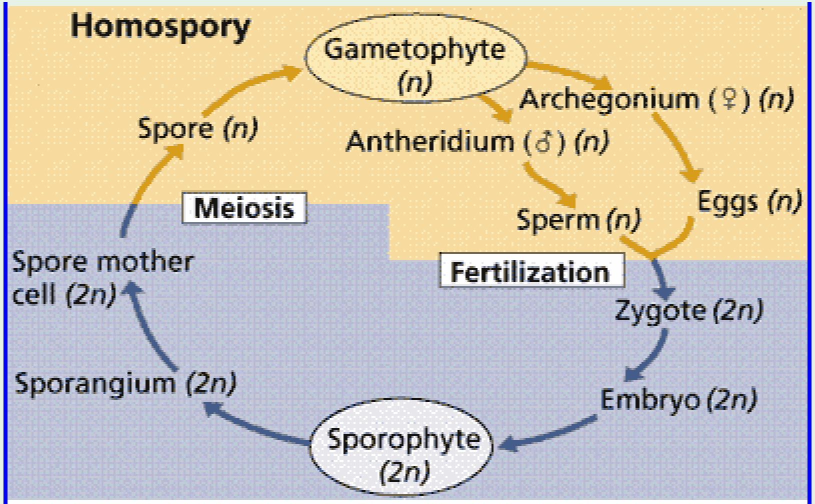
Histological: relating to tissue. Usually used to distinguish tissue-level organization or structure, as opposed to organization or structures at the molecular, cellular, organ, or organismal level.

Holdfast: algal organ for attachment.

Homoplasy: parallel evolution. The evolution of similar structures independently in two different lineages.

Homosporous: having one type of spore. *Compare heterospory*.

Homospory: a condition in which an organism produces only one type and size of spores,



Typical life cycle of a homosporous plant.

(microspores).

Hydroid: The water storage or water vascular cells of Bryophyta. Analogous to *xylem* in tracheophytes.

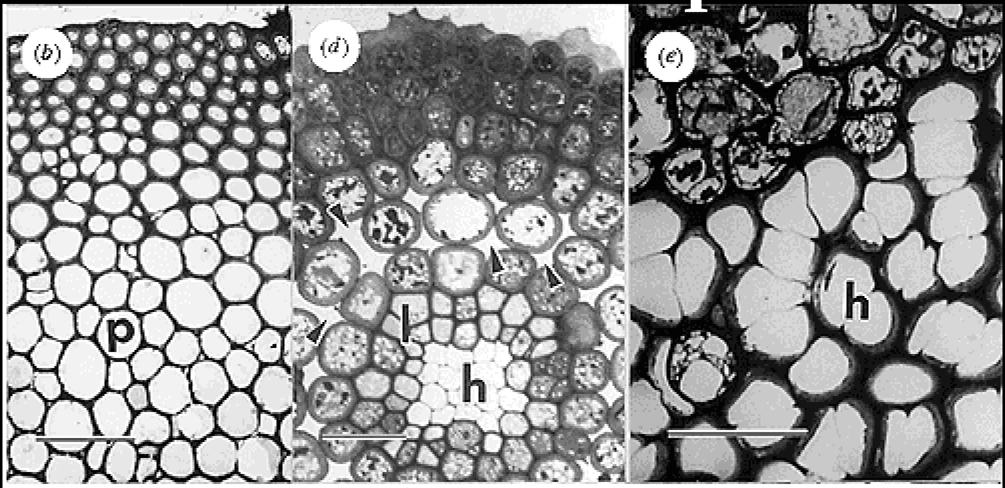
Hygroscopic: hygroscopic substances are those which extract water from the medium (usually referring to air).

-I-

Integument: the outermost layer(s) of an *ovule* which will develop into the seed coat; most seed plant ovules have one integument, angiosperm ovules have two integuments (see double integument).

Intercalary meristem: *see* meristem.

Isotomous: branching pattern. Dichotomous branching with both branches essentially equal. *Compare anisotomous*.



Moss vascular tissues from Ligrone *et al.* (2000) showing range of specializations. (b) undifferentiated parenchyma in *Neckera* (d) hydroids and leptoids in *Pogonatum*, and (e) complex association of hydroids in *Polytrichum*.

-K-

Karyogamy: fusion of two (haploid) nuclei.

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A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

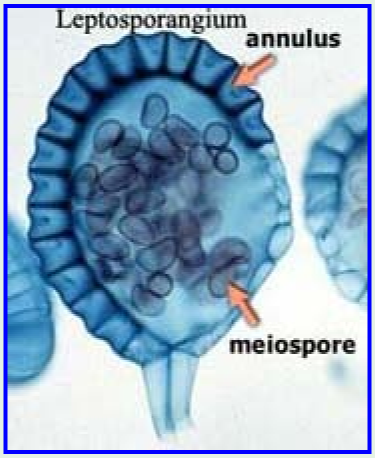
-L-

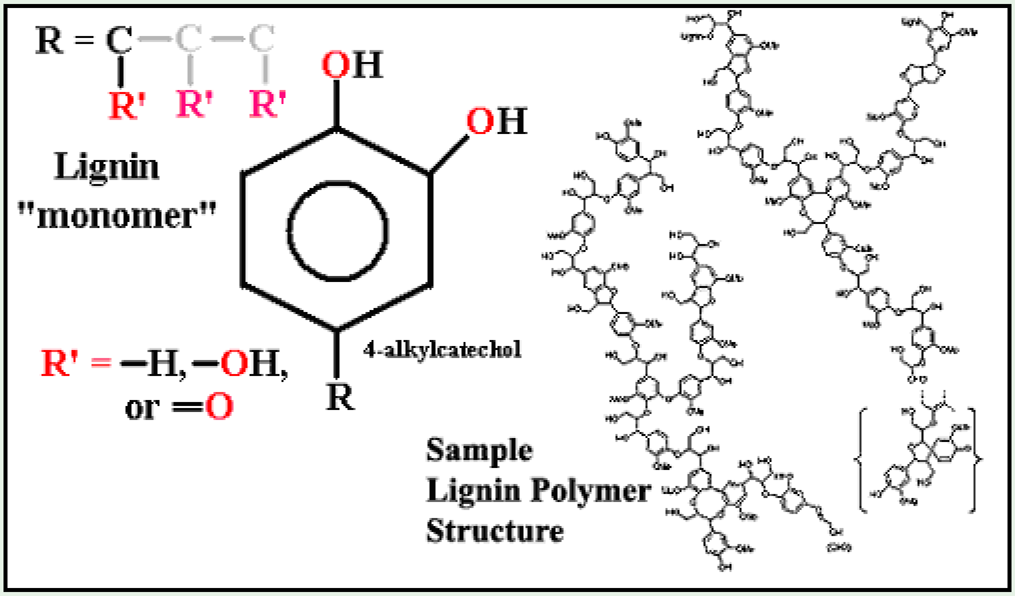
Lateral meristem: same as vascular cambium. *See* cambium.

Leaf: a flattened, photosynthetic structure of a plant arranged on a stem.

Leptoid: Cells involved in solute storage and transport in Bryophyta. Analogous, possibly even homologous, to the *phloem* of tracheophytes. Ligrone *et al*. (2000). *See* image at *hydroid*.

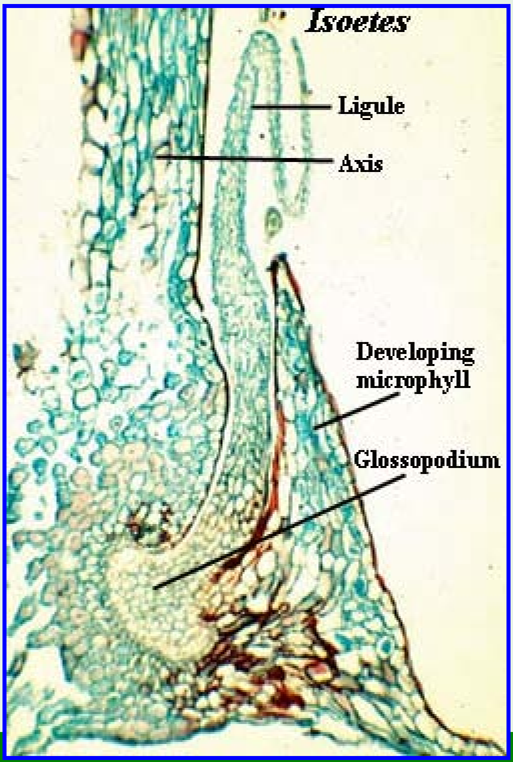
Leptosporangium: sporangium developed from a single superficial cell. **Leptosporangiate**: having leptosporangia. This is a derived character state in the fern clade; compare to *eusporangium*. Image from the **Botany 125** site of Prof. Curtis Clark, California State Polytechnic Univ. at Pomona.





Lignin: wood. Lignin is formed by the removal of hydroxyl groups from sugars, creating phenolic compounds and short-chain alcohol ligands. Lignin polymers are heavily cross-linked. There is great variation in lignin, even within the same plant. Undoubtedly, it has evolved to have a somewhat random structure to foil enzymatic attack. Lignin is, in fact, extremely difficult to dissociate -- so much so that even as late as 1980 almost nothing was known of the detailed chemistry of lignin, the second most common biopolymer on the planet (next to cellulose). Fortunately, considerable progress has been made since then. The basic monomer of lignin can be thought of as 4-alkylcatechol. The alkyl ligand is a 1 to 3 carbon chain which may be substituted with hydroxy or keto ligands at any or all positions. Both phenol groups and the alkyl substitutions may cross-link to other monomers or their side chains, yielding a fairly light, but strongly cross-linked and randomly ordered mass, *i.e.*, wood. What is more, the chemical structure virtually guarantees that any intermediate degradation product will be a highly toxic phenolic compound. Lignin was a rather early product of plant evolution. The necessary implication is that, contrary to most current thought on the subject, land plants were subject to biological attack (although not necessarily attack by herbivorous animals) by at least the Middle Devonian, and probably even earlier.

Ligule: small protuberance from the base of a *leaf*. "The ligule is a small, leaflike structure situated on the *adaxial* side of vegetative leaves and sporophylls ... . Once thought characteristic only of heterosporous lycopsids, a ligule has recently been documented in the homosporous fossil lycopsid *Leclercqia complexa* ... ." Kenrick & Crane (1997). These authors believe that the ligule in lycopsids is homologous to both the *sporangium* and the *microphyll*. Image: lingitudinal section of the extant lycopsid *Isoetes*, showing a ligule. Image adapted from the **Plant Fossils and Evolution** site of Prof. Kathleen Pigg (Arizona State Univ.).



Lobed margin (leaves) margin indented one quarter or more of the distance from the margin to the mid-vein or (where this is lacking) to the long axis of the leaf; compare *entire margin* and *toothed margin* leaves

Locule, alternatively **loculus** (pl. **loculi**)**:** a chamber, compartment or other limited volume which is used to accumulate or store either gametes or spores. Typically, the locule contains *only* gametes or spores. Thus a sporangium is a spore-producing organ, but a locule within the sporangium is where the spores are accumulated before release.

-M-

Manoxylic: wood type that contains abundant *parenchyma*; typical of cycads; compare with *pycnoxylic*.

Megagamete: the "female" gamete, analogous to an egg and sometimes referred to as an ova (Latin for *egg*).

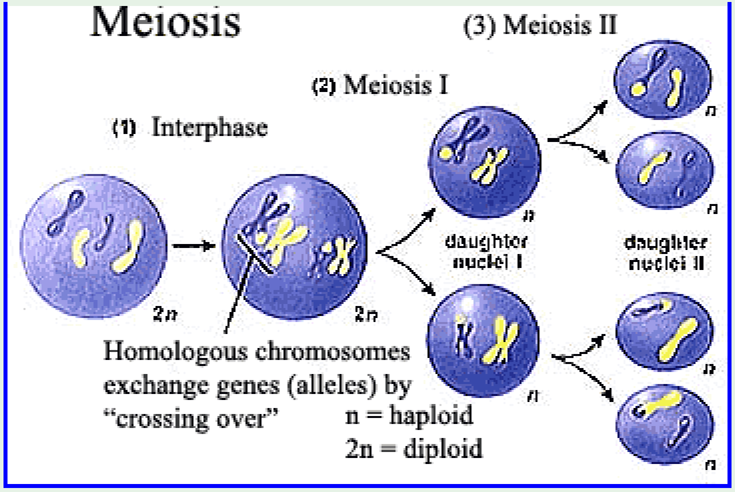
Megagametophyte: in *heterosporous* plants and in seed plants, the female *gametophyte* produced by a *megaspore*.

Megaphyll a leaf with branched veins and a flat area for receiving sunlight.

Megasporangium: a sporangium that produces megaspores; see also heterosporous.

Megaspore: a large, haploid (N=1) spore of a heterosporous plant that produces a megagmetophtye (female gametophyte)

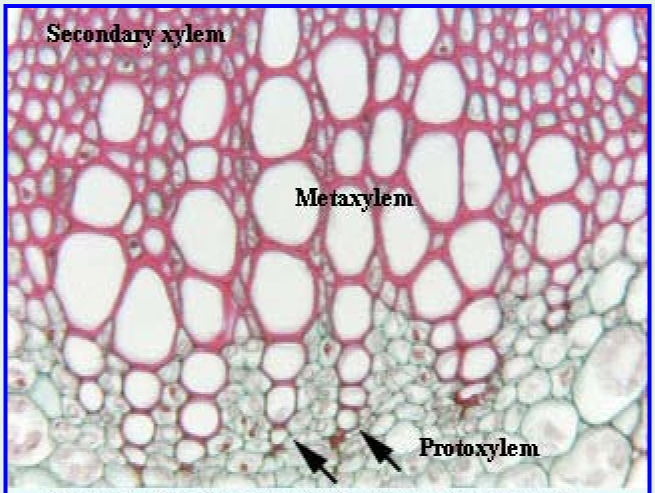
Meiosis: A process common to almost sexual reproduction in eukaryotic cells. The homologous chromosomes of a diploid nucleus first exchange homologous genes (alleles) on a roughly random basis, so that the resulting chromosomes carry a mixture of genes from each parent. The nucleus then divides normally (by mitosis) to yield two diploid daughter nuclei. Finally, the nuclei divide again, but now without DNA replication, to yield four haploid cells. Image from the **Online Biology Book** by Dr. Mike Farabee of Estrella Mountain Community College.



Meristem: a plant tissue containing cells that are actively dividing (or have the potential to do so). Meristem found in the tip of roots and stems, the ***apical meristem***, is responsible for the growth in length (primary growth) of these organs. The cambium is a ***lateral meristem*** that is responsible for increase in girth (*secondary growth*) in perennial plants. Some plants also have ***intercalary meristem***, as in the stems of grasses, for example. These are responsible for their continued growth after cutting or grazing has removed the apical meristem of the shoots. **Tiscali**.

Mesarch: "a type of xylem maturation in which the protoxylem is embedded in the metaxylem and development proceeds both centripetally (from the outside in) and centrifugally (from the inside out)." **Virtual Paleobotany Laboratory Glossary**. Compare *centrarch*, *endarch*, *exarch*.

Mesophyll: *parenchymal* tissue between the upper and lower epidermis of a leaf.



From the Plant Anatomy Lab site of Prof. James D. Mauseth, University of Texas

Metaxylem: the outer part of the *primary xylem*, or woody tissue of a plant, generally consisting of wider, thick-walled and/or pitted cells. The metaxylem frequently includes living *parenchymal* cells. The defining feature of metaxylem is that it develops after the protoxylem but before secondary xylem. Wikipedia. "Two types of vessels mature in characteristic positions [when] primary xylem tissue ... differentiates from the procambium during the early ontogeny of a plant. The *protoxylem* vessels, which commonly have annular and spiral thickenings, mature before the surrounding organs have elongated. These are frequently destroyed by the extension of the surrounding tissues. The metaxylem vessels, which usually have reticulate and pitted thickenings, mature after the surrounding organs complete their growth. In contrast to protoxylem vessels, they are not destroyed, and constitute the water-conducting tubes of the mature plant ... ." Kubo *et al*. (2005).

Microgamete: the "male" gamete, analogous to sperm.

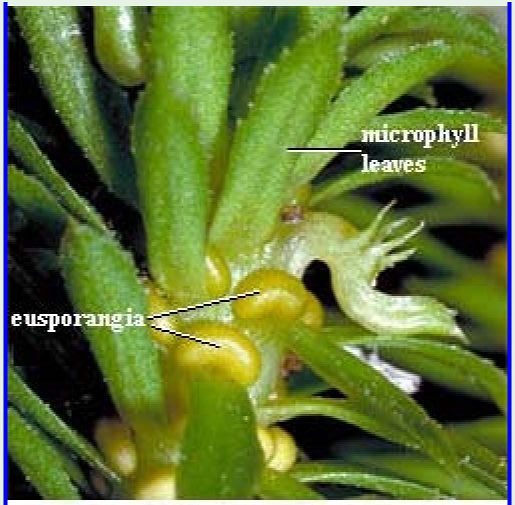
Microgametophyte: in *heterosporous* plants and in seed plants, the male *gametophyte* produced by a *microspore*.

Microphyll: a *leaf* with only one vascular bundle. Kenrick & Crane (1997) apply a developmental definition: "a stem outgrowth that influences the differentiation of axial vascular tissue." Image from the website of **Prof. Gerald Carr** at the Univ. of Hawaii at Manoa.

Microsporangium: a sporangium that produces microspores. Also see heterosporous.

Microspore: a small, haploid (N=1) spore of a heterosporous plant that produces a microgametophyte (male gametophyte).

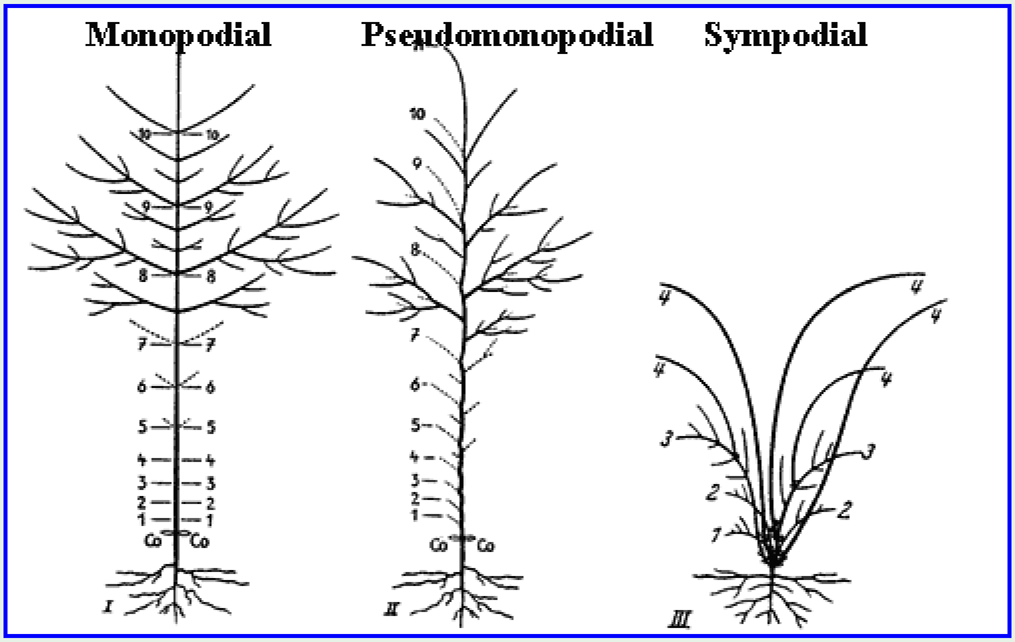
Monocarpic: a plant that produces reproductive propagules only once in its lifetime.



Huperzia serrata

Monoecious: used to describe a species in which a single plant produces both male and female gametes.

Monophyletic: a group descended from a single common ancestor within the group being studied. The term is also used in a slightly different sense. A "monophyletic group" usually refers to a *clade*, i.e. an organism and *all* of its descendants. Thus *Sinraptor* and *Allosaurus* are (very likely) monophyletic within Allosauroidea. However they are not, by themselves, a clade, because they do not include all descendants of their last common ancestor.



Monopodial: of branching patterns, Monopodial branching is a pattern of branching in which there is one main shoot with lateral branches emerging from it. Many firs and spruces exhibit monopodial branching patterns, therefore the Christmas tree image is a good example of monopodial branching. Monopodial branches develop some distance behind the tip of the apical meristem (the growing shoot of the plant). The important implication is that the monopodial branch does not develop from *apical meristem*. That is, the growing tip of the plant doesn't simply divide in two. Instead, a whole new growth axis is formed -- a *lateral meristem*. Compare *sympodial*, *pseudomonopodial*. Minimally, "In contrast to the pseudomonopodial condition, in monopodial branching there is a developmental lag in the lateral branch trace compared to the xylem in the main axis." Kenrick & Crane (1997: 109). These terms are also used with reference to growth patterns of rhizomes, flowers, etc. They are also quite frequently used wrongly. Some writings define these terms by reference to the branch angle. Monopodial branches are typically >45° from the vertical axis, but the term monopodial refers to a development course, not gross morphology. Other materials restrict *monopodial* to (?multiple) branches from nodes. That's closer, but too restrictive. It misses the evolutionary point and isn't consistent with the established uses of this term in paleobotany, or its application to structures other than stems which also arise by formation of a secondary growth axis. Image from the **Professur für Forstbotanik site** of the Universität Freiburg.

Monosaccate: a pollen grain with one saccus or buoyant bladder. Compare bisaccate.

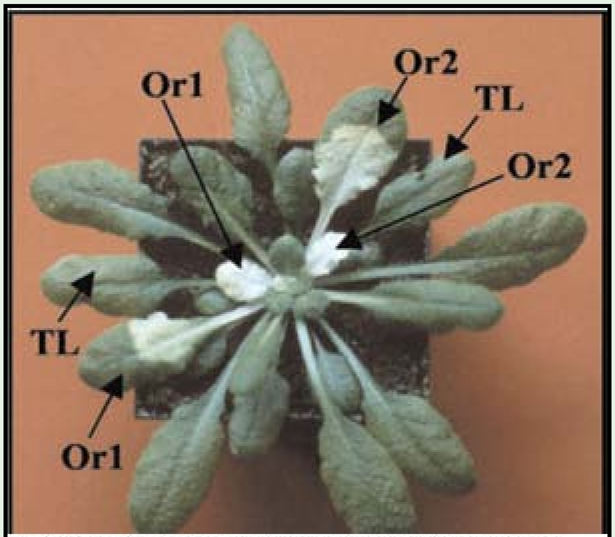
-N-

Nucellus: *ovule* tissue within which an embryo develops (embryo sac); homologous with the *megasporangium* of a seed plant.

-O-

Oogamy: reproduction in which the female gamete is large and non-motile and the male gamete small and motile.

Operculum: *L.* for *lid* or *cover*. In botany, nearly any kind of lid or cover.

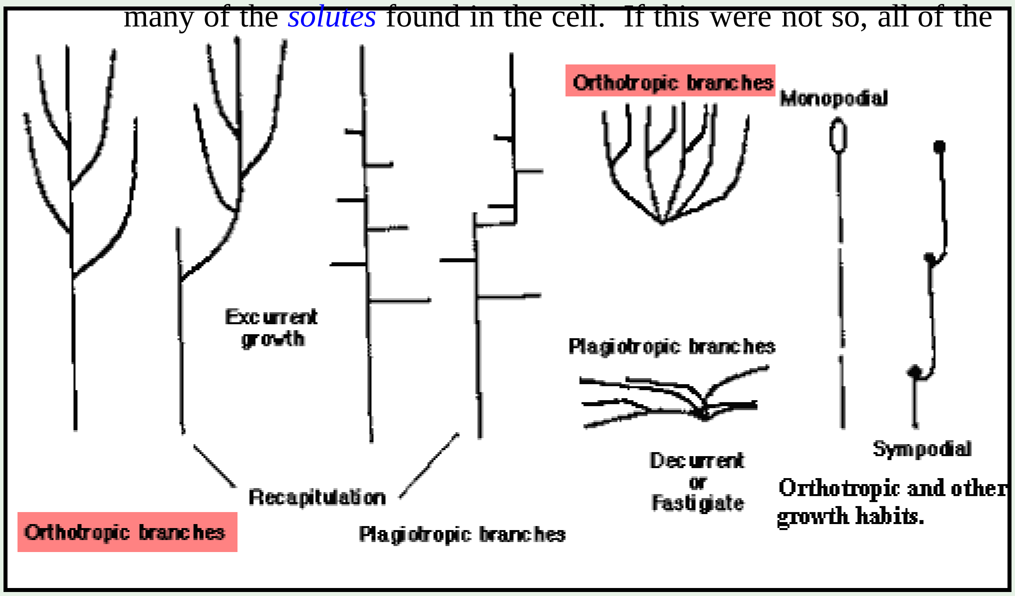


Arabidopsis plant showing preferential transport of a virus between leaves on two orthostichies (Or1 and Or2). From Kiefer & Slusarenko (2003).

Orthostichy: like a number of terms in botany, this word has two meanings -- one morphological and one physiological -- which are usually, but not invariably, equivalent. Morphologically, an orthostichy is "a longitudinal rank, or row, of leaves along a stem," to quote the usual copyright-expired Webster's dictionary. Physiologically, an orthostichy is a series of leaves with a direct vascular connection. Kiefer & Slusarenko (2003). Typically these are the same. That is, leaves with a direct vascular connection lie directly above or below each other, looking down the long axis of the stem. However, this is apparently not *always* the case. Kenrick & Crane (1997: 297) (referring to "helical orthostichies" in *Archaeopteris*).

Orthotropic: orthotropic growth of branches indicates that the branches grow in the same (*ortho*) direction as the main shoot, i.e. upwards. *Compare* *plagiotropic*. Huber & Hutchings (1997). Image from the **Biology of Horticulture** site (Ohio State University).

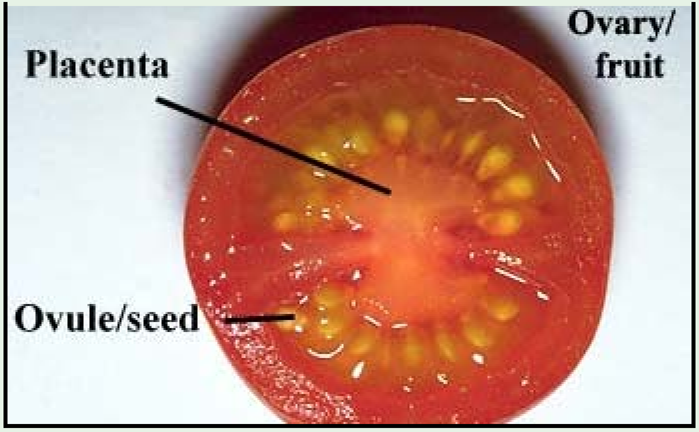
Osmotic pressure: Most biological membranes are impermeable to many of the *solutes* found in the cell. If this were not so, all of the valuable biomolecules in the cell would simply diffuse out and be lost. However, the same membranes are often more or less permeable to water. Since there are many solutes trapped in the cell, the "concentration" of water is lower in the cell than outside, *i.e.*, there are more water molecules per unit volume outside the cell than inside. Diffusion of water through the membrane works both ways and is completely random. However, water "concentration" is higher outside the cell. That is, there are more water molecules in contact with the membrane on the outside than on the inside. So, there will be a net flux of water into the cytoplasm until the concentrations equalize. The **osmotic potential** is the measure of the net tendency of water to enter the cell. Real cells can't usually behave in this fashion, since the cell will expand and ultimately burst. The problem is handled in numerous different ways, depending on the cell type. In plant cells (and various others), the cell membrane is confined within a semi-rigid cell wall. Water enters the cell only until the elastic reaction force of the cell wall equals the outward force caused by water molecules crowding into the cell. At steady state, the plant cell then maintains a rather high internal pressure, referred to as **turgor pressure**. Turgor pressure serves as a sort of internal hydrostatic skeleton which helps to support -- and even move -- the plant structures. [I have lost the original source for most of this useful paragraph -- my apologies to the author.]



Orthotropic and other growth habits.

Ovary: the enlarged basal portion of a carpel, where the *ovules* are borne; the ovary differentiates into the fruit.

Overtopping: overtopping or *pseudomonopodial* growth is a growth habit in which branches depart from a main (usually vertical) axis, rather than by more or less even bifurcation of the axis. To put the matter more simply, overtopping means



branching more like a tree and less like a bush. A type of branching in which the apical meristem appears to divide to form two branches, one of which is dominant resulting in an upright main axis with distinct side branches.

Ovule: unfertilized seed; the ovule contains the megasporangium with the megagametophyte, surrounded by one or two integuments. *See* sclerotesta for detailed anatomy of a (fossil) seed.

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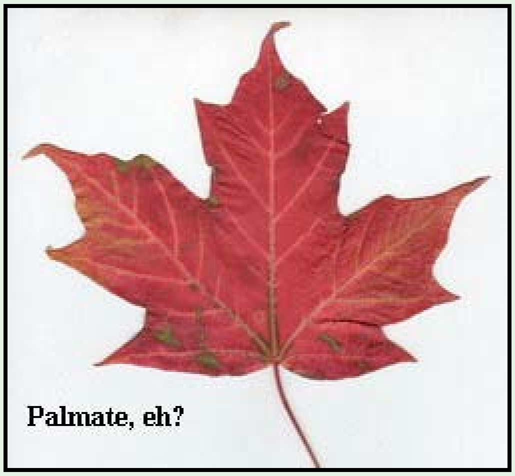
Glossary P-Q

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

-P-

P-Type Tracheid: *See tracheid types.*



Palmate: a pattern of leaf venation in which several main veins radiate in different directions from a (more or less) central point, *e.g*. the emblematic Canadian maple leaf. *Compare pinnate*, *parallel-veined*.

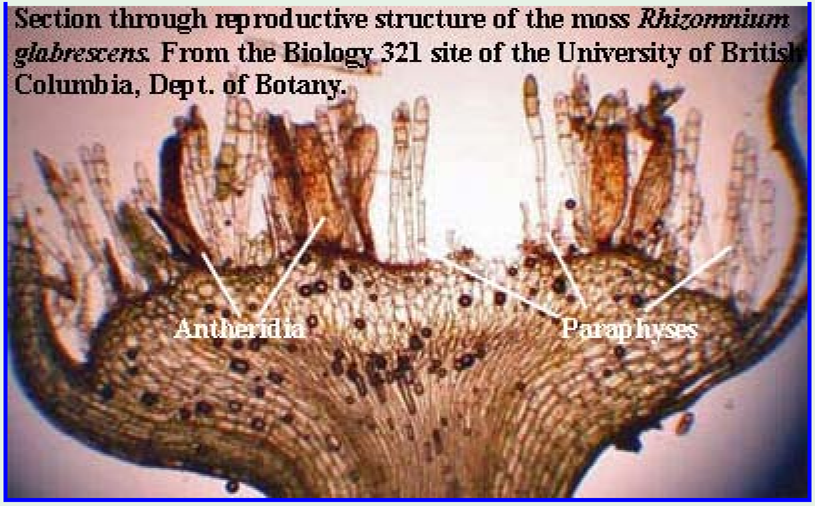
Palynomorph: a fossil *spore* or *pollen* type.

Parallel-veined: a pattern of leaf venation in which several main veins extend through the leaf in parallel. *Compare palmate*, *pinnate*.

Paraphyletic: a taxon is said to be paraphyletic if it does not contain all descendants of its last common ancestor. So, for example, "seedless plants" is paraphyletic because its last common ancestor would also be the ancestor of plants *with* seeds. A clade must contain all descendants of its last common ancestor. It is usually fairly important to stick to a consideration of clades. However, that importance can often be outweighed by the utility of being able to discuss the earliest forms of some group. We normally signal that we are talking about such a paraphyletic group by saying "*basal* seedless plants" or "*paraphyletic* seedless plants" or by the use of some other, similar linguistic artifice.

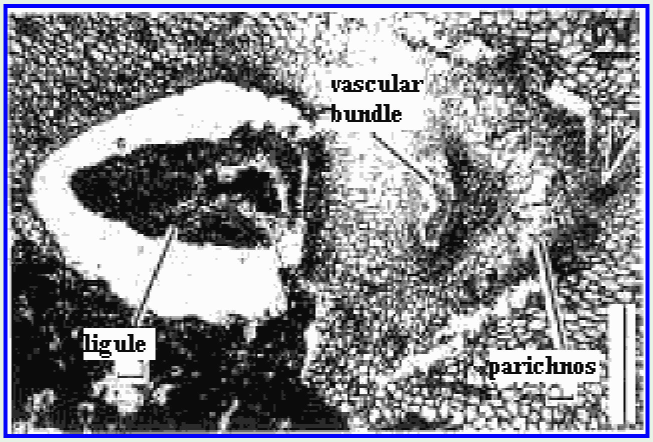
Paraphysis: "Paraphyses are sterile, multicellular, generally uniseriate [a single row of cells], chlorophyllous hairs found among the gametangia of most mosses ... ." Kenrick & Crane (1997).

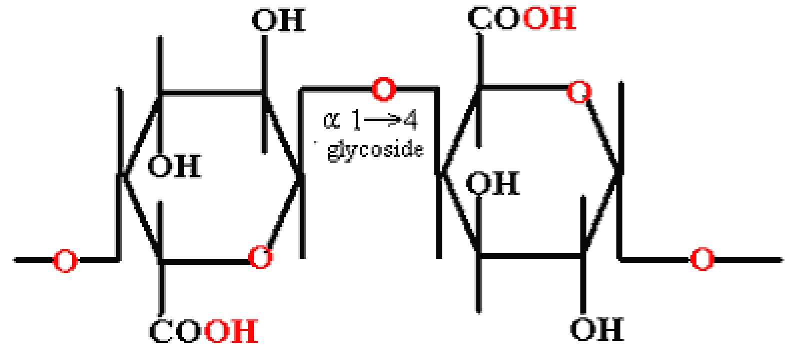
Parenchyma: the most common type of plant cell; thin-walled cells varying in size, shape, and function. Parenchyma cells are usually loosely packed cubed-shaped or elongated cells that contain a large central vacuole and have thin, flexible cell walls.


Section through reproductive structure of the moss *Rhizomnium glabrescens*. From the Biology 321 site of the University of British Columbia, Dept. of Botany.

Parenchymal cell walls are enriched in *pectins* and therefore stain pink with Toluidine Blue. They also have simple *pits*. Parenchymal cells are found in large numbers in the *pith* and *cortex*. They are the least specialized cells in the plant and normally act as a sort of reserve of stem cells. They may also serve a number of functions, including food storage (either water or nutrients), photosynthesis, as well as tissue repair. Compare *cholenchyma*, *sclerenchyma*.

Parichnos: an interconnected system of parenchymous strands with many air spaces that extend throughout the vegetative organs of some *arborescent* lycopsids. Essentially, parichnos tissue is *parenchyma* with lots of air space between cells. This tissue probably aided photosynthetic gas exchange in much the same way as do the lenticels of modern trees. Image: oblique section through a leaf base of "*Lepidodendron*" from Zhou *et al*. (2004). Scale bar = 500µ.





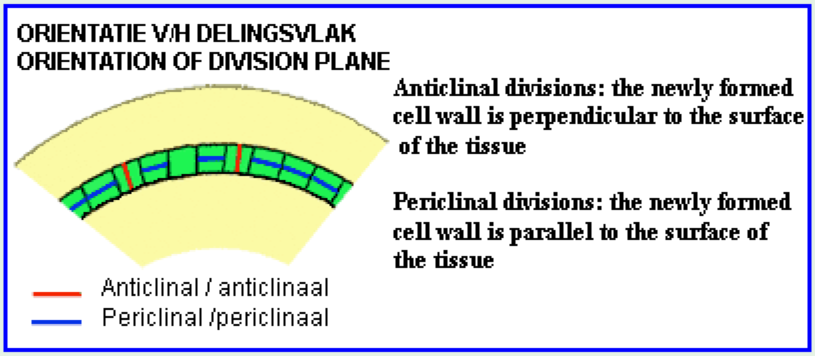
Basic Unit of pectin: poly[α-(1>4)-D-galacturonic acid]. Blocks of this simple polymer alternate with "hairy," non-gelling regions containing side-chains with other unusual sugars

Pectin: yet another sugar polymer. In plants, pectin occurs on cell walls of *parenchyma* and related cell types where it apparently strengthens the cell wall and assists in cell-to-cell adhesion. It is frequently extracted and used as a thickener for preserves.

Peltate: "Of a leaf, having the stalk attached to the lower surface of the blade, not to the margin (also applied, in the same sense, to other stalked structures)." Biology Online. In other words, the leaf is held like an umbrella, instead of a frying pan.

Perennial: a plant without a definite lifespan.

Periclinal: directional term referring (perhaps unexpectedly) to the radial direction. The image, from **Virtual Classroom Biology** (Radboud Univ. Nijmegen) makes more sense than any amount of explanation we could add. Another image we found very useful is **here**. However, that image is the from the incredible set of University of Hawaii Botany pages by Prof. David Webb. We have already so far exceeded our self-imposed quota of images from Prof. Webb's site, that we must leave it as a link.


ORIENTATIE V/H DELINGSVLAK
ORIENTATION OF DIVISION PLANE

Anticlinal divisions: the newly formed cell wall is perpendicular to the surface of the tissue

Periclinal divisions: the newly formed cell wall is parallel to the surface of the tissue

Perine: "The perine is the normal outer wall layer of the spores of *homosporous* ferns and lycopsids and is also found in the *microspores* of the Isoetaceae and Selaginellaceae. A distinct perine layer is present in mosses but is absent in liverworts, hornworts, and *Coleochae*." Kenrick & Crane (1997) (citation omitted).

Peristome: a combination of Greek roots roughly meaning "stuff around the mouth." In mosses, this means the ring of **peristome teeth** around the orifice of the spore capsule that control spore dispersal. See discussion of the moss sporophyte.

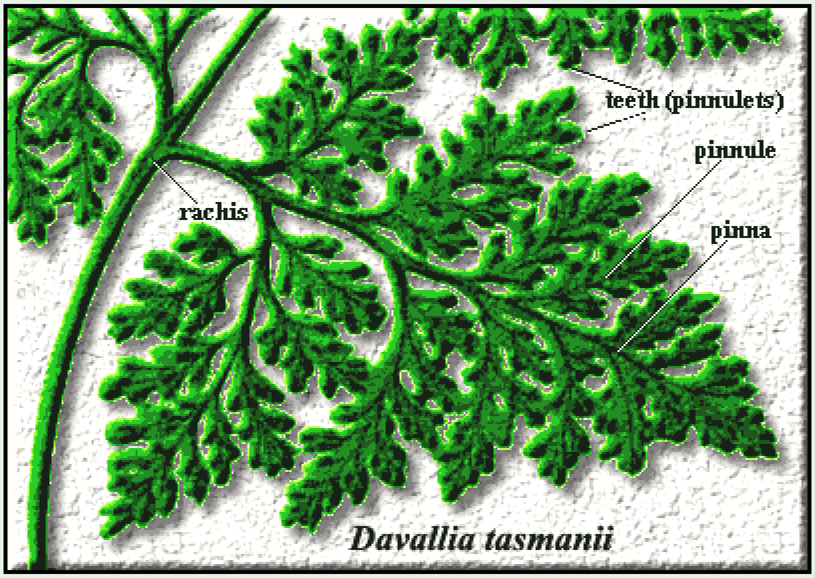
Petal: one of the whorls of a flower; petals may be brightly colored.

Phloem: conducting tissue of vascular plants. Phloem differs from xylem both structurally and functionally. Functionally, phloem transports solutes both up and down the plant, while xylem functions as a one-way transport system for moving water from the roots to the leaves (or equivalent). Phloem carries sugars and other direct or indirect products of photosynthesis to the stem and roots, generally during the day. Phloem also carries ions and soil nutrients up from the roots to the stem and leaves, generally at night. Xylem makes considerable use of the cell walls of dead or enucleated cells. Phloem uses living cells. Xylem uses capillary action and suction, like a straw, to transport water. Phloem uses *osmotic pressure* to move solutes. A high concentration of solute is loaded inside cells of the phloem at a source, such as a leaf where sugars are produced. This creates a diffusion gradient that draws water into the cells. The resulting pressure causes a flow to occur. If the dissolved sugars or other chemicals carried along with the sugars are removed from the phloem at another place in the tree for use (a sink such as a root or fruit), the decline in concentration of sugar causes water to move out of the phloem cells. Because water is moving in at a source and out at a sink, there is a mass flow of water and substances in the phloem. In trees, phloem is shed annually with the bark. **Water and Chemical Movement Beneath the Bark**

Phyllid: the leaf of a bryophyte. By many more exacting definitions, this does not constitute a *leaf*, hence the purported need for this apparently pointless addition to your vocabulary.

Phyllotaxy: the pattern in which leaves are arranged around a stem.

Pinna: first order of subdivision of a compound leaf or fern frond. *Davallia tasmanii* image adapted from vonKonrat *et al*. (1999).

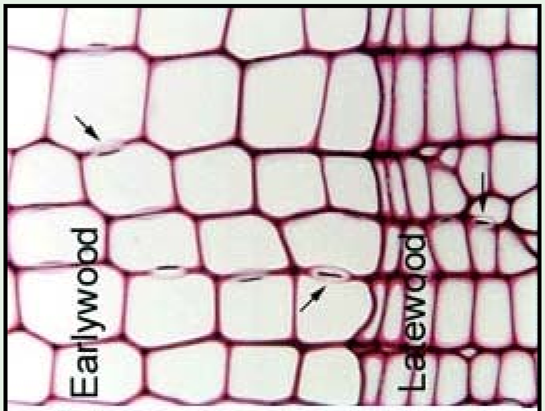


Pinnate: a type of leaf venation in which all of the veins of the leaf arise from a central mid-rib. *Compare palmate*, *parallel-veined*.

Pinnule: the second order of segments of a compound leaf or fern frond.

Pinnulet: as you have undoubtedly guessed, the *third* order of segments of a compound leaf or fern frond.

Pistil: the "female" organs (*megagasporangium*) of a *flower*, including the *stigma*, *style*, *ovary*, and *ovule*.



Pine tracheids. Arrows point to pits.

Pit: the thin, remnant primary wall of *tracheids*, *i.e.*, primary wall which has not been covered by *lignified* secondary wall. Pits are involved in *translocation* of fluids from the *xylem*. See also, *pit membrane*.

Pit membrane: in many sources, the term *pit* refers to the absence of secondary wall, *i.e.* the "hole" in the secondary wall, while the primary wall is the pit membrane. The distinction becomes important in detailed xylem anatomy because vessels may have pits but usually lack pit membranes. In that case the pit is simply a hole in the vessel wall.

Pith: a central unspecialized parenchymous ground tissue in monocot roots and dicot stems.

Plagiotropic: plagiotropic growth of branches is growth at = 90° to the direction of growth of the main axis (i.e. the branches grow directly outward or downward, in the usual case). *Compare orthotropic*. Huber & Hutchings (1997).

Plasmodesma: (pl. **plasmodesmata**) "Plasmodesmata are narrow channels that act as intercellular cytoplasmic bridges to facilitate communication and transport of materials between plant cells. The plasmodesmata ... are extremely specialized channels that allow for intercellular movement of water, various nutrients, and other molecules (including signalling molecules) ... . Plasmodesmata are located in narrow areas of cell walls called primary pit fields, and they are so dense in these areas (up to one million per square millimeter) that they make up one percent of the entire area of the cell wall." **Plasmodesmata**.

Plesiomorphic: a plesiomorphic character of a taxon is one which it shares with an ancestral group. It is not a unique, derived character (*synapomorphy* or *apomorphy*), but a primitive character which tells us nothing about its evolutionary position.

Pollen: the *microspore* of seed plants that contains the *microgametophyte* (male gametophyte)

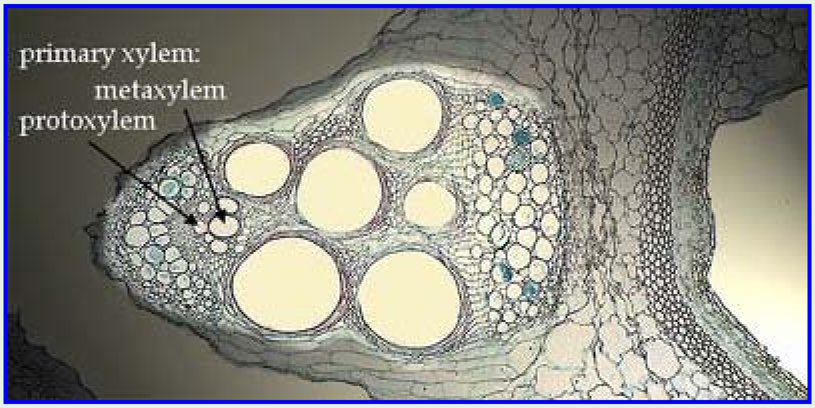
Pollination: the transfer of *pollen* from the pollen organ to the *ovule*; for example in flowering plants from *stamens* to the *stigmatic* surface of the *carpel*.

Polystelic: having more than one *stele*.

Primary growth: growth in length, controlled by the *apical meristem*

Primary pinna: leaflet of first subdivision of a fern frond or compound leaf.

Primary xylem: xylem is found in leaves and young stems or in young roots it is referred to as primary xylem. Primary xylem is *xylem* derived from *apical meristem*, rather than *cambium*. It contains *fiber* cells and *tracheids* (pipe-like) elements which progressively develop secondary, *lignified* walls until little of the primary wall is left except at *pits*. These pits operate to permit fluids to move between tracheids. The precise centrifugal series of secondary wall structures, and the shape and pattern of mature pits are useful in taxonomic and forensic work.



Propagule: in plants, a propagule is whatever structure functions to reproduce the species: a *seed*, *spore*, stem or root cutting, etc.

Protocorm: The cell mass formed during the earliest phase of germination. "The term *protocorm* was first proposed by Melchior Treub in 1890 to describe the early stages in the germination of lycopsids. Orchid protocorms resemble those of lycopsids — according to Bermard's use of the term—and it has been used extensively (Arditti, 1992). Protocorms have round or elliptical shapes with some unicellular absorbing hairs on the basal part and an apex meristem on the tip." Chang *et al*. (2005).

Protonema: first growth from a germinating spore, especially, the thread-like process from a germinating moss (Bryophyta) spore.

Protostele: a type of *stele* with a solid core of *primary xylem*. Compare *siphonostele*. Image from the **Pink Monkey** site.

Protoxylem: the first xylem cells to develop. They are relatively small because the cells "stopped expanding while they – and all the surrounding internode tissues – were still young and close to the shoot apical meristem." Protoxylem.

Pseudomonopodial: a type of branching characterized by the presence of a main branch which has outgrown the other of the dichotomous pair, resulting in a main axis with smaller lateral branches. A type of branching where the apical meristem divides to form two branches, one of which is dominant resulting in an upright main axis with distinct side branches. Compare (and see fuller discussion at) *monopodial*, *sympodial*.

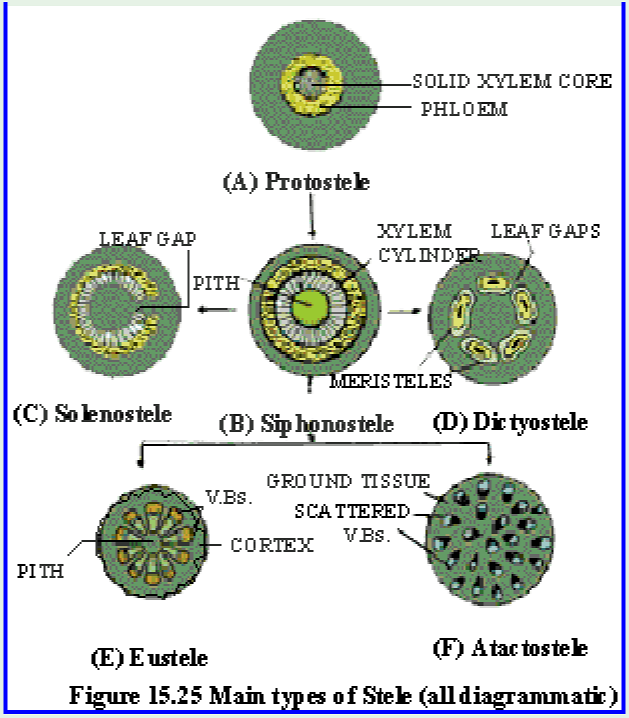


Figure 15.25 Main types of Stele (all diagrammatic)

Pteridophyte: a paraphyletic group including (roughly) all Tracheophyta except Spermatophytata, *i.e.* rhyniophytes, lycophytes, ferns and horsetails. Plants which are tracheophytes, but not seed plants. The term has also been used more restrictively, to refer to leptosporangiate ferns, for example. Cantino *et al*. (2007)

Pychnoxylic: dense wood that contains little *parenchyma*; typical of *Archeopteris*, and conifers; compare to *manoxylic*.

Pyrenoid: a starch storage structure found in the chloroplasts of green algae.

-Q-

Quadriseriate: in four ranks or rows.

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Palaeos
Παλαιός
GLOSSARY
PLANTS
GLOSSARY R-SE

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Glossary R-Se

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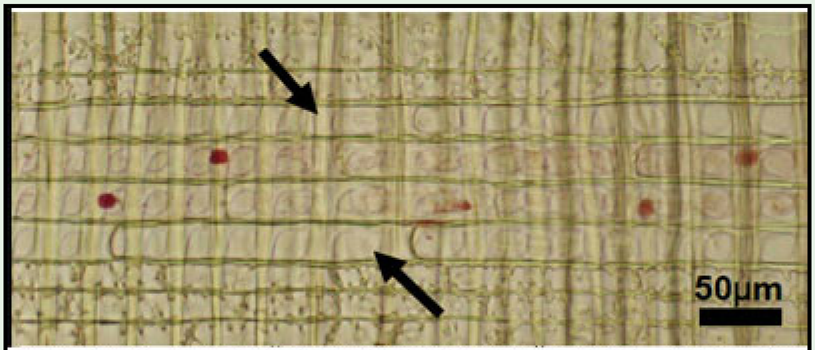


Ray cells in *Pinus*. The ray cells grow across annual growth rings. Note the two adjacent living cells in the center (with red-staining bodies). From Nakaba *et al.*

Ray cell: xylem cells which are extended radially. In wood, ray cells hold annual growth rings together and allow the products of photosynthesis to move in and out of storage in the xylem tissues. Ray cells contain two populations of cells. Most are short-lived tracheids which are similar to ordinary xylem, except for their growth outwards from the center, rather than along the axis of the stem. A few are long-lived parenchymal cells which presumably form a pool of living tissue to extend or repair the system of radial tracheids. Image from Nakaba *et al.*

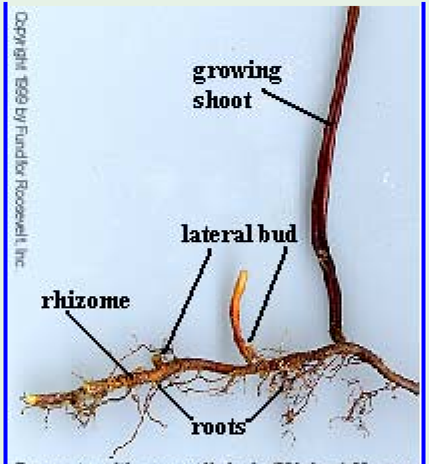
Rhizoid: hair-like filamentous projection for anchorage or absorption.

Rhizomatous root-like.

Rhizome: a (usually) underground stem that is horizontally oriented; rhizomes may appear like roots, but have a definite node and internode architecture. Image from the site: **Flora of Roosevelt Monmouth County, New Jersey** by Ross Tulloss & Mike Hamilton.

Rhynie Chert: *See* Devonian Sites and Paleozoic Sites. A critical Pragian site in Scotland with plant tissues preserved to the subcellular level. The Rhynie Chert has recently been dated to 396 ± 12 million years. "The site is interpreted as a series of ephemeral freshwater pools within a hot springs ecosystem. The organisms were rapidly fossilized, perhaps as a result of a silica gel fixing." Taylor *et al*. (2005).

Rhyniophyte: a *paraphyletic* group of basal tracheophytes which might be defined as all tracheophytes other than Eutracheophyta.



Dennstaedtia punctilobula (Michx.) Moore
Loc.: Roosevelt, Monmouth Co., New Jersey
Date: 2 July 1999 Photo: R. E. Tulloss

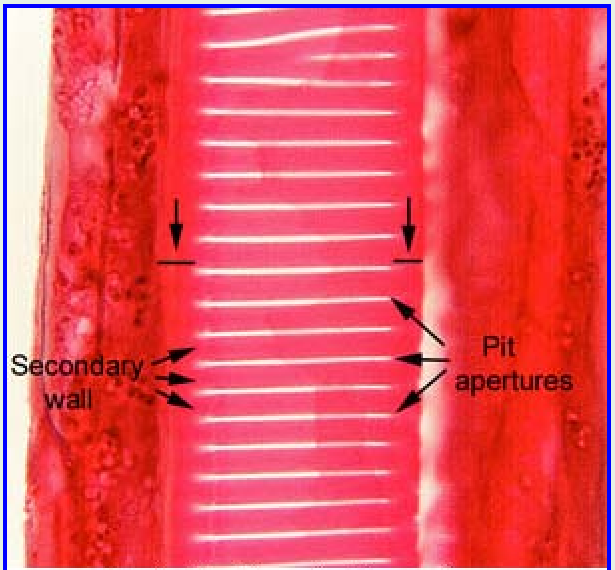
Root: axial structure of the *sporophyte* which has all or most of the following characteristics: (1) direction of growth (on average) within 90° of gravitational field; (2) growth away from light (negative phototropism); (3) elongation growth is strictly *apical*, without bifurcation of the *meristem* (*root cap*); (4) possession of a *histologically* distinct root cap; (5) *endodermis*; (6) *protostele* (sometimes with a pith); (7) endogenous origin of lateral roots, *i.e.*, branching by the initiation of an entirely new meristematic growth region from the *stele*. Raven & Edwards (2001) (parts of this definition are directly quoted from the reference).

-S-

S-Type Tracheid: *See tracheid types.*

Saccate pollen: pollen with a *saccus* or sacci; characteristic of many conifers. *See* image at *bisaccate*.

Saccus: (pl. *sacci*) a wing-like or bladder-like extension on a pollen grain. *See* image at *bisaccate*.

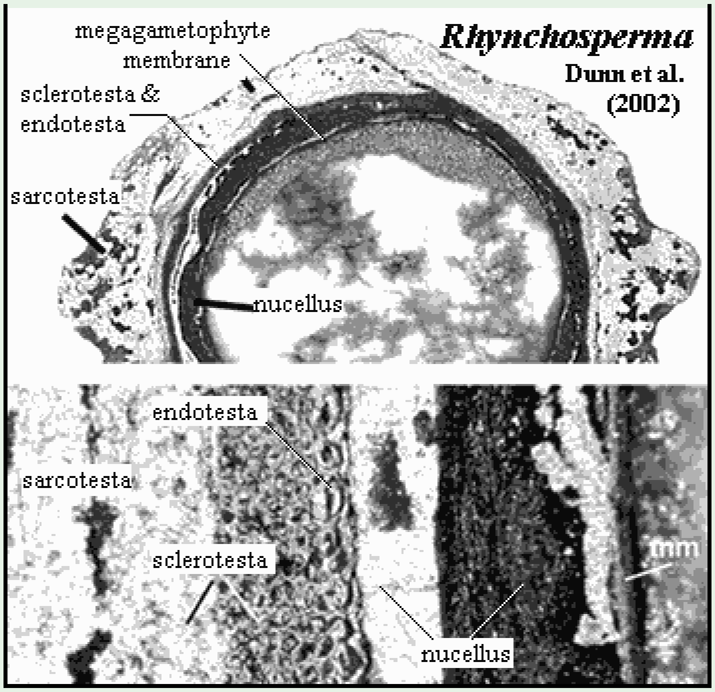


Tracheid with scalariform pits

Scalariform: ladder-like, like the rungs on a ladder. Image from Dr. James Mauseth's **Plant Anatomy Laboratory** site (U. Texas).

Sclerenchyma: tissue composed of (usually dead) cells having walls thickened with *lignin*; sclerenchyma tissue functions primarily in strengthening and support. Compare *chollenchyma*, *parenchyma*. Image from Michael Muller's **Bios 100 Summer 2005 site** (Univ. Ill. at Chicago).

Sclerotesta: the middle,



fibrous layer of the integument in some seeds. Image from Dunn *et al*. (2002) showing cross sections of a *Rhynchosperma quinii* seed from the late Mississippian (Serpukhovian?) of Arkansas.

Secondary growth: growth in width initiated and maintained by the vascular cambium and cork cambium. *See cambium*. The vascular cambium surrounds the core of the stem, branch, or root. It creates *xylem* medially and *phloem* radially. If present, the cork cambium, a second, outer layer of cambium, creates a new outer layer (typically bark) radially. There is a really good explanation of secondary growth at **Stem - Secondary Growth**.

Secondary phloem: phloem produced by the vascular cambium. *See phloem*, *cambium*, *secondary growth*.

Secondary xylem xylem produced by the vascular cambium. *See xylem*, *cambium*, *secondary growth*.

Seed: a fertilized *ovule; megasporangium* that contains an embryo enclosed in an integument. A seed has been described as "a baby sporophyte in a jacket with a lunch sack." Gymnosperm Evolution. The advantage of a seed is that it can combine the dispersal functions of a spore with sexual reproduction.

Seed fern: any of a number of extinct seed-bearing plants with fern-like leaves. Image of *Neuropteris* from the **Kentucky Paleontological Society** web site.

Seed plants: a monophyletic clade of plants that reproduces by seeds; *megagametophyte* is retained on the parent *sporophyte* and enclosed in an integument; *microgametophyte* is transferred to the megagametophyte.

Sepal: a whorl of a *flower*; sepals often resemble reduced *leaves* and function in the protection of the bud; sepals may be modified to function more like a *petal*.

Seta: This incredibly over-used anatomical term is simply Latin for a bristle or a stiff hair. It is used in a variety of contexts, not only for things that look like bristles (or, to be sure, stiff hairs), but also for things like the stalk of the *sporophyte* in mosses, which looks nothing like a bristle (or, for that matter, a stiff hair).

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Glossary Si-Sz

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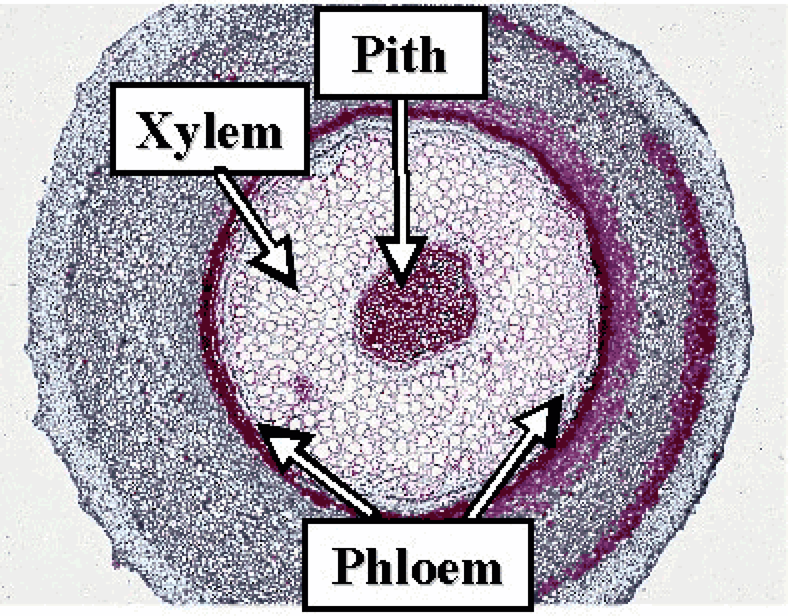
Simple tissue: tissue composed of only one cell type

Sinus: the indentations of a lobed *pinna* or *pinnule* of a fern or of a dicot *leaf*.

Siphonostele: a type of *stele* in which the vascular tissue forms a cylinder around a central column of cellular or acellular pith. Compare *protostele*. Image from Prof. David Webb's (U. Hawaii) **Botany 201** site.



Stem cross-section showing siphonostele. This image shows an *ectolophic* siphonostele -- a stele with phloem outside the xylem. *Amphilophic* steles have phloem on both sides of the xylem.

Solute: anything dissolved in a solvent. In salt water, the water is the solvent, and the salts are solutes.

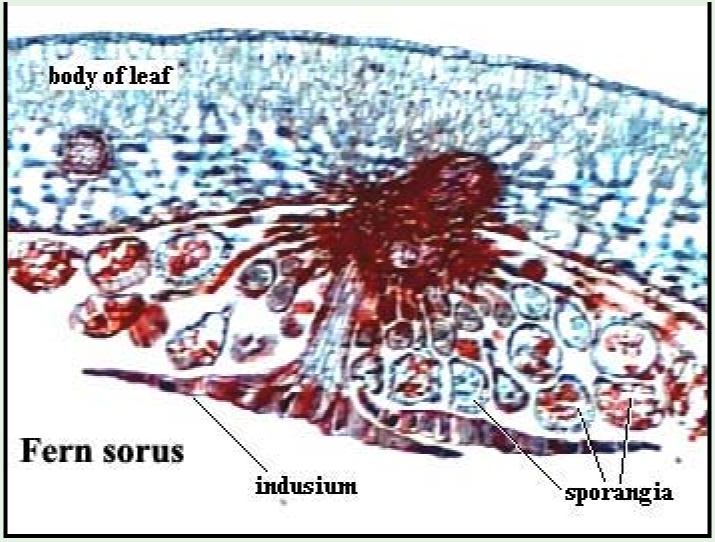
Sorus: (pl *sori*) a cluster or group of *sporangia* of a fern; most frequently applied to clusters of fern sporangia attached to the bottom of fern leaves. Image from the **General Biology Lab** site by Diane Jokinen and Patrick Duffie of Loyola University Chicago.

Spline: cell biology. In the developing spermatids of euphyllophytes, "a lamellar strip and a narrow band of microtubules ... which extend around the cell providing a framework for positioning of organelles." Renzaglia *et al*. (2000).

Sporangiophore: modified branch on which the *sporangium* is attached.

Sporangium: (pl. *sporangia*) hollow, unicellular or pluricellular structure in which *spores* are produced.

Spore: a *haploid* (1N) reproductive cell capable of developing directly into a *gametophyte* without uniting with another cell.



Sporophyll: a *spore*-bearing leaf (microphyll, not a "true" leaf); a modified leaf bearing *sporangia*. In some lycophytes, the megaspore (and so the developing megagametophyte) stay with the sporophyte and its sporophylls (i.e., the *strobilus*). It is fertilized in situ by microspores, and develops into sperm-producing microgametophytes. This lycopsid system is analogous, but clearly not directly related, to reproduction in the seed plants. Image from the **Vascular Plant Image Library** (Texas A&M Univ.).


Botrychium sporophyll with sporangia

Sporophyte: the *spore* producing, *diploid* (2N) phase of the life cycle; compare to *gametophyte*.

Sporopollenin: A major chemical constituent of the outer walls of plant spores. "The chemical composition of sporopollenin is not exactly known, due to its unusual chemical stability and resistance to degradation by enzymes and strong chemical reagents. Analyses have revealed a mixture of biopolymers, containing mainly long chain fatty acids, phenylpropanoids, phenolics and traces of carotenoids. Tracer experiments have shown that phenylalanine is a major precursor, but other carbon sources also contribute. It is likely that sporopollenin derives from several precursors that are chemically cross-linked to form a rigid structure." Wikipedia.

SSU rDNA: DNA coding for RNA associated with the small *ribosomal* subunit, *i.e.* for *"18S" RNA*.

Stamen: the "male" structures of a flower, consisting of a supporting filament and the *anther*, a sac which produces and holds the *microgametophytes* (pollen).

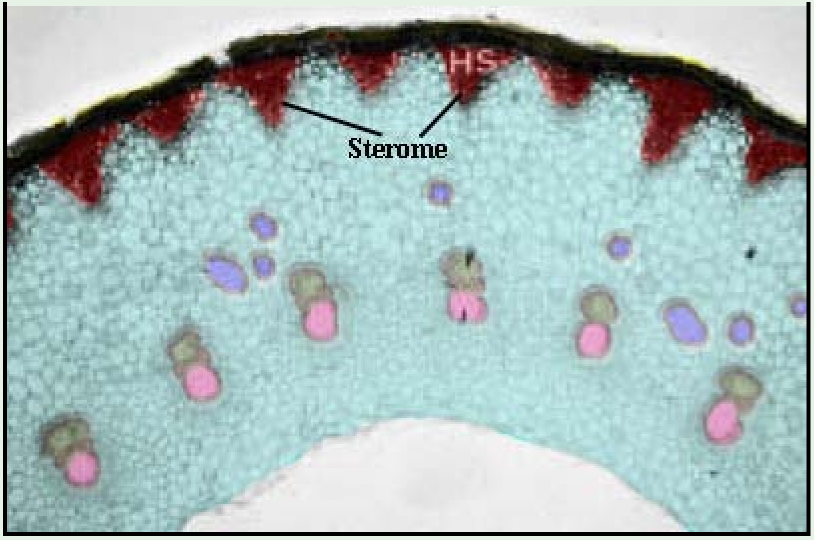
Central stele of the buttercup, *Ranunculus*. From Biodidac.

Stele: vascular tissue (the *xylem* and *phloem* together) bundle; the vascular cylinder in stems and roots where the vascular tissue is located.

Stem: same as *axis*; a plant axis with *leaves* or *enations*.

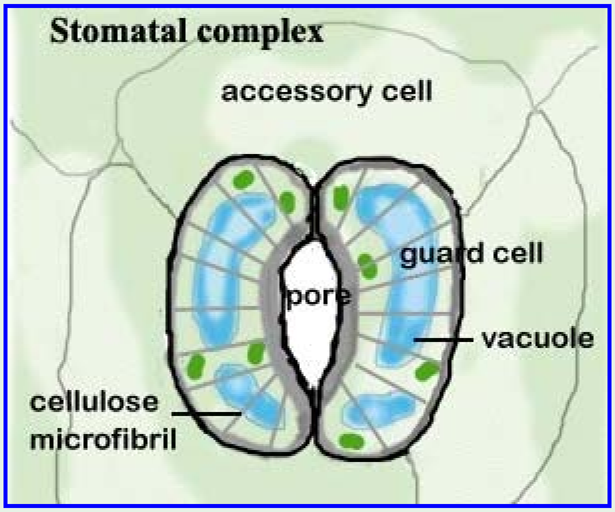
Sterome: "The stems of many early polysporangiophytes [our tracheophytes] have a well-developed peripheral zone (sterome) consisting of several layers of thick-walled, decay-resistant cells ... . This zone is continuous in many zosterophylls, including *Gosslingia*, *Sawdonia*, and *Crenaticaulis*. No equivalent tissue has been recorded in the basal members of the Lycopodiales, and although thick-walled cortical tissues are present in extant Lycopodiaceae, these tissues are unlignified in the basal members of the clade (e.g., *Huperzia*)." Kenrick & Crane (1997).

Stigma: (pl. *stigmata*) the distal part of the pistil, the



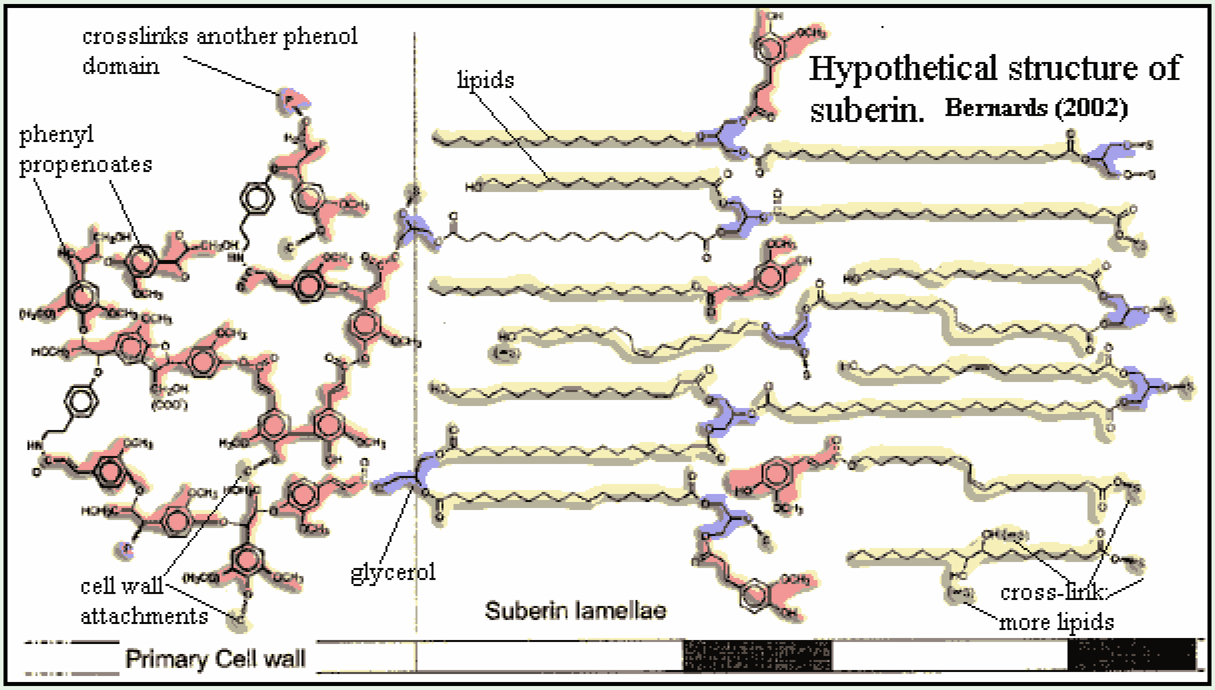
organ that receives the pollen. Stigmata may be quite varied in shape and structure. They are often button-shaped and studded with hair-like papillae ("dry" stigmata) or coated with a sticky film ("wet" stigmata) to capture pollen.

Stigmarian: originally meaning "similar to the roots of *Stigmaria*." As it turned out, stigmarian roots are neither roots nor attributable to a genus *Stigmaria*. Instead, they are the basal branch systems of tree-like lycopsids. Stigmarian "root" systems probably lay on, or just under, the surface, with a photosynthetic upper surface. They radiate from the central axis and bifurcate equally, as do lycopsid branches. The "roots" bear scars which probably, like the scars on lycopsid branches, indicate the positions of small (microphyllous) leaves. Prof. Ralph Taggart (Michigan State Univ.) has some good images at **Arborescent Lycopods**.



Stoma: (pl. *stomata*) tiny pores or opening in the epidermis of leaves; stomata are flanked by two guard cells that regulate opening and closing of the pore and thus regulate gas exchange (respiration) and *transpiration*. Image from the **Ecotree** site by Martin Cocks of the University of the Western Cape (South Africa).

Strobilus: (pl. *strobili*) a cone a cone-shaped cluster of spore-bearing leaves (*e.g.*, a pine cone), an aggregation of *sporophylls* on a common *axis*. Kenrick & Crane (1997) define *strobili* as "aggregations of micro- and megasporangiophores, typically around an unbranched determinate axis." They note that all strobili are not necessarily homologous: "strobili usually comprise *sporangia* and the associated *sporangiophores*, which are clearly modified *microphylls* in lycopsids, are probably highly modified *megaphylls* in seed plants, and are reduced branches in the Equisetopsida. In the Zosterophyllopsida, sporangia are aggregated into strobili in which microphylls and sporophylls are generally absent ("naked strobili" ...). Early fossil members of the Euphyllophyta, including taxa in the Spermatophytata, Equisetopsida, and Filicopsida stem groups, seldom possess strobili although sporangia are typically aggregated into terminal clusters (*e.g.*, *Psilophyton* ...)."



Suberin: waxy, waterproof chemical in some plant cells, notably cork (in stems) and endodermis cells (in roots). Suberin is an extremely complex and irregular material, like *lignin* -- with which it shares some similarities. Suberin is composed of two physically separated domains: the aliphatic and phenolic. The phenolic domain is rather lignin-like, but with even greater variability, and built on the same basic unit of a di- or tri-hydroxyphenyl group attached to a three-carbon chain, variously oxidized and integrated with the carbohydrates of the cell walls. Perhaps the most common building block is ferulic acid: formally, 3-(2'-methoxy-3'-hydroxyphenyl)-propenoic acid. Distally, the phenolic domain is attached at points by ester linkages to glycerol. The remaining hydroxyls of the glycerol molecule are ester-linked to some strange-looking C-18 to C-30 lipids. These lipids are substituted at C9-10 with one or two hydroxyls, or even with an epoxide link between the two carbons. Finally the **ω** position may be oxidized to a carboxylate (alone or esterized to glycerol) or hydroxyl (alone or esterised to ferulic acid). Variations allow for cross-linkage to other suberin molecules via the 9-10 or **ω** positions. Image adapted from Bernards (2002).

Style: a tubular column in the *pistil* of a *flower*, through which the *pollen* is transported from the *stigmata* to the *ovary*.

Succulent: a plant that is able to store water in its tissues and then withdraw it during times of drought. *e.g.* a cactus. The water storage tissue may be found in the stem, leaves, or roots depending on the species. Stem succulents, leaf succulents, and root succulents are types of growth forms.

Sympodial: of branching patterns. Sympodial branching is a a developmental pattern in which branches arise from division of the *apical meristem*. That is, the growing tip of the plant simply divides in two, although the division may not be equal. A new growth axis is not formed. Instead, the old axis heads off in two different directions. Compare *monopodial*, *pseudomonopodial*. These terms are also used with reference to growth patterns of rhizomes, flowers, etc. They are also quite frequently used wrongly. Some writings define these terms by reference to the branch angle. Sympodial branches are typically <45° from the vertical axis, but the term *sympodial* refers to a development course, not gross morphology. Other materials restrict *monopodial* to (?multiple) branches from nodes. That's closer, but too restrictive. It misses the evolutionary point and isn't consistent with the established use of this term in paleobotany.

Synangium: (pl. *synangia*) a reproductive unit composed of fused sporangia.

Synapomorphy: a unique character which is shared by all basal members of a clade and is derived from their common ancestor, but not shared with ancestral groups. A synapomorphy may be secondarily lost in later descendants. Only a synapomorphy may be used to infer phylogeny.

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Glossary T-Z

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-T-

Terete: "Smooth, cylindrical and tapering. Often used in describing vascular cells in plants (esp. xylem cells)." **Glossary**.

Tetrastichous: of branches etc. Arranged in four rows (looking down from the top of the main axis).

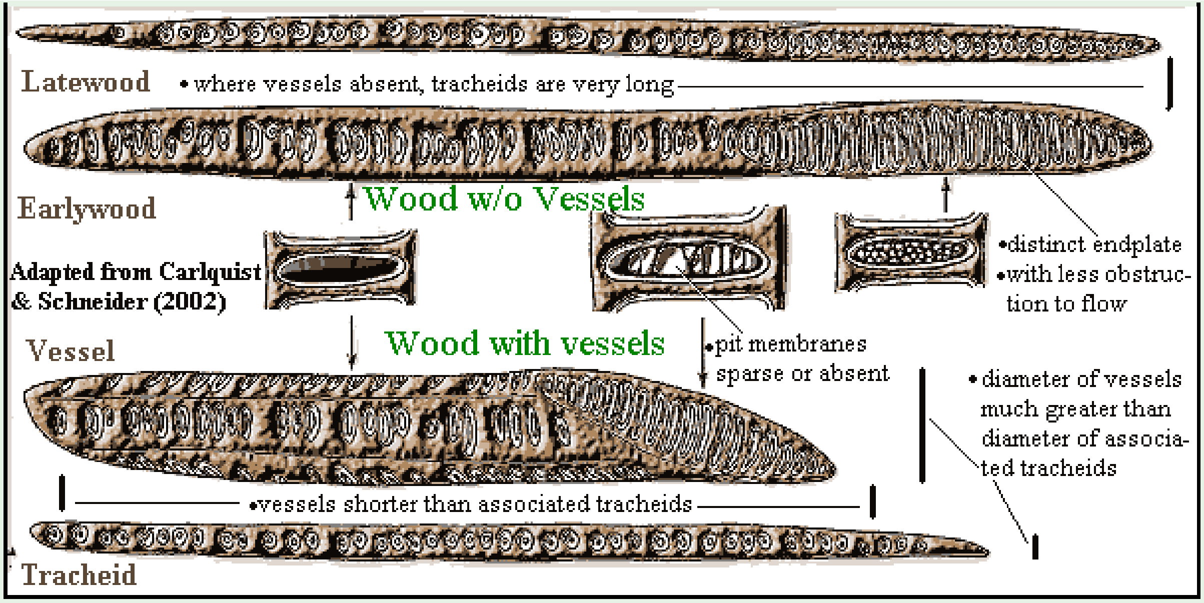
Thallus: term given to the body of a lower plant which has no recognizable shoot, root, leaf regions. Most of the things this term is used to describe are not even plants, ***e.g.*** lichen. However, the term does apply to plants like the liverwort shown in the image. Image from the **Majors Biology** site of Tyler Junior College (Texas).

Thalloid: with reference to a growth habit, recumbent, spreading along the substrate (***e.g.***, mosses and liverworts); as opposed to ***axial***, growing upward from the substrate (***e.g.***, trees).

Thallophyte: an organism not differentiated into shoot and root, the cells of which have a cell wall; originally used for bacteria, Fungi and algae.

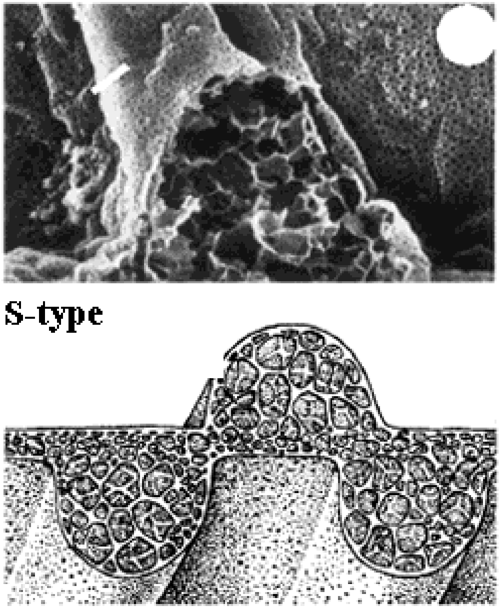
Toothed margin: (leaves) margin having projections or serrations with pointed apices, indented less than one quarter of the distance to the midvein or long axis of the leaf; compare entire margin and lobed margin leaves.

Tracheid: This definition used to be so ***simple***. Its like this. In the good old days, xylem had two kinds of tube-like systems, **vessels**

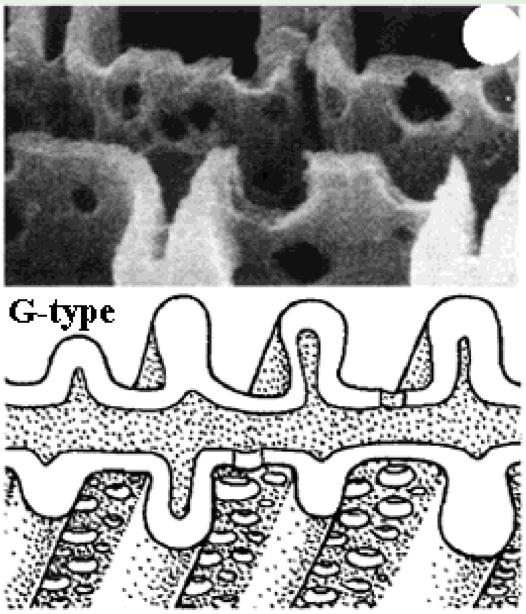


and **tracheids**. Vessels were wide, open, short and dead. Tracheids were narrow, closed-ended, long, and mostly had some living cell associated with them. Then came Carlquist & Schneider (2002). These folks unfairly used actual observations, rather than generations of classroom dogma. This was an utterly rotten thing to do because it messed up a lot of perfectly good, if slightly faded, lecture notes. C&S pointed out that there are at least six character states involved, and that any given plant may have tubular things of several different kinds falling almost anywhere in that morphospace. To complicate matters further, in plants with vessels, the tracheids may have specialized as structural support tissues (biological rebar). In plants without vessels, tracheids often differ strongly between vessel-like earlywood and latewood tracheids. The morphological characters identified by C&S are shown in the figure.

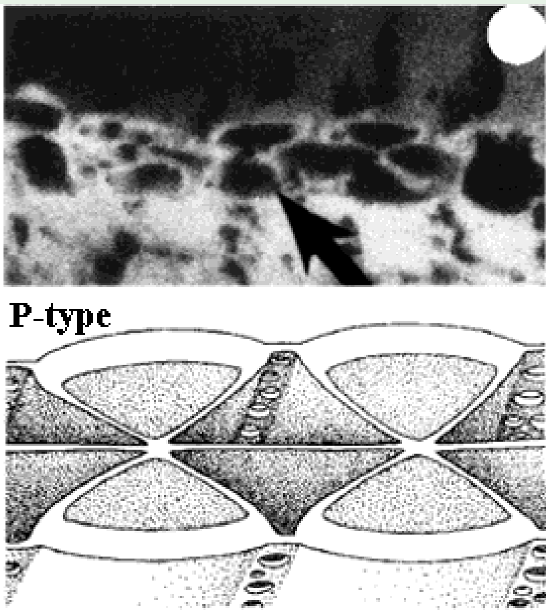
Tracheid types: early plants developed several distinct types of tracheids. ***See*** Friedman & Cook (2000); Kenrick & Crane (1997). These are described in the figure:



S-type tracheids: basal Rhyniophyta. Walls with annular or helical thickenings made of spongy material. Thin, decay-resistant layer which may be microporose on the internal face.



G-type tracheids: zosterophylls. Annular or helical thickenings probably of non-resistant material plus thick resistant (lignified?) layer between thickenings. Pits or perforations present between interior and resistant layer.



P-type tracheids: basal Euphyllophyta. As in G-type, secondary thickenings hollow or non-resistant to decay. Perforations open into a pit cavity. **Adapted from Friedman & Cook (2000).**

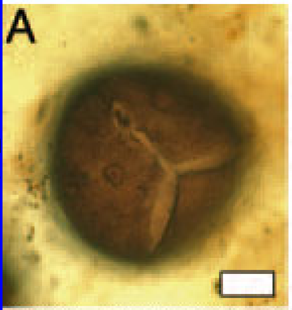
Tracheophyte: plants with true vascular tissue, i.e. xylem and phloem;. Includes all land plants higher than bryophytes (mosses) and liverworts.

Translocation: the process whereby solutes are transported through the phloem. Unlike ***xylem***, phloem is essentially a chain of living cells. The most widely accepted explanation for translocation of substances in the phloem is the Münch pressure flow hypothesis. The proposed mechanism is as follows: a high concentration of solute (***e.g.***, sugars) is loaded into cells of the phloem, presumably by active transport, at locations, such as a leaf, where sugars are produced by photosynthesis. The high solute concentration in the phloem cell creates an osmotic gradient which draws water into the phloem. The resulting high turgor pressure causes flow to occur. If the dissolved sugars or other chemicals carried along with the sugars are removed from the phloem at another place in the tree for use (a sink such as a root or fruit), the decline in concentration of sugar causes water to move out of the phloem cells. Because water is moving in at a source and out at a sink, there is a mass flow of water and substances in the phloem.

Transverse section cross section. A section perpendicular to the main axis of the plant or organ.

Triarch: consisting of three; for example a triarch stele has three lobes.

Trilete: a term used to describe spores with a 'Y'-shaped suture. This is believed to represent the attachment point of a spore tetrad (group of 4). "This scar results from the splitting of the spore mother cell into four equivalent reproductive cells in such a manner that the four are all in contact at a single point. When these cells separate, they carry a remnant of the point of commonality and the lines of contact with adjoining cells, forming the "Y" shaped mark or suture. The same effect can be produced by pressing four balls of clay or plasticine tightly together, then carefully separating them again." **Earth History Research Center**. Image from Taylor ***et al.*** (2005).



Trilete spore of *Aglaophyton* Taylor *et al.* (2005). Scale bar = 15 µ.

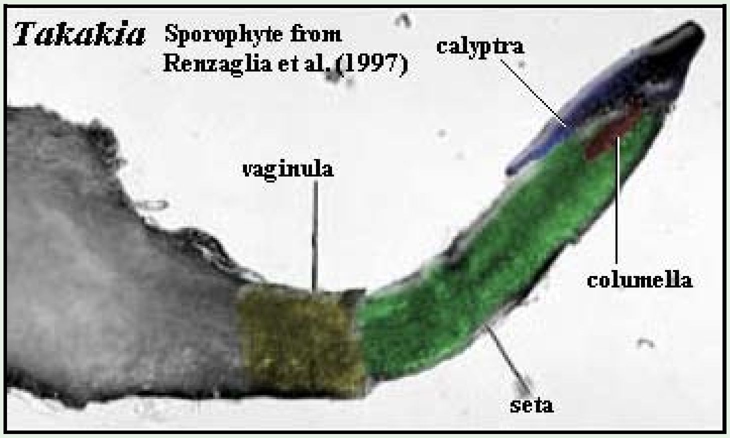
Turgor: ***see*** osmotic pressure.

-U-

Unifacial Cambium:

Urn: a term used for anything even vaguely vase- or gourd-shaped, ***e.g.*** the sporangium in mosses.

-V-



Vaginula: in mosses, a derivative of the ***archegonium*** forms a hard, protective ***epigonium*** around the developing sporophyte. Later the epigonium breaks up, but the sporophyte retains a conical "dunce cap" or ***calyptra*** over its distal end and sometimes a ring around the base. The term calyptra refers to the "dunce cap," and the piece of the epigonium retained around the base (if any) is the ***vaginula***.

Vascular: relating collectively to the conductive plant tissues, xylem and phloem. Analogous vascular tissues in bryophytes are referred to as hydroids and leptoids, respectively.

Venter: swollen basal region of the archegonium where the sporophyte develops in bryophytes.

-W-

Wood: ***see*** lignin.

Wood ray: a radially oriented tier of parenchyma cells that conducts food, water, waste products and other materials laterally in stems and roots of woody plants; rays are usually continuous across the vascular cambium between the secondary phloem and xylem.

-X-

Xylem: Vascular tissue specialized to transport water and solutes. Generally composed of lignified (woody) dead cells. Unlike phloem, which does not accumulate but instead is shed with the dead bark, the old xylem is retained, may be used to conduct water for a few years, and eventually just provides structural support as the tree grows larger. At least 90% or more of the trunk of a tree is xylem or wood.

Xylem, primary: ***see primary xylem***.

Xerophyte: a plant well adapted to withstand prolonged drought. The typical xerophyte is a deciduous shrub with tiny leaves and a shallow root system that extends well beyond the crown of the shrub.

-Z-

Zygote: according to Wikipedia, from Greek ζυγωτός zugootos "joined" or "yoked", from ζυγοῦν zugoun "to join" or "to yoke". We believe this etymology is absolutely correct. The term refers to the fertilized egg and the earliest stages of development of the embryo. In botany, this represents the earliest developmental stages of the ***diploid***, ***sporophyte*** generation.

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-B-

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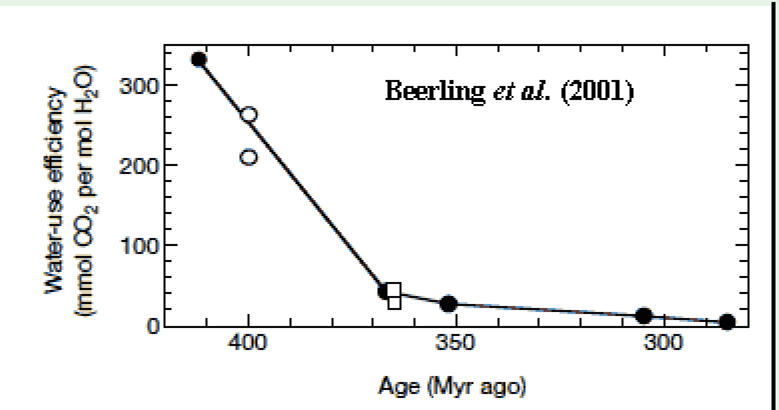

Figure 2 Stimulated and isotopically derived changes in leaf and axis water-use efficiency during the Late Palaeozoic era. Black circles, estimate from soil organic $\delta^{13}C$; white circles, simulated Early Devonian axis; white squares, simulated Early Carboniferous planate leaf.

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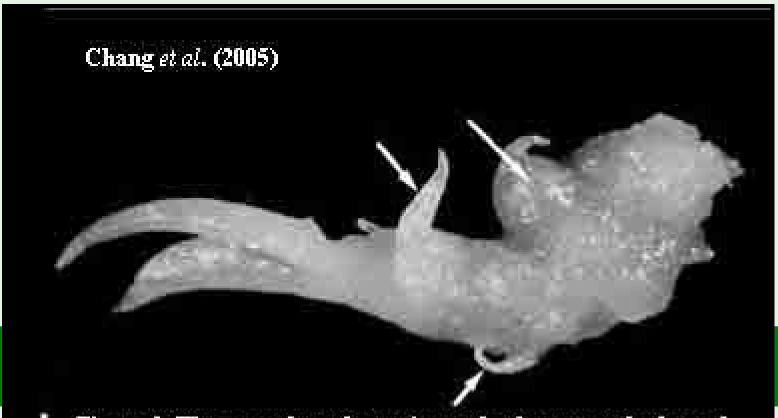

Figure 2. The apex shoot formation and subsequent the lateral bud (è) developed of rhizome of C. dayanum. (bar = 400 µm)

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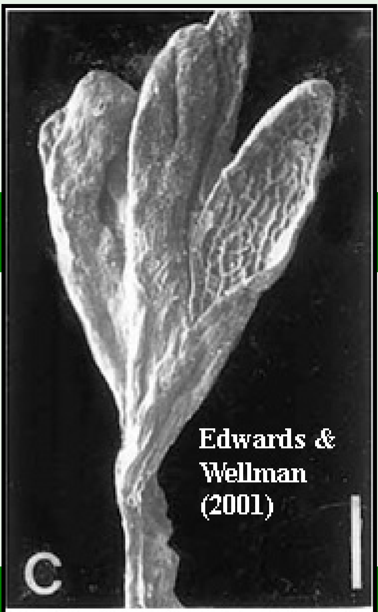

Fig. 2C. Scanning electron microscopy of mesofossils. C: *Salopella cf marcensis*. **NMW93.98G.8. Scale bar = 100 µm.**

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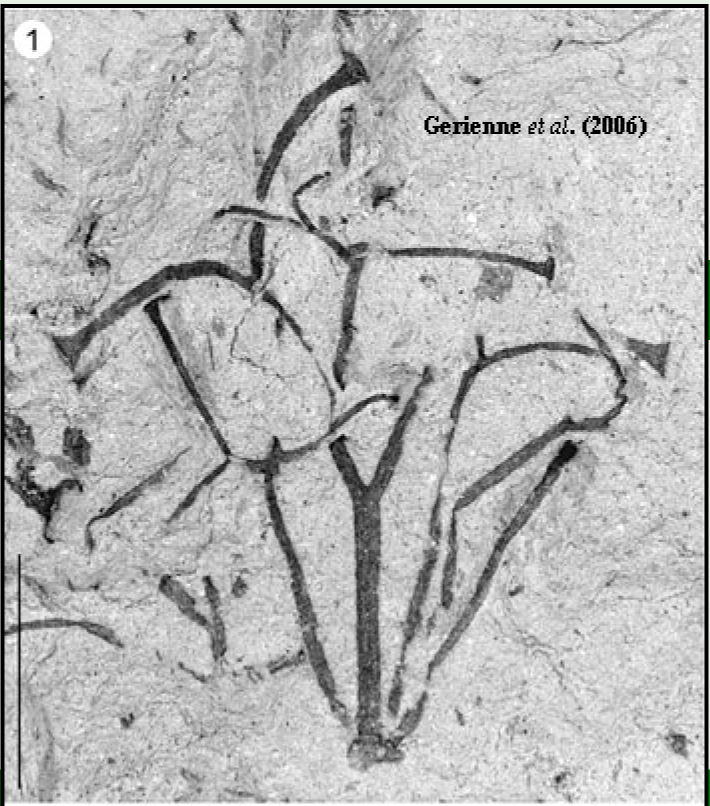

Cooksonia paranensis **from the Early Devonian of the Paraná Basin (Brazil), interpreted [as] ... five sporophytes attached to a thalloid gametophyte. [Scale bar = 1 cm].**

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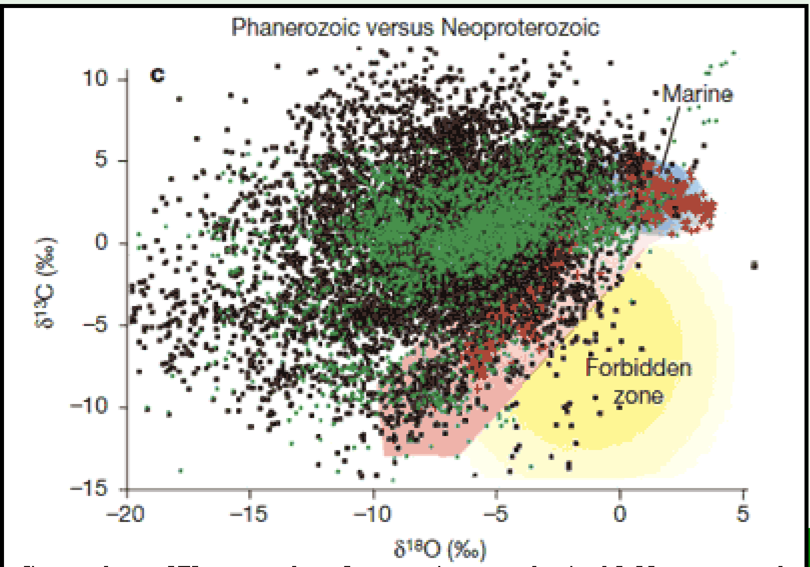

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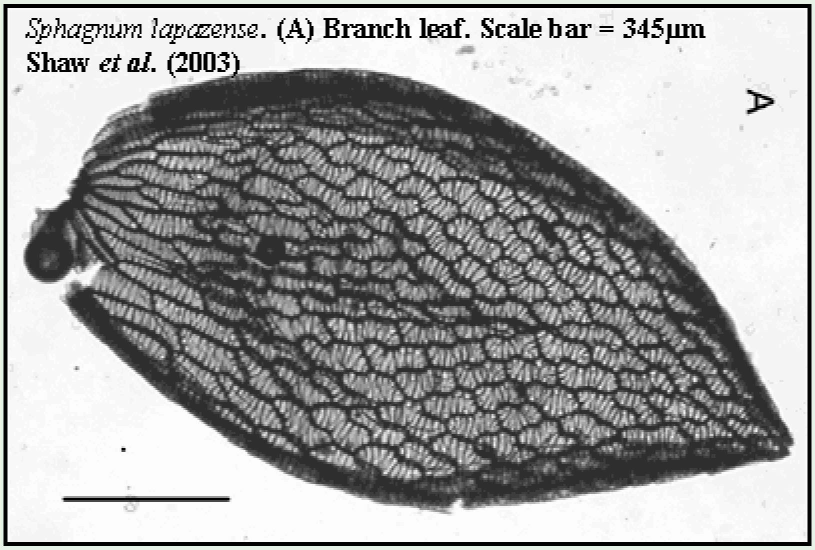

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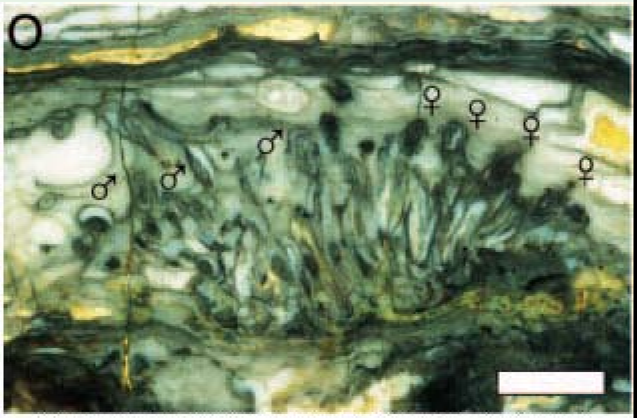
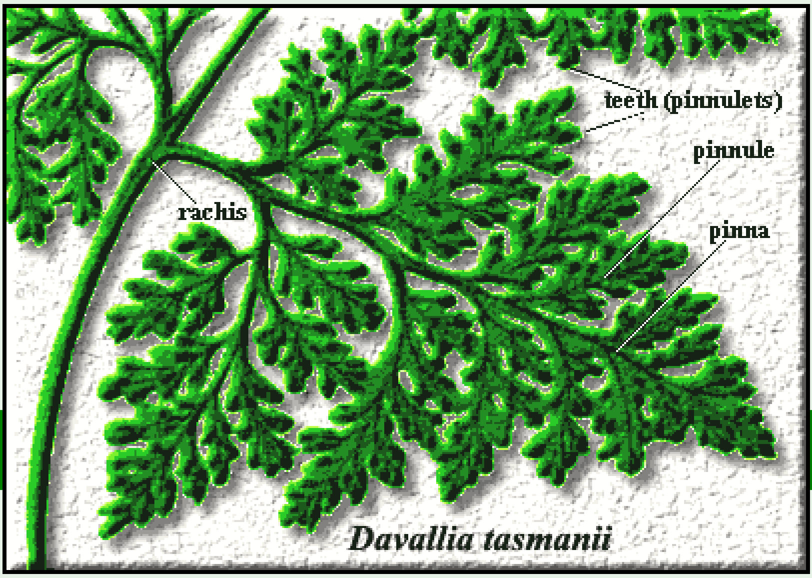


Dense cluster of *Rhynia* gametophytes in the Rhynie Chert. Scale bar = 6.5 mm. From Taylor *et al.* (2005).

-V-



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Bryophyta - 1

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CHLOROBIONTA
|--Chlorophyta
`--Charophyta
   |--(various green algae)
   `--Embryophyta
      |--BRYOPHYTA
      |  |--Sphagnum
      |  `--+--Andreaeids
      |     `--+--Polytrichales
      |        `--Bryopsida
      `--Tracheophyta "rhyniophytes"
         |--Lycophytina
         `--Euphyllophyta
            |--Monilophyta
            `--Spermatophytata
               |--trimerophytes
               `--SPERMATOPSIDA
```

The Mosses

If the mosses had not survived into the present, we would be forced to invent them as just the sort of intermediate we might expect between essentially aquatic algae and fully terrestrial plants. Mosses and, to a lesser extent, other basal plants, do have differentiated shoots. Although these are generally only a few millimeters tall, they are still designed to provide mechanical support against gravity on land -- the first such structure in any kingdom. Bryophytes also have leaves of a sort (*phyllids*). These are typically one cell thick and lack veins, although they may have a central thickening for support. Mosses also have *rhizomes*. These may have some function in extracting soil nutrients, although their primary function seems to be mechanical attachment to the substrate. Thus they are not true roots, but do approach that condition.

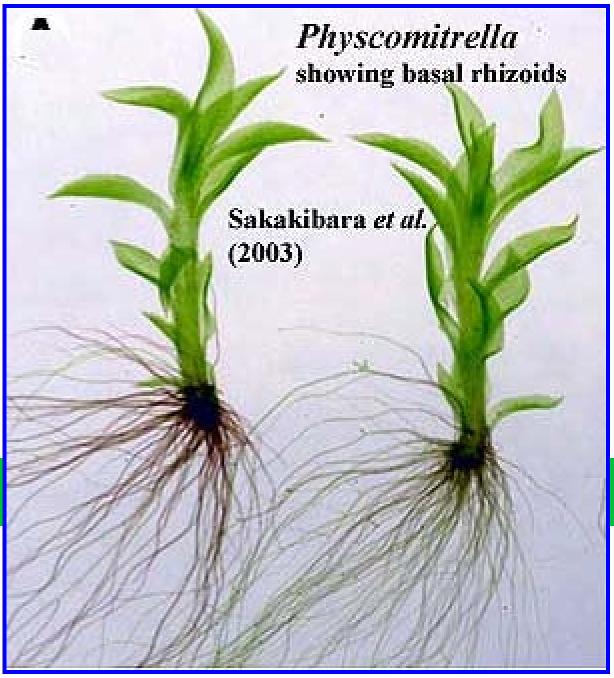
The bottom line is that, structurally, mosses really differ from rhyniophytes in only one aspect: mosses lack the particular, specialized *vascular* tissues of tracheophytes. That alone is sufficient to explain the lack of big leaves, long stems, and true roots. This whole complex of characters is thus probably primitive. The other distinctive character of mosses is that the plant we normally observe is the *haploid*, *gametophyte* stage. But this character is shared with liverworts (basal embryophytes) and so is also probably *plesiomorphic*.

Curiously, in hornworts (also basal embryophytes) the *sporophyte* generation is dominant. In addition, it turns out that the leaves of moss probably evolved independently from the leaves of higher plants. So the relationships of the mosses and basal embryophytes are still uncertain. What really seems to set mosses apart is their unique form of leaf. What may unite mosses with higher plants is (a) the presence of *stomata* to control water loss and (b) *meristem* (apical growth) in the sporophyte generation. *See*, Friedman *et al.* (2004). However, even these similarities may not be strictly homologous. Phylogenetically, we treat Bryophyta as Moss > *Quercus*.

A word about terminology. "Bryophyta" was formerly used, and is still used by many to include the liverworts and hornworts, as well as the mosses. Since the branch order and monophyly of the mosses and the two liverworts (Marchantiophyta) and hornworts (Anthocerotophyta) remains unclear, this is understandable. However, we prefer the more restrictive use of the term to mean just mosses, since the mosses are probably *monophyletic*. The wort + moss group, however structured, is almost certainly *paraphyletic*. That is, the broader definition takes in all of the basal radiation of embryophytes (land plants), including the direct ancestors of the "higher plants."

Image: moss on rocks in Iceland from **Arrakeens Site**.

The Gametophyte

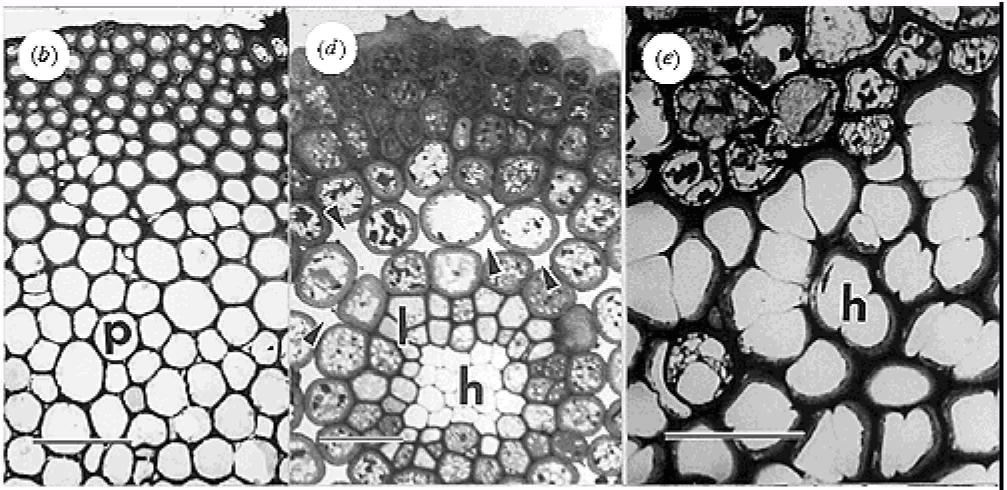


As mentioned, the gametophyte (haploid) generation is dominant in the life cycle of mosses. The sporophyte (diploid) form remains attached to and dependent on the gametophyte at all times. That being the case, we can best describe the mosses starting from the bottom and working up to the gametic structures, then proceeding from the *archegonium* (ovary) to the developing sporophyte as if it were an extension of the gametophyte, which is essentially the case. There is considerable variety among mosses; but, when in doubt, we sometimes defer to the peat moss *Sphagnum*, which is not only the most basal living moss, but also the most common. (Unfortunately, it is also, in some respects, quite atypical. Shaw *et al*. (2003))

Rhizoids

Mosses manage to look like small tracheophytes, but behave more like liverworts. So, for example, mosses have small, threadlike basal processes which look like roots. In fact, these are simply *rhizoid* holdfasts, not very different from those found in algae. It is likely that the rhizoids absorb water, but only because almost *everything* in a moss absorbs water. However, a moss lacks a highly specialized vascular system, so the water is usually stored in the ubiquitous moss water storage cells. From these cells, water probably diffuses, very slowly, to other parts of the plant; but, in most cases, the probable function of the water storage cell is structural. Since mosses have no wood, either, they use the *turgor* pressure of these storage cells to satisfy much of their modest need for structural support. Another common moss strategy for structural support is to grow very densely. So, like academic communities, they grow progressively larger and denser, maintaining their continued existence by sheer bulk without having any real roots in the environment which supports them.

Actually, we may further extend this dubious simile, since mosses have likewise developed elaborate designs for clinging to each other, so that the entire mass behaves like a foam rubber pillow -- conforming to the slightest pressure, but springing back to business as usual when the pressure is removed.



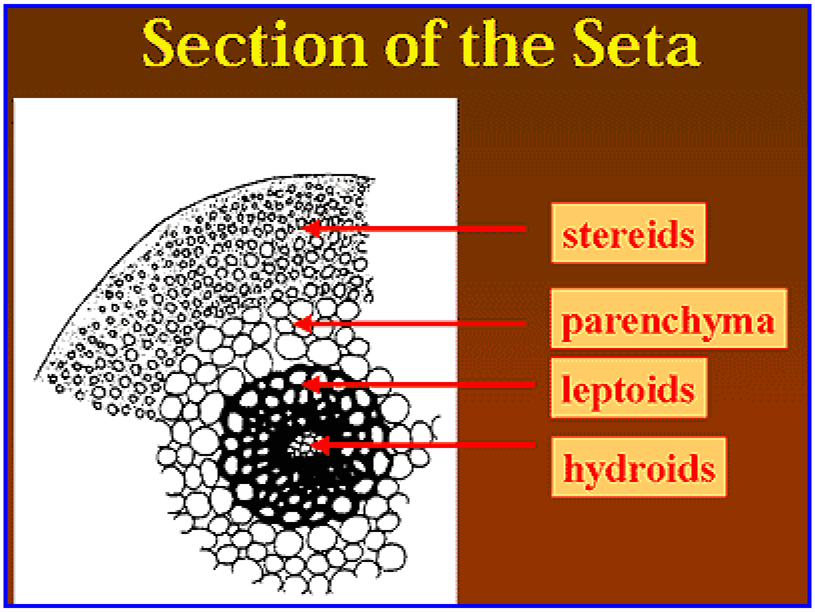
Moss vascular tissues from Ligrone *et al.* (2000) showing range of specializations. (b) undifferentiated parenchyma in *Neckera* (d) hydroids and leptoids in *Pogonatum*, and (e) complex association of hydroids in *Polytrichum*.

One such strategy is the use of yet more rhizoids, growing from the shoot, which entangle adjacent shoots and their rhizoids.

Sakakibara *et al.* (2003) have shown that rhizoids on *gametophores* of *Physcomitrella* differentiate in response to the ubiquitous plant hormone auxin, followed by a (presumably more specific) signal from HD-ZIP homeodomain genes. This is essentially the same mechanism which is involved in the development of roots in higher plants. *Id.*. However, before you get excited, note that it is also the same mechanism involved in, *e.g.* the specification of leaf morphology in higher plants. Micol & Hake (2003). It appears to be a general mechanism for developing lateral structures. Still, this all encourages us to think that there is a broad, underlying homology between roots and rhizoids.

Shoot

Mosses generally have a well-defined shoot in the gametophyte generation. In early development, the plant may take a flattened form, suspiciously similar to the thallus of an alga or liverwort. More typically, the spore develops a long thread-like, recumbent growth, the *protoneme*, which in turn buds off lateral *caulonemata* which develop into stem-like gametophore structures on which the gametes will develop in a terminal *gametangium*. This structure typically has a well-developed pattern of leaves, as in the image of *Physcomitrella* above. It is common to see this referred to as a "stem" or "shoot" although it has no *xylem* or *phloem* and is therefore not really similar to an axis of a vascular plant.

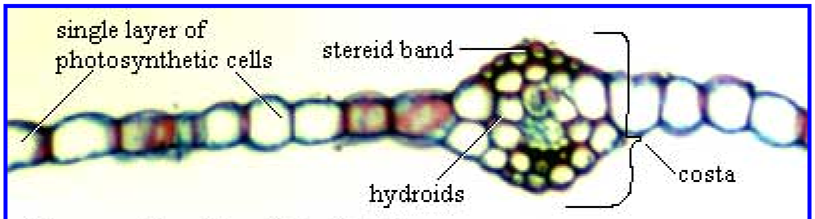


Rather than the xylem or phloem of tracheophytes, mosses have tissues made up of *hydroid* and *leptoid* cells. These are frequently referred to as "vascular tissues," and they do probably serve analogous functions. The subject has been reviewed by Ligrone *et al.* (2000). However, they are not *lignified*. The hydroid tissues, in particular, are the general run of moss water storage cells and are probably only remotely related to the xylem of tracheophytes. Leptoids are not as well understood, but might be homologous to phloem. However there is great variation in the structure and degree of specialization of these tissues, and their phylogenetic distribution is somewhat unexpected. Unfortunately, we have to break off with these vague and enigmatic generalities, or we will never get on with the rest of the job. As it turns out, most water and nutrient transport is actually accomplished external to the shoot, using a variety of rather *ad hoc* tools -- small channels on the surface, gutters and catchments formed by leaves, playing games with mucous and surface tension, etc.

One more cell type worth mention is the *stereid*. These are thick-walled cellulosic support cells found near the perimeter of the shoot (and also in leaves and setae) which presumably function as rebar. They are easily seen on the perimeter of the shoot in the cross-section of *Neckera* in the image above. Growth and differentiation of the shoot, and of nearly everything else in mosses, is driven by a single apical cell.

Image: Seta cross-section from the course web site of **Prof. Robert S. Eagan**, University of Nebraska at Omaha (who has an excellent pdf on bryophyte anatomy).

Leaves & Peripheral Structures



Cross-section of bryophyte phyllid

Bryophyte leaves are generally arranged in a very stereotyped way around the shoot, typically a spiral with four positions (*e.g. Physcomitrella*). The bryophyte leaf typically consists of a single layer of photosynthetic cells with a midline vein, rib, nerve or *costa* (all the same thing) containing hydroids and/or rows of stereids for mechanical support. Botanists who prefer a more exacting definition of *leaf* refer to them as *phyllids*, since moss leaves lack many of the advanced features of tracheophyte leaves. The polytrichid mosses may have much more elaborate structures in both leaves and shoot. By contrast, many mosses lack even the customary costal thickening.

Antheridium of unidentified moss

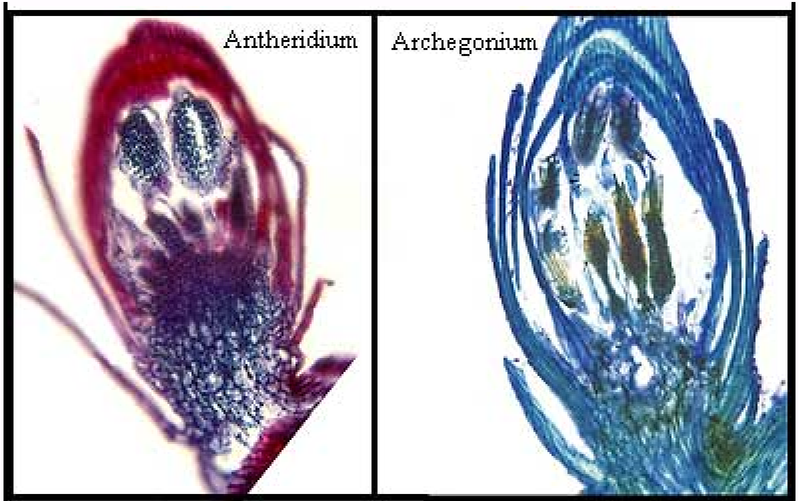
In addition to leaves, moss stems may bear structures for aesexual reproduction -- *gemmae* or *bulbils*. These are not complex. Mosses have great powers of regeneration and can regenerate an entire plant from an isolated segment of a shoot. The gemmae therefore consist of a small ball of undifferentiated cells. Finally, mosses may, like higher plants, also have a waxy cuticle and stomata to help control evaporation. The stomata are restricted to the sporophyte generation -- not only in mosses, but in all land plants, with the exception of the extinct polysporangiophytes -- and many mosses lack stomata entirely. Nevertheless, general statements to the effect that mosses lack cuticles and/or stomata are simply incorrect. *See*, generally, review by Raven (2002).

Image: phyllid cross-section from website of **Dr. George P. Chamuris**, Bloomsburg University.

Gametangia

Mosses may be either *monoecious* (hermaphroditic) or *dioecious*. Similar species within the same genus may differ in this character, and there is little phylogenetic consistency. The gametangia are normally located in terminal clusters at the end of the shoot. However, in *Takakia* and *Sphagnum*, generally considered two of the most basal mosses, gametangia are associated with leaves along the shoot. As we might expect in such a regime, the male and female gametangia have somewhat similar structures. *See* the image from Alejandro (2004). Notwithstanding their general similarity, the archegonia of mosses differ externally from antheridia in having a longer neck and longer stalk. The neck encircles a tube which leads to the cavity (*venter*) containing the female gamete.

Both gametangia form from a stereotyped series of divisions of a terminal apical cell, unlike the gametangia of liverworts and hornworts. However, once the initial division are complete, the developmental pattern of the archegonium is the same in all three groups. "In all three groups, the process involves three longitudinal divisions that form a central triangular axial cell surrounded by three peripheral cells. The peripheral cells form the neck and venter while the axial cell gives rise to the



Gametangia of Neckeropsis. Adapted from Alejandro (2004)

neck canal cells, ventral canal cell and egg. Further divisions in the peripheral cells typically result in a neck of five or six cell rows." Renzaglia *et al*. (2000: 775).

The following description of the structure and function of the antheridium from **Phylum Bryophyta** is better than anything we could come up with, so we quote it *in extenso*: "Antheridia are equally elongated with a long narrow stalk and banana-shaped antheridial body. The sterile jacket is one layered except at the tip where an operculum forms. When mature, the operculum cells dissociate and release blocks of spermatozoids individually enclosed in "vesicles". Spermatozoids are biflagellated [sic], coiled and thread-like [and, we might add, absolutely bizarre in both development and appearance]. Transport of spermatozoids may be effected by rain droplets encountering the cup-like antheridial shoot and splashing packets of cells to adjacent plants." Interestingly, this method of dispersal, by raindrops agitating a cup-like structure, is essentially the same as the method used to disperse gemmae during aesexual reproduction in both moss and other basal plants. *Compare* the very different dispersal method for spores, discussed on the next page.

Credits: the Phylum Bryophyta page quoted above is part of **Land Plants On Line**, the product of Dan Nickrent and Karen Renzaglia (both well-known botanists) of the University of Southern Illinois at Carbondale. Antheridium image from the **Biology 211 Lab** site of Iowa State University.

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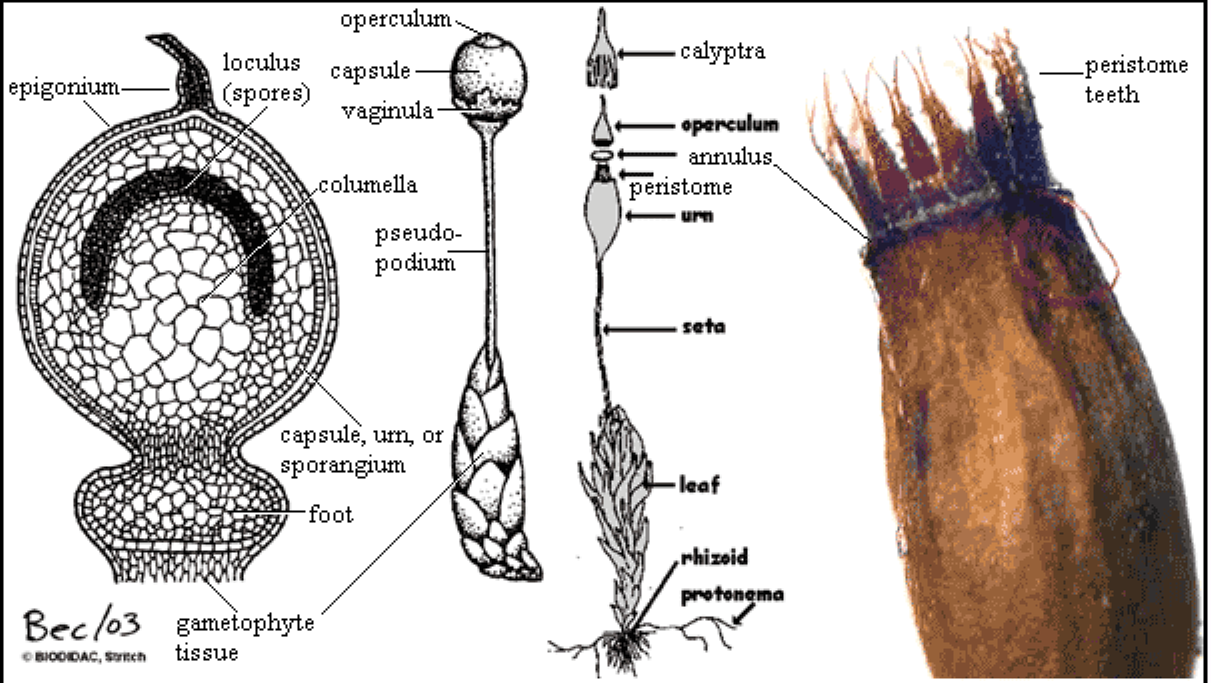
Bryophyta - 1

```
CHLOROBIONTA
|--Chlorophyta
`--Charophyta
   |--(various green algae)
   `--Embryophyta
      |--BRYOPHYTA
      |  |--Sphagnum
      |  `--+--Andreaeids
      |     `--+--Polytrichales
      |        `--Bryopsida
      `--Tracheophyta "rhyniophytes"
         |--Lycophyta
         `--Euphyllophyta
            |--Monilophyta
            `--Spermatophytata
               |--trimerophytes
               `--SPERMATOPSIDA
```

The Sporophyte

The sporophyte generation of mosses is completely dependent on the gametophyte and never makes independent contact with the substrate. Accordingly, we treat it as an anatomical extension of the gametophyte. A generalized bryophyte sporophyte can be considered as having three parts: a "foot" which connects the embryo to the gametophyte



Development of the moss sporophyte. Left two images are of *Sphagnum*. Right two images reflect development of the sporophyte in Polytrichales

to extract nutrients,
a seta which lifts the mature sporophyte clear of the gametophyte body, and a terminal sporangium capsule. Shaw & Renzaglia (2004). In addition, we might add the protective structures formed by the gametophyte.

The figure shows roughly how the structure works in development. **(1)** Initially, the sporophyte is completely surrounded by the *epigonium*, a protective coat supplied by the gametophyte. As the sporophyte grows, it elongates and grows wider, eventually fracturing the calyptra. The last remnants form a loose, pointed apical dunce cap, the *calyptra*, and sometimes a ring around the base, the *vaginula*. At the same time (approximately -- the timing is quite variable) three other things are going on. **(2)** the inner sporophyte capsule (a/k/a *urn* or *sporangium*) is developing and hardening. **(3)** the sporophyte is levitating itself clear of the mother-ship on a long extension tube, the *seta*. **(4)** Inside the sporophyte, cells on the surface of a central *columella* (think of it as a little internal shoot) are undergoing meiotic divisions to create haploid spores. The small spaces where this is going on are called *loculi*. *Loculus* may be translated to mean, oddly enough, "small space." Perhaps fortunately, people tend to avoid Latin these days and refer to it as a *locule*.

Later, the calyptra dries up completely and falls off, and the capsule is exposed, with the end sealed by a small *operculum*. Eventually, this, too, is lost. Many derived mosses have yet another control on spore dispersal: a *peristome* with peristome teeth arranged around an *annulus*. The teeth are quite diagnostic of the species and are much sought after by species-level taxonomists for this reason. The teeth are so constructed that they bend outward as they dry out, causing the opening to widen and release the spores. Note that that this entire system is designed to promote spore dispersal in relatively sustained dry weather and moderate winds. That seems an odd sort of requirement for a plant that requires flowing water for sexual reproduction.

Bear in mind that that this describes sporophyte development in an imaginary "typical" moss. As we keep saying, there is a great deal of variation. *Sphagnum*, for example, has no seta. In *Sphagnum* and other basal mosses, the sporophyte is raised by the *pseudopodium*, a structure produced by the parent gametophyte.

These last three paragraphs will get you by the usual, garden-variety botany mid-term. Because we are kindly and avuncular, but mostly because you must be quite desperate if you are trying to prepare for an examination using this site, we will also add that most teachers of botany have their own, favorite moss -- the one they learned bryology on. It might be wise to bone up on the idiosyncrasies of that plant as well. And don't forget the mandatory life cycle diagram. Best of luck ...

Diversity

Here we have deliberately picked a mixed bag of Latin endings: *Sphagnum*, "Andreaeids," Polytrichales, and Bryopsida. In a cladistic scheme, it makes no sense to agonize over the rank of the groups. Instead we've simply used a variety of rank suffixes to convey other information -- or possibly just to be obnoxious. In any case, *Sphagnum* is a single genus, so there's no sense in dressing it up as anything else. The Andreaeids are a paraphyletic collection of (probably) three small genera, two of which may have a good deal in common. We've added *Takakia* because it has no obvious place anywhere else. Polytrichales is a moderately diverse bunch of "typical" mosses -- probably monophyletic. Hyvönen *et al*. (2003). Bryopsida is an extremely speciose, but fairly uniform, set of plants -- a large and distinct monophyletic assemblage. Consequently, we've given it the highest "rank" consistent with common usage.

Sphagnum

Sphagnum is different from all other mosses in many ways. There has never been much doubt that it is the sister group of all other mosses. *Sphagnum* is the moss which forms peat. There are 250-400 living species (Shaw *et al*., 2003) which collectively have the distinction of covering 2-3% of the entire land surface of the Earth (an oft-repeated statistic -- but how was this computed?). The plants create an environment


Sphagnum moss with sporophytes. Note the extended pseudopodia.

which is antiseptic and acidic, thus the plants (and anything in them) are extremely slow to decompose.

Many of *Sphagnum*'s unique features may be plesiomorphic ("primitive") traits. The fossil record of mosses is so poor that we can't tell if these are unique specializations or traits left over from the distant common ancestor of all mosses. For example, the phyllids contain a very high proportion of hydroids mixed in with the photosynthetic cells -- to the point that the plants often look grey-green rather than the bright green of other common mosses. The spore expulsion (*dehiscence*) is explosive. These characters, and *Sphagnum*'s acid, antiseptic secretions, appear highly specialized. However, unlike other mosses, *Sphagnum* does not retain a calyptrum "cap." You can see the naked operculum in the image. *Sphagnum* sporophytes also lack a peristome. On germination, the spores may (not always) form a structure which looks suspiciously like the flat thallus of a liverwort. As mentioned above, *Sphagnum* forms a pseudopod from the gametophyte, rather than a seta from the sporophyte.

Other peculiar features of *Sphagnum* have been recently summarized by Shaw *et al*. (2003). One deserves special mention because of its possible implications. In all mosses except *Sphagnum*, the spores themselves are formed from the central, invaginating *endothecium* tissues -- very much in the manner of mesodermal structures developing from the developing coelom in the gastrula embryo of animals. In *Sphagnum*, the spores develop from the outer *amphithecium* -- just as, in some basal, "acoelomate" animals normally "mesodermal" tissues are derived from ectoderm. ... Compare the *Sphagnum* sporophyte (the leftmost image in the collection above) with a typical microlecithal animal embryo at gastrula, and ponder that one a while. This is undoubtedly a case of convergence, but moderately mind-blowing all the same.

Image: *Sphagnum* from the website of **Dr. George P. Chamuris**, Bloomsburg University.

"Andreaeids"


Andreaea (left) and *Takakia* (right) gametophytes

The Andreaeidae, as generally described, include *Andreaea* and *Andreaeobryum*. In most respects they created a smooth and continuous path of character acquisition from *Sphagnum* up through the Bryopsida. The genus *Takakia* was originally considered to be a very peculiar liverwort. However, when the sporophyte of *Takakia* was ultimately described, it became obvious that *Takakia* was a moss. *See* discussion in Renzaglia *et al*. (1997). This dug a raw and unseemly pot-hole in the phylogenetic pathway, since *Takakia* has an odd mix of characters. The current best guess is that *Takakia* is closest to the Andreaeidae -- but it is perhaps more bryopsid-like in some ways.

As mentioned, the Andreaeidae themselves are more cleanly intermediate forms. The gametophyte is almost indistinguishable from the gametophyte of the Polytrichales. However, the sporophyte has a number of primitive features. As in *Sphagnum*, the gametophytic coat over the sporophyte, the *epigonium*, is retained until just before *dehiscence*. Similarly, they the sporophytes are elevated on a pseudopodium, rather than a *seta*. Unlike *Takakia* or bryopsids, *Andreaea* has a relatively short sporophyte foot. However, the foot in *Andreaeobryum* is elongate. The

Andreaeidae are also primitive in (probably) producing spores from *endothecial* tissue, although this tissue grows over the *outer* wall from the base of the columella, rather than covering the columella as in *Sphagnum*. The capsule wall itself is even less specialized than in *Sphagnum*. It rests directly on the spore mass, is single-layered, and lacks a distinct operculum. Dehiscence in all Andreaeids is accomplished by slitting the lateral walls of the capsule. Renzaglia *et al*. (1997).

Images: *Andreaea* from **Images of California Bryophytes**. *Takakia* from the **Interactive Malesian Moss Database** (Nat. Univ. of Singapore).

Polytrichales

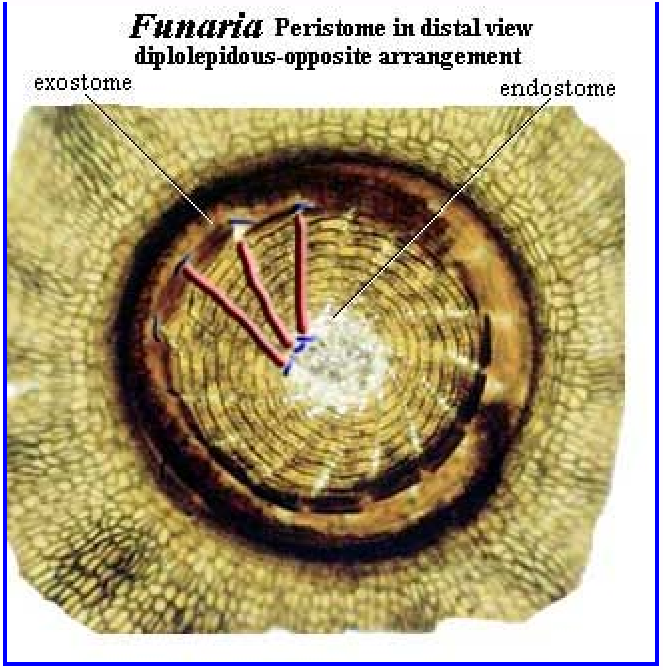
Our previous tiresome remarks notwithstanding, botanists have drawn a real distinction between Polytrichopsida and Polytrichales in that the former includes the Tetraphidales, encompassing such genera as *Buxbaumia*, *Oedipodium*, *Tetraphis*, and sometimes even *Andreaeobryum* and *Takakia*. Hyvönen *et al*. (2003). The possible inclusion of the last two genera strongly signals the likelihood that this is a garbage taxon. So, for the moment, we will ignore it and collapse Polytrichopsida into Polytrichales.

Polytrichales includes about 19 genera and perhaps 200 species. The following general description is derived from Hyvönen *et al.* (2003) with only minor changes. Polytrichales are typically pioneer plants of open, sometimes even dry, habitats. The group exhibits great diversity: from miniature plants with reduced leaves such as *Pogonatum pensilvanicum* of eastern North America, to giants of Australasia and New Zealand like *Dawsonia superba* (height up to 50 cm) with the best-developed gametophyte of all land plants. The most typical features of the gametophyte are closely spaced adaxial lamellae on the leaves, forming a pseudoparenchyma, and differentiation of leaves into a distinct blade and sheathing base. The calyptra is typically hairy in many common species of the Northern Hemisphere, enveloping the developing capsules of the sporophyte generation. This has given the whole group its name, although most genera have a practically naked calyptra. Capsules of the Polytrichales normally have a well-developed peristome with at least 16 teeth formed of whole cells. The epiphragm covering the mouth of the capsule is a unique character that distinguishes Polytrichales from all other groups of mosses. Size and shape of the capsule vary greatly among genera.

Image: *Dawsonia superba* from **The Hidden Forest**.

Bryopsida

The Bryopsida include 90% of all moss species. Given this fact, and given the long history of the group, it ought to be a simple matter to list the characteristics which identify these as the definitive moss lineage. In fact, it is not. Bryopsids *typically* have a number of characteristics, many of which are mentioned by Renzaglia *et al*. (1997). Thus, bryopsid sporophytes generally have vertically aligned plates embedded between multiple layers of cells in the amphithecium. They possess stomata which may or may not be homologous with those in higher plants (but *Sphagnum* also has stomata of a sort). The sporophytes also develop opercula, peristomes, continuous columella, and a spongy layer between the amphithecium and the spore mass. The setae frequently twist



at some stage of sporophyte development.

However, only one characteristic seems to be both unique and universal among bryopsids. All bryopsid gametophytes are arthrodontous or descend from ancestors which were *arthrodontous*. That is, these mosses have *peristome teeth* which are formed by walls growing between the rows of cells making up the mouth of the spore capsule. This and other critical concepts in moss dentistry are explained and illustrated at the Tree of Life page on Bryopsida, thereby saving us the bother.

According to Newton *et al*. (2000) this clade is strongly supported using both morphology and molecules. Further, the basal three genera are all, like *Funaria* in the image, *diplolepidous-opposite*. That is to say, *Funaria* has two rows of plates (*exostome* and *endostome*) which line up to form radial teeth between them.

Image: *Funaria* peristome from the **Bot 125 Plant Morphology site**.

Evolution

Most of the general features of moss evolution are implicit in the descriptions above, but we include two odd speculations that may be worth the effort of explaining.

First, we have, somewhat speciously, compared the sporophyte to the gastrula of an animal embryo. Those similarities probably reflect the inherent advantages, and limited number of ways to create, an additional population of specialized developmental cells which can do their job in a tightly controlled internal environment. The best geometrical solution to that problem is probably the one represented by the gastrula or columellar sporophyte. This creates a controlled volume, closely bordered by two layers of different types of cells. One might evolve such a system simply by having a flat embryo -- or sporophyte, as the case may be. However, the advantage of creating the space by localized invagination is that it automatically creates proximo-distal polarity, and thus a fundamental tool for differentiation between separate parts of the organism. Although plants never went this direction, the mechanism also creates the further possibility of dorsoventral polarity, if the invagination can be consistently flattened in a particular plane. In mosses the "mesodermal" compartment was co-opted almost completely for the production and storage of gametes. The same is true of many basal invertebrates. However, the elaborate peristomal structures of mosses show that mosses developed the potential of this system to some extent. Evolution is driven by low-probability random events. There does not need to be a "reason" for matters to arrange themselves in any particular way. Still, we wonder why the potential of the system was not expressed in further specializations.

Second, it is a little bit unusual to see this kind of evolutionary tree -- with a few, sometimes strongly divergent basal forms and an enormous radiation of a single derived lineage. This signals an unusually poor fossil record, which is indeed the case with mosses, and/or a very old taxon. Either can result in a "patchy" record of basal forms, with most of the early diversity completely unknown. One of the oddest things about the whole embryophyte story is, in fact, its antiquity. The first known embryophyte remains are, if correctly identified, from the Middle Ordovician, or about 470 Ma. It is usually thought that complex plant communities date from the Earliest Devonian (415 Ma) and forests from perhaps 390 Ma. This is not unreasonably slow. After all, the vertebrates probably subsisted as an only moderately successful type of oddly specialized worm for longer than 60 Ma. However, unlike vertebrates, plants were exploiting an entirely new environment. Typically, this sort of evolutionary invasion leads to explosive radiation. If mosses, liverworts, and perhaps a slew of similar forms, developed early, why didn't things move faster? We, certainly, have no answer. However, we are struck with the fact that, in the Late Ordovician, an ice age was triggered by (it is thought) a sudden draw-down in atmospheric carbon dioxide. This rapid reduction in carbon dioxide has, thus far, eluded explanation. Could these matters be related? A similar event in the Mississippian was almost certainly due to the growth of inland forests **[1]**. Even the "Snowball" episodes of the Cryogenian may have begun with the spread of eukaryotic algae into fresh water (small volume, but very rich in sunlight, nitrates and iron). After all, no law states that every invasion, military or evolutionary, must necessarily result in a successful or permanent conquest. History, and life, are recorded by the winners. Thus, we don't know much about the failures.

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[1] We may, one day, complete our discussion of that event. The series begins at **A Lot of Rot**.

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Rhyniophyta

```
CHLOROBIONTA
|--Chlorophyta
`--Charophyta
   |--(various green algae)
   `--Embryophyta
      |--Bryophyta
      `--RHYNIOPHYTA
         |--Horneophytopsida
         `--+--Aglaophyton
            `--+--Rhyniopsida
               `--+--Cooksonia
                  |--Eutracheophyta
                  |  `--Lycophytina
                  |     |--Zosterophylopsida
                  |     `--Lycopodopsida
                  |        `--Isoetopsida ?
                  `--Euphyllophytina
                     |--Moniliformopses
                     `--Spermatophytata
                        |--trimerophytes
                        `--SPERMATOPSIDA
```

Status

The Rhyniophytes are a paraphyletic taxon comprising the first vascular land plants (Rhyniopsida) and their morphologically similar, but avascular, cousins. They thus have a key position in the history of life. The coverage includes a brief discussion of their structure and importance on this page. Individual pages are included on two very early forms, *Horneophyton* and *Aglaophyton*, as well as on two well-known, derived members of the monophyletic Rhyniopsida, *Cooksonia and Rhynia*.

Index

Rhyniophyta: this overview page.

Horneophyton: a very simple, dichotomously branching form with terminal sporangia -- may or may not be vascular.

Aglaophyton: a larger (to 60 cm), and apparently more terrestrial version of *Horneophyton* -- probably not vascular.

Cooksonia: a Silurian vascular plant.

Rhynia: a very well-known plant from the Rhynie Chert.

The flora that existed in the Upper Silurian to Lower Devonian was probably an assemblage of marsh inhabitants with structural feature transitional between aquatic non-vascular and land vascular plants. Of these, the *Rhyniophyta* are a small but prominent group that include some of the earliest and most primitive terrestrial plants.

The Early Rhyniophytes

stylised Rhyniophyte

In these very primitive land plants in which there was little differentiation between the different parts. They had simple shoots rise from a creeping axis which hardly differs in structure from the upright shoots themselves. These shoots or stems often branched in a simple manner, forking into two, and then into two again, and sometimes the shoots terminated in spore capsules called sporangia. These ancient plants lacked leaves, seeds, and flowers. Instead of roots they had horizontal stems, connected with the soil by root hairs. The whole plant was generally less than 50 cm in height. At least one form, Taeniocrada is thought to have been aquatic, although whether a transitional forms from fresh water to land or secondarily aquatic is not clear

Included in the rhyniophytes are ancestral forms are the ancestral genus *Cooksonia*, from the late Silurian to early Devonian (Wenlock to Frasnian). By the Early Devonian more advanced types like *Rhynia* had evolved. Fossils of *Rhynia* from Devonian chert of Rhynie in Aberdeenshire, Scotland are so perfectly preserved that the individual cells within the plant tissue is recognizable.

There are also a number of related forms, like *Aglaophyton*, apparently not even true tracheophytes,

Systematics

The following represents a suggested Linnean classification and time-line for the rhyniophytes and related forms. Not that the most primitive forms are not necessarily the oldest, indicating that either the evolutionary sequence presented here is incorrect, or that a lot of early plant evolution occurred in regions away from conditions allowing fossilization

```
Subphylum Rhyniophytina
    Class not specified
        Order not specified
            Aglaophyton         - Pragian
    Class Horneophytopsida
        Order Horneophytales
            Family Horneophytaceae - Pragian
    Class Rhyniopsida
        Order not specified
            Cooksonia           - Wenlock to Frasnian
            other rhyniophyte fossils
        Order Rhyniales
            Family Rhyniaceae      - Lochkovian to Emsian
```

Occurrence

Period	**Silurian**			**Devonian**		
Epoch/Age	**Wen.**	**Lud.**	**Prid.**	**Loch.**	**Prag.**	**post- Prag.**
Aglaophyton					***	
Horneophytaceae					***	
Cooksonia	***	***	***	***	***	***

Rhyniaceae				***	***	***

Links

Links

The Biota of Early Terrestrial Ecosystems: The Rhynie Chert - Ongoing research into the stratigraphy, sedimentology and paleontology of an Early Devonian hot spring, by The Rhynie Chert Research Group: Aberdeen See especially **The Rhynie Chert Flora**

Rhynie Chert

Rhynie Research Index - The Rhynie Chert and its Flora.

Rhynie Chert Pictures - includes coverage of the most important flora

LES CORMOPHYTES (=premières plantes terrestres) - Description et évolution des premières plantes terrestres - evolution of early land plants - in French

Early Land Plants

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Tracheophyta

Vascular Plants: Maple > Moss

From the Wenlock

```
CHLOROBIONTA
|--Chlorophyta
`--Charophyta
   |--(various green algae)
   `--Embryophyta
      |--Bryophyta
      `--Tracheophyta
         |--Horneophyton
         `--+--Aglaophyton
            `--+--Rhynia
               `--+--Cooksonia
                  `--Eutracheophyta
                     |--Lycophyta
                     `--Euphyllophyta
                        |--Monilophyta
                        `--Lignophyta
                           |--Archaeopteris
                           `--SPERMATOPSIDA
```

Introduction

What we here call *Tracheophyta* is more exactly referred to as *Pan-Tracheophyta*. Cantino *et al*., (2007). As we will discuss, the correspondence is not exact. The definition we apply here is *Quercus* > *Polytrichum*, or maples > mosses. Generally speaking, the Tracheophyta are the vascular land plants and their morphologically similar, but avascular, cousins. They thus have a key position in the history of life.

We can think of the Tracheophyta as including three sorts of plants: (a) a disorganized and grossly paraphyletic collection of basal "rhyniophytes," mostly

Baragwanathia, a Silurian lycopsid, is one of the oldest known tracheophytes.

from the Silurian and Early Devonian; (b) lycophytes and their relatives; and (c) the Euphyllophyta, a huge group made up of the ferns and woody plants. The coverage on this page deals with the rhyniophytes and only the most basal forms of the others. Elsewhere, we include individual pages on the rhyniophytes *Horneophyton* and *Aglaophyton*, as well as on two well-known, probably more derived, members of the group, *Cooksonia and Rhynia*.

The earliest fossil tracheophytes are of Wenlock age; but the clade probably diverged in the Llandovery -- possibly even the Late Ordovician. The history of photosynthesis on land keeps getting pushed back (*see, e.g.*, Knauth & Kennedy, 2009), so its hard to be sure. Most of these basal forms disappeared by the end of the Devonian as seed plants (Spermatopsida) began to appear. Bateman *et al.* (1998).

Aglaophyton Taylor *et al.* (2005)

Fig. 1. Life history of *A. major*/*L. rhyniensis* showing stages in the development of the dimorphic gametophytes. The mature sporophyte (lower left) bears sporangia with spores of two types. Blue spores develop into mature antheridiophores; orange spores develop into archegoniophores.

Tracheophytes are often referred to as "vascular plants," which is close enough for most purposes. With few exceptions, tracheophytes have specialized water conducting elements (*xylem*) made up of dead cells (*tracheids*), with some kind of *woody* (or at least polyphenolic) reinforcement. Long strands of xylem conduct water because water is continuously removed from the upper parts of the plant by evaporation. This, in turn, occurs because water vapor escapes through pores, *stomata*. The presence of at least some stomata is thus likewise characteristic of tracheophytes. Sperry (2003). Actually, some non-tracheophyte groups have internal water-conducting elements, polyphenols, stomata, etc. But the phylogenetic distribution of these characteristics is spotty and does not point uniquely to one lineage as the sister group of tracheophytes. Ligrone *et al*. (2000).

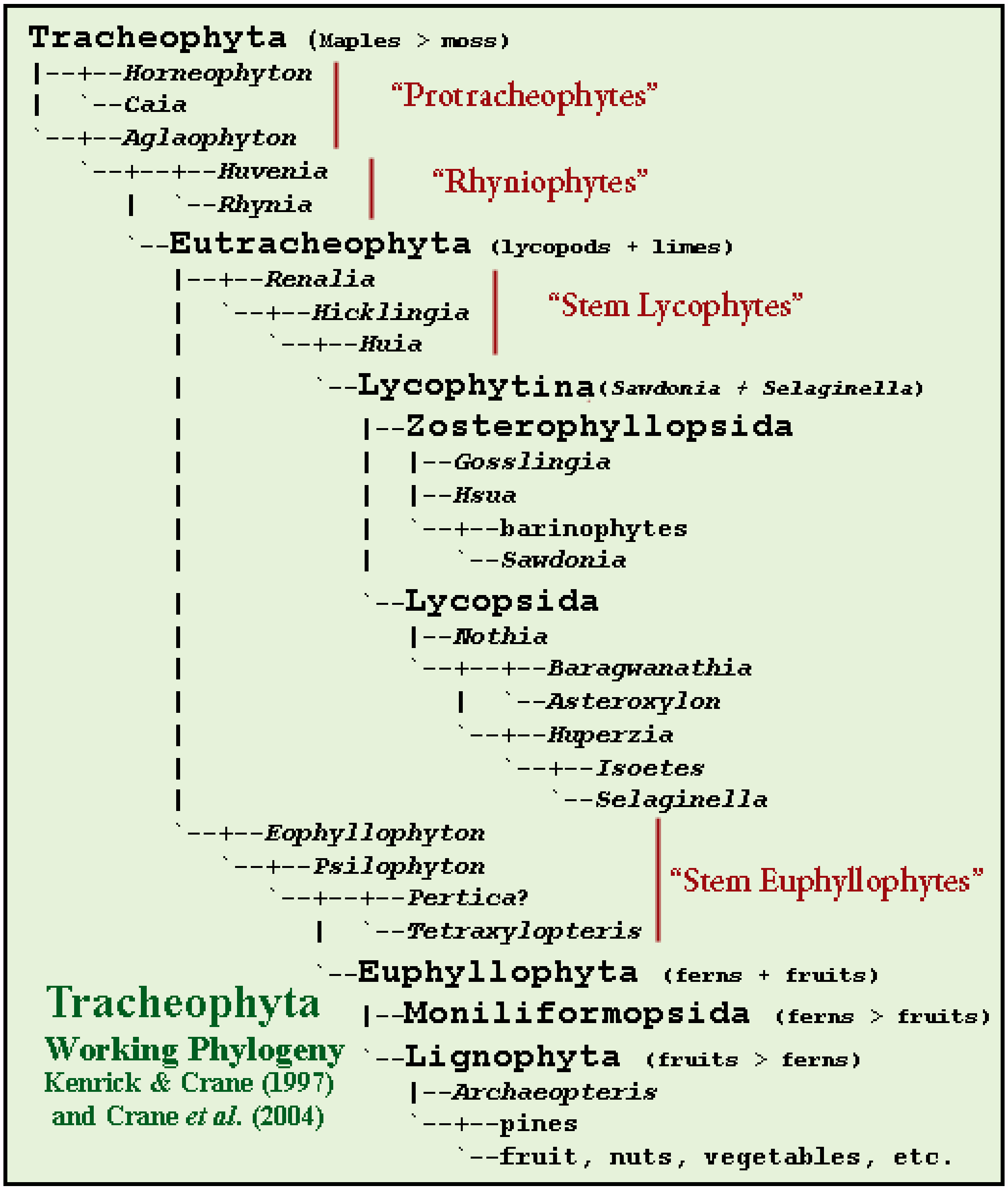
An even better indicator of tracheophytes is their life cycle. Plants, you may recall, alternate between *haploid* (*gametophyte*) and *diploid* (*sporophyte*) generations. In all tracheophytes, the diploid, sporophyte phase of the life cycle is physically larger than the gametophyte, more or less independent of the haploid phase, and establishes direct contact with the substrate. Ligrone *et al*. (2000). This combination of features features seems to be truly unique to the Tracheophyta.

Definition

Cantino *et al*., (2007) define Pan-Tracheophyta under Phylocode as "the total clade of Tracheophyta" and Tracheophyta as "The most inclusive *crown clade* containing *Zea mays* L. 1753 (Spermatophyta) but not *Phaeoceros laevis* (L.) Prosk. 1951 (Anthocerotophyta) or *Marchantia polymorpha* L. 1753 (Marchantiophyta) or *Polytrichum commune* Hedw. 1801 (Bryophyta)." Translated, this means everything more closely related to corn than to hornworts, liverworts, or mosses.

This definition is intended to promote stability. Cantino *et al*., (2007). Stability isn't usually that high on our agenda, and we prefer definitions that explicitly incorporate a specific hypothesis about the way things evolved. That usually works well enough for a platform like Palaeos. If we change our minds, we can go back and change everything. We have done just that, any number of times. However, our "maples > moss" definition (or "corn > moss" if you prefer) is more likely to be off base than most of the phylogenetic definitions we apply. For example, otherwise credible molecular phylogenies sometimes find that hornworts are more closely related to maples than to mosses. Nickrent *et al.* (2000); Qiu *et al.* (2006). If true, that would be awkward for us. And, certainly, few paleobotanists would clamber so far out on their respective limbs as to claim certain knowledge of the sister group to the tracheophytes. Nonetheless, we will stick to our short definition for the present.

Phylogeny



Tracheophyta marks an important and relatively sharp phylogenetic boundary. On the downstream side, the orderly and familiar succession of early tracheophyte clades are diplayed like the sunlit paths of a well-tended English garden. On the upstream side, we observe a dark and howling wilderness of mosses, liverworts, and hornworts in no comprehensible sequence or arrangement. We have -- somewhat arbitrarily -- chosen to cast our lot with the mosses as the sister group of Tracheophyta, at least for purposes of crafting a clade definition. That no longer seems as good a bet as it did just a few years ago. But no potential sister group seems capable of attracting a consensus of paleobotanists. Palmer *et al*. (2004). To be sure, paleobotanists are a flighty lot; but their lack of commitment seems amply justified in this case.

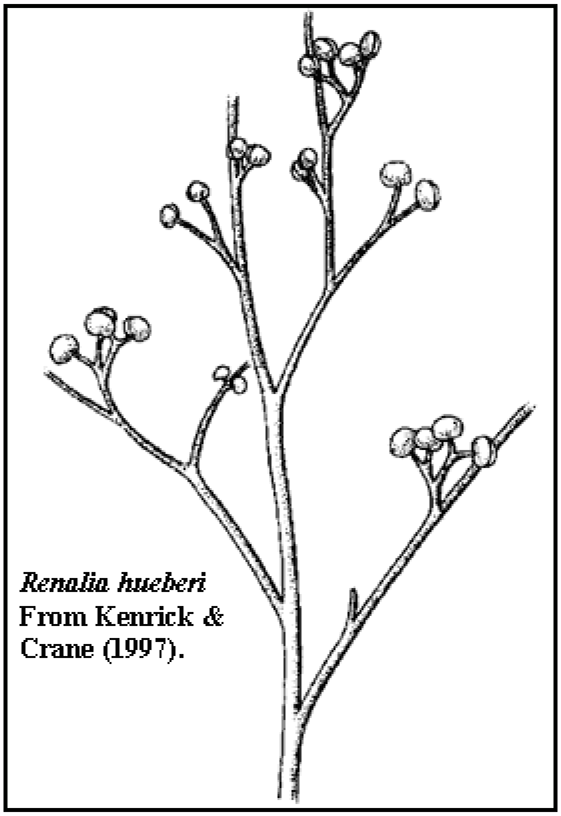
Kenrick & Crane's (1997) massive morphological study found that mosses were probably the closest living relatives of tracheophytes; but the conclusion was not strongly supported. The two main molecular studies have not added much clarity. Nickrent *et al.* (2000); Qiu *et al.* (2006). As mentioned above, they suggest that the hornworts may actually be closer, and that relationship is only slightly less parsimonious from a morphological perspective. Unfortunately, the DNA studies leaned heavily on chloroplast DNA. It turns out that, among the basal plants, rate heterogeneity is an even greater problem than in most organelle DNA. Soltis *et al*. (2002).

The Consensus Phylogeny Within Tracheophyta

By contrast, within the tracheophytes, the main branches are remarkably uncontroversial. Magallón & Sanderson (2002) (*chloroplast* DNA); Kenrick & Crane (1997a) (morphology). With one exception, the outline determined by Kenrick & Crane (1997) has survived almost unchallenged.

According to this consensus view, the "***protracheophytes***" (*e.g. Horneophyton*, *Caia*, *Aglaophyton*), which lack *xylem* altogether, are the most basal tracheophytes. Kenrick & Crane (1997). Other well-known fossil plants from the Pragian Rhynie Chert (***"rhyniophytes"***: *e.g. Huvenia*, *Rhynia*) are identified as more derived grades of the same basal tracheophyte stock. Of these, *Rhynia* may form a small clade with *Stockmansella* and *Taeniocrada*. Bateman *et al*. (1998). *Cooksonia*, known almost worldwide, often from much older deposits (Boyce, 2008), is said to be probably paraphyletic. Kenrick & Crane (1997a); Bateman *et al*. (1998). That is, some *Cooksonia* specimens are rhyniophytes, while others are believed to belong to more derived groups.

The term ***"pteridophyte"*** is sometimes used to refer to the paraphyletic group of all seedless Tracheophyta. The *crown group* of tracheophytes (limes + lycopsids) is the ***Eutracheophyta***. This clade contains all living, and most fossil, vascular plants. Bateman *et al*. (1998).


Renalia hueberi
From Kenrick & Crane (1997).

The lycophyte branch from this crown group presents some difficulties. The greatest difficulty is the problem of names. The taxon names *Lycophyta*, *Lycophytina*, *Lycopodiophyta*, *Lycophytopsida*, *Lycopsida*, etc. are used to mean very different things by different authors. We have been unable to find any real consistency -- even on our own website, much less in the literature. For our purposes we have made the following arbitrary choices.

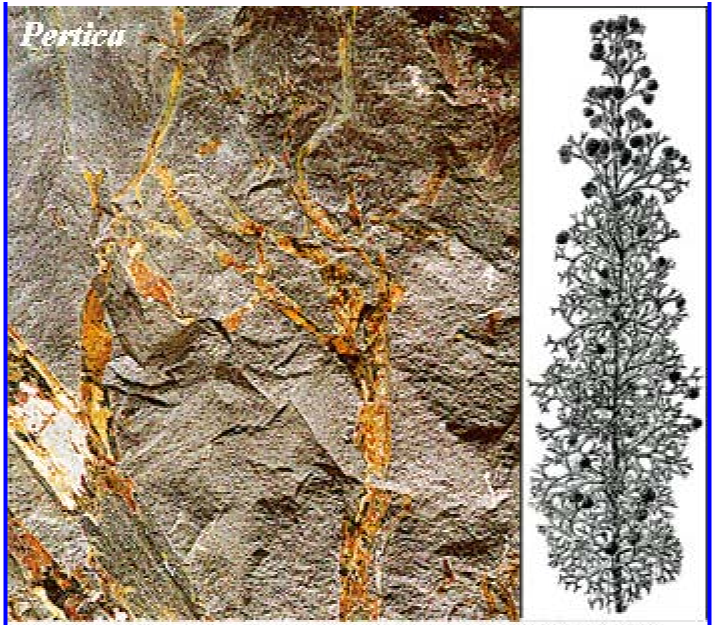
Lycophyta will be about the same as the Kenrick & Crane's (1997) *Lycophytina* or the Phylocode *Pan-Lycopodiophyta*: lycopsids > limes. It may turn out to include the same genera as Lycopsida. Then again, it may not. Tentatively, we follow Kenrick & Crane by placing *Huia*, *Renalia*, and *Hicklingia* inside Lycophyta but basal to Lycophytina. Crane *et al.* (2004). We will informally call this small, paraphyletic band of misfits ***"stem lycophytes***." *Huia* is not to be confused with *Hsua* (a zosterophyll), an error which baffled us for some time. Not to mention *Huperzia* (an extant lycopsid) and *Huvenia* (a rhyniophyte).

Lycophytina doesn't have a close Phylocode equivalent. We use it to mean *Sawdonia* + *Selaginella*, that is, zosterophylls plus conventional lycopsids. This is an idiosyncratic use of this name. Don't even *think* about using it that way in public. However, we have to call this group something, and *Lycophytina* suggests a diminutive of *Lycophyta* -- which is exactly what we intend.

Lycopsida will mean *Selaginella* > *Sawdonia, i.e.*, plants closer to living lycophytes than to zosterophylls. Again, Phylocode has no equivalent. To be completely honest, we envision Lycopsida as an intense, but somewhat homely teen-age girl with glasses, living in Queens. Zosterophyllopsida is her exotic, lesbian older sister from Paramus, New Jersey who drives a yellow Porsche. You will probably not find this to be a helpful *aide memoire*, but it may be worth a try. Almost anything is better than raw systematics.

Traditionally, the zosterophylls were thought to be just a basal grade of Lycophytina. Bateman *et al*. (1998). However, the current view is that zosterophylls are generally monophyletic and the sister group to an equally monophyletic Lycopsida. A few classical zosterophyll species are still of uncertain affinities. Crane *et al.* (2004). The zosterophylls are structurally simple, leafless plants, but they "strongly resemble lycopsids in sporangium morphology and in certain anatomical details." Examples: *Sawdonia, Zosterophyllum*, *Huperzia*. Kenrick & Crane (1997).

The exact placement of basal, non-lycopsid Eutracheophyta is not well understood. Crane *et al.* (2004). Below Eutracheophyta, after some uncertain phylogenetic interval, we



Fossil and reconstruction of *Pertica quadrifaria*, both from the Maine Secretary of State's site.

arrive at the crown group ***Euphyllophyta*** (a/k/a Euphyllophyta) = ferns + fruits. The stem group eutracheophytes -- below Eutracheophyta but above Euphyllophyta -- probably include early (mostly Late Devonian) fossils such as *Eophyllophyton*, *Psilophyton*, and *Pertica*. Bateman *et al*. (1998); Kenrick & Crane (1997: 129, fig. 4.33) (except as to *Pertica*); Schneider (2006). Stem euphyllophytes are sometimes called the ***"trimerophytes."*** Kenrick & Crane (1997).

The monophyly of Euphyllophyta is strongly supported by, among other things, "a unique 30-kb inversion in the chloroplast genome." Kenrick & Crane (1997a); Qiu *et al*. (2006) (criticized by Palmer *et al*., 2004, who argue that rare genomic events are no more privileged than rare morphological events). Euphyllophyta is, in turn, supported by two clades we will treat as stem groups: ***Monilophyta*** (ferns > fruits) and ***Lignophyta*** (fruits > ferns).

Monilophyta probably includes *Equisetum* (horsetails) as well as the ferns. The monophyly of the two was often doubted, but now seems increasingly accepted. Schneider (2006). The most basal known lignophyte is the famous Late Devonian forest-maker, *Archaeopteris*. Schneider (2006).

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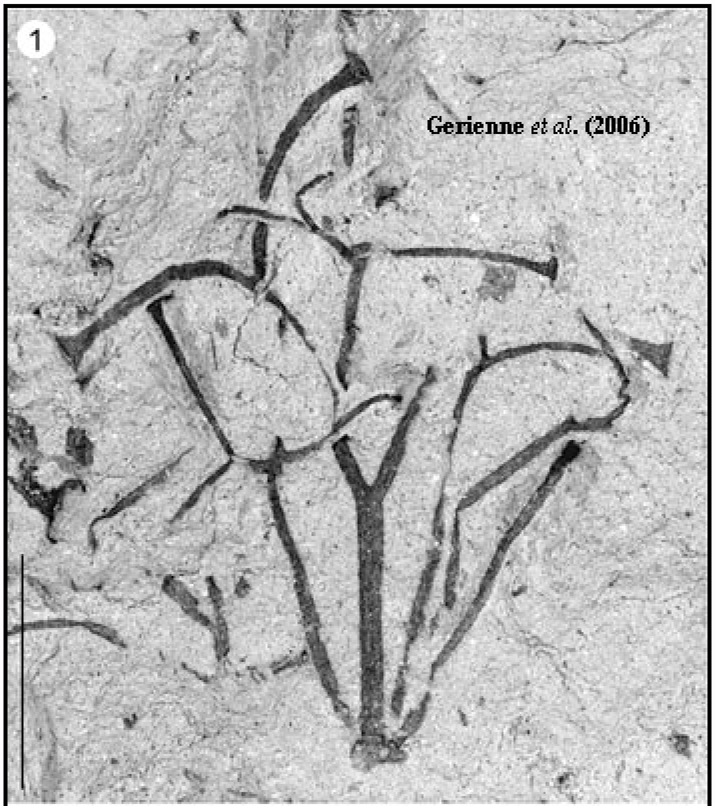
A Misplaced Root?



Cooksonia paranensis from the Early Devonian of the Paraná Basin (Brazil), interpreted [as] ... five sporophytes attached to a thalloid gametophyte. [Scale bar = 1 cm].

The main phylogenetic outline above is essentially undisputed. However, Boyce (2008) has raised a powerful dissenting argument about the position of the root. That is, even if the various groups are connected in the right way, we may be connecting them to the other Embryophyta in the wrong place. "Dissent" may be too strong a term to describe Boyce's position. Boyce is very cautious about drawing strong phylogenetic conclusions. However, he does point out some serious problems with the consensus structure.

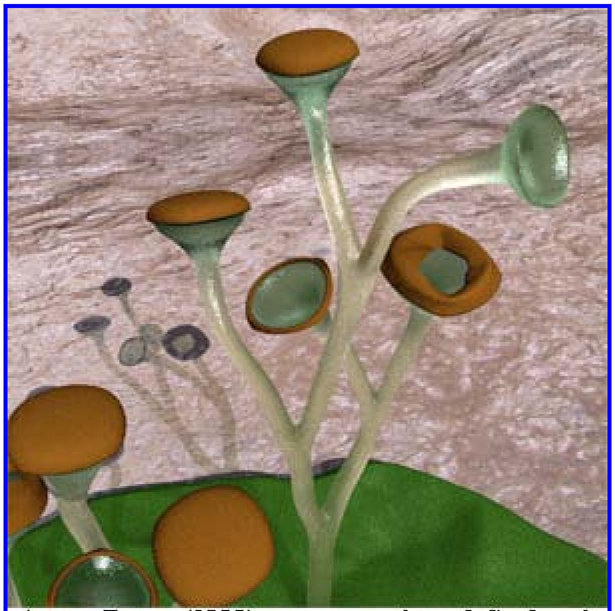
First, as everyone has known for many years, there's a timing problem. The protracheophytes and rhyniophytes are all Early Devonian except for *Cooksonia*. Yet -- despite many attempts to discredit the evidence -- undoubted Lycophytina are known from the Wenlock. Kotyk *et al*. (2002). That leaves a very long ghost lineage of protracheophytes, rhyniophytes and assorted stem Lycophyta. This is not impossible, but it *is* unsettling. Second, Devonian species of *Cooksonia* appear to eutracheophytes. One species in particular appears to be a zosterophyll (although it lacks a Porsche). This is also possible, if also disturbing. *Cooksonia* may not actually be a monophyletic genus. It may consist of a group of unrelated plants, or it may be grossly paraphyletic. That is, all eutracheophytes may be actually descended from *Cooksonia*.

But here's the real kicker. Early *Cooksonia* (or "cooksonioids," including *Cooksonia, Salopella, Tarrantia, Tortilicaulis*) have stems which are 100µ or less in diameter. Boyce shows that this is simply too skinny to support both vascular and photosynthetic systems. The combination requires a minimum stem diameter of about 700µ -- much stouter than Silurian *Cooksonia*. It is hard to imagine a plant the height of *Cooksonia* (several cm) without a water transport system. Even the miniature sporophyte axes of mosses generally have dedicated water transport systems. Boyce (2008).

Therefore, the implication is that *Cooksonia* lacked enough photosynthetic capacity to be self-sustaining. If so, Silurian *Cooksonia* were not independent *sporophytes*, as is usually supposed, but were "parasitic" on a *gametophyte* -- just like the sporophytes of mosses, liverworts, and other early embryophytes. This supposition is confirmed by other evidence: the similarity of *Cooksonia* proportions to other non-photosynthetic stalks, the low density of *stomata*, the presence of a supporting cortical *sterome* (taking up even more of the limited space in the stem), and the absense of *roots* or root analogues. If correct, then *Cooksonia* is the otherwise missing link between early plants and true tracheophytes. That is, it is clearly a large (by Silurian standards) sporophyte, which looks like a tracheophyte, but was not fully independent. Boyce (2008). Recently Gerienne *et al.* (2006) have reported a very large specimen of *Cooksonia* which they tentatively interpret as five sporophytes emerging from a *thalloid* gametophyte.

If Boyce is correct, we should redraw the phylogeny of tracheophytes with the same branches, but with the root moved to look more like this:

```
       Embryophyta
       |--Bryophyta
      `--Cooksonia
     |--+--"Rhyniophtes"
   |   `--"Protrachophytes"
`--+--+--Zosterophyllopsida
        |   `--Lycopsida
        `--Euphyllophyta
```


A post-Boyce (2008) reconstruction of *Cooksonia* by Smith609 from Wikipedia Commons

Or, since some species of *Cooksonia* are very zosterophyll-like:

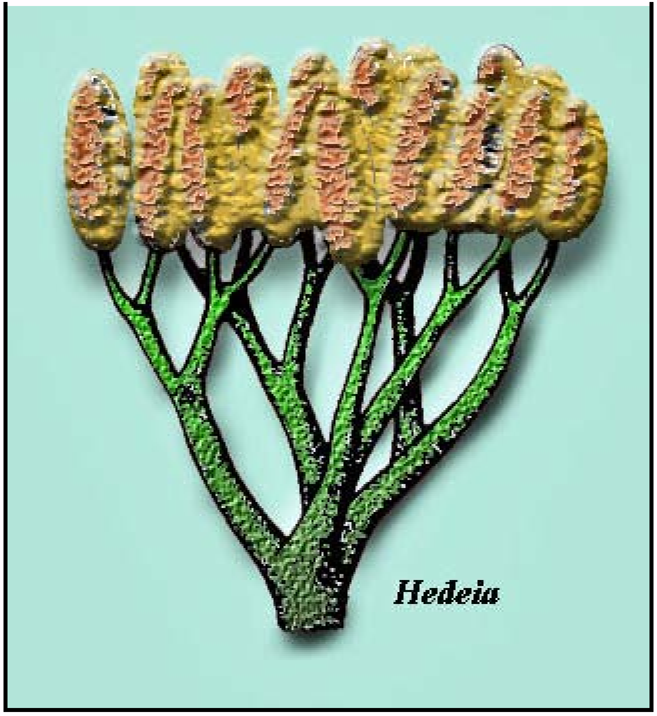
```
     Embrophyta
    |--Bryophyta
    `--Cooksonia
          |--
Zosterophyllopsida
   `--+--Lycopsida
      `--+--+--
   "Rhyniophtes"
|   `--"Protracheophytes"
     `--Euphyllophyta.
```

Actually, we are quite fond of this last one. First, it comes closest to explaining why we find *Cooksonia* and lycopsids in the Silurian, rhyniophytes in the Early Devonian, and euphyllophytes only later. The thesis does require secondary simplification in rhyniophytes, but this is entirely possible. In fact, it has long been suspected that the Rhynie Chert plants are secondarily simplified as an adaptation to a very unusual, wet, acid environment. *See, e.g.*, Bateman *et al*. (1998); Arnold (1947: 80) (referring to even earlier work). *Psilotum* looks very much like a rhyniopsid, but is actually a living, secondarily simplified euphyllophyte.

Second, Boyce's thesis also explains why *Cooksonia* species often distribute themselves so widely in most cladograms. The genus appears to be paraphyletic -- not because it is a garbage taxon -- but because it *is* paraphyletic. Ultimately, the only reason we have not adopted this revisionist phylogeny is that Boyce himself has chosen not to assert it directly.

Diversity and Occurrence

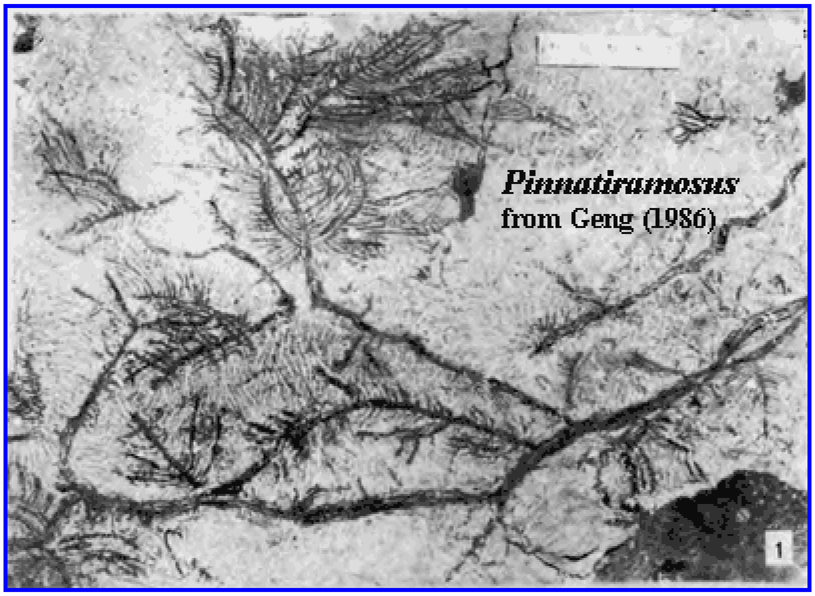
Tetrahedral spores (suggesting *haploid* cells produced by *meiosis*)



with decay-resistant walls (presumably including *sporopollenin*) are diagnostic of land plants. These spores appear in the fossil record as early as the Middle Ordovocian. Kenrick & Crane (1997a); Bateman *et al*. (1998). Tracheophyte body fossils are not known before the Wenlock. However, Silurian tracheophyte fossils already include lycopsids (like *Baragwanathia*, pictured above) and zosterophylls, as well as the less-easily classified *Salopella*, *Hedeia*, and the amazingly advanced -- but equally controversial -- *Pinnatiramosus* (Geng, 1986).

Pinnatiramosus is controversial because it has a number of features which seem to have no business on a plant from the Llandovery. For example, it has well-developed pitted *tracheids* and fairly regular, plainly *monopodial* branching. Geng (1986). The branching pattern is particularly startling because this kind patter of development requires *lateral meristem*. As we will see, that is unexpected in a plant from the Silurian. The ultimate order of branch is 400-800 µ in diameter -- just possibly stout enough to be a fully developed photosynthetic structure. Boyce (2008). *Pinnatiramosus* does not appear to bear *leaves* of any sort, nor even *enations*; and no reproductive structures are described. Geng (1986). Some relatively recent work (which we were not able to lay our hands on) argues that *Pinnatiramosus* is actually the intrusive root system of an unidentified plant from overlying deposits of Permian age.

On the other hand, there is quite solid evidence of lycophytines of various sorts from Ludlow exposures in both Australia and Canada. In addition to the lycopsid *Baragwanathia*, the Australian Ludlow flora includes *Salopella*, *Hedeia*, and zosterophylls. Kotyk *et al*. (2002) have documented an extensive zosterophyll fauna from the Ludlow of arctic Canada. This suggests that tracheophytes diverged from other embryophytes in the Llandovery or even the Late Ordovician. Thus, by the time that plant fossils become abundant in the Early Devonian, the pace of plant evolution -- while relatively brisk -- could not quite be described as explosive. Kenrick & Crane (1997a).



The genera treated as the most basal tracheophytes in the consensus phylogeny (*e.g.*, *Aglaophyton* and *Horneophyton*) are referred to as "protracheophytes" because they lack tracheids. Bateman *et al*. (1998). However they don't appear in the fossil record until the Early Devonian. This is the age of the remarkable Rhynie Chert fossils, which have structures perfectly preserved at the cellular level. "Unfortunately, the supposedly archetypal Rhynie Chert flora appears to be an unusual assemblage specialized for life in a low-pH, periodically flooded habitat; the flora may have included species secondarily reduced for aquatic life habits." Bateman *et al*. (1998).

Euphyllophytes (ferns and lignophytes) appear in the Late Devonian. By the end of the Devonian, well-developed forests of the basal lignophyte *Archaeopteris* covered broad areas of lowlands. Thus morphologically identifiable representatives of all the main tracheophyte groups all appear in the fossil record over a period of only about 70 million years, during the late Silurian and Devonian. Bateman & DiMichele (2003).

Tracheophyta - 2

```
CHLOROBIONTA
|--Chlorophyta
`--Charophyta
   |--(various green algae)
   `--Embryophyta
      |--Bryophyta
      `--Tracheophyta
         |--Horneophyton
         `--+--Aglaophyton
            `--+--Rhynia
               `--+--Cooksonia
                  `--Eutracheophyta
                     |--Lycophyta
                     `--Euphyllophyta
                        |--Monilophyta
                        `--Lignophyta
                           |--Archaeopteris
                           `--SPERMATOPSIDA
```

Introduction
Definition
Phylogeny
Diversity and Occurrence
Anatomy

Anatomy

An Early Devonian landscape. Original painting in the NMNH by Mary Parrish (2000).

We have reorganized this section several times, generally ocillating between phylogenetic anatomy and anatomical phylogeny. We ultimately reached the conclusion that there is no reasonable way to organize this material. We suspect that Kenrick & Crane (1997) found the same problem a dozen years ago, since they ultimately describe the anatomy of early plants several times, using various different schemes of organization. In fact, we strongly recommend Kenrick & Crane (1997) to the interested reader. The review below is written -- as is most of Palaeos -- solely for the purpose of educating ourselves. For that purpose, we will take an anatomical approach, trying to make sense of the evolution of the various organ types using the consensus phylogeny. Kenrick & Crane (1997), who *invented* the now consensus phylogeny, do this far better than we could ever hope to do.

It is worth noting that the traditional organization used by paleobotanists is neither anatomical nor phylogenetic, but temporal. As we've noted elsewhere, there is some tendency for plants of all lineages to develop the same sorts of structures at about the same time. So for example, the density of *stomata* increase through the Devonian in all groups. The development of *monopodial* branching, the tree body plan, reduction of the *gametophyte*, the evolution of *leaf* structures, and the differentiation of *roots* all occur in rough synchrony across land plant groups. It is possible, but rather unlikely, that our ideas of tracheophyte phylogeny are grossly mistaken. It is more likely that broadly parallel (*homoplastic*) evolution actually occurred and that it occurred because all land plants were experiencing parallel changes in their environment. For this reason numerous articles have tried to make sense of tracheophyte evolution in terms of secular change in broad environmental factors. We like this approach, but apply it with caution. It is too easy to slip from this type of analysis into purely scenario-based speculation. We really don't know all that much about terrestrial environments in the Middle Paleozoic (Silurian and Devonian), and the fossil record of plants at the time is only good for the Early and Late Devonian.

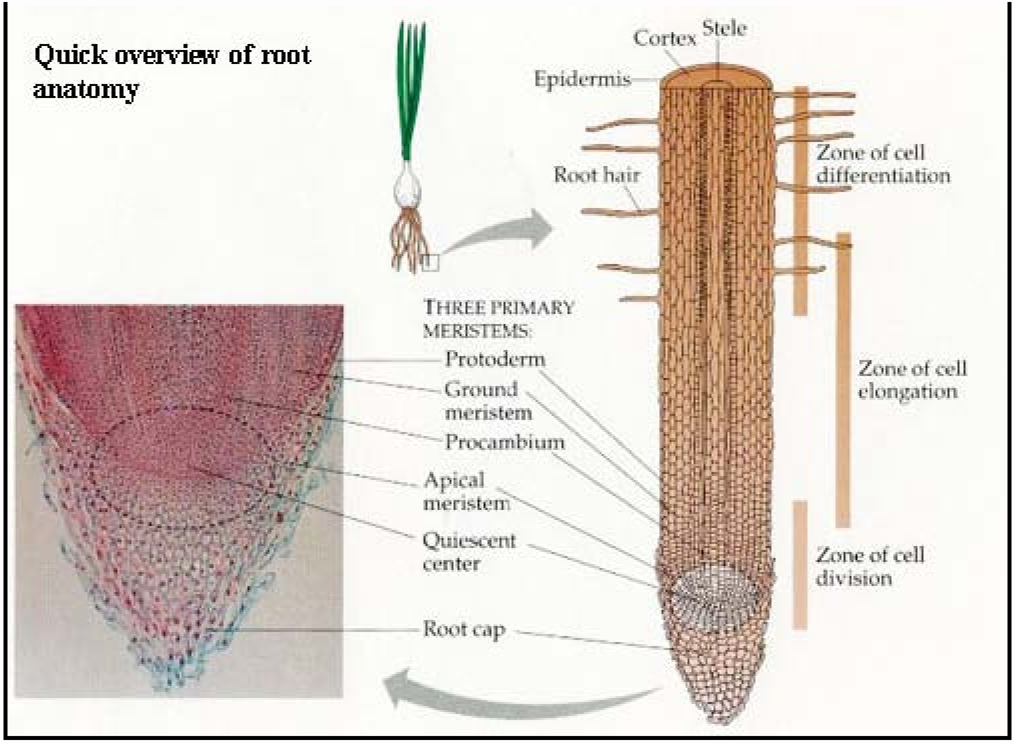
Another common approach is to view the plant body plan as simply having fewer possibilities than (for example) the animal body. Viewed from this perspective, early plant evolution is the constrained development of a delicate balancing act between "[t]he functions essential for nearly all independently growing terrestrial plants — desiccation resistance, structural support, hydraulic and solute transport, and photosynthesis." Boyce (2008).

However, this pattern of evolution is not necessarily due to some inherent limitation of plant genetics. The dynamic of early evolution in terrestrial plants differs from that in terrestrial animals in several fundamental ways. Early terrestrial animals were all motile predators or detritovores. Terrestrial herbivores were either non-existent or of minimal significance right into the Permian. Labandeira & Allen (2007). So animals chased each other around for food or sex, from the very start. What is more, they chased each other around in an environment already partitioned by plants. Shear & Selden (2001). In contrast, early terrestrial plants were sessile. They had no macroscopic predators at all and were expanding into an environment which possibly abiotic or, at the most, was only very thinly conditioned by other living organisms. Therefore it is perhaps not surprising that -- in general -- terrestrial animals evolved more by environmental specialization through genotypic plasticity; while early plants tended towards large monotypic stands which created their own environment and by greater reliance on *phenotypic* plasticity. The kinds of constraints imposed by the two modes of terrestrial evolution were quite different **[1]**.

But this is all rather high level speculation. Let's look at the practical details.

The Roots of Roots

To decide how roots evolved, we must decide what *roots are*. This has proven difficult. The most careful approach to a modern definition is that of Raven & Edwards (2001). Rather than provide a definition, Raven & Edwards assert that a *root* is any axial structure of the *sporophyte* which has all or most of the following characteristics: (1) direction of growth (on average) within 90° of gravitational field; (2) growth away from light (negative phototropism); (3) elongation growth is strictly *apical*, without bifurcation of the *meristem* (*root cap*); (4) possession of a *histologically* distinct root cap; (5) *endodermis*; (6) *protostele* (sometimes with a pith); (7) endogenous origin of



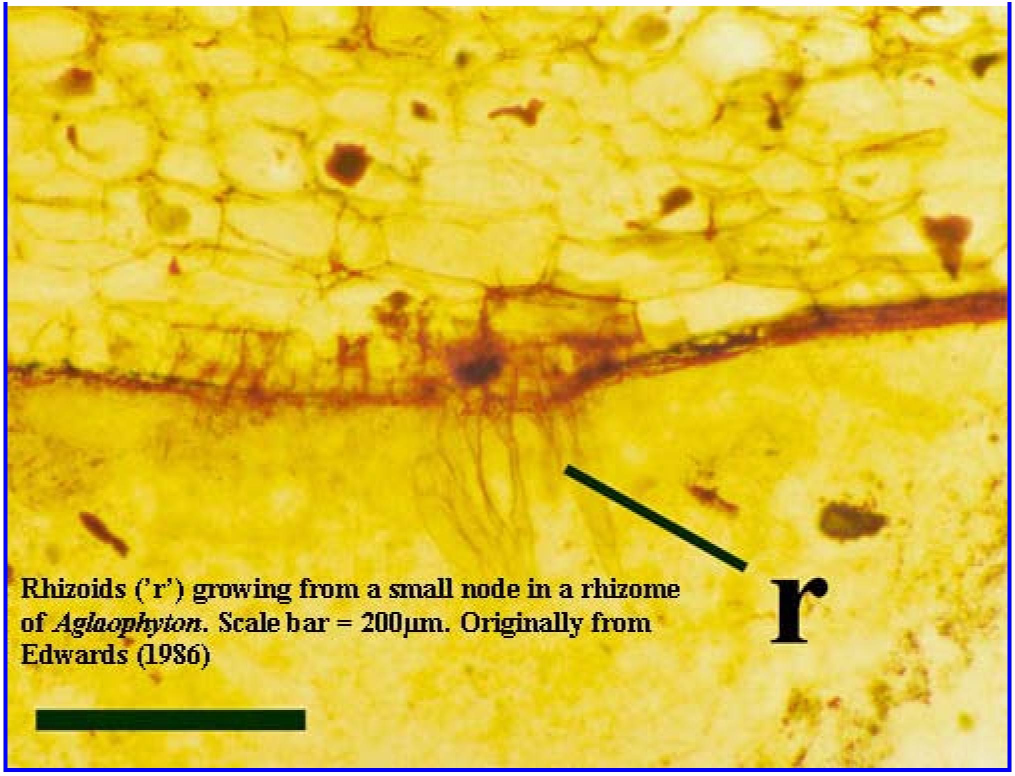
lateral roots, *i.e*., branching by the initiation of new meristem growth region from the *stele*. Of these characters, (2), (4), (5), and (6) aren't very useful for fossils or have too many exceptions. Endodermis (5) and protostele (6) may also be *plesiomorphic* for tracheophytes. Characters (3) and (7) are two related aspects of meristem development. Root meristem does not divide, nor does it branch superficially. A root has true *monopodial* (single main axis) development and branching occurs by new growth continuous with the central vascular strand.

Thus, the short explanation is that a root is something that grows like a tree, only downward. That being the case, you will be unsurprised to learn that real roots and real trees developed about the same time -- probably no earlier than the Middle Devonian. Kenrick & Crane (1997a); Bateman *et al*. (1998); Raven & Edwards (2001). The main technical obstacle to root and tree evolution seems to have been finding a reliable method for putting parts of the active, apical meristem to sleep for a while, then waking them up to form secondary axes continuous with the original stele. We'll talk a little more about this problem when we get to branches.

Root-like impressions are known from the Late Silurian. Structures that *really* look like roots are first found associated with Early Devonian tracheophytes. However, even these fossils are probably the remains of rhizomes. Rhizomes are not roots. They are part of the main trunk of the plant which grows more or less horizontally along the surface of the earth. Typically, rhizomes generate nodes at intervals. From these nodes grow aereal branches and/or root hairs (or even true roots in more recent plants). Mosses have essentially the same system.

Essentially all land plants have root *hairs* (*rhizoids*) for absorbing water and soil ions. Rhizoids are one or a few cells wide and are thus rarely preserved in fossils. However, they are common where conditions permit preservation in detail, as in the Rhynie Chert. Kenrick & Crane (1997). "Many germinating spores in the Rhynie chert are associated with microbial mats that contain cyanobacteria and other microbes. In modern microbial mats extracellular polymeric substances are important components of the mat that are involved in attaching microbes to the substrate and forming a matrix around the organisms" Taylor *et al*. (2005).

Fungal associations important in early



Rhizoids ('r') growing from a small node in a rhizome of *Aglaophyton*. Scale bar = 200µm. Originally from Edwards (1986)

plant history Kenrick & Crane (1997a). Probable functional predecessor of roots. Raven & Edwards (2001). "Fungal associations are widespread in gametophytes of pteridophytes, liverworts and hornworts, but are lacking in mosses (Duckett et al. 1991). Fungal hyphae facilitate absorption and translocation of minerals, water and organic molecules within the plant. In nature, heterotrophic subterranean gametophytes of pteridophytes rely exclusively on endophytic fungi for nutrient uptake." Renzaglia *et al*. (2000).

BUT: "Rhynie Chert tracheophytes and protracheophytes -- all of roughly similar axis diameter to extant *Psilotum* ... possess *rhizoids* (*Aglaophyton, Horneophyton, Rhynia*), other rooting structures (*Asteroxylon*), or rhizomatous growth (*Aglaophyton, Asteroxylon, Nothia, Rhynia*) ... ." Boyce (2008).

Aglaophyton (and some other Rhynie plants) have underground axes bearing rhizoids; these axes have arbuscular mycorrhizas, but mycorrhizas also occur on above-ground axes. Raven & Edwards (2001)

Unicellular rhizoids present in all Rhynie plants, but are rarely preserved in other fossils. Kenrick & Crane (1997). Image at 66. On observe dans les axes de certaines espèces (comme *Aglaophyton*) des champignons symbiotiques rappelant les mycorrhizes des racines des arbres actuels. DuBuisson *et al*. (2005).

In these very primitive land plants in which there was little differentiation between the different parts. They had simple shoots rise from a creeping axis which hardly differs in structure from the upright shoots themselves. Instead of roots they had horizontal stems, connected with the soil by root hairs.

Diameter seems to help in growth rate, cytoplasmic streaming, life-span and structural maintenance; hurts in surface/volume. Raven & Edwards (2001).

Rhyniophytes: still no roots. Raven & Edwards (2001).

Rhizoids of *Rhynia* are borne on hemispherical projections near the base of presumed aerial axes. Raven & Edwards (2001).

Nothia included by some, but its a lycopsid per Crane *et al.* (2004).

Eutracheophyta: Just as nearly all vascular plants have stomata, nearly all have an endodermis with a waterproofing casparian strip of lignin and suberin (Schreiber 1996; Raven and Edwards 2001), whether or not the absorbing organs are true roots or are limited to stems. An interesting exception is *Lycopodium*, where an endodermis is lacking in roots but present in stems; however, an “endodermoid layer” in the roots seems to have the equivalent function (Raven 1984). The earliest appearance of an endodermis in the fossil record is from the Carboniferous (Raven 1984), but it likely originated at least as early as the split of the tracheophytes into the lycophyte and euphyllophyte clades (fig. 1). Sperry (2003). BUT endodermis (seen only in roots of higher plants, but also in stems of *Psilotum*), Lecture.

Lycophyta: "Roots in zosterophylls, "stigmarian" roots arborescent lycopsids (*Lepidodendron*) and *Isoetes* may all be morphologically analogous leaves. "This root-like organ develops into the 'stigmarian root system' bearing 'stigmarian rootlets'. and the stigmarian axis and its rootlets is considered homologous to the shoot system (Rothwell, 1984; Rothwell and Erwin, 1985). This view is supported by the presence of a pith cavity in the stigmarian root system, and by the exogenous production of lateral organs (stigmarian rootlets) (Stewart and Rothwell, 1993; Taylor and Taylor, 1993). The 'stigmarian rootlets' have thus been interpreted as morphologically equivalent to leaves, and are closely similar in anatomy to the roots of the extant *Isoetes spp*. where, as one might expect of modified leaves. the roots have a major role in CO_2 uptake by the plant." Raven & Edwards (2001). R&E argue that absence in Silurian and Early Devonian lycophytes means independent origin, but note that this "requires that such features of roots as a root cap, and endogenous origin of laterals evolved independently from the original relatively undifferentiated axis of the lycophytes and the euphyllophyte."

The anaromy of rootjng systems is unknown in nearl)' all of the early fossil lycopsids and zo .. uel'oph)·IL~.K&C

Zosterophylls: The published information on roots or root-like structures in the early Devonian (Pragian-Emsian) (Gensel et al., 2001) has been reviewed, and new data presented on Lower Devonian fossils from Bathurst Island, Arctic Canada, and from New Brunswick and Gaspe, Canada. These plants with root-like structures are zosterophyllophytes or lycophytes sensu lato." These had "(1) The rooting structures are attached to aerial ones, but have no emergences or microphylls. (2) The rooting structures are generally much narrower in diameter, and shorter, than are the aerial axes that bear them. (3) The rooting structures are either unbranched or are irregularly branched; this contrasts with the more predictable branching of the aerial axes. (4) The rooting structures may have a sinuous or delicate appearance. (5) The rooting structures proceed in a direction opposite to that in which the aerial axes grow. These authors point out that characteristics 2-5 are also applicable to plants with naked axes, and that the rooting structures show no evidence of root caps or indisputable root hairs; furthermore, the anatomy of the rooting structures is not yet known. Raven & Edwards (2001). Authors argue unconvincingly that these and *Drepanophycus qujingensis* don't have roots since no evidence of root cap, endodermis, etc. none of which is to be expected in fossils lacking the spectacular preservation of Rhynie Chert specimens.

"[Bathurst Is.] *Zosterophyllum sp. nov.* with tufted rooting structures which occur as descending naked axes from plants with dense aggregations of branching aerial shoot systems." Raven & Edwards (2001).

"The Quebec and New Brunswick fossils comprise *Crenaticaulis verruculosus* and *Sawdonia ornata: C. verruculosus* has smooth, spinous. slender (0.5 mm wide) rooting structures departing at right angles to aerial or rhizomatous axes in regions where there are otherwise no branches (Gensel *et al*., 2001). *Sawdonia ornata* fossils have [similar] structures " Raven & Edwards (2001).

Rhizomatous axial systems; ? Aerial axes that are dichotomous or pseudomonopodial, an elliptical exarch protostele; ? Axes with randomly arranged spines in some genera; ? Cauline (occurs on the axis) globose or reniform sporangia, trilete spores G.

Lycopsids: Lycopodiophyta: "The least inclusive clade containing *Lycopodium clavatum* L. 1753, *Huperzia selago* (L.) Schrank & Mart. 1829, *Isoëtes lacustris* L. 1753, and *Selaginella apoda* (L.) Spring 1840." That's the crown clade. For this clade: "association of a single axillary or adaxial sporangium with a sporophyll; absence of vasculature in the sporangium; metaxylem tracheids pitted; root stele bilaterally symmetrical, with phloem located on only one side of the stele (but there are a lot of missing data for fossils outside the crown, so this trait may be synapomorphic of a more inclusive clade); crescent-shaped root xylem (but there are a lot of missing data for fossils outside the crown). The following characters are synapomorphies of this crown clade relative to other crowns but are apomorphic at a more inclusive level when fossils are considered (Kenrick & Crane, 1997: Fig. 6.18, Table 7.2): microphylls ("lycophylls"; Schneider & al., 2002; Pryer & al., 2004a); exarch xylem differentiation in stem (Kenrick & Crane, 1997; Doyle, 1998; Schneider & al., 2002); stellate xylem strand in stem; reniform sporangia with transverse dehiscence (Doyle, 1998). This list is not exhaustive; see Kenrick & Crane (1997: Table 7.2) and DiMichele & Bateman (1996) for other synapomorphies listed under Lycophytina and Lycopsida." Cantino *et al*. (2007).

"earliest roots in the fossil record have diameters ranging from 3 mm at their attachment to less than 0.7 mm in the smallest branches recovered." Raven & Edwards (2001). Early Devonian lycopsids.

Asteroxylon mackiei is one of the earliest known Lycopods from the Rhynie Chert with microphyllous leaves; rhizome creeping, naked, developed repeatedly bi-furcating root-like structures (these were not true roots as the root-cap was absent), *Baragwanathia:* but we have little knowledge of the underground structures which, it is widely believed, such plants must have possessed if they were to have been adequately anchored, and to have had a sufficient capacity for uptake of water and soil-derived nutrients ... It is clear from the size of the erect aerial axes of Baragwanafhia that substantial below-ground structures would be needed." Raven & Edwards (2001).

"The Bathurst Island fossils (Gensel et al., 2000) comprise *Drepanophycus* and *Bathurstia* spp. with aerial axis-borne rooting structures scattered along what appear to be trailing or rhizomatous structures, or forming parts of the so-called 'K-branching' structures" Raven & Edwards (2001).

Rayner argues that *Drepanophycus spinaeformis* had roots on the basis of the branching pattern and the attitude in the sediment of the smooth axes in relation to the bedding plane (Schweitzer, 1980). However, there is no anatomical evidence (e.g. endogenous branching) to support this view. Li and Edwards have looked at *Drepanophycus qujingensis* (Li and Edwards, 1995), was shown to have roots, i.e. structures borne by both fertile and sterile leafy shoots, which branch dichotomously at least five times. The roots appear to be inserted randomly, and the largest branching root system extends up to 30 mm from the stem. The diameter of the roots is about 3 mm at their attachment and rapidly decrease with branching; the smallest branches recovered have a diameter of less than 0.7 mm (Fig. 37D of Li and Edwards, 1995), and it is likely that the unpreserved, more apical, portions had an even smaller diameter. It is of interest that these roots were borne on leafy axes which were presumably above-ground but were probably prostrate, as the rooting system itself extends down into the rock, at an angle to the bedding plane in which the leafy axes were exposed. Raven & Edwards (2001).

Isoetes only survivor with "rootlets" of the type developed in tree-like lycopsids. Donoghue (2005).

"anatomical studies of arborescent lycopsids raise certain matters with regard to their physiology (Phillips & DiMichele, 1992). The lack of a clear phloem connection between root and shoot, the generally limited phloem throughout the plant's aerial shoot, the leaf-like rootlets borne on the stigmarian axes, and the long leaves on stems and cones, are all consistent with extremely localized use of photosynthate and perhaps even self-supporting root systems in terms of carbon fixation." DiMichele & Gastaldo (2008).

Stem Euphyllophyta: Euphyllophyta crown group: ""Synapomorphies (relative to other crown clades). — Roots with monopodial branching and endogenous lateral roots (Schneider & al., 2002); ... (these features characterize the earliest members of /Pan-Euphyllophyta and were modified in most extant representatives); Cantino *et al*. (2007).

Psilophyton "emerged from rhizomatous mat." K&C

Furthermore. the zosterophyllophyte-lycophyte sensu lata clade possessed root-like structures in the Lower Devonian, although there is no corresponding evidence for root-like structures on euphyllophytes at this time. The earliest convincing euphyllophyte roots occur in the Middle Devonian cladoxylalean *Lorophyton goense*. thought to derive from trimerophytes (Fairon-Demart and Li, 1993) where bifurcating structures arise in tufts from a swollen stem base. This is consistent with the polyphyletic origin of roots, a point considered in more detail below. Raven & Edwards (2001).

[Theory] suggest a height for *Archaeopteris* of 10-30 m. Corresponding to this increase in height is an increased plant biomass per unit land area and depth of penetration of roots *sensu lato*. ... there is independent evidence of an increasing depth of penetration of roots ... up to 2 mm in diameter and up to 0.9 m long in the Emsian (late Early Devonian) have been found." Raven & Edwards (2001).

The "Original Condition"

Bryophytes: "Possibly the earliest upright cylindrical structures among embryophytes were erect gametophores embedded in thalloid structures. Because the cylindrical structures lacked specialized vascular tissues or hypodermal steromes, the diameter and height of such columns would have been severely restricted by potential conductance (105) and relied on turgor pressure to maintain an upright stance. The height ... may have conferred greater dispersal potential than that possessed by forms sporulating directly from the thallus surface, allowing spores to reach uncolonized areas beyond the dense, extensive clonal mat." Huh? Bateman *et al*. (1998).

Mosses transitional in having erect gametophyte tissues with conducting tissue. Bateman *et al*. (1998).

Polyphenols in hydroid walls. Sperry (2003).

No branching in sporophyte, then some dichotomous. Kenrick & Crane (1997: 299)

Protracheophytes: *Aglaophyton*, *Caia*, *Horneophyton*

No synapomorphies for Pantracheophyta. "An independent sporophyte and multiple sporangia are listed by Kenrick & Crane (1997: Table 7.2) as synapomorphies of Polysporangiomorpha (a slightly less inclusive clade than /Pan-Tracheophyta ; see Synonymy) but only the latter would be a synapomorphy of Polysporangiomorpha if it were given an apomorphy-based definition based on the etymology of the name. The order in which the two features evolved is not known. Sunken archegonia are also cited as a possible synapomorphy of Polysporangiomorpha by Kenrick & Crane (1997: Table 7.2), but it is unknown whether sunken archegonia evolved before or after multiple sporangia. Moreover, sunken archegonia also occur in Anthocerophyta (op. cit., Fig. 3.33, pp. 63–64) and thus may be a synapomorphy of a more inclusive clade if hornworts are the closest extant relatives of tracheophytes (e.g., Qiu & al., 2006b). Synonymy. — The name Polysporangiomorpha (poly- sporangiophytes) sensu Kenrick & Crane (1997: Table 7.2)" more or less. Cantino *et al*. (2007).

Early loss of dessication-resistance and development of homoiohydry (??). Sperry (2003).

Stems: In these very primitive land plants in which there was little differentiation between the different parts. They had simple shoots rise from a creeping axis which hardly differs in structure from the upright shoots themselves. Instead of roots they had horizontal stems, connected with the soil by root hairs.

La dispersion des spores peut être favorisée par une grande taille verticale. DuBuisson *et al*. (2005).

Vascular Tissue: There are also a number of related forms, like *Aglaophyton*, apparently not even true tracheophytes, other basal tracheophytes had G-type. Kenrick & Crane (1997a). Not much contribution to mechanical strength. Bateman *et al*. (1998).

"*Aglaophyton* and *Horneophyton*, [lack] tracheids with well-defined thickenings." Kenrick & Crane (1997a); Bateman *et al*. (1998). Such tracheid-like structures as they had were centrally located and seem to have evolved to with stand negative pressure of transpiration, rather than support the plant. Bateman *et al*. (1998). Central vascular strand almost indistinguishable from bryophytes. Kenrick & Crane (1997).

"Tissue differentiation within the seta of many mosses is quite pronounced and shows similarities to early fossil vascular and nonvascular plants, including the possession of a central conducting strand and a peripheral cortical layer of thickwalled cells. There is a central region of elongated and unthickened cells, possibly conducting tissue, surrounded by a poorly preserved, presumably parenchymatous, tissue and a layer of thickwalled epidermal cells (Halle 1916a, 1916b, 1936a). No thick-walled cortical tissue has been observed." Also applies to branches. Kenrick & Crane (1997). Evidence from the fossil record indicates that cells with helical or annular thickenings are more general than pitted cells because many early vascular plant fossils possess tracheids with only helical thickenings (Kenrick and Crane 1991). Well-defined wall thickenings are absent in the early polysporangiophyte fossil *Horneophyton*." Kenrick & Crane (1997).

They had simple shoots rise from a creeping axis which hardly differs in structure from the upright shoots themselves. These shoots or stems often branched in a simple manner, forking into two, and then into two again. Donoghue (2005). The whole plant was generally less than 50 cm in height. Basal tracheophytes developed the branched sporophyte. That is, "enlargement and branching of the sporophyte preceded the acquisition of tracheids." Dichotomous branching characterizes the polysporangiophytes. More spores per fertilization event and increased size. Donoghue (2005).

"Elements" of auxin metabolism known from the early embryophyte grade. Kenrick & Crane (1997a).

Protracheophytes still maintained largely by turgor pressure. Cortex took the strain. 20-30 cm max height. Bateman *et al*. (1998). However, "plant axes in the size range of smaller cooksonioid axes can rely exclusively on turgor from the hydrostatic core (Niklas 1997). Nonetheless, a stereome is preserved in some of the narrowest cooksonioids." Boyce (2008).

"The simplest conduits were thin and smooth-walled microperforate tubes of the now extinct protracheophytes (fig. 3A; *Aglaophyton, Horneophyton*; Kenrick and Crane 1991). These resemble the hydroids of some mosses and may have a common ancestry (fig. 1; Mishler and Churchill 1984; Kenrick and Crane 1997a; but Ligrone et al. 2000). These fossil tubes do not appear to have been lignified but may have been impregnated with lignin-like polyphenols, as are extant hydroids." Sperry (2003). Gametophyte of *Aglaophyton* also had conducting tissue. Taylor *et al*. (2005).

"pitting is absent from the tracheid cell walls of many basal taxa (Kenrick and Crane 1991). In these early fossils, all tracheids have conspicuous helical or annular thickenings that strongly resemble the early-formed protoxyem elements of extant groups ...

"The persistence of this plesiomorphic cell type in the protoxylem of extant vascular plants is probably strongly linked to functional constraints. In xylem tissues, cell elongation cannot occur by further growth after differentiation because metabolic death must occur before the cell is able to function. In vascular plants, most differentiation of primary tissues, including metaxylem, occurs after a period of cell elongation at a distance below the apex. This constraint means that the developing metaxylem tissue is unable to immediately supply the metabolically demanding growing point with xylem product (e.g., water and mineral nutrients). The role of the protoxylem is to ensure an uninterrupted supply of xylem product to the apex, and the protoxylem achieves this by early differentiation within the zone of tissue elongation immediately below the apex. Ultimately, many of the protoxylem cells become nonfunctional through severe distortion by cell elongation in the neighboring tissues, and the role of supplying water is taken over by the differentiating metaxylem with its more robust, heavily lignified, and pitted secondary walls. During the brief functional period of protoxylem, the helical-annular thickenings serve a dual role in resisting the lateral collapse (cavitation) of the cell walls while allowing axial elongation of the cell through stretching in response to growth of the surrounding tissues (Bailey 1953). The critical role of protoxylem in vascular plant ontogeny explains the persistence of the plesiomorphic helical-annular thickened cell wall and its widespread occurrence among extant groups." Kenrick & Crane (1997: 300)

Branches: Branching "set the stage" for development of more advanced vascular tissues. Donoghue (2005). [branching connected the vascular system to sites of transpiration and photosynthesis, thus creating need for tracheids] Branched sporophyte and multiple sporangia developed at the avascular level (*Aglaophyton, Horneophyton*). Kenrick & Crane (1997).

Branching pattern irregular [lack of long-range order]. Kenrick & Crane (1997). "Among early polysporangiophytes, branching is relatively simple (Rothwell 1995, see above) and may contain a significant stochastic component (Niklas 1982). A series of more complex and increasingly deterministic branching systems appear early within the major clades of vascular plants." Kenrick & Crane (1997: 298)

Leaves: External surface not elaborated for additional photosynthetic area as in some early embryophytes, Boyce (2008).

These ancient plants lacked leaves, Bateman *et al*. (1998). *Aglaophyton* and *Horneophyton* lacked leaves Kenrick & Crane (1997a).

Stomata: *Stomata* probably already present. Known from both *Aglaophyton* and *Horneophyton*. Kenrick & Crane (1997).

Stomatal density increase in all lines? through Devonian. Raven & Edwards (2001).

Many hornworts and mosses have stomata, but they are absent in liverworts. Benton & Harper (1997).

Sporangia: "in basal polysporangiophytes, they are often solitary at the ends of the main branching system, for example in *Aglaophyton* (Figure 4.7), *Cooksonia*" Kenrick & Crane (1997).

... sometimes the shoots terminated in spore capsules called *sporangia*. ... lacked seeds, and flowers.

Aglaophyton and *Horneophyton* branched, nutritionally independent sporophyte. Bateman *et al*. (1998). "two fundamental growth forms predominate in basal tracheophytes: (i) green epiterrestrial forms with irregular upright lamellae and (ii) thick, fleshy subterranean forms with a fungal symbiont. The latter type, exemplifed by *Huperzia* (figure 1a), *Lycopodium*, *Diphasiastrum*, *Phegmariurus*, Psilophytes (figure 1b), *Botrychium* and *Ophioglossum*, is generally considered ancestral. These gametophytes may persist for several years and they have the capacity to produce multiple sporophytes and form abundant regenerants." Renzaglia *et al*. (2000).

Aglaophyton sporangia are terminal and produce trilete spores.Taylor *et al*. (2005).

Unlike those of pteridophytes, gametangia of mosses and liverworts are stalked and extend from the epidermal surface (Bold et al. 1987). Gametangia of basal pteridophytes are never stalked and are either entirely sunken within the thallus or form conspicuous epidermal mounds (Bierhorst 1971). Renzaglia *et al*. (2000).

"In vascular plants the sporophyte is initially dependent on the gametophyte (its foot absorbs nutrients from the gametophyte) but develops complete physiological independence during early ontogeny (Bierhorst 1971). In liverworts, horn worts, and mosses, the sporophyte remains in intimate contact with gametophytic tissues during spore production." Kenrick & Crane (1997).

"The basal members of the Polysporangiomorpha clade are “protracheophyte”-grade genera such as *Horneophyton* and *Aglaophyton*. They exhibit branched, independent sporophytes isomorphic with gametophytes that possess sunken archegonia." Bateman *et al*. (1998); and multiple sporangia above this level. Kenrick & Crane (1997). That is, "transition to sporophyte dominance moved through a stage in which gametophyte and sporophyte phases were more or less similar in structure (so-called isomorphic alternation of generations." Donoghue (2005) (citing K&C). *Contra* Boyce (2008). [and Taylor et al. (2005)?]

Horneophyton unique in having branched *sporangium*. Kenrick & Crane (1997).

Aglaophyton and *Horneophyton* had terminal sporangia. Bateman *et al*. (1998). *Horneophyton* even retained a *columella*, a pillar of sterile tissue in the sporangium which supports the spore capsule. This is a feature typical of mosses, but virtually unknown in tracheophytes. Bateman *et al*. (1998).

the Rhynie chert plants can also reproduce by various asexual meansTaylor *et al*. (2005). All of the Rhynie chert plants can reproduce both sexually and by vegetative methods, and thus clonality may have served as the primary method of species invasion into new niches (54). Sections of rhizomes that supported a single sporophyte suggest that fragmentation and dieback may have been an important form of vegetative reproduction, as in some modern clonal plants (55). Other structures in the fossils that may have functioned in asexual reproduction include reduced branches as fragmentation propagules, bulbils (Fig. 2Q), and bulges containing poorly organized vascular tissue (56).Taylor *et al*. (2005).

"Terminal sporangium attachment on longcr axes is the general condition in polysporangiophytes." Kenrick & Crane (1997).

Gametophyte: "Mature *gametophytes* [of *Aglaophyton*] consist of a fleshy *protocorm* attached to the substrate by basal *rhizoids*; arising from the upper surface are one to several upright *gametangiophores* bearing multiple *gametangia*. *Stomata* are present on the upper surface of the protocorm and gametangiophore, and *endomycorrhizal* fungi extend throughout the gametophyte. Gametophytes are unisexual, producing either *antheridiophores* or *archegoniophores*. There is no evidence that gametophytes later become *hermaphroditic*. The sexual dimorphism of the *Rhynie chert* gametophytes is inconsistent with theoretical ideas about the *haploid* phase of early land plants." Taylor *et al*. (2005).

Earliest vascular plants had elaborate gametophyte. "Early gametophytes ... are more complex than in living plants and have branched stems bearing sexual organs on terminal cupor shield-shaped structures ... . Archegonia (female gametangia) are flask-shaped with a neck canal and egg chamber, and are sunken as in hornworts and most vascular plants (Fig. 2c). Antheridia (male gametangia) are roughly spherical, sessile or with a poorly-defined stalk, and superficial (Fig. 2b). Gametophytes are very similar to associated sporophytes, and shared anatomical features (waterconducting tissues, epidermal patterns, and stomates) have been used to link corresponding elements of the life cycle. ... after the development of a simple, unbranched, ‘parasitic’ sporophyte among early land colonizers ... there was elaboration of both gametophyte and sporophyte in vascular plants. ... The small, simple, often subterranean and saprophytic gametophytes of [lycopsids] and ferns ... result from morphological loss. ... gametophyte reduction was independent in clubmosses and the fern–seed plant lineage." Kenrick & Crane (1997a). [use image?]

Horneophyton with sunken archegonia (probably -- ID of gametophyte is not 100% certain). Kenrick & Crane (1997)

"Antheridial development is essentially identical to archegonial development in pteridophytes (figure 4c) (Bierhorst 1971). The process begins with a transverse division in an epidermal cell. The outer cell gives rise to a sterile jacket and the inner cell forms the spermatogenous tissue. So similar are these division patterns in the two sex organs of pteridophytes that it is virtually impossible to differentiate antheridia from archegonia in early stages of organogenesis. Moreover, in protandrous lycophytes, when the transition between male and female sex organs occurs, it is possible to find bisexual gametangia that contain developing sperm in the `neck region' and an egg cell at the base (figure 5) (K. S. Renzaglia and D. P. Whittier, unpublished data)." Renzaglia *et al*. (2000). *Compare* "The shape and general appearance are like that of the exosporic gametophytes of living nonseed vascular plants. The first cell division of the gametophyte is transverse and divides the globular mass into nearly equal segments (Fig. 2 B and C). The outer cell continues to divide to form a mass of cells that will ultimately give rise to the gametophyte proper (Fig. 2 D and E); the inner cell also divides a few times to form a small cell mass that remains within the confines of the spore wall. Oblique cell divisions of the outer cell give rise to an apical cell that subsequently divides to form cells of two types (Fig. 2F). On the outside is an outer ring of slightly flattened cells that will form the epidermis; on the inside is an inner core of cells that are more isodiametric in outline. During elongation, apical cells of the inner core continue to divide so that the gametophyte becomes teardrop-shaped and 10 cell layers thick" Taylor *et al*. (2005). Taylor et al. emphasize that gametophores are morphologically very distinct and never hermaphroditic. This appears specialized compared to the pattern in lycophytes described by Renzaglia et al.

"Gametophytes of *Lyonophyton* are unisexual ... nor is there any evidence that gametangia are mixed on a single gametangiophore. Gametangiophores are morphologically distinct ... . Mature antheridiophores are upright, unbranched, and ~2.0 cm long. The distal ends are cup-shaped and lobed (Figs. 1 and 2K) and produce 10–40 antheridia, each spherical and =600µ in diameter. Antheridia are stalked and columellate (Fig. 2L), with delicate parenchyma strands extending from the columella to the inner wall of the antheridium; on the distal surface, a small pore is formed in mature antheridia through which flagellated gametes (Fig. 2M) are released. The distal ends of the archegoniophores consist of several closely spaced dichotomies (Fig. 1), each possessing conducting strands. The tip is slightly expanded with a shallow central depression. Archegonia are slightly sunken on the inner surface of the depression or are subterminal along the axis just beneath the tip. Each archegonium is hemispherical and consists of 8–10 cell rows, with each row one to three cells thick and up to six cells high (Fig. 2N)." Taylor *et al*. (2005).

"A cutinized epidermis covers both the antheridophores and archegoniophores; beneath this layer is a two-celled hypodermis. To the inside of this layer is a one- to two-cell-thick zone of slightly opaque isodiametric cells (Fig. 2H), some of which contain arbuscules (Fig. 2I) of the endomycorrhizal fungus *Glomites* (17). Hyphae enter the gametophyte at the base in the region of the rhizoids and extend through the intercellular spaces of the cortex (Fig. 2H)." Taylor *et al*. (2005).

"Free-living gametophytes are known for three of the Rhynie chert macroplants (Aglaophyton, Rhynia, and Horneophyton); to date, only antheridiophores are known for Nothia. All gametophytes consist of unisexual, axial, and upright structures (gametangiophores) that develop from the distal surface of a protocorm; on the base are tufts of rhizoids. Gametangiophores are small (5 cm tall) and possess specialized conducting elements. The distal end of the gametangiophore is variously modified in different gametophyte taxa. Antheridia are large and stalked; archegonia are slightly sunken." Taylor *et al*. (2005).

All homosporous. Intersporangial heterospory (anispory) is typically regarded as an early stage in the evolution of heterospory and is well documented in several groups of fossil plants -- but not found in Rhynie plants. Taylor *et al*. (2005) "These spore aggregates (Fig. 2P) are known at least for the Rhynie chert sporophytes Aglaophyton and Horneophyton, and we suggest that they may represent a dispersal strategy that resulted in maintaining the close proximity of both types of unisexual gametophytes, thus ensuring fertilization. If Aglaophyton is functionally anisporous, then spore dispersal becomes an important factor in maintaining the next generation, because proximity of sperm and egg is critical." Taylor *et al*. (2005).

"A slightly different morphology is present in ... the gametophyte of *Horneophyton ligneri*, and ... the [male] gametophyte of *Nothia aphylla*. Both ... are ... more complex, with the distal ends ... *gametangiophores* modified into large cups that contain conducting elements. ... [T]he elaboration of the distal ends of the gametangiophores has little if any phylogenetic significance but rather reflects the physiological complexity of the tips, because it appears that more *gametangia* are produced per gametangiophore in these gametophytes, compared with those of *Aglaophyton*... or even *Rhynia*... . Very little is known about ... the development of these two gametophyte types. Early stages in the germination of *Horneophyton* spores appear similar to those described in *Aglaophyton*." Taylor *et al*. (2005).

"sexual expression in these gametophytes was not labile like that in modern homosporous plants. ... the unisexual gametophytes of the Rhynie chert plants suggest that sex determination may occur in the sporangium of the sporophyte " Taylor *et al*. (2005)

In bryophytes, "Bryophytes also are homosporous but possess a life history in which the sporophyte is reduced and physiologically dependent on the gametophyte, which is the dominant part of the life cycle. Unisexual gametophytes occur in 50% of the taxa (47) and can be directly correlated with spores of two different sizes produced in the same sporangium (48). Some unisexual bryophytes have sex chromosomes, and for several, gametophytes that only produce archegonia are more common (49). Sex expression in bryophytes may be both labile and environmentally controlled (44)," Taylor *et al*. (2005)

"In vascular plants, the embryo phase is relatively short and the sporophyte soon establishes direct contact with the substrate, thus becoming independent from the gametophyte. Moreover, the sporophyte develops specialized vascular tissues, the xylem and phloem. In particular, the xylem contains waterconducting cells (WCCs), the tracheids and vessel elements, whose developmental pattern includes the deposition of a secondary lignified wall and final cytoplasmic lysis. The bryophytes traditionally include those embryophytes in which the sporophyte is permanently associated with the gametophyte and never establishes direct contact with the substrate." Ligrone *et al.* (2000).

"Today, the concept of isomorphic early vascular plants is widely accepted." Gerienne *et al.* (2006).

phytes isomorphic with gametophytes that possess sunken archegonia." Bateman *et al*. (1998); and multiple sporangia above this level. Kenrick & Crane (1997). That is, "transition to sporophyte dominance moved through a stage in which gametophyte and sporophyte phases were more or less similar in structure (so-called isomorphic alternation of generations." Donoghue (2005) (citing K&C). *Contra* Boyce (2008). [and Taylor et al. (2005)?]

Rhyniophytes: *Cooksonia*, *Rhynia*

Stem: "*Cooksonia* (Figure 10.5) is composed of cylindrical stems that branch in two at various points and which are terminated by cap-shaped sporangia, or spore-bearing structures, at the tip of each branch. The specimens of *Cooksonia* range from tiny Silurian examples, as little as a few millimetres long, to larger Devonian forms up to 65 mm long." Benton & Harper (1997).

- Small plant attaining heights of 10 cm, dichotomous branched with globose terminal sporangia. Found in monotypic stands. G

The later "rhyniophytes," for example the more derived species of *Cooksonia*, have steromes, but are still essentially supported by turgor pressure and thus required continuous supply of water. Bateman *et al*. (1998).

Rhyniophytes with *S-type tracheids*. Kenrick & Crane (1997a). Not much contribution to mechanical strength. Bateman *et al*. (1998).

Regardless of whether they have true xylem, these sporophyte axes have intercellular spaces [which *Baragwanathia* does not], cuticle and stomata [which Silurian *Baragwanathia* spp. do not], and sporangia. Among those with true xylem are representatives with smooth axes (*Rhynia gwynne-vaughanii*). Raven & Edwards (2001).

"The vascular conducting tissues of early Devonian examples [of *Cooksonia*] have thickened walls, and there are stomata on the outer surfaces of the stems." Benton & Harper (1997).

"Water-conducting cells (xylem elements, tracheids) with differentially thickened cell walls are characteristic of the sporophytes of extant vascular plants ... . In nearly all extant vascular plants, conspicuous pits characterize the metaxylem cells, whereas annular or helical thickenings are typical of the earliest protoxylem elements to differentiate (Figure 3.27; Bierhorst 1960). Kenrick & Crane (1997). La présence de xylème chez le fossile Cooksonia du Silurien moyen à supérieur, qui est sans conteste la polysporangiophyte la plus ancienne retrouvée à ce jour (fig. 5), est fortement contestée [peut-être car le lieu phylogénétique de *Cooksonia* et aussi tant contesté]. Cooksonia partagerait avec d'autres polysporangiophytes du Dévonien inférieur (comme Aglaophyton, fig. 5), la présence de tissus conducteurs non xylémiens proches de ce qui est observé chez les bryopsides. DuBuisson *et al*. (2005).

S-type tracheids. "The two-layered cell wall comprises a very thin decay-restant inner layer facing cell lumen and a "spongy" outer layer ... . Minute plasmodesmata-sized perforations occur over the entire inner surface of the cell wall." Kenrick & Crane (1997).

Pits allow flow between tracheary elements [equalize pressure, presumably], but allowing air through seeds cavitation and colapse. Sperry (2003). "pitted tracheids evolved independently at least twice (Lycopsida, Euphyllophyta) and that xylem composed entirely of tracheids with helical-annular thickenings is the plesiomorphic condition in vascular plants. Kenrick & Crane (1997: 300)

Water-conducting tissue and stomatal regulation go hand in hand. They appear at essentially the same time in the fossil record and co-occur in the vast majority of extant plants (fig. 1). Sperry (2003). Stomata are characteristic of the sporophyte in basal land plants.

Both rhyniophytes and eutracheophytes had "annular or helical thickenings in the warcr-conducting cells ... .Another possible synapomorpny at this level is lignin deposition on the inner surface of the tracheid cell wall." Kenrick & Crane (1997). "In many early taxa, cells with annular thickenings show occasional diagonal bars connecting adjacent helical-annular rings (e.g., G-type tracheid: Figure 7.27; ... In basal tracheophytes the frequency of diagonal bars is quite low, and their position and number varies such that the cell has a mixture of helical-annular thickenings and simple pits ... We suggest that tracheid pitting evolved through an increase in the regularity and frequency of diagonal bars to produce a more complex pattern of regular pits." Kenrick & Crane (1997: 300-301)

"True tracheids have been defined as single-celled conduits with lignified and ornamented walls, either banded or pitted (Kenrick and Crane 1997a; Doyle 1998). They may have evolved once, uniting all tracheophytes (fig. 1, all taxa below the protracheophytes). The banded type (fig. 3B, 3C) superficially resembles the modern protoxylem tracheid. It is thought to be ancestral because it is the only type found in the basal tracheophyte group, the extinct rhyniopsids. Sperry (2003).

"Cortical sclerenchyma inbasal Euphyllophyta, such as the relatively plesiomorphic Psilophyton, forms a continuous hypodermal band or sterome several cells thick (Figure 7.26). This feature is common in other basal tracheophytes such as the Zosterophyllopsida, Lycopsida, and some Cooksonia- like stem group vascular plants and is probably plesiomorphic in the Euphyllophyta [Eutracheophyta??]" Kenrick & Crane (1997: 297).

Branching still without long-range order in *Rhynia*, *Aglaophyton*, *Huvenia*. Kenrick & Crane (1997). *Rhynia* and some close relatives show branching from small hemispheres. These vascular strands of these branches are not continuous with the main axis system. Kenrick & Crane (1997). See Fig 1C -- a Silurian form -- in Bodzioch *et al.* (2003).

Spiny *enations* common in various rhyniophytes, *Psilophyton*, *Huvenia*. Kenrick & Crane (1997).

"Sporangia in *Rhynia* and *Stockmansella* are lateral and sessile, whereas in *Huvenia* they terminate short, branched axes." Kenrick & Crane (1997). "(*Stockmansella*, *Huvenia*, *Rhynia gwynne-vaughanii*), there is a distinctive pad of tissue into which the sporangium is slightly sunken (Figures 4.27 and 4.28). This pad is situated on the end of a short axis or attached laterally on the main axes." Kenrick & Crane (1997). Dehisence through multiple helical slits. Kenrick & Crane (1997).

Gametophyte: "The biological relationship between *gametophyte* and *sporophyte* [of *Rhynia*] is based on the *S-type* secondary wall thickenings of the conducting elements. The tightly compacted cluster of ... gametophytes (Fig. 2O) consists of 200 globular to bowl-shaped protocorms, each bearing rhizoids on the basal surface and one to several upright unisexual *gametangiophores* on the distal surface. Of these, 27 are unbranched *archegoniophores*, and at least 69 additional ones are unbranched *antheridiophores*. Most gametangiophores grow *orthotropically*, however, some develop *plagiotropically* and display a more sinuous growth pattern. This pattern is common in many modern *exosporic* gametophytes, where crowding is the result of many spores germinating at approximately the same time and becoming intermingled during growth. [*Rhynia*] antheridiophores are short (=15 mm) with *antheridia* located on shield- to cup-like tips; *archegonia*-bearing axes are longer (=2.0 cm) with slightly flared tips and archegonia either terminal or subterminal. The morphology and structure of antheridia and archegonia are similar to those of *Aglaophyton*. Taylor et al. (2005).

"gametophytes from the Rhynie Chert is based on- gametangiophores from three taxa (Remy, Gensel, and Hass 1993). All are small, probably dichotomously branched plants bearing terminal gametangiophores. Anatomically, the gametophyte axes are indistinguishable from those of the associated sporophytes and contain welldeveloped water-conducting tissues as well as an epidermis with stomates." Kenrick & Crane (1997: 302)

"Cladistic analysis indicates that fossils with isomorphic life cycles are related to stem group tracheophytes and probably even to basal Lycophyta (e.g., *Nothia aphylla*: Table 7.8). This evidence points to a significant elaboration of both the gametophyte and sporophyte in early polysporangiophytes and implies that the gametophytes of extant pteridophytes are highly reduced compared to those of some of the earliest protracheophytes." Kenrick & Crane (1997: 305).

"The specimen [of *Cooksonia*] is a cluster of five individual sporophytes still attached to the remains of a small female or bisexual gametophyte. In the latter case, this fossil is evidence that reduced thalloid gametophytes and branched axial sporophytes are plesiomorphic among the earliest eutracheophytes. We suggest that a major difference in life cycle defines a basal dichotomy in tracheophytes. Eutracheophyta, including all living vascular plants, have a heteromorphic sporophyte dominant alternation of generations, whereas their extinct sister-group Rhyniopsida (renamed here Paratracheophyta) is characterised by a more or less isomorphic alternations of generations." Gerienne *et al.* (2006). "implies that the early eutracheophyte Cooksonia had already a heteromorphic sporophyte dominant alternation of generations." Gerienne *et al.* (2006) Authors acknowledge this is not the only possible interpretation. "According to our Hypothesis # 3, the haploid generation in *Cooksonia* was much smaller and inconspicuous compared to the diploid phase. Therefore, we propose that *Cooksonia* had a heteromorphic, diploid dominant, alternation of generations, with axial sporophytes and thalloid prothallus-like gametophytes. This type of life cycle is similar in many respects to that of most freesporing vascular plants living today, and it implies that *Cooksonia* and all the earliest eutracheophytes had a diplobiontic life cycle with a conspicuous and independent sporophyte. As all previously described *Cooksonia* specimens (including those of *Cooksonia paranensis*) consist only of isolated individual sporophytes, it is assumed that the gametophyte/sporophyte association illustrated in the specimen described here is an exception." Gerienne *et al.* (2006).

"One of the most puzzling nearly whole plants is *Cooksonia* W. H. Lang, often touted as the earliest vascular land plant but known only from aerial parts (Edwards et al., 1992). Where were the prostrate axes to which these organs presumably were attached? Rothwell (1995) suggested that *Cooksonia* may have been a sporophyte incapable of a free-living existence, instead growing attached to a photosynthetic gametophyte, much like modern moss sporophytes and, thus, far from completely known morphologically. Gerrienne et al. (2006) found a cluster of Early Devonian *Cooksonia* axes attached to a thalloid-like pad and offered three possible interpretations, among which was the possibility that the axes represented sporophytes attached to a gametophyte. This hypothesis has been given biomechanical and physiological support by Boyce (2006), who demonstrated that most *Cooksonia* species are too narrow to have had sufficient photosynthetic tissues to sustain themselves independently." DiMichele & Gastaldo (2008).

Eutracheophytes

Cantino's Tracheophyta. "Synapomorphies. — walls of water-conducting cells with a thick, lignified, decay-resistant layer. Free-living sporophyte and multiple sporangia per sporophyte are synapomorphies relative to other crown clades; however, when fossils are considered, these traits are synapomorphies at a more inclusive level (see /Pan-Tracheophyta). Sterome (a well-developed peripheral zone of the stem consisting of thick-walled, decay-resistant cells) and pitlets in the tracheid wall are listed by Kenrick & Crane (1997: Table 7.2, pp. 11 4, 120) as synapomorphies of “eutracheophytes” (= /tracheophyta), but the extent of missing data for fossils combined with the apparent loss of these traits in extant tracheophytes reduces confidence in their inferred originations." Cantino *et al.* (2007).

Apical growth and branching coupled with ... were important innovations of vascular plants. In both [eutracheophyte] lineages, however, meristem dormancy and abortion were early innovations, providing evidence of hormonal control and substantial phenotypic flexibility. Kenrick & Crane (1997a). Meloche & Diggle (2001) (explanation of how hormonal control of dormancy and abortion controls branching and phenotypic variability) [Note how this allows overtopping to evolve into true branching by delaying the development of the minor shoot].

Renalia - Longest axis recorded is 11 cm, dichotomous, with round to reniform (kidney-shaped) terminal sporangia.

Pseudomonopodial in growth habit of monotypic stands. Displays characteristics of both Rhyniophytes and Zosterophyllophytes. G

Synapomorphies: xylem thickening and loss of columella. Kenrick & Crane (1997). But says that no evidence for columella in *Aglaophyton*. Kenrick & Crane (1997: 56). So may have evolved earlier. "The eurracheophyte dade (01 = 2) is defined by two structural features of the tracheid eel! wall: a thick, decay-resistant wall, and pitlets between thickenings or within pits (Figure 4.26)." Kenrick & Crane (1997).

"Centrarch maturation of conducting tissues appears to be present in some basal polysporangiophytes such as *Nothia* [lycopsid by our def and Crane *et al.* (2004)] and *Yunia* [stem lycophyte by same criteria] (diarch in part). However, in other taxa, which are often described as centrarch (e.g., *Horneophyton, Rhynia*), and in other basal polysporangiophytes such as *Aglaophyton* and *Stockmansella*, the distinction between protoxylem and metaxylem on the basis of cell size is difficult." Kenrick & Crane (1997). Some had lobes and protoxylem was mesarch in lobes.

"annular or helical thickenings in the water-conducting cells. Another possible synapomorpny at this level is lignin deposition on the inner surface of the tracheid cell wall. ... Include the reduction of sporangium dehiscence to a single well-defined slit and the presence of a sterorne (Figure 4.32.). Character optimization on our preferred most parsimonious tree (Figure 4.32) also indicate a change in sporangium shape at this node from fusiform and radially symmetrical to elliptical wlth bilateral symmetry. This change is reversed in the Euphyllophyta from node 59 to node 58." Kenrick & Crane (1997).

Dropping CO2 with loss of water use efficiency. Increases cavitation pressure. 17-fold variation Silurian to Pennsylvanian. "Similarly, a given internal storage capacity (pcapacitance) would supply transpired water for 17 times longer under Silurian compared to late Carboniferous conditions. High CO2 conditions would have favored relatively low hydraulic conductance systems with high capacitance." Sperry (2003).

Wood developed in both branches, perhaps independently. Sperry (2003). The additional presence of pitted elements (fig. 3D) resembling metaxylem characterizes most other tracheophyte groups (Kenrick and Crane 1991). Sperry (2003). The lignified secondary walls of tracheary elements provide a significant increase in the compressive strength of the wall—from negligible in nonlignified walls to over 40 MPa (Niklas 1992). The negative pressure required to implode a tubular conduit is a function of the wall thickness divided by the conduit lumen diameter. Sperry (2003). Propping open tracheary elements was probably the original function of lignin and secondary walls in plants (Raven 1987). The thickened and presumably lignified walls of early Devonian vascular plants are limited to tracheary elements of a protostele—a cylindrical strand in the stem center. Sperry (2003). Lignin rigidifies the cell wall in part by replacing water in the cell wall matrix and pore space (Donaldson 2001). In so doing, it reduces the permeability of the walls to water—both by reducing wall porosity and because lignin is hydrophobic. This water-proofing action is not necessary to prevent leakage of water from the conduits as long as the water is under negative pressure, and it has the disadvantage of increasing resistance to water and solute flow across the conduit walls. Sperry (2003).

"The presence of irregular pitlike openings (pitlets) in the cell wall is a common feature in many early polysporangiophyte taxa (Figures 4.25 and 4,26). Such structures are found between annular and helical bars in zosterophylls and basal lycopsids." Kenrick & Crane (1997). And reasonably-well developed xylem known from Silurian *Bagwanathia*. DuBuisson *et al*. (2005).

Sterome of similar type in zosterophyls, *C. pertoni* [stem eutrachophyte], and *Psilophyton[same?]*; but not *Nothia* or *Asteroxylon* [both lycopsids by our def and Crane *et al.* (2004)]. Kenrick & Crane (1997).

"Biflagellated sperm cells are produced by charophycean algae (except Zygnematales), bryophytes and most [but not all! r et al. note high diversity of types in lycophytes] lycophytes (figures 6 and 7), while all other tracheophytes with motile sperm produce multiflagellated cells (figures 8 and 9). The mature biflagellated cell in bryophytes is a helical cylinder, with an anteriorly positioned locomotory apparatus and four organelles: an anterior mitochondrion, a compacted central nucleus and a posterior plastid with an associated mitochondrion (figure 6b-d). In addition to flagella and basal bodies, the locomotory apparatus consists of a lamellar strip and a narrow band of microtubules (the so-called spline), which extend around the cell providing a framework for positioning of organelles." Renzaglia *et al*. (2000).

Le cylindre des sporophytes des polysporangiophytes avec ses épidermes verticaux est par contre moins efficace pour capter la lumière. La capture de la lumière peut être favorisée par la sélection de structures horizontales. DuBuisson *et al*. (2005). la microphylle. Les microphylles vont se généraliser chez les lycophytes et par convergence chez les sphenopsides au Dévonien moyen à supérieur. DuBuisson *et al*. (2005).

"Extant plants such as horsetails, club mosses, and most ferns are characterized by a haplodiplontic life history in which the sporophyte produces morphologically similar spores (homosporous) that germinate to form free-living, sometimes photosynthetic gametophytes. Sex expression in most is regarded as labile and determined by age andor presence of an antheridiogen produced by an adjacent gametophyte (44). Slight differences in spore size in homosporous plants have been correlated with stored food, time to germination, and gametophyte development; large spores produce rapidly growing bisexual gametophytes that, in turn, influence smaller spores to produce slower-growing gametophytes with only antheridia. In *Equisetum*, patterns of sex determination are controlled by various environmental parameters (45). *In vitro* studies show that crowding, mineral deficiency, high temperatures, drought, and increased sucrose concentrations result in the production of more gametophytes with antheridia. In wild populations, environmental stress appears to have the same effect (46). " Taylor *et al*. (2005).

"In extant vascular plants, only one sporophyte usually develops, but the presence of multiple sporophytes on one gametophyte is known in extant Sphenophyta, isosporous Lycophyta and Psilotophyta." Gerienne *et al.* (2006). "On the basis of our Hypothesis # 3, we believe that another characteristic of eutracheophytes might be the presence of a heteromorphic, sporophyte dominant, alternation of generations, while Rhyniopsida would exhibit an alternation of more or less isomorphic generations. Accordingly, we believe that the sets of characters exhibited by the Rhyniopsida and the eutracheophytes respectively differ from each other significantly and therefore we propose the erection of new divisions for the clades: Eutracheophyta and Paratracheophyta. Most fossil vascular plants and all living vascular plants belong to the Eutracheophyta. The oldest known representatives of Eutracheophyta are mid-Silurian (Edwards and Feehan, 1980). Members of the Paratracheophyta (ex Rhyniopsida) include sporophytes (*Rhynia*, *Stockmansella*, *Huvenia*), gametophytes (*Remyophyton, Sciadophyton*), and morphotypes (*Sennicaulis hippocrepiformis*, *Taeniocrada dubia*). Based on current evidence, Paratracheophyta evolved during the early Devonian and became extinct during the late Devonian." Gerienne *et al.* (2006).

Lycophytes

"The names Lycophyta and Lycopodiophyta have been widely applied to the same set of clades (referring variably to the crown, total clade or something intermediate). Since the former is apparently based on the name Lycopodium, it should be corrected to Lycopodiophyta under the ICBN (Arts. 16.1 and 18.1). The names Lycopsida and Lycopodiopsida are also widely applied to this set of clades" Cantino *et al*. (2007).

Pan-Lycopodiophyta: "Definition. — The total clade of /Lycopodiophyta. Composition. — /Lycopodiophyta and all extinct plants (e.g., Zosterophyllum) that share more recent ancestry with /Lycopodiophyta than with /Euphyllophyta. ... Synapomorphies. — Possibly sporangium dehiscence by a transverse, apical slit. Doyle (1998) showed this character as arising at or near the base of the (unnamed) lycophyte total clade. Kenrick & Crane (1997: Table 4.6) cited it as a possible synapomorphy of node 52, which is near the base of the total clade" Cantino *et al*. (2007).

protoxylem generally exarch Kenrick & Crane (1997).

Cambium present but unifacial, with *Isoetes* the only survivor of this line. Not produce that much wood, since diameter could not increase. "cambial cells in unifacial plants apparently did not divide anticlinally. Consequently, any increases in the cambial ring were brought about by the growth of cambial initials in length, spreading apart the cambial initials situated just above and below them in the cambial cylinder." Donoghue (2005). **[show part of figure 6, p.10]**

"The Lycophytina are defined by a change from terminal to lateral sporangia (reversed in *Hsua*)" Kenrick & Crane (1997). "Other synapomorphies appearing in the Lycophytina stem group include (1) isovalvate dehiscence along rhe distal sporangium rim (Figure 4.32, Table 4.6: node 60 -+ node 52), (2) conspicuous cellular thickening of the dehiscence line; (3) reniform sporangia (Figure 4.32, Table 4.6: node S2 -+ node 50), and (4) exarch xylem differentiation (Figure" Kenrick & Crane (1997).

Or toute plante croît d'abord par son extrémité où sont localisées une à plusieurs cellules à forte capacité de division (le méristème). Cette croissance uniquement en longueur se traduit par une limitation dans le diamètre maximal que peut atteindre la tige. Pour croître en épaisseur, l'axe a besoin de tissus supplémentaires. Chez les plantes, la croissance en épaisseur est assurée par la mise en place de méristèmes dits secondaires. DuBuisson *et al*. (2005). Since lycophytes lack phloem or bifacial cambium, had to grow fat first.

"G-type cell wall with annular-reticulate thickenings typic:al of many zosterophylls and early lycopsids. The two-layered cell wall comprises a decay-resistant inner layer facing cell lumen (white) and a nonresistant outer layer ... ." Kenrick & Crane (1997).

Basal lycophytes of all lineages (*Asteroxylon*, *Drepanophycus*, *Zosterophyllum*) show more evidence of structural support, but most was still supplied by turgor pressure. Bateman *et al*. (1998).

in the lycophyte line a peculiar bark-like "periderm" tissue (situated in the outer cortex, beneath the persistent leaf bases) was ‘‘invented’’ to stiffen the trunk" Donoghue (2005).

The transition from hydrostatic support to cell-wall support of primary growth was probably first achieved by the evolution of sclerenchyma tissue located peripherally in the stem (Raven 1987; Speck and Vogellehner 1988). Even in the arborescent lycopsids with secondary xylem (e.g., Lepidodendrales; fig. 1), the wood was of limited extent near the stem center, and mechanical support was provided by an expanded cortex and periderm (Gifford and Foster 1989; Kenrick and Crane 1997a). Sperry (2003).

Microphylls developed which are either vascularized or at least influence the growth of axial vascular tissue. Kenrick & Crane (1997). The potential microphyll homologue-the lateral sporangium with a helical sporangiotaxis and a single vascular strand-defines a more inclusive clade that contains zosterophylls and lycopsids. Kenrick & Crane (1997: 291)

"In zosterophylls and lycopsids, sporangia are attached laterally on short stalks (Figures 5.1 and 5.24); in some basal taxa, such as *Zosterophyllum myretonianum*, *Nothia*, and *Asteroxylon*, these stalks are known to he vascular." Kenrick & Crane (1997). Sporangia are symmetrical and isovalvate.

"One variation of the sterilization hypothesis predicts that stem group Lycopsida will have strobilar regions composed of sporangium pairs or sporangia with sporangium-shaped sporophylls on otherwise naked axes. Paired sporangia have not been recorded in the fossil record of this group but would be difficult to recognize in plants with relatively compact strobilate regions. However, sporangium-like sporophylls bearing functional sporangia have been documented in a plesiomorphic member of the zosterophyll-lycopsid clade recently described from China. *Adoketophyton subverticillatum* bears conspicuous fan-shaped sporophylls, each with a single, adaxial, reniform sporangium on otherwise naked axes" Kenrick & Crane (1997: 291)

Zosterophylls

Gosslingia - Aerial stems up to 0.5 m in height with dichotomous branching but a strong centralized axis resulting in an imperfect pseudomonopodial habit. Small short vascularized branches (<2 mm long) occur along the axis. Commonly found as monotypic assemblages Rebuchia - Plant of densely branched, tufted aspect with distinct upright. G

Sawdonia - Aerial parts up to 30 cm tall (may have attained heights of 0.5 m), pseudomonopodial (anatomically the axes appear dichotomous, but the plant takes on the appearance of a central axis with laterals) from rhizome with lateral dichotomous axes. Apices are coiled (circinate or fiddle-heads such as found in ferns). Lateral spines have no vascular tissue. Reniform (kidney-shaped) sporangia are loosely aggregated into spikes. Commonly found in monotypic assemblages. G.

"*Zosterophyllum* (Figure 10.5e), a zosterophyllopsid, shares many features with the rhyniopsids, but has numerous lateral sporangia, instead of a single terminal one, on each vertical stem." Benton & Harper (1997).

Zosterophylls had cortical fibers which supplied some mechanical support. Highly developed in derived lycophytes, but lignified core with secondary xylem development required for trees (??) Bateman *et al*. (1998).

Lack of secondary phloem, limiting transport from photosynthetic areas to growth areas. Consequently, shallow, masive roots with microphylls. Trunk not maintained for long. Donoghue (2005).

Branching may have been planar in basal zosterophylls. Kenrick & Crane (1997). In addition to the main branching system, small subordinate (often undeveloped) axes are common in many zosterophylls. Kenrick & Crane (1997). In zosterophylls, "One common type of branching pattern involves the production of a single, usually small, undeveloped, *circinate* axis slightly below each dichotomy of the main branching system (Figure 5.15). These small axes are oriented perpendicular to the plane of the main branching system" Kenrick & Crane (1997).

Tree grade independently here, and in both euphyllophyte groups. Donoghue (2005).

Silurian zosterophylls with *isotomous* branching. Kotyk *et al.* (2002).

Enations independently acquired in zosterophylls Kenrick & Crane (1997: 291)

"The most likely microphyll homologues occur in the Zosterophyllopsida and closely related taxa" Kenrick & Crane (1997: 290)

Cauline sporangium attachment is the general condition within me Zosterophyllopsida Kenrick & Crane (1997). "Zosterophyllopsida, and these leafless plants bear simple, cauline, lateral sporangia on short, unbranched stalks (Figure 5.1)." Kenrick & Crane (1997).

Lycopsids

Lycopodiophyta: "The least inclusive clade containing *Lycopodium clavatum* L. 1753, *Huperzia selago* (L.) Schrank & Mart. 1829, *Isoëtes lacustris* L. 1753, and *Selaginella apoda* (L.) Spring 1840." That's the crown clade. For this clade: "association of a single axillary or adaxial sporangium with a sporophyll; absence of vasculature in the sporangium; metaxylem tracheids pitted; root stele bilaterally symmetrical, with phloem located on only one side of the stele (but there are a lot of missing data for fossils outside the crown, so this trait may be synapomorphic of a more inclusive clade); crescent-shaped root xylem (but there are a lot of missing data for fossils outside the crown). The following characters are synapomorphies of this crown clade relative to other crowns but are apomorphic at a more inclusive level when fossils are considered (Kenrick & Crane, 1997: Fig. 6.18, Table 7.2): microphylls (“lycophylls”; Schneider & al., 2002; Pryer & al., 2004a); exarch xylem differentiation in stem (Kenrick & Crane, 1997; Doyle, 1998; Schneider & al., 2002); stellate xylem strand in stem; reniform sporangia with transverse dehiscence (Doyle, 1998). This list is not exhaustive; see Kenrick & Crane (1997: Table 7.2) and DiMichele & Bateman (1996) for other synapomorphies listed under Lycophytina and Lycopsida." Cantino *et al*. (2007).

Nothia - Naked invaginated axes with pear-shaped sporangia (apical dehiscence) on adaxially (downward) recurved stalks. Sporangia may be helical or whorled in arrangement. Found with other rhyniophytes. G

"[Rhynie Chert] sporophytes have branched aerial axes (i.e. are polysporangiophytes: Kenrick and Crane, 1997) which are endohydric, but do not always have true xylem (i.e. water conducting cells with unevenly but regularly thickened walls typical of tracheids); an example of an endohydric plant without true xylem is *Nothia aphylla*

Asteroxylon attained a height of 0.5 meters and consisted of erect monopodial branches originating from a flat-lying (prostrate) rhizome. The xylem cylinder is an actinostele (star-shaped). Axes are covered with "enations" (appear to be leaves but lack vascular tissue) with stomata. Kidney-shaped sporangia (reniform) are borne in the axil of an enation. Vascular tissue has been identified in the sporangial area. G.

Asteroxylon with microphylls. Raven & Edwards (2001). The leaf of the early fossillycopsid Asteroxylon is often cited as evidence favoring the enation hypothesis because of the leaf's enation- like morphology. Unlike in other lycopsids, the leaf trace of the fossil terminates at the base of the leaf. *Asteroxylon* is unique in this respect, but it is equally parsimonious to interpret the absence of vasculature within the leaf as a loss. Kenrick & Crane (1997: 290). Microphylls independently acquired in Lycopsida. Kenrick & Crane (1997: 290-291) "lycophyte *Baragwanathia*, cuticle, stomata, tracheids, and (probably) intercellular gas spaces are known from above-ground structures in Lower Devonian specimens (but not so far from the less well preserved Upper Silurian fossils) (Hueber, 1983), Raven & Edwards (2001).

"anatomical studies of arborescent lycopsids raise certain matters with regard to their physiology (Phillips & DiMichele, 1992). The lack of a clear phloem connection between root and shoot, the generally limited phloem throughout the plant's aerial shoot, the leaf-like rootlets borne on the stigmarian axes, and the long leaves on stems and cones, are all consistent with extremely localized use of photosynthate and perhaps even self-supporting root systems in terms of carbon fixation." DiMichele & Gastaldo (2008).

"In lycopsids, *antheridia* are embedded individually within the tissues of the *gametophyte*, whereas antheridia in other vascular plants, such as the Ophioglossaceae, Equisetaceae, Psilotaceae, and leptosporangiate ferns, are sessile on the surface of the gametophyte." Kenrick & Crane (1997).

Wood developed early, but fairly deep withing the lycopsid lineage (Lepidodendrales) Sperry (2003).

"secondary vascular tissues evolved independently in at least two major groups of vascular plants. These two lineages of secondary vascular tissues were not homologous (Cichan, 1985). ... Species of the second group (or groups) produced either a unifacial vascular cambium or a cambium that differentiated secondary vascular tissues only toward the inside, and except for the quillwort *Isoetes* (Lycopsida), are all extinct" Rothwell & Lev-Yadun (2005).

The association of a single sporangium with a sporophyll is a unique feature of lycopsids ... Usually, the sporangium is axillary to the sporophyll or positioned on the basal part of its adaxial surface, but in some taxa it is well out on the leaf. ... In certain early fossils, such as *Asteroxylon* ... and *Drepanophycus* ... sporangia clearly are cauline and do not appear to be associated with specific "sporophylls." but in others. such as *Baragwanathia*, the condition is unclear ... . It is uncertain whether the cauline sporangia of such plants as *Asteroxylon* are loosely associated with a leaf or completely dissociated from leaf phyllotaxy (Kenrick & Crane, 1997: 201). [not certain this is consistent with k&C:289]

"Three hypotheses concerning the origin of the lycopsid microphyll focusing on the sporophyll-sporangium appendage (transitions occurring from left to right). (a) The reduction hypothesis interprets the sporangium-sporophyll appendage in lycopsids as a highly reduced lateral branch. Sporophylls of putative extinct intermediates are characterized by branched "leaves" and multiple sporangia. Modified after Stewart and Rothwell 1993. (b) The enation hypothesis interprets the sporophyll as a new structure that evolved as a sterile outgrowth of the stem. Sporophylls of putative extinct intermediates are characterized by unbranched and nonvascular or partially vascular "leaves" (path of vascular tissue indicated within stem). [as K&C note, these fail to explain association of sporophyll with leaf] (c, d) The sterilization hypothesis interprets the sporophyll as a sterilized sporangium. Sporophylls of putative extinct intermediates are characterized by unbranched and partially vascularized leaves that may be reniform or spatulate in shape (path of vascular tissue indicated within stem). In (c), the sporangiumsporophyll association arises by sporangium duplication prior to sterilization. In (d), the sporangium-sporophyll association arises by subsequent association of sporangium and microphyll." Kenrick & Crane (1997: 289)

We suggest that the lycopsid microphyll is a transformational homologue of the sporangium.... Sporangium and sporophyll share similar positions on the stem, and the expression of this positional similarity is continued in the phyllotaxis of vegetative leaves. Both organs also have a similar ontogeny, developing as lateral structures from epidermal initials close to the stem apex.... Similarity of sporangium vascularization among early members of the Lycophytina to vascularization of microphylls in Lycopsida is also significant. Kenrick & Crane (1997:291)

In *Asteroxylon*, both microphylls and sporangia possess their own vascular trace. The absence of vasculature within the microphyll of *Asteroxylon* is consistent with the absence of vasculature in equivalent areas of the sporangium. Kenrick & Crane (1997: 291)

"During gametophyte ontogeny in the Lycopodiaceae, apical growth ceases at a very small size, and the peripheral cells on the apical flanks become meristematic, forming a ring meristem. Subsequent cell divisions in the ring meristem produce an expanded, disk-shaped apex that is typically 3- 15 mm in diameter and has a smooth or convoluted margin (Figure 7.28). The archegonia and antheridia are located on the upper surface of the disk." Kenrick & Crane (1997: 305) The disk-shaped gametangiophores in the permineralized Rhynie Chert plant Kidstonophyton (sporophyte = Nothia aphylla) and in the compression fossils of the Sciadophyton type strongly resemble gametangiophore morphology in extant Lycopodiaceae (Figure 7.28). Both Kidstonophyton and Lycopodium clavatum gametangiophores comprise an expanded, disk-shaped structure of similar size and shape. Both bear gametangia on the convex upper surface and have a raised marginal rim without gametangia. Kenrick & Crane (1997: 305)

"It is worth pointing out that the gametophyte of *Lycopodium* is perennial, and may persist at the base of the mature sporophyte (Raven et al., 1999)." Gerienne *et al.* (2006).

Stem Euphyllophytes

Euphyllophyta crown group: "The most inclusive crown clade containing *Ginkgo biloba* L. 1771 (/Spermatophyta), *Equisetum telmateia* Ehrh. 1783, and *Pteridium aquilinum* (L.) Kuhn 1879 (/Leptosporangiatae) but not *Selaginella apoda* (L.) Spring 1840 (/Lycopodiophyta)." ... "Synapomorphies (relative to other crown clades). — ... sporangia terminating lateral branches (Pryer & al., 2004a) and dehiscing longitudinally (Doyle, 1998) (these features characterize the earliest members of /Pan-Euphyllophyta and were modified in most extant representatives); lobed, mesarch primary xylem strand (Stein, 1993; Kenrick & Crane, 1997: Fig. 7.10 and p. 241; Doyle, 1998), which has been modified in the stems of most extant members; multiflagellate spermatozoids (apparently convergent in *Isoëtes*) (Garbary & al., 1993; Kenrick & Crane, 1997: 240, 275); a 30-kb inversion in the chloroplast genome (Raubeson & Jansen, 1992a). Megaphylls (euphylls) are sometimes cited as a synapomorphy of /Euphyllophyta (Schneider & al., 2002), but analyses that include fossils suggest that the compound, fernlike megaphylls of monilophytes and seed plants evolved independently (Stewart & Rothwell, 1993; Kenrick & Crane, 1997; Doyle, 1998; Boyce & Knoll, 2002; Friedman & al., 2004). Even within /Lignophyta, the small, wedge-shaped leaves of *Archaeopteris* may not be homologous with the whole fernlike fronds of seed ferns but rather with individual leaflets of such fronds (Doyle & Donoghue, 1986a; Doyle, 1998)." Cantino *et al*. (2007).

Pan-Euphyllophyta: "Euphyllophyta and all extinct plants (e.g., *Psilophyton*) that share more recent ancestry with /Euphyllophyta than with /Lycopodiophyta. Synapomorphies. — Several synapomorphies were listed by Kenrick & Crane (1997: 240, Table 7.2, and pages listed below), most of which have been lost or modified in some or all extant members of the clade: pseudomonopodial or monopodial branching (pp. 109, 359) (although if the fernlike leaves of early seed plants were derived from pseudomonopodial branch systems of more basal lignophytes (Doyle, 1998), the axillary monopodial branching of seed plants and the pseudomonopodial branching of more basal lignophytes may not be homologous); helical arrangement of branches (pp. 11 0, 360); dichotomous appendages (pp. 11 3, 361); recurvation of branch apexes (pp. 11 2–11 3, 360); paired sporangia grouped into terminal trusses (pp. 121–122, 364); sporangium dehiscence along one side through a single longitudinal slit (pp. 125, 366). Kenrick & Crane also cited scalariform bordered pitting of metaxylem cells as a synapomorphy, but it does not occur in Eophyllophyton and therefore is synapomorphic for a slightly less inclusive group than the total clade (op. cit., pp. 120, 363, Fig. 7.10)." Cantino *et al*. (2007).

Psilophyton - Variable branching of the erect stem (pseudomonopodial, dichotomous or trichotomous) that emerged from rhizomatous mat. Stem with variously shaped spines. Paired sporangia terminate ultimate dichotomy of the lateral branches; homosporous. Central axis may be as much as 3.5 cm in diameter; maximum height may have been > 1m. G.

Pertica - Lateral branches are tetrastichous (four branches in an opposite pattern), forming a clockwise spiral, and originate from a main axis Individual branches dichotomize many times at right angles to each other. Axes have small bumps (papillae). Clusters of sporangia (32-256) terminate branches; trilete spores are homosporous. Main axis 1.5 cm in diameter; maximum height may have been several meters. G

"The Euphyllophyta are supported as a group by six synapomorphies: (1) pseudomonopodial or monopodial branching, (2) a basically helical arrangement of branches, (3) small, "pinnulelike" vegetative branches (nonplanare in basal taxa), (4) recurvation of branch apexes, (5) sporangia in pairs grouped into terminal trusses, and (6) multicellular appendages (spines)." "Other synapomorphies appearing in this stem group indude (1) meta xylem pitting, (2) aligned xylem, (3) radial sporangium symmetry (reversal), (4) fusiform sporangia (reversal) (Figure 4.32, Table 4.6: node 59 ~ node 58), (51 the loss of multicellular spines (reversal) (Figure 4.32, Table 4.6: node 58 ~ node 57), (6) a lobed xylem strand, and (7) a change from 3 continuous sterome to discrete hundles of fibers in the stem correx (Figure 4.32, Table 4.6: node 57 4 node 56). This result supports the independem origins of pseudomonopodial branching, meta xylem pitting, and lohed xylem strands in the lycophytina and toc Euphyllophyta." Kenrick & Crane (1997).

True tracheids in basal euphyllophytes. Donoghue (2005).

Protoxylem generally mesarch to centrarch. Kenrick & Crane (1997).

"P-type cell with scalariform pitting typical of plesiomorphic Euphyllophyta (e.g., *Psilophyton*). The two-layered cell wall comprises a decay-resistant inner layer facing the cell lumen, pit chambers, and a nonresistunt inner layer within the scalariform bars ... . Characteristically, the scalariform pit apertures are covered with a perforate sheet of decay-resistant material." Kenrick & Crane (1997).

"overtopping (or *pseudomonopodial* growth) evolved at the base of the euphyllophytes" possibly in multiple lineages. Enabled the evolution of *megaphyllous* leaves. Branching equivalent to development of *hox* polarity in animals and may involve similar genes (i.e. *knox*). Donoghue (2005). Computer simulations suggest that overtopping preceded planation, which preceded webbing. Niklas (2004). Interestingly, Niklas notes this occurs on the assumption that light interception and mechanical stability are the main criteria (i.e. not spore dispersal or water conservation). He does not say what happens when these are factored in or substituted. His series reproduces *Psilophyton* wonderfully from a very basal *Cooksonia*. It does not reproduce lycophytes or *Archaeopteris*. Suggests that other factors (competition? predation?) were more significantly limiting than light and mechanical stability in those cases.

"basal eupbyllophytes many taxa exhibit a radial alignment of the metaxylem, but there is often no histological evidence of *cambial* activity, and *ray cells* are absent." However, "Radially aligned xylem, whether or not the product of cambial activity, has been noted in tbe larger axes of [some species of] *Psilopbyton*." Kenrick & Crane (1997). *Psilophyton* shows aborted branches, although quite different from zosterophylls. Kenrick & Crane (1997).

But branch structure in *Psilophyton* like the simplest axes of *Aglaophyton*. Kenrick & Crane (1997). Branch *pattern* was helical. Kenrick & Crane (1997). Development of various kinds of long-range order in lineages.

"In ferns and seed plants, much morphological diversity is clearly attributable to modifications of branching systems into a variety of leaf-like organs, whereas the relatively conservative clubmoss bauplan has a dearth of organ systems that can be interpreted as modified branches." Kenrick & Crane (1997a). But see Kotyk *et al". (2002).

"Much of the morphological diversity in the Euphyllophyta seems attributable to profound modifications to the branching systems, whereas morphological conservatism within the Lycophytina is reflected in the absence of elaborate branching and the dearth of organ systems that can be interpreted as transformed branches." Kenrick & Crane (1997: 298)

Leaves appeared as a result of falling carbon dioxide concentrations. Prior to Mid-Devonian, expanses of photosynthetic area would have killed the plant from heat stress. Beerling *et al.* (2001). Associated with 100x increase in density of stomata. Earliest leaves in *Eophyllophyton*. See also image here.

"Isotomously branching, nonplanar, small, ultimate appendages are present in many taxa of the Euphyllophyta. These structures are leaflike in several respects but are unwebbed." Includes *Psilophyton*. Kenrick & Crane (1997). Les euphyllophytes sont caractérisées par un mode de croissance particulier qui se traduit par une latéralisation des rameaux, c'est-à-dire qu'on l'on a un axe principal vertical et des ramifications latérales (elles-mêmes ramifiées) de diamètre plus petit que celui de l'axe principal (ce qui s'observe dès le Dévonien inférieur chez *Psilophyton*). DuBuisson *et al*. (2005). La vraie feuille ou mégaphylle serait une ramification latérale transformée avec mise dans un même plan horizontal de toutes les ramifications du rameau et développement d'un limbe (le tissu aplati qui constitue les feuilles) réunissant ces ramifications. L'apparition de cette feuille est néanmoins relativement tardive, au Dévonien supérieur, par convergence chez les filicopsides et chez les premières gymnospermes. DuBuisson *et al*. (2005).

"The enation hypothesis predicts that the microphyll character will be nested within a more general clade defined by the presence of enations. Although nonvascular enations are common in many early land plants, this feature is highly homoplastic (see Chapter 3). Bower (1935) used the enations of *Psilophyton princeps* as a model for an intermediate stage in microphyll evolution, but our analysis shows that enations in *Psilophyton* evolved independently from those in the Lycophytina" Kenrick & Crane (1997). Really? See "Multicellular spines are common in many zosterophylls, where they may be filiform ... or deltoid in shape ... . Morphologically similar spines are found in some rhyniophytes, such as *Huvenia* and *Dutoitea*, and also in some species of *Psilophyton* ... . Microphylls of basal homosporous lycopsids generally are somewhat larger than the spines discussed above and are either fully vascularized or clearly influence the differentiation of vascular tissue in the adjacent axis (e.g., *Asteroxylon*: Figure 6.16). We define the microphyll as a stem outgrowth that influences the differentiation of axial vascular tissue." Kenrick & Crane (1997: 113) Enation hypothesis still possible. K&C favor idea that "all the appendicular structures of lycopsids (microphylls, ligules, sporangia) as iterative modifications of a single basic developmental pathway (Figure 7.21). We suggest that the lycopsid microphyll is a transformational homologue of the sporangium." Kenrick & Crane (1997: 291)

Our preliminary c1adogram for the Euphyllophyta supports a hypothesis of homology among megaphylls in seed plants, ferns, and *Equisetum* (highly reduced) at the level of dichotomous, threedimensional lateral branches of the *Psilophyton* type. This result is consistent with the independent evolution of planation, webbing, and fusion in the major clades of megaphyllous plants. Thus, many of the similarities between megaphylls in ferns and in basal seed plants are convergent. Probably only the open dichotomous vasculature typical of many basal members of these clades can be viewed as homologous. Kenrick & Crane (1997: 295). This consistent with the hypothesis of forcing by lowered CO_2, increased stomata. Osborne *et al*. (2004).

"In trimerophytes, progymnosperms., and many early fernlike taxa [including *Psilophyton*], sporangia are paired in densely hranched clusters at the ends of smaller branches." Kenrick & Crane (1997). Dehisence in *Psilophyton*, *Pertica* seems to be from a single slit on one side of the sporangium. Kenrick & Crane (1997).

Sperm are larger, all multiflagellate, with more abundant organelles (suggesting bigger investment in sperm durability and mobility). Also, "Cellular elongation or streamlining reduces excess baggage and, perhaps even more importantly, is instrumental in movement of the spermatozoid through the narrow tube of the archegonial neck." Renzaglia *et al*. (2000).

. "pteridophytes, in which the single epidermal initial first divides transversely (periclinal division). The outer cell then further divides to form the neck while the inner cell divides periclinally to produce neck canal cells, ventral canal cell and egg (figure 2f, g, j) (Bierhorst 1971; Kenrick & Crane 1997a). With expansion, the archegonium projects from the epidermal surface. The neck invariably consists of four vertical rows of cells (figure 2h, i). Clearly, there are no parallels in development between the sunken archegonia of hornworts (figure 2e) and similar embedded archegonia in pteridophytes (figure 2j)." Renzaglia *et al*. (2000).

Monilophyta

Unifacial cambium. Donoghue Tree habit through support from roots or intertwining of numerous small stems. (2005).

Some developed wood, but (per fossil record) not until Jurassic. Sperry (2003).

"Synapomorphies (relative to other crown clades). — A possible synapomorphy is the exclusively centrifugal development of the spore *exine* (Schneider & al., 2002)" Cantino *et al*. (2007) This for the crown group -- not for Pan-Monilophyta which is actually Cantino *et al*.'s equivalent of this clade. Definition is the total clade of "the most inclusive crown clade containing *Equisetum telmateia* Ehrh. 1783 and *Pteridium aquilinum* (L.) Kuhn 1879 (/Leptosporangiatae) but not *Ginkgo biloba* L. 1771 (/Spermatophyta) or *Selaginella apoda* (L.) Spring 1840 (/Lycopodiophyta)." Cantino *et al*. (2007).

Modern *Equisetum* may be viewed as an example of an analogous stage in the evolution of the breeding system that we hypothesize in the *Rhynie chert* plants. *Equisetum* spores contain a pair of *hygroscopic elaters* that function in dispersing spores from the *sporangium*. However, these appendages also become entangled with those of other spores so that clusters of spores are dispersed together. This event results in the development of multiple *gametophytes* in close juxtaposition and optimizes the opportunity for fertilization and the development of new sporophytes while reducing the chances for outbreeding. Gametophytes of Equisetum may be photosynthetic and long-lived and may produce either antheridia or archegonia initially; gametophytes with archegonia eventually develop antheridia, whereas those with antheridia rarely produce archegoniaTaylor *et al*. (2005).

Lignophytes

When developed in early lignophytes, originally limited to main axis. *Id.*

Wood common to all Sperry (2003)

Trimerophytes had P-type. Kenrick & Crane (1997a).

Bifacial cambium developed by end of Devonian. "Cambial cells in lignophytes can undergo both periclinal and anticlinal cell divisions, the periclinal ones adding xylem and phloem and the anticlinal ones adding extra cells to the ring of cambium. Donoghue (2005). Un premier méristème se forme entre les phloème et xylème primaires, c'est le cambium et il produit au moins un nouveau xylème dit secondaire qui croît radialement. Ce nouveau xylème est le bois que l'on trouve dans les troncs. Un deuxième méristème (nommé phellogène) se forme vers la périphérie de la tige et donnera l'écorce. La présence d'un bois et d'un tronc définit l'arborescence, et donc l'arbre, et autorise de très grandes tailles, via non seulement l'augmentation du diamètre mais aussi via l'ajout de nouveaux tissus lignifiés plus ou moins rigides. DuBuisson *et al*. (2005). Developed fully by *Archaeopteris*. DuBuisson *et al*. (2005) (fig 7).

"secondary vascular tissues evolved independently in at least two major groups of vascular plants. These two lineages of secondary vascular tissues were not homologous (Cichan, 1985). The first was in a clade that includes the extinct progymnosperms (Crane, 1985; Rothwell and Serbet, 1994) and seed plants, where a bifacial vascular cambium usually forms xylem toward the inside and phloem toward the outside (Larson, 1994)." Rothwell & Lev-Yadun (2005)

"When various obstacles such as buds, branches, and wounds disrupt the axial polar auxin flow in or near the cambial region of seed plants (conifers and dicotyledons), polar auxin flow whirlpools are formed in the cambial zone (Sachs and Cohen, 1982). These auxin whirlpools induce the differentiation of characteristic circular tissue patterns of tracheary elements above axillary buds of woody plants ... and at branch junctions in the wood of conifers (Lev-Yadun and Aloni, 1990) (Fig. 2) and dicotyledonous woody plants (Lev-Yadun and Aloni, 1990) (Fig. 3). Identical circular patterns also occur at the same positions in the secondary wood of the Upper Devonian fossil progymnosperm *Archaeopteris* (Figs. 4, 5), thus providing the first clear fossil evidence of polar auxin flow. Such spiral patterns do not occur in the primary xylem of either fossil progymnosperms or extant seed plants. They are also absent from the primary xylem strands of living ferns and other nonseed plants such as *Psilotum nudum* (L.) Beauv., and from the Lower Devonian fossil land plants that we have examined [ca. 390-385 million-years-old *Aglaophyton major* (Kidston and Lang) D. Edwards; *Renallia hueberi* Gensel; and *Psilophyton dawsonii* Banks, Leclercq & Hueber]." Rothwell & Lev-Yadun (2005).

Reproduction

"enlargement and branching of the sporophyte preceded the acquisition of tracheids" Donoghue (2005).

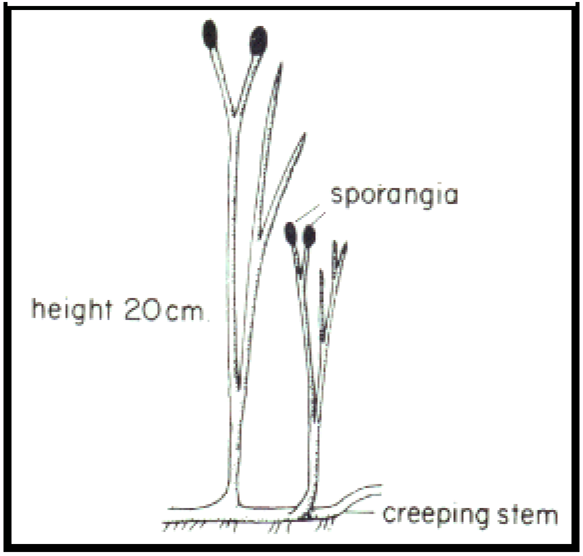
Included in the rhyniophytes are ancestral forms are the ancestral genus *Cooksonia*, from the late Silurian to Late Devonian (Wenlock to Frasnian). By the Early Devonian more advanced types like *Rhynia* had evolved.

delayed initiation of spore-bearing organs Kenrick & Crane (1997a). Note zosterophylls with spores on retarded branches approaching a Pseudomono condition. Kotyk *et al.* (2002).

Ecology

"The evolution of roots is thought to have been an important factor in the reduction of atmospheric CO_2 concentrations through increased weathering of Ca–Mg silicate minerals brought about by mechanical disruption and soil acidification." Kenrick & Crane (1997a). Raven & Edwards (2001).

"the maximum observed aerial axis diameter of vascular plant fossils from the late Silurian to the Devonian-Carboniferous boundary [increases] from some 3 mm diameter in the latest Silurian, via an approximately linear increase in the logarithm of diameter with time, to



almost 2 m at the end of the Devonian in the progymnosperm *Archaeopteris* (*Callixylon*). [Theory] suggest a height for *Archaeopteris* of 10-30 m. Corresponding to this increase in height is an increased plant biomass per unit land area and depth of penetration of roots *sensu lato*. ... there is independent evidence of an increasing depth of penetration of roots ... up to 2 mm in diameter and up to 0.9 m long in the Emsian (late Early Devonian) have been found." Raven & Edwards (2001). Uncertain effects, but presumably large. R&E miss the point that the change of cycling could have been way out of balance.

Siluro-devonian increase in oxygen and decrease in CO_2. *But see* Scott & Glasspool (2006).

Herbivory by Middle Devonian? Bateman *et al*. (1998).

least one form, *Taeniocrada* is thought to have been aquatic, although whether transitional forms from fresh water to land or secondarily aquatic is not clear.

Expansion into an empty ecospace, with rapid radiations in a "fractal" pattern. Bateman *et al*. (1998).

Notes

[1] These generalizations lose much of their force over the course of the Mesozoic. We are speaking only of the Paleozoic pattern. A Paleozoic naturalist would rarely find 100 temnospondyls of the same species in one place, but -- if he did -- he could count on each one having exactly the same number of limbs. For Paleozoic plants, the case would be exactly the reverse.

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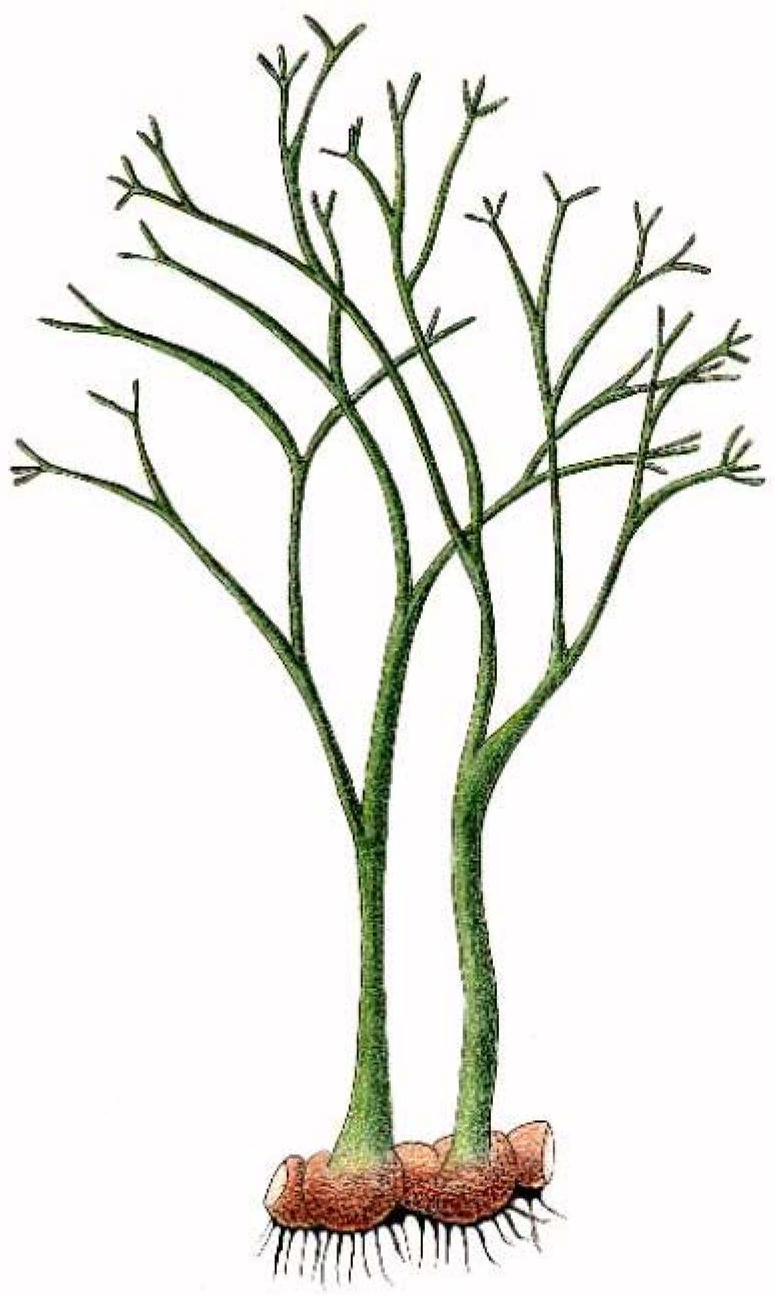
Edwards (1986) found that Rhynia major was probably not a true vascular plant, but possessed non-lignified water-conducting (hadrom) and food-conducting (leptom) tissues similar to those found in mosses. He therefore renamed it, Aglaophyton major. It is believed that the gametophyte generation also had water-conducting tissue, cuticle, and stomata, making this species isomorphic. This species (as well as species of Horneophyton originally classified as rhyniophytes) is certainly transitional between mosses and vascular plants and, therefore, is considered a protracheophyte.

Horneophyton



Horneophyton lignieri
Class Horneophytopsida - Order Horneophytales - Family Horneophytaceae
Pragian of Scotland (Euramerica)

Illustration © Francoise Gantet, 1997 - from Le Monde des V�g�taux - Cooksonia caledonica (illustration) page

Horneophyton represents a distinct evolutionary form which may have been more primitive than the rhyniopsids. It has dichotomously-branched above-ground axes that terminate in sporangia, but is unique in the presence of a swollen base bearing numerous rhizoids, and the cylindrical and branched sporangia. The sporangia have a central column similar to that of some mosses, but the tracheids in the center of *Horneophyton*'s axis remove it from the moss lineage. *Horneophyton* also appears to have a free-living gametophyte.

Horneophyton seems to have preferred damp to wet conditions, growing on sandy and organic-rich substrates, as well as being an early colonizer of sinter (a chemical sedimentary rock deposited by precipitation from hot spring mineral waters, and forming the characteristic gray rock formations seen in the geyser basins) surfaces. The subterranean corm-like rhizomes that form the base of the plant were probably easily able to cut through pre-existing plant litter, as well as helping to anchor the plant. Like many Rhynie species, and indeed early plant assemblages in general, *Horneophyton* is commonly present as monotypic stands, indicating the low biodiversity of the time. It is only rarely associated with *Rhynia gwynne-vaughanii*

Links

Horneophyton - from the Biota of Early Terrestrial Ecosystems: The Rhynie Chert - **best on the web**

The Rhynie Flora--Elaborations on a Theme

The Rhynie Chert and its Flora - VII. Nothia and Horneophyton - includes photographs showing details of microstructure

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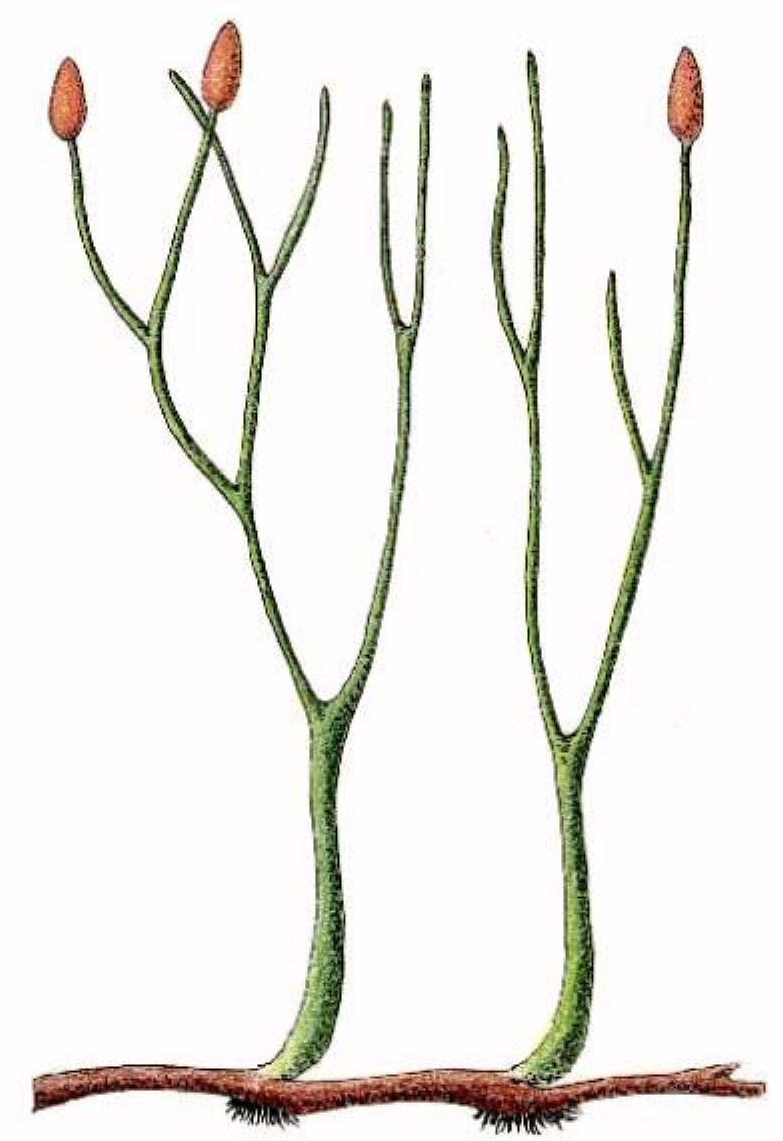
Aglaophyton major



Aglaophyton major
Pragian of Scotland (Euramerica)

Illustration © Francoise Gantet, 1997 - from Le Monde des V�g�taux - Cooksonia caledonica (illustration) page

At least one plant originally considered rhyniophytes (and hence primitive vascular plants) is now known not to belong in that group at all. Edwards (1986) found that the structures in *Rhynia major* the structures originally interpreted as tracheids in a central vascular strand turned out on closer examination to be conducting tubes more like those of some mosses, indicating this was probably not a true vascular plant, even though, like the rhyniophytes this plant lacked leaves and roots, and had terminal sporangia on branching axes. He therefore renamed it *Aglaophyton major*. It is believed that the gametophyte generation also had water-conducting tissue, cuticle, and stomata, making this species isomorphic.

This species is therefore either transitional between mosses and true vascular plants, or represent one of a number of experimental lineages that were evolving during the late Silurian and early Devonian (similar analogies of parallel straight-line evolution can be found among the early synapsids, where several lineages independently evolved towards the mammalian condition). These plants are therefore considered protracheophytes.

In any case, *Aglaophyton major* coexisted alongside primitive true vascular plants like *Rhynia* and *Asteroxylon*. All these plants have been found perfectly preserved in fossil form in the Rhynie Chert (Pragian epoch, Devonian period of Euramerica). They were among a variety of plants apparently growing together in an ancient community. Although very primitive, *Aglaophyton major* was a relatively large plant for this time, with branched aerial stems up to about 60 cm in height

The gametophyte of *Aglaophyton* appears to be *Lyonophyton*, another Rhynie Chert plant with naked axes and dichotomous branches; these branches terminate in antherida. Lyonophyton has some sort of conducting strand at the center of its axis, but the nature of the tubes is questionable. The two generations are linked together by shared epidermal features.

Aglaophyton was a common plant in the Rhynie ecosystem, and seems to have preferred growing on litter-covered, organic-rich surfaces. While occasionally found in monotypic stands it more often occurred with other species, particularly *Nothia*, *Asteroxylon*, *Horneophyton* and occasionally *Rhynia*. The cuticle and stomata display adaptations to prevent water loss, suggesting adaptation to drought-like conditions, although wet conditions may have been necessary for spore germination.

Links

Edwards, DS, 1986. Aglaophyton major, a non-vascular land-plant from the Devonian Rhynie Chert. - *Botanical Journal of the Linnean Society*, 93: 173-204.

Aglaophyton major

Aglaophyton - from the Biota of Early Terrestrial Ecosystems: The Rhynie Chert - **best on the web**

The Rhynie Flora--Elaborations on a Theme - Aglaophyton

The Rhynie Chert and its Flora - III. Rhynia and Aglaophyton - includes photographs showing details of microstructure

The Rhynie Chert and its Flora - VI. Growth Forms of Rhynia and Aglaophyton - includes photographs showing details of microstructure

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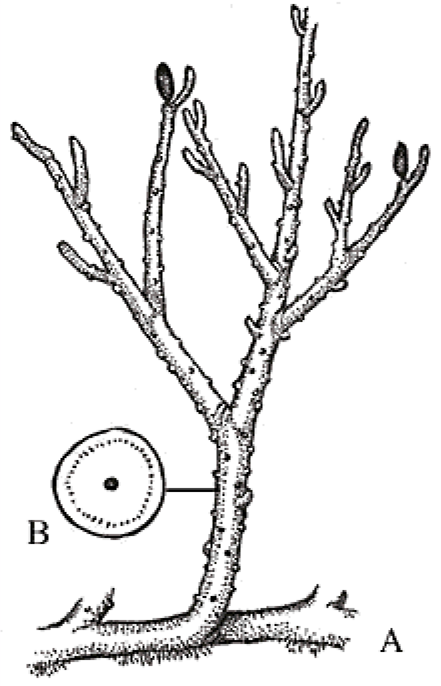
Rhynia gwynne-vaughanii



Rhynia gwynne-vaughanii
Class Rhyniopsida - Order Rhyniales - Family Rhyniaceae

(A) Whole plant reconstruction
schematic protostele in transverse section.

image courtesy of the University of California Museum of Paleontology web site

Rhynia gwynne-vaughanii is a primitive vascular plant with branching leafless stems that reached a height of about 18 cm and culminated in fusiform-shaped sporangia. The upright stems branched from creeping branching horizontal rhizomes that bore delicate hair-like roots. The lateral branches could overtop the sporangia bearing stems, and the upright portions of the plant would have had a thicket-like appearance.. Small bumps along the stems may contain archegonia, which indicate a possible bryophyte-like life history, although this is still unclear. But there is also a distinct protostele composed of distinct phloem and only a handful of xylem cells.

Rhynia is named after the Rhynie Chert (Pragian epoch, Devonian period of Euramerica), a fossil paleocommunity of which it is a the most common member, both numerically and in terms of ground cover.

The species is commonly present as monotypic stands, and seems to have been an early colonizer of well-drained sinter (hot spring sedimentary deposits) and sandy substrates. It is also found associated with all other Rhynie plants except (apart from very rarely) *Horneophyton*, suggesting that *Rhynia* was a vigorous, perhaps weed-like, form tolerant of a wide range of habitats and able to withstand interspecies competition within the Early Devonian ecosystem.

Links

Rhnia - from the Biota of Early Terrestrial Ecosystems: The Rhynie Chert - **best on the web**

The Rhynie Flora--Elaborations on a Theme - Rhynia

III. Rhynia and Aglaophyton - includes photographs showing details of microstructure

The Rhynie Chert and its Flora - VI. Growth Forms of Rhynia and Aglaophyton - includes photographs showing details of microstructure

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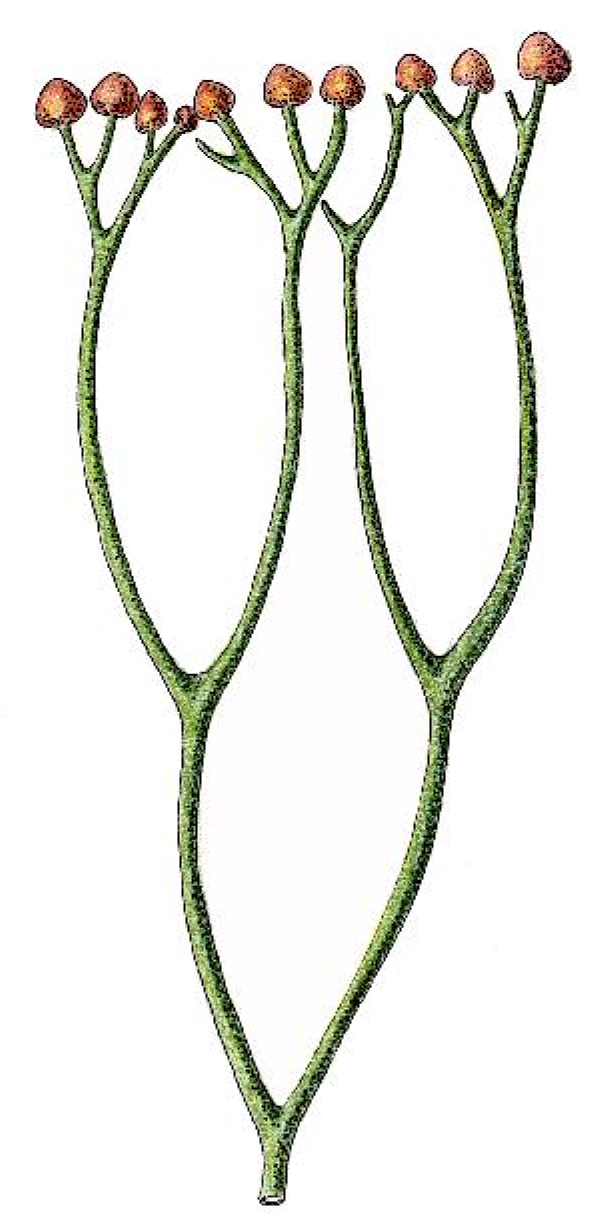
Cooksonia



Cooksonia caledonica
late Ludlow and Pridoli of Wales,

Illustration © Francoise Gantet, 1997 - from Le Monde des V�g�taux - Cooksonia caledonica (illustration) page

The earliest well-known plant, which flourished during the late Silurian and early Devonian is called *Cooksonia*. It is named after Isabel Cookson, who occupied herself with intensive collecting and describing plant fossils. The little plant was only a few centimeters in height and very simple in structure, in fact it is the most primitive known vascular land plant. It consists of a stem which bifurcated several times, and ended in small spheres (sporangia) in which the spores were formed. It is possible that horizontal growing stems, connected with the soil by root hairs, functioned as roots. It was nevertheless a true vascular plant, with tracheid-resembling internal conducting cells (revealed by fossil microstructure), and already equipped for life in an aerial, terrestrial environment

The earliest fossils of *Cooksonia* have been found in Middle Silurian Wenlock strata from Tipperary, Ireland. They consist of small bifurcations some centimeters in size. During the latest Silurian Cooksonia becomes more common, and by the early Devonian has been supplanted by other species of land-plants.

Cooksonia has been found widely across Euramerica (fossils are known from Wales, Scotland, Ireland, Czechoslovakia, Kazakhstan, New York, and Ontario) and Siberia, all of which seem to have part of a singly phytogeographical province or biome. Interestingly, the fauna of the northern hemisphere was very different from that of the possibly contemporary or later Barragwanathia fauna of Gondwanaland

Four species are known - *Cooksonia pertoni*, *C. caledonica*, *C. cambrensis*, and *C. hemisphaerica*. These differ only in minor ways, chiefly in the form and structure of the spore-case, but already *Cooksonia* includes plants related to the lycophytes (*Cooksonia cambrensis*). This means that the genus *Cooksonia* is a paraphyletic grade rather than a monophyletic clade; a group of similar plants that are near to the major evolutionary branching that leads to the Lycophytes (*more on grades vs clades*). Organisms like *Cooksonia* give the lie to claims by Christian Creationists that no intermediate forms have ever been found in the fossil record.

Links

- Early Land Plants (1) includes some good info on *Cooksonia*
- The Oldest land plants - includes material on *Cooksonia*
- *Cooksonia pertoni* - photo of specimen
- *Cooksonia pertoni* - photo showing sporangia
- Early Land plants - includes material on *Cooksonia*
- How plants conquered the land - includes info on *Cooksonia*
- Megan's Research on the First Land Plants - this is quite cute and easy to follow

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Class Lycopsida

Club-mosses and Scale Trees

Lycopsids, are a group of very ancient vascular plants that are only distantly related to other land plants. They have a long history stretching back possibly to the late Silurian period. Their living representatives include club mosses and quillworts, but in past ages they dominate the landscape with huge forests.

Lycopsids have roots, simple or branched stems and small, spirally arranged leaves (microphylls). The sporangium is either borne on a fertile leaf (a sporophyll) or is associated with one; it is thick-walled, and is either homosporous (producing only one kind of spore) or heterosporous (producing two kinds of spore). The sperm cells are mobile and have two or many flagella. Gametophytes are complex, with multicellular gametangia.

The earlier forms, such as *Baragwanathia* from the late Silurian / early Devonian of Gondwanaland, were small soft-bodied, low-growing plants which reached a typical height of 25 centimetres.

The group became especially successful and important during the late Carboniferous period, when the great Lepidodendrales formed huge swamp forests, with trees such as *Lepidodendron* reaching over 40 metres in height.

The drying out of the climate during the latest Carboniferous was catastrophic for the lycopsids, which require moist conditions to reproduce. All the giant "pole trees" like *Lepidodendron* died out, leaving only a number of small herbaceous types.

Today the Lycopsids are represented by five living genera with about 1100 species, all small creeping plants such as *Lycopodium* which reach only about 5 cm in height.

The following is a suggested classification

- Class Lycopsida ("club-mosses')
  - Order Drepanophycales (ancestral types)
  - Order Protolepidodendrales
  - Order Lycopodiales (Club "mosses")
  - Order Selaginellales (Spike "mosses")
  - Order Lepidodendrales = Lepidocarpales (Scale trees)
  - Order Miadesmiales
  - Order Pleuromeiales (intermediate forms)
  - Order Isoetales ("quillworts')

Links

Introduction to the Lycophyta - evolutionary history of the group - **best on the web**

History of Palaeozoic Forests - Fossil and Extant Lycophytes - description and links to photos of recent and extinct forms.

Lecture Notes

Lycophytes - readable palaeobotanical intro to the Lycopsids

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Palaeos | Παλαιός | Lycopodiophyta
Plants | Classification & Dendrogram

Page Back	Unit Back	Unit Home	Paleozoic Plants	Plants Glossary	Plant Kingdom
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Lycophyta Home	Drepanophycales	Protolepidodendrales	Lycopodiales	Selaginellales
Lepidodendrales	Miadesmiales	Pleuromeiales	Isoetales	Dendrogram

Lycophyta after Cleal

```
Class Lycopsida ("club-mosses')
    Order Drepanophycales
        Family Drepanophycaceae
    Order Protolepidodendrales
        Family Protolepidodendraceae
        Family Eleutherophyllaceae
    Order Lycopodiales
        Family Lycopodiaceae
    Order Selaginellales
        Family Selaginellaceae
    Order Lepidocarpales
        Family Cyclostigmaceae
        Family Flemingitaceae
        Family Sigillariostrobaceae
        Family Lepidocarpaceae
        Family Spenceritaceae
        Family Caudatocarpaceae
        Family Pinakodendraceae
        Family Sporangiostrobaceae
        Family Pleuromeiaceae
    Order Miadesmiales
        Family Miadesmiaceae
    Order Isoetales ("quillworts')
        Family Isoetaceae
        Family Chaloneriaceae
```

Palaeozoic Palaeobotany of Great Britain as well as listing British sites and the history of discovery of plant fossils in Britian, this is an excellent intro to Palaeobotany in general.

C.J. Cleal, 1993, in *The Fossil Record 2*, Chapman & Hall, London

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Lycophyta cladogram (various sources)

```
<==o LYCOPHYTA
   |--+--o �ZOSTEROPHYLLOPSIDA
   |  |  |-- �Zosterophyllum
   |  |  |-- �Gosslingia
   |  |  |-- �Rebuchia
   |  |  |-- �Bathurstia
```


ZOSTEROPHYLLUM

```
|  |  |-- �Crenaticaulis
|  |  |-- �Serrulacaulis
|  |  |--o �Sawdonia
|  |  |  |-- �S. ornata
|  |  |  `-- �S. acanthotheca
|  |  |-- �Discalis longistipa
|  |  |-- �Drepanophycus spinaeformis
|  |  |-- �Kaulangiophyton akantha
|  |  `-- �Asteroxylon mackiei
|  `--+--o �ASTEROXYLALES
|     `--+--o �DREPANOPHYCALES
|        `--+?- �Baragwanathia longifolia
|           |?- �Archaeosigillaria
|           `--o LYCOPODIOPSIDA)
|              `--o LYCOPODIALES
|                 `--o Lycopodiaceae
|                    |--o Huperzia
|                    |  `-- H. selago
|                    |--o Lycopodiella
|                    |  `-- L. inundata
|                    |--o Lycopodium
|                    |  |-- L. annotinum
|                    |  `-- L. clavatum
|                    `--o Diphasiastrum
|                       |-- D. alpinum
|                       `-- D. complanatum
`--+--o �PROTOLEPIDODENDRALES
   |  |--o �Prolepidodendron
   |  |  `-- �P. scharyanum
   |  |--o �Estinnophyton
   |  |  |-- �E. wahnbachense
   |  |  `-- �E. gracilis
   |  |-- �Sugambrophyton
   |  |-- �Colpodexylon
   |  |-- �Leclercqia complexa
   |  `--o �Spencerites
   |     |-- �S. moorei
   |     `-- �S. insignis
   `--+?-o SELAGINELLALES
      |  `--o Selaginellaceae
      |     |-- �Selagibellites hallei
      |     |-- �Miadesmia
      |     `--o Selaginella
      |        |-- �S. harrisiana
      |        `-- S. selaginoides
      `--o ISOETOPSIDA
         |--o LEPIDODENDRALES
         |  |-- �Valmeyerodendron triangularifolium
         |  |-- �Cyclostigma
         |  |-- �Bisporangiostrobus
         |  |-- �Lepidosigillaria
         |  |--o �Sigillariaceae
         |  |  `--o �Sigillaria
         |  |     |-- �(Eusigillaria)
         |  |     |-- �(Subsigillaria)
         |  |     `-- �(Sigillaria)
         |  `--o �Lepidodendraceae
         |     |--o �Lepidodendron
         |     |  |-- �L. hickii
         |     |  `-- �L. aculaetum
         |     |-- �Paralycopodites brevifolius
         |     |--o �Diaphorodendron
         |     |  |-- �D. vaskulare
         |     |  |-- �D. phillipsii
         |     |  |-- �D. scleroticum
         |     |  `-- �D. dicentricum
         |     `--o �Lepidophloios
         |        `-- �L. halli
         `--o ISOETALES
            |--o Isoetaceae [Iso�taceae]
            |  `--o Isoetes [Iso�tes]
            |     |-- I. lakustris
            |     `-- I. echinospora
            |--o Pleuromeiales
            |  |-- �Pleuromeia sternbergi
            |  |-- �Nathorstiana arborea
            |  `-- �Chaloneria
```

```
          |-- �Paurodentron fraipontii
          |-- �Oxroadia
          `-- �Prostigmaria eggertiana
```

Reference(s):

H�met-Ahti, L., Suominen, J., Ulvinen, T., Uotila, P. & Vuokko, S., 1984: Retkeilykasvio. --Suomen Luonnonsuojelun Tuki Oy & Forssan Kirjapaino Oy, Forssa, 1984, 1-544

--iNet: The Tree of Life

Steward, W. N. & Rothwell, G. W., 1993: Paleobotany and the Evolution of Pants, 2nd Edition. --Cambridge University Press, Cambridge, U.S.A., xii-521

Links

Systematics of the Lycophyta, at the UCMP site has a simplified and incomplete lycopsid phylogeny -- but useful for getting oriented to the main groups. Another fine introduction, which will probably not be on the web very long, can be found at An Overview of Green Plant Phylogeny. A nice student paper with an interesting phylogeny: Brautigam, S, C Li, A Mudry, G Miller & E Prebil (2001), *An analysis of the evolution of the vascular cryptogams, Lycopodophyta, Sphenophyta, and the Pteridophyta, through examination of extinct and extant genera*. **J. Sys. Biol. Susq. Univ.** 8(4). *See* Brautigam *et al*. (2001). The ultimate collection of lycopsid links in general is, as usual, on the Links for Paleobotanists site. *See* Lycophyta, Introductions to both Fossil and Recent Plant Taxa. Having little to do with lycopsid phylogeny *per se*, but well worth reading: Bateman, RM, PR Crane, WA DiMichele, PR Kenrick, NP Rowe, T Speck & WE Stein (1998), *Early evolution of land plants: Phylogeny, physiology, and ecology of the primary terrestrial radiation*. **Ann. Rev. Ecol. Syst.** 29: 263�92 *See* Bateman *et al*. (1998). ATW050803.

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Barinophytopsida

This is a class of primitive pteridophytic plants, similar to Zosterophylls. There is only one family, the Barinophytaceae, which ranged from the Pragian (Early Devonian) to the Tournaisian (Early Carboniferous)

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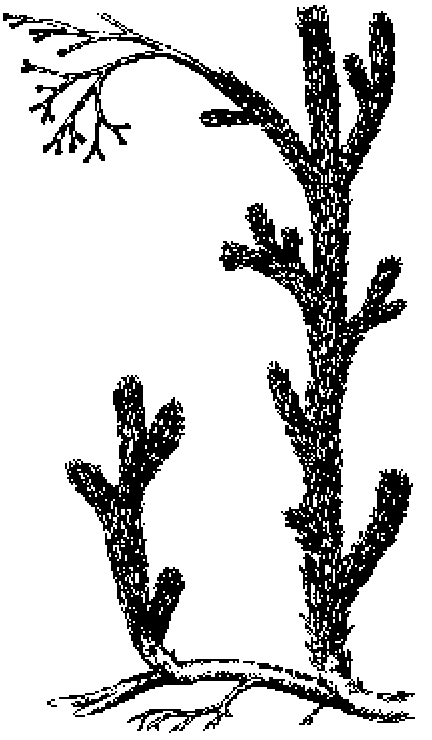
Drepanophycales

Ancestral Lycophytes

Baragwanathia, one of the earliest known Land Plants,
from the Late Silurian or Early Devonian of Victoria, Australia

The Asteroxylales were originally included under the Protolepidodendrales, but they are a much more primitive lineage and have been given their own taxon (of ordinal rank). They stand midway between the Zosterophyllopsida and the more developed lycopsids. During the mid-Devonian this lineage split into two: the extant Lycopodium and the Protolepidodendrale - Selaginella - Lepidodendralean lineage



drawing of *Asteroxylon* from *The Fossil Book* - Fenton & Fenton, 1958, Doubleday & Co., p.283 - new edition *The Fossil Book : A Record of Prehistoric Life* by Pat Vickers Rich (Editor), Thomas Hewitt Rich, Mildred Adams Fenton, Patricia V. Rich, Carroll Lane Fenton

The most primitive member of this group, *Asteroxylon* (Pragian to Emsian of Euramerica, family Asteroxylaceae) attained a height of 0.5 meters and, like most early land plants, consisted of erect branches originating from a horizontal rhizome. The branches were covered with "enations" (organs that appear to be leaves but lack vascular tissue). *Asteroxylon* could be seen as an intermediate in the evolution of true leaves in the Lycopsida.

True leaves are found in *Baragwanathia* and *Drepanophycus*, which represent the family Drepanophycaceae.

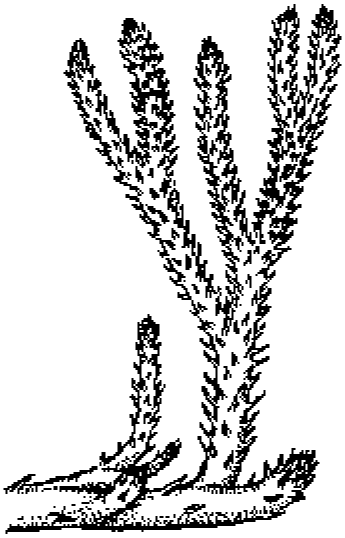
Baragwanathia longifolia is an Australian lycophyte. Its fossil imprints have been found in Yea, Victoria and other localities. This plant has been controversial for some time because of its supposed age as Ludlovian (late Silurian), corresponding in age with *Cooksonia*, a very much more primitive ancestral vascular plant. This dating is based on graptolites found associated with *Baragwanathia.* It has been suggested that the *Baragwanathia* represents a Gondwanan flora which was much more advanced than the contemporary northern hemisphere flora.

An alternative explanation is that the graptolite dating is wrong. *Baragwanathia* is very similar to *Drepanophycus* (below left) from the early and middle Devonian of the northern hemisphere. Since it is unlikely that a spore-reproducing plant from one continent would not spread to or exert any influence on the landscape and flora of another continent for many millions of years, a later age for *Baragwanathia* (probably Early Devonian) may be more plausible.

Drepanophycus (Lochkovian-Frasnian) was a larger plant, the stems of which are up to 4 cm in diameter, bearing stout thorn-like to curved leaves with vascular tissue. The sporangia are kidney-shaped. *Drepanophycus* may have attained heights of several meters.

Image courtesy of the University of California Museum of Paleontology web site

This image from The Clade Lycopsida slightly modified



Links

- ***Asteroxylon*** - from the Biota of Early Terrestrial Ecosystems: The Rhynie Chert - **best on the web**
- The Clade Lycopsida

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Isoetales

Isoetes

The order Isoetales includes the modern "quillwort", the living genus, *Isoetes* with about 70 species, which has a worldwide distribution, and very similar fossils (*Isoetites* a mid-Cretaceous plant resembling modern *Isoetes*). These are small, often aquatic plants with a short stem and elongate leaves. These are highly reduced plants that have effectively "telescoped" the body into a small corm-like stem that lacks vegetative leaves (all the leaves are fertile sporophylls). Fossil forms are sometimes placed in the modern genus *Isoetes*. Like the more primitive Selaginellales, the Isoetales are heterosporous, producing two kinds of spore.

The Isoetales are the most advanced of the lycopsids, and many unusual features with the great Carboniferous scale trees (Lepidodendrales) including secondary tissue development (both wood and bark), a modified shoot system that acts as a rooting system, bipolar growth and an upright plant habit. Despite the superficial difference in size and form, they could actually be considered miniaturized versions of the mighty scale trees. Although the scale trees died out with the drying of the climate during the latest Carboniferous, their tiny aquatic relatives the Isoetales survived as living fossils to the present day.

The Order Isoetales and Lepidodendrales are sometimes included in the Subclass Ligulatae - defined by the presence of ligules, heterospory, and endospory. There is also a tendency now to include the *Chaloneria*, *Pleuromeia*, and *Nathorstiana* under the order Isoetales, although *Pleuromeia*, is sometimes also considered a late and specialized Lepidodendrale. Because of the uncertainty of placing these transitional forms, I have retained the old order Pleuromeiales for them, at least for now

Order Isoetales
Isoetaceae (*Isoetes*, *Stylites*, *Isoetites*)

Links

The Isoetes Page, Laboratorio Fisiologia Vegetale e Micropropagazione, Universita degli Studi di Palermo, Italy - everything there is to know about *Isoetes*

Quillworts: a small page on *Isoetales* with some useful diagrams

The delayed resurgence of equatorial forests after the Permian ..: a scientific paper which discusses the ecological importance of Isoetales in the recovery from the end-Permian extinctions. This paper is discussed in more detail in connection with the Olenekian Age of the Early Triassic.

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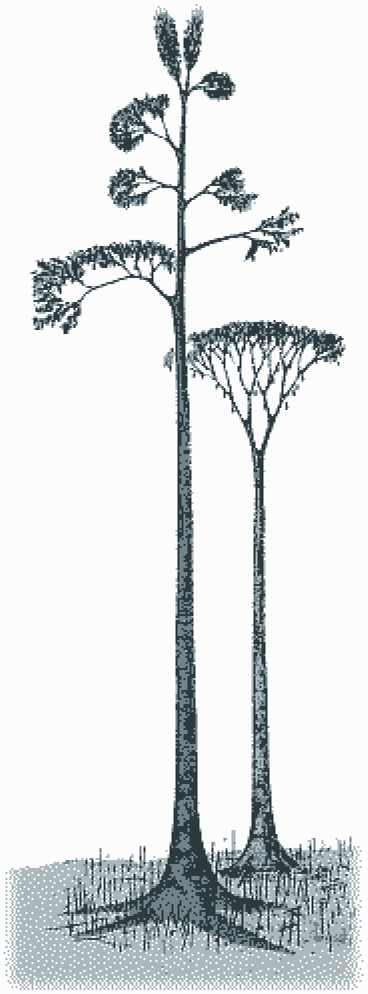
Order Lepidodendrales (=Lepidocarpales)



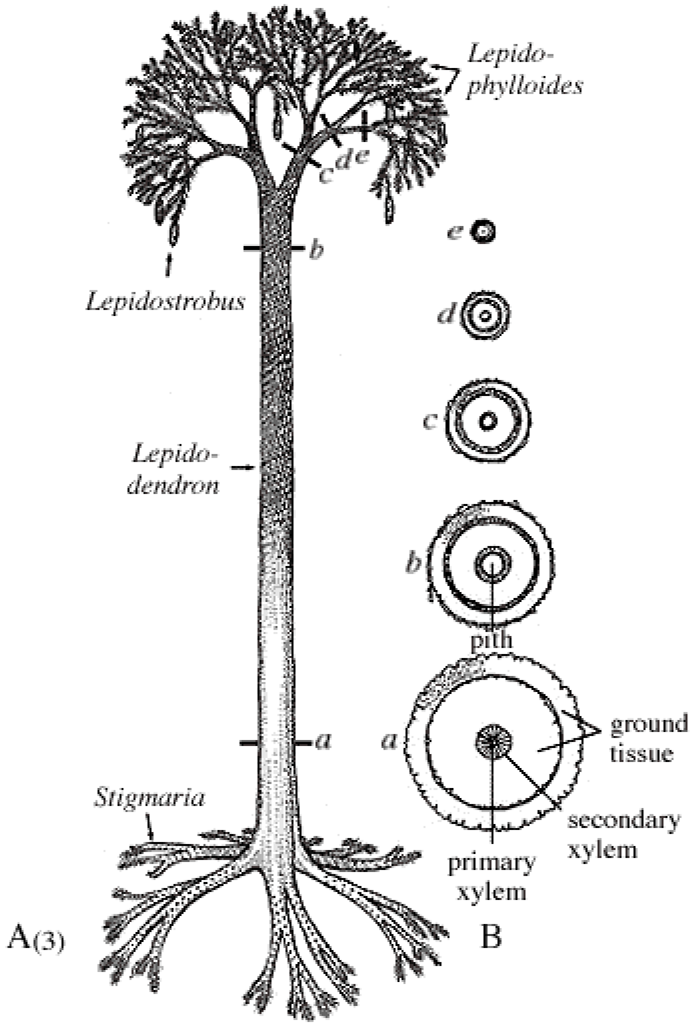
Two Late Carboniferous Lepidodendrales.
left: *Diaphorodendron scleroticum* , right: *Lepidophloios hallii*
(from Bateman et al.)

This extinct order of giant scale trees includes relatives of the modern quillworts (Isoetes). These striking plants reached their greatest diversity and development in the tropical swamps of the Late Carboniferous, when they formed forests of trees 30 to 40 metres or more in height.   some, like the Late Carboniferous *Lepidocarpon*, show elaborate dispersal adaptations that operated almost like seeds. The trunks of these trees were unlike those of modern trees which possess a trunk composed mainly of wood with a thin outer covering of bark. Lycopsids had only a thin central core of wood surrounded by a thick layer of tissue [see figure]. For this reason it has been suggested that the forests of the Carboniferous swamps could have been easily flattened by high winds and storms.

A Carboniferous storm

from *Life Before Man* by Zdenek V. Spinar, illustrated by Zdenek Burian

The fossilized stems or trunks are notable for their scale-like bark which show a characteristic external pattern formed by the leaf-scars, showing a distinctive diamond-shaped pattern.



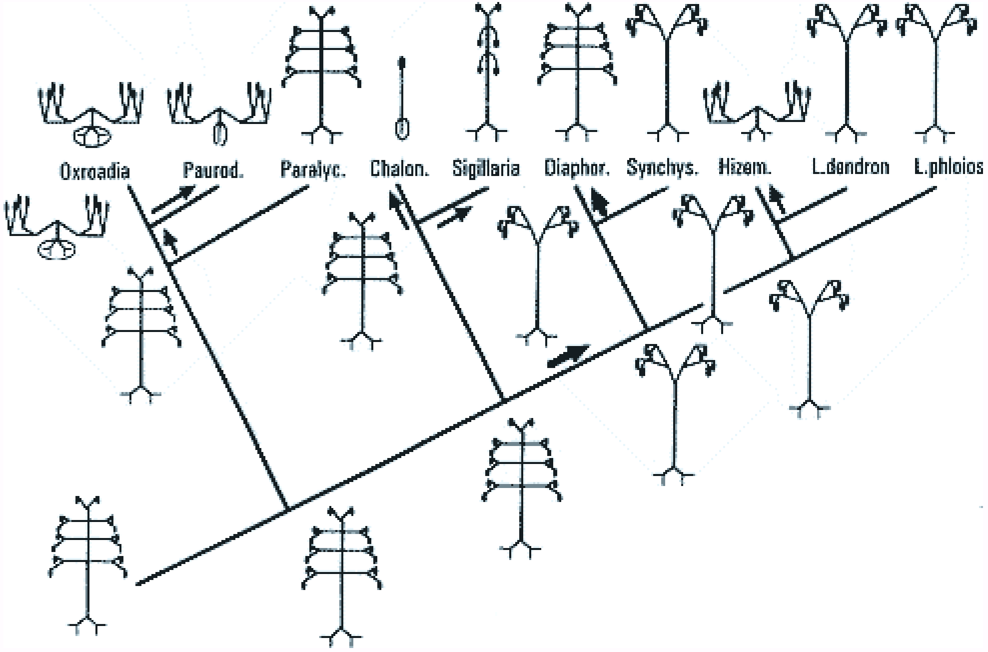
Lepidodendron "form genera" - four different names applied to the same plant!
The cross-sections on the right reveal how little of the plant was actually wood (xylem)

image courtesy of the University of California Museum of Paleontology web site

Lepidodendron and similar great trees grew in the hot humid swampland of the Carboniferous period. It possessed branching rooting organs, called *Stigmaria*, by which it was anchored in shallow soil. The *Stigmaria* had spirally arranged roots coming from them. Attached to the *Stigmaria* of *Lepidodendron* was a long pole-like trunk which had no branches for most of its length. The trunk terminated in a crown of simple branches which were covered with spirally arranged grass-like leaves, called *Lepidophyllum.* At the end of the branches were cigar-shaped reproductive cones, called *Lepidostrobus*, which contained spores. These different names (called "form genera") have been applied to different parts of *Lepidodendron* because they were originally discovered and scientifically described as separate parts. It was only later when more complete specimens were found that it was realized that the separately described parts in fact belonged to the same plant). In some cases the form genus turns out to belong to different families when the complete plant is considered. For example *Stigmaria* may belong to genera assigned to Lepidodendraceae, Sigillariaceae, or Lepidocarpaceae

Many of the larger lepidodendrid trees had monosporangiate cones, with highly specialized megasporangia that mimic the seed habit. A good example is *Lepidocarpon*. In *Lepidocarpon* cones, there is a single megaspore present that remains within the megasporangium, and the megasporangium remains tucked inside a leafy sporophyll that encloses it. The entire cone breaks up and these units thus serve as propagules. Because plants bearing this type of cone were living in a wet coal swamp, some paleobotanists have suggested that this dispersal unit acted as a small boat capable of aquatic dispersal.

The Lepidodendrales were the most elaborate and diversified of al the lycopsids, and dominated the Carboniferous, but with the drying of the climate during the latest Carboniferous and early Permian they went into a steep decline. By the middle Permian, they were all gone. Inefficient movement of water and nutrients through the stems of these tall plants, resulting from a lack of secondary xylem is cited as one of the reasons for their extinction.



Dendrogram of late Carboniferous Lepidodendrales, showing generalized growth habit. Only the diminutive unbranched *Chaloneria* managed to continue the lineage into the Mesozoic (see Pleuromeiales)

diagram by Reinhard Junker

Links

Bateman RM, DiMichele WA & Willard DA (1992) Experimental cladistic analysis of anatomically preserved arborescent lycopsids from the Carboniferous of Euramerica: an essay on paleobotanical phylogenetics. *Ann. Miss. Bot. Gard.* 79, 500-559.

see also general links section for more (almost all these pages will have info on Lepidondendrales)

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Lepidodendrales | Miadesmiales | Pleuromeiales | Isoetales | Dendrogram

Lycopodiales

Lycopodium

The Lycopodiales are the most primitive living lycopsids and among the most ancient members of this group. They first appear for certain in the late Devonian (Famennian) with *Lycopodites* , although *Huperzia*. might extend as far back as the Middle Devonian (Eifelian), predating the first tetrapods. Recent forms (Lycopodium) are known as club-mosses. Unlike more advanced lycophytes, they are homosporous, producing only one kind of spore. The Lycopodiales evolved into the Protolepidodendrales during the Middle Devonian, initiating a great evolutionary radiation of lycophyte shrubs and trees.

This order includes the recent genus *Lycopodium* (known commonly as club moss, ground pine, or "wolf foot,"), with some 200 living species. Surviving species are mainly tropical, but several occur in Arctic and subalpine regions. Recent authorities suggest splitting *Lycopodium* into several genera. All are trailing plants from a rhizome. In some species, variations and gradations between dichotomous and monopodial growth patterns occur.

Order Lycopodiales

family Lycopodiaceae (*Lycopodium*, subgenera: *Lycopodium Phylloglossum*, *Huperzia*, *Diphasium*, *Lycopodites*)

Links

Order Lycopodiales: images and brief descriptions of living species

Clubmosses: same, but with more detail

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The Bashkirian (middle Carboniferous) *Miadesmia* was a quasi-seed-bearing herbaceous plant, much like the recent *Selaginella*, although possibly an epiphyte. This was one of two lineages of Paleozoic lycopsids that independently evolved seed-like structures, the other being the large Lepidodendrales like *Lepidocarpon*. The seeds of the two genera are differently in structure, and hence evolved independently.

Links

XII. The Palaeontological Record. - II. Plants by D.H. Scott, F.R.S. - some information here on trends in seed-development in Carboniferous lycopsids; in *Darwin and Modern Science* by A.C. Seward, Book Rags e-book

Margaret Benson (1908), ***Miadesmia membranacea***, *a new Palaeozoic lycopod with a seed-like structure*, **Phil. Trans. Roy. Soc. B** 199:

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Order Pleuromeiales

This extinct paraphyletic group, 1 to 2 meters tall, were reduced relatives of the *Lepidodendrale* lineage. They were heterosporous and bore ligulate leaves.

With the late Carboniferous (Kazimovian) drying out of the climate the mighty scale trees disappeared and smaller unbranched "woody" plants like *Chaloneria* and *Pleuromeia* continued to flourish throughout the Permian and into the Early Triassic.

Family Chaloneriaceae - Carboniferous (Bashkirian to Kasimovian)

Although large specialized lycopsid trees (Lepidodendrales) dominated the Carboniferous swamps, they were dependent on very wet environments, and inevitably died out as the climate changed during the Late Pennsylvanian and into the Permian.

Smaller, unbranched forms like *Chaloneria cormosa* of the Upper Pennsylvanian (Kazimovian Epoch) of western euramerica fared better. This species was up to 2 meters in height with axes up to 10 cm in diameter. It is structurally quite similar to representatives of the Pleuromeiaceae (Triassic period). *Typha latifolia* may be a synonym. It was unbranched with a terminal fertile zone for spore production, and grew in dense strands in swampy areas. The base of the plant was similar to the base of the corm in *Isoetes* (roots of the Stigmaria-Isoetes type). It is known from North American coals balls.

Family Pleuromeiaceae - Triassic (?Scythian / Anisian to Carnian)

This family of extinct lycopsids is made up of several Mesozoic genera and would seem to be allied with the Isoetaceae. They were small trees of around a meter in height with a branchless trunk, possibly transitional between the Carboniferous Lepidodendrales and the Isoetales. The family Pleuromeiaceae is variously included among other order, as well as its own order. There is also distinct similarity between *Pleuromeia* to *Chaloneria*. However, the Pleuromeiales are not known from anatomically preserved species, so our knowledge of them is somewhat more limited than for *Chaloneria*. The lower part of the plant resembles Isoetes. *Pleuromeia* is structurally intermediate between the Paleozoic genus *Sigillaria* and the Cretaceous genus *Nathorstiana*.

Pleuromeia is known from fossil remains from Germany, Russia, Australia, Japan, and China and without doubt had a global distribution. These plants, the last humble representatives of the great Lepidondendrales, grew in monotypic stands in coastal swamps, before succumbing to the increasing aridity of the later Triassic age.

Family unspecified (*Nathorstiana*) - Cretaceous

Nathorstiana - This Early Cretaceous plant is sometimes included in the Pleuromeiaceae but resembles *Isoetes*, especially in the leaves and the base of the stem. although a distinct stem region is still present. The roots were of the Stigmarian type. It was about 10 to 30 cm in height.

Links

VASCULAR PLANT MORPHOLOGY LABORATORY 4 Class Lycopsida

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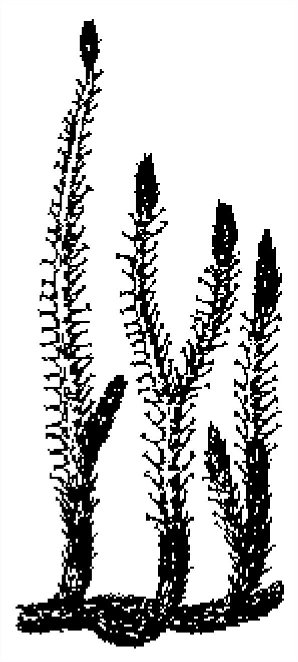
Order Protolepidodendrales



Protolepidodendron
Middle Devonian of Europe

from *The Fossil Book* - Fenton & Fenton, 1958, Doubleday & Co., p.283 - new edition *The Fossil Book : A Record of Prehistoric Life* by Pat Vickers Rich (Editor), Thomas Hewitt Rich, Mildred Adams Fenton, Patricia V. Rich, Carroll Lane Fenton

The Protolepidodendrales are a group of mostly small plants that had an apparently world-wide distribution during the Devonian and early Carboniferous (Mississippian) periods. They were probably ancestral to later lycophyte groups like the Lepidodendrales and Selaginellales. They differ from other lycophytes in the possession of leaves which were forked at the tips. Well-known genera include *Archaeosigillaria* and *Leclercqia*. The latter plant grew to half a meter or more in height. Both *Archaeosigillaria* and *Colpedoxylon* have leaves that trifurcate, or have three-pointed tips. The most complex of these forms, *Leclercqia*, had five-forked or -pointed leaves, each of which bore a ligule (a small scale-like outgrowth), while the xylem resembled that of the primary xylem of the huge Carboniferous scale-trees like *Lepidodendron*. *Leclercqia* is an important linking taxon, as homospory and the presence of a ligule are not found together in any living lycophyte.

The Protolepidodendrales evolved tree-like characteristics independent of other tracheophytes. They probably developed leaves both by enations and by planation of a branching system. They were also the first members of the Lycophyte lineage to evolve wood and bark, a modified shoot system that acts as a rooting system, bipolar growth and an upright plant habit. Some of them had large stems and bark superficially resembling that of the Carboniferous scale trees, implying that some, such *Protolepidodendropsis*, were a few metres high, and by the late Devonian had evolved into proper trees like *Cyclostigma*.

The lycopsid *Archaeosigillaria* (center) together with the pteridosperm *Aneurophyton*, representatives of the flora from the Gilboa Forest (Givetian of what is now New York)
from *The Fossil Book* - Fenton & Fenton, 1958, Doubleday & Co., p.284 - new edition *The Fossil Book : A Record of Prehistoric Life* by Pat Vickers Rich (Editor), Thomas Hewitt Rich, Mildred Adams Fenton, Patricia V. Rich, Carroll Lane Fenton

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Introduction to the Protolepidodendrales - **best on the web**

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Order Selaginellales

Selaginella

The Selaginellales or "spike mosses" are a very ancient group that includes the modern genus *Selaginella* with about 700 species and a worldwide distribution, and fossil forms called *Selaginellites*. They are more reproductively complex and more widely distributed in the tropics than *Lycopodium*, although they have similar dichotomous branching.

These plants first appeared and diversified during the Carboniferous period (at least the Bashkirian and possibly as early as the Visean epoch, or even the Famennian (latest Devonian)). They seem to be transitional between the primitive Lycopodiales and the rather more advanced Isoetales, and probably evolved from Protolepidodendrales some time during the middle Devonian. Like these other forms they are herbaceous, and like the Protolepidodendrales and their other descendents they produce two types of spores (are heterosporous). They share with the Isoetales a small flap-like structure called a *ligule* on the upper surface of their leaves.

Order Selaginellales
family Selaginellaceae (*Selaginella*, *Selaginellites*)

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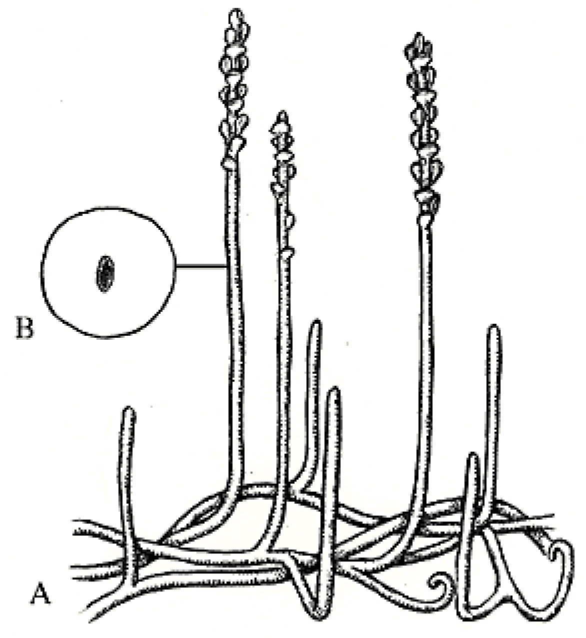
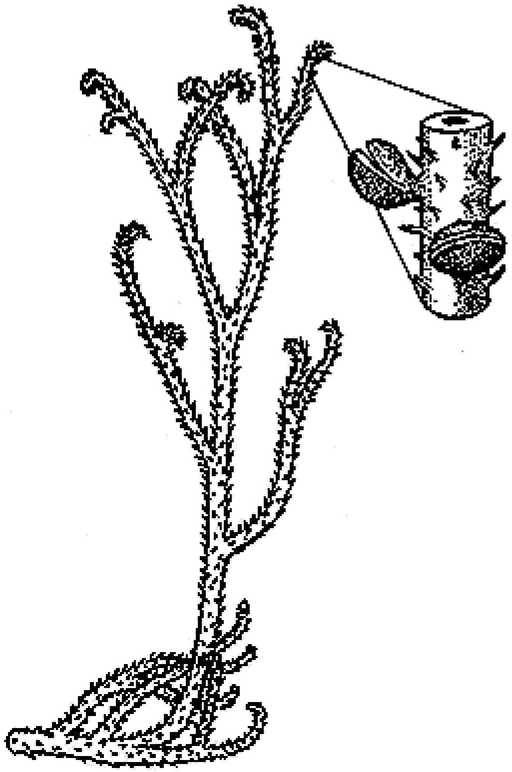
Zosterophyllopsida



Zosterophyllum deciduum whole plant reconstruction; (B) ovale protostele of *Zosterophyllum*.
Class: Zosterophyllopsida - Order Zosterophyllales - Family Zosterophyllacea
Frasnian of Euramerica
image Lab V - Lycophytes (1)

The zosterophylls are a small group of extinct primitive plants that may have been ancestral to the lycopsids. They are best known from the Early and Middle Devonian. Zosterophylls looked very much like the contemporary rhyniophytes and like trimerophytes. Like them, Zosterophylls lacked true leaves and roots, and photosynthesis was probably carried out all over the stems. As with the rhyniophytes each stem dividing into two branches of equal size (*dichotomous branching*).

Zosterophylls differed from other plants by having round to kidney-shaped sporangia (spore-cases) that were born on small stalks arranged in clusters along branches. That is, they had many lateral, rather than terminal, sporangia. The branch tips unrolled like the head of a fern.



Sawdonia ornata
Class: Zosterophyllopsida - Order Zosterophyllales - Family Zosterophyllacea
Devonian of Euramerica

image courtesy of the University of California Museum of Paleontology web site

Some genera, such as *Zosterophyllum* (top of page) and *Gosslingia* (up to 50 cm tall) had smooth stems. Others, like *Sawdonia* (above, up to 30 cm tall), *Serrulacaulis*, and *Crenaticaulis* had stems covered with saw-tooth or scale-like spiny flaps of tissue that lacked vascularization and so were not true leaves. These same organs also occur among the trimerophytes.

Links

Introduction to the Zosterophylls

Early Devonian Zosterophylls

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Anthophyta

(Magnoliaphyta)

The angiosperms

Cretaceous to recent

The angiosperms or flowering plants are by far the most important and best known group of plants. They appeared and rose to importance during the later Cretaceous period. By the early Tertiary angiosperms had spread worldwide and become the dominant form of land plant, supplanting the Coniferales and other gymnosperms.

The angiosperms include all living flowering plants and have traditionally been divided into the dicotyledons and the monocotyledons according to the structure of their seeds. It is now known that this is something of an artificial grouping.

Plant Kingdom

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