PLANT MORPHOLOGY

Important plant fossils

Aneurophyton: outgroup to seed plants (not incl. Tetraxylopteris, Rellimia)

- three dimensional branching systems; helical or decussate of lateral branches
    - 2-3 x dichotomizing branchlets
- protostelic stems w/ secondary growth
    - mesarch
    - pycnoxylic xylem
    - tracheids with bordered pits
- terminal fusiform sporangia
    - tendency for planation, but also circinate
    - in A. germanicum, ultimate, fertile branchlets dichotomize once, both branchlets curve inwards and have two rows of fusiform sporangia on inner surfaces
    - homosporous

Archaeopteris: composite genus; historically the basis of "progymnosperms"

- frondlike branching systems
- eustelic
    - mesarch vascular bundles
    - pyncoxylic secondary wood w/ circular bordered pits on radial walls of tracheids
    - ultimate branching systems of "planate, variously dissected webbed leaves" are spirally arranged
    - planate lateral branching, not fronds
- axial primordia, not from axillary buds
- fusiform sporangia, adaxial on terminal leaflike, dichotomous appendages
- fertile branches are helically arranged on penultimate branches in planate branching systems
- homosporous/heterosporous (prob. heterosporous in most if not all)

FOSSIL SEED PLANTS

Lyginopterids: composite genus (Lyginopteris, stems; Lagenostoma, petrified ovules; Calymmatotheca, lobed campanulate cupules; Sphenopteris, compressed fronds; Crossotheca, Telangium, Telangiopsis & Feraxotheca, microsporangiate organs)

- Carboniferous
- eustelic stems
    - stems w/ anastomosing, radially elongate bands of fibers in outer cortex (Oliver & Scott)
    - branching pattern interpreted as dichotomous with occasional close dichotomies that superficially mimic axillary branching by Nixon et al (vs. axillary by other workers)
- microsporangiagia pinnate and laminar w/ abaxial sporangia in Crossotheca and Feraxotheca, but terminal in Telangium and Telangiopsis
- stems, lvs & cupules have capitate epidermal glands ("used by Oliver & Scott, 1904) to recognize 'seed ferns'")

* - "...in future analyses this terminal would be divided into subunits based on observed variation within the group." Nixon et al.

Medullosans: (see citations pg. 491 in Nixon et al. 1994 for series of studies of this group)

- Carboniferous-Permian
- characterized by large bifurcate fronds
- eustelic
- large noncupulate ovules
- complex synangia
- variation of key vegetative characters
- M. endocentrica vine-like growth habit and axillary branching (unique for genus)
- others with treelike habit and lack axillary branching
- controversies over origin of polystelic stem and homology of large and complex pollen-bearing organs accd to but not addressed byNixon et al.

Callistophyton: first recognized by Delevoryas & Morgan (1954)

- Pennsylvanian (Taylor)
- petrified axes superficially similar to Cordaites were very similar in morphology to Lyginopteris
- shrub w/ spirally arranged fronds
- axillary branches & occasional adventitious roots at nodes
- synangia and ovules borne on abaxial surfaces of pinnules
- ovules not borne in cupules, but were platyspermic (nucellus free from the inner integumentary layer except at the base)
- synangia: ring of laterally fused elongate sporangia
- pollen is monosaccate with distal sulcus and two lateral lobes (Callandrium and Idanothekion) often with branched pollen tube and intact microgametophyes within the walls similar to extant conifers. (Callistophytaceae-cordaites-conifers??)

Cordaites: "conspicuous group of plants" from Late Paleozoic; Northern Hemisphere

- tall, much-branched trees or shrubs
- eustelic
    - endarch (Cordaixylon) or mesarch (Mesoxylon)
    - secondary xylem pits are araucarioid
    - pith is "conspicuous" with septation of parenchyma tissue
- pycnoxylic wood
- spiral phyllotaxis
- large strap-shaped and lanceolate leaves
    - no midvein, but numerous dichotomizing veins running nearly parallel in leaf lamina
- compound pollen and seed-bearing cones borne on central bracteose axis in either planate pattern or spirally arranged
- sterile appendages mixed with sporophylls
- microsporophylls laminar, simple, with 4-6 free microsporangia
    - dehisence by longitudinal slits
    - pollen grains eusaccate or monosaccate and inaperaturate
- megasporophylls are stalklike; either single bearing a single terminal ovule (C. zeilleri; more recent) or dichotomous, bearing two ovules (C. pseudofluitans).
- ovules are platyspermic; single integument of inner sclerotesta and outer sarcotesta.
    - nucellar cuticle is distinct and free from the integument and thick megaspore wall
- microsporangiate cone (Gothania) compound with sporangia in a single row on the apex of sporophyll

Glossopterids: "..signal group of the Gwondwana flora...imprecisely understood assemblage..." "...minimal if any evidence for monophyly." (Nixon et al. '94)

- Permian to Triassic (Taylor)
- leaves w/ "multiveined midrib w/ anastomosing lateral venation that is not hierarchical with respect to vein order diameters" (Nixon et al, '94)
- sporangia (seed or pollen-bearing) on simple or branched stalks subtended by foliar structures
- sporangia variously adenate to foliar structures; seeds sometimes seemingly borne directly on foliar structures while others "appear to be completely enclosed by foliar organ." (Nixon et al, '94)
- ovules orthotropous; connected by parenchymatous cells "that might be interpreted as participating in pollination" (see citations in Nixon et al, '94)
- pollen bearing organs composed of "variously branched axes terminating in clusters of microsporangia" (Nixon et al, '94)
- pollen bisaccate or quasisaccate (?)
- reproductive structures regarded "as axillary branch systems with variously modified fertile appendages adnate to a subtending bract." (Nixon et al, '94) (i.e., interpreted as axillary not foliar structures).
- Axial complexes vs megasporophylls: "The close association of and/or fusion of fertile axillary structures to foliar appendages is consistent with the morphology of reproductive structures in most other seed plants with axillary branching such as the conifers, Ginkgo, and gnetopsids, and is also consistent with some interpretations of the angiosperm carpel/placenta complex." (Nixon et al, '94)

Peltasperms: (Peltaspermum, Lepidopteris (lvs), Antevsia (microsporangia) and numerous other lf form and reproductive structure genera). Upper Triassic; Greenland and South Africa (Taylor).

- prob. woody plants with system of long and short shoots
- lvs spirally arranged; bi- or tripinnately compound w/ conspicuous tuberculate bodies and folds along the main rachis...folds interpreted as scale lvs (Schimper, 1869 cited in Nixon et al. 1994)
- "frond" of Lepidopteris interpreted as a "branch system with the main axis bearing scale leaves alternating with lateral branches borne in a planate arrangement. The lateral branches bear scale leaves as well as larger laminar leaves." (Nixon et al, '94)
  - venation is open dichotomizing, fan-shaped or pinnate..pinnules lacking or having indistinct mid-vein.
- microsporangiate organs branched structures with spirally arranged lateral appendages that bifurcate once or twice
  - microsporangia are borne on the ultimate segments in groups of eight; these are free sporangia in two rows; dehiscence by longitudinal slit opening to the center of sporangial clusters
  - pollen monocolpate, w/ smooth outer surface, thick lamellate endexine and thick homogenous ektexine (Pedersen, 1981).
- ovulate organs (on main axis with stalked peltate and radially symmetrical discs in a spiral arrangement
- Salpingocarpus: platyspermic, unitegmic, w/ nucellus free from integument, w/ distinct salpinx

Corystosperms: Gwondwanan group of plants; Triassic of South Africa, Australia, Argentina, and & India

-Representative genera: Umkomasia, Pilophorosperma (ovulate structures), Spermatocodon (seeds), Pteruchus (microsporangia), Dicroidium (leaves)

- woody habit for some (at least); possibly several wood types present..
- lvs once-pinnate with dichotomizing mid-vein (citations in Nixon et al. 1994)

- microsporangiate structures of a central axis with stalked lateral appendages, these unbranched and terminating in a "laminar-peltate structure bearing 20-100 abaxially arranged sporangia" (Nixon et al., '94)
    - sporangia were free and dehisced by longitudinal slit (Thomas, 1933 *in* Nixon et al, '94)
- ovulate structures: compound branching systems of a central axis w/ lateral branches arising in axils of bracts; "..branches are apparently in one plane" (Nixon et al, '94)
    - one to several pairs of stalked or rarely sessile ovulate units are borne along the lateral branches, the distal pair being distinctly bifurcate (Nixon et al, '94)
    - each seed is enclosed (partially, at least) by a recurved cupule
    - each ovule has a slightly curved, bifid micropylar canal (Taylor, 1981, Nixon et al, '94)
- reproductive structures interpreted as branching systems, not sporophylls by Nixon et al ('94) based on radially symmetrical vascular bundles in the central axis of Pteruchus (Yao et al., 1992)

Caytoniales: "...best known group of Mesozoic seed ferns." (Taylor, 1981)

- Known from Jurassic, Triassic and Cretaceous sediments
- first described by Thomas in 1925 as a new group of angiosperms

- palmately compound leaves with 3-6 leaflets (up to 7 cm long), each with a midvein and anastomosing laterals that form a reticulate venation pattern (Taylor, '81)
    - stomata present on lower surface; cuticle is thin.
- Caytonanthus (pollen-bearing structure) is synangiate w/ 3-5 sporangia borne on the abaxial surface of pinnate microsporophylls (Thomas, 1925 *in*Nixon et al, '94)
- Caytonia (ovulate structures) consists of "an axis about 5.0 cm long that bears stalked, multiovulate cupules in subopposite pairs" (Taylor, '81); the cupules were recurved and had a liplike projection near the point of attachment with the central axis. Each cupule contains 8-30 seeds. The "cupule" was wrongly interpreted at first as an outer seed layer with the lip of the cupule thought to form a stigmatic surface and fine strands of cuticle were said to be remnants of pollen tubes, but pollen was subsequently found within the micropylar end of seeds thus there was not stigmatic surface formed by the "cupule" and while certain workers have considered the cupule as homologous to the second integument of angiosperm seeds, it is interpreted by Nixon et al., ('94) as a "seed envelope" but not homologous to the second integument of angiospermous seeds. The discussion in Nixon et al, '94 describes a "stoma" created between the lip of the cupule and the adaxial wall of the pedicel of the whole ovule-bearing structure...this is different than a micropyle of an angiosperm that is formed solely by the integuments. Nixon et al, '94 go on to say that the seed envelope ("cupule") is "more similar in form to a planate leaflike appendage that has curved inward upon itself (semi-circinate) with connate margins, forming a saclike structure." In this interpretation, the seeds can be seen as being borne directly on a foliar appendage or that an axillary stem system has become adnate to the subtending bract (envelope) that folded over to form the seed envelope.

Pentoxylon: "small group of Jurassic gymnosperms" (Taylor, '81)

- Composite genus: Pentoxylon (stems), Nipaniophyllum (leaves), Carconites (ovulate heads) & Sahnia (branched pollen-bearing organs)
- known from northeastern India & Mesozoic of New Zealand
- small trees or shrubs with both long and short shoots
- eustelic; unusual and similar to Medullosaceae
    - comprised of 5-6 [16] triangular wedges of primary and secondary wood; wedges are separated by parenchymatous areas analogous to rays
- primary xylem is mesarch

- wood is pycnoxylic w/ uniseriate rays; secondary wood is more developed toward the center of the stem
    - tracheids with uni- & biseriate round bordered pits
    - some specimens with radially aligned cells in cortex suggestive of a periderm (Taylor & Taylor, '93)
    - no evidence of wood parenchyma, resin canals or ray tracheids
- leaves strap-shaped; up to 20 cm long, "w/ entire margin and a midrib that extends to the apex and consists of several parallel veins" (Nixon et al, '94)
    - petioles very short
    - stomata on the abaxial surface

Pollen-bearing organs (Sahnia) consist of "receptacles with raised rim that bears a whorl of delicate axis approximately 2 cm high" (Nixon et al, '94) OR "...pollen cones consist of numerous branches, which have been termed microsporophylls (approximately 24) that are fused at their bases [note: others have claimed these are free at their bases]to form a shallow ring around a dome-shaped receptacle at the end of a spur shoot. Each microsporophyll is about 1.5 cm long and contains numerous helically arranged branches." (Taylor, '81) At the end of each branch are borne numerous sporangia ("pollen sacs" of Nixon et al, '94).

- pollen is monosulcate w/ "complex exine structure that appears endoreticulate with an inner lamellate layer" Osborn et al., 1991 cited in Nixon et al, '94)

Ovule-bearing organs (Carnoconites) borne terminally on short shoots and consist of a central branching peduncle or axis with each branch terminating in a cone that is about 2.0 cm long and contains ca. 20 seeds

- seeds are platyspermic, attached directly to the axis of the cone with the micropyles pointing away from the central axis.
- two layered integument (sarcotesta and sclerotesta) is free from the nucellus except at the chalazal end.

Bennettitales: two families, Williamsoniaceae and Cycadeoidaceae (Taylor & Taylor, 1993)

- well represented in Triassic through Cretaceous sediments from North America, Europe, India, and Greenland.
- share striking characters with flowering plants; discovered in 19th century and early work by Wieland (1906) revealed cosexual strobili in Cycadeoidea from the Black Hills (S.D./N.D.) which later incl. evidence of insect pollination (Crepet, 1972, 1974).
- habit: from delicate branched forms that lack persistent leaf bases (Wielandiella) to more robust, sparsely branched columnar trunks with persistent leaf bases (Williamsonia) to ovoid or stout columnar trunks which are sparsely branching (Cycadeoidea & Monanthesia)
- leaves: from entire-leaved taxa to pinnate
- cones: located at lateral branch terminals and surrounded by sterile bracts (Williamsonia) or terminal and subtended by two short lateral branches (Wielandiella) or terminal on short lateral branches with cone-surrounding bracts (Cycadeoidea, Monanthesia).
- ovulate receptacles are fleshy and conical or dome-shaped that bear hundreds to thousands of orthotropous ovules; tubular micropyles extend beyond the armored surface formed by the tangential walls of the polygonal heads of the interseminal scales
- microsporophylls are based on a pinnate groundplan; borne in a single whorl which in cosexual cones subtend the ovuliferous portion of the receptacle
    - sporangia are enclosed in elongate or kidney-shaped synangia that are borne on microphylls

*- questions remain about the distribution of bisexual (cosexual) vs unisexual reproductive structures in Bennettitales

- timing of maturation of microsporangia and megasporangia, poorly understood fossils, etc.., but Weltrichia spp. have microsporangia without associated ovulate parts.

- analyses suggest that Bennettitales initially evolved as unisexual plants

*- the corona of Cycadeoidea is noted as being not a fleshy extension of the ovulate receptacle but is made of "elongated modified interseminal scales that have elongate cells with spiral thickenings similar to those found in transfusion tissue in conifers" (Crepet, 1974 cited in Nixon et al., '94) ...in other words, it may not be homologous with the corona of Williamsoniella.

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