BDB 2014 Picea study day, an introduction, by Paul Goetghebeur, BG Ghent University
Scan Jan De Langhe :
Picea_asperata_(not_heterolepis)_NPVBM19842407_2950JDL_15022007_10.JPG

From ferns to Gymnosperms : from sporangia to seeds

Seed ferns : Medullosaceae (fossil) (Kalkman 1972)
A. *Medullosa noei*, habit
B. Id., stele in cross section
C. *Medullosa solmsii*, id.
D. *Medullosa luckartii*, id.
E. *Alethopteris lancifolia*, pinna
F. *Neuropteris*, pinna with seed
G. *Trigonocarpus*, ovule longitudinal section
H. Id., cross section

Seed ferns (fossil) (Stewart 1983)
1. *Archaeosperma arnoldii,* ovules
The integument is almost entirely united with the nucellus (except for the top).
In the nucellus a large macroprothallium (= female gametophyte) is evident.
2. Reconstruction of a semophylesis explaining the origin of the ovule.
A : basic pattern with dichotomous branching and terminal sporangia
B : start of heterospory, with one macrosporangium surrounded by many microsporangia
C : microsporangia are reduced, their telomes are “sterile”
D : webbing of the “sterile” telomes around the macrosporangium resulting in the formation of a new layer, this new layer = the integument (later on forming the seed coat !)

Development of the ovule in Gymnosperms (Kalkman 1972)
A : full grown ovule
B : primordium of ovule, with a small nucellus, surrounded by an incipient integument
C : differentiation of the macrospore mother cell (still diploid !) in the nucellus (= macrosporangium wall)
D : meiosis of the macrospore mother cell, yielding 4 haploid macrospores
E : degeneration of three macrospores, only the most internal one functional
F : the functional macrospore is growing into a female gametophyte (= macroprothallium)
on top of the micropyle a pollination drop is formed (in many Gymnosperms)
G : several pollen grains were captured in the pollination drop, and have sunken into the micropyle, on top of the nucellus in the pollen chamber, where several pollen grains have germinated and are growing a pollen tube
H : seed, with seed coat (developed from the integument), a thin layer as a remnant of the nucellus, the primary endosperm (developed from the female gametophyte tissue), and the embryo (the result of the sexual process, uniting an egg cell with a sperm cell)

Phylogeny of the Seed Plants : 5 monophyletic groups
Gymnosperms are now considered as a monophyletic group.
The Gymnosperms themselves are composed of 4 living clades (Cycadopsida, Ginkgoopsida, Gnetopsida, Pinopsida), and each of these is also considered monophyletic.

Cycadales : pachycaul species with a crown of stiff leaves
Cycads *Dioon* with female cone
Cycads *Ceratozamia* with female cone
Cycads *Cycas* with male cone
Cycads female *Cycas* with ovules
Fossil cycads : *Williamsonia*, in Blake & Mortimer, by E.P.Jacobs

Ginkgoales : feeling very lonely
Ginkgo biloba, the only survivar of its group.

Ginkgo biloba : pollination drop on micropyle

Ginkgo biloba, without and with pollen grains
Top row : no pollen is entering the pollination, and the secretion of fluid is continuing for several days (blue line).
Bottom row : pollen has entered the pollination drop, secretion of fluid stops abrupt (pink line), and the pollen grains finally are entering the micropyle.

Ginkgo biloba + pollen of Ginkgo, Cycas, Pinus, Abies
Pollination drop on top of ovule of *Ginkgo biloba*
1. With pollen of *Ginkgo biloba*. The pollen grains are sinking to the bottom of the drop, secretion stops immediately, the pollen grains are rehydrating and enter the micropyle and will germinate in the pollen chamber.
2. With pollen of *Cycas revoluta*. Idem as 1.
3. With pollen of *Pinus thunbergii*. The pollen grains do not sink, do not rehydrate, do not enter the micropyle, except for a few which do not germinate. Secretion holds on for a longer period.
4. With pollen of *Abies firma*. Idem as 3, but not a single pollen grain is entering the micropyle.

Life cycle of Ginkgo biloba, pollen tube = haustorium
Figure to the left :
In these two basalmost clades (Cycadales & Ginkgoales) the pollen tube is acting as a haustorium, providing food for the two growing spermatozoides.
Fertilization is achieved by zoidogamy.
In the two next clades (Conifers & Gnetales) the pollen tube has developed into a new function for transporting the non-motile sperm cells towards the egg cell.
Fertilization is achieved by siphonogamy.

Ginkgo biloba, habit : short shoots with seeds
Seed coat thick and multi-layered, with a thin outer coat, a thick fleshy layer, and a bony inner layer.

Gnetales : three bizarre genera

Gnetum, "flowers" and seeds
Leaves broad, pinnately nerved, decussate.
Pantropical rain forest trees & lianas.

Ephedra viridis (Mojave desert)
A genus from dry, often mountainous regions.
Leaves decussate, but reduced to scales.

Ephedra distachya : dry seeds included by fleshy scales
The ovules develop into dry seeds, but they are often surrounded by fleshy scales, producing a berry-like diaspore.

Welwitschia mirabilis in the Namib desert
One of the most bizarre plants, living in the Namib desert.
Leaves decussate, but reduced to one single pair, that is living on for centuries due to a basal meristematic tissue.

Welwitschia mirabilis
The species is dioecious, with "male" and "female" specimens.
Both are producing cone-like structures, strobili. In the "female" strobili are formed winged seeds.

Conifers : producing complex cones
Conifers are recognized by their complex cones.
Cones of *Pseudotsuga* do show this complex nature very clearly : a real bract (3-toothed), with a scale-like structure in its axil, the seed-bearing "scale".
This seed-bearing scale is now understood as a flattened short shoot, i.e. a phyllocladium.

The complex cones of Conifers explained (1 : Florin 1951. 2 : Kalkman 1972)
Figure to the left : Semophylesis, showing the transition from a cone with bract + axillary branch transforming into a bract bearing a broad, flattened “seed scale”.
Figure to the right : Cones of different groups of Conifers, with bract (striped) and seed scale (dotted)
L : Cordaitales (fossil)
M : Pinaceae
N : Araucariaceae
O : Taxodiaceae
P : Cupressaceae
R : Podocarpaceae
S : Cephalotaxaceae

Phylogenetic tree of the six families of Conifers.
Podocarpaceae is often divided into Podocarpaceae sensu stricto and its sister group Phyllocladaceae.
Taxaceae is often divided into Taxaceae sensu stricto and its sister group Cephalotaxaceae.

Family name, with number of genera.

Araucariaceae	3
Podocarpaceae	19

The genus *Phyllocladus* is often kept in a separate family Phylllocladaceae, the sister group of Podocarpaceae.

Sciadopityaceae	1
Cupressaceae	29
Taxaceae	6

The genera *Amentotaxus* and *Cephalotaxus* are often separated as the family Cephalotaxaceae, the sister group of Taxaceae.

Pinaceae : new branches becoming woody in 1st year
All genera and species of the family Pinaceae are easy recognized by their new branches becoming woody soon in their first year.
Scan Jan De Langhe : Picea_rubens_ARLR2551_3009JDL_11032007_02a.jpg

Pinaceae : 11 genera, 232 species
Pinaceae
The eleven genera are readily separated into 2 subfamilies, Abietoideae & Pinoideae.

Abietoideae vs Pinoideae

	Abietoideae	Pinoideae
Ovulate cones	erect (exc. Tsuga)	hanging
Cone scales	narrow base deciduous or persistent	broad base persistent
Resin vesicles on seed	present	absent

Apart of these differences, there are more data from wood anatomy, clearly separating the two subfamilies.

Pinaceae : list of genera, with their respective number of species.

Abies	50
Cathaya	1
Cedrus	4
Keteleeria	3
Larix	11
Nothotsuga	1
Picea	37

Pinus	111
Pseudolarix	1
Pseudotsuga	4
Tsuga	9
11	232

Picea : leaf base very prominent & soon woody
As a result all needles will be shed when drying during the preparation of a herbarium specimen, yielding unsightly naked branches and many loose needles.
Scan Jan De Langhe : Picea_jezoensis_NPVBM19652433_2944JDL_15022007_02a.jpg

Picea : leaf base very prominent & soon woody
Scan Jan De Langhe : Picea_jezoensis_NPVBM19790188_2943JDL_15022007_03a.jpg

Picea phylogeny (Lockwood et al. 2013)
Phylogenetic tree based on genome analysis of the three sources, cpDNA, mtDNA and nrDNA.
None of the previous or current morphology-based classifications is congruent with this tree…
Picea abies is non-monophyletic !

Picea phylogeny (Lockwood et al. 2013)
Summary of the previous phylogenetic tree.
Basalmost clade = Asian species (part 1) + the European species.
The position of *Picea breweriana* is unresolved, but somewhere basal.
The North American species and the second part of the Asian species each are forming a monophyletic clade, but with unresolved position.
Picea morrisonicola is the sister group of the other species of the Asian clade part 2.
Concluding :
- three monophyletic clades are evident,
- the position of *Picea breweriana* is unclear,
- the backbone is not yet resolved,
- clade 1 + *Picea breweriana* + *Picea morrisonicola* are characterized by a plesiomorphy, mitotype D.

Area of all species of Picea (Lockwood et al. 2013)
See list with text.

The take home message
Seed plants are spore-forming plants with specialized macrosporangia
Gymnosperms : 4 monophyletic groups
Many gymnosperms are producing pollination drops
Cycads & *Ginkgo* with haustorial pollen tube & motile spermatozoids
Pinales and Gnetales pollen tube : transporting sperm cells to egg cell
Pinales = Conifers : complex ovulate cones, 6 families
Pinaceae : new shoots becoming woody in their first year, 11 genera
Picea : leaf base very prominent and soon woody
Picea : morphology rather uniform, not congruent with molecular phylogeny

A sincere « Thank you » to :
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Matthias Goerne, listen to : Oh du mein holder Abendstern

Picea jezoensis
Scan Jan De Langhe : Picea_jezoensis_NPVBM19790188_2943JDL_15022007_06a.jpg