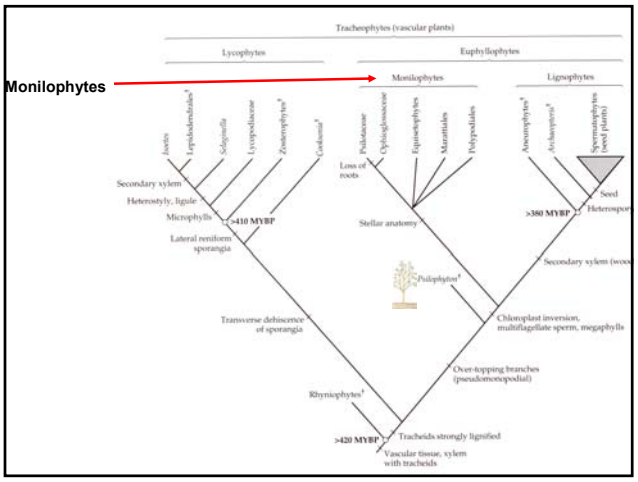
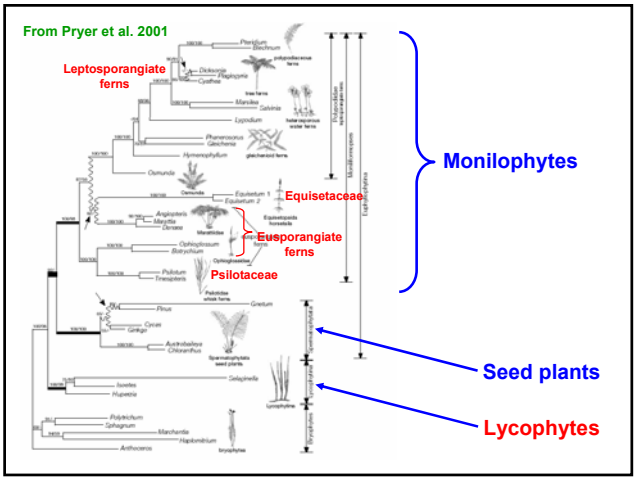
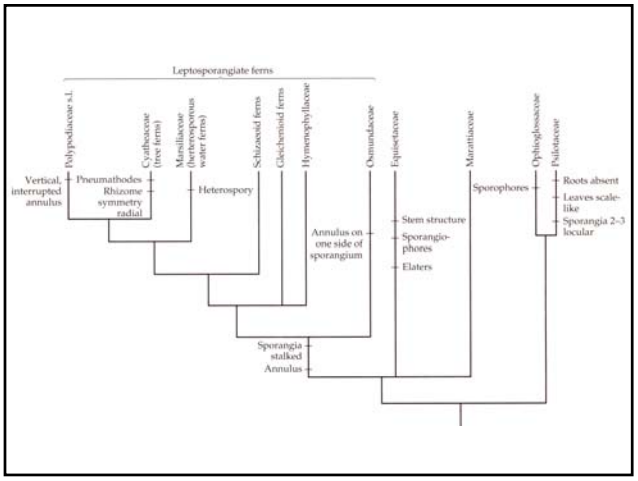

Fabulous Ferns
The Monilophyte Lineage


Monilophytes
Tracheophytes (vascular plants)
Lycophytes
Euphyllophytes
Monilophytes
Lignophytes
Secondary xylem
Heterostyly, ligule
Microphylls
~410 MYBP
Lateral reniform sporangia
Loss of roots
Stellar anatomy
>380 MYBP
Seed
Heterospory
Secondary xylem (wood)
Transverse dehiscence of sporangia
Chloroplast inversion, multiflagellate sperm, megaphylls
Over-topping branches (pseudomonopodial)
>420 MYBP
Tracheids strongly lignified
Vascular tissue, xylem with tracheids


From Pryer et al. 2001
Leptosporangiate ferns
Equisetaceae
Eusporangiate ferns
Psilotaceae
Monilophytes
Seed plants
Lycophytes

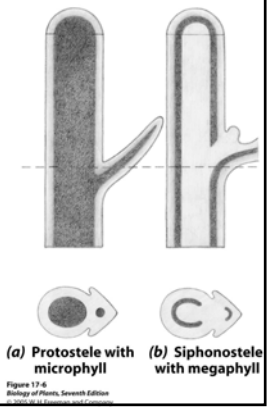

Leptosporangiate ferns
Polypodiaceae s.l.
Cyatheaceae (tree ferns)
Marsileaceae (heterosporous water ferns)
Schizaeoid ferns
Gleicheniod ferns
Hymenophyllaceae
Osmundaceae
Equisetaceae
Marattiaceae
Ophioglossaceae
Psilotaceae
Vertical, interrupted annulus
Pneumathodes
Rhizome symmetry radial
Heterospory
Annulus on one side of sporangium
Stem structure
Sporangio-phores
Elaters
Sporangia stalked
Annulus
Sporophores
Roots absent
Leaves scale-like
Sporangia 2–3 locular

Megaphylls

- Leaf gap
- More than 1 branched vein
- Telome theory of megaphyll evolution

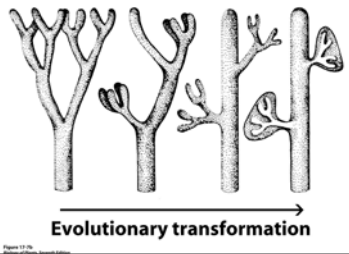
Micro- vs. Mega-phyll Evolution

- Microphyll: single, unbranched vein with no leaf gap (left side)
- Megaphyll: Vein branching multiple times with a leaf gap (right side)
- Review microphyll evolution from Lycophyte lecture

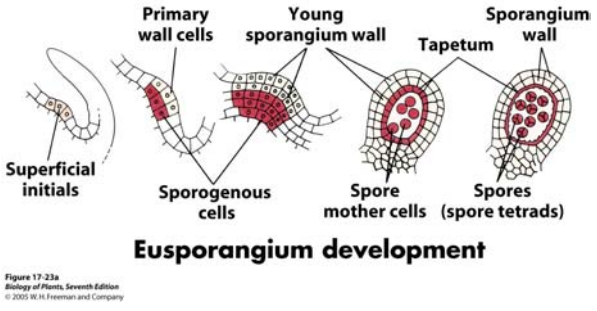


Telome Theory of Megaphyll Evolution

- Leaves (megaphylls) of arthrophytes, ferns & seed plants evolved from branch systems (telomes) by overtopping, planation & webbing

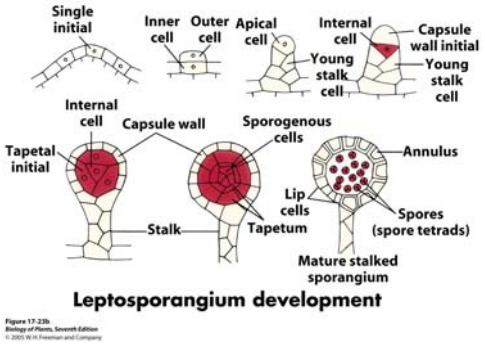


Eusporangium



Found in most plant lineages

Leptosporangium



Only in the "true ferns," Polypodiophyta

Eusporangium

- Relatively large
- Thick-walled (several cell-layers)
- Many spores (100s-1,000s)
- No specialized dehiscence mechanism
- No stalk
- Form from several initial cells

Leptosporangium

- Relatively small
- Thin-walled (1 cell-layer thick)
- (Usually) 64 spores
- Dehisce via annulus
- Stalked
- Form from just 1 initial cell

Location of Vascular Tissue

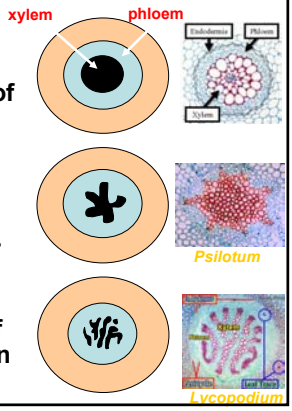
- Evolutionary progression in complexity & location of vascular tissue (esp. stems)
- Related to megaphyll development
  - Large, numerous leaf traces = many large leaf gaps
- Location of stele = equilibrium between location of strengthening & conducting cells
- Ideal location for strengthening tissue is just beneath the surface of a cylindrical structure at the center of the axis
  - Least likely to break when stems are bent by wind

The Stele

- Arrangement (pattern) of vascular tissue
- Root & stem morphology usually different from each other
  - How we can tell a rhizome is a modified stem, not a root
- Useful for distinguishing between different taxonomic groups
- Roots, which do not produce leaves, have the most simple stelar types & the stele is in the center of the axis
  - Mostly an *Actinostele*

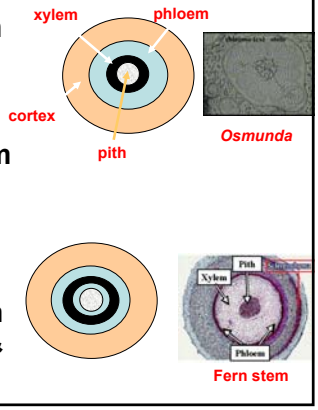
Stele Types: Protostele

- Simplest type of stele
- Solid core of xylem surrounded by a cylinder of phloem
- 3 general variations
- **Haplostele**: solid cylinder of xylem
- **Actinostele**: radiating cog-like ridges of xylem
- **Plectostele**: cylindrical xylem core with masses of phloem interspersed within



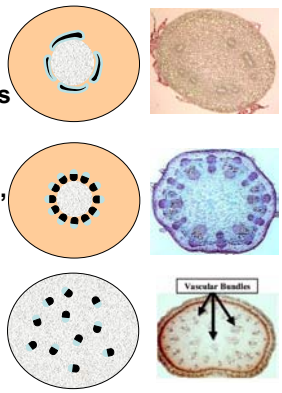
Stele Types: Siphonosteles

- Xylem & phloem form concentric cylinders around central pith
- **Ectophloic siphonostele:** phloem restricted to outer surface of xylem
- **Amphiphloic siphonostele (solenostele):** phloem found both external & internal to xylem



Siphonostele Types

- Fault of leaves!
  - Don't blame me
- **Dictyostele:** stele appears as discrete strands or bundles in cross section
- **Eustele:** discrete strands, xylem inner & phloem outer (dicots)
- **Atactostele:** bundles scattered, xylem/phloem random facing
  - Monocots



Psilotophyta: *Psilotum*

Psilotophyta
Psilotopsida
Psilotales
Psilotaceae
Psilotum
Tmesipteri

Psilophyta

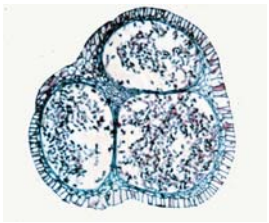
- Until recently, though to be most primitive, extant lineage of vascular plants
- 2 genera
  - *Psilotum* (pantropical)
  - *Tmesipteris* (New Zealand)
- Homosporous
- Cultivated in Japan for 400-500 years as an ornamental
- Whiskferns

Sporophyte Morphology

- Naked stems
- Dichotomous branching
- Rhizomes & rhizoids
  - No true leaves or roots
  - Enations
- Similar to Rhyniophytes, *but*:
  - Enations (leaf-like flaps of tissue)
  - Sporangia axillary (not terminal)
  - Sporangia fused into synangium

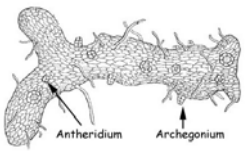
Synangium

- 3 fused sporangia (in *Psilotum*)
- In axils of enations (axillary)

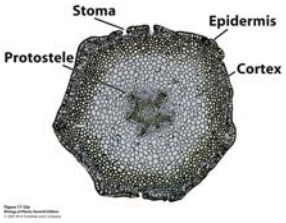


Gametophytes

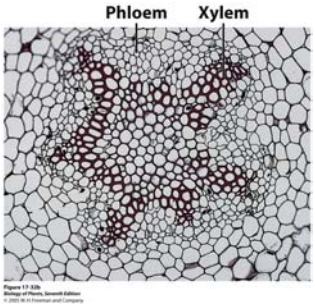
- Small
- Subterranean
- Lack chlorophyll
  - Mycotrophic
  - Depend on fungal partners for nutrition



Psilotum Stems



Protostele (Actinostele)



Primitive Lineage?

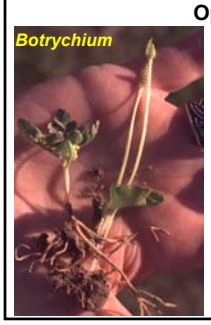
- Many believe that *Psilotum* (& *Tmesipteris*) closest living relatives to Rhyniophytes.
- BUT there are alternative hypotheses
- Psilotophyta are highly modified group of ferns which have lost many fern-like characters
  - Why? Large fossil gap; gametophyte similarities
- Chemical & morphological features suggest affinity with "eusporangiate"

Tmesipteris

- Similar to *Psilotum*, but with leaf-like structures
- Enations or flattened stem?
  - Vascular tissue (rules against enation)
- Only 2 sporangia in synangium

Ophioglossophyta

Ophioglossophyta
Ophioglossopsida
Ophioglossales
Ophioglossaceae
Ophioglossum
Botrychium



Ophioglossophyta

- Dimorphic fronds
  - Sporangia borne on fertile fronds
  - Other segment is flattened & vegetative
- Leaves are megaphylls
- True roots
- Homosporous
- Gametophytes
  - Subterranean
  - Lack chlorophyll
  - Mycotrophic

The Players

- *Ophioglossum*
  - Adder's-tongue ferns
- *Ophioglossum reticulatum* has largest known chromosome # (2n = 1,260!)
  - 84-ploid!
  - *Haplopappus gracilis* = lowest #, 2n = 4
- *Botrychium*
  - Grape ferns; rattlesnake ferns

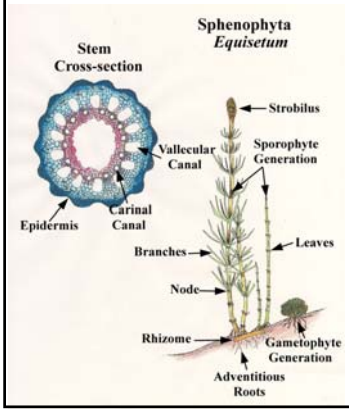
Equisetophyta: *Equisetum*

Equisetophyta
Equisetopsida
Equisetales
Equisetaceae
Equisetum

Equisetum

- Horsetails, scouring rushes
- Near-cosmopolitan
- Many fossil taxa
  - Up to large trees
- Dates back to Triassic
- Toxins include nicotine & thiaminase (breaks down thiamine)
- May help with Alzheimer's

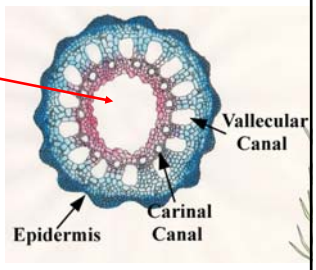
Equisetum Stem



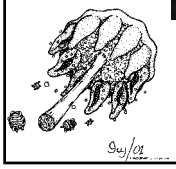
- Jointed at nodes
  - Point of attachment for leaves & lateral branches)
- Ridged (or ribbed)
- Accumulate silica in epidermis
- Photosynthetic
  - Leaves reduced

Equisetum Stem

- 3 series of canals
- Central (inner)
  - Aeration
- Carinal (middle)
  - Associated with xylem & phloem
  - Opposite ridges
  - Aids conduction
- Vallecular (outer)
  - Alternate with ridges; function?



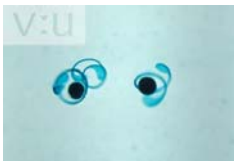
Strobilus & Sporangiophore

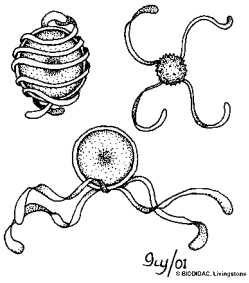


- Sporangia in strobilus
- But in sporangiophores
  - Stem tissue, not sporophylls
  - Peltate (umbrella-shaped)
- Homosporous

Spores

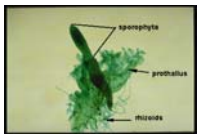
- Elaters
  - Modifications of outer spore wall
- Dispersal
  - Uncurl when dry
  - Coiled when wet





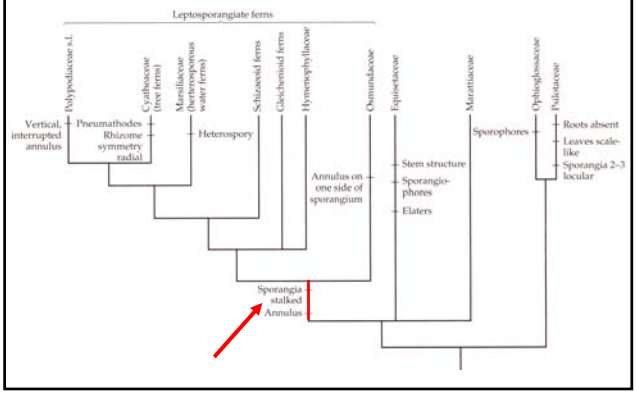
Gametophyte

- Photosynthetic
- Unisexual – but plant homosporous!
- Sex due to environmental cues, e.g., light intensity, quality (e.g., red light)
- Some female gametophytes exude a chemical that turns neighboring ones male



Pteridophyta: "True" Ferns

Phylogenetically Speaking



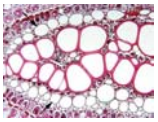
Leptosporangiate Fern Taxonomy

Polypodiophyta
- **Polypodiopsida**
  - **Polypodiales**
    - **Polypodiaceae *sensu lato***
      - **Many genera; Various families (we'll put them just in this one for now)**
    - **Osmundaceae**
      - ***Osmunda***
    - **Marsileaceae**
      - ***Marsilea***
      - ***Azolla***
      - ***Salvinia***

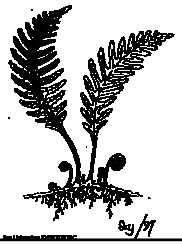
Polypodiophyta

- Date to Devonian (like lycophytes & eusporangiate Monilophytes)
- Abundant in Carboniferous (Pennsylvanian)
- Modern fern genera date back to Tertiary & Cretaceous (not as old as extant lycophyte genera)
- Largest group of extant cryptogams (> 12,000 spp.)
- Morphologically diverse
- Variety of habitats
  - Still require water for fertilization

General Morphology



- Leptosporangiate
- Dictyostele
- Leaves simple to compound
  - Very variable across fern groups
  - Megaphylls
- Circinate vernation
- Sporophyte dominant
  - Free-living



Circinate vernation

- Distinctive uncoiling of young leaves
  - Also in cycads (convergence)
- Fiddleheads (or croziers)
  - Prior to uncoiling

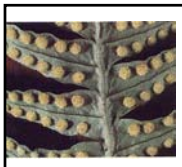
Reproductive Morphology

- Mostly homosporous
- Sporophylls = megaphylls anatomically
- Sporangia mostly in sori
  - Underside of leaves
  - That brown stuff that most people think is fungus or dirt

Fern Sporangia

- **Sorus:** clusters of sporangia
- **Indusium:** covering of sorus
- **Annulus:** specialized dehiscence mechanism
  - Ring of thickened cells
  - Contract sharply when dry
  - Scatter spores

Exindusiate



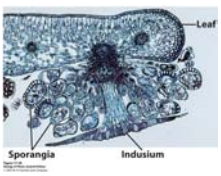
E.g., *Phymatosorum*

Indusium completely lacking

E.g., *Platysereus*

Exindusiate

Peltate Sorus



Peltate indusium

E.g., *Cyrtonium*

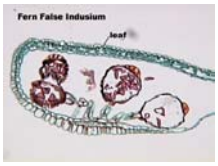
Peltate: umbrella-shaped

Reniform Sorus

Reniform: kidney-shaped

E.g., *Nephrolepis*

False Indusium



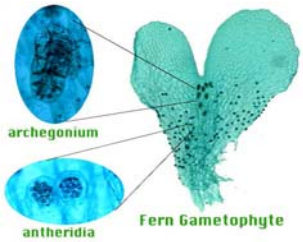
False indusium

E.g., *Adiantium*

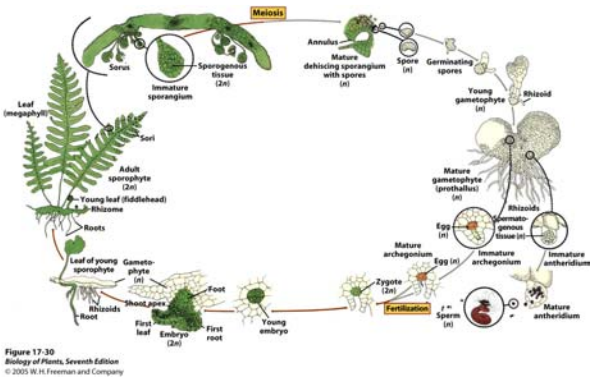
False indusium

Gametophyte

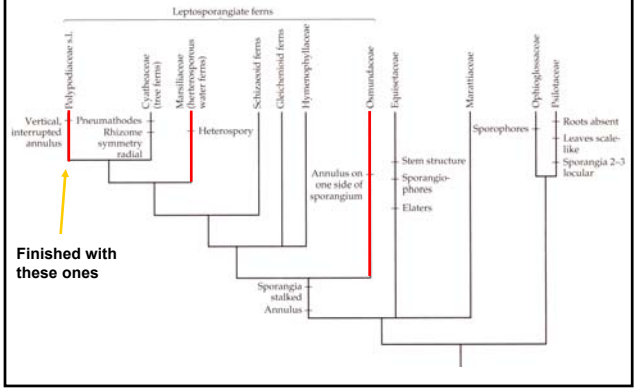
- Prothallus generally heart-shaped
- Dorso-ventrally flattened



Pteridophyte Life Cycle



OK, So Where Are We?



Osmundaceae

Osmunda cinnamomea (cinnamon fern)

Osmundaceae

- Basal lineage
  - Lack of sorus
  - Primitive annulus
  - Molecular data
- E.g., royal fern, cinnamon fern
- Dimorphic leaves
  - Separate fertile/sterile (cinnamon)
  - Both on one (royal)

Osmunda regalis (royal fern)

Heterosporous Water Ferns

- ONLY heterosporous "true" fern lineage
  - Marsileaceae & Salviniaceae (sister groups)
- Not particularly fern-like to look at
- Sporocarps: specialized adaptations to living in water
  - Modified sporophylls with tightly clustered sori; sporophyll fronds are hardened
  - Morphology varies across groups

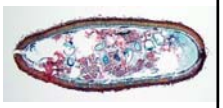
Marsileaceae

- Water clovers
- Cosmopolitan in warm temperate & tropical areas

Marsilea

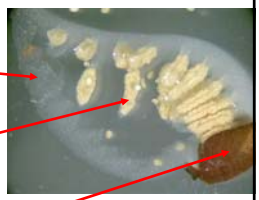
Marsilea Sporocarp

- Paired at sterile leaf base
- Burst when hydrated
- Each sorus with micro- & mega sporangia
- Can keep spores viable up to 100 years
  - Adaptations for growth in arid regions?
- Dispersed by waterfowl
- Sporangia lacking annulus



Sporocarps: Sorophore

- Sorophore: gelatinous backbone
  - Swells when hydrated
  - Sporangia attached



Spores & Gametophytes

- Megasporangia with just 1 megaspore
  - Megagametophyte with 1 archegonium
- Microsporangia with 16-64 microspores
  - Microspores burst as sperm released
- Gametophytes minute, endosporic

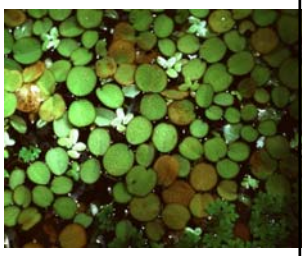
Salviniaceae

- *Salvinia*
  - Floating ferns

- *Azolla*
  - Mosquito ferns

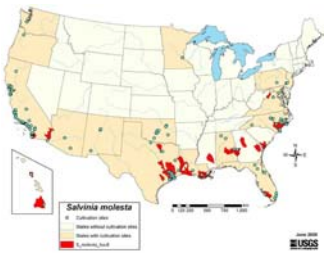
Salvinia

- Rootless
- 3 leaves
  - 2 floating, leaf-like
  - 1 pendant, root-like
    - Produce sporocarps



Salvinia molesta

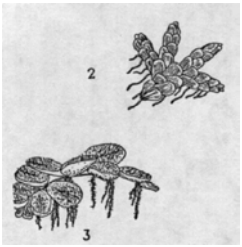
- Giant *Salvinia*, from SE Brazil
- WORLDWIDE NOXIOUS WEED!



Salvinia molesta

- Aggressive weed with wide ecological tolerance
- Very rapid growth
- A single plant has been described to cover 40 square miles in 3 months!
- Rapidly expanding populations can overgrow & replace native plants
- Resulting dense surface cover prevents light & atmospheric oxygen from entering water
- Decomposing material drops to bottom, consuming dissolved oxygen needed by fish & other aquatic life

Azolla



Azolla: Mosquito Ferns

- 1 leaf with 2 lobes
- Upper lobe houses *Anabaena*
  - Filamentous blue-green alga
  - Fixes atmospheric nitrogen
- Was important in past rice crops
  - Fertilizer for rice plants
  - Still used in many places for same reason