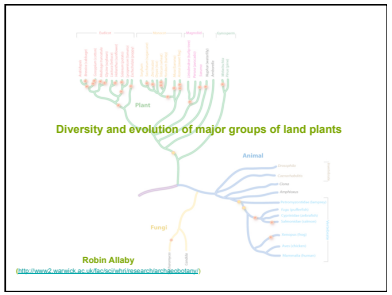

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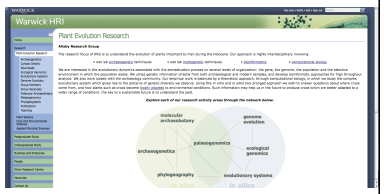
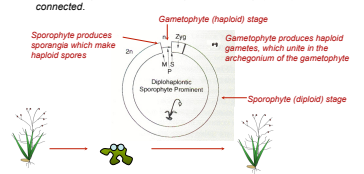


What is a land plant?

- Any photosynthetic eukaryote that can survive and sexually reproduce on land
- All land plants are embryophytes (= embryo bearing plants)

Embryophytes

- Defined by a true alternation of generations with *multicellular* diploid and haploid phases, and the two phases *remain physically connected*.



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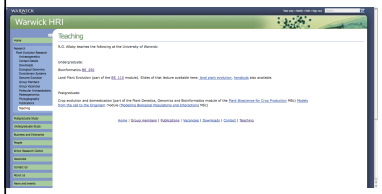
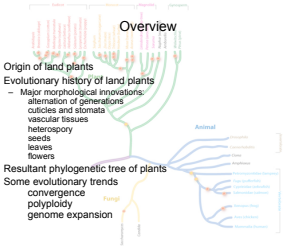
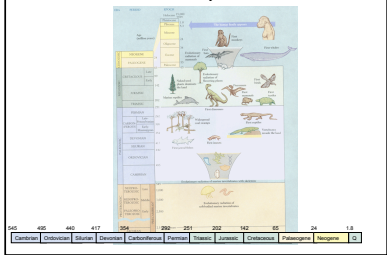


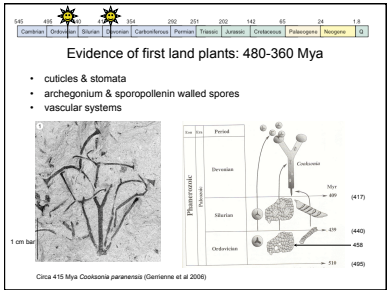
Overview



- Origin of land plants
- Evolutionary history of land plants
  - Major morphological innovations:
    - alternation of generations
    - cuticles and stomata
    - vascular tissues
    - heterospory
    - seeds
    - leaves
    - flowers
- Resultant phylogenetic tree of plants
- Some evolutionary trends
  - convergence
  - polyploidy
  - genome expansion

A brief history of time





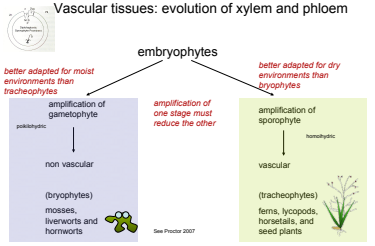
Invasion of land was really an invasion of the air

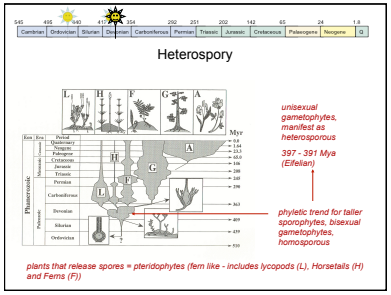
- dessication and support are the principal problems
- adaptation to dessication requires :
  - a cuticle (and consequentially stomata)
  - spores and seeds (ultimately)
  - vascular tissue (when plants are above a certain size)

What is a land plant?

- Any photosynthetic eukaryote that can survive and sexually reproduce on land

Vascular tissues: evolution of xylem and phloem

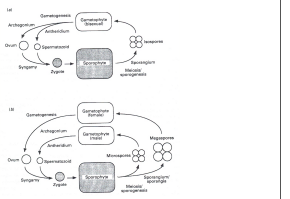




Heterospory

homospory

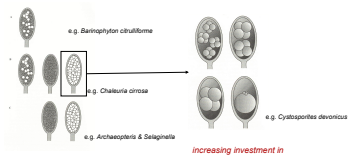
heterospory



Heterospory

- Seems odd - reduces the chances of fertilization by separating egg and sperm. Cannot be good in a harsh environment, this is a cost.
- Once separated, makes sense to increase energy investment in the "female" gametophyte which must support the sporophyte, and maximize chances of successful fertilization by making male spore numerous, (and consequently small).
- Gives rise to out-crossing. Perhaps this is the advantage (?).
- That it is an advantage is proven by the convergence on the habit - possibly as many as 11 times! (Bateman & DiMichele 1994).

The logical progression of heterospory



increasing investment in megaspore causes reduction in megaspore number

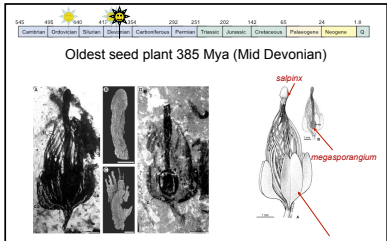
Seed habit - the next step after heterospory

- *retain* megaspore in megasporangium
- reduce functional megaspores to 1
- *retain* megagametophyte (elimating requirement for external water for fertilization)
- modification of megasporangia to receive microspores
- modification of microspores to enable them to deliver sperm cells to eggs (ie pollen tube)
- integument develops around megasporangia (later)

all seed plants = spermatophytes

first seed plants = gymnosperms (naked seeds)

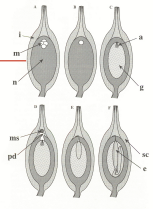
Oldest seed plant 385 Mya (Mid Devonian)



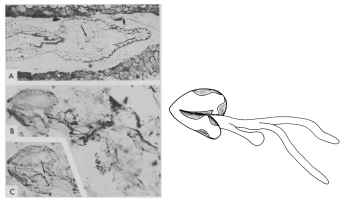
Runcaria heinzelinii (Gerrienne et al 2004)

Basic Gymnosperm architecture

integument + megasporangium uncovered

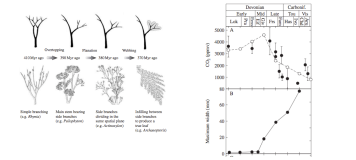


Pollen tubes by early Carboniferous



(Rothwell 1972)

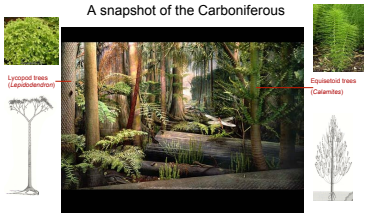
The late arrival of leaves: 360 Mya!! (end of Devonian)



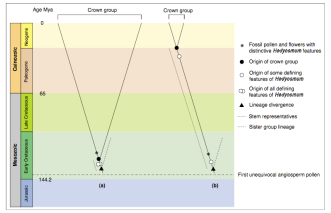
Leaf evolution associated with falling CO_2 levels (first plants evolved in a CO_2 rich atmosphere)

(Beerling 2005)

A snapshot of the Carboniferous



Angiosperms appear 144 Mya (early Cretaceous)

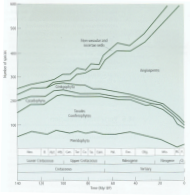


Asteropollis sp. Pollen (Laurales) (Friis et al 2005)

Evolution of Angiosperms

- Angio = container - megasporangium (and integuments) enclosed in carpel.
- Flower structure (a determinate shoot built from leaves).
- 2 integuments not one (as in gymnosperms).
- Double fertilization (resulting in triploid endosperm).
- Xylem structure (vessel members and sieve tubes).
- Other features to such as endopolyploidy ability (weed technology!), vegetative reproductive ability (weed technology!).
- Very versatile - numerous floral strategies possible - a single mutation can result in sexual isolation and new species formation.
- Introduction of animal based pollination strategies.

Explosion in Angiosperm speciesGnetales is gymnosperm group closest to flowering plants

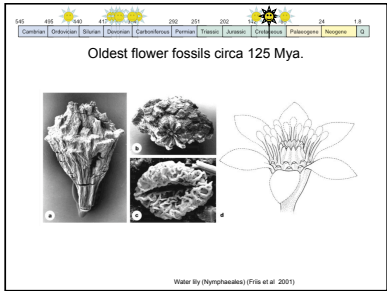


Angiosperms	220 000 species
Bryophytes	22 400 species
Pteridophytes	9 000 species
Gymnosperms	750 species

Fabaceae alone have 14000 species

Also only land plant group to reinvade the sea (*Zostera sp.*)

2/23/11



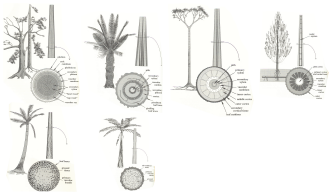
Oldest flower fossils circa 125 Mya.

Water lily (Nymphaeales) (Friis et al. 2001)

The diversification of angiosperms: Darwin's abominable mystery

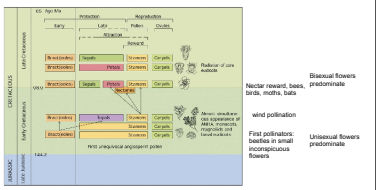
- The rapid appearance of so many species of angiosperm was a problem for Darwin's theory
- In his version of events, evolution proceeds gradually, selecting minute changes
- Saltation was an opposing view point – gives more emphasis to mutation (internally driven) than Natural Selection (externally driven)
- Darwin discovered the reason, and founded 'pollination biology'

Evolutionary Trends: convergence (on tree habit)



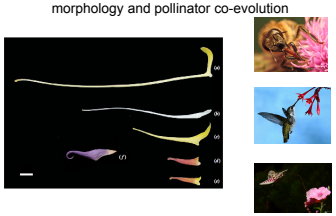
Evolutionary Trends: convergence (on cactus habit)

Floral evolution – protection to attraction

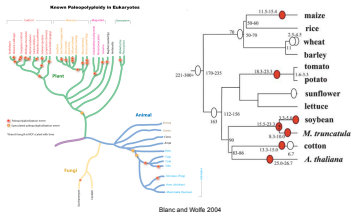


Friis et al 2006

Angiosperms diversified because of floral morphology and pollinator co-evolution

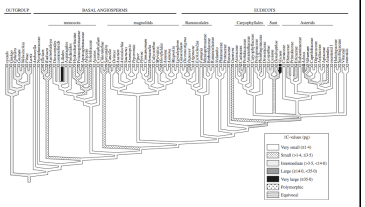


Evolutionary trends: polyploidy

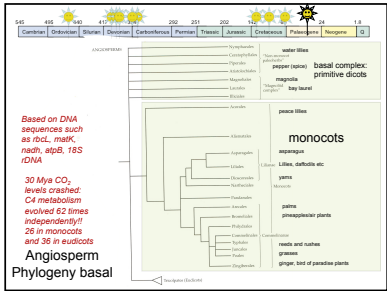


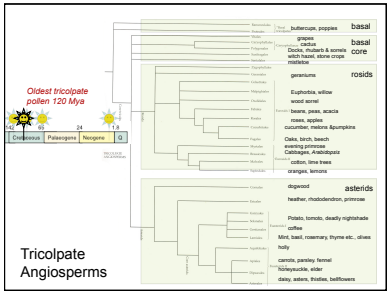
Blanc and Wolfe 2004

Evolutionary trends: genome obesity



Leitch et al 2005





Obesity in the Liliales

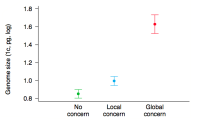
Fritillaria (Liliales) 127 000 Mb

Large cells, slow replication - good for bulbs

Arabidopsis (Brassicales) 157 Mb

Small cells, fast replication - good for weed habit

Endangered species?



Why is there an over-representation of large genomes in the plant Red List?

Vinogradov 2003, but read also Cavalier-Smith 2005

Suggested reading
Crane PR, Friis EM, Pedersen KR (1995) The origin and early diversification of angiosperms. *Nature* 374: 27-33.
Friis EM, Pedersen KR, Crane PR (2005) When the earth started blooming: insights from the fossil record. *Current Opinion in Plant Biology* 8:5-12.
Judd WS, Campbell CS, Kellogg EA, Stevens PF (1999). *Plant Systematics: A Phylogenetic Approach.* Sinauer Associates, Sunderland, Massachusetts.
Kenrick P and Crane PR (1997) The origin and early evolution of plants on land. *Nature* 389:33-39.
Niklas K (1997) *The evolutionary biology of plants.* University of Chicago Press, Chicago.

Other source material
Bateman RM and DiMichele WA (1994) Heterospory: The most iterative key innovation in the evolutionary history of the plant kingdom. *Biological Reviews of the Cambridge Philosophical Society* 69:345-417.
Boerling DJ (2005. Leaf Evolution: Gases, Genes and Geochemistry. *Annals of Botany* 96:345-352.
Blanc G, Wolfe KH (2004) Widespread paleopolyploidy in mode plant species inferred from age distributions of duplicate genes. *The Plant Cell* 16:1667-1678.
Cavalier-Smith T (2005) Economy, sped and size matter: evolutionary forces driving nuclear genome miniaturization and expansion. *Annals of Botany* 95:147-175.
Cavalier-Smith T (2004) Only six kingdoms of life. *Proceedings of the Royal Society of London Series B* 271:1251-1262.
Friis EM, Pedersen KR, Crane PR (2001) Fossil evidence of water lilies (Nymphaeales) in the early cretaceous. *Nature* 410: 357-360.
Friis et al 2006 Cretaceous angiosperm flowers: Innovation and evolution in plant reproduction. Palaeogeography, Palaeoclimatology, Palaeoecology 232 (2006) 251–293
Friis et al 2010 Diversity in obscurity: fossil flowers and the early history of angiosperms. *Phil. Trans. R. Soc. B* 2010 **365, 369-382**
Gerrienne P, Meyer-Berthaud B, Fairon-Demaret M, Streel M, Steemans P (2004) *Runcaria*, a Middle Devonian Seed Plant Precursor. *Science* 306 856-858.
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Leitch IJ, Soltis DE, Soltis PS, Bennett MD (2005) Evolution of DNA amounts across land plants (Embryophyta). *Annals of Botany* 95:207-217.
Proctor M (2007) Ferns, evolution, scale and intellectual impediments. *New Phytologist* 178:504-506.
Rothwell GW (1972) Evidence of Pollen Tubes in Palaeozoic Pteridosperms. *Science* 175:772-774.
Vinogradov AE (2003) Selfish DNA is maladaptive: evidence from the plant Red List. *Trends in Genetics* 19:609-614.