Primitive Vascular Plants

- Small & simple in structure
- Sporophyte a dichotomously branching stem
  - 1-2” high
  - Sporangia terminal
  - No leaves or roots
- Did not produce true tracheids in xylem
  - Used turgor pressure to remain upright
- Tracheids then evolved, giving rise to tracheophytes

Early Life Cycles

- Early vascular plants had alternation of more or less similar generations
  - Sporophyte & gametophyte (which was also branched) ~ same size
- Compared to bryophytes, both generations initially elaborate
Geological Time Scale

The Rhynie Chert & Its Flora
- Found 1912, Rhynie, Scotland
- ~396 MYA
- Extremely important for our understanding of early plants, including vascular plants

Rhynie Chert Discoveries

<table>
<thead>
<tr>
<th>Cyanobacteria</th>
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<tbody>
<tr>
<td>Archeaolithium contexta</td>
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<tr>
<td>Archeaolithium oscillatorium</td>
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<tr>
<td>Kieleria lutea</td>
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<tr>
<td>Langiella acutifida</td>
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<tr>
<td>Rhynia aeriformis</td>
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<tr>
<td>Rhyniomorus uniformis</td>
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<table>
<thead>
<tr>
<th>Fungi</th>
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<tbody>
<tr>
<td>Allomyces sp.</td>
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<tr>
<td>Gomphidium rhyniensis</td>
</tr>
<tr>
<td>Kriptomyces discoides</td>
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<tr>
<td>Miltenomyces rhyniensis</td>
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<tr>
<td>Palaeoblastocladia milleri</td>
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<tr>
<td>Palaeomyces agglomerata</td>
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<tr>
<td>Palaeomyces asterioides</td>
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<tr>
<td>Palaeomyces gondwana</td>
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<tr>
<td>Palaeomyces hornae</td>
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<tr>
<td>Palaeomyces simpsonii</td>
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<tr>
<td>Palaeomyces simpsonii</td>
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<tr>
<td>Several Chytridiomycetes</td>
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<tr>
<td>Ascomycetes</td>
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<thead>
<tr>
<th>Lichens</th>
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<tbody>
<tr>
<td>Winfrenella reticulata</td>
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<tr>
<td>Nematophytes</td>
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<tr>
<td>Nematophyton salii</td>
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<tr>
<td>Nematophyta rhyniensis</td>
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<tr>
<th>Algae c.f.</th>
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<tbody>
<tr>
<td>Mackiella rotundata</td>
</tr>
<tr>
<td>Palaeonitella crassii</td>
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<tr>
<td>Rhynia verruciformis</td>
</tr>
<tr>
<td>Various other undescribed fungi</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Tracheophytes (Sporophytes):</th>
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</thead>
<tbody>
<tr>
<td>Aglaophyton major</td>
</tr>
<tr>
<td>Asteroxylon mackiei</td>
</tr>
<tr>
<td>Horneophyton lignieri</td>
</tr>
<tr>
<td>Nothia aphylla</td>
</tr>
<tr>
<td>Rhynia geometrica</td>
</tr>
<tr>
<td>Trichophyton lydiianum</td>
</tr>
<tr>
<td>Vendura lymnae</td>
</tr>
</tbody>
</table>

<table>
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<tr>
<th>Tracheophytes (Gametophytes):</th>
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<tbody>
<tr>
<td>Langiophyton macrleri</td>
</tr>
<tr>
<td>Lyonophyton rhyniensis</td>
</tr>
<tr>
<td>Kidstonophyton discoides</td>
</tr>
<tr>
<td>Still undescribed female gametophyte of Aglaophyton major</td>
</tr>
<tr>
<td>Still undescribed female and male gametophytes of Rhynia geometrica</td>
</tr>
<tr>
<td>Still undescribed male gametophyte of Horneophyton lignieri</td>
</tr>
</tbody>
</table>

Aglaophyton
- Fossil taxon
- Aglaophyton best-known taxon from Rhynie Chert
  - New studies have shown that the conducting cells of Aglaophyton major are strongly reminiscent of those of certain mosses
  - Some authors, therefore, do not regard Aglaophyton as a real vascular plant
Asteroxylon

- *Asteroxylon mackiei*, one of the earliest lycopsids, is the only plant from the Rhynie Chert which had already small leaf-like structures
  - Lacked a vein
- Central stele = star-shaped xylem surrounded by phloem (actinostele)
- Resulted in a much greater plant stability
- Comparatively complex architecture

Asteroxylon

- Up to 40 cm high
- Leaves up to 5 mm long
- Reniform sporangia on short stalks in leaf axils

Asteroxylon

- Rhizome formed repeatedly bifurcating root-like organs up to 20 cm deep
  - Not true roots, calyptra missing (cap-like structure on root tip)
- Leaves considerably increased photosynthetic surface
- Better able to regulate humidity
  - Keep dew drops between leaves
  - Better water regulation than other Rhynie Chert plants
- Stomatal density of *Asteroxylon* is about 10X more than *Aglaophyton*
  - Unlike other Rhynie Chert plants, could likely survive in temporarily drier environments
Let’s walk through the phylogeny...

**Phylogenetic Context**

Let’s start with the Charales...

- **Anthocerophyta**
- **Hepatophyta**
- **Lycopodiophyta**
- **Polypodiophyta**
- **Gymnosperms**
- **Angiosperms**

**Cooksonia**

**Lycophytes**

- **Isoëtes** (Quillwort)
- **Selaginella** (Resurrection Plant)
- **Lycopodium** (Club Mosses)

**Sporophyte or Gametophyte?**

- Bryophytes – dominant gametophyte generation
- Everything above them on the phylogeny – dominant **sporophyte**
- Gametophyte becomes successively reduced in size as we go along all the way up to angiosperms

**Lycophytes**

- **Heterosporous**
- **Homosporous**
Shared Lycophyte Characters

- Contain true stems, roots & leaves
- Microphyll-type leaves
- Leaves densely spirally arranged
- Stems/ & roots often have dichotomous branching
- Sporangia borne on leaves
  - “Sporophylls”
- Sperm biflagellate

Microphylls

Enation Theory of Microphyll Origin

- Remember Asteroxylon?
  - Leaves without veins?
  - Enations!

Extant Lycophyte Taxonomy

- Lycopodiophyta
- Lycopodiopsida
  - Lycopodiales
    - Lycopodiaceae
    - Selaginellaceae
    - Isoëtaceae
Lycopodiophyta

- An ancient group
- First fossils ~ 400 MYA (lower Devonian)
- Some extant genera known all the way back to ~300 MYA (Pennsylvanian epoch of Carboniferous)
- Today, a very small group, but once a dominant life form

Geological Time Scale

- Rhynie Chert (Includes first lycophytes)
- Some extant lycophytes

Lycopodiaceae

- Clubmoss, ground pine, running cedar
- Fossils date back to Pennsylvanian (300 MYA)
- Homosporous & leaves non-ligulate
  - Distinguish it from rest of order
- Strobilus = terminal cluster of sporophylls
  - Some spp. lack strobili; sporophylls elsewhere
- Sporangia kidney-shaped, opening by a transverse slit; solitary in leaf axils or borne on leaf bases
**Lycopodium Sporangia**

- Longitudinal slit

**Lycopodium Strobilus**

- Note all spores are the same size
- Contrast this with heterosporous plants

**Homosporous Life Cycle**

- Epiterrestrial or subterranean
- ~0.5” long
- Bisexual

**Gametophyte**

- Anthridia
- Archegonia
Archegonia

Spermatozoids

Economics
- Christmas garlands/wreaths
- Oily, highly flammable compounds in spore wall
  - Magicians/sorcerers in Middle Ages (flash of light)
  - The 'flash' of old-time photography
  - Early (experimental) photocopiers
  - Industrial lubricants
  - Formerly prevention of rubber cohesion in condoms & surgical gloves
- Used to count Avogadro’s Number in chemistry lab

Heterosporous Lycophytes
- Selaginellaceae & Isoëtaceae
- Produce 2 types of spores
  - Microspores (“male”)
  - Megaspores (“female”)
- Microspores develop into microgametophytes
  - Produce antheridia & sperm
- Megaspores develop into megagametophytes
  - Produce archegonia & eggs
Heterospory

- Note the 2 different spore sizes
- Microspores are much smaller than megaspores

Selaginella strobilus

Heterosporous Lycophytes

- Ligulate leaves
  - Leaves with a small flap of tissue at base

Selaginella ligule

Isoëtes ligule

Endosporic Gametophytes

- Mega- and microspores produce endosporic gametophytes in the heterosporous lycophytes
- Gametophyte produces wholly within spore wall (until mature)

Selaginella microgametophyte

Selaginellaceae: Selaginella

Isoëtes megagametophyte
Selaginellaceae

- 1 genus (*Selaginella*)
  - c. 750 spp. (38 in FNA)
- Most moist tropics
  - But many adapted to xeric habitats
- Leaves small (< 2 cm long)
- Sporangia usually in strobili
- Vegetatively similar to *Lycopodium*

Selaginella Sporangia

- Both sporophyll-types still *microphylls* anatomically
- Megaspores produced in megasporaniga (megasporophyll)
- Microspores produced in microsporangia (microsporophyll)

Megagametophyte

- Endosporic
  - Bursting out when mature
- Anchored by rhizoids

Resurrection Plant

- Adaptation to xeric environments
  - Dormancy
  - Come back when conditions favorable

Selaginella lepydophylla
Isoëtaceae: Isoëtes

- 2 genera in family, but we'll look at Isoëtes (150 spp.; 24 spp. in FNA)
- Cosmopolitan, except for Pacific islands
- Fossils similar to Isoëtes as far back as the Triassic (213-248 MYA)
  - Some with leaves 1 m long! NB. Still microphylls
- Usually aquatic or marshy-areas
- Similar looking to grasses & rushes
  - Often overlooked
- Leaves - elongated microphylls (up to 1 ft [30 cm], but can be as small as several centimeters)

Isoëtes

- Stem – short, corm-like, 2(-4) lobed
- Shoot & root apices sunken
- Dichotomously branched
**Sporangia**

- Microsporangia produce ~ 150,000-1,000,000 microspores
- Megasporangia produce ~ 50-300 megaspores

**As Aquarium Plants?**

- Several species of *Isoëtes* can be used as aquarium plants

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**Isoëtes Life Cycle**

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*Isoëtes kirkii*