E-kursuse
Soontaimede evolutsioon ja süstemaatika
LOOM.01.015, 3 EAP
Loenguslaidid

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Tartu Ülikool 2011

BGBO.01.038 SOONTAIMEDE EVOLUTSIOON JA SÜSTEMAATIKA 3 EAP

Soovitatav kirjandus:

Mitmesugused evolutsiooniõpikud (soovitavalt uuemad)

Judd & Campbell 2002 või 2007, Plant Systematics

Bremer, Bremer & Thulin 2003, Introduction to Phylogeny and Systematics of Flowering Plants

Muud tänapäevased (>2000) taimesüstemaatika õpikud

Vanemad õpikud, sh Botaanika II teatud infoks

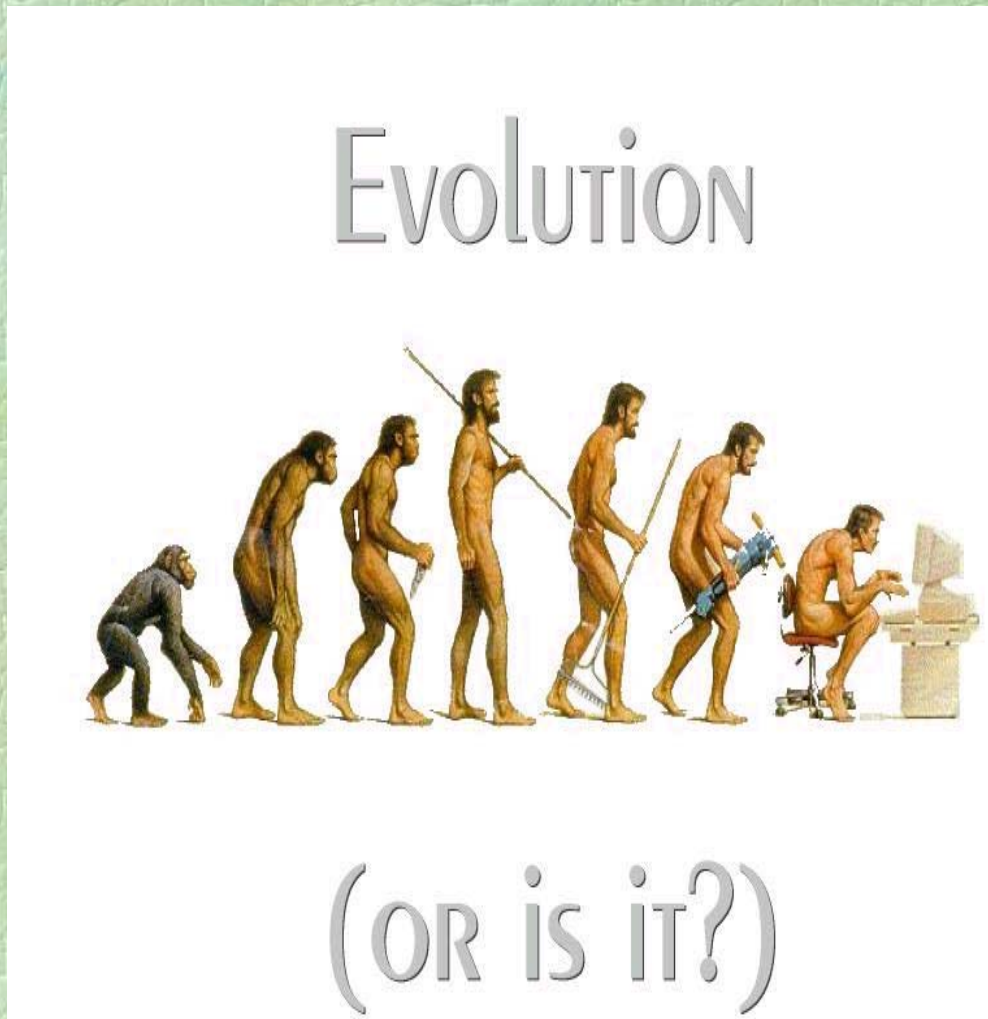
Loengute teemad

- Sissejuhatav loeng
- Ajaloolis-süstemaatiline osa
- Evolutsiooniprotsessid taimedel
- Seminarid (näited)

Täna

- Mis on ja mida hõlmab evolutsioon?
- Evolutsiooni uurimine, fossiilid
- Evolutsiooniteooria ja botaanika ajalugu

- **"Nothing makes sense in biology except in the light of evolution"-- Theodosius Dobzhansky, 1973**

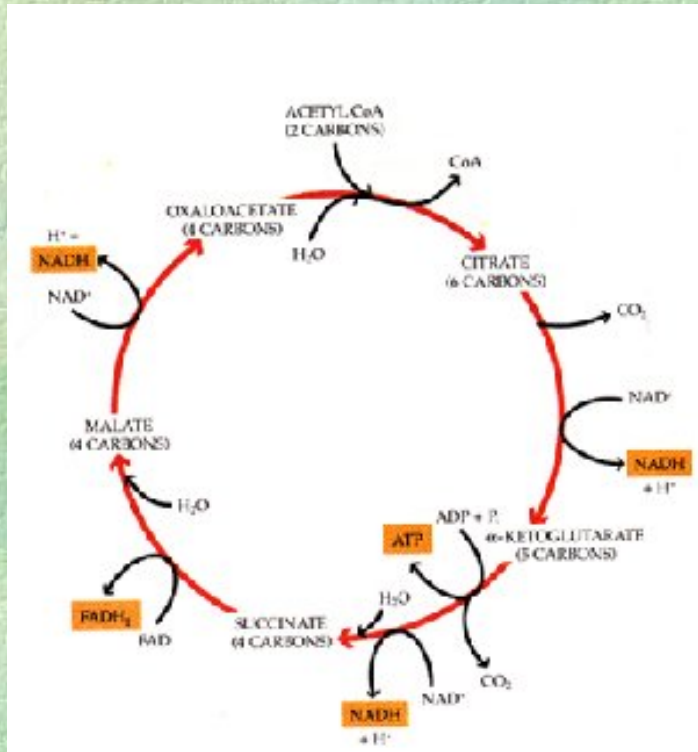


Mis on evolutsioon?

- Päritavate tunnuste pöördumatu muutumine põlvkonnast põlvkonda organismide populatsioonides (Wikipedia)
- Keerukamate organismide järkjärguline arenemine lihtsamatest
- Elusa looduse ajalooline areng liikide üksteisest põlvnemise kaudu
- Organismide grupid, eriti liigid muutuvad ajas nii, et järeltulijad erinevad esivanematest morfoloogiliselt ja füsioloogiliselt
- Sugulasorganismide grupi ajalooline areng = fülogenees

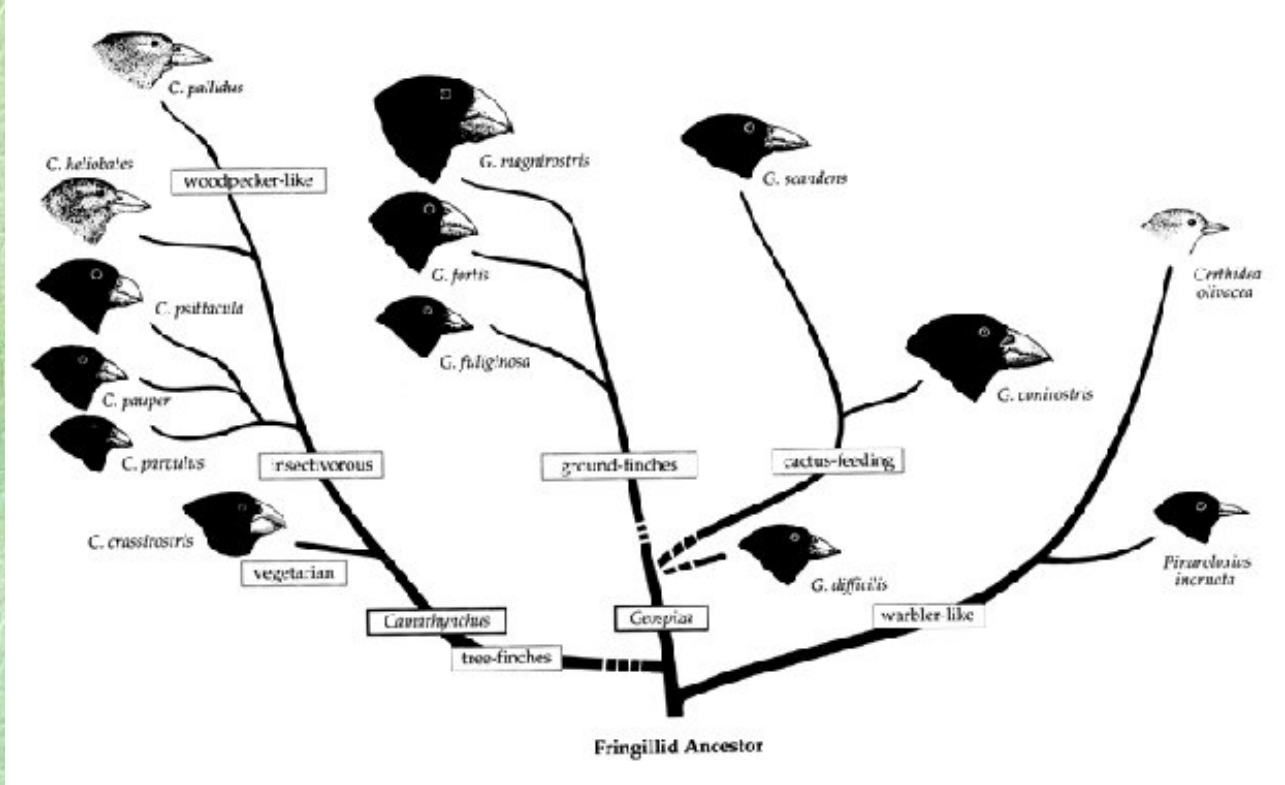
Evolutsiooniprotsessid

- Pärilikkus, metabolism ja replikatsioon
- Anatoomia ja füsioloogia



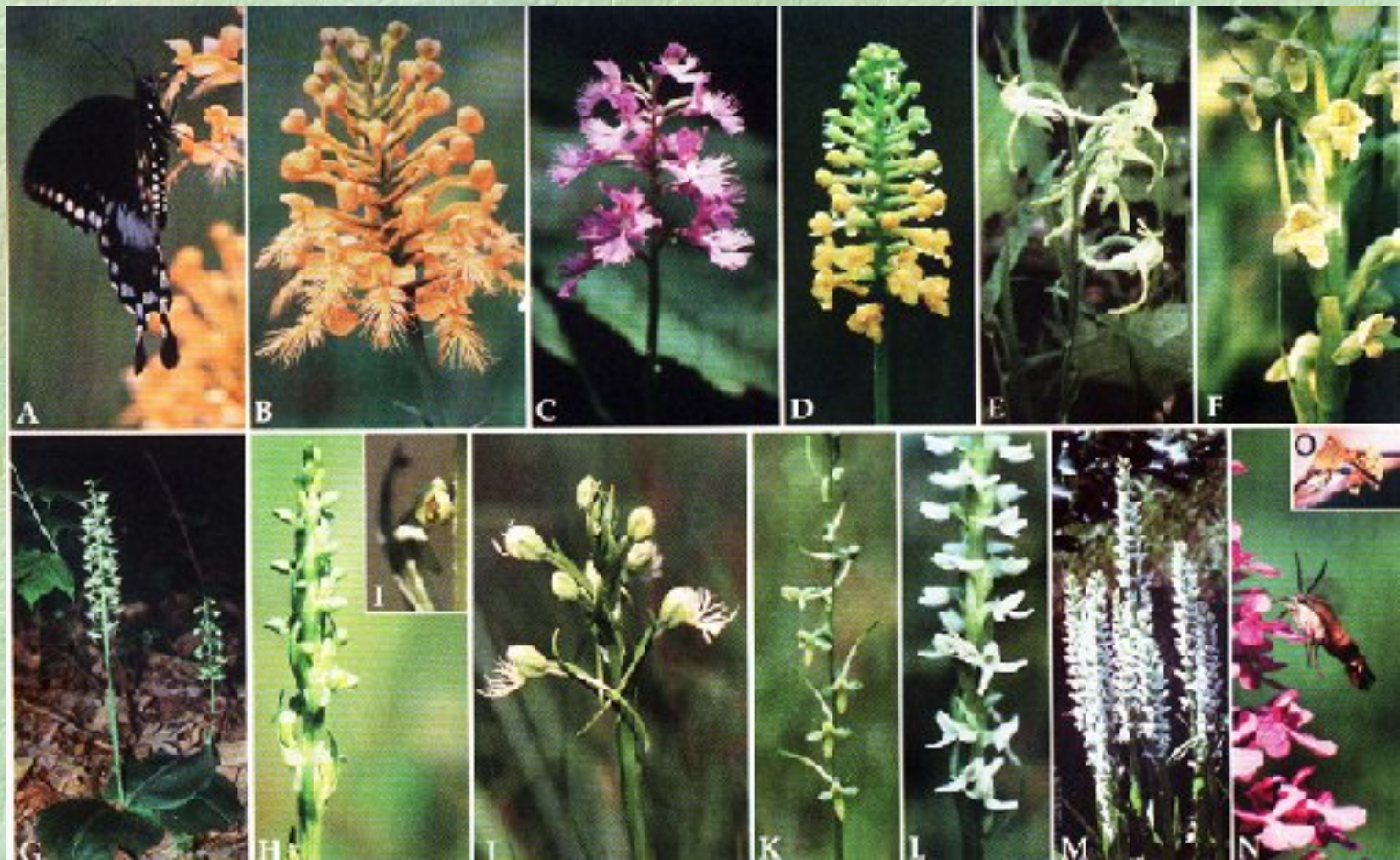
Evolutsiooniprotsessid

- Divergeerumine ja konvergents
- “Radiatsioonid”



Evolutsiooniprotsessid

- Liigiteke ja liikide interaktsioonid
- Liigisisene varieeruvus



Evolutsiooni uurimine (tõendid)

- **(otsene)**
  - eksperiment, sh kunstlik aretustöö
  - paleontoloogia (paleobotaanika) – fossiilid
- **(kaudne)**
  - võrdlev morfoloogia, anatoomia
  - molekulaar-bioloogia
  - arengubioloogia (evo-devo)
  - fülogeneetiline süstemaatika

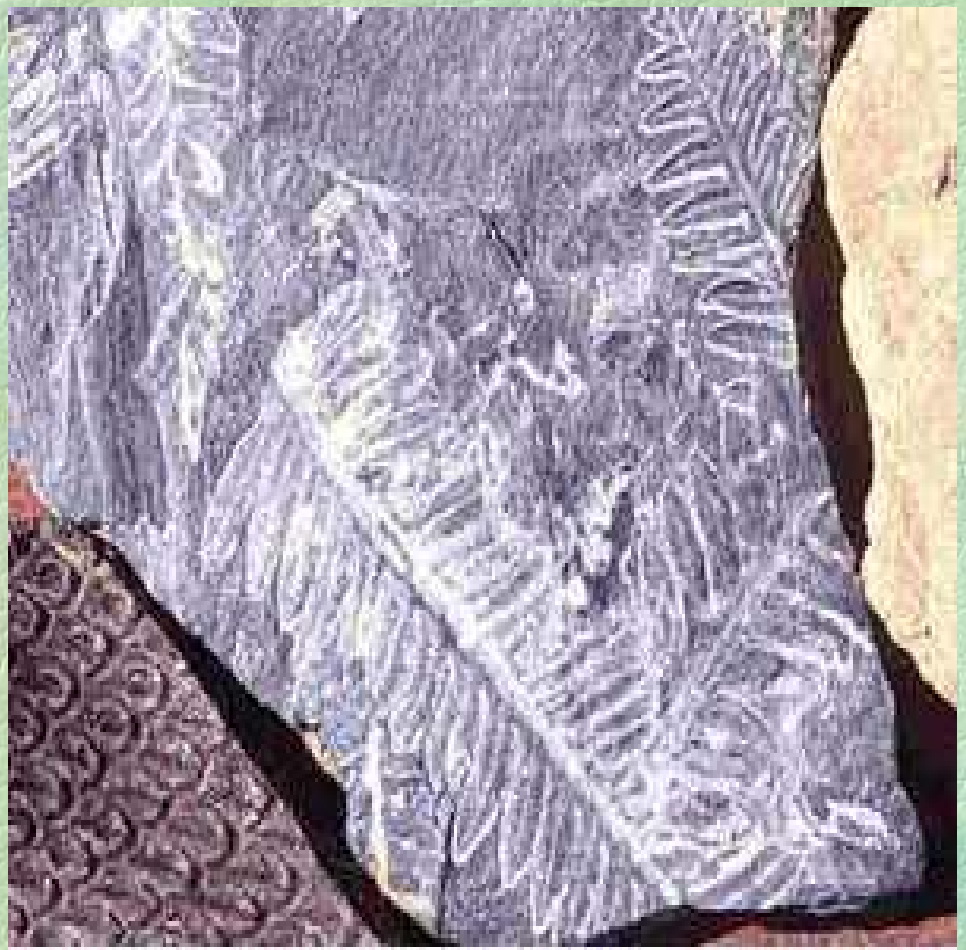
Fossiilid

- settekivimites (lubjakivi ja dolomiit, kivisüsi ja pruunsüsi, diatomiit ja merevaik)
- erilised keskkonnatingimused (O_2 puudus, ekstr temp, pH, kuivus, vesi või jää)

Fossiliseerumine

Makrofossiilid:

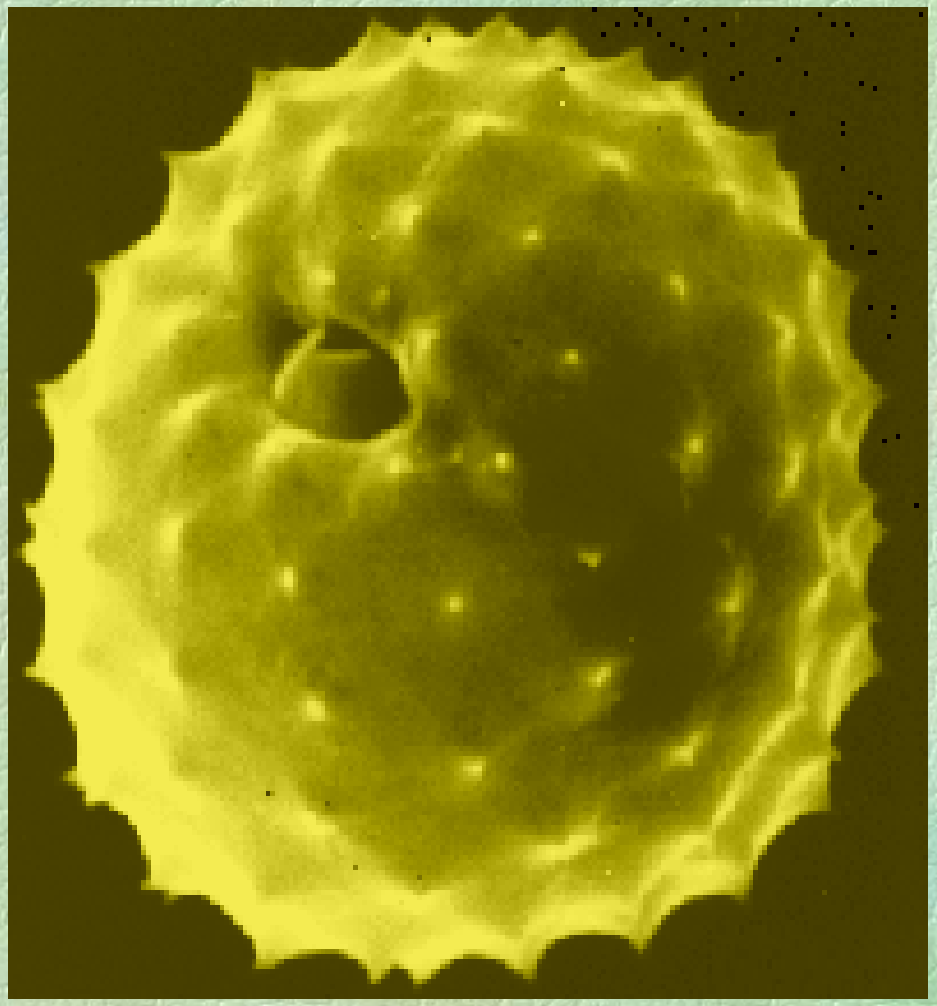
- Impressioonid, nt tsementeerumine, rauakonkretsioonid jm
- Permineralisatsioon ehk petrifikatsioon
- Karboniseerunud kompressioonid
- **Mikrofossiilid, harvem makrofossiilid:** duripartiline fossiliseerumine (erijuhtum: merevaik)



Carbonization

Indeksfossiilid

- kiire evolutsioon ja rohke esinemine
- **palünomorfid** (spoorid, tolmuterad, dinoflagellaadid jm orgaanilise kestaga mikrofossiilid)
- stratigraafiliste kihtide identifitseerimiseks ja dateerimiseks



Fossiilide vanuse määramine

- **radiomeetriline**
  - Pegmatiidis: $^{238}U \rightarrow ^{206}Pb + 4H$, poolestusaeg 4500 mlj a
  - Settekivimites: $^{40}K \rightarrow ^{40}Ca + ^{40}Ar$, poolestusaeg 1250 mlj a
  - Eelnevad vanematele fossiilidele kui 100 000 a
  - Pleistotseeni fossilidele (40 a – 50 000 a) radiosüsiniku meetod ^{14}C poolestusaeg 5568 ± 30 a
  - **geomagnetiline polaarsus**
  - **luminestsents**
  - **korrelatsioon (bioloogiline või geoloogiline)**

Ajalugu (botaanika ja evolutsiooniteooria)

Botaanika enne evolutsiooniteooriat

- nn. rahvabotaanika
- antiikbotaanika: **Theophrastus** (370–287 e Kr) De Historia Plantarum
- "pime keskaeg"
- **Camerarius** (1665-1721) – taimede "seks" (tolmukad, emakad, seemne teke)
- **J.P. de Tournefort** (1656-1708) perekonnad
- **John Ray** (1628-1705) Methodus Plantarum Nova,
- 18 000 liiki, palju tunnuseid

Karl Linné (1707–1778)

- Systema Naturae 1735,
- Genera Plantarum 1737 – nn seksuaalsüsteem,
- Species Plantarum 1753 - binomiaalne nomenklatuur
- liigid on loodud Jumala poolt
- liigid on muutumatud
- kõik liigid on ühevanused
- kindel hierarhia

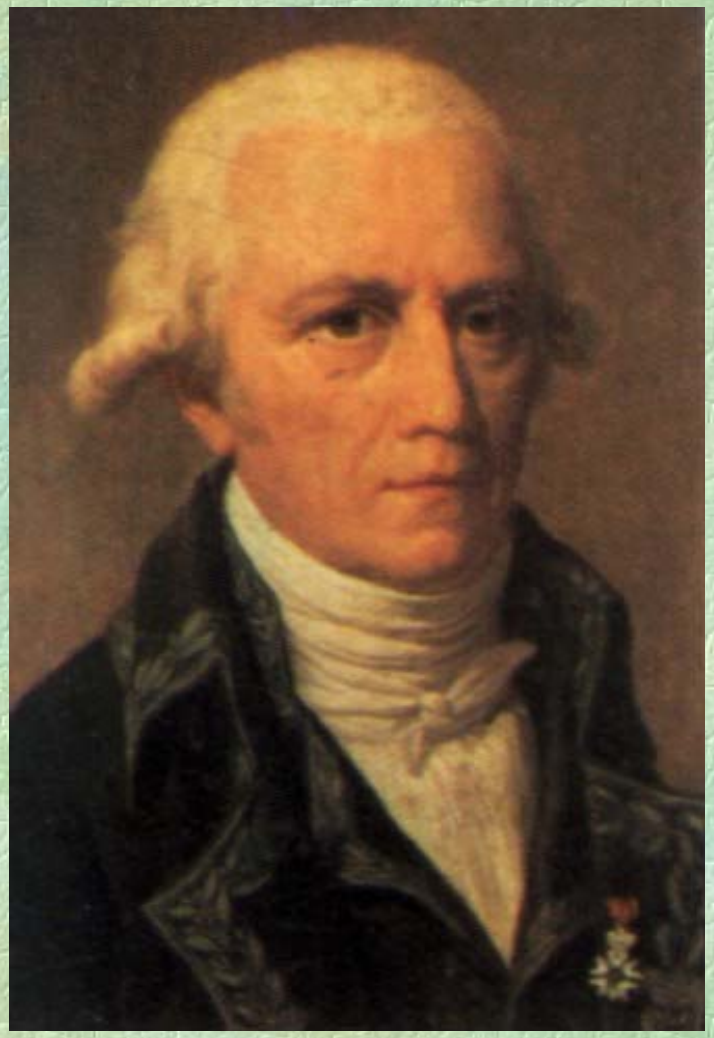
Linné-järgsed “loomulikud” süsteemid

- **M. Adanson** (1727-1806) prantslane
- Familles des Plantes 1763

- **A.P. (1778-1841)** ja **A. de Candolle (1806-1893)**, šveitslased
- Prodromus Systematis Naturalis Regni Vegetabilis 1823-187

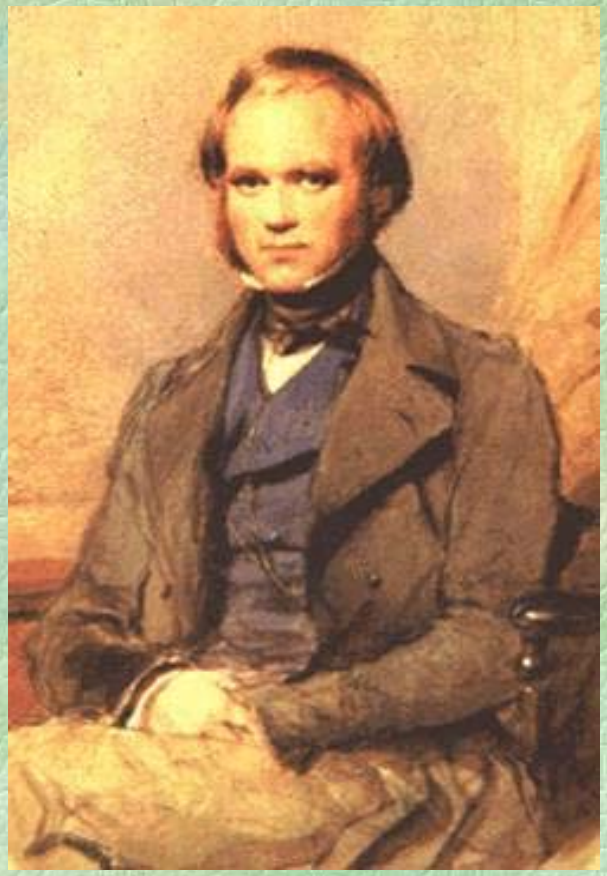
Evolutsiooniteooria areng

- **Jean-Baptiste Lamarck** (1744-1829)
- 1809 Philosophie zoologique
- liigid ei ole ühevanused
- liigid muutuvad erinevates keskkonnatingimustes
- modifikatsioonid on pärilikud
- taimetaksonoomilised tööd, dihhotoomsed määramistabelid



Charles Darwin (1809-1882)

- 1859 The Origin of Species



Alfred Russel **Wallace** (1823-1913)

- sarnased ideed Darwiniga
- loomaliikide biogeograafia, ökoloogia eelkäija

http://entomologia.net/wallace.htm

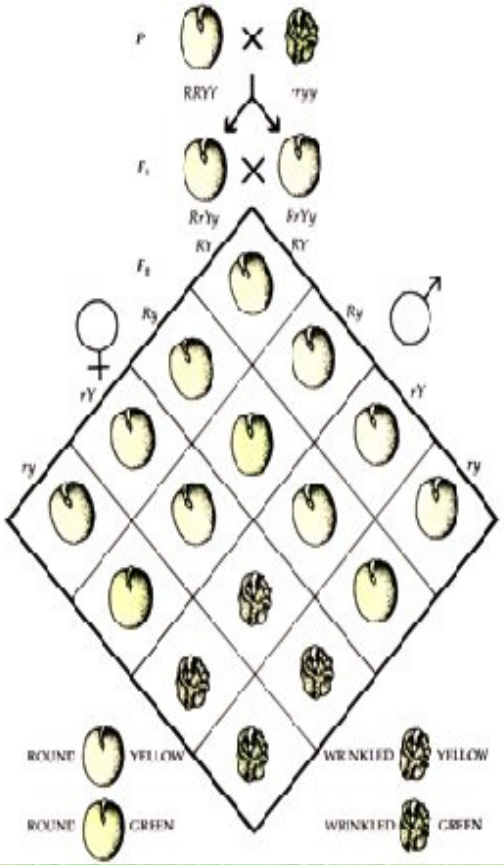
Darwini (ja Wallace'i) teooria looduslikust valikust

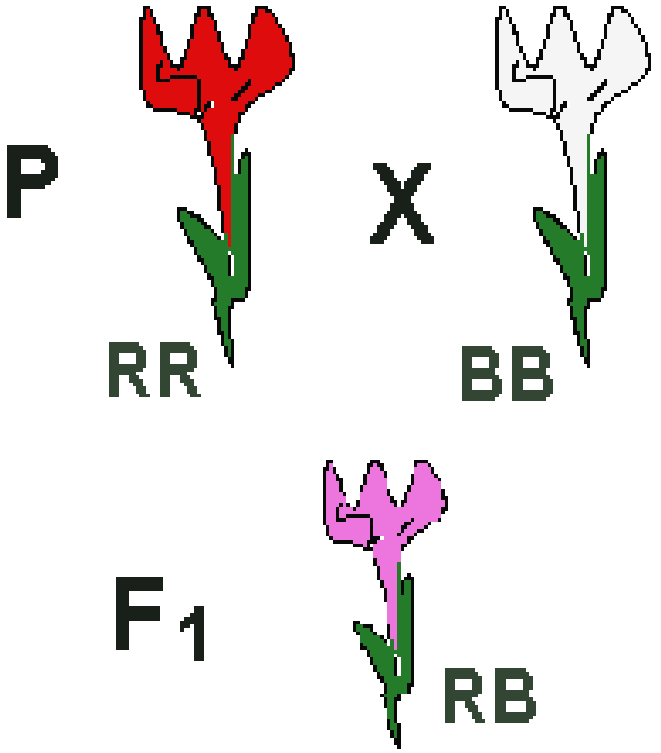
- taime- ja loomaliigid varieeruvad
- välismõjudeta paljuneksid organismid geomeetrilises progressioonis
- kuna ressursid on limiteeritud, jäävad ainult osad järglastest ellu
- looduslik valik soosib eelistatud tunnustega isendite ellujäämist
- eelistatatud tunnused kanduvad edasi järglastele
- valik toimub tuhandete generatsioonide vältel
- muutuvates tingimustes asendavad uued vormid eelnenud

Evolutsiooniteooria areng pärast Darwinit

- **Eksperimendid, transplantatsioonikatsed** 19. saj lõpul, 20. saj algul
  - Bonnier - alpitaimede ökotüübiline varieeruvus
  - von Wettstein 1895 silmarohud
  - Turesson kortslehed
  - de Vries (1905) muutlikkuse teooria teatud paljunemistüüpidel, *Oenothera*

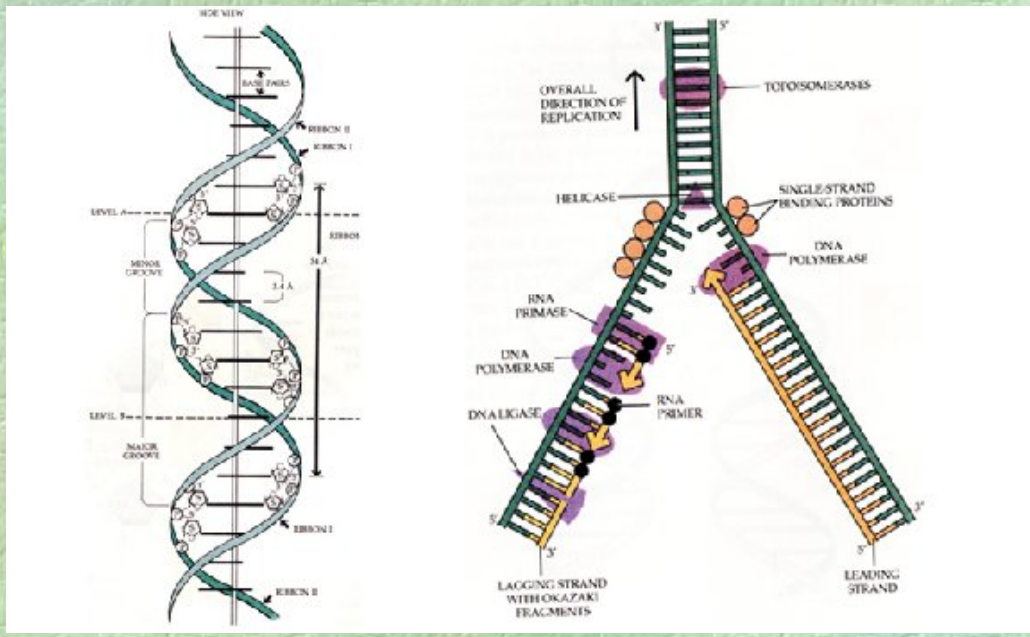
Gregor **Mendel** (1822-1884)
geneetika rajaja





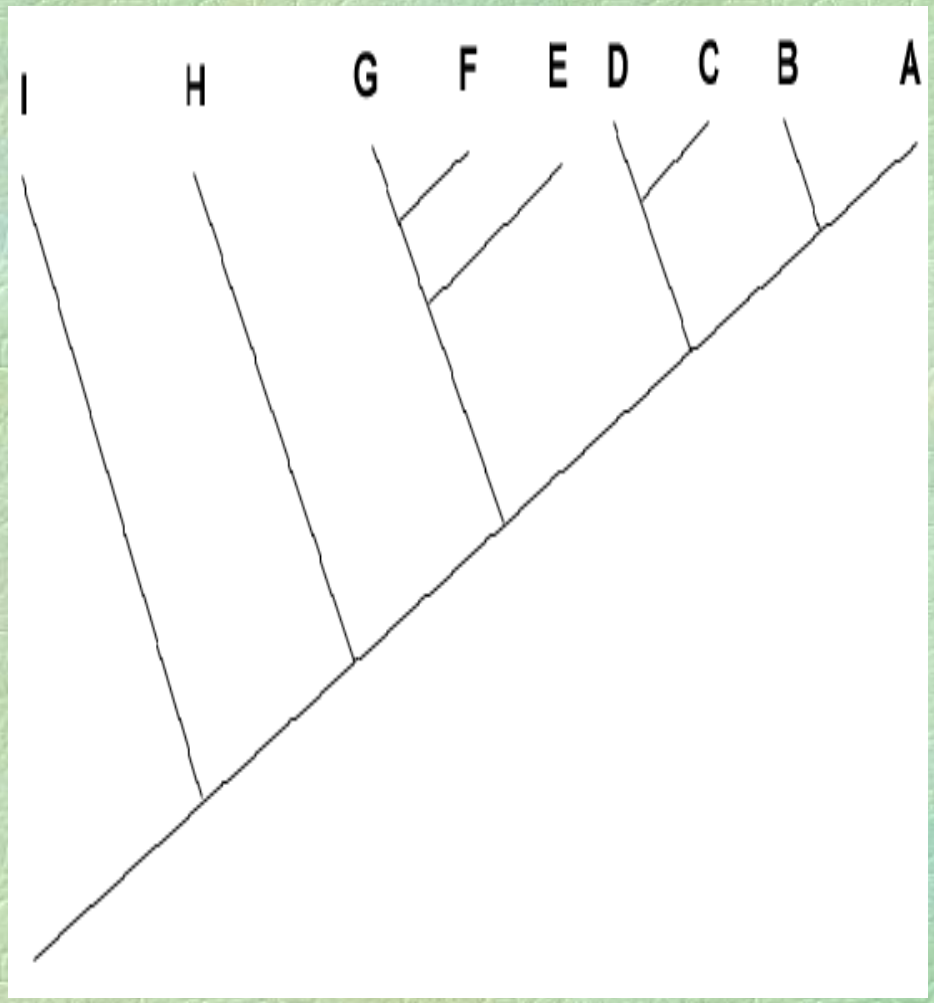
Geneetiline “revolutsioon” (20. saj)

- Mendeli geneetika füüsikaline alus - **geenid, alleelid, kromosoomid**
- **DNA struktuur** (Watson ja Crick), replikatsioon, translatsioon, mutatsioonid
- **populatsioonigeneetika** (Fisher, Haldane ja Wright)



Fülogeneetiline süstemaatika

- **W. Hennig**
  Phylogenetic Systematics
  1960 (saksa keeles 1950)
  kladistika ehk fülogeneetiline süstemaatika



Fülogeneetiline süstemaatika

- Klassifitseerib taksoneid nende ajaloolise arengu ehk **fülogeneesi** alusel
- **Parsimoonia**- ehk säästuprintsiip
- **Monofüleetilised** rühmad
- Plesio- ja apomorfsed tunnused, **sünapomorfid**
- **Fülogeneesipuu** on falsifitseeritav hüpotees

Tänapäev: uusdarvinistlik ehk sünteetiline evolutsiooniteooria

- Evolutsioon on alleelisageduste muutus populatsiooni geenifondis paljude põlvkondade vältel.
- Liikide geenifondid on üksteisest isoleeritud, iga liigi geenifondi säilitab geenisiire.
- Seksuaalselt paljuneva liigi üks isend annab poole järglase alleelidest.
- Isendi alleelikombinatsiooni moodustavad kahe vanema alleelid ja seda võivad muuta mutatsioonid.
- Mutatsioonid on uute geenide allikaks.

Sünteetiline evolutsiooniteooria (järg)

- Looduslikus valikus edukamad isendid annavad rohkem oma geenidest järgmise põlvkonna geenifondi.
- Alleelisageduste muutused populatsioonides toimuvad eelkõige loodusliku valiku tulemusel, kuid sageli esineb ka **geenitriivi.**
- Liikide osapopulatsioonide vahelised barjäärid on vajalikud osapopulatsioonide divergeerumiseks.
- Uus liik on tekkinud, kui geenisiiret eristunud populatsiooni ja vanemliigi populatsiooni vahel enam ei toimu.

Taimede fülogeneetilised süsteemid

- süstemaatilise ühikute eraldamise aluseks taimede sugulus
- süsteem peab peegeldama taimeriigi evolutsiooni

Taimede fülogeneetilised süsteemid

- **Adolf H.G. Engler** (1844-1930) süsteem 1892, koos K.A.E. **Prantl'**iga
- Die Natürlichen Pflanzenfamilien 1887-1915, 14 hõimkonda
- **Melchior**'i toim. uus versioon 1964
- kasutusel BÖI üldherbaariumis, Botaanika II lk 687

Taimede fülogeneetilised süsteemid

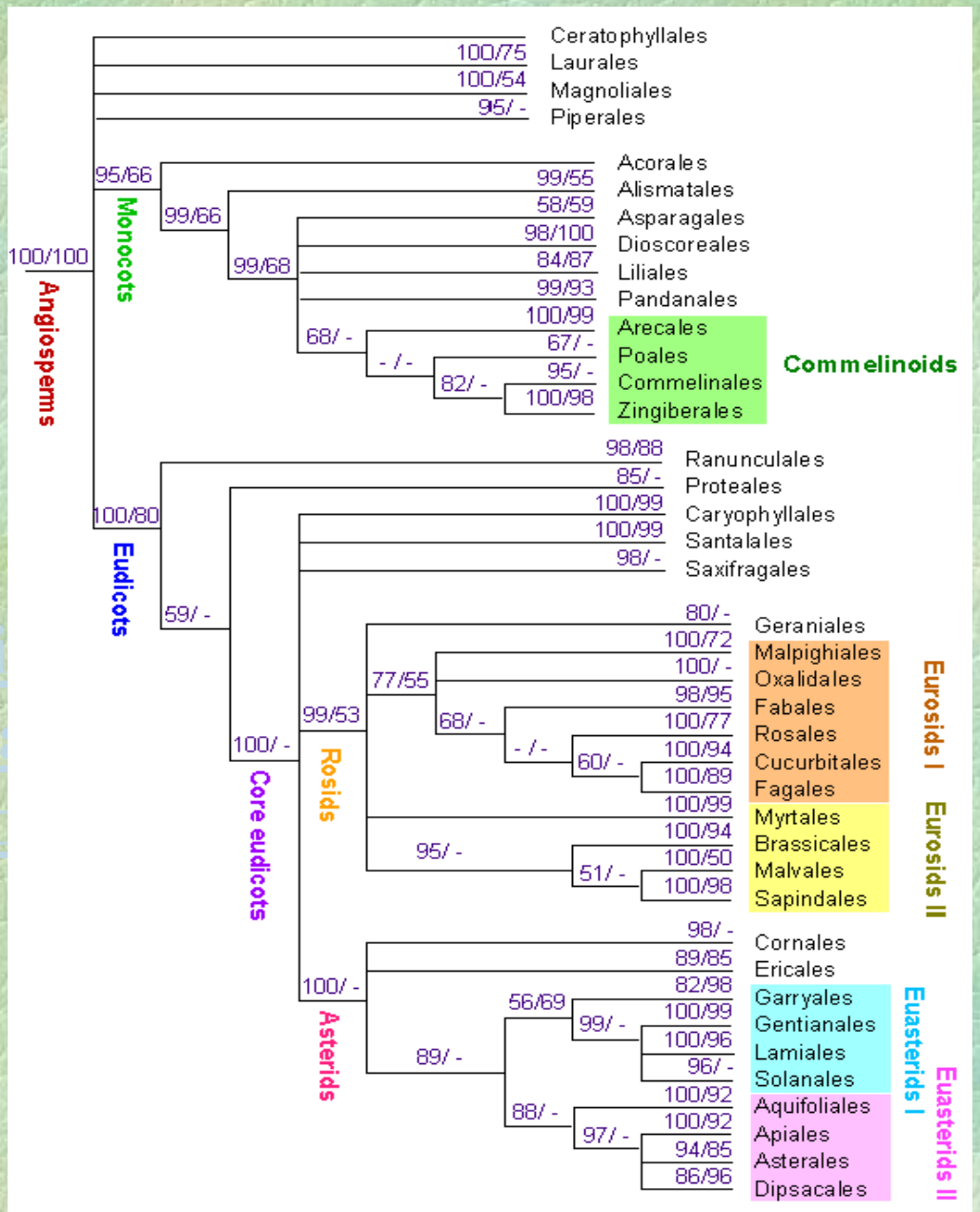
- **N.I. Kuznetsov**
- Vvedenie v sistematiku tsvetkovykh rastenij 1914
- Tartu Ülikool (1895-1914)
- Süsteem Botaanika II lk 691
-

Taimede fülogeneetilised süsteemid

- **A. Cronquist (1939-1992)**
- Evolution and Classification of Flowering Plants 1968, uuemad 1978, 1988
- Sarnaneb Takhtajan'i süsteemiga
- **Armen Takhtajan**
- Die Evolution der Angiospermen 1959
- System and Phylogeny of Flowering Plants 1966
- Sistema Magnoliofitov 1987
- Botaanika II lk 696, 699

Molekulaarsüstemaatika

- Angiosperm Phylogeny Group (APG) 1998, 2003, 2009
- http://www3.interscience.wiley.com/journal/121583649/grouphome/home.html



Kas on midagi veel teha?

- Liigitekke mudelite ja evolutsiooniprotsesside testimine konkreetsete hüpoteeside kaudu
- Radiatsioonide ja adaptatiivsete sündroomide uurimine molekulaarbioloogia meetoditega
- Evolutsiooniliselt oluliste tunnuste ja evolutsioonilise divergentsi molekulaarse baasi selgitamine
- Fülogeneesiuuringud, biogeograafilised uuringud
- Jne, jne

Maismaataimede tekkimine

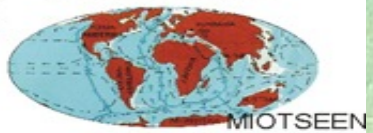
EELLUGU JA SAMBLAD

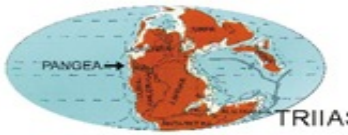
Silvia Pihu

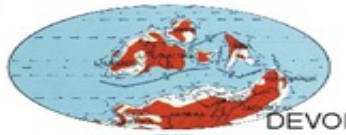
GEOKRONOLOOGILINE TABEL

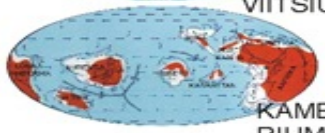
EOON	AEGKOND	AJASTU	AJASTIK	VANUS MILJ. A
Fanerosoikum	Kainosoikum *Uusaegkond*	Kvaternaar Q	Holotseen	0,0115
			Pleistotseen	1,806
		Neogeen N	Pliotseen	5,332
			Miotseen	23,03
		Paleogeen E	Oligotseen	33,9
			Eotseen	55,8
			Paleotseen	65,5
	Mesosoikum *Keskaegkond*	Kriit K	Hilis-Kriit	99,6
			Vara-Kriit	145,5
		Juura J	Hilis-Juura	161,2
			Kesk-Juura	175,6
			Vara-Juura	199,6
		Triias T	Hilis-Triias	228
			Kesk-Triias	245
			Vara-Triias	251
	Paleosoikum *Vanaaegkond*	Perm P	Loping	260,4
			Guadalup	270,6
			Cisural	299
		Karbon C	Pennsylvania	318,1
			Mississippi	359,2
		Devon D	Hilis-Devon	385,3
			Kesk-Devon	397,5
			Vara-Devon	416
		Silur S	Pridoli	418,7
			Ludlow	422,9
			Wenlock	428,2
			Llandovery	443,7
		Ordoviitsium O	Hilis-Ordoviitsium	460,9
			Kesk-Ordoviitsium	471,8
			Vara-Ordoviitsium	488,3
		Kambrium Є	Furong	501
			Kesk-Kambrium	513
			Vara-Kambrium	542
Proterosoikum	Neoproterosoikum	Ediacara		600
		Krüogeen		850
		Ton		1000
	Mesoproterosoikum	Sten		1200
		Ectas		1400
		Calymm		1600
	Paleoproterosoikum	Stather		1800
		Orosir		2050
		Rhyac		2300
		Sider		2500
Arhaikum	Neoarhaikum			2800
	Mesoarhaikum			3200
	Paleoarhaikum			3600
	Eoarhaikum			~4600

PALEO-GEOGRAAFIA









IUGS, 2004;

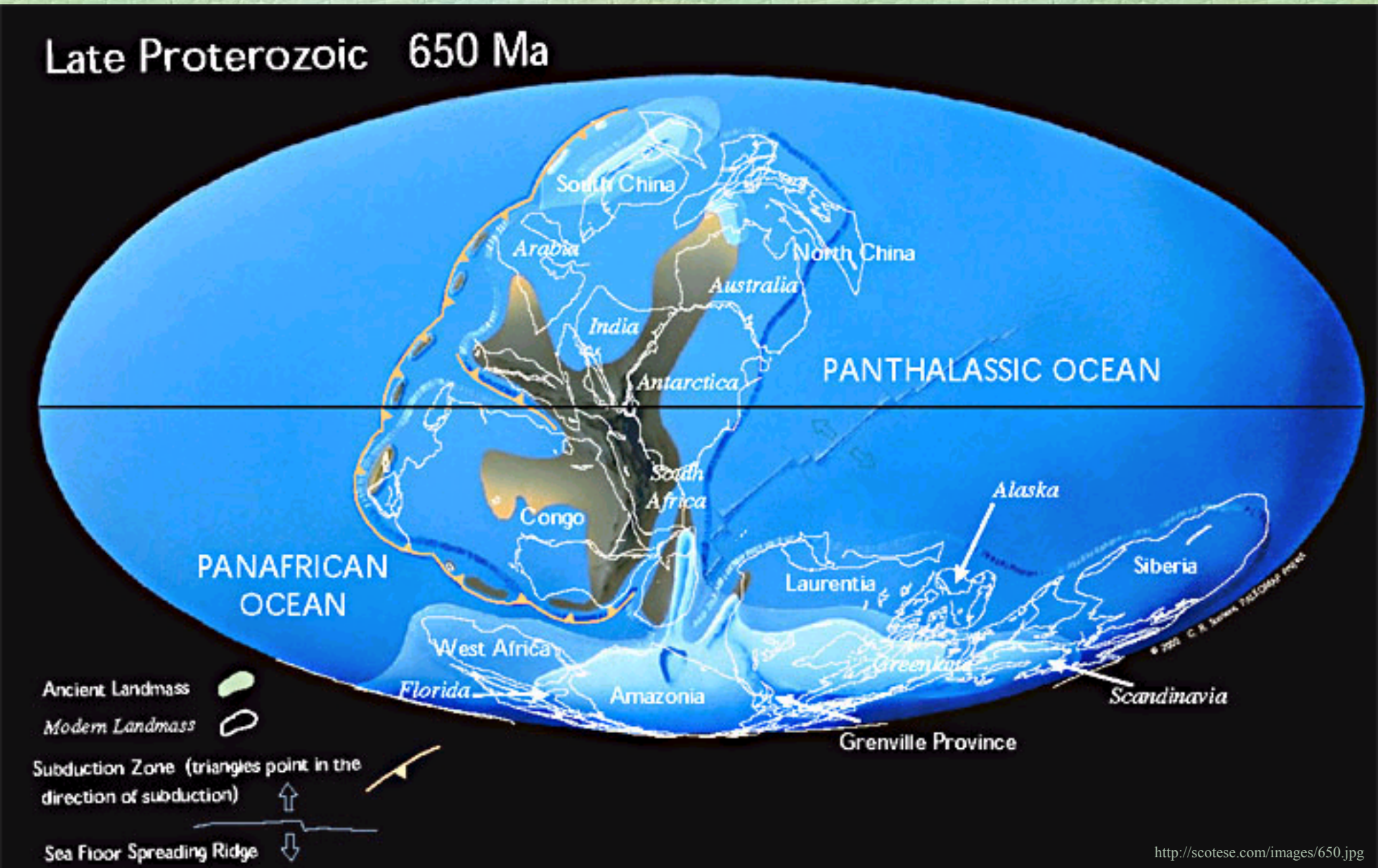
http://lepo.it.

da.ut.ee/~mi/

geokrono.jpg

www. stratigraphy.org

Mandrid proterosoikumis

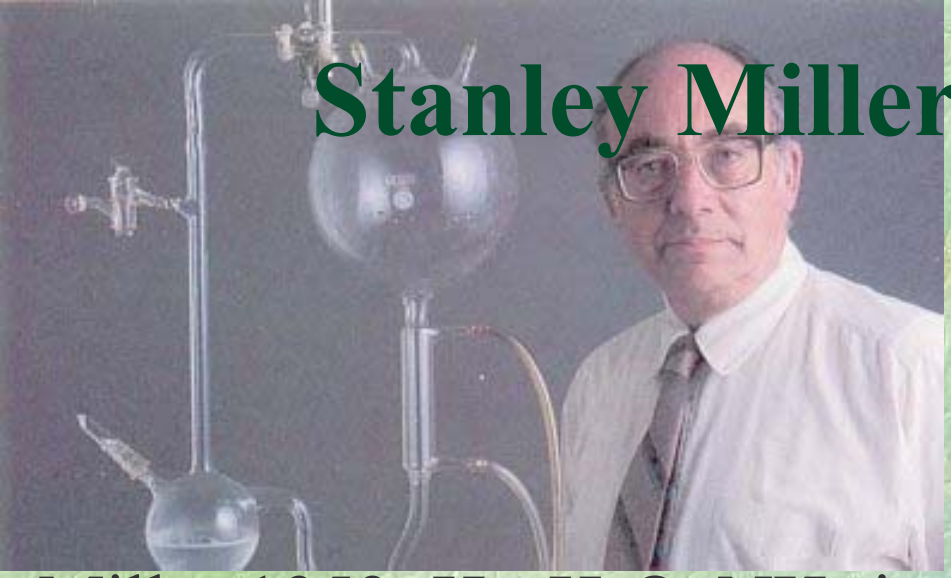


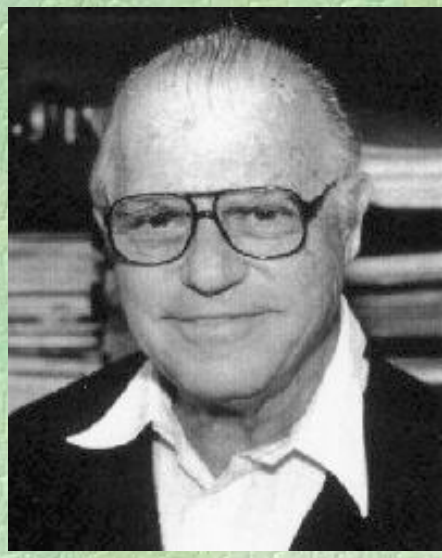
http://scotese.com/images/650.jpg

Tingimused Maal ca 4 miljardit aastat tagasi

- Sagedased vulkaanipursked
- Puudus mullakiht
- Maa oli suures osas kaetud madalate soojaveeliste meredega
- Vulkaanilistest gaasidest moodustus esialgne atmosfäär (N_2, CO_2, SO_2, H_2, NH_2, CH_4)
- Atmosfääris puudus vaba hapnik
- Puudus osoonikiht ning UV-kiirgus jõudis takistamatult Maale

Stanley Miller ja Sidney Fox





Miller 1953: H_2, H_2O, NH_3 ja CH_4 segust võib saada elektrilaengu toimel aminohappeid.

http://www.biologie.uni-hamburg.de/b-online/fo41/3b.jpg

Fox 1960: aminohapete segu kuumutamisel laavatükil tekivad polüaminohapped, mis kokkupuutel veega moodustavad nn **mikrokerasid**, mis sarnanevad mõnede väljasurnud bakteritega

Tähtsündmused kauges minevikus

- 4600-4500 Mat Maa teke
- 3800-3500 Mat grafiit, stromatoliidid
- ? 3800-3400 Mat fotosüntees
- 2700 Mat tõestatud elu olemasolu Maal (tsüanobakterid)
- 2200 Mat O_2 hulga oluline suurenemine
- 2100 Mat eukarüoodid (nt *Grypania*)
- 1500-1000 Mat akritarkide divergeerumine ja radiatsioon
- Vahepeal korduvad jääajad, väljasuremised
- 900-700 Mat hulkraksus; 600 Mat selgrootud

http://www.fas.org/irp/imint/docs/rst/Sect20/stromatolites.jpg

Stromatoliidid

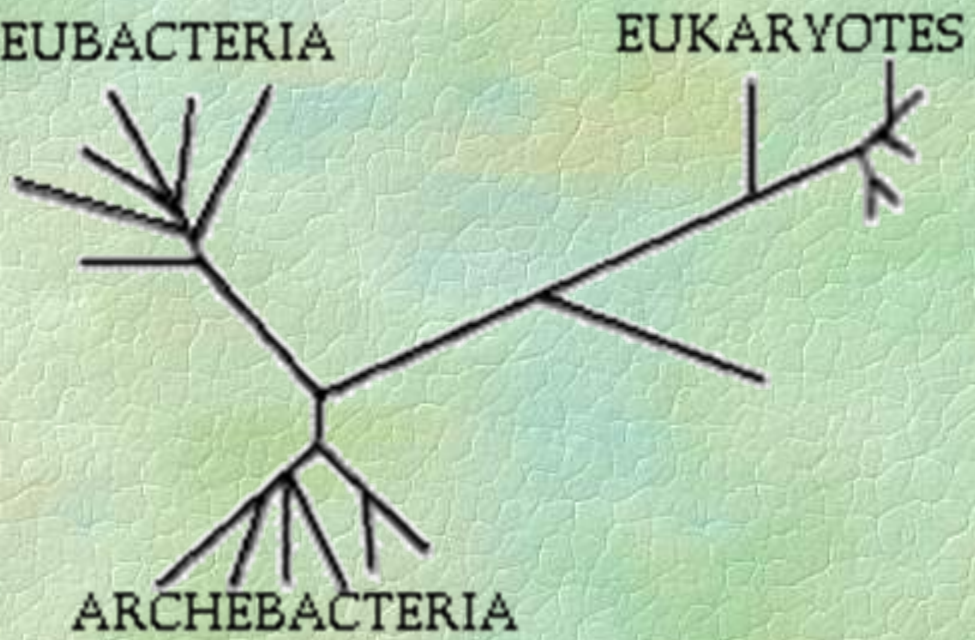
3500 Mat

Schopf 1993

elu jäljed või amorfne grafiit?

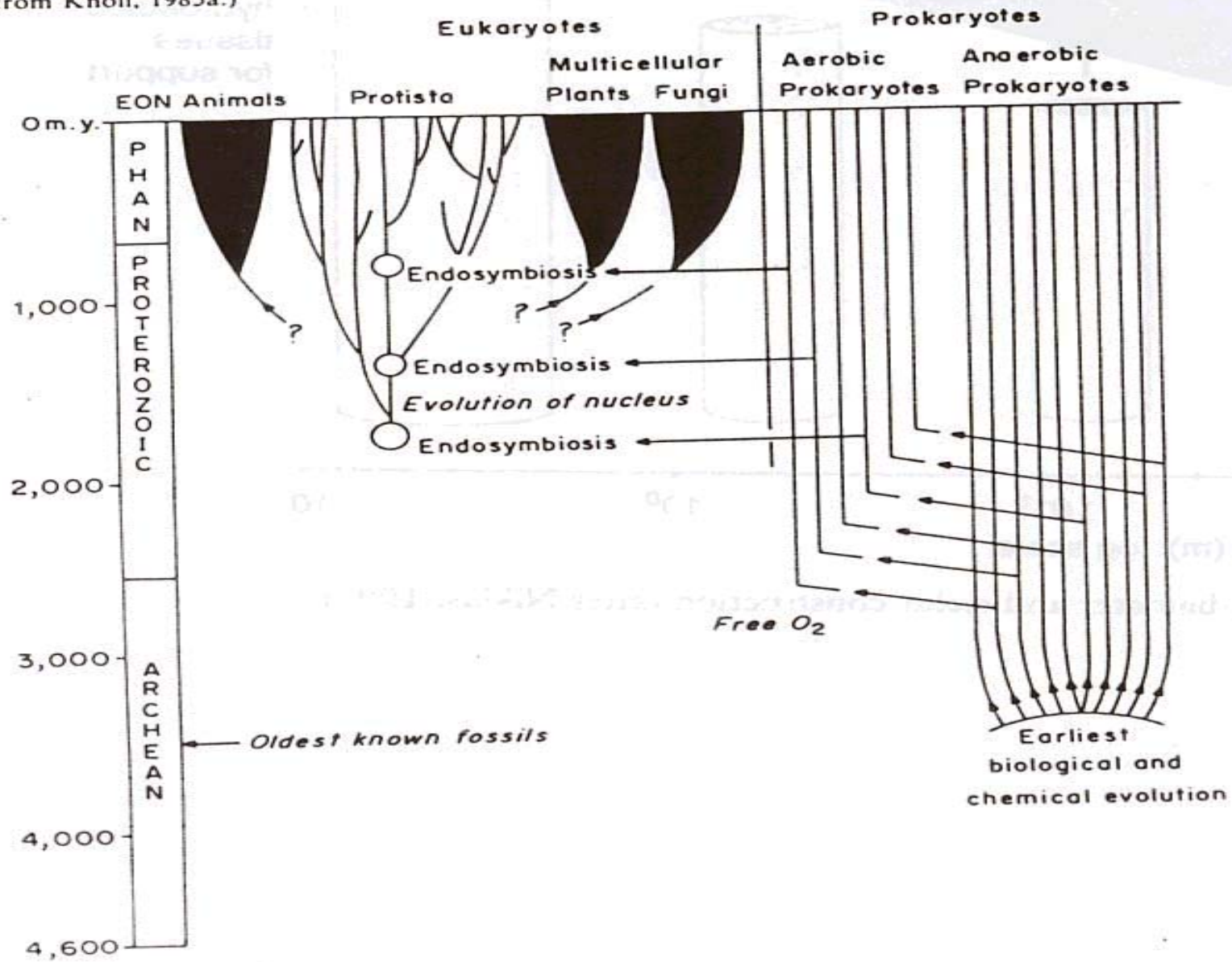
http://www.ut.ee/BGGM/eluareng/stromatoliit1.jpg

http://www.rockhounds.com/grand_hikes/images/fossils/stromatolites_hamelin_pool1.jpg



Esimesed organismid – kemotroofsed anaeroobsed arhed?

Chart 4.2. Representation of major patterns of evolution in the Precambrian. See text for clarification. (Modified from Knoll, 1985a.)



Eukarüoodid ja hulkraksus

- Endosümbioos
- Eukarüootsus võimaldas hulkraksust
- Tekkis aeroobne respiratsioon e hingamine
- Koed ja organid – tööjaotus
- Eraldatud, püsiv sisekeskkond
- Palju uusi organismitüüpe
- Taimed, seened ja loomad

Grypania

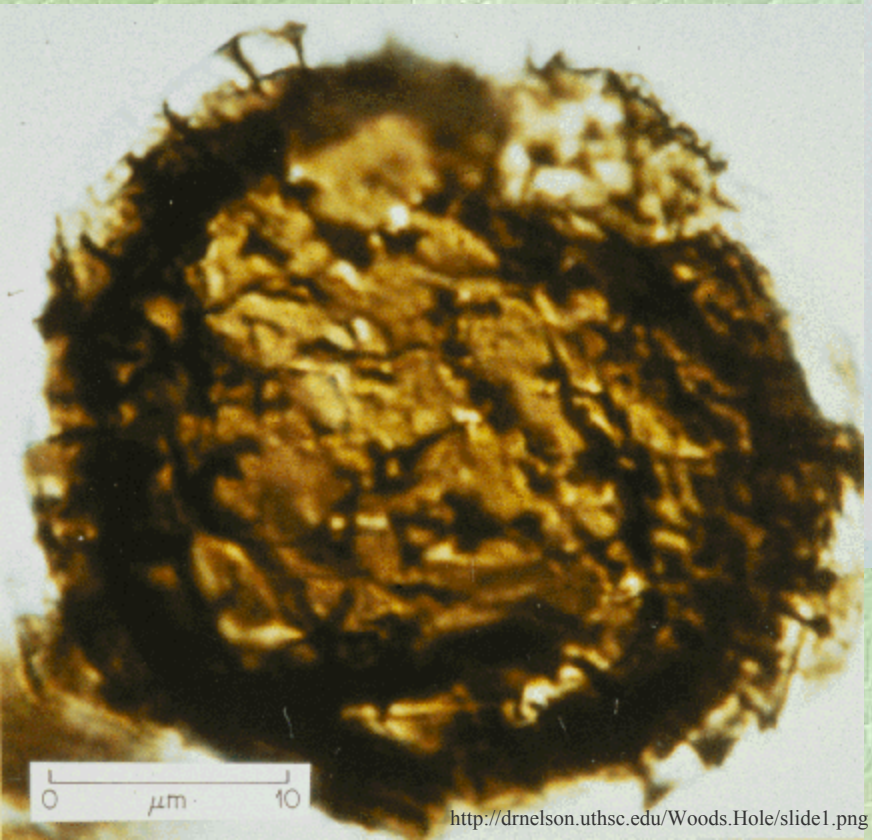
http://www.fas.org/irp/imint/docs/rst/Sect20/pmg31.jpg

2100 Mat
?misidentified

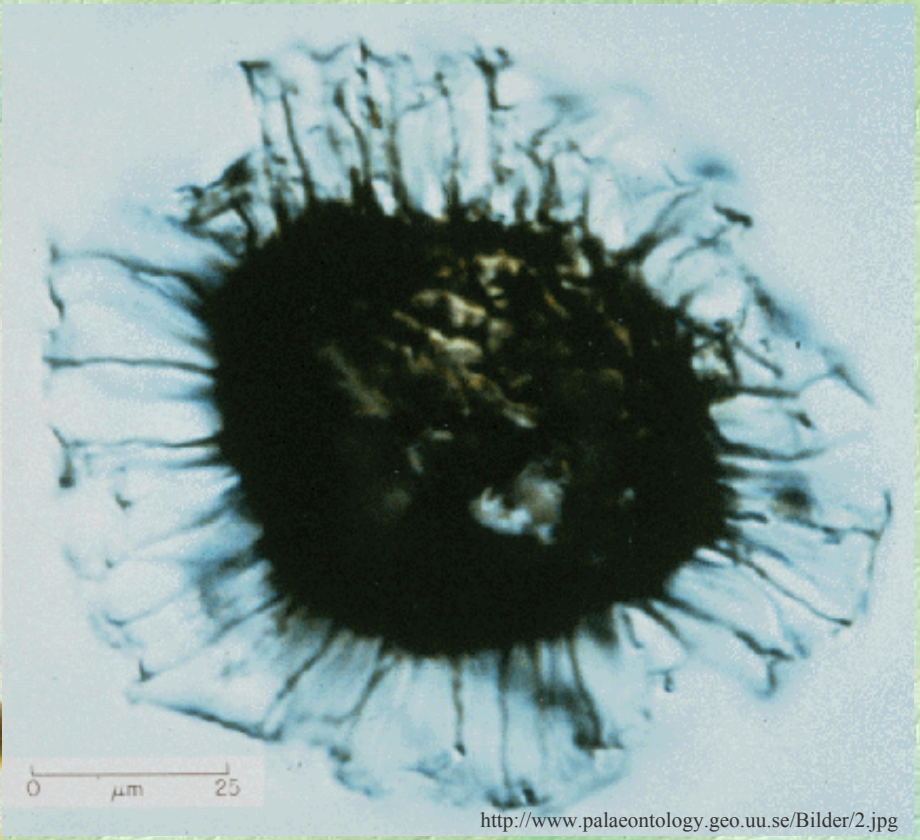
http://web.eps.utk.edu/research/kah/images/Grypania.jpg

Akritarkid

Esimesed ca 1850 Mat



http://drnelson.uthsc.edu/Woods.Hole/slide1.png



http://www.palaeontology.geo.uu.se/Bilder/2.jpg

Kes on taimed (I)?

- Vanasti samblikest ja vetikatest kuni õistaimedeni
- Sageli hõlmati isegi seened

- **Taim** on autotroofne **eukarüootne** organism, kes muudab valgusenergia keemiliseks energiaks fotosünteesi käigus, $CO_2 + H_2O \rightarrow$ (klorofüll kloroplastides) $\rightarrow$ süsivesikud.

Kes on taimed (II)?
Nn Elupuu

- Liitvetikad ehk glaukotsüstofüüdid
- Punavetikad
- Rohevetikad
- Ikkesvetikad
- Mändvetikad
- Maismaataimed

Kes on taimed (III)? Nt Judd ja Campbell

Rohelised taimed (*Chlorophyta, Viridiplantae*) on monofüleetiline rühm, mille autapomorfideks on klorofüll IIb, tärklis varuainena, kiirjas viburi struktuur, tülakoidid ja transposoonid.

- rohevetikad
- mändvetikad
- ikkesvetikad
- maismaataimed

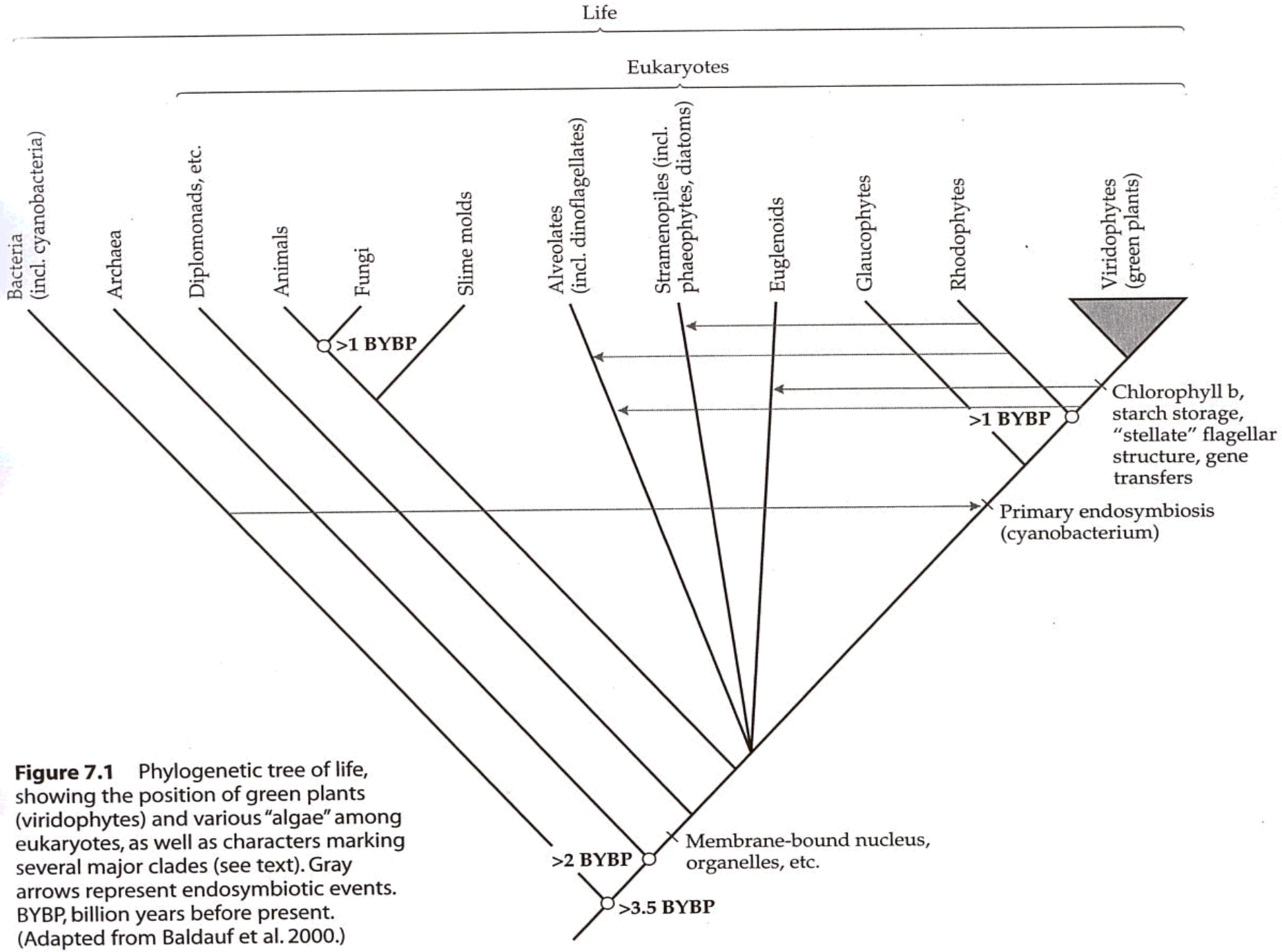


Figure 7.1 Phylogenetic tree of life, showing the position of green plants (viridophytes) and various "algae" among eukaryotes, as well as characters marking several major clades (see text). Gray arrows represent endosymbiotic events. BYBP, billion years before present. (Adapted from Baldauf et al. 2000.)

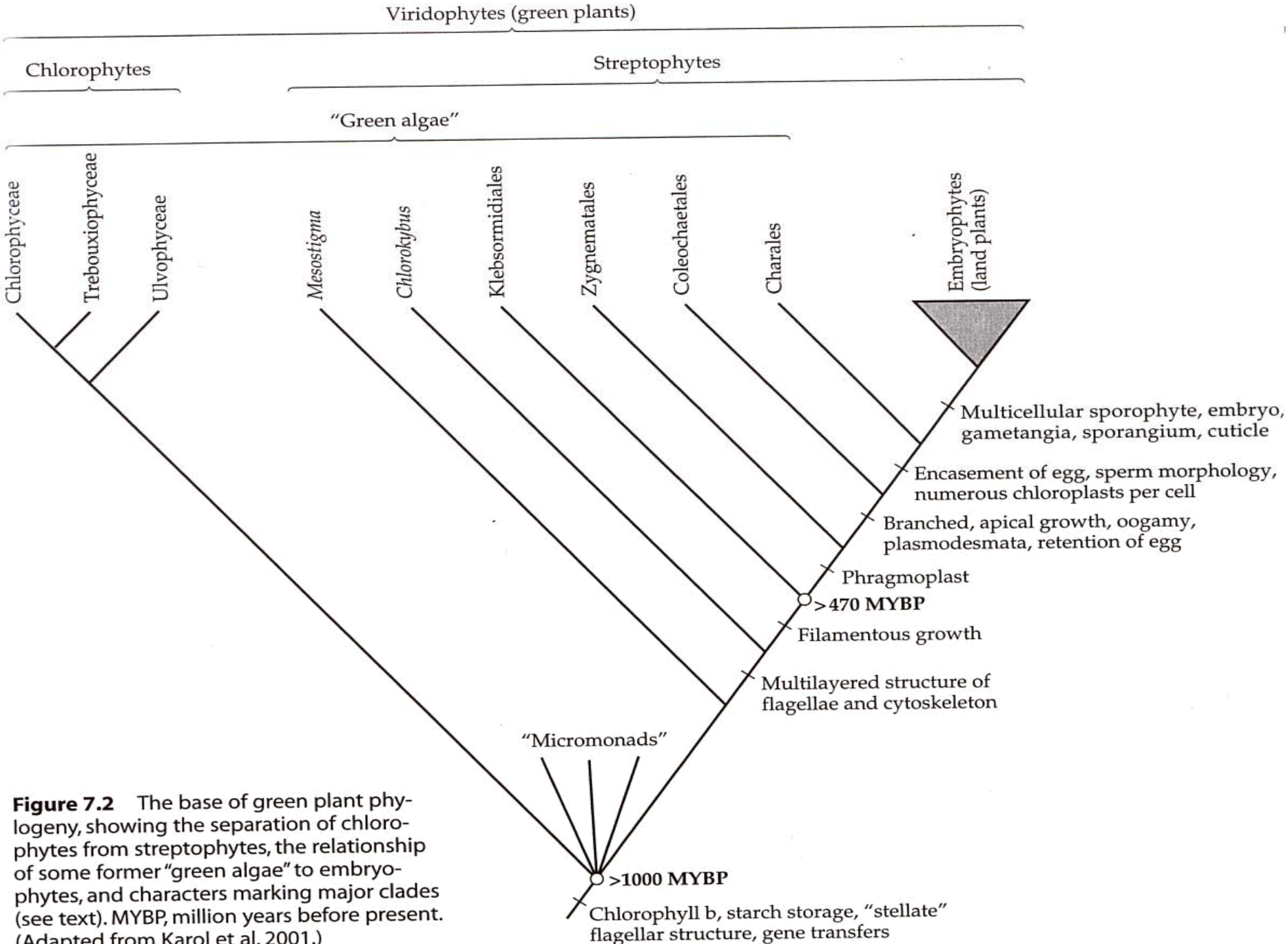


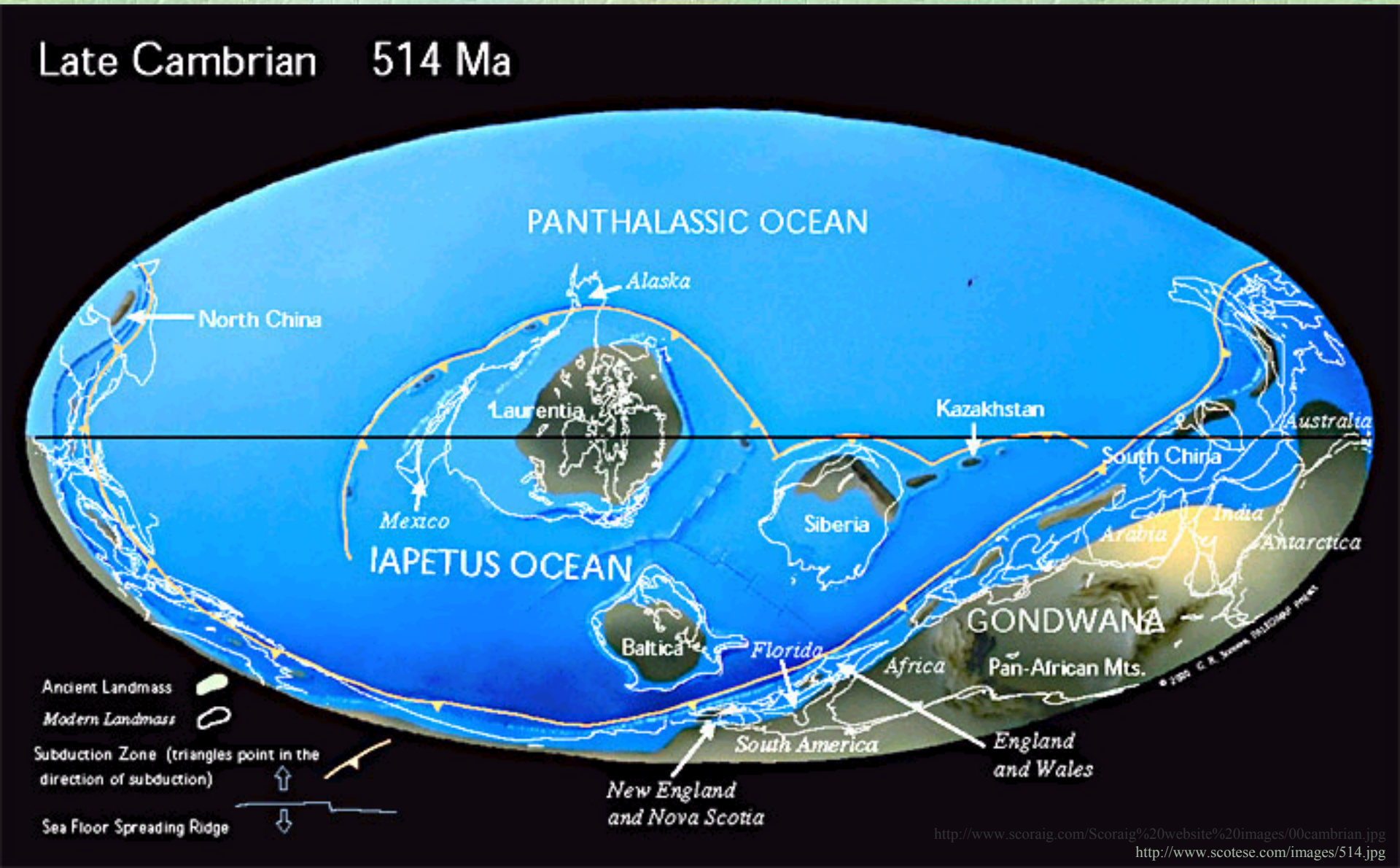
Figure 7.2 The base of green plant phylogeny, showing the separation of chlorophytes from streptophytes, the relationship of some former "green algae" to embryophytes, and characters marking major clades (see text). MYBP, million years before present. (Adapted from Karol et al. 2001.)

Kes on taimed (IV)? Nt Raven

- Ainult maismaataimed ehk embrüofüüdid
- Samblad+soontaimed

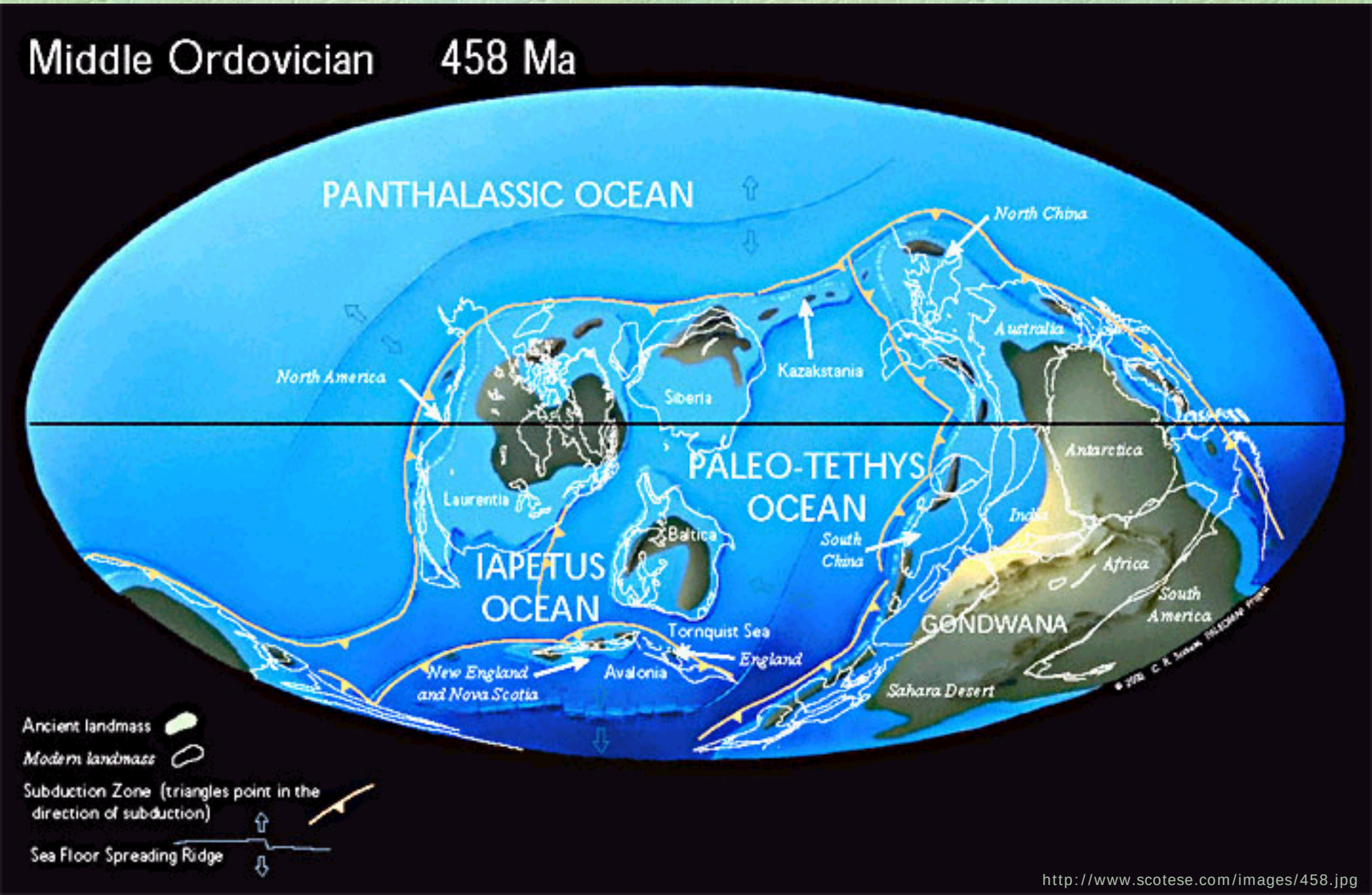
- **Lõplikku vastust ei ole**
- Selles kursuses räägime maismaataimedest ja eelkõige soontaimedest

Paleosoikum
Mandrid Kambriumis



http://www.scoraig.com/Scoraig%20website%20images/00cambrian.jpg
http://www.scotese.com/images/514.jpg

Mandrid Ordoviitsiumis



http://www.scotese.com/images/458.jpg

Tingimused Kambriumis ja Ordoviitsiumis

- 540 Mat algas planktonvetikate suur divergeerumine
- “Kambriumi plahvatus”
- 440 Mat jääaeg - avatud rannad
- muldade areng Ordoviitsiumi lõpuks
- kliima muutused

Rohevetikas *Cyclocrinites spasski* Eichwald, Anija, Ordoviitsium

Kes on maismaataimede eellased?

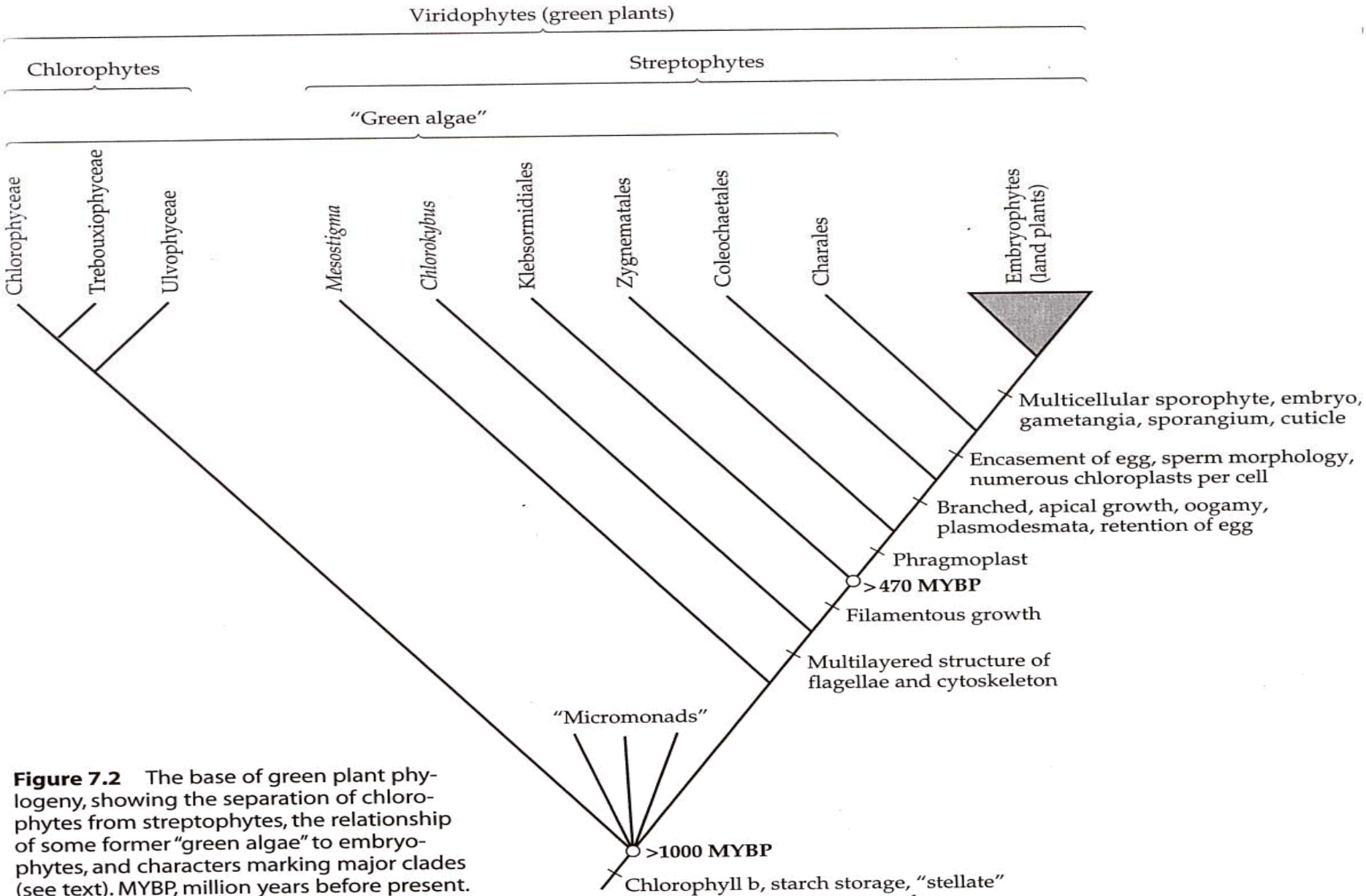
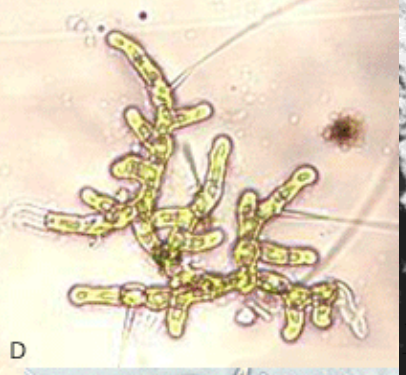
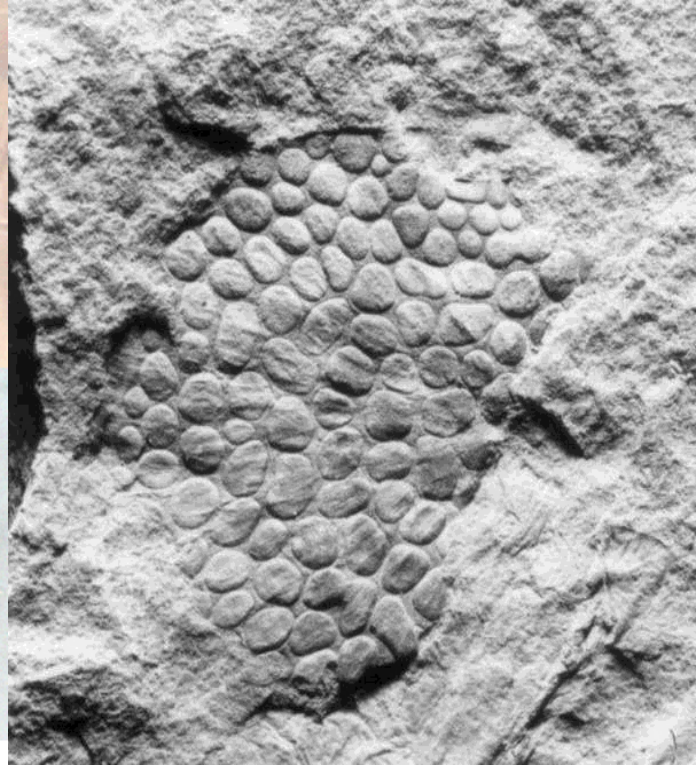
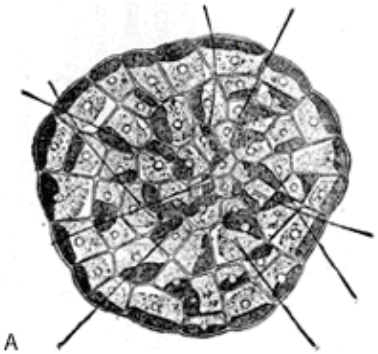


Figure 7.2 The base of green plant phylogeny, showing the separation of chlorophytes from streptophytes, the relationship of some former "green algae" to embryophytes, and characters marking major clades (see text). MYBP, million years before present. (Adapted from Karol et al. 2001.)

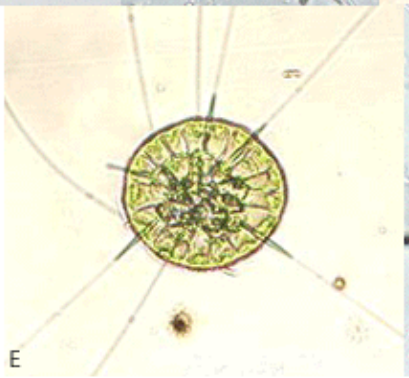
Coleochaete



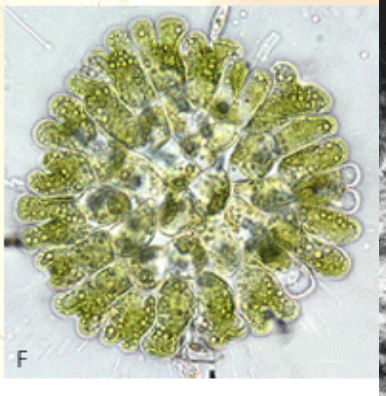




A



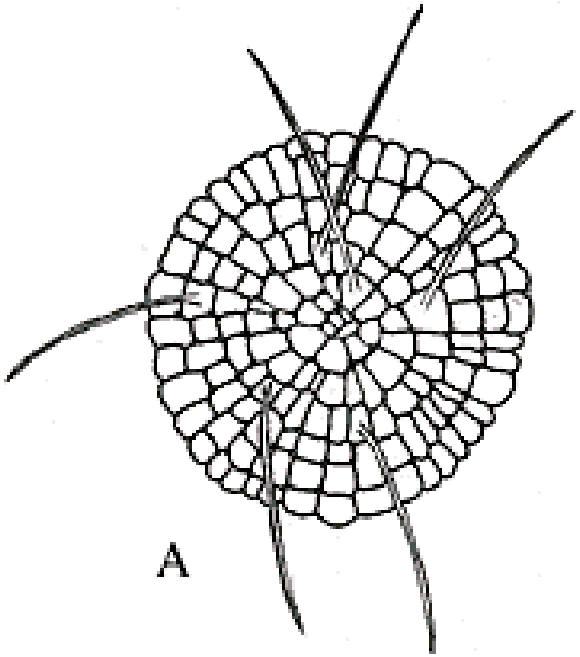
E



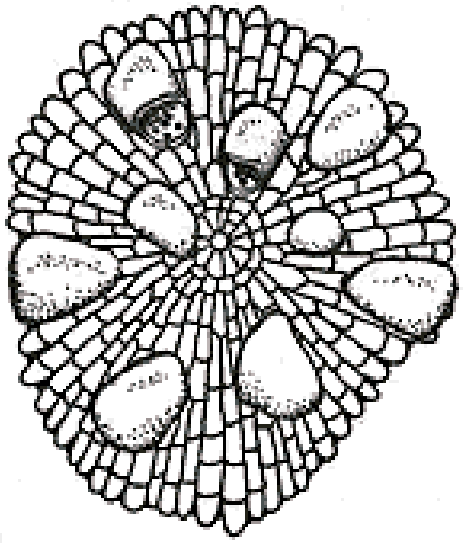
F

A after Smith (1950)

B, C, D, E, F © J. Kinross, see http://www.lifesciences.napier.ac.uk/JK/algalweb/alg



A

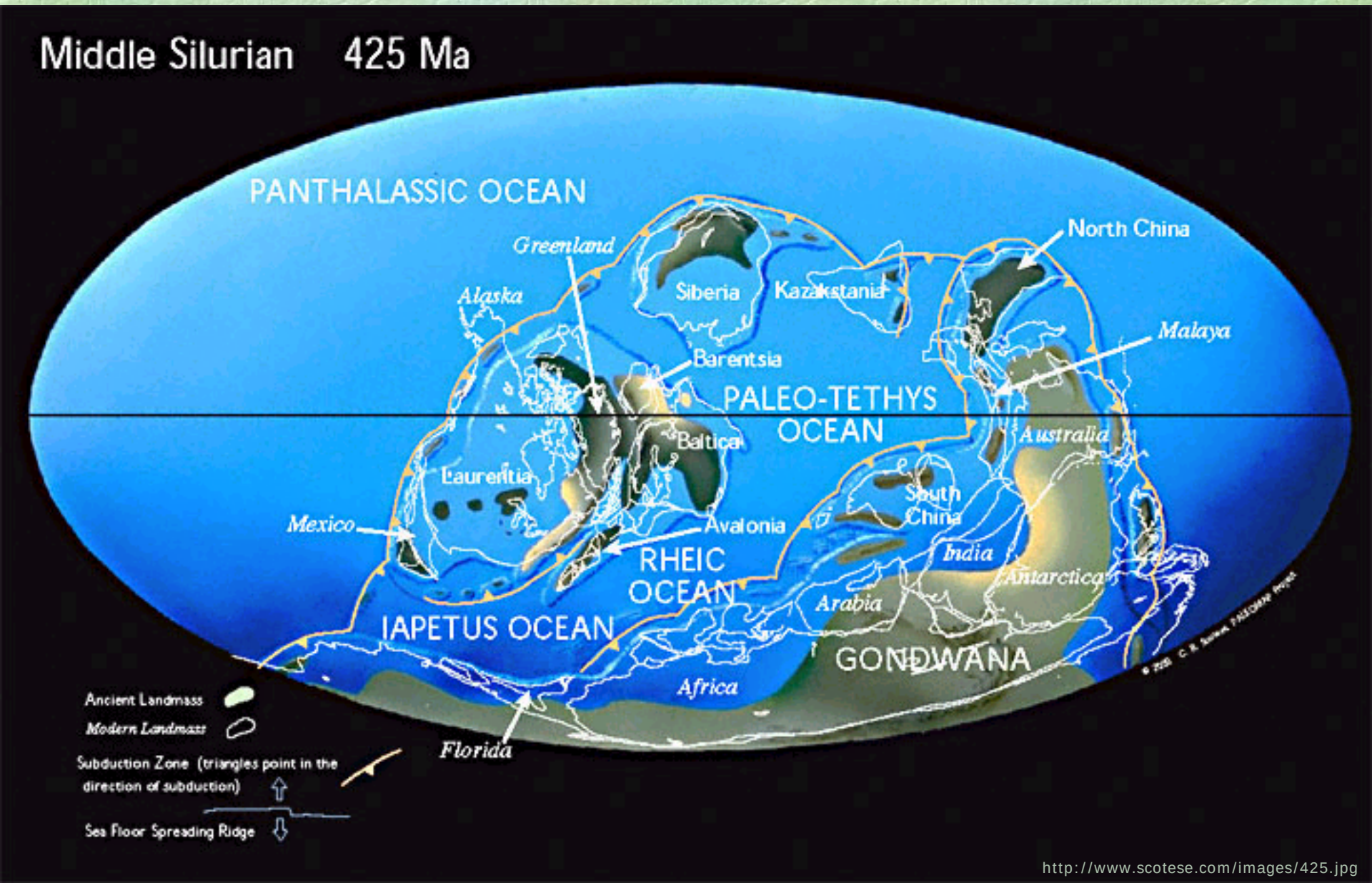


B

http://t2.gstatic.com/images?q=tbn:ANd9GcSBkDRCapVXLcbOkk-tkz3S_z3WL4tk0YhtlsxxAJbbNURxxn0ftw

http://algaekey.com/pictures/chara.PNG

Mandrid Siluris

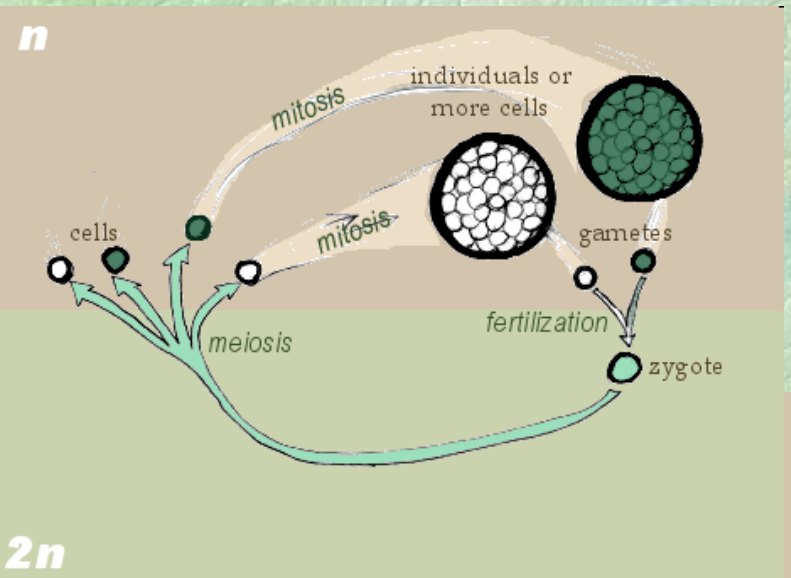


http://www.scotese.com/images/425.jpg

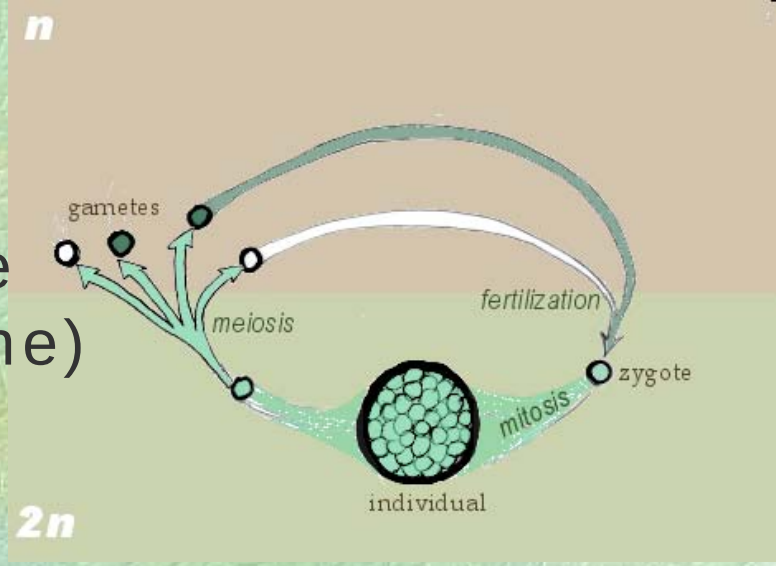
Faaside (generatsioonide) vahelduse teke

- Vahelelükke (antiteetiline) teooria
- Transformatsiooni (homoloogne) teooria

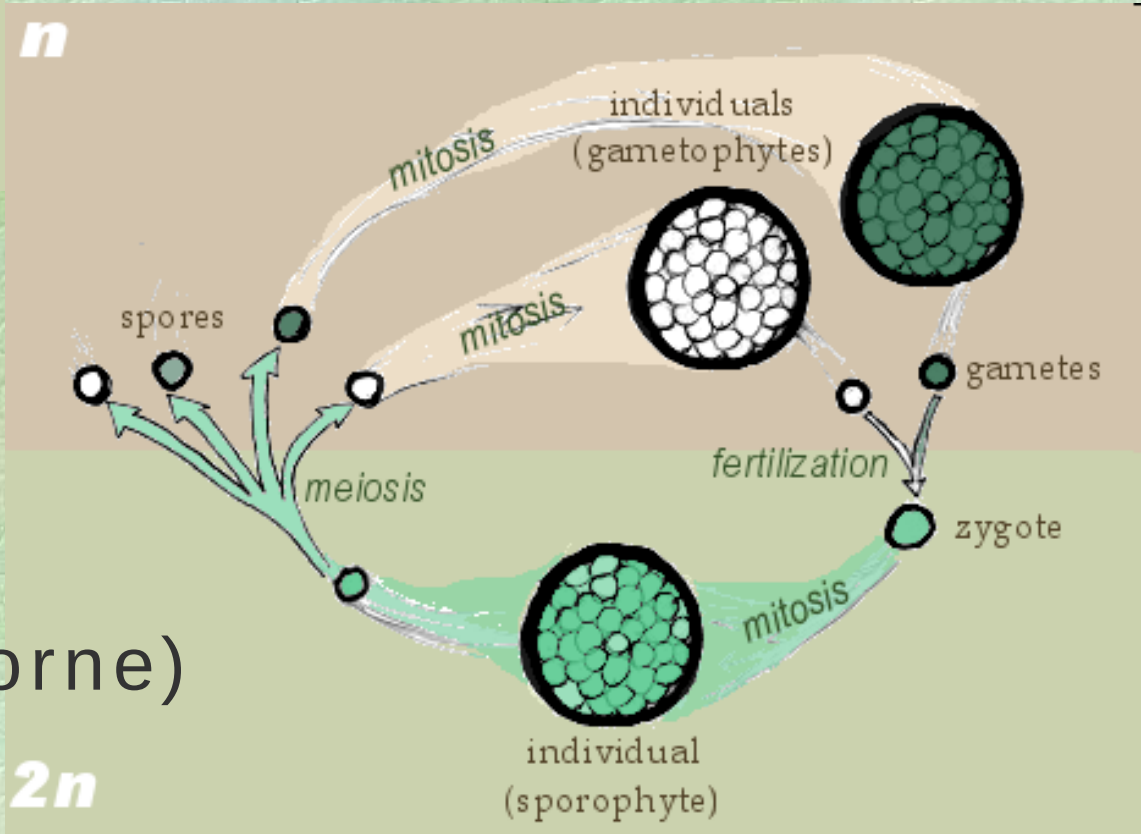
Elutsüklid



haplontne (sügootne)



diplontne (gameetne)



diplobiontne (spoorne)

http://en.wikipedia.org/wiki/Biological_life_cycle

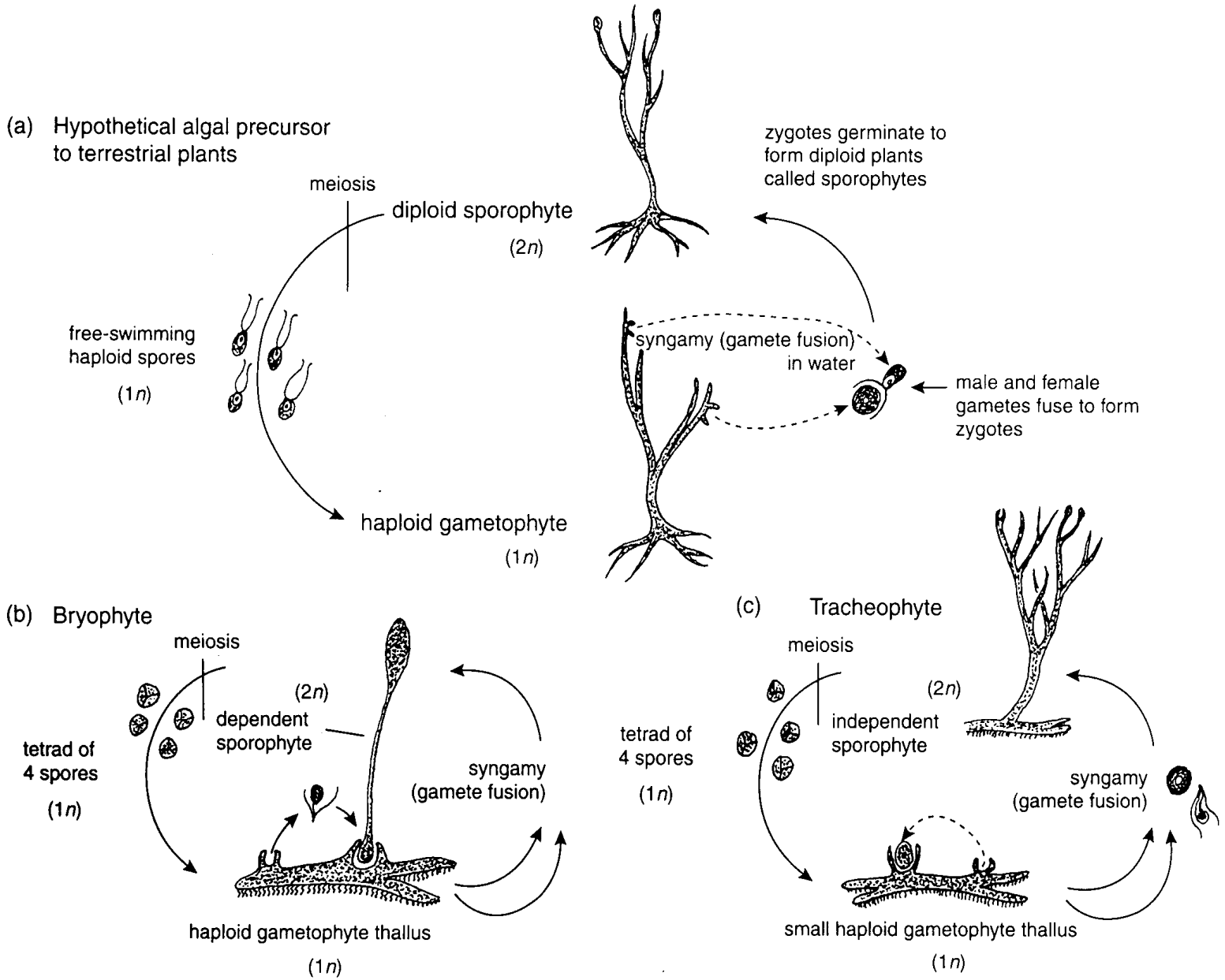
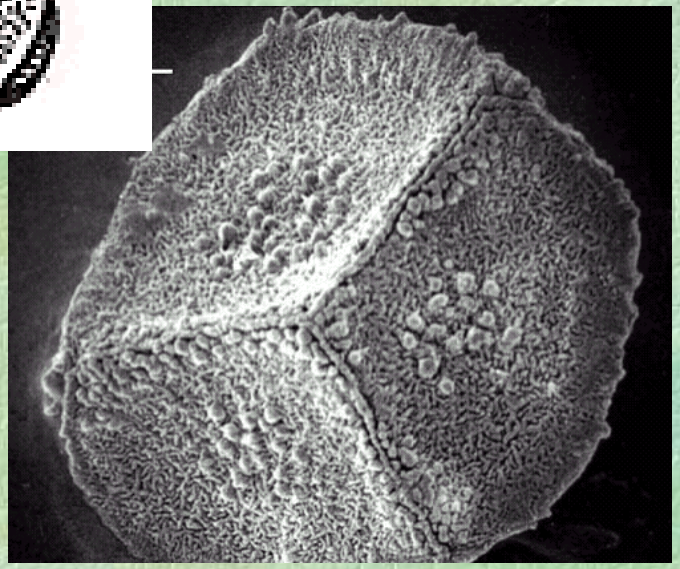


Figure 3.6 Diagram of simplified plant life cycle, showing alteration of generation phases. (a) Simplified diagram to indicate the alteration of two phases of generation in algal reproduction; (b) the cycle with an amplified gametophyte generation—most bryophytes follow this mode of reproduction; and (c) the cycle with an amplified sporophyte generation—all vascular plants follow this mode of reproduction (redrawn from Price, 1996).

Maismaataimede kohastumused

- **Paljunemisviisi veesõltuvuse vähenemine**
- trileetsed spoorid, tetraadidena 450 Mat
- sporopolleniin
- paljunemis-tsükkel - faaside vaheldus



http://www.ucmp.berkeley.edu/IB181/VPL/Elp/ElpD/ElpD2.gif

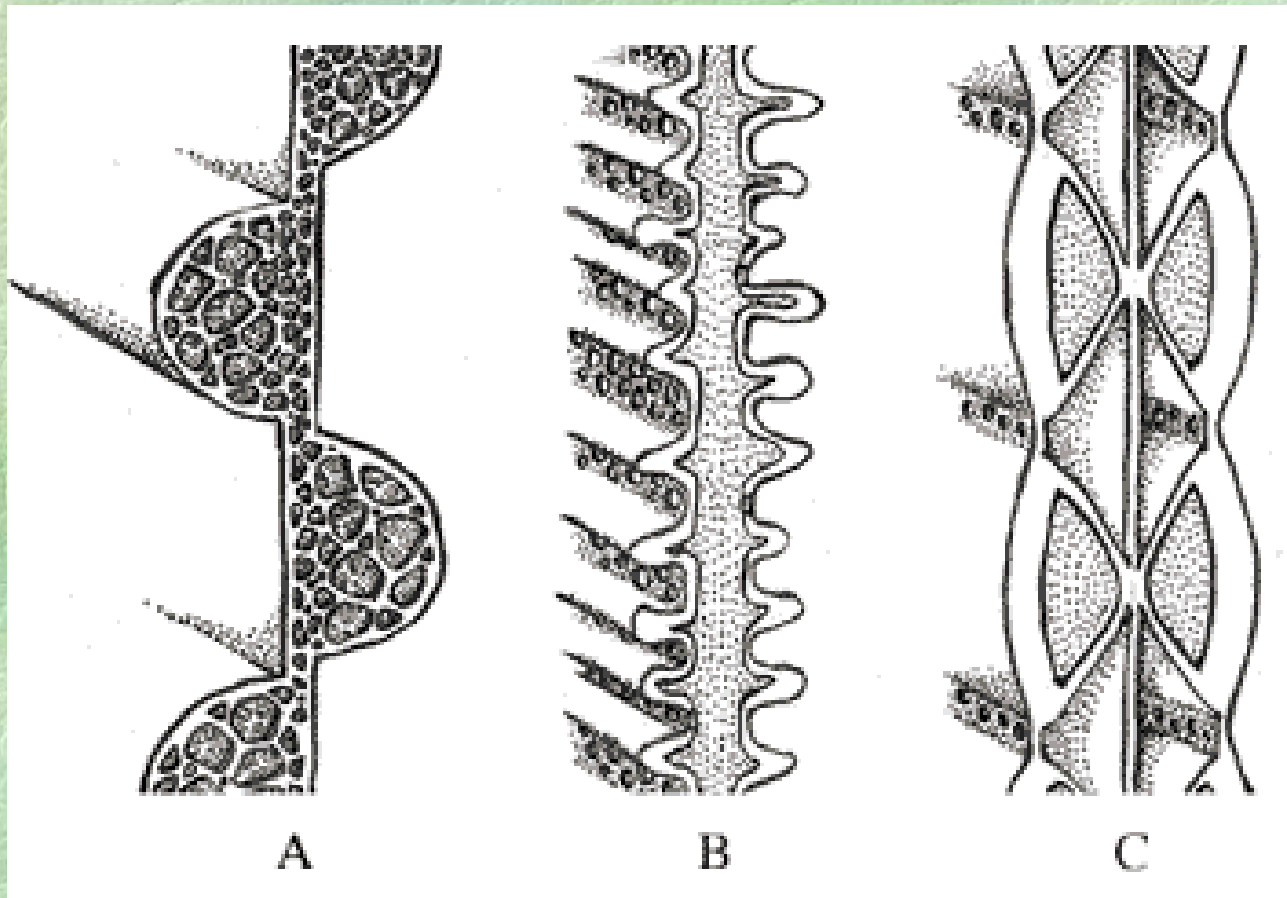
Maismaataimede kohastumused

- **Kaitse kuivamise eest**
- kutiikula
- õhulõhed

http://sciencerevolution.net/stoma.jpg

Maismaataimede kohastumused

- **Juhtkoe elemendid**
- 430 Mat
- trahheiidid, sooned
- ligniin
- G, S, P-tüüpi trahheiidid
- **Juured** 408 Mat



Maismaataimede kohastumused

- Mehhanilised ehk tugikoed

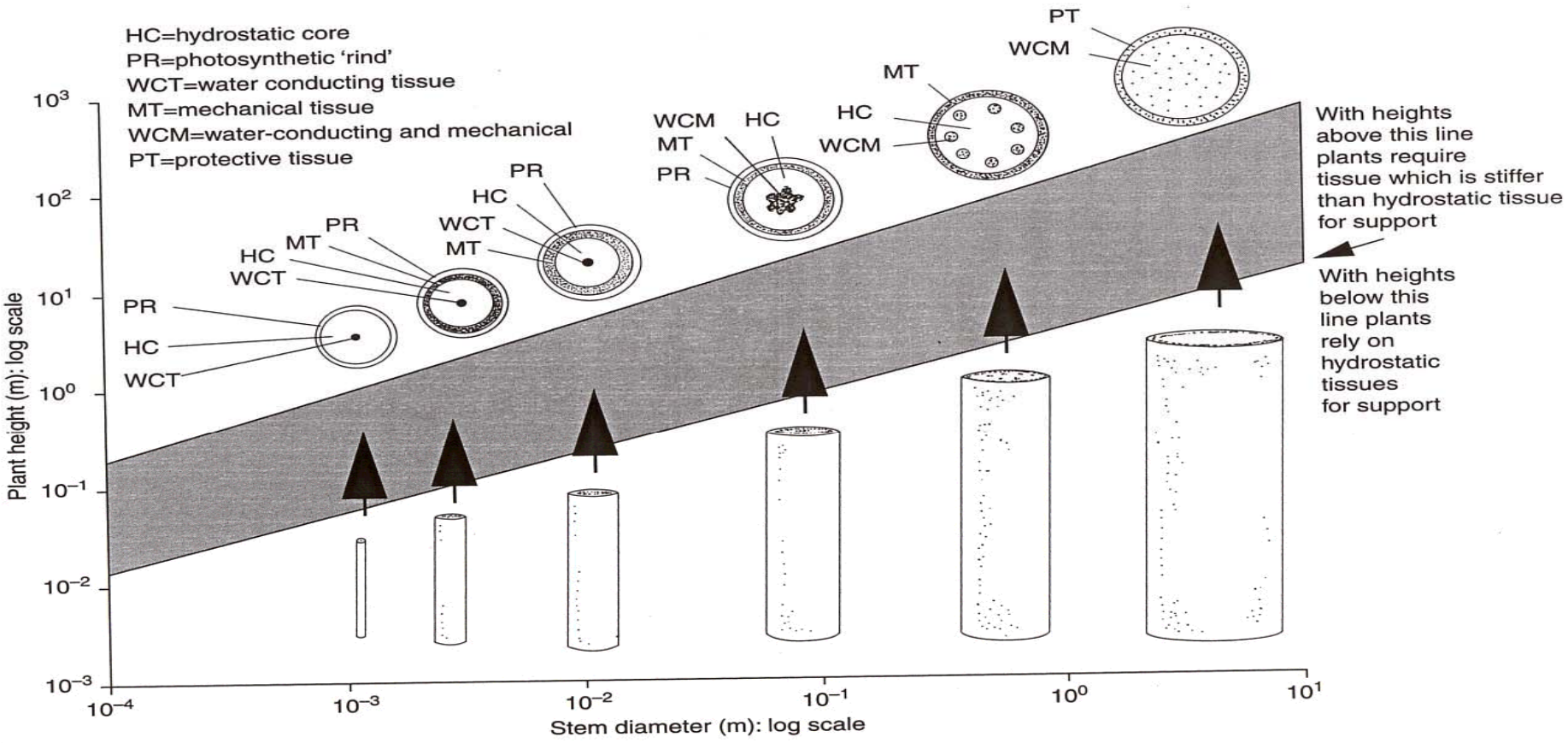
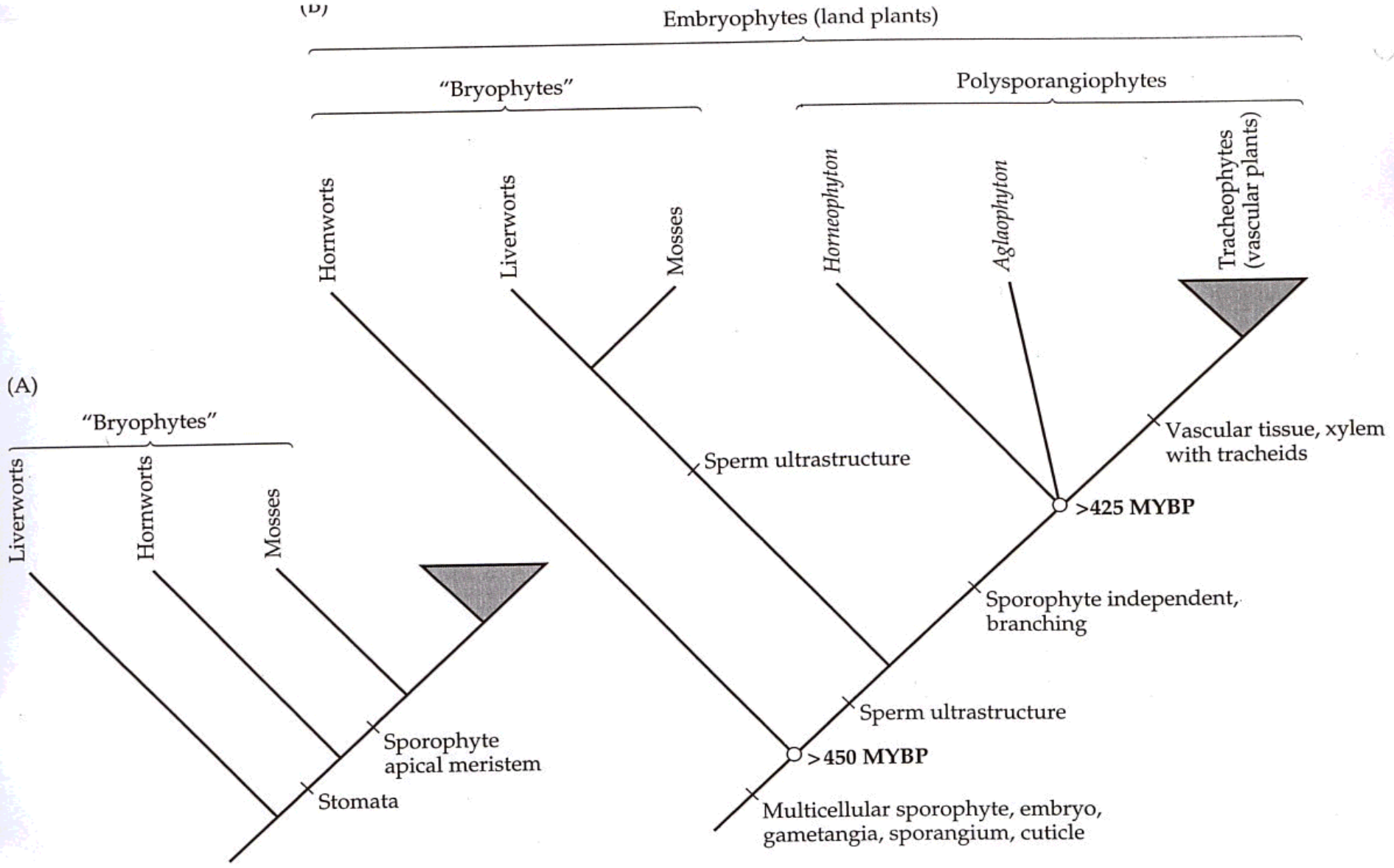


Figure 3.10 Relationship between stem diameter and stelar construction (after Niklas, 1997).

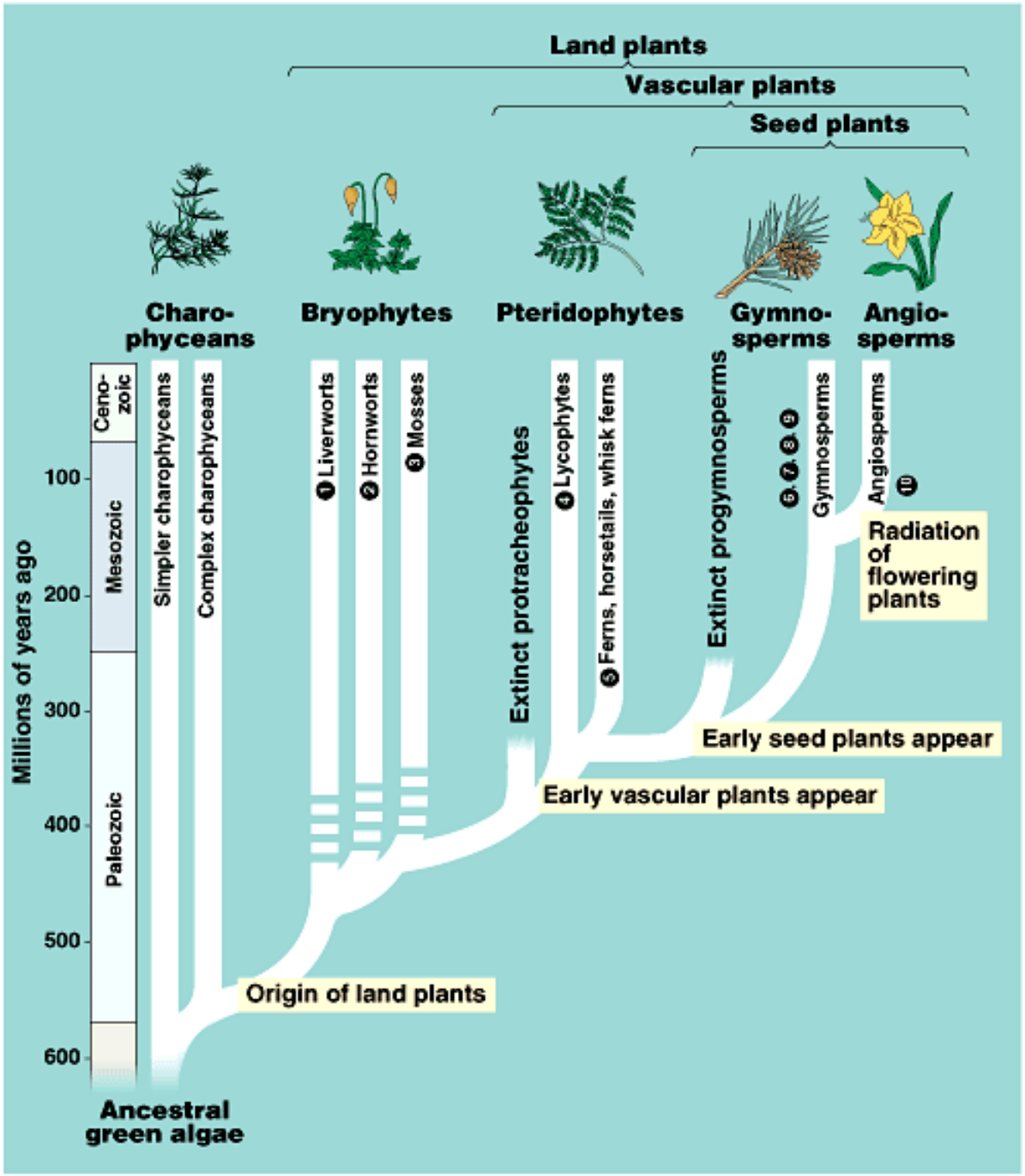
Viis evolutsioonifaasi maismaataimede arengus

- Schopf 1992, Kenrick-Crane 1997
  - **Krüptospoori-kutiikula faas** Ordoviitsium – Alam-Silur
  - **Sporofüüdi-trileetse isospoori faas** Alam-, Kesk-Silur
  - ***Cooksonia* – skulptureeritud sporomorfi faas** Kesk-, Ülem-Silur
  - **Õhulõhede – juhtkudede faas** Ülem-Silur
  - **Sporofüüdi arengufaas** alates Alam-Devonist

Maismaataimed ehk embrüofüüdid



Judd, Campbell 2002.

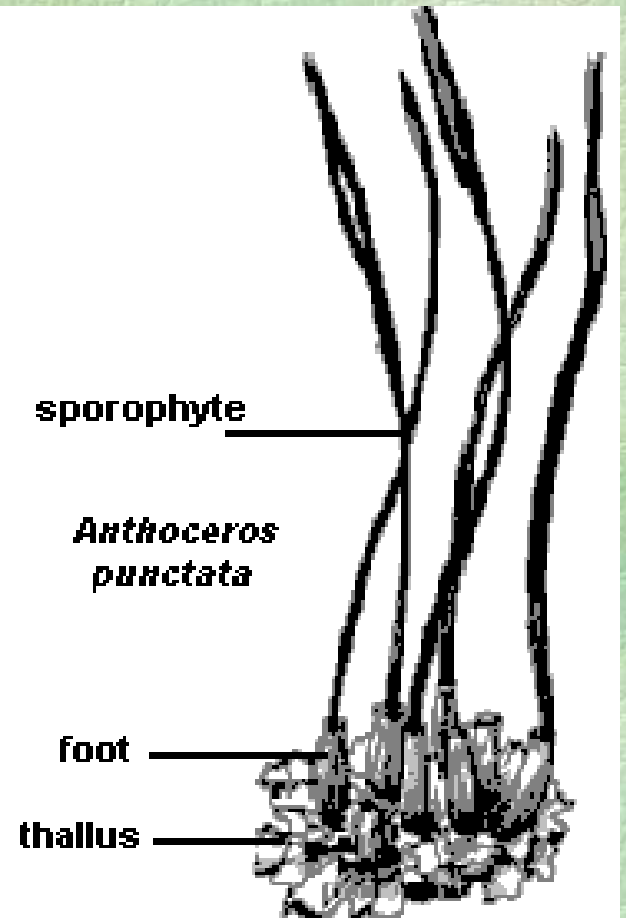


“Sammaltaimed”

- Parafüleetiline või monofüleetiline rühm?
- Elutsükkel
- Gametofüüt domineeriv, sporofüüt sõltuv
- Juhtkoed puuduvad või primitiivsed (hüdroidid ja leptoidid), trahheiidid ja sõeltorud puuduvad
- Suhteliselt väikesed

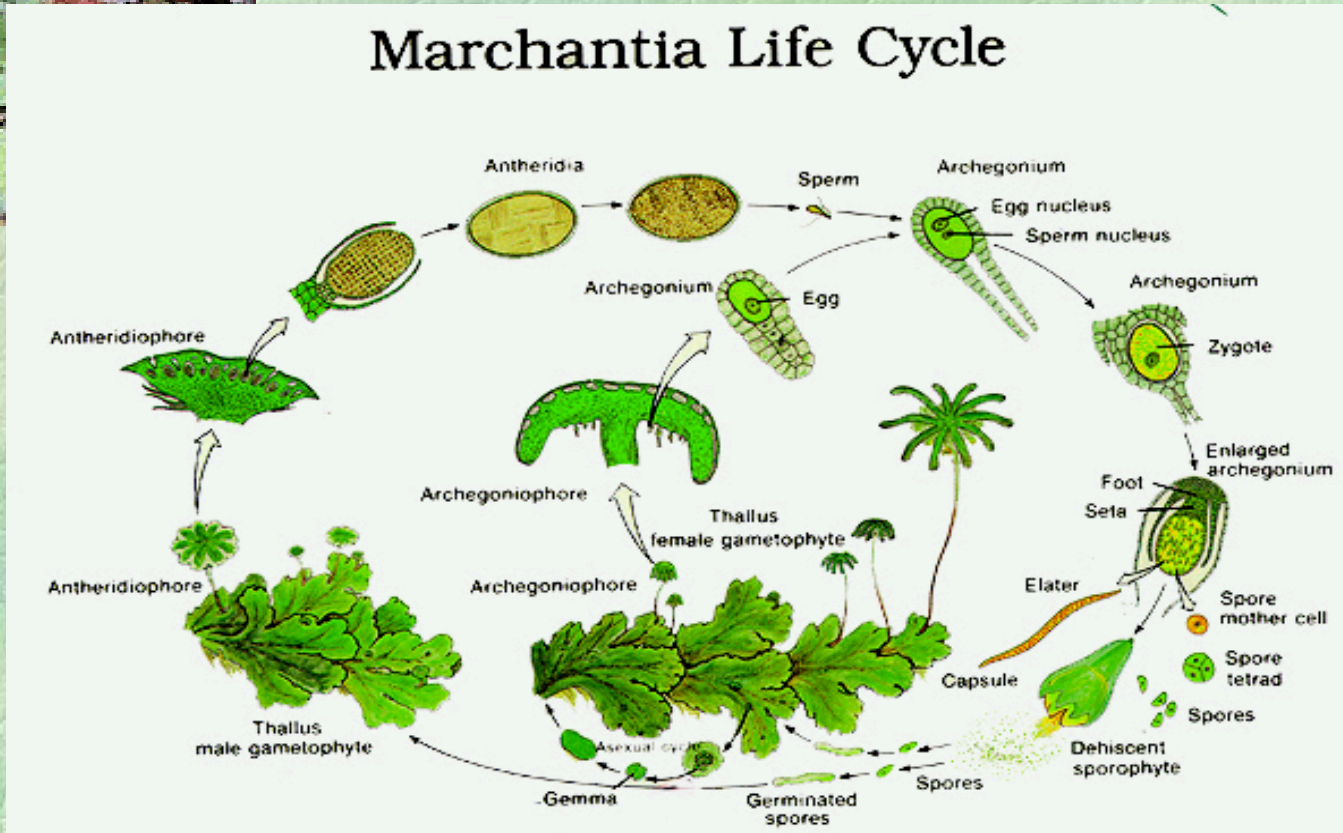
Anthoceratophyta - kõdersamblad

- Tallus
- Rakus üks suur kloroplast
- Sporofüüt fotosünteesiv, piiramatult k
- Soontaimede sõsarrühm?



Hepaticophyta - maksasamblad

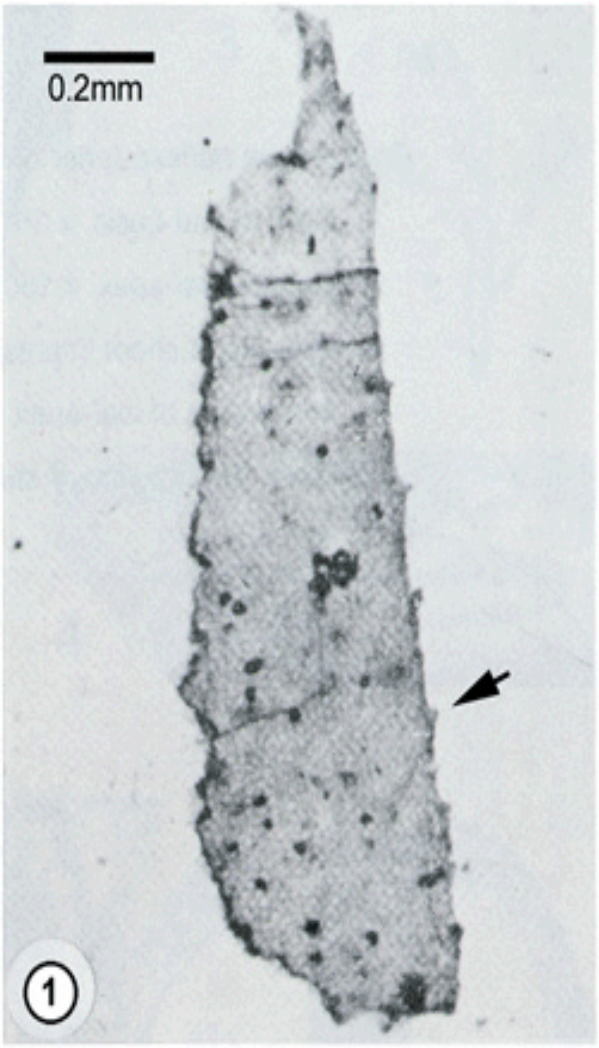
- Tallus (lihtne või keerukam)
- või vars ja lehed



http://t2.gstatic.com/images?q=tbn:ANd9GcSbNOdDMHCpNd4rLudoLJ8ieOxCzAdFc9dT41smf1ngou8btGDeLQ

http://www.bio.miami.edu/dana/pix/marchantia_lifecycle.jpg

- Eosed Ordoviitsiumis
- Lehed Devonis

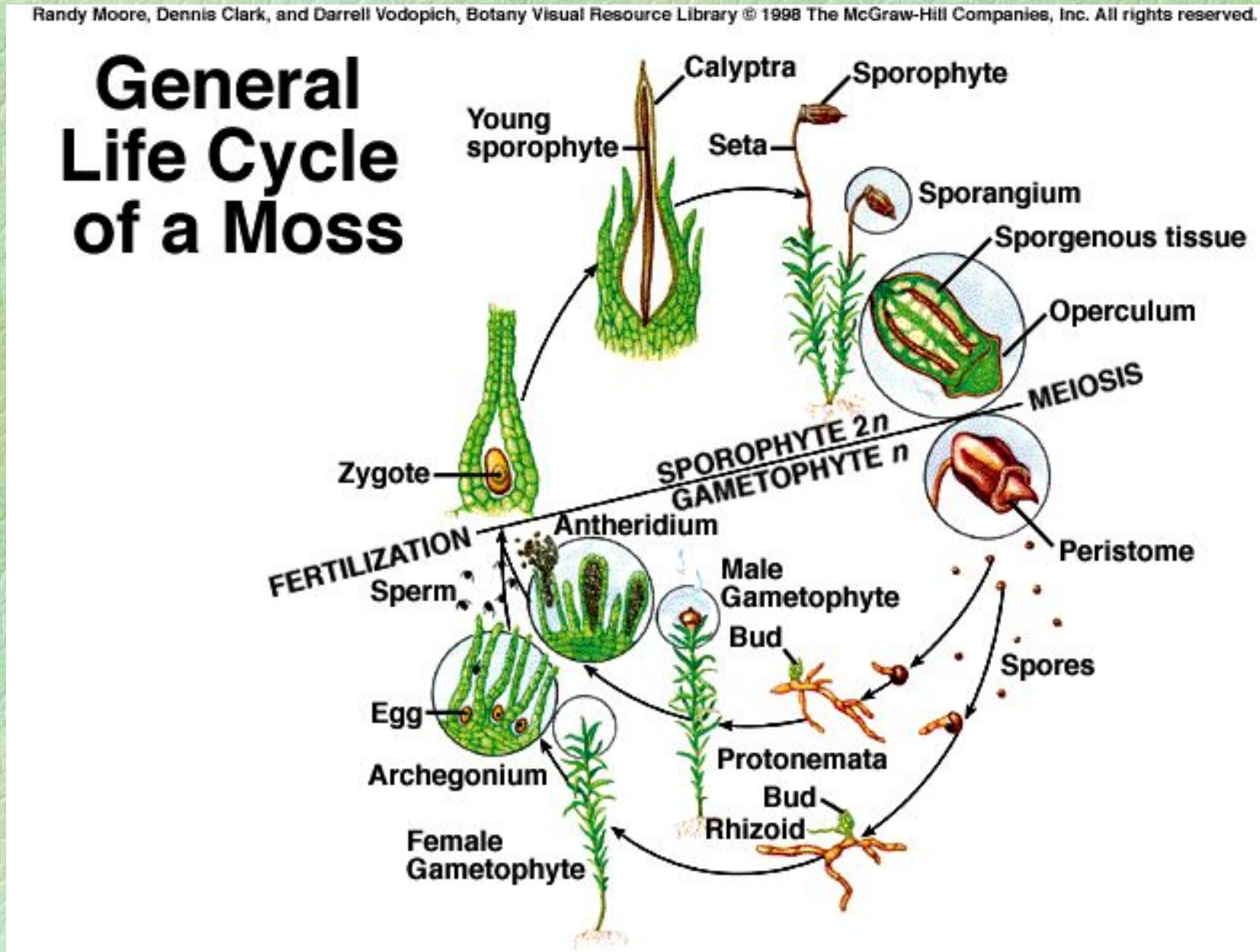


Pallavicinites devonicus

Pallavicinia xiphoides

http://t2.gstatic.com/images?q=tbn:ANd9GcS0Rhob6Pn-NjsKWXAJKuh7LF0EYMg16bzNdcbB8l5OXaP1gWUG

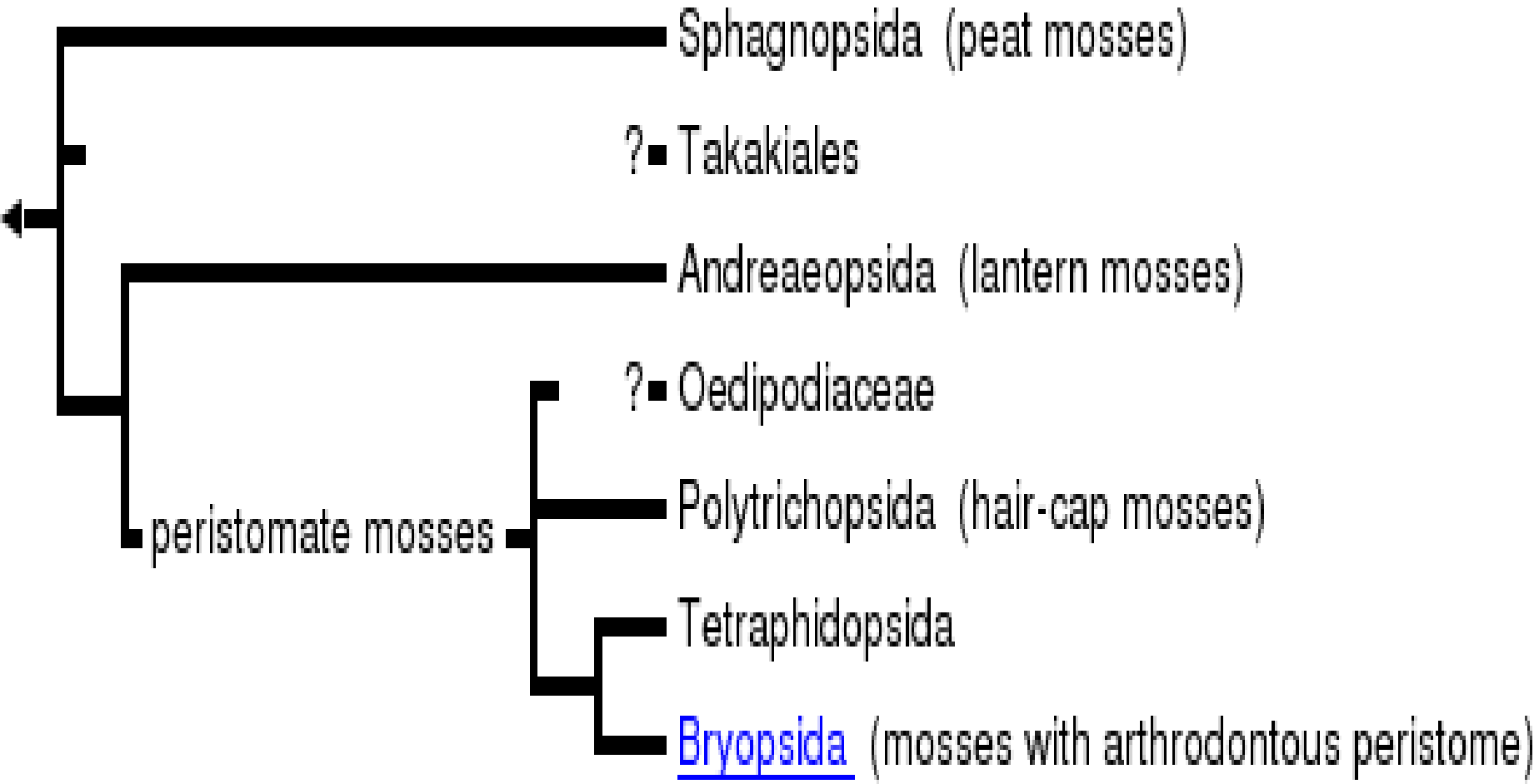
Bryophyta - lehtsamblad



Bryophyta - lehtsamblad

- Varred, lehed, risoidid
- Akrokarpsed (gametangiumid varre tipus, parafüleetilised) ja pleurokarpsed (gametangiumid lehtede vahel, monofüleetilised)
- Eoskupra peristoomi tüüp oluline

Bryophyta - lehtsamblad

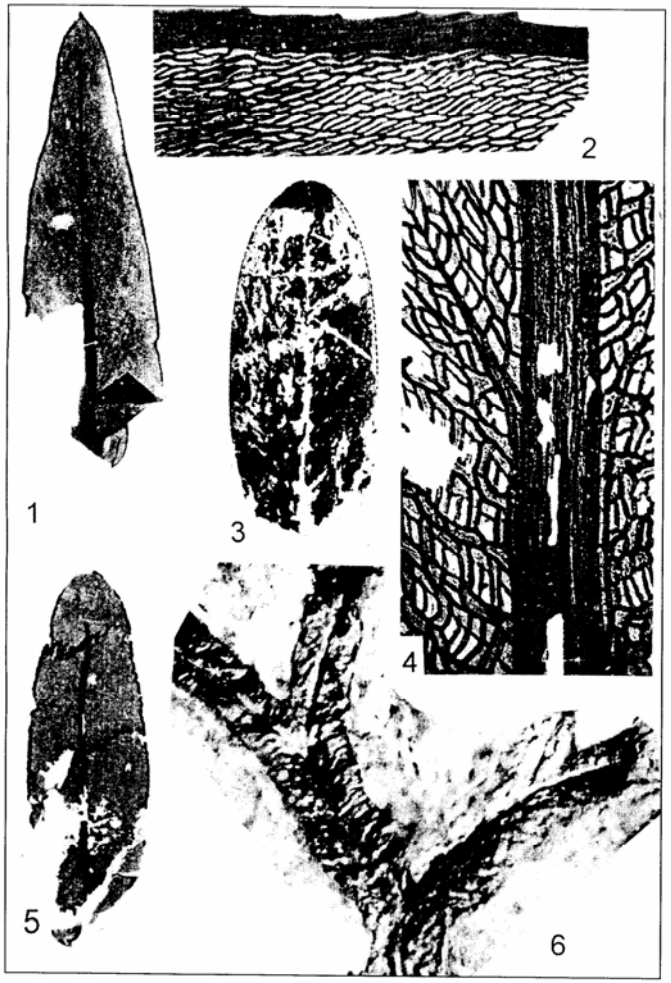


Judd, Campbell 2002

Lehtsammalde fossiilid

- Halb säilivus, alates Karbonist
- *Protosphagnum*
- *Muscites plumatus, tortifolius*

http://www.sammlerpage.de/Bucher/Bu...stein/Atlas_der_Pflanzen/at.mos...



http://www.amjbot.org/content/97/9/1511/F4.small.gif

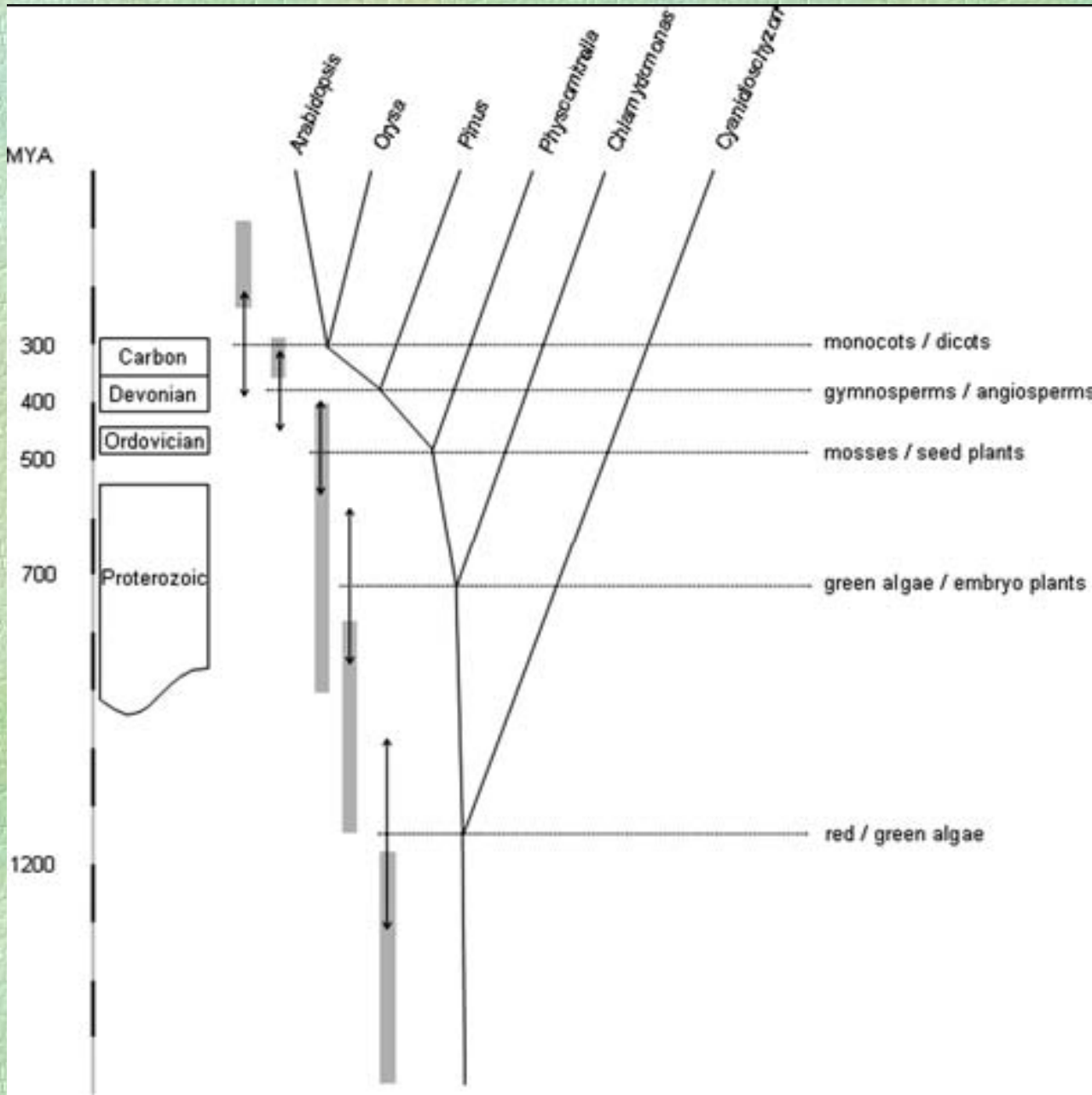
Taimeriigi evolutsioon maismaal	Loomariigi evolutsioon maismaal
410-440 miljonit aastat tagasi **ÜRGRAIKAD** • Esinevad varred, risoomid • Puudusid tõelised lehed ja juured	**400 miljonit aastat tagasi** **LÜLIJALGSED**
280-360 miljonit aastat tagasi **SÕNAJALGTAIMED** • Paljunevad eostega • Tõelised lehed • Mulla teke taimejäänuste lagunemisest ja kivimite murenemisest	**395-345 miljonit aastat tagasi** **KAHEPAIKSED** • Paljunemine vees • Elavad maismaal
300-350 miljonit aastat tagasi **PALJASSEEMNE TAIMED** • Paljunemine seemnetega	**280-300 miljonit aastat tagasi** **ROOMAJAD** • Kehasisene viljastumine
100-130 miljonit aastat tagasi **KATTESEEMNETAIMED** • Õite ja viljade esinemine	**200 mln. a. tagasi** **IMETAJAD** • Püsisoojasus • Areng emaüsas **150 mln. a. tagasi** **LINNUD** • Lennuvõime • Püsisoojasus **2 miljonit aastat tagasi** **INIMENE**

Soontaimede tekkimine

Peamised süstemaatika ühikud taimedel

- Riik (kingdom)
- **Hõimkond** (phylum, division) – **phyta**
- Klass (class) **- opsida**
- Alamklass (subclass) – **idae**
- Selts (order) – **ales**
- **Sugukond** (family) **- aceae**
- Perekond (genus)
- Liik (species)

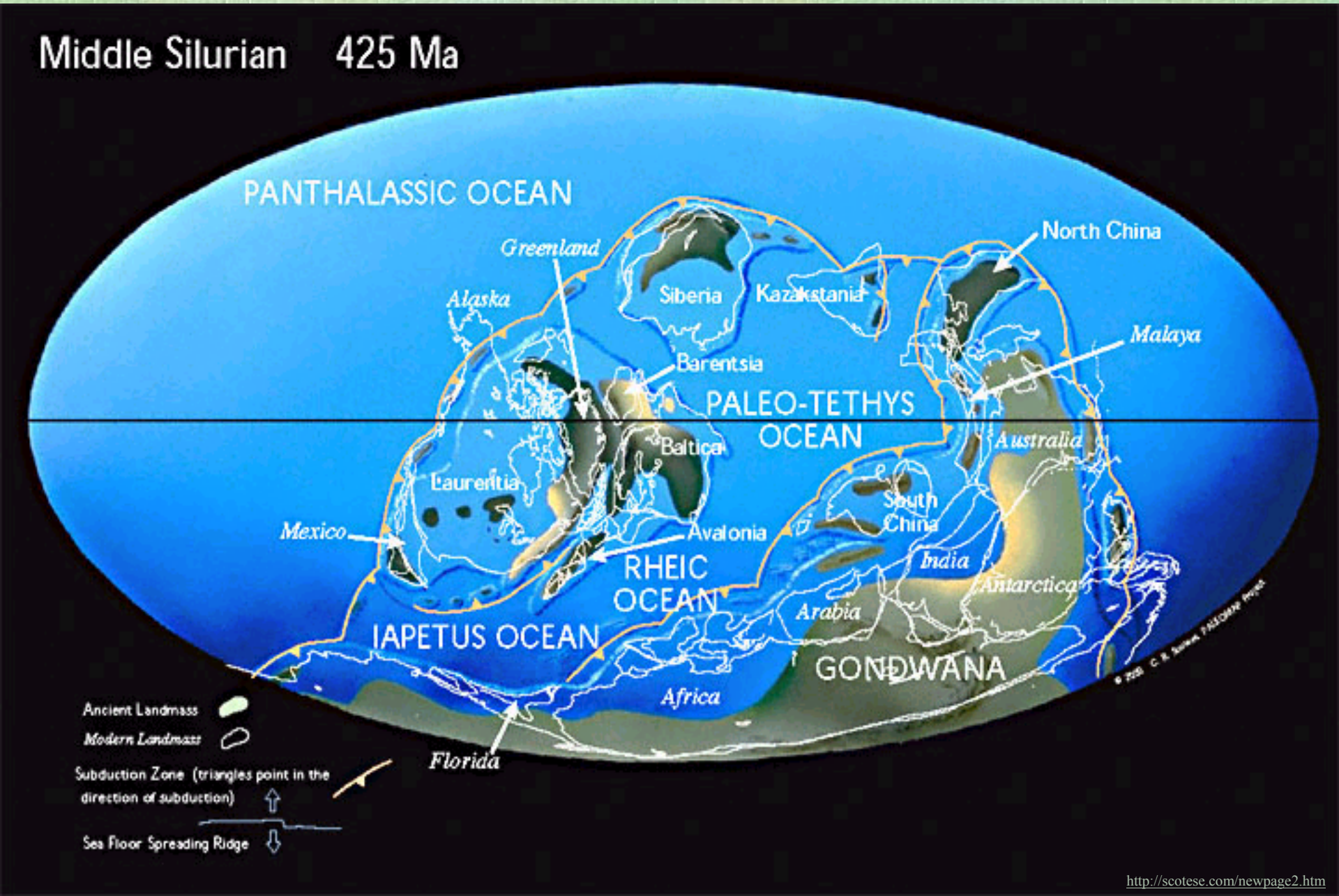
Divergentsiajad molekulaarse kella järgi (Zimmer et al. 2007)



Riik Chlorophyta
Alamriik Embryophyta

- Ülemhmk helviksammaltaimed *Marchantiomorpha*
- Kõdersammaltaimed *Anthoceromorpha*
- Lehtsammaltaimed *Bryomorpha*
- Ülemhmk *Polysporangiomorpha*

Mandrid Siluris



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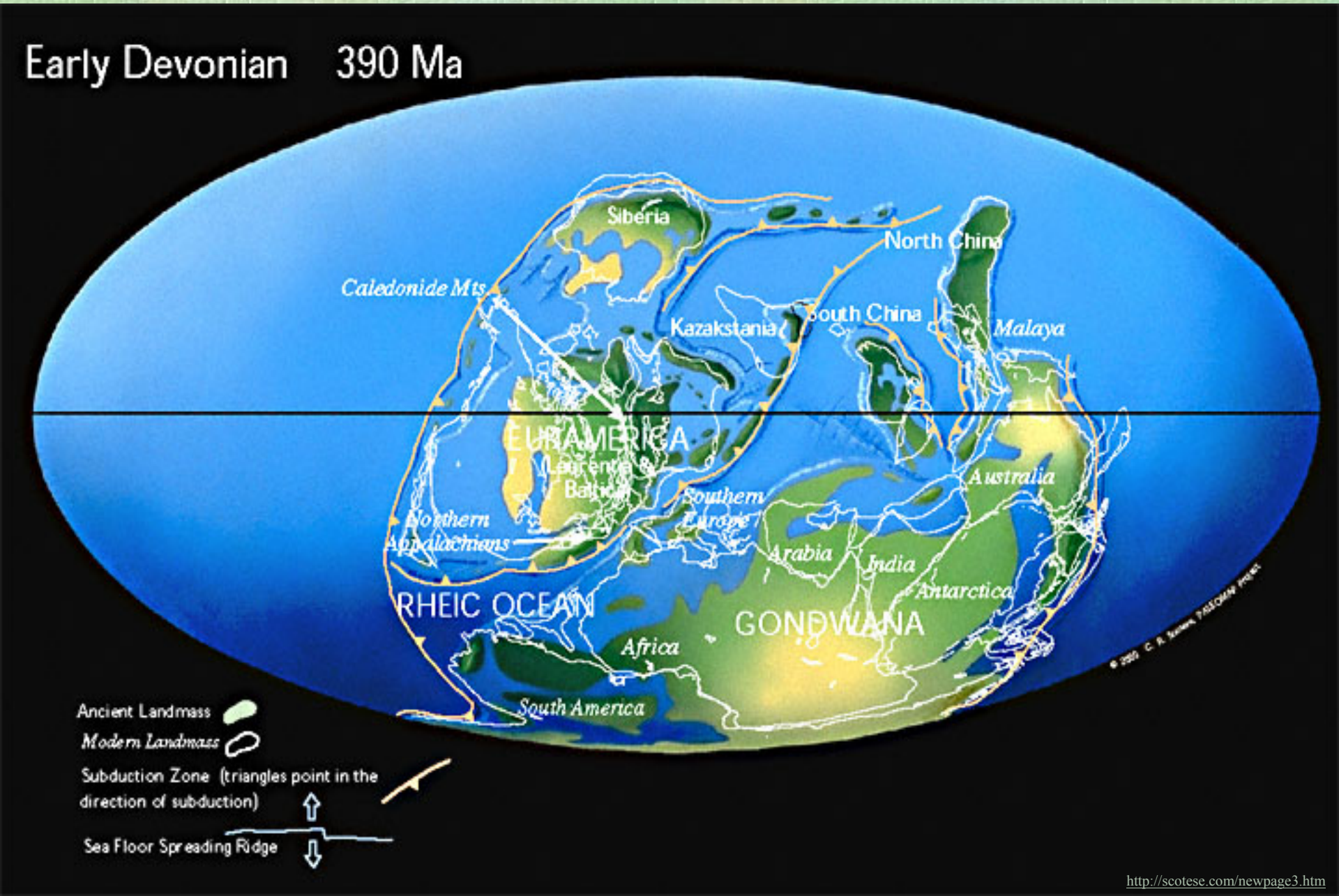
Mandrid Devonis



http://scotese.com/newpage3.htm

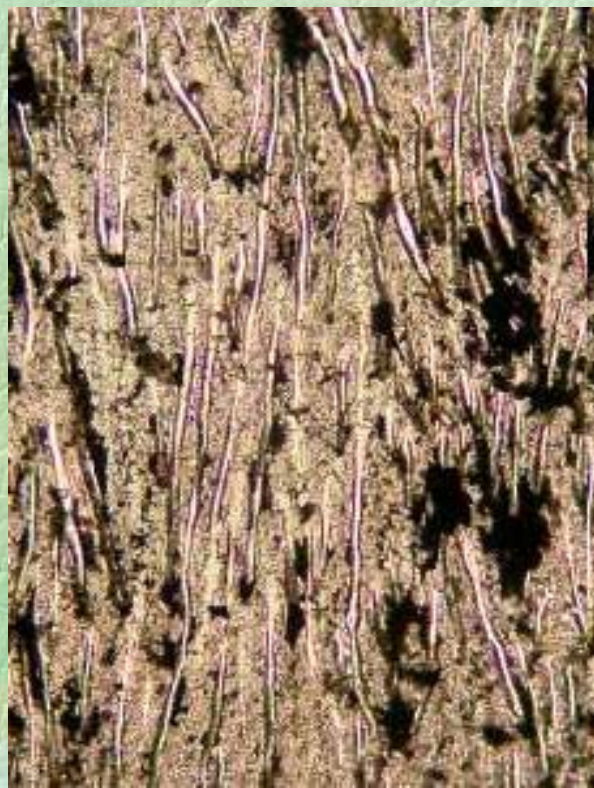

http://steurh.home.xs4all.nl/engprot/eprototx.html

Enigmaatilised organismid

Vetikas, seen, samblik või soontaim?

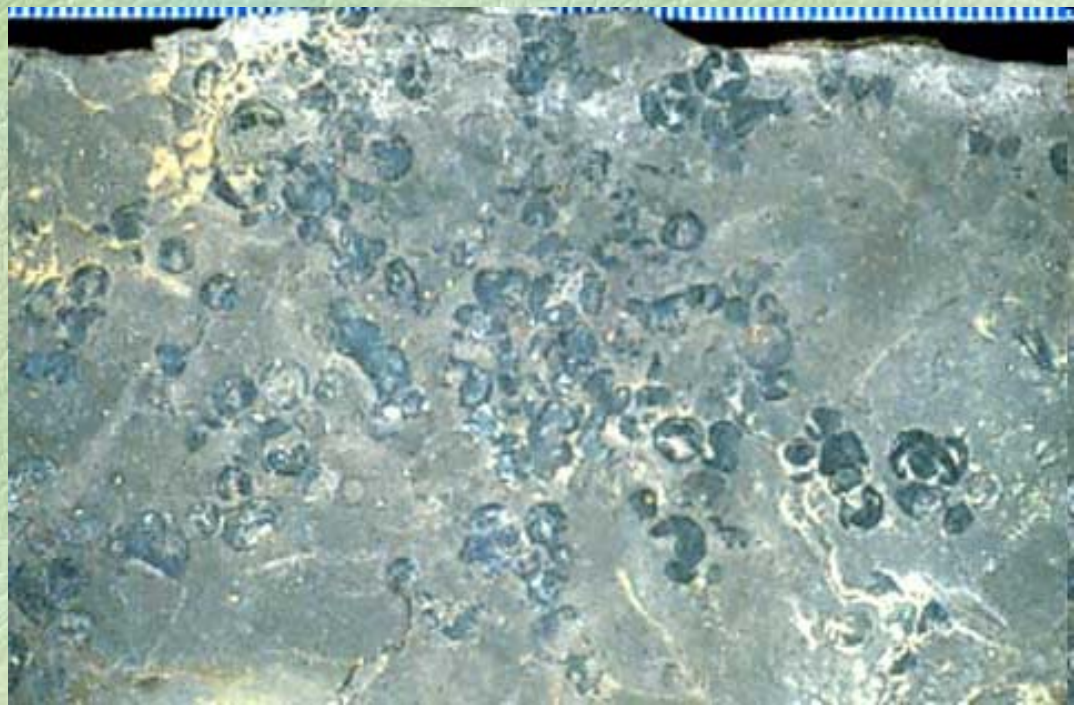
Prototaxites

Kuni 8m x 1.25m



Enigmaatilised organismid

- *Protosalvinia*
- **Vetikas, maksasammal või koguni sõnajalgtaim?**

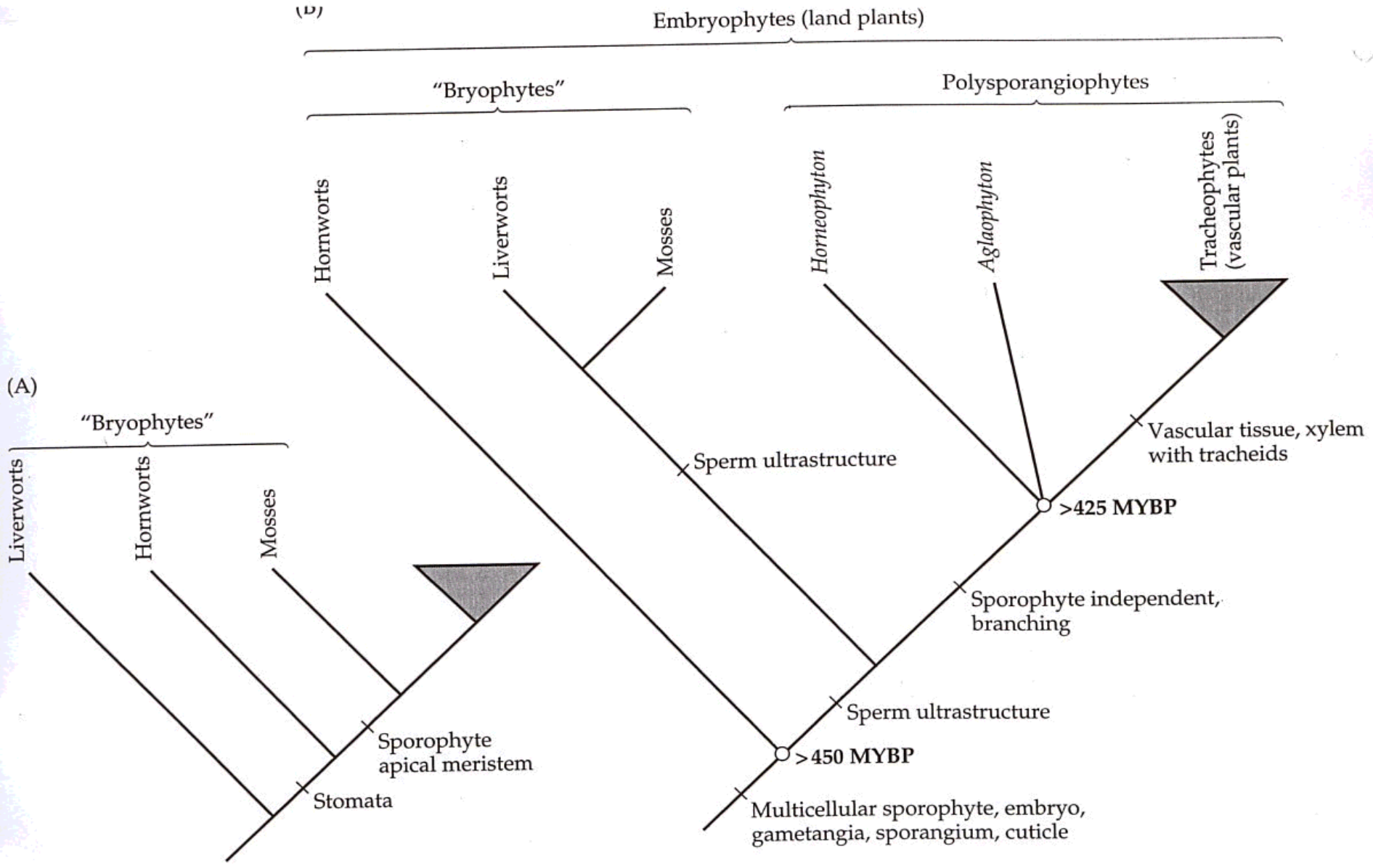


http://en.wikipedia.org/wiki/Protosalvinia

Aldanophyton atiquissimum

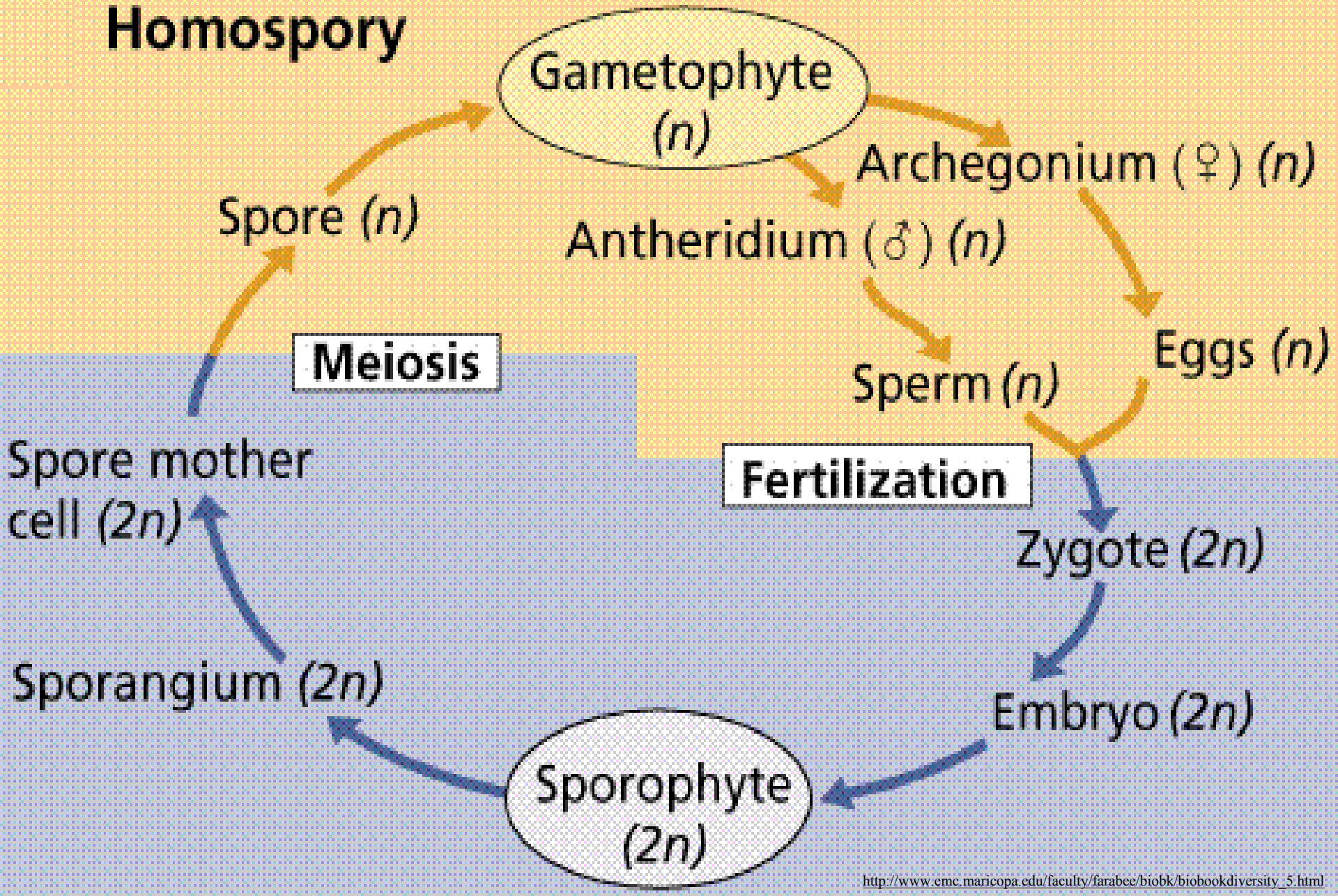
- Varaseim soontaim Kambriumist?
- Venemaa, Ida-Siber
- Kollataoline
- Kahtlane, kas õigesti dateeritud

Polysporangiomorpha



Judd, Campbell 2002

Homospoorne elutsükkel



http://www.emc.maricopa.edu/faculty/farabee/biobk/biobookdiversity_5.html

Varaste taksonite suhted (morfoloogia)

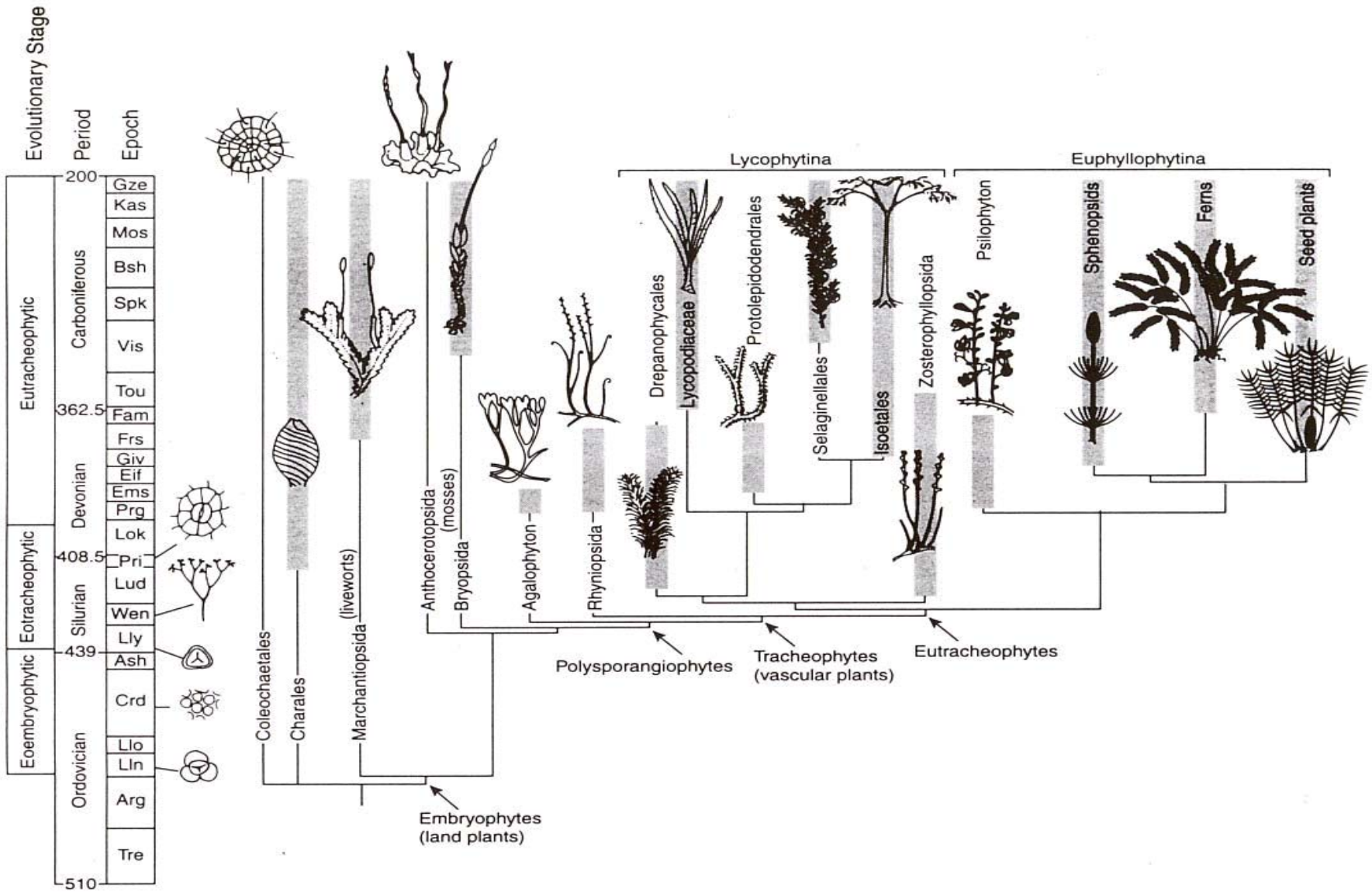
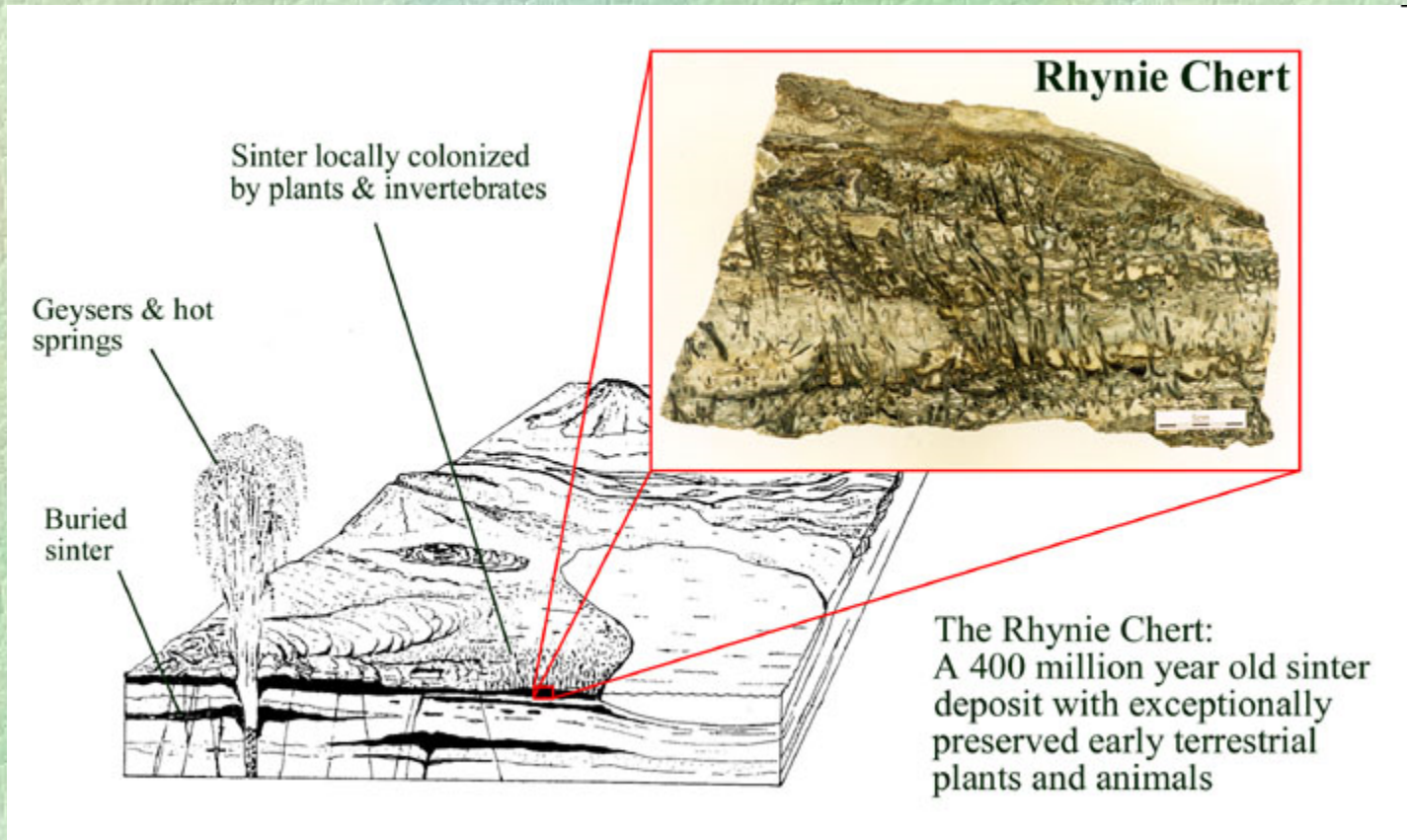


Figure 4.25 Phylogenetic relationship between extinct and extant early plants (redrawn from Kenrick and Crane, 1997b).

- Ülemhmk *Polysporangiomorpha*
  - Klass *Horneophytopsida*
- Hmk Soontaimed *Tracheophyta*
  - Klass rüüniad – *Rhyniopsida* (osa ürgraigastest)
- Alamhmk raigastaimed *Lycophytina*
  - Klass *Zosterophyllopsida*
  - Klass ürgraikad *Psilophytopsida = Trimerophytopsida*
  - Klass pärisraikad *Lycopsida*
- Alamhmk pärislehttaimed *Euphyllophytina*

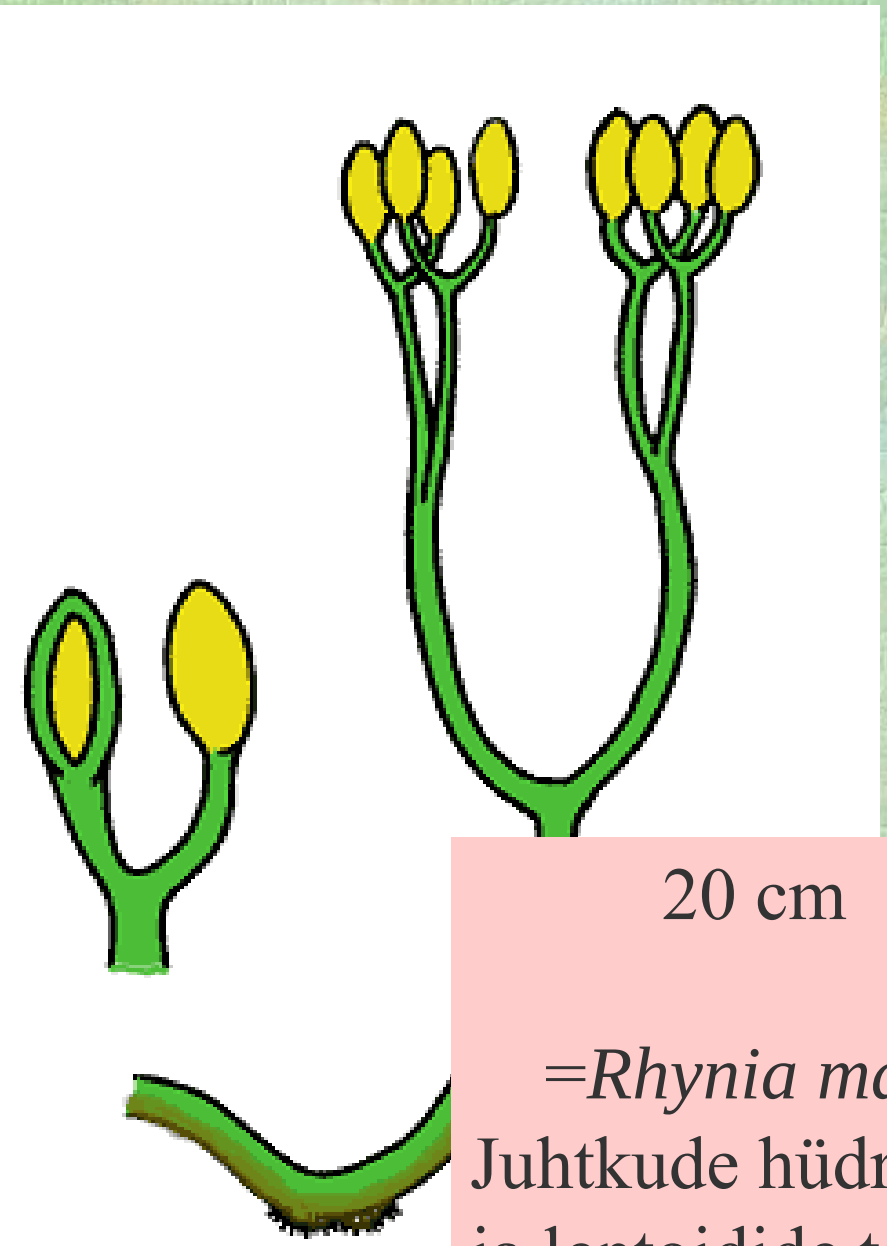
Rhynie Chert

- Vara-Devon (ca 400 Mat)
- Ränistunud taimede ja lülijalgsete fossiilid
- Šotimaal



http://www.abdn.ac.uk/rhynie/

Horneophytopsida: *Aglaophyton major*



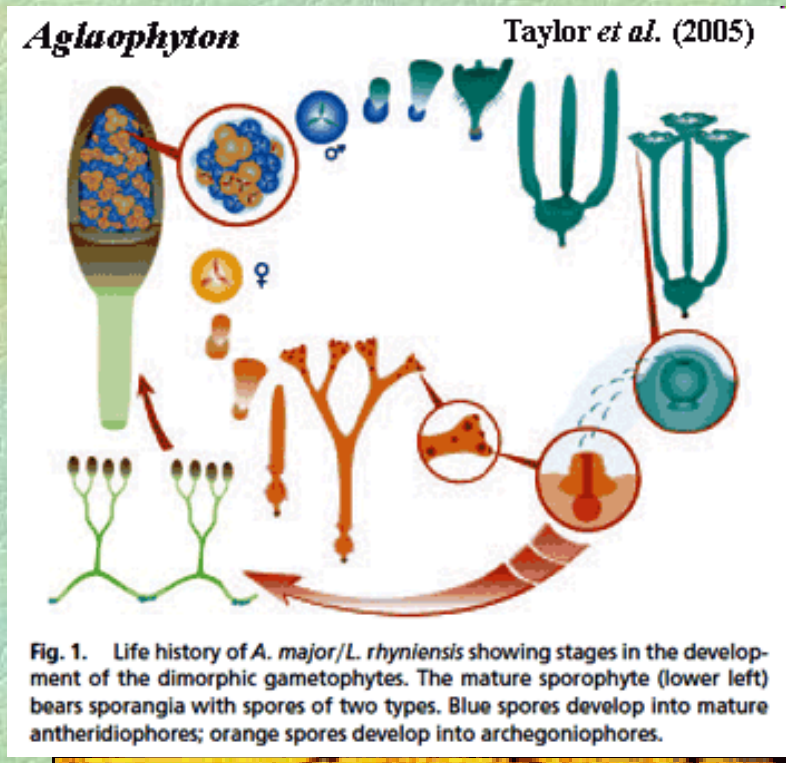
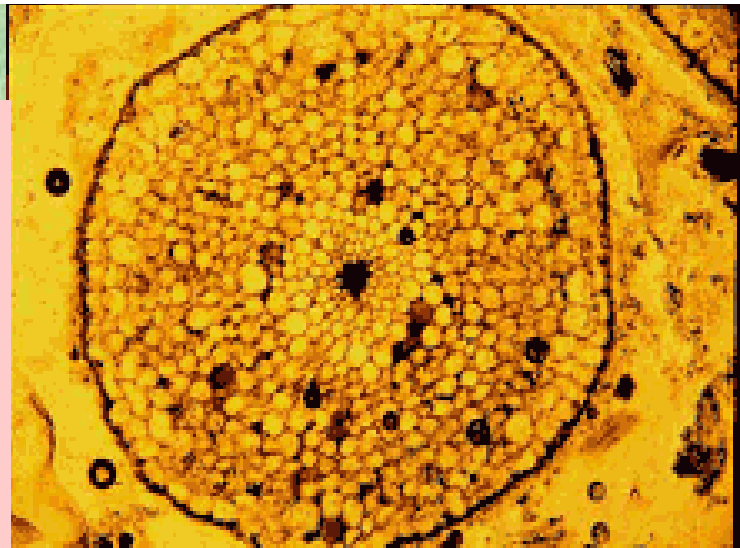


Fig. 1. Life history of *A. major*/*L. rhyniensis* showing stages in the development of the dimorphic gametophytes. The mature sporophyte (lower left) bears sporangia with spores of two types. Blue spores develop into mature antheridiophores; orange spores develop into archegoniophores.

20 cm

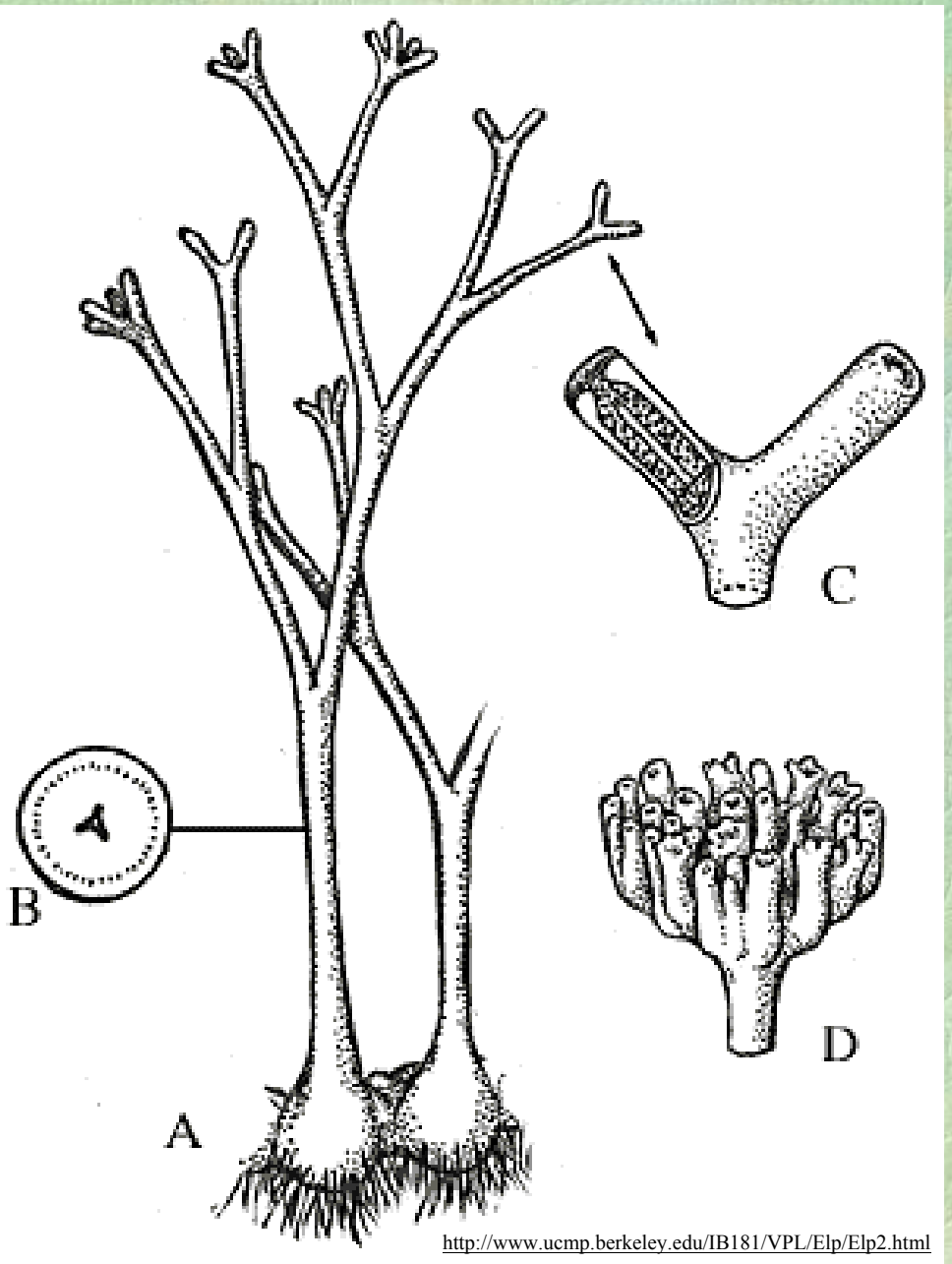
=*Rhynia major*

Juhtkude hüdroidide ja leptoidide taoline



Horneophyton lignieri

- Kolumella nagu sammaldel
- Trahheiidid?
- 20 cm



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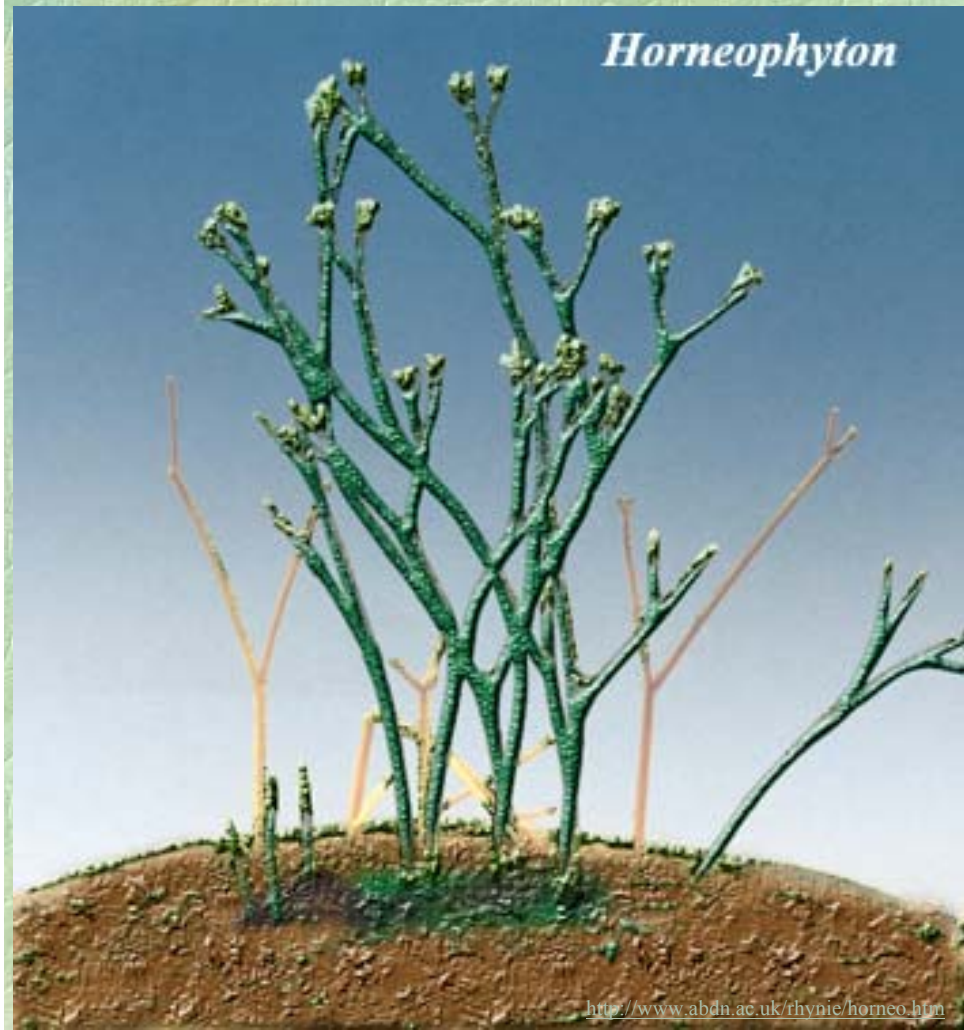
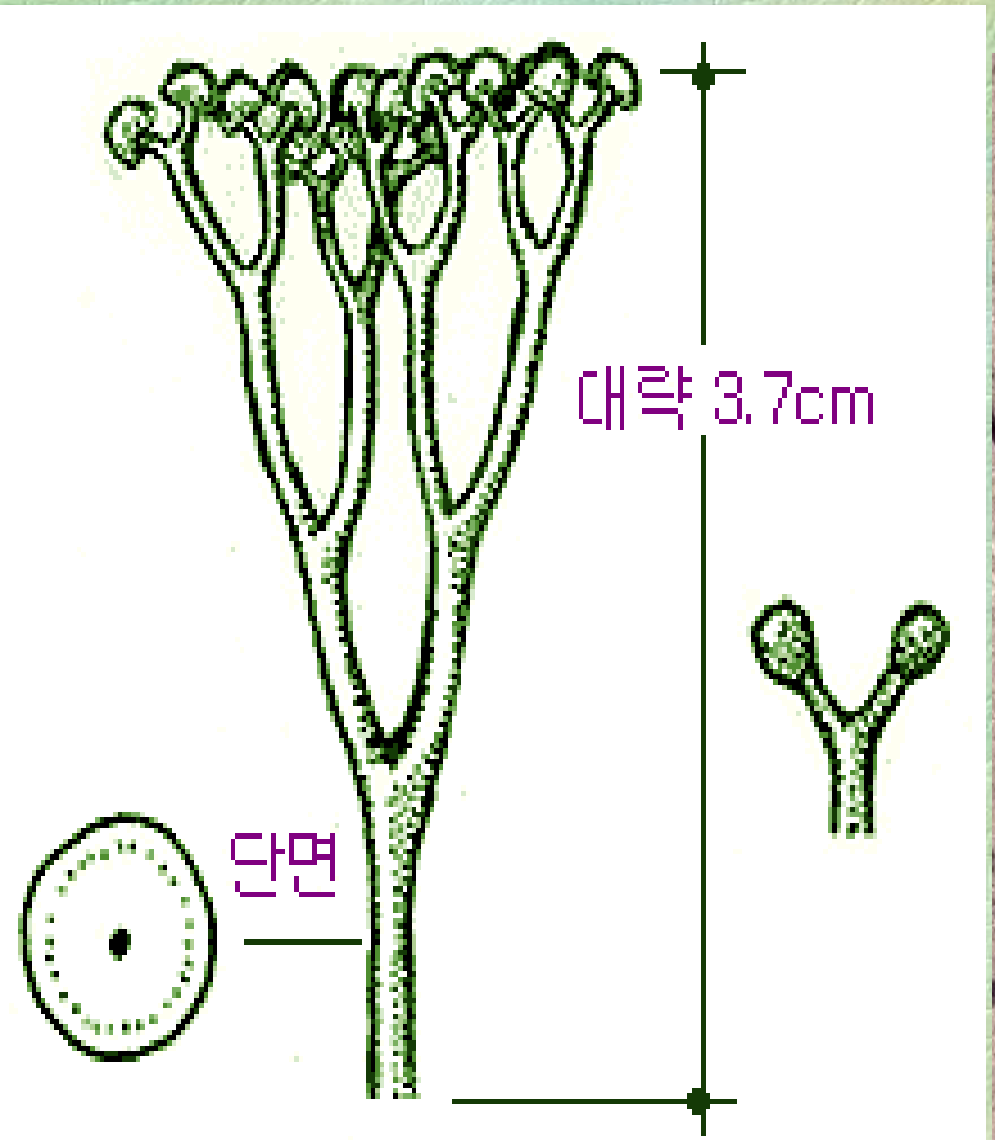


http://www.abdn.ac.uk/rhynie/horneo.htm

Rhyniopsida: *Cooksonia pertonii*

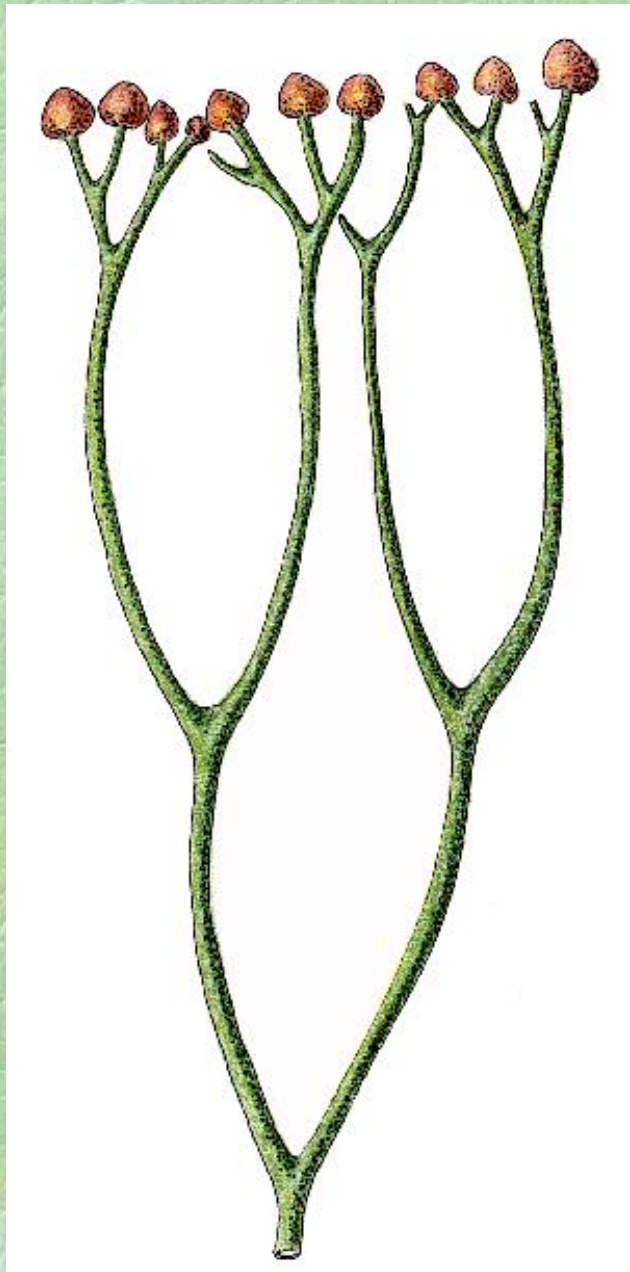
Silur (428 mat)



http://www.ucmp.berkeley.edu/silurian/silulife.html

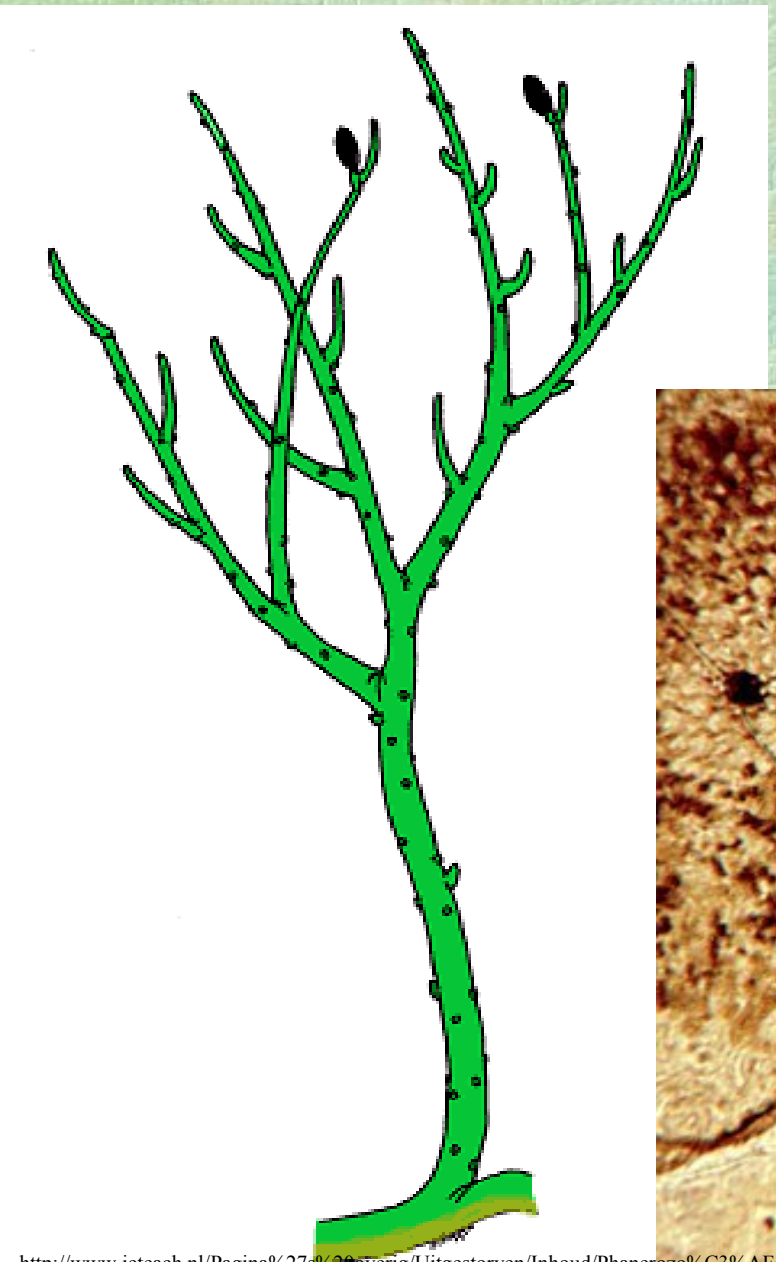
http://steurh.home.xs4all.nl/engcook/ecooks.html

Cooksonia caledonica



http://www.creaweb.fr/perso/bv/banque/cormo-cooksonia.html

Rhynia gwynne-vaughanii



http://www.uni-muenster.de/GeoPalaeontologie/Palaeo/Palbot/rhynneu3.htm

http://www.icteach.nl/Pagina%27s%20overig/Uitgestorven/Inhoud/Phanerozo%C3%AFcum/Paleozo%C3%AFcum/Devoon/Flora/devoon_flora.htm

Lyonophyton ja *Sciadophyton*

http://www.abdn.ac.uk/rhynie/aglao.htm

http://www.senckenberg.de/root/index.php?page_id=1818


http://www.earthhistory.org.uk/recolonisation/first-plants

"Tõelised" soontaimed

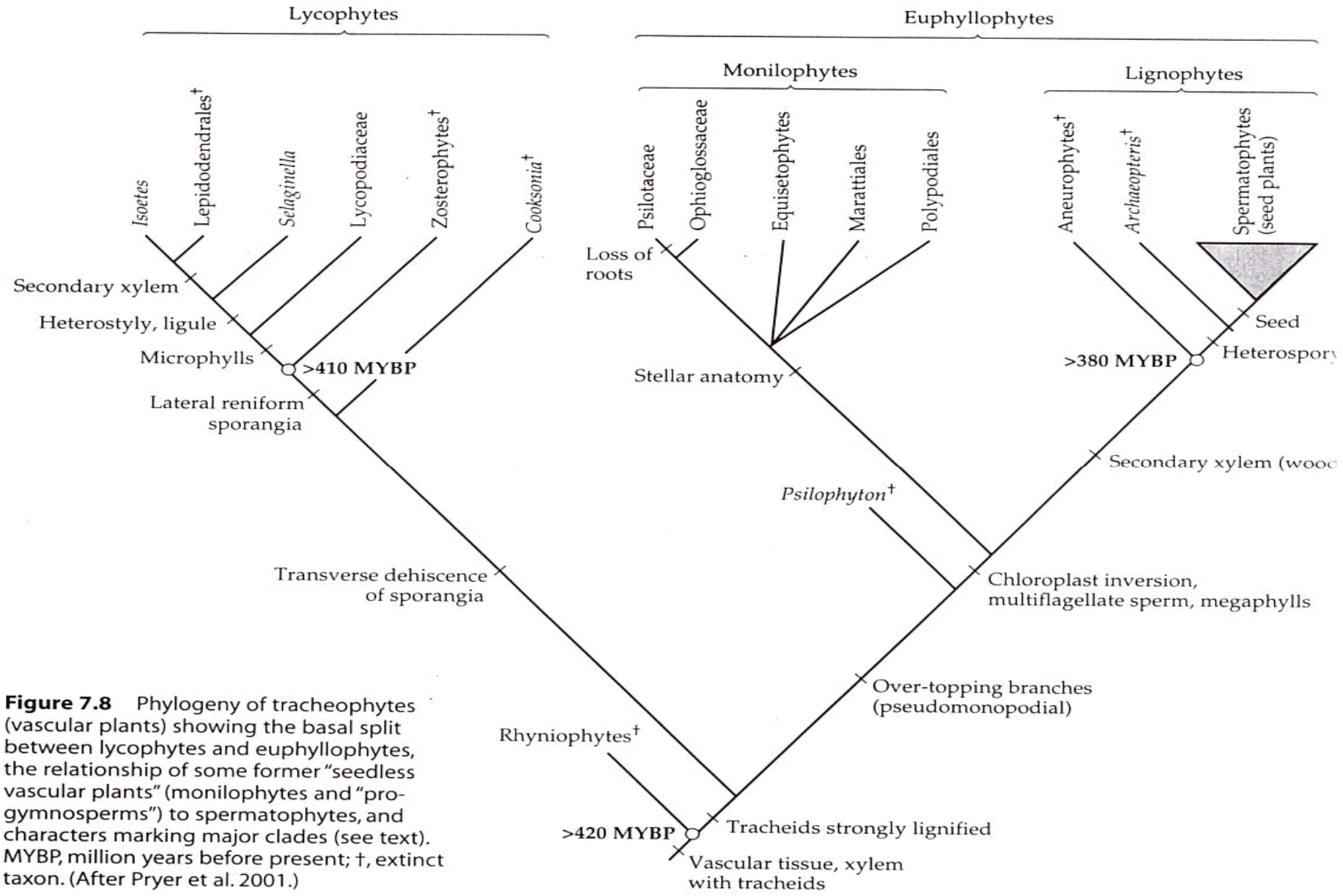
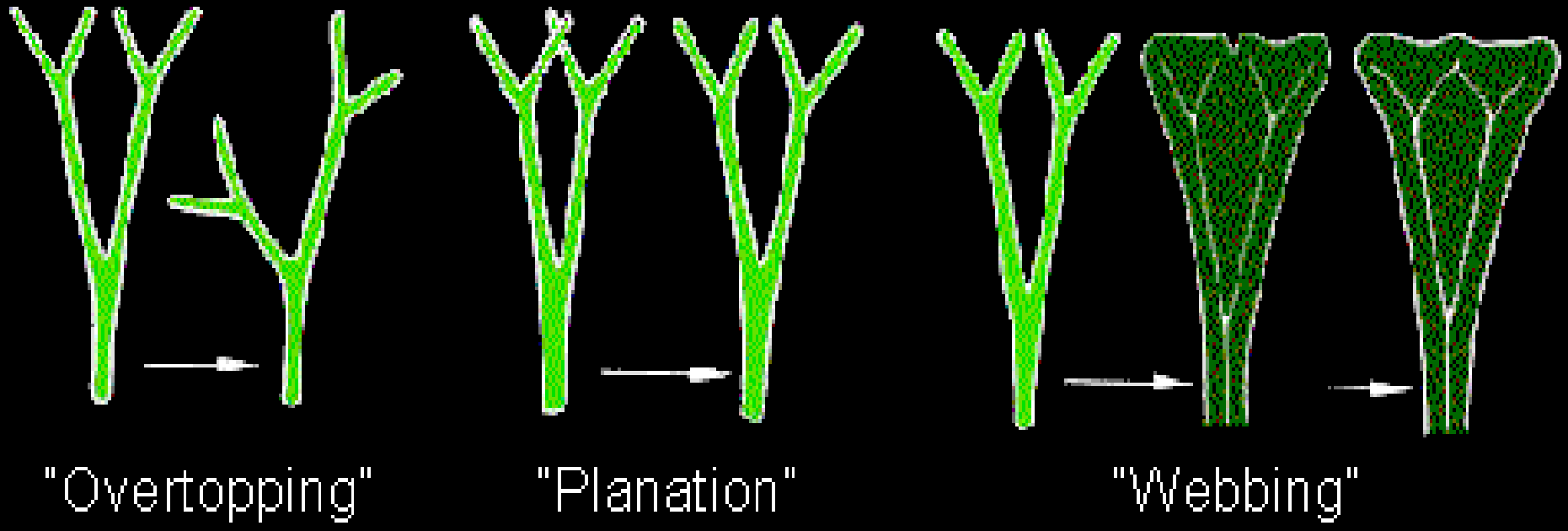
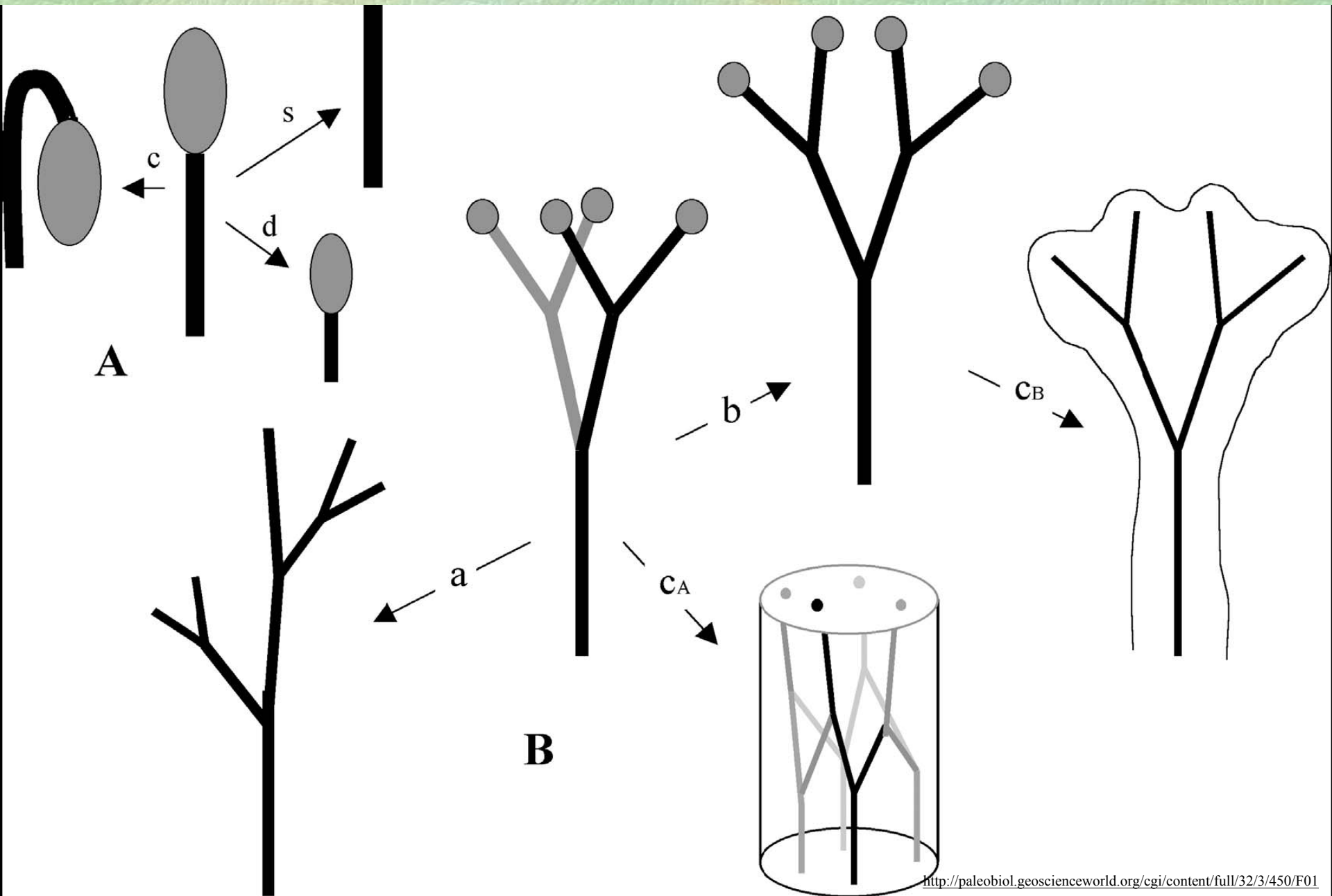


Figure 7.8 Phylogeny of tracheophytes (vascular plants) showing the basal split between lycophytes and euphyllophytes, the relationship of some former "seedless vascular plants" (monilophytes and "progymnosperms") to spermatophytes, and characters marking major clades (see text). MYBP, million years before present; †, extinct taxon. (After Pryer et al. 2001.)

Zimmermanni teloomiteooria



Teloomiteooria



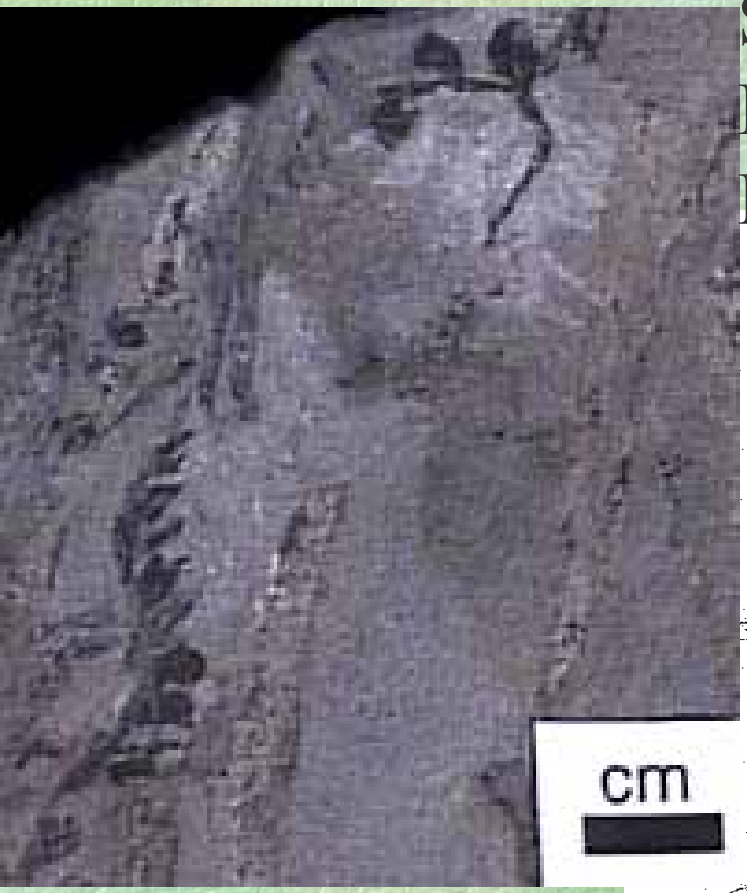
http://paleobiol.geoscienceworld.org/cgi/content/full/32/3/450/F01

Zosterophyllopsida: *Zosterophyllum divaricatum*

Silur –devon

Lateraalsed sporangiumid

Dihhotoomsed /pseudomonopodiaalsed



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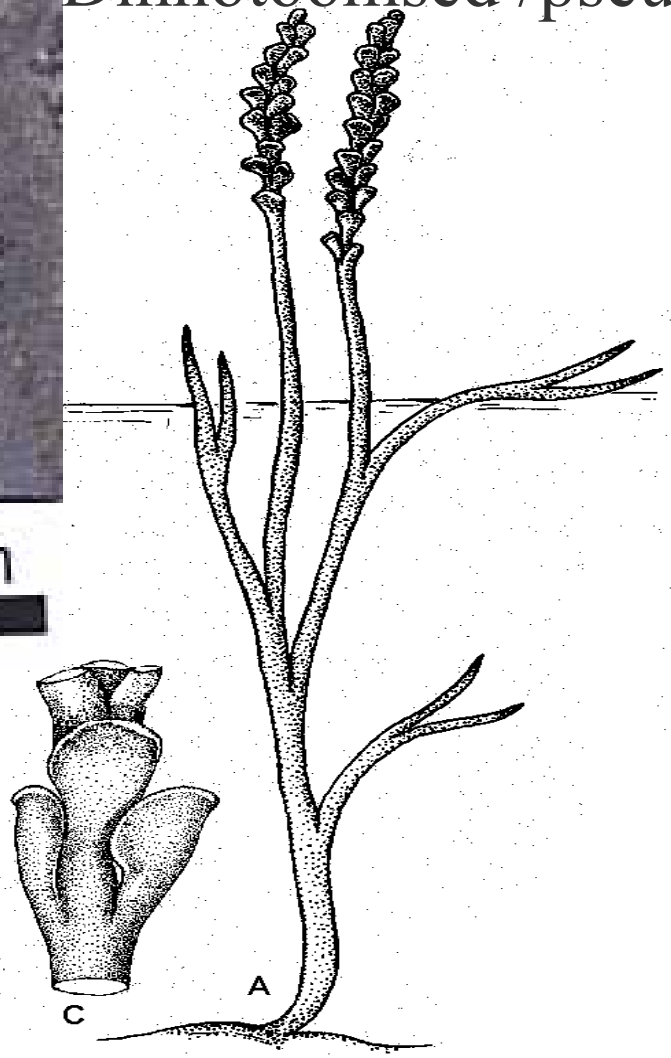
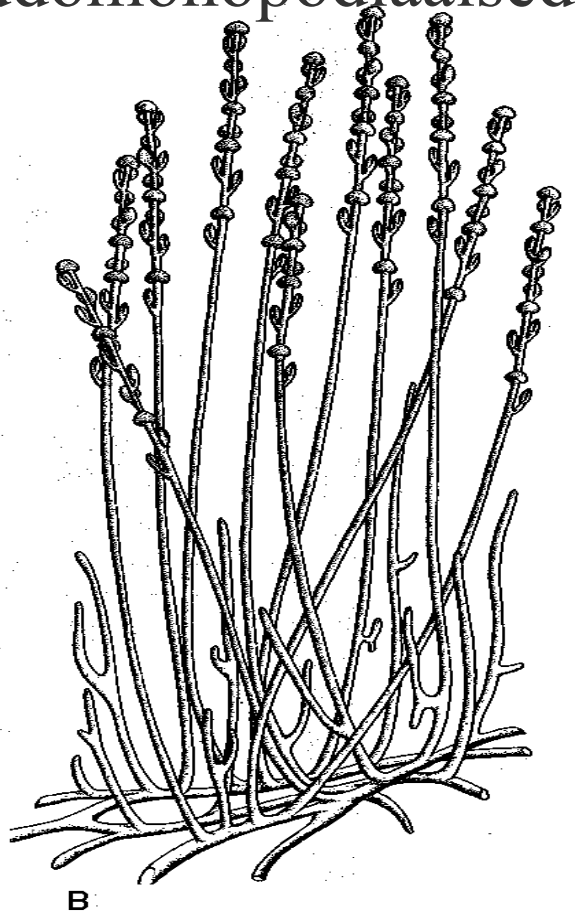
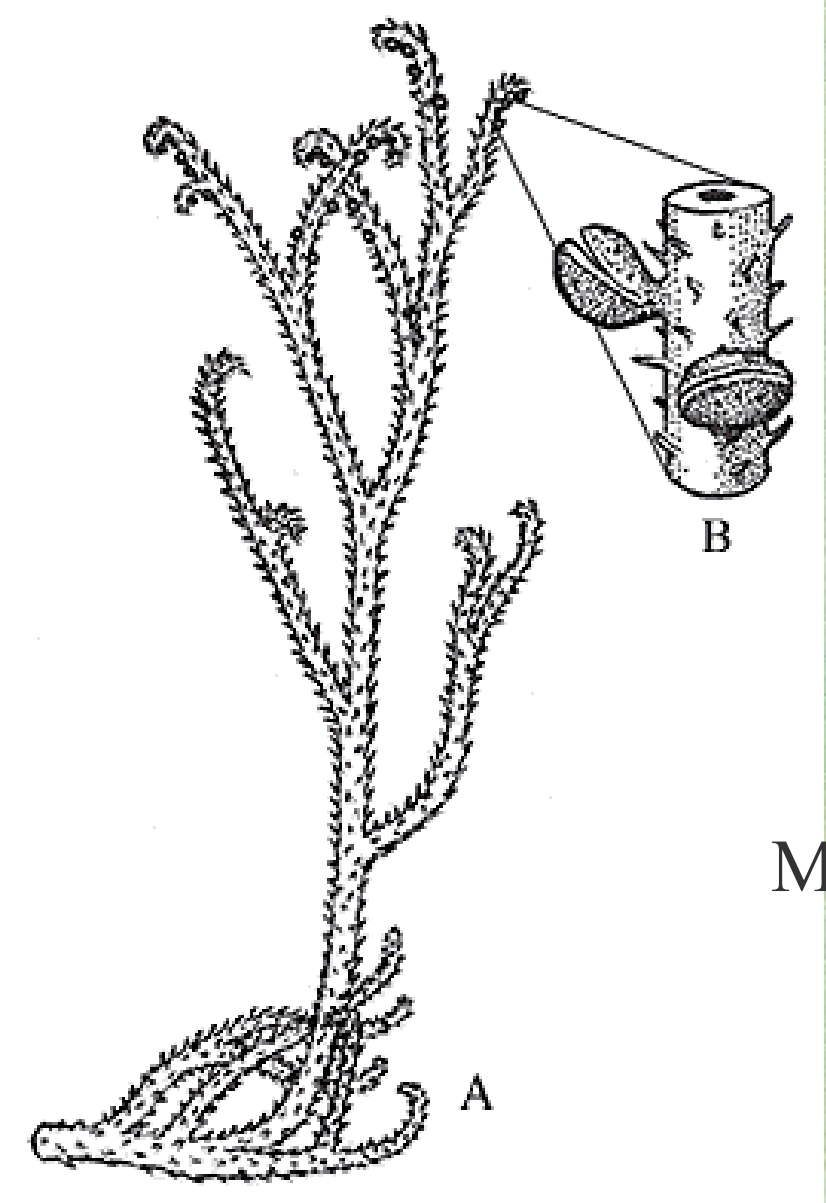




http://www.uua.cn/Paleobotany/show-6163-1.html

Sawdonia ornata



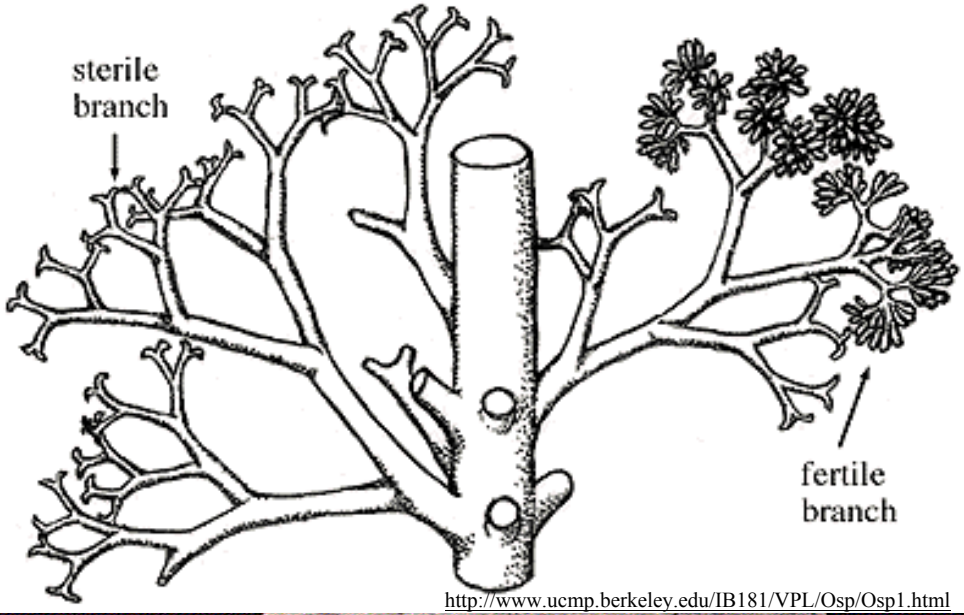
Mikrofüllid

http://en.wikipedia.org/wiki/Sawdoniales

Ürgraikad: *Psilophyton dawsonii*

Monopodiaalne harunemine Eufüllofüüt?

http://lifeofplant.blogspot.com/



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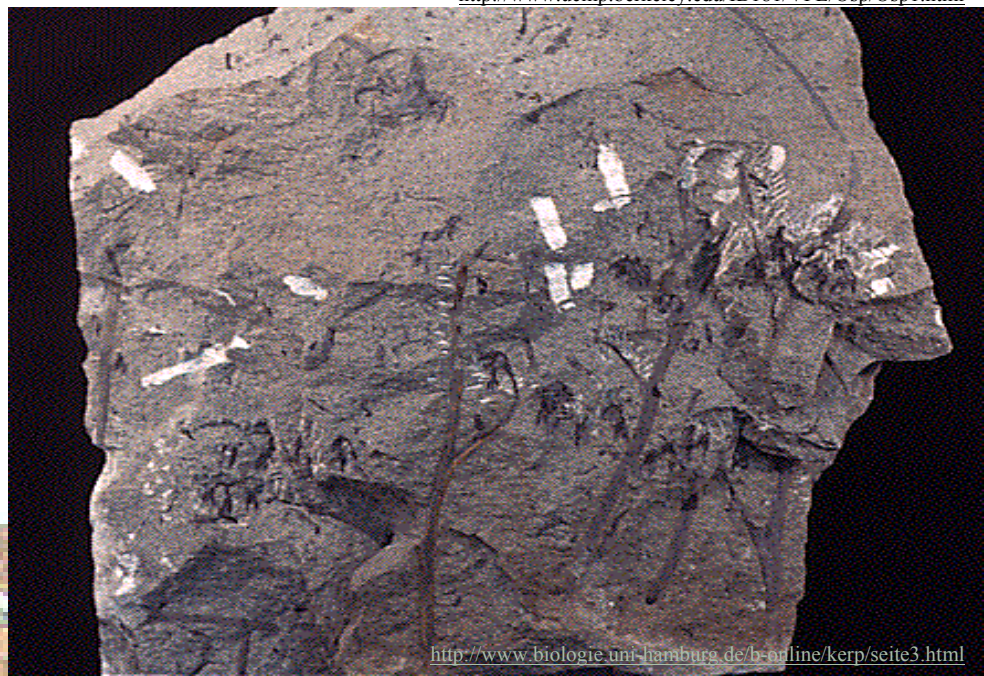
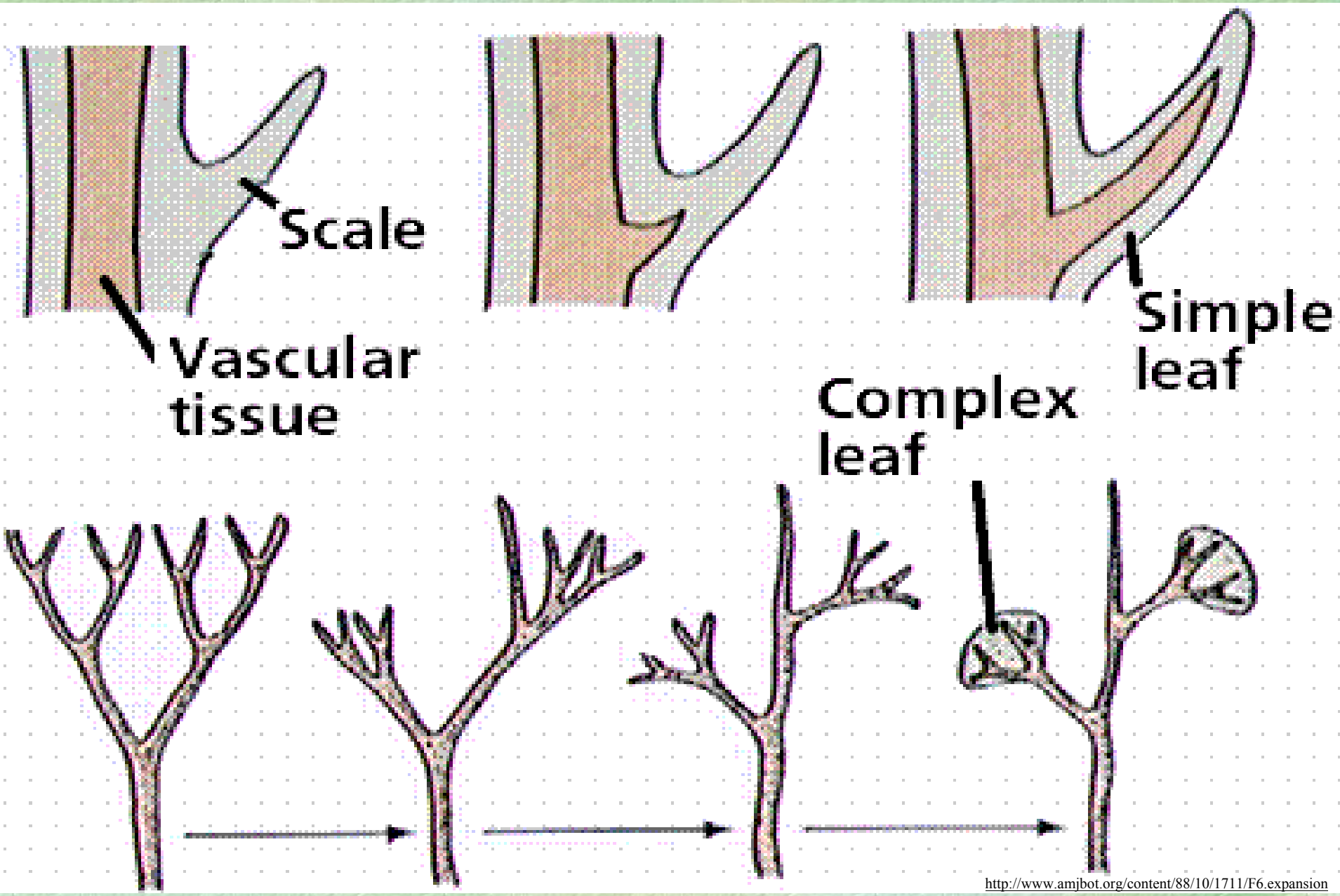


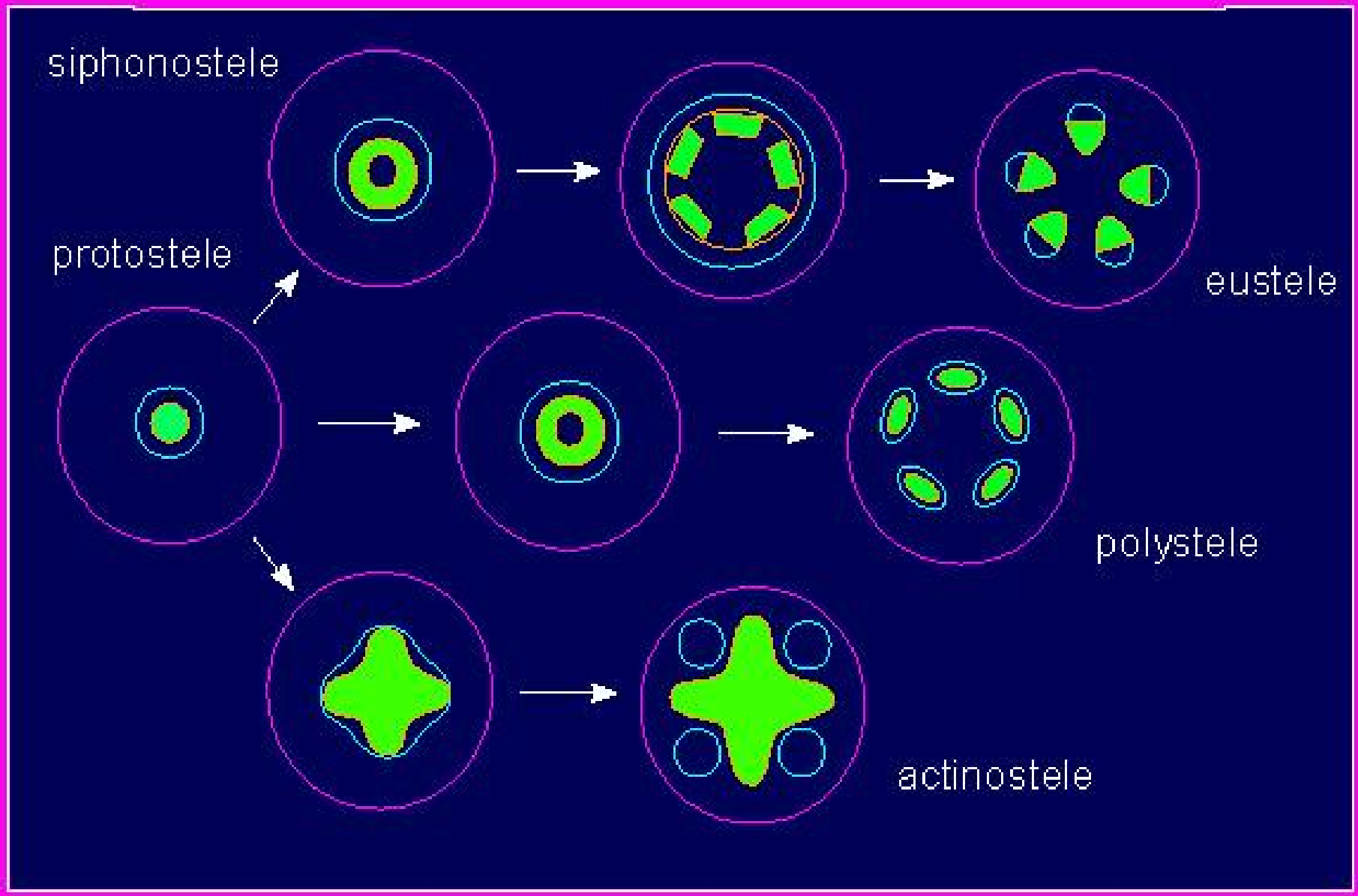
http://www.biologie.uni-hamburg.de/b-online/kerp/seite3.html

Mikrofüllide teke



http://www.amjbot.org/content/88/10/1711/F6.expansion

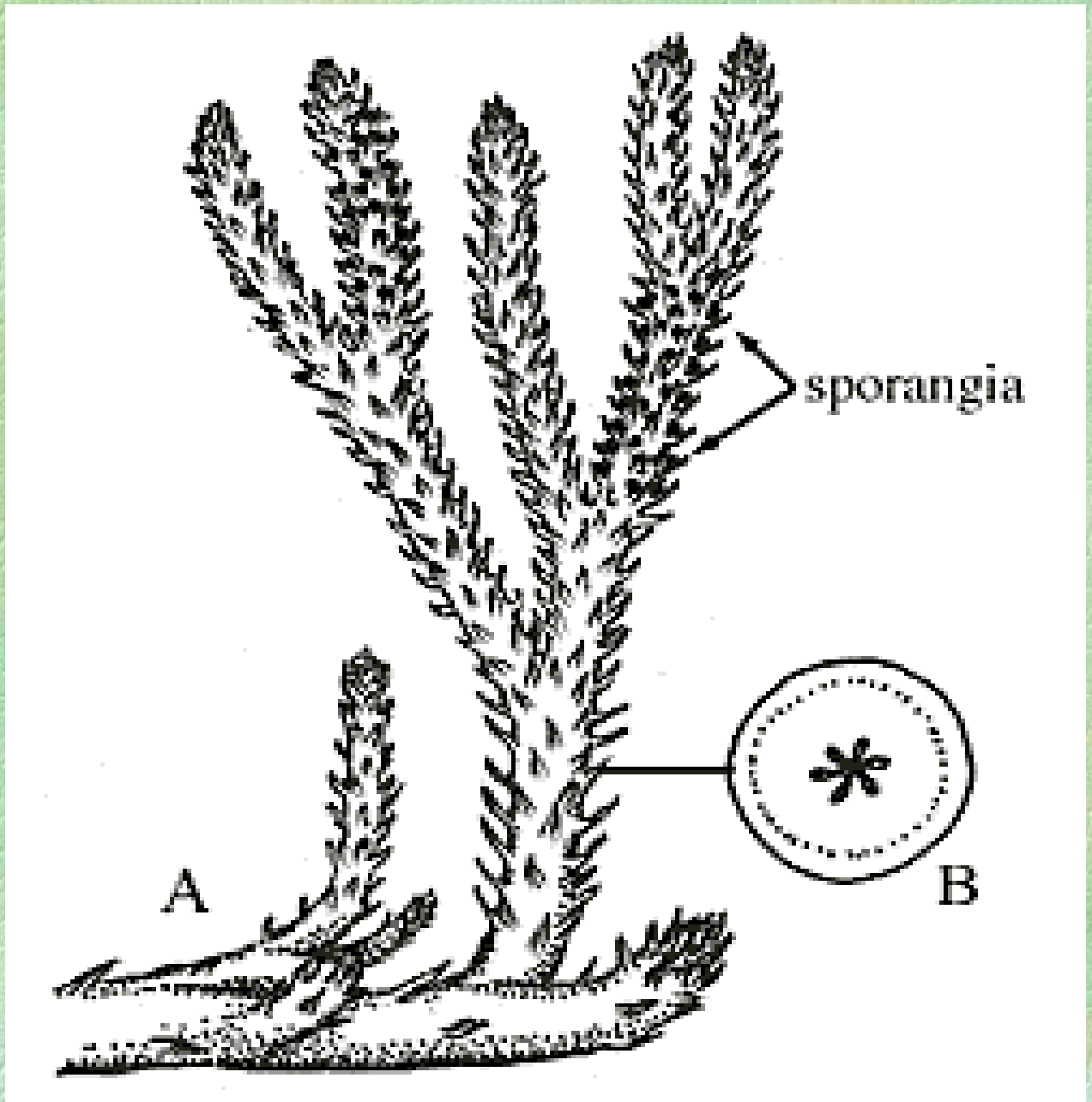
Juhtkudede areng - stellaarteooria



http://www.biologie.uni-hamburg.de/b-online/e06/06i.htm

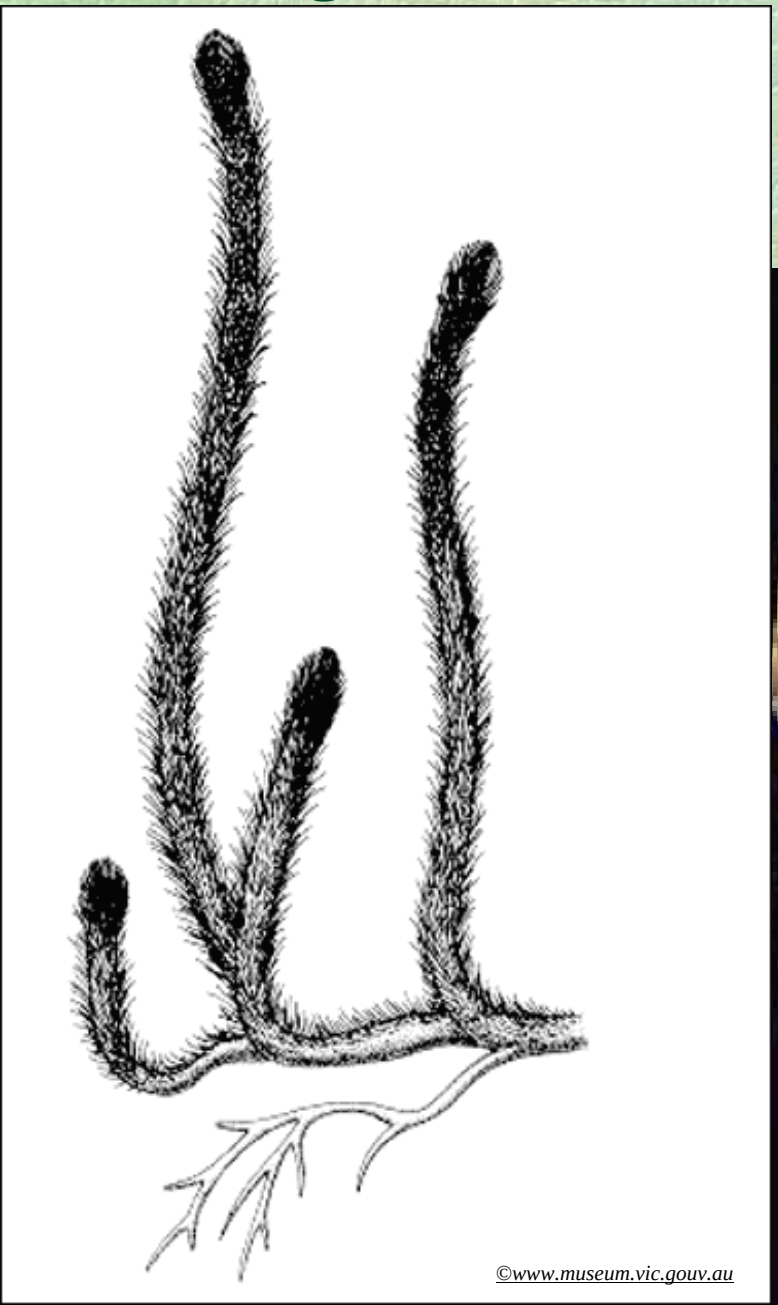
Lycopsida

Drepanophycales

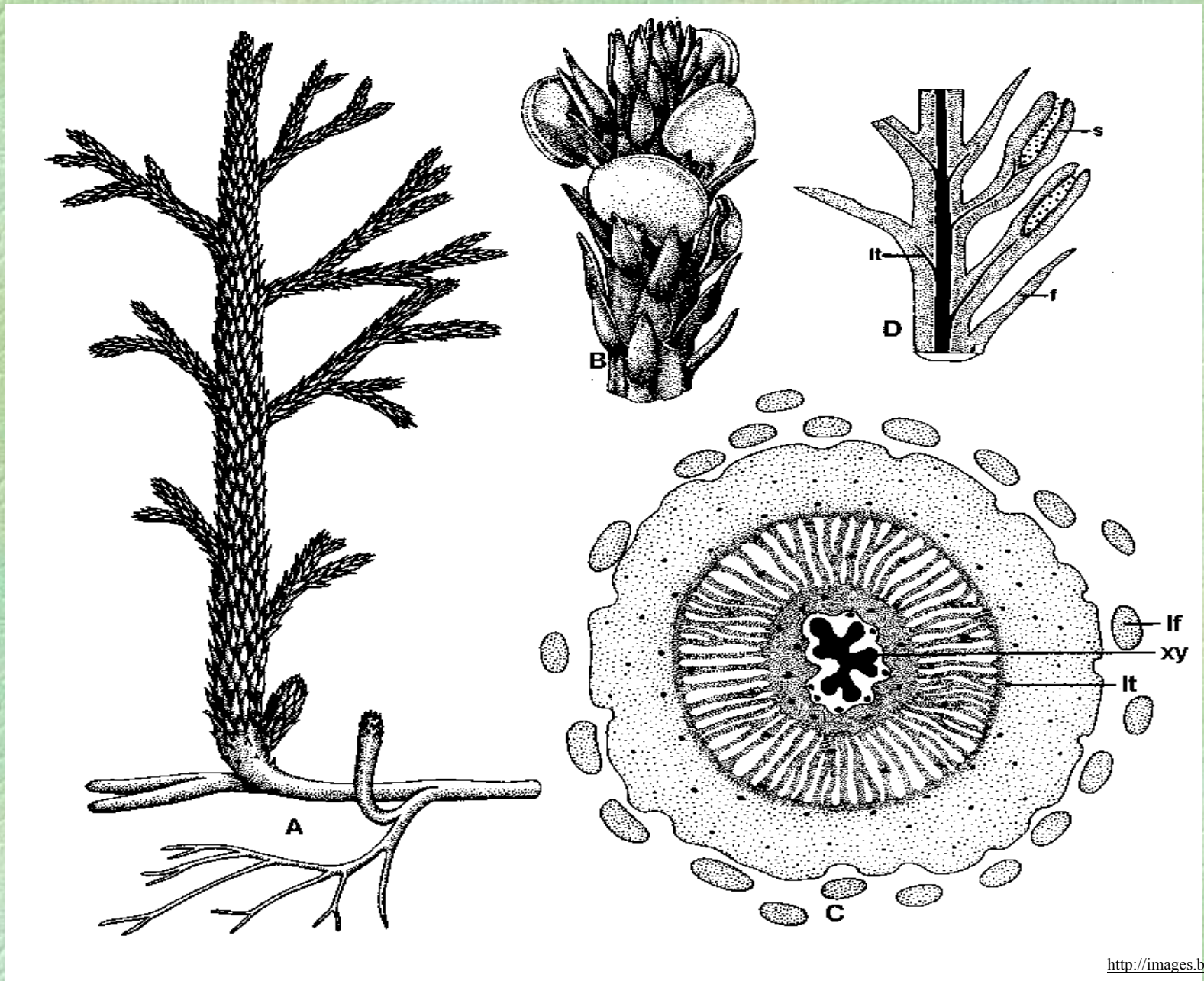


Baragwanathia longifolia - ogalehik

420 Mat!



Asteroxylon mackiei - ürgkold



http://images.botany.org/set-18/png1.html

Kollalaadsed - *Lycopodiales*

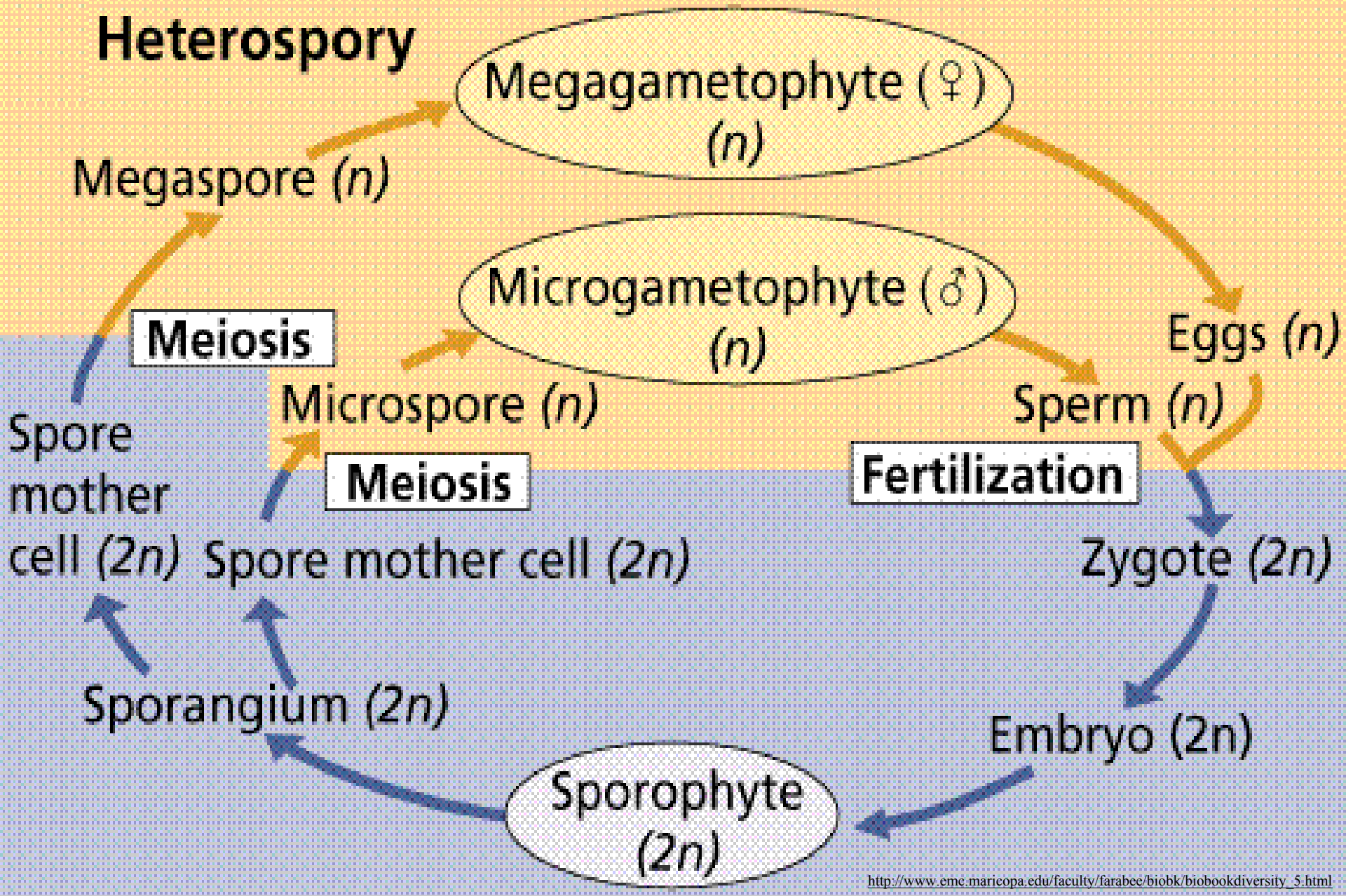
- 1 sugukond, 2-5 perekonda, 201 liiki
- Eestis 6 taksonit

Kollalaadsed - *Lycopodiales*

Lycopodium annotinum

Lycopodium clavatum

Heterospooria teke



http://www.emc.maricopa.edu/faculty/farabee/biobk/biobookdiversity_5.html

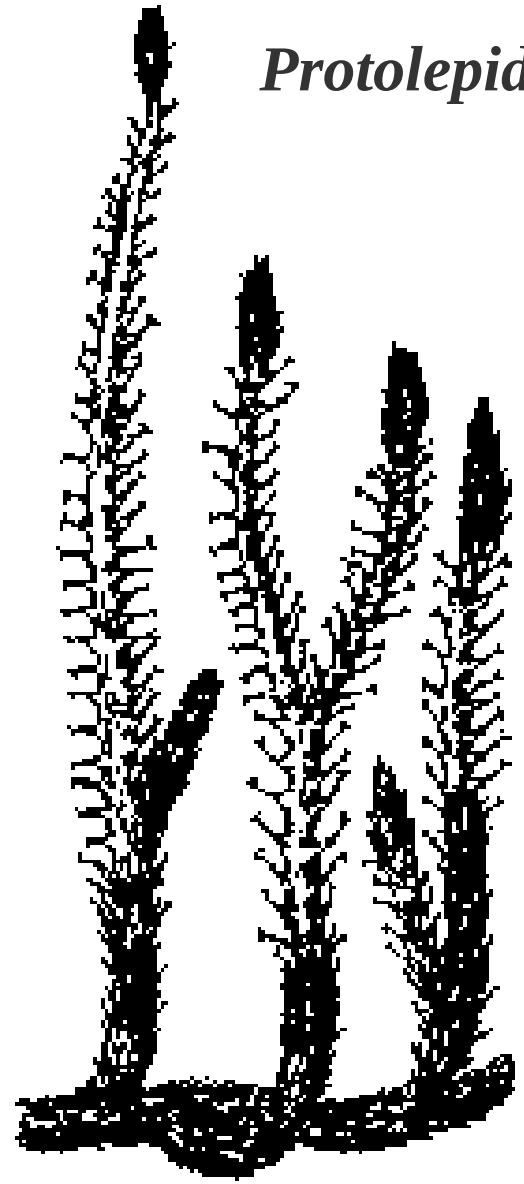
Selaginellilaadsed *Selaginellales*

Selaginella selaginoides

1 suguk, 1 perek, 500-750 liiki

Kuni 2 cm

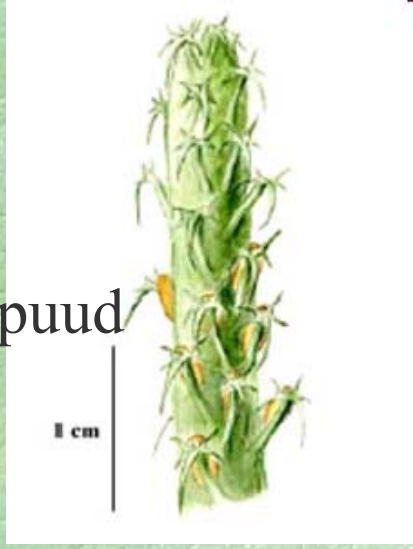
Ürgsoomuspuulaadsed - *Protolepidodendrales*



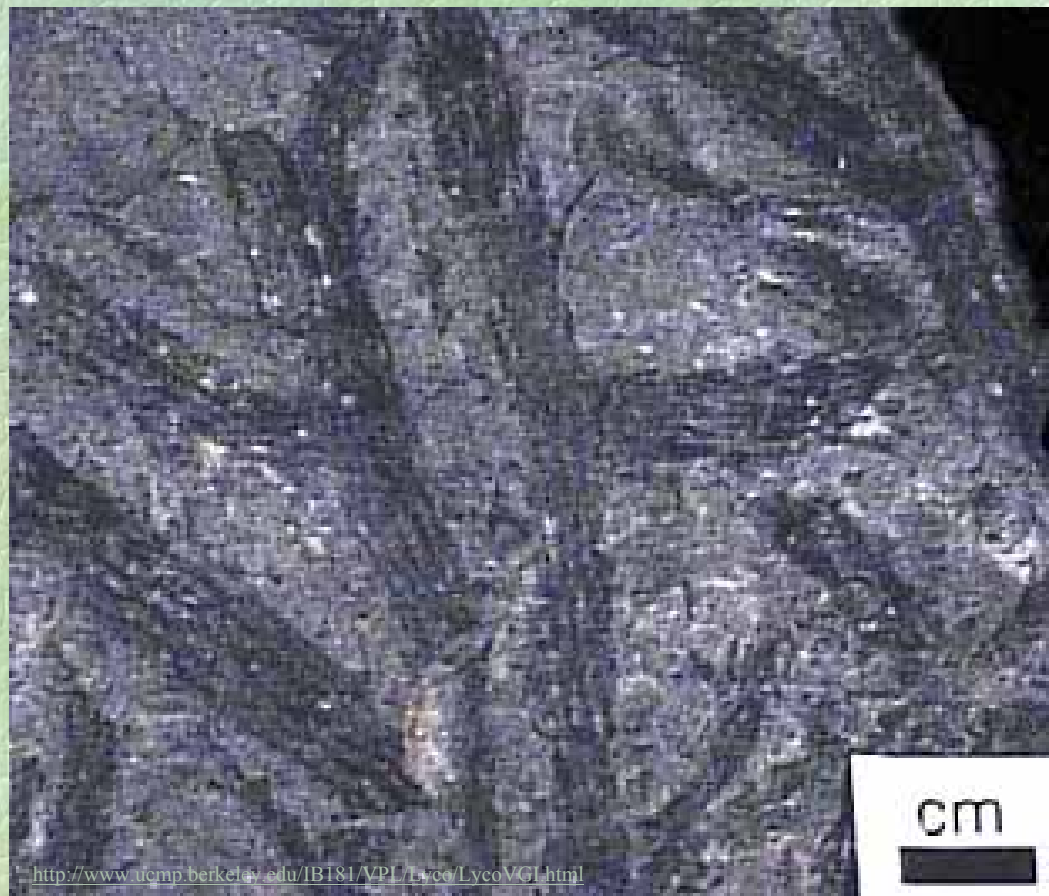
Protolepidodendron

Devon-karbon

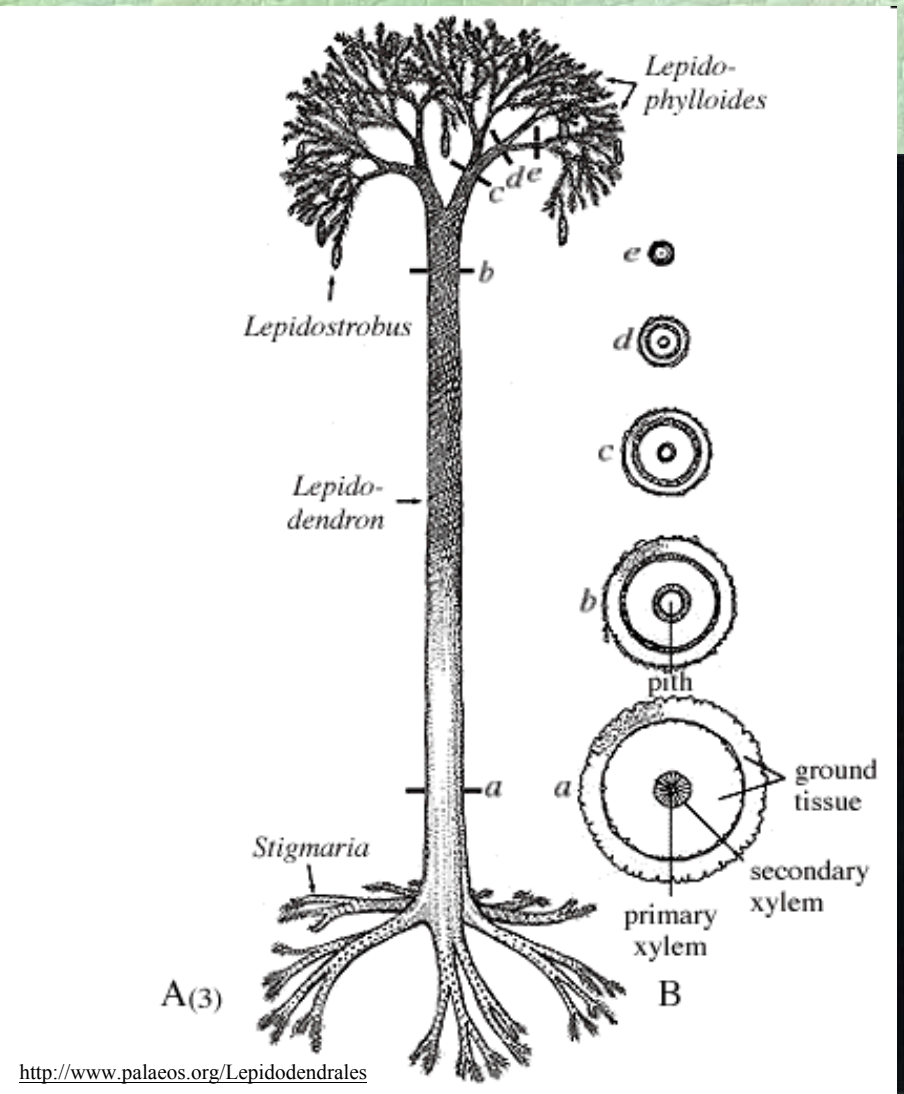
Rohttaimed-väikesed puud



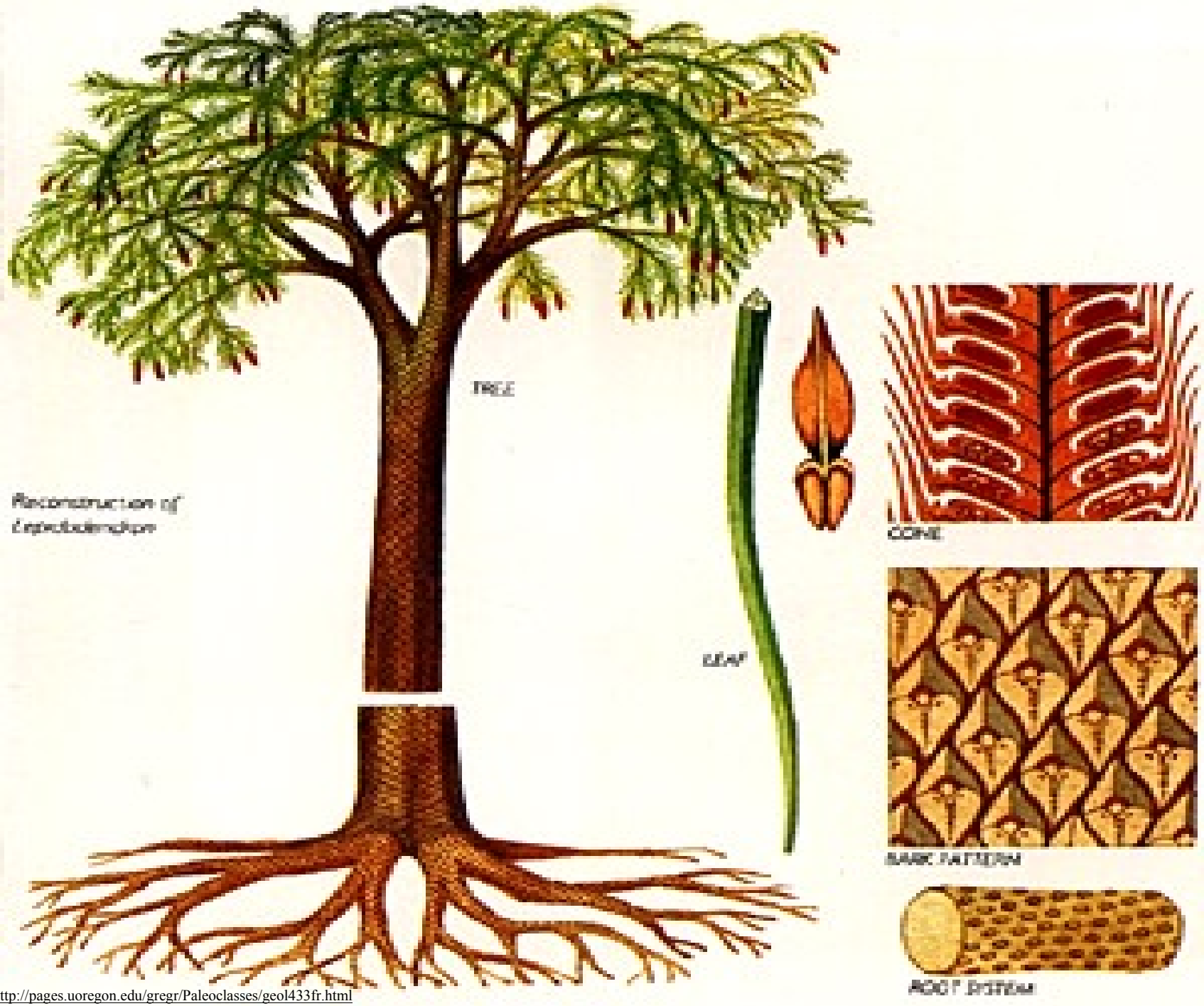
Leclercqia complexa



Lepidodendrales
Soomuspuu - *Lepidodendron*



http://www.palaeos.org/Lepidodendrales



http://pages.uoregon.edu/gregr/Paleoclasses/geol433fr.html

Soomuspuulaadsed *Lepidodendrales*

Sammaspuu - *Pleuromeia*

http://www.nickolai.de/Lichtenberg/Geschichte/Erdgeschichte/Trias/trias.html

faculty.jsd.claremont.edu

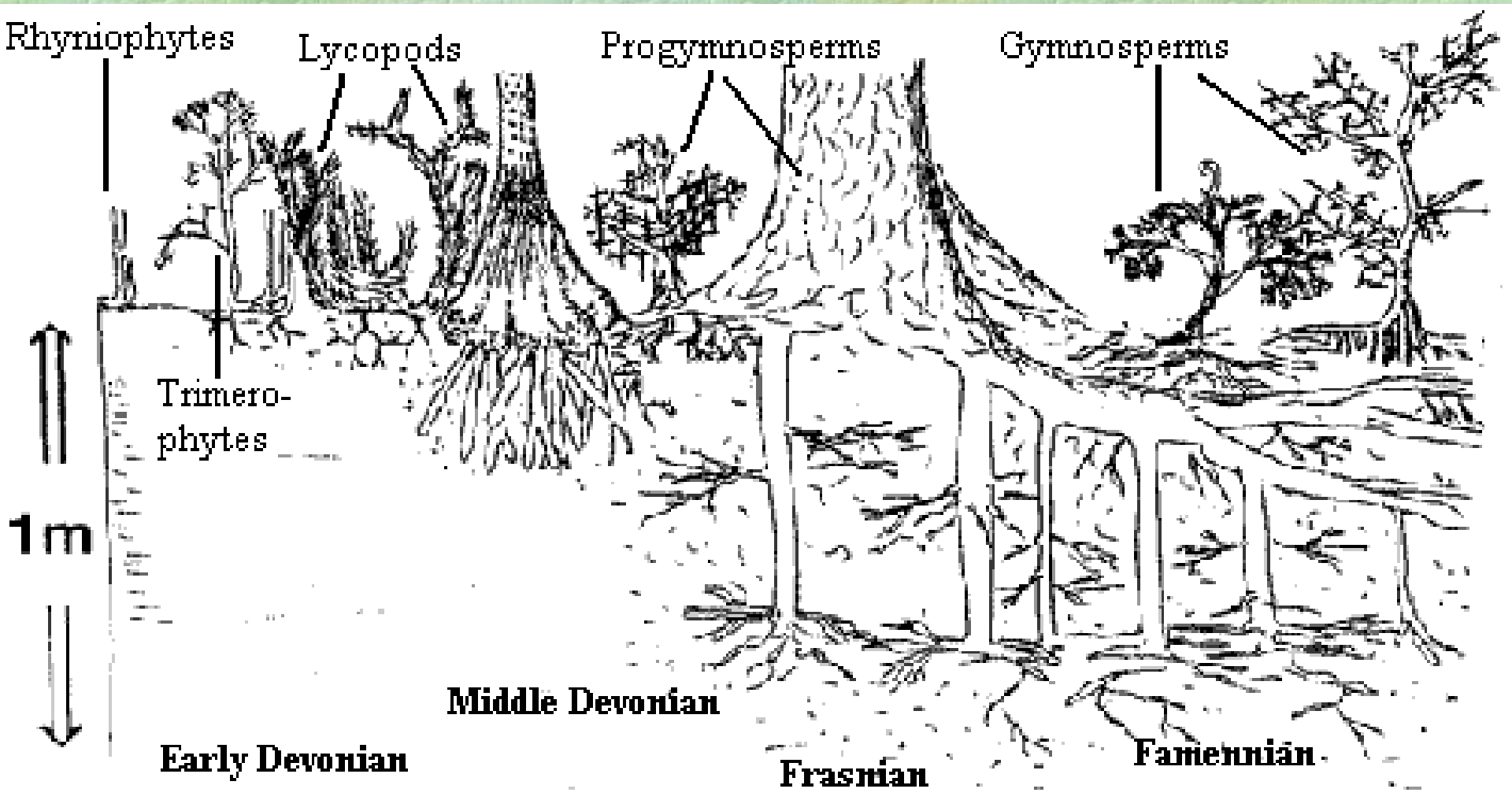
10-35 m

Pitsatipuu-
Sigillaria

http://www.devoniantimes.org/who/pages/lycopsid.html

Esimesed “metsad”

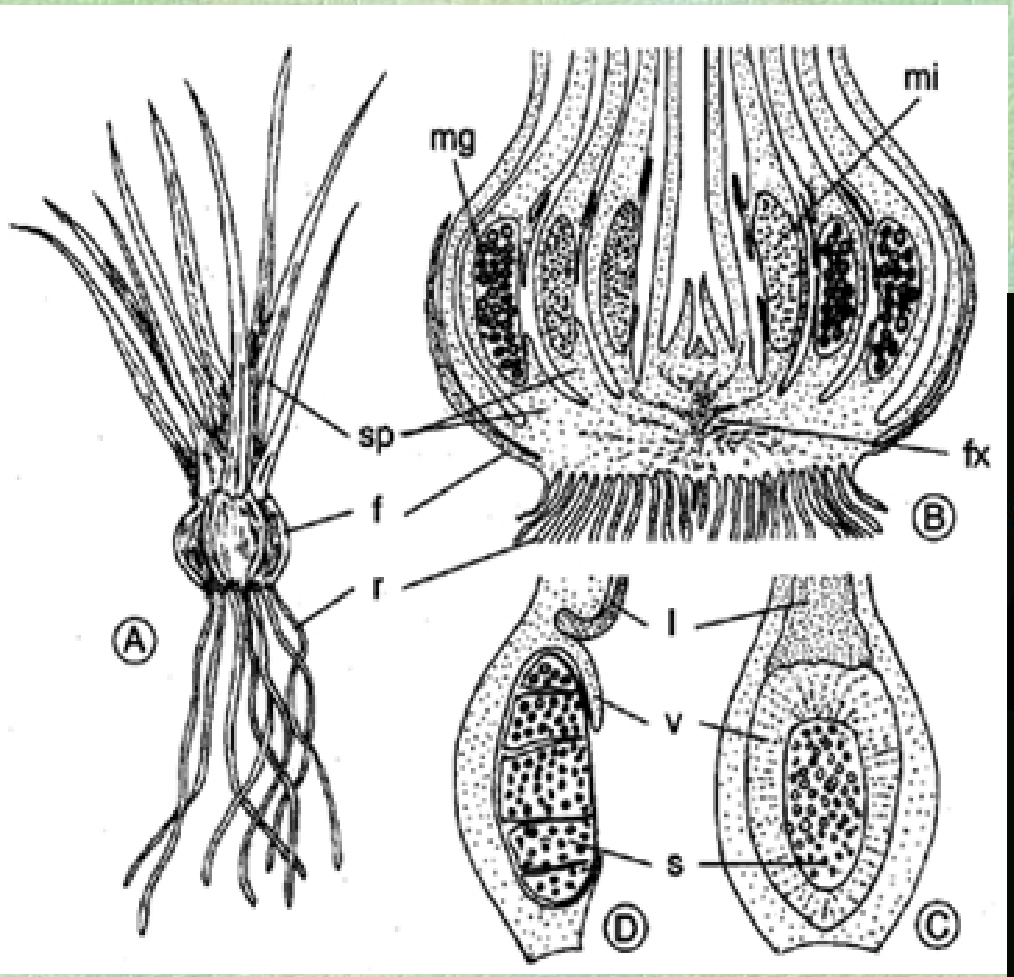
http://www.palaeos.org/Embryophyta



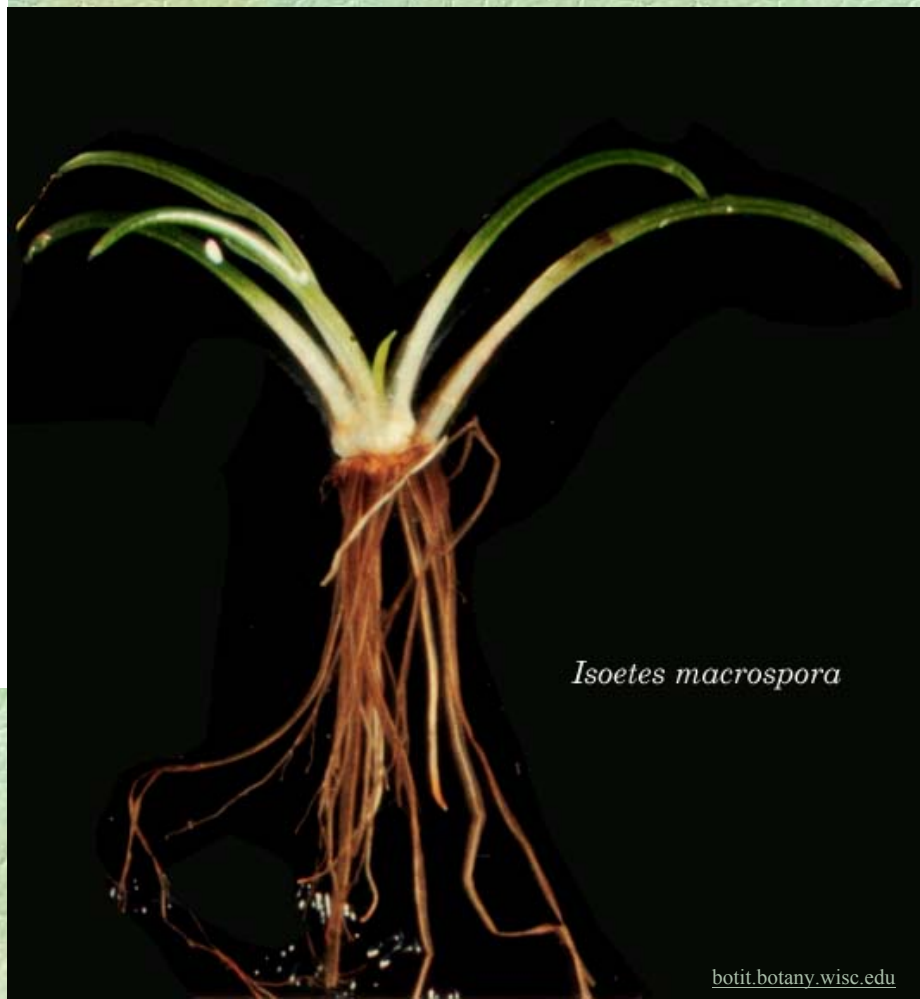
Pleuromeiales
Pleuromeia sternbergii

http://www.cindylooy.org/palynology/palynology_2.html

Lahnarohulaadsed - *Isoetales*



Rohtsed veetaimed
Vars redutseerunud
1-2 perek, 150-200 liiki, E 2 1



Alamhõimkond pärislehttaimed Euphyllophytina

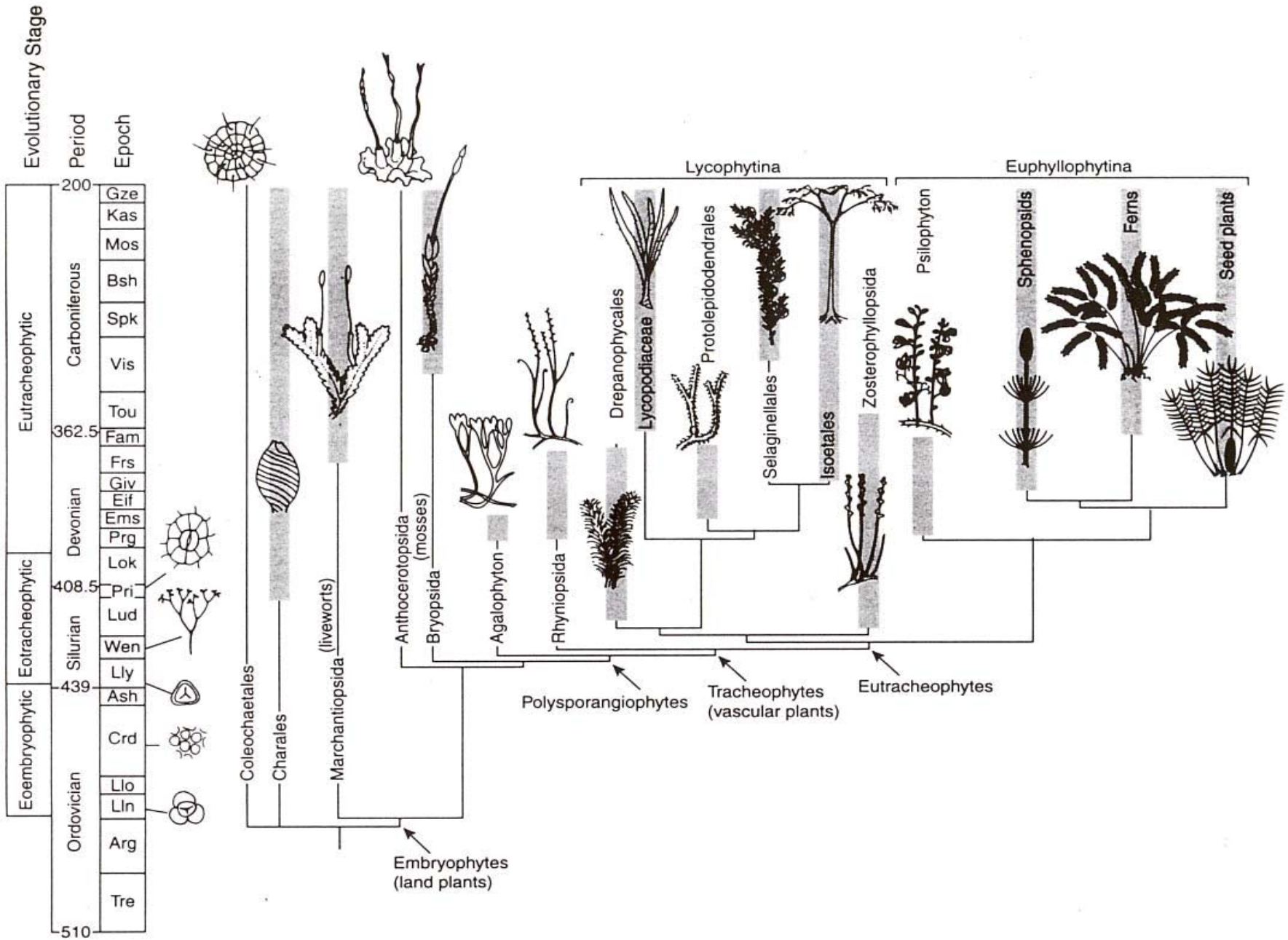
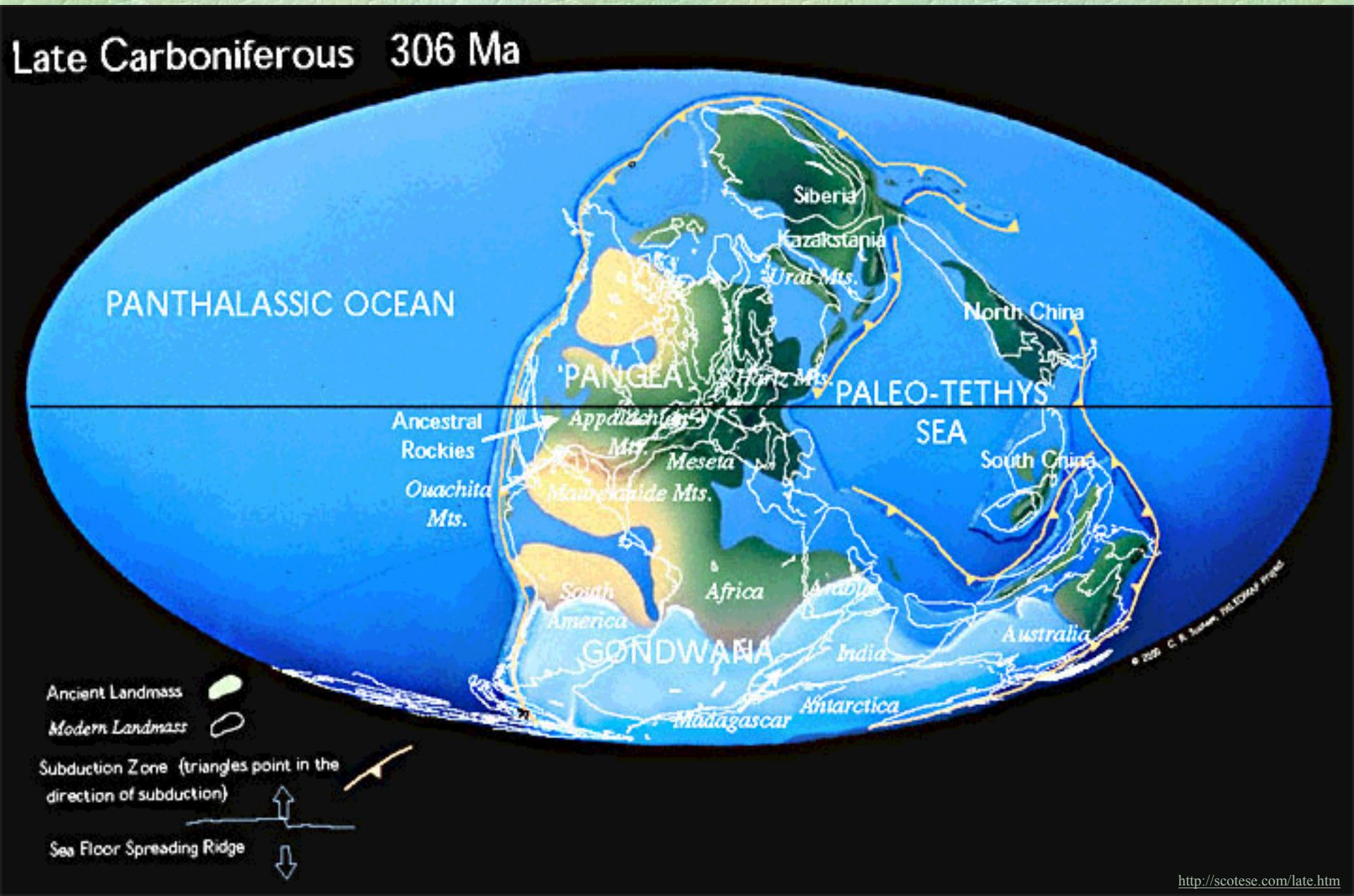
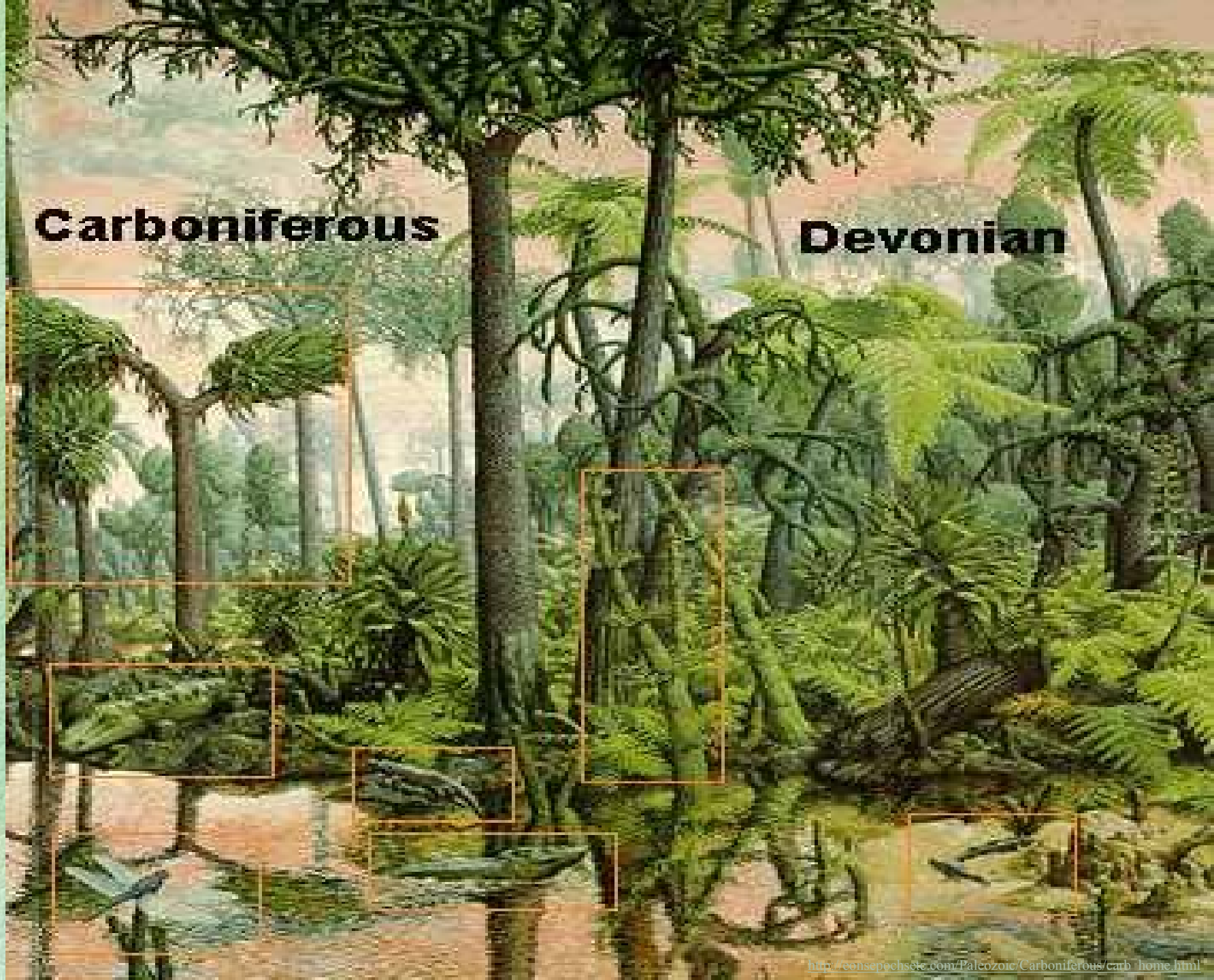


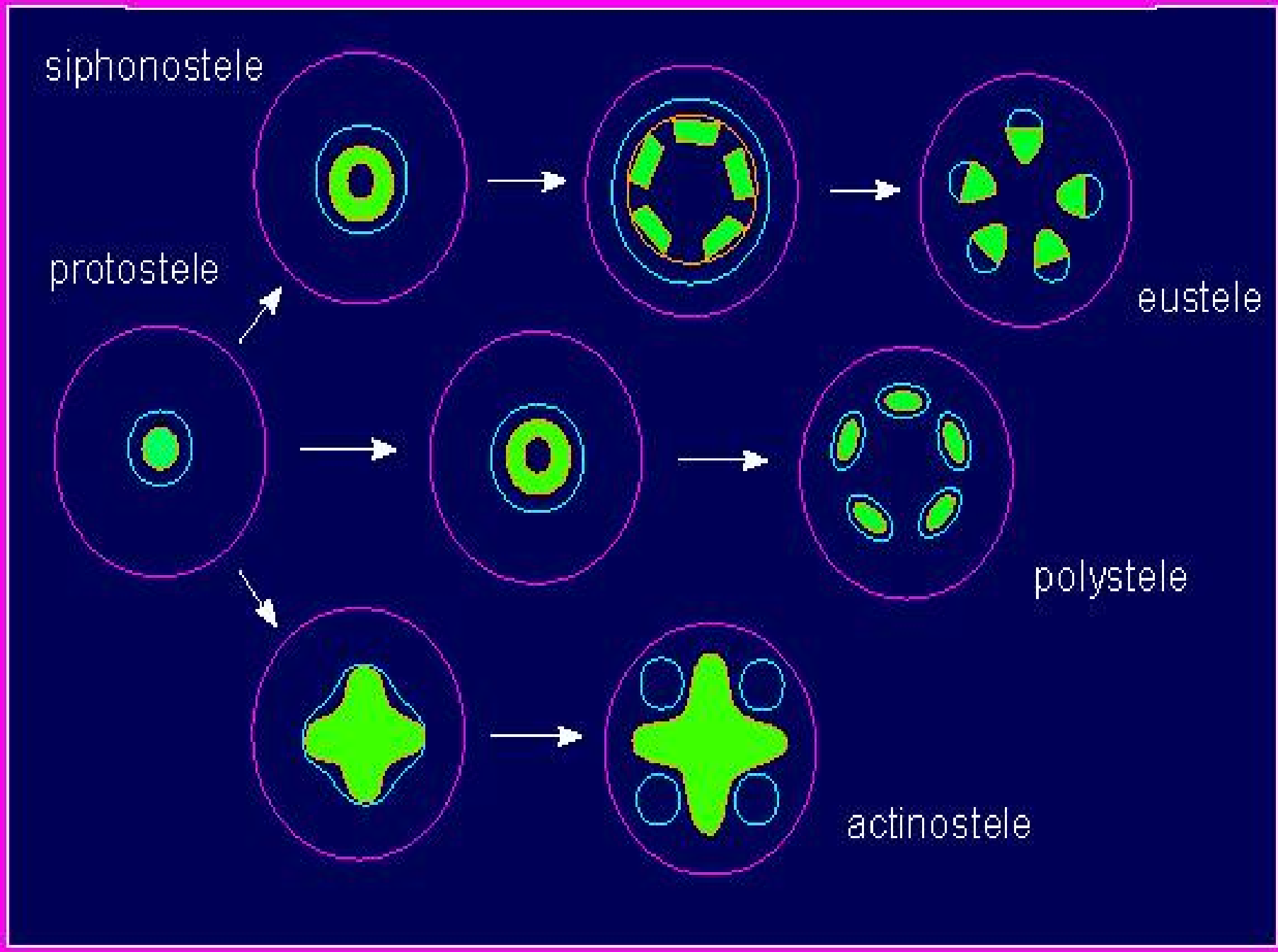
Figure 4.25 Phylogenetic relationship between extinct and extant early plants (redrawn from Kenrick and Crane, 1997b).

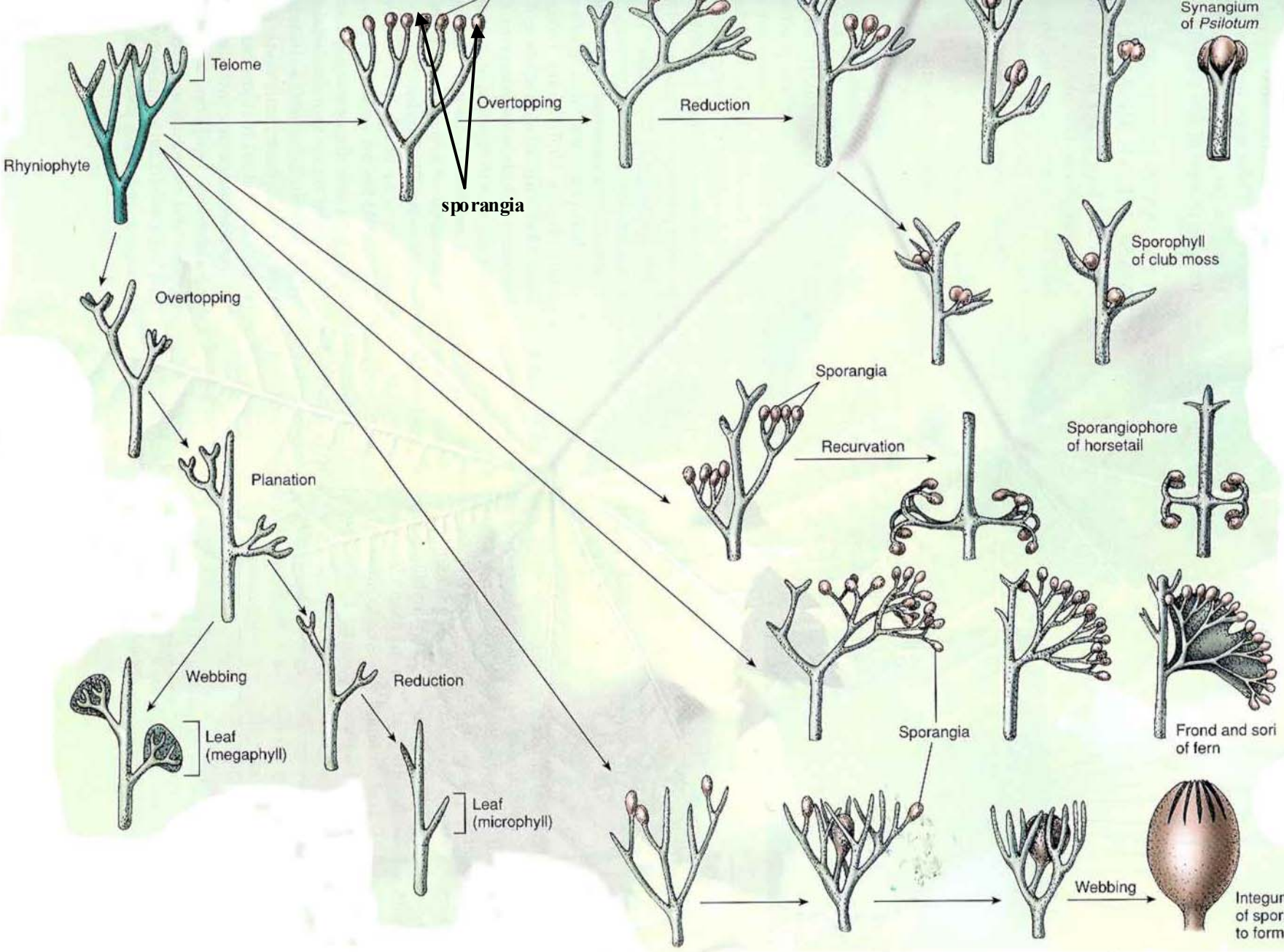
Mandrid Karbonis



http://scotese.com/late.htm

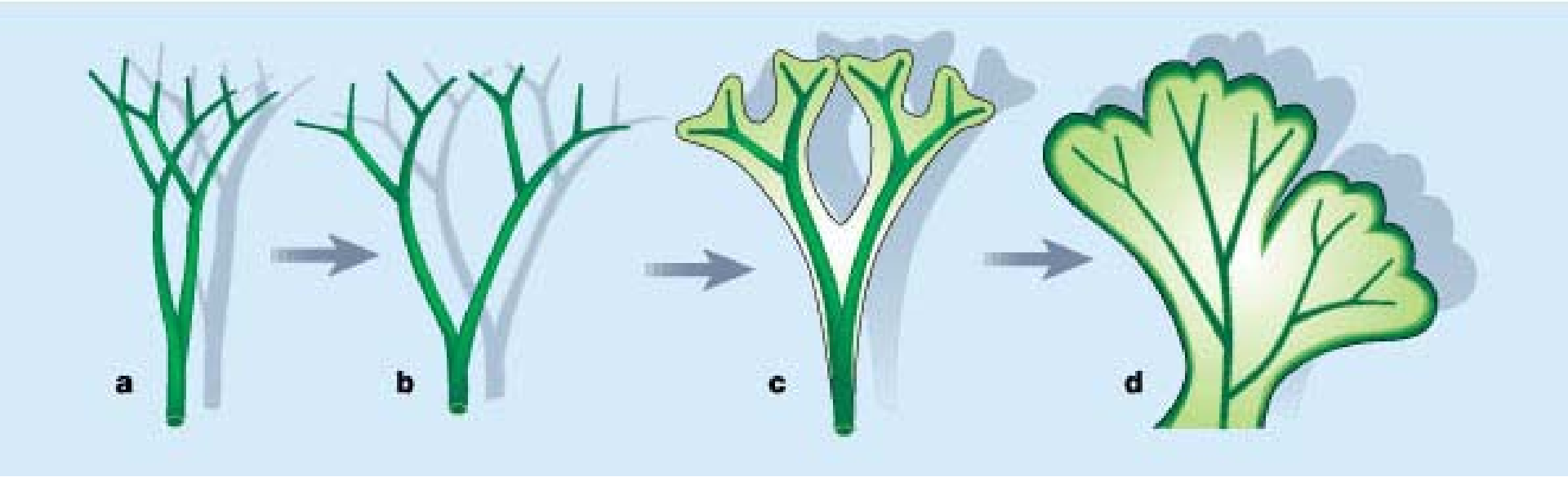

Carboniferous
Devonian
http://emsepochsete.com/Paleozoic/Carboniferous/carb_home.html


siphonostele
protostele
eustele
polystele
actinostele



Diagrammetic representation of the evolution of leaves and reproductive structures according to telom theory. (Botanical World: Northington and Schneider 1

Leaf evolution

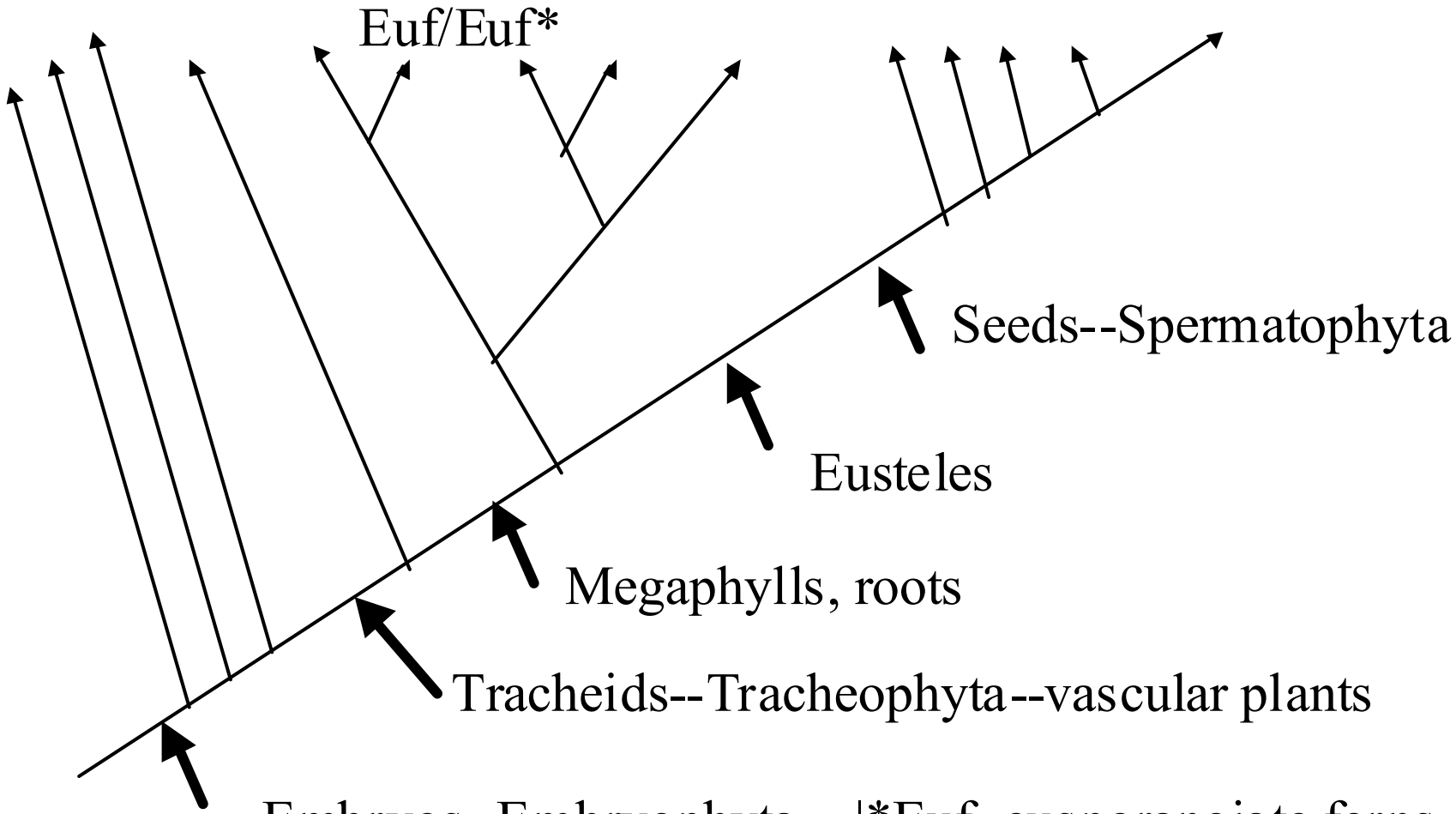


Fossil evidence shows that megaphylls evolved from simple, leafless photosynthetic branching systems in early land plants (a, b) to dissected (c) and laminate (d) leaves over a period of at least 40 million years. (Beerling, Osborne & Chaloner. 2001. Nature 410:352-354)

The new phylogeny

Pryor, et al., 2001. Nature 409: 618-622

Mosses		Ferns & Fern Allies			Seed plants	
Bryo (s.l.)	Lyco	Psilo	Spheno	Ptero	Gymnosperms	Angiosperms



|*Euf=eusporangiate ferns

Alamhmk *Euphyllophytina*

- Ülemkl *Moniliformopses*

  Klass ürgsõnajalad *Cladoxylopsida*

  Klass kidad *Equisetopsida* e *Sphenopsida*

  Klass keerdlehikud *Filicopsida*
- Ülemkl *Radiatopses*

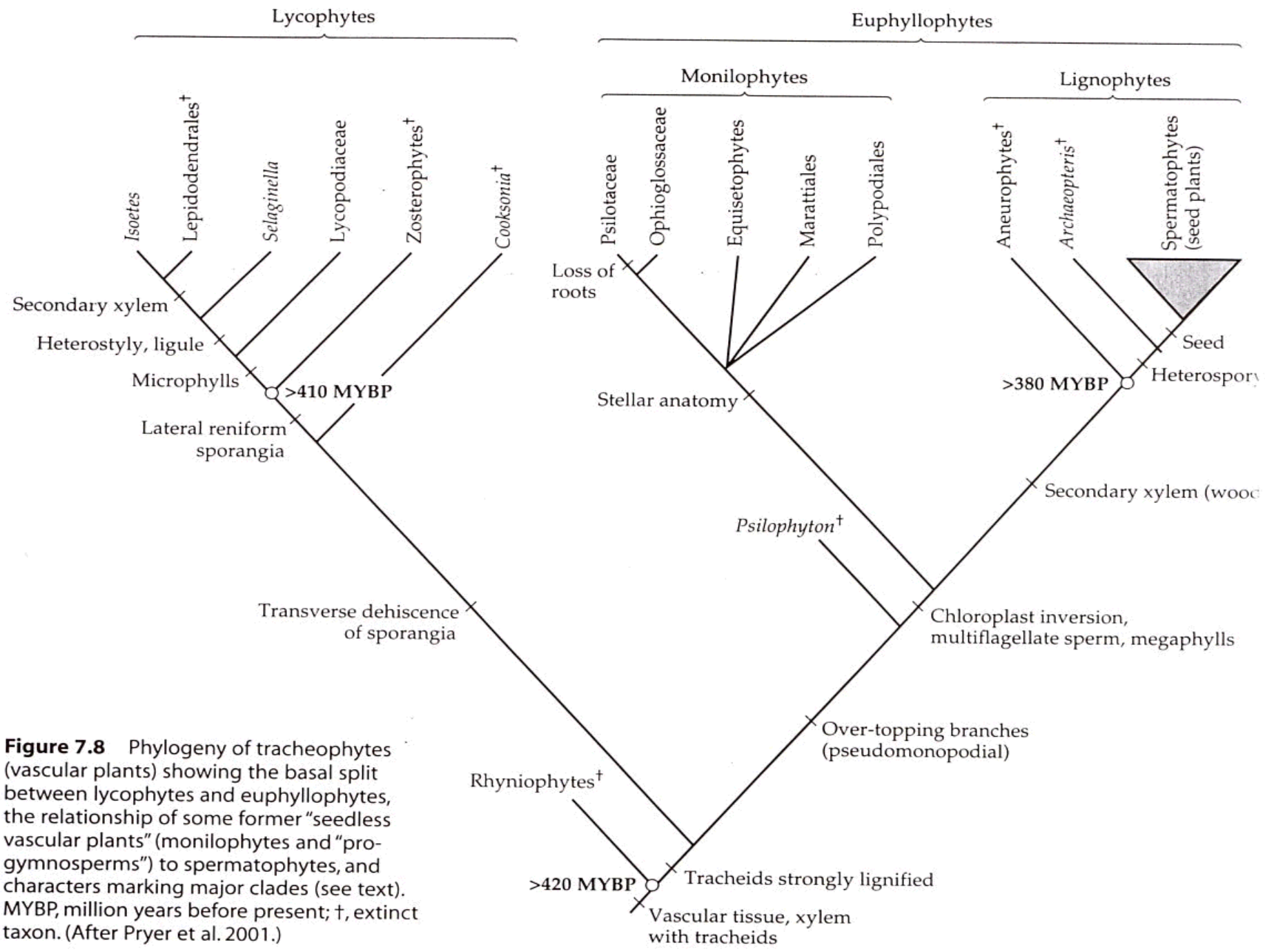
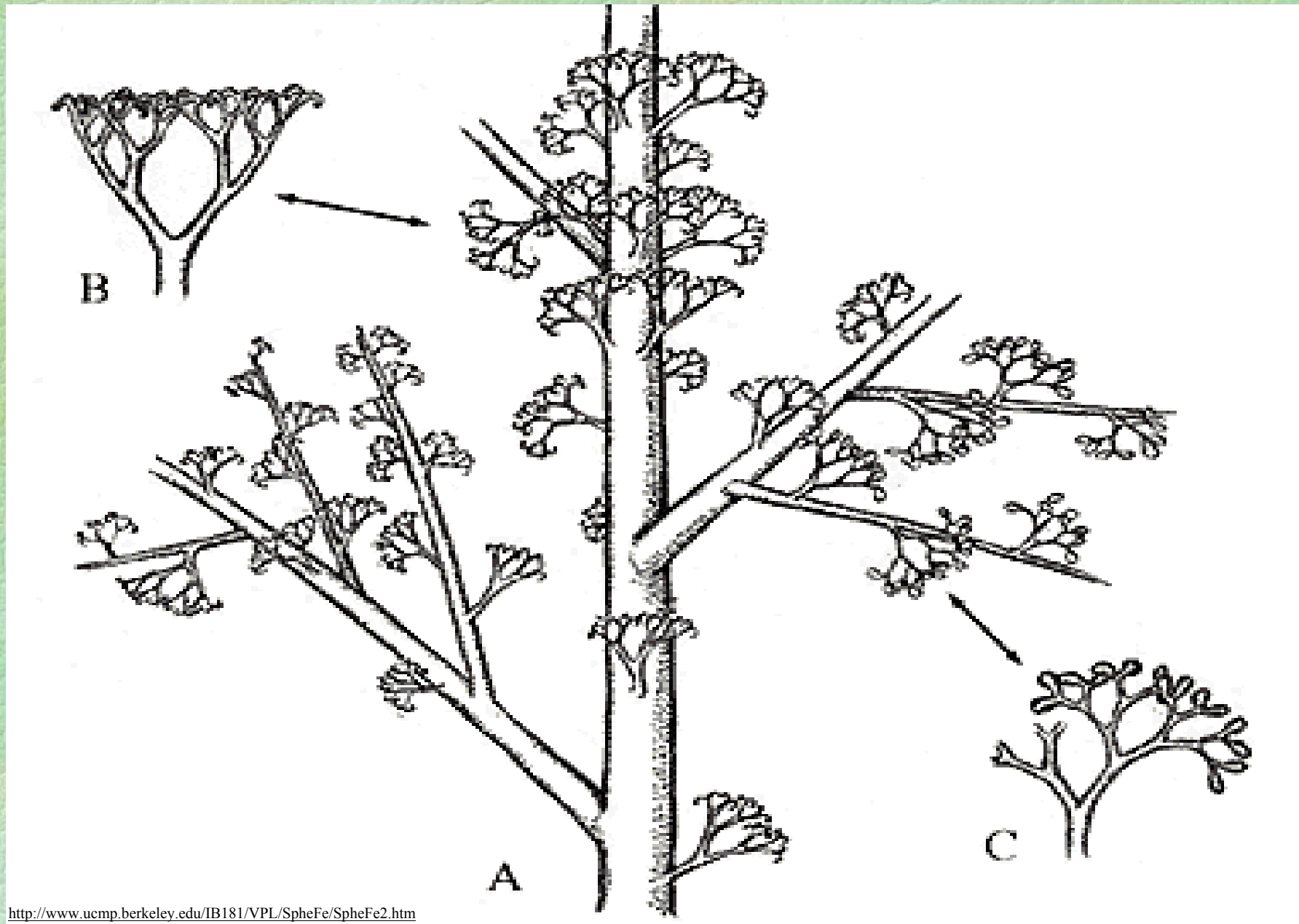
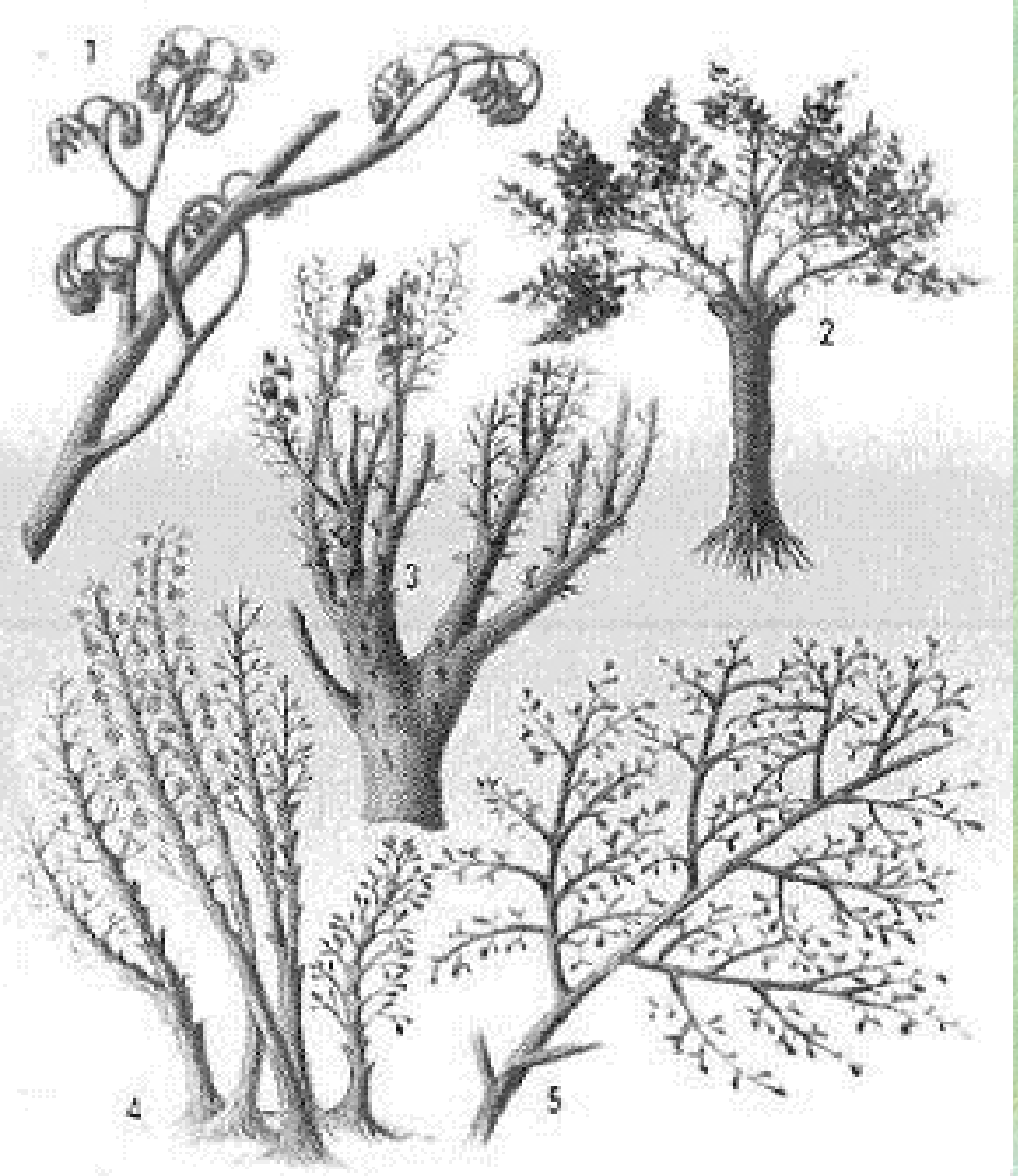


Figure 7.8 Phylogeny of tracheophytes (vascular plants) showing the basal split between lycophytes and euphyllophytes, the relationship of some former "seedless vascular plants" (monilophytes and "progymnosperms") to spermatophytes, and characters marking major clades (see text). MYBP, million years before present; †, extinct taxon. (After Pryer et al. 2001.)

Kidad – Sphenopsida: *Ibyka*



http://www.ucmp.berkeley.edu/IB181/VPL/SpheFe/SpheFe2.htm

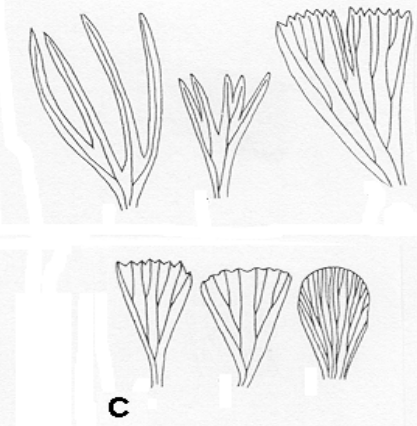

1
2
3
4
5

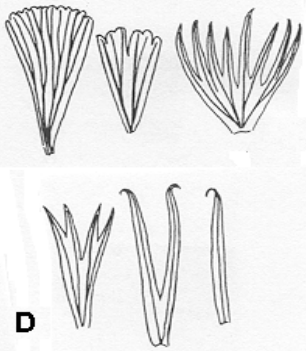
Ürgkidalaaadsed: *Hyenia* ja *Calamophyton*

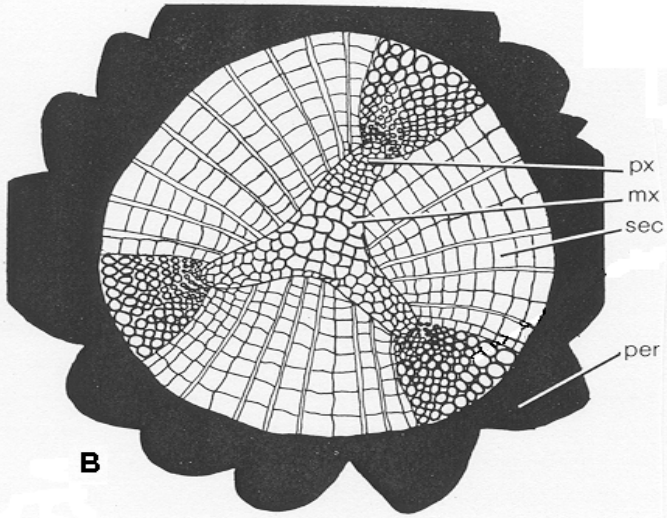
http://www.ucmp.berkeley.edu/IB181/VPL/SpheFe/SpheFeVGI.html

http://www.ucmp.berkeley.edu/plants/cladoxylopsida/cladoxylopsida.html

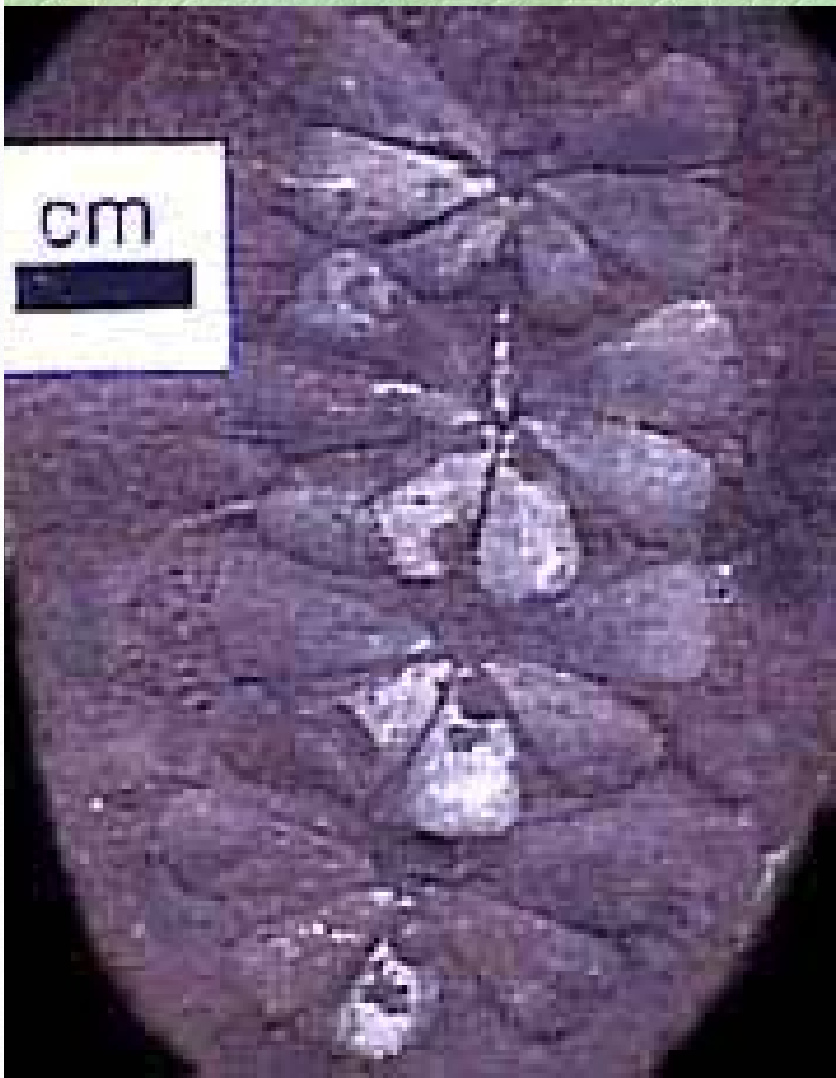
Talblehik – Sphenophyllum



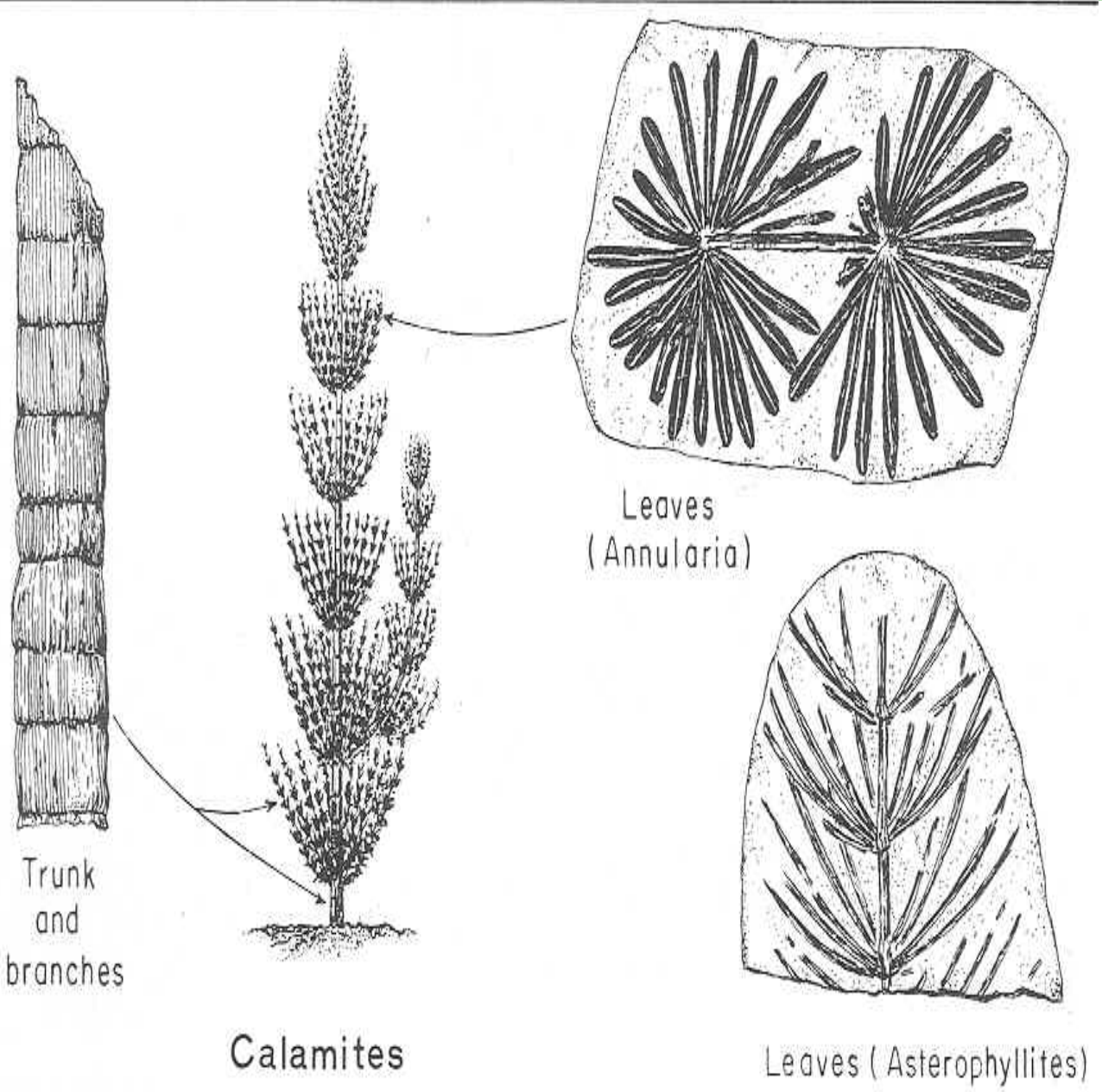


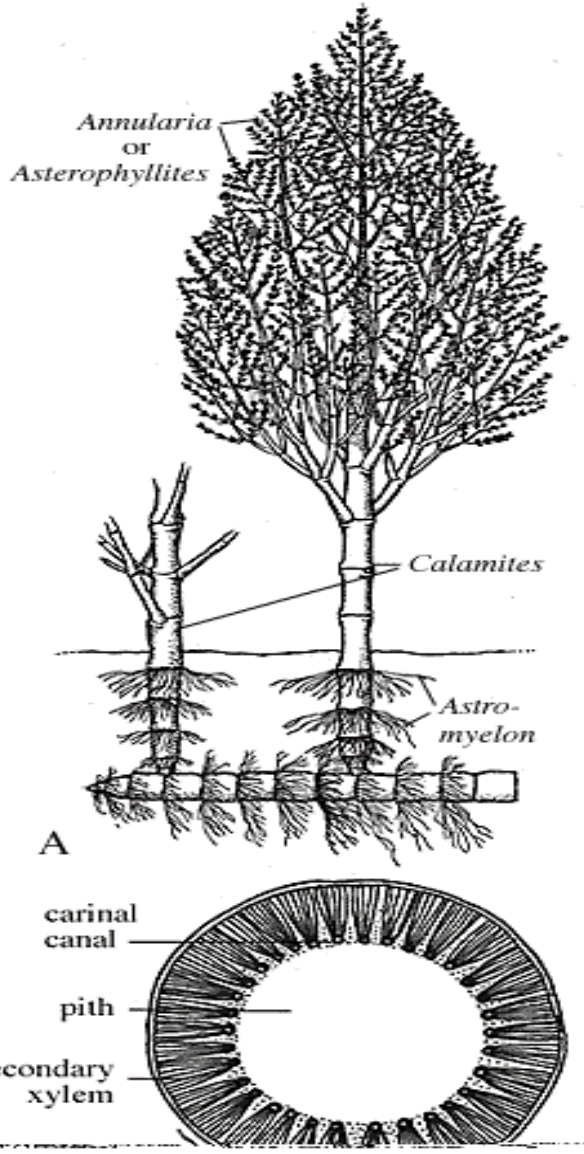


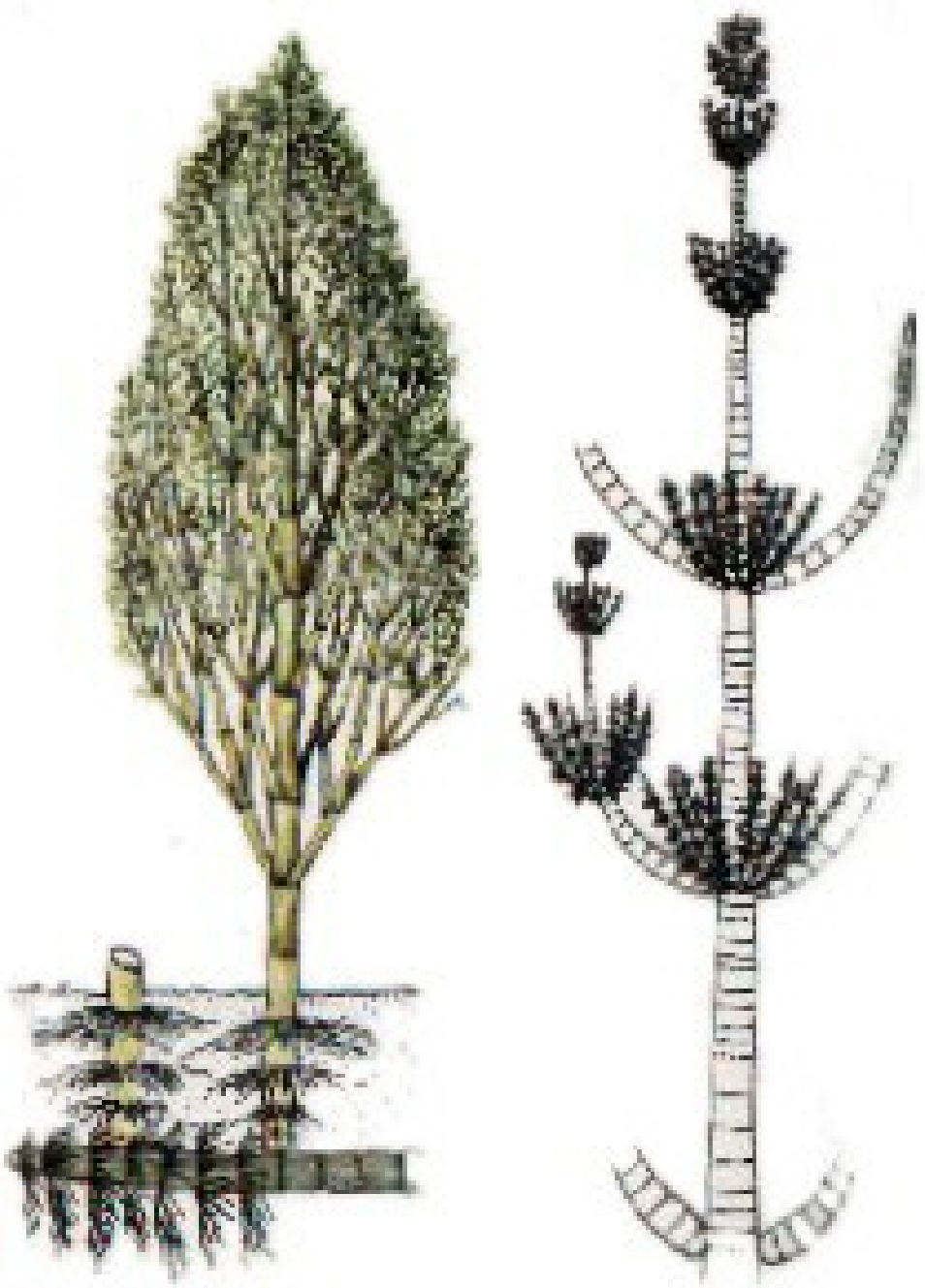
accessscience.com



Kalamiidilaadsed - *Calamitales*





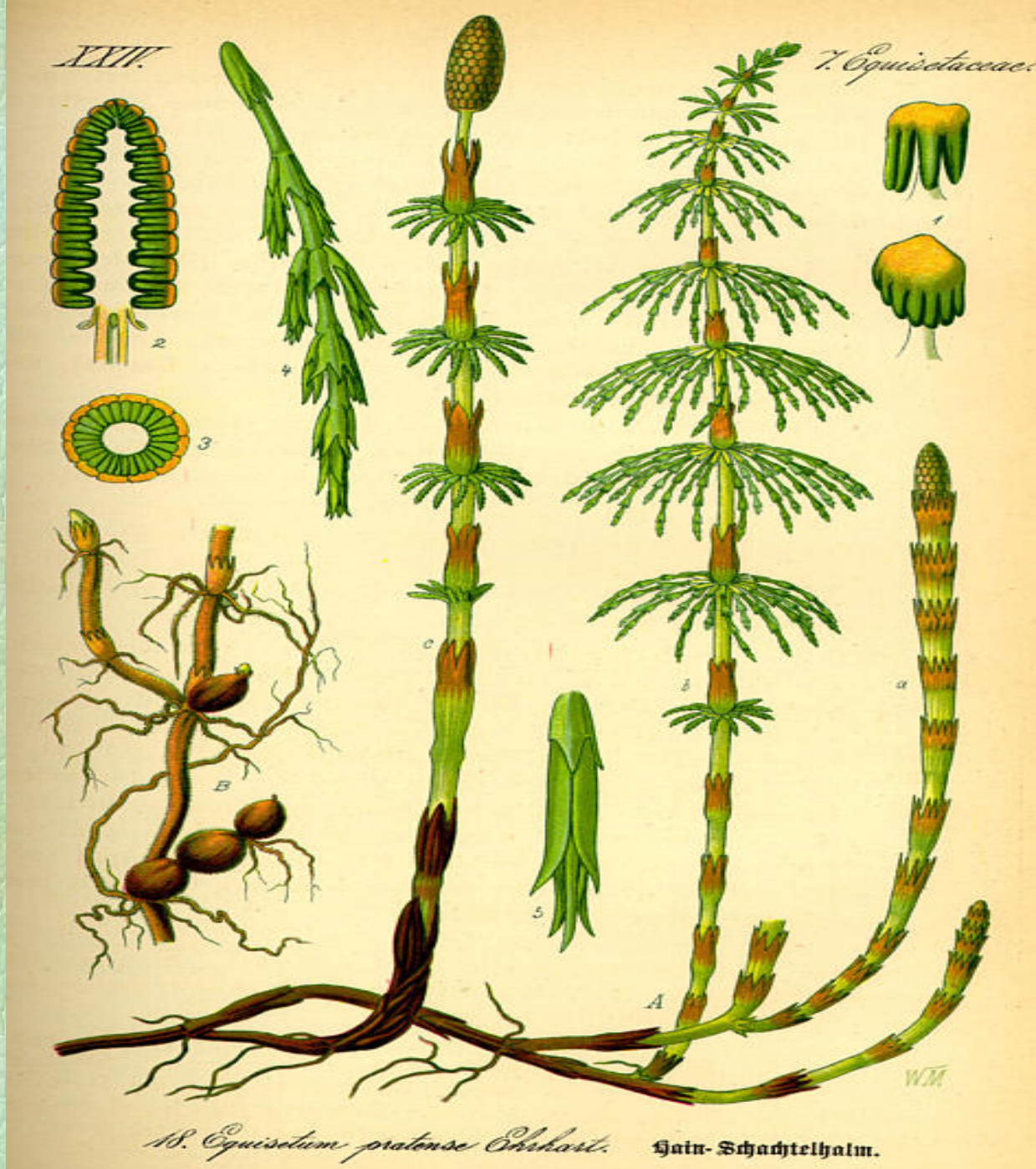


ricostruzione di Calamites

Equisetales

Equise-taceae

Equisetum

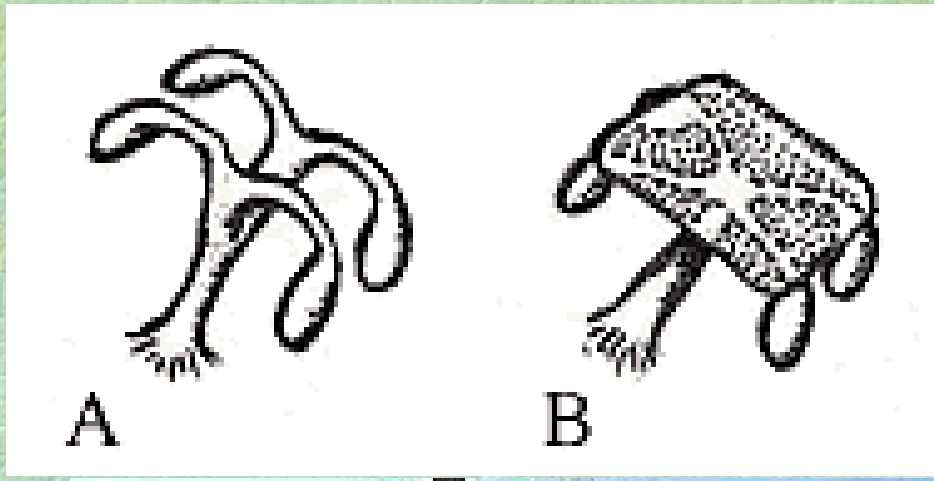


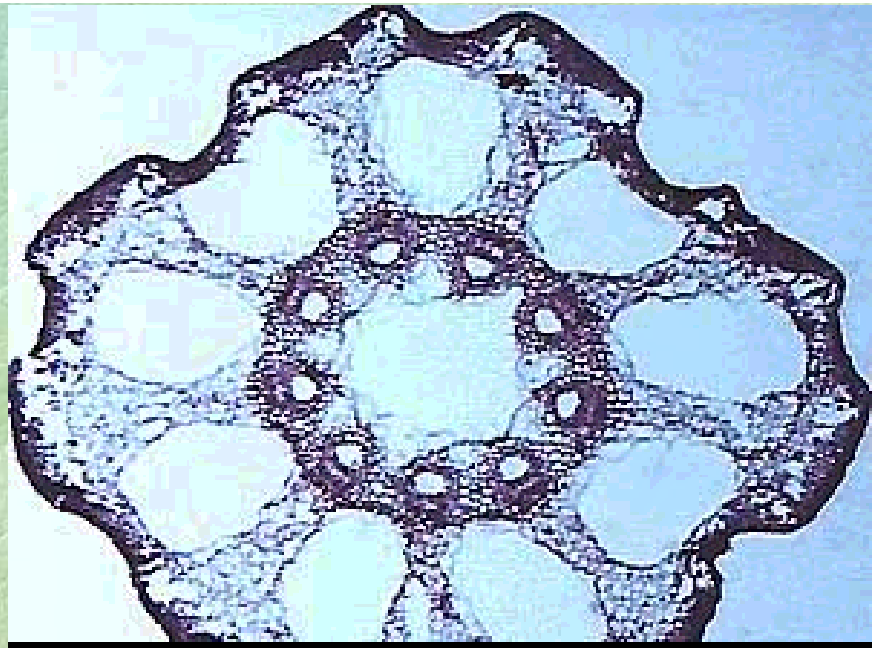
http://caliban.mpiz-koeln.mpg.de/thome/band1/tafel_018_small.jpg

Equisetum arvense

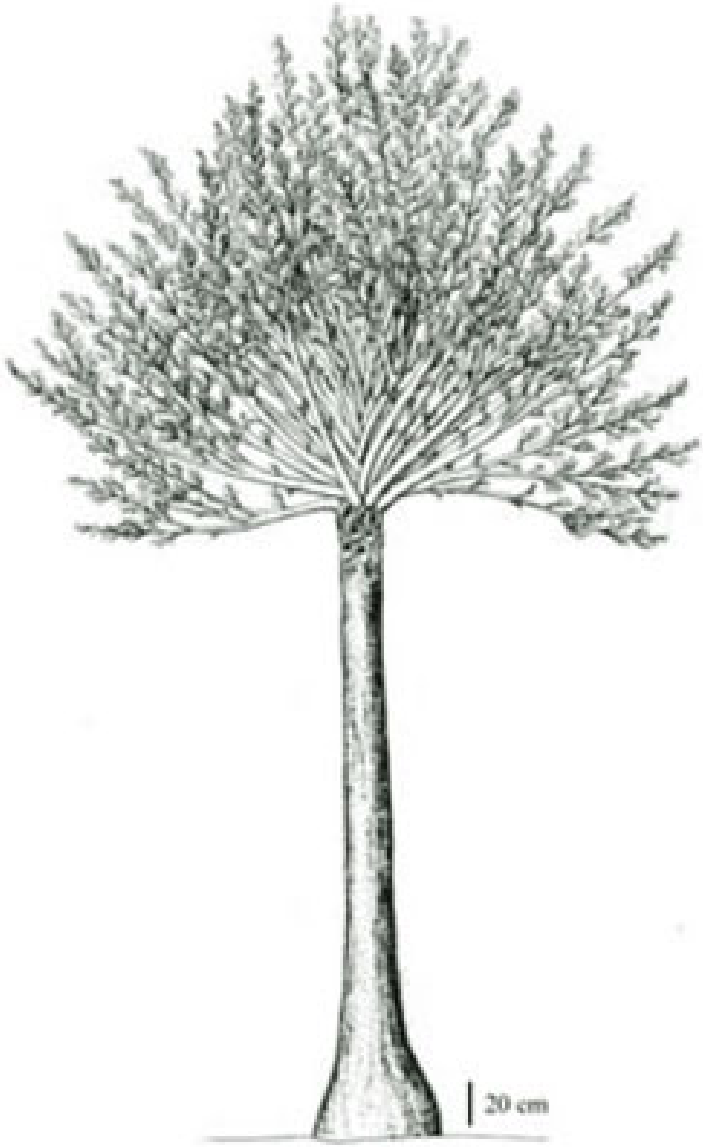
Equisetaceae

Equisetum giganteum





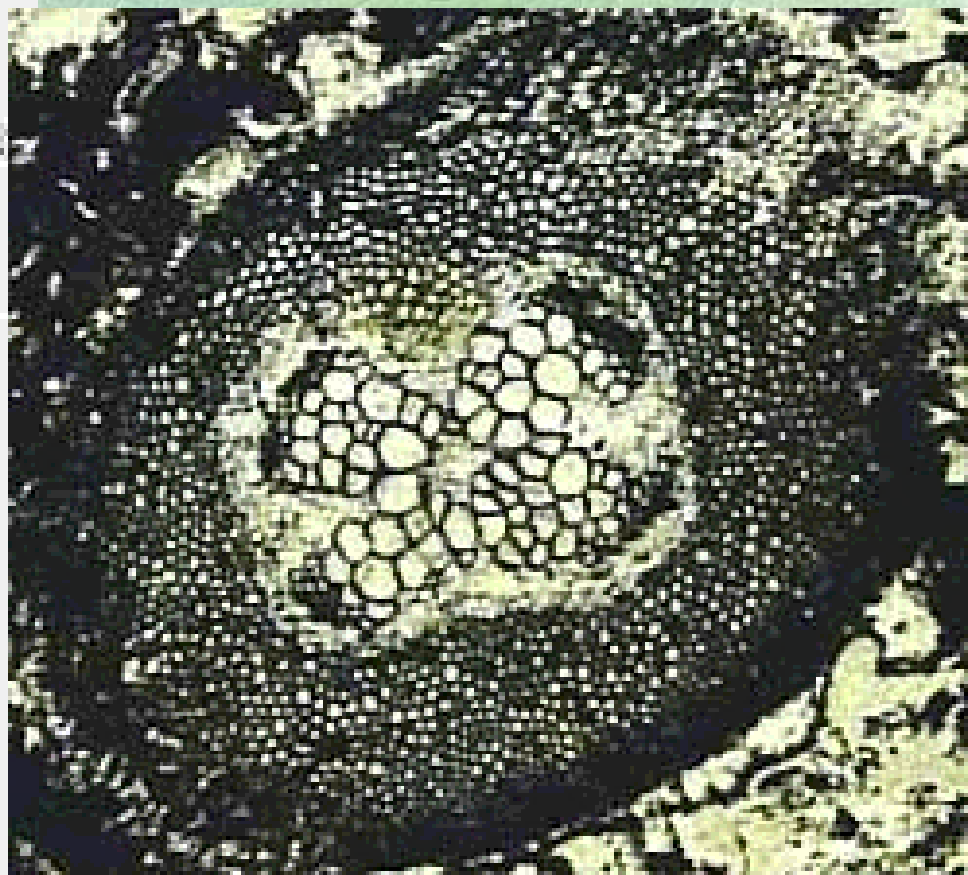
Cladoxylopsida: *Pseudosporochnus*



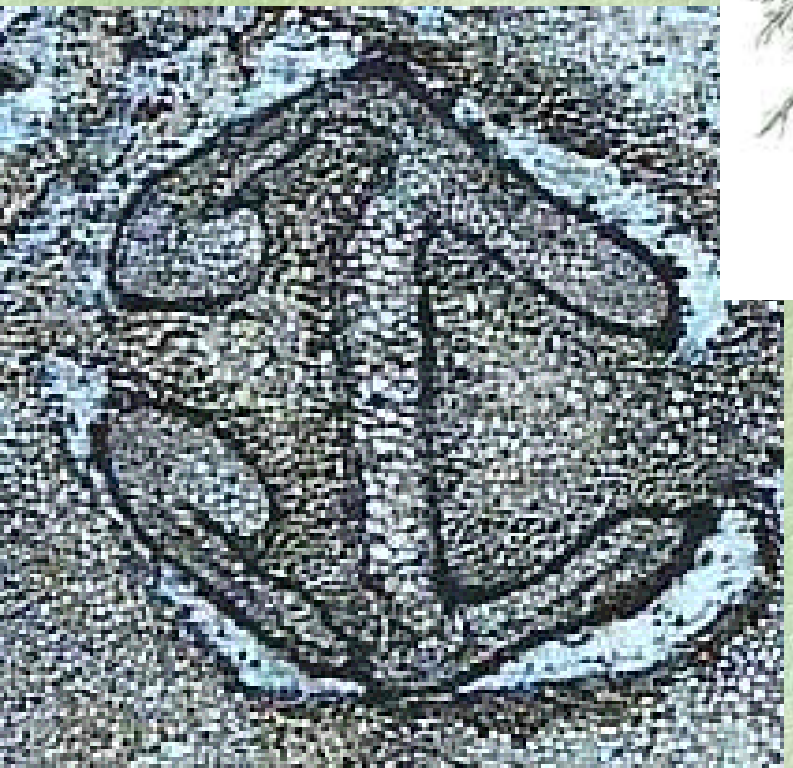
futura-sciences.com

Ristsõnajalg - *Stauropteris*

http://www.ucmp.berkeley.edu/IB181/VPL/SpheFe/SpheFeVGII.html



Seigsõnajalad - *Zygopteris, Rhacophytron*

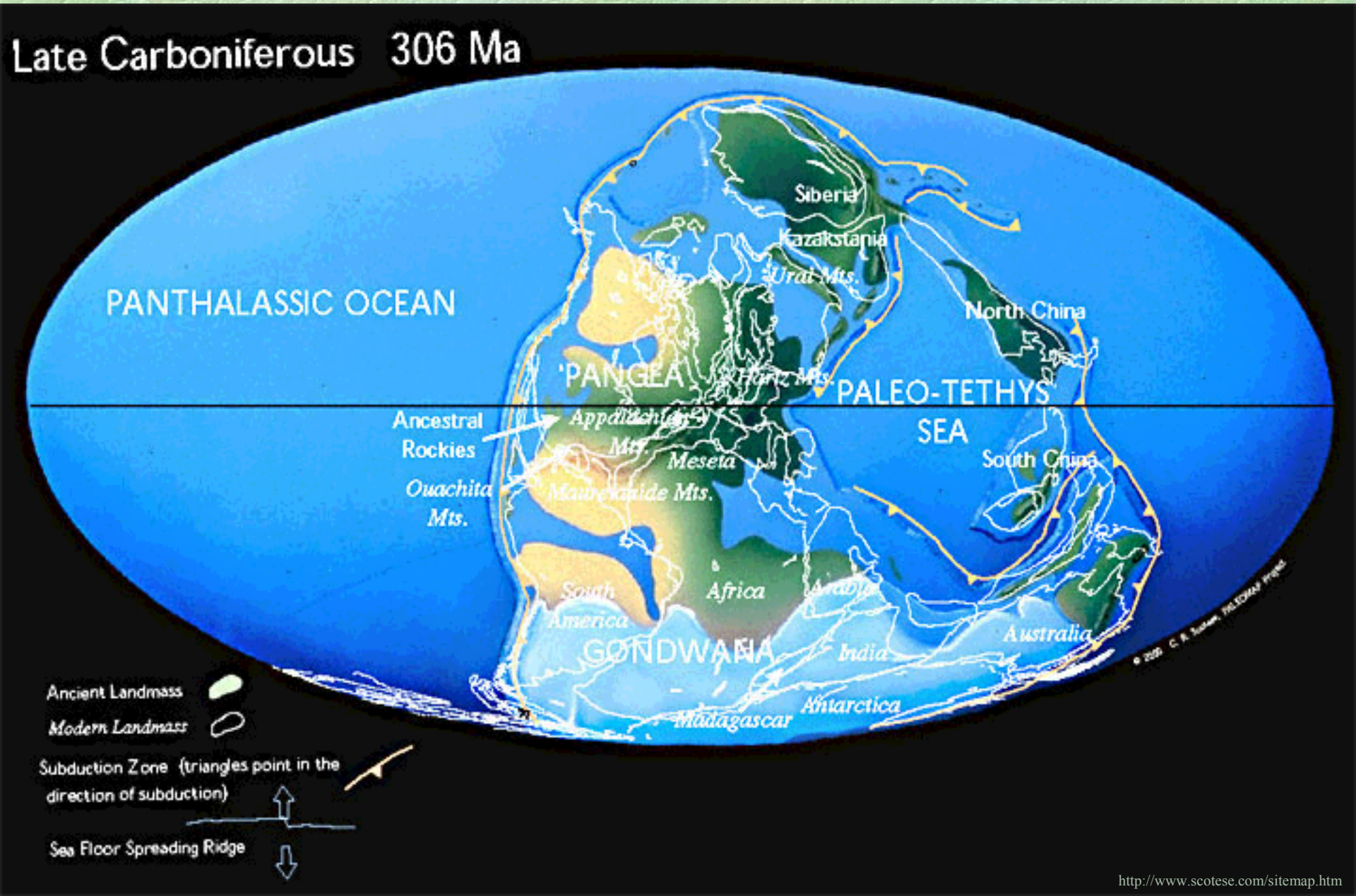


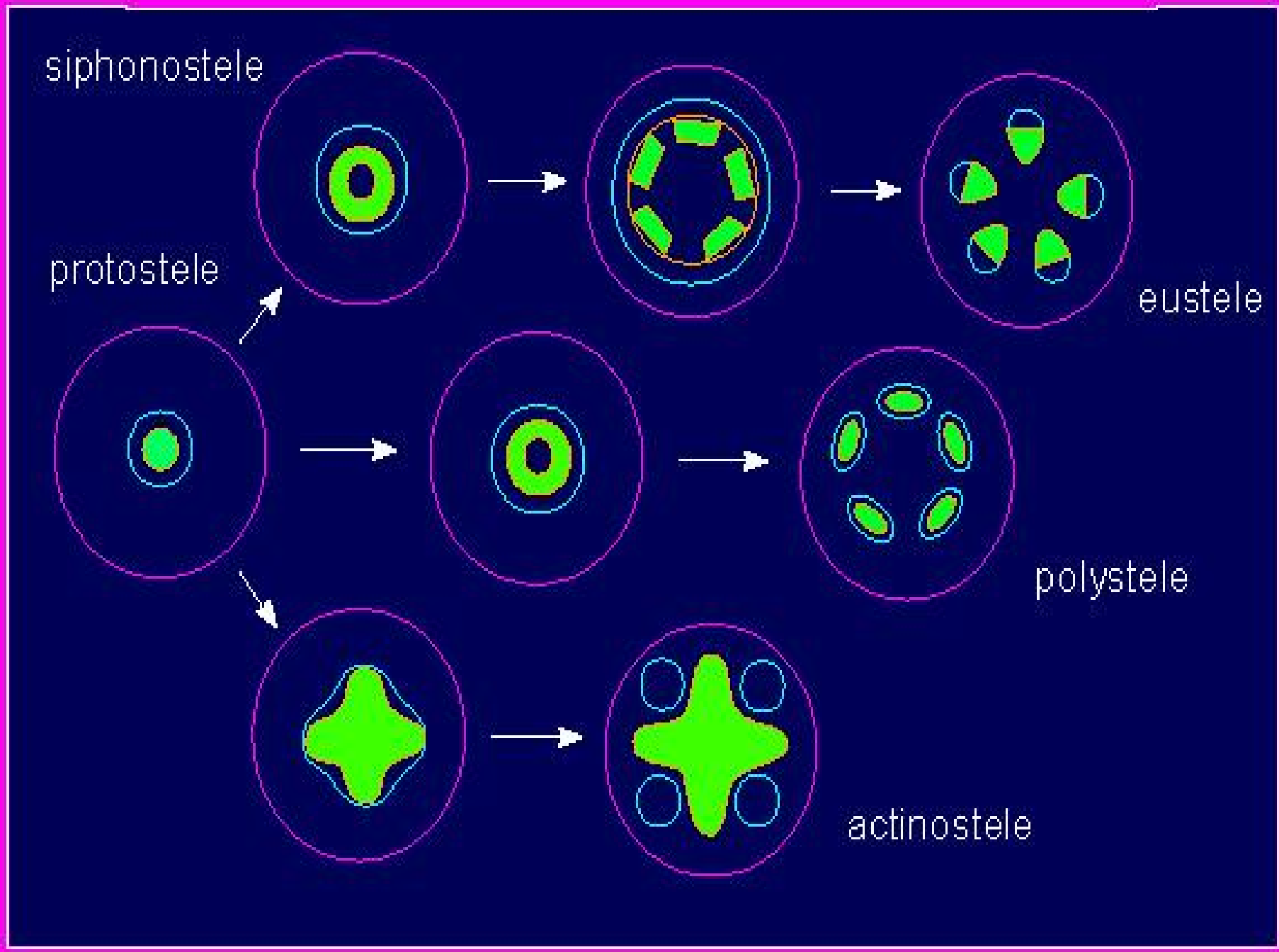
http://www.devoniantimes.org/who/pages/rhacophyton.html

Karboni ajastu mets

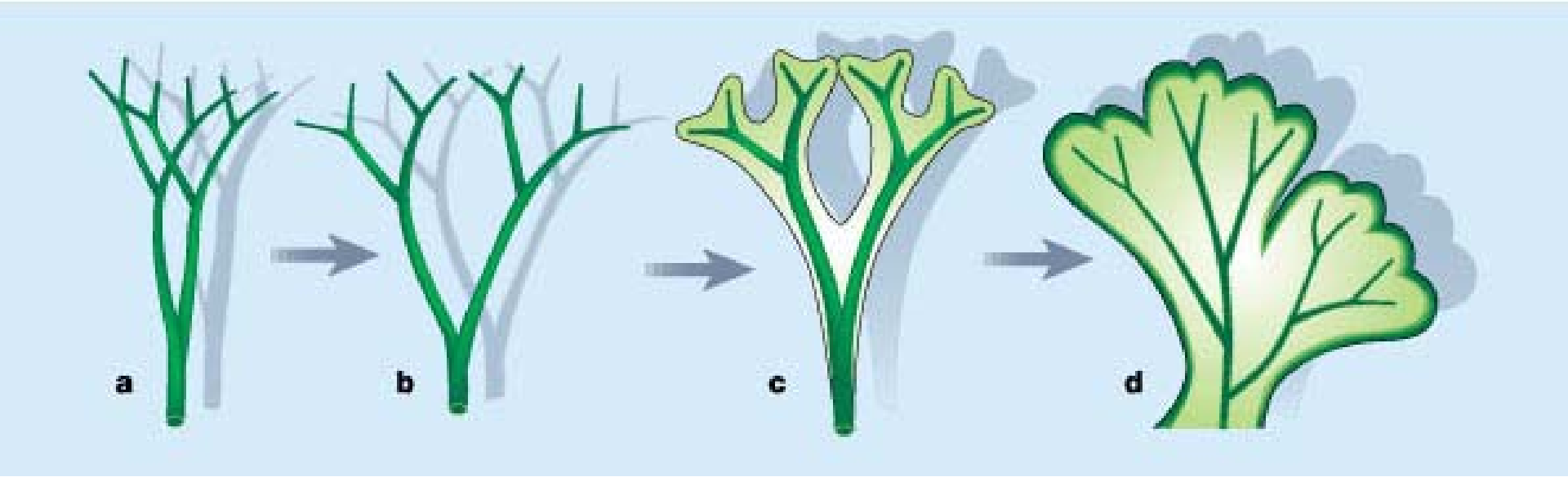
Alamhõimkond pärislehttaimed *Euphyllophytina*

Mandrid Karbonis





Leaf evolution

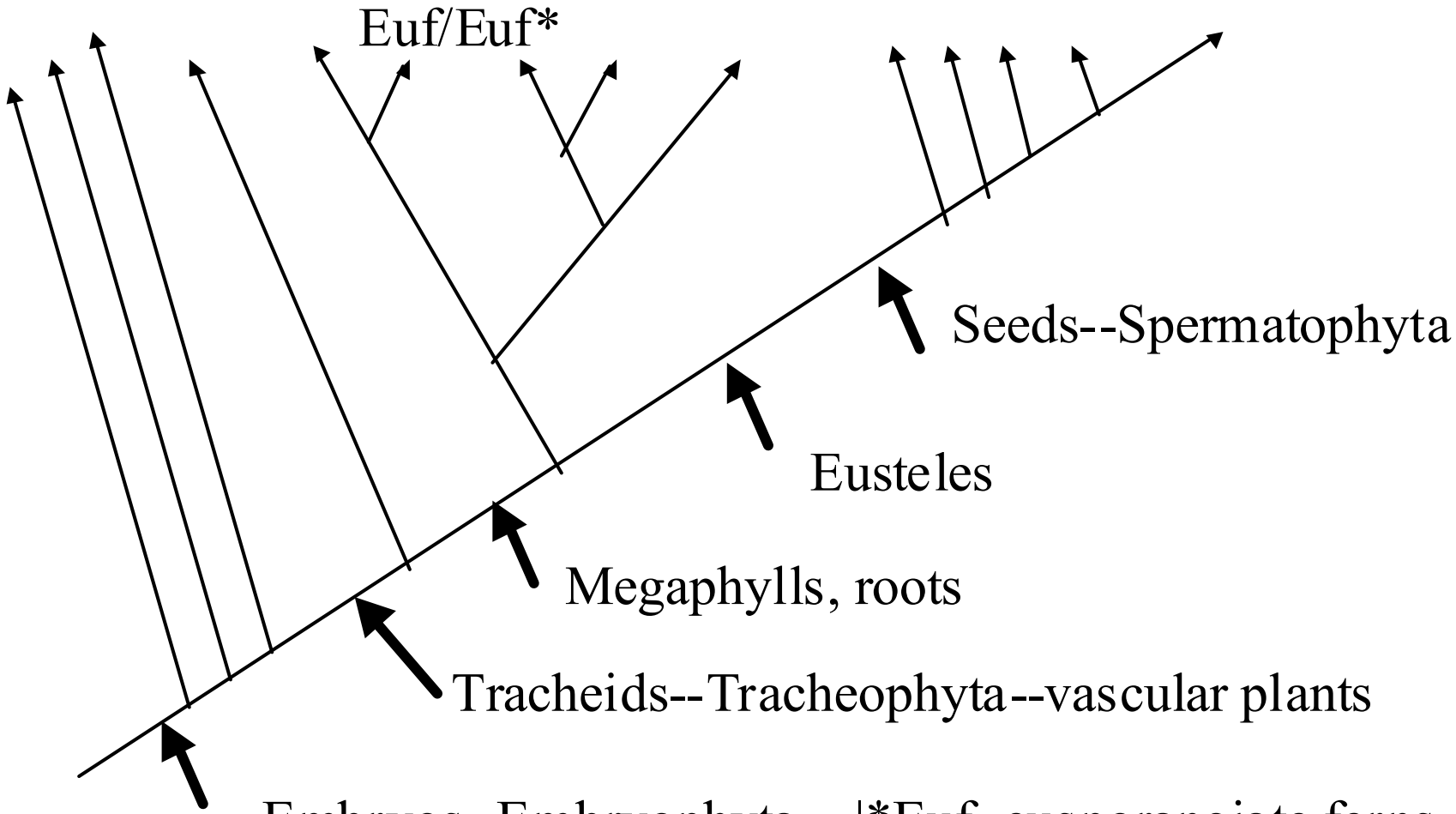


Fossil evidence shows that megaphylls evolved from simple, leafless photosynthetic branching systems in early land plants (a, b) to dissected (c) and laminate (d) leaves over a period of at least 40 million years. (Beerling, Osborne & Chaloner. 2001. Nature 410:352-354)

The new phylogeny

Pryor, et al., 2001. Nature 409: 618-622

Mosses		Ferns & Fern Allies			Seed plants	
Bryo (s.l.)	Lyco	Psilo	Spheno	Ptero	Gymnosperms	Angiosperms



|*Euf=eusporangiate ferns

Alamhmk Euphyllophytina

- Ülemkl *Moniliformopses*

  Klass ürgsõnajalad *Cladoxylopsida*

  Klass kidad *Equisetopsida* e *Sphenopsida*

  Klass keerdlehikud *Filicopsida*
- Ülemkl *Radiatopses*

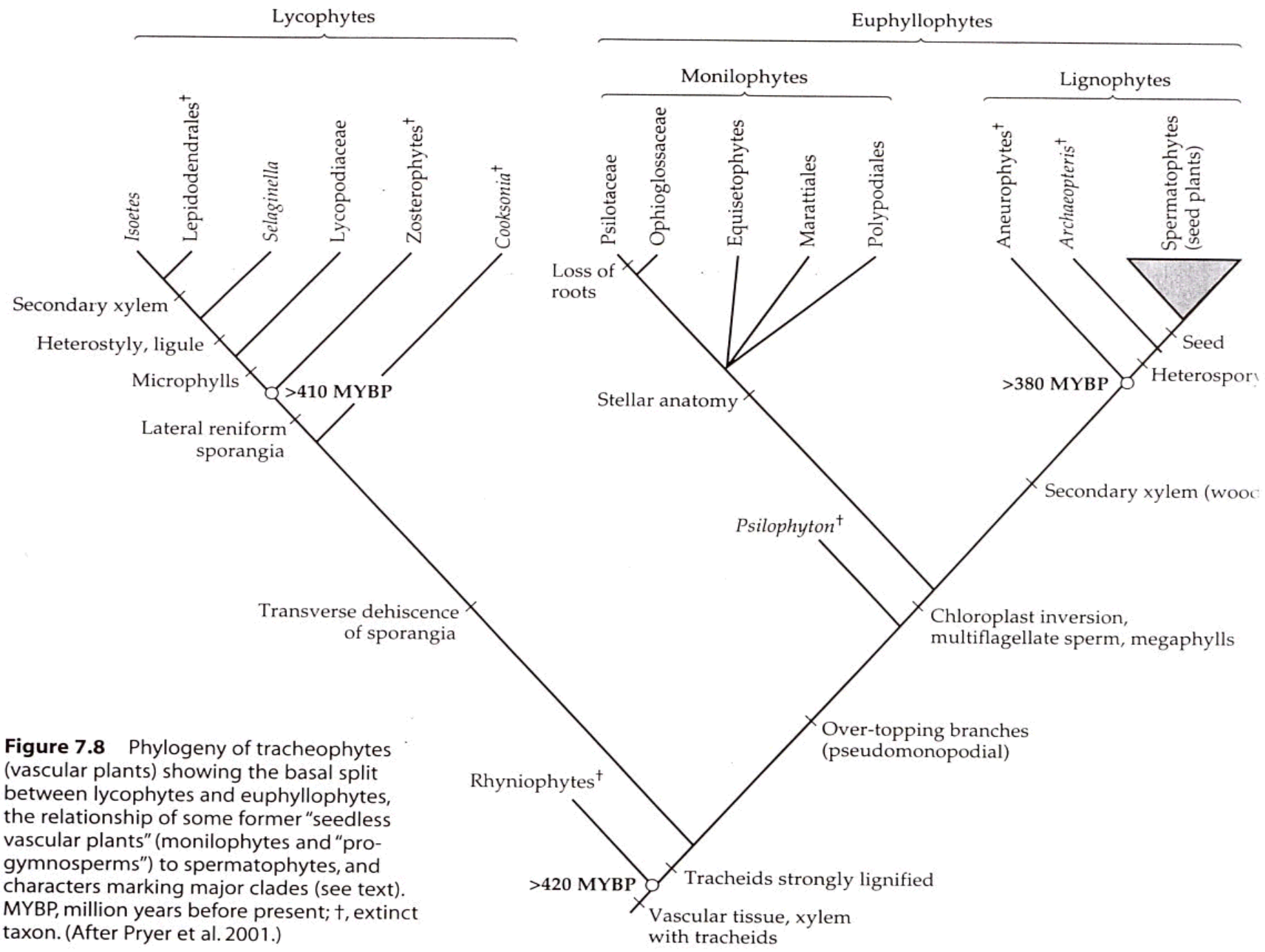


Figure 7.8 Phylogeny of tracheophytes (vascular plants) showing the basal split between lycophytes and euphyllophytes, the relationship of some former "seedless vascular plants" (monilophytes and "progymnosperms") to spermatophytes, and characters marking major clades (see text). MYBP, million years before present; †, extinct taxon. (After Pryer et al. 2001.)

Kidad Sphenopsida

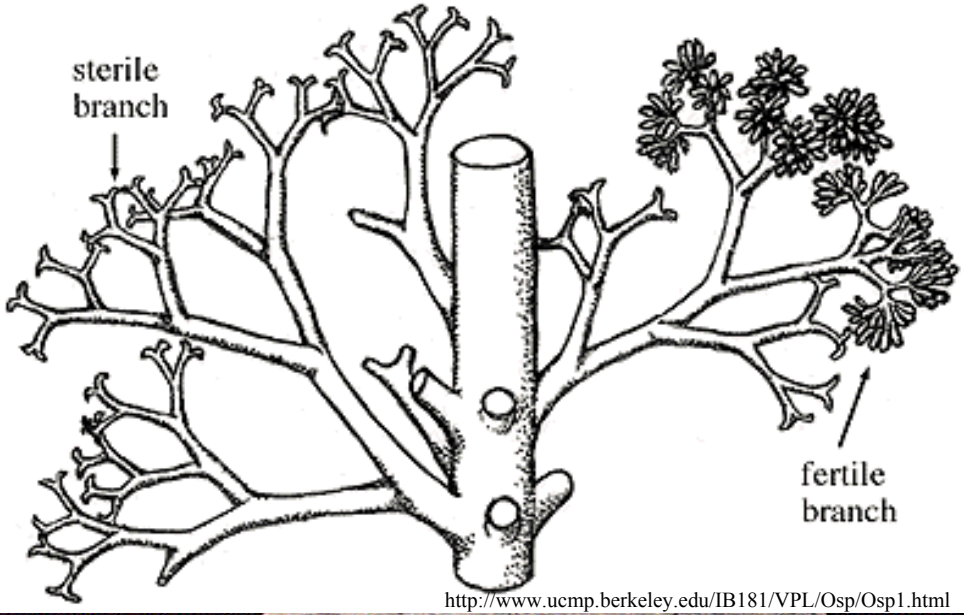
- Ürgkidalaadsed *Hyeniales*†
- Talblehikulaadsed *Sphenophyllales*†
- Kalamiidilaadsed *Calamitales*†
- Alamkl osjad *Equisetidae*

Ürgraikad: Psilophyton dawsonii

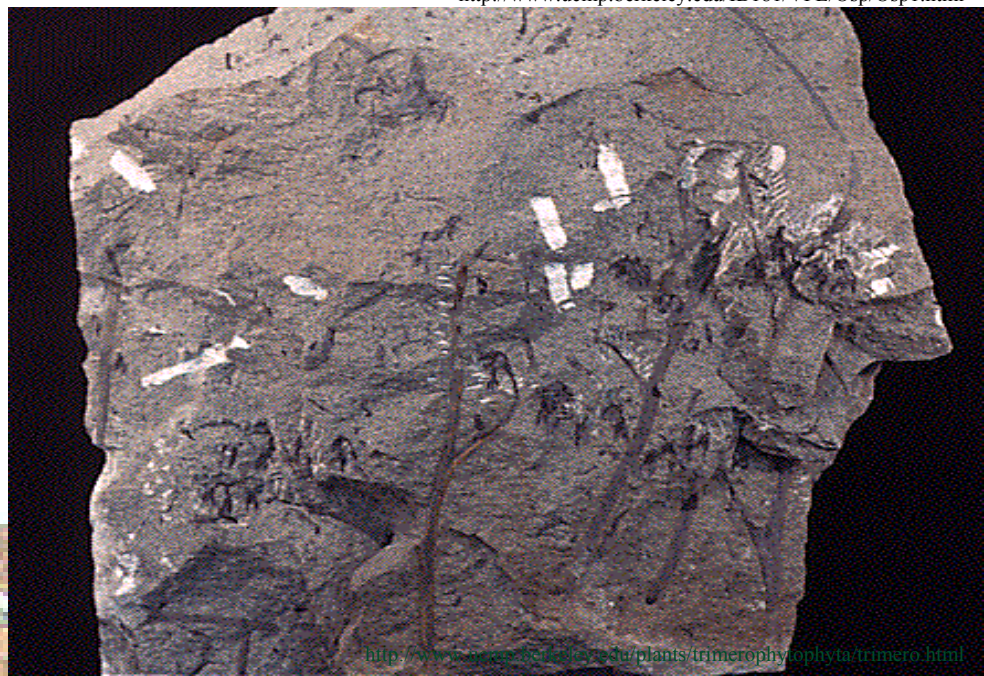
Monopodiaalne harunemine

Eufüllofüüt?

http://taggart.glg.msu.edu/isb200/fland.htm

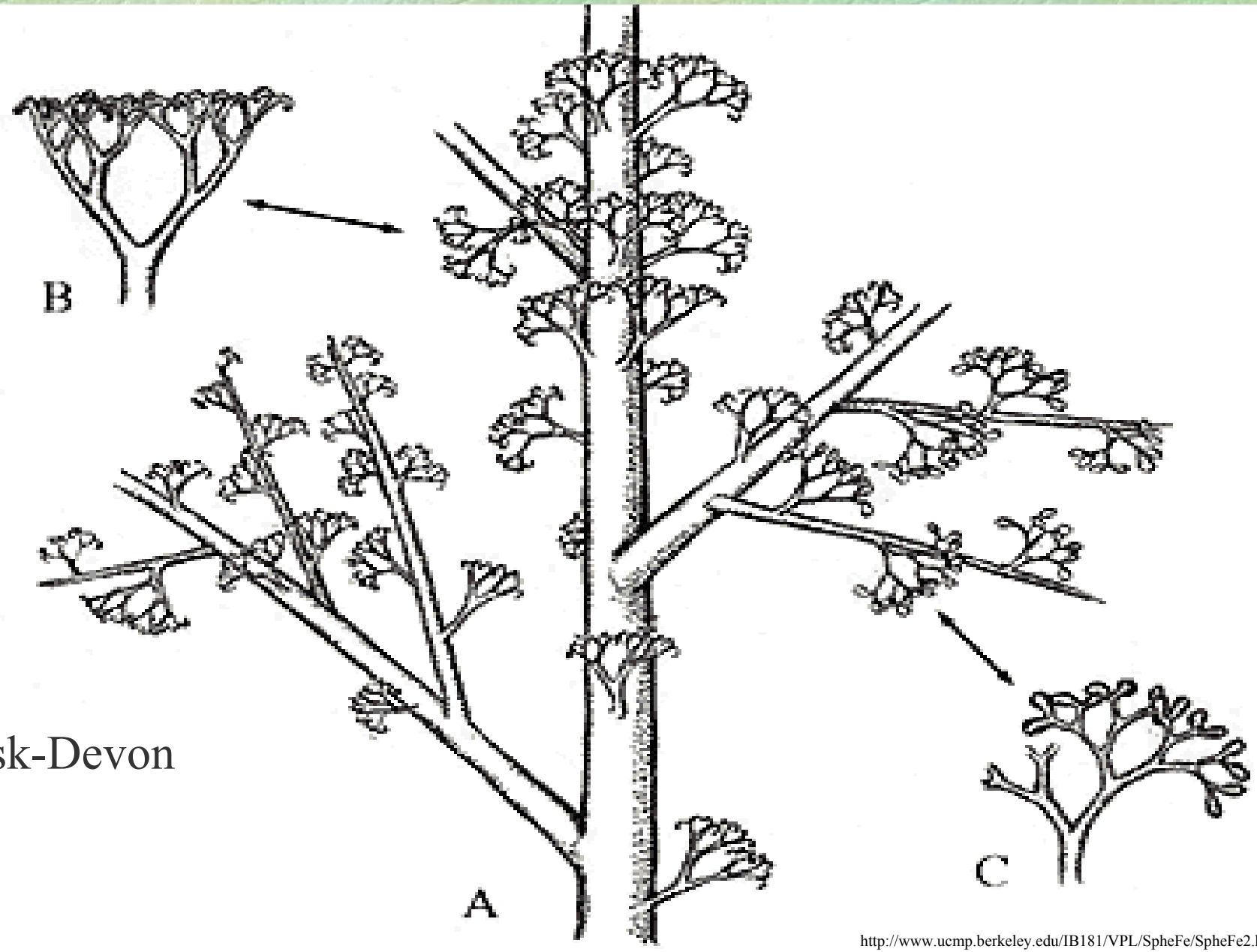


http://www.ucmp.berkeley.edu/IB181/VPL/Osp/Osp1.html



http://www.ucmp.berkeley.edu/plants/trimerophytophyta/trimero.html

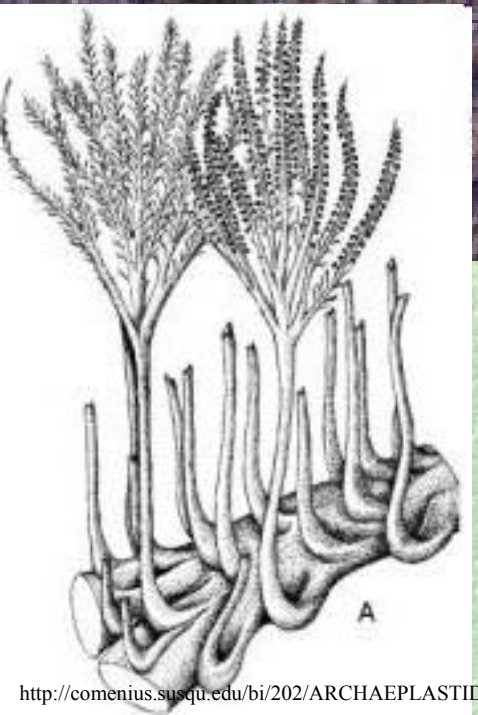
Ibyka

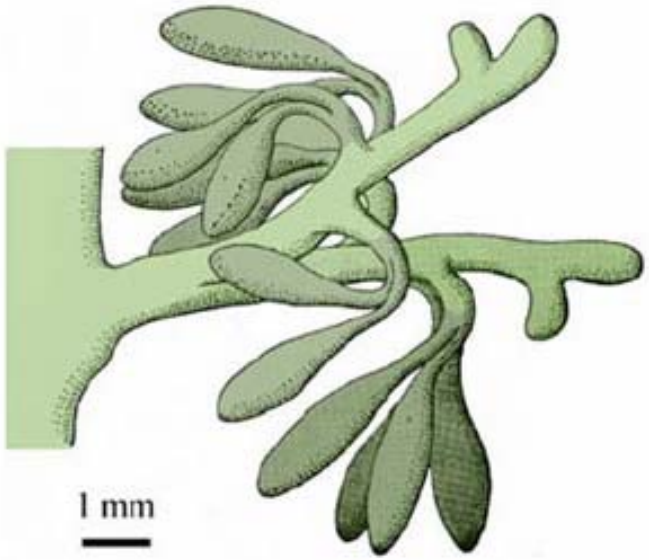


Kesk-Devon

http://www.ucmp.berkeley.edu/IB181/VPL/SpheFe/SpheFe2.html

Ürgkidalaadsed: Hyenia *ja* Calamophyton

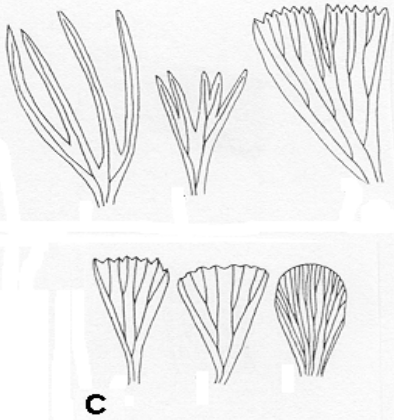


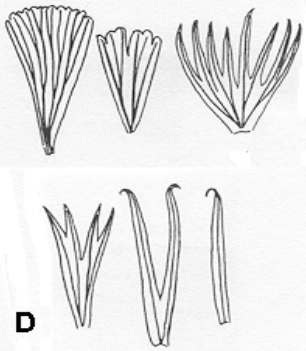


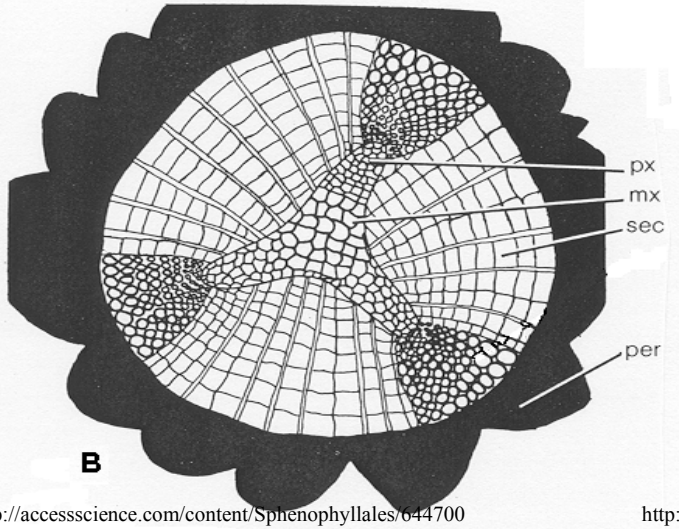
http://comenius.susqu.edu/bi/202/ARCHAEPLASTIDA/VIRIDIPLANTAE/Vascular%20Cryptogams/PTERIDOPHYTA/pteridophyta.htm

http://www.ucmp.berkeley.edu/IB181/VPL/SpheFe/SpheFe1.html

Talblehik – Sphenophyllum

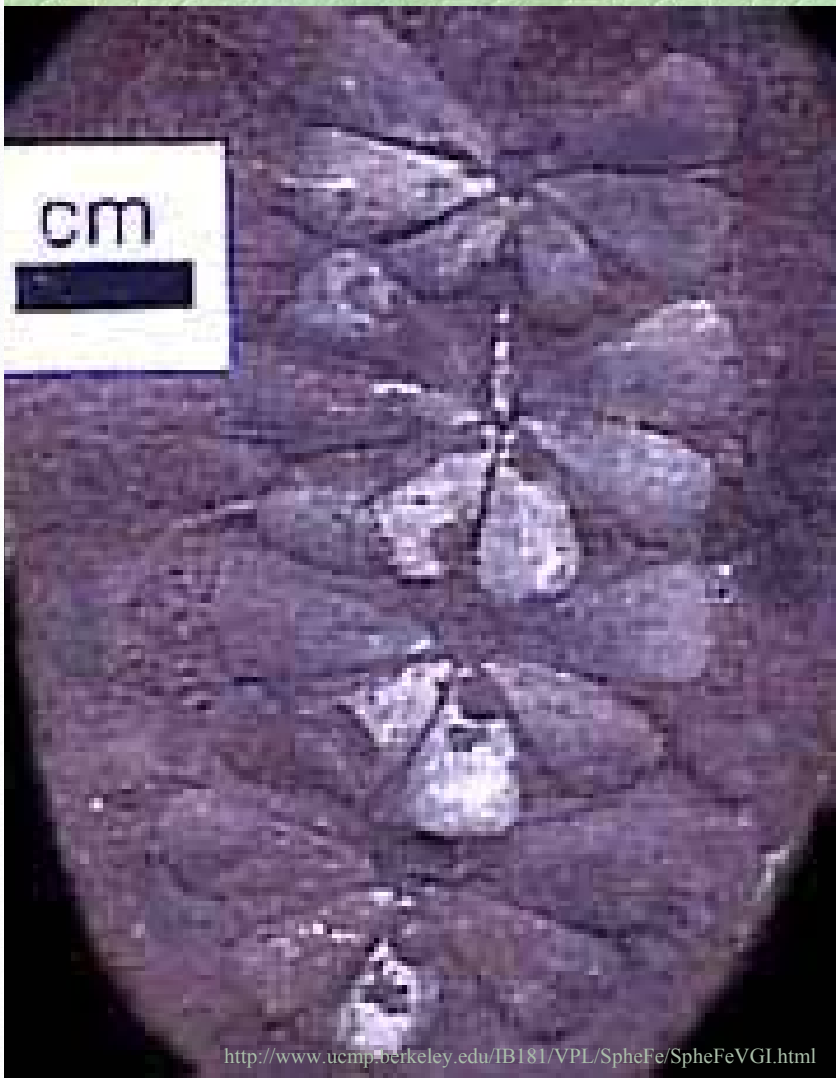






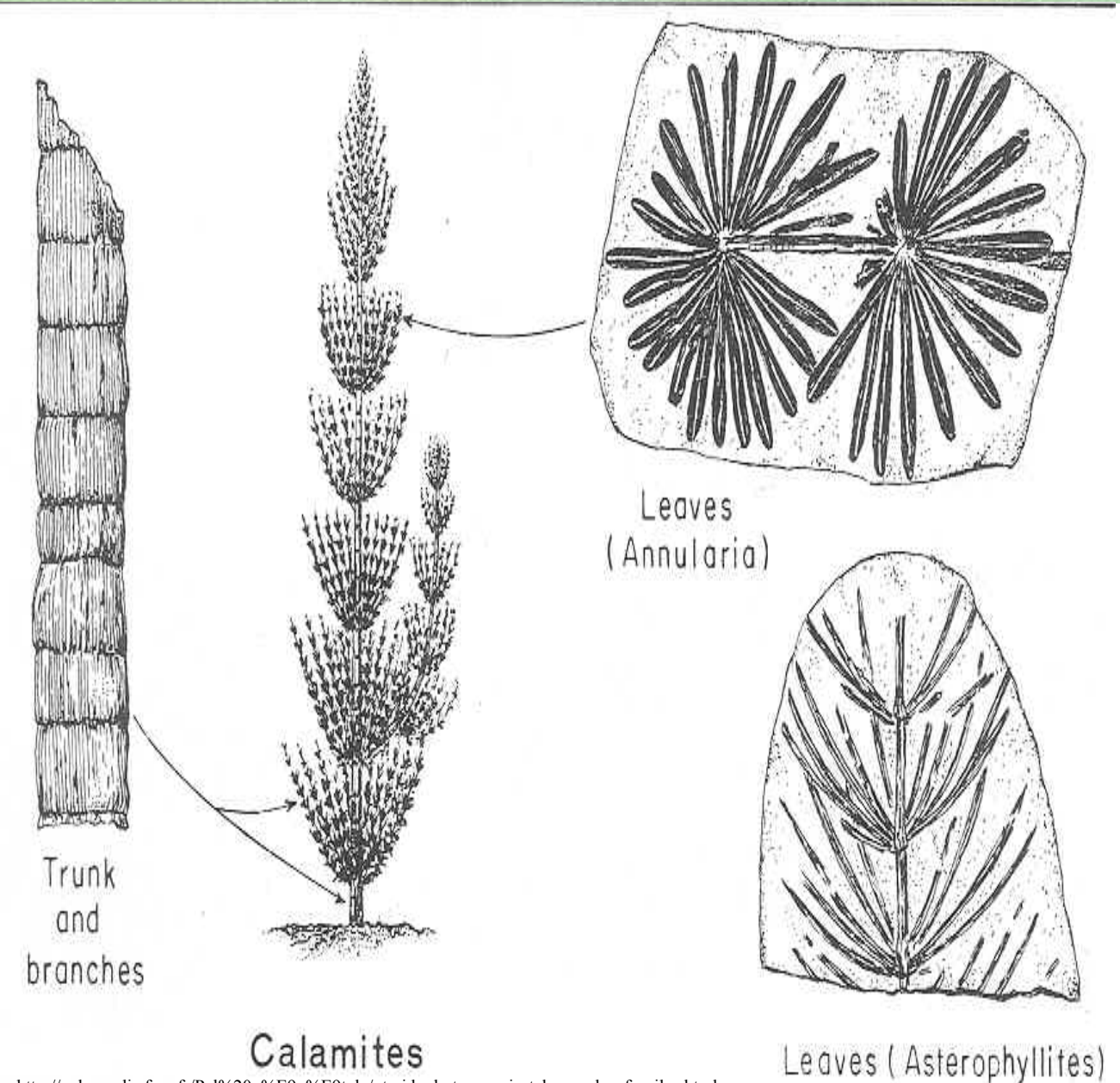
http://accessscience.com/content/Sphenophyllales/644700

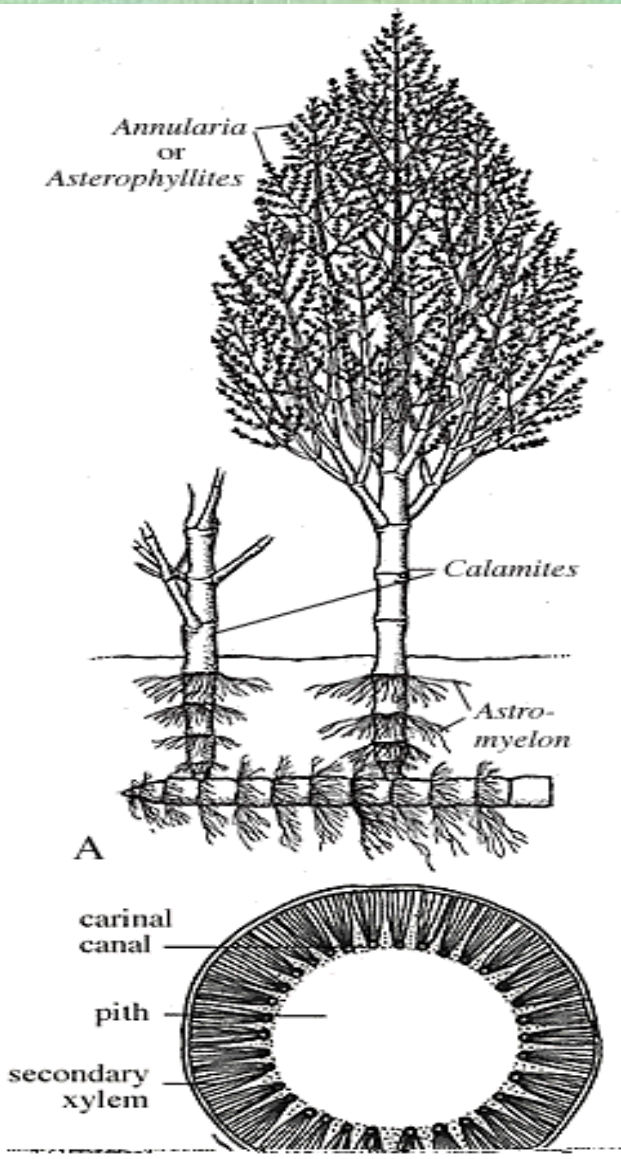
http://images.botany.org/set-18/png5.html



http://www.ucmp.berkeley.edu/IB181/VPL/SpheFe/SpheFeVGI.html

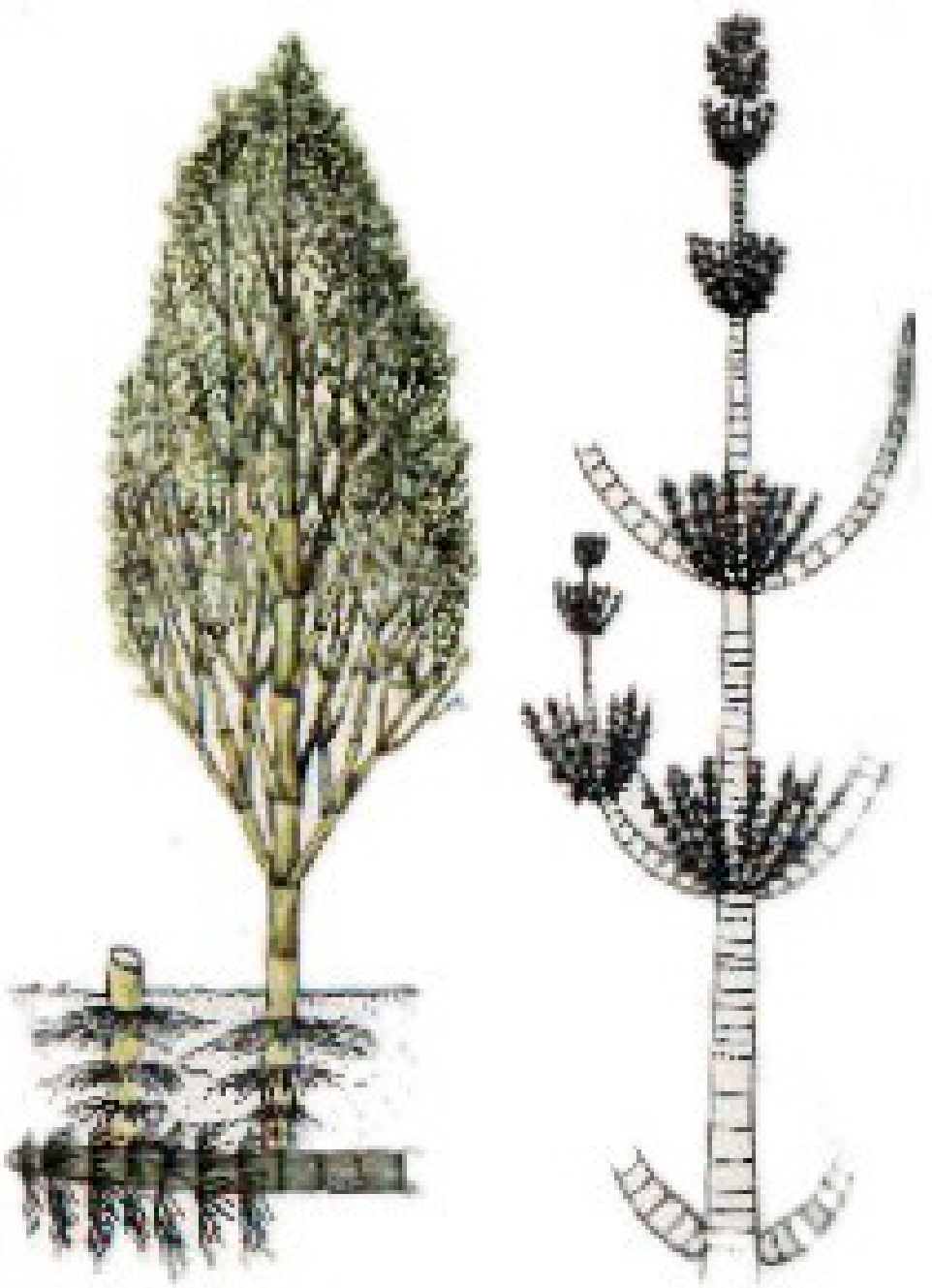
Kalamiidilaadsed - Calamitales





http://paleopedia.free.fr/Pal%20v%E9g%E9tale/pteridophytes_equisetales_preles_fossiles.html

http://bio1903.nicerweb.com/Locked/media/ch29/

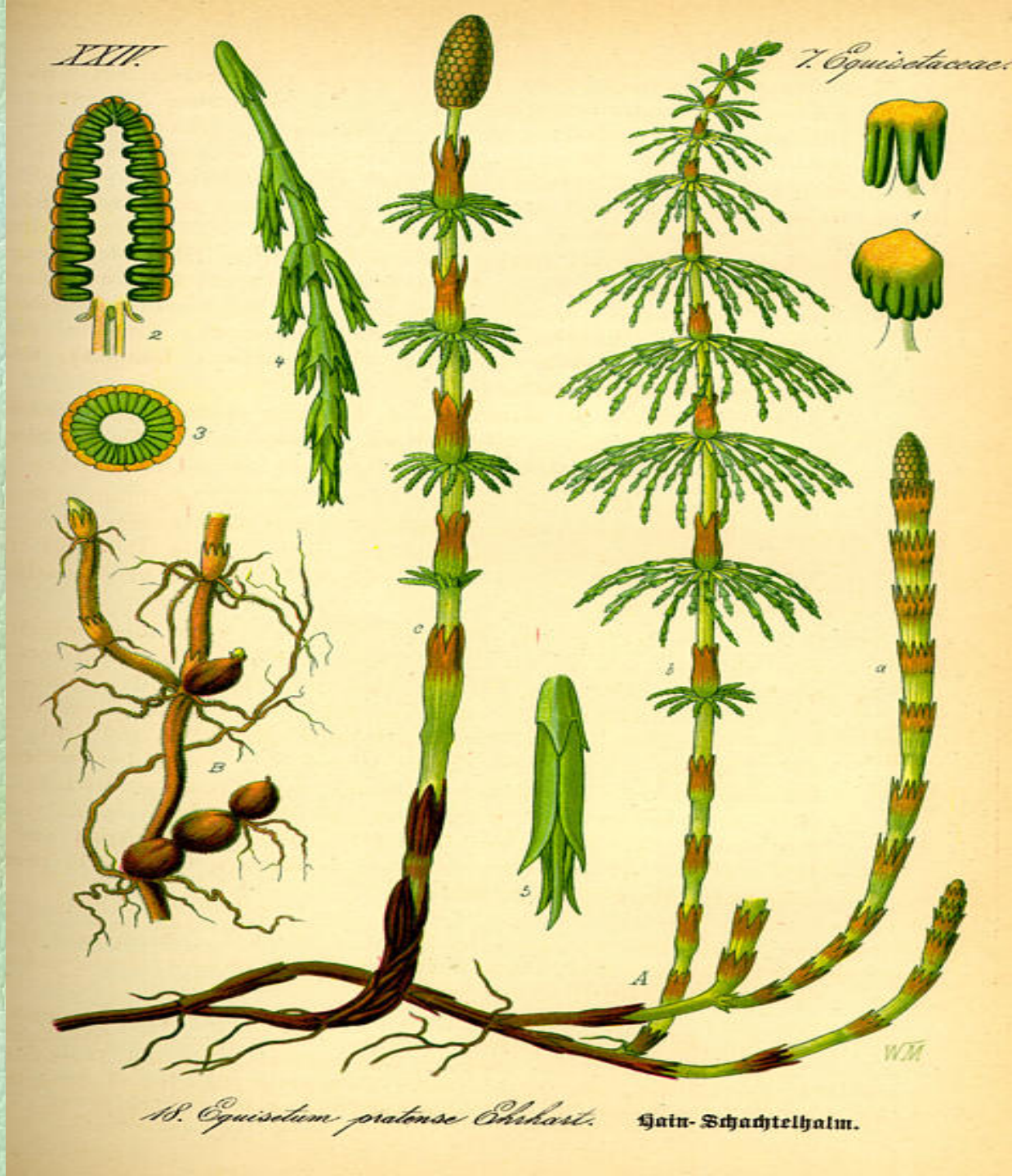


ricostruzione di Calamites

http://www.museum.state.il.us/exhibits/mazon_creek/gallery.php?RollID=roll02&FrameID=Calamites

Equisetales
Equise-taceae
Equisetum

15-30 liiki
Eestis 11



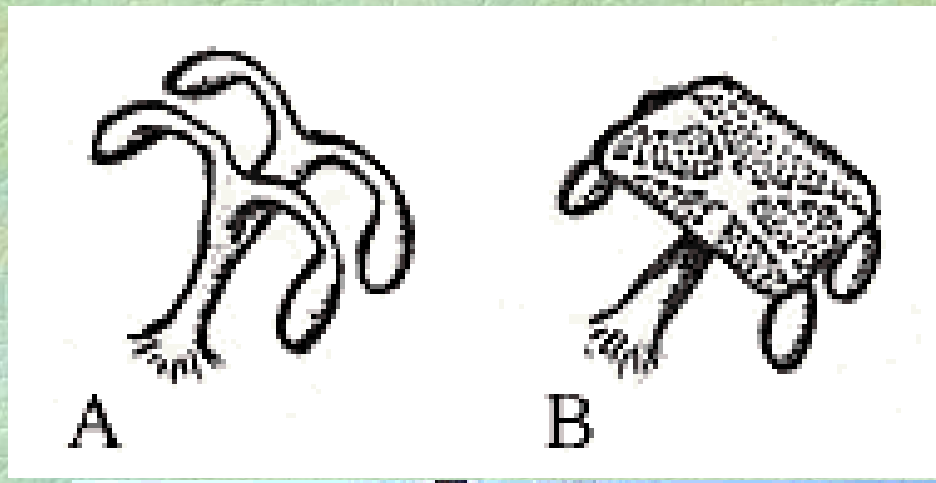
http://de.academic.ru/dic.nsf/dewiki/430050

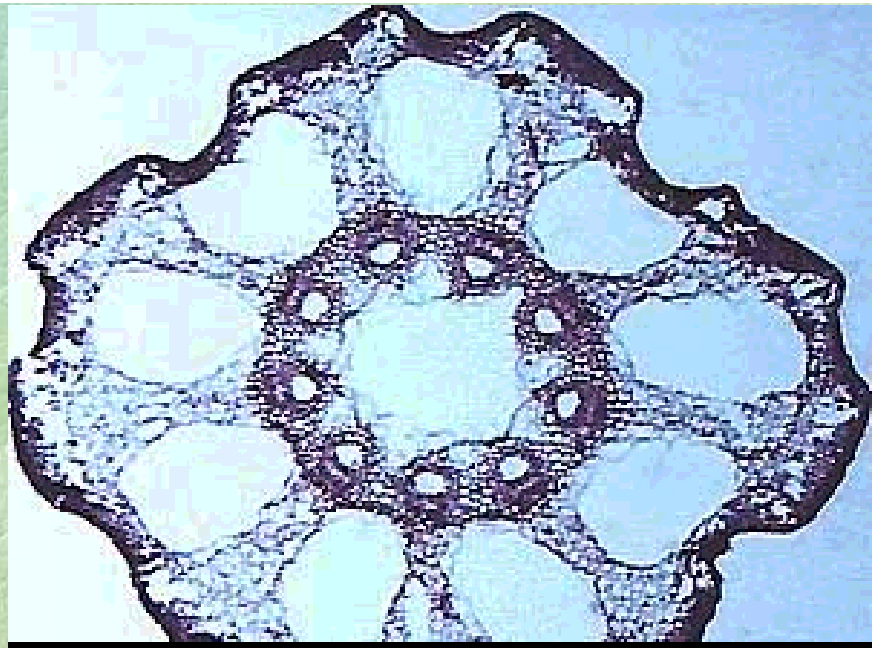
Equisetum arvense

Equisetaceae

Equisetum giganteum

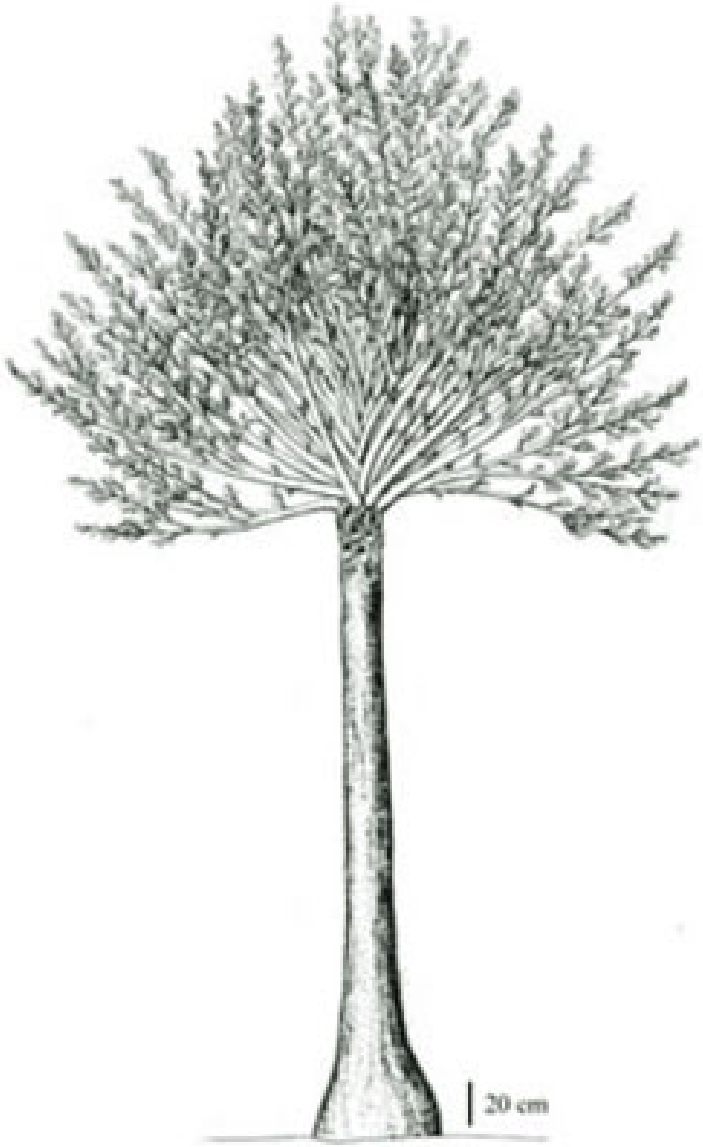
http://w3.fiu.edu/husby/





http://www.ucmp.berkeley.edu/IB181/VPL/SpheFe/SpheFe2.html

Cladoxylopsida: *Pseudosporochnus*



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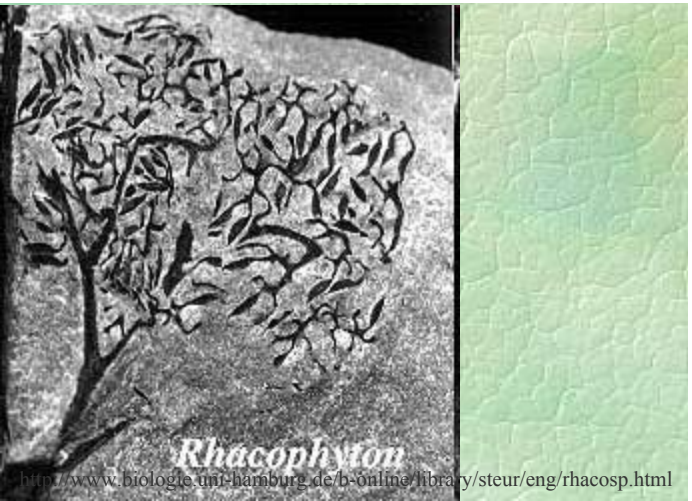
Klass keerdlehikud Filicopsida

- *Rhacophytales*†
- *Stauropteridales*†
- *Zygopteridales*†
- Alamkl raagraikad *Psilotidae*
- Marattiad *Marattiidae*
- Maokeeled *Ophioglossidae*
- Sõnajalad *Polypodiidae*
  - *Osmundales*
  - *Filicales*
  - *Polypodiales*
  - *Salviniales*

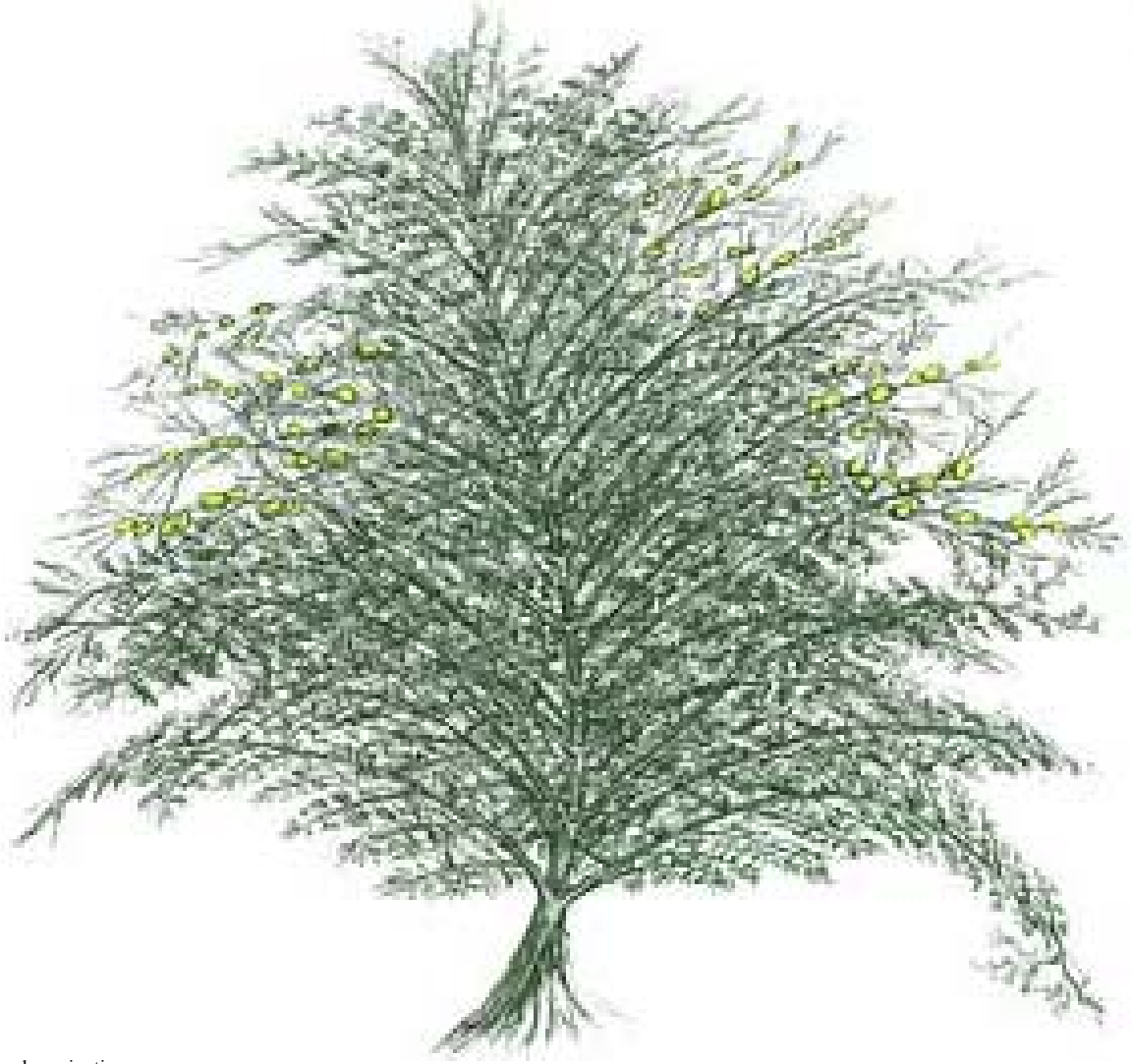
Calamites/Annularia **(far left, Late Carboniferous),** ***Polystichum*** **(upper left, extant),** ***Phlebopteris*** **(upper right, Triassic),** ***Osmundia*** **(far right, extant),** ***Todites*** **(lower right, Jurassic),** ***Psaronius*** **(center, Late Carboniferous), and** ***Rhacophyton*** **(lower left, Late Devonian).**

http://www.devoniantimes.org/who/pages/ferns.html

Rhacophyton

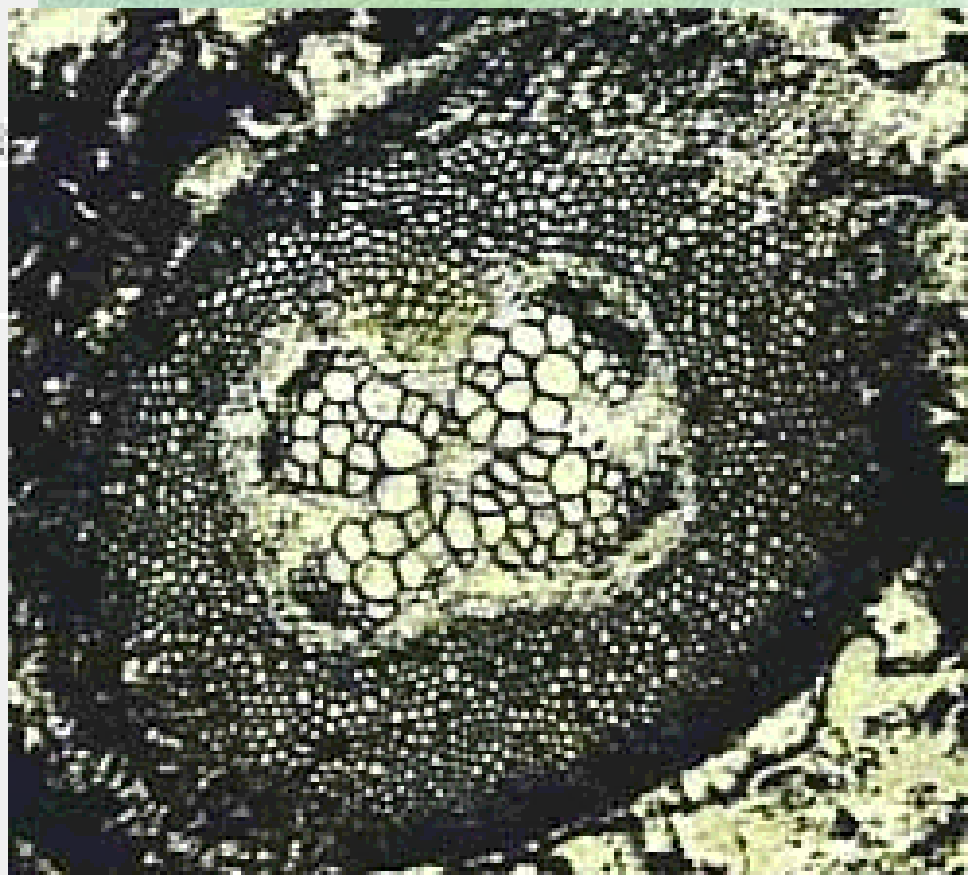


http://www.biologie.uni-hamburg.de/b-online/library/steur/eng/rhacosp.html

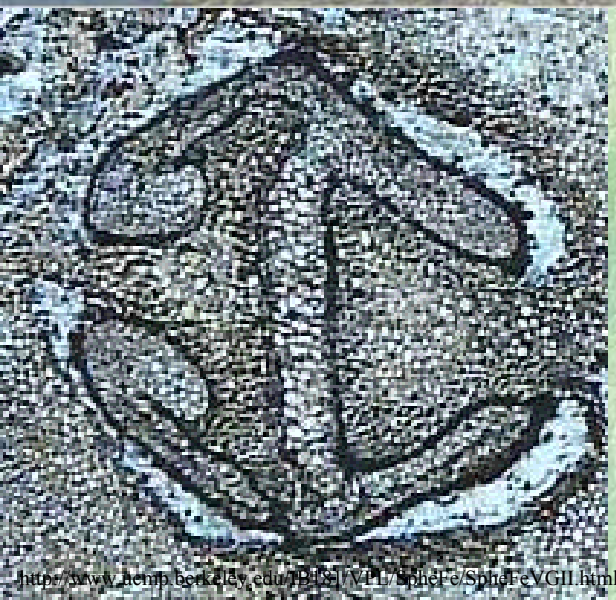


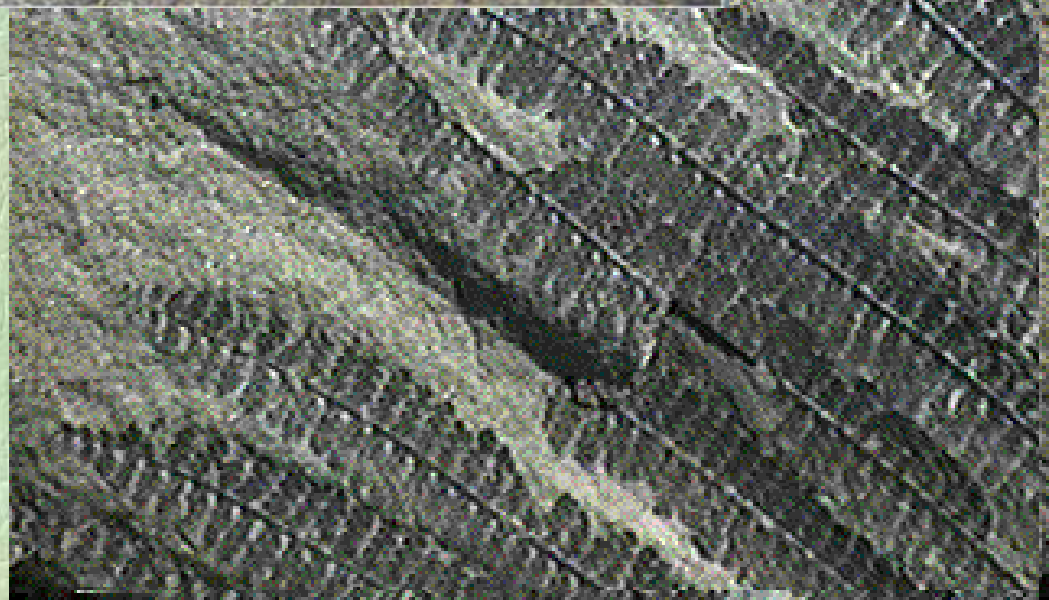
devoniantimes.org

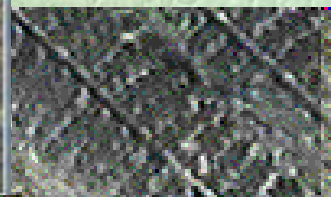
Ristsõnajalg - Stauropteris



Seigsõnajalalaadsed - Zygopteridales





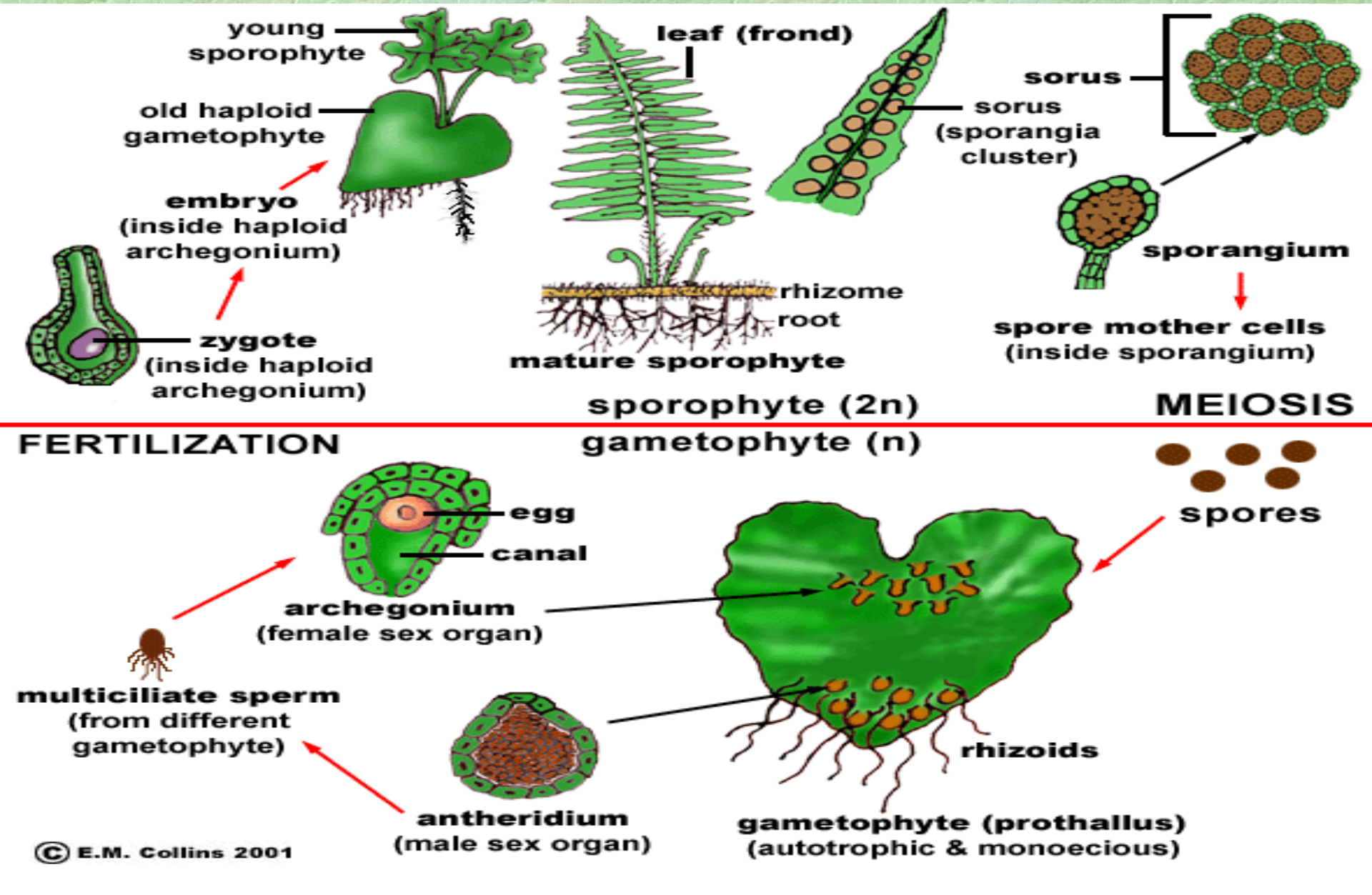


http://www.ucmp.berkeley.edu/IP/IVPL/SpheFe/SpheFeVGII.html

Karboni ajastu mets

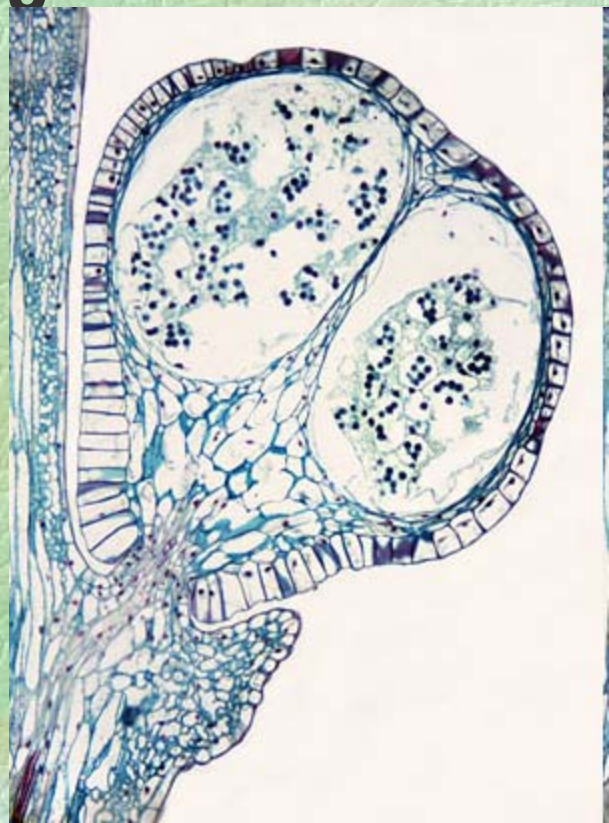
http://www.naturenorth.com/dragonfly/DOM/Page03_Palaeobiology.html

Sõnajala elutsükkel



Eusporangiumilised sõnajalgtaimed

- Eusporangium – tekkinud epidermise rakkudest, mitmekihilise seinaga



http://www.botany.org/plantimages/ImageData.asp?IDN=25-007

Psilotidae, Psilotales *raagraikalaadsed*

- Puuduvad juured, osadel ka lehed
- Epifüüdid või rohttaimed peam troopikas
- Dihhotoomne harunemine
- Homospoorsed, sünangiumid
- Peetud primitiivseteks soontaimedeks, aga molekulaarsed, arengulised, osad morfoloogilised tunnused viivad eusporangiumiliste sõnajalgade hulka
- Reduktsioon seoses mükoriisaga?
- 2 perekonda, 17 liiki

Raagraigas - *Psilotum*

http://www.ucmp.berkeley.edu/plants/pterophyta/psilotales.html

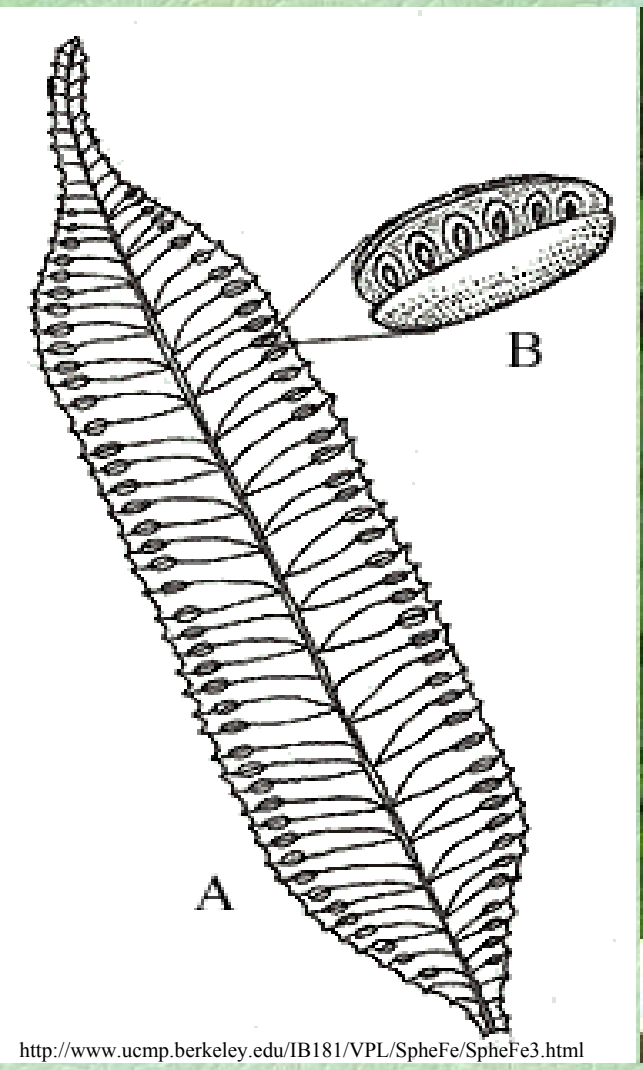
http://www.plantoftheweek.org/week055.shtml

Sammalraigas -*Tmesipteris*

Marattiidae Marattiales
marattialaadsed

- Sarnanevad sõnajalgadega
- Põõsa- või puukujulised, muguljad varred
- Abilehed
- Sünangiumid lehe all, homospoorsed
- 6 perekonda, 90 liiki

Marattia



http://www.ucmp.berkeley.edu/IB181/VPL/SpheFe/SpheFe3.html

http://www.creaweb.fr/perso/bv/banque/pteri...

Pecopteris

http://steurh.home.xs4all.nl/engpsar/epsstam3.html

http://go2add.com/paleo/Carboniferous.php

Ophioglossidae
Ophioglossales - Maokeelelaadsed

- Rohttaimed
- Steriilne leht ja sporofoor, homospoorsed
- 3 perekonda, 70-90 liiki, üle maailma
- Eestis 5 liiki

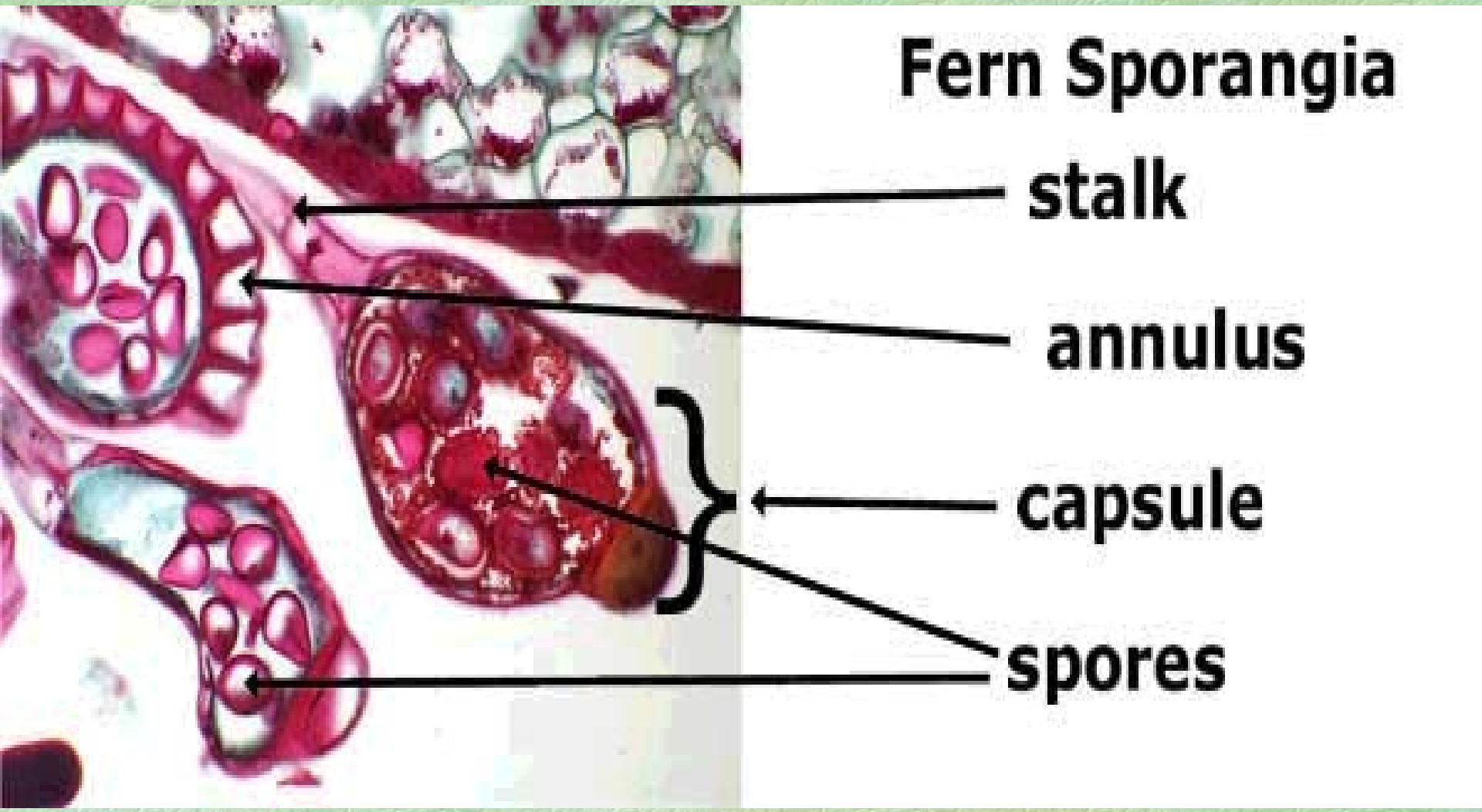

Botrychium


Ophioglossum

Polypodiidae, Polypodiales - *imaralaadsed*

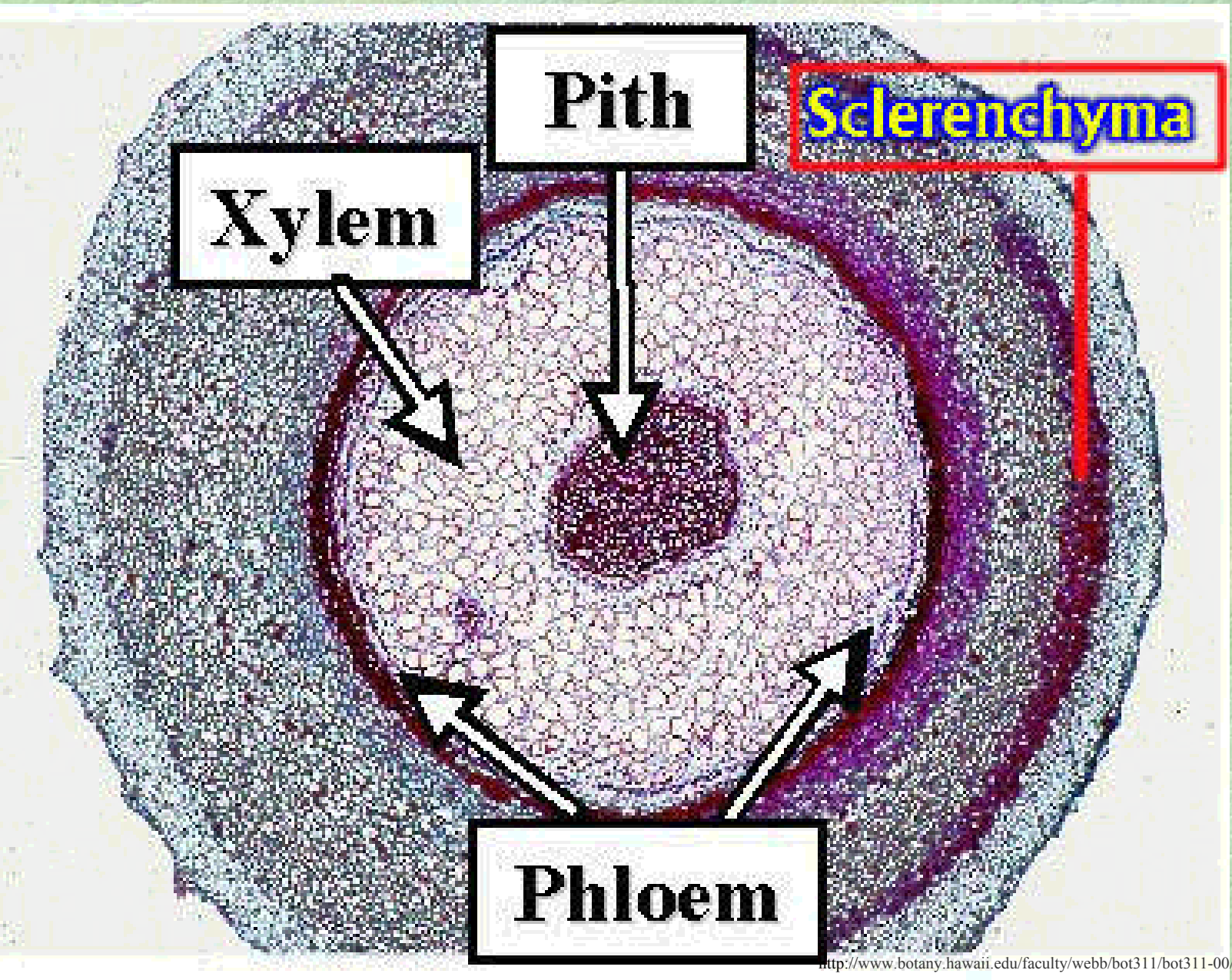
- Leptosporangium
- Lahtikeerduv megafüll
- Polüsteel, astriktrahheiidid

Leptosporangium



http://www.esu.edu/~milewski/intro_biol_two/lab_2_moss_ferns/Fern_sporangia.html

Sõnajala varre ristlõige



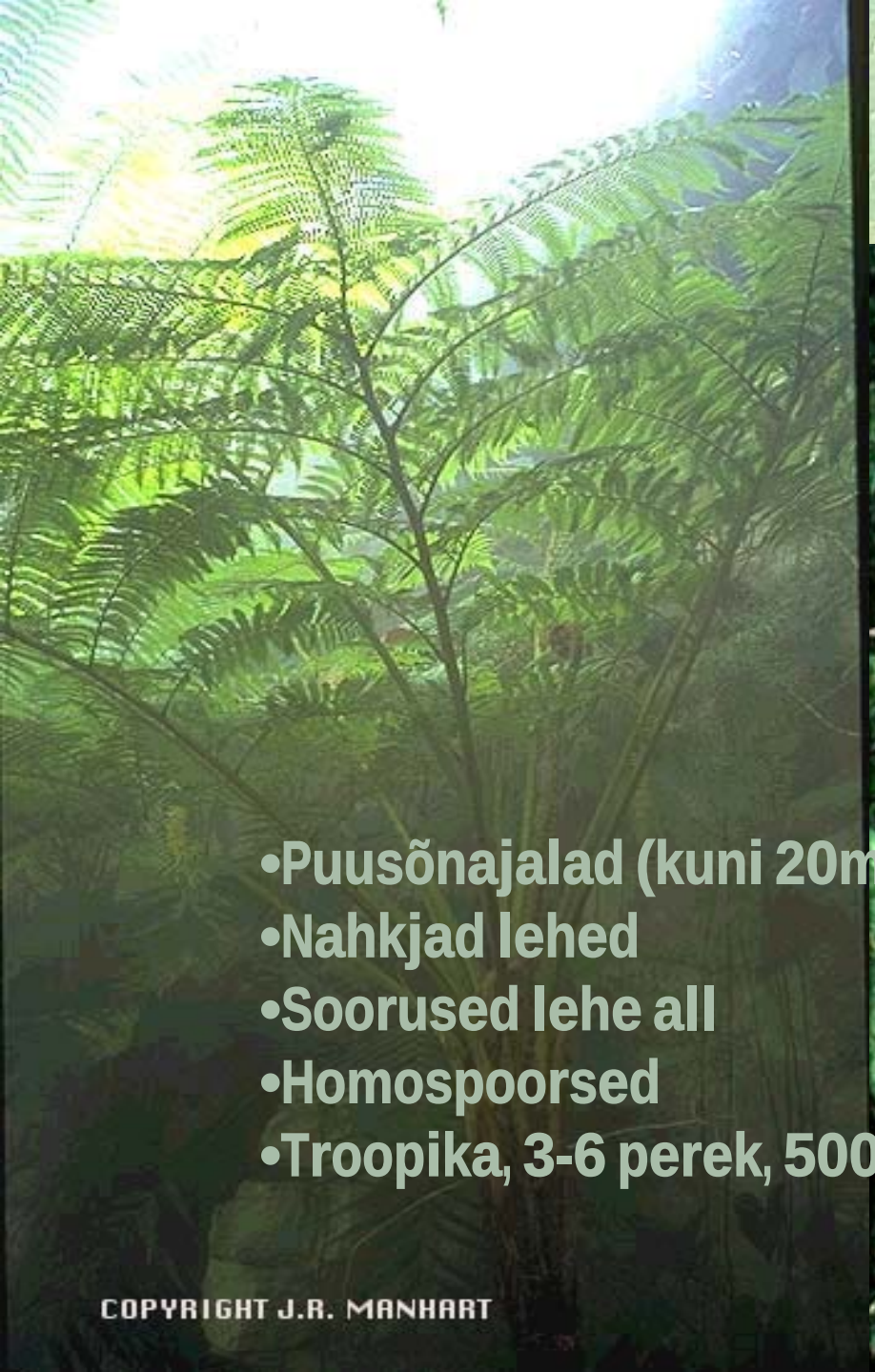
http://www.botany.hawaii.edu/faculty/webb/bot311/bot311-00/Transition/invasion_landStele.htm

Osmundaceae
Osmunda

- annulus sporangiumi ühel küljel
- Soorusi ei ole
- Soojas kliimas üle maailma
- 3 perek, 18 liiki

http://cs.wikipedia.org/wiki/Soubor:509_Osmunda_regalis.jpg

Cyatheaceae



- Puusõnajalad (kuni 20m)
- Nahkjad lehed
- Soorused lehe all
- Homospoorsed
- Troopika, 3-6 perek, 500 l

Marsileaceae – *marsiilealised ja* Salviniaceae - *salviinialised*

- Veetaimed
- Heterospoorsed
- Marsiilealistel pikarootsulised lehed
- Soorused induusiumita, sporokarpides
- 3 + 2 perek, ca 90 liiki, troopika ja soe parasvööde

Marsilea *ja* Salvinia

http://nas.er.usgs.gov/taxgroup/plants/docs/marsilea/marsilea.html

Imaralised – Polypodiaceae s.l.

- Sporangiumil arenenud vertikaalne annulus, jalg
- Soorused, induusium
- Suured lõhestunud või liitlehed
- Homospoorsed
- Risoom
- Üle maailma, ca 200 perek, 7500 liiki
- Varem 11 suguk

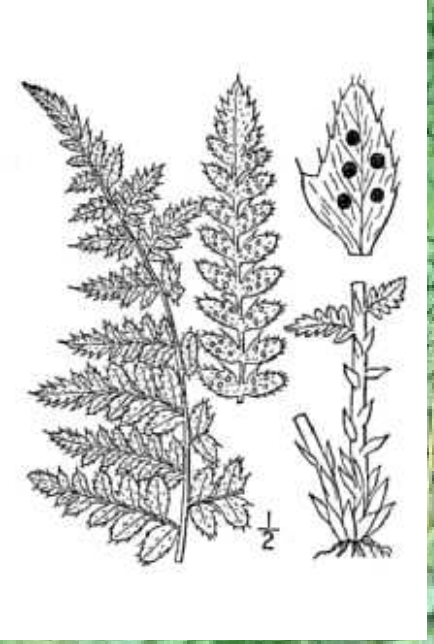
Imaralised – Polypodiaceae s.l

- Eestis perekonnad *Polypodium (1), Pteridium (1), Thelypteris (1), Phegopteris (1), Asplenium (3), Athyrium (1), Cystopteris (2), Woodsia (1), Gymnocarpium (2), Matteucia (1), Polystichum (2), Dryopteris (5), Blechnum (1)*

Pteridium aquilinum

ja

Dryopteris filix-mas



Polystichum braunii

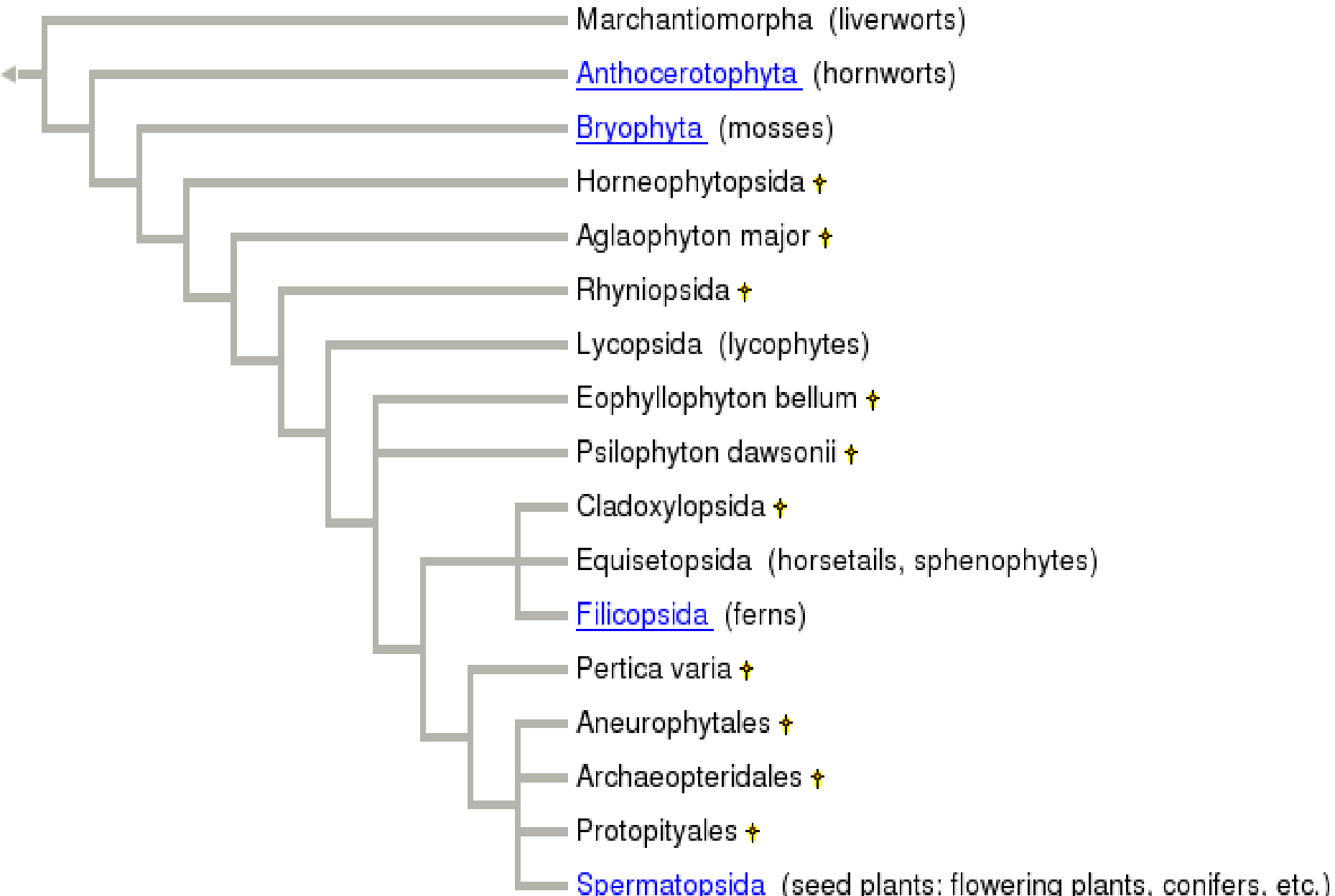
http://luirig.altervista.org/flora/polystichum.htm

http://delta-intkey.com/britfe/www/asplsept.htm

APG III järgi

- Class *Equisetopsida* MAISMAATAIMED
- Subclass *Anthocerotidae*
- Subclass *Bryidae*
- Subclass *Marchantiidae*
- Subclass *Lycopodiidae*
- [monilophytes]
- Subclass *Equisetidae*
- Subclass *Marattiidae*
- Subclass *Ophioglossidae*
- Subclass *Polypodiidae*
- Subclass *Psilotidae*
- [gymnosperms, angiosperms)

Embrüofüüdid - maismaataimed



Judd, Campbell 2002

Seemnetaimede kujunemine

Paljasseemnetaimed

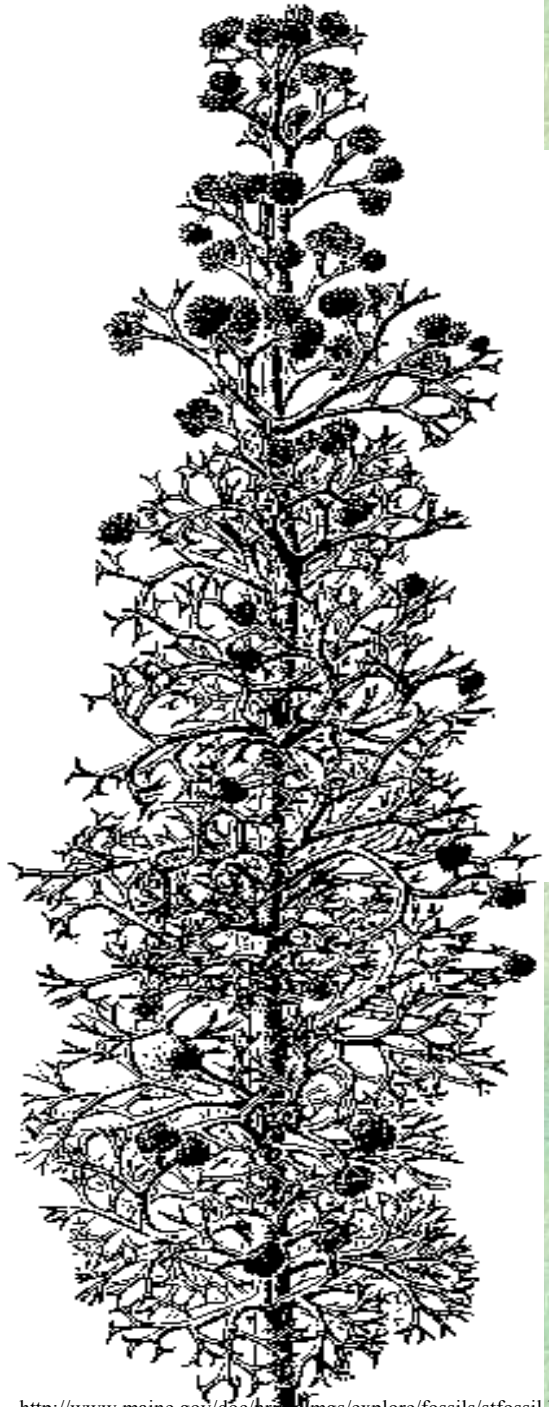
Seemnetaimede eellased

- Alamhmk ***Radiatopses***

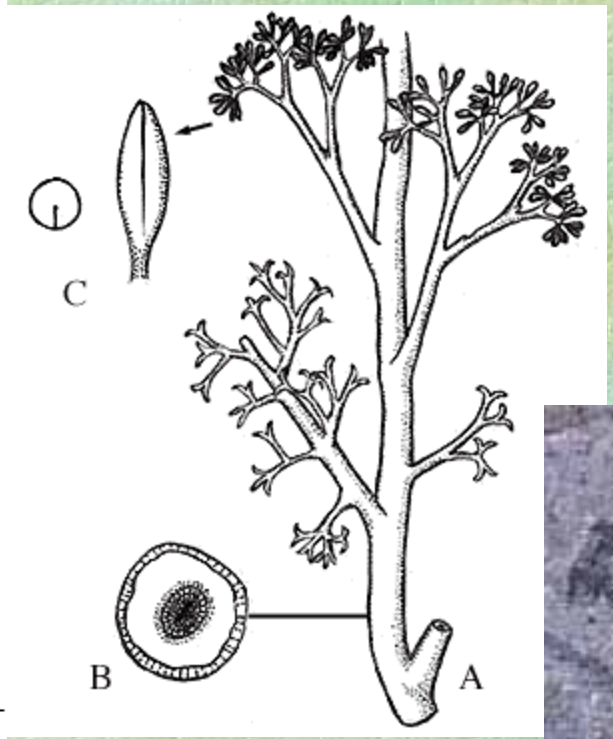
  Pertica varia

  - Ülemkohort ***Lignophytia***
    - Selts ***Aneurophytales***
    - ***Archaeopteridales***
    - ***Protopityales***
    - Kohort seemnetaimed - ***Spermatophyta***
      - Suguk *Calamopityaceae*
      - *Hydraspermaceae*
      - *Lyginopteridaceae*
      - *Medullosaceae* jne

Pertica



http://www.maine.gov/doc/nrimc/mgs/explore/fossils/stfossil.htm

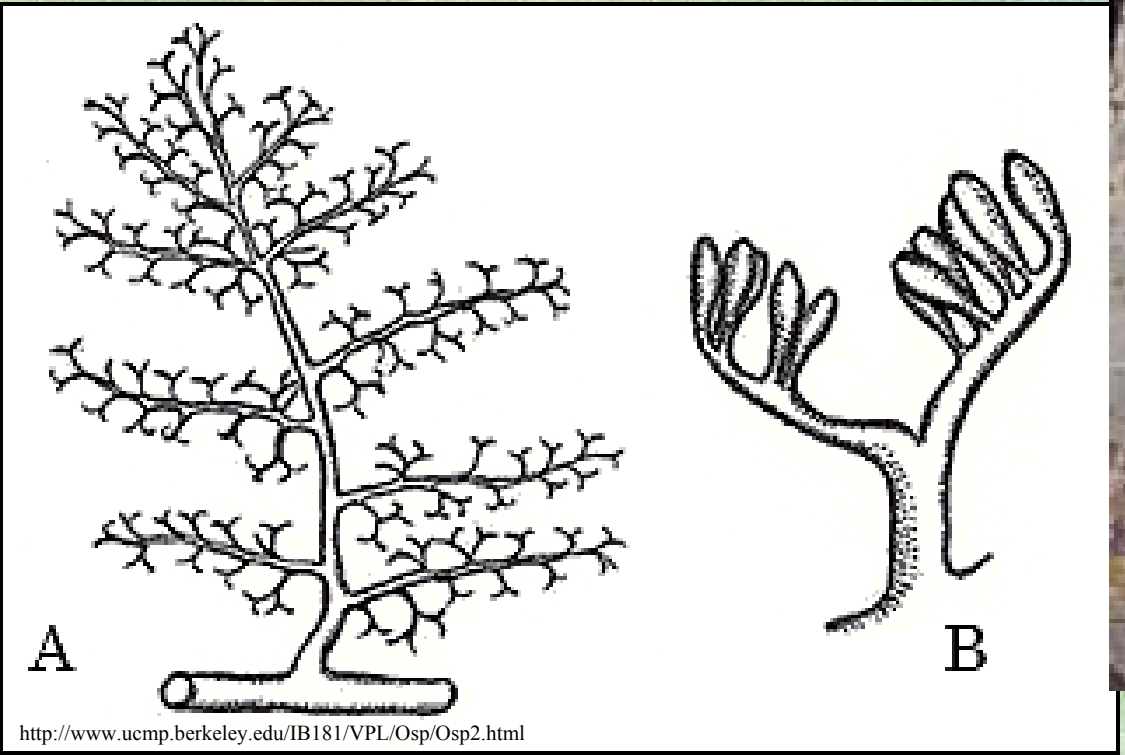


http://www.ucmp.berkeley.edu/IB181/VPL/Osp/Osp1.html

*Psilophyton*i sarnane Teispuit

http://www.uni-muenster.de/GeoPalaeontologie/Palaeo/Palbot/seite3.html

Aneurophyton



http://www.ucmp.berkeley.edu/IB181/VPL/Osp/Osp2.html

http://www.senckenberg.de/root/index.php?page_id=2877

Archaeopteris

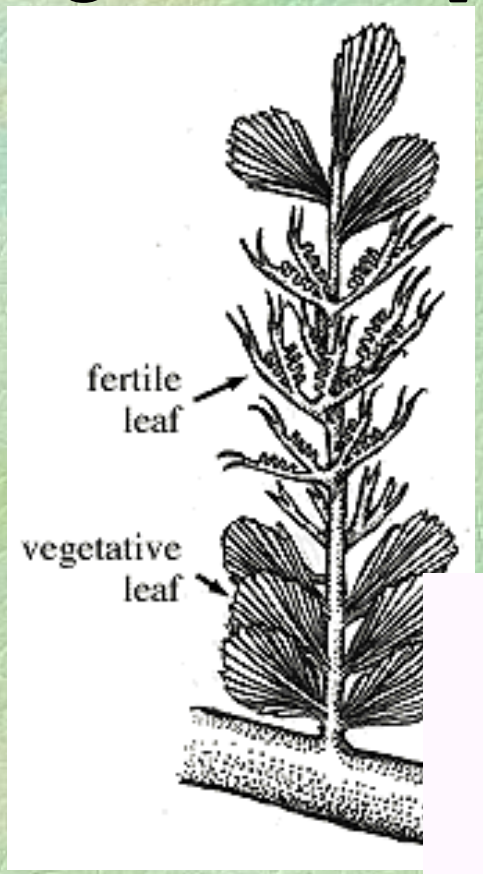
http://www.devoniantimes.org/who/pages/archaeopteris.html

http://www.uccsocieties.ie/wiki/index.php/History_of_Geology_in_UCC

http://www.ucmp.berkeley.edu/IB181/VPL/Osp/OspVG.html

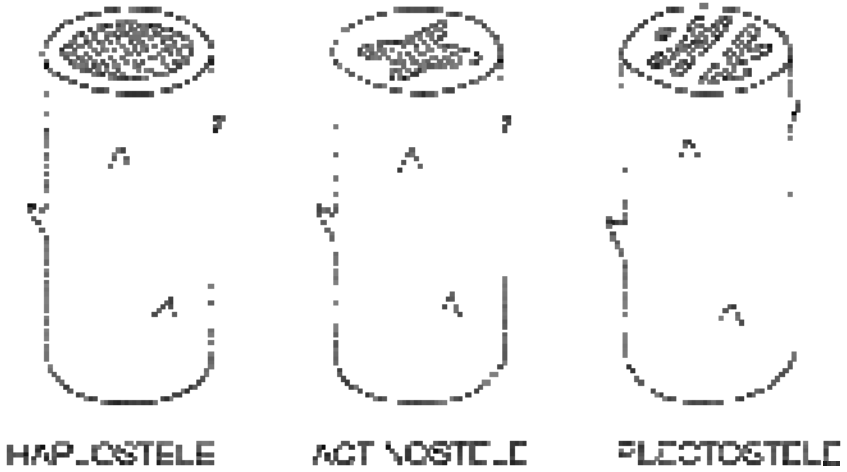
Nn progümnospermid

- al. Devoni keskelt
- Devoni lõpul – *Archaeopteris*
- puit – *Callixylon*
- heterospoorne
- õietolm trileetne, 33 –70 mikromeetrit
- megagametofüüdid vabalt liikuvad
- seemnetaimede eellane??
- Ka *Protopityales*

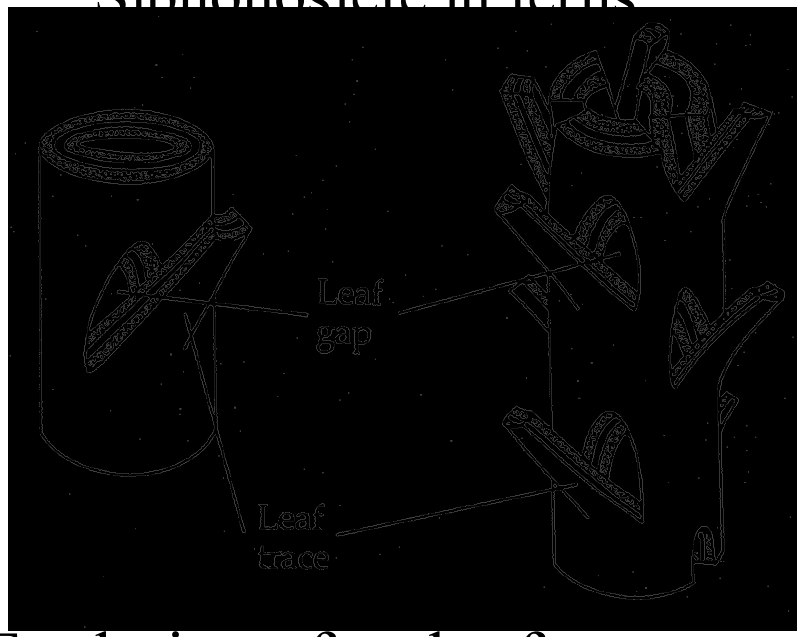


http://www.normalesup.org/~clanglois/Fossiles-epoques/Carbonifere.html

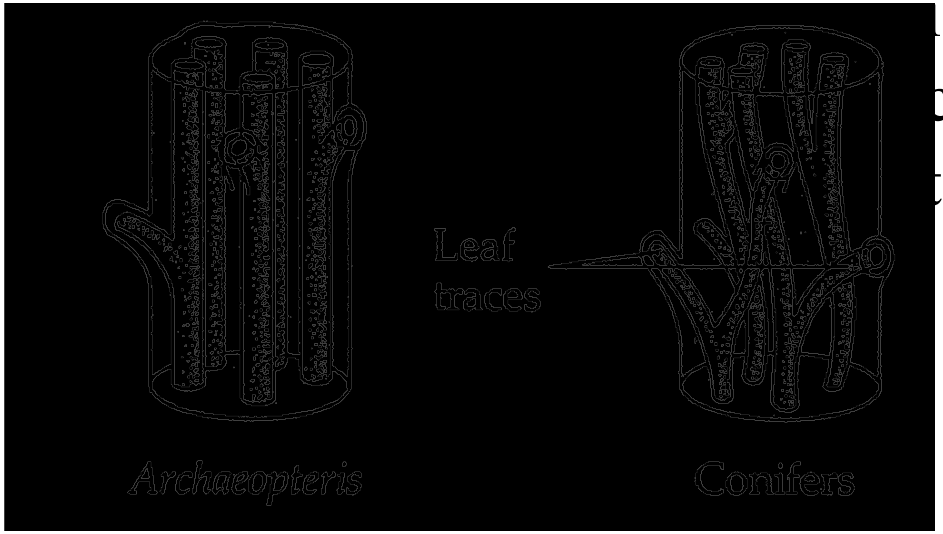
Protostele



Siphonostele in ferns

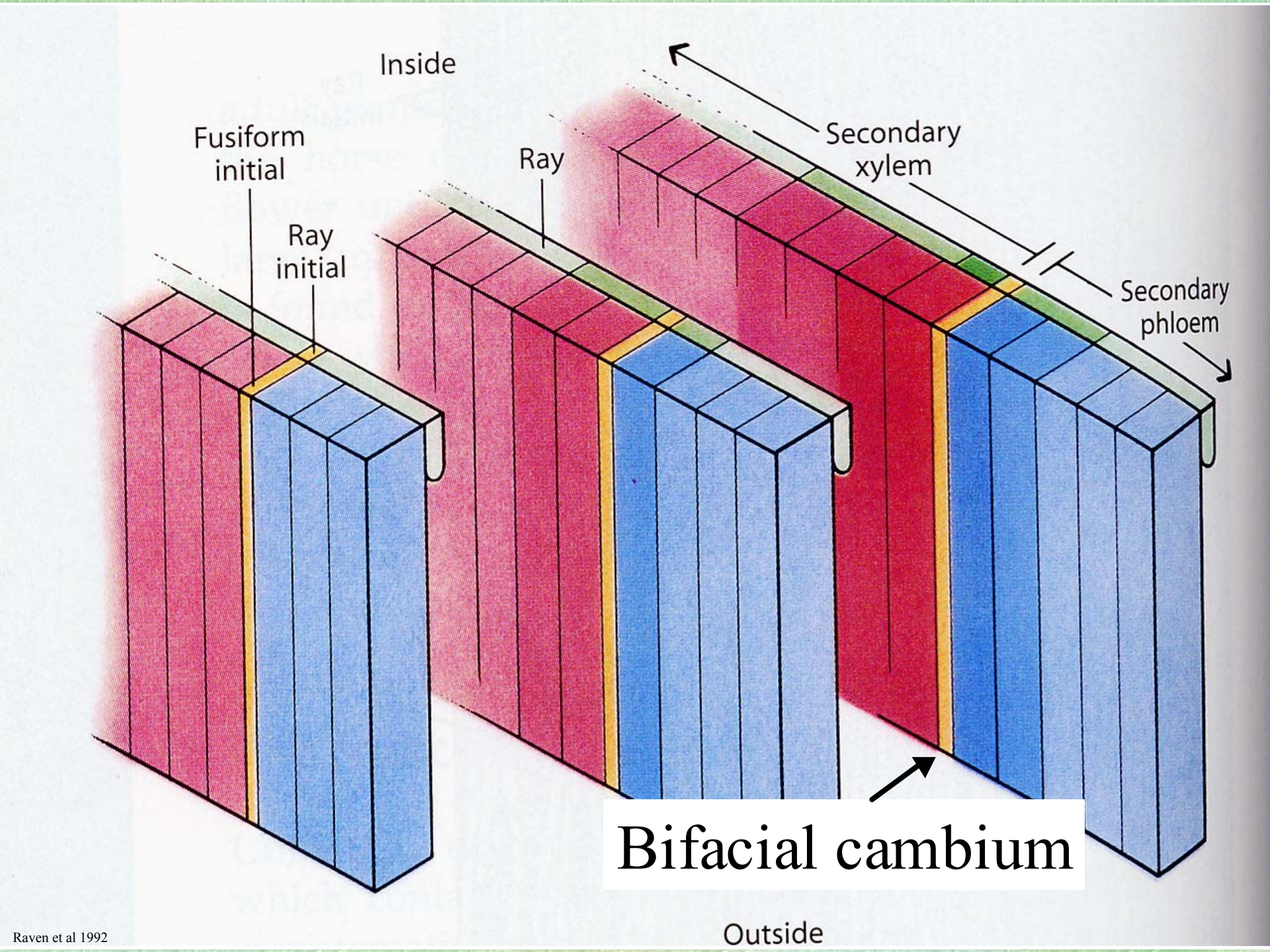


Eustele



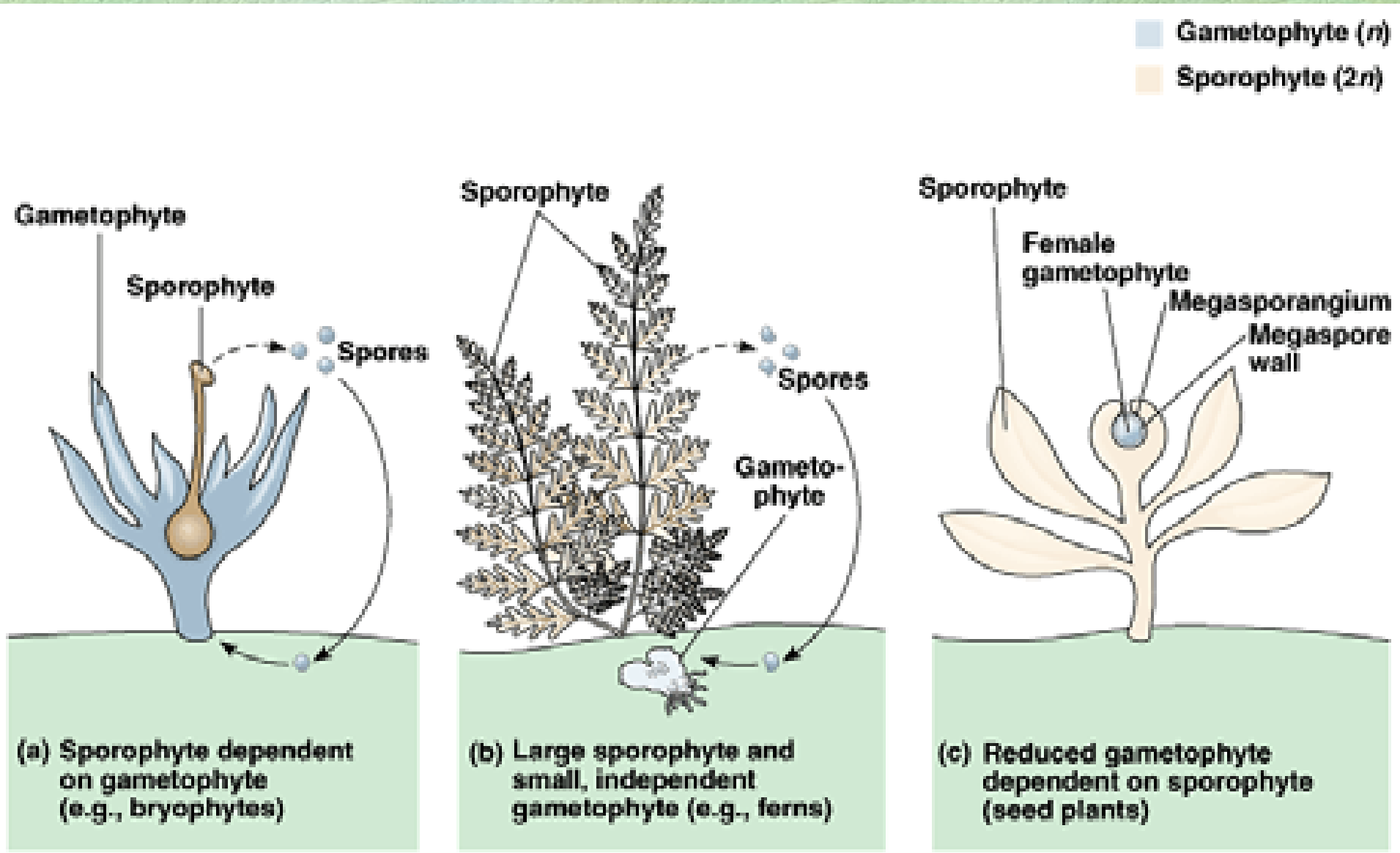
Evolution of stelar form
increased efficiency of water
conduction and unit strength of
the skeleton.

Dr Richard Saunders
Department of Ecology & Biodiversity
Hong Kong University
http://web.hku.hk/~saunders/28211/stem.htm

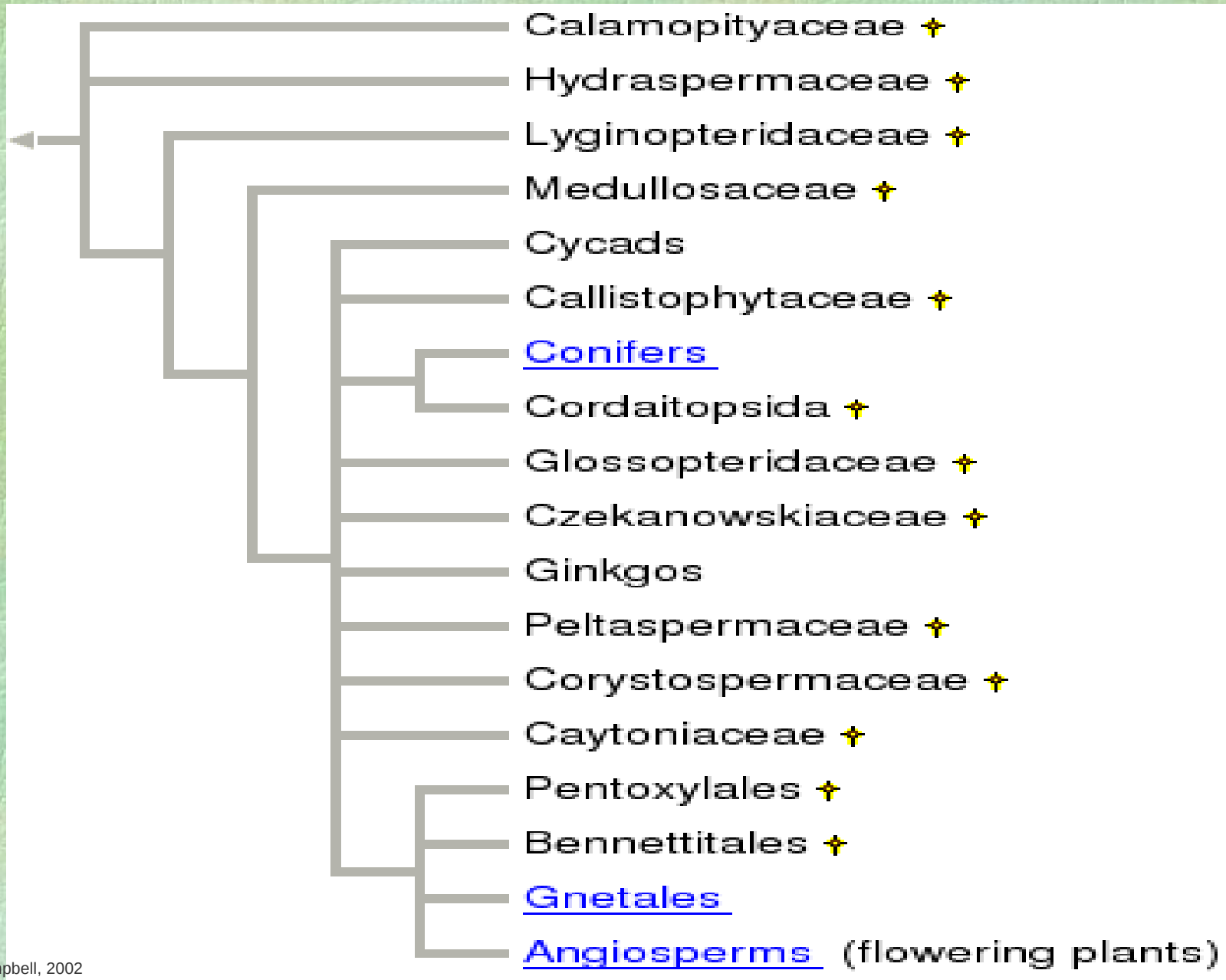


Raven et al 1992

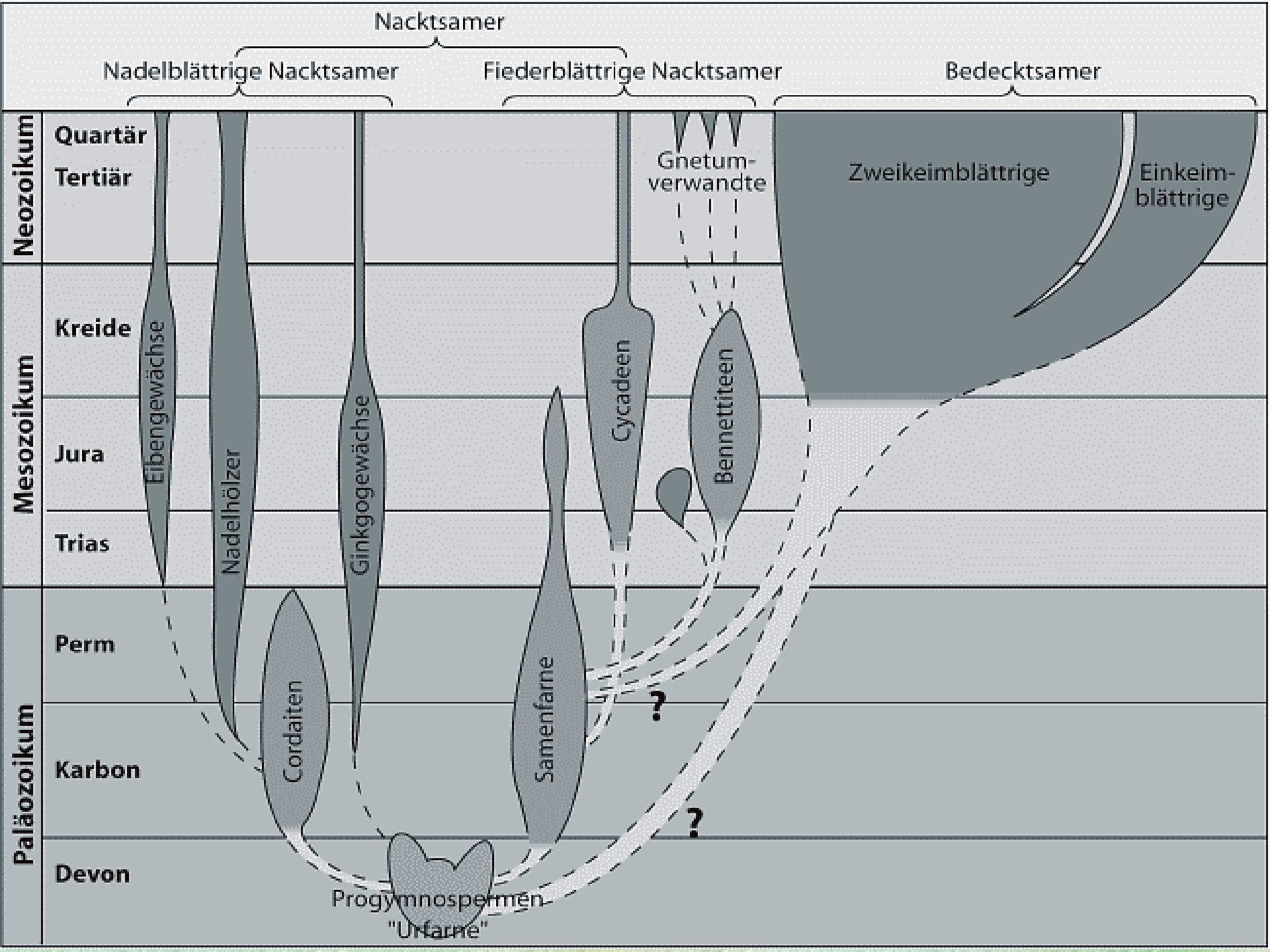
Seemnetaimed



Seemnetaimed



Judd, Campbell, 2002


Nacktsamer
Nadelblättrige Nacktsamer
Fiederblättrige Nacktsamer
Bedecktsamer
Neozoikum
Mesozoikum
Paläozoikum
Quartär
Tertiär
Kreide
Jura
Trias
Perm
Karbon
Devon
Eibengewächse
Nadelhölzer
Ginkgogewächse
Cordaiten
Samenfarne
Cycadeen
Bennettiteen
Gnetum-
verwandte
Zweikeimblättrige
Einkeim-
blättrige
?
?
Progymnospermen
"Urfarne"

Heterospooria areng

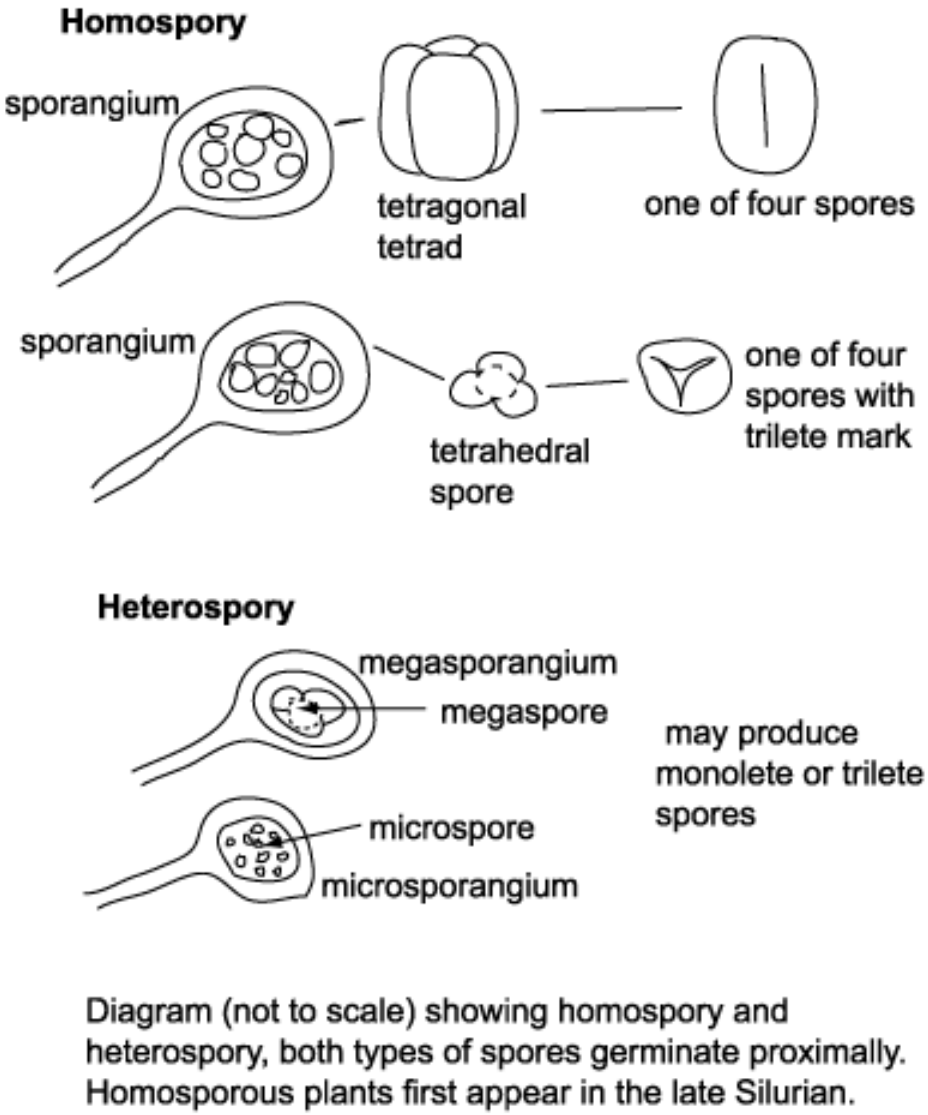
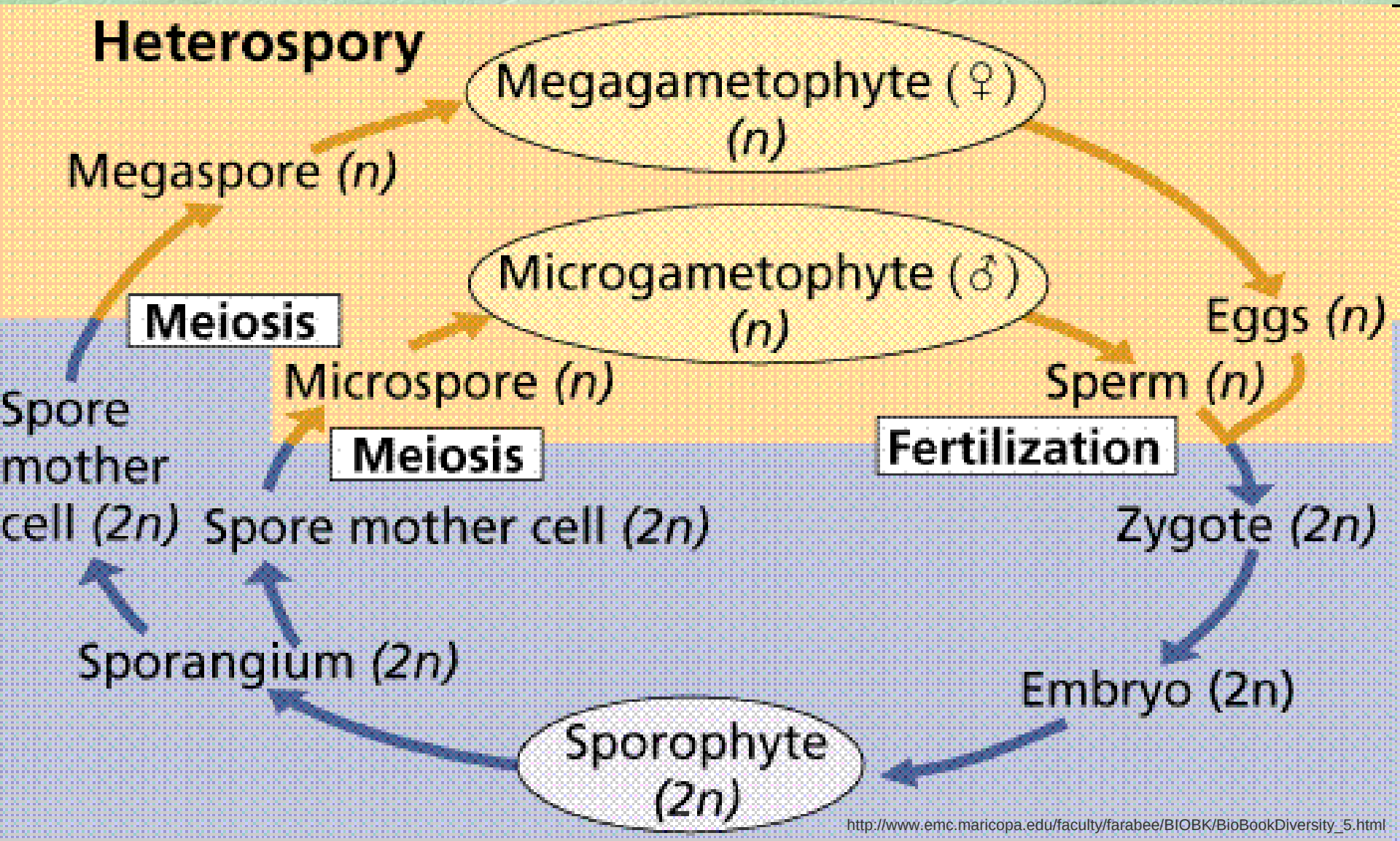


Diagram (not to scale) showing homospory and heterospory, both types of spores germinate proximally. Homosporous plants first appear in the late Silurian.

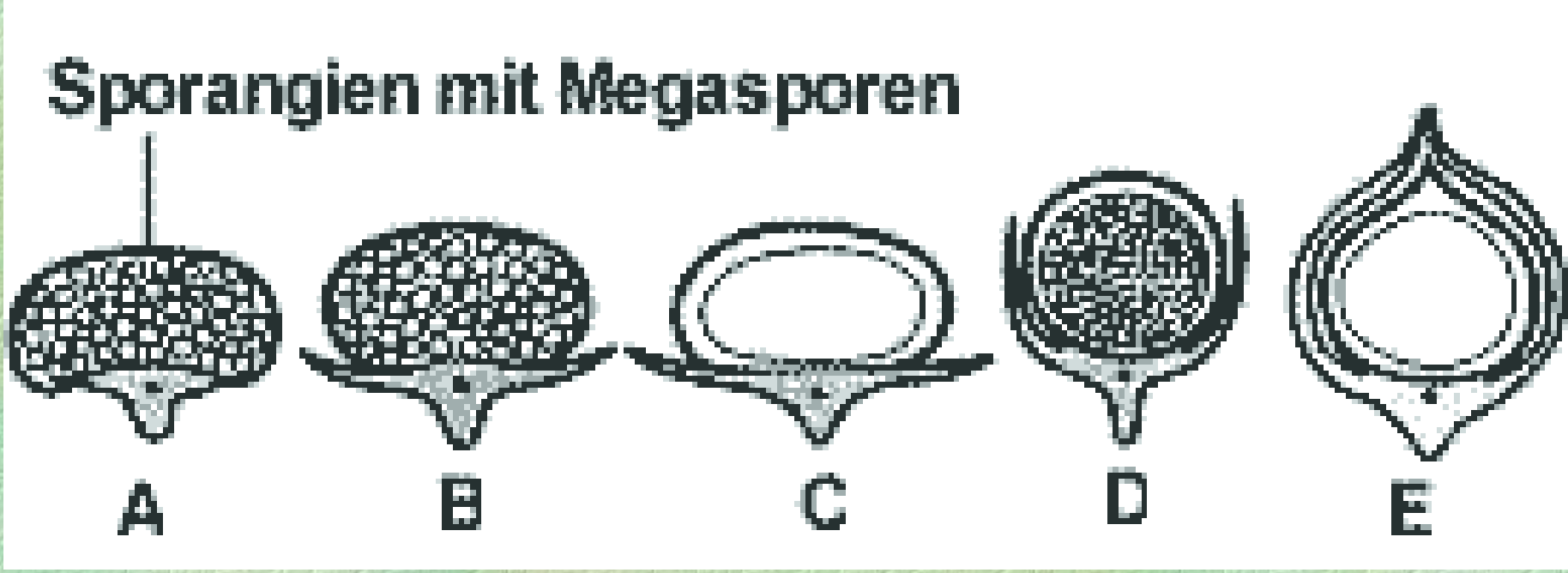
http://www.ucl.ac.uk/GeolSci/micropal/spore.html

Heterospoorse taime elutsükkel



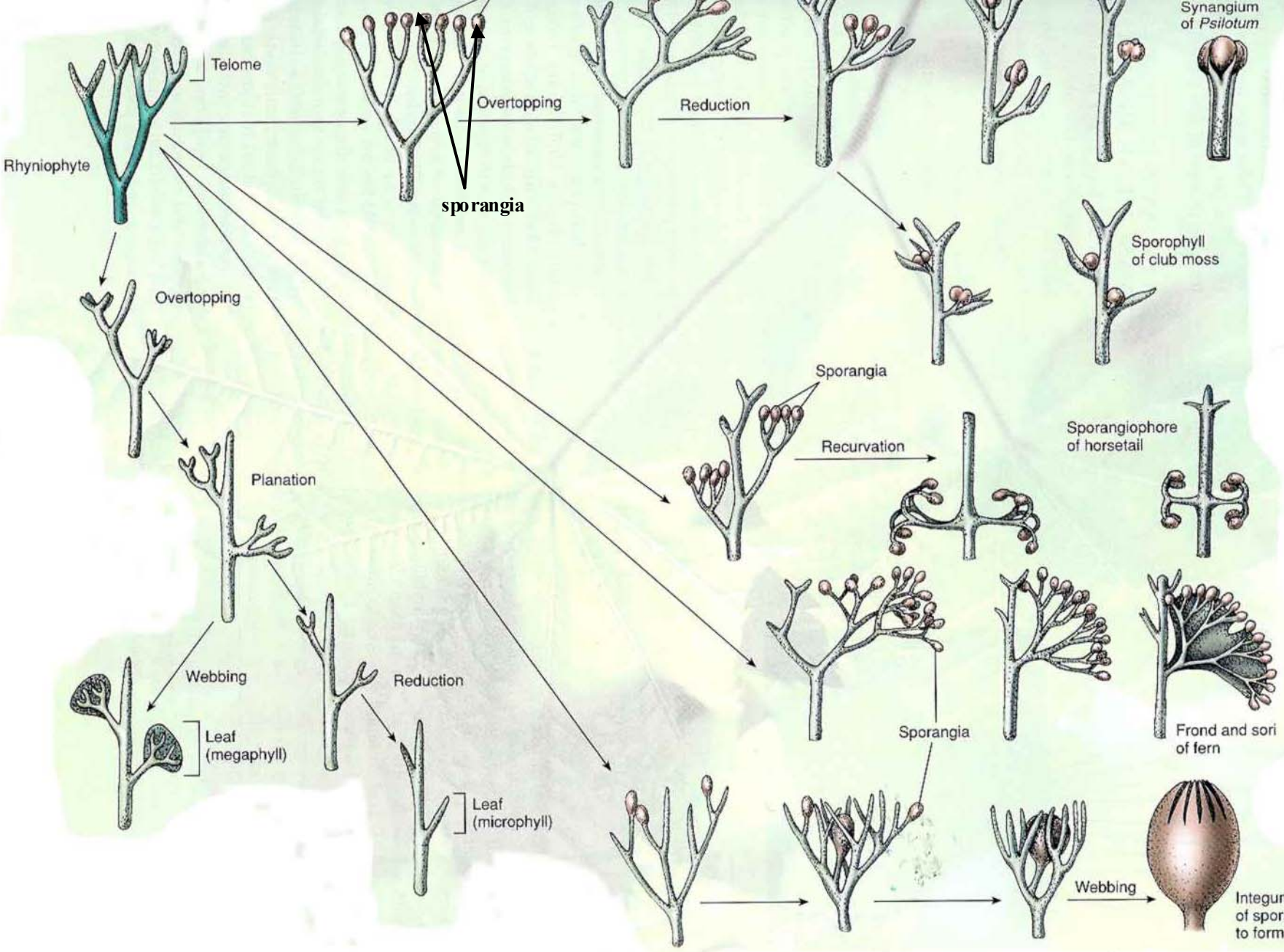
http://www.emc.maricopa.edu/faculty/farabee/BIOBK/BioBookDiversity_5.html

Megasporangiumi areng



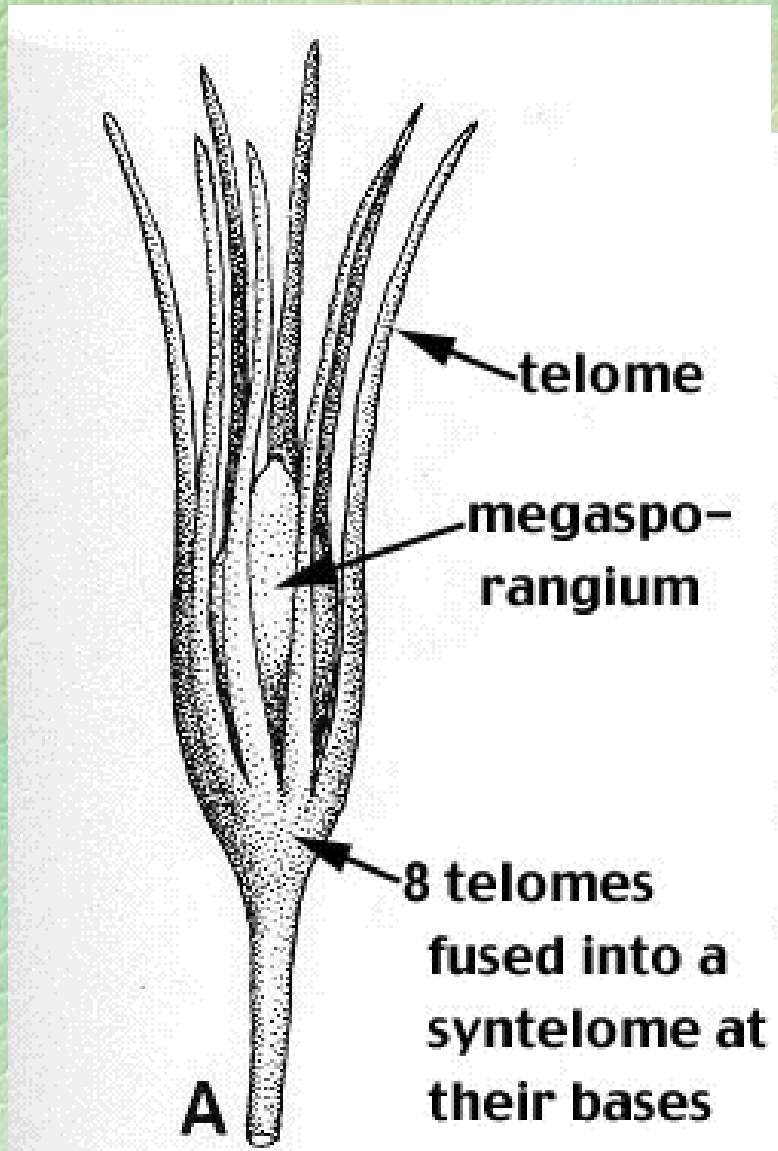
A. Lepidostrobus, B. Lepidostrobopsis,
C-D. Lepidocarpopsis, E. Lepidocarpon

Integumentide areng

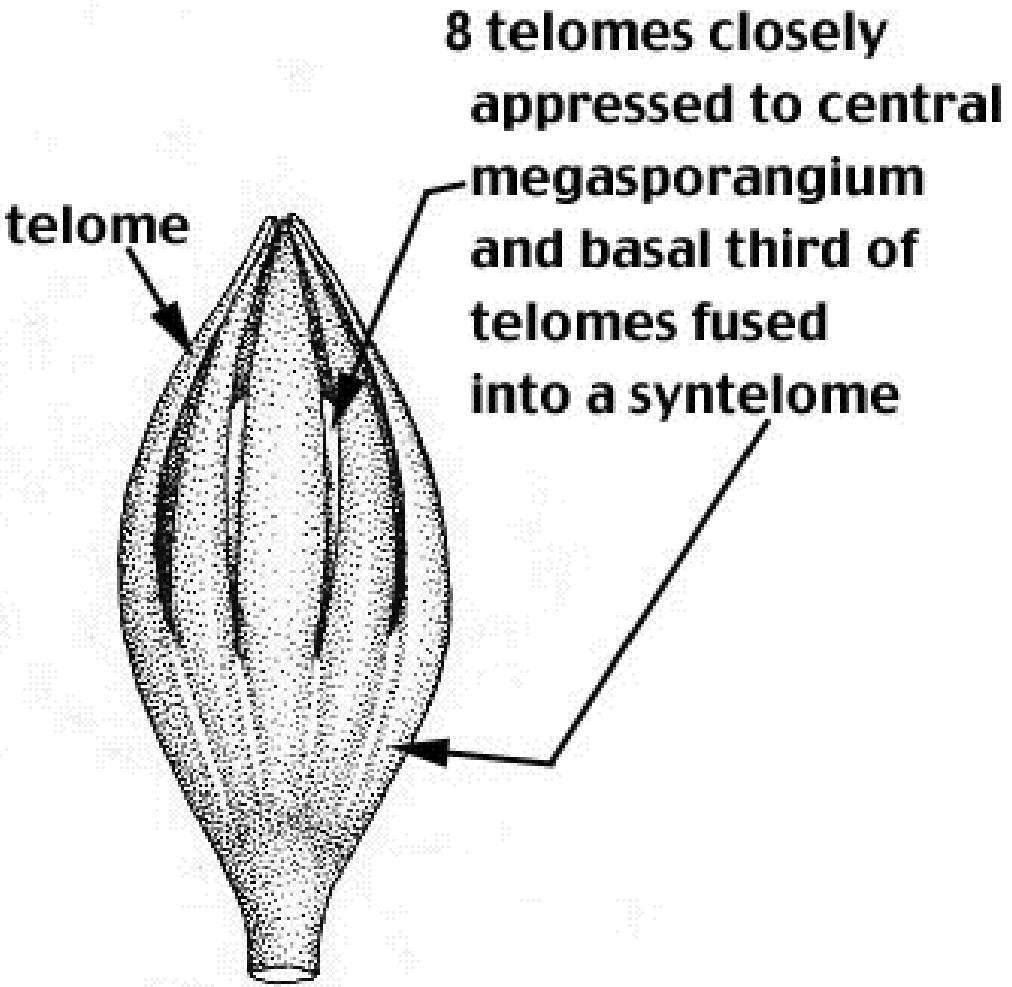


Diagrammetic representation of the evolution of leaves and reproductive structures according to telom theory. (Botanical World: Northington and Schneider 1

Integumendi evolutsioon



Genomosperma kidstonii

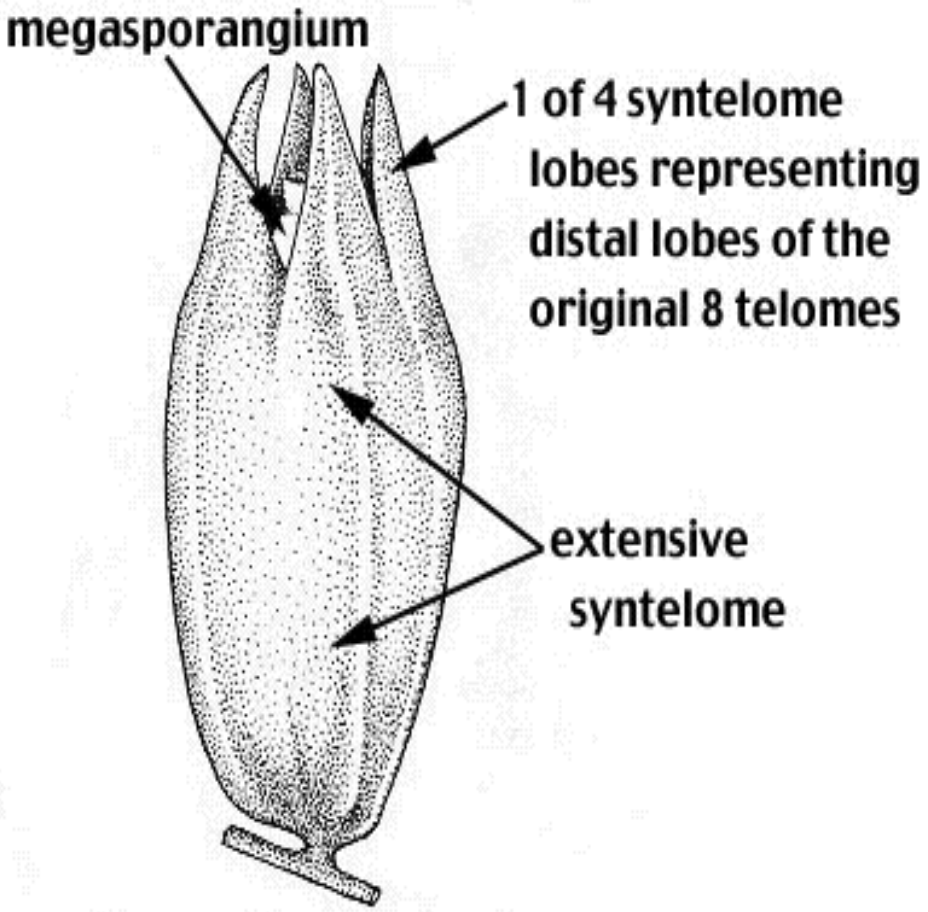


Genomosperma latens

http://www.plantbiology.siu.edu/plb304/lecture08gymnos/gymnos.html

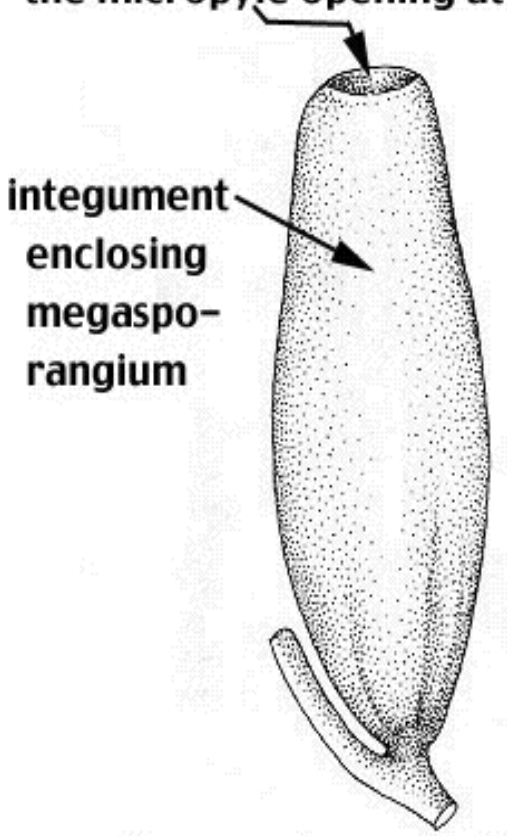
Integumendi evolutsioon

More extensive fusion of 8 original telomes into a syntelome that forms a more complete integument around the central megasporangium



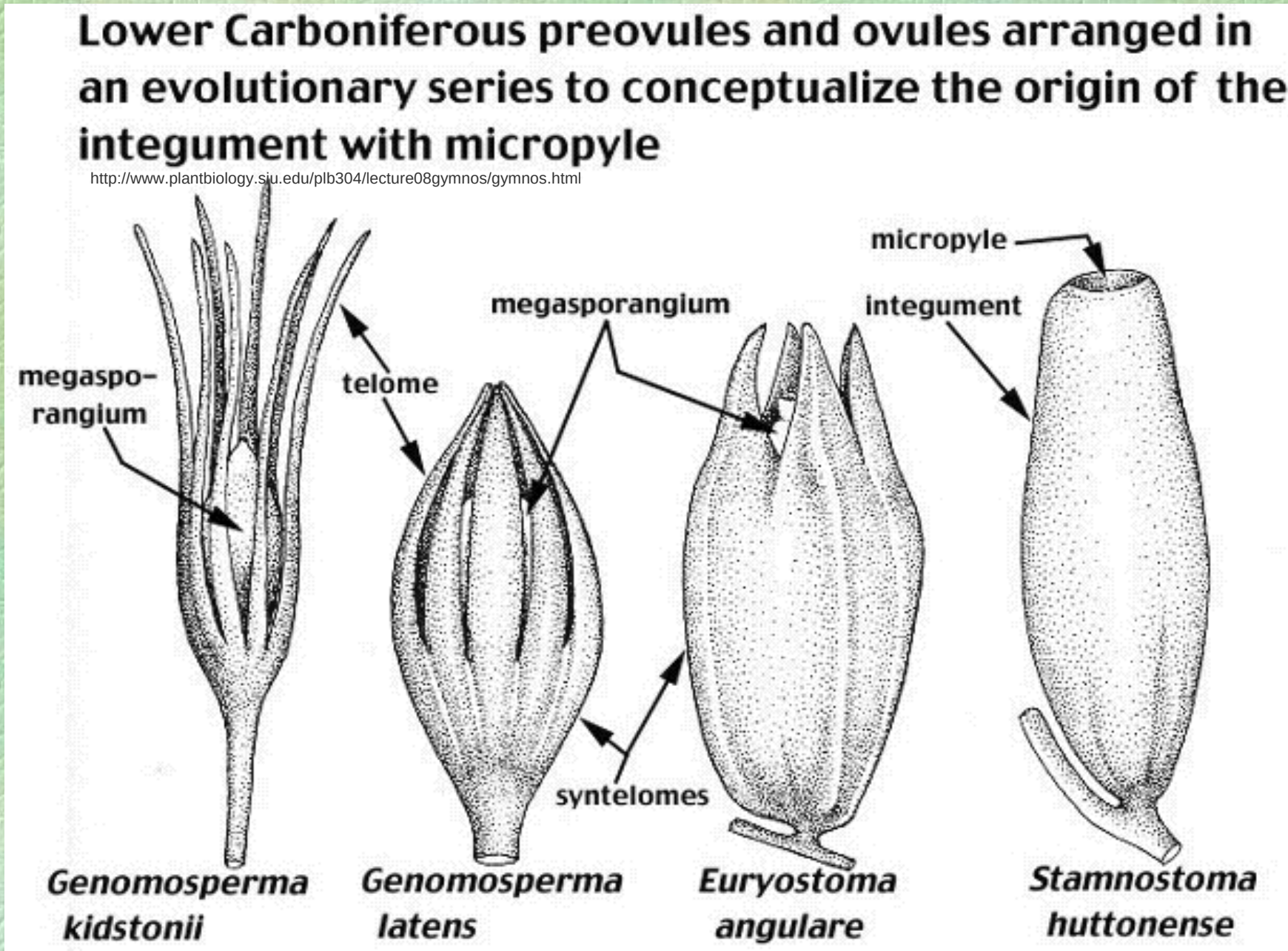
Euryostoma angulare

Ovule formed by complete fusion of telomes into a syntelome that is now the integument enclosing the megasporangium except for the micropyle opening at the tip

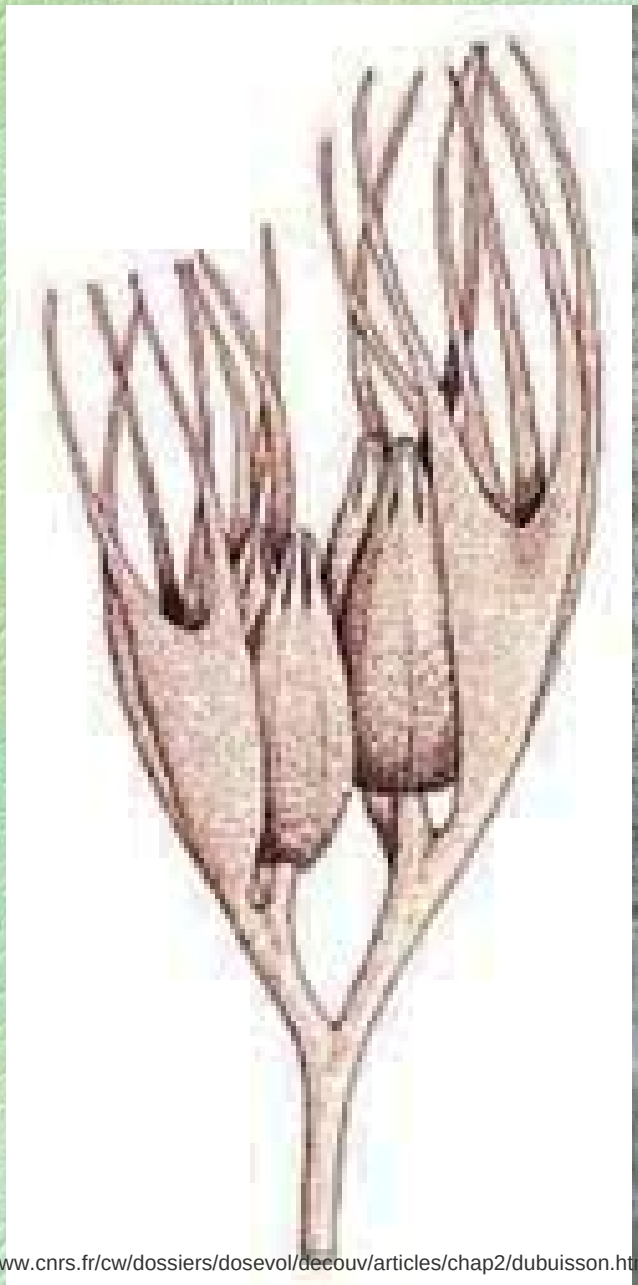


Stamnostoma huttonense

Integumendi evolutsioon



Moresnetia



http://www.cnrs.fr/cw/dossiers/dosevol/decouv/articles/chap2/dubuisson.html

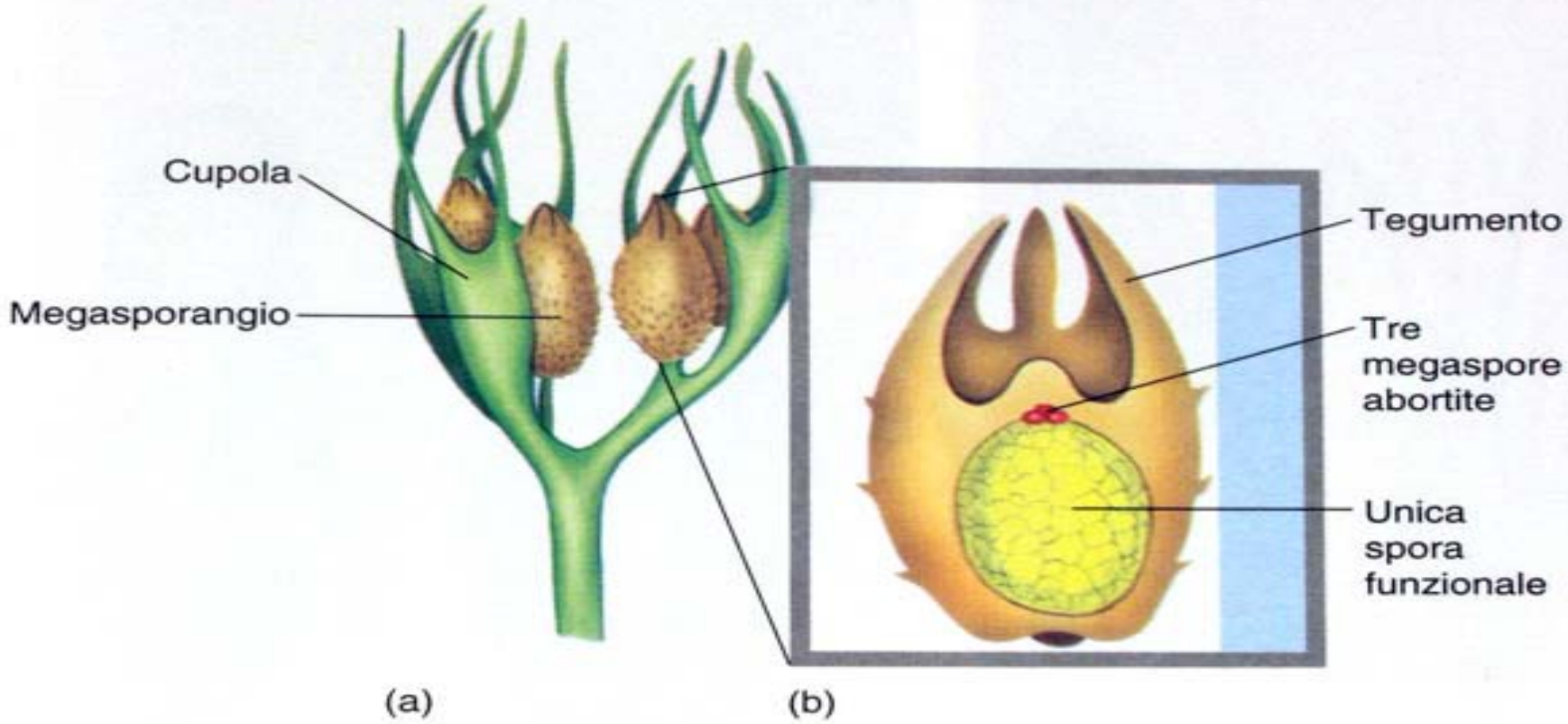


Figura 24.7
Una ricostruzione del megasporangio (b) e dei telomi adiacenti (a) di *Archaeosperma arnoldii*. Ciascuno sporangio conteneva solo una grande megaspora; le altre tre prodotte dalla cellula madre durante la meiosi, apparentemente degeneravano precocemente. Il tessuto che circondava la megaspora era la parete del megasporangio. Un tessuto monostratificato, chiamato tegumento, era attaccato alla parete dello sporangio e si estendeva verso l'alto con proiezioni digitiformi. L'esatta natura del tegumento non è conosciuta, potrebbe essere derivato da telomi adiacenti allo sporangio (*vedi* fig. 24.8). Sopra lo sporangio c'era uno spazio circondato dal tessuto tegumentale, una quieta camera pollinica senza vento dove arrivavano e si fermavano il polline o le spore. Intorno a ciascun megasporangio e al tegumento c'era un altro gruppo di telomi parzialmente fusi.

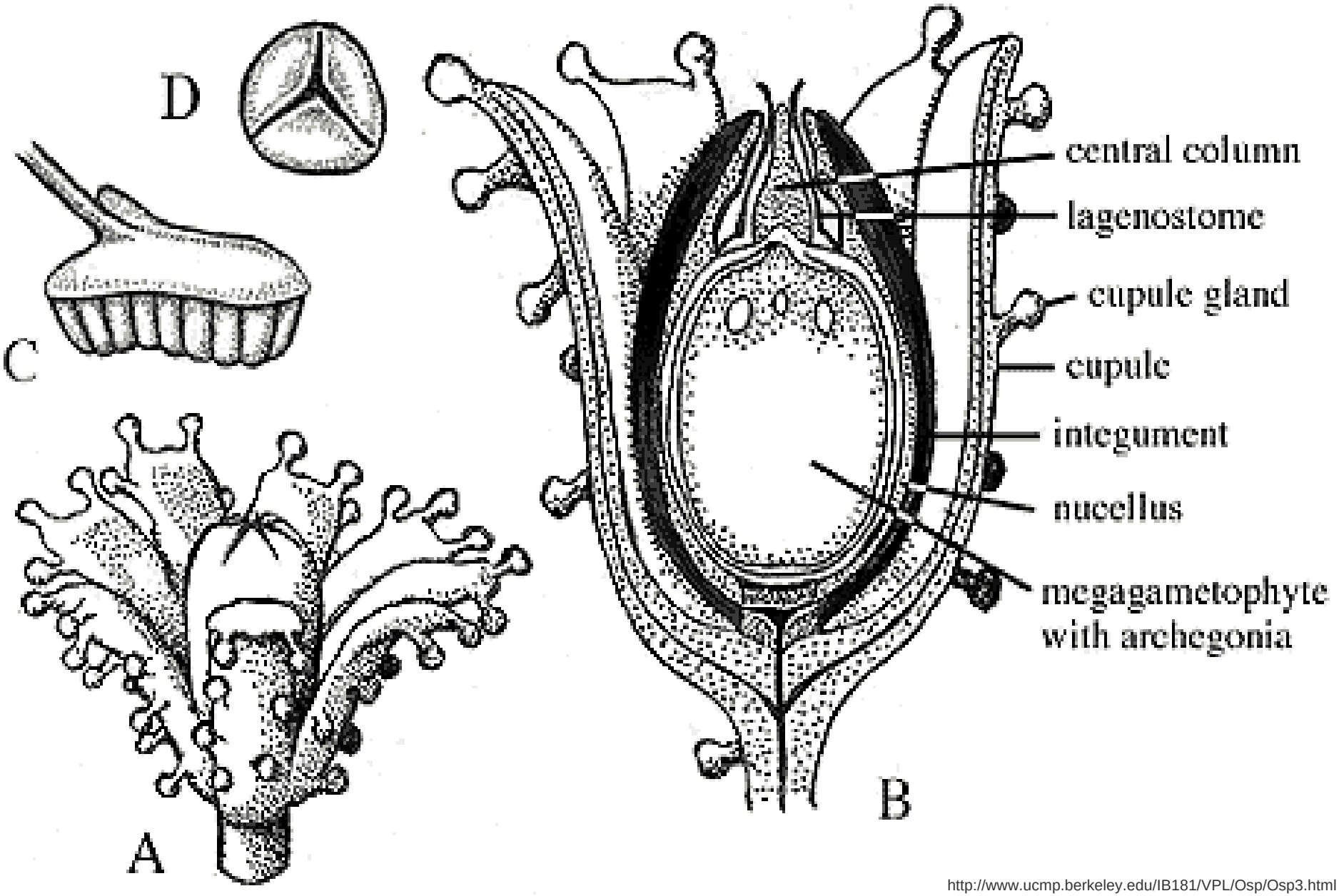
Seemnealgme ja tolmeldamise areng

Lyginopteris

http://ademir.comtercy.free.fr/fossiles/familles.htm/lyginopteris.html

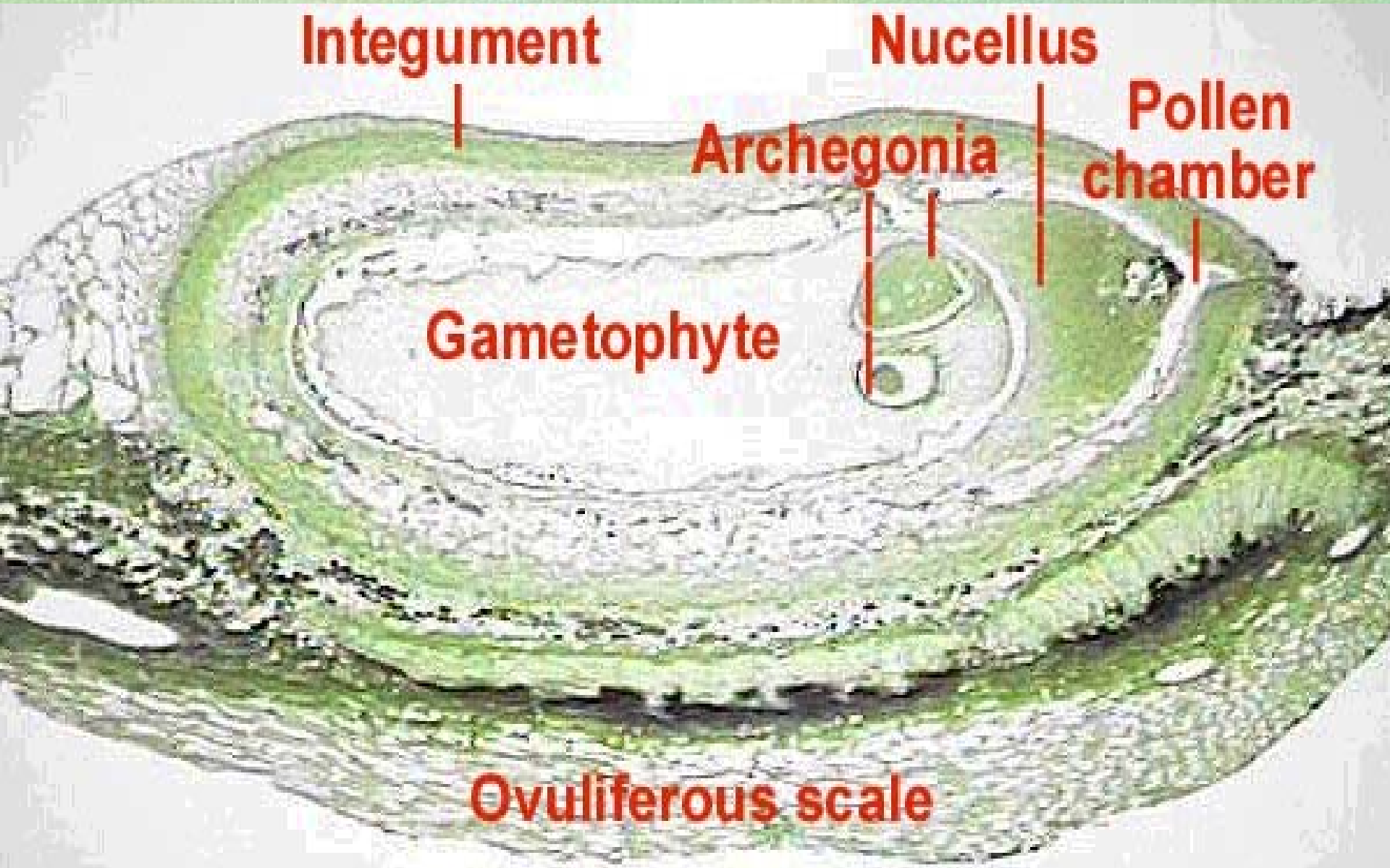
http://www.ucmp.berkeley.edu/IB181/VPL/Osp/Osp3.html

Lyginopteris



http://www.ucmp.berkeley.edu/IB181/VPL/Osp/Osp3.html

Seemnealge

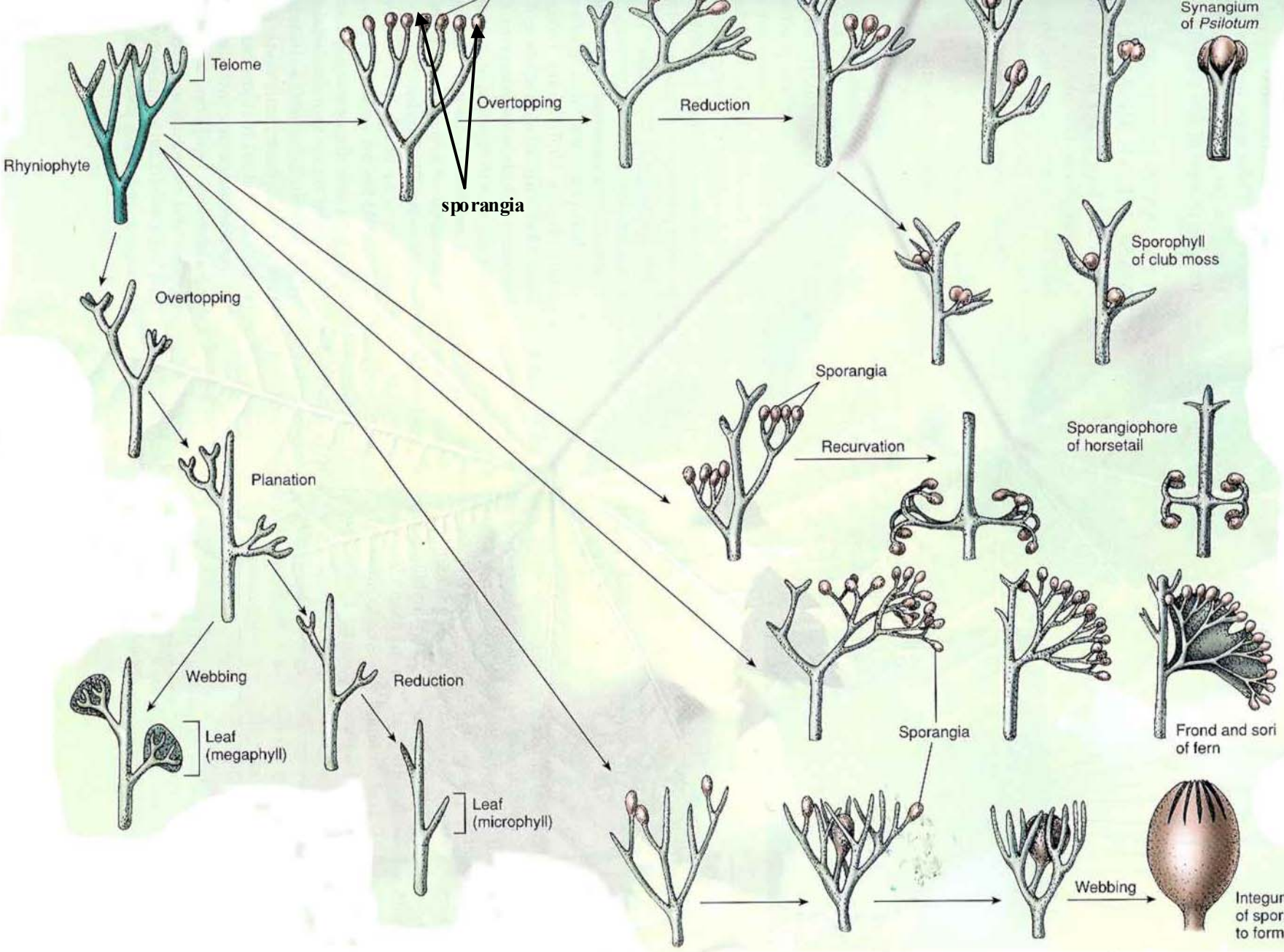

Integument
Nucellus
Archegonia
Pollen chamber
Gametophyte
Ovuliferous scale

Seemnetaimede areng

Kokkuvõtteks: evolutsioonilised uudsused Paleosoikumi seemnesõnajalgadel

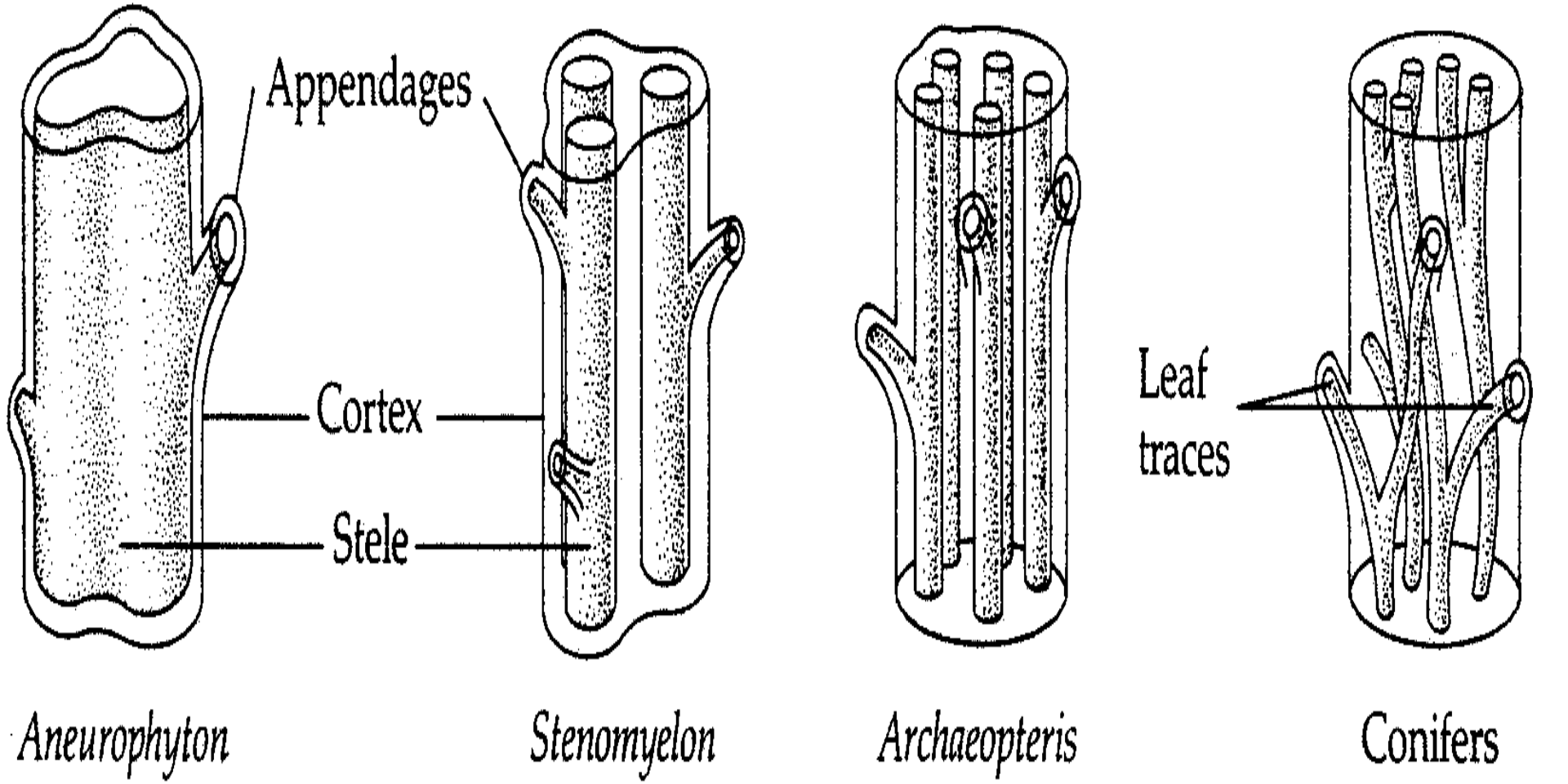
bilateraalsummeetriline leht, mis on arenenud kolmedimensionaalsest radiaalsest teloomikimbust

2. Paljunemisorganite paiknemine lehtedele fertiilsete teloomikimpude modifitseerumise teel



Diagrammetic representation of the evolution of leaves and reproductive structures according to telom theory. (Botanical World: Northington and Schneider 1

3. Eusteeli areng protosteelist



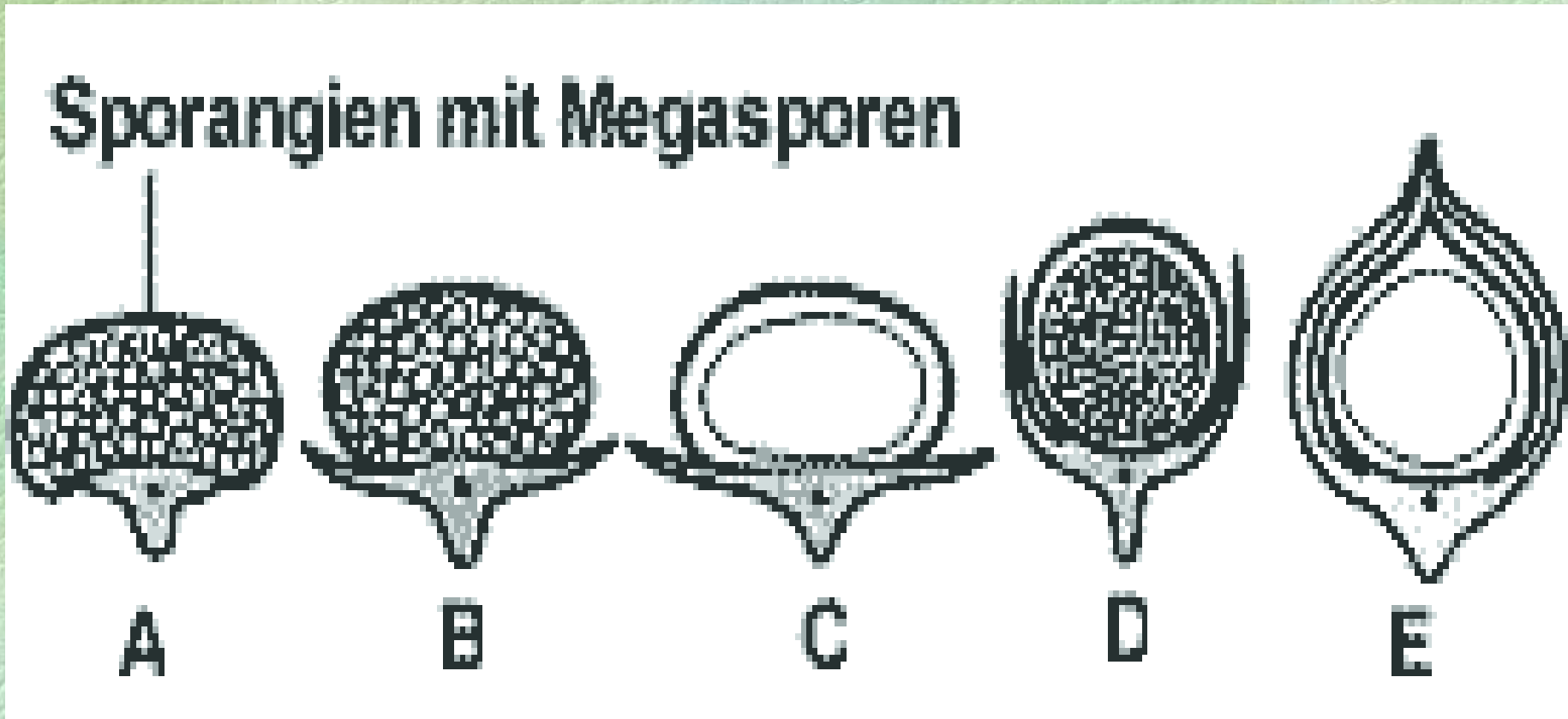
http://www.users.muohio.edu/smithhn/natepage.htm

4. Manoksüülse teispuidu areng

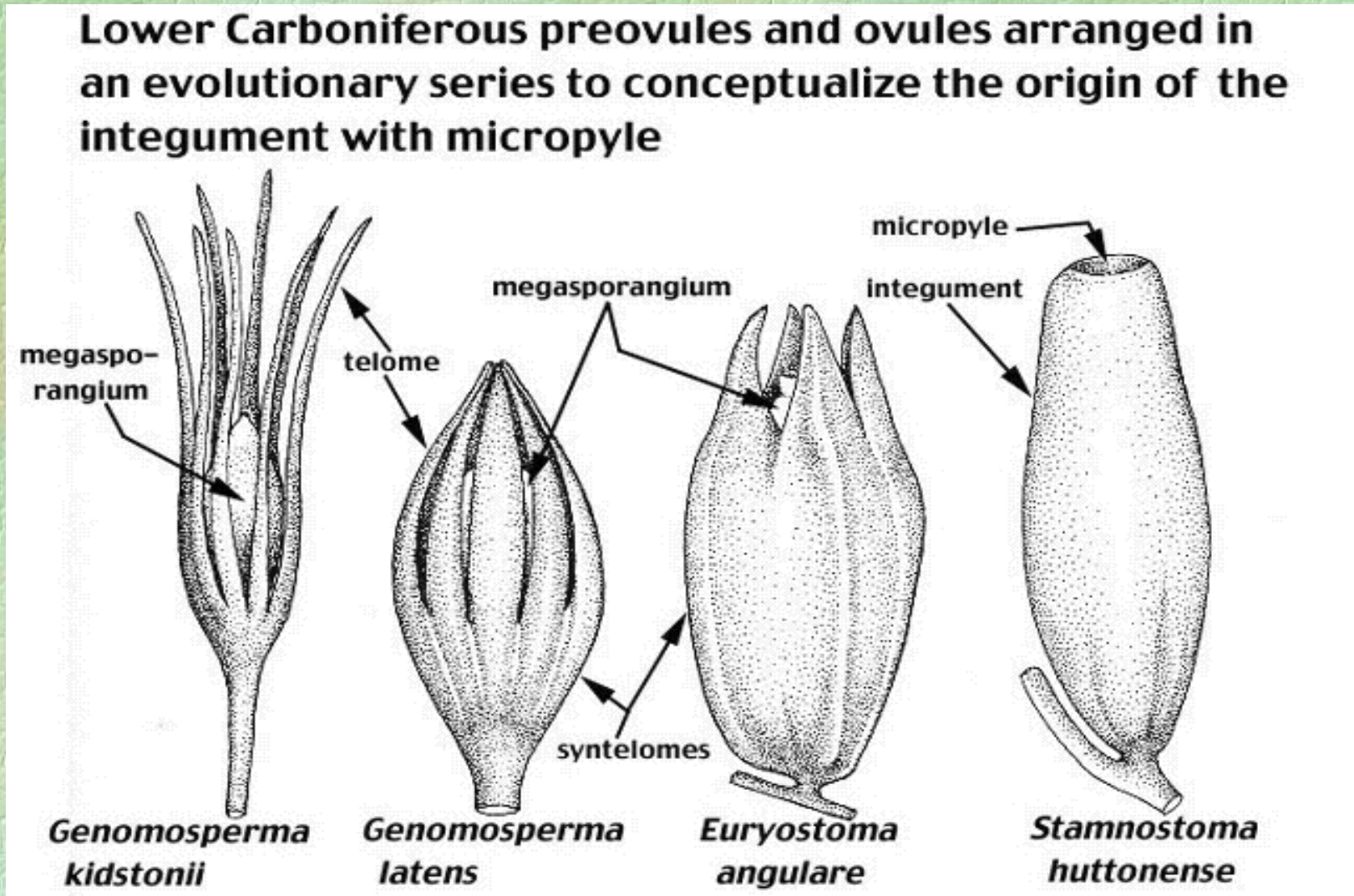
http://www.sbs.utexas.edu/mauseth/weblab/webchap15wood/15.2-8.htm

5. Heterospooria ja endospooria areng

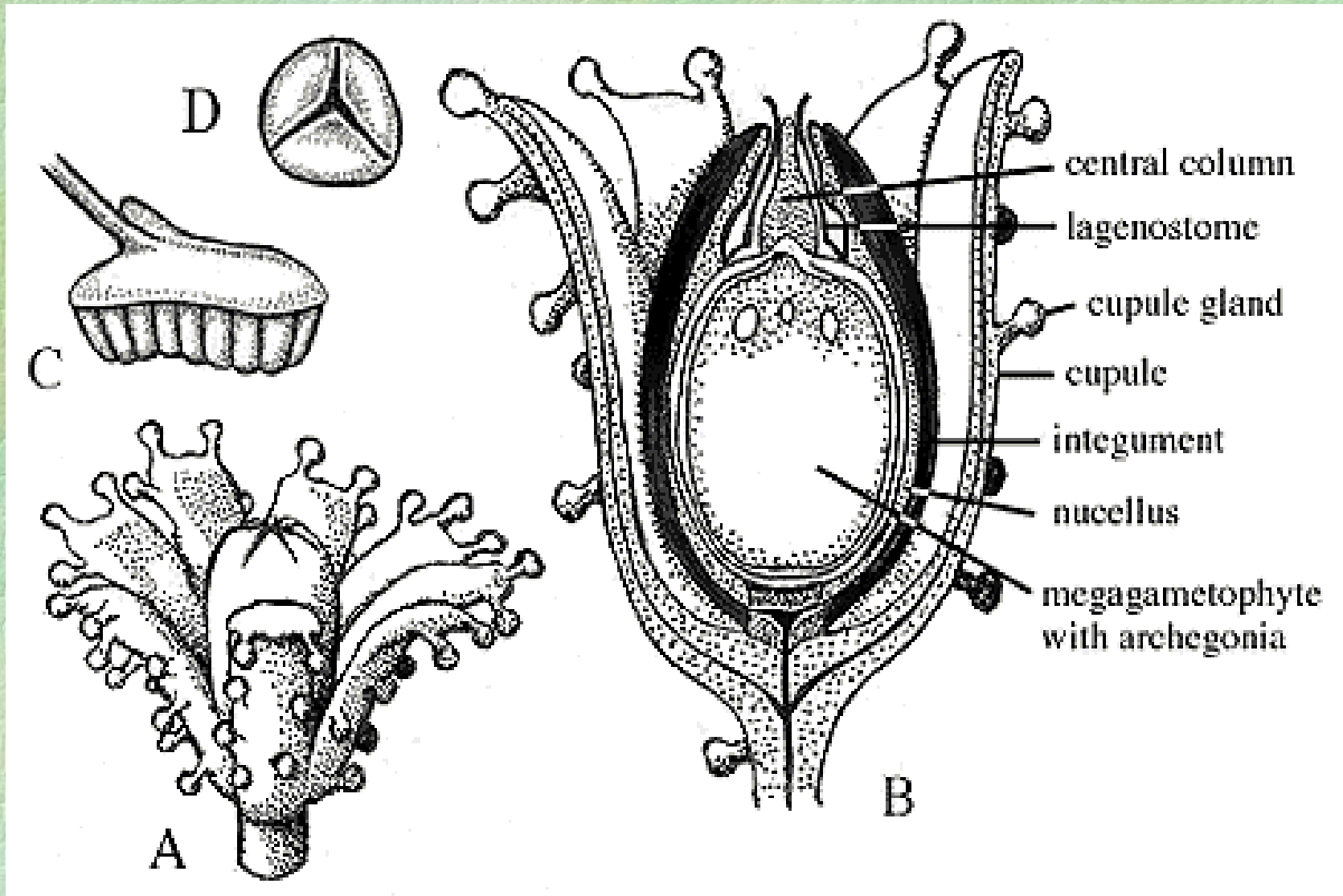
- mitteavanevate megasporangiumide teke



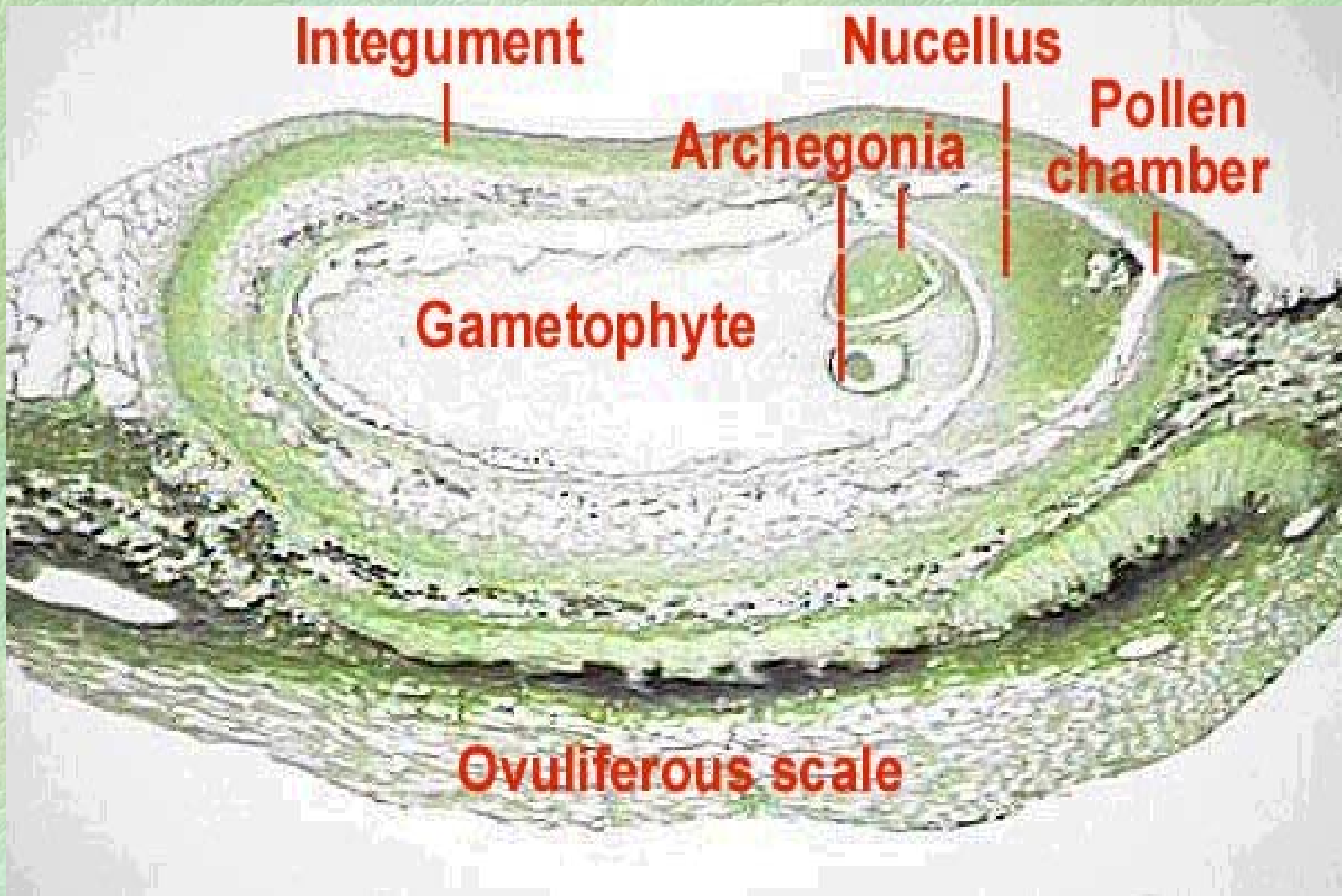
integumentide ja kuupuli arenemine ümber megasporangiumi



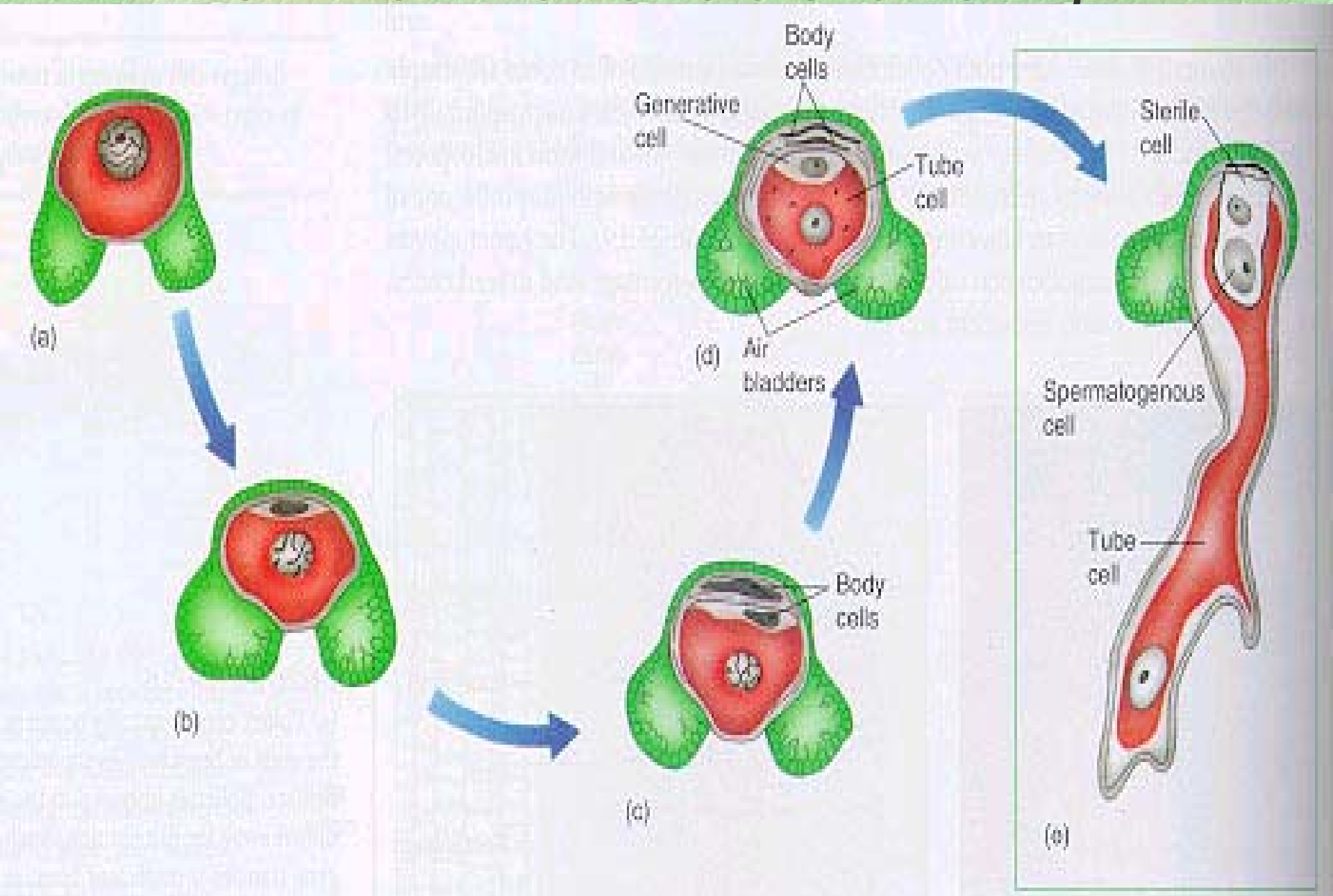
7. Tolmlemise arenemine, hüdraspermne paljunemisviis (lagenostoom)



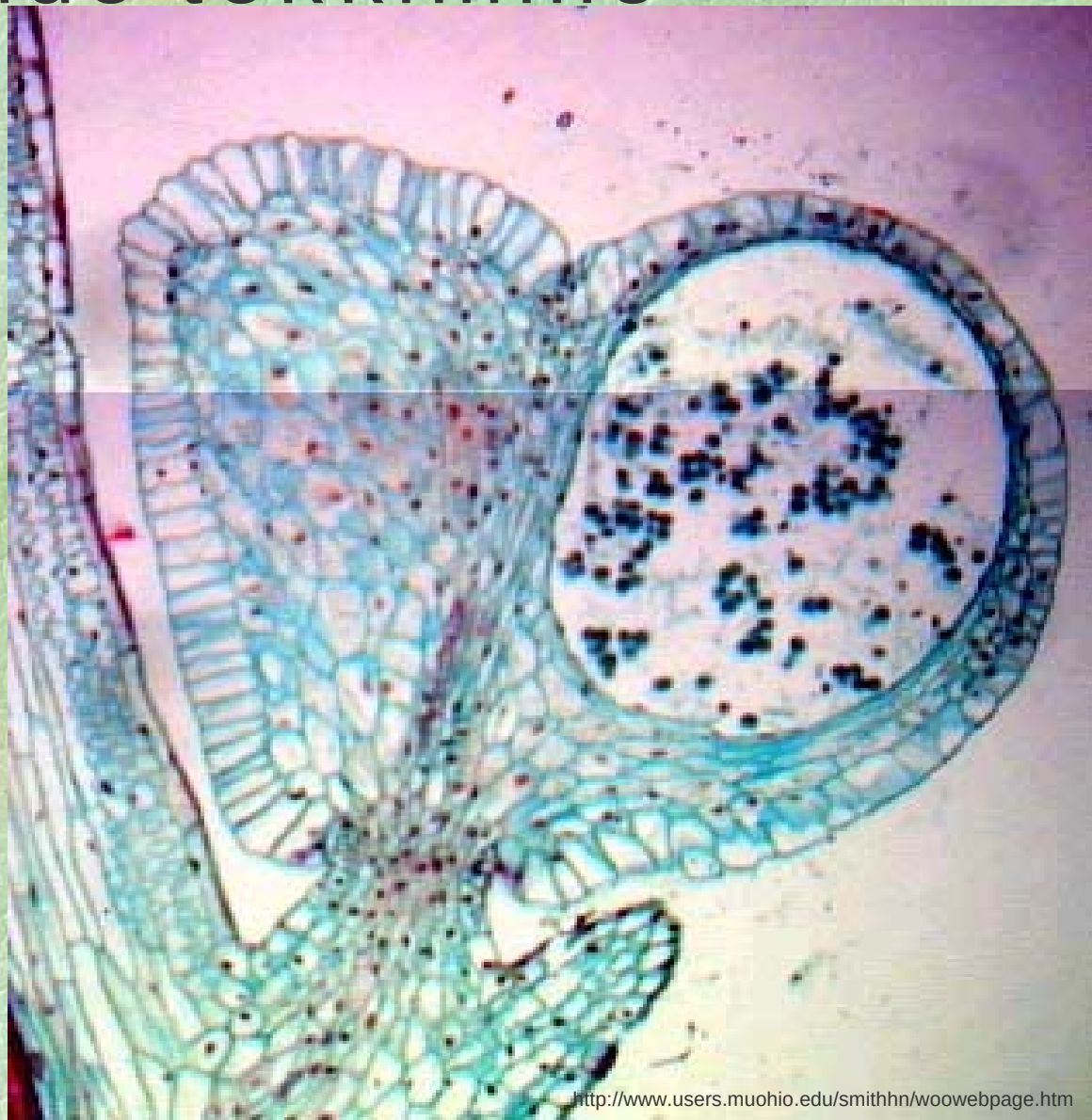
väljaarenemine – integumendid funktsionaalse mikropüüliga



9. Tolmutorude areng



10._Mikrosporangiumide klastritest kerajate sünangiumide tekkimine



http://www.users.muohio.edu/smithhn/woowebpage.htm

tolmuterade erinevate tüüpide areng trileetsetest mikrospooridest

Figure 4.3 Some pore and furrow patterns (adapted from Kapp 1969:22–25, 27).

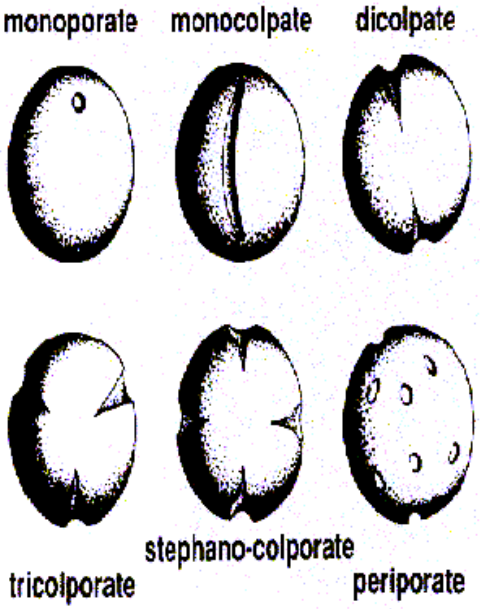
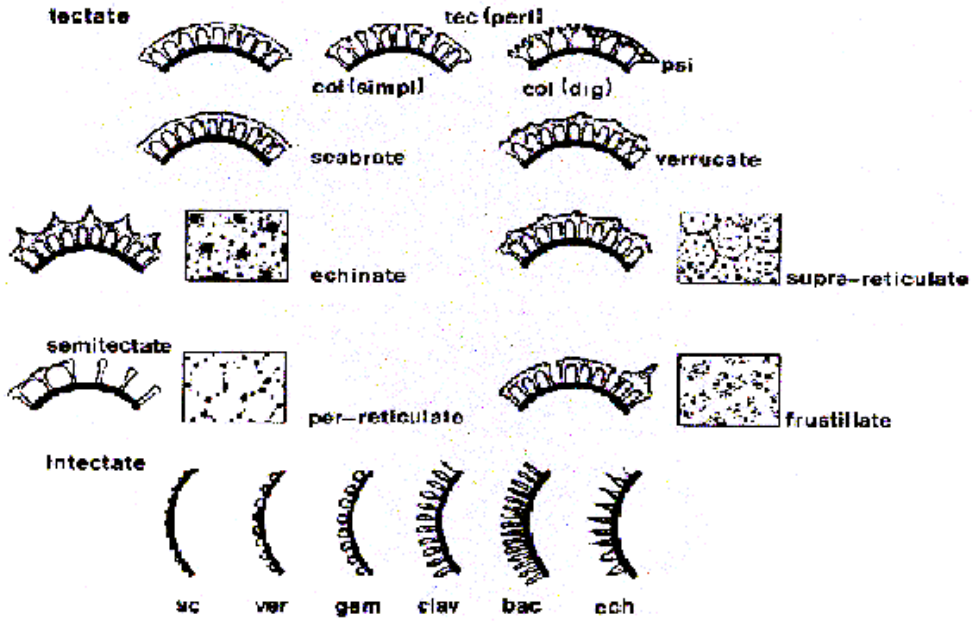
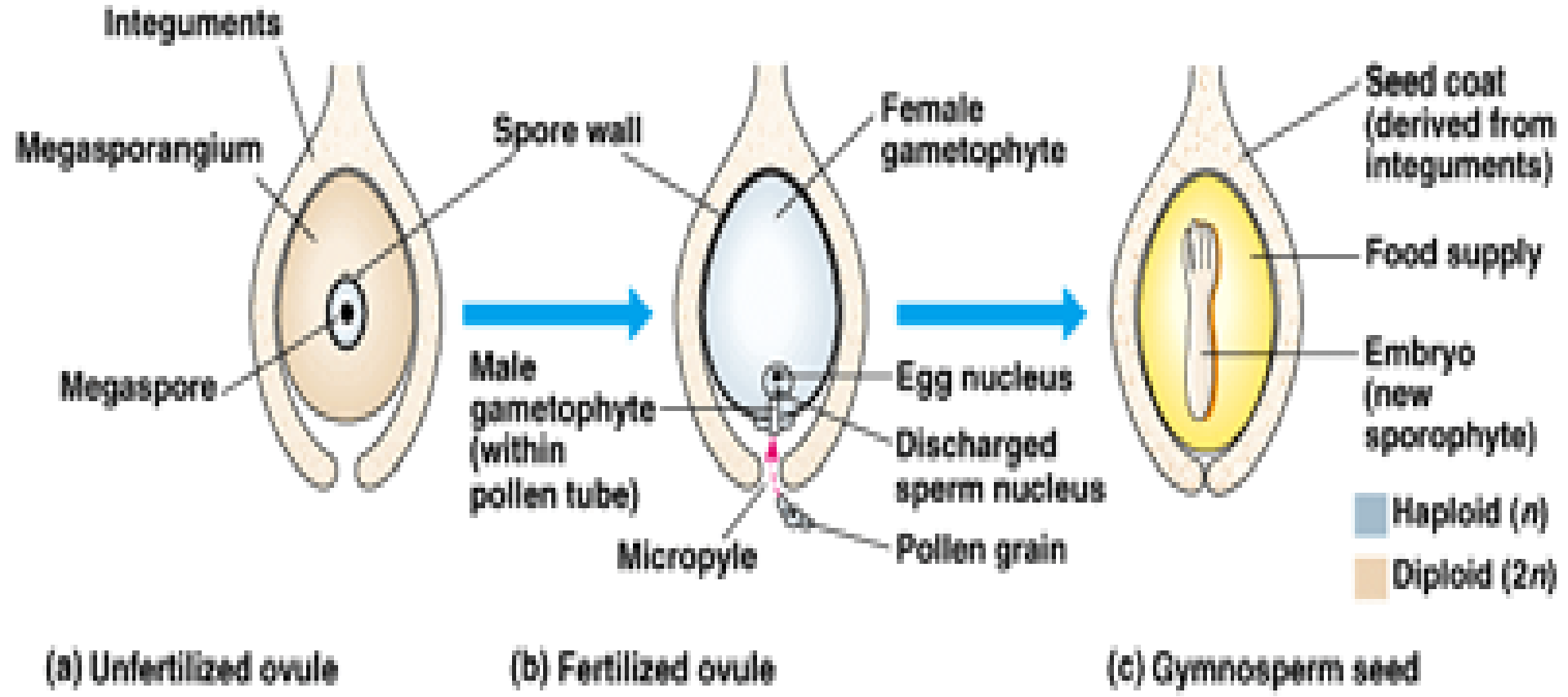


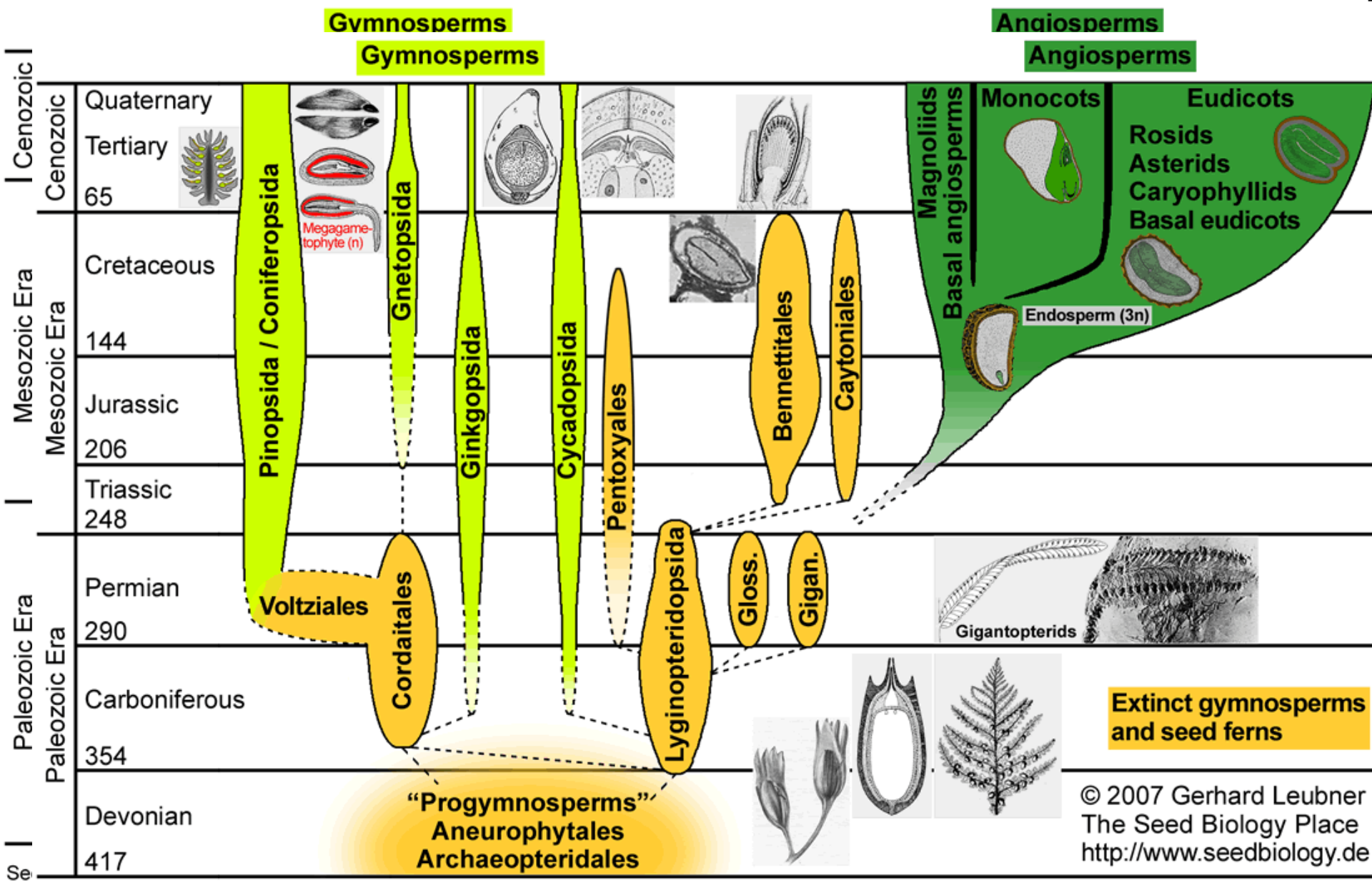
Figure 4.4 Variations of exine structure and sculpturing. Endexine, black; ektexine, dotted. col, columellae (simpl = simple, dig = digirate); tec (perf), perforate tectum; Psi, psilate. Bottom row: scabrate, verrucate, gemmate, clavate, baculate, and echinate sculpturing (from Faegri and Iversen 1975:30).



Paljasseemnetaime paljunemine



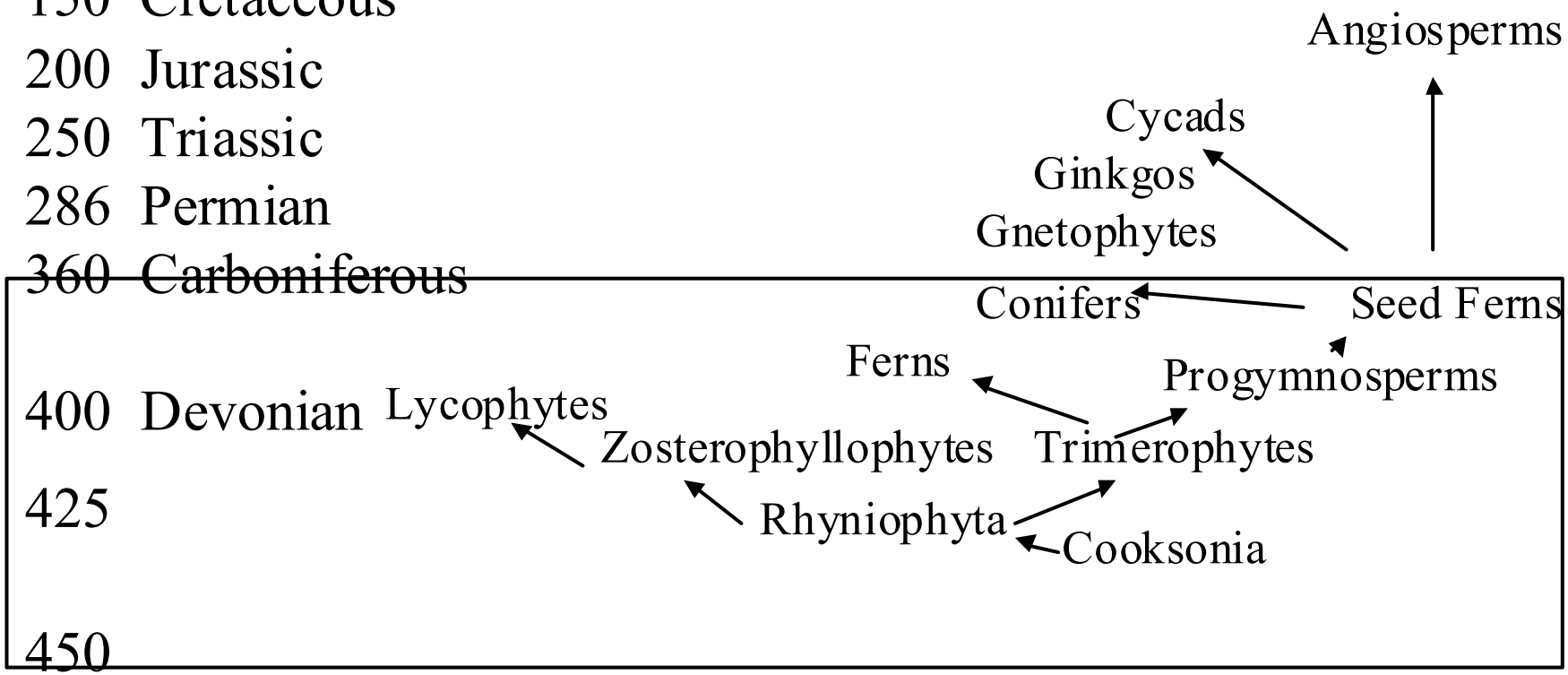
Paljasseemnetaimed

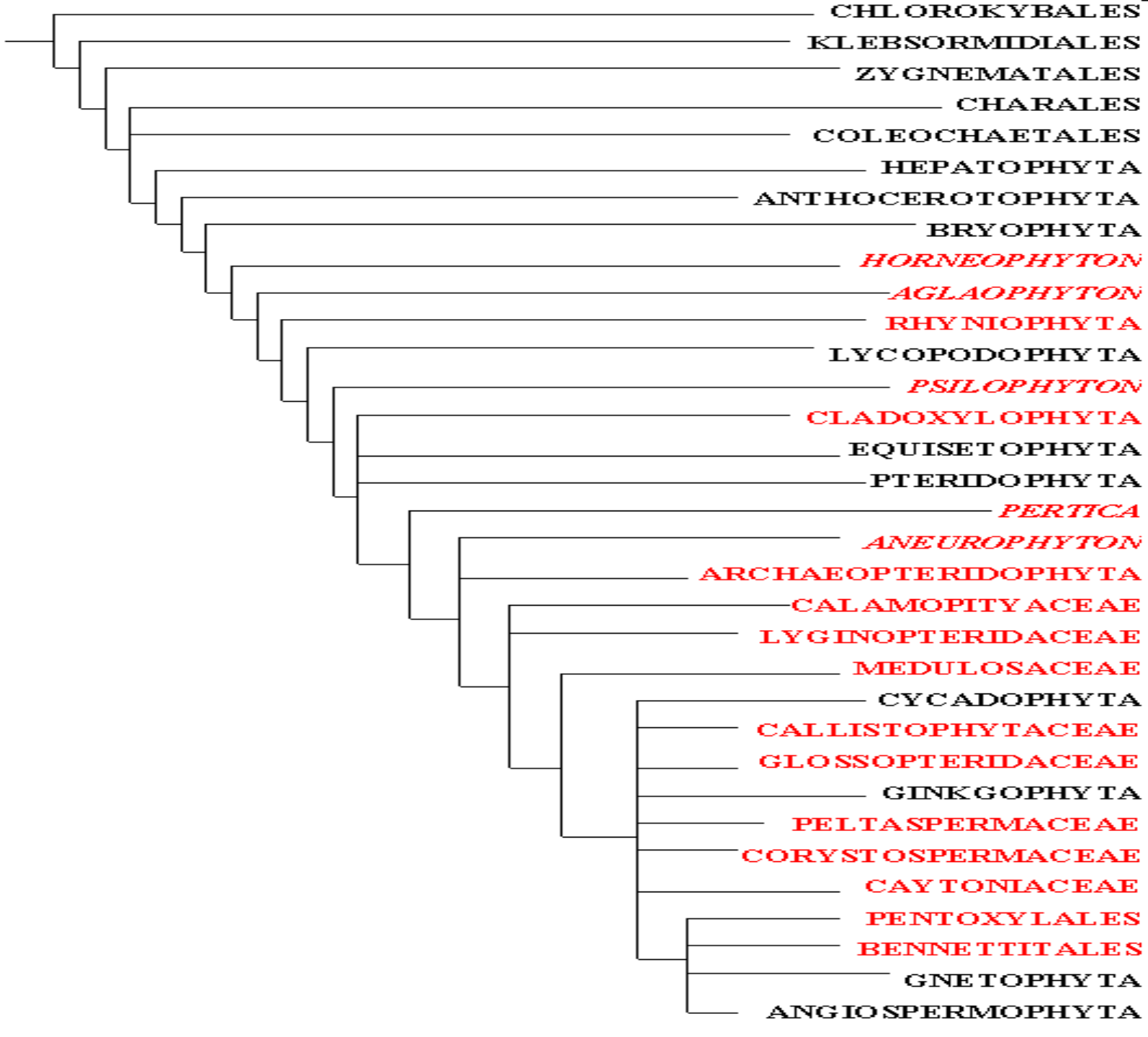


Seed plant phylogenetic tree considering major gymnosperm and angiosperm clades. Note that the precise evolutionary connections between the differe gymnosperm groups are unknown and that the ancestors of angiosperms are unknown. Typical seed types visualize steps in the evolution of the see Extinct gymnosperm groups (fossils): Lyginopteridopsida (seed ferns, "Samenfarne", includes Devonian/Carboniferous Lyginopterids and Carboniferou Permian Medullosans and other subgroups), Cordaitales, Voltziales, Pentoxylales. Bennettitales (cycadeoids), Caytoniales, Glossopteridales (glossopteric Gigantopteridales (gigantoperids). Extant gymnosperm groups: Pinopsida/Coniferopsida (conifers, "Nadelbäume"), Ginkgopsida (ginkgos), Cycadopsic (cycads, "Palmfarne"), Gnetopsida (gnetophytes: Ephedridae, Gnetidae, Welwitschiidae). Angiosperms (flowering plants): Most important groups depicte

Gymnosperm phylogeny is in flux. They may be four separate lineages, a single clade, or maybe in between.

MYA--Epoch
50 Tertiary
100
150 Cretaceous
200 Jurassic
250 Triassic
286 Permian
360 Carboniferous
400 Devonian
425
450
500 Silurian
600 Cambrian--Ordovician



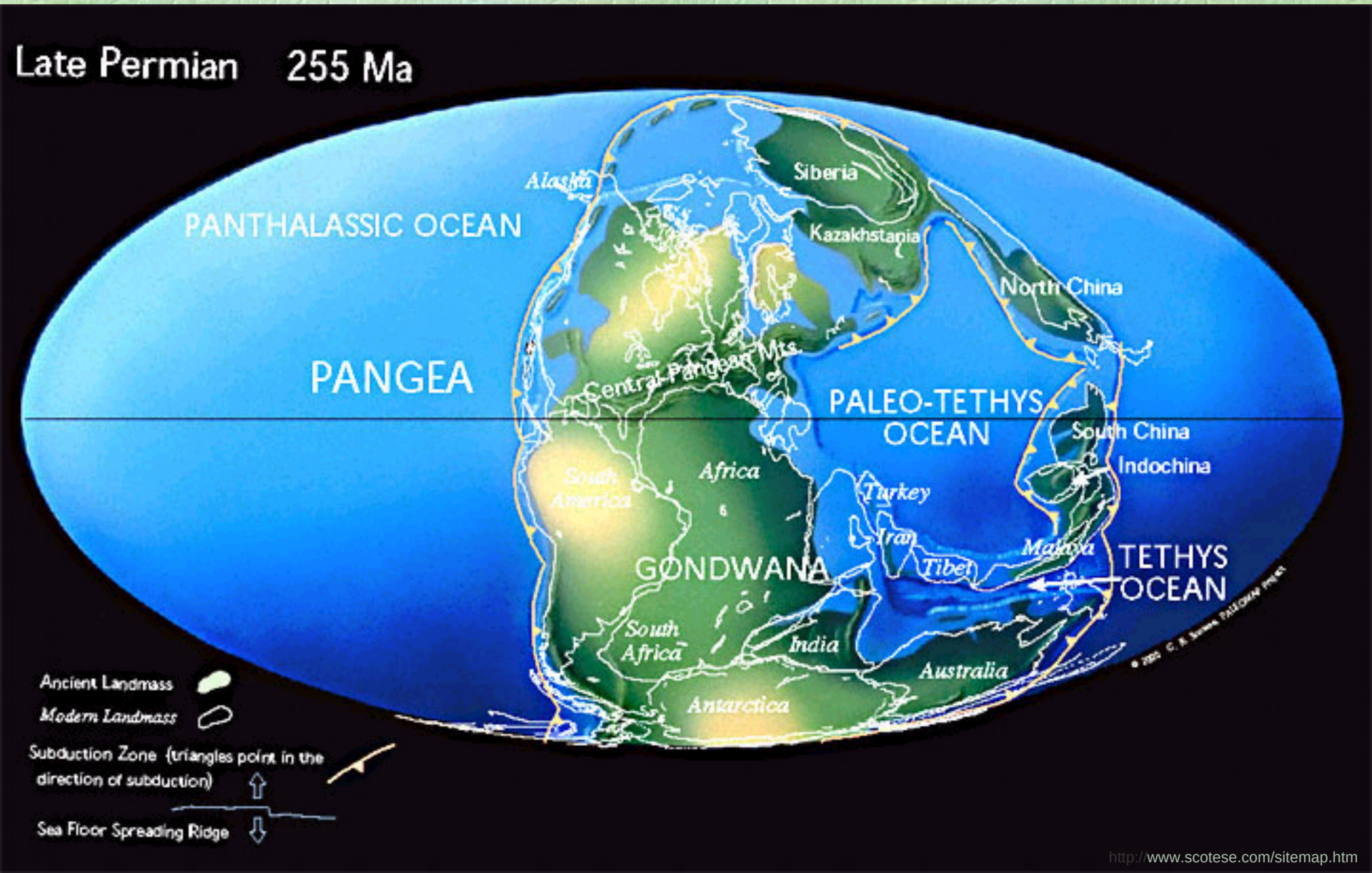


Judd, Campbell 2002

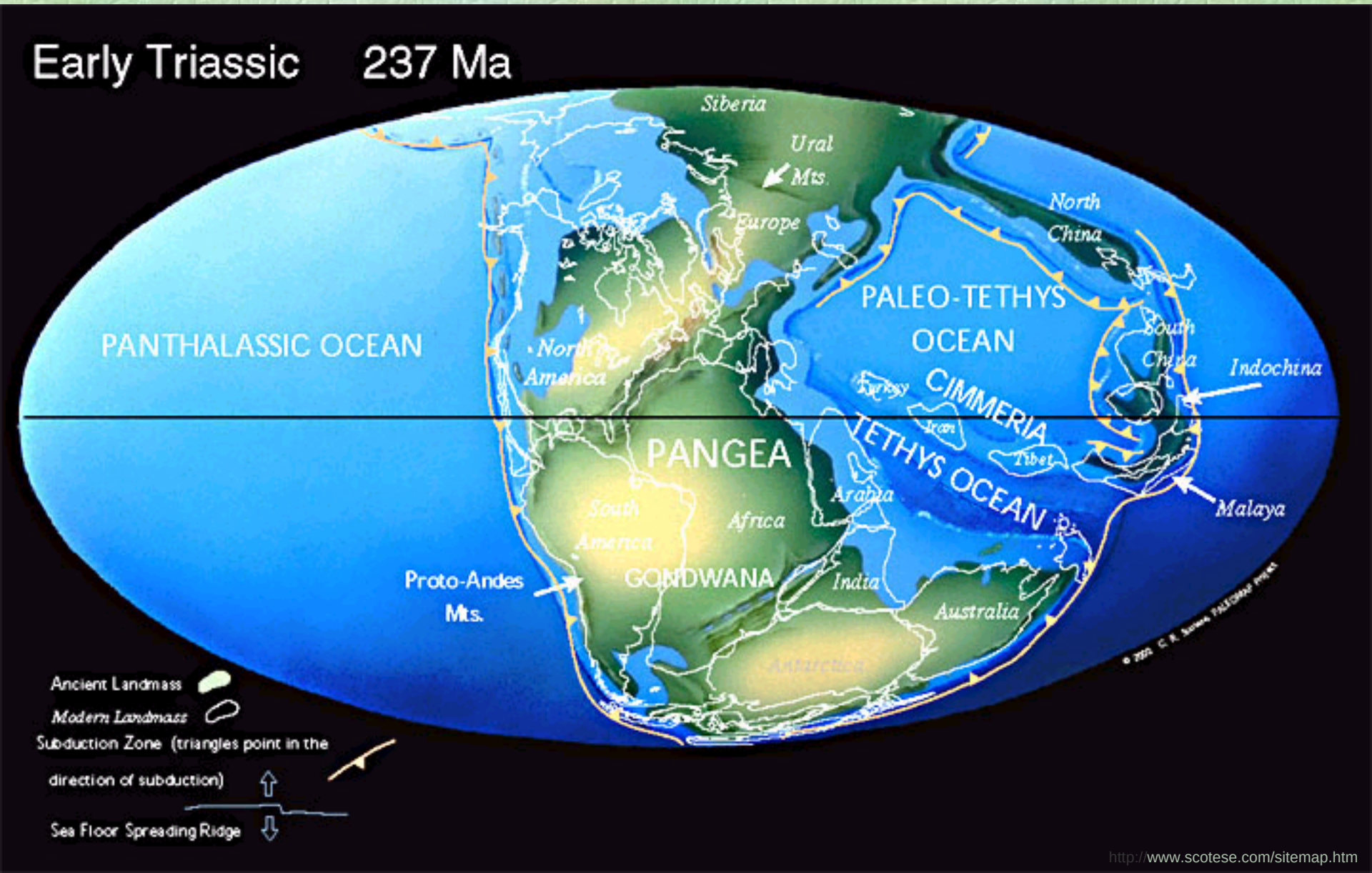
Seemnetaimed

- Väljasurnud "seemnesõnajalad" (4 suguk) †
- Alamklass palmlehikud *Cycadidae*
- Suguk *Callistophytaceae* †
- Alamklass okaspuud *Piniidae*
  - ihnlehikulaadsed *Cordaitales* †
  - männilaadsed *Pinales (Coniferales)* †
- Suguk *Glossopteridaceae* †
- Alamklass hõlmikpuud *Ginkgooidae*
- Suguk *Caytoniaceae, Corystospermaceae, Peltaspermaceae* †
- Seltsid Pentoxylales, Bennetitales †
- Alamklass vastaklehikud *Gnetidae*

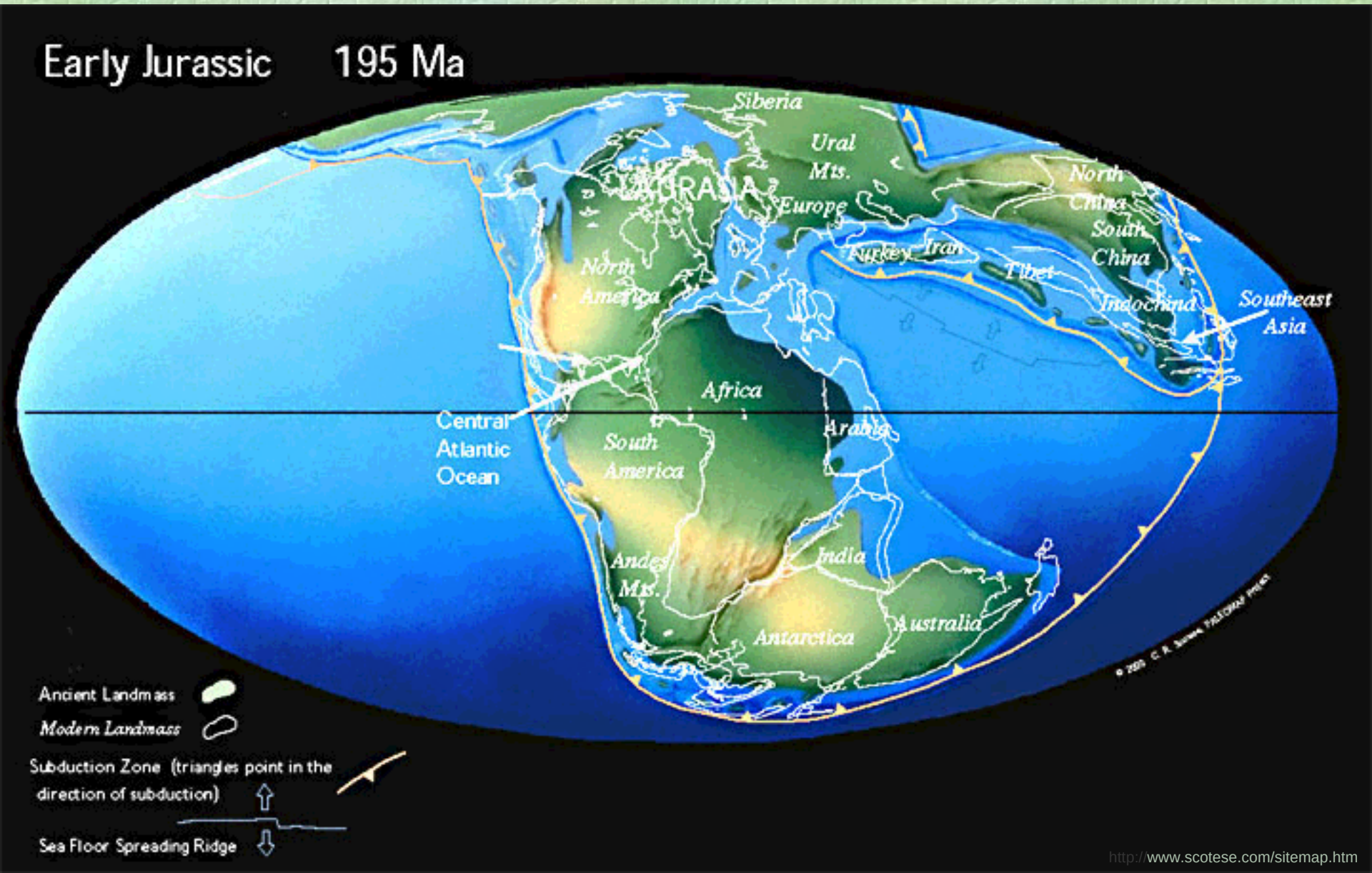
Mandrid Permis



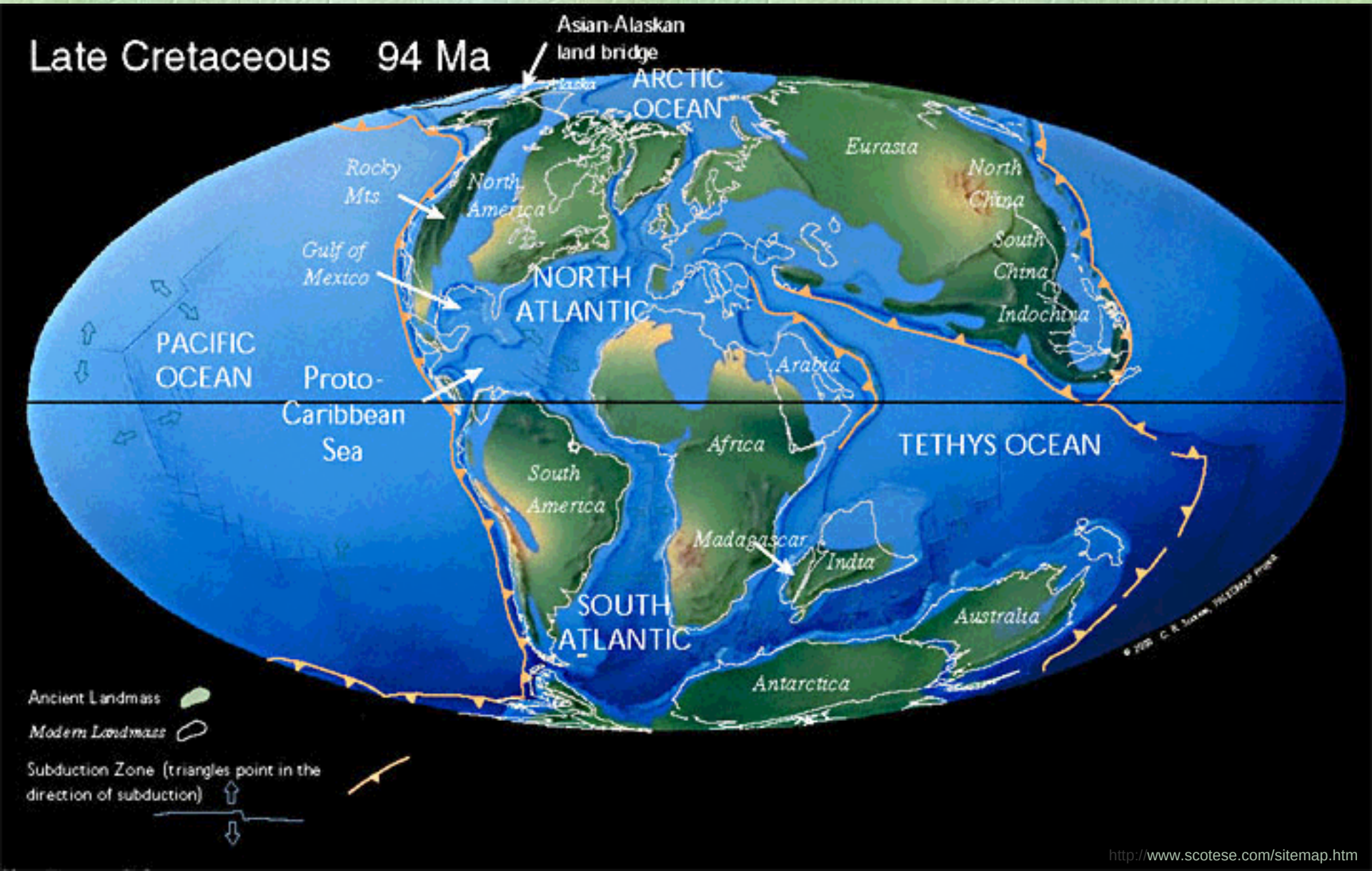
Mesosoikum
Mandrid Triiases



Mandrid Juuras



Mandrid Kriidis

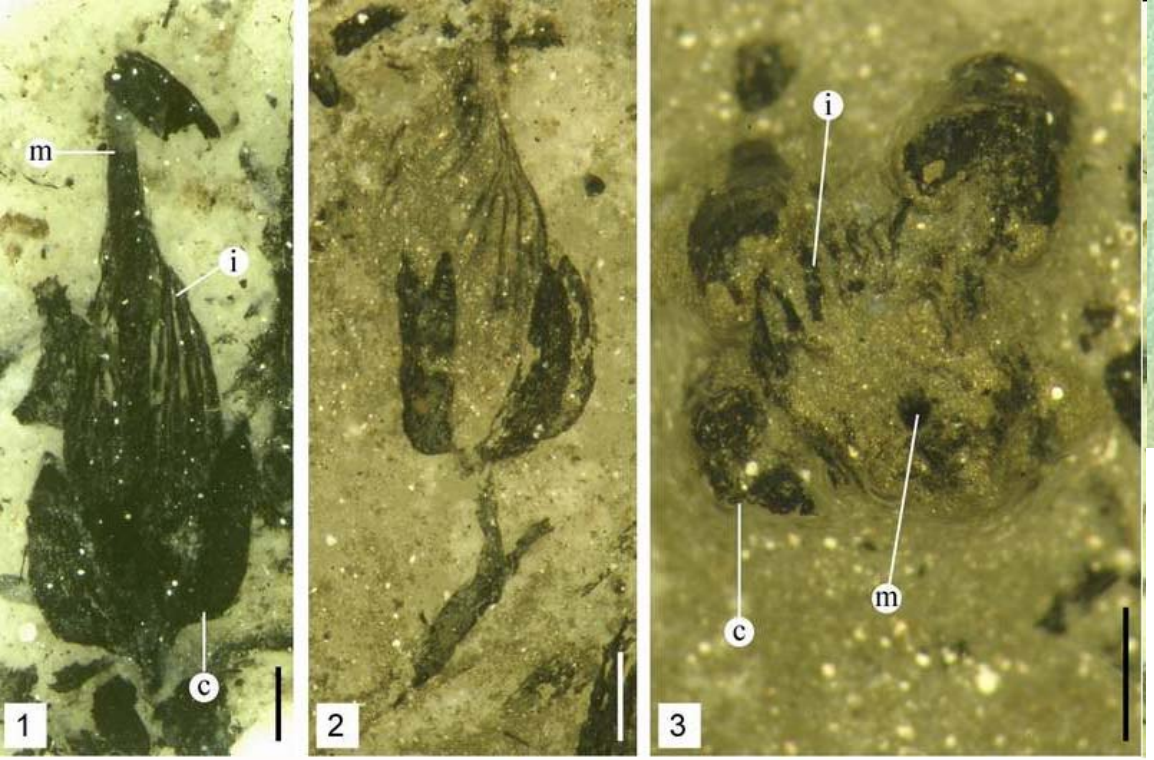


Väljasurnud seemnesõnajalad

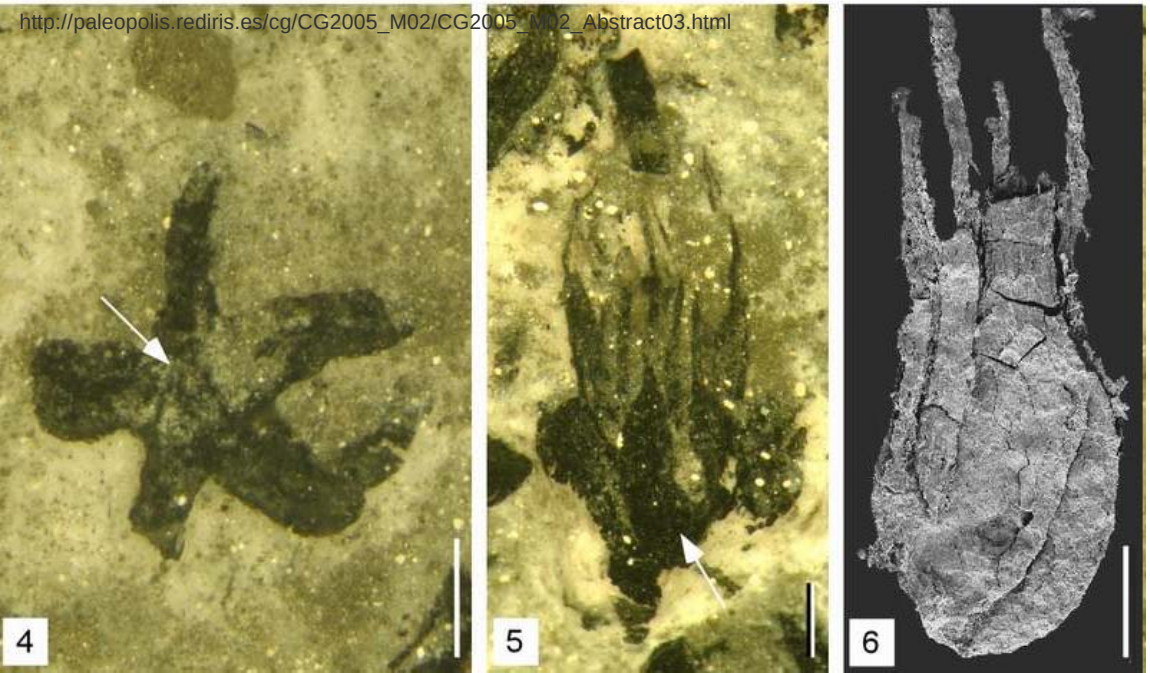
- *Runcaria*
- Calamopityaceae
- Hydraspermaceae
- Lyginopteridaceae
- Medullosaceae

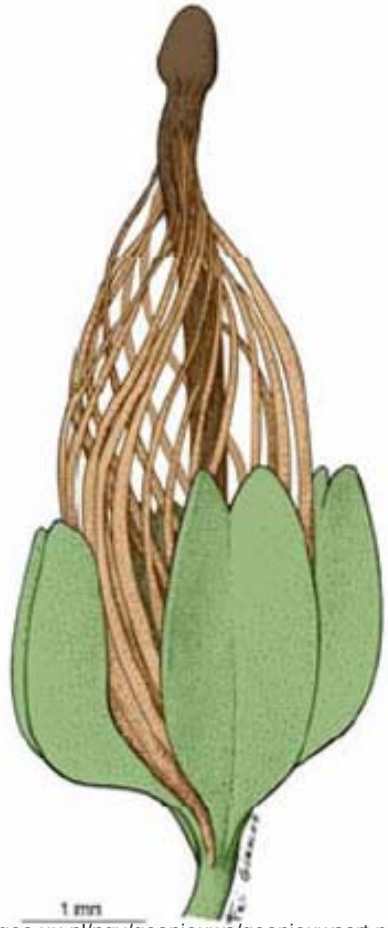
Runcaria

385 MAT!



http://paleopolis.rediris.es/cg/CG2005_M02/CG2005_M02_Abstract03.html





http://www.geo.uu.nl/ngv/geonieuws/geonieuwsart.php?artikelnr=523

Elkinsia polymorpha

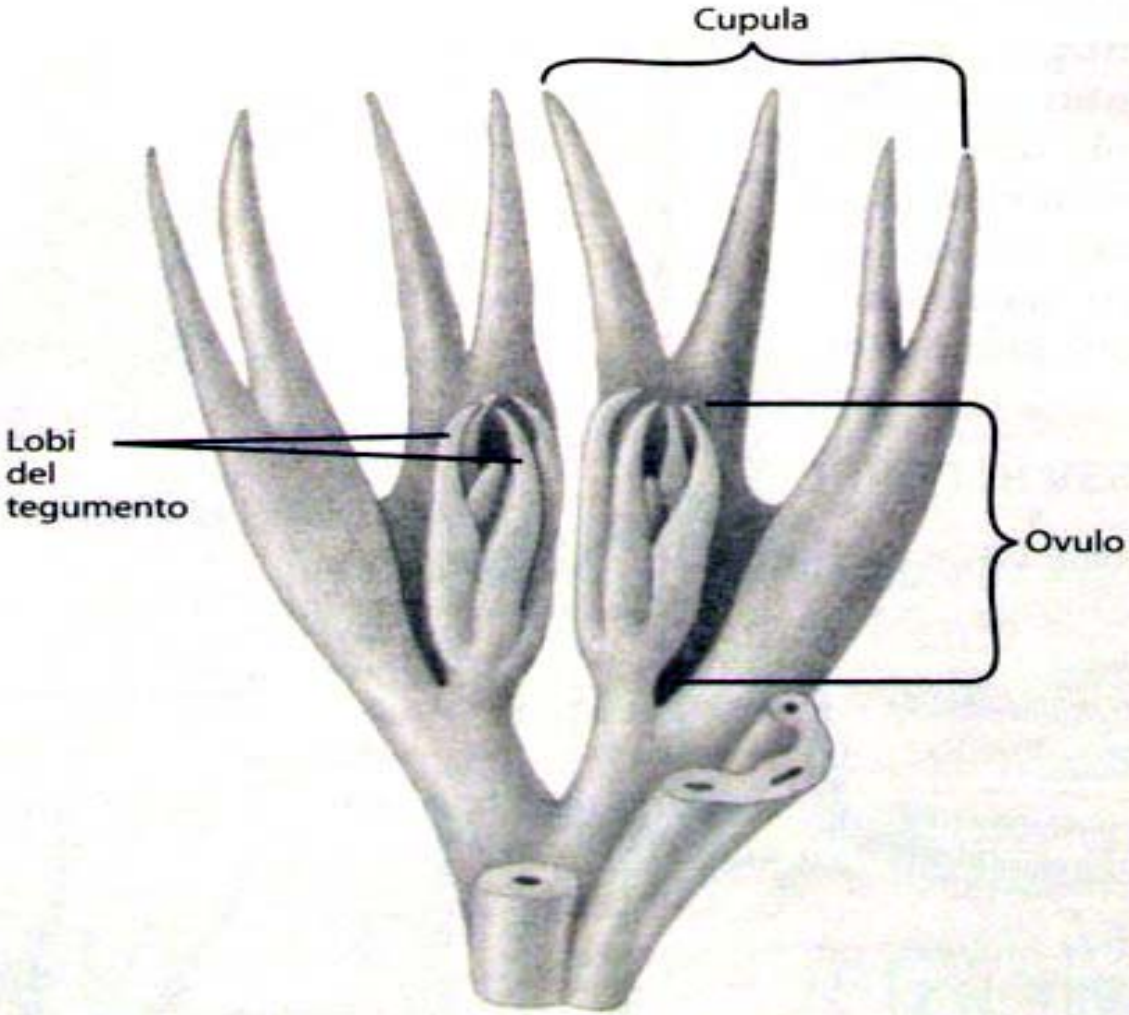
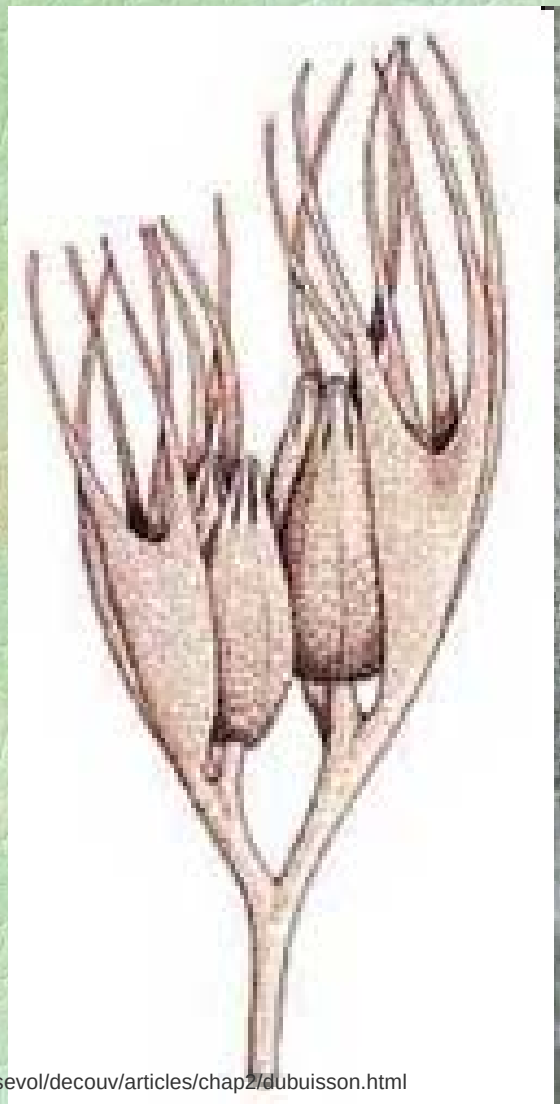


Figura 20.3 Ricostruzione di un ramo fertile di *Elkinsia polymorpha*, una pianta del Devoniano superiore, con gli ovuli. Ciascun ovulo era sovrastato dalla cupula, una struttura sterile ramificata dicotomicamente. Sono visibili i lobi del tegumento più o meno liberi.

Archaeaosperma ja *Moresnetia*



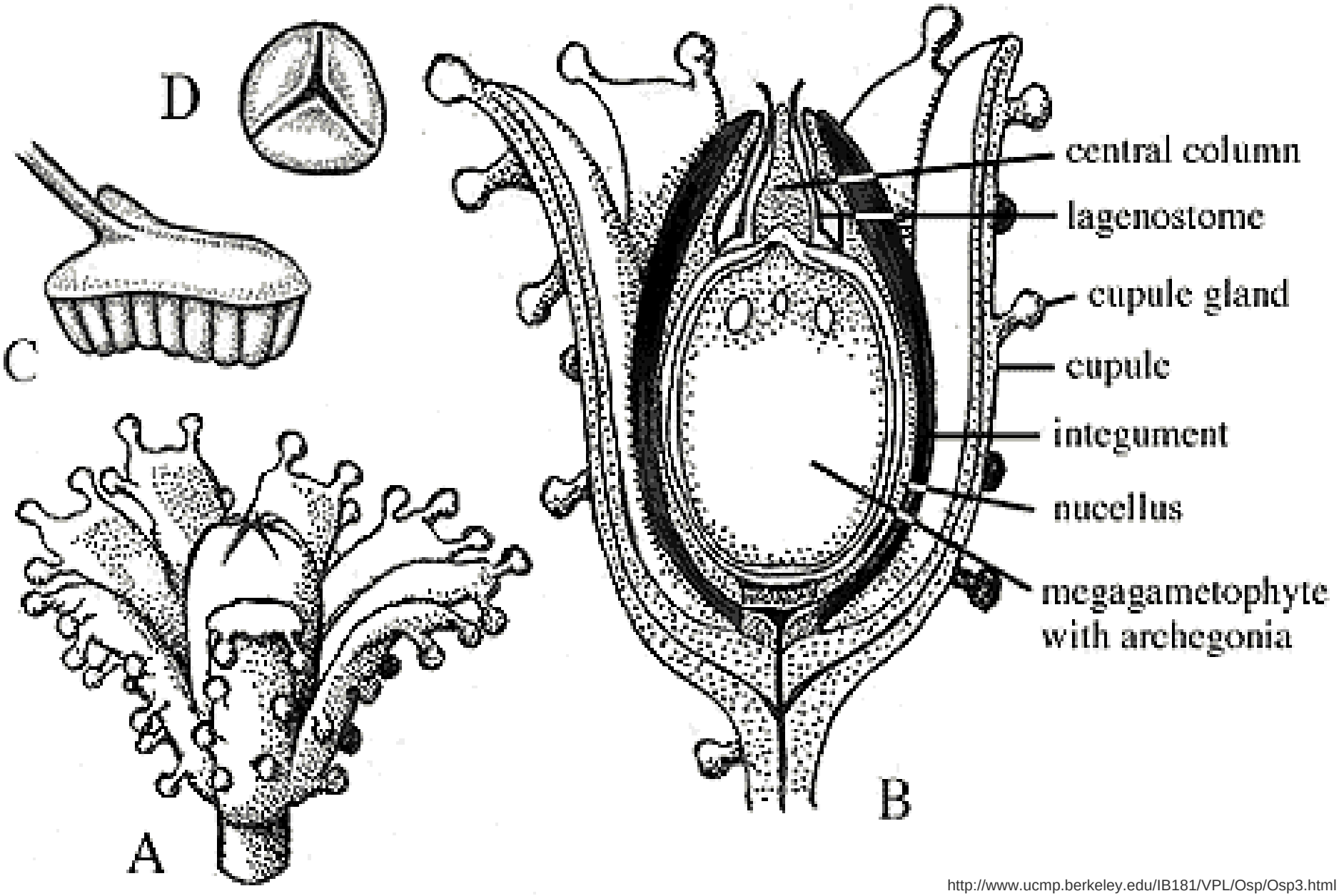
http://www.cnrs.fr/cw/dossiers/dosevol/decouv/articles/chap2/dubuisson.html

Lyginopteris

http://ademir.comtercy.free.fr/fossiles/familles.htm/lyginopteris.html

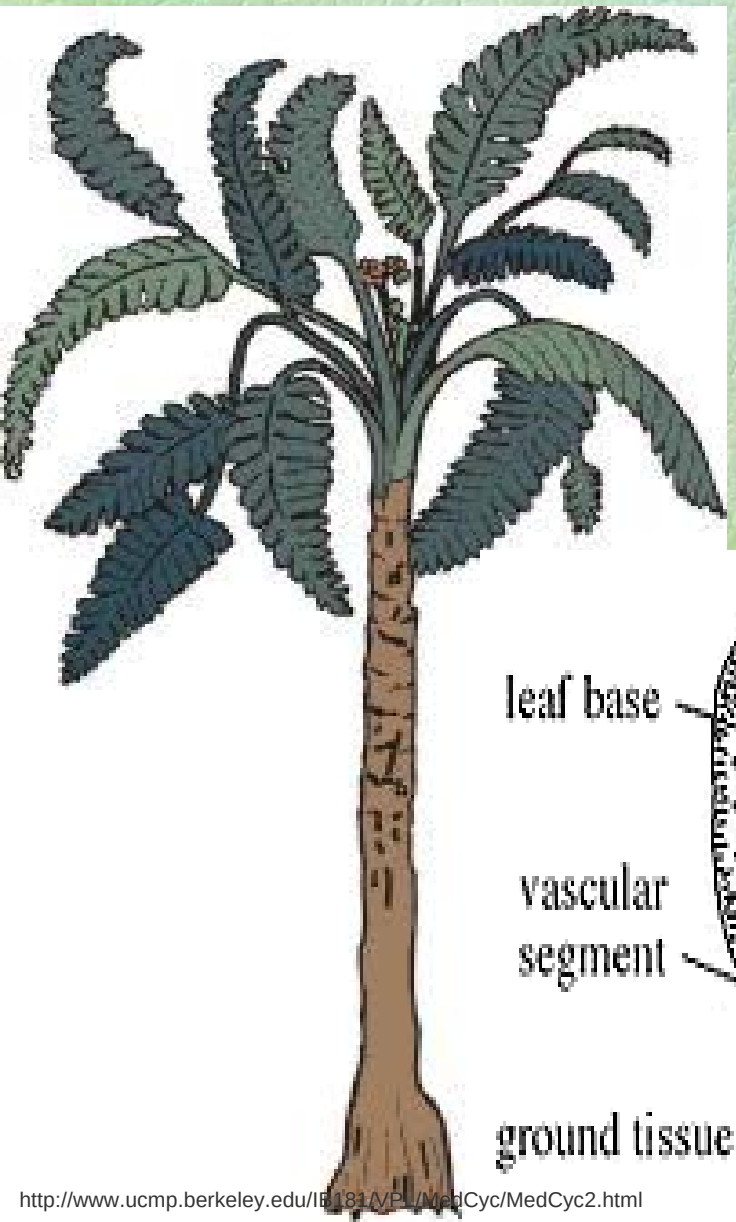
http://www.ucmp.berkeley.edu/IB181/VPL/Osp/Osp3.html

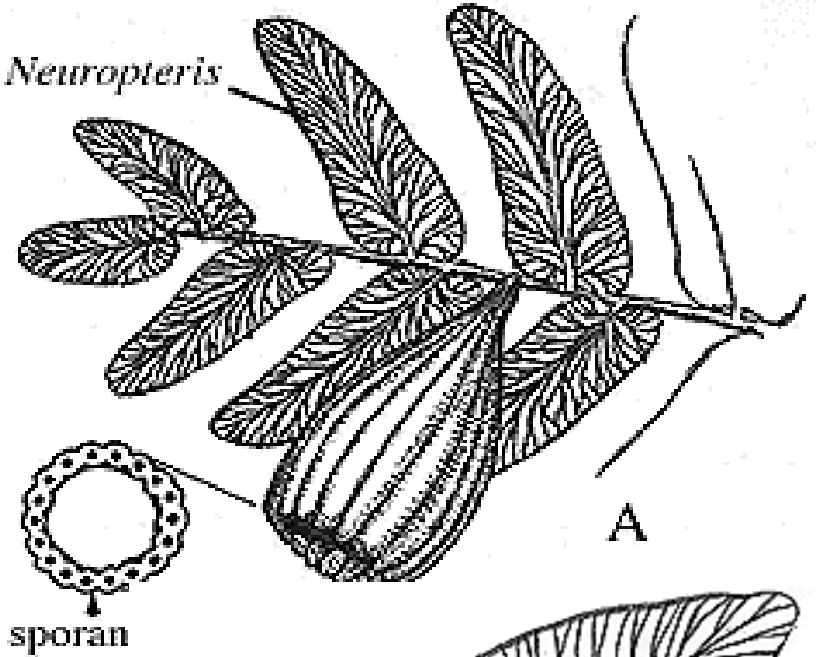
Lyginopteris

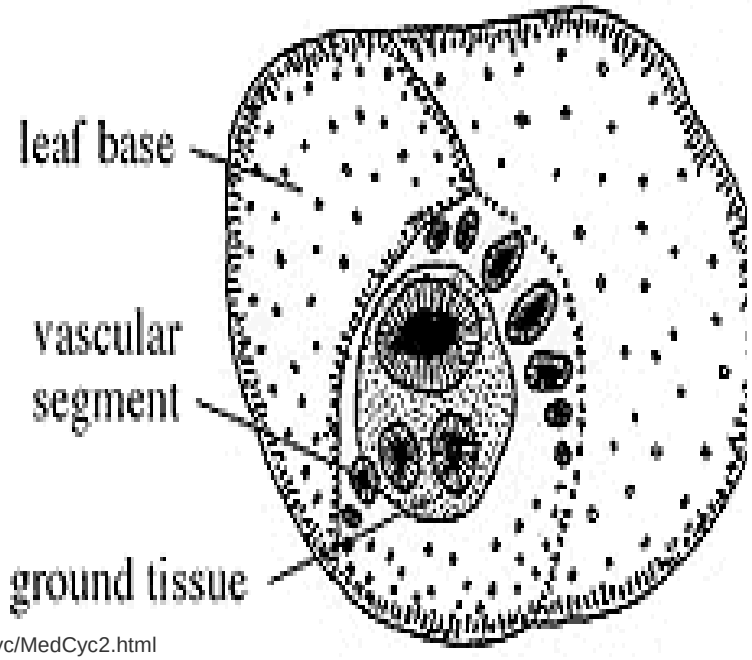


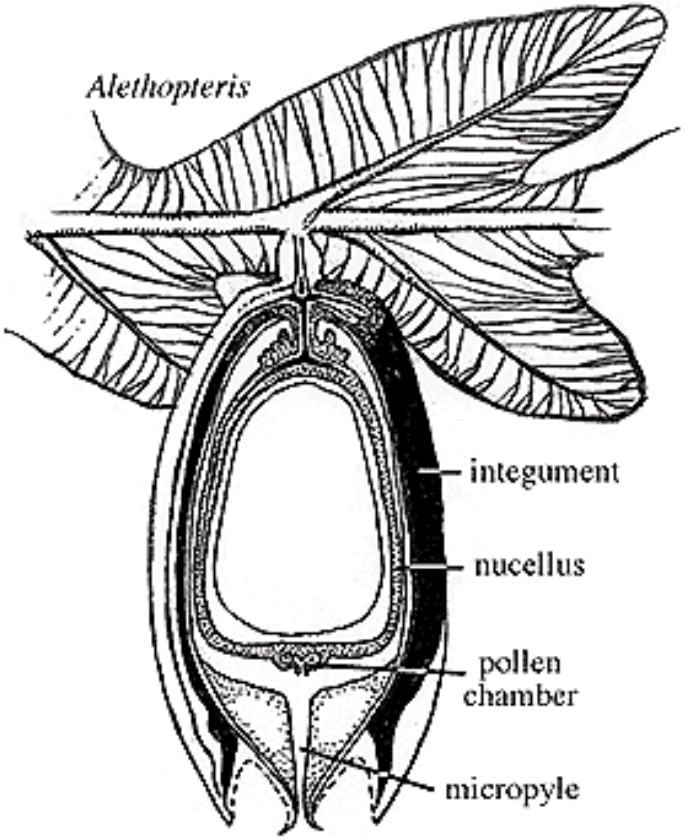
http://www.ucmp.berkeley.edu/IB181/VPL/Osp/Osp3.html

Medullosa



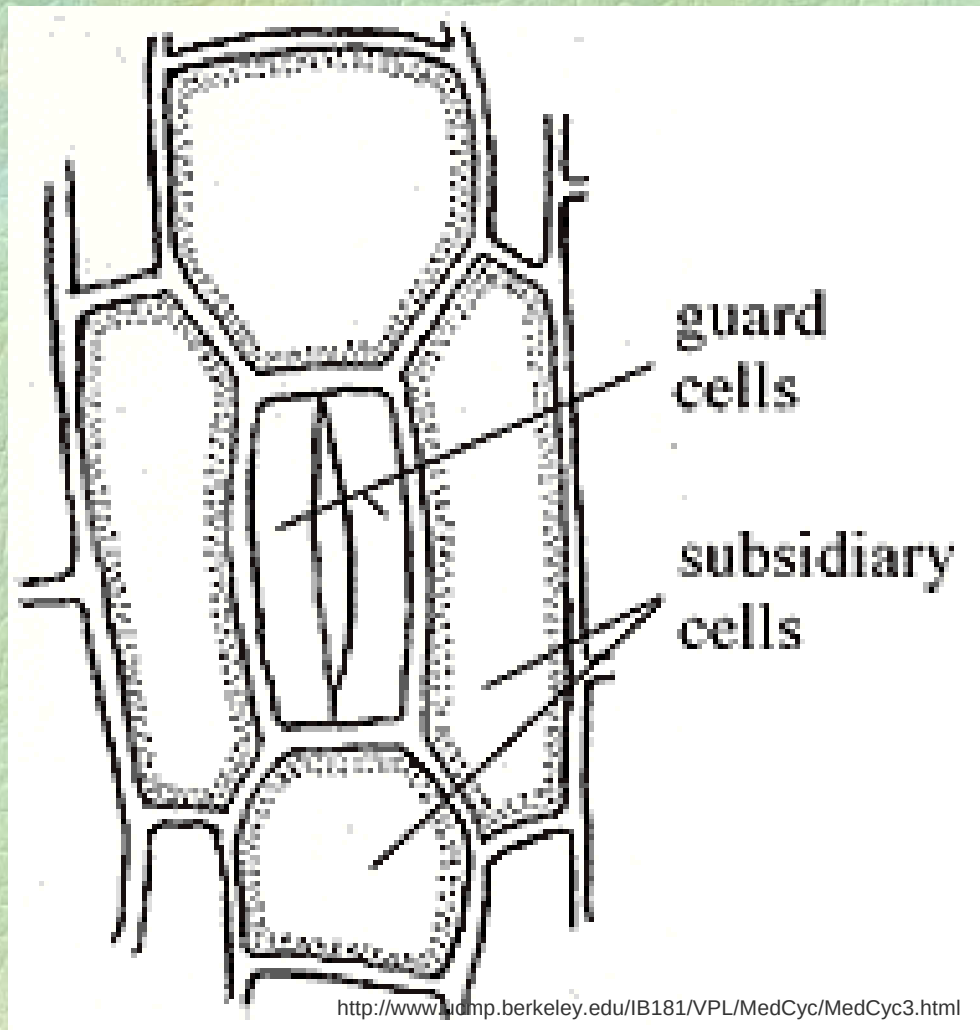

Neuropteris
A
sporan


leaf base
vascular segment
ground tissue


Alethopteris
integument
nucellus
pollen chamber
micropyle

Palmlehikud – *Cycadidae, Cycadales*

- Eriline juhtkimpude paigutus leherootsus
- Glükosiidid tsükasiinid
- Erilist tüüpi õhulõhed (ka okaspuudel)
- Katafüllid
- Käbid
- Koralloidsed juured
- Sulgjad liitlehed



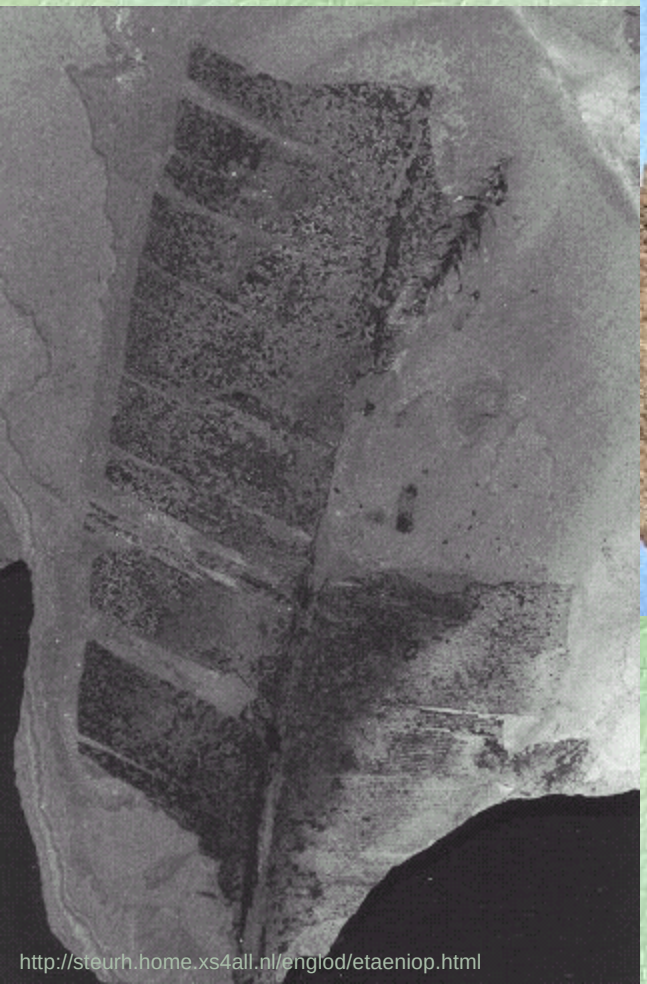
http://www.ucmp.berkeley.edu/IB181/VPL/MedCyc/MedCyc3.html

Cycadales

- Palmi- või sõnajala-taolised puud, 18-20 m
- Troopikas, eriti lõunapoolkeral
- Cycadaceae, Zamiaceae
- 10-11 perek, 130 liiki
- Reliktid, endeemid

Väljasurnud palmlehikud

Taeniopteris



Leptocycas

http://steurh.home.xs4all.nl/englod/etaeniop.html

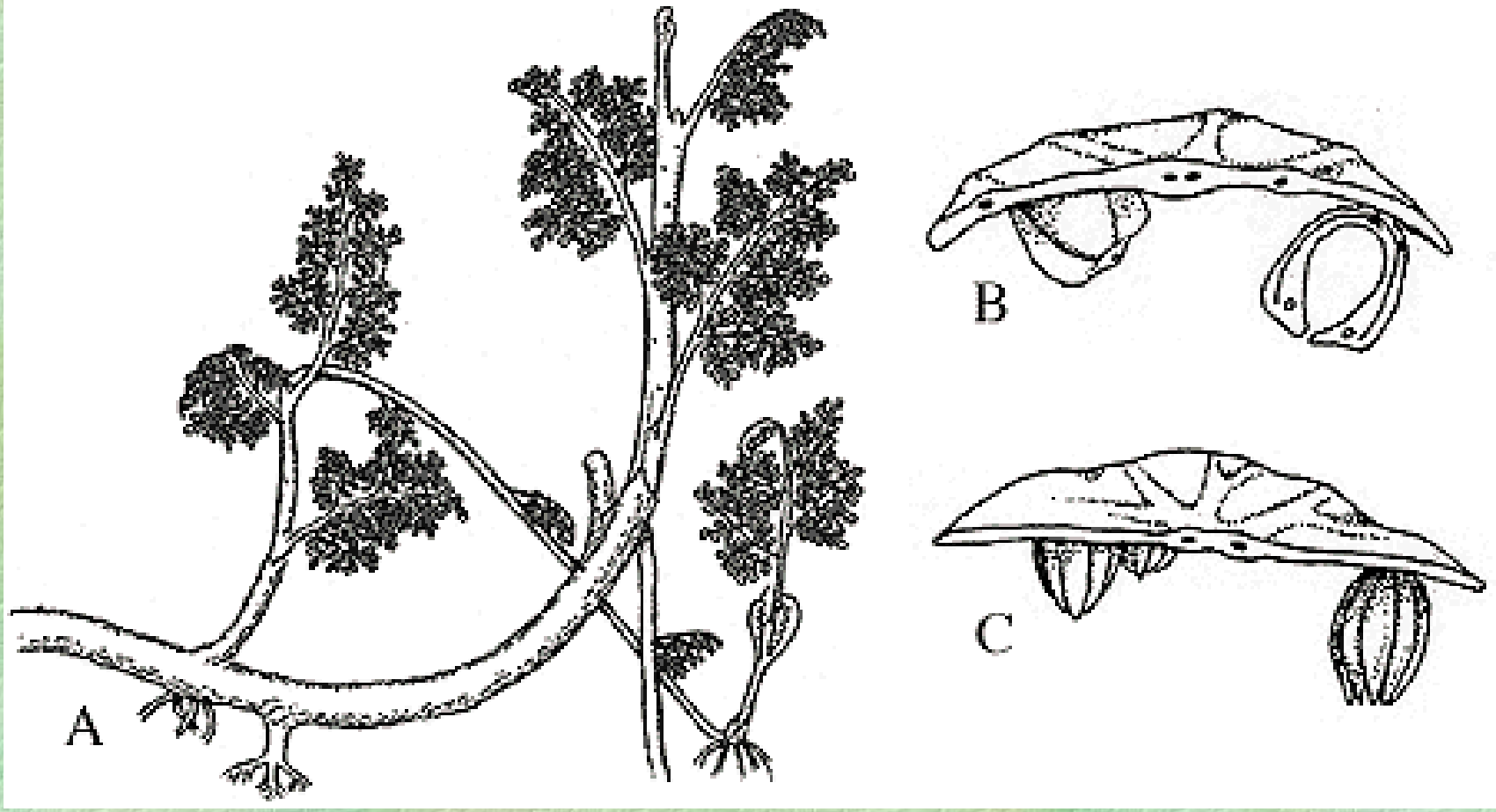
http://www.ucmp.berkeley.edu/IB181/VPL/MedCyc/MedCyc3.html

Rahu-palmlehik *Cycas revoluta*

Cycas revoluta

Moore’i suurkäbikas
Macrozamia moorei

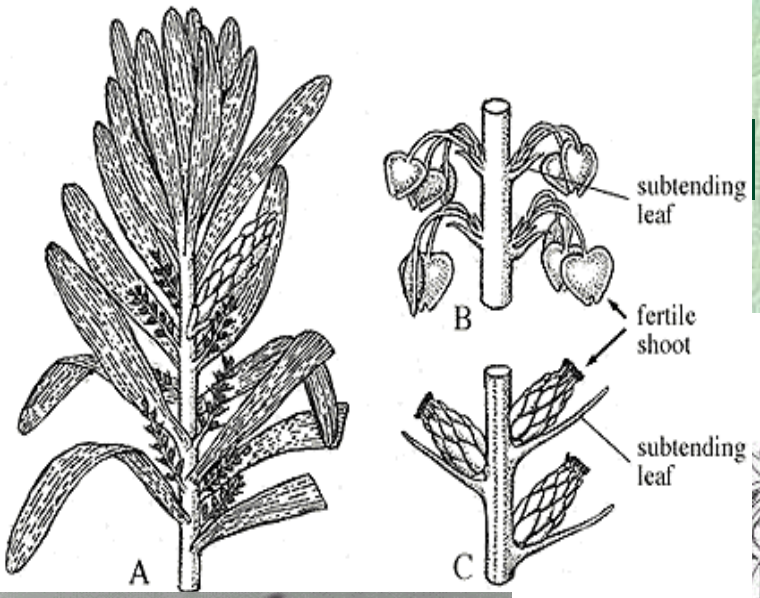
Callistophyton

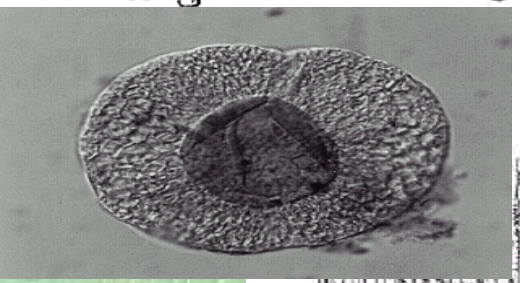


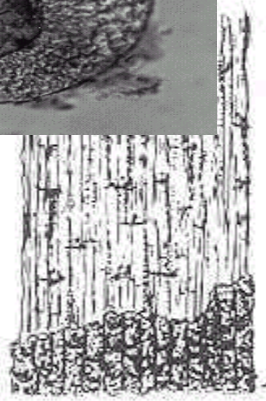
(A) Whole plant reconstuction showing vine-like growth form and leaf attachment. (B) *Callospermaroin* ovules attached to pinnules of *Callistophyton* (in transverse section). *(C) Idanothekion* microsporangia attached to pinnule (in cross section).

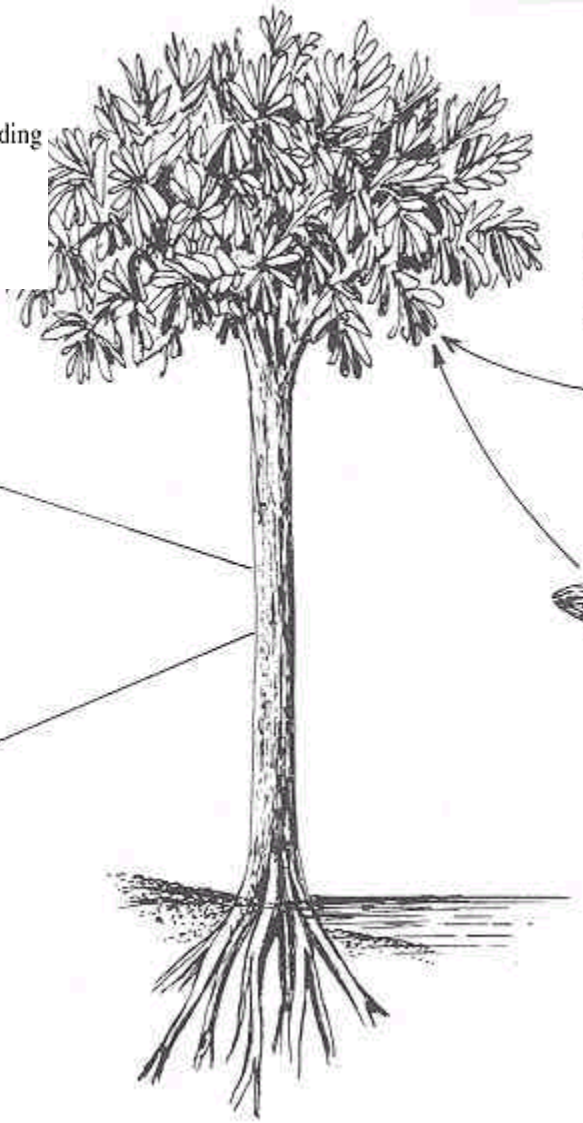
http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup2.html

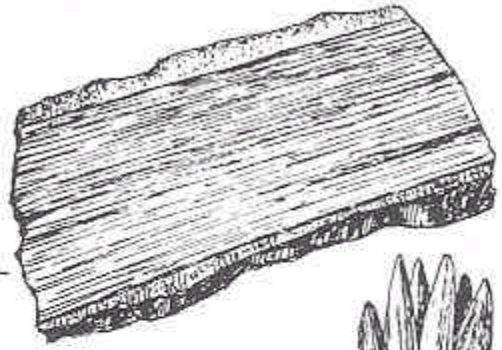
Cordaitales
Ihnlehik *Cordaites*

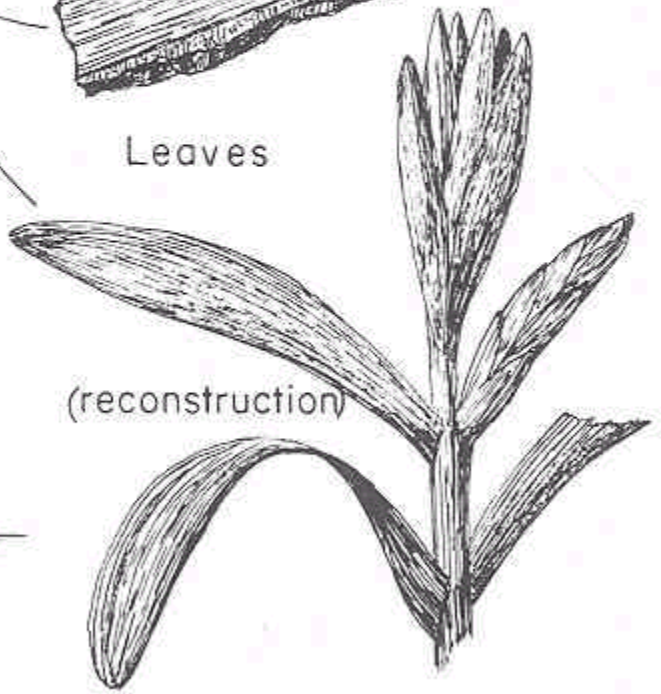





Trunk



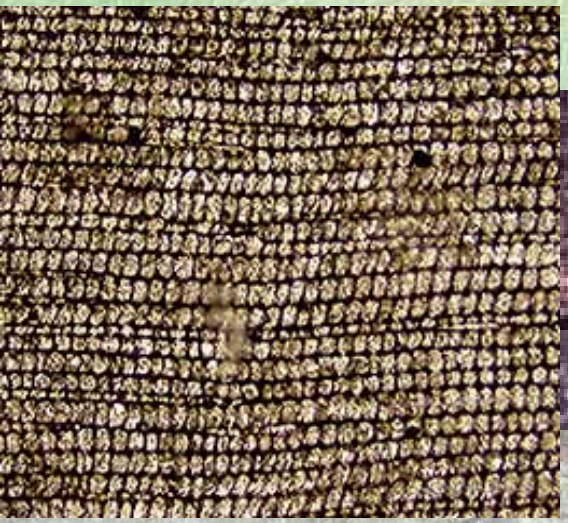

Leaves


(reconstruction)

Cordaites

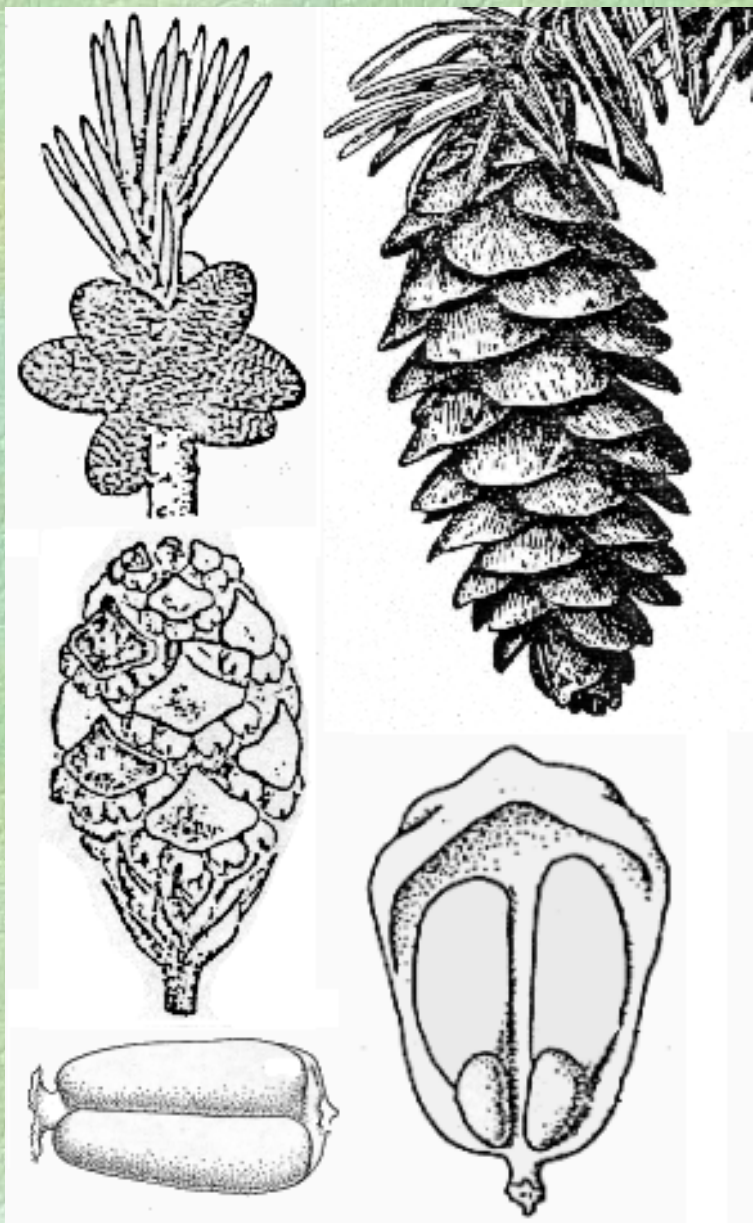
http://www.geology2.pitt.edu/GeoSites/fossils.htm
http://www.ucmp.berkeley.edu/IB181/VPL/CorCon/CorCon2.html

Ihnlehik *Cordaites*



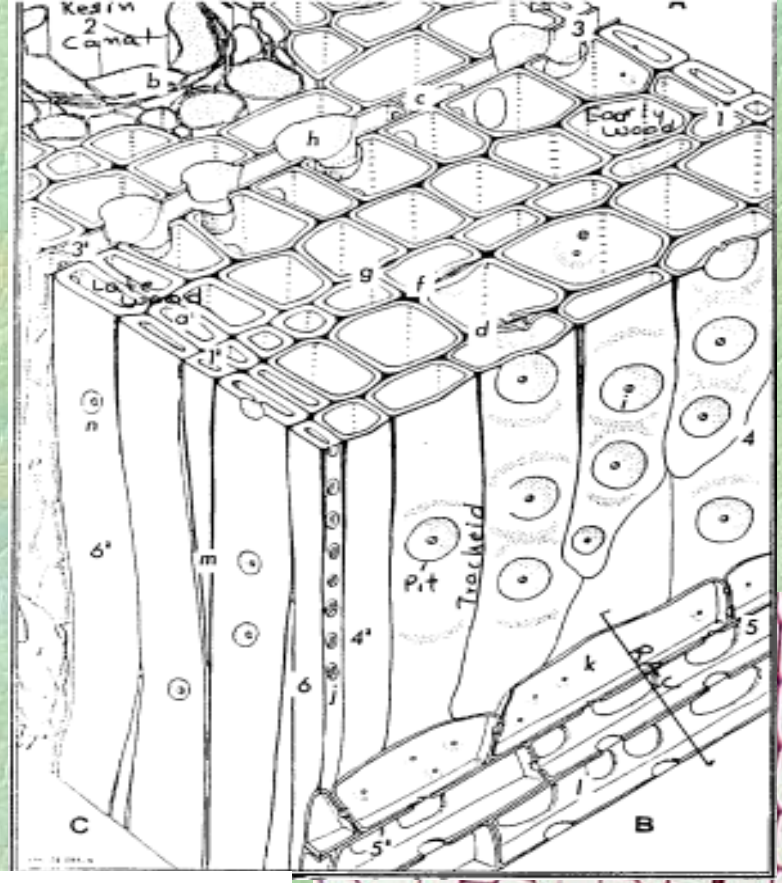
Okaspuud

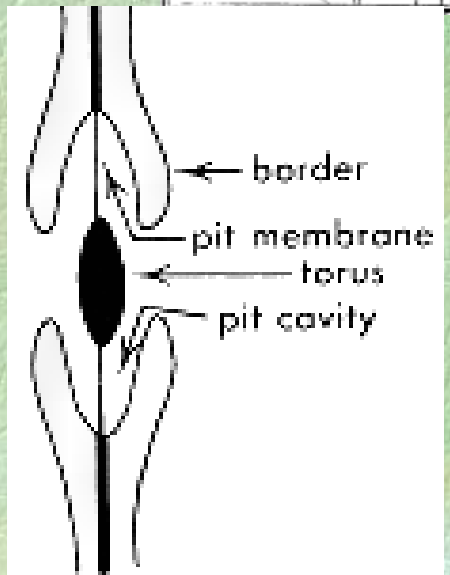
- Käbi, tuultolmlemine
- Embrüoloogia
- Monopodiaalne harunemine
- Igihaljus, okkad
- Puidu eripärad

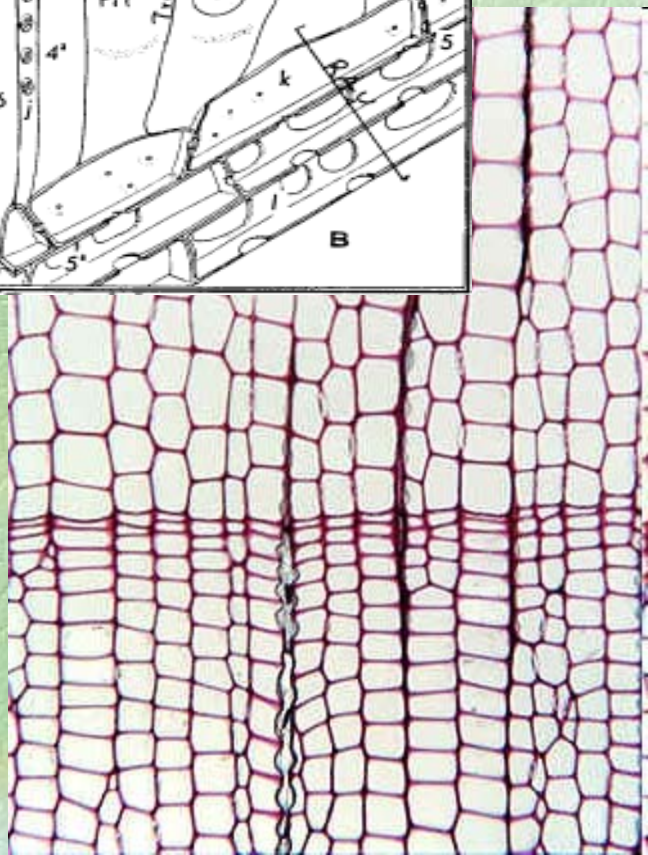


Okaspuude pui

- Püknoksüülne puit
- Vaigukäigud
- Koobaspoorid







Esimesed okaspuud

- Karboni lõpul
- allakäik Tertsiaaris
- *Lebachia, Walchia*
- ühekojalised, kuid eraldi emas-isaskäbid

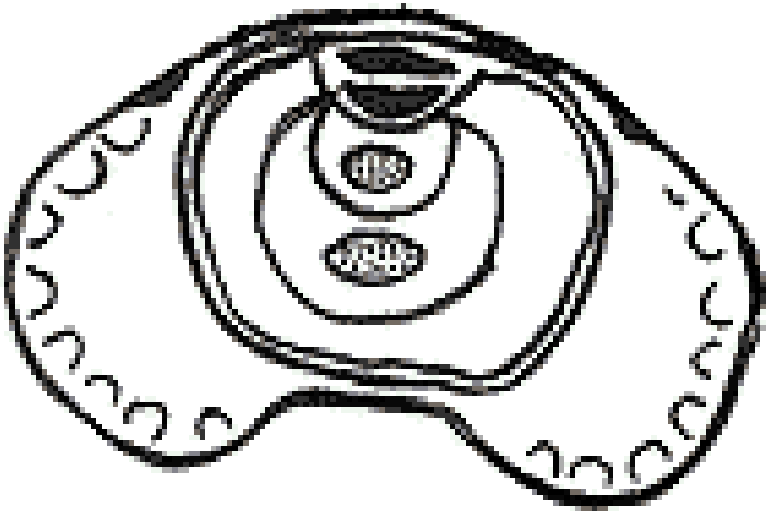
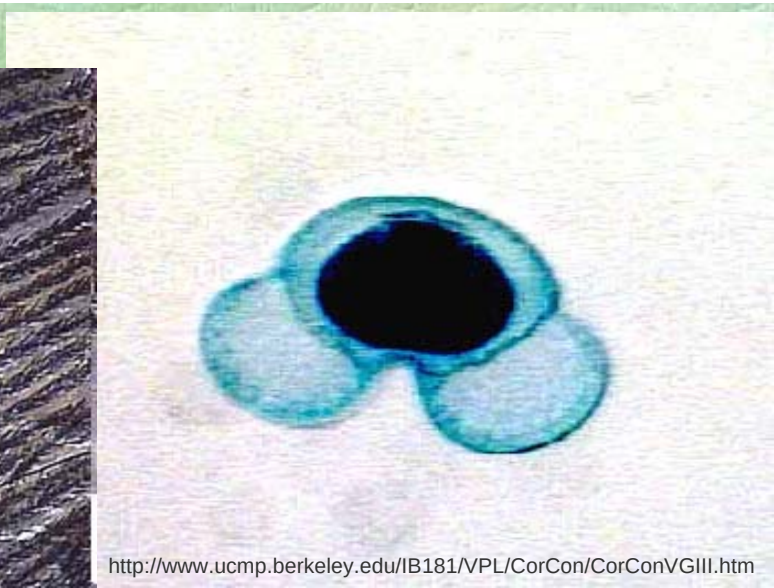
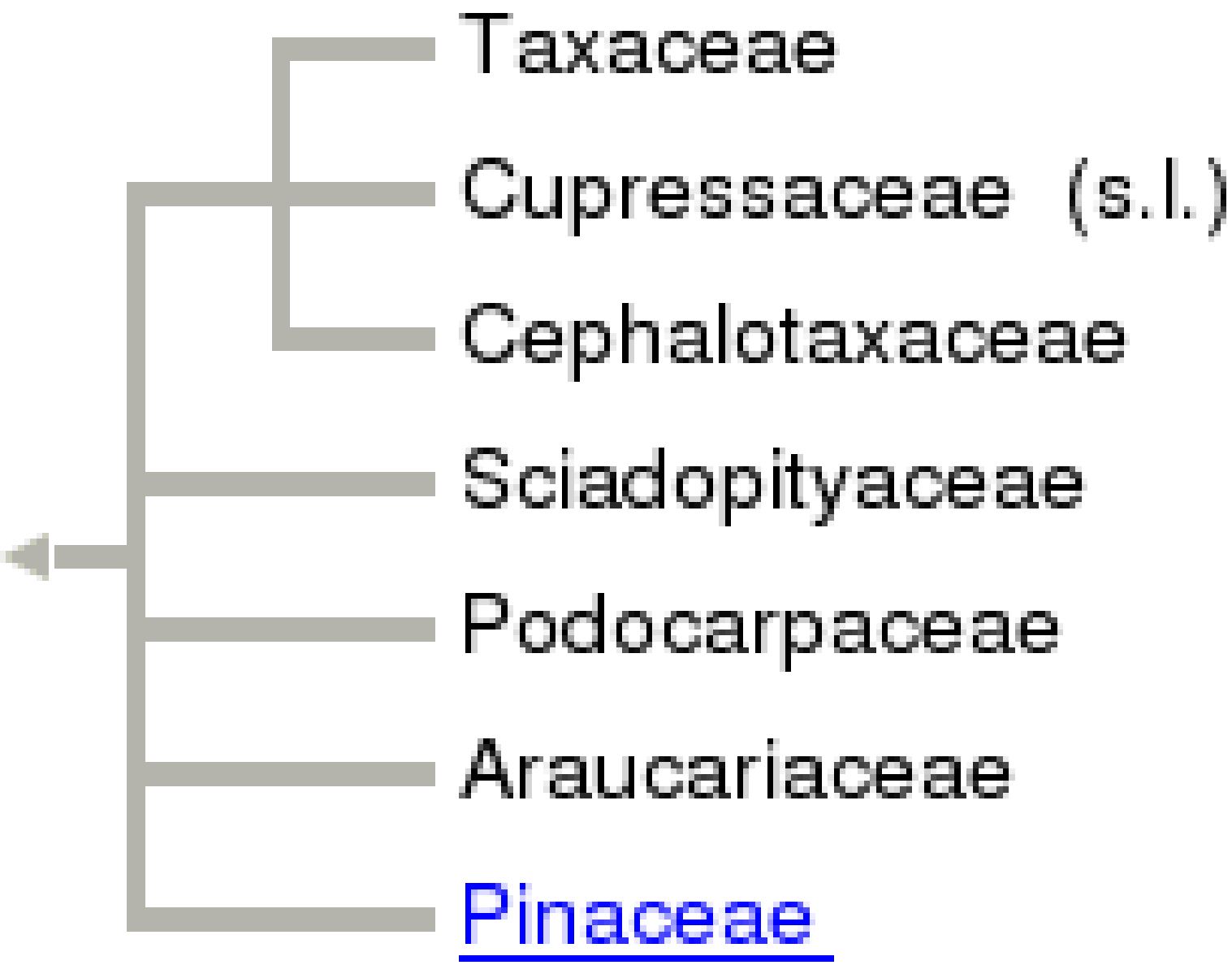


Рис. 185. Лебахия сосновидная (Lebachia piniformis); боковая ветвь с прямостоячими собраниями мегастробилов и висячими микростробилами.



http://www.ucmp.berkeley.edu/IB181/VPL/CorCon/CorConVGIII.htm

Okaspuud



Judd, Campbell 2002

Jugapuulised *Taxaceae*

- Üksik seemnealge
- Tõelised käbid puuduvad, nn marikäbi:
- Seemned kõva kesta ja lihaka arilliga
- Põhjapoolkeral
- 5 perek, 20 liiki

H. jugapuu *Taxus baccata*

Peajugapuulised *Cephalotaxaceae*

- Käbid olemas, soomused 2 seemnealgmega
- Seemned sukulentse arilliga, luuviljataolised
- Aasias

Fortune’i peajugapuu
Cephalotaxus fortunei

Sciadopityaceae

Sciadopitya verticillata

- Elav fossiil Jaapanis
- 2 tüüpi lehed
- Sugulus kivijugapuu-listega?

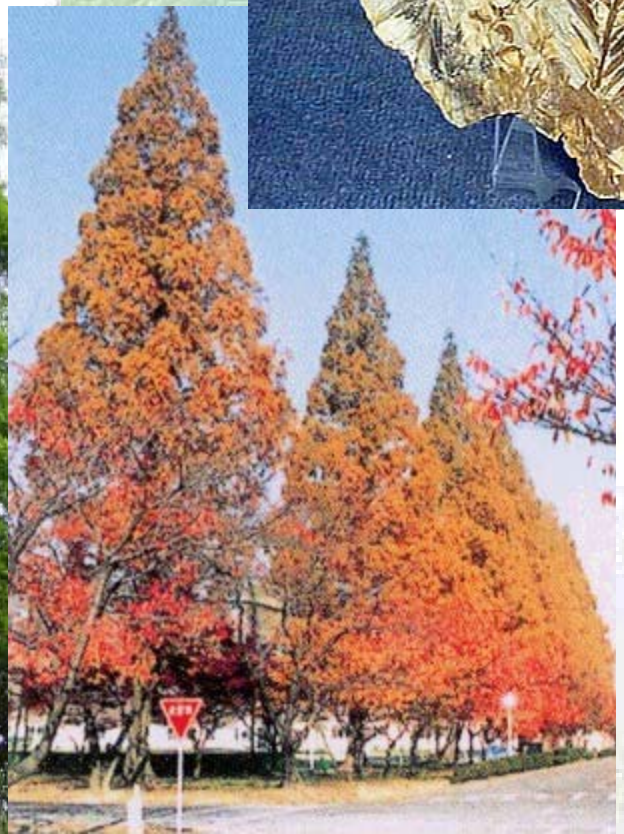
Küpressilised Cupressaceae

- Emaskäbides soomused kokku kasvanud, mõnel lihakad, 1-20 seemnealget, püstised
- Isaskäbides 2-10 mikrosporangiumi soomuse alaküljel
- Lehed tihti soomusjad, sageli dimorfsed
- Puud või põõsad vaiguga, aromaatsed
- Ca 30 perek, 110-140 liiki
- Kosmopoliitne, enamik põhjapoolkeral

Hiidsekvoia e mammutipuu
Sequoiadendron giganteum

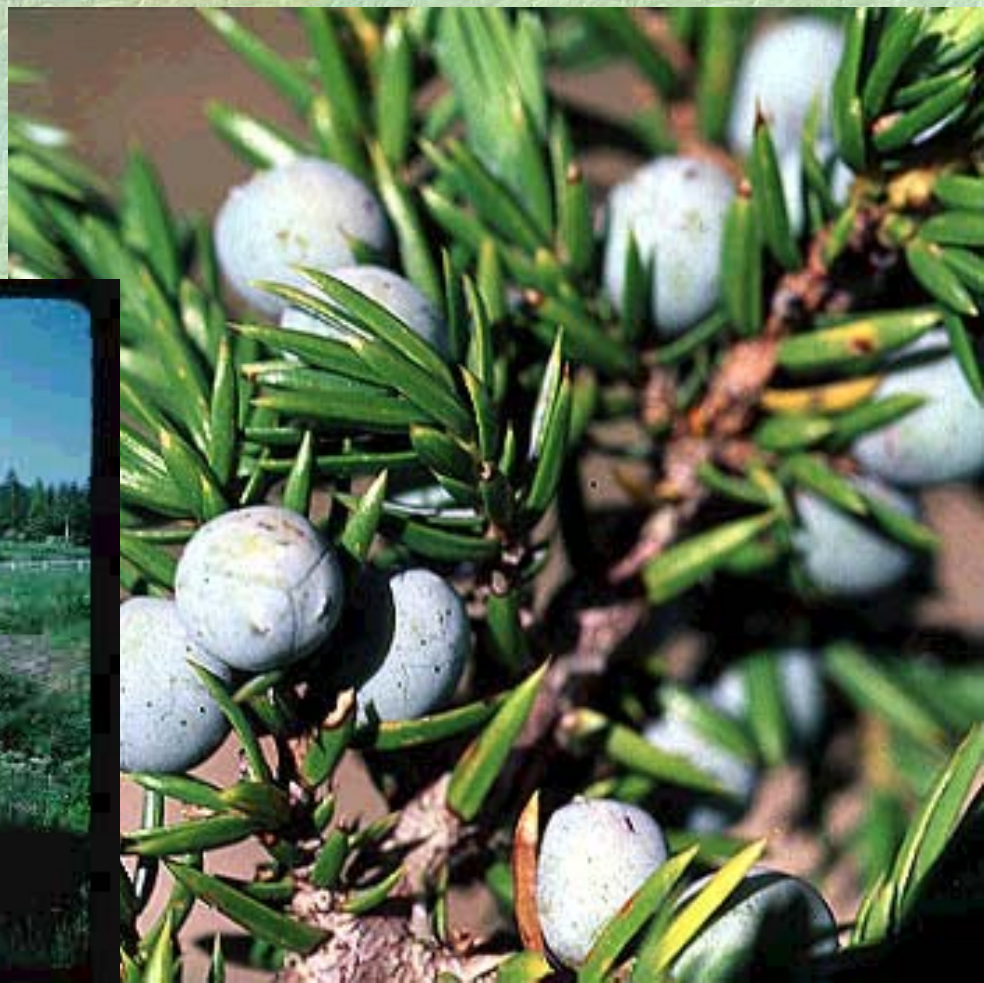
http://www.monumentaltrees.com/en/trees/giantsequoia/giantsequoia

Metasequoia glyptostroboides



H. kadakas

Juniperus communis



Kivijugapuulised *Podocarpaceae*

- Emaskäbi 1-mitme soomusega, igaüks 1 seemnealgmega, kokku kasvanud, moodustab lihaka epimaatsiumi
- 17 perek, 170 liiki
- Troopikas ja subtroopikas, eriti lõunapoolkeral (Australaasia, L-Aafrika)

Kivijugapuu *Podocarpus*

Araukaarialised Araucariaceae

- Seemnealgmed ühekaupa, soomus seemnega kokku kasvanud, aga pole lihakad
- Tolmutera eksiin auguline
- Lõunapoolkera vihmametsades
- 3 perek, 40 liiki

Araucaria

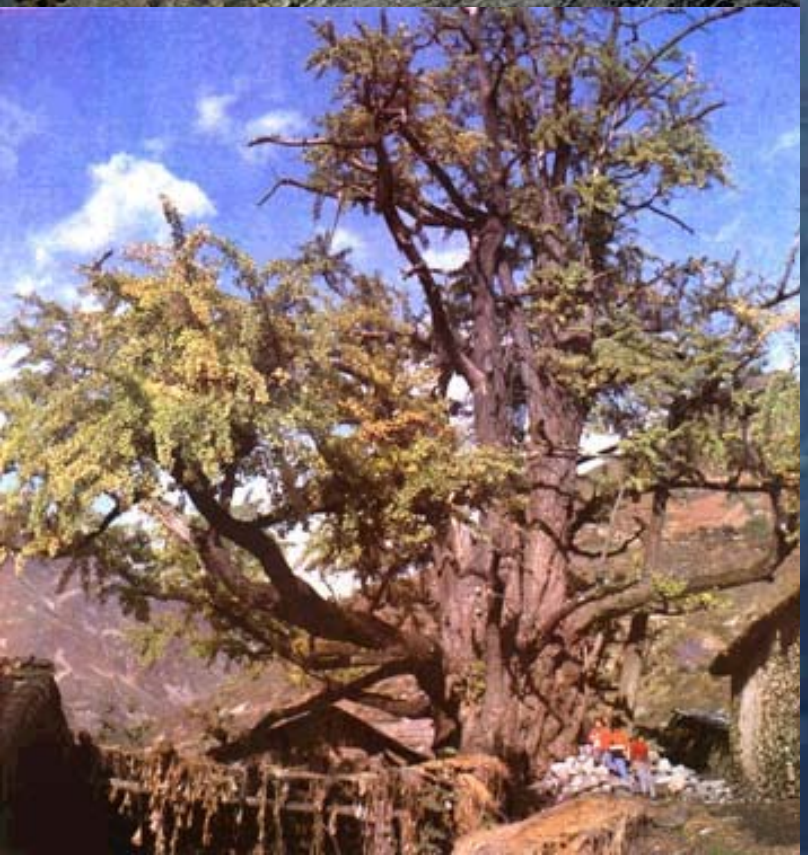
Männilised *Pinaceae*

- Arenenud käbid, vabad seemnesoomused
- Kaks pööratud seemnealget
- Seemned pika lennutiivaga, mis tekkinud soomusest
- 10-11 perek, 220-230 liiki
- Põhjapoolkeral

Pinus sylvestris

http://www.conifers.org/pi/Pinus_sylvestris.php

Picea abies



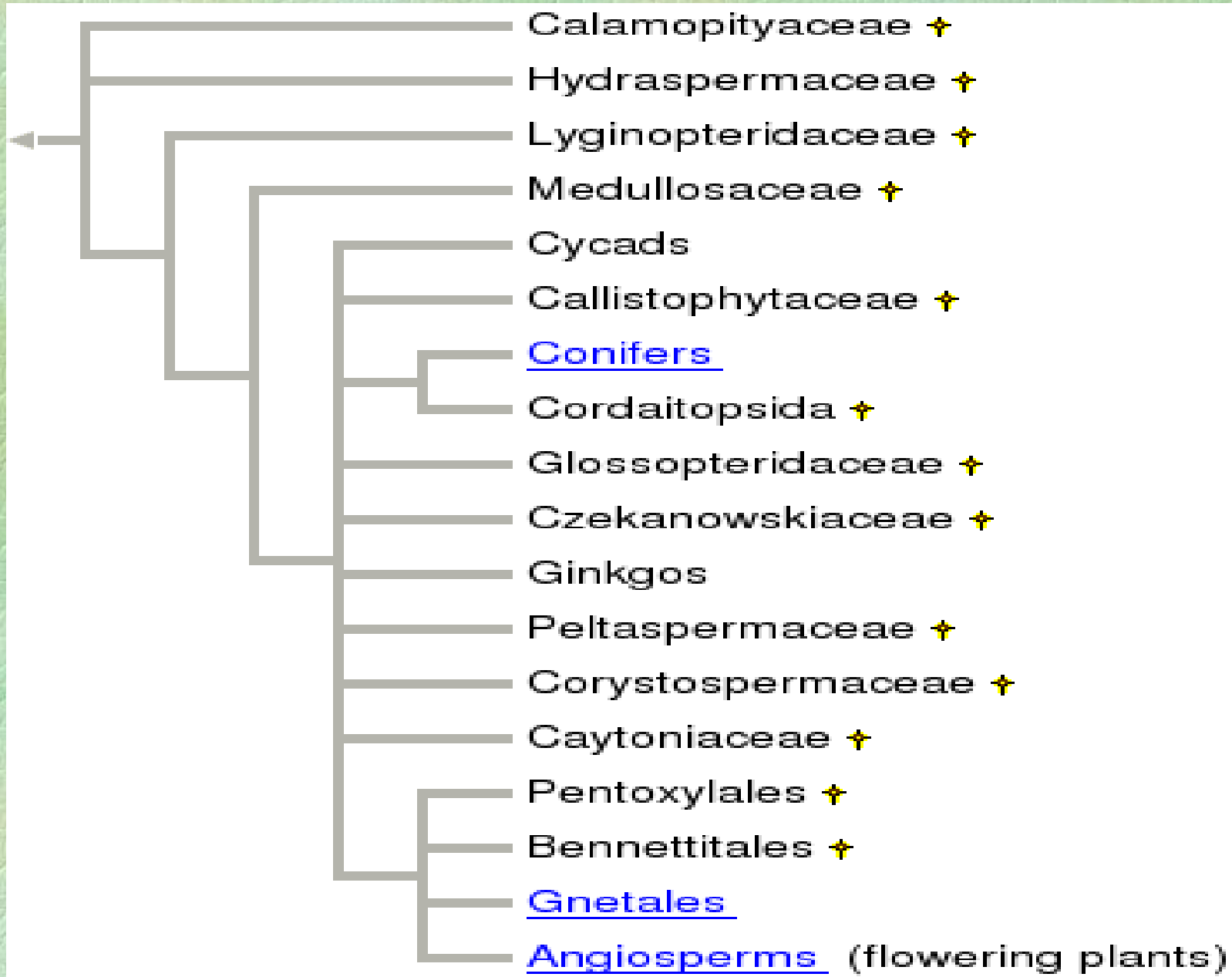
Ginkgoidae
Hõlmikpuu
Ginkgo biloba

Paljasseemnetaimed (järg)

Oistaimede tekkimine

microsporangium
microsporophyll
♂
♀
megasporangium
megasporophyll
2n sporophyte
meiosis
meiosis
microspores
megaspores
(only one lives)
2n zygote
pine embryo
mitosis
mitosis
1n ♂ gametophyte
= pollen
pollination,
then fertilization
archegonium
with egg
1n ♀ gametophyte

Seemnetaimed

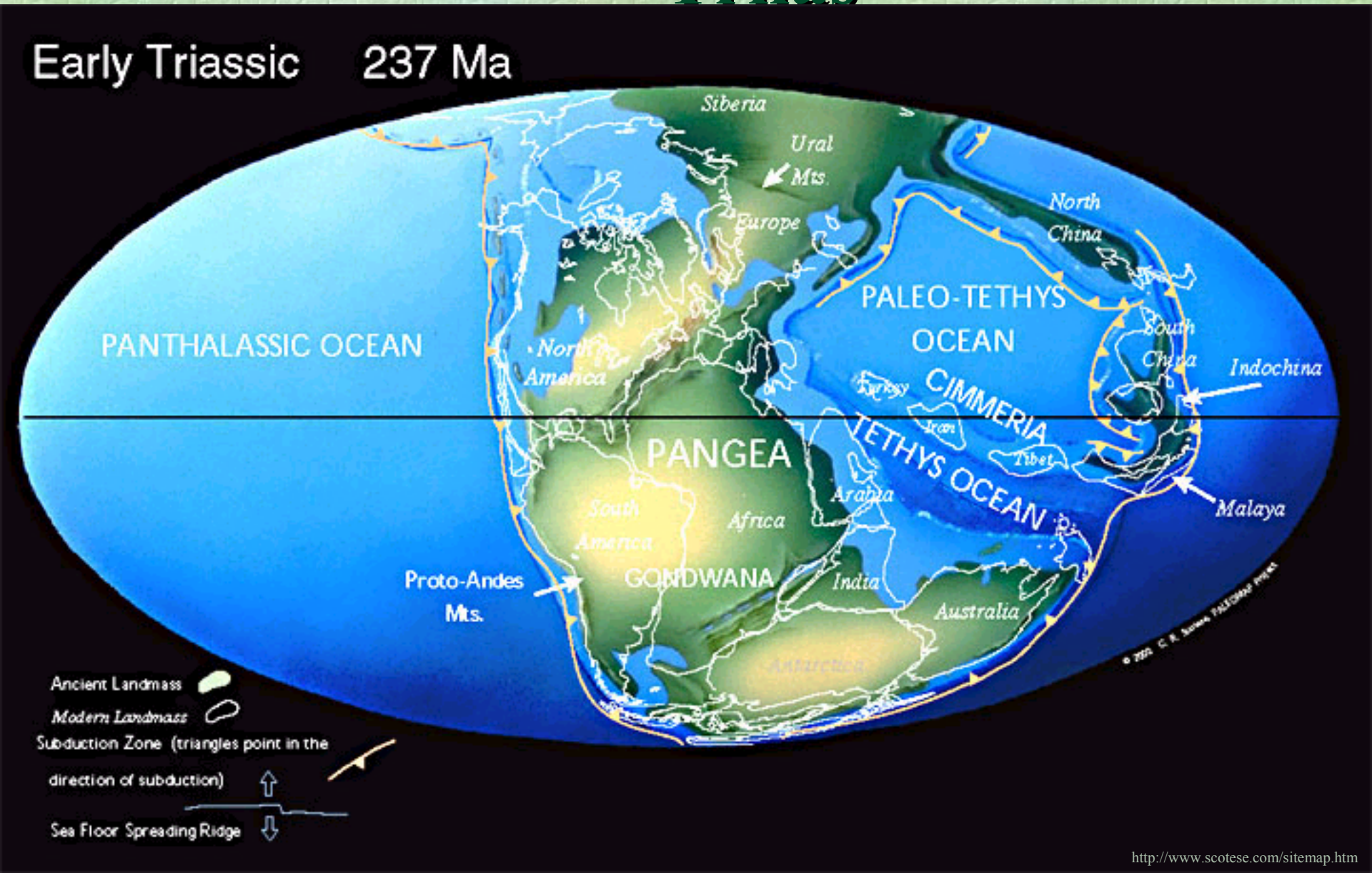


Judd, Campbell 2002

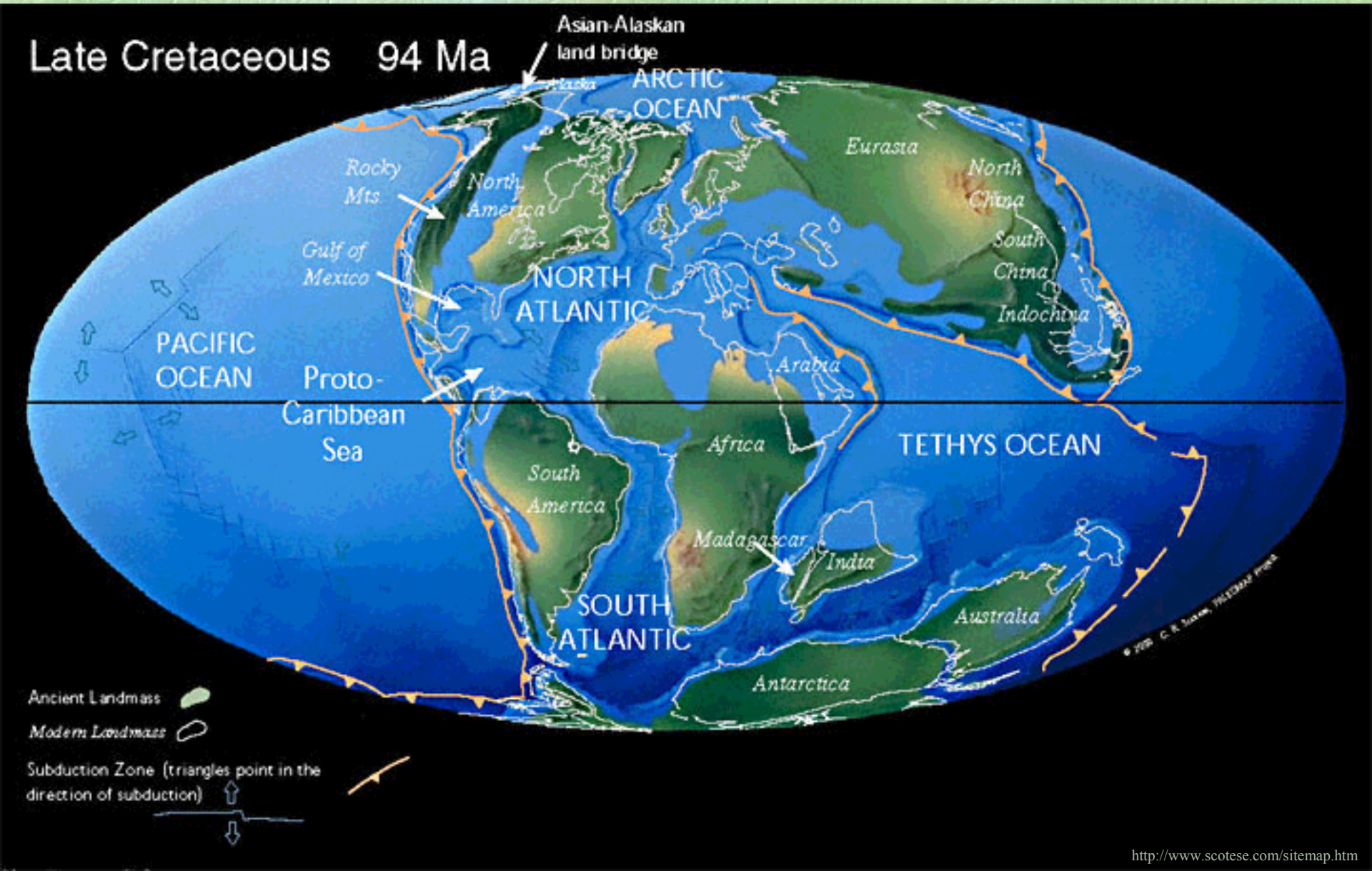
Seemnetaimed (hmk rühm, hmk, kohort *Spermatophyta)*

- Väljasurnud “seemnesõnajalad” (4 suguk) †
- Alamklass **palmlehikud *Cycadidae***
- Suguk *Callistophytaceae* †
- Alamklass **okaspuud *Piniidae***
- Alamklass **hõlmikpuud *Ginkgooidae***
- Suguk *Glossopteridaceae* †
- Suguk *Caytoniaceae, Corystospermaceae, Peltaspermaceae* †
- Nn antofüütidid (alamkohort *Anthophytatae)*
- Seltsid *Pentoxylales, Bennetitales* †
- Alamklass **vastaklehikud *Gnetidae***
- Alamklass õistaimed *Magnoliidae*

Mesosoikum
Triias



Kriit



http://www.scotese.com/sitemap.htm

Origin of flowering plants and their rise to dominance.

Widespread dominance by most conifers, cycads, ferns

Ferns, conifers diversity.

Most lycophytes, horsetails become extinct, origin of ginkgos, cycads.

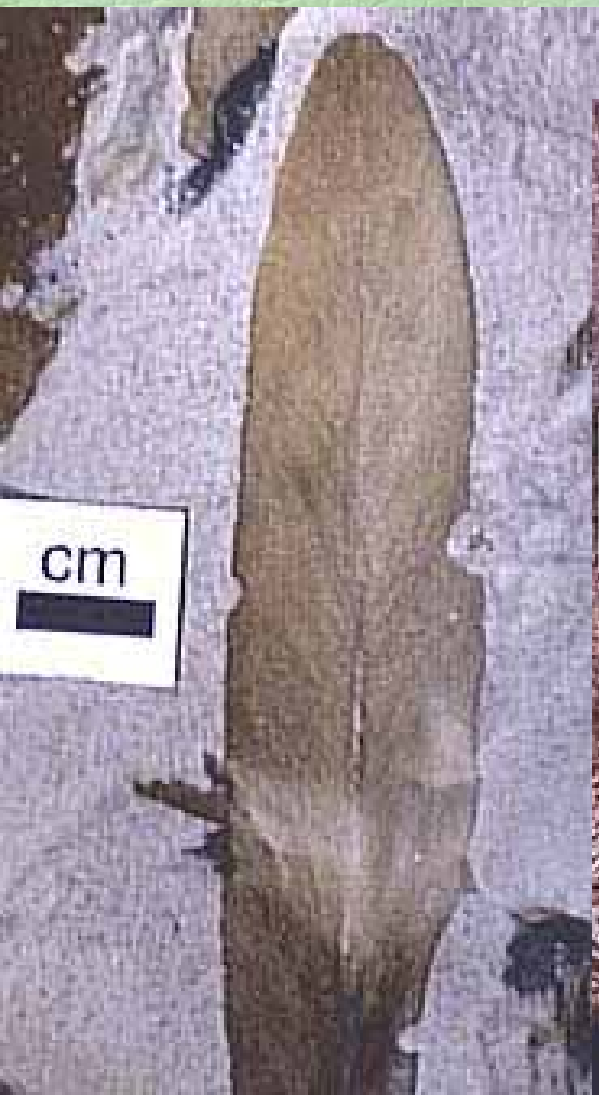
Vast forests and coal swamps with diverse fungi, bryophytes, lycophytes, horsetails, and ferns. Origin of conifers.

Origin of bryophytes (liverworts), vascular plants (lycophytes, horsetails, ferns, progymnosperms) by end of Devonian.

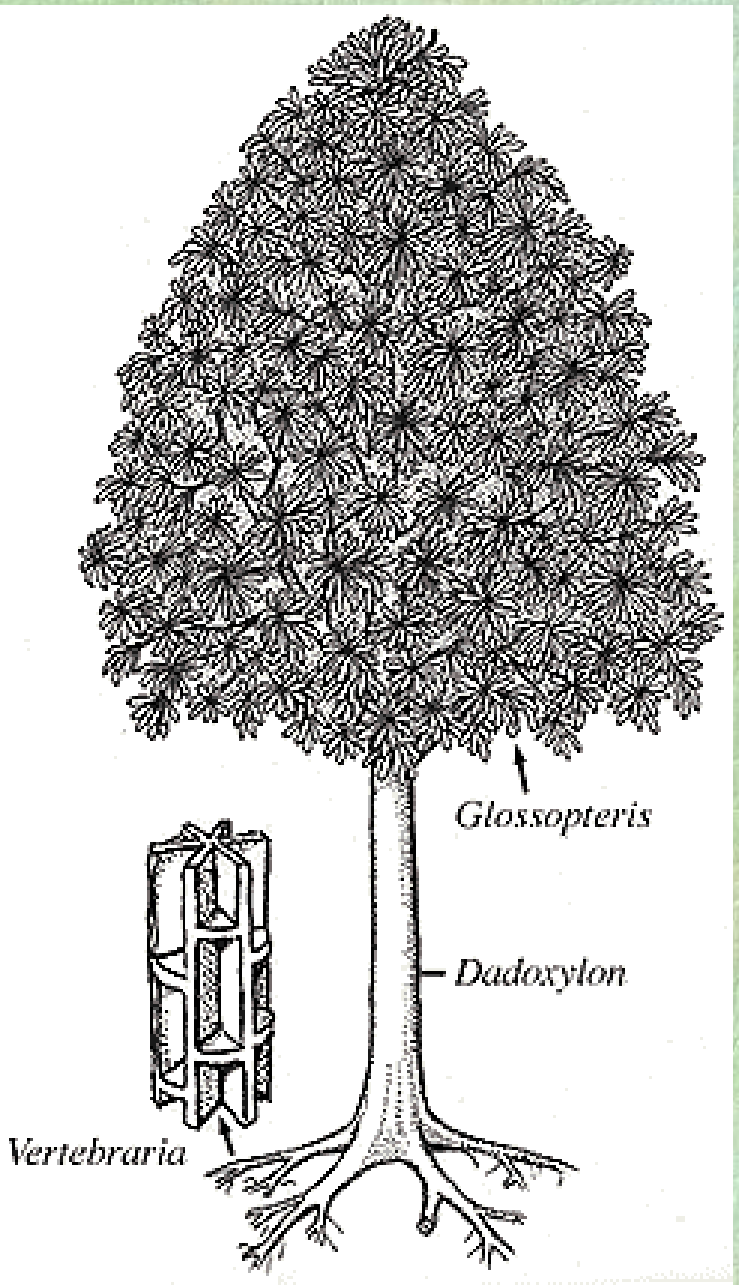
Earliest known vascular land plants, origin of rhyniophytes by mid-Silurian.

Origin of land plants by 435 mya.

Glossopteridaceae



Glossopteridaceae



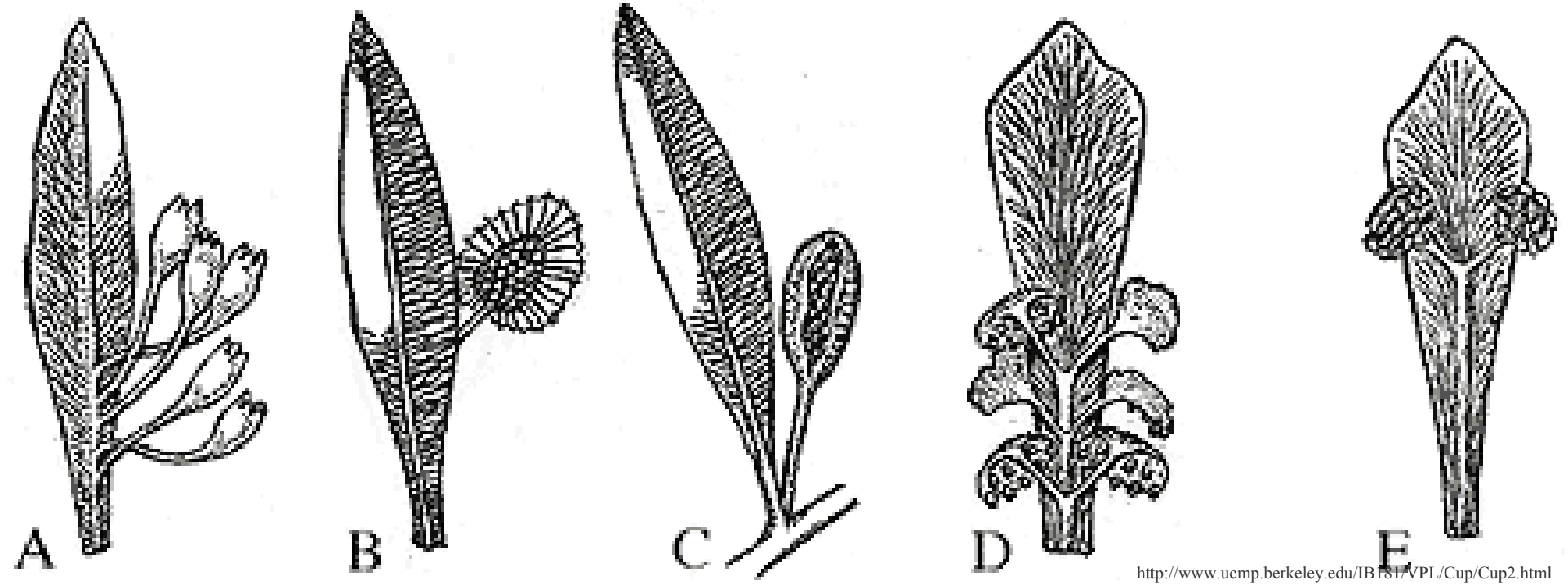
http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup2.html

Glossopteridaceae

(A) *Denkania* (ovulate), (B) *Scutum* (ovulate),

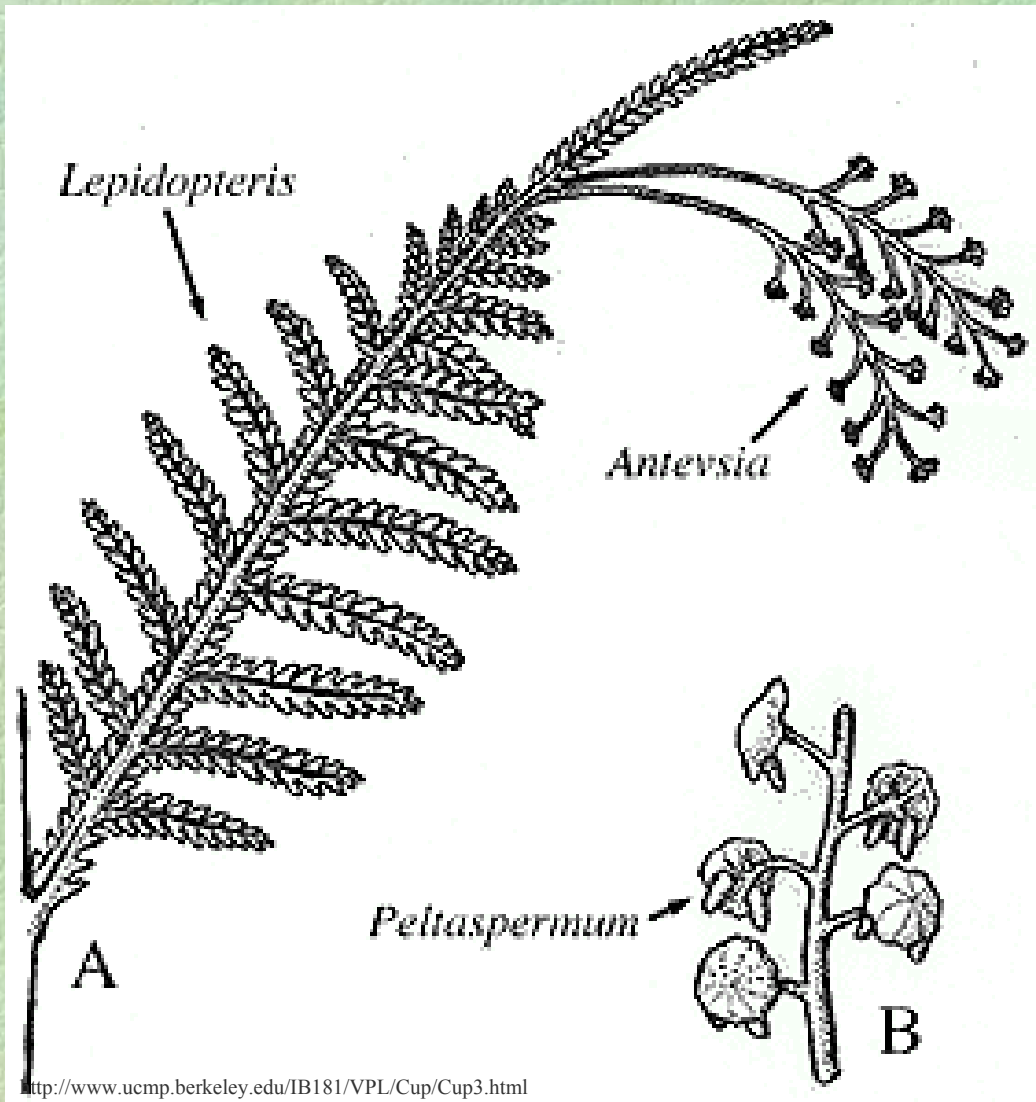
(C) *Dictyopteridium* (ovulate),

(E) *Eretmonia* (pollen-producing).



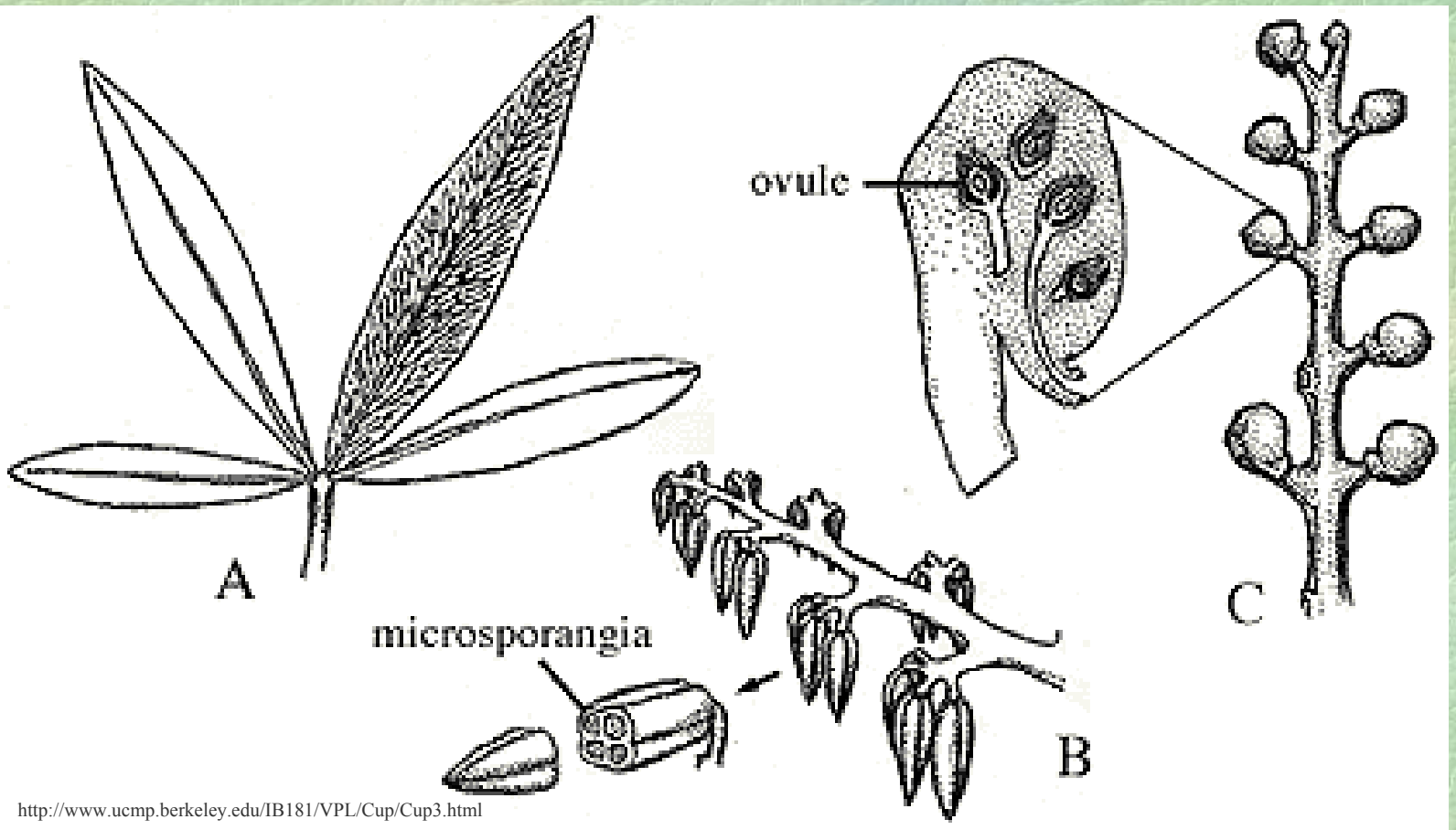
http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup2.html

Peltaspermaceae



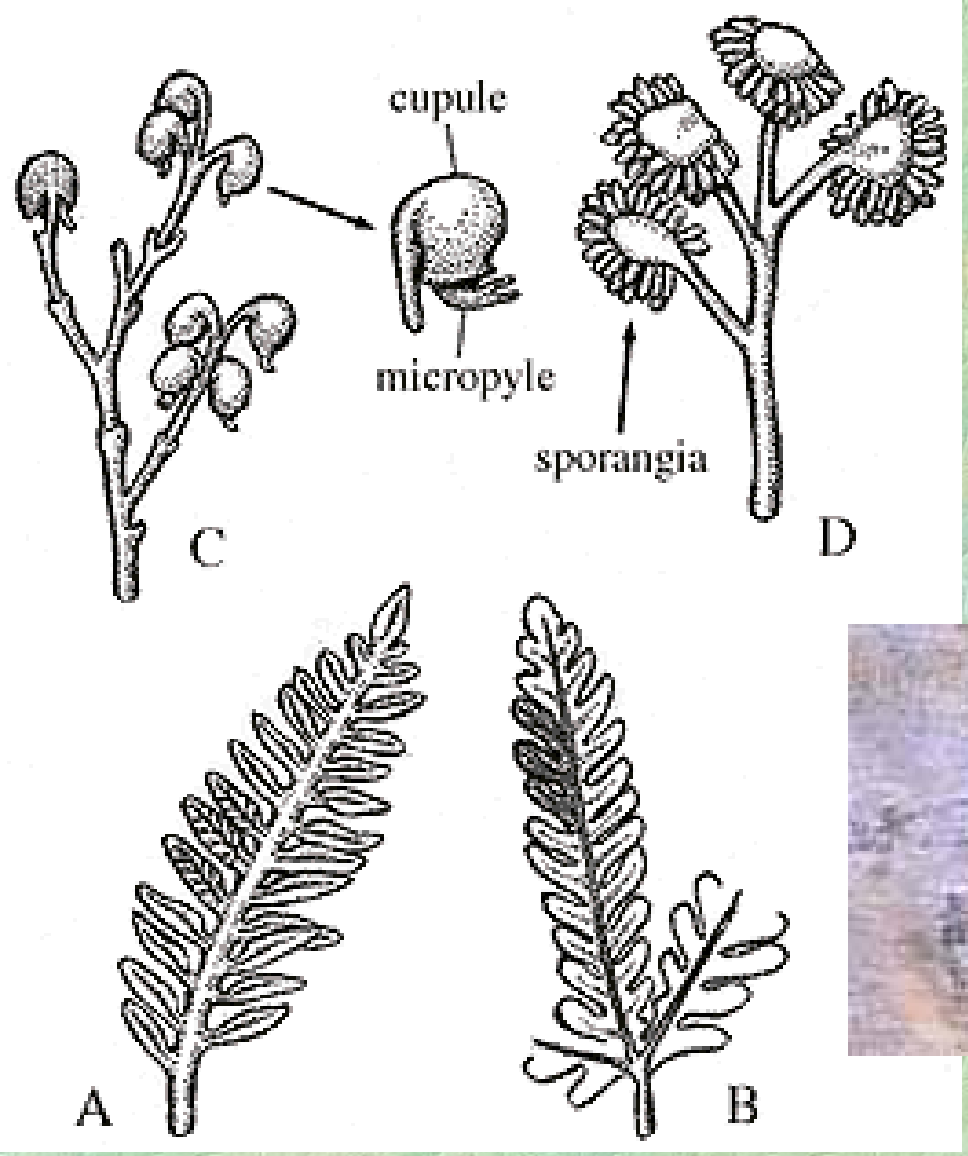
http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup3.html

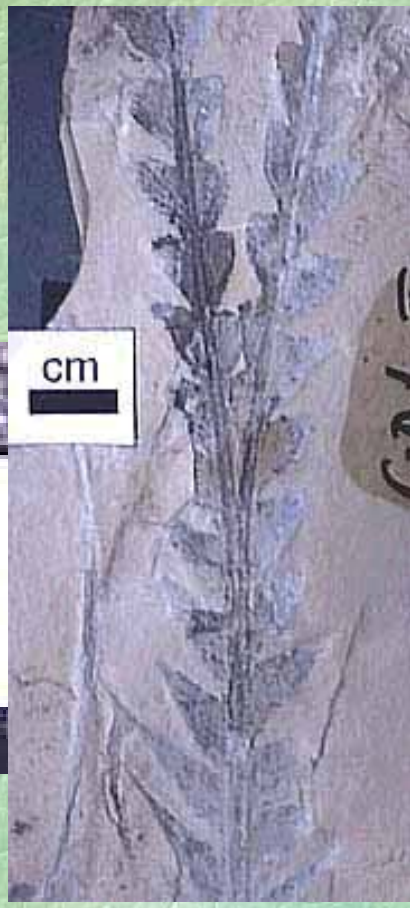
Keitoonia *Caytonia*



http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup3.html

Corysto-spermaceae





A *Dicroidium* and B *Pachypteris* foliage; C *Umkomasia* megasporophyll with cupules, bifurcating micropyle; D *Pteruchus* microsporophyll.

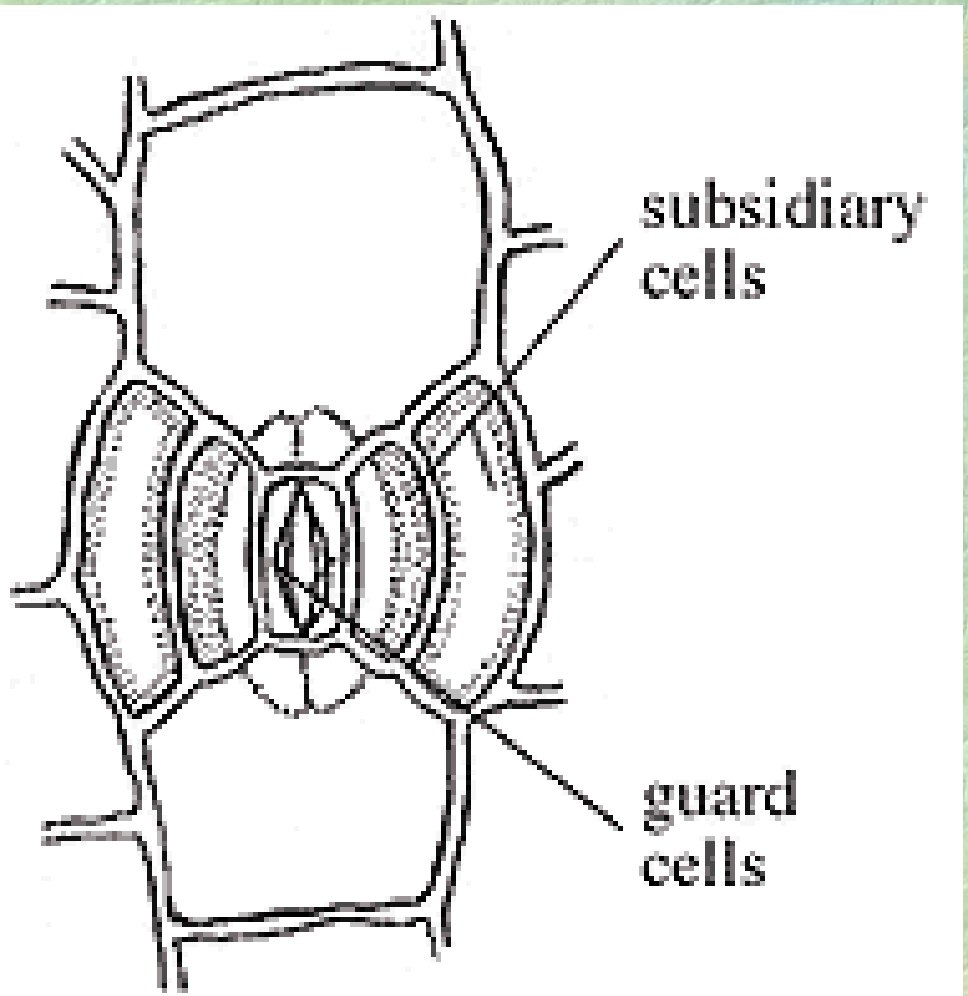
http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup3.html

Antofüüdid

- Selts *Pentoxylales*
- Selts bennetiidilaadsed *Bennetitales*
- Alamkl vastaklehikud *Gnetiidae*
- Alamkl õistaimed *Magnolidae*

(Angiospermae)

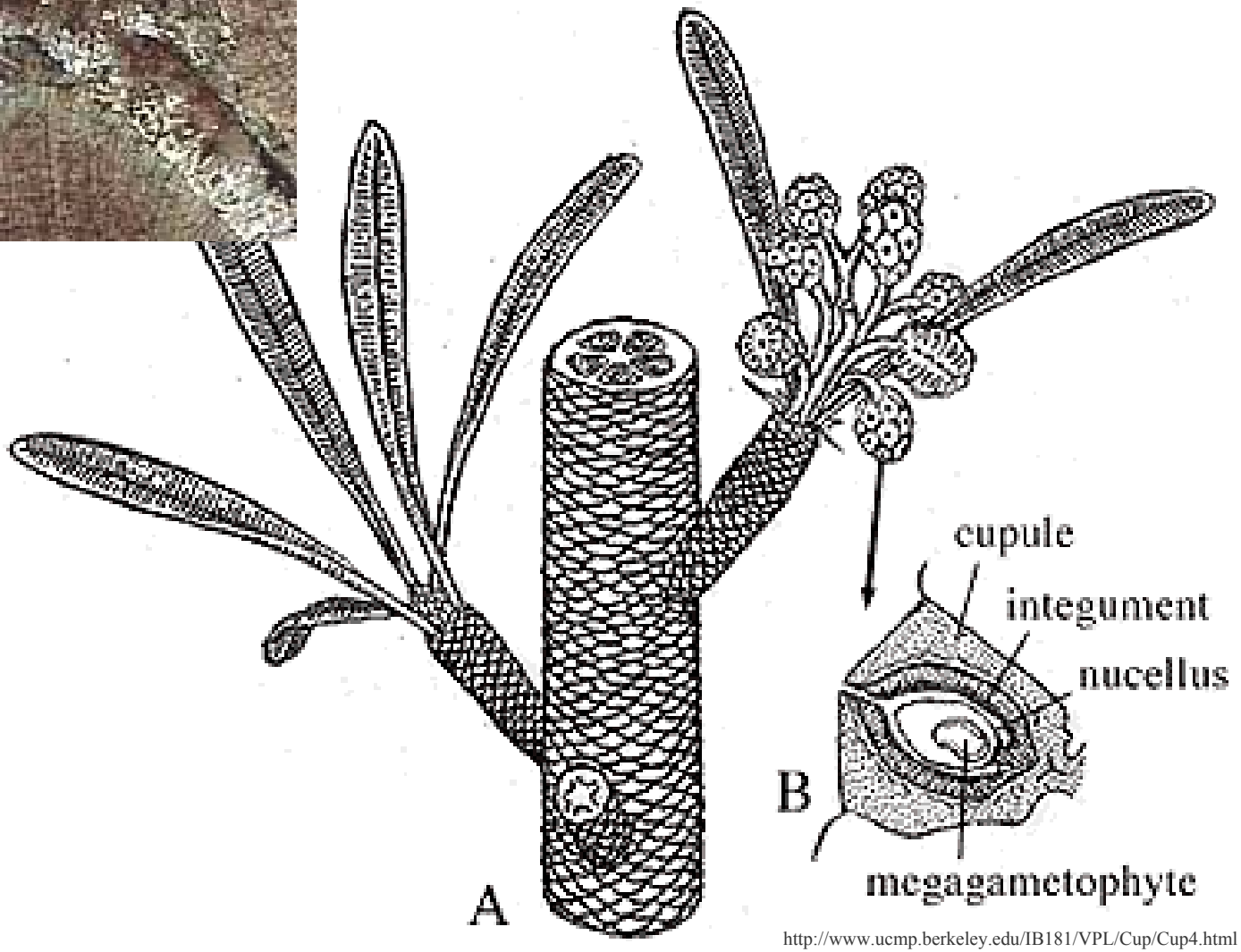
Antofüüdid



- trahheiidid/trahheed P-tüüpi paksenditega
- lihtsulgjad mikrosporofüllid
- üks seemnealge kuupulis
- arenenud tolmutera granulaarse eksiiniga
- **õhulõhede ehitus**
- (biseksuaalsed) õie-taolised struktuurid

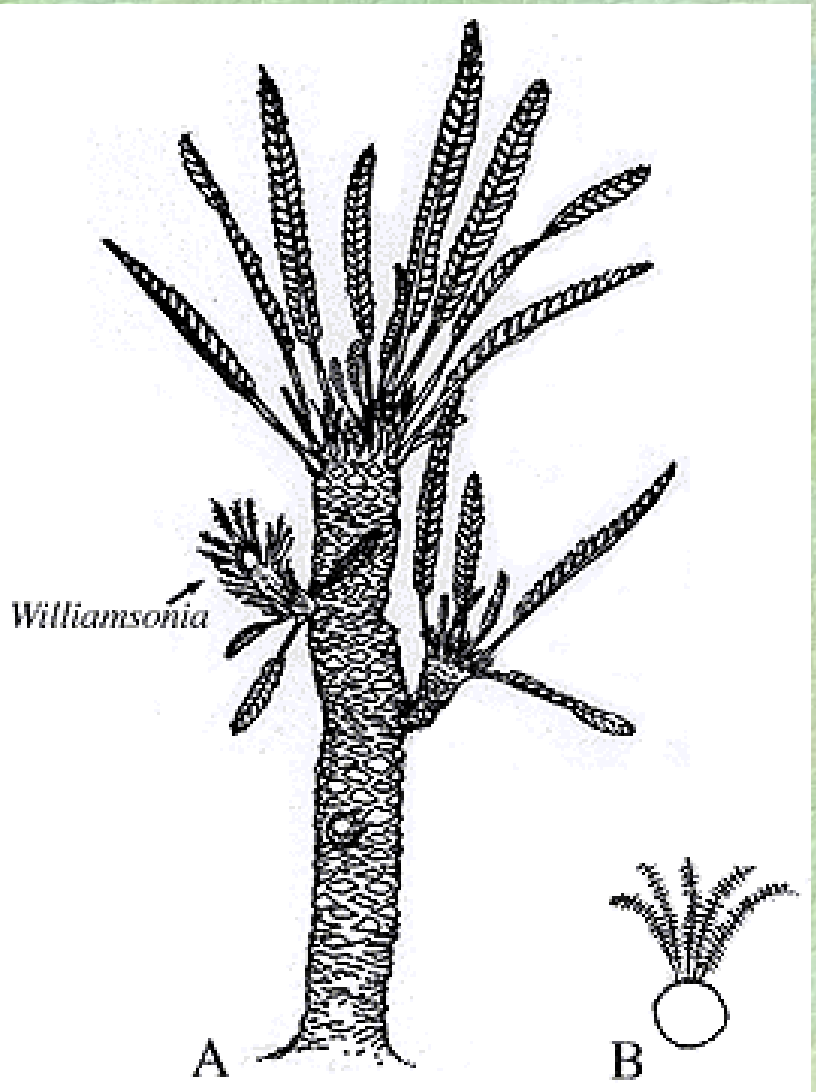
http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup4.html

Pentoxylon

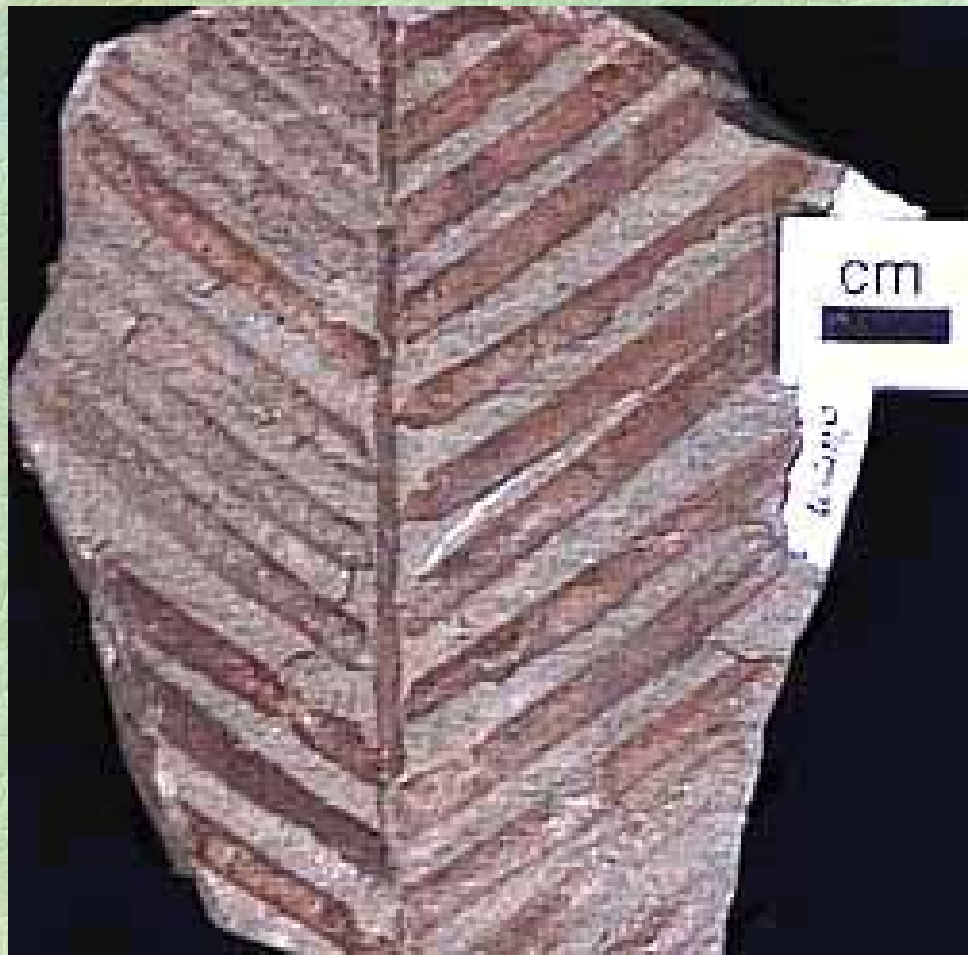


http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup4.html

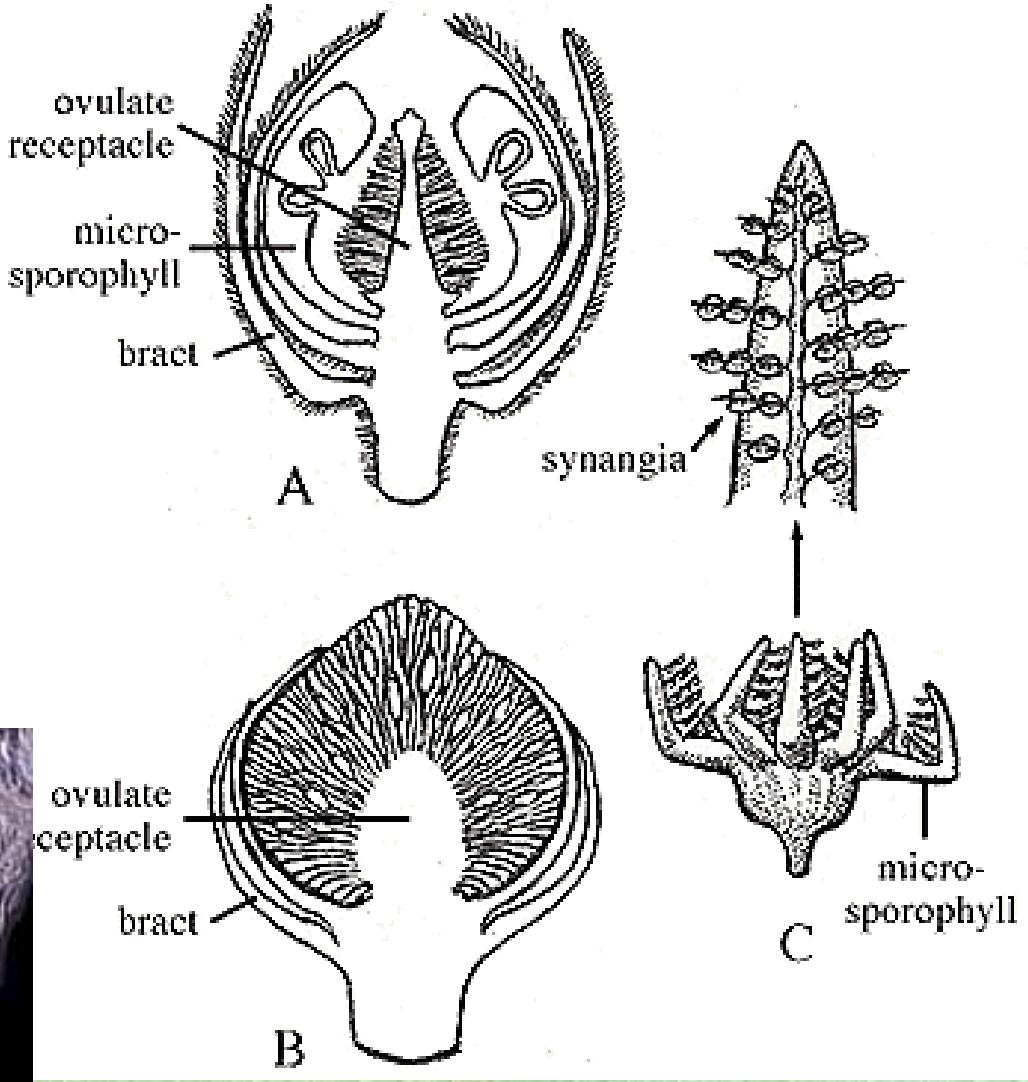
Bennetiidid *Bennettitales*



http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup4.html



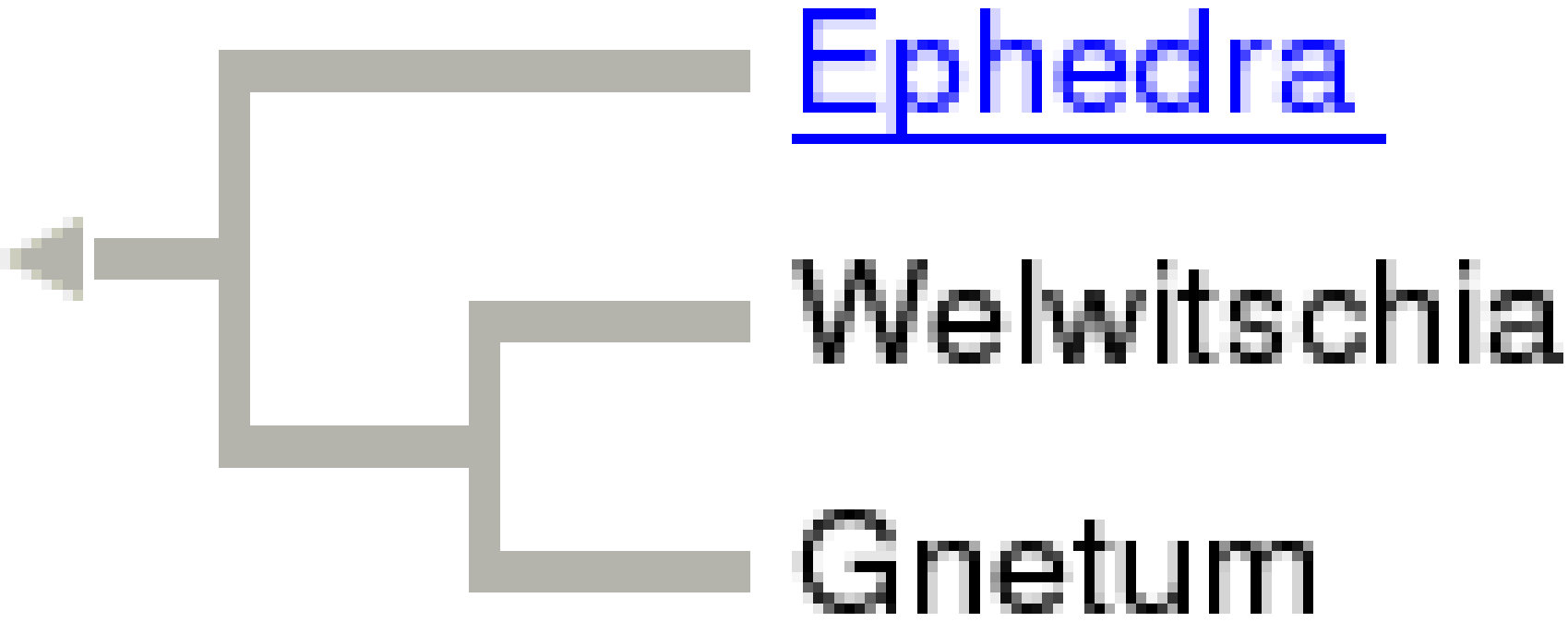
Bennettitales



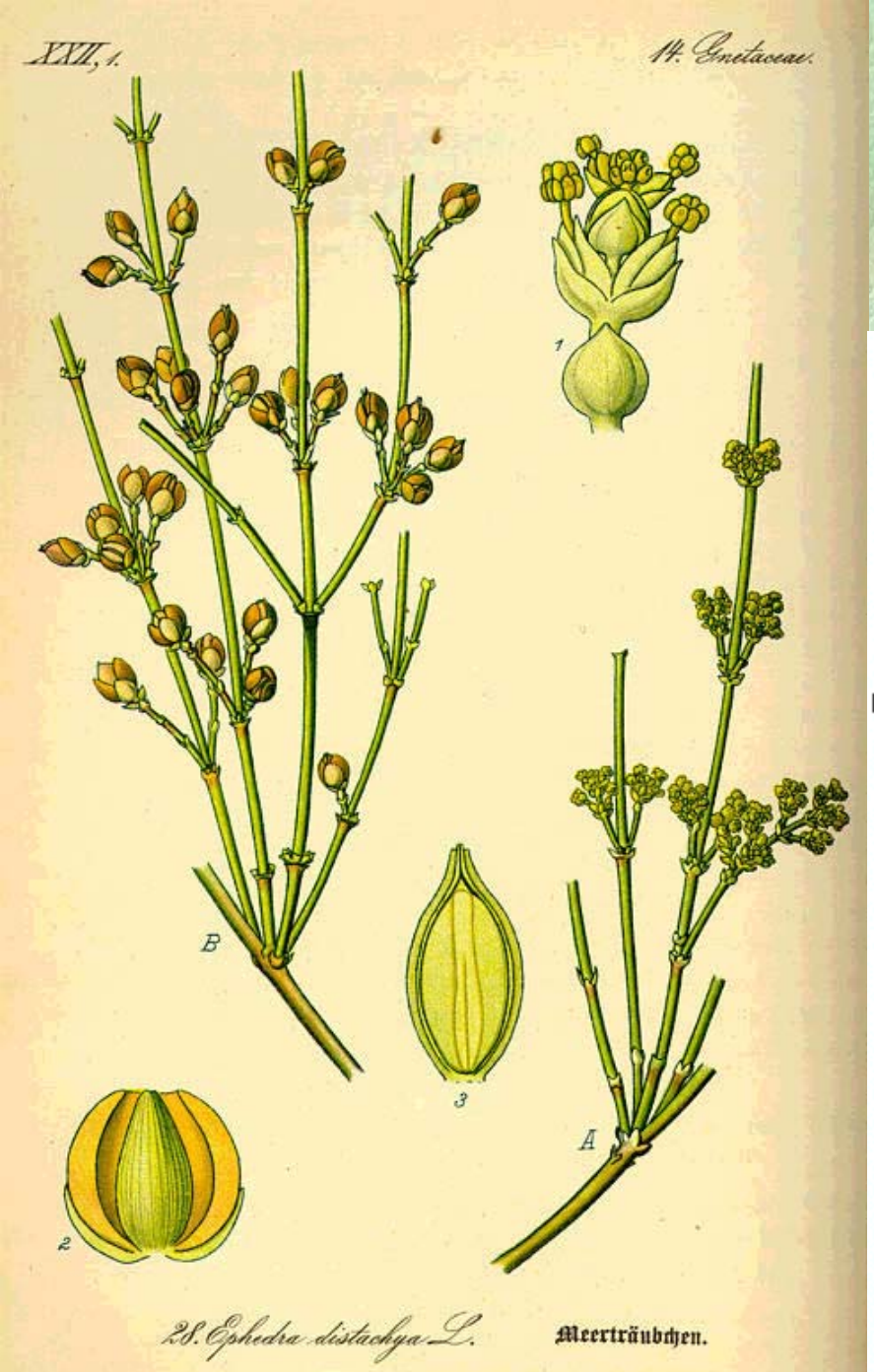
A. *Williamsoniella*,
B. *Williamsonia*, C. *Weltrichia*

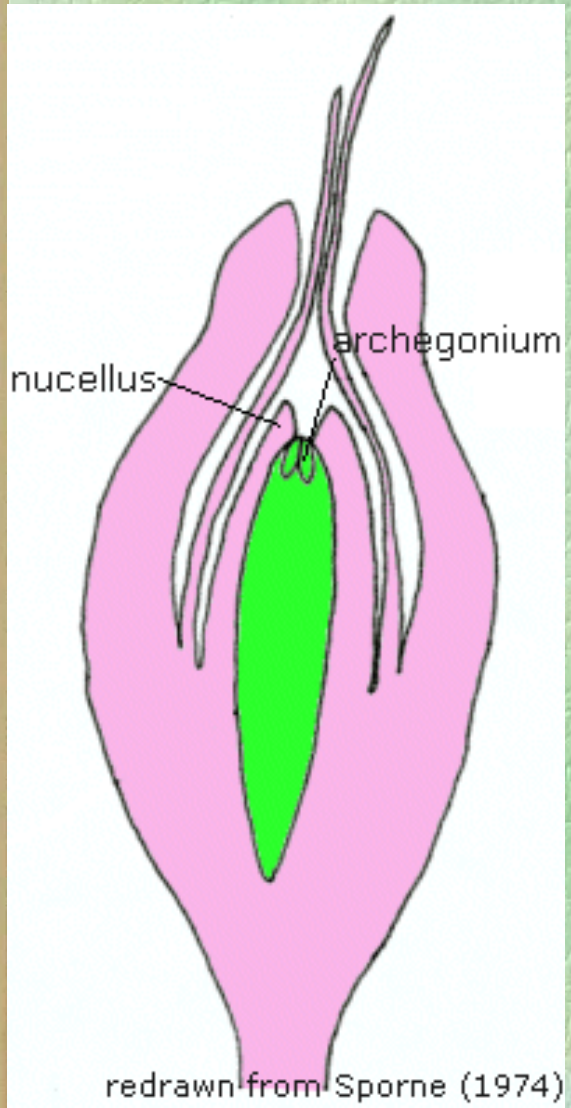
http://www.ucmp.berkeley.edu/seedplants/bennettitales.html

Vastaklehikud *Gnetopsida*



Efedra *Ephedra*

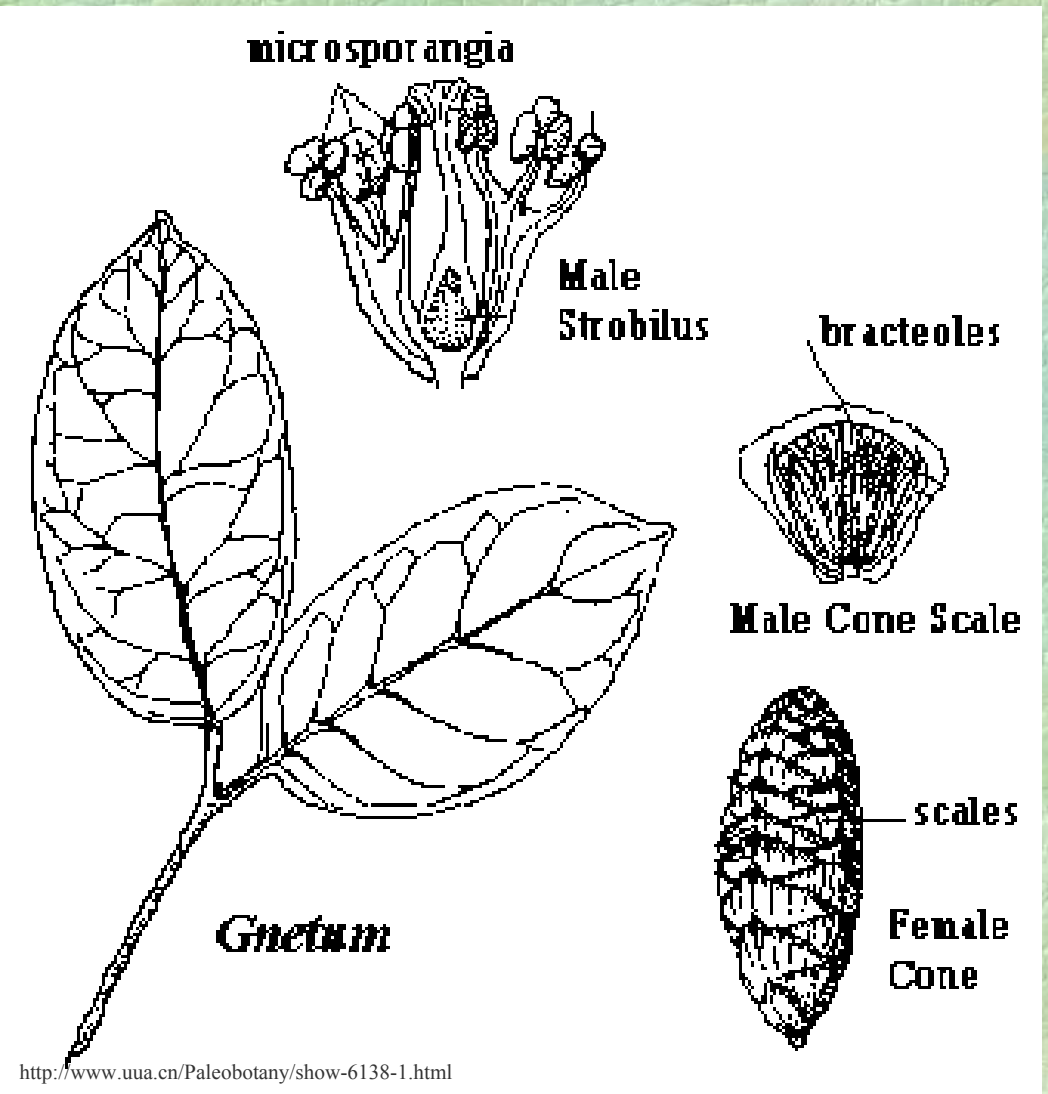




Ephedra

http://tolweb.org/Ephedra/21721

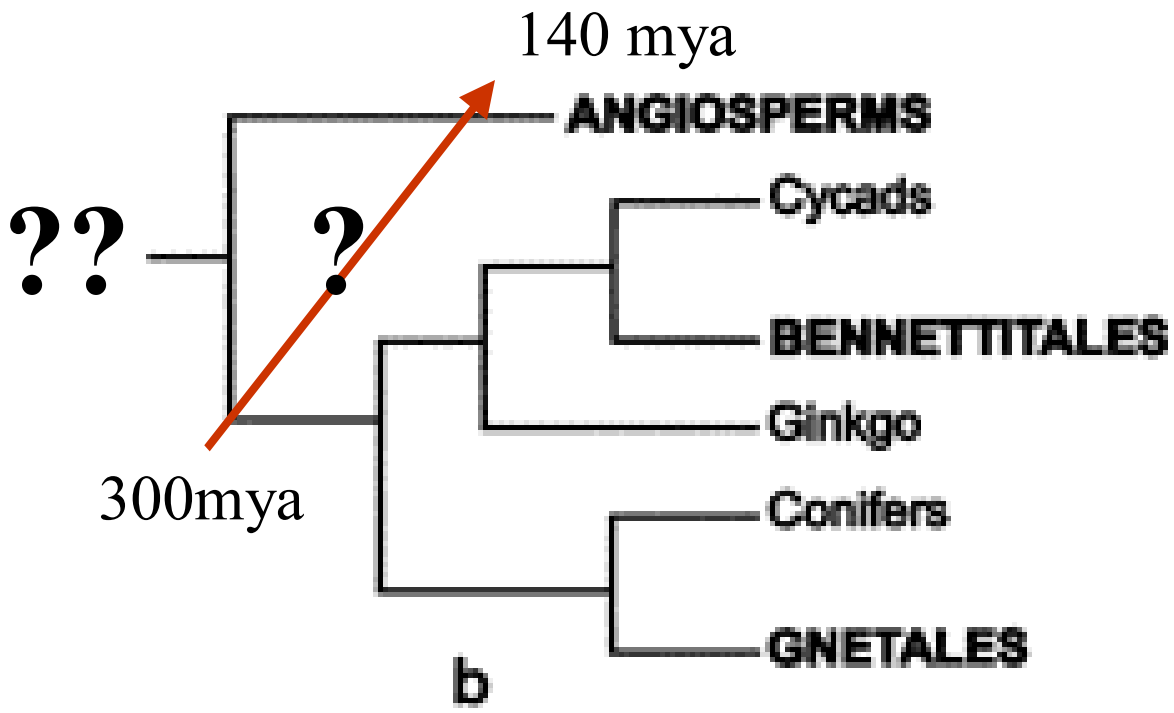
Vastaklehik *Gnetum*



http://www.uua.cn/Paleobotany/show-6138-1.html

Gnetum

Velvitšia *Welwitschia*



But it leaves us with missing links between 300 mya and 140 mya, as well as few clues about the common answer of angiosperms and gymnosperms

This figure from Crepet (2000).

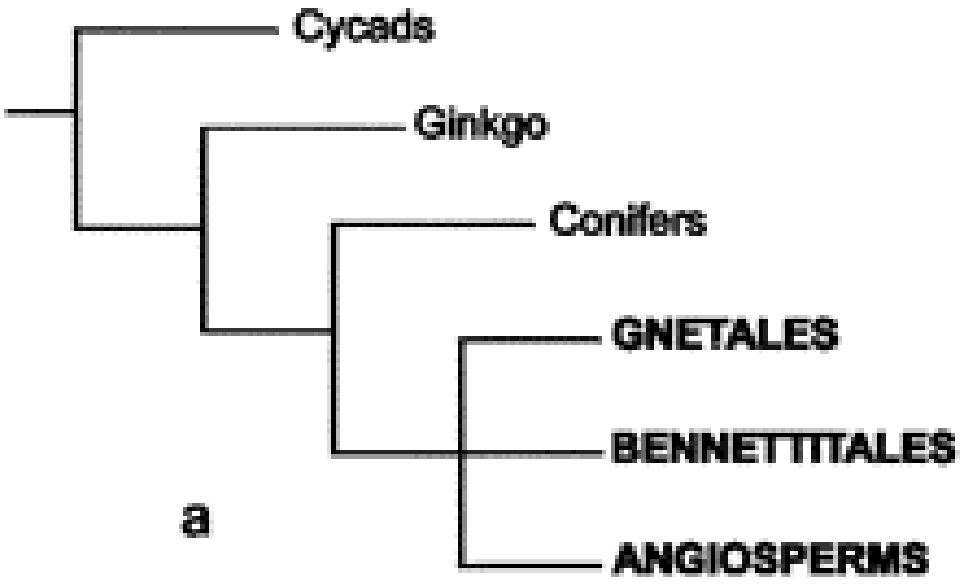
http://www.sunstar-solutions.com/sunstar/Why02/why.htm

Gigantopteridales

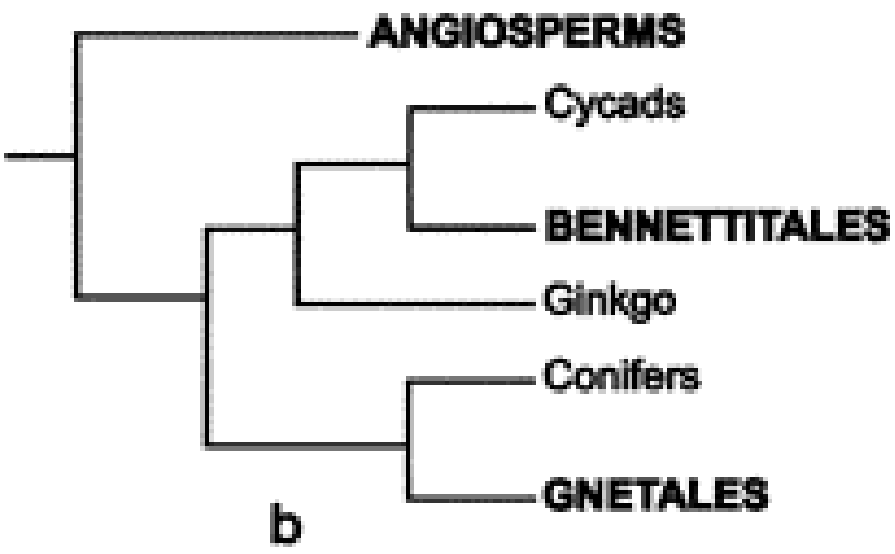
oleanaanid

http://www.amjbot.org/content/86/11/1563.full

Anthophyte hypothesis



Gnetifer hypothesis

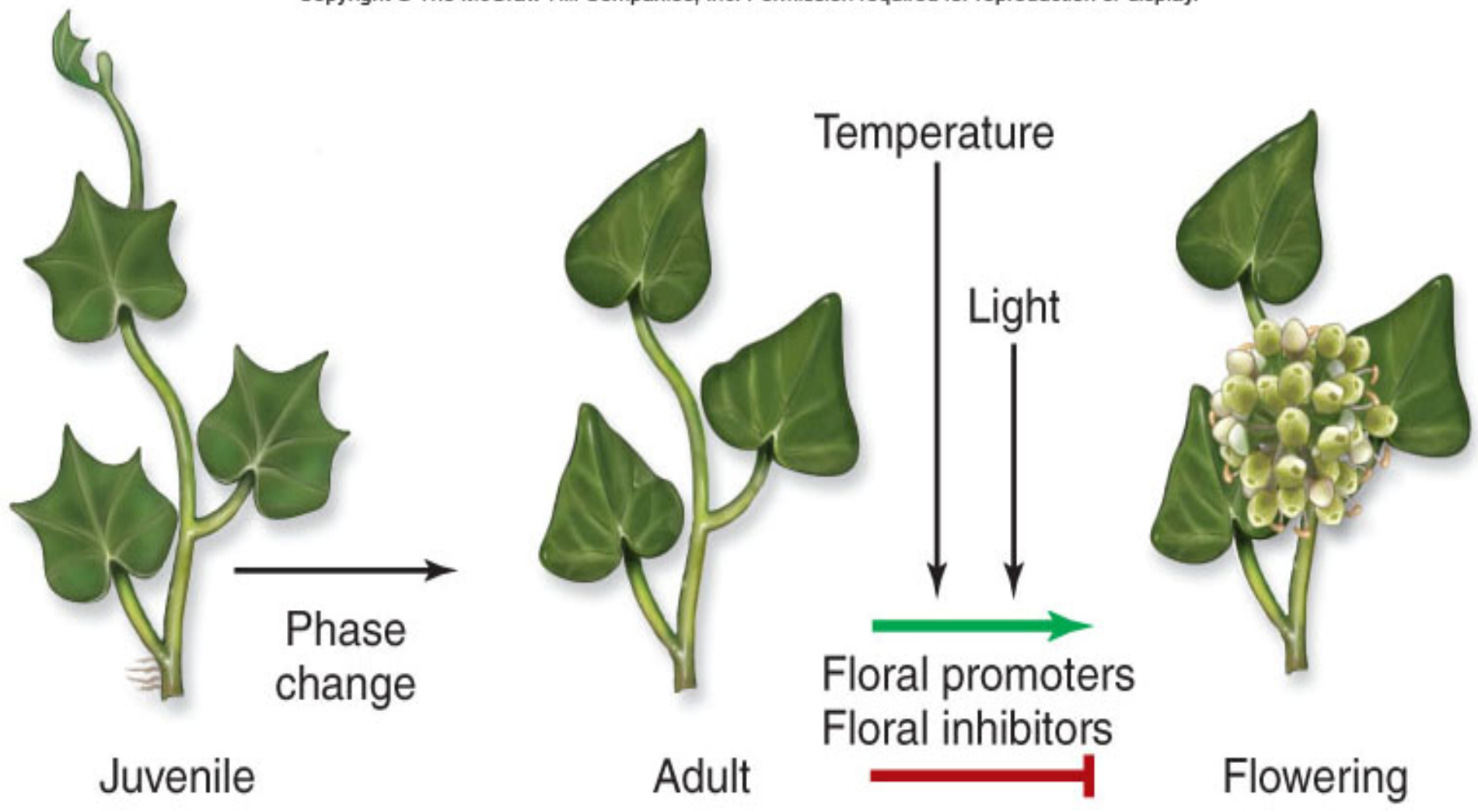


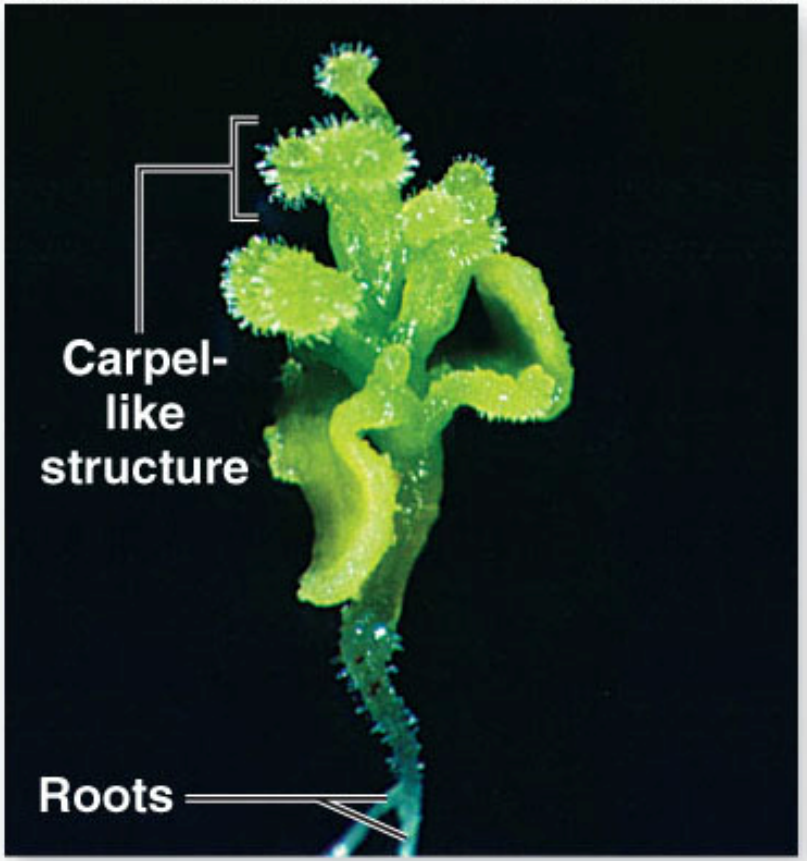
The Gnetifer hypothesis helps resolve the paradox of the age of the Bennettitales (225 MY) relative to known Angiosperms (140 MY)

(a) A typical morphology-based phylogeny of existing seed plants (plus the extinct Bennettitales) illustrating (in bold type) the anthophyte clade.
(b) A composite phylogeny illustrating the realignment of Bennettitales and Gnetales based on ITS and new morphological data (Goremykin et al 1996). This figure from Crepet (2000).

Õie teke

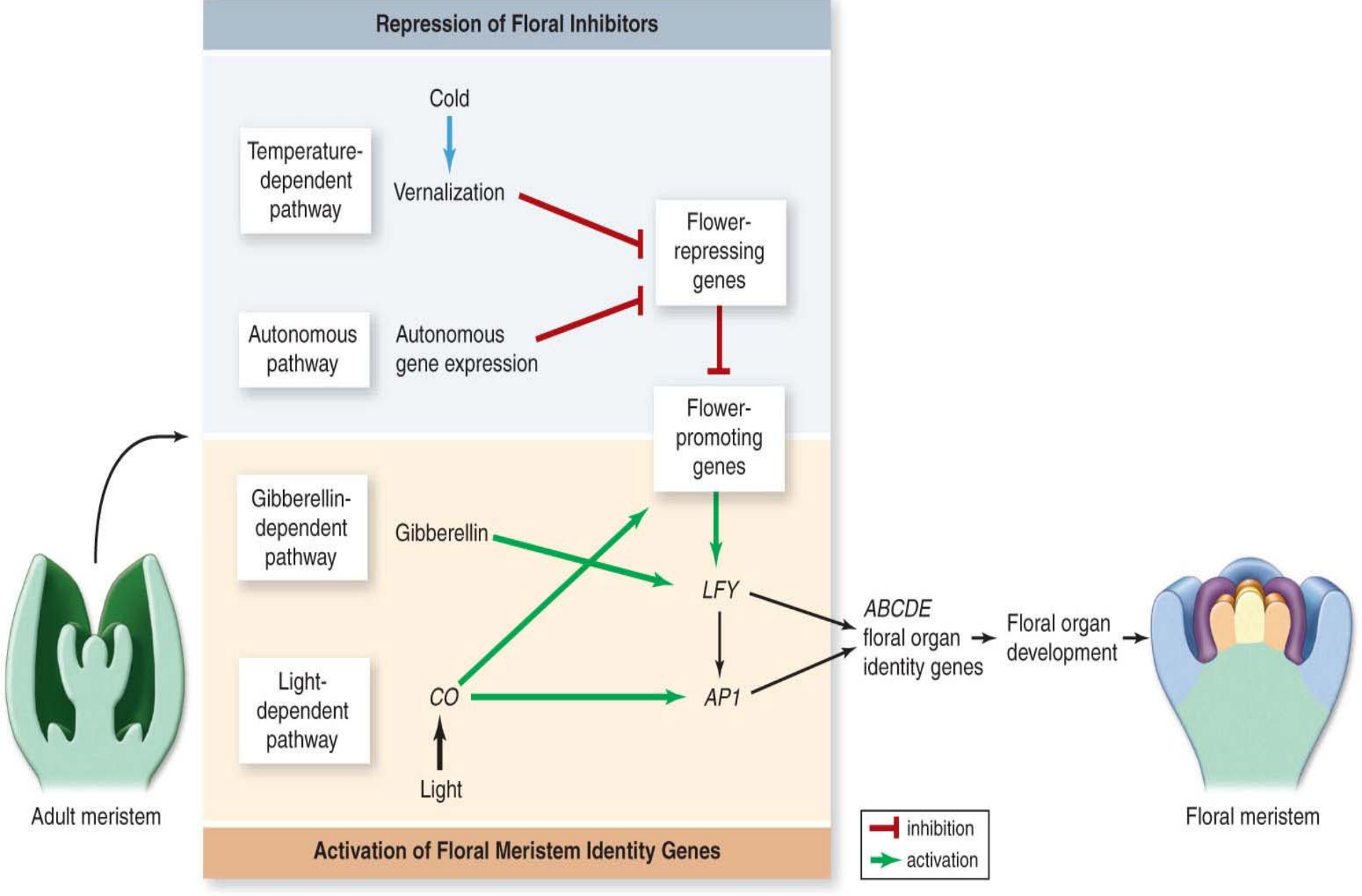
Faasinihe





- Mudeltaim müürlook *Arabidopsis thaliana*
- Geen *LEAFY* (*LFY*) põhjustab varast õitsemist

Flowering Plants
Gnetales
Conifers
Ginkgo
Cycads
WelLFY
WelNdly
GnegnLFY
PRFLL
Needly
GinLFY
GinNdly
ZamfuLFY
ZamfuNdly
Out-
groups
Loss of NEEDLY
a
Duplication-->LFY & NEEDLY


Repression of Floral Inhibitors
Cold
Temperature-dependent pathway
Vernalization
Flower-repressing genes
Autonomous pathway
Autonomous gene expression
Flower-promoting genes
Gibberellin-dependent pathway
Gibberellin
LFY
ABCDE floral organ identity genes
Floral organ development
Light-dependent pathway
CO
AP1
Light
Adult meristem
Floral meristem
inhibition
activation
Activation of Floral Meristem Identity Genes

ABC(DE) mudel

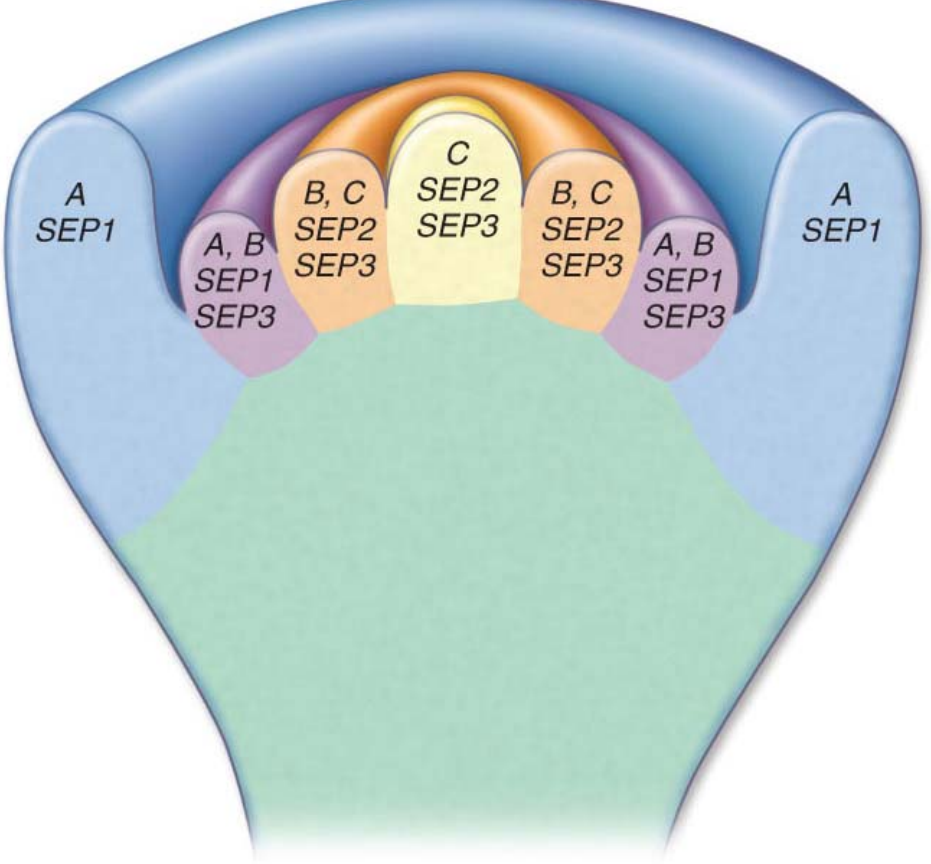
- A – tupplehed
- A ja B – kroonlehed
- B ja C – tolmukad
- C ja D – emakas

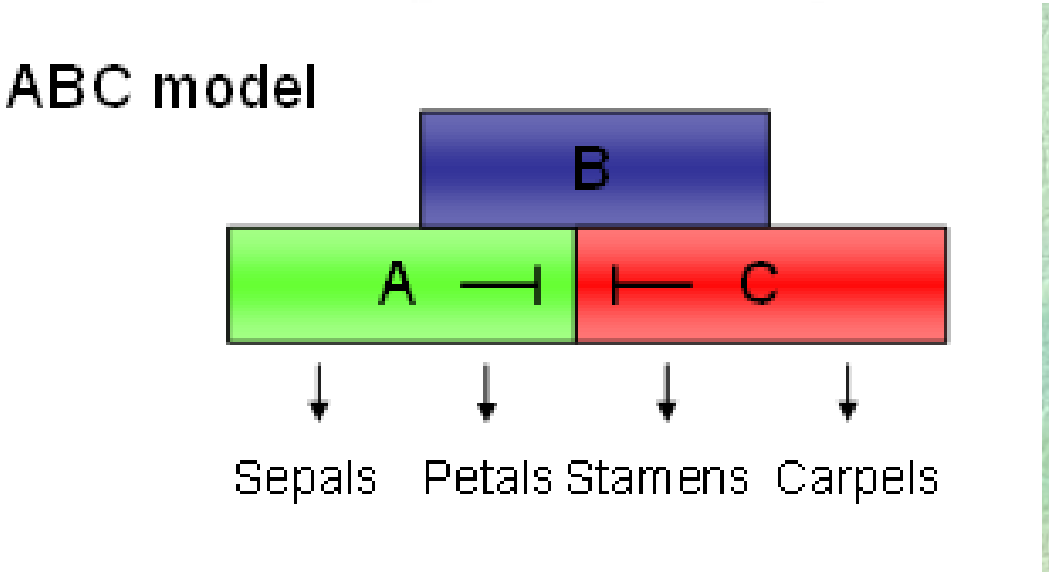
(viljalehed)

- E (SEPALATA)

Reguleerib A,B,C

- MADS-box





Whorl 1 sepals
Whorl 2 petals
Whorl 3 stamens
Whorl 4 carpels

A
B and C
C
B and C
A and B
A

Wild-type floral meristem

Development

Cross section of wild-type flower

Sepals
Petals
Stamens
Carpels

Wild-type Flower

C
B and C
C
B and C
C

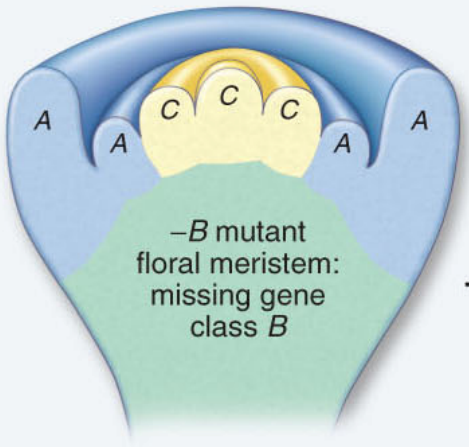
–*A* mutant floral meristem: missing gene class *A*

Development

Cross section of –*A* mutant flower

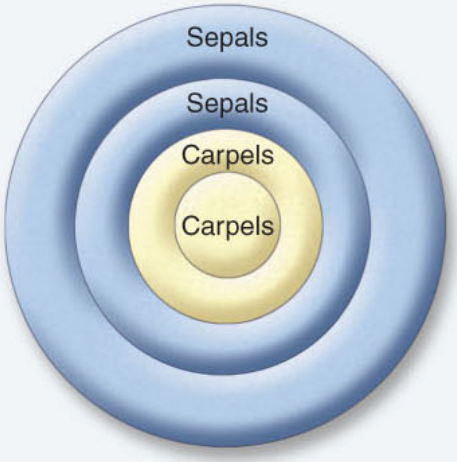
Carpels
Stamens
Stamens
Carpels

–*A* Mutant Flower

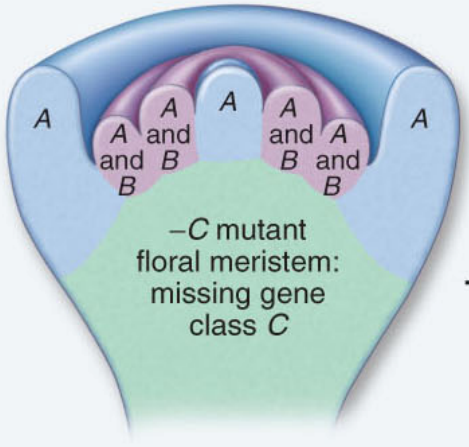


Development

Cross section of –*B* mutant flower

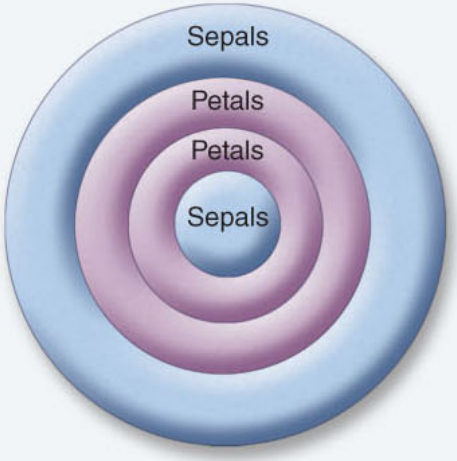


–*B* Mutant Flower



Development

Cross section of –*C* mutant flower

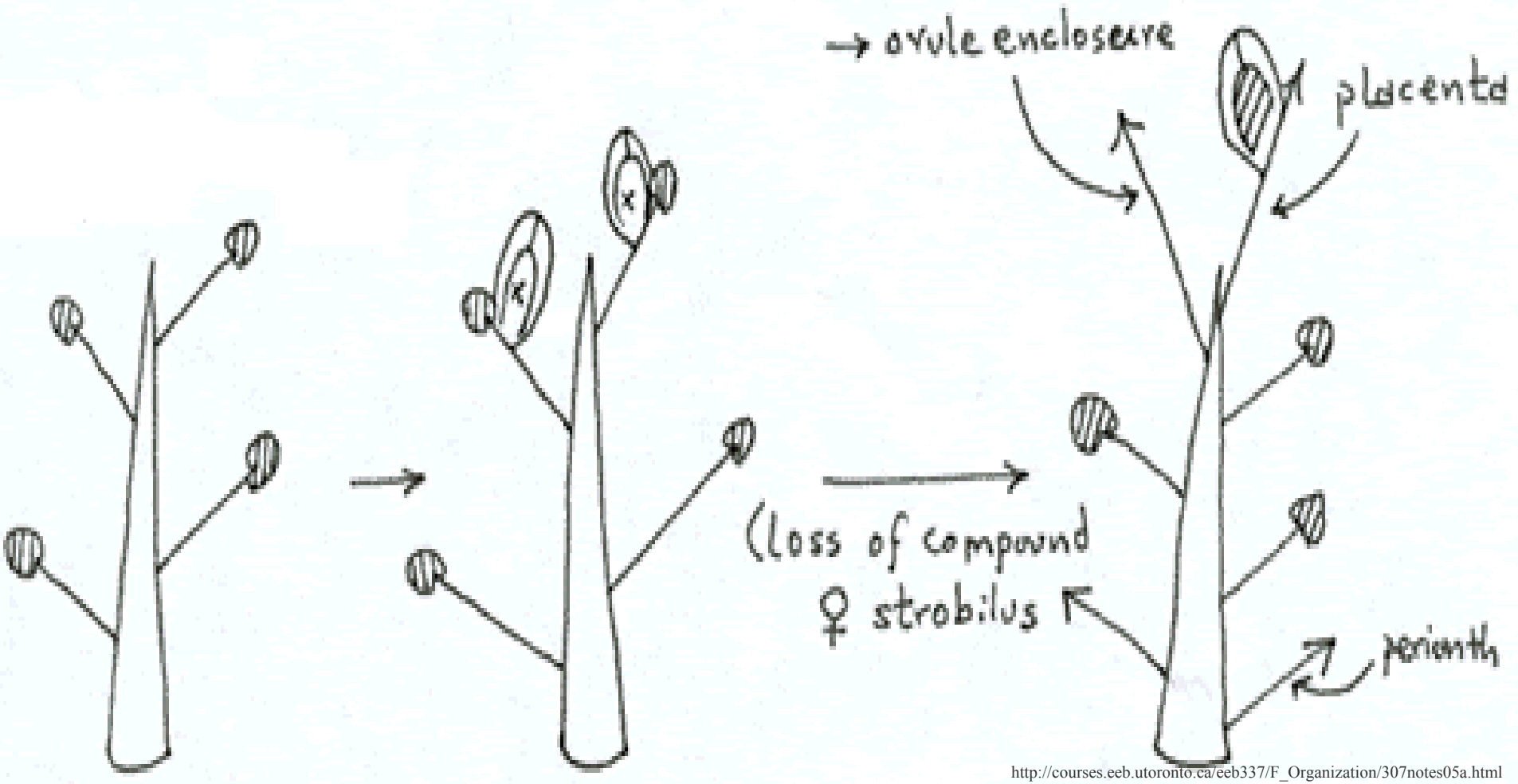


–*C* Mutant Flower

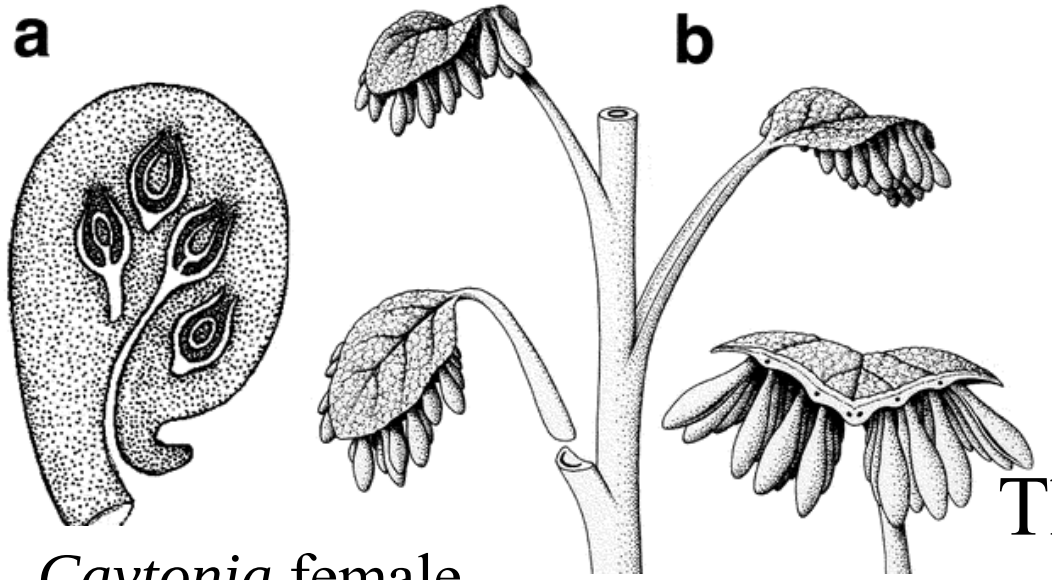
Õie teke

- *Euanthium* – kahesugulisest käbist (*Cycadoidea/Bennettitales/Caytoniales*), primitiivsed õied (*Magnolia, Nymphaea)* periandiga, õieosad lehelist päritolu; antofüütide ja *Neopseudanthium* teooria (vastaklehikud õistaimede eellased); AGA Gnetiidae MADSbox lähem okaspuudele
- ***Pseudanthium*** ühesugulisest paljunemisorganitest seemnesõnajalgadel, primitiivsed õied periandita (*Archaefructus),* tolmukad ja viljalehed otse teloomset päritolu; ÕIGEM; AGA kuidas kahesuguliseks?

Eelisasuse teooria (mostly male theory)



http://courses.eeb.utoronto.ca/eeb337/F_Organization/307notes05a.html



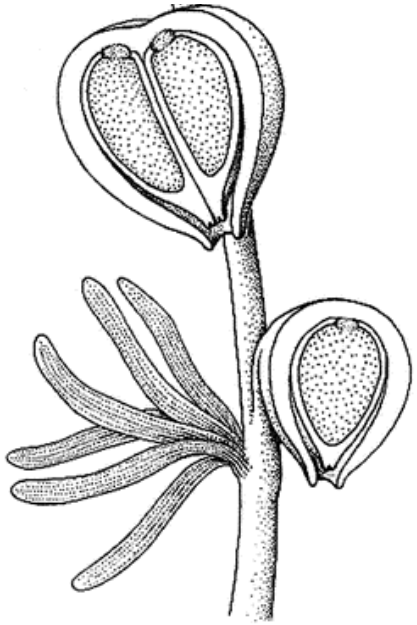
Caytonia female

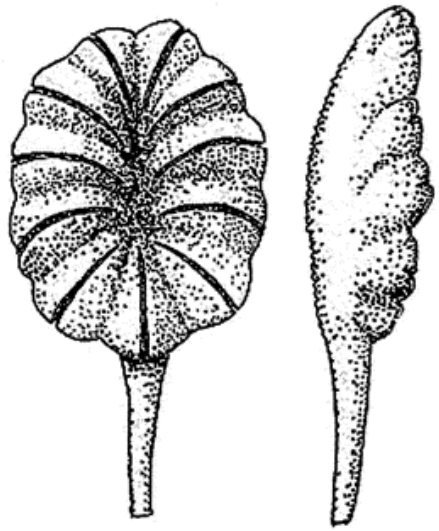
Pteruchus male

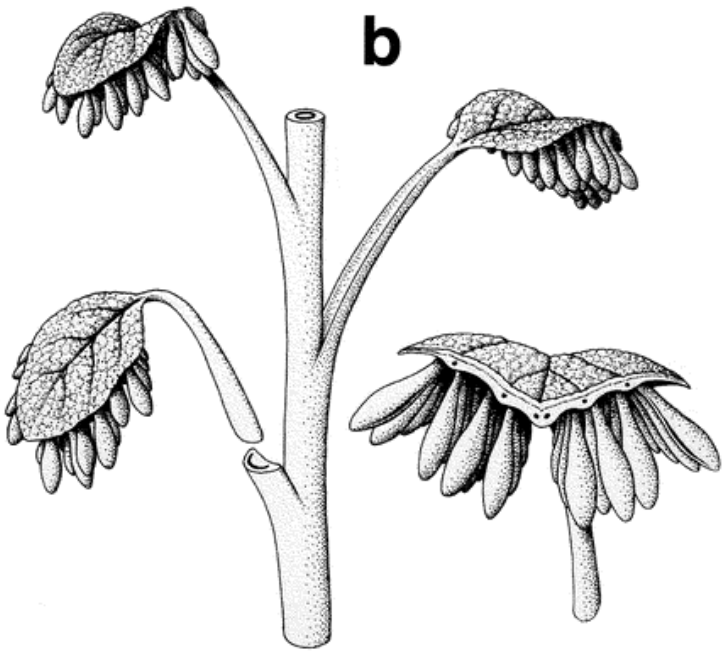
The broad, flat male organs of Corystosperms (*Pteruchus*, *Pteroma*) would make good carpels.

Ktalenia female

Pteroma male







Pteruchus male

Archaefructus female parts

Did angiosperms originate by a simple homeotic mutation that puts ovules where microsporangia was supposed to go?

Sun et al 2002

Eelemasuse teooria

- Emaskäbid redutseerisid alumises osas B-geenide ekspressiooni ja tekkisid isasorganid

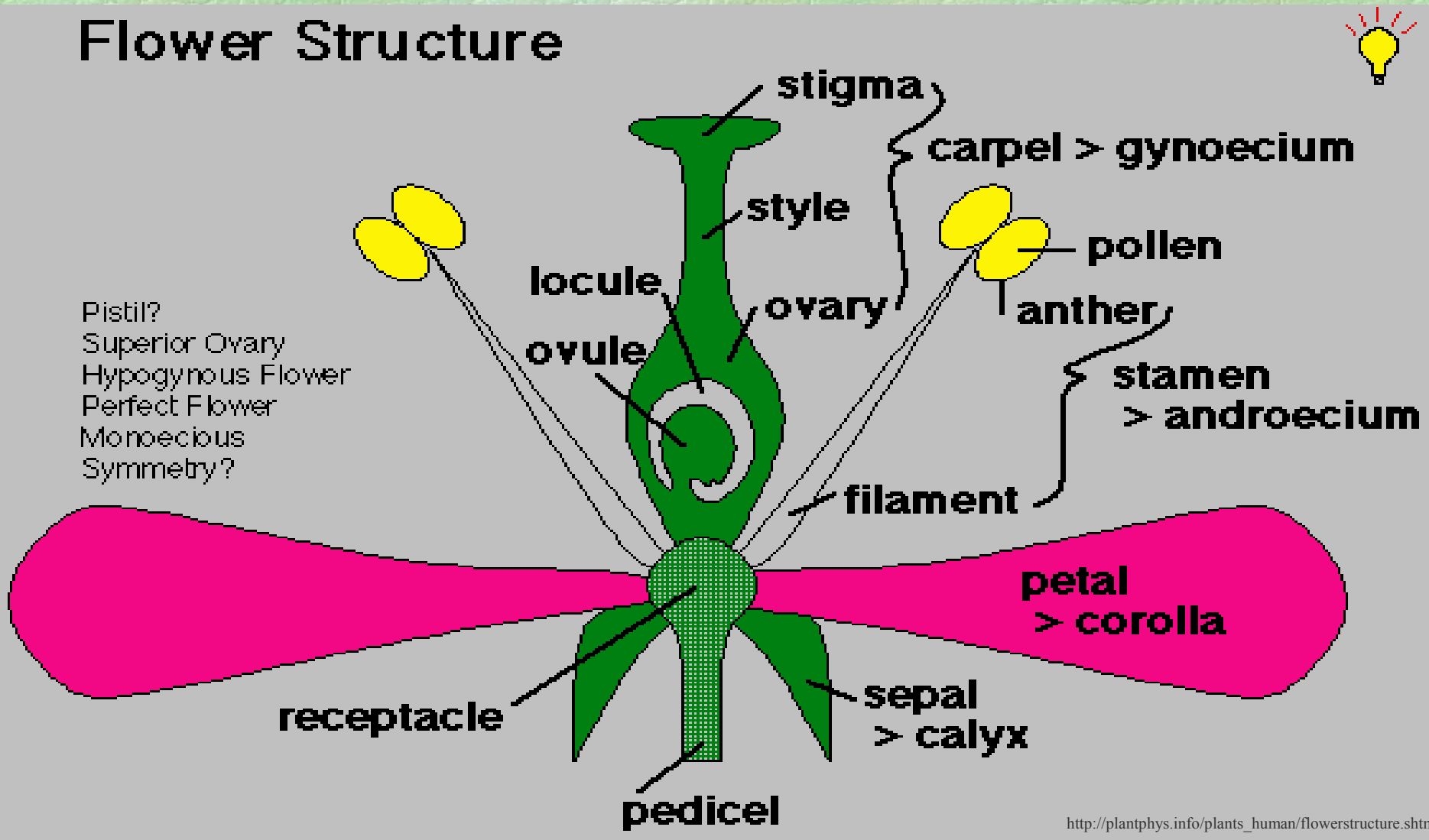
Õistaimede sünapomorfid

- Õis (õiekate, tolmukad, emakas)
- Suletud viljalehed,vili
- Lihtsad mikro-ja megagametofüüdid (tolmukad, arhegoon puudub)
- Anatroopne seemnealge, kaks integumenti
- Tolmuterade idanemine emakasuudmel
- Kaheliviljastamine ja polüploidne endosperm
- 8-tuumaline lootekott

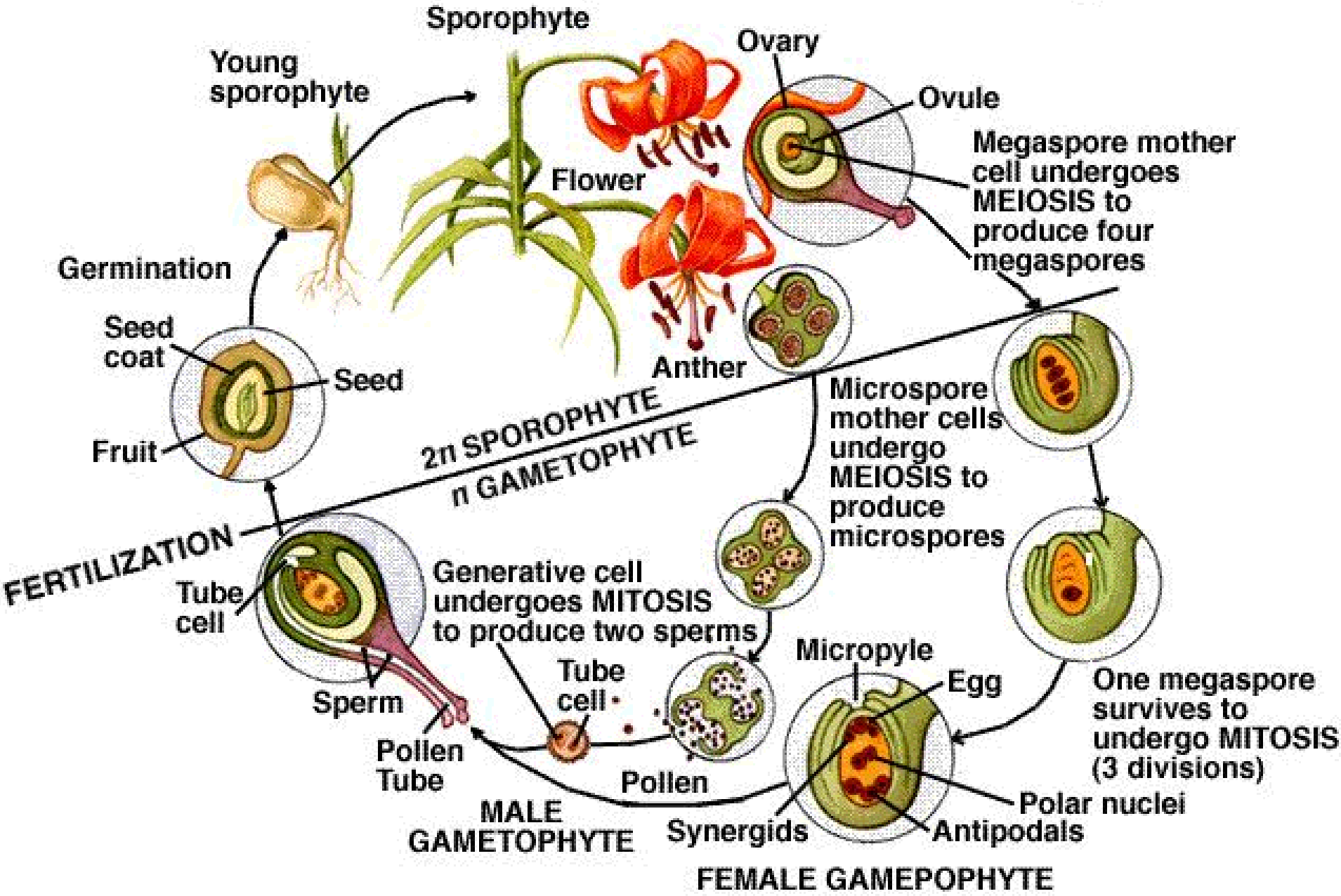
Õistaimede sünapomorfid

- **Tolmuterade eksiin ribiline**
- **Trahheed**
- **Lignifitseerunud puidukiud ja sõeltorud**
- **Võrkjas roodumine**
- **Alkaloidid**

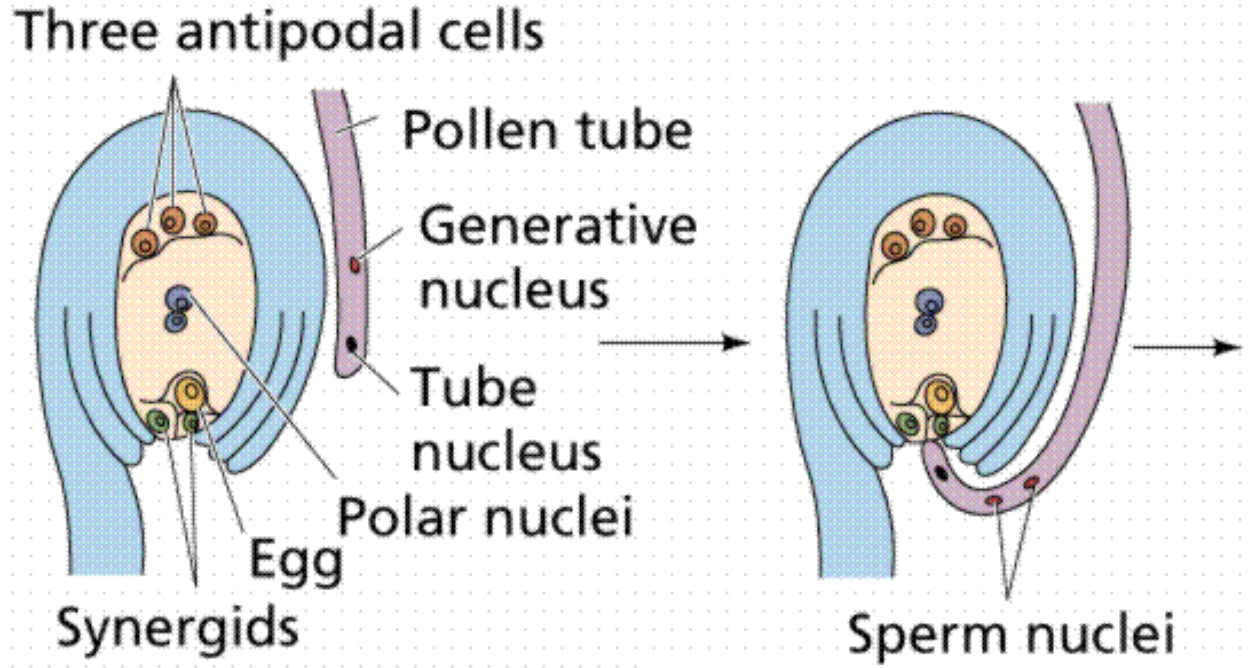
Õistaimede sünapomorfid



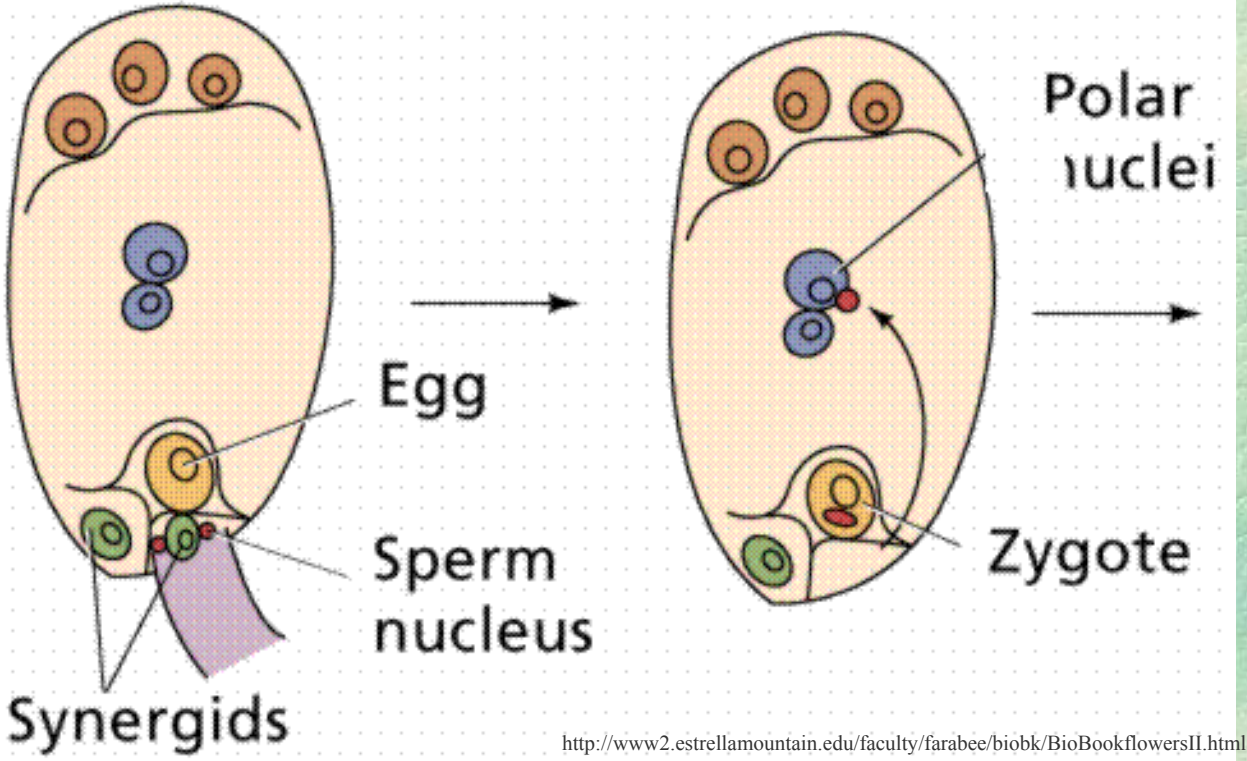
Generalized Life Cycle of Flowering Plants



8-tuumaline lootekott

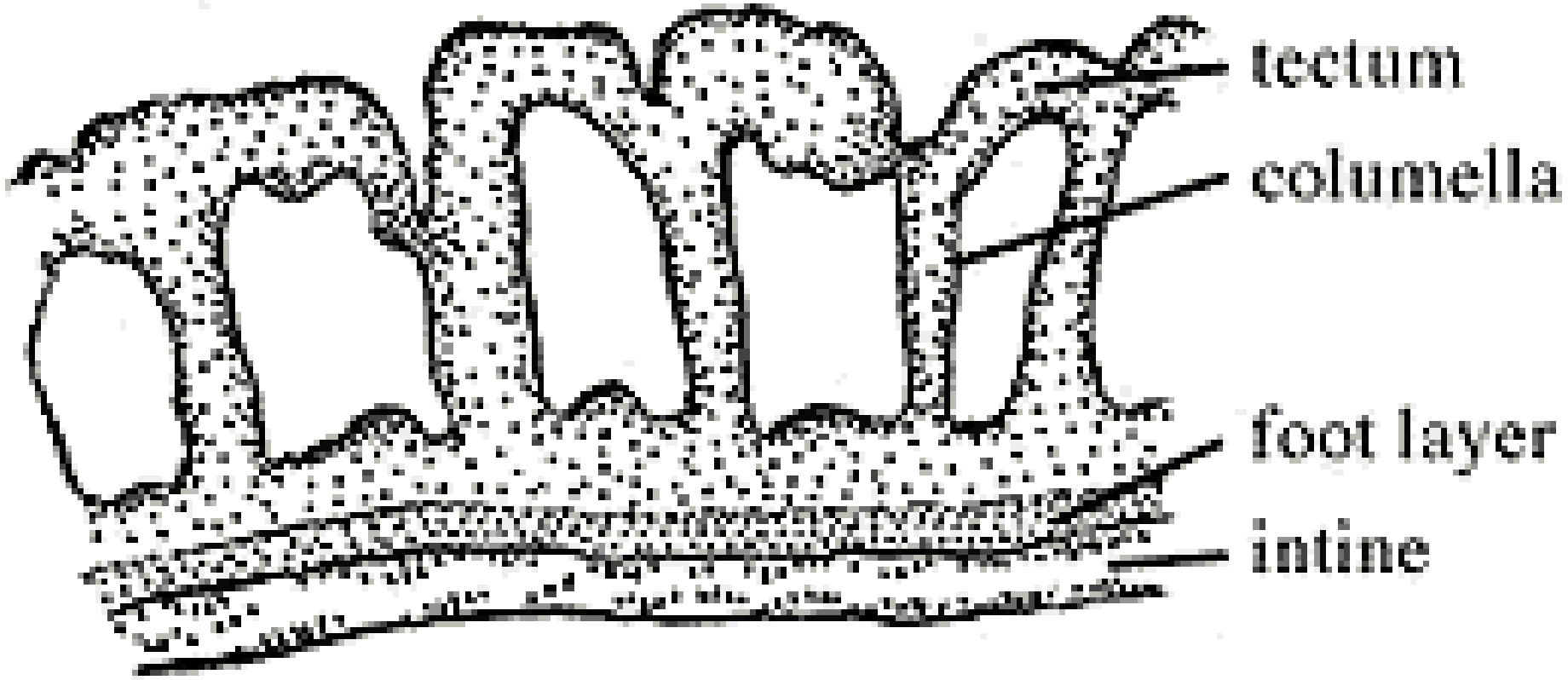


Kaheli-viljastamine, polüploidne endosperm

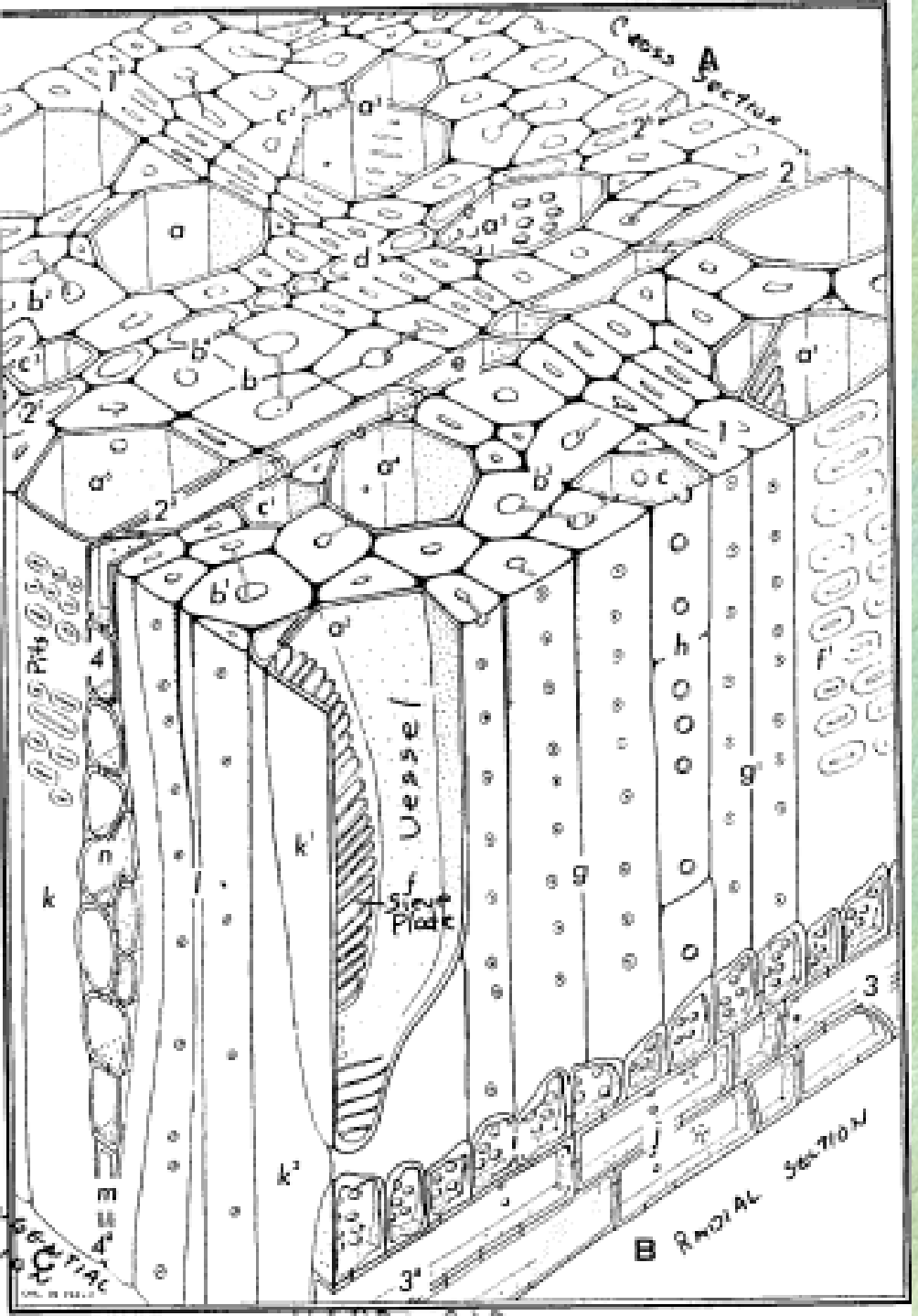


http://www2.estrellamountain.edu/faculty/farabee/biobk/BioBookflowersII.html

Tolmutera eksiini ehitus



http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup5.html

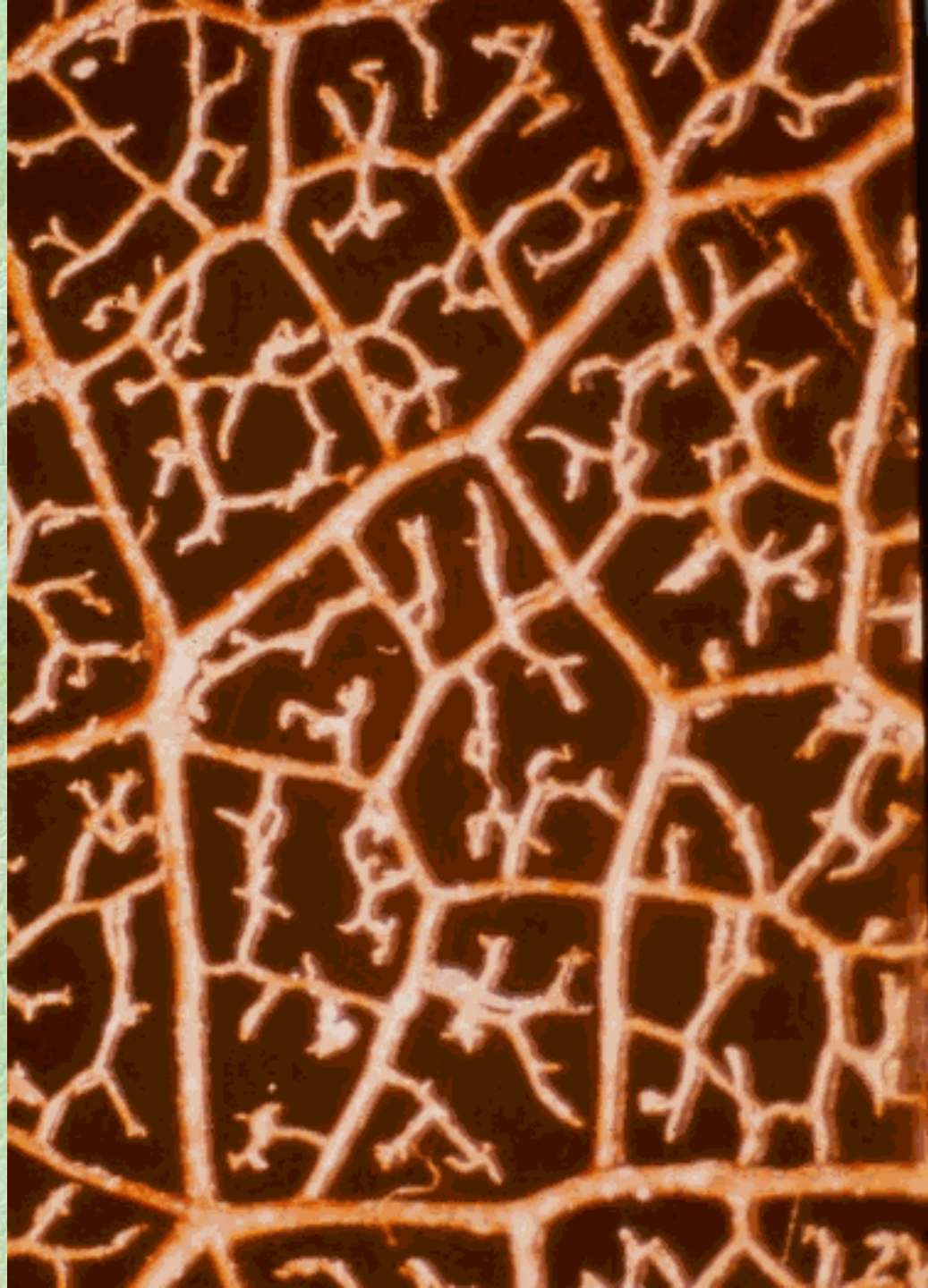


Sooned e trahheed

Sõeltorud ja saaterakud

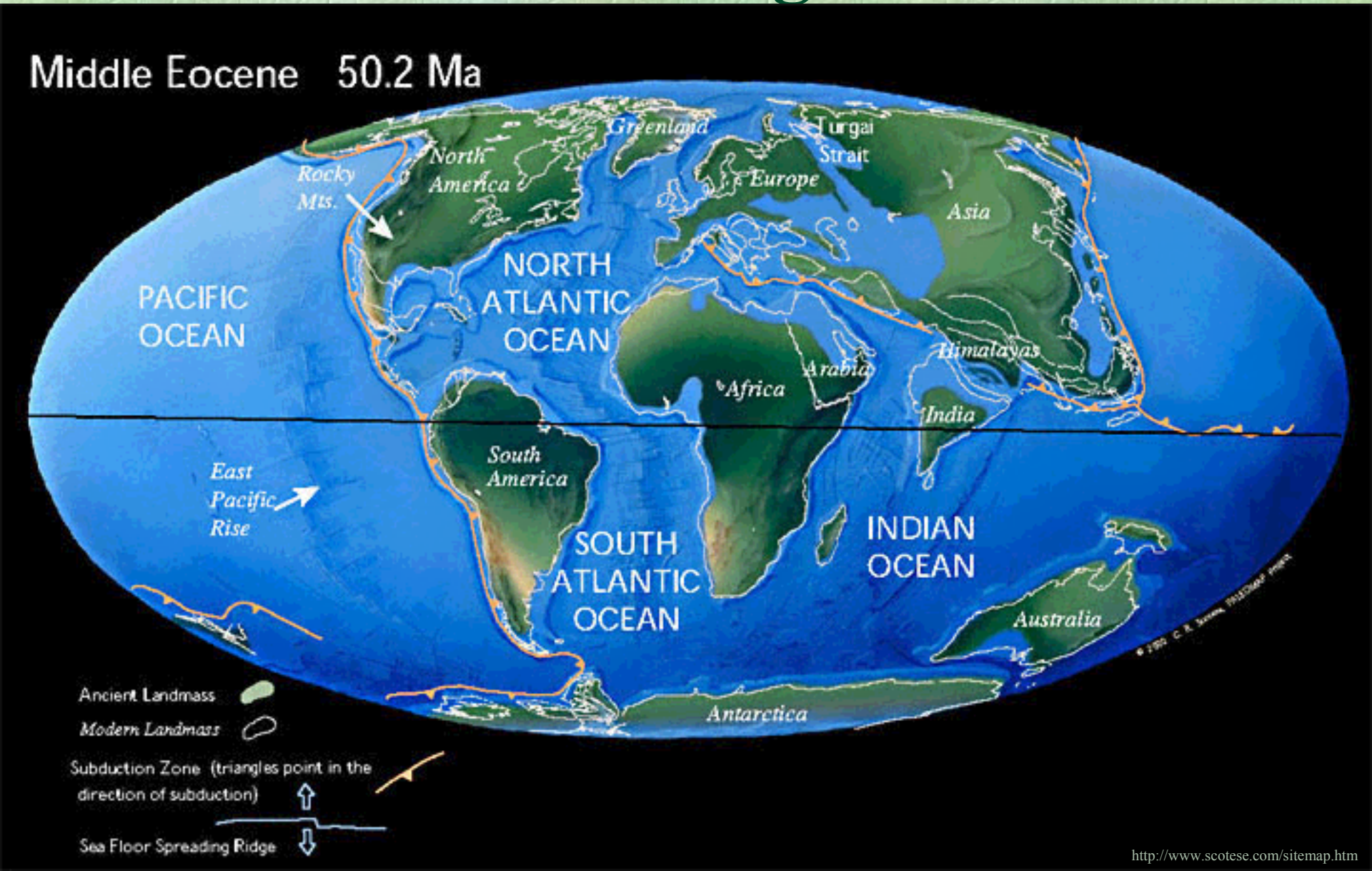
http://geo.arizona.edu/palynology/geos581/lec_13.html

Võrkjas roodumine

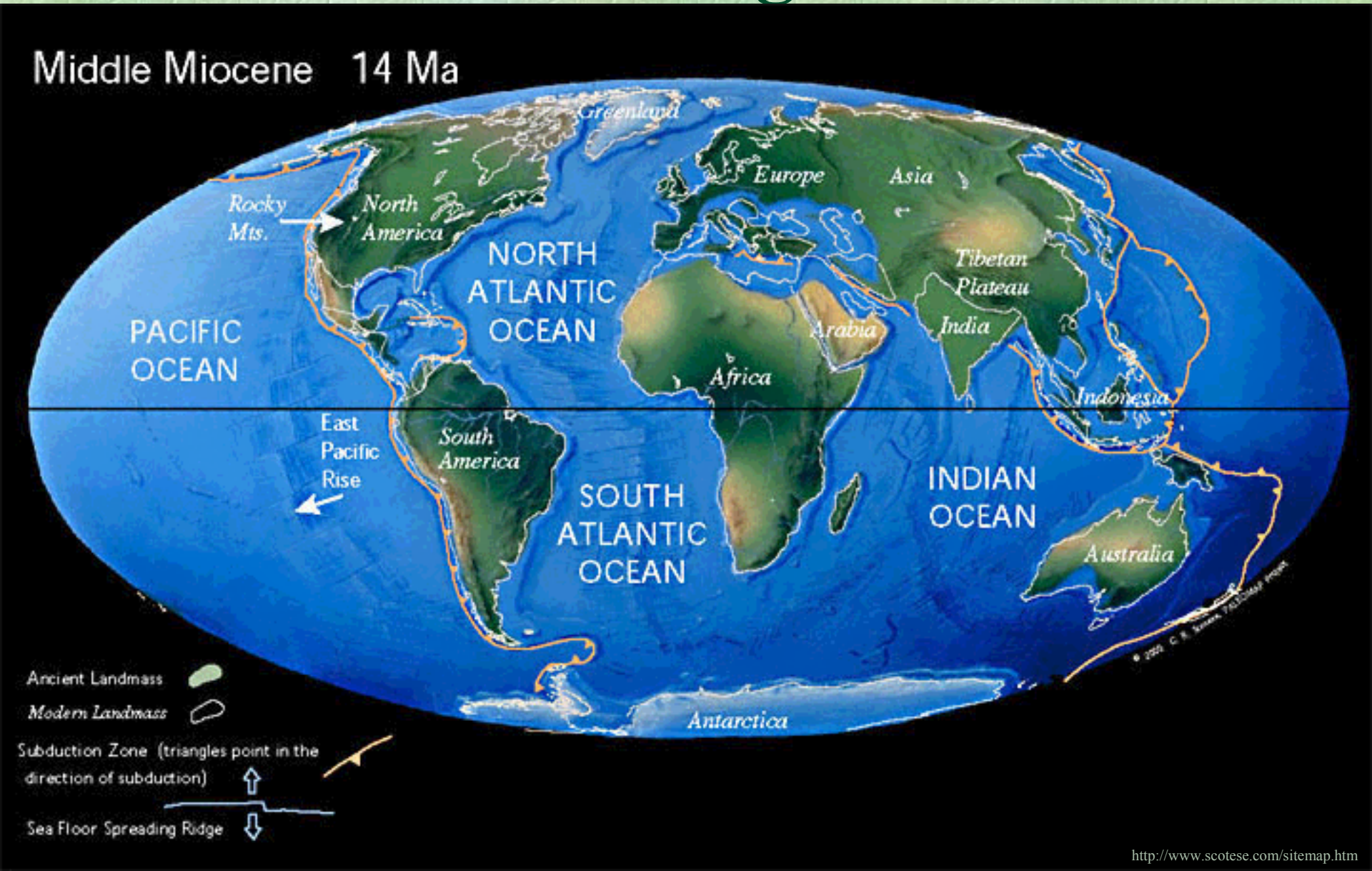


Esimesed õistaimed

Paleogeen

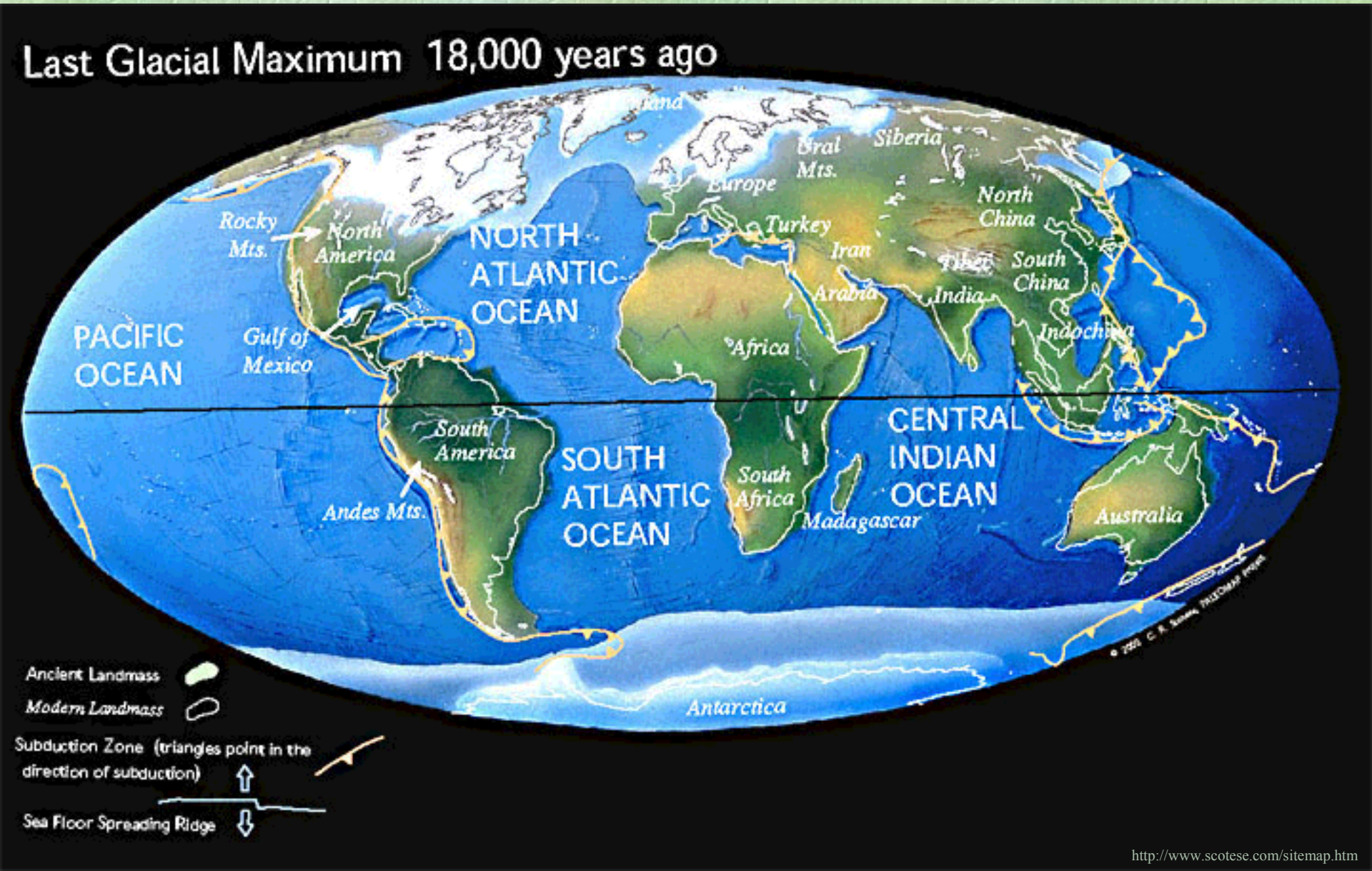


Neogeen



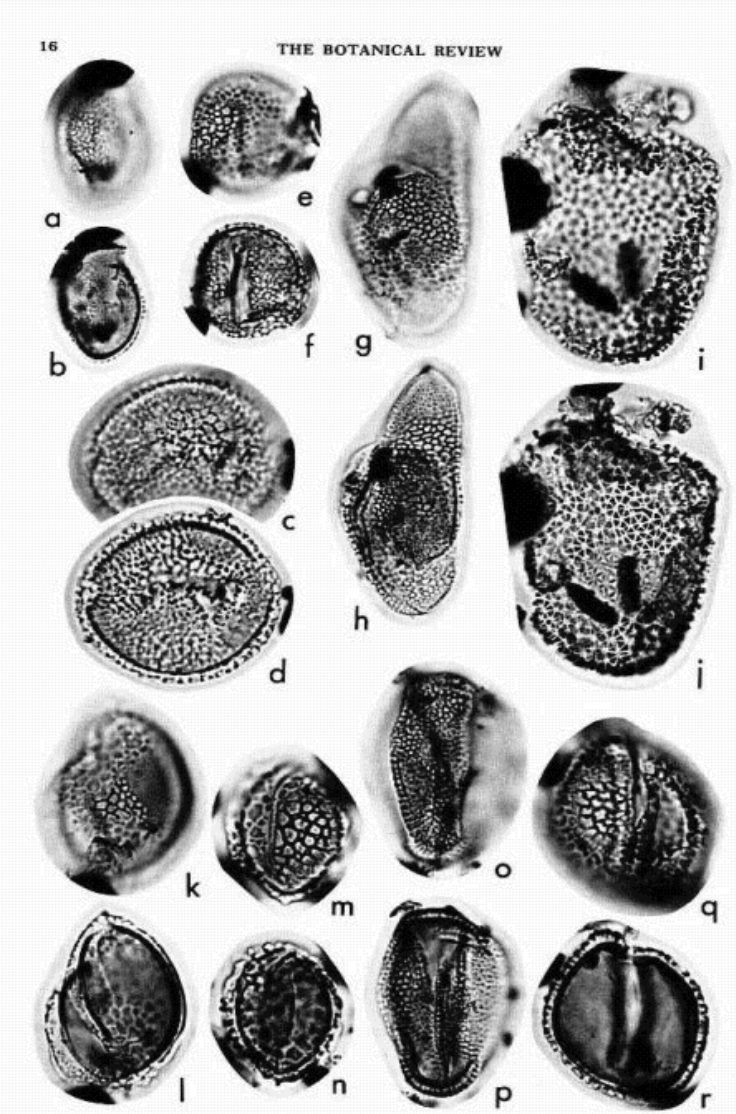
http://www.scotese.com/sitemap.htm

Kvaternaar



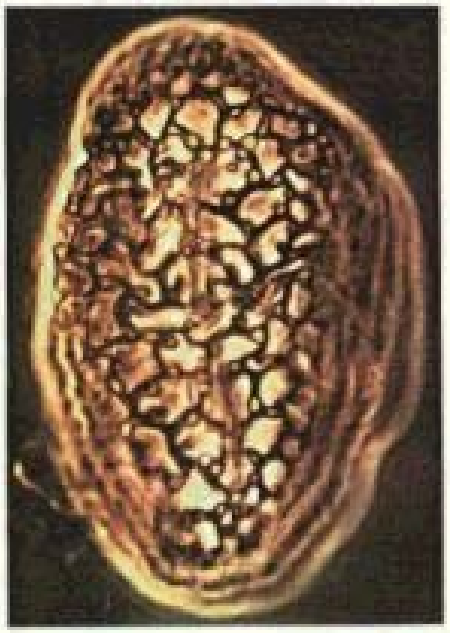
http://www.scotese.com/sitemap.htm

Õietolm Triiasest

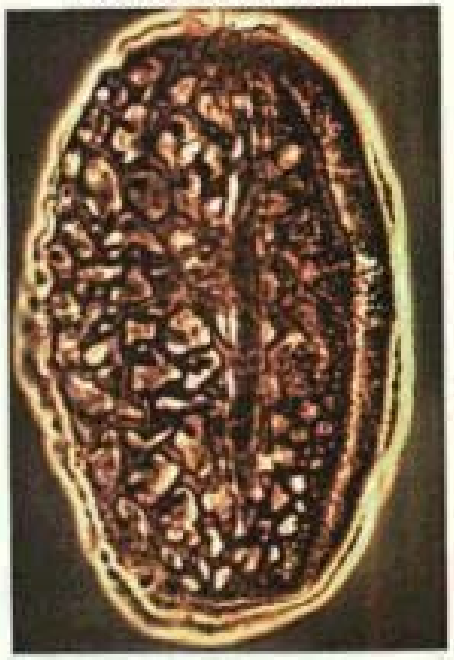


PENTASULCATE SP. 1

PENTASULCATE SP. 1



LATE MIDDLE CARNIAN



TRISULCATE SP. 4

http://www.sunstar-solutions.com/sunstar/Why02/why.htm

Sanmiguelia lewisii

Text-Fig. 6. Reconstruction of *Sanmiguelia lewisii* Brown.

http://www.ucmp.berkeley.edu/IB181/VPL/Cup/CupVGIII.html

http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup5.html

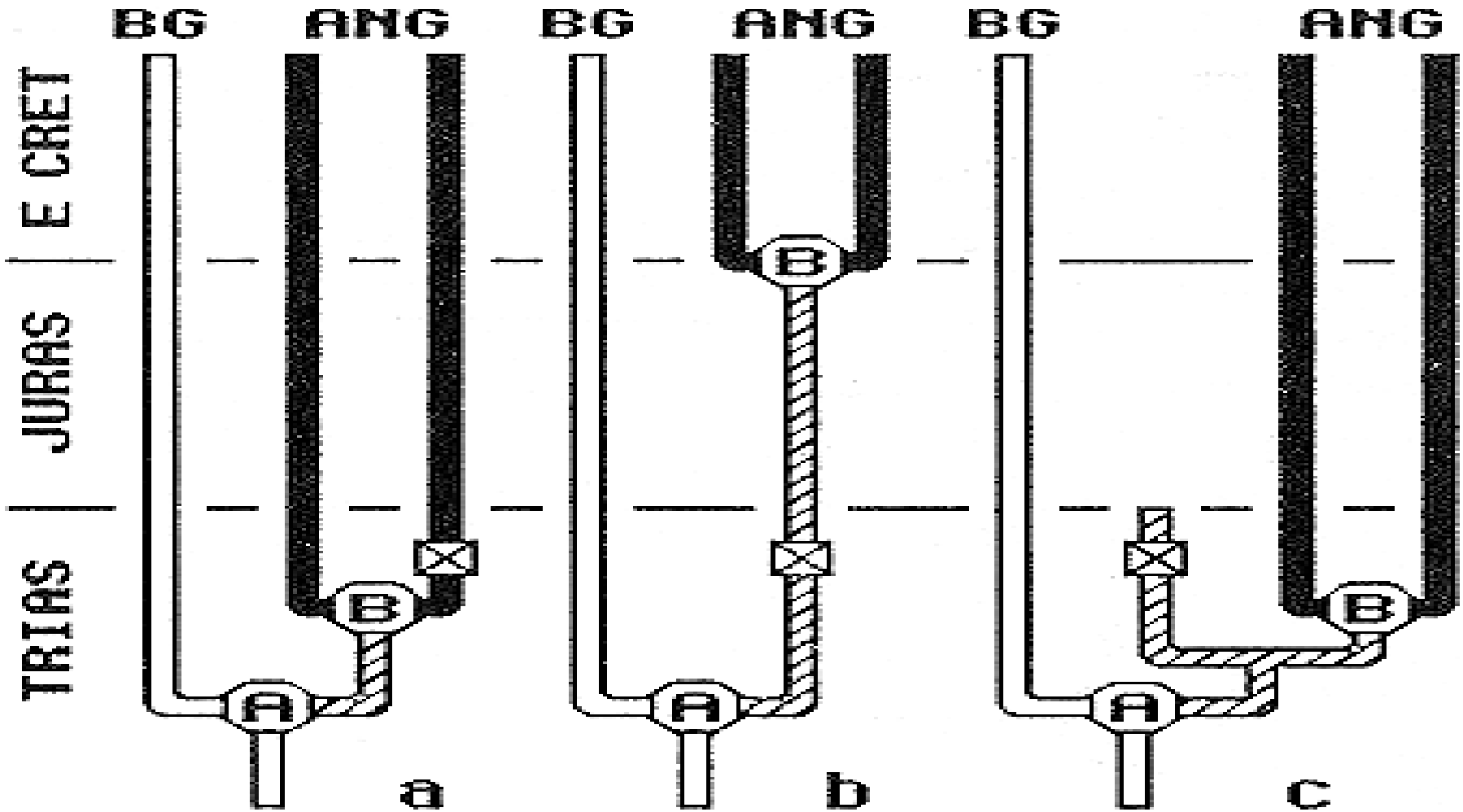


FIGURE 15. Implications of Late Triassic angiosperm-like fossils (*Sanmiguelia*, Crinopolles) for the age of node B, depending on whether they are angiosperms (a) or stem angiophytes; in the latter case, the crown-group could be much younger (b), or it could exist at the same time (c). BG, Bennettitales, *Pentoxylon*, and Gnetales.

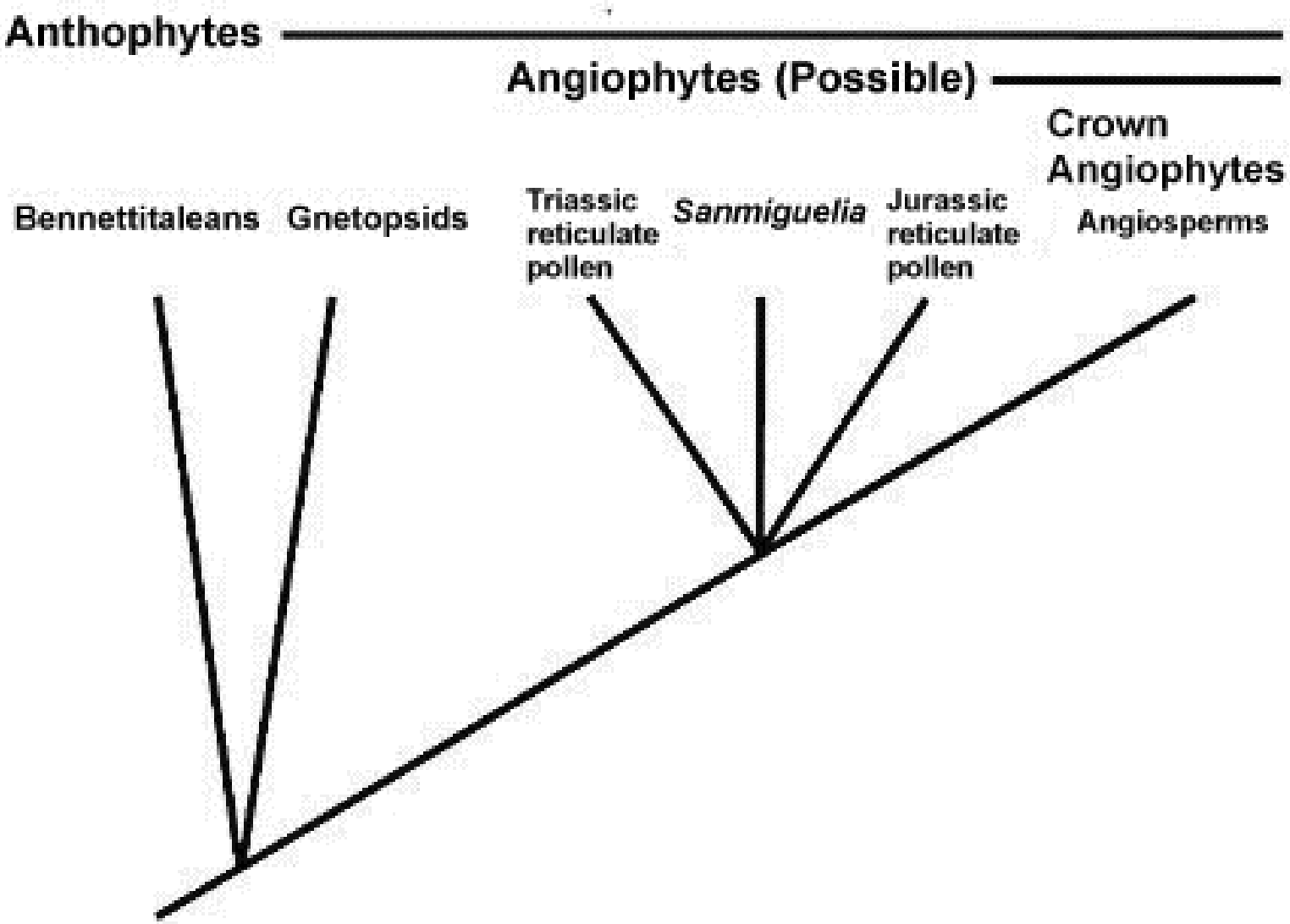
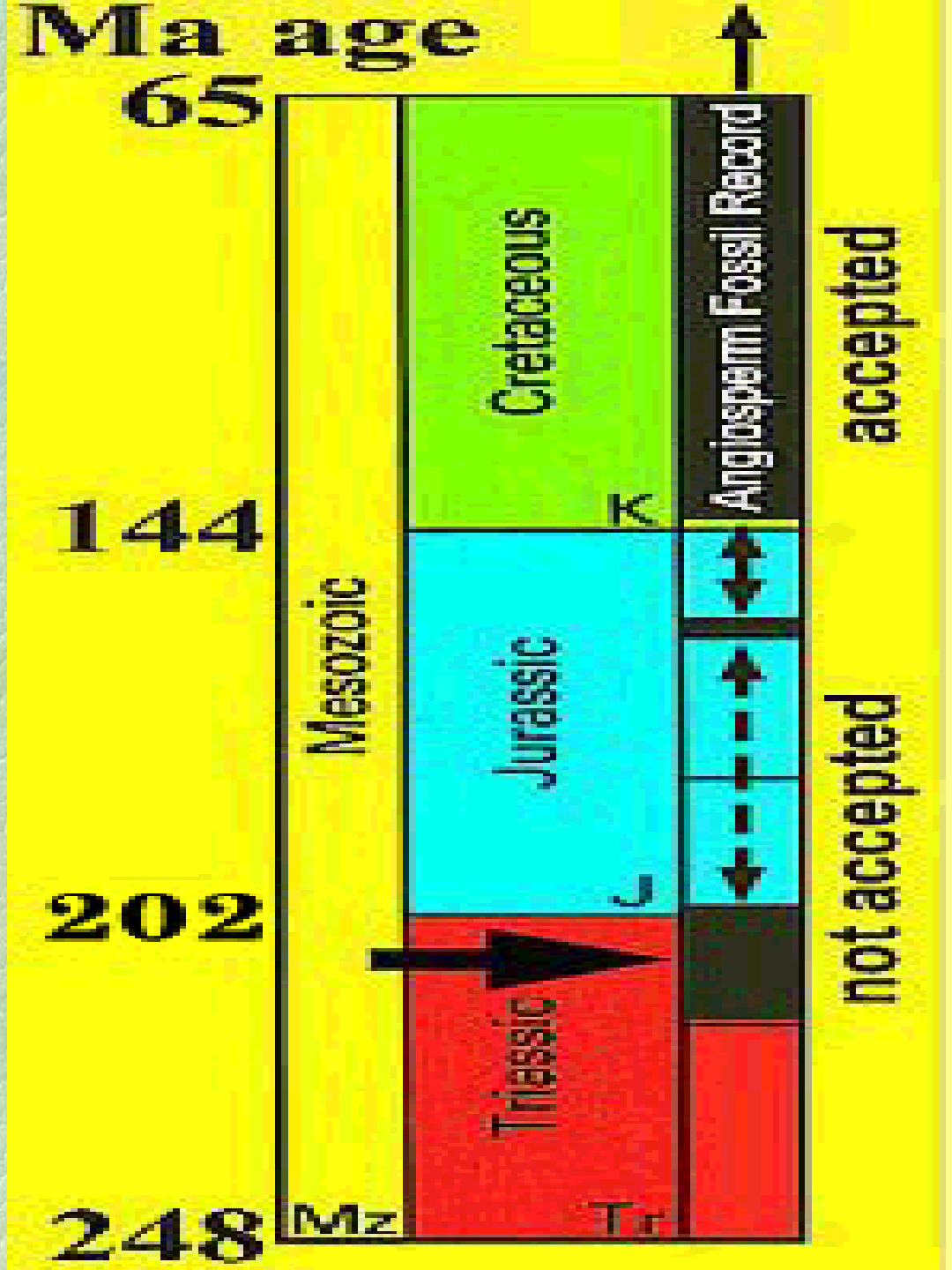


Figure 9.1. A consensus phylogeny showing the Anthophytes including the angiosperm sister groups, Angiophytes including the possible stem angiophytes, and the Angiosperms, the crown angiophytes. The conceptual basis for this hierarchy is based on the work of Doyle and Donoghue (1993).

Taylor & Hickey, 1996. Evidence for and implications of an herbaceous origin for Angiosperms. Chapman & Hall, 232-266.

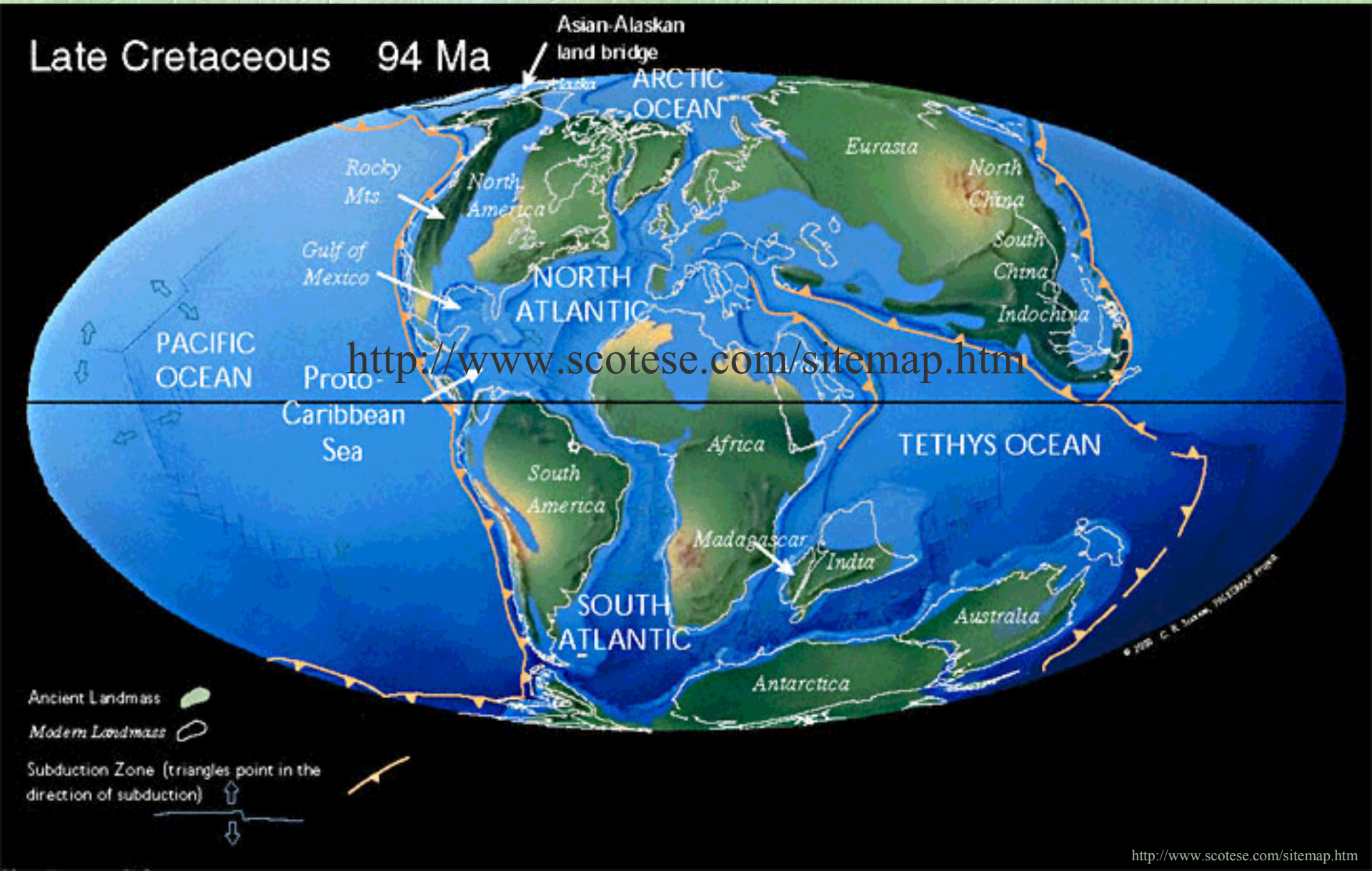
Õistaimed II

Esimesed õistaimed



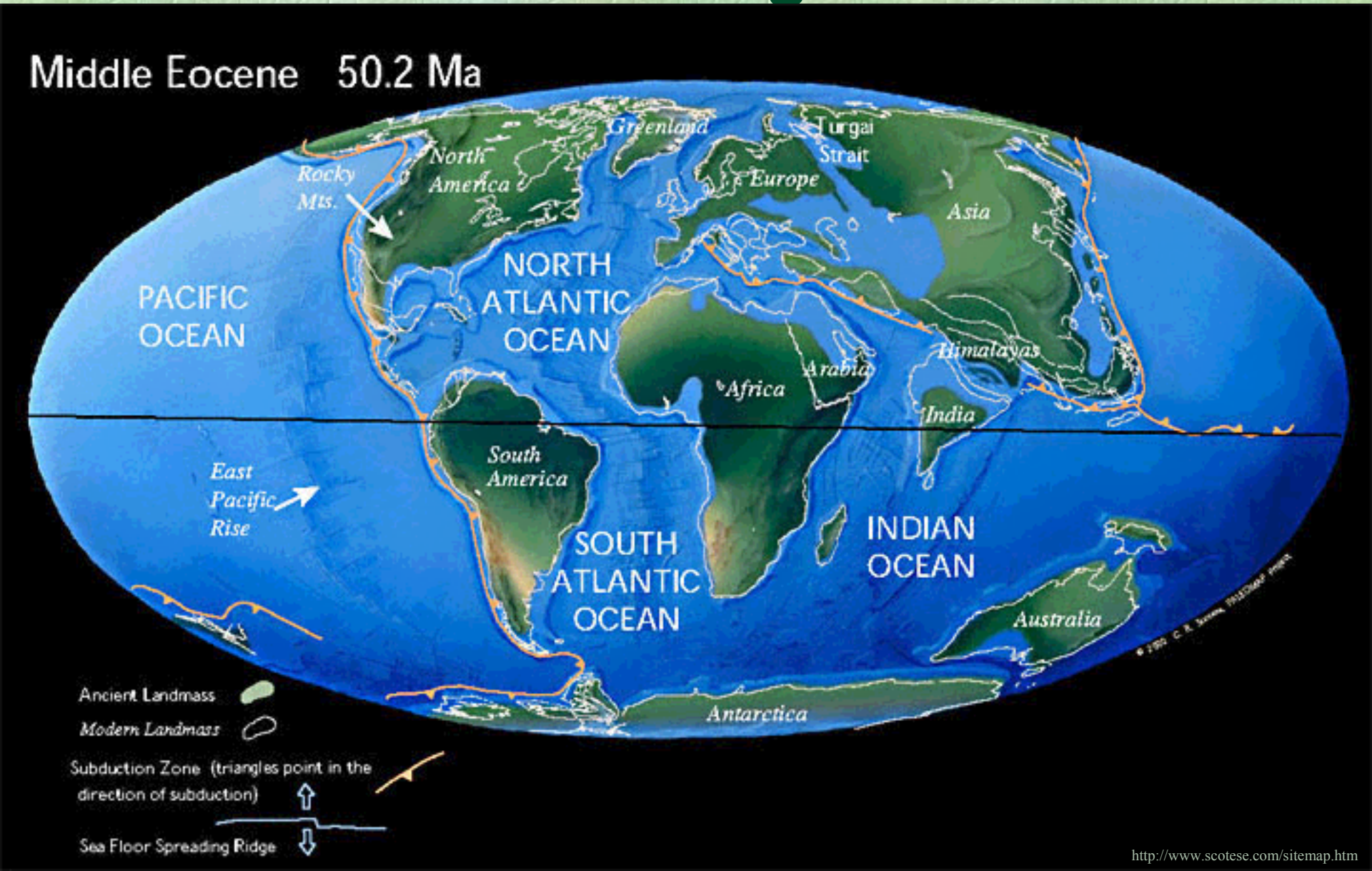
http://www.sunstar-solutions.com/sunstar/Why02/why.htm

Kriit



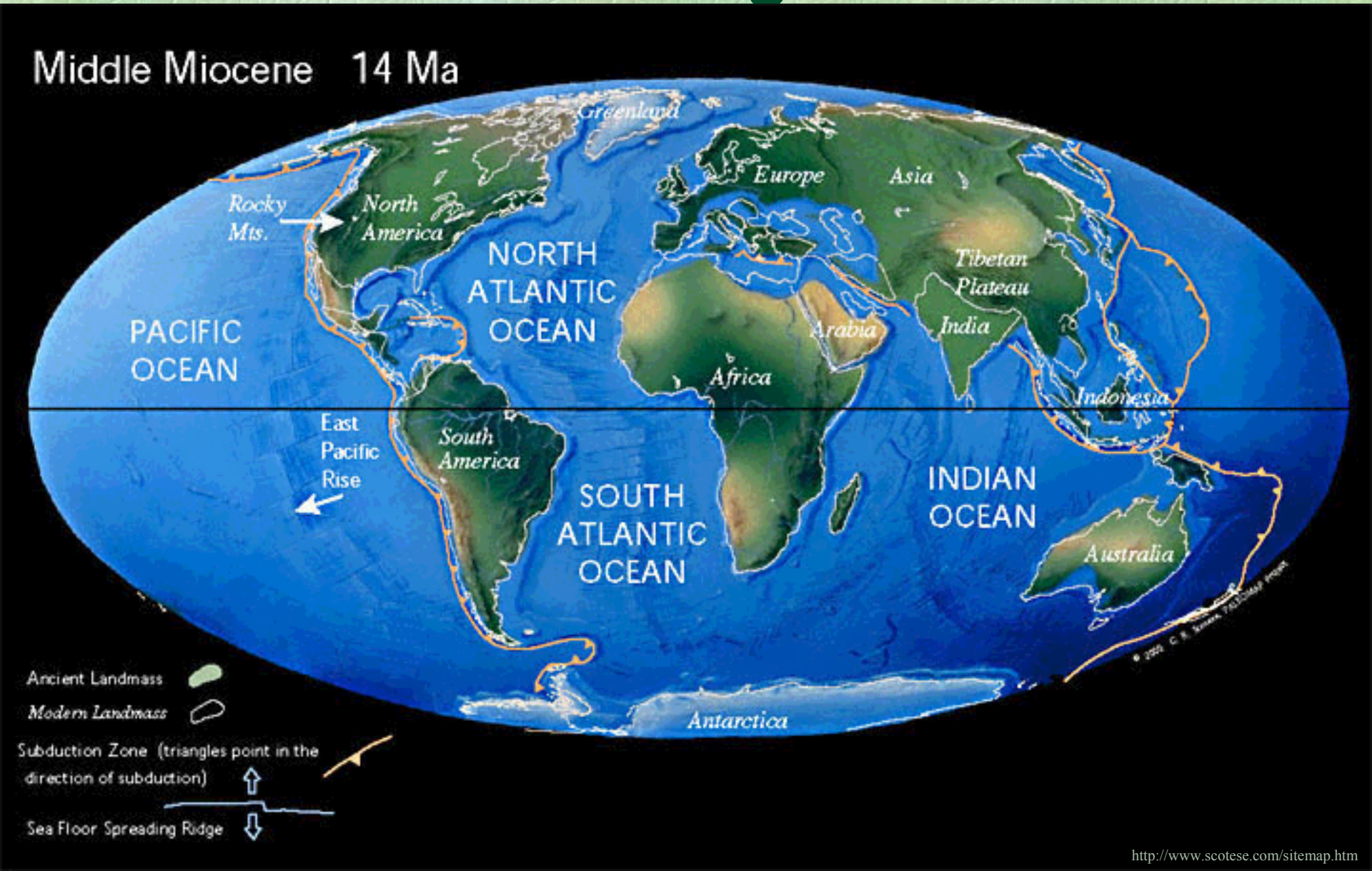
http://www.scotese.com/sitemap.htm

Paleogeen



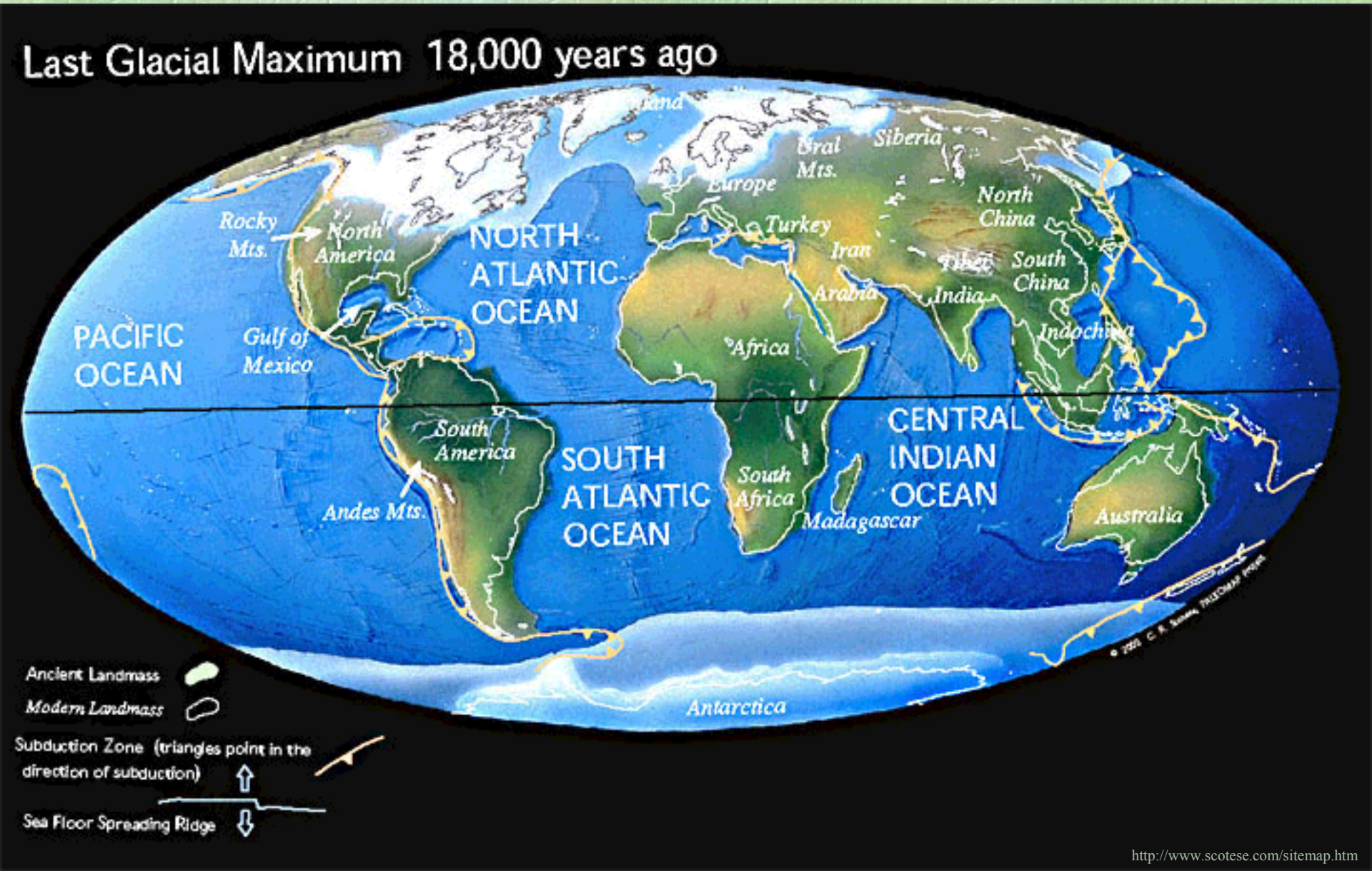
http://www.scotese.com/sitemap.htm

Neogeen



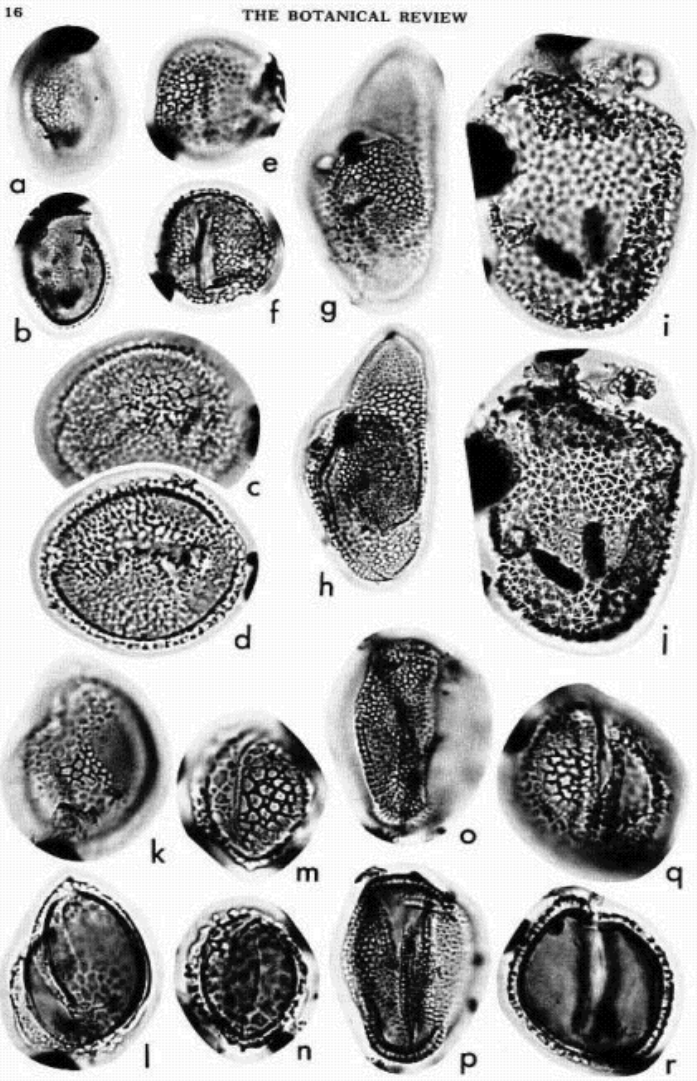
http://www.scotese.com/sitemap.htm

Kvaternaar



http://www.scotese.com/sitemap.htm

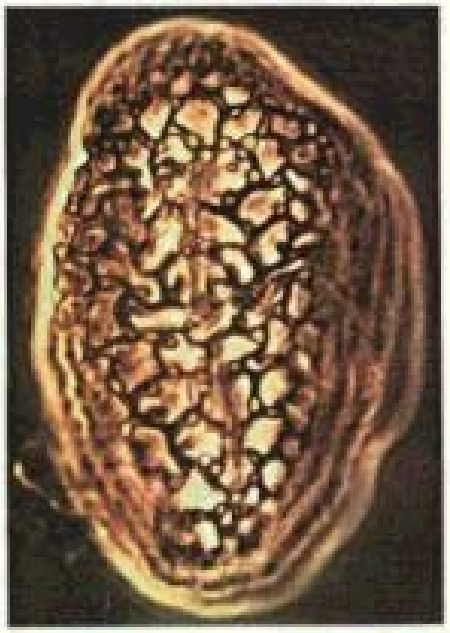
Õietolm Triiasest



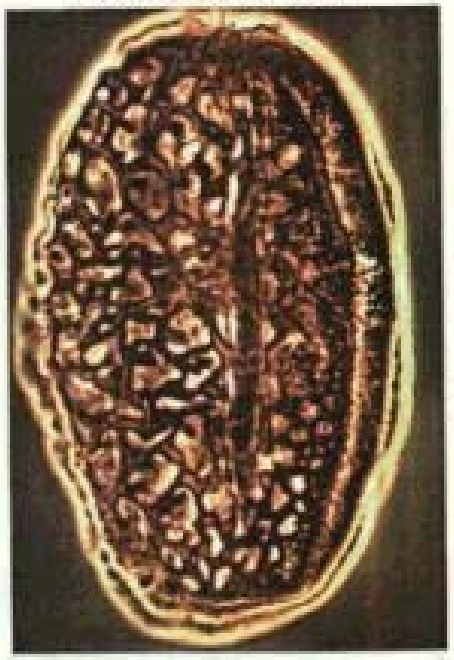
http://www.sunstar-solutions.com/sunstar/Why02/why.htm

PENTASULCATE SP. 1

PENTASULCATE SP. 1



LATE MIDDLE CARNIAN



TRISULCATE SP. 4

Sanmiguelia lewisii

Text-Fig. 6. Reconstruction of *Sanmiguelia lewisi* Brown.

http://www.ucmp.berkeley.edu/IB181/VPL/Cup/CupVGIII.html

http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup5.html

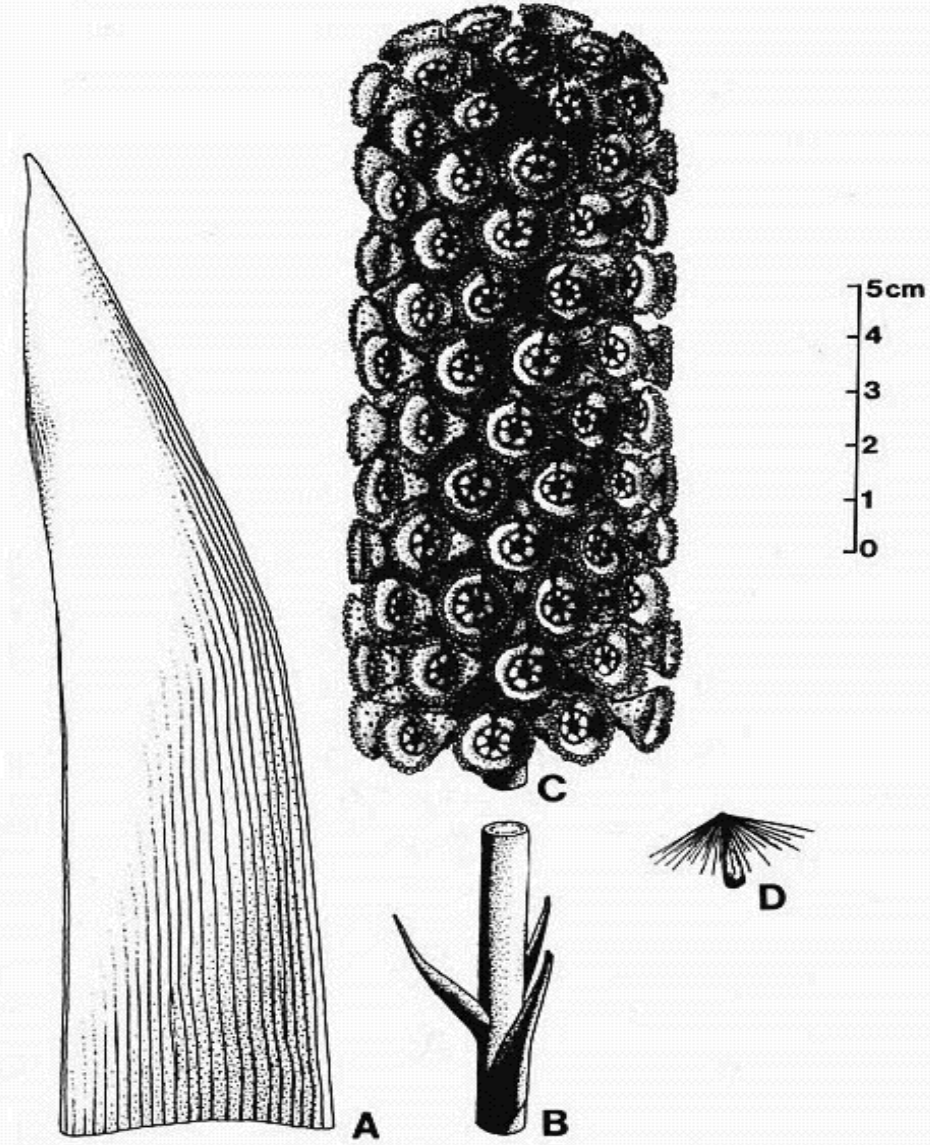
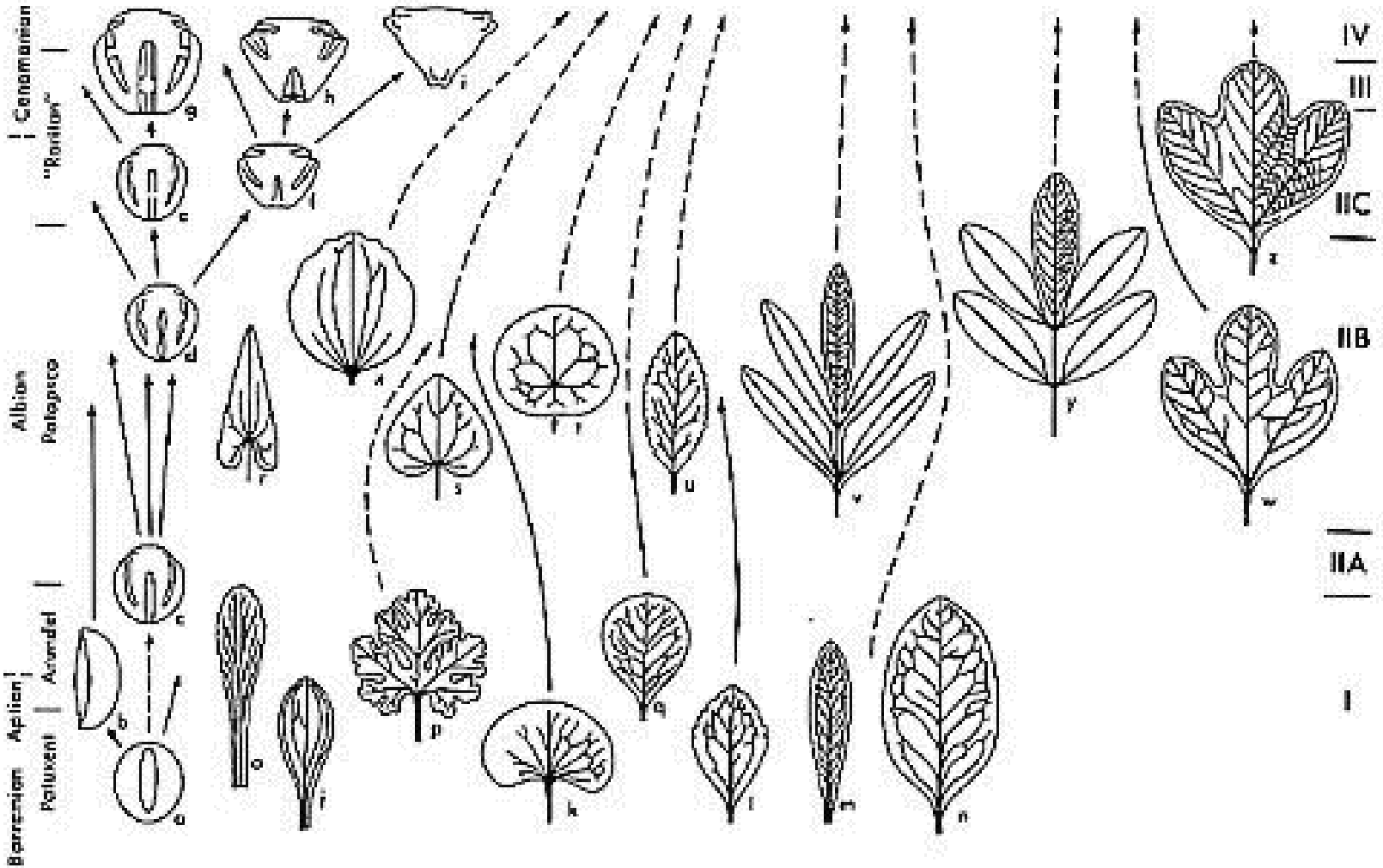


Figure 3.43. Reconstruction of *Archaestrobilus cupulanthus* and isolated organs related by morphology and association. (*A*) Associated leaf of *Pelourdea poleoensis*; most dichotomies occur near leaf base; cross-veins unknown. (*B*) Associated sterile lower part of strobilus. (*C*) Female strobilus (holotype). (*D*) Dispersed seed (Carnian, Dan River basin, NC) showing floater apparatus; same type of seed recovered from holotype.

Archaestrobilus cupulanthus

http://bcornet.tripod.com/Cornet96/Archaestrobilus.htm

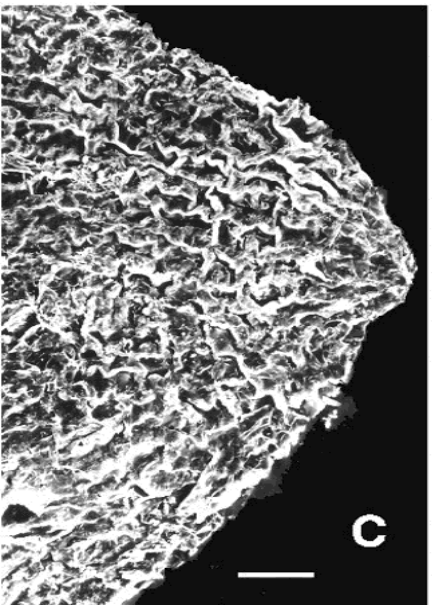
Lehtede ja tolmuterade areng Kriidiajastul

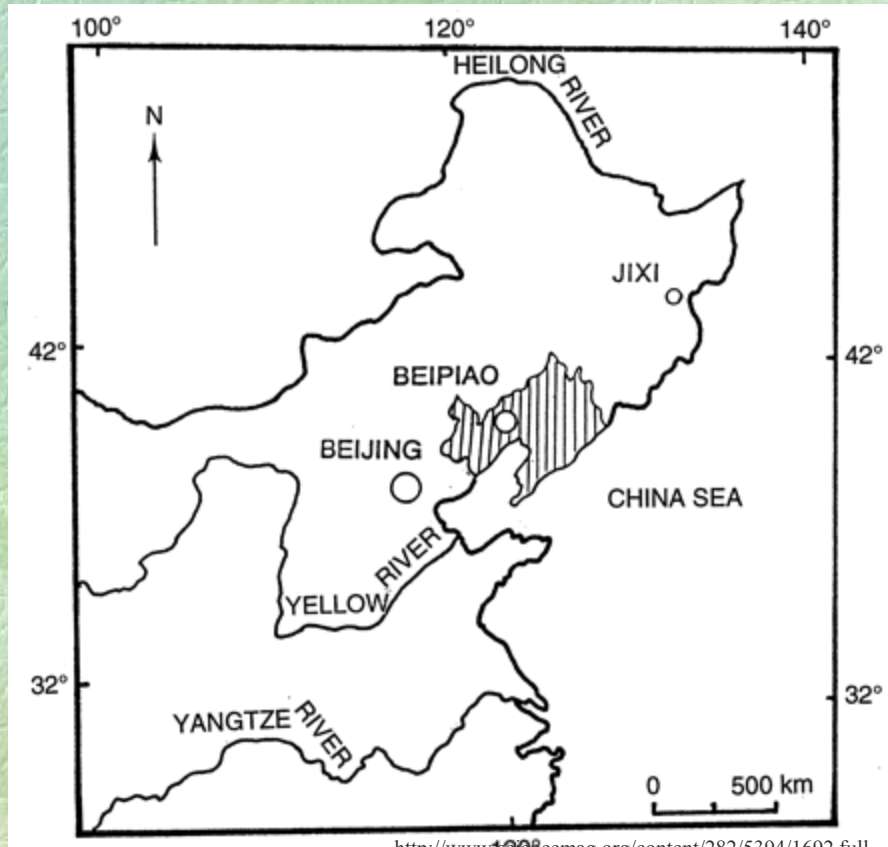


http://www.sunstar-solutions.com/AOP/SOW/paleobot.htm

Archaefructus liaoningiensis

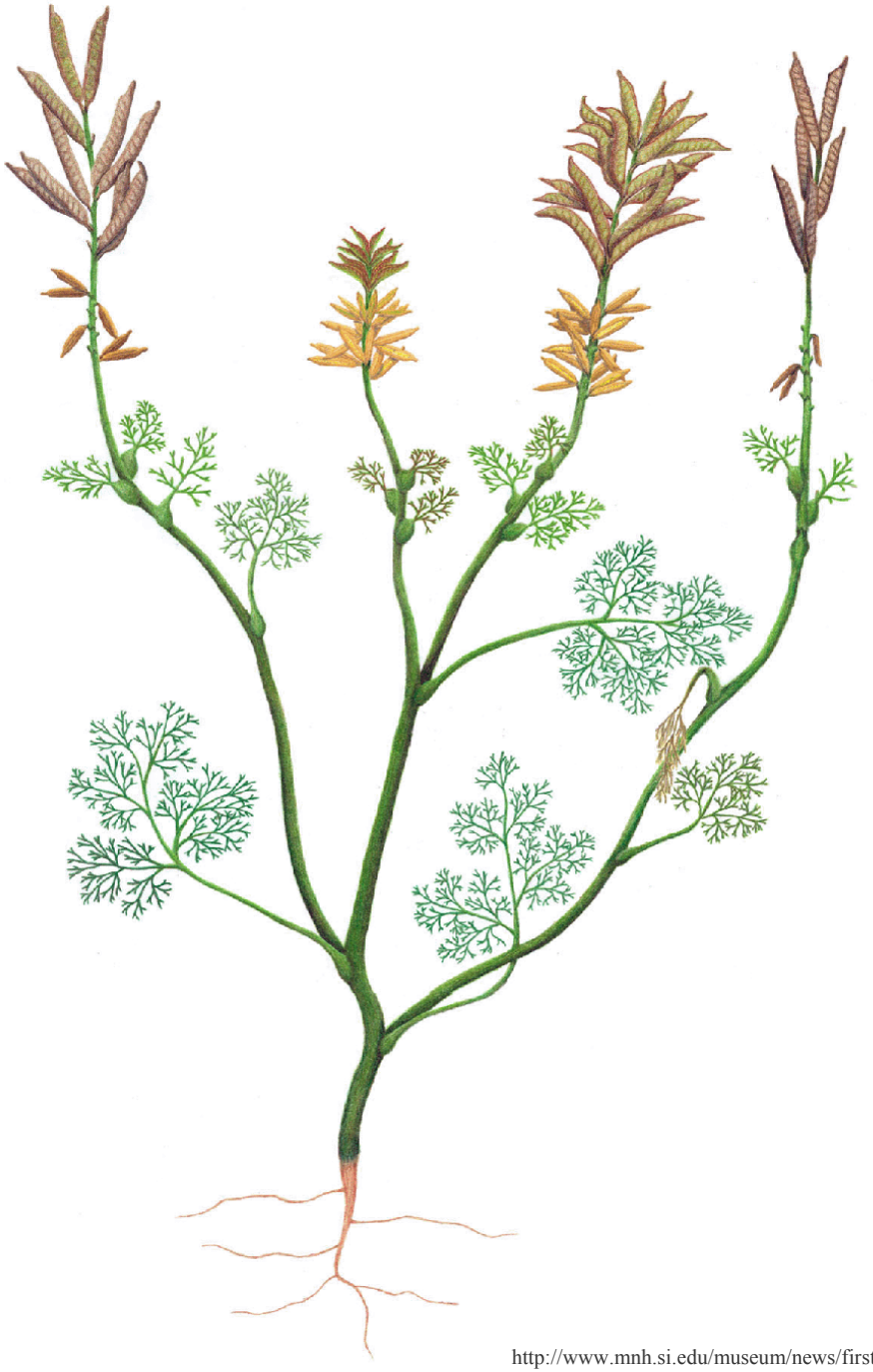
http://www.sciencemag.org/content/282/5394/1692/F2.expansion



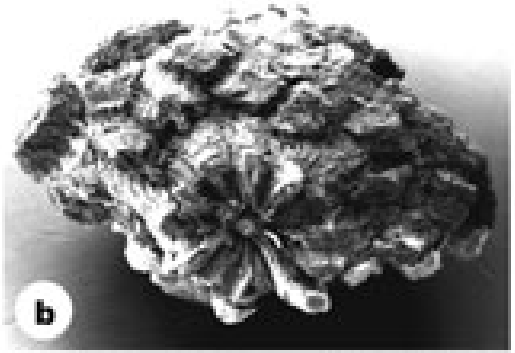


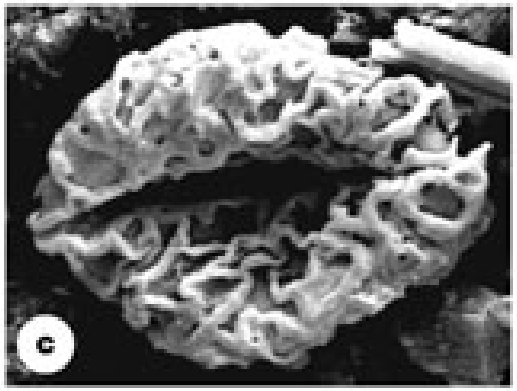
http://www.sciencemag.org/content/282/5394/1692.full

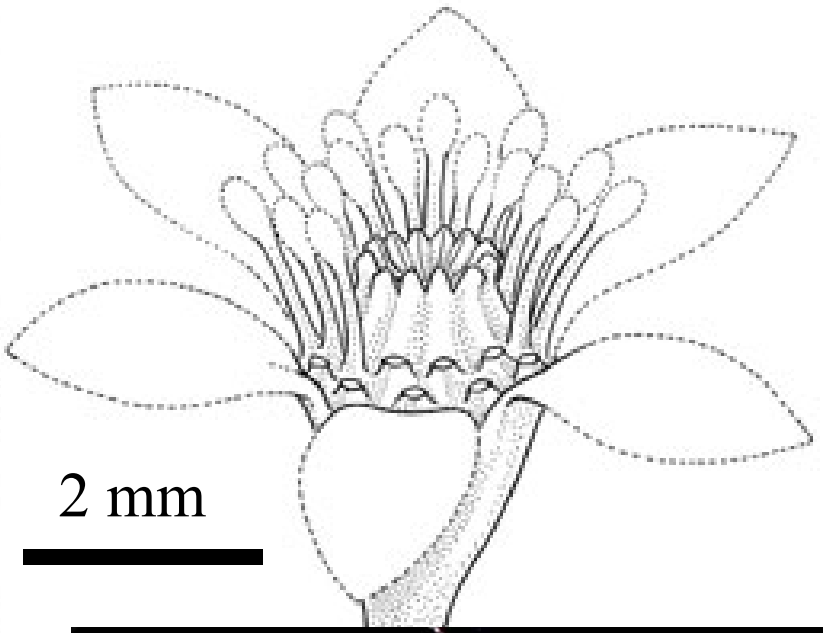
Archaefructus sinensis



http://www.mnh.si.edu/museum/news/firstflower/







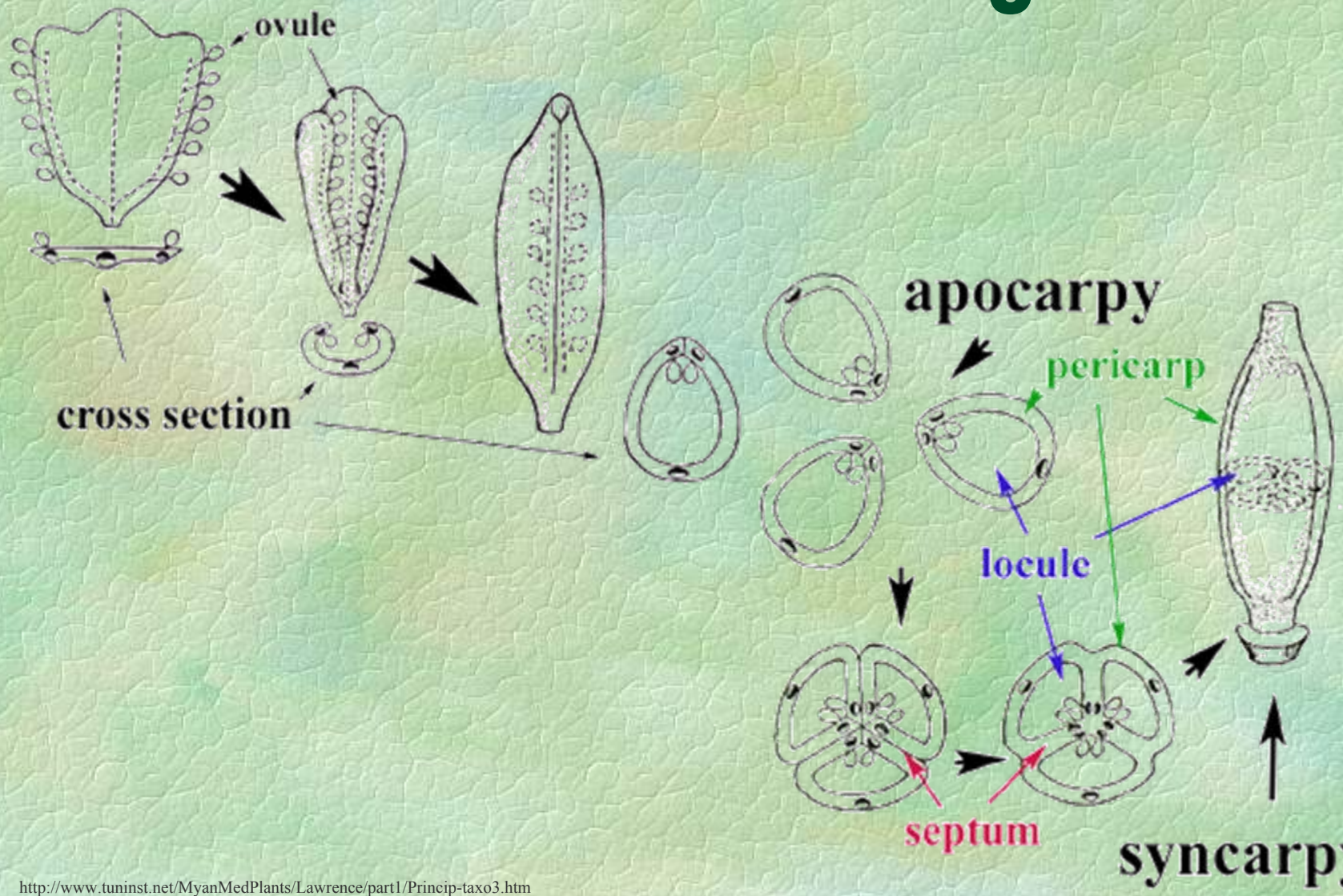
New fossil evidence--a 125 million-year-old water lily from Portugal

Friis, Pederson & Crane. 2001. Nature 410

Archae-anthus

http://www.flmnh.ufl.edu/paleobotany/

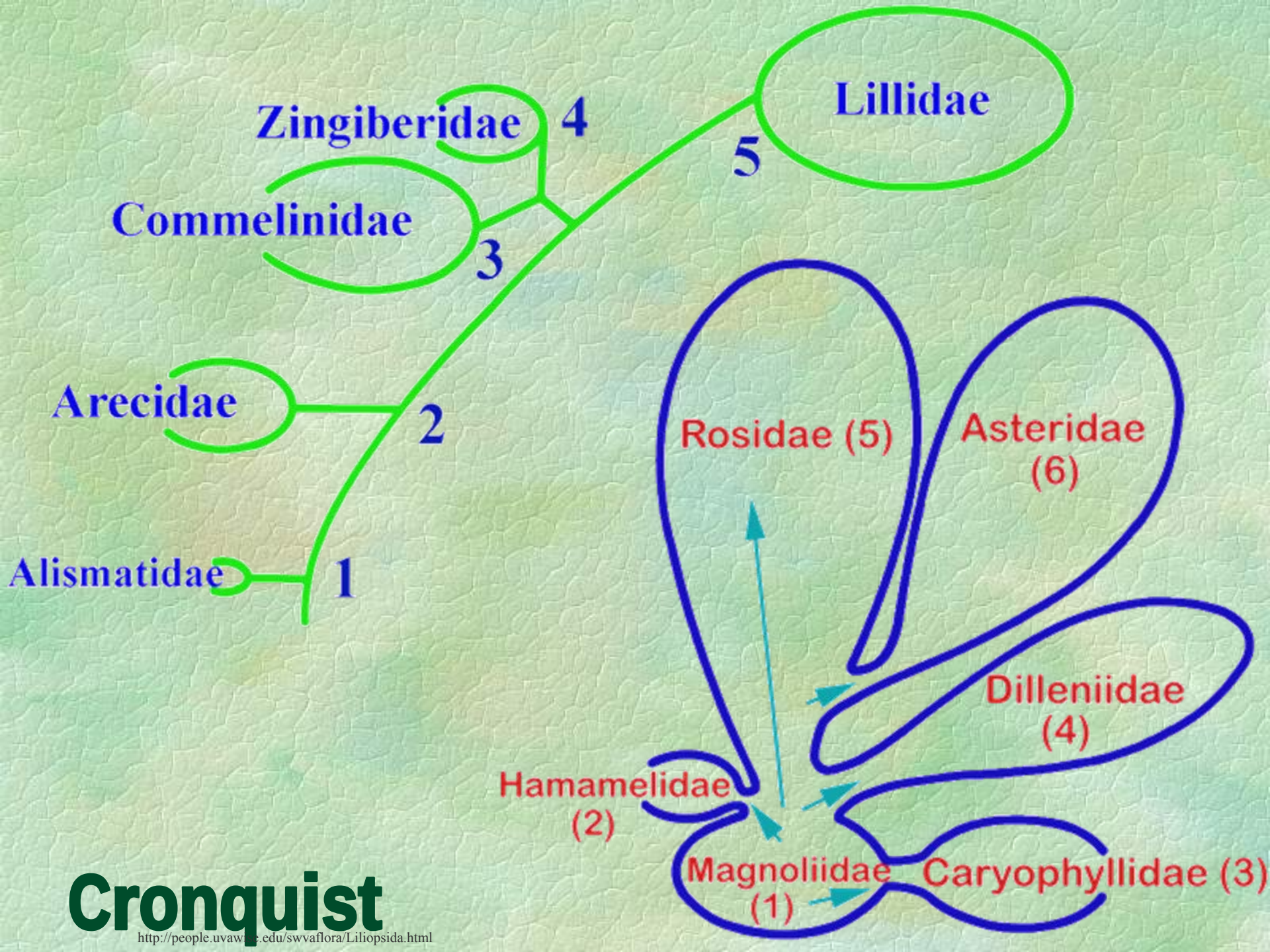
Emaka oletatav areng

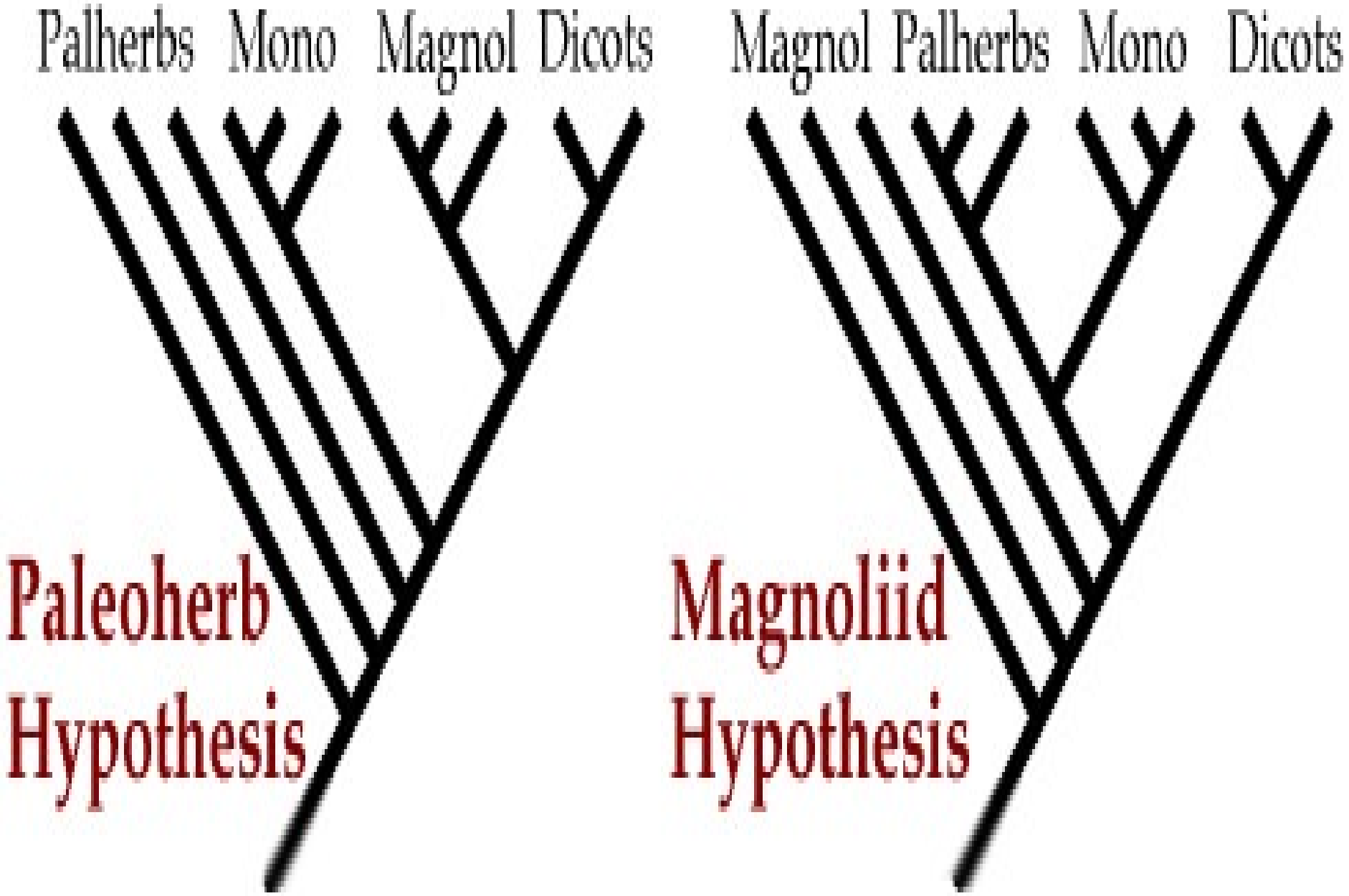


http://www.tuninst.net/MyanMedPlants/Lawrence/part1/Princip-taxo3.htm

Küsimused, millele fossiilid vastust ei anna

- Kas esivanem oli puu (*Magnoliidae*) või rohttaim (*Nymphaeales*)?
- Kas esimene oli suur “käbijas” õis (*Magnoliidae*) või väike väheseosaline õis (*Chloranthaceae*)?
- Kas enne oli lame tolmukas (lehest) või niitja varrega (teloom sünangiumiga)?


Zingiberidae
4
Lillidae
5
Commelinidae
3
Arecidae
2
Alismatidae
1
Rosidae (5)
Asteridae
(6)
Dilleniidae
(4)
Hamamelidae
(2)
Magnoliidae
(1)
Caryophyllidae (3)
Cronquist
http://people.uvawise.edu/swvaflora/Liliopsida.html



http://www.ucmp.berkeley.edu/anthophyta/anthophytafr.html

Plate I. Comparison of primitive and advanced floral features.

PRIMITIVE

Parts many
Parts indefinite in number
Parts free
Spiral arrangement of parts
Sepals, petals, stamens, carpels all present
Bisexual
Ovary superior
Symmetry regular (actinomorphic)

Magnolia campbellii

Nymphaea elegans

ADVANCED

Parts few
Parts definite in number
Parts fused
Whorled arrangement of parts
Loss of sepals, petals, stamens, or carpels
Unisexual
Ovary inferior
Symmetry irregular (zygomorphic)

Lamium maculatum

Helianthus decapetalus

Miks õistaimed nii edukad?

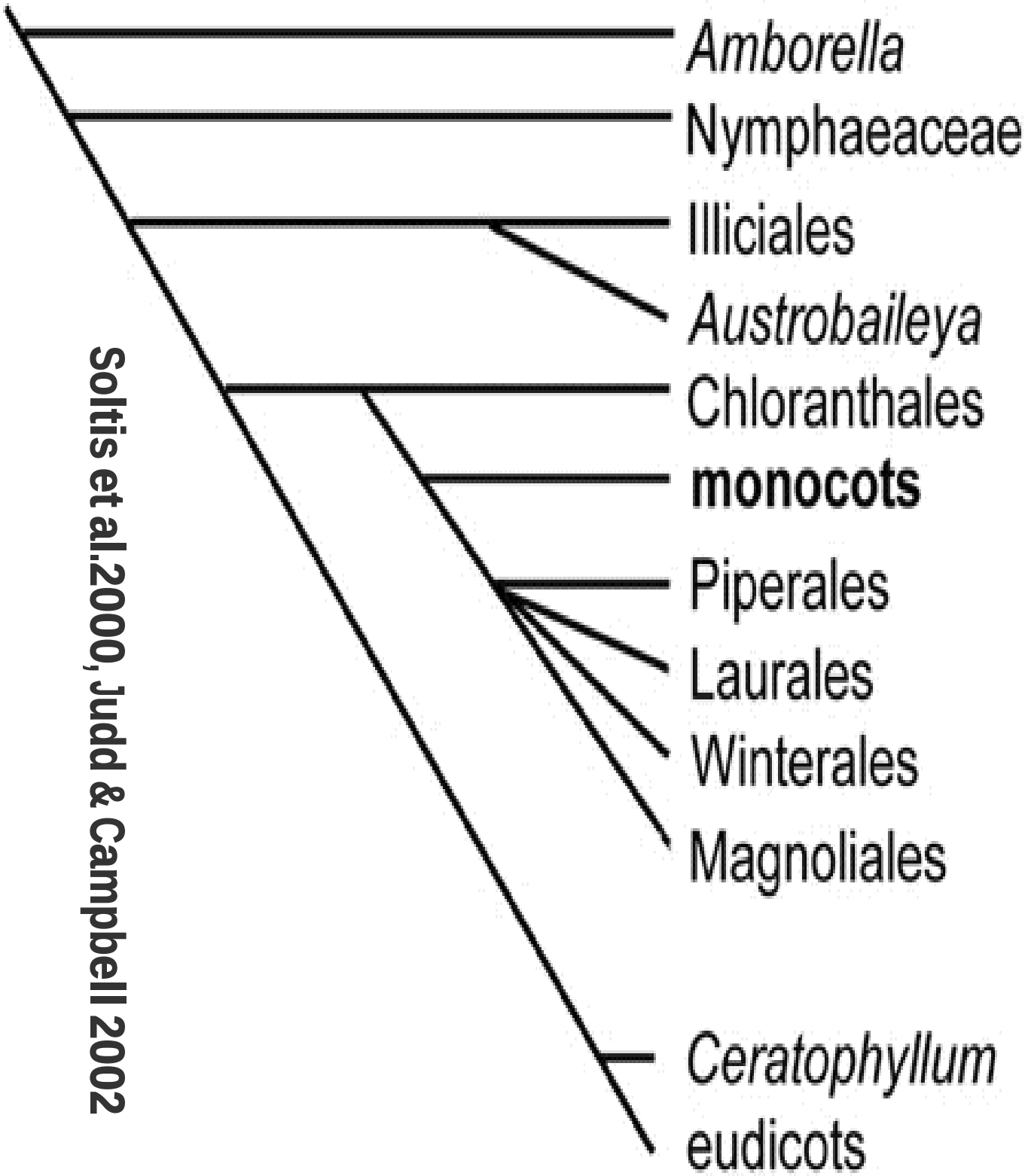
- Ca 250 000 liiki, 350 sugukonda
- Hästi kaitstud seeme
- Efektiivsed tolmeldamise ja leviku viisid
- Efektiivsed transpordi elemendid (trahheed)
- Heitlehisus
- Sekundaarsed metaboliidid
- Rohtne kasvuviis (ühe- ja mitmeaastased)

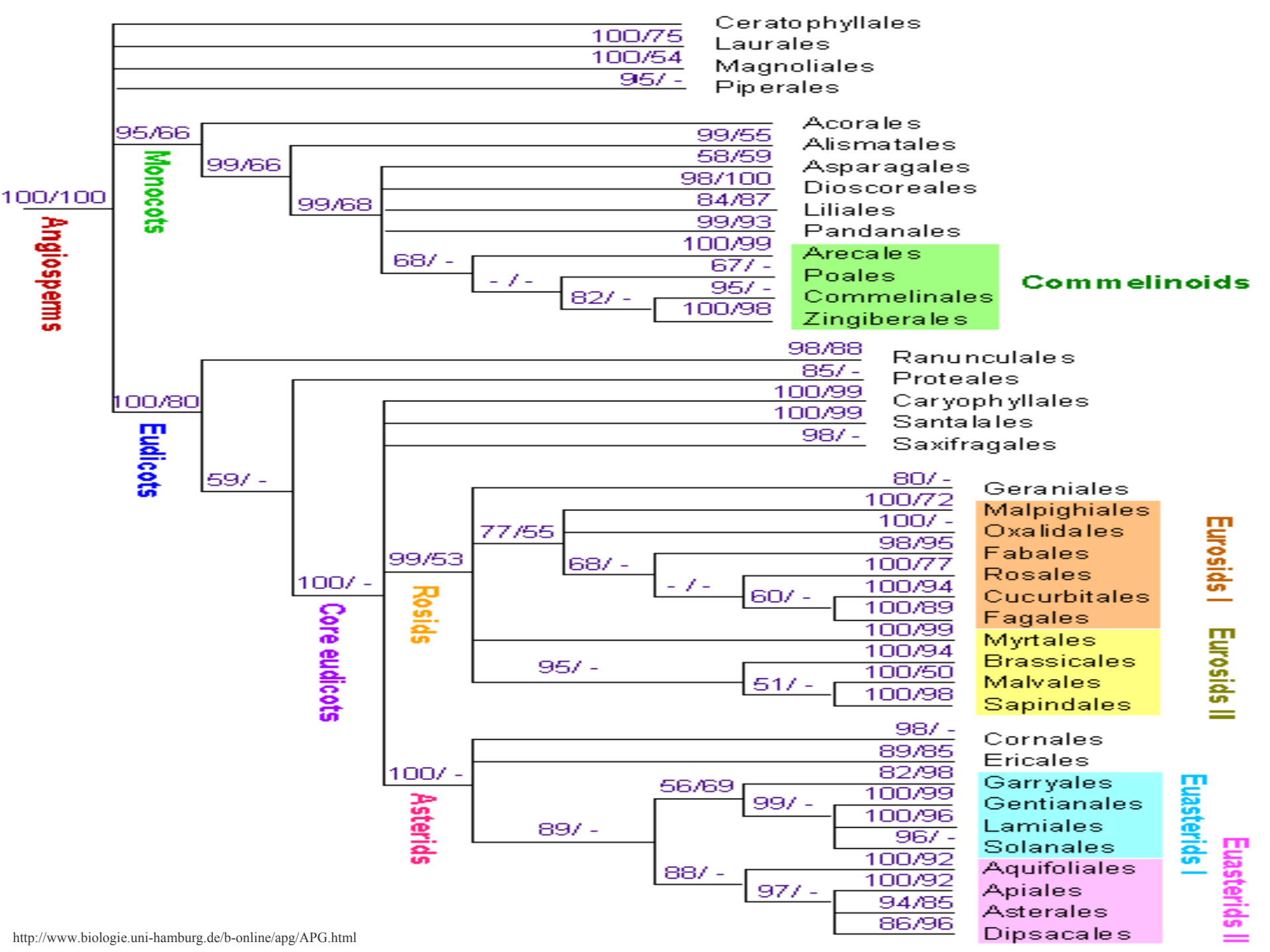
Angiosperm Phylogeny Group
APG

APG I 1998

APG II 2003

APG III 2009


Amborella
Nymphaeaceae
Illiciales
Austrobaileya
Chloranthales
monocots
Piperales
Laurales
Winterales
Magnoliales
Ceratophyllum
eudicots
Soltis et al.2000, Judd & Campbell 2002


Ceratophyllales
Laurales
Magnoliales
Piperales
Acorales
Alismatales
Asparagales
Dioscoreales
Liliales
Pandanales
Arecales
Poales
Commelinales
Zingiberales
Commelinoids
Ranunculales
Proteales
Caryophyllales
Santalales
Saxifragales
Geraniales
Malpighiales
Oxalidales
Fabales
Rosales
Cucurbitales
Fagales
Myrtales
Brassicales
Malvales
Sapindales
Cornales
Ericales
Garryales
Gentianales
Lamiales
Solanales
Aquifoliales
Apiales
Asterales
Dipsacales
Angiosperms
Monocots
Eudicots
Core eudicots
Rosids
Asterids
Eurosids I
Eurosids II
Euasterids I
Euasterids II
100/100
95/66
99/66
99/68
68/ -
- / -
82/ -
99/55
58/59
98/100
84/87
99/93
100/99
67/ -
95/ -
100/98
100/80
98/88
85/ -
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100/99
98/ -
59/ -
100/ -
99/53
77/55
68/ -
- / -
60/ -
80/ -
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98/95
100/77
100/94
100/89
100/99
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100/94
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89/85
82/98
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97/ -
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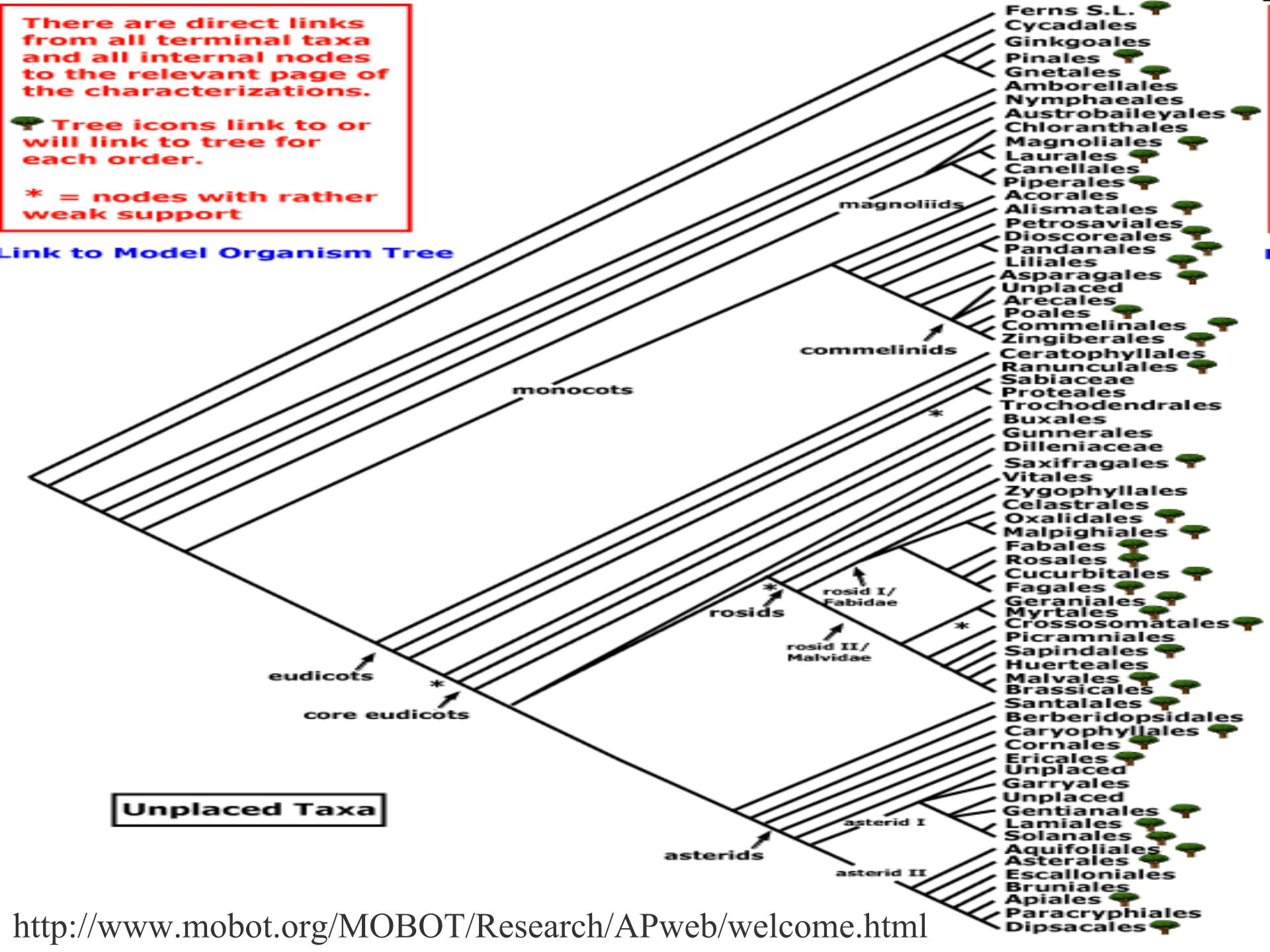
94/85
86/96



http://www.mobot.org/MOBOT/Research/APweb/welcome.html

Magnoliidae (Magnoliophyta, Magnoliopsida)

- Õis
- suletud viljalehed, tolmukad
- redutseerunud mikro-ja megagametofüüdid
- anatroopne seemnealge
- 2 integumenti
- tolmuterade idanemine emakasuudmel
- 8-tuumaline lootekott (modifikats. sekund.)
- kaheliviljastamine, endosperm
- sõeltorud saaterakkudega
- võrkjas roodumine

Ülemselts Amborallanae *Amborella trichopoda*

- Ülejäänute sõsarrühm
- Trahheed puuduvad
- Kahekojaline
- Tolmuterad ühepoorilised, eksiin pole ribiline
- Luuvili

Õistaimed v.a. *Amborellanae*

- Trahheed e sooned olemas
- Molekulaarsed tunnused

Ülemselts Vesiroosilaadsed

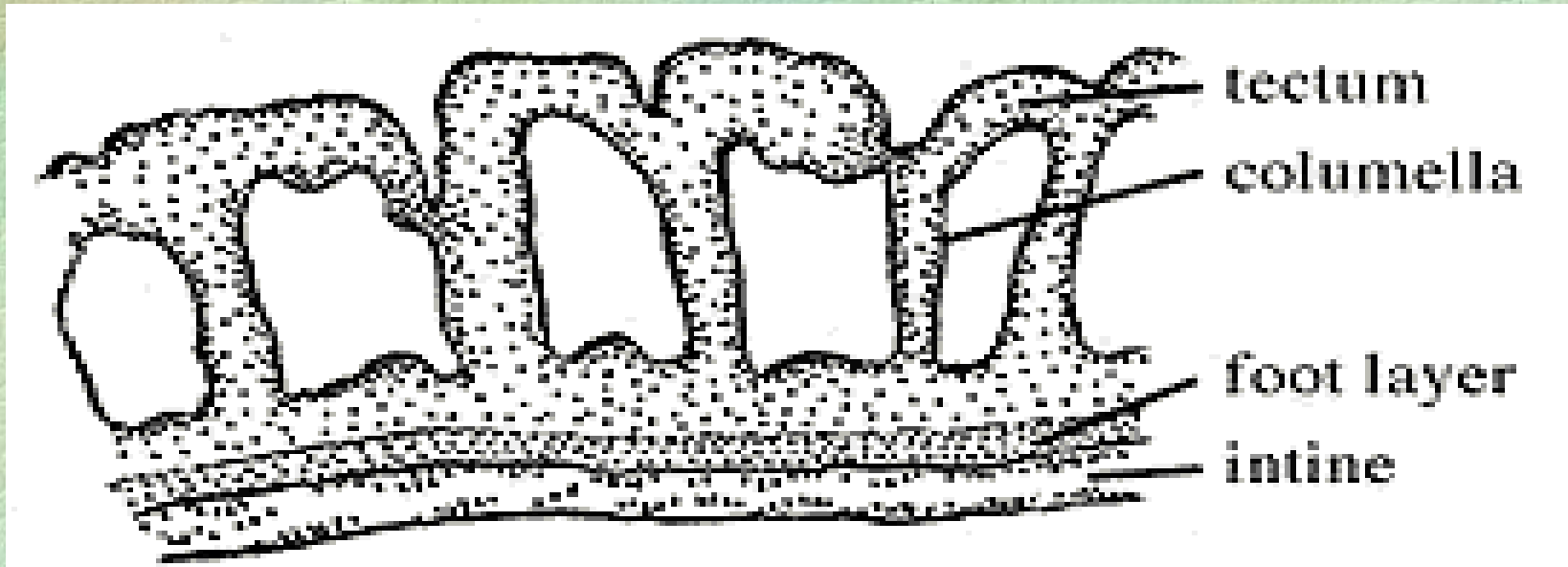
Nymphaeanae

- risoomsed veetaimed
- limakarvad
- suured pika raoga õied
- Seemned avanevad kaanega

http://www.scientific-web.com/en/Biology/Plants/Magnoliophyta/NupharLutea01.html

Kõik õistaimed v.a. Amborellanae ja Nymphaeanae

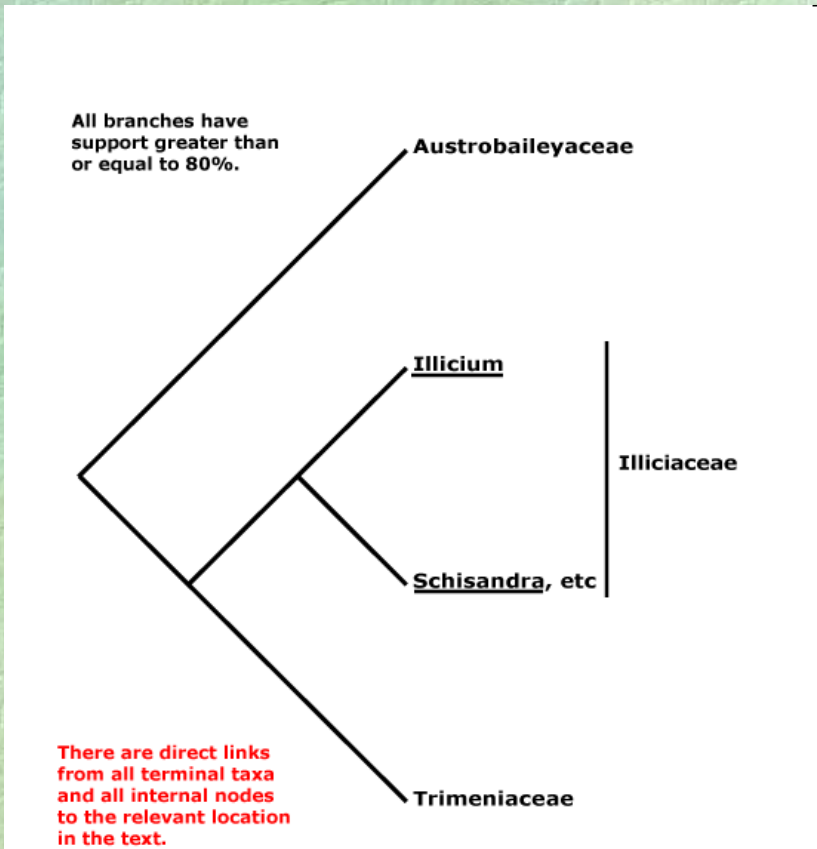
- Eeterlikud õlid (idioblastides)
- Tolmutera eksiin ribiline
- Trahheed skalaarsete paksendustega (P-tüüpi)
- Teatud deletsioon genoomis



http://www.ucmp.berkeley.edu/IB181/VPL/Cup/Cup5.html

Austrobaileyanae

- *Illiciaceae* - tähtaniisipuulised
- vili ühest viljalehest
- kõvenenud mesokarbi rakud



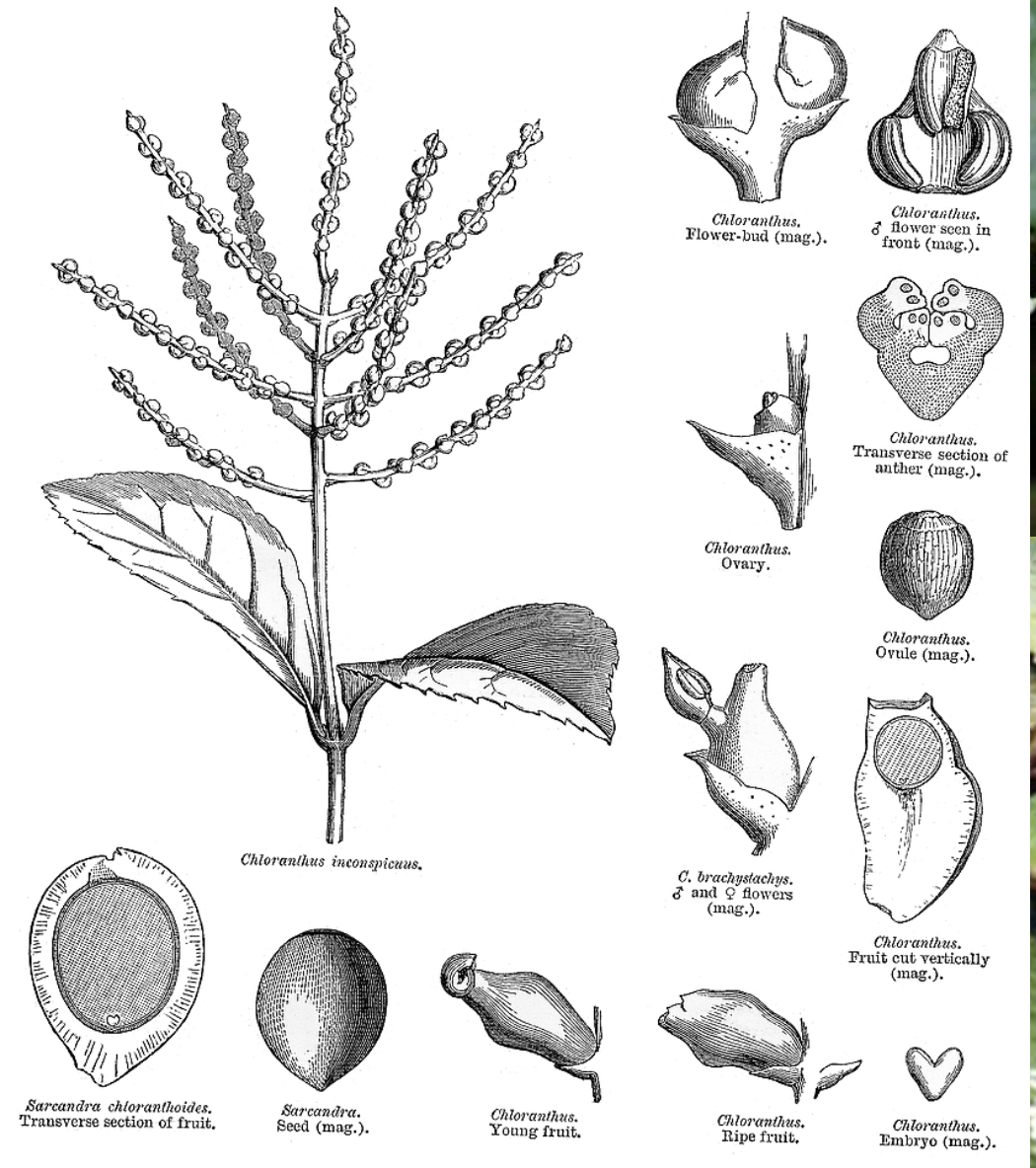
http://www.mobot.org/mobot/research/apweb/

Tähtaniisipuu *Illicium*

ÕISTAIMEDE TÜÜMRÜHM "(MESANGIOSPERMS; V.A. AMBORELLALES, NYMPHAEALES JA AUSTROBAILEYALES):

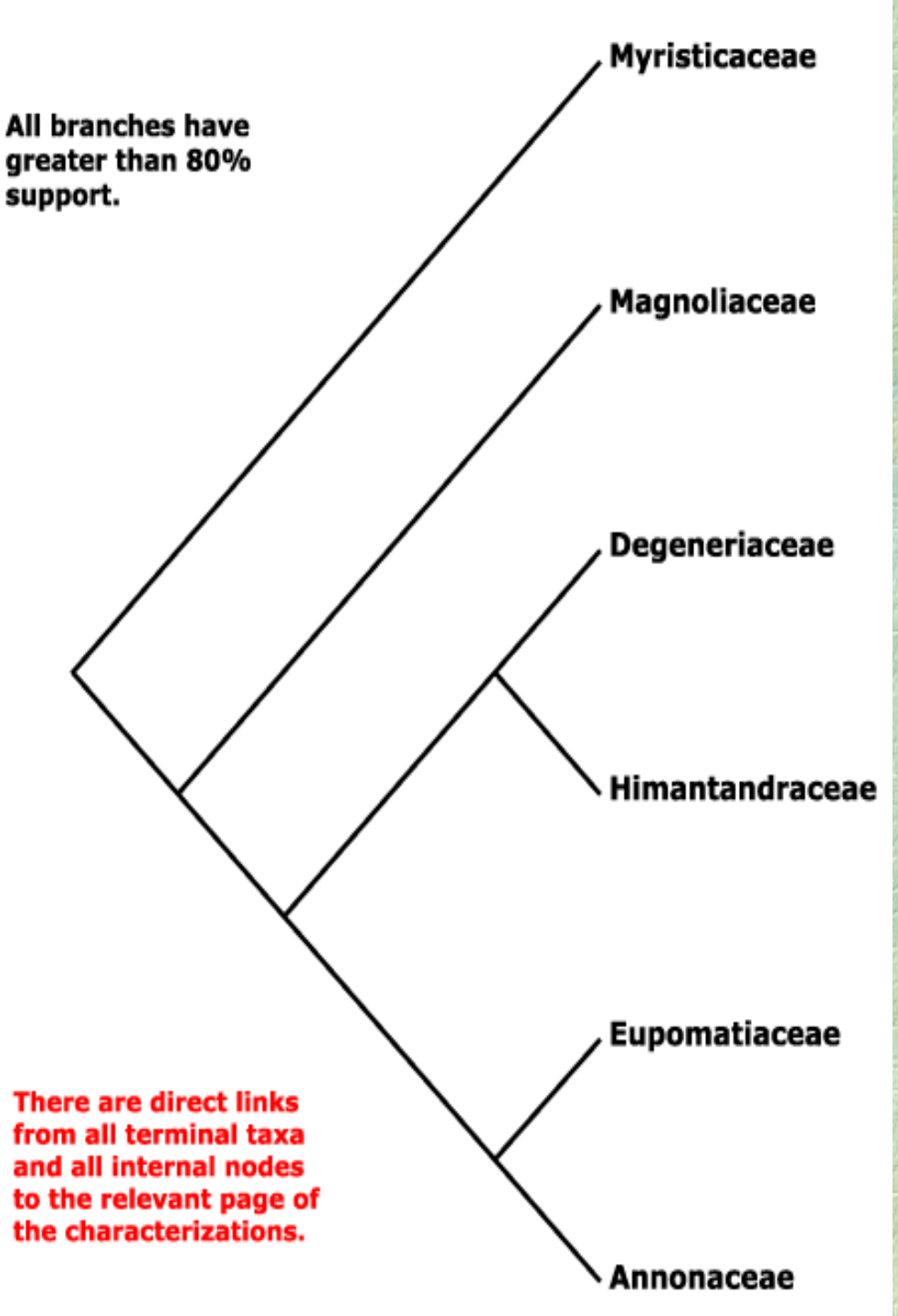
- Õiekate ja tolmukad ringidena
- Viljalehed kokkuvolditud, kokkukasvanud
- Lootekott ühe seemnealgmega, bipolaarne, 8-tuumaline
- Endosperm triploidne
- Vesikulaar-arbuskulaarne mükoriisa

"Asetamata" selts *Chloranthales*



Ülemselts magnoolialaadsed *Magnolianae*

- Terved leheservad
- Tolmukaid palju, spiraalselt
- Seemnealgme iseärasused
- MAGNOLIALES
- LAURALES
- CANELLALES
- PIPERALES

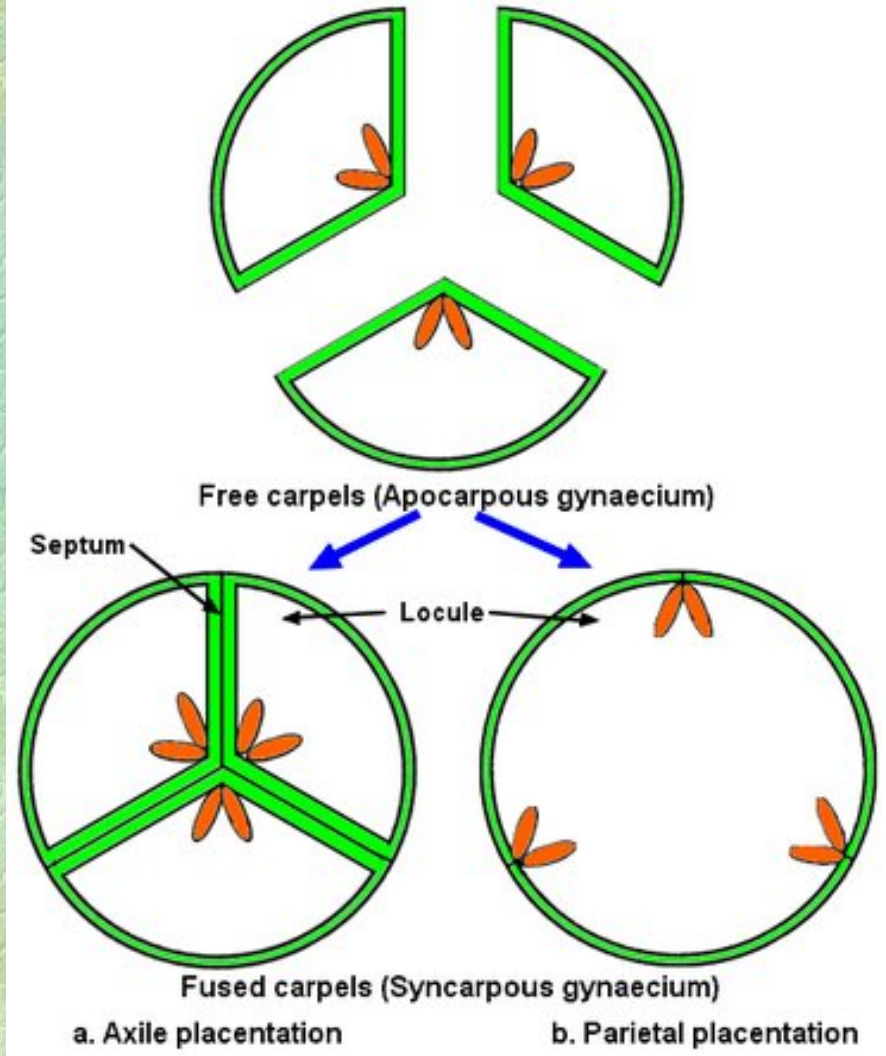


Magnoolia-laadsed *Magnoliales*

http://www.mobot.org/mobot/research/apweb/

Magnoliales

- Puittaimed
- Eeterlikud õlid, alkaloidid
- Suured üksikud õied
- Palju tolmukaid, spiraalselt
- Palju viljalehti
- Apokarpne sigimik



http://www.botanique.org/2/reproduction-in-angiosperms/

Magnoliaceae

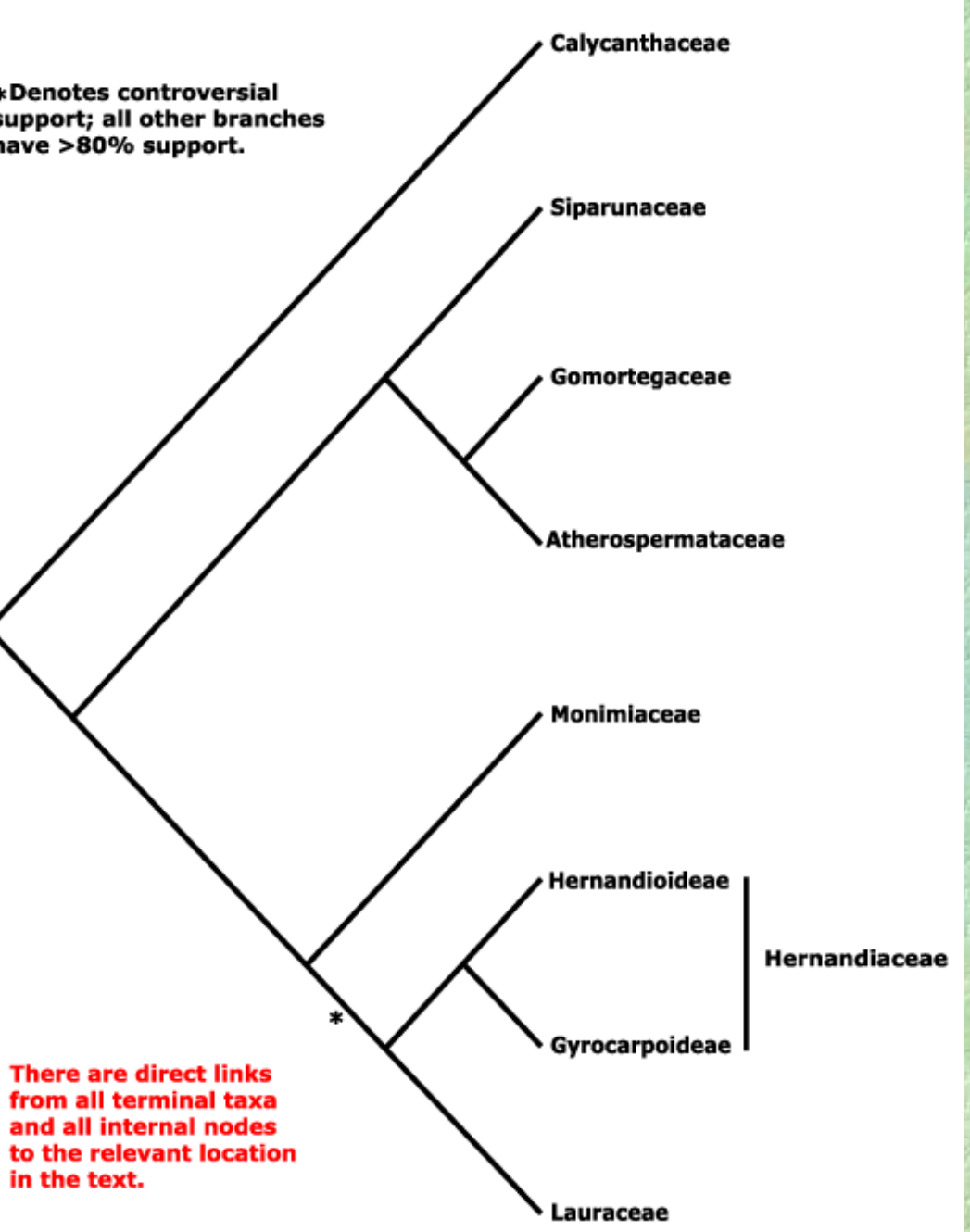
Magnolia grandiflora

Liriodendron tulipifera

Annonaceae

Annona muricata

Cananga odorata



Loorbeerlaadsed *Laurales*

http://www.mobot.org/mobot/research/apweb/

Loorberilaadsed *Laurales*

- Puittaimed
- Eeterlikud õlid
- Väikesed ühesugulised õied
- Tolmukad kolmekaupa ringides
- Üks viljaleht
- Apokarpne sigimik

Lauraceae

Cinnamomum

Lauraceae

Persea americana

Laurus nobilis

Pipralaadsed *Piperales*

- Rohttaimed või põõsad
- Ümarad eeterlike õlide rakud
- Alkaloidid
- Väikesed õied
- Tolmukad kolmetiselt
- Sõlmekohad sageli paisunud
- **5 sugukonda**

Piperaceae

Piper nigrum

Peperomia

Aristolochiaceae - tobiväädilised

Aristolochia fimbriata

Asarum europaeum

Kardheinalaadsed + üheidulehelised

- Peajuur nõrk
- Varre juhtkimbud suletud (interfastsikulaarne kambium puudub)

Kardheinalaadsed + päriskaheidulehelised

- Tolmukapea ja tolmukaniit diferentseerunud
- Eeterlikud õlid kadunud

Kardheinalaadsed Ceratophyllanae

- Veetaimed
- Eeterlikud õlid puuduvad
- Juured puuduvad
- Trahheed puuduvad
- Õhulõhed ja kutiikula puuduvad
- Endosperm puudub
- Lehed männastes, ogalishambulised
- Õied väikesed, ühesugulised
- Vili ogaline seemnis

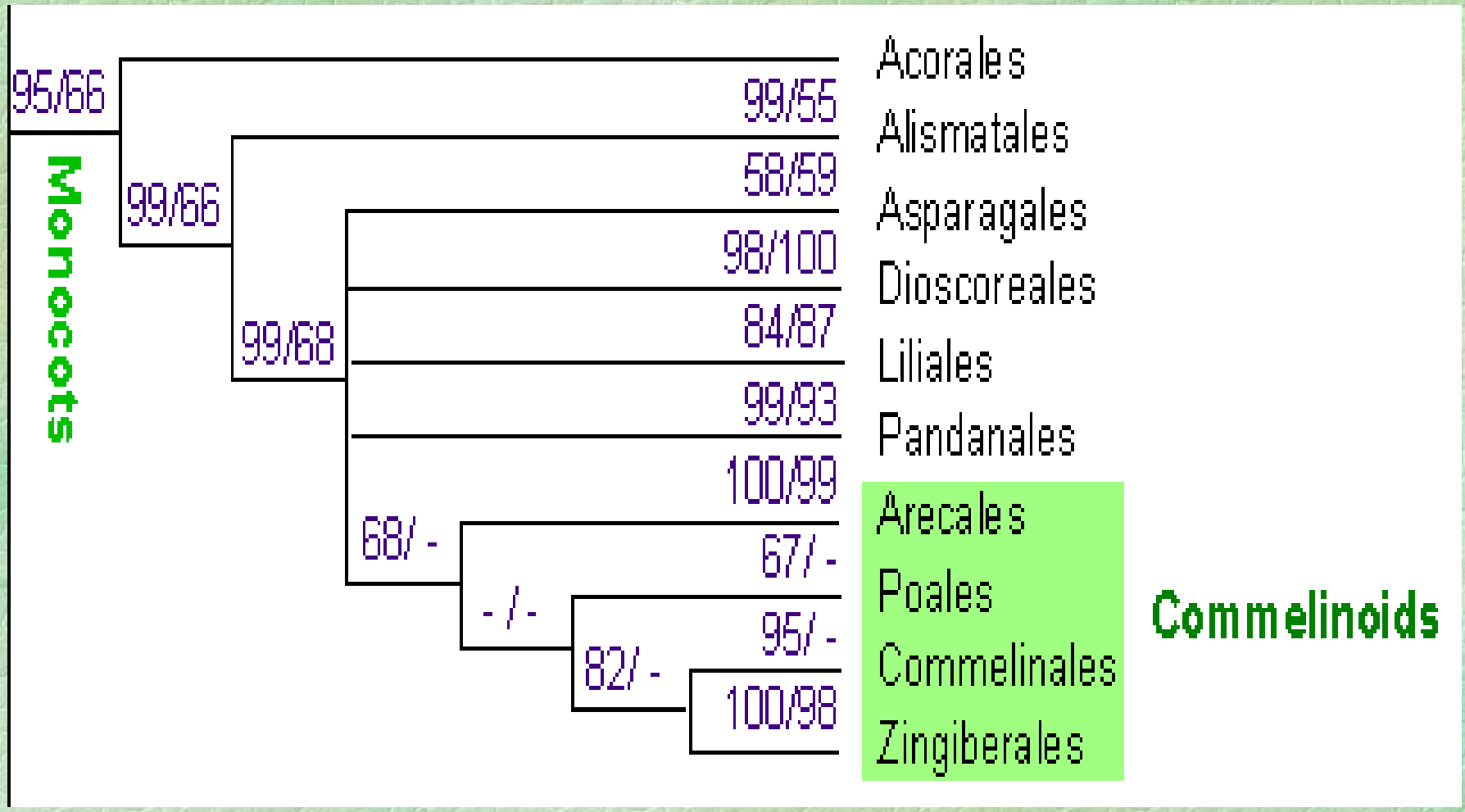
Räni-kardhein
Ceratophyllum demersum

Õistaimed III - üheidulehelised

Täpsustatud geokronoloogiline skaala (Mat)

- Kvaternaar 2,588
- Neogeen 23,03
- Paleogeen 65,5+-0,3
- Kriit 145,5+-4,0
- Juura 199,6+-0,6
- Triias 251+-0,4
- Perm 299+-0,8
- Karbon 359,2+-2,5
- Devon 416,0+-2,8
- Silur 443,7-+1,5
- Ordoviitsium 448,3+-1,7
- Kambrium 542+-1,0
- Ediacara - u. 635

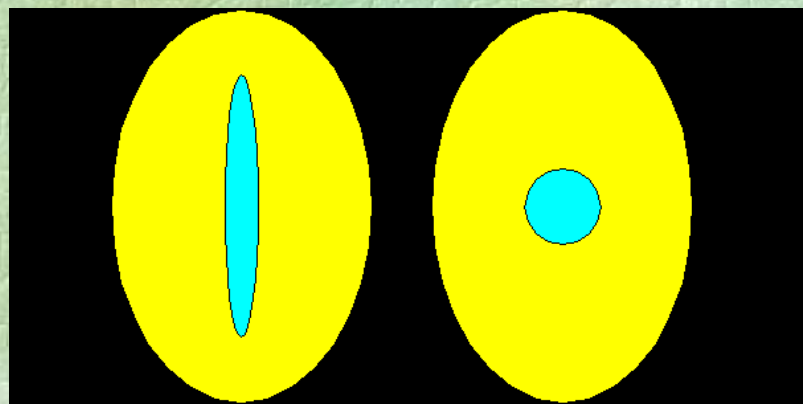
Ülemselts liilialaadsed *Lilianae* (üheidulehelised)



Lilianae (üheidulehelised)

- Üks iduleht
- Narmasjuurestik
- Juhtkimbud hajusalt, suletud
- Lehed rootsuta, rööp- või kaarroodsed
- Õied kolmetised, pentatsüklilised

  $\mathbf{P_{3+3}\ A_{3+3}\ G_3}$
- Sigimik nektaariumidega vaheseintel
- Ühekaviline, monosulkaatne tolmutera
- 1/4 õistaimedest



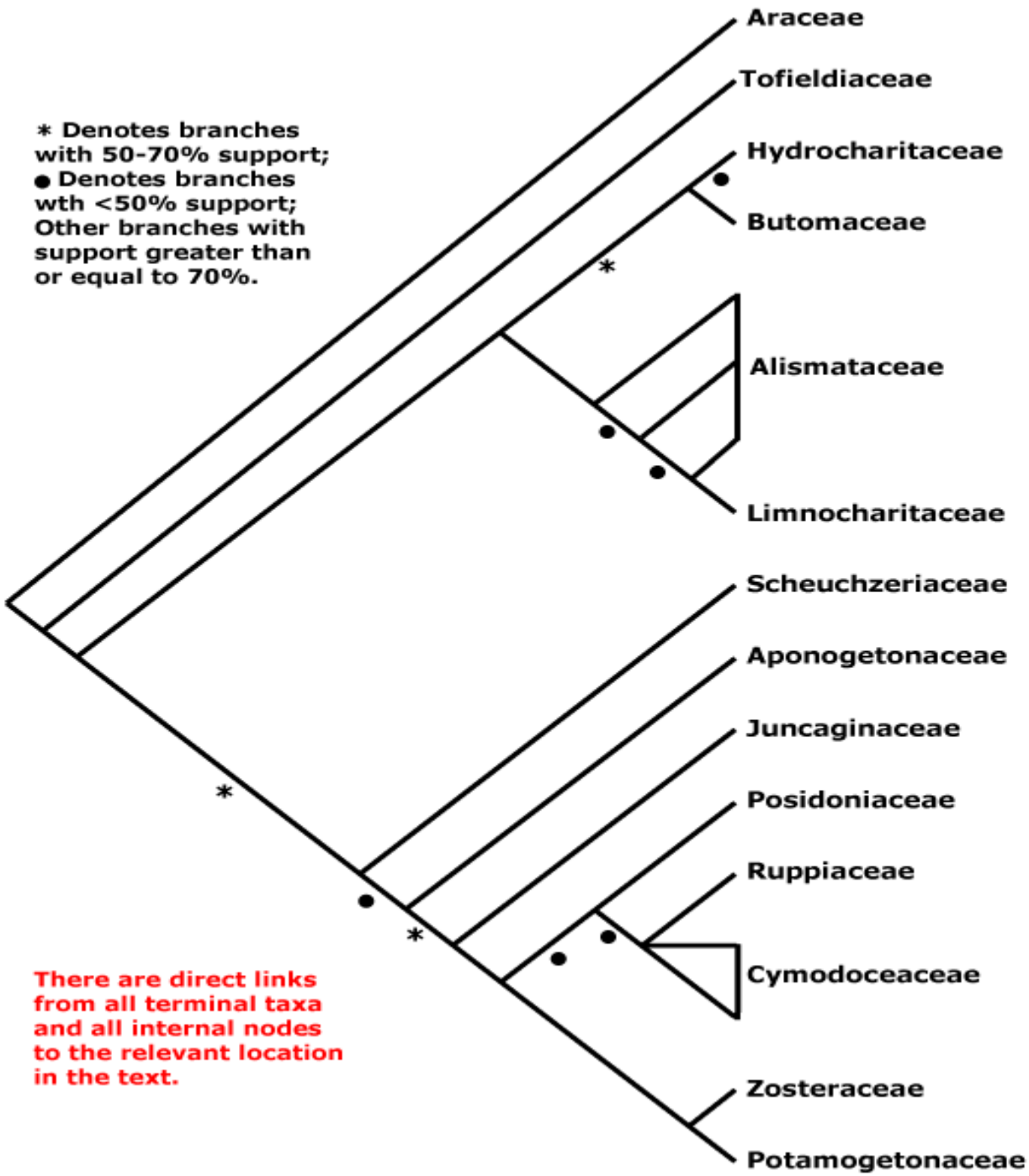
http://www.pollen.mtu.edu/glos-gtx/glos-p3.htm

Kalmuselaadsed *Acorales*

- Õisik tihe tähk, lateraalselt
- Magusalt lõhnavad
- Lehed saduljalt, kahes reas

Kalmus
Acorus calamus

Konnarohu-laadsed *Alismatales*



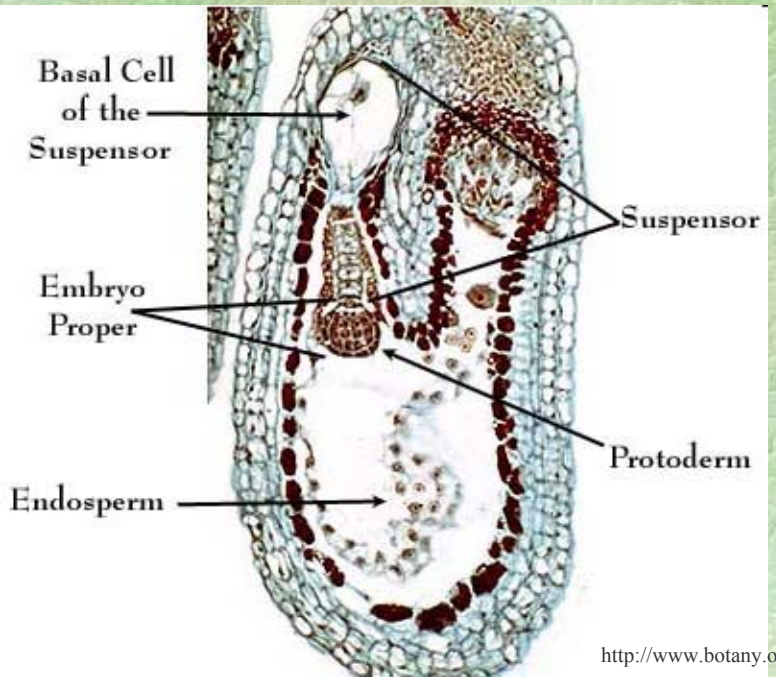
http://www.mobot.org/mobot/research/apweb/

Konnarohulaadsed *Alismatales*

- Veelised või poolveelised taimed
- Õied pööristes või tähkades
- Tolmukaid ja viljalehti palju
- Endosperm helobiaalne, valminud seemnetes puudub
- Mükoriisa puudub

Endospermi tüübid

- Nukleaarne
- Tsellulaarne
- Helobiaalne



http://www.botany.org/plantimages/ImageData.asp?IDN=20-011

Konnarohulised Alismataceae

Sagittaria sagittifolia

Alisma plantago-aquatica

Võhalised Araceae

Amorphophallus campanulatus

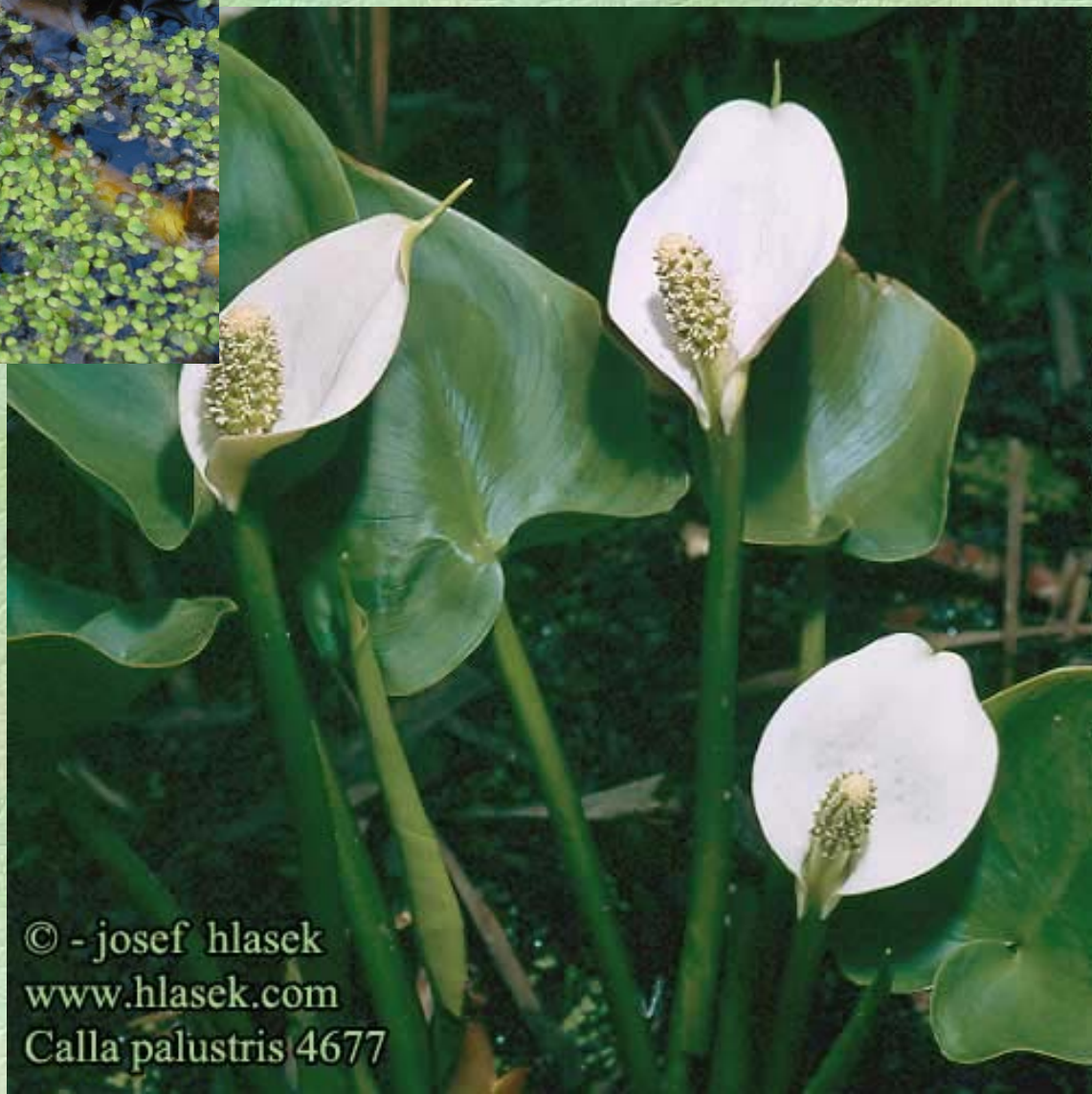
Zantedeschia aethiopica

Võhalised Araceae

Philodendron

Dieffenbachia

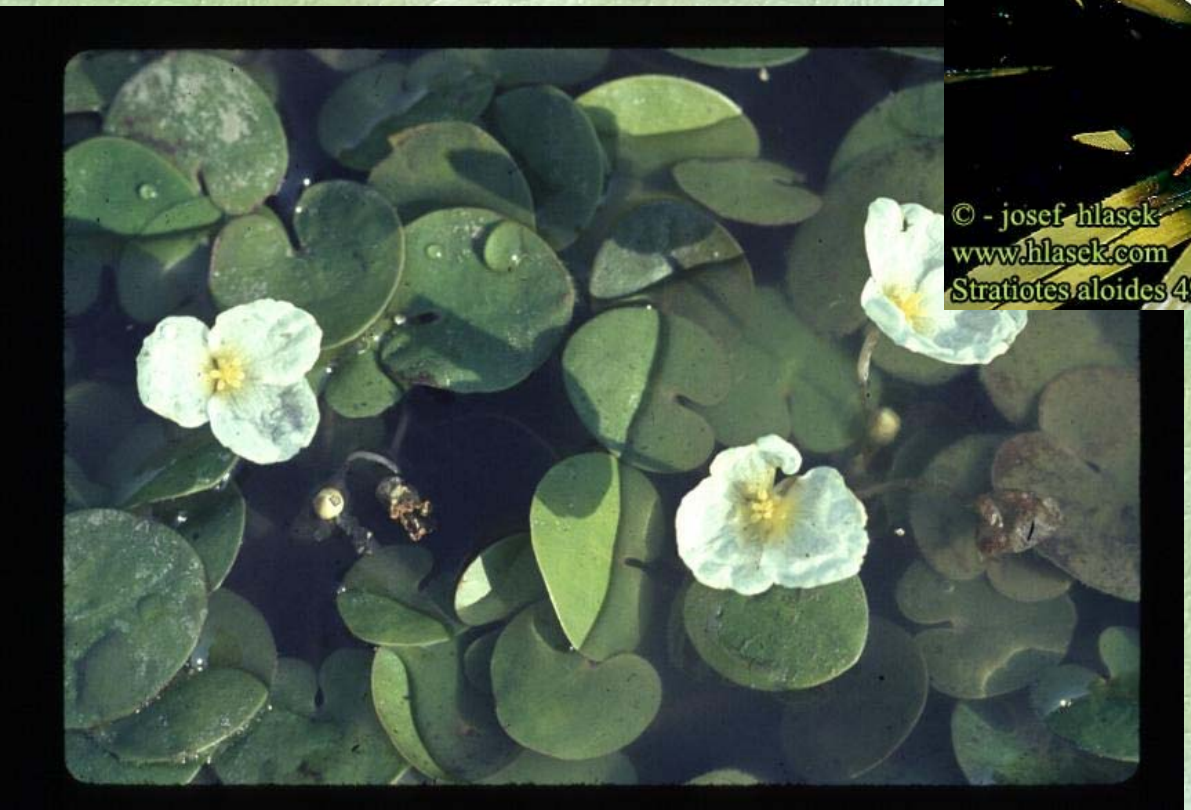
Calla palustris - soovõhk



Lemna minor – väike lemmel

Kilbukalised *Hydrocharitaceae*

Konnakilbukas-
Hydrocharis morsus-ranae



Vesikarikas –
Stratiotes aloides

Kilbukalised *Hydrocharitaceae*

Kanada vesikatk –
Elodea canadensis

Meri-näkirohi-
Najas marina

Butomaceae

Butomus umbellatus

Scheuchzeriaceae

Scheuchzeria palustris

Penikeelelised- *Potamogetonaceae*

Juncaginaceae

Triglochin palustre

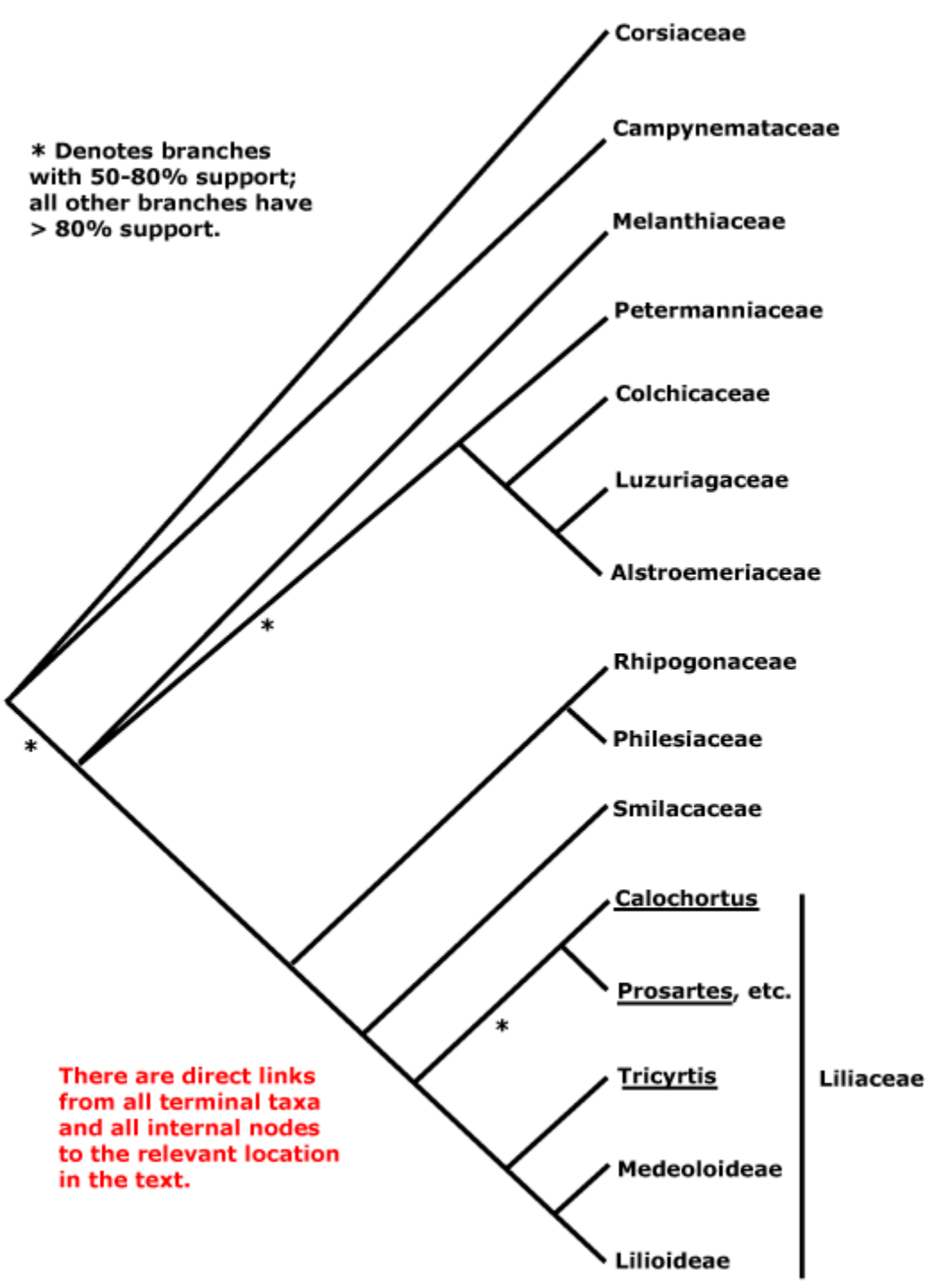
T. maritimum

Ruppiaceae, Zosteraceae, Zannichelliaceae, Tofieldiaceae

Pikk merihein
Zostera marina

Lemmelill
Tofieldia calyculata

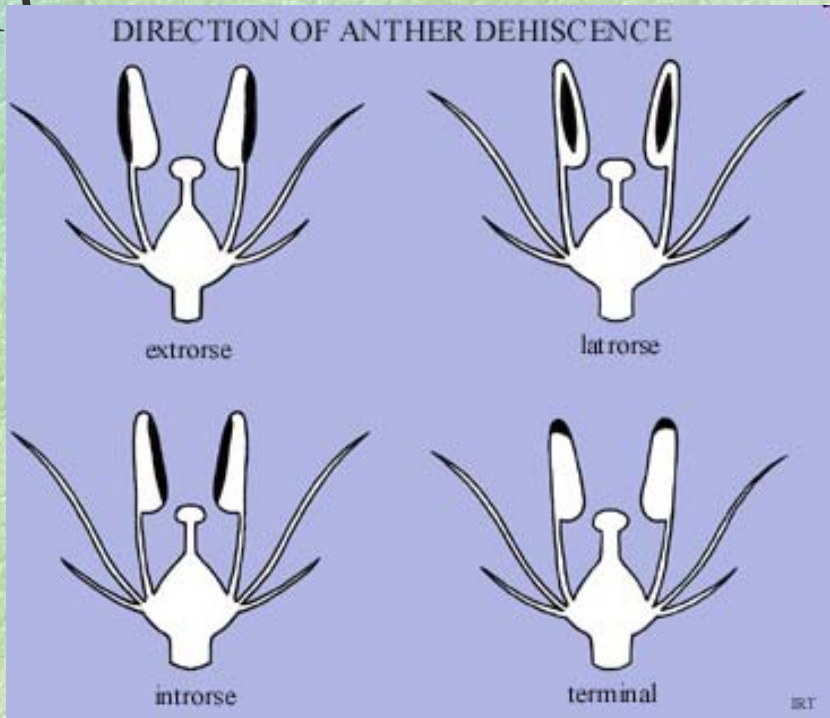
Liilialaadsed
Liliales



http://www.mobot.org/mobot/research/apweb/

Liilialaadsed *Liliales*

- Õiekattelehed basaalsete nektaariumidega
- Tolmukad ekstrorssed
- Geofüüdid (risoom, sibul)



http://www.environment.gov.au/biodiversity/abrs/online-resources/glossaries/vascular/anthdire.html

Liilialised

Kirju liilia
Lilium martagon

Metstulp *Tulipa sylvestris*

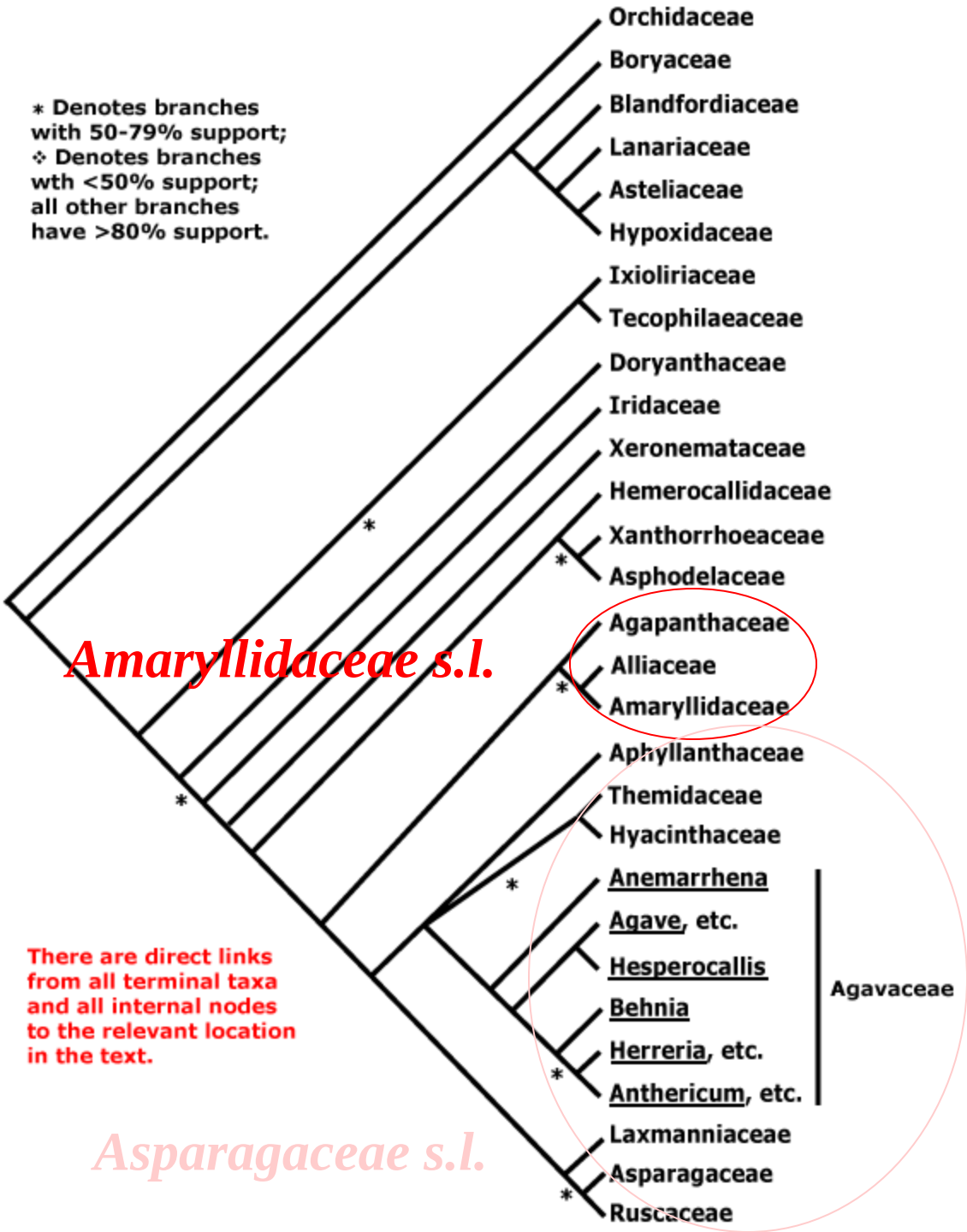
Kollane kuldtäht *Gagea lutea*

Sügislillelised *Colchicaceae*

Melanthiaceae

Paris quadrifolia

Aspari-laadsed *Asparagales*



http://www.mobot.org/mobot/research/apweb/

Asparilaadsed *Asparagales*

- Geofüüdid: sibulad, mugulad või risoomid
- **Seemnekest must**, sisaldab **fütomelaani**
- Nektaariumid sigimiku seintes
- Helidoonhape

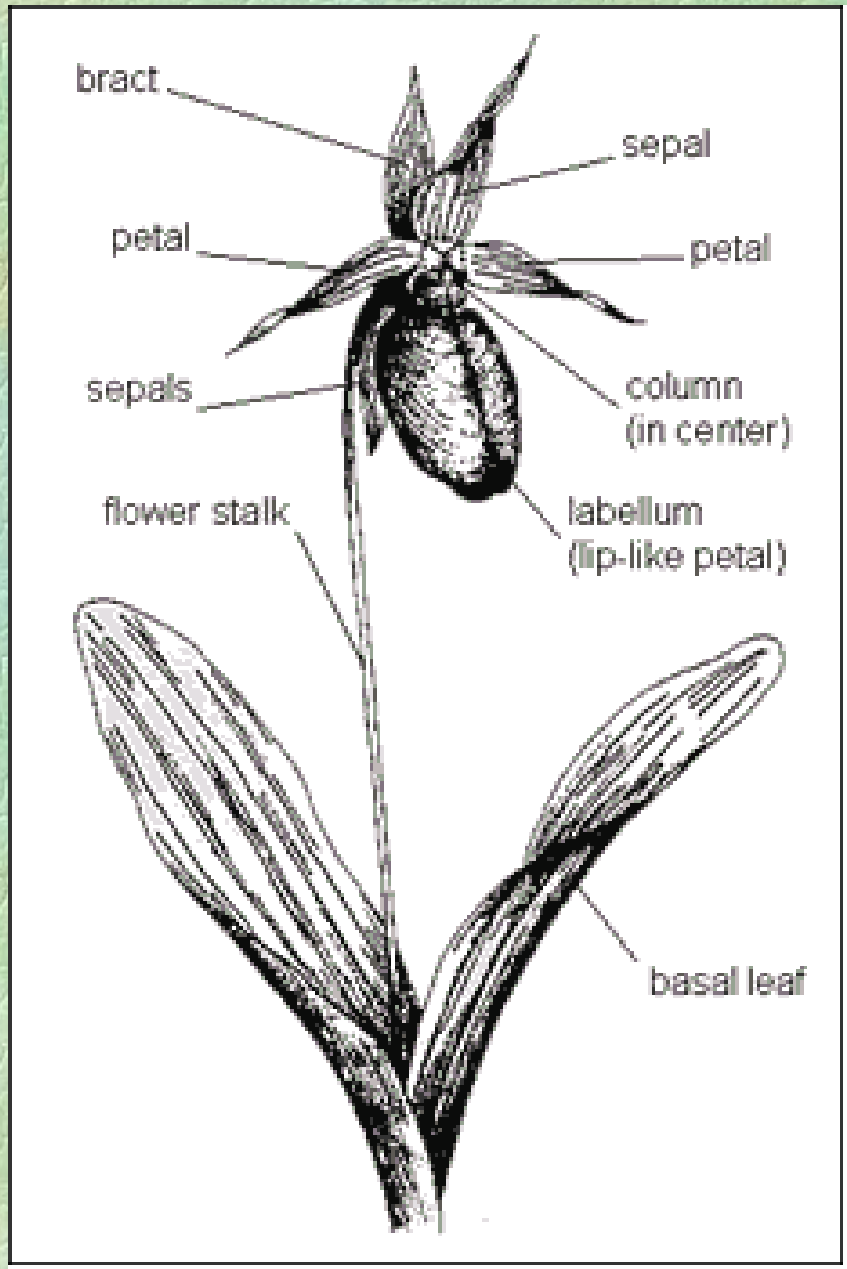
Käpalised *Orchidaceae*

Vanilla

Dendrobium

Käpalised *Orchidaceae*

- **Eestis:**
- *Dactylorhiza 10, Orchis 4, Epipactis 3*
- *Platanthera, Listera, Cephalantera, Gymnadenia 2*
- Veel 12 ühe liigiga esindatud perekonda



Pruunikas pesajuur
Neottia nidus-avis

Kahelehine käokeel
Platanthera bifolia

Kaunis kuldking *Cypripedium calceolus*

Saaremaa sõrmkäpp *Dactylorhiza osiliensis*

Võhumõõgalised *Iridaceae*

Iris sibirica

Iris pseudacorus

Freesia

Niidu-kuremõõk
Gladiolus imbricatus

Crocus sativus

Amaryllidaceae

Amaryllis

Hippeastrum

Narcissus

Lauk *Allium* 9l

Allium schoenoprasum

Allium ursinum

Allium sativum

Asparilised

Convallaria majalis

Scilla sibirica

Yucca filamentosa

Agave americana

Kommeliniidid

- Lignifitseerumata rakukestad
- Ränikehakesed lehtedes
- **Õiekate diferentseerunud**
- Õisik kõrglehtedega
- **Tärkliserohke endosperm**
- **Epikutikulaarne vaha**

Palmilaadsed *Arecales*

- **Puud**
- **Lehed suured, sõrmjalt või sulgjalt jagunenud** ja roodunud
- **Õied suurtes keerukates õisikutes**
- Vili luuvili või mari

Palmilised
Arecaceae

Cocos nucifera

Serenoa repens

Kommeliinilaadsed
Kommeliinilised *Commelinaceae*

- Sukulentsed
- Lehed tupega
- Tolmukaniidid karvased
- Suured õisikud
- Seemned kaanega

Komme-liinilised

Tradescantia ohiensis

Commelina communis

Ingverilaadsed *Zingiberales*

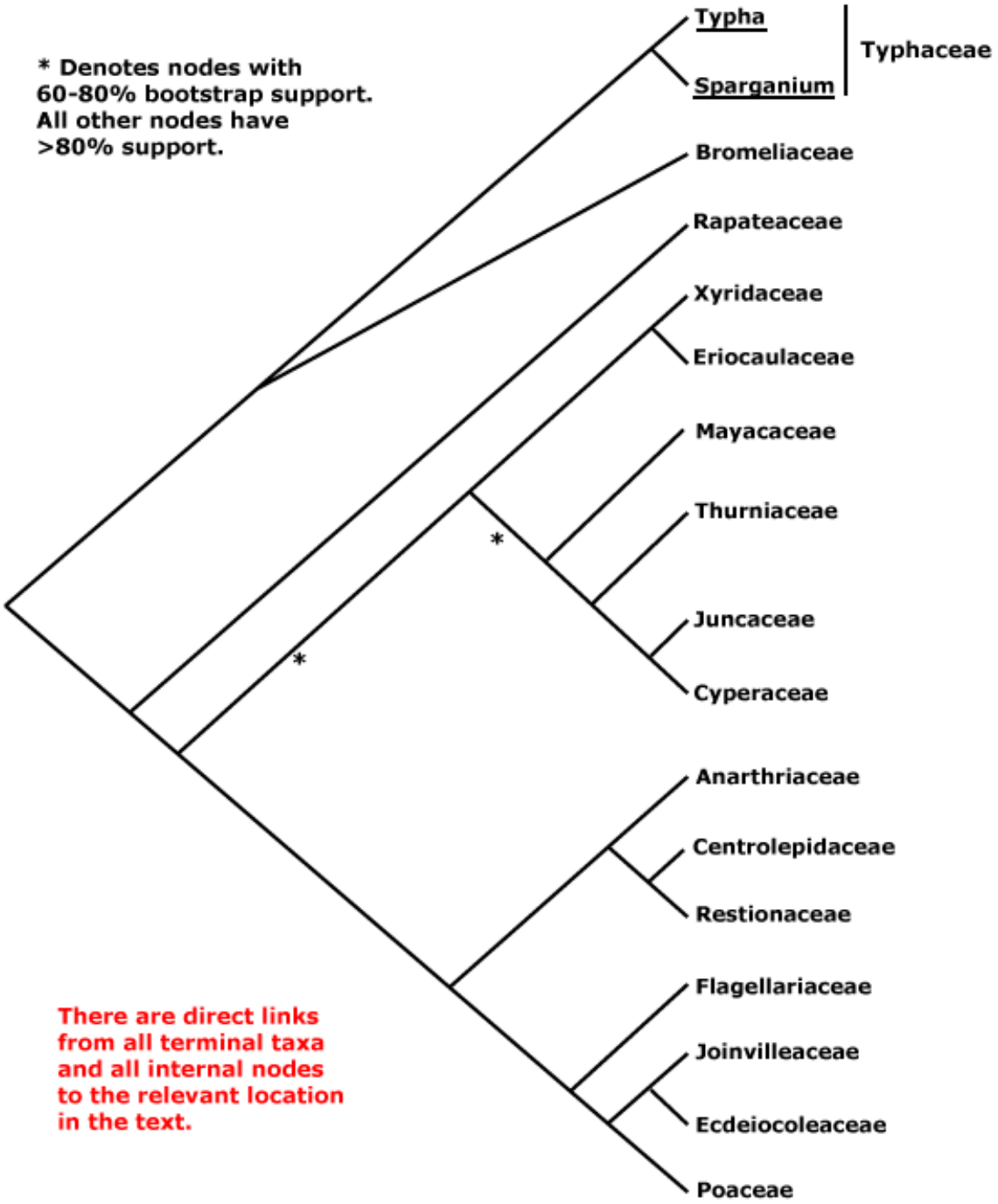
- Risoom
- Lehed vahelduvad, suured, rootsuga, sulgroodsed
- Õied sügomorfsed, epigüünsed, sageli suurtes eredavärvilistes õisikutes

Ingverilaadsed

Zingiber officinalis

Musa paradisiaca

Kõrrelise-laadsed *Poales*



http://www.mobot.org/mobot/research/apweb/

Kõrreliselaadsed *Poales*

- Lehed 2-realiselt, tupega
- Väikesed õied
- Üks seemnealge viljalehe kohta
- Nukleaarne endosperm
- Õhulõhe kaasrakud erilise kujuga
- Ränikehakesed epidermis

Bromeelialised

Loalised

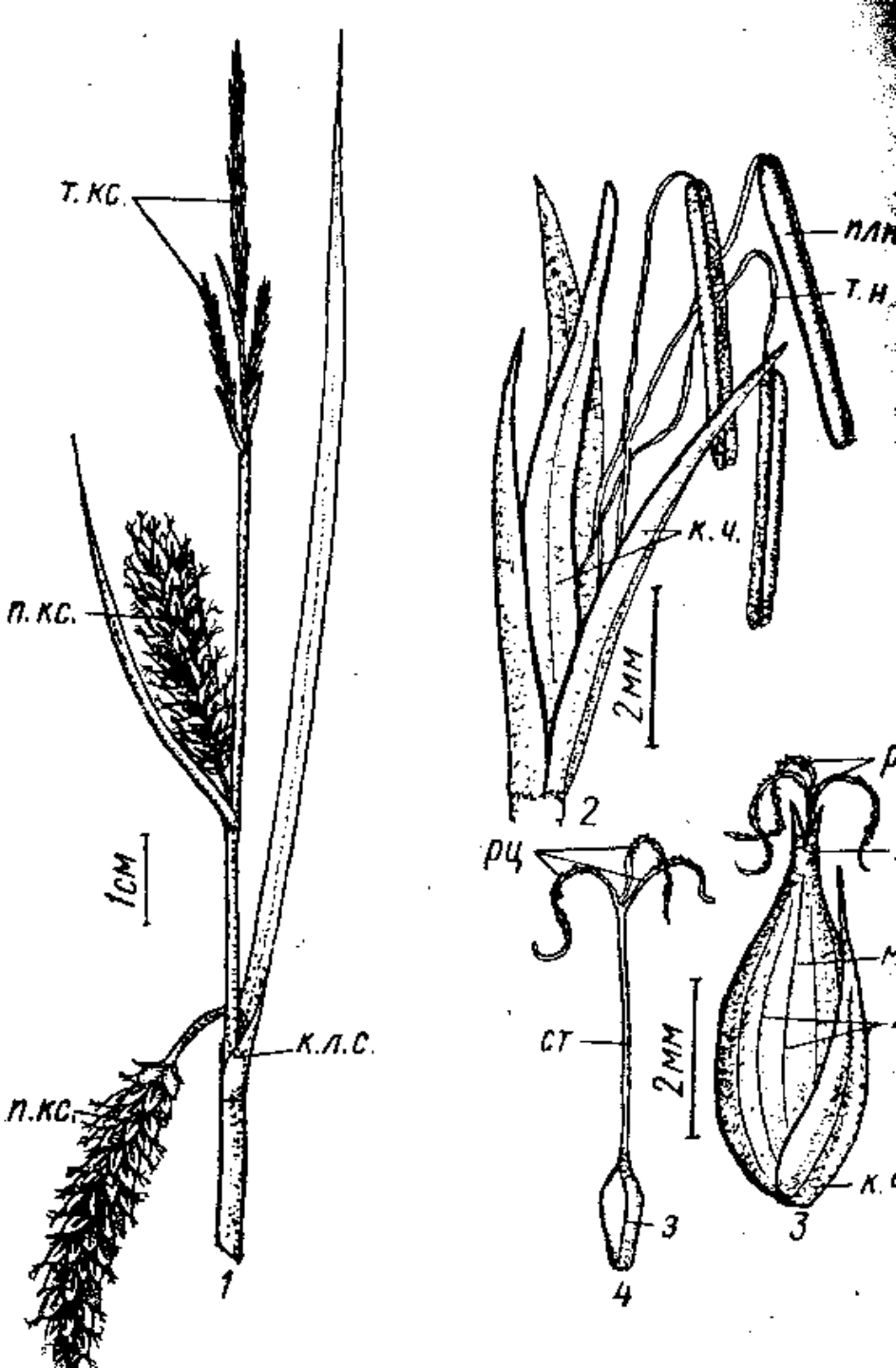
- Siledad
- Avatud tupega lehed kolmes reas
- Pöörisjad õisikud kõrglehega

Luzula pilosa

Juncus effusus

Lõikheinalised
Cyperaceae

- Kolmekandiline vars
- Lehed suletud tupega kolmes reas
- Õied koondunud pähikutesse, need liitõisikutesse
- Vili pähklike



Lõikheinalised *Cyperaceae* Eestis

- **12 perekonda, üle 100 liigi**

- ***Carex* 77*l***

- ***Eleocharis* 7*l***
- ***Eriophorum* 4*l***

- *Trichophorum, Scirpus, Schoenoplectus, Blysmus, Schoenus, Rhynchospora 2l*

Eleocharis palustris

Blysmus compressus

Eriophorum angustifolium

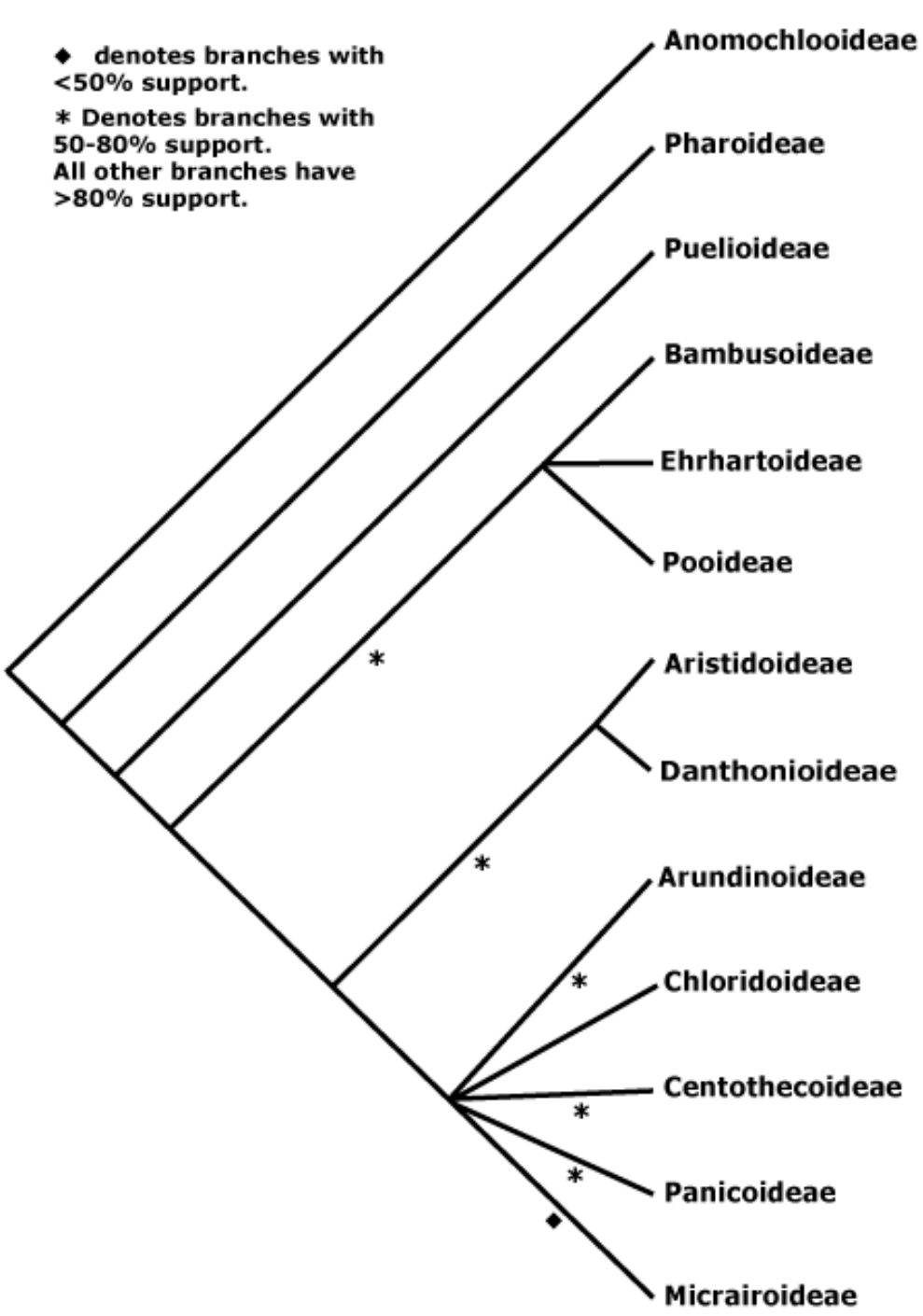
Trichophorum alpinum

Bolboschoenus maritimus
Schoenoplectus tabernaemontanii

Rhynchospora alba

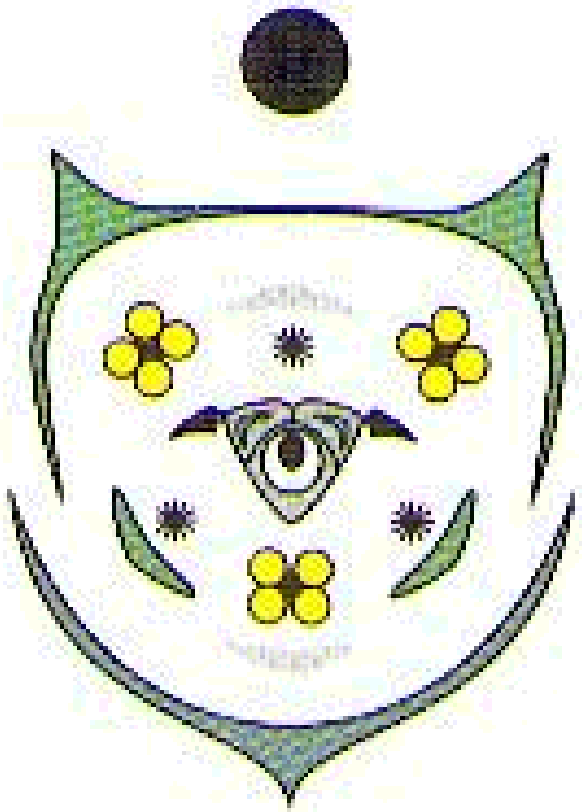
Schoenus ferrugineus

Kõrrelised
Poaceae



http://www.mobot.org/mobot/research/apweb/

Kõrrelised



Poaceae (Abb. 58)
(*Poa*)
P(2)+2 A3 G(3)

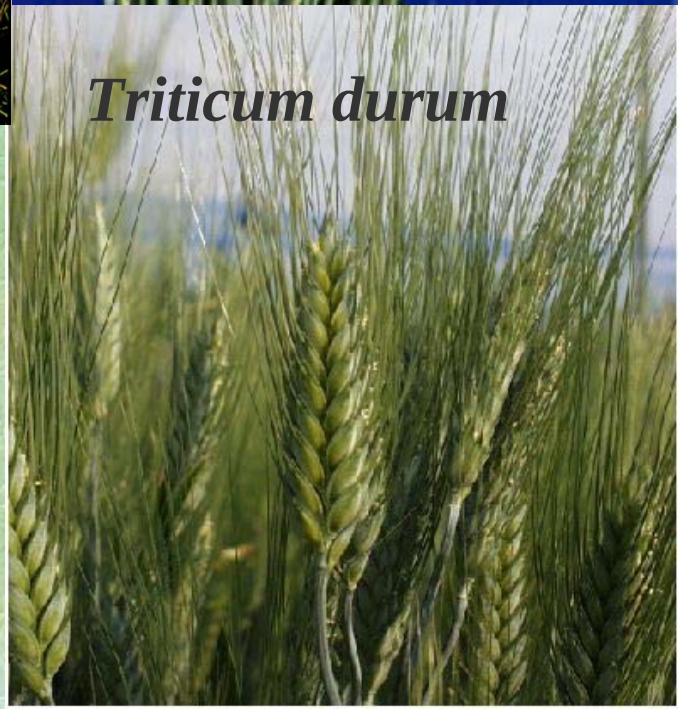
- Õõnsad, ümarad, sõlmilised varred
- Avatud lehetupp, keeleke
- Õie ehitus
- Vili teris

Teraviljad

Zea mays

Triticum aestivum

Triticum durum



KA
hirss, sorgo

Avena sativa

Secale cereale

Hordeum vulgare

Bambusa

Saccharum officinarum

Eestis

- Enamik ***Pooideae***
- 48 perekonda, üle 100 liigi
- Sh 7 liiki teravilja, ajuti metsistuvad
- *Poa* 10 l
- *Festuca* 9 l
- *Bromus* 7 l
- *Agrostis* 6 l
- *Calamagrostis*, *Alopecurus* 5 l
- *Glyceria* 4 l
- *Setaria*, *Hierochloe*, *Koeleria*, *Puccinellia*, *Lolium*, *Elymus*, *Hordeum*, *Avena* 3 l

Poa pratensis

Alopecurus pratensis

Phragmites australis

Hundi-nuialised *Typhaceae*

Typha latifolia
Foto: Norman Hagen

Jõgi-takjas *Sparganium*

Päriskaheidulehelised

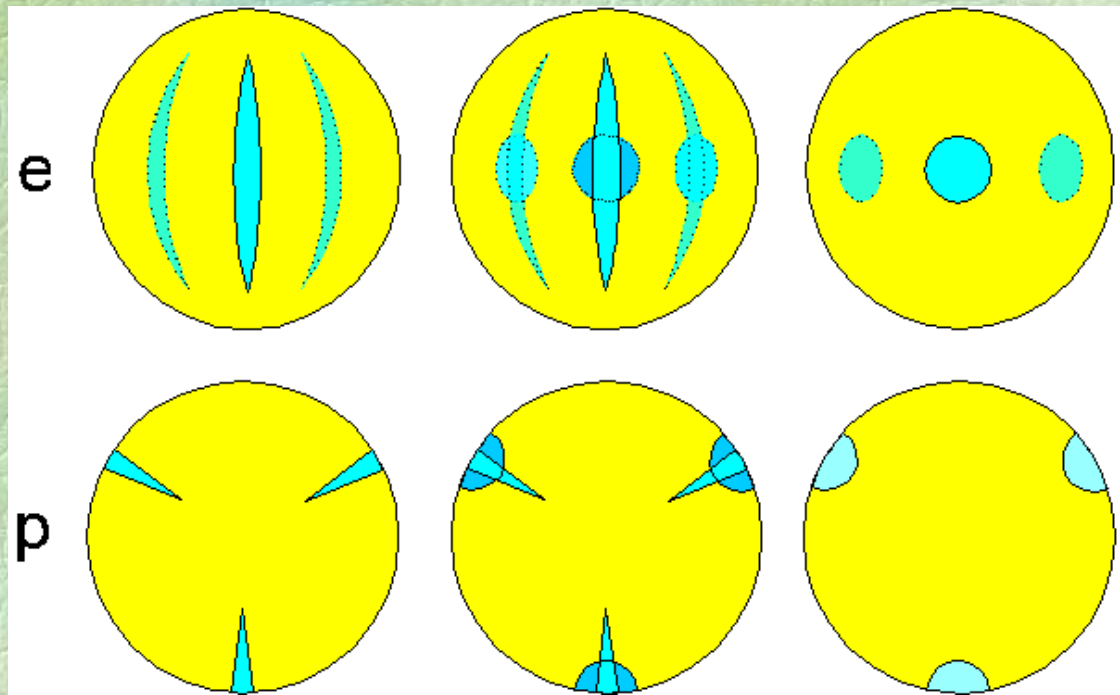
Mitteformaalne rühm

I osa: basaalsed rühmad ja rosiidid

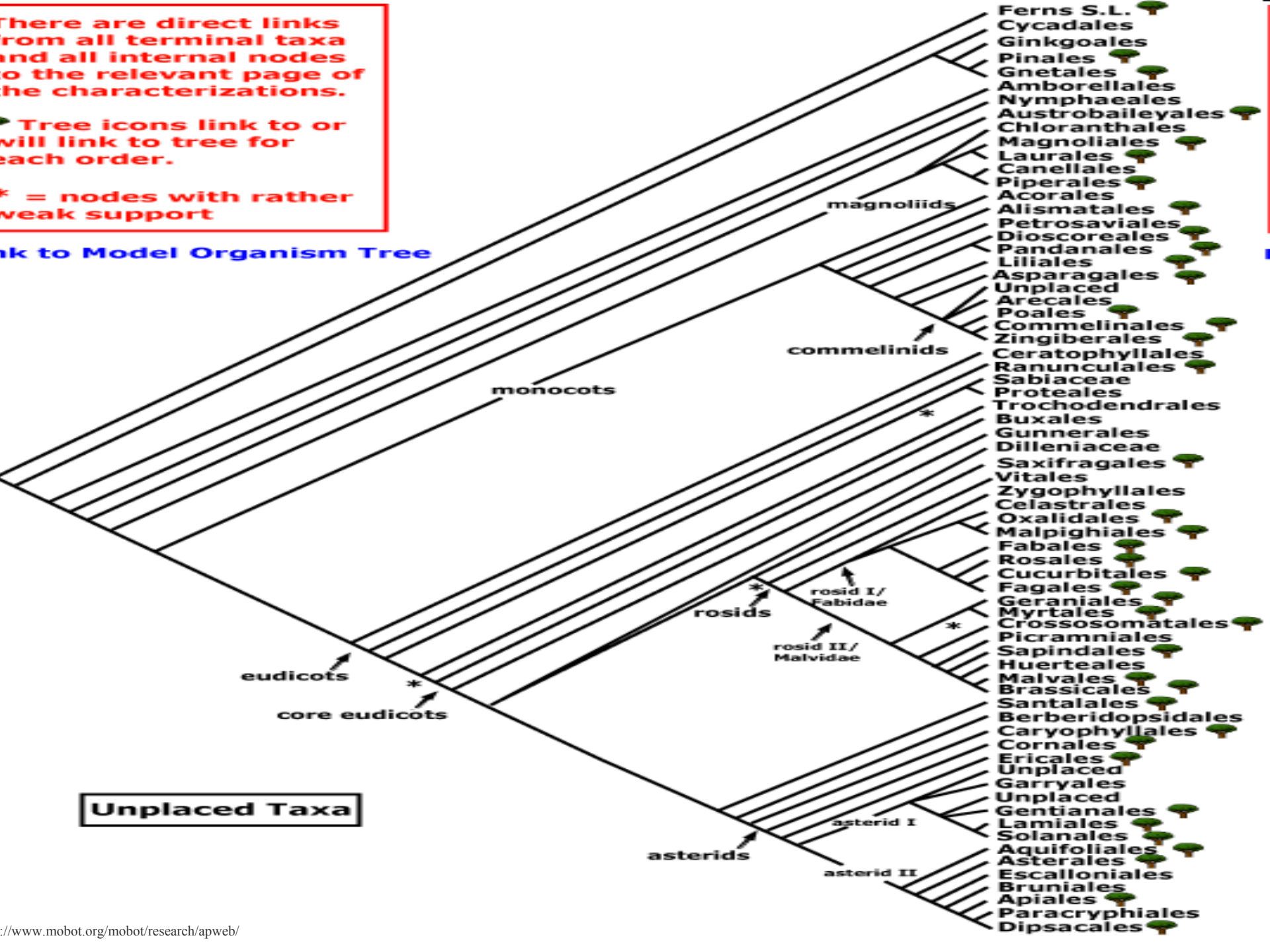
Päriskaheidulelehelised

- Kolmepooriline tolmutera
- Õiekate diferentseerunud tupeks ja krooniks, ringides vaheldumisi
- Eeterlikud õlid sageli puuduvad
- Trahheed

lihtsad

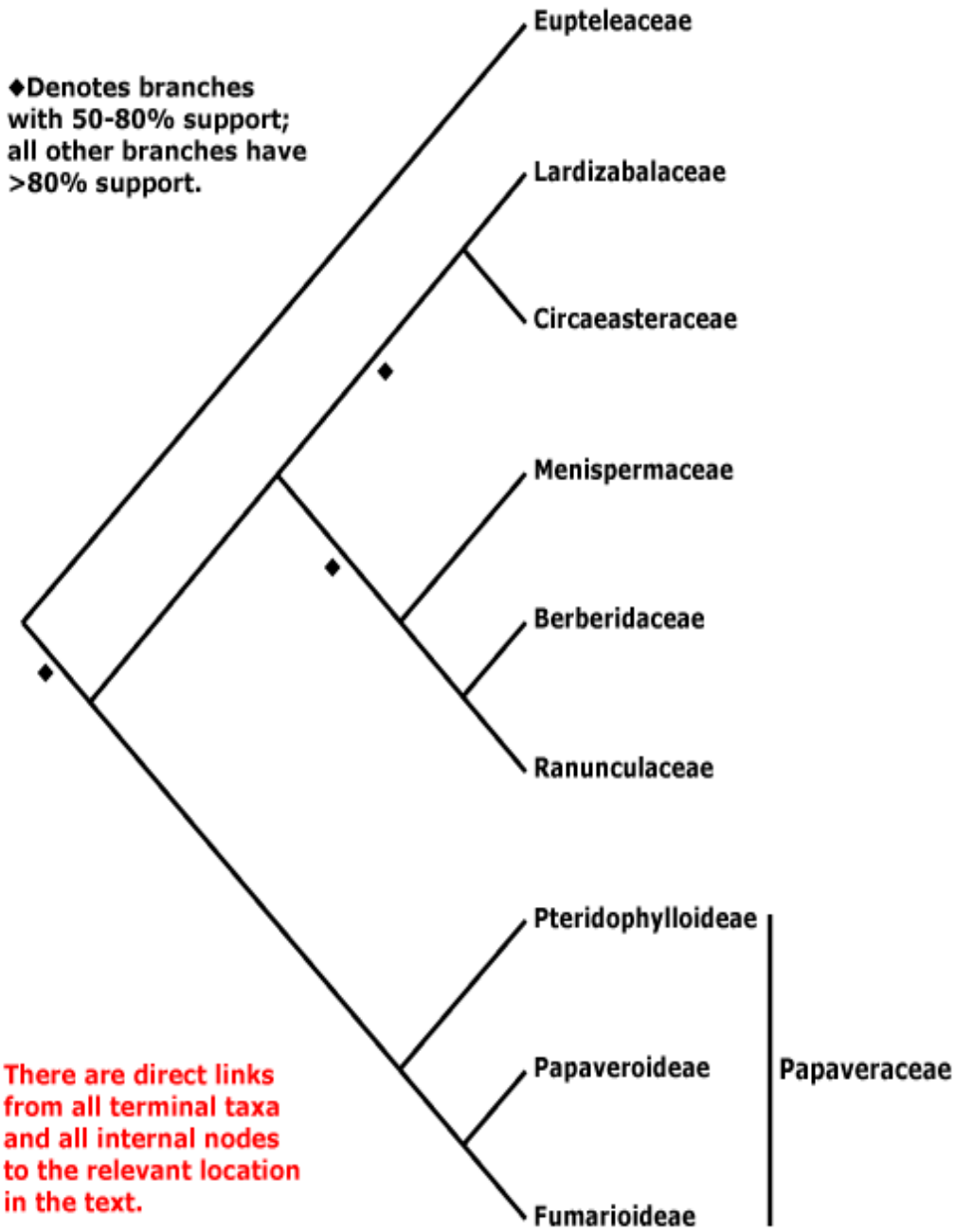


http://www3.bio.uu.nl/palaeo/glossary/glos-p2.htm


There are direct links
from all terminal taxa
and all internal nodes
to the relevant page of
the characterizations.
Tree icons link to or
will link to tree for
each order.
* = nodes with rather
weak support
nk to Model Organism Tree
Ferns S.L.
Cycadales
Ginkgoales
Pinales
Gnetales
Amborellales
Nymphaeales
Austrobaileyales
Chloranthales
Magnoliales
Laurales
Canellales
Piperales
magnoliids
Acorales
Alismatales
Petrosaviales
Dioscoreales
Pandanales
Liliales
Asparagales
Unplaced
Arecales
Poales
Commelinales
Zingiberales
commelinids
monocots
Ceratophyllales
Ranunculales
Sabiaceae
Proteales
Trochodendrales
Buxales
Gunnerales
Dilleniaceae
Saxifragales
Vitales
Zygophyllales
Celastrales
Oxalidales
Malpighiales
Fabales
Rosales
Cucurbitales
Fagales
rosid I/
Fabidae
Geraniales
Myrtales
Crossosomatales
rosids
rosid II/
Malvidae
Picramniales
Sapindales
Huerteales
Malvales
Brassicales
eudicots
core eudicots
Santalales
Berberidopsidales
Caryophyllales
Cornales
Ericales
Unplaced
Garryales
Unplaced
Gentianales
asterid I
Lamiales
Solanales
Aquifoliales
Asterales
asterids
asterid II
Escalloniales
Bruniales
Apiales
Paracryphiales
Dipsacales
Unplaced Taxa

Basaalsed päriskaheidu-lehelised **Tulikalaadsed** ***Ranunculanae***

- Lehed sageli lõhestunud
- Tolmukaid ja viljalehti palju
- Bensüülisokinoon-alkaloidid
- Õiekatte välimine ring kroonjas



http://www.mobot.org/mobot/research/apweb/

Tulikalised *Ranunculaceae* Eestis

- Eestis 12 perekonda, 36 liiki
- *Ranunculus* 19 l
- *Thalictrum* 5 l
- *Anemone* 3 l
- *Aconitum, Pulsatilla* 2 l

Ranunculus acris

Ranunculus aquatilis


Anemone sylvestris


Hepatica nobilis SCHREBER
©Bernd Liebermann


Pulsatilla patens
© M. Hassler


© - josef hlasek
www.hlasek.com
Myosurus minima 4855

Magunalised

Papaveraceae

Fumaria officinalis

Papaver somniferum

Kukerpuulised *Berberidaceae*

Berberis vulgaris

Prootealaadsed *Proteanae*

Nelumbonaceae

Platanaceae

Proteaceae

Leucadendron

Protea obtusifolia

Päriskaheiduleheliste tuumrühm

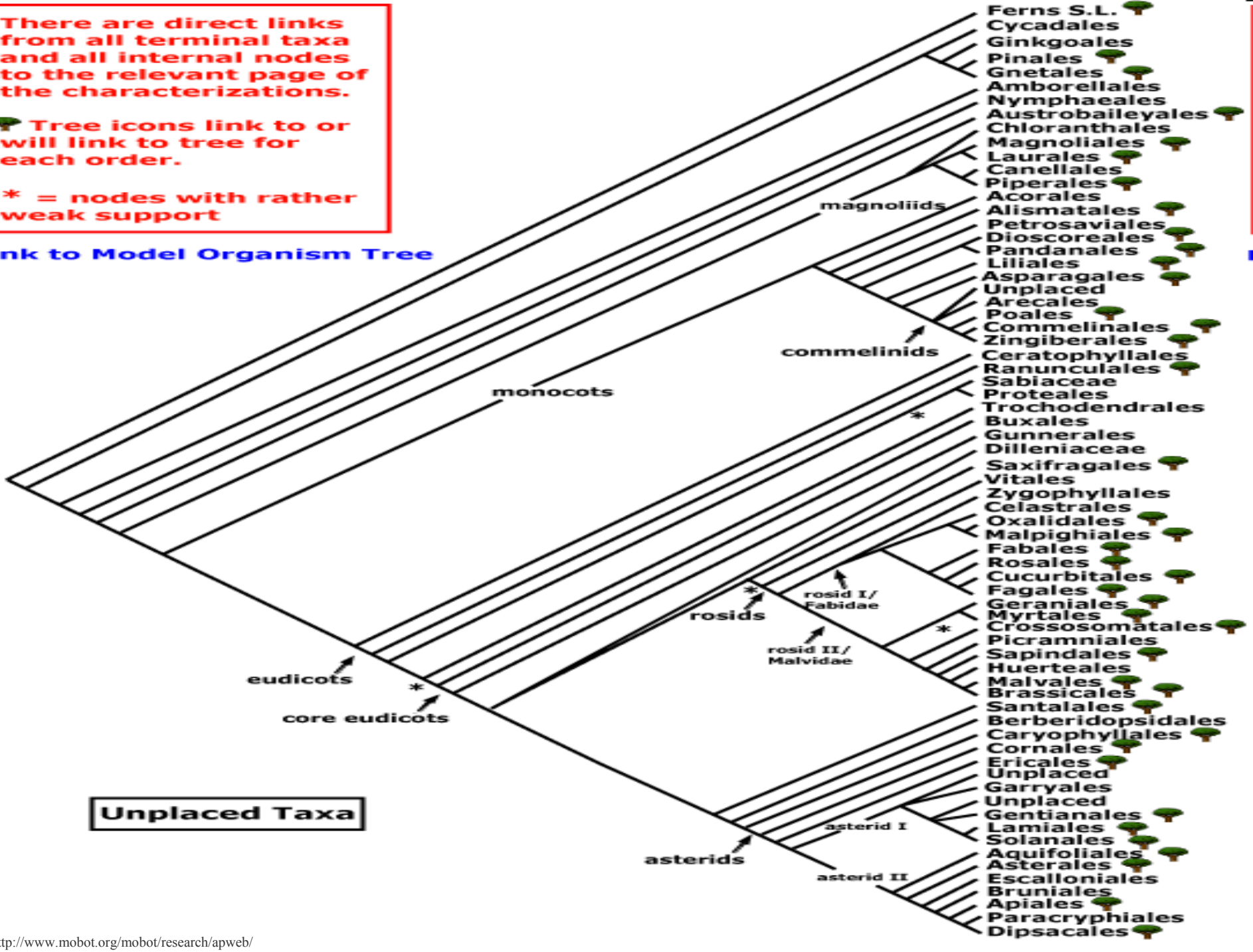
- Õied viietised
- Tupp ja kroon eristunud
- Kolmekaviline (trikolpaatne) tolmutera
- Endosperm nukleaarne
- Juure apikaalne meristeem suletud
- Seemnekesta ehitus
- Spetsiifilised geenid

There are direct links from all terminal taxa and all internal nodes to the relevant page of the characterizations.

Tree icons link to or will link to tree for each order.

* = nodes with rather weak support

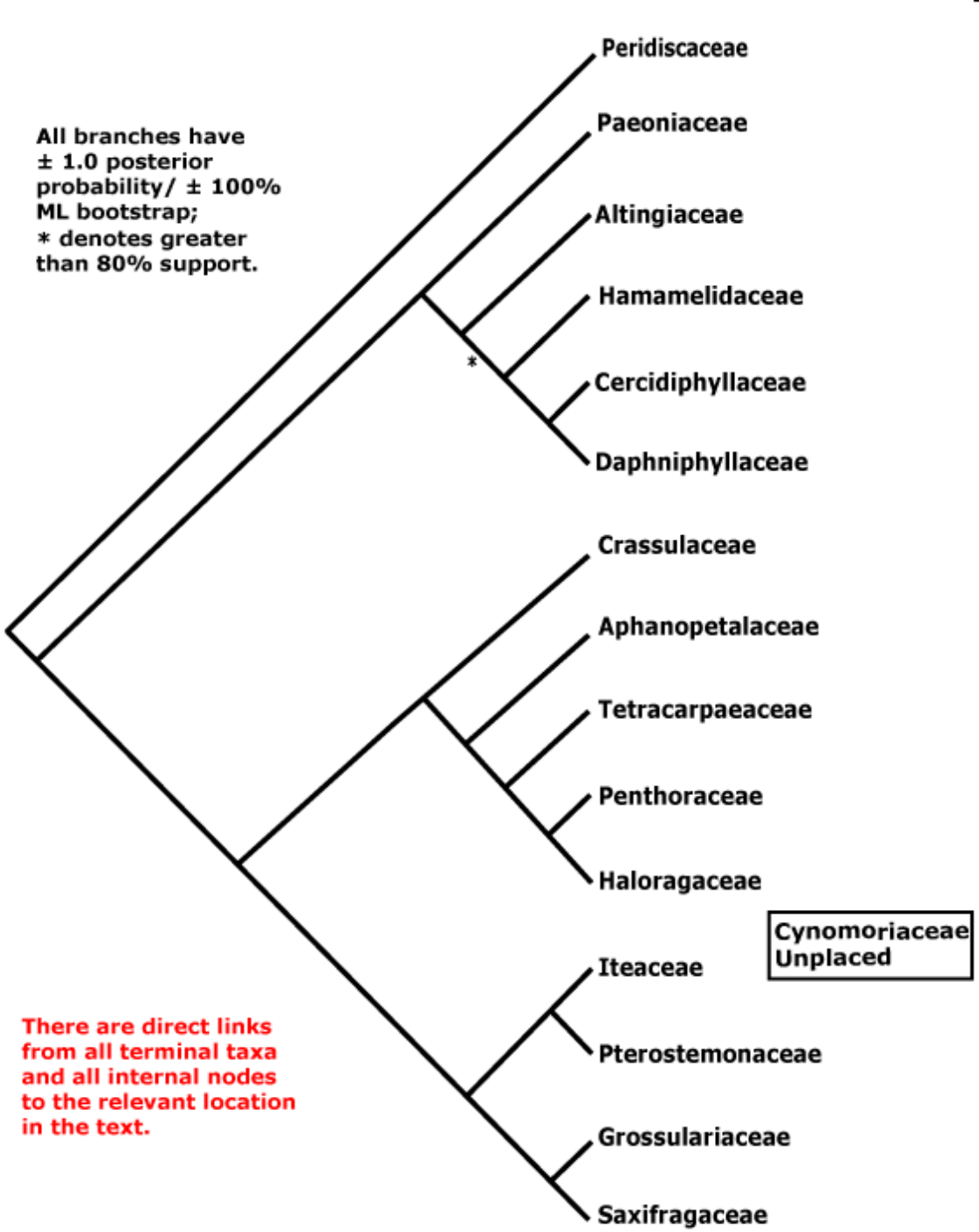
Link to Model Organism Tree



Unplaced Taxa

Kiviriku-laadsed *Saxifragales*

- Asetamata selts
- Viietised kiirjad õied
- Viljalehed alusel kokku-kasvanud või peaaegu vabad, eraldi emakakaeltega
- Endosperm tsellulaarne
- Lehed hambulised, näärmetega



http://www.mobot.org/mobot/research/apweb/

Nõiapuulised
Hamamelidaceae

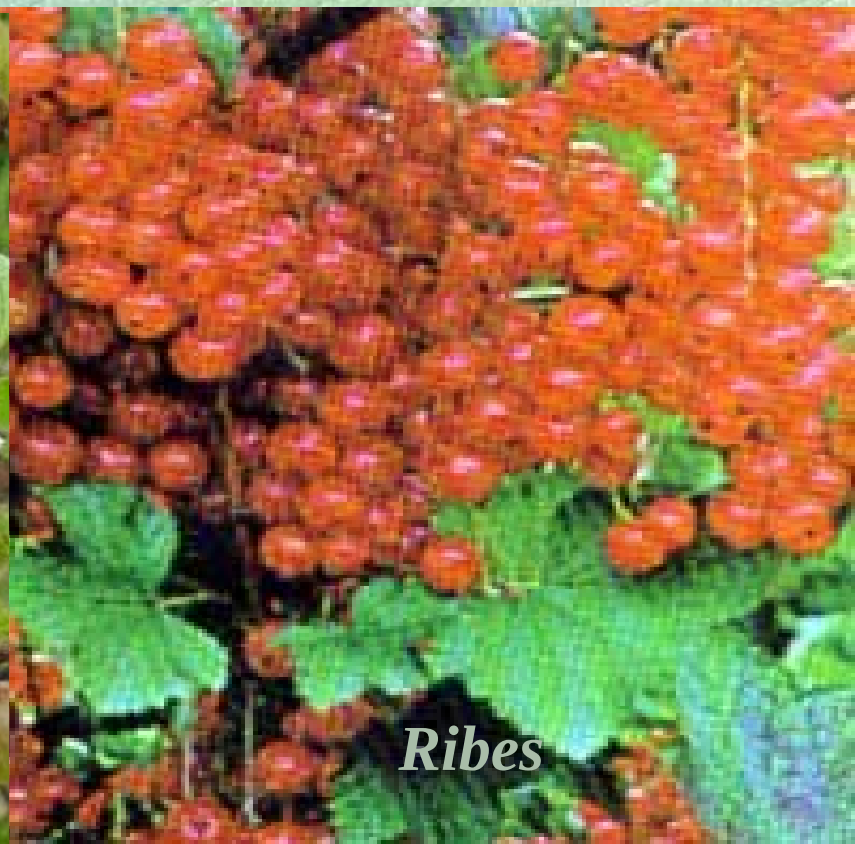
http://www.pfaf.org/user/Plant.aspx?LatinName=Hamamelis+virginiana

Paksulehelised
Crassulaceae

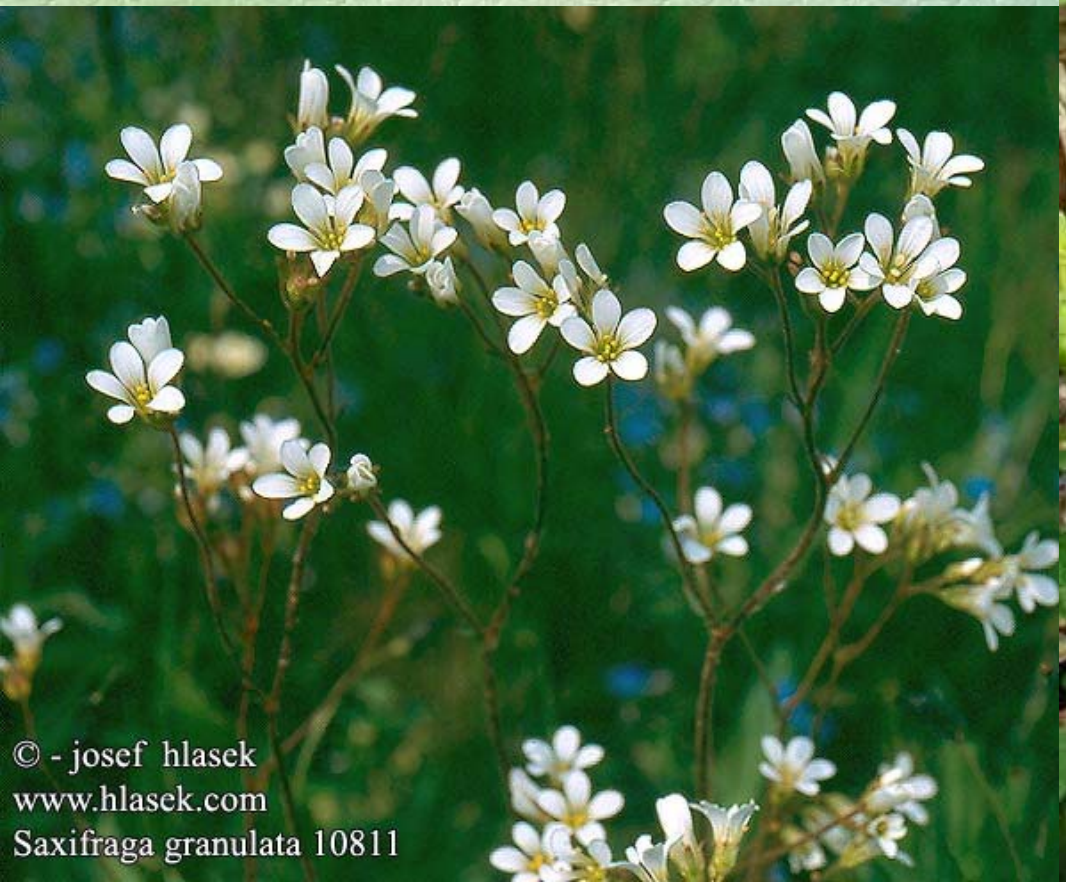
Jovibarba globifera

Sedum

Sõstralised
Grossulariaceae

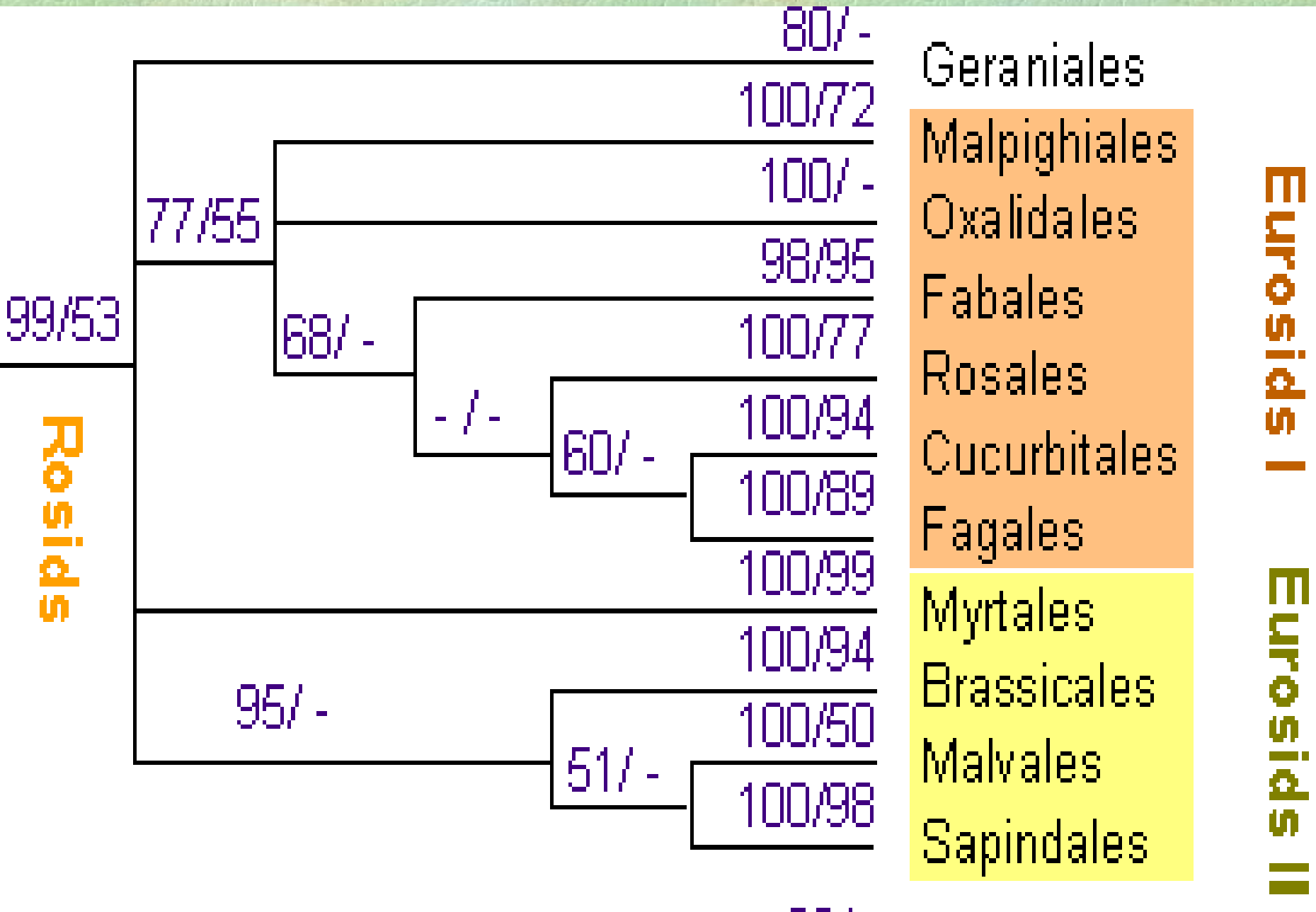


Kivirikulised
Saxifragaceae



“Rosiidid” *Rosanae*

- Abilehed
- Diplostemoonsed õied (tolmukad kahe või enama vahelduva ringina)
- Tanniinid
- Pikk embrüo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51/ -
100/98
Geraniales
Malpighiales
Oxalidales
Fabales
Rosales
Cucurbitales
Fagales
Myrtales
Brassicales
Malvales
Sapindales
Rosids
Eurosids I
Eurosids II

Viinapuulaadsed *Vitales*

Vitis vinifera

Pärisrosiidide
I rühm ehk “fabiidid”

- Endosperm puudub või väike
- Molekulaarsed tunnused

Malpiigia-laadsed *Malpighiales*

Lisaks
Linaceae

http://www.mobot.org/mobot/research/apweb/

orbiaceae

Mercurialis perennis

phorbia canariense

Euphorbia helioscopia

Manglipuulised *Rhizophoraceae*

Pajulised *Salicaceae*

Kannikeselised *Violaceae*

Linalised *Linaceae*

Linum catharticum
Foto: Jan Wesenberg

Clusiaceae + Hypericaceae

Clusia lanceolata

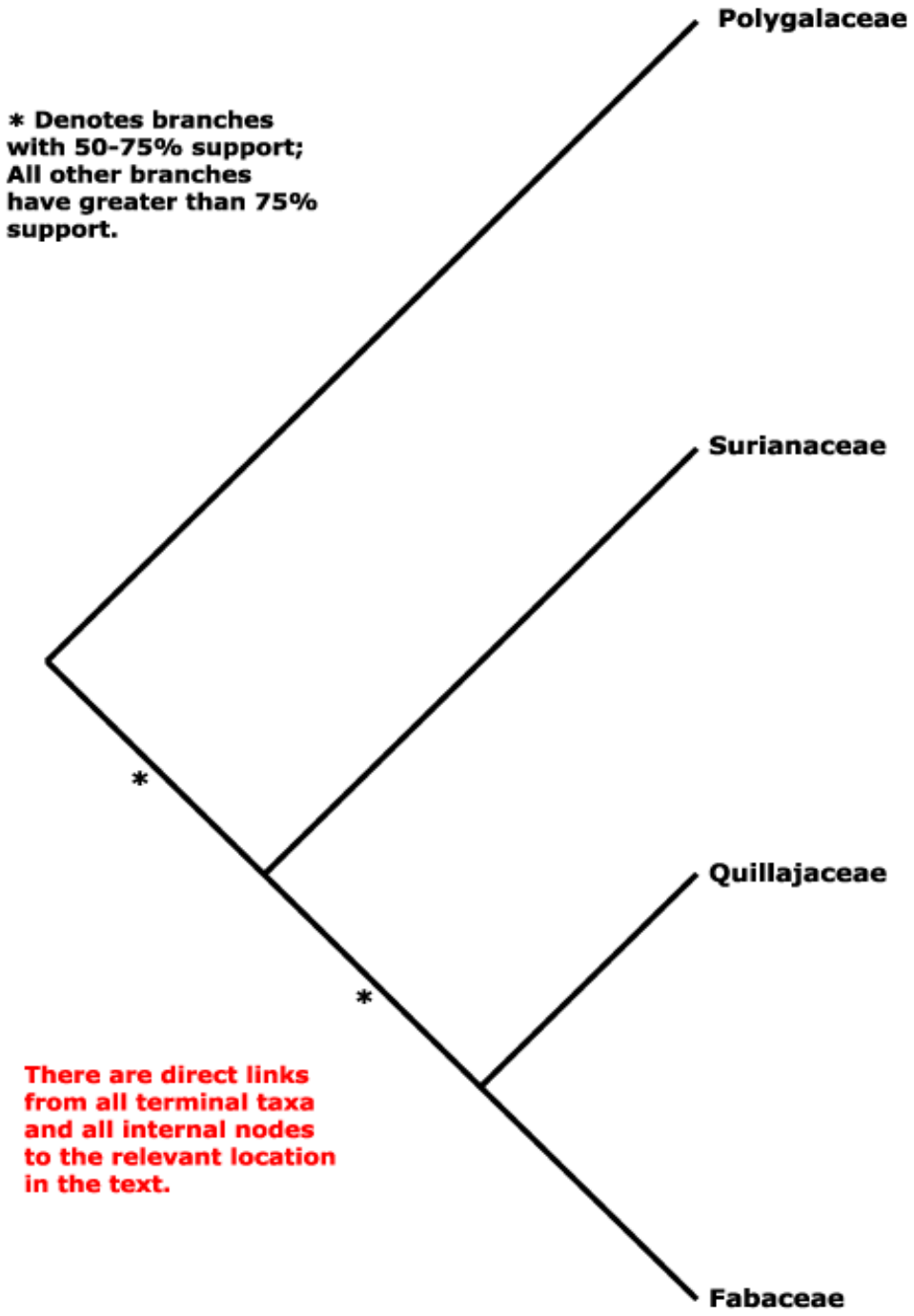
Hypericum perforatum

Rafflesiaceae + Passifloraceae

Jänesekapsalaadsed *Oxalidales*
Oxalidaceae

Oalaadsed
Fabales

Fabaceae:
Caesalpinioideae
Mimosoideae
Faboideae



Liblikõielised (oalised)
Fabaceae

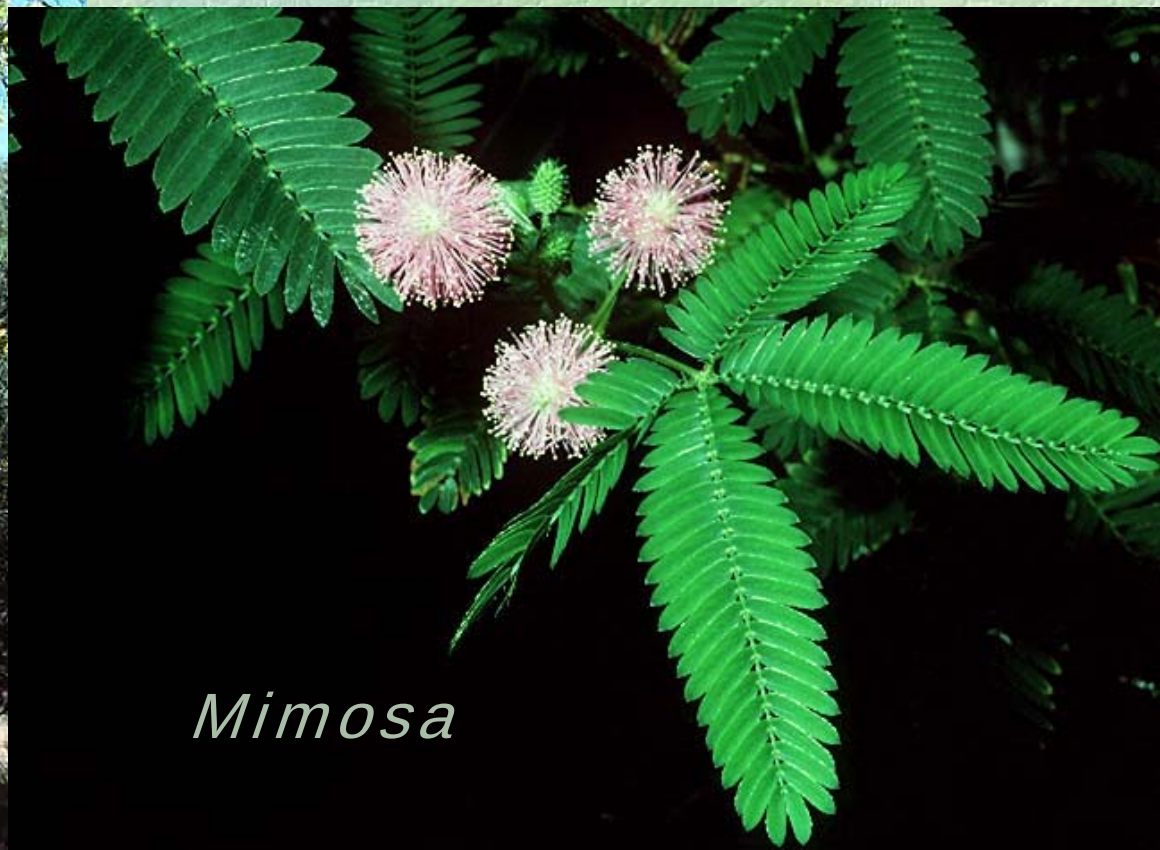
- Juuremügarad
- Sulgjad liitlehed
- Vabad kroonlehed, sügomorfne õis
- 10 tolmukat
- Üks viljaleht
- Vili kaun

Tsesalpiinialised *Caesalpinioideae*

Senna

Caesalpinia

Mimoosilised *Mimosoideae*



Liblikõielised *Faboideae*

- Rohttaimed
- Liblikõis
- *Astragalus* maailmas ca 3000 l
- toidutaimed
- E 23 perek, 70 liiki
- *Trifolium* 12
- *Vicia* 11, *Lathyrus* 10
- *Anthyllis* 8, *Lotus* 7+1
- *Medicago* 6

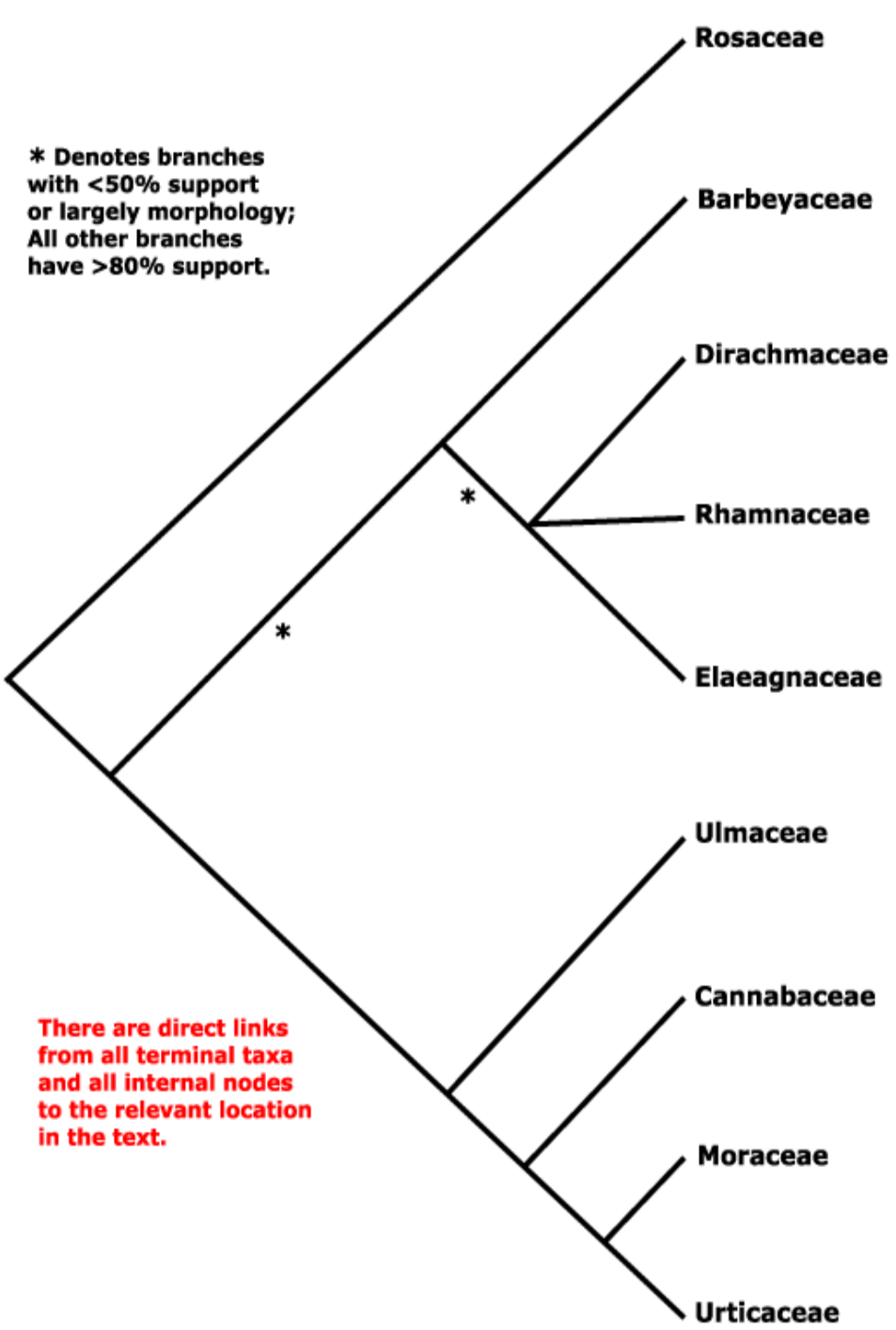
Arachis

Vahulillelised
Polygalaceae

Polygala fruticosa

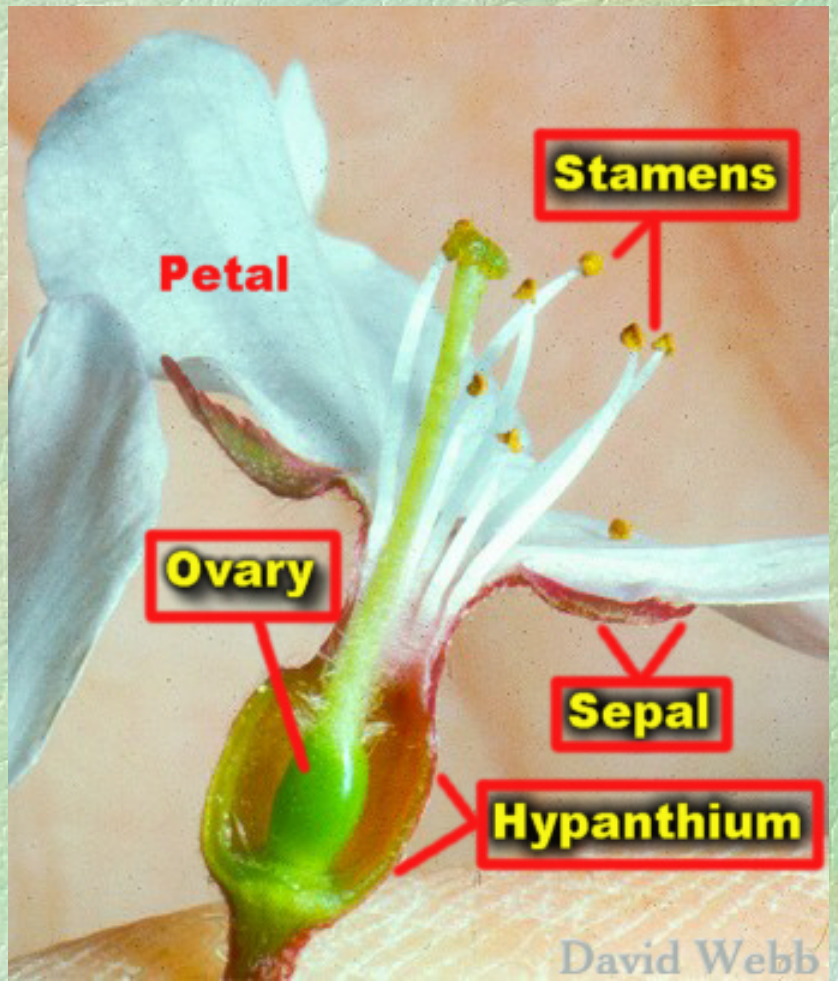
Roosilaadsed
Rosales

- Redutseerunud endosperm
- Hüpantium
- Molekulaarsed tunnused



http://www.mobot.org/mobot/research/apweb/

Hüpantium



Roosõielised *Rosaceae*

- Lehed liitlehed või lõhestunud, abilehtedega
- Hüpantium nektaariumiga
- Kroon lahklehine, palju tolmukaid
- Lihakad viljad
- *Rosoideae, Spiraeoideae, Amygdaloideae, Pyroideae*
- Eestis 22 perek, üle 100 liigi
- *Alchemilla* 24 (1)
- *Potentilla* 19
- *Rosa* 16
- *Crataegus* 9
- *Rubus* 7

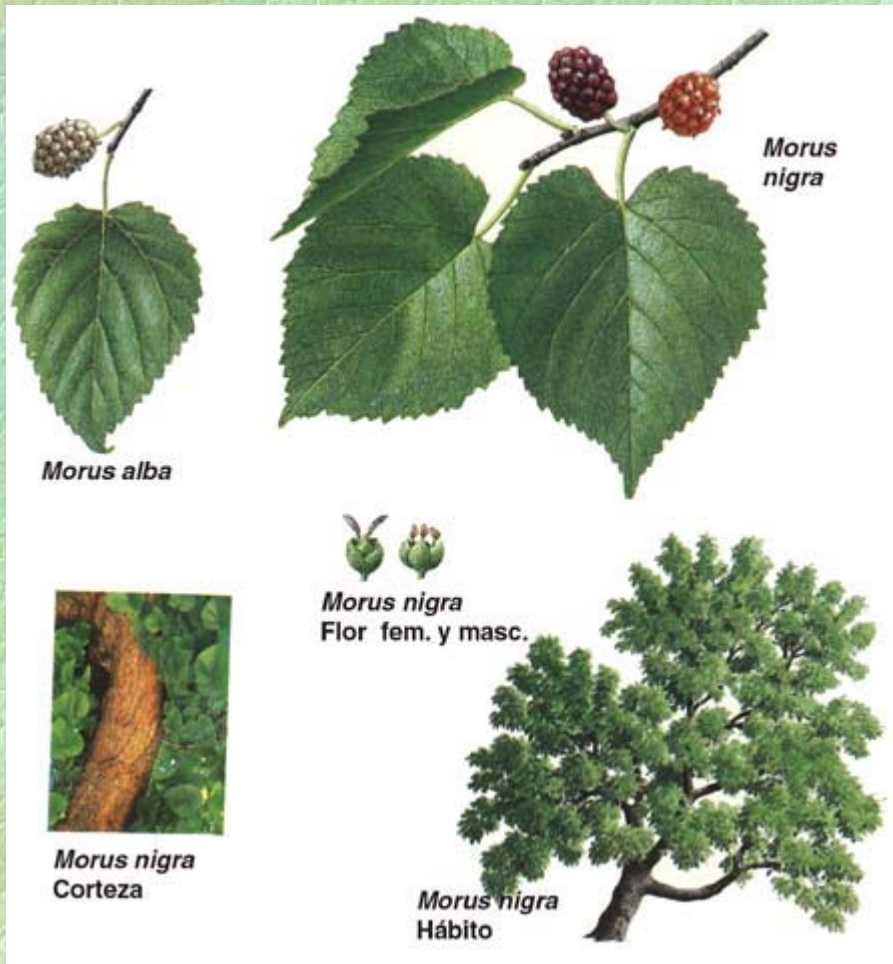
http://en.wikipedia.org/wiki/File:Cleaned-Illustration_Malus_domestica.jpg


Potentilla erecta
© M. Hassler


Rubus idaeus


Fragaria vesca
Foto: Per M. Hagen

Mooruselised *Moraceae*



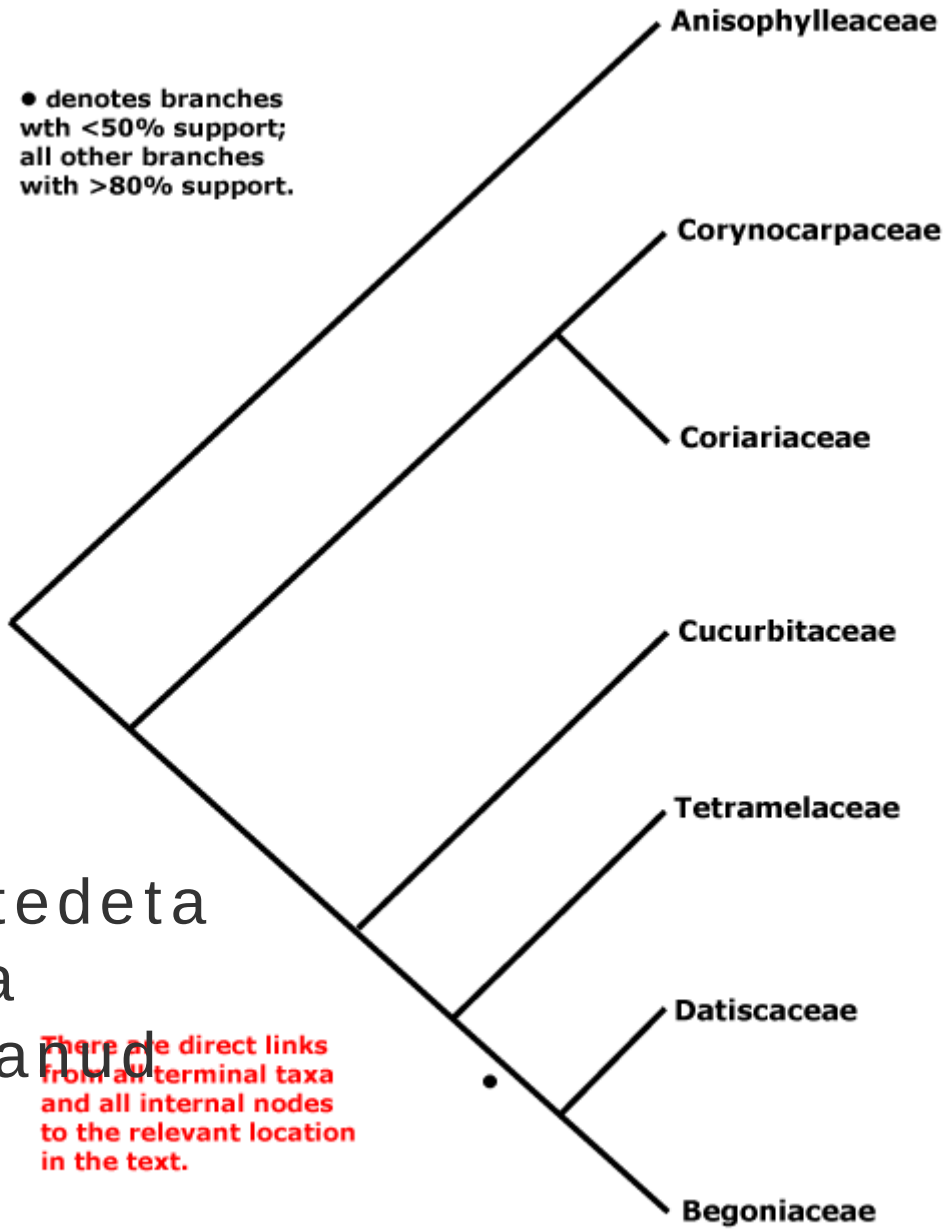
Kanepilised *Cannabaceae*

Rhamnaceae ja *Ulmaceae*

http://www.discoverlife.org/mp/20q?search=Rhamnaceae

Nõgeselised *Urticaceae*

Kõrvitsa-laadsed *Cucurbitales*



Cucurbitaceae:

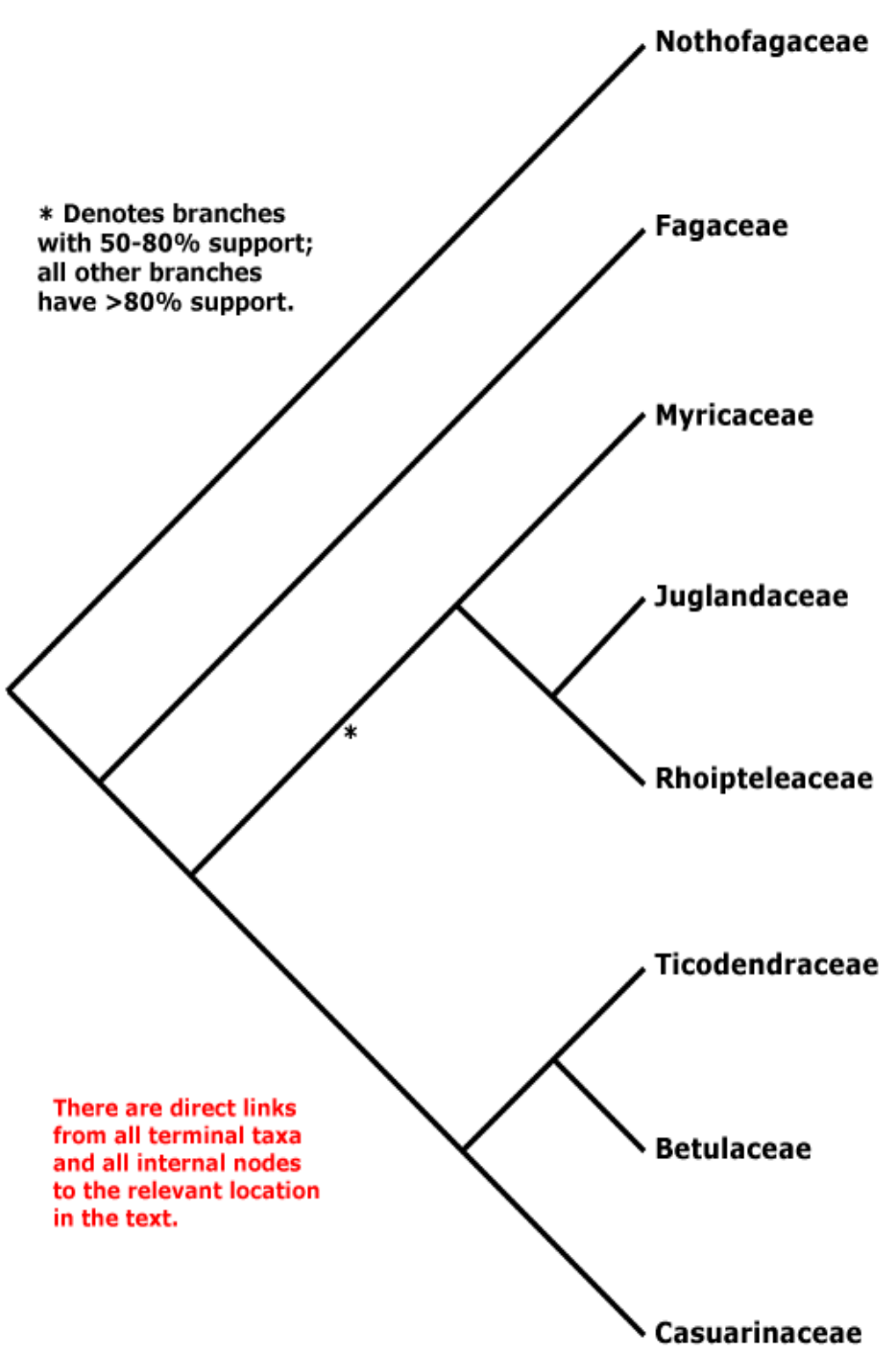
- Ronivad, köitraagudega
- Sõrmroodne leht abilehtedeta
- Kiirjas õis hüpantiumiga
- Kroonlehed kokku kasvanud
- Lihakas sünkarpne vili

http://www.mobot.org/mobot/research/apweb/

Kõrvitsalised *Cucurbitaceae*

Pöögilaadsed
Fagales

- Tuultolmlejad
- Väikesed ühesugulised õied õisikutes (urvad)
- Lihtne õiekate
- 1-seemneline vili: luuvili või pähkel



http://www.mobot.org/mobot/research/apweb/

Pöögilised *Fagaceae*

Foto: Arne Anderberg

Foto: Arne Anderberg

Kaselised *Betulaceae*

Foto: Arne Anderberg

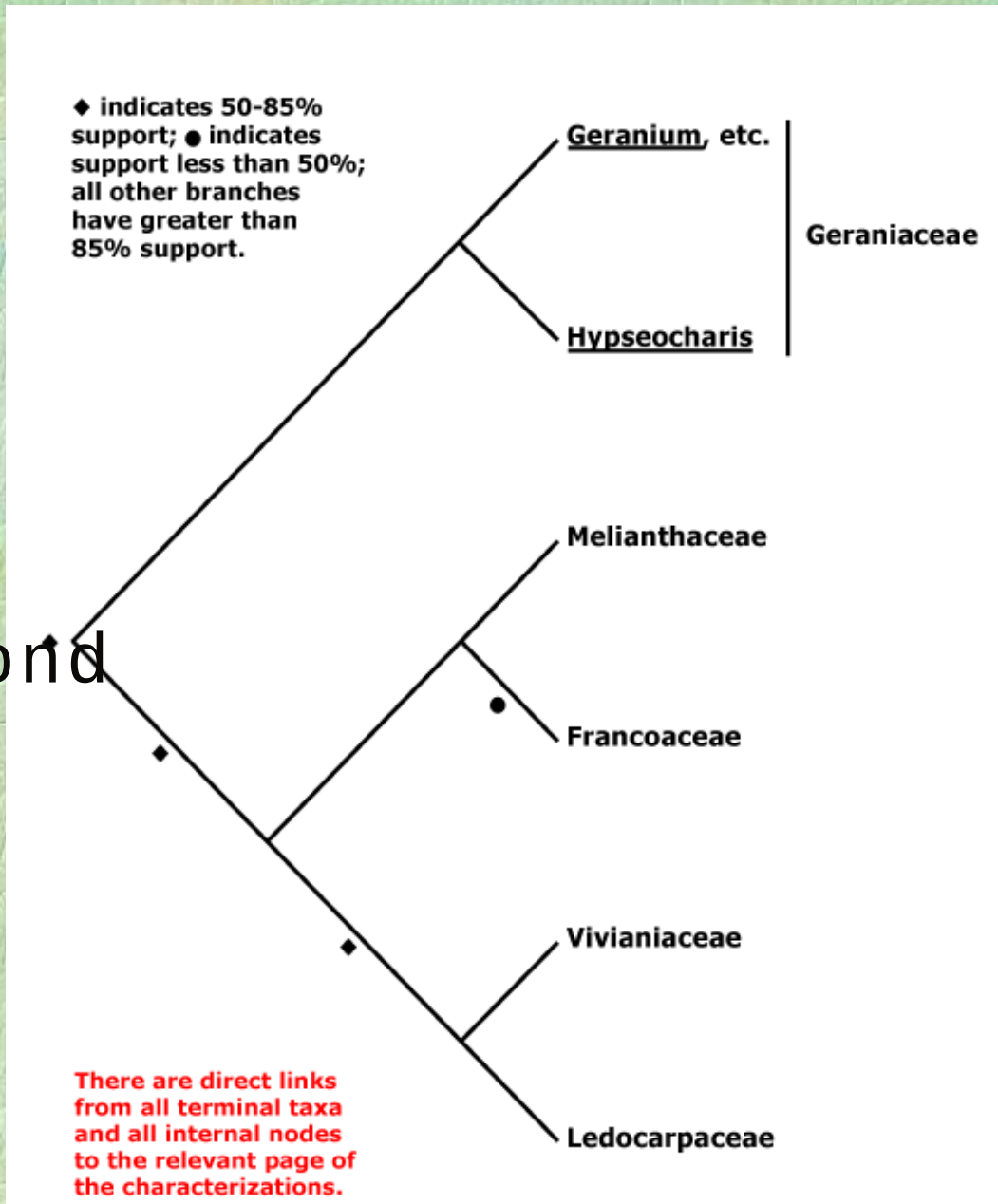
Pärisrosiidide II rühm ehk “malviidid”

- Flavonoolid
- Üks emakakael
- Molekulaarsed tunnused

Kurerehalaadsed *Geraniales*

Geraniaceae

- Näärmekarvad
- Lõhestunud lehed
- 10-15 tolmukat
- Sünkarpne emakkond ühe emakakaelaga

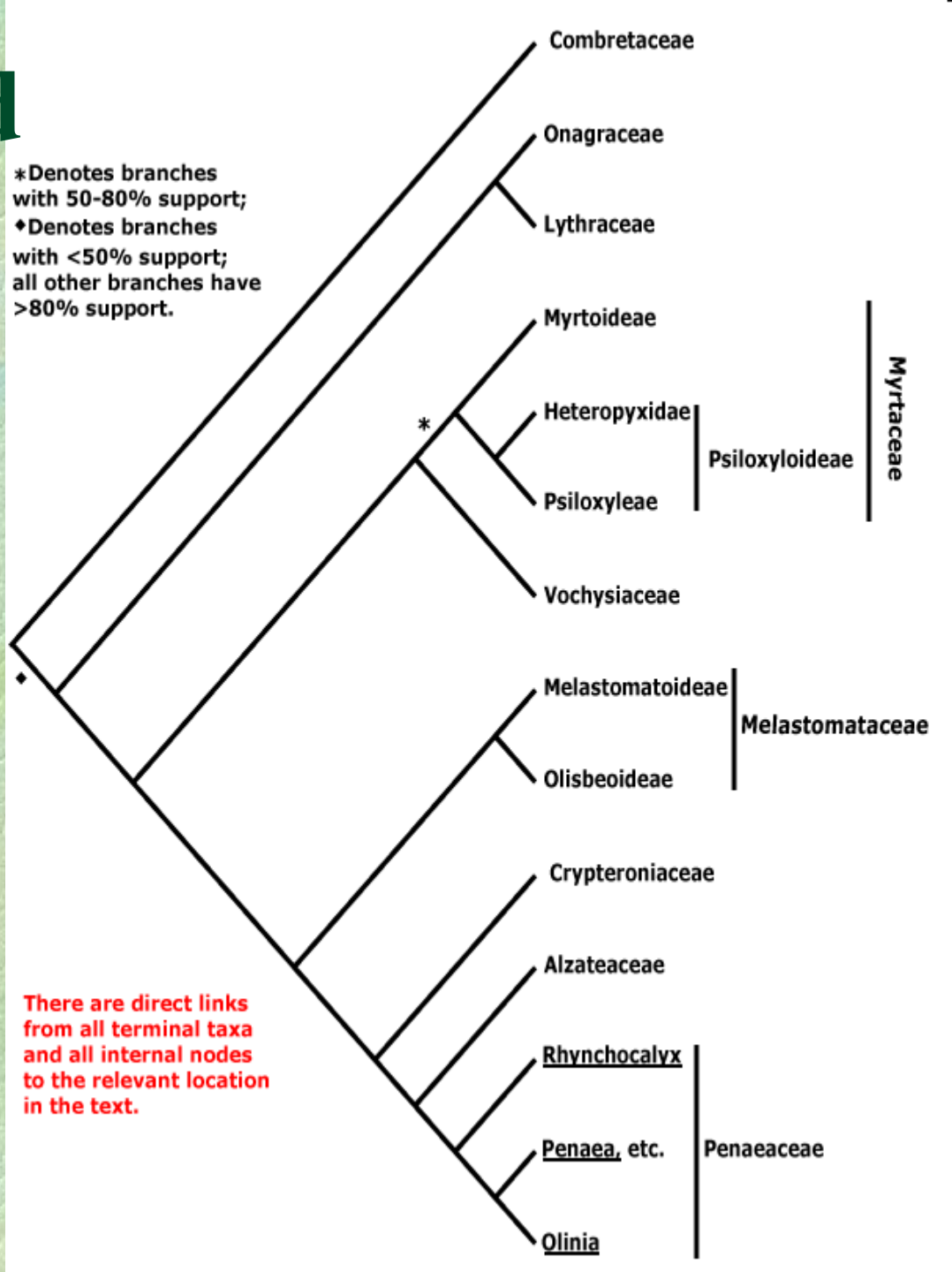


http://www.mobot.org/mobot/research/apweb/

Kurerehalised

Mürdilaadsed
Myrtales

- Lehed vastakud
- Puit sisemise floeemiga
- Hüpantium nektaariumiga
- Tolmukad pungas painutatud



http://www.mobot.org/mobot/research/apweb/

Mürdilised
Myrtaceae

Roodlehelised *Melastomataceae*

Kukesabalised *Lythraceae*

Peplis portula

Lythrum salicaria

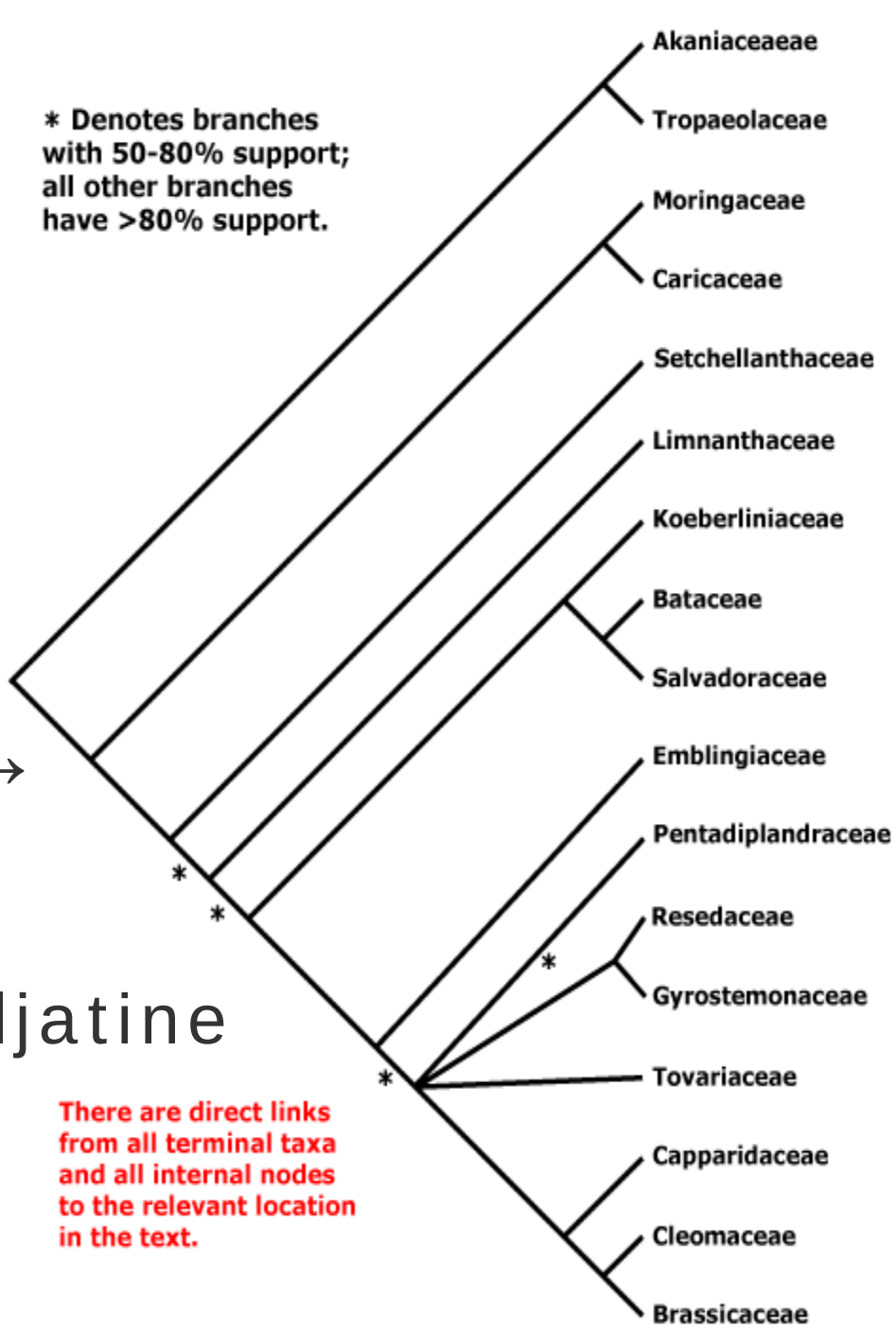
Pajulillelised
Onagraceae


Oenothera biennis


Epilobium angustifolium

Kapsa-laadsed *Brassica-les*

- Glükosinolaadid → sinepiõlid mürosiinirakkudes
- Õiekate sageli neljatine



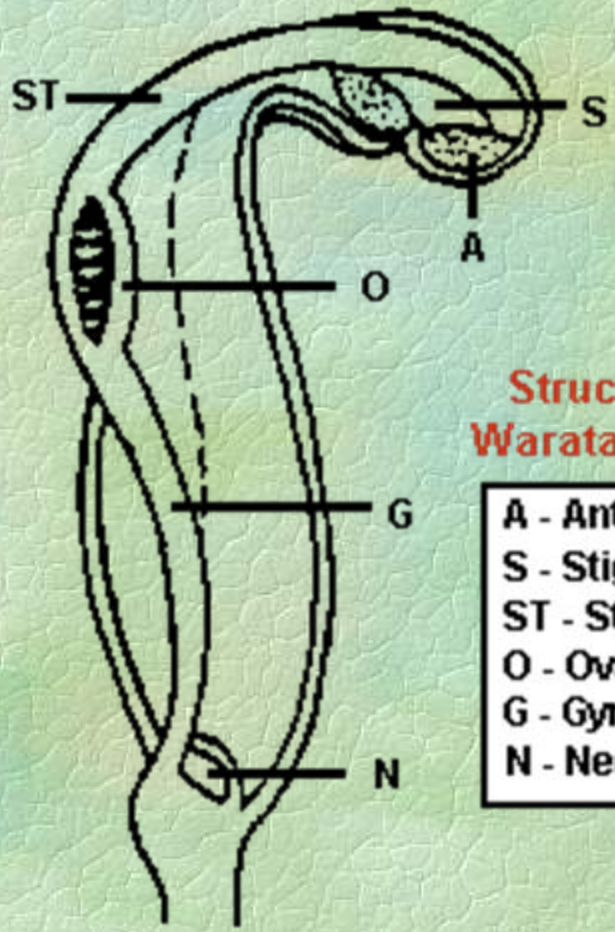
http://www.mobot.org/mobot/research/apweb/

Ristõielised *Brassicaceae*

- Aktinomorfne lahklehine õis: 4 tupplehte, 4 kroonlehte, 6 tolmukat, 2 viljalehte
- Sigimik sünkarpne, jaotatud kaheks kambriks sekundaarse vaheseina poolt
- Günofoor
- Vili avanev kõder
- Eestis 40 perekonda, 77 liiki
- *Sisymbrium, Cardamine* 6
- *Erysimum, Rorippa, Brassica, Lepidium, Camelina* 4

Waratah bud showing curved apical swelling

Figure 1



Structure of Waratah flower

A - Anther
S - Stigma
ST - Style
O - Ovary
G - Gynophore
N - Nectary

Figure 2

Bud showing the "hook" typical of the Waratah and its allies

Figure 3

Brassica oleracea zelje, ohrovt, cvetača itd.

Harilik müürlook
Arabidopsis thaliana

Sinapis alba

Sinapis arvensis

Crambe maritima

Capsella bursa-pastoris

Bunias orientalis
Foto: Jan Wesenberg

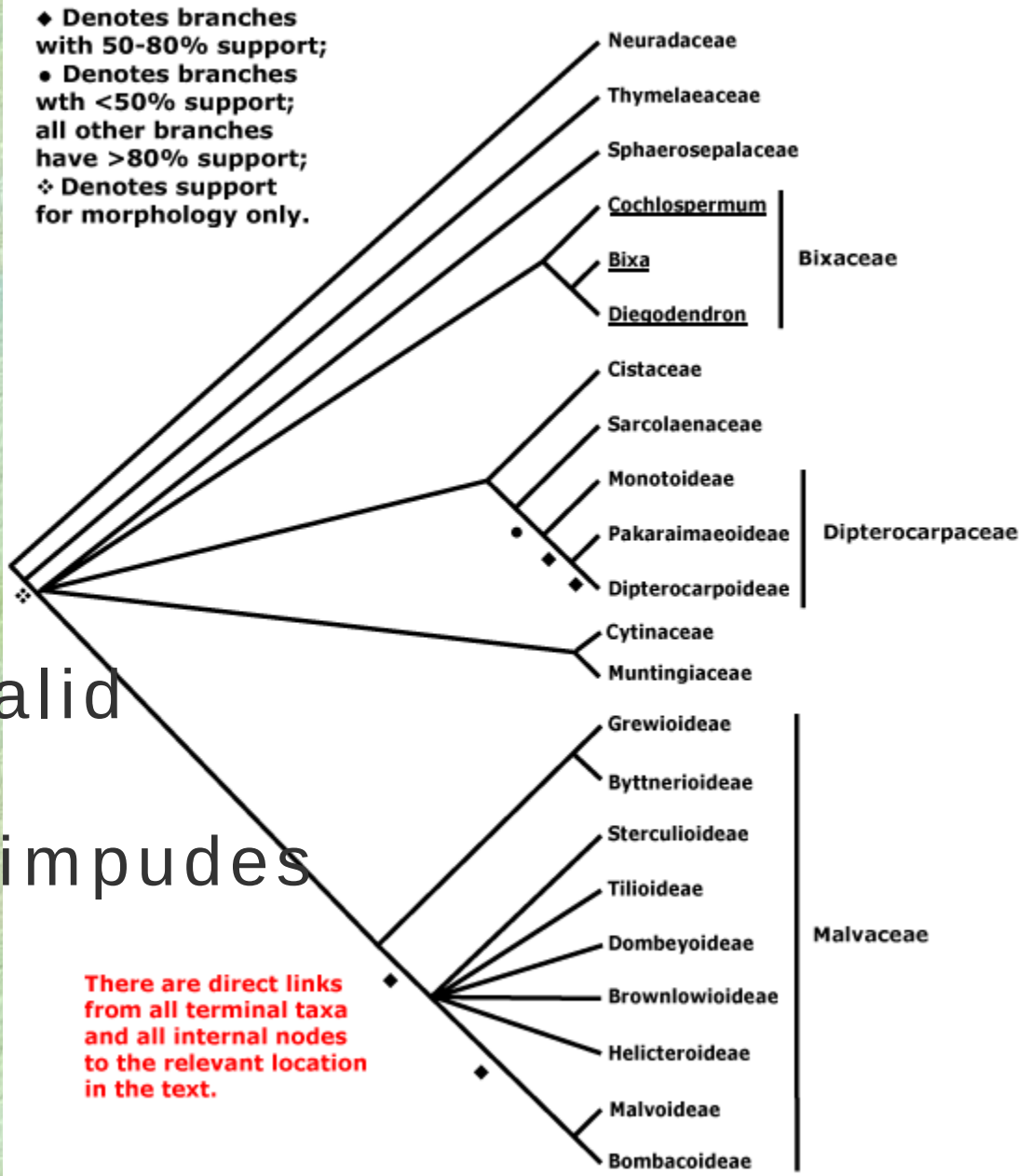
Cardamine pratensis

Kapparilised
Capparidaceae

Capparis spinosa

Kassinaeri-laadsed *Malvales*

- Tähtkarvad
- Limarakud ja –kanalid
- Sõrmjad lehed
- Tolmukaid palju, kimpudes



http://www.mobot.org/mobot/research/apweb/

Kassinaerilised *Ma*

Hibiscus

Malva

Cola

Gossypium hirsutum
Mo Fayyaz

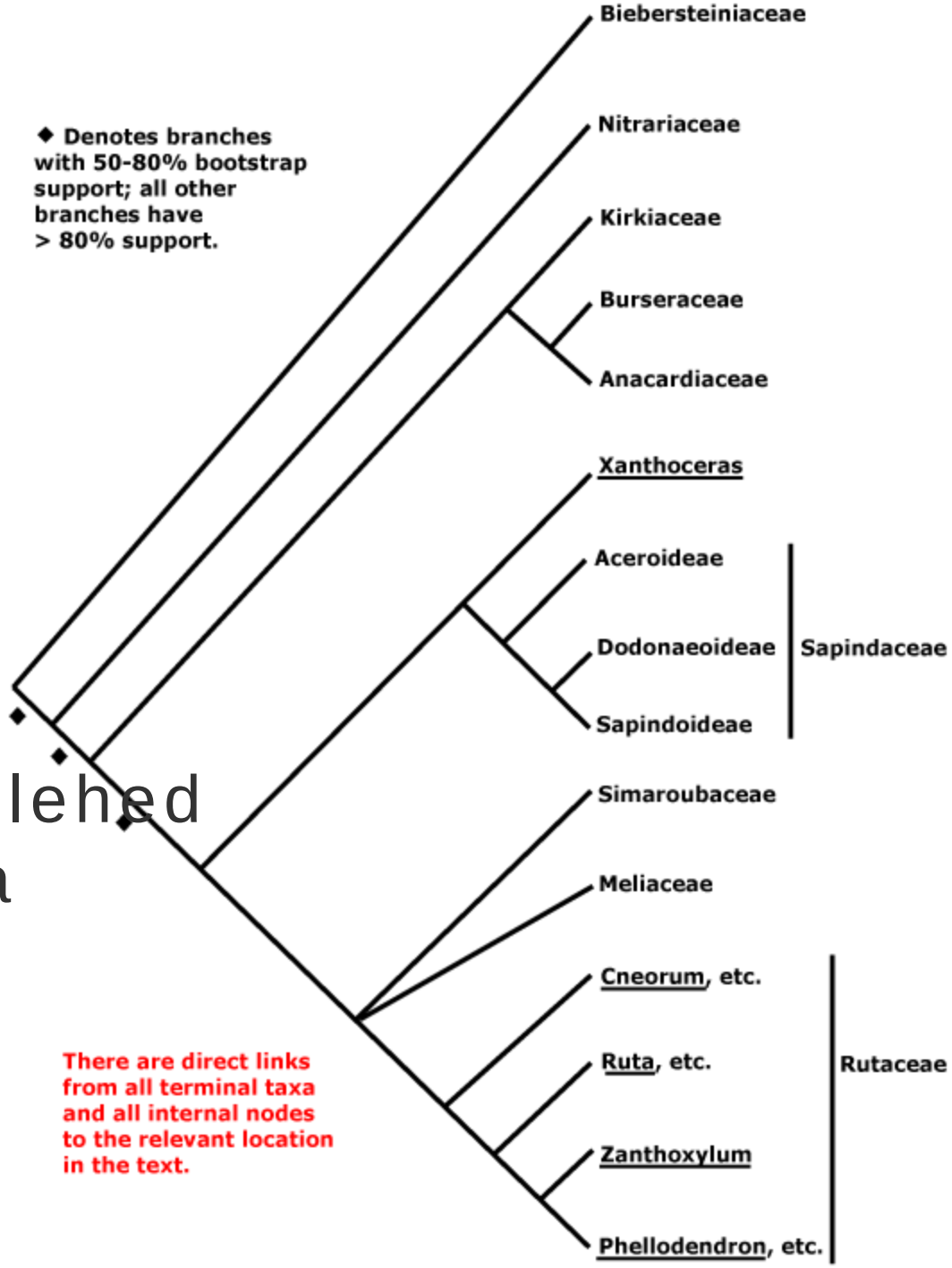
Tilia cordata

Theobroma

Kuldkannilised
Cistaceae

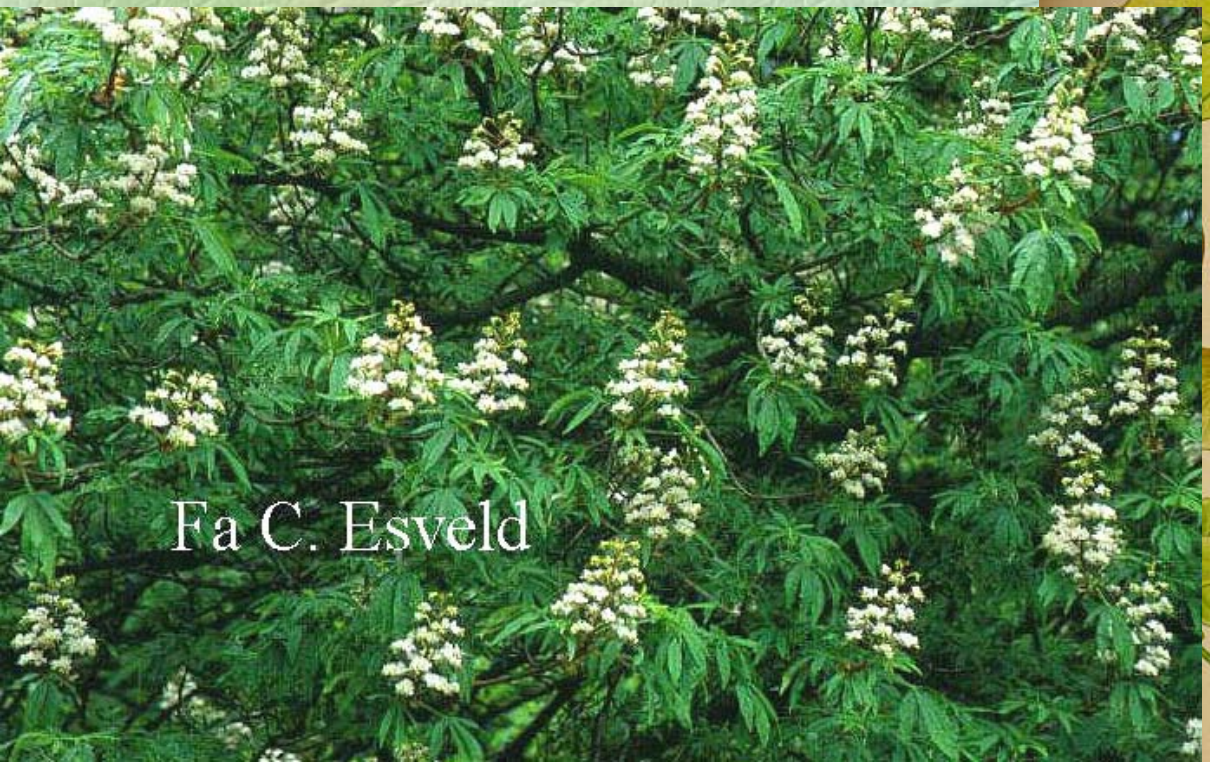
Seebipuu-laadsed *Sapindales*

- Puittaimed
- Liit- või lõhestunud lehed
- Õied nektarikettaga



http://www.mobot.org/mobot/research/apweb/

Seebipuulised *Sapi*



Fa C. Esveld

Ana-kardilised *Anacar-diaceae*

Ruudilised
Rutaceae

Õistaimed (järg)

Päriskaheidulehelised (järg)

Rosiidid (järg)

Nelgilaadsed

Asteriidid

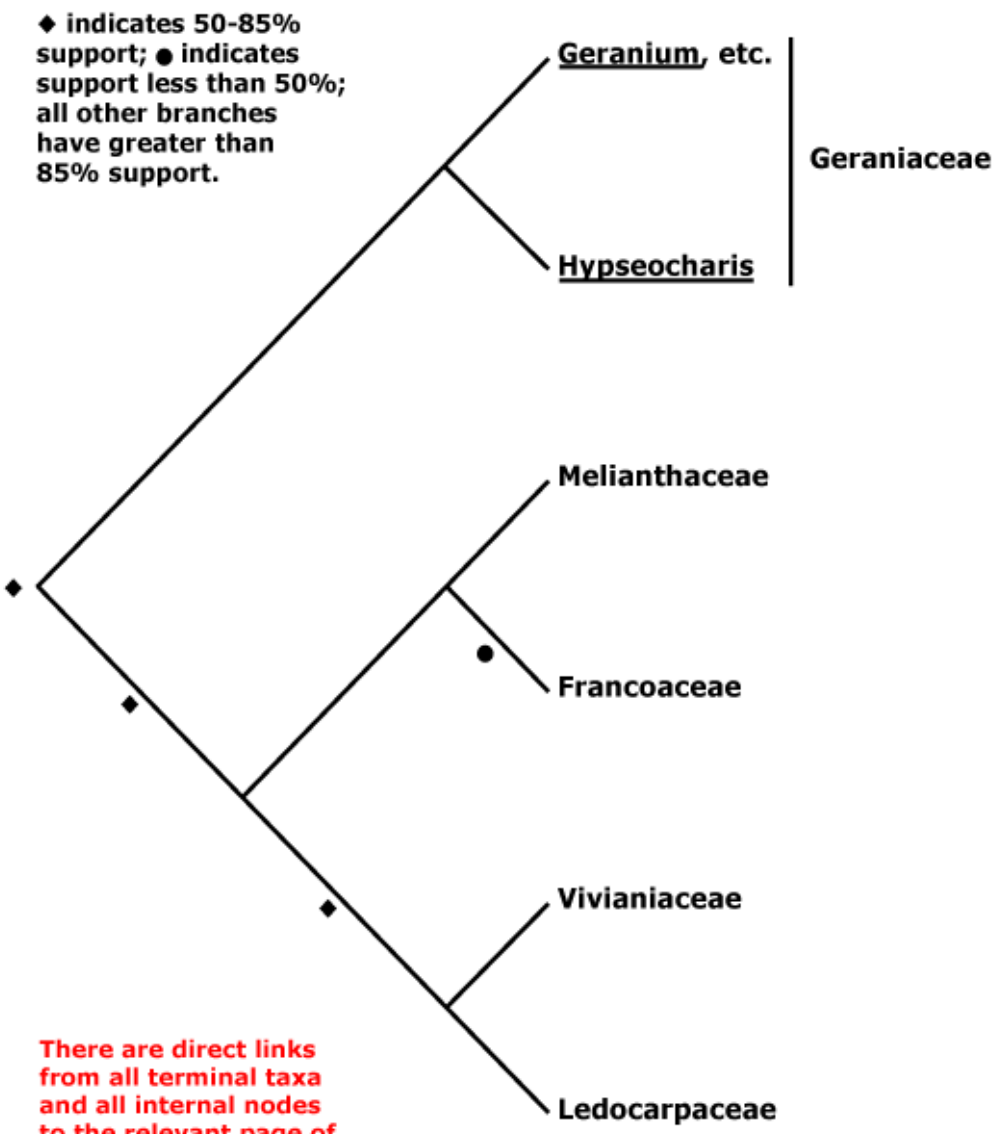
Pärisrosiidide II rühm ehk "malviidid"

- **Flavonoolid**
- Enamasti **üks emakakael**
- **Molekulaarsed tunnused**

Kurerehalaadsed Geraniales

Geraniaceae

- Näärmekarvad
- Lõhestunud lehed
- 10-15 tolmukat
- Sünkarpne emakkond ühe emakakaelaga



http://www.mobot.org/mobot/research/apweb/

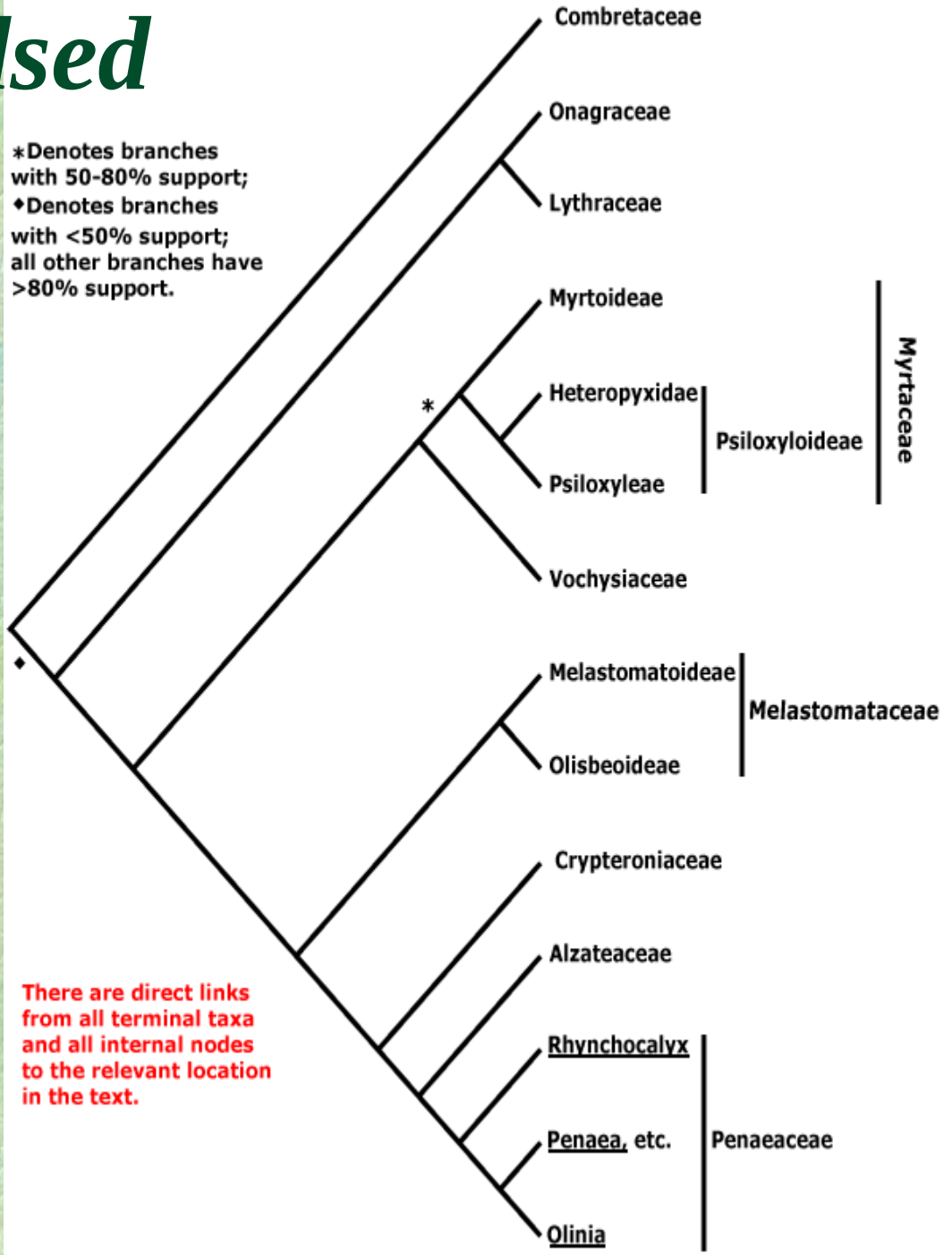
Kurerehalised

Geranium sanguineum

Pelargonium zonale

Mürdilaadsed
Myrtales

- Lehed vastakud
- Puit sisemise floeemiga
- Hüpantium nektaariumiga
- Tolmukad pungas painutatud



Mürdilised
Myrtaceae

Roodlehelised Melastomataceae

Kukesabalised Lythraceae


Peplis portula


Lythrum salicaria

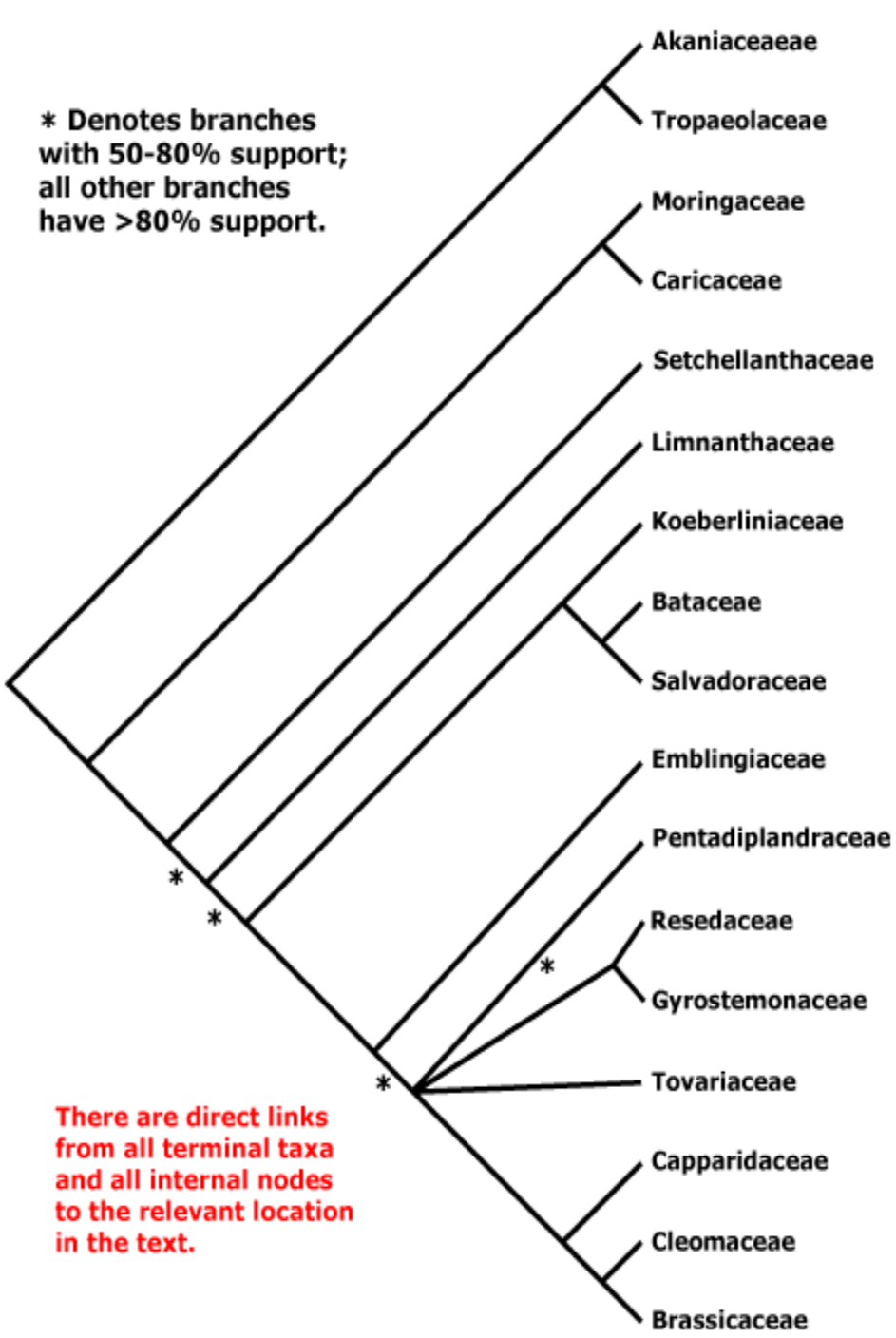
Pajulillelised
Onagraceae

Oenothera biennis

Epilobium angustifolium

Kapsa-laadsed Brassicales

- **Glükosinolaadid →** sinepiõlid mürosiinirakkudes
- **Õiekate** sageli **neljatine**



http://www.mobot.org/mobot/research/apweb/

Ristõielised Brassicaceae

- **Aktinomorfne lahklehine õis:** 4 tupplehte, 4 kroonlehte, 6 tolmukat, 2 viljalehte
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Waratah bud showing curved apical swelling

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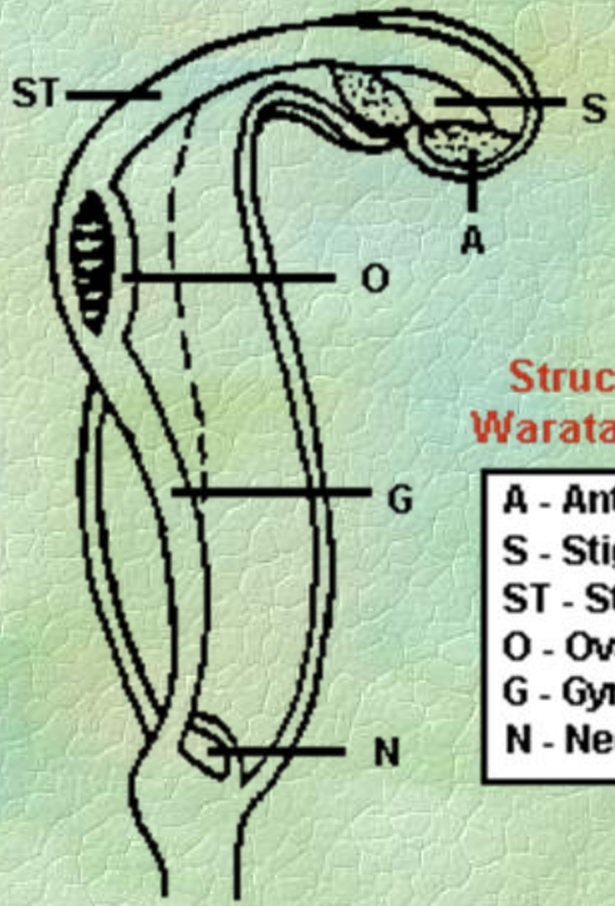

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O - Ovary
G - Gynophore
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Bud showing the "hook" typical of the Waratah and its allies

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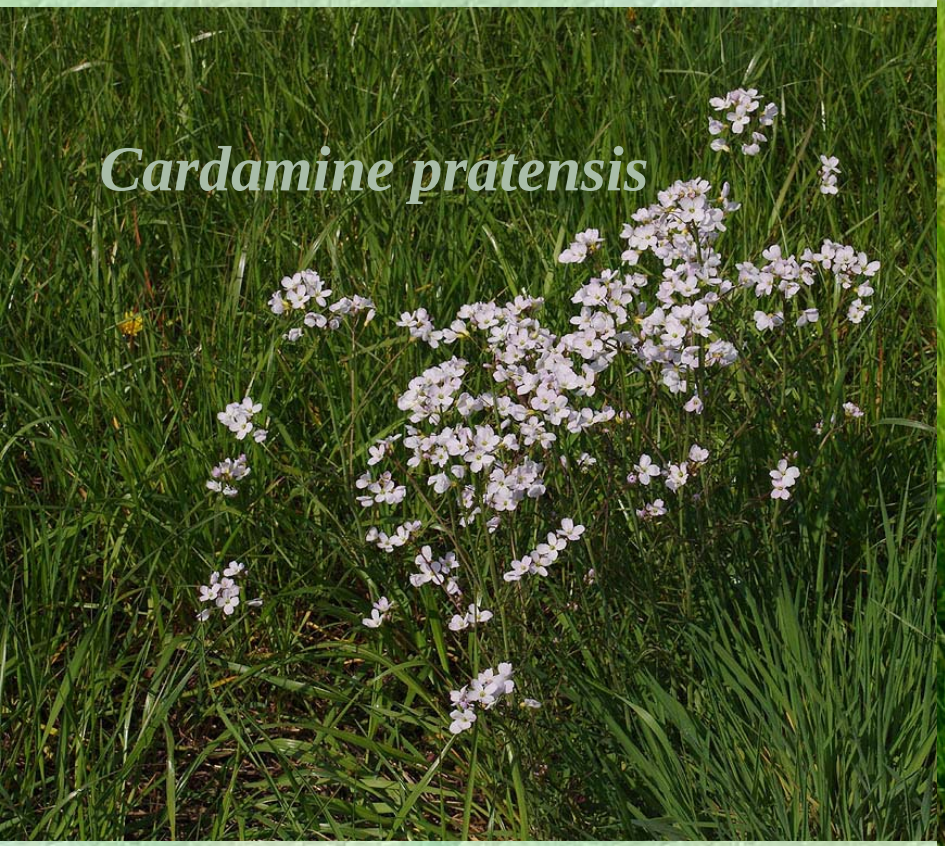
Harilik müürlook
Arabidopsis thaliana

Sinapis alba

Sinapis arvensis

Capsella bursa-pastoris

Crambe maritima


Cardamine pratensis

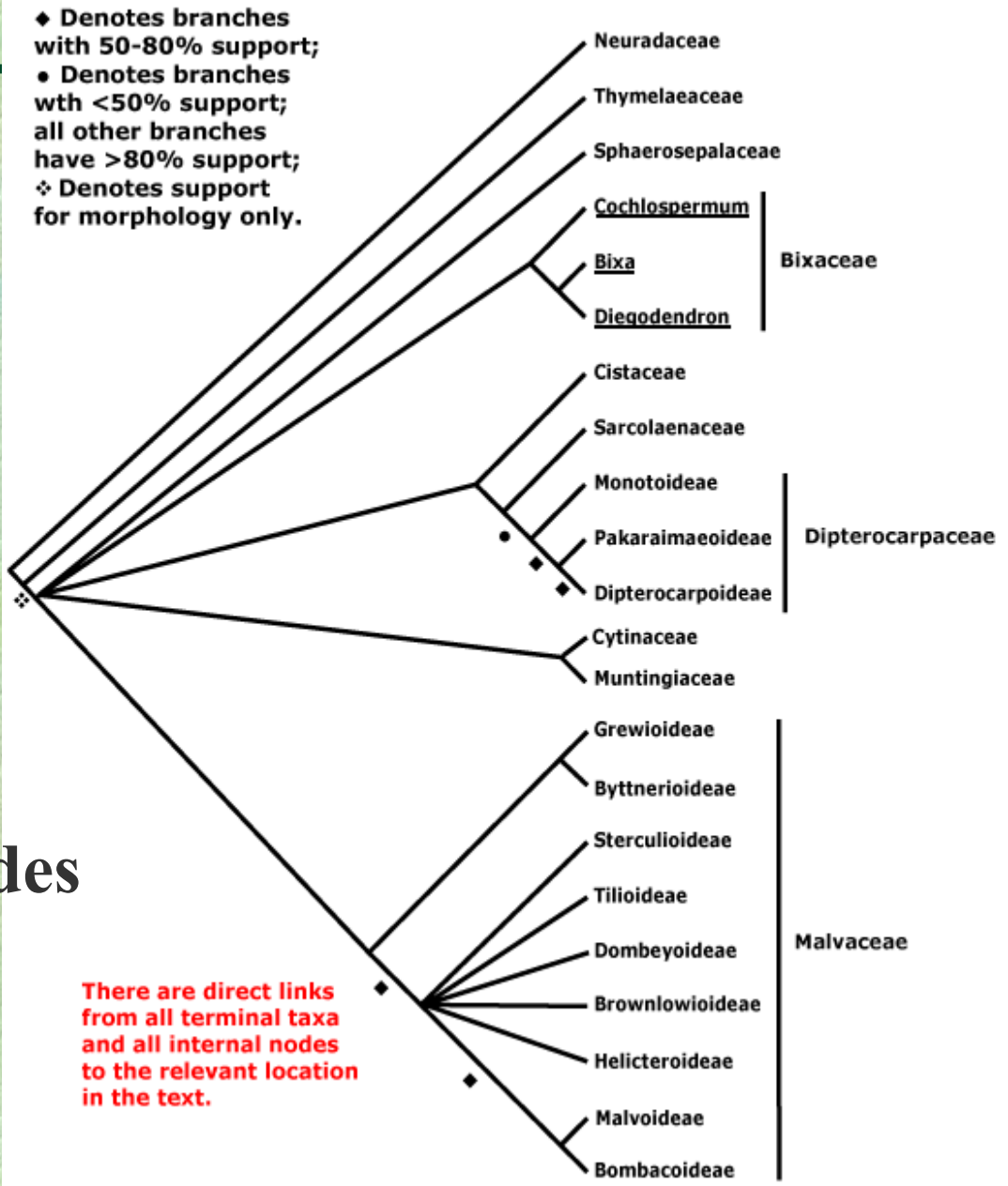

Bunias orientalis
Foto: Jan Wesenberg

Kapparilised
Capparidaceae

Capparis spinosa

Kassinaeri-laadsed Malvales

- Tähtkarvad
- Limarakud ja –kanalid
- Sõrmjad lehed
- Tolmukaid palju, kimpudes



http://www.mobot.org/mobot/research/apweb/

Kassinaerilised Malvaceae

Hibiscus

Malva

Cola

Gossypium hirsutum
Mo Fayyaz

Tilia cordata

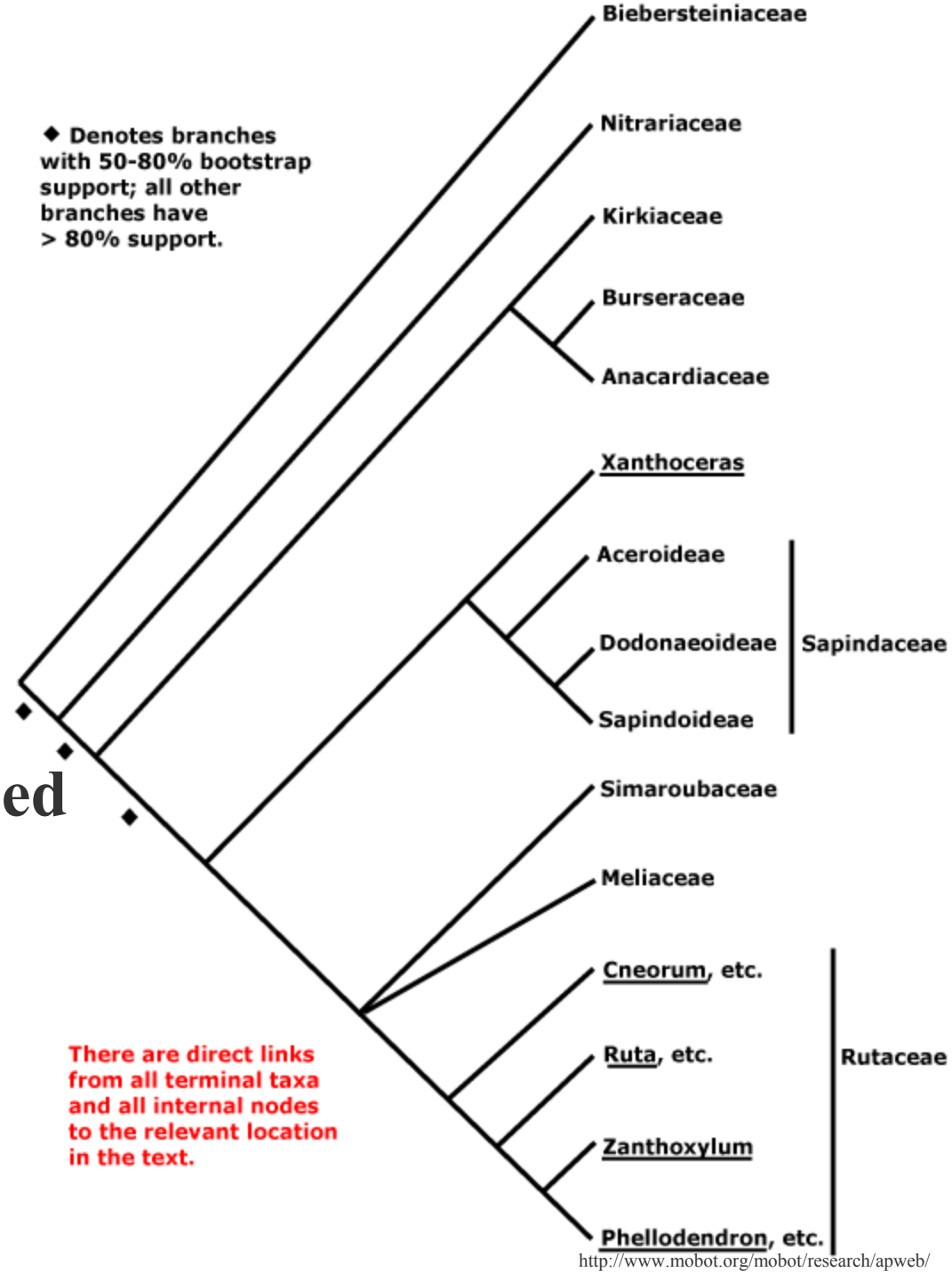
Theobroma

Kuldkannilised
Cistaceae

Helianthemum nummularium

Seebipuu-laadsed
Sapindales

- Puittaimed
- Liit- või lõhestunud lehed
- Õied nektarikettaga



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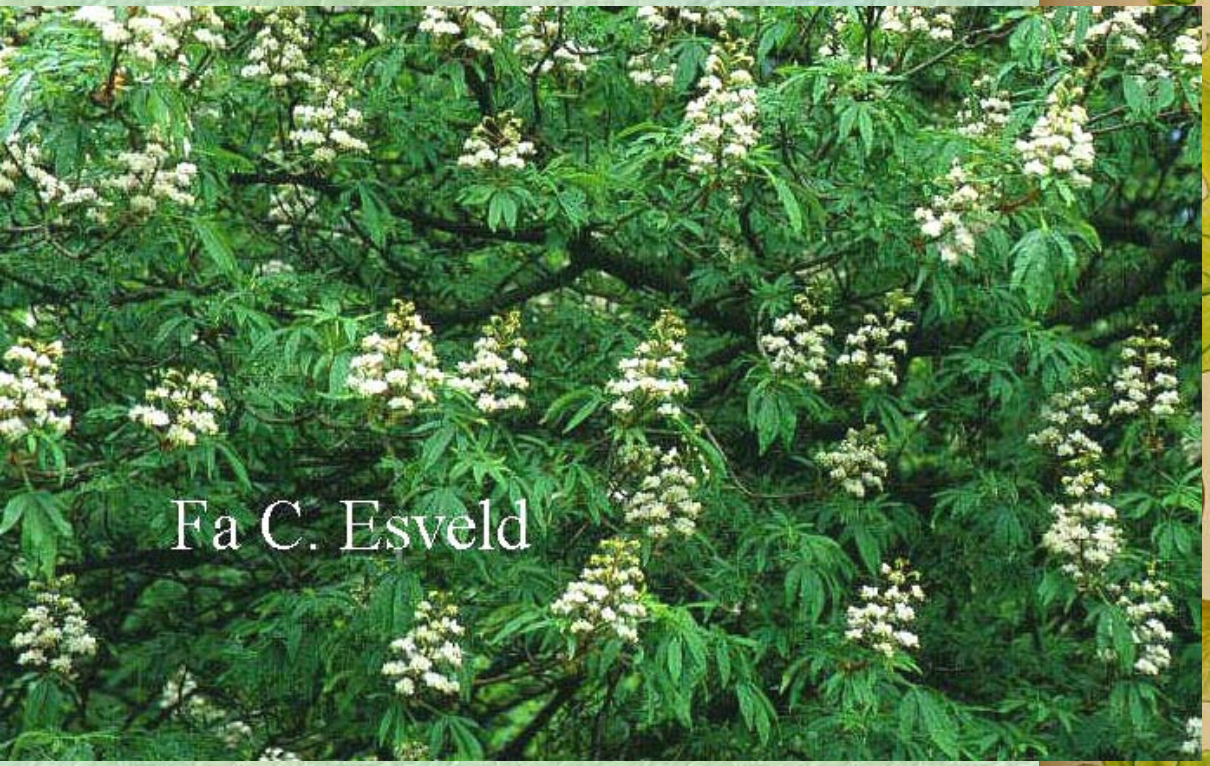
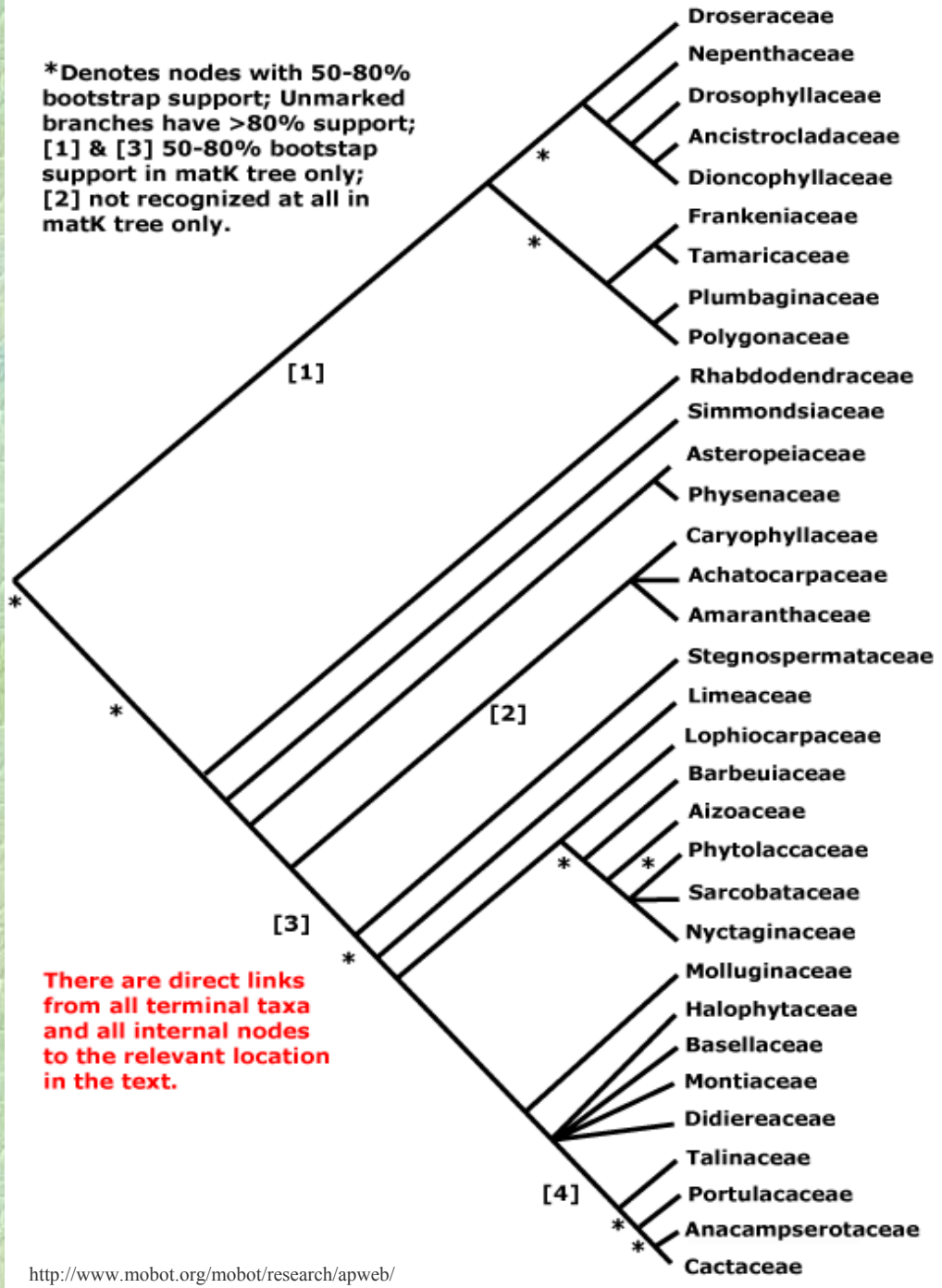
Seebipuulised
Sapindaceae



Ana-kardilised Anacar-diaceae

Ruudilised
Rutaceae

Nelgi-laadsed Caryo-phyllanae



http://www.mobot.org/mobot/research/apweb/

Nelgilaadsed

- Antotsüaniinide asemel sageli **betalaiinid**
- **Sigimik** sageli **ühepesaline**
- Platsentatsioon tsentraalne vaba või basaalne
- **Perisperm tärkliserohke**
- Enamasti **terved lehed**
- Sageli **üks ring õiekattelehti**
- **Puudub mükoriisa**

Tatralised Polygonaceae

Fagopyron esculentum

Rheum rhabarbarum

Foto: Anna-Lena Anderberg


Rumex acetosa


Polygonum bistorta
Foto: Trond Steen

Huul-heinalised Droseracea

Drosera rotundifolia

Tinajuurelised Plumbaginaceae

Limonium ja *Armeria*

Nelgilised Caryophyllaceae

- **Rohttaimed**
- Lihtsad **vastakud lehed**
- **Viietised aktinomorfsed õied**, diferentseerunud tupp ja kroon
- **Ebasarikõisik**
- **Antotsüaniinid**
- Eestis 18 perekonda, 52 liiki
- *Stellaria* 9, *Silene* 8
- *Cerastium* 5, *Dianthus* 4
- *Sagina, Spergularia, Lychnis, Gypsophila* 3

Nelgilised

Silene cucubalus

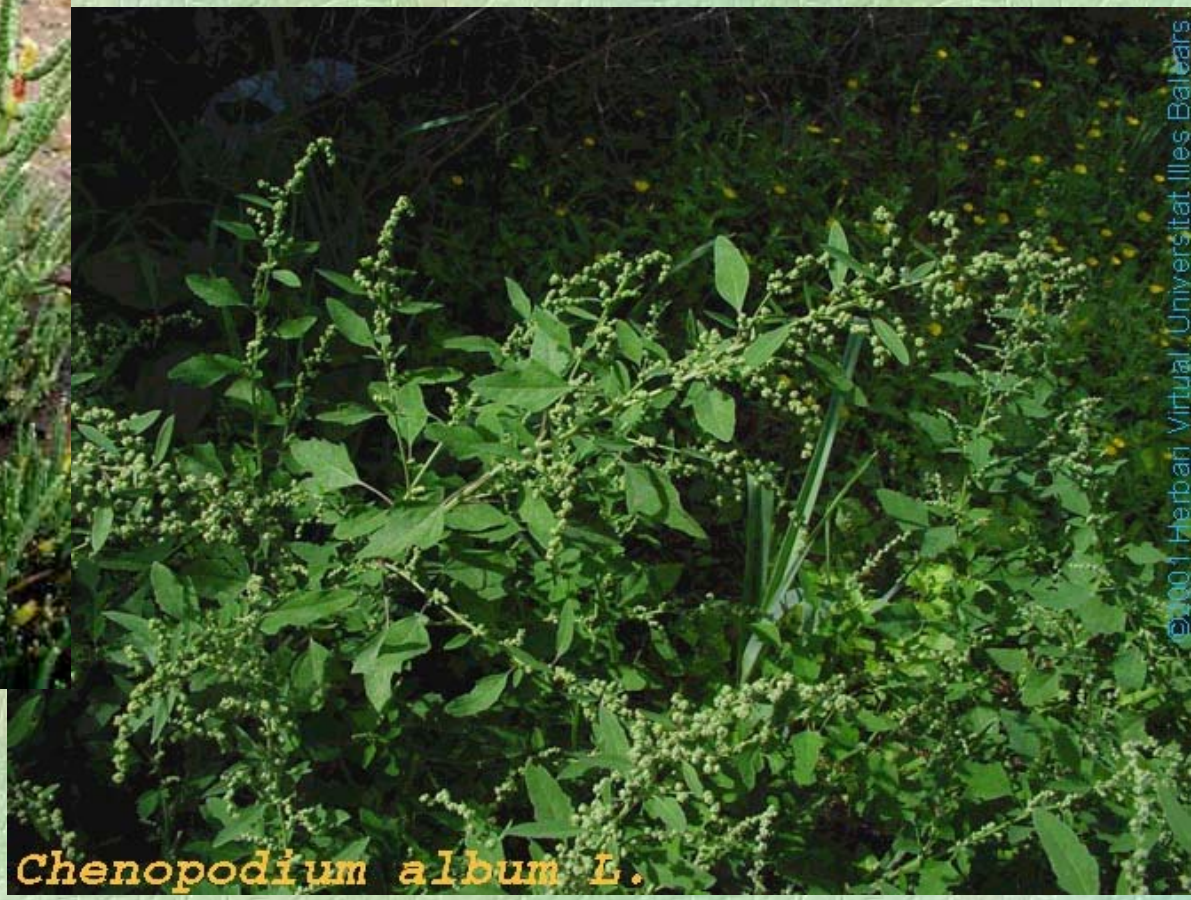
Stellaria media

Nelgilised

Dianthus arenarius

Rebasheinalised Amaranthaceae

Salicornia europaea

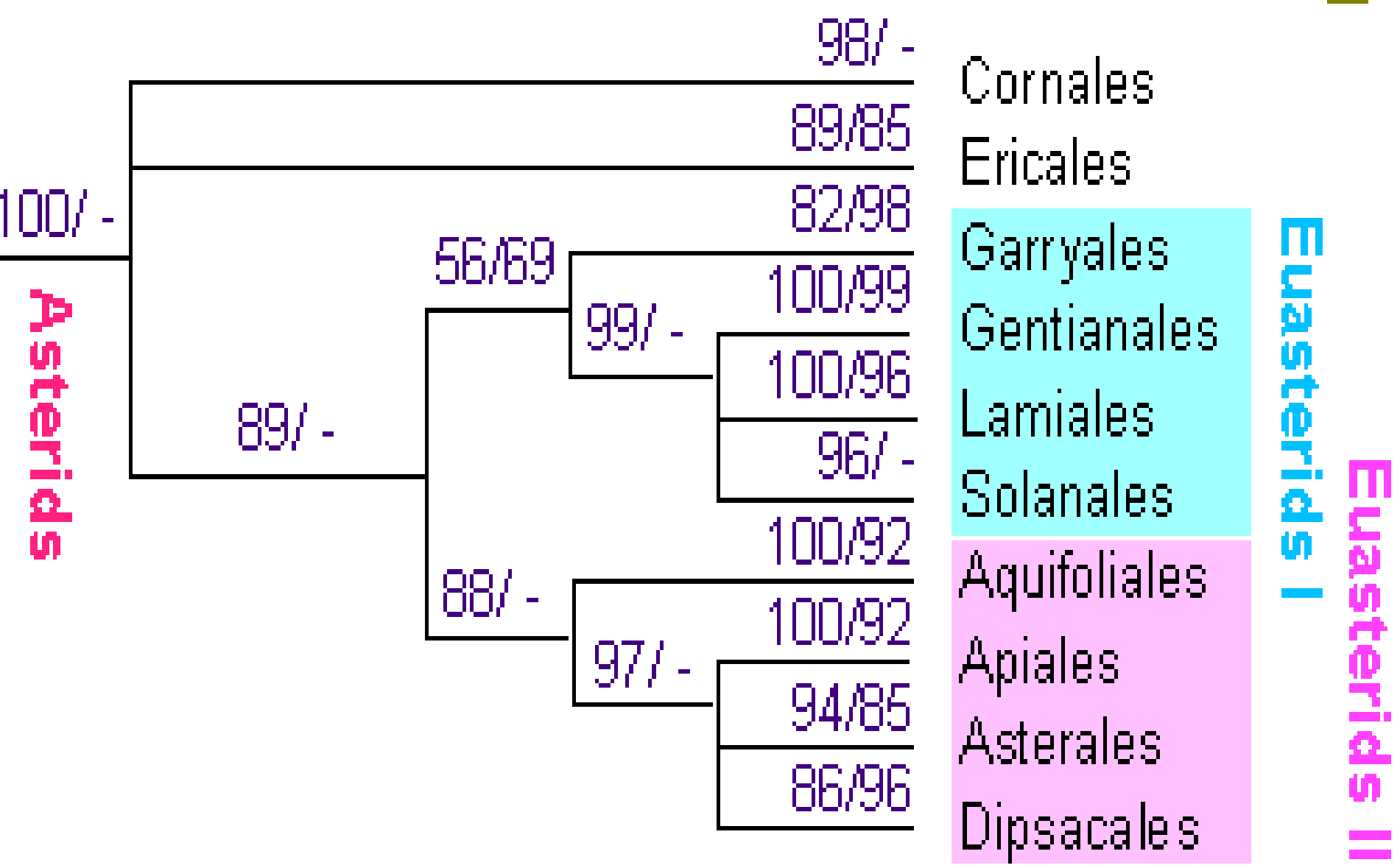


Kaktuselised
Cactaceae

Kann-taimelised
Nepenthaceae

Asteriidid Asteranae

- Enamik **rohttaimed**
- **Kroonlehed** enamasti **kokku kasvanud**
- Paljudel **kahest viljalehest emakkond**
- **Väikese nutselliga ühekattelised seemnealgmed**
- Enamasti **tsellulaarne endosperm**
- Paljudel **iridoiidid**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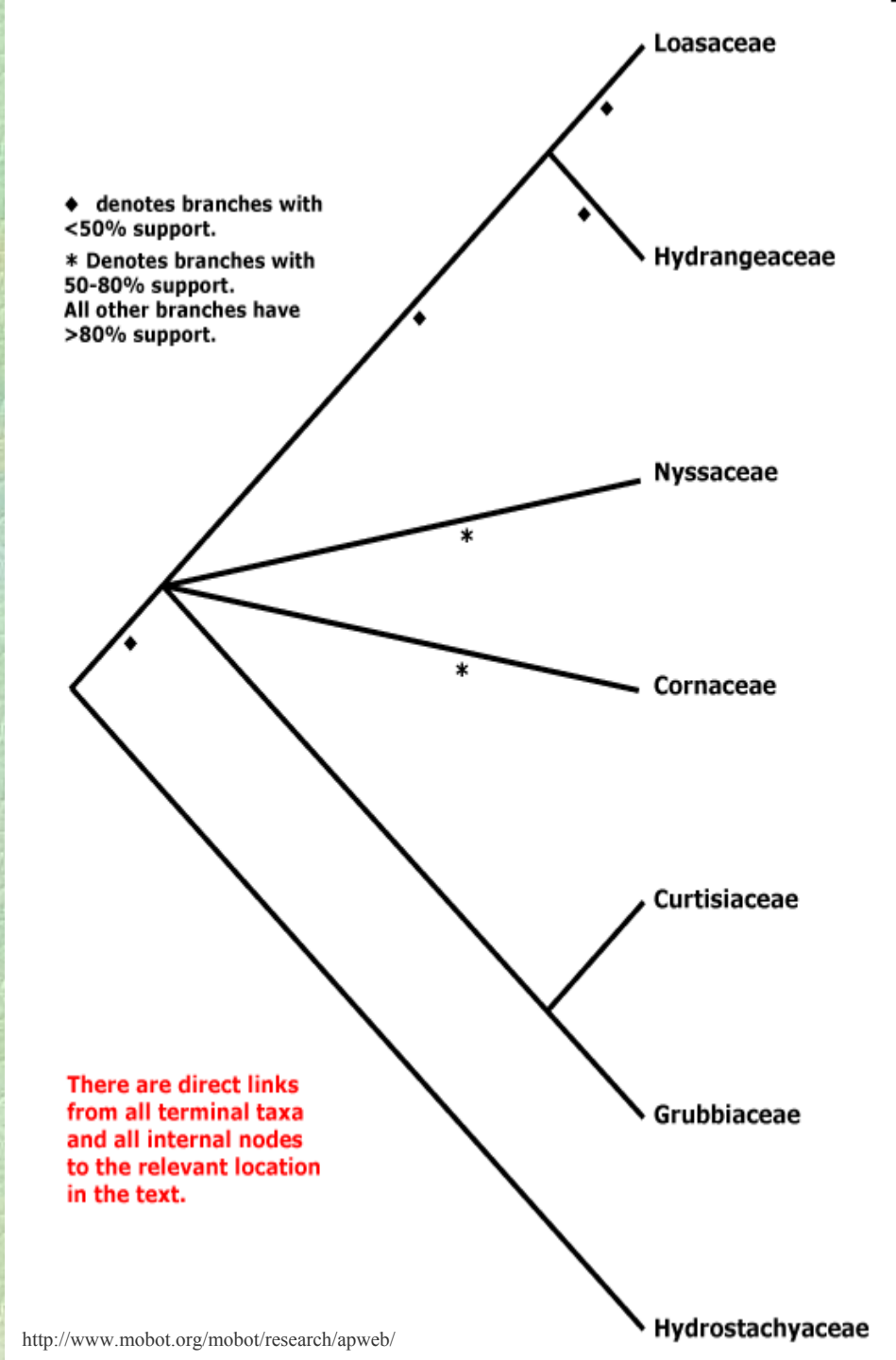
88/ -
97/ -
100/ -
Asterids
Cornales
Ericales
Garryales
Gentianales
Lamiales
Solanales
Aquifoliales
Apiales
Asterales
Dipsacales
Euasterids I
Euasterids II

Kontpuu-laadsed *Cornales*

Cornaceae:

- **Vastakud lihtsad lehed**
- **Õied väikesed, neljatised**
- **Kroonlehed vabad**
- **Suured õisikud**
- **Luuvili**



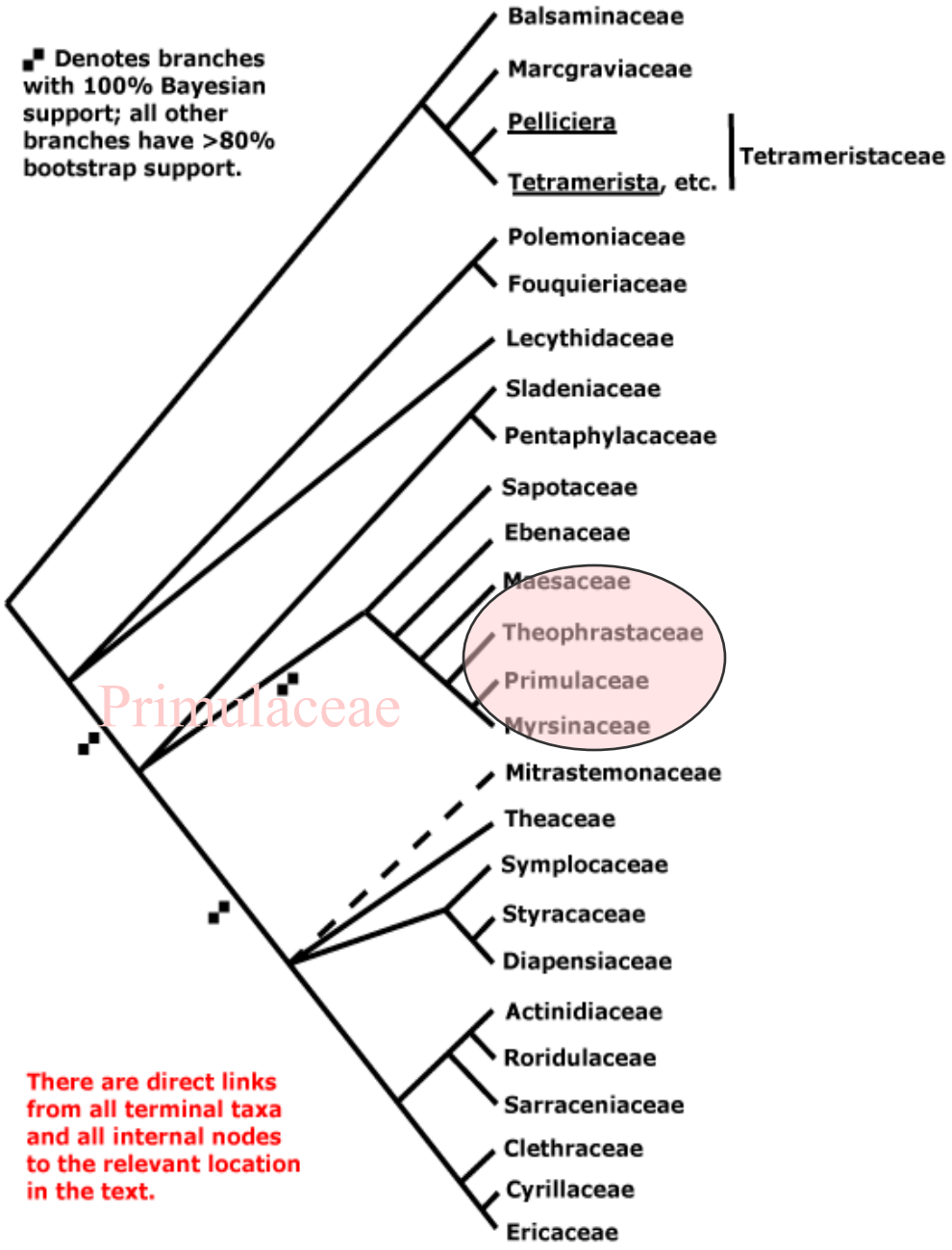
http://www.mobot.org/mobot/research/apweb/

Chamae-periclymenum suecicum

Cornus sanguinea

Kanarbiku-laadsed *Ericales*

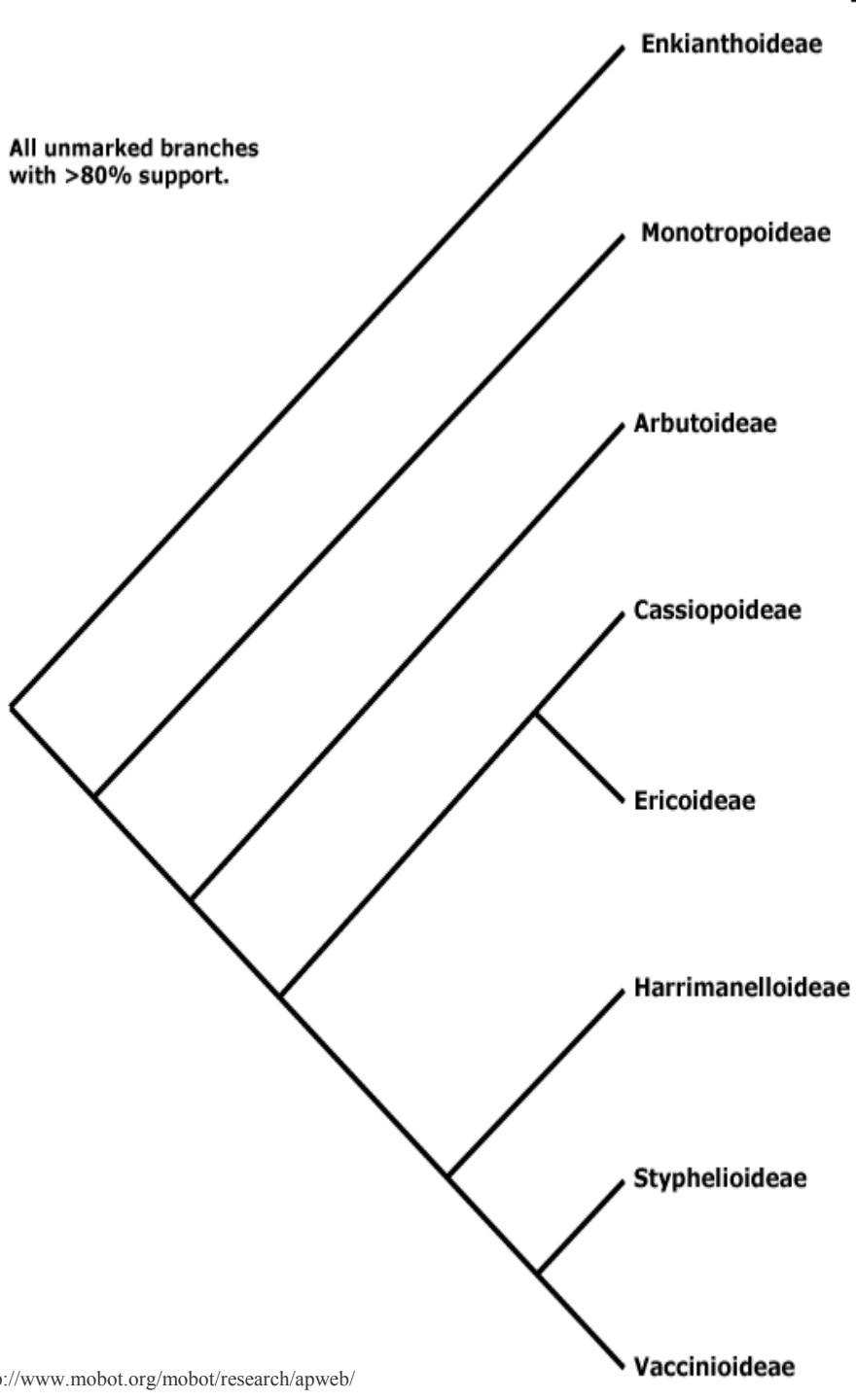
- Enamasti **puitunud**
- **Lihtsad vahelduvad lehed** eriliste hammastega
- Enamik **aktinomorfse õiega**
- **Palju tolmukaid**



http://www.mobot.org/mobot/research/apweb/

Kanarbiku-lised *Ericaceae*

- **Puittaimed**
- **Erikoidsed lehed**
- **Aktinomorfsed õied**
- **Kokkukasvanud kroon**
- **10 tolmukat**
- **Erikoidne mükoriisa**
- Eestis 20 liiki



http://www.mobot.org/mobot/research/apweb/

Ericoideae: Rhododendron


© - josef hlasek
www.hlasek.com
Empetrum hermaphroditum 4745


Calluna vulgaris


Erica tetralix
Foto: Norman Hagen

Vaccinioideae

Monotropoideae

Pyrola rotundifolia

Nurmenukulised Primulaceae

Primula veris

Androsace septentrionalis


Lysimachia vulgaris
Foto: Jan Wesenberg


Glaux maritima


Trientalis europaea

Ebenaceae *ja* Sapotaceae

Diospyros kaki

Pouteria sapota

Sarraceniaceae *ja* Theaceae

Sarracenia

Camellia sinensis

Balsaminaceae *ja* Polemoniaceae

Impatiens noli-tangere

Foto: Jan Thomas Johansson

Polemonium caeruleum

Pärisasteriidide I rühm ehk lamiidid

- **Molekulaarsed tunnused**
- **Trahheed lihtsate perforatsioonplaatidega**
- Enamasti **vastakud lehed**
- **Kaks viljalehte**
- **Nektaridisk**

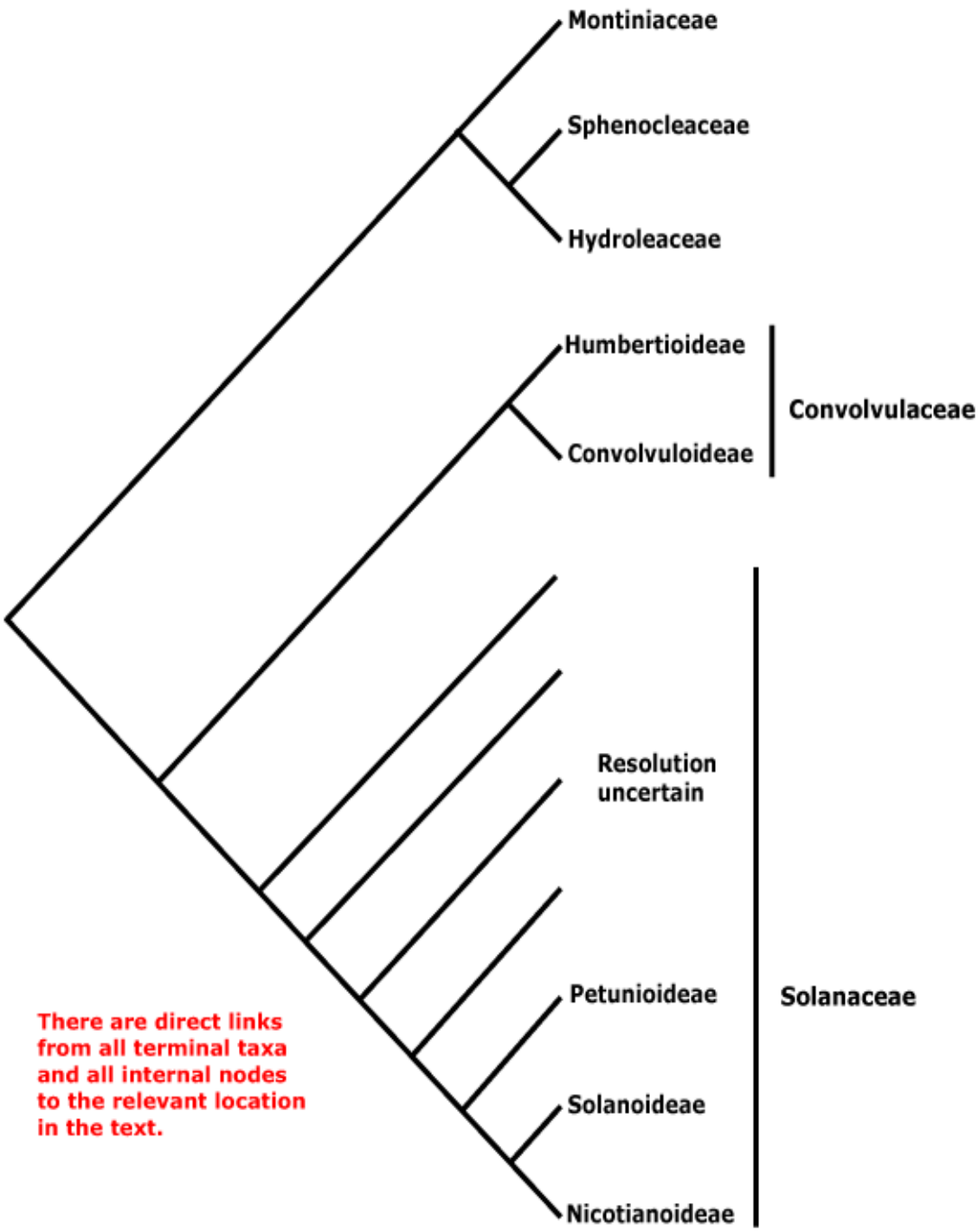
Boraginaceae *karelehelised*

- **Asetamata sugukond**
- **Jäigad karvad**
- Spiraalsed või sirpjad **ebasarikõisikud**
- **2pesaline, 4pesaliseks muutuv sigimik**
- **Laguvili või luuvili**
- Eestis 22 liiki, 13 perek
- *Myosotis* 7

Boraginacea

Maavitsa-laadsed *Solanales*

- Lehed vahelduvad
- Alkaloidid



http://www.mobot.org/mobot/research/apweb/

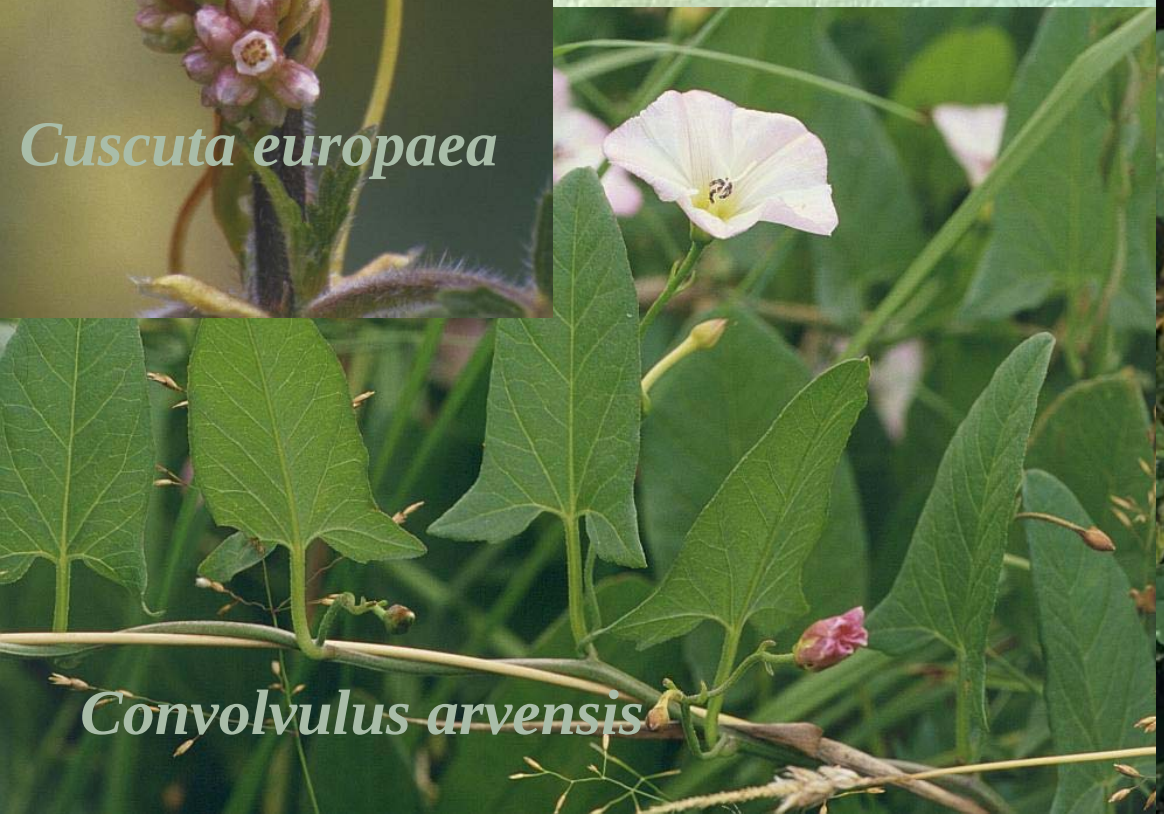
Maavitsalised Solanaceae

Solanum dulcamara, tuberosum, lycopersicum

Hyoscyamus niger

Convolvulaceae

Cuscuta europaea

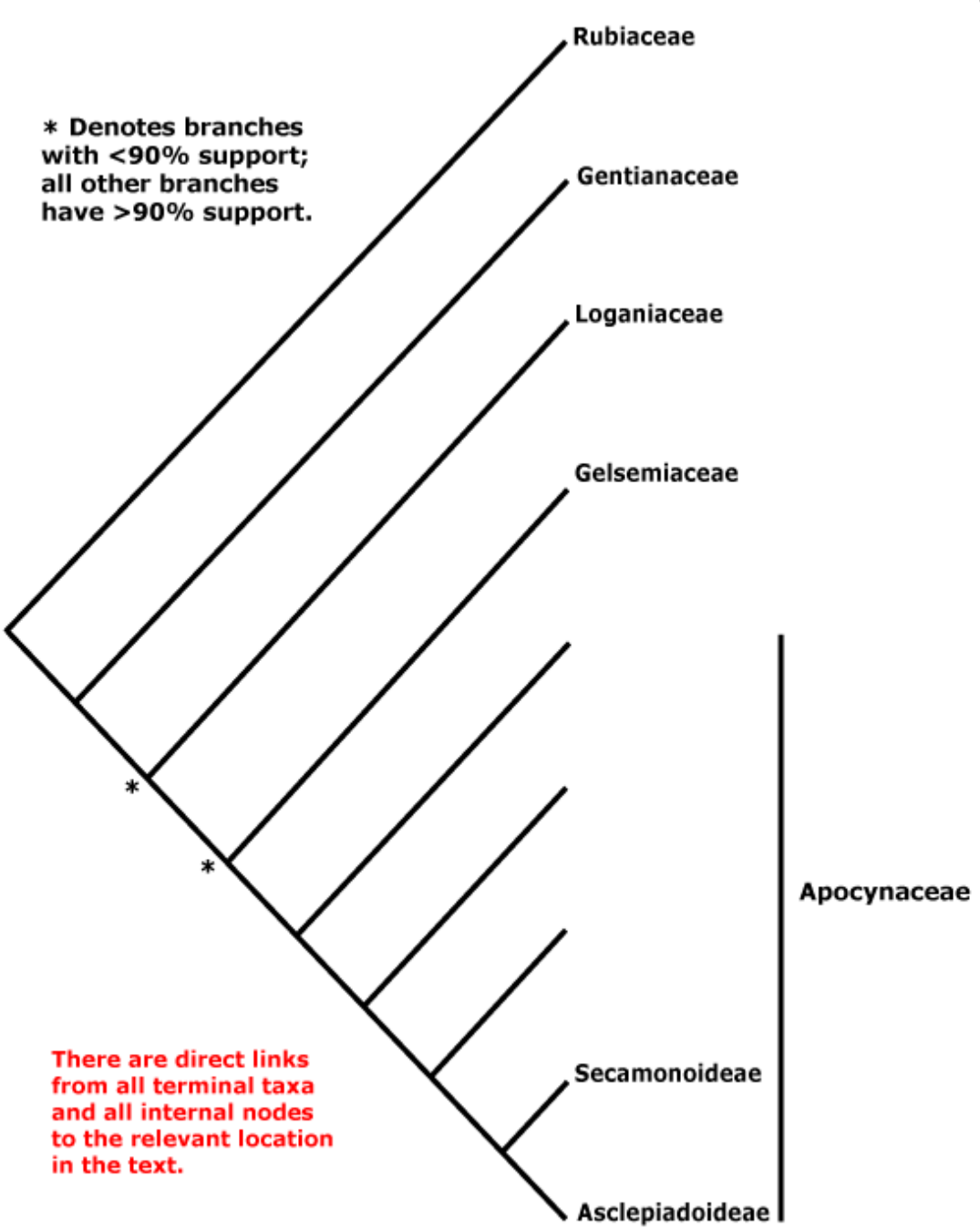


Convolvulus arvensis

Ipomoea

Emajuure-laadsed Gentianales

- **Alkaloidid**
- **Vastakud lehed**
- **Näärmed**
- **Puit** sageli **sisemise floeemiga**



http://www.mobot.org/mobot/research/apweb/

Madaralised Rubiaceae

- **Vastakud, abilehtedega lehed**
- **Alumine sigimik**
- Maailmas neljas, 10 000 liiki
- Eestis 4 perek, 21 liiki
- *Galium* 16

Psychotria

Coffea arabica

Emajuurelised
Gentianaceae

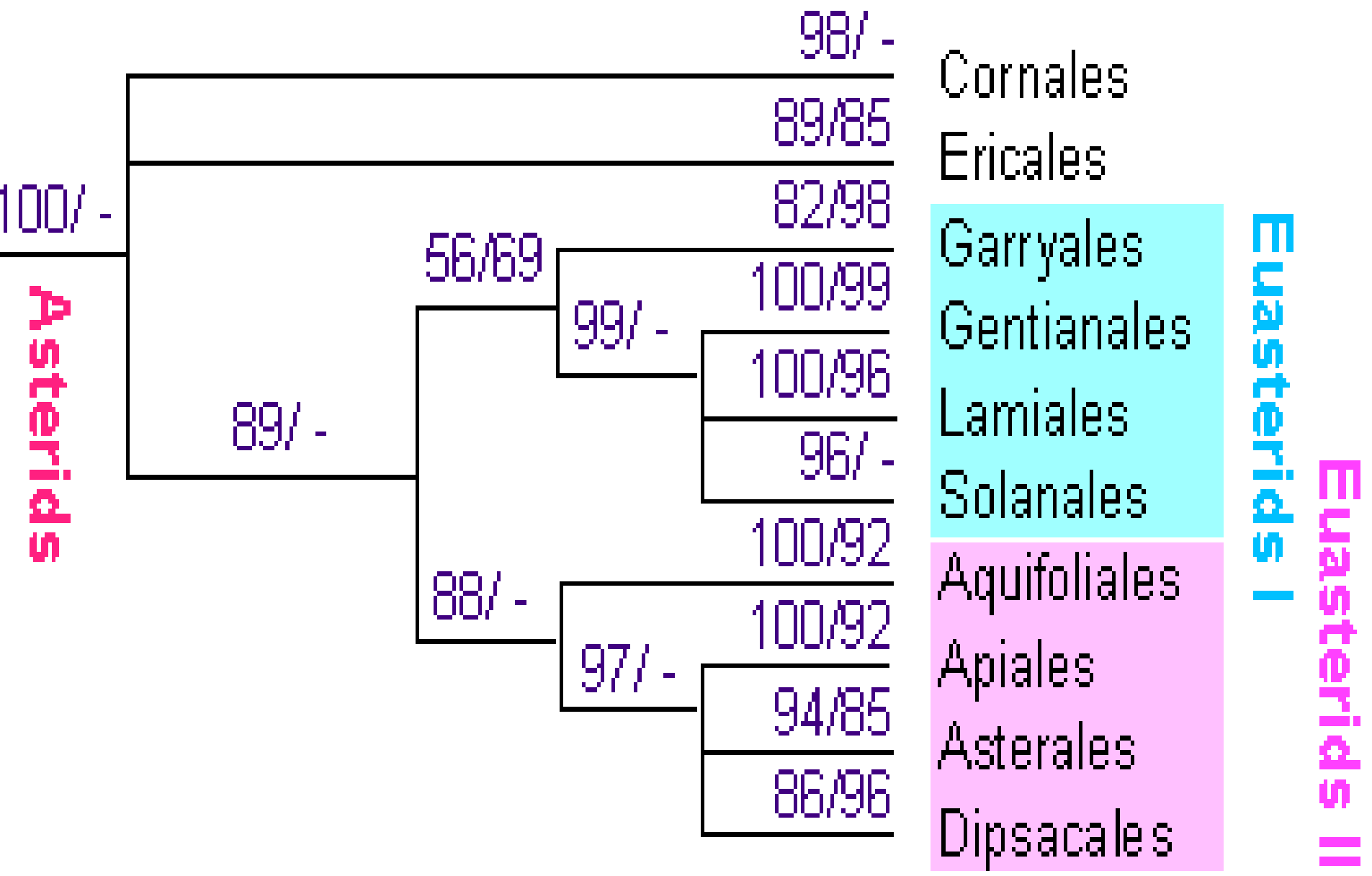
Koera-koolulised
Apocynaceae


Vinca minor

Asclepias

Apocynum

Asteriidid (järg)
Asteranae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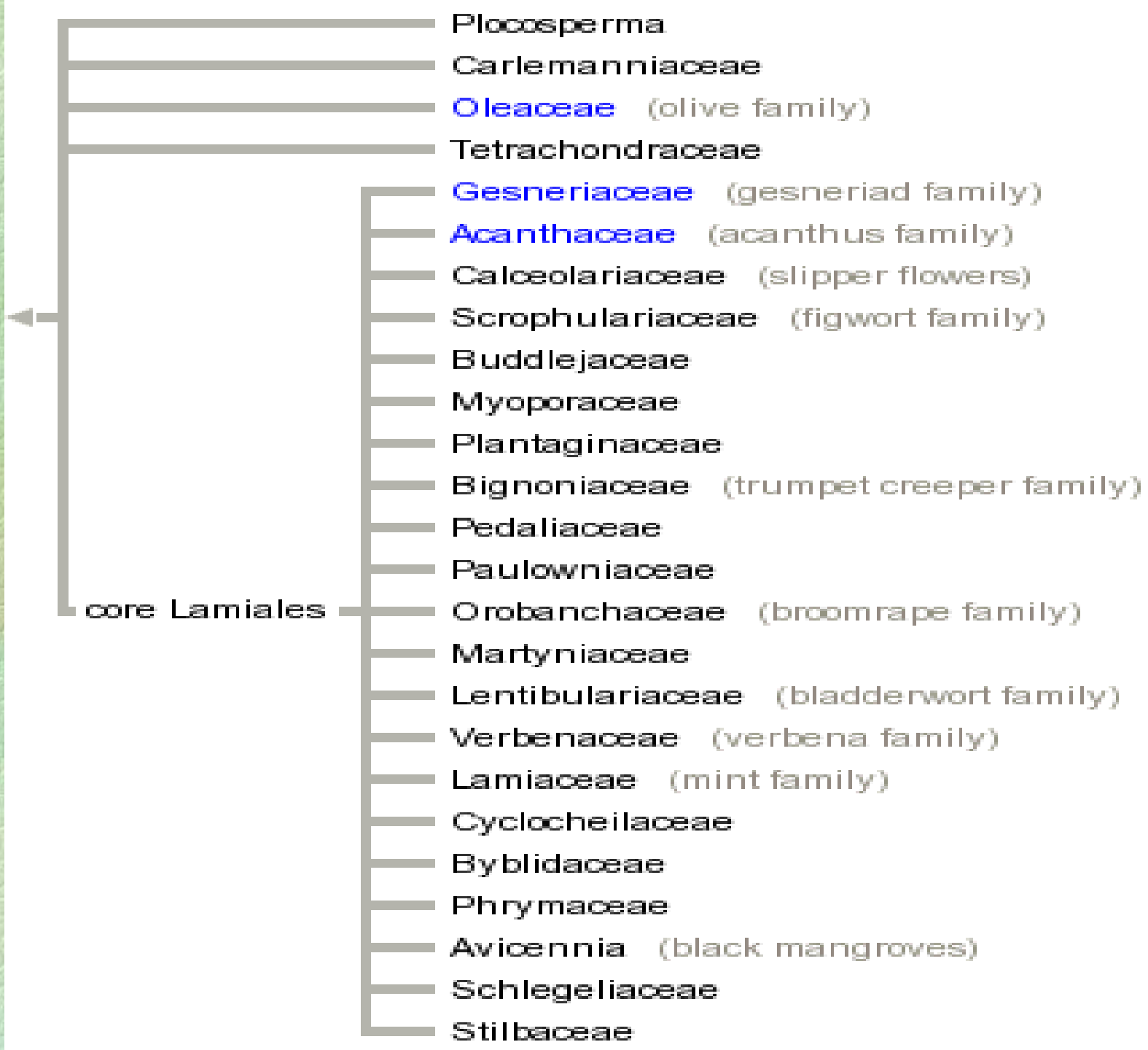
86/96
Cornales
Ericales
Garryales
Gentianales
Lamiales
Solanales
Aquifoliales
Apiales
Asterales
Dipsacales
Asterids
Euasterids I
Euasterids II

Pärisasteriidide I rühm ehk lamiidid (järg)

- Molekulaarsed tunnused
- Trahheed lihtsate perforatsioonplaatidega
- Enamasti vastakud lehed
- Kaks viljalehte
- Nektaridisk
- *Boraginaceae, Gentianales, Solanales, Lamiales*

Iminõgeselaadsed *Lamiales*

- Enamasti **vastakud lehed**
- **Sügomorfsed õied**
- Sageli värvunud kõrglehed
- **Tolmukaid 4 või 2,** spetsiifilise ehitusega
- **Näärmekarvad**
- Keemilised, embrüoloogilised, molekulaarsed tunnused


Ploccosperma
Carlemanniaceae
Oleaceae (olive family)
Tetrachondraceae
Gesneriaceae (gesneriad family)
Acanthaceae (acanthus family)
Calceolariaceae (slipper flowers)
Scrophulariaceae (figwort family)
Buddlejaceae
Myoporaceae
Plantaginaceae
Bignoniaceae (trumpet creeper family)
Pedaliaceae
Paulowniaceae
core Lamiales
Orobanchaceae (broomrape family)
Martyniaceae
Lentibulariaceae (bladderwort family)
Verbenaceae (verbena family)
Lamiaceae (mint family)
Cyclocheilaceae
Byblidaceae
Phrymaceae
Avicennia (black mangroves)
Schlegeliaceae
Stilbaceae

Õlipuulised
Oleaceae

Gesneerialised *Gesneriaceae* ja karusõralised *Acanthaceae*

Streptocarpus

Scrophulariaceae
sealõuarohulised

Sügomorfne kokkukasvanud krooniga õis

Teelehelised *Plantaginaceae*

- **Rohttaimed**
- Sügomorfsed (kahehuulelised) kuni peaaegu aktinomorfsed õied
- **Seinavanev kupar**
- **Spetsiifilised näärmekarvad**
- Maailmas ca 2000, Eestis 32 liiki
- *Veronica* 16, *Plantago* 6


Linaria vulgaris


Veronica officinalis
Foto: Norman Hagen


Plantago major
©Cavy Things - http://cavies.lightskies.net/

Digitalis purpurea

Antirrhinum

Soomukalised *Orobanchaceae*

- **Parasiidid või poolparasiidid**
- **Viietised sügomorfsed (kahehuulelised) õied kobarõisikus**
- Maailmas ca 2000, Eestis 25 liiki
- *Euphrasia* 8 (1), *Melampyrum* 5, *Orobanche* 4, *Rhinanthus*, *Odontites* 3, *Pedicularis* 2

Euphrasia officinalis

Pedicularis palustris

Melampyrum nemorosum

Orobanche elatior

Rhinanthus osiliensis

Huulõielised *Lamiaceae*

- **Aromaatsed näärmekarvadega**
- **Vastakud hambulised lehed**
- **Neljakandilised varred**
- **Kahehuulelised õied** ebasarikates, 2-4 tolmukat
- **Kahest viljalehest neljapesaline emakas**, laguvili
- Maailmas ca 7000, Eestis 46 liiki
- *Mentha* 6, *Lamium*, *Galeopsis* 5, *Stachys* 4


Thymus serpyllum

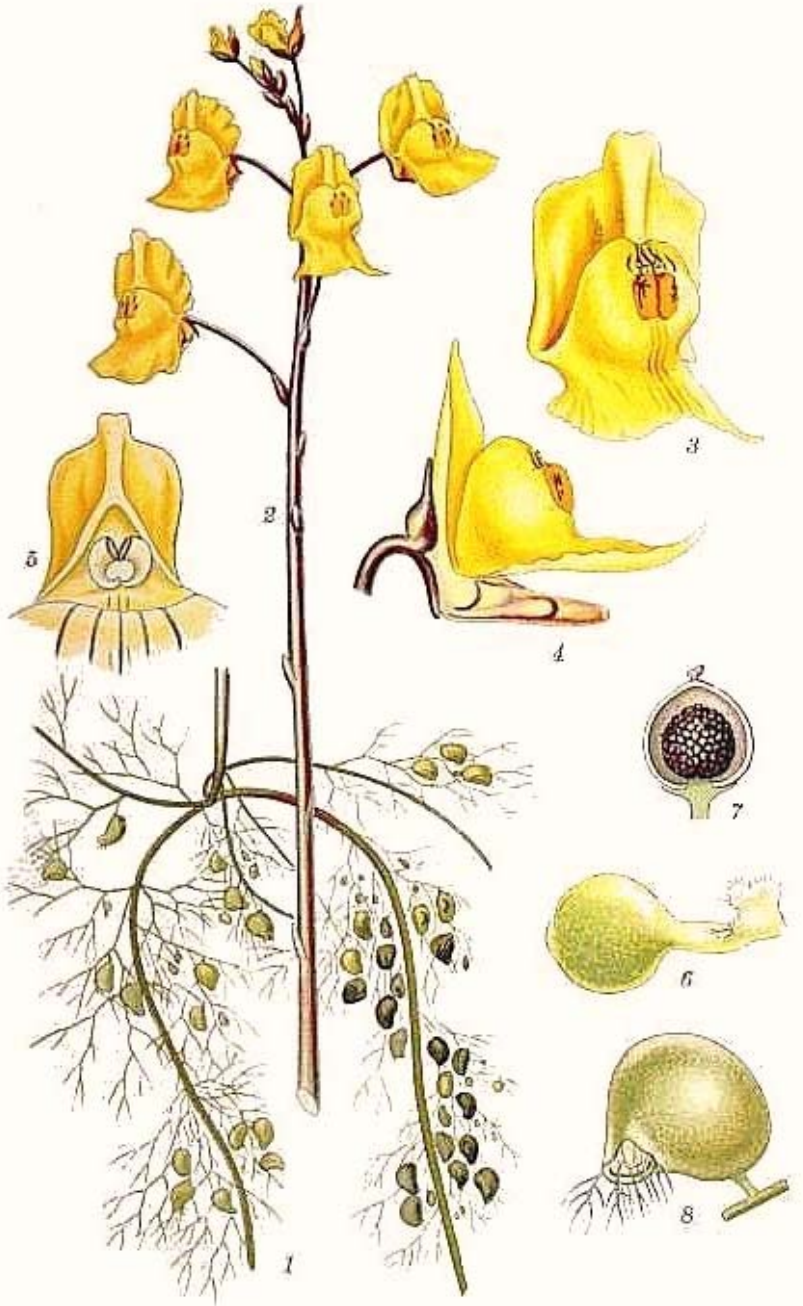

Mentha aquatica


Lamium album
Foto: Jan Wesenberg
Lamium album


Glechoma hederacea

Vesihernelised
Lentibulariaceae

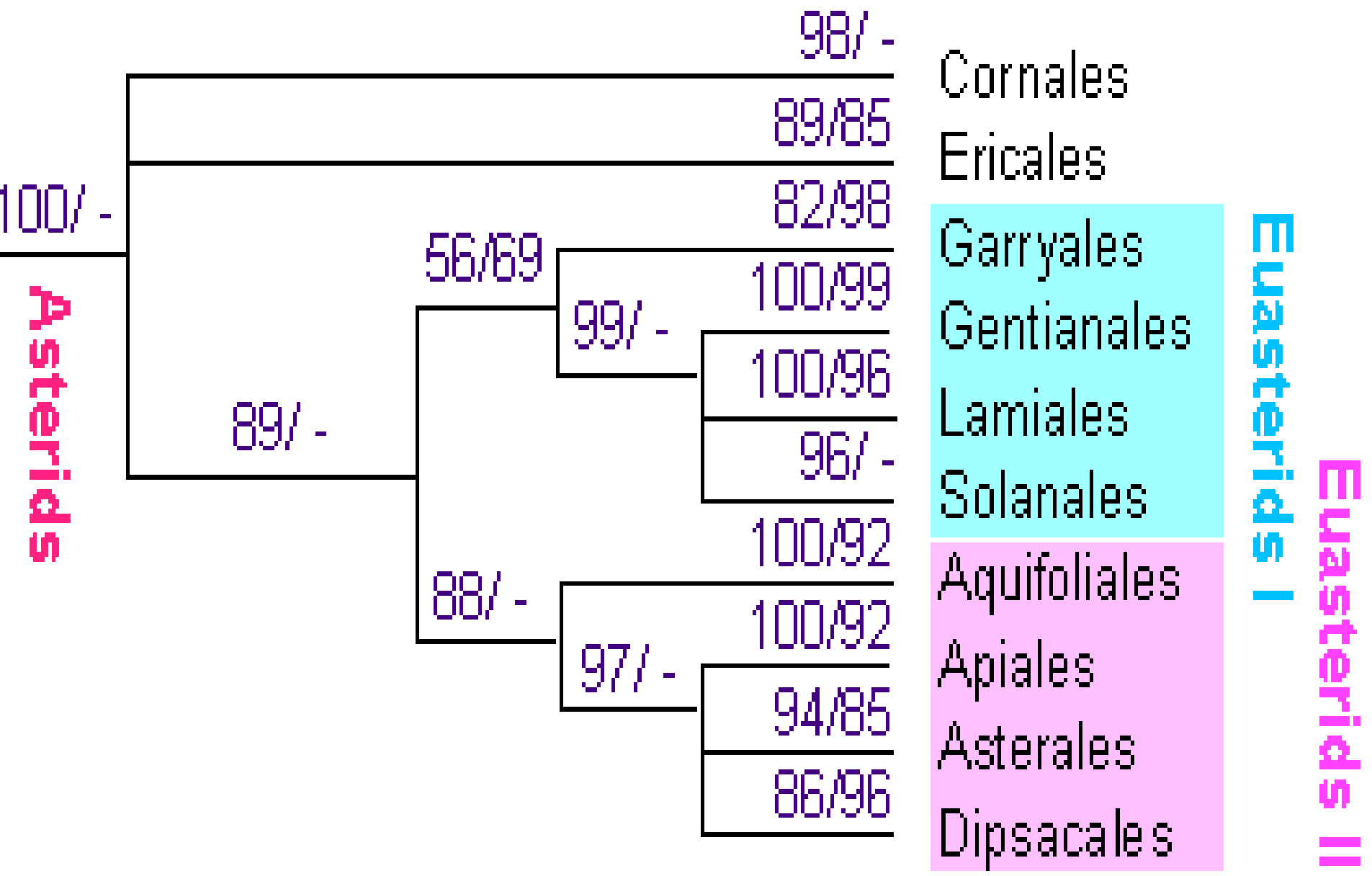
http://commons.wikimedia.org/wiki/Category:Utricularia_australis



BLÅSÖRT, UTRICULARIA MAJOR SCHMID.

Pärisasteriidide II rühm ehk “kampanuliidid”

- Enamus **rohttaimed**
- Enamasti **vahelduvad lehed**
- Õie ontogeneesi tunnused
- **Alumine sigimik** (epigüünne õis)
- Polüatsetüleenid ja seskviterpeenid iridoiidide asemel
- Molekulaarsed tunnused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Cornales
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Lamiales
Solanales
Aquifoliales
Apiales
Asterales
Dipsacales
Asterids
Euasterids I
Euasterids II

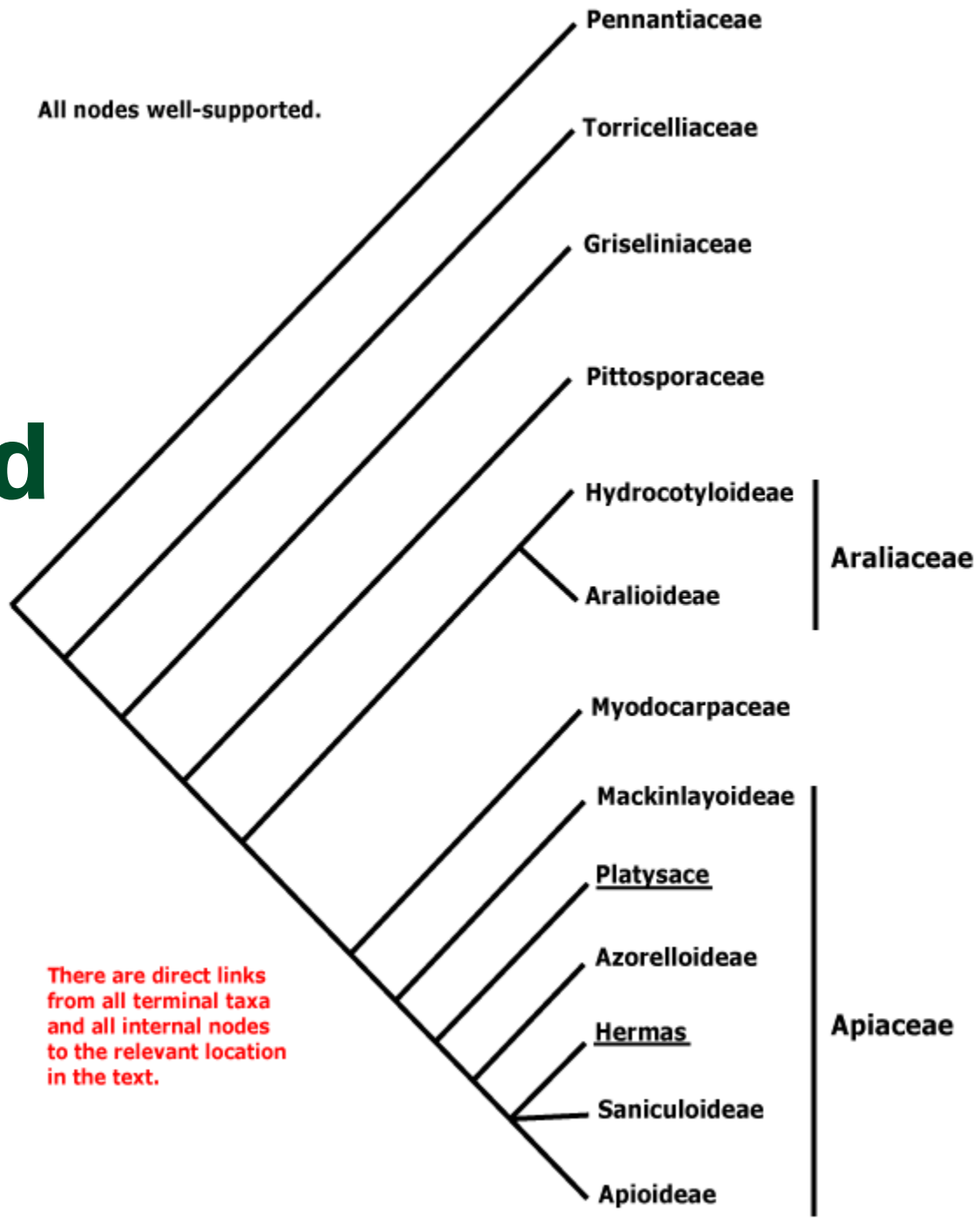
Astelpõõsalaadsed *Aquifoliales, Aquifoliaceae*

- Puittaimed
- Ühesugulised ülemise sigimikuga õied
- 1/450: *Ilex*

Sellerilaadsed *Apiales*

- Liit- või lõhestunud lehed
- **Erituskanalid**
- **Sarikõisik**
- **Kroonlehed vabad**
- **Stülopood**

Sellerilaadsed
Apiales



http://www.mobot.org/mobot/research/apweb/

Araalialised
Araliaceae

Sarikalised *Apiaceae*

- **Rohttaimed**
- (enamasti **liit)sarikas**
- **Kaksikseemnis**
- Enamasti liitlehed
- Erituskanalid
- Maailmas ca 3000,

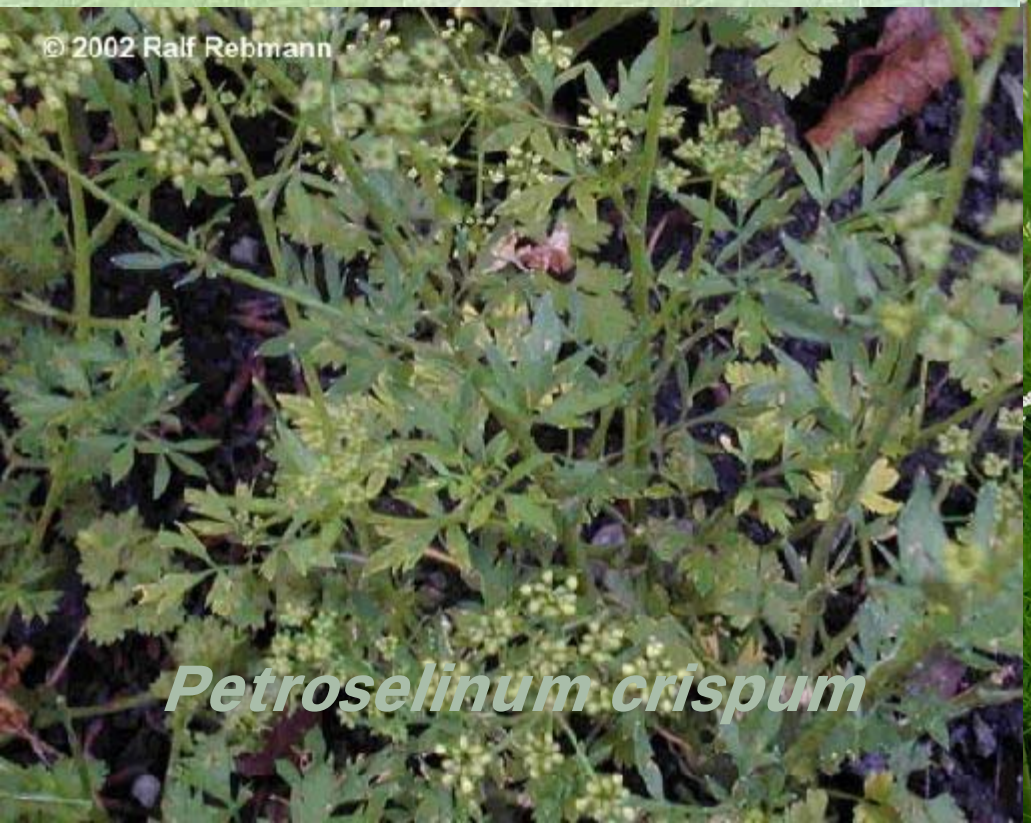
Eestis 43 liiki

Saniculoideae

Eryngium maritimum

Sanicula europaea

Apioideae



Petroselinum crispum

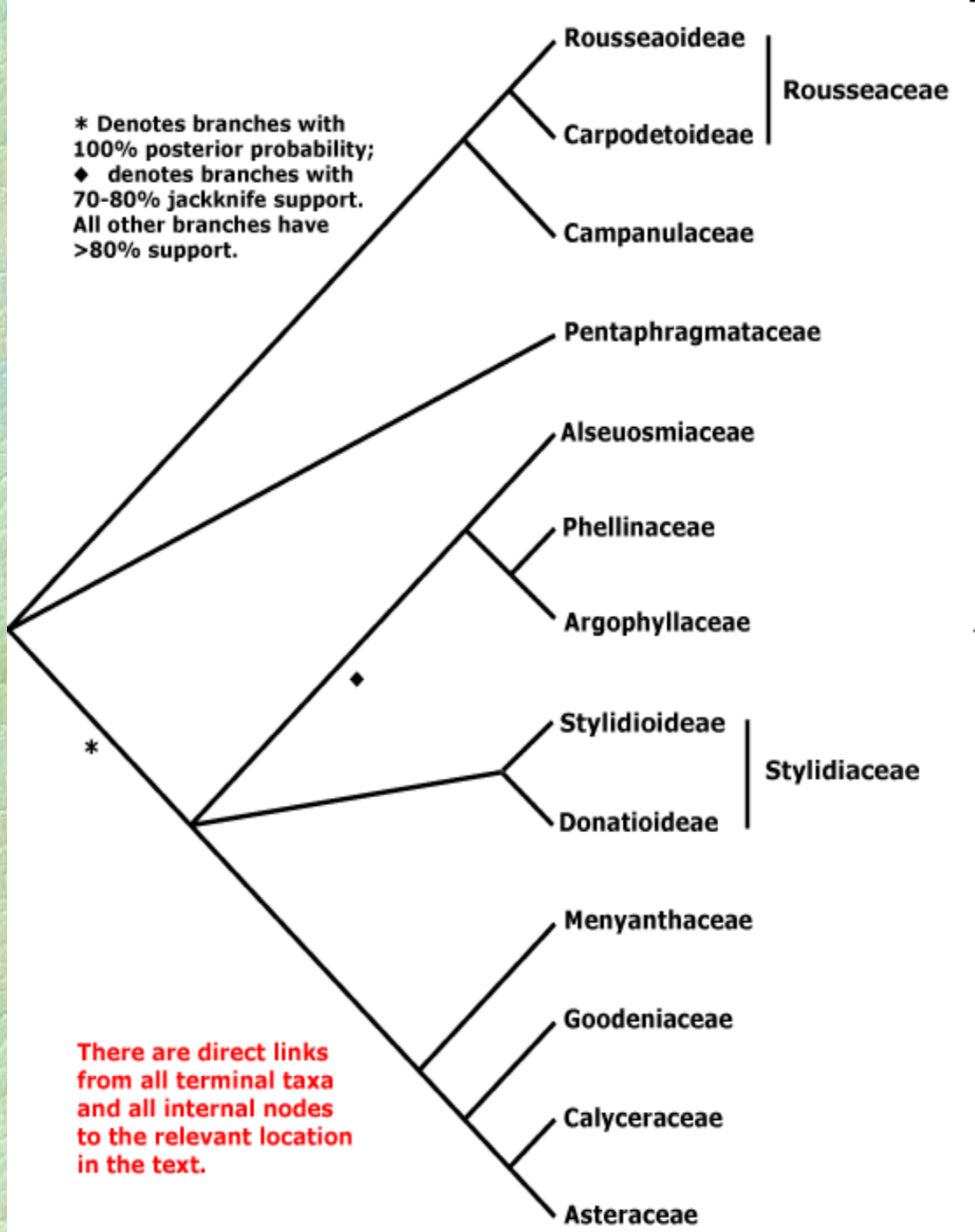
Carum carvi
Foto: Jan Wesenberg

Conium maculatum

Heracleum sosnowskyi

Astri-laadsed *Asterales*

- Varuaine **inuliin**
- **Sekundaarne õietolmu eksponeerimine tolmeldajatele**



http://www.mobot.org/mobot/research/apweb/

Kellukalised *Campanulaceae*

- **Rohttaimed**
- **Õietolmu sekundaarne eksponeerimine**
- Pehmed, spiraalselt paiknevad lehed
- **Piimmahl**
- Campanuloideae: kellukjas õis
- Lobelioideae: sügomorfne õis
- Maailmas ca 2000, Eestis 12 l

Campanu-loideae

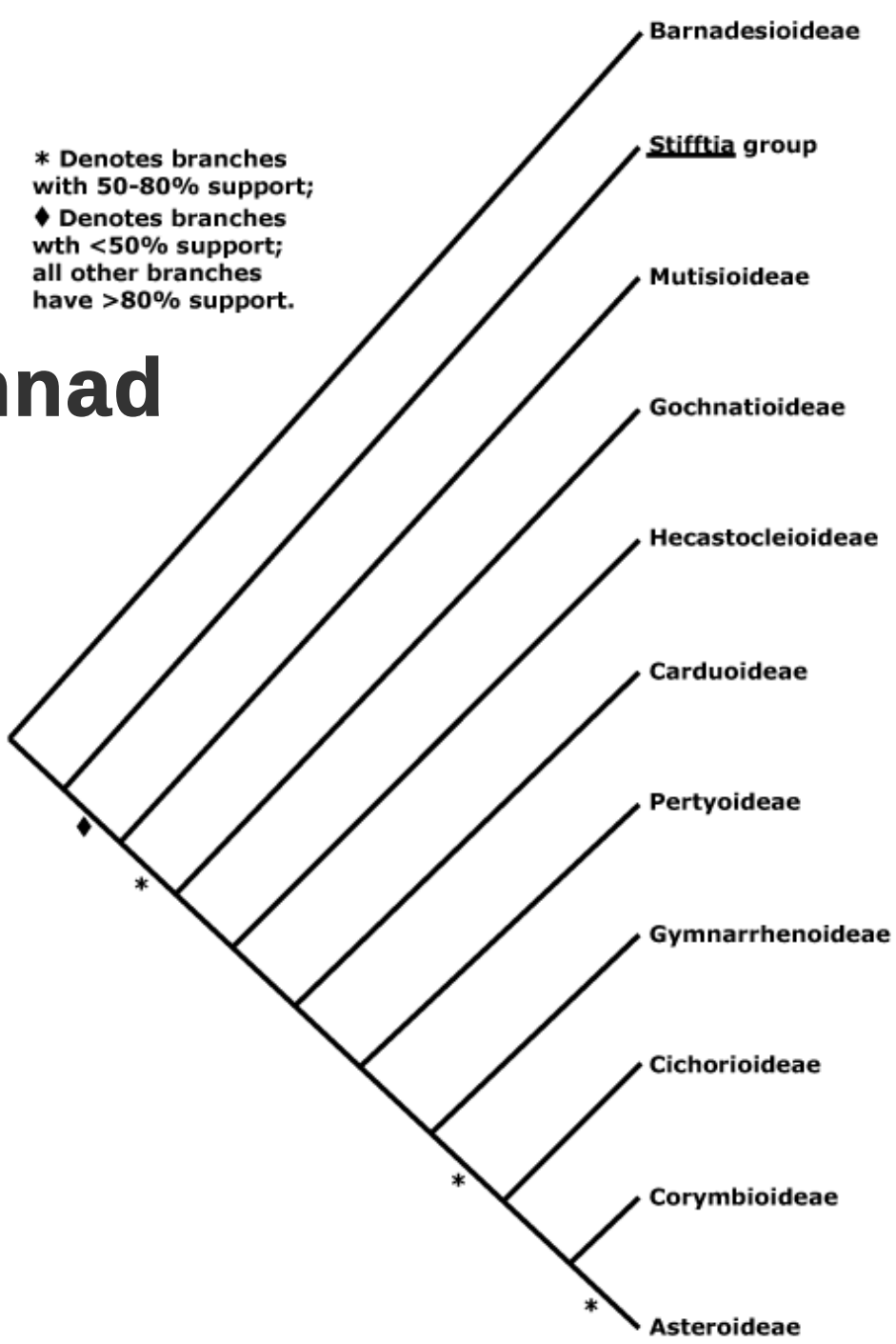
Lobelioideae


Lobelia dortmanna
Foto: Norman Hagen

Korvõielised *Asteraceae*

- Rohttaimed
- **Piimmahl kanalites**
- **Korvõisikud**
- **Tolmukad toruna**
- **Vili pappusega seemnis**
- **Suurim taimesugukond** maailmas: **23 600 liiki**, 1/10 õistaimedest, Eestis üle 130 + mikroliigid (*Hieracium*, *Pilosella*, *Taraxacum*)

Korvõieliste alamsugukonnad



http://www.mobot.org/mobot/research/apweb/

Carduoideae

Cirsium vulgare

Centaurea cyanus

Cichorioideae

Asteroideae

Senecio jacobaea

Anthemis arvensis

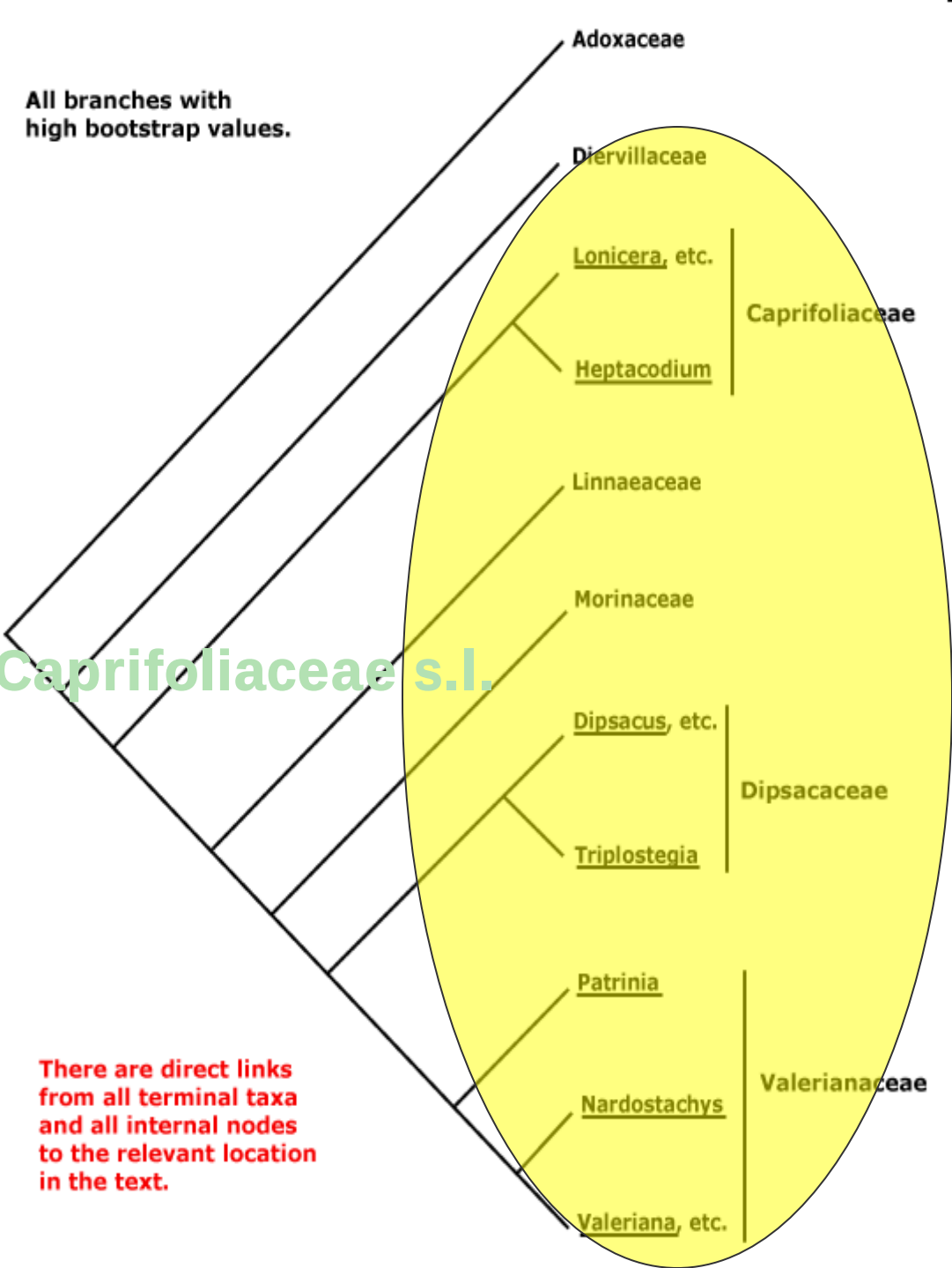

Artemisia vulgaris


Antennaria dioica
Foto: Norman Hagen


Antennaria dioica
Foto: Einar Værnes

Uniohaka-laadsed *Dipsacales*

- Roht- ja puittaimi
- **Vastakud lehed**
- Õied keerukates **ebasarikates või peades**
- Õied aktinomorfsed kuni sügomorfsed, enamasti kokkukasvanud krooniga



Kuslapuulised *Caprifoliaceae*

Lonicera xylosteum

Harakkuljuselised
Linnaeaceae

Palderjanilised *Vale*

http://www.herbfactory.at/valeriana_officinalis.html

Uniohakalised *Dipsacaceae*

Knautia arvensis

Muskuslillelised *Ado*

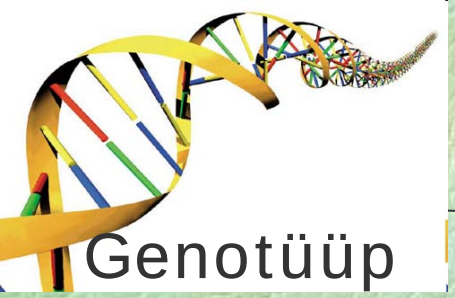
Adoxa moschatellina

Sambucus

Viburnum

Taimede varieeruvus

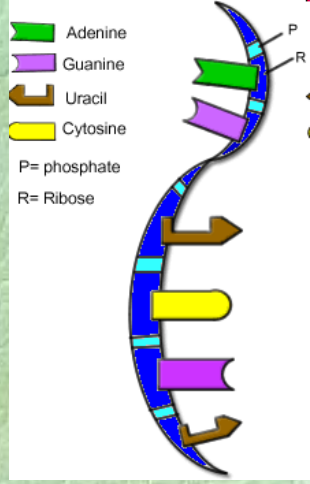
- Geneetiline varieeruvus
- Fenotüübiline varieeruvus
- Populatsioonid
- Geenisiire



Genotüüp

transkriptsioon

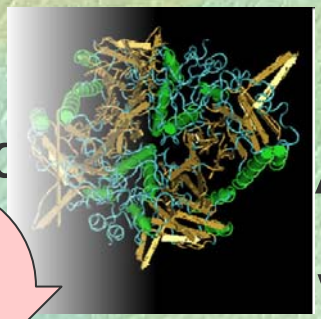
RNA



DNA

“Mälu”

translatsioon



keskkond

valik

Aminohapped

valgud

mitoos

areng

Meioos

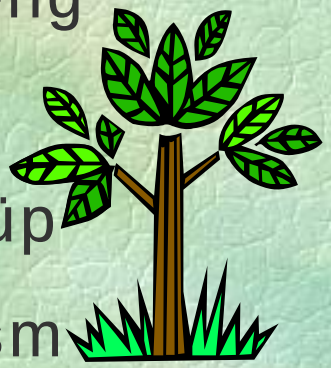
Replikatsioon

Pärilik varieeruvus

Embrüoloogia

Fenotüüp

Organism



Geneetilise varieeruvuse allikad-mutatsioonid

- **Avaldumine fenotüübis**

  letaalne, morfoloogiline, biokeemiline jm
- **Mutageenid**

  UV ja radioaktiivne kiirgus, ekstr temp, kemikaalid, vanadus jm
- **Sagedus**: haruldased gameedi või indiviidi kohta, aga üle populatsiooni või liigi muutuvad oluliseks

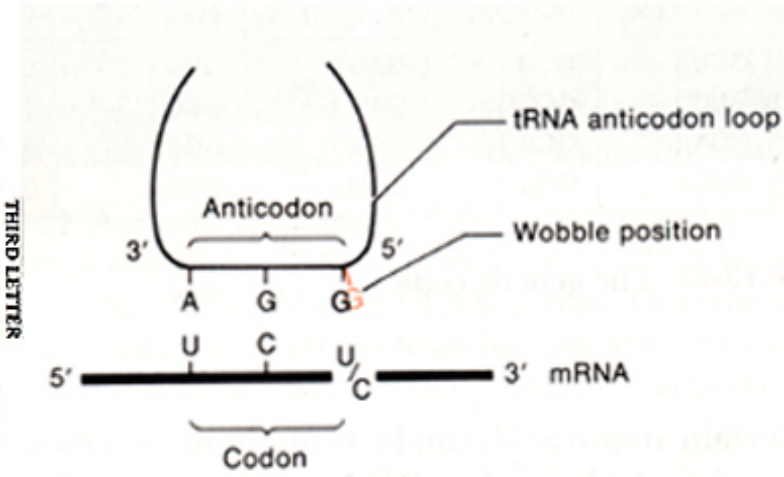
Mutatsioonid

- **Suund ja mõju**
  - “Tagasimutatsioonid” erakordselt harva
  - Enamik on letaalsed
  - Mitteletaalsed põhjustavad väikesi muutusi
  - Väikeste muutuste akumulatsioon võib viia suurte muutuste, uute sündroomideni

Mutatsioonid

- **Kodeeriv ja mittekodeeriv, sünonüümsed ja mittesünonüümsed**

FIRST LETTER	SECOND LETTER: U	SECOND LETTER: C	SECOND LETTER: A	SECOND LETTER: G	THIRD LETTER
U	UUU phe	UCU ser	UAU tyr	UGU cys	U
	UUC phe	UCC ser	UAC tyr	UGC cys	C
	UUA leu	UCA ser	UAA stop	UGA stop	A
	UUG leu	UCG ser	UAG stop	UGG trp	G
C	CUU leu	CCU pro	CAU his	CGU arg	U
	CUC leu	CCC pro	CAC his	CGC arg	C
	CUA leu	CCA pro	CAA gln	CGA arg	A
	CUG leu	CCG pro	CAG gln	CGG arg	G
A	AUU ile	ACU thr	AAU asn	AGU ser	U
	AUC ile	ACC thr	AAC asn	AGC ser	C
	AUA ile	ACA thr	AAA lys	AGA arg	A
	AUG met	ACG thr	AAG lys	AGG arg	G
G	GUU val	GCU ala	GAU asp	GGU gly	U
	GUC val	GCC ala	GAC asp	GGC gly	C
	GUA val	GCA ala	GAA glu	GGA gly	A
	GUG val	GCG ala	GAG glu	GGG gly	G



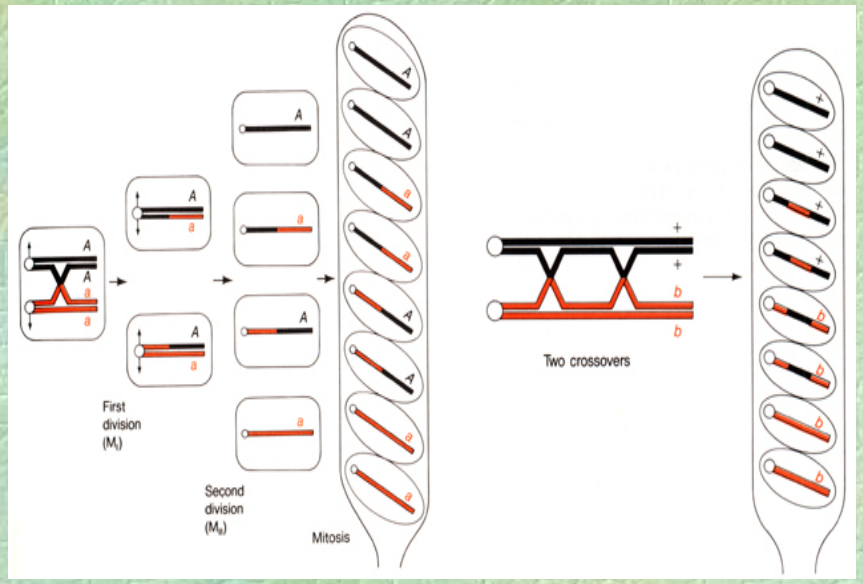
http://biology.kenyon.edu/courses/biol114/Chap05/Chapter05.html

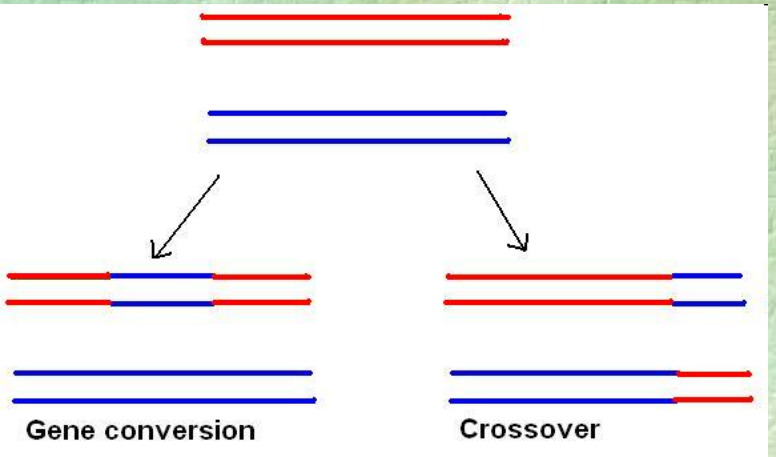
Mutatsioonid

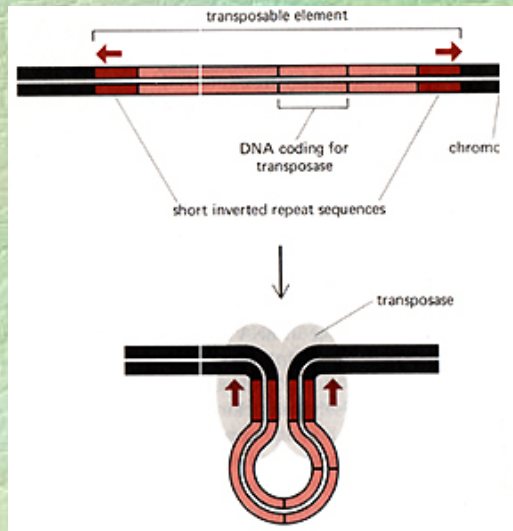
- “Kuumad punktid”
- **Punktmutatsioonid** ja suuremad “ümberkorraldused”
- Asendused: transitsioonid ja transversioonid
- Insertsioonid ja deletsioonid
- **Mittesünonüümsete asenduste mõju**
- Valkude struktuur muutub
- Raaminihe

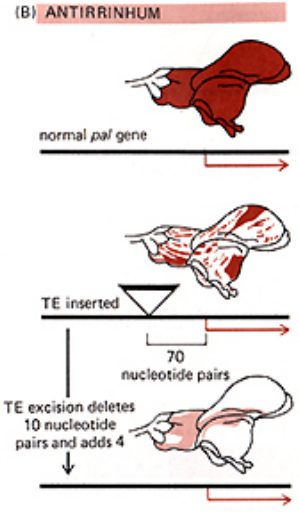
Suuremad ümberkorraldused

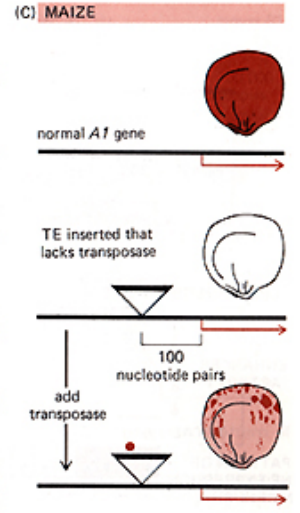
- **Genoomisisesed**
- Krossingover
- Geenikonversioon
- Transposoonid





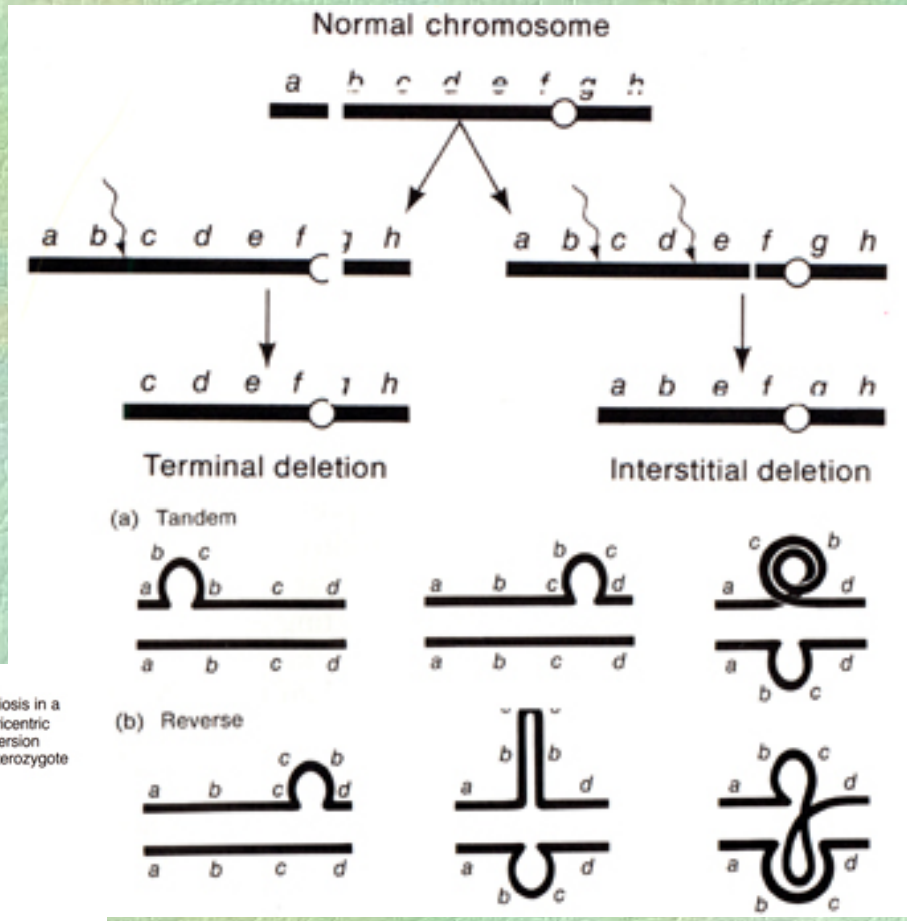


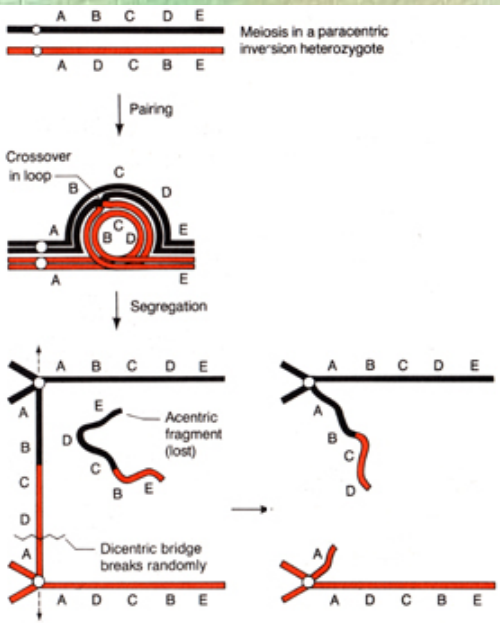


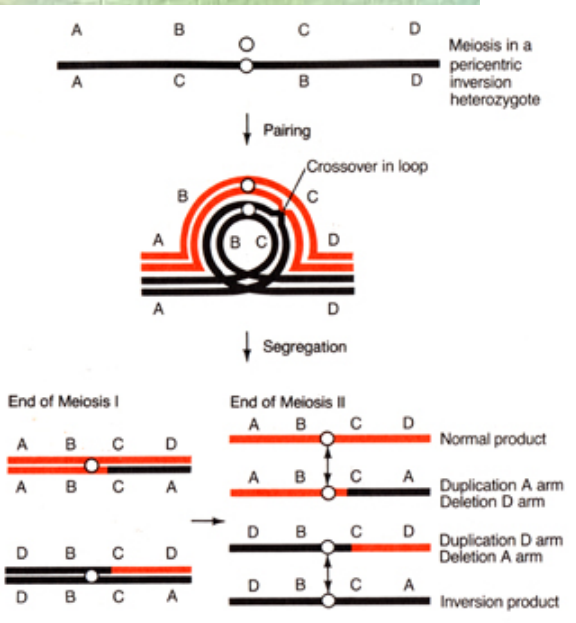


Kromosoommutatsioonid

- Deletsioonid
- Duplikatsioonid
- Inversioonid

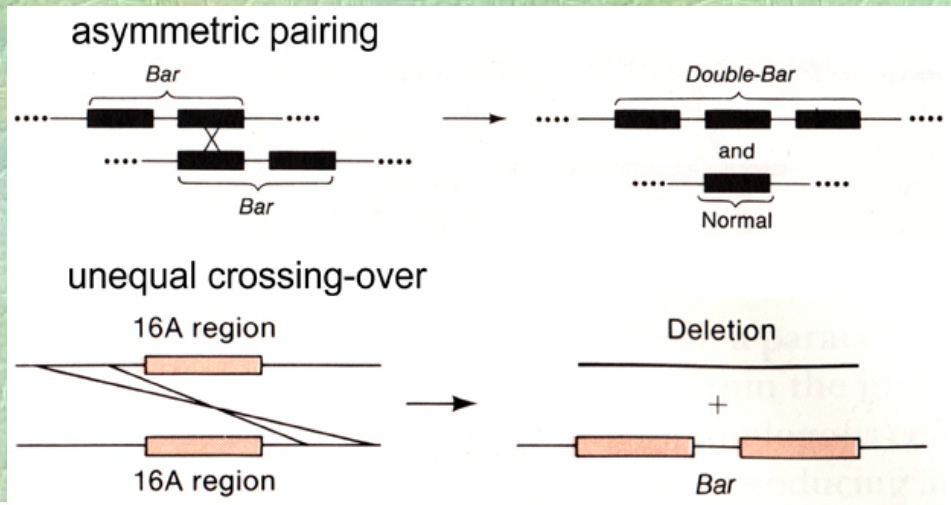


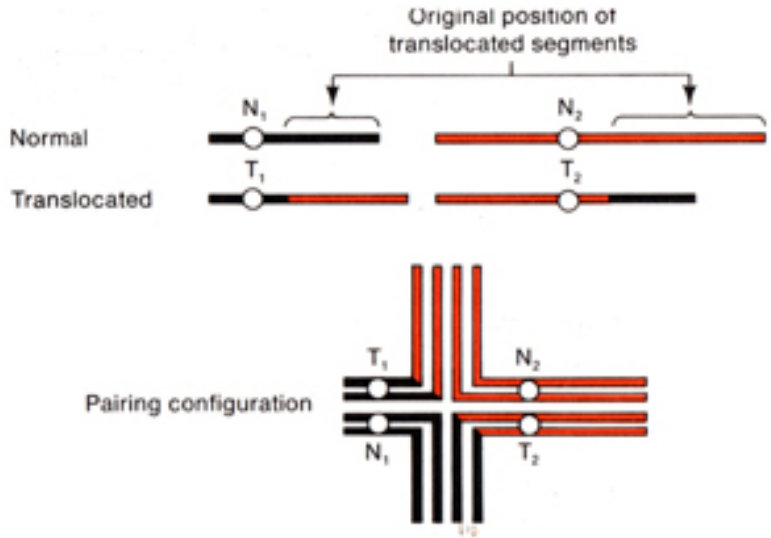




Kromosoommutatsioonid

- Translokatsioonid
- Ebavõrdne krossingover
- Asümmeetriline paardumine





Two types of segregations:

		Products	
Adjacent-1			
to north	$T_1 + N_2$	Duplication of colored, deletion of black translocated segment	(often inviable)
to south	$T_2 + N_1$	Duplication of black, deletion of colored translocated segment	
Alternate			
to north	$T_1 + T_2$	Translocation genotype	(Both complete and viable)
to south	$N_1 + N_2$	Normal	

Kromosoomiarvu muutused

Polüploidsus

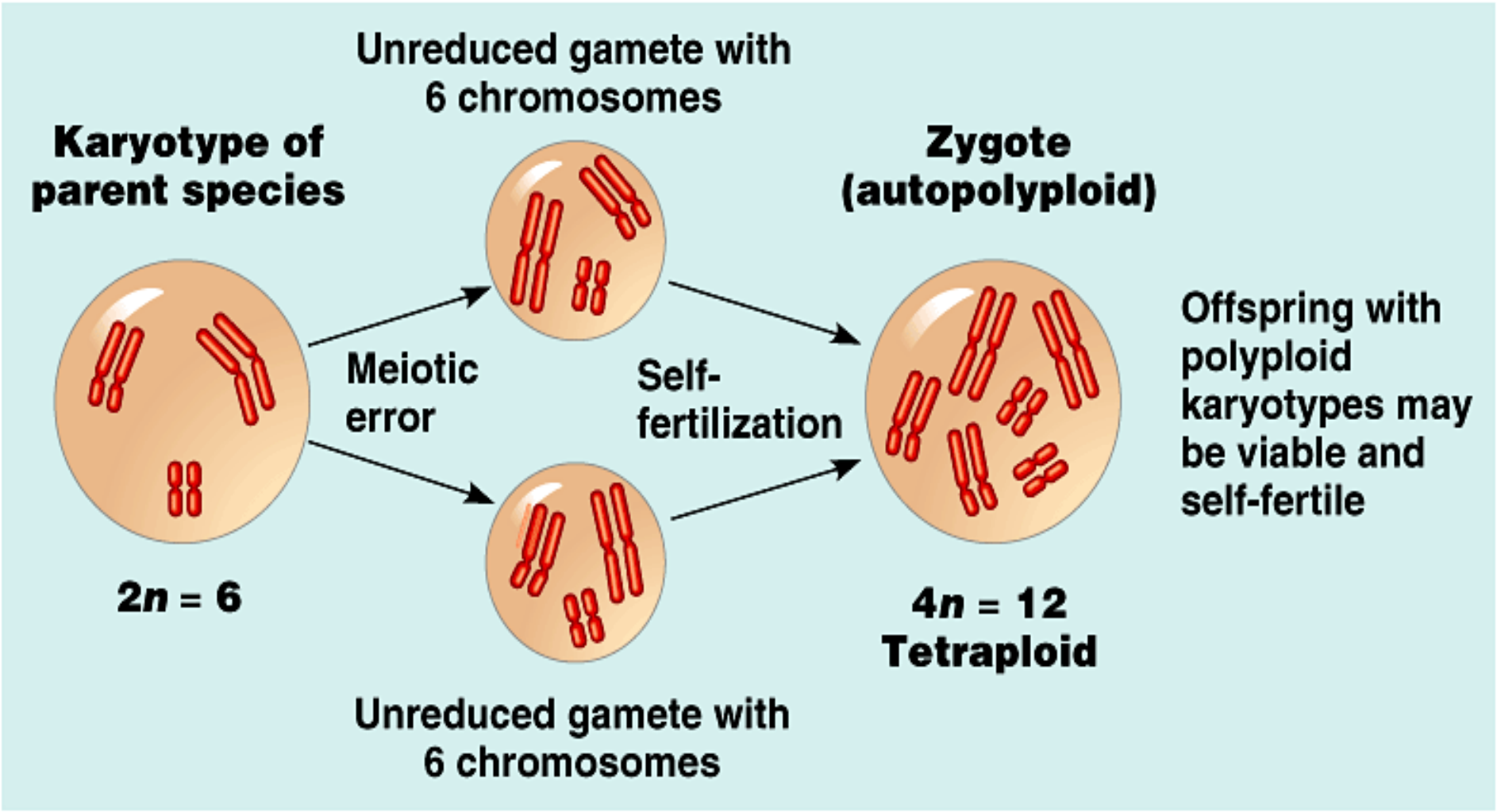
Polüploidide liigid

- **Euploidid**
- Autopolüploidid **AAAA**
- Allopolüploidid ehk amfiploidid **AABB**

(käsitleme hiljem põhjalikumalt)

- **Aneuploidid**
  - Esimene jagunemine-->2n+1 ja 2n-1 gameedid
  - Teine jagunemine-->1n+1, 1n-1, normaalsed gameedid
  - Monosoomid (2n-1) and nullisoomid (2n-2)
  - Trisoomid (2n+1)

Autopolüploidide teke



Autopolüploidide omadused

– meioosis multivalentide moodustumine

– alleelsete geenide multisoomne lahknevus

– geneetilistest iseärasustest tulenevad fenotüübilised kõrvalekalded

– vähene fertiilsus

– aeglustunud areng

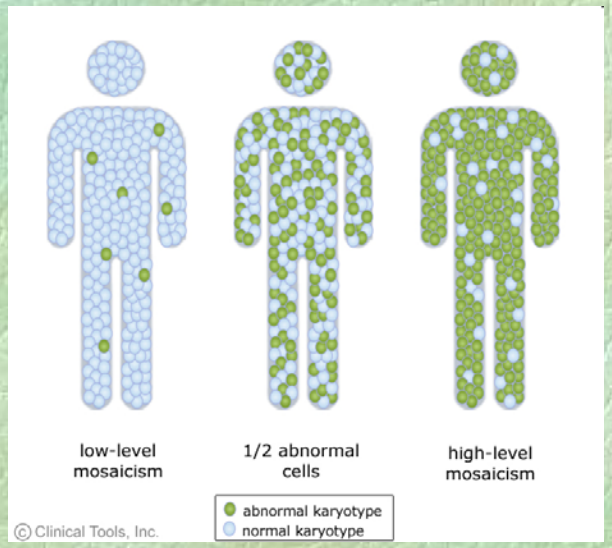
– morfoloogiliste parameetrite suurenemine

Polüploidide evolutsioonilised omadused

- suurem mutatsioonide taluvus ⇒
- mutatsioonide akumuleerumise tendents ⇒
- suurem evolutsiooniline potentsiaal
- adaptiivsete ja heteroossete genotüüpide fikseerumine
- kohastumisvõime laienemine, despetsialiseerumine
- steriilsusbarjääride nõrgenemine, hübridiseerumine
- paljunemisviisi muutus autogaamialt allogaamiale või agamospermiale
- **Polüploidid on sagedasemad ja edukamad äärmuslikes elutingimustes**
- **Üks tee hüppeliseks liigitekkeks**

Sugurakkude ja somaatilised mutatsioonid

- **Geneetilise mosaiiksuse hüpotees** (Whitham & Slobodchikoff 1981; Gill 1986)



Meetodid taimede molekulaarse varieeruvuse ja fülogeneesi uurimisel

- Valgud, eriti allosüümid
- **DNA**
- Tuuma, kloroplasti ja mitokondri DNA
- Geenide ja mittekodeerivate alade nukleotiidsed järjestused (sekventsid)
- Korduv DNA kui oluline varieeruvuse allikas
- Minisatelliidid (10-60 bp)
- Mikrosatelliidid (1-6 bp)

Fragmentanalüüs või DNA “sõrmejäljed”

- RFLP
- Hübridiseerimine (Southern blot, lookusespetsiifiline ja multi-lookuseline)
- **PCR-il baseeruvad meetodid**
- PCR-RFLP ehk CAPS
- RAPD
- Mini- ja mikrosatelliidid (SSR), tuuma ja kloroplasti; erim ISSR
- AFLP
- Konformatsiooni polümorfismi analüüsid
- jm

Fenotüübiline varieeruvus

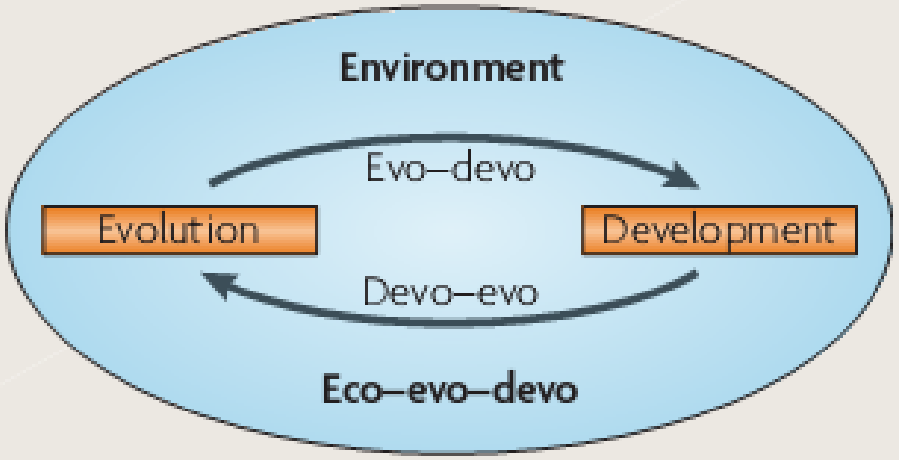
Fenotüüp

- **Ei ole üksühest vastavust fenotüüpide ja genotüüpide vahel**
- Geneetiliselt on määratud **reaktsiooninorm**
- **Fenotüübiline varieeruvus**
- Geneetiline varieeruvus
- Arenguline varieeruvus
- Fenotüübiline plastilisus s.s.

Arenguline varieeruvus

Evo–devo questions

- How did development originate?
- How did the developmental repertoire evolve?
- How are developmental processes modified in evolution?



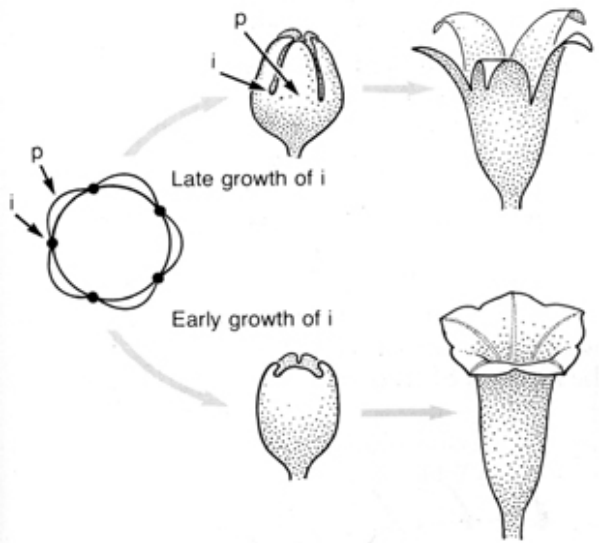
Devo–evo questions

- How does development influence phenotypic variation?
- How does development contribute to phenotypic novelty?
- How does development affect the organization of phenotypes?

Eco–evo–devo questions

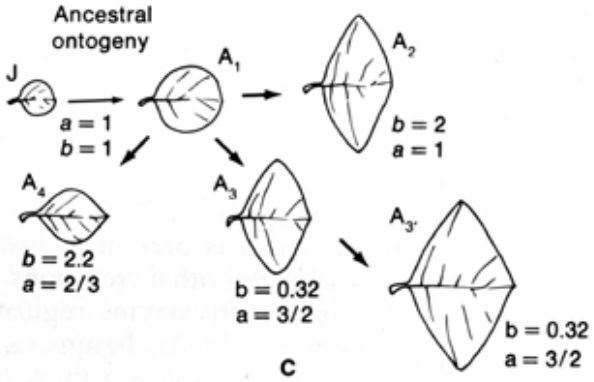
- How does the environment interact with developmental processes?
- How does environmental change influence phenotypic evolution?
- How does developmental evolution affect the environment?

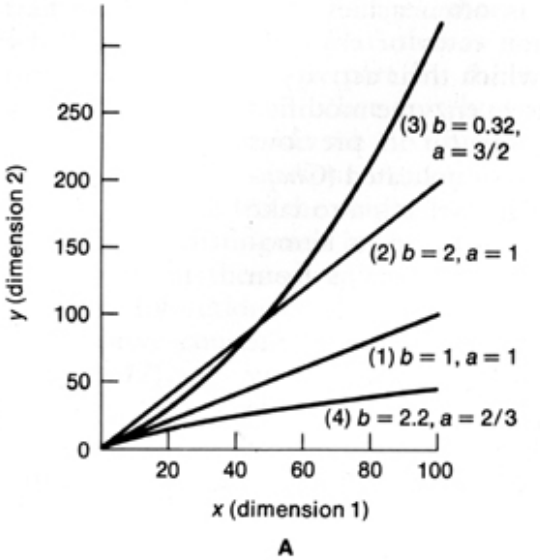
Müller, 2007



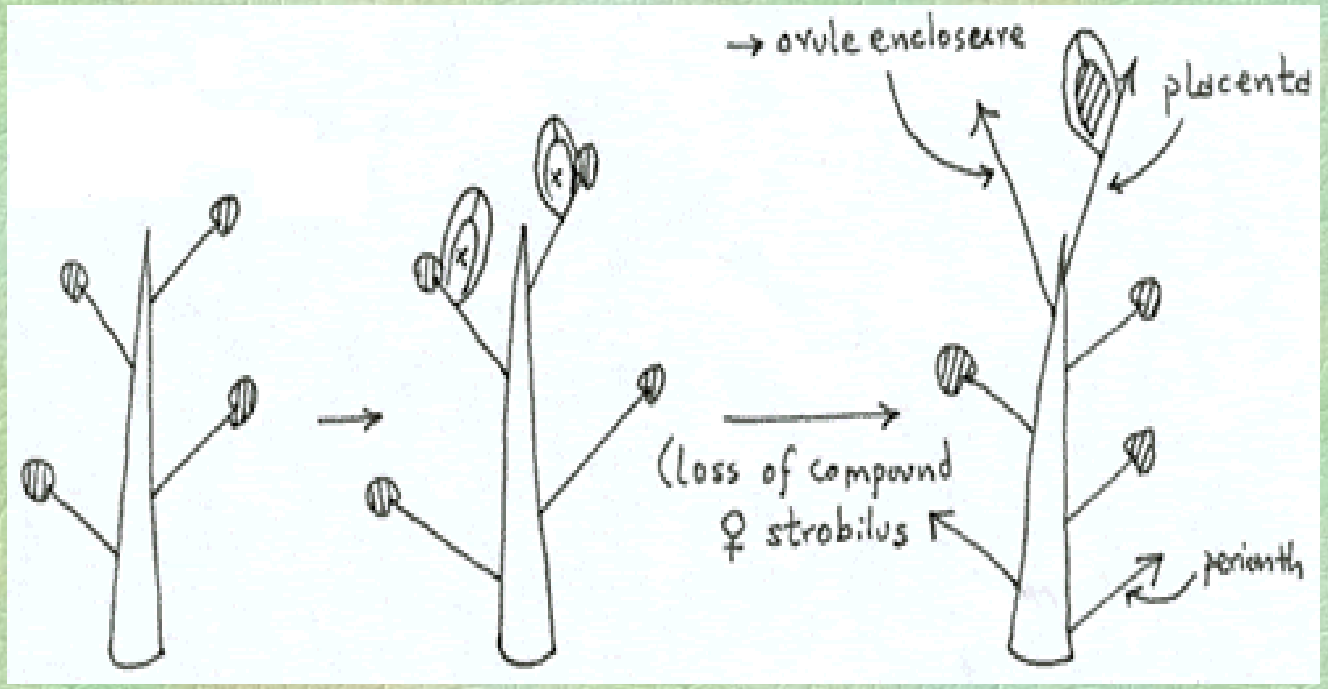
15

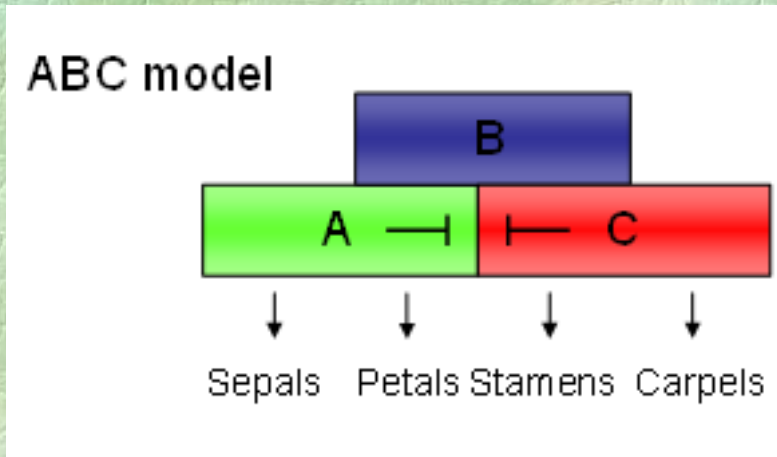
Effects of developmental timing on form. The developing flower, shown from above at left, has petal primordia (*p*) separated by intercalary cells (*i*). If these begin dividing only after the petal primordia grow, the petal lobes of the mature flower (side view, at right) are well separated. If the intercalary cells develop along with the petal primordia, a largely fused (sympetalous) corolla is formed. (Adapted from Stebbins 1974, after Payer 1857)





Allometric growth. (A) Arithmetic plot of the lengths y and x of two structures or dimensions. Curves 1 and 2 show isometric growth ($a = 1$); structure 2 equals structure 1 in curve 1 ($b = 1$) and is twice as long in curve 2 ($b = 2$). Curve 3 shows positive allometry ($a > 1$); curve 4 shows negative allometry ($a < 1$). (B) Logarithmic plot of the same curves. The slope equals 1 in curves 1 and 2, which differ only in intercept (cf. Figure 6); it is greater than 1 in curve 3 ($a > 1$), less than 1 in curve 4 ($a < 1$). (C) Illustration of hypothetical evolution of leaf shape, according to these graphs. As the ancestral species doubles in length (x) during its growth from juvenile (J) to the mature form (A_1), it doubles in width (y); that is, $a = 1$, $b = 1$. Descendant A_2 is twice as wide when mature, for b has evolved from 1 to 2. If a evolves from 1 to 2/3, a narrower leaf (A_4) results. If a evolves from 1 to 3/2, a wider leaf (A_3) is formed. With this allometric relation, evolution of greater length results in disproportionately greater width ($A_{3'}$).


ovule enclosure
placenta
loss of compound
♀ strobilus
perianth


ABC model
B
A
C
Sepals
Petals
Stamens
Carpels

Heterokroonia

- Neoteenia ja akstseleratsioon
- Arenguetapi hilinemine või varanemine
- Progenees ja hüpermorfoos
- Ühiste nimedega:

pedomorfoos ja peramorfoos

- Võib põhjustada fenotüübilist plastilisust

Fenotüübiline plastilisus

- Valik toimib populatsioonis fenotüüpidele
- Tunnuse reaktsiooninorm on fenotüübiliste väärtuste kogum, mida antud genotüüp ekspresseerib.
- Valik toimib indiviidide vahel tunnuse seisundile
- **Plastilisus taimedel**

  vegetatiivsetel organitel suur

  generatiivsetel väike

“Plastilisusgeenid”

- Alleelide ekspressioon võib erinevates keskkonnatingimustes avaldada erinevat mõju fenotüübile ⇒ **fenotüüpne modulatsioon ehk “pidev” plastilisus**
- Nt lehtede kuju
- Regulaatorgeenid põhjustavad teiste geenide “sisse- ja väljalülitamist” erinevates keskkonnatingimustes ⇒ **arengukonversioon ehk “diskreetne” plastilisus**
- Nt õite värvus

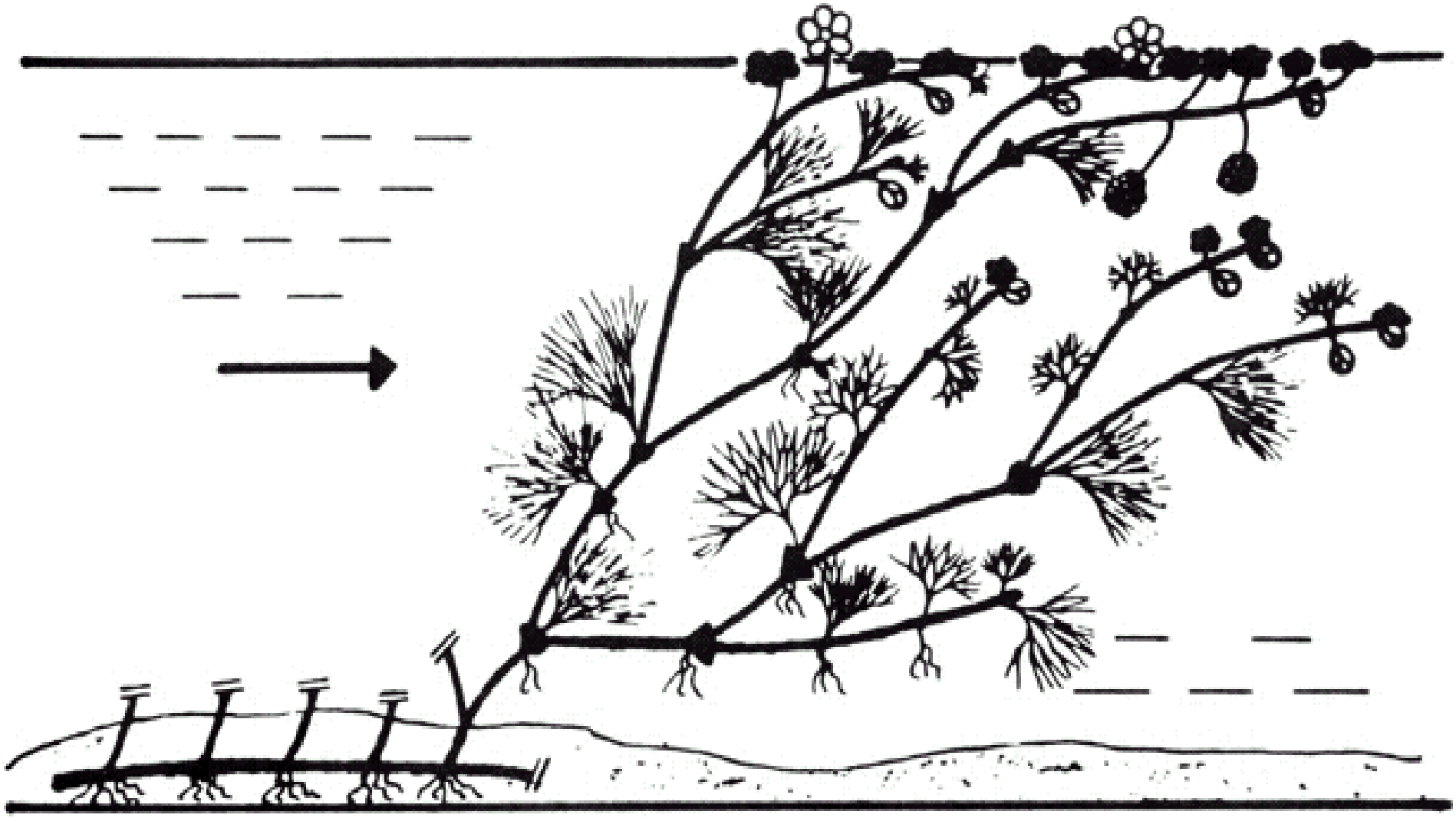


Fig. 6.18. Generalised diagram showing heterophylly in *Ranunculus* subgenus *Batrachium*. For convenience only one shoot is illustrated. Close examination has revealed seasonal variation in leaf form, especially in the submerged leaves. (From Zander & Wiegleb, 1987.)

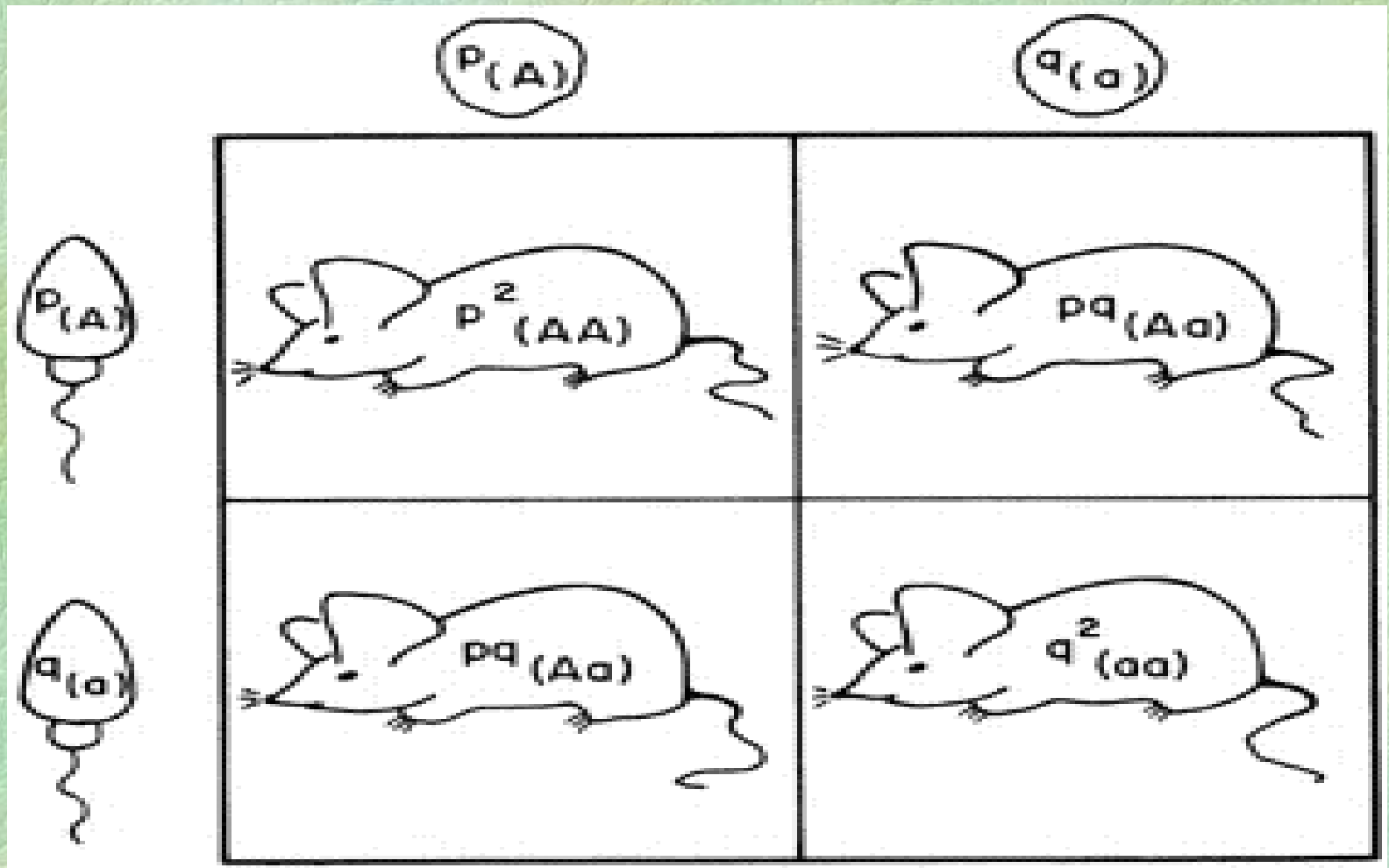
Evolutsioon toimub populatsioonides

- Populatsioonigeneetika TÜMRIs
- Toomas Tammaru, Evolutsiooniline ökoloogia

Alleelisagedused

- Populatsioonis, kus N diploidset isendit, Mendeli järgi:
  - N11 = genotüüp A1A1 (homosügoodid)
  - 2N12 = genotüüp A1A2 (heterosügoodid)
  - N22 = genotüüp A2A2 (homosügoodid)
  - N11 + 2N12 + N22 = N
- Genotüüpide proportsioonid
  - A1A1: P11 = N11/N
  - A1A2: P12 = N12/N
  - A2A2: P22 = N22/N
- Allelisagedused
  - p = (N11 + N12)/N = P11 + P12
  - q = (N22 + N12)/N = P22 + P12

Hardy-Weinbergi võrrand



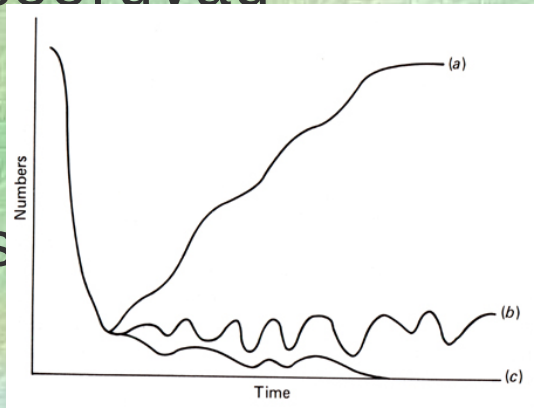
$$p_{(A)} + q_{(a)} = 1$$

$$p^2_{(AA)} + 2pq_{(Aa)} + q^2_{(aa)} = 1$$

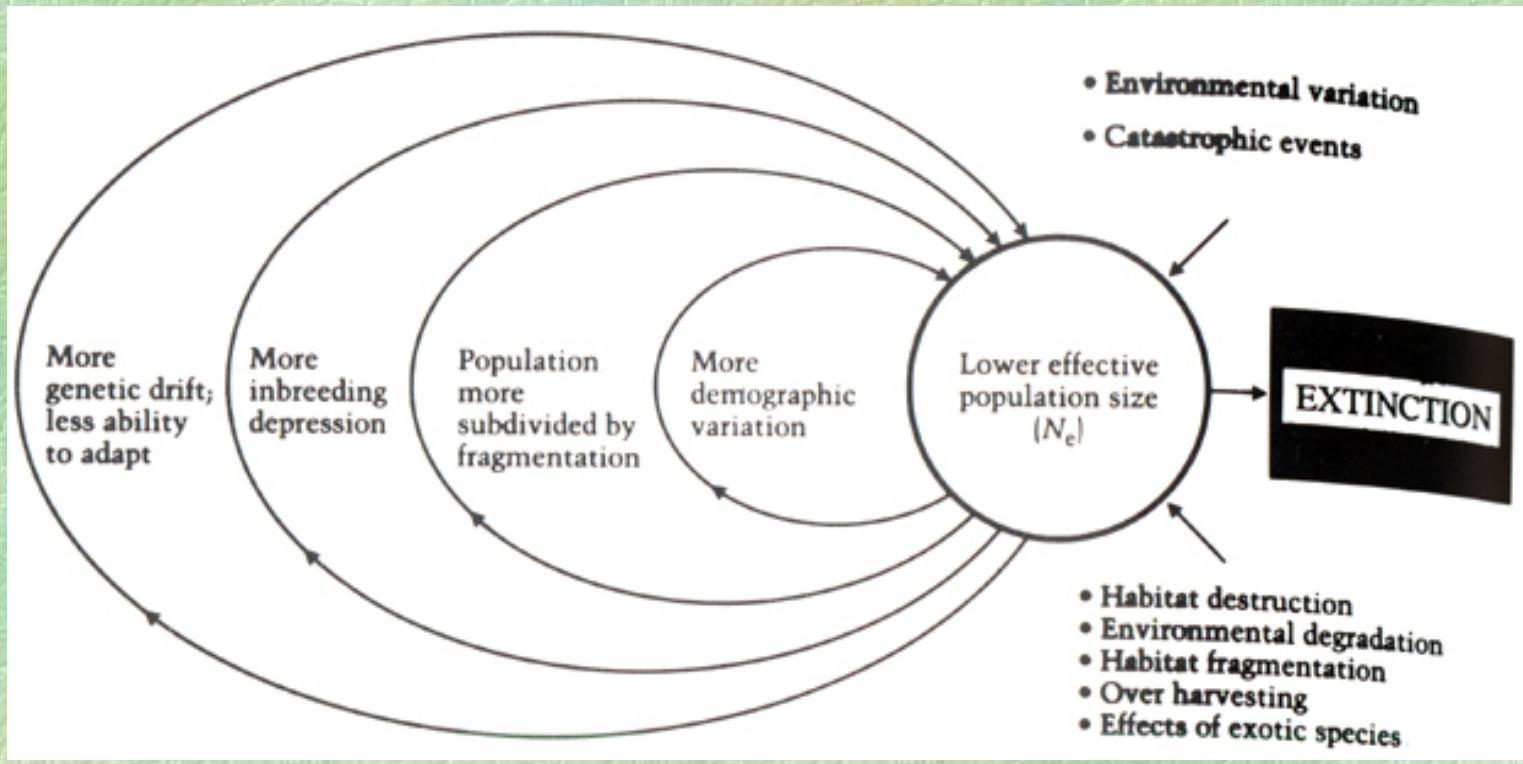
“Lõplik” populatsioon

- **Hardy-Weinbergi tasakaal reaalselt ei kehti**
- Valiku vm tegurite puhul alleelisagedus muutub

  $\Delta p = spq^2 / (1 - sq^2)$
- **Mittejuhuslik paaritumine**
  - eelistused fenotüübi järgi
  - sugulusristumine
  - Iseviljastumine
- Geenitriiv, juhuslikud protsessid: homosügootsus suureneb $f_t = 1/2N + (1 - 1/2N)f_{t-1}$
- Väga väikesed populatsioonid läbivad “pudelikaelu”
- Alleelid “fikseeruvad” juhuslikult
- Migratsioon
- Polüploidsus



Väljasuremine



Briggs & Walters (1997)

Taimepopulatsioonid looduses

- Paljud liigid esinevad **valdavalt** väikeste populatsioonidena
- Populatsioonid on fragmenteeritud ja isoleeritud
- Paljudel liikidel piiratud levikuvõime
- Sugulusristumine on tavaline
- Inbriiding

Geenisiire

Määravad-mõjutavad:

- Eluvorm
- tolmeldamisviis ja paljunemistüüp
- leviku mehhanismid, nt seemnete leviku tüübid
- liigi geograafiline levik
- isendite asetus ruumis
- liigisisene ja liikidevaheline konkurents
- kasvukohatingimused
- migratsioon populatsioonide vahel

Tolmlemine

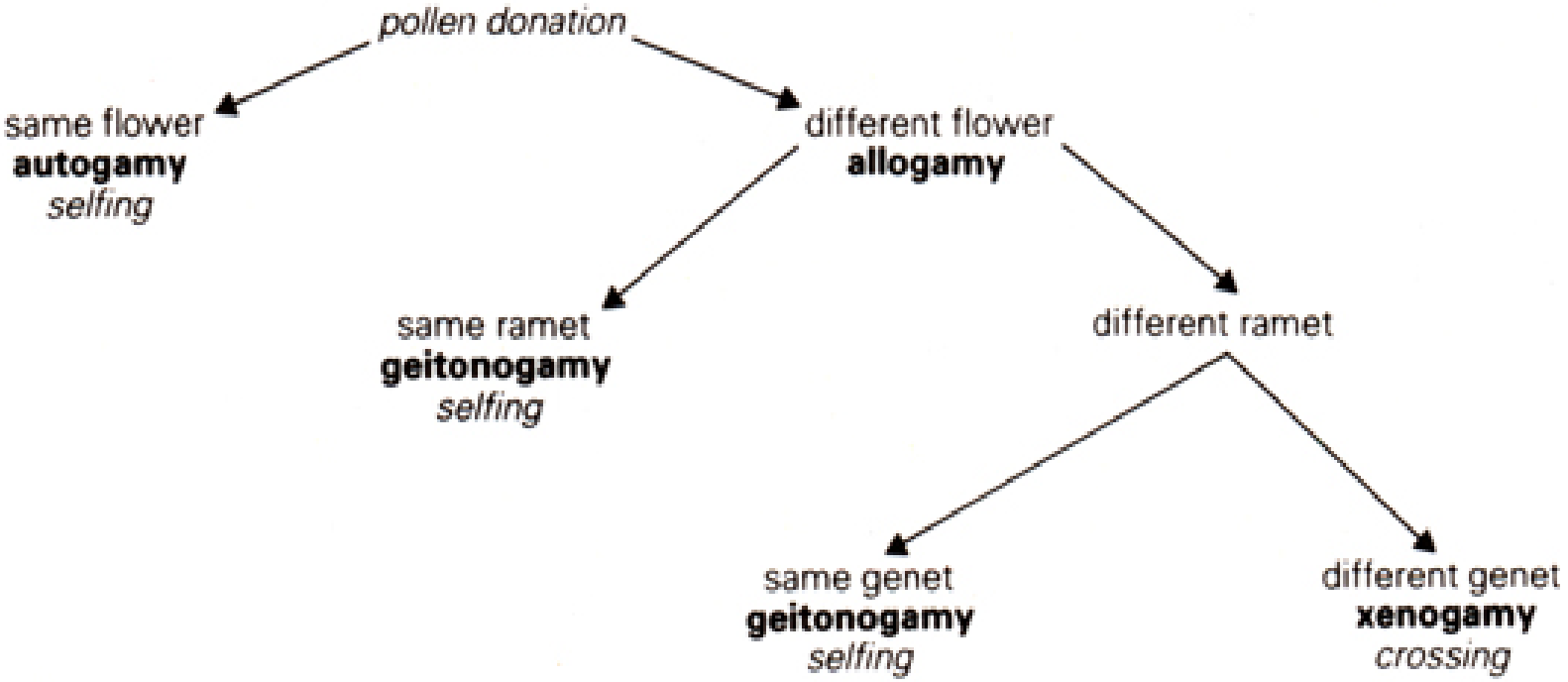


FIGURE 22.4 Patterns of pollen transfer within and between flowers and plants. (From Richards 1986:3)

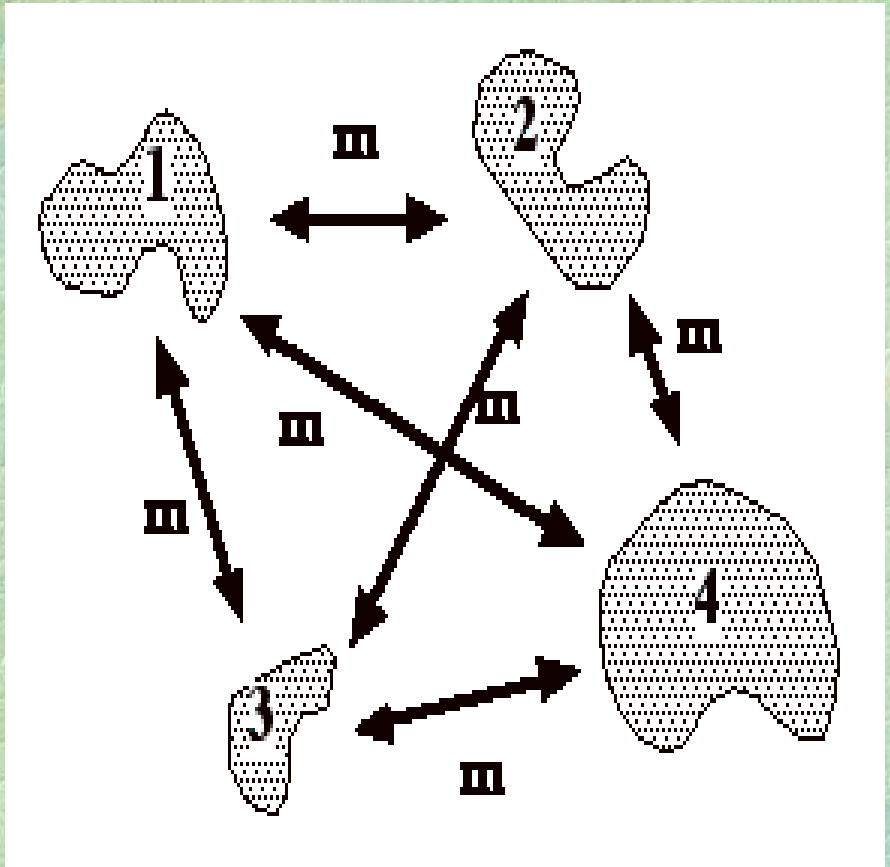
Risttolmlemise agendid: tuul, putukad, ka vesi, linnud jm

Seemnelevi

- Aktiivne (paiskviljad)
- Aktiivne kandjate abiga (tuul, vesi, loomad)
- Passiivne (gravitatsioon)

Mudelid

- kivilt kivile (stepping stone)
- saarte mudel
- kontinendi-saare mudel
- kauguse mudel



Populatsioonidevaheline geneetiline erinevus

Soltis & Soltis 1989

Kõrge	Madal
Isetolmlemine	Risttolmlemine
Hermafrodiidid	Ühe- ja kahekojalised
Gravitatsiooniline seemnelevi	Tuul- ja loomlevi
Üheaastane	Mitmeaastane
Monokarpne	Polükarpne
Suktsessioonis varane	Suktsessioonis hiline

Looduslik valik ja adaptatsioonid

“Selection is the statistically consistent differential survival and/or reproduction of two or more classes of entities.” (**Futuyama 1979**)

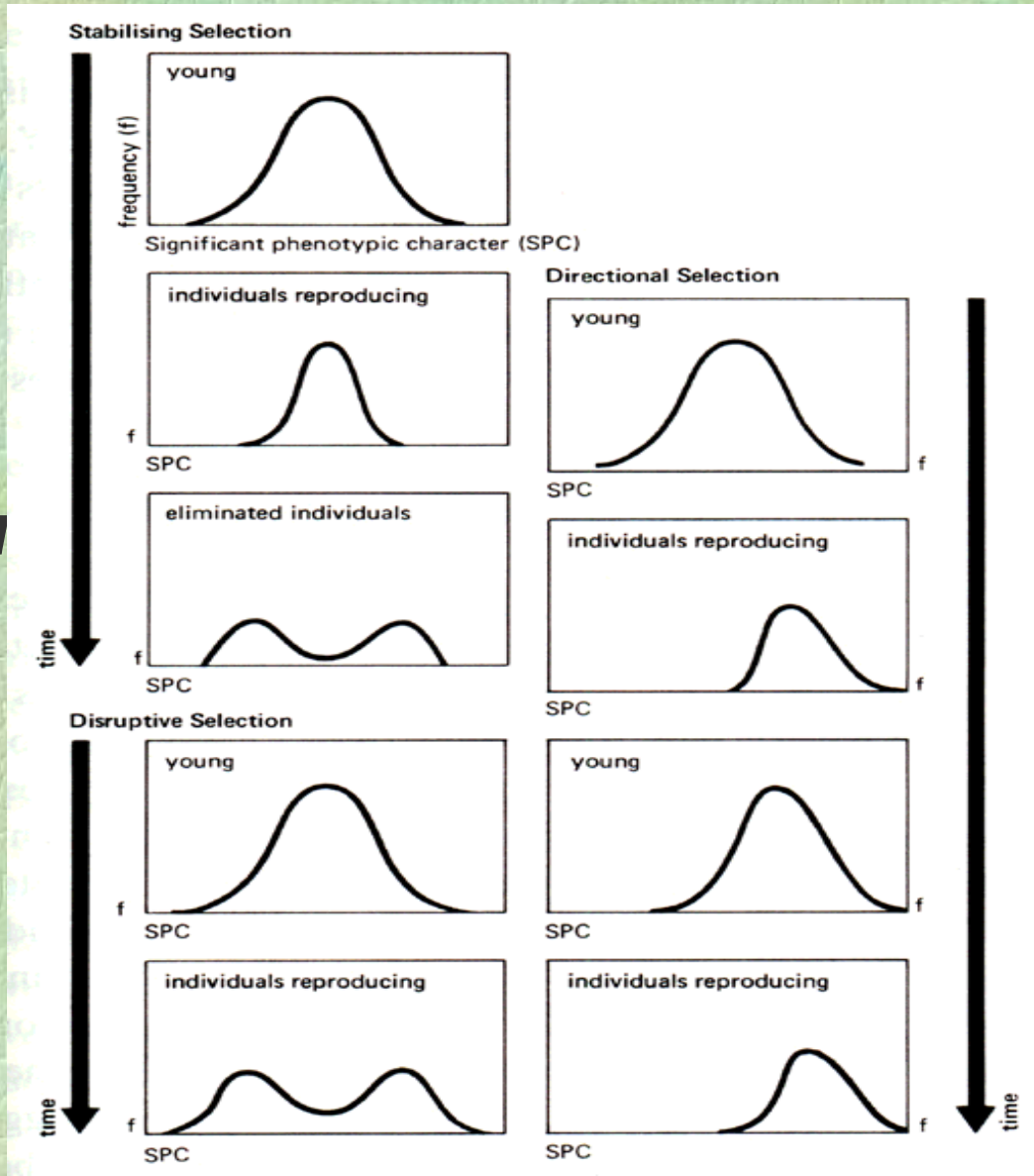
Looduslik valik

- Pärilik replikatsiooni kiiruse variatsioon põhjustab evolutsiooni valiku kaudu
  - Replikatsiooni kiiruse valik on otsene, fenotüübi kaudu
  - Tunnused, mis mõjutavad kiirust, on kaudse valiku all
- Evolutsioon toimub vähemsobivate variantide järjestikulise asendumise teel sobivamatega
- Uus tunnus areneb vaid siis, kui ta on individiidile kasulik
- Valik parandab toimetulekut konkreetsetes tingimustes
- Adaptatsioon ühtedes tingimustes võib olla kahjulik teistes tingimustes
- Selektsiooni põhjustab indiviidide

Valiku liigid

- **Stabiliseeriv**
- **Suunav**
- **Divergeeriv**

- **Valik toimib fenotüübile *sensu lato***
- Valiku edukust saab hinnata **kohasusega** – järglaste suurema arvuga



Briggs & Walters (1997)

Valiku näiteid

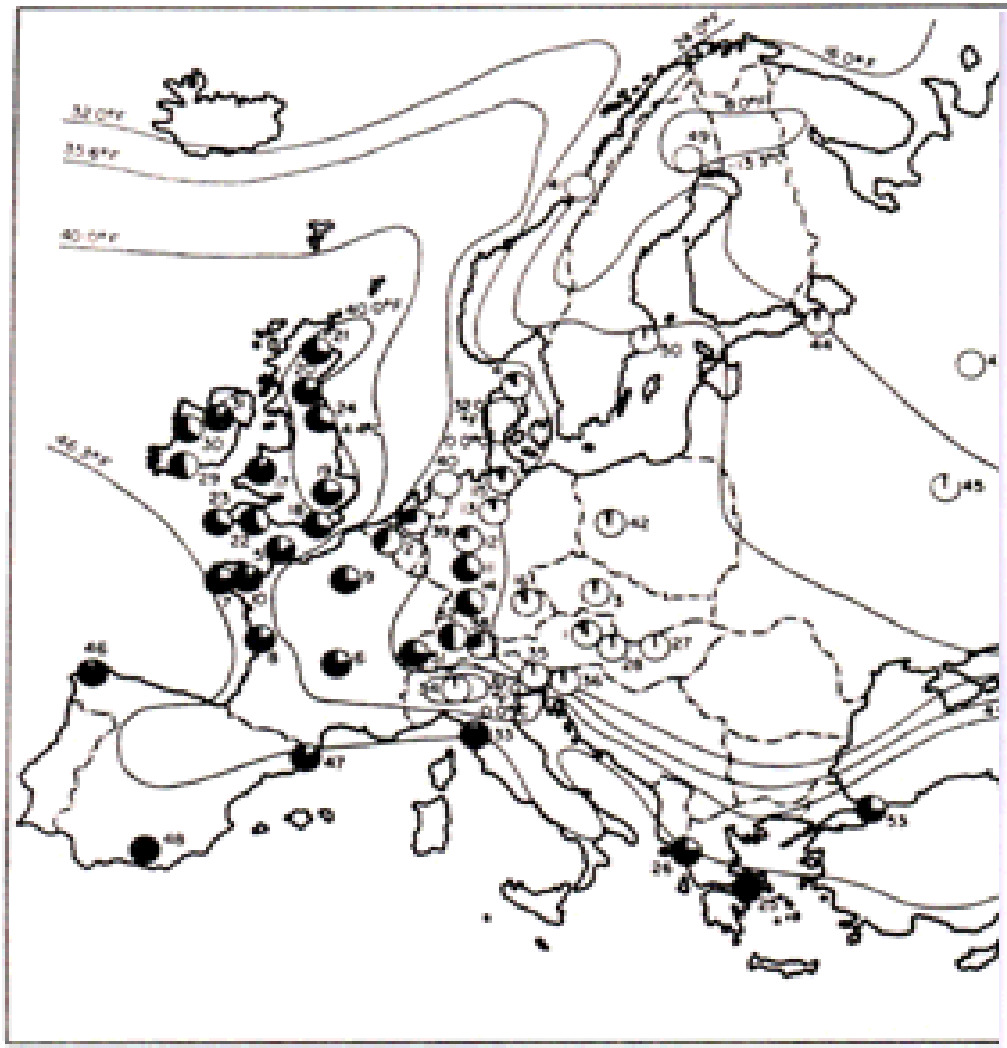


Fig. 9.6. Distribution and frequency of the cyanogenic variant in Europe
near eastern wild populations of *Trifolium repens*. Black section: frequen
the cyanogenic variant. White section: frequency of the acyanogenic vari
January isotherms. (From Jones, 1973, after Daday, 1954*a*.)

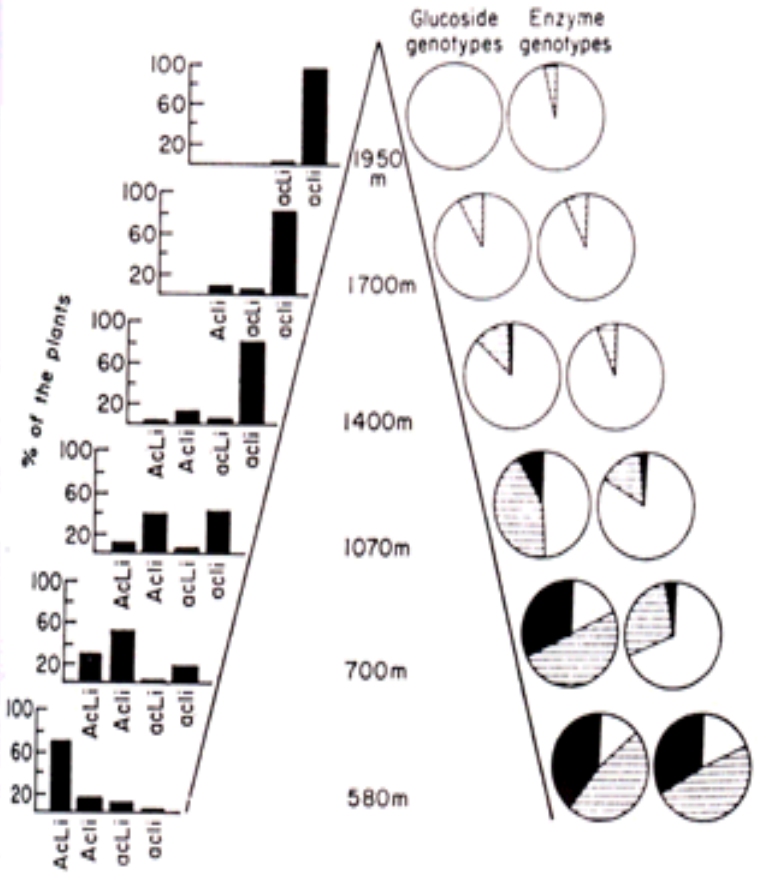


Fig. 9.7. Phenotypic and genotypic frequencies in wild populations of *Trifolium repens* from different altitudes. (From Jones, 1973, after Daday, 1954*b*).

Phenotypes (left):
AcLi – glucosides and enzyme
Acli – glucosides only
acLi – enzyme only
acli – neither glucosides nor enzyme

Estimated genotypes (right):
Black section = dominant homozygotes
Lined section = heterozygotes
White section = recessive homozygotes

Briggs & Walters (1997)

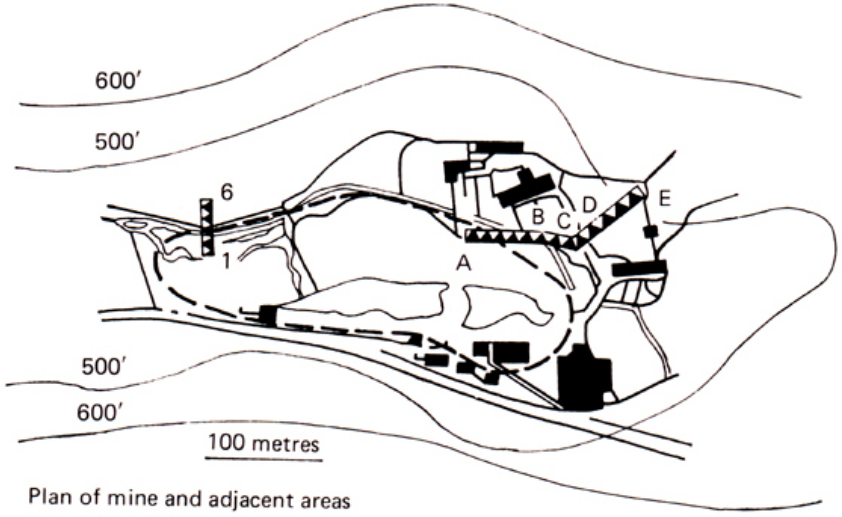
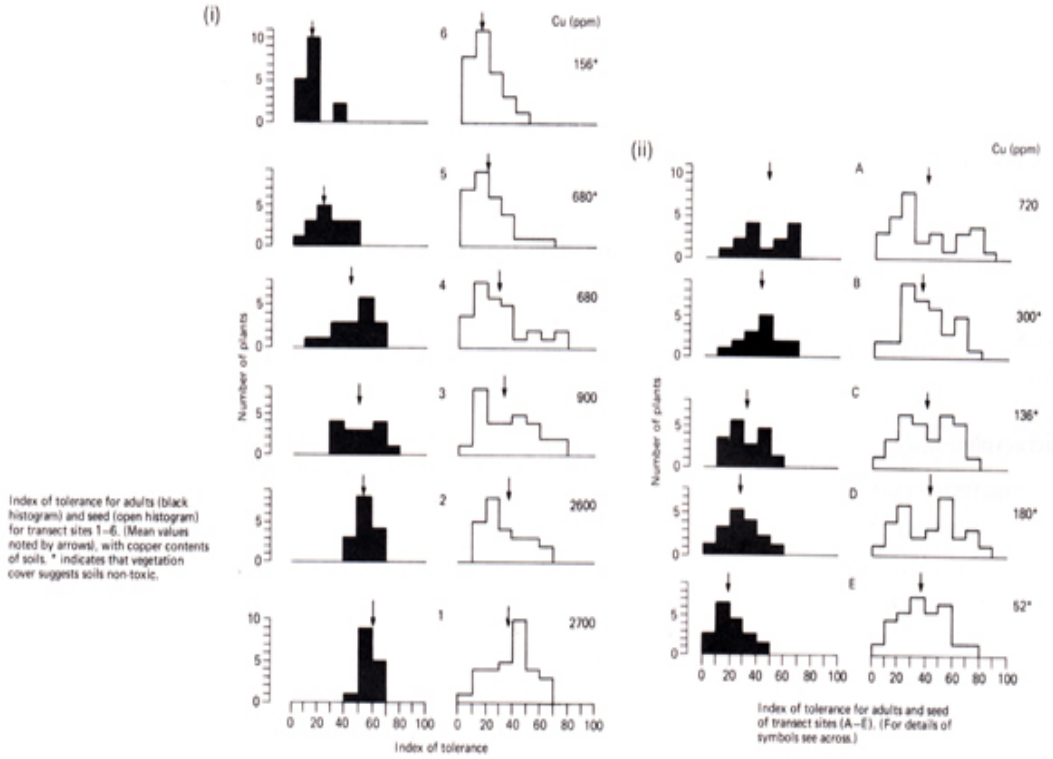
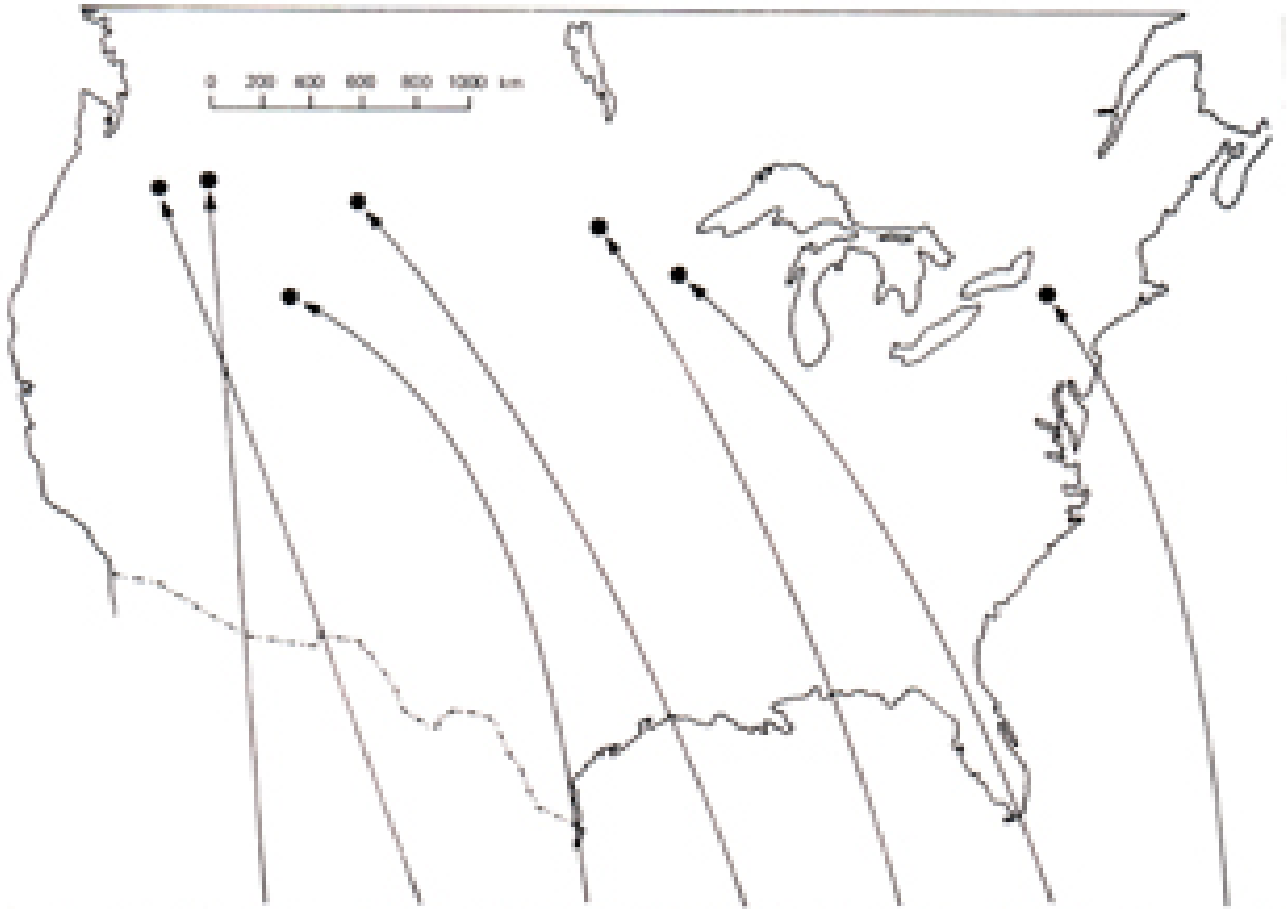


Fig. 9.10. Map of old copper mine workings at Drws y Coed, Caernarvon, Wales, showing positions of transects sampled by McNeilly (1968). In his studies of *Agrostis capillaris* (*A. tenuis*), using a water culture technique, an index of copper tolerance for adult plants and seed produced by different ac was determined for material from two transects: (i) sites 1–6; and (ii) sites A Adults from the mines proved to be more copper tolerant than plants from non-contaminated pasture adjacent to the mine. Studies of the seedlings, produced from wild collected seeds, revealed a wider spectrum of variation in the adult plants. This pattern was particularly clear in transect A–E, whe evidence for considerable gene flow of copper-tolerance genes downwind of mine was discovered in progeny of copper-sensitive plants. This experiment consistent with the view that strong natural selection occurs on the variable products of sexual reproduction. The only seedlings to survive to adulthood likely to be copper tolerant on the contaminated areas and non-tolerant variants (which have been shown to be better competitors than copper-toler plants) on pasture areas. (From McNeilly, 1968.)



Index of tolerance for adults (black histogram) and seed (open histogram) for transect sites 1–6. (Mean values noted by arrows), with copper contents of soils. * indicates that vegetation cover suggests soils non-toxic.

Briggs & Walters (1997)



Varieties	Pullman Washington	Moro Oregon	Aberdeen Idaho	Moccasin Montana	Fargo North Dakota	St. Paul Minnisota	Ithaca New York
Coast & Trebi	150	125	159	102	156	121	76
Gatami	1	3	20	73	29	16	46
Smooth Awn	5	10	6	54	23	37	47
Lion	3	3	21	44	14	34	44
Mebay	6	3	9	12	0	5	6
White Smyrna	276	226	119	89	17	5	1
Hannchen	30	48	109	55	152	215	17
Svanhals	23	26	33	31	80	57	8
Deficiens	5	0	7	2	1	0	6
Manchuria	1	6	17	38	37	10	262

Number of plants of each variety in a sample of 500– figures for 1930

Briggs & Walters (1997)

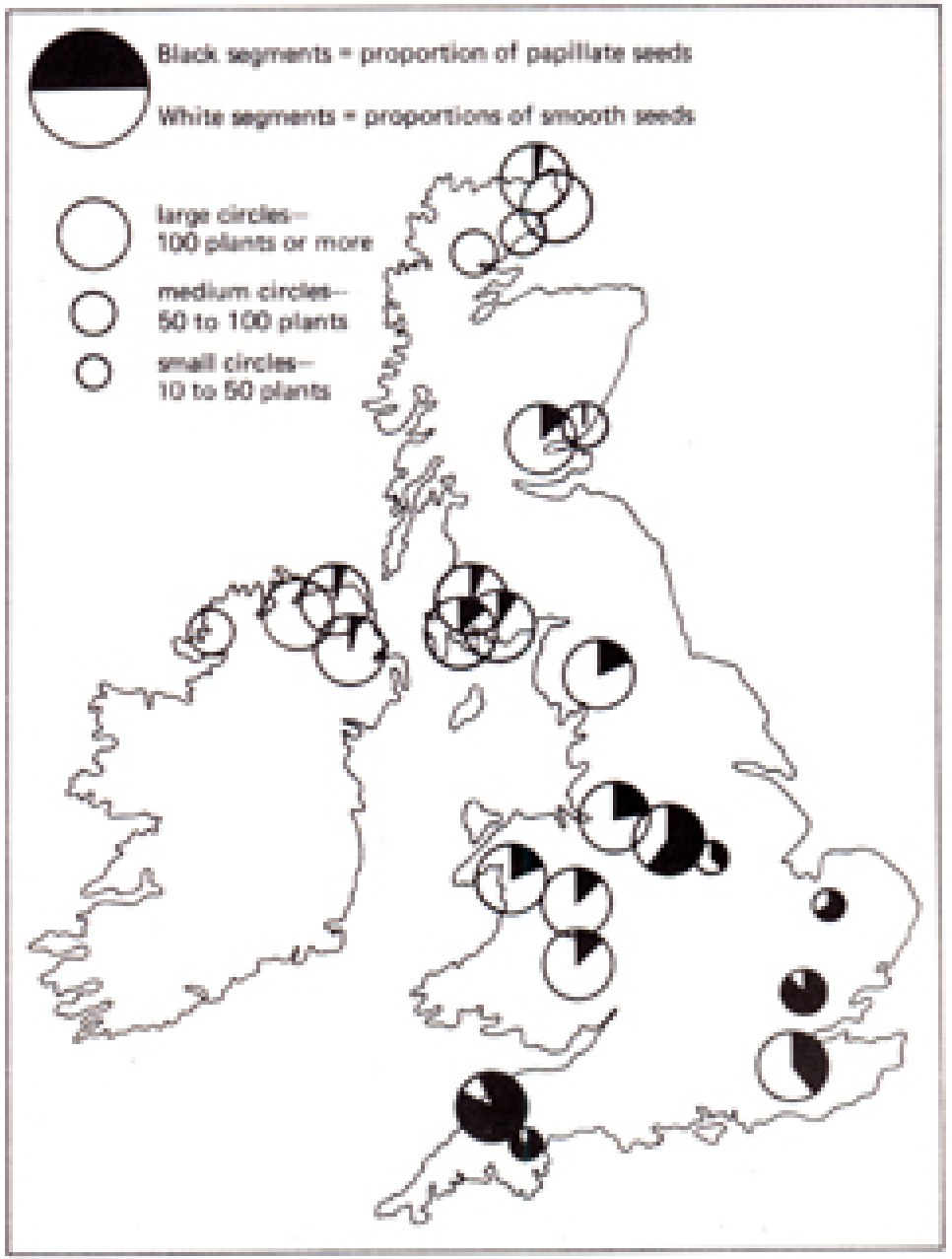
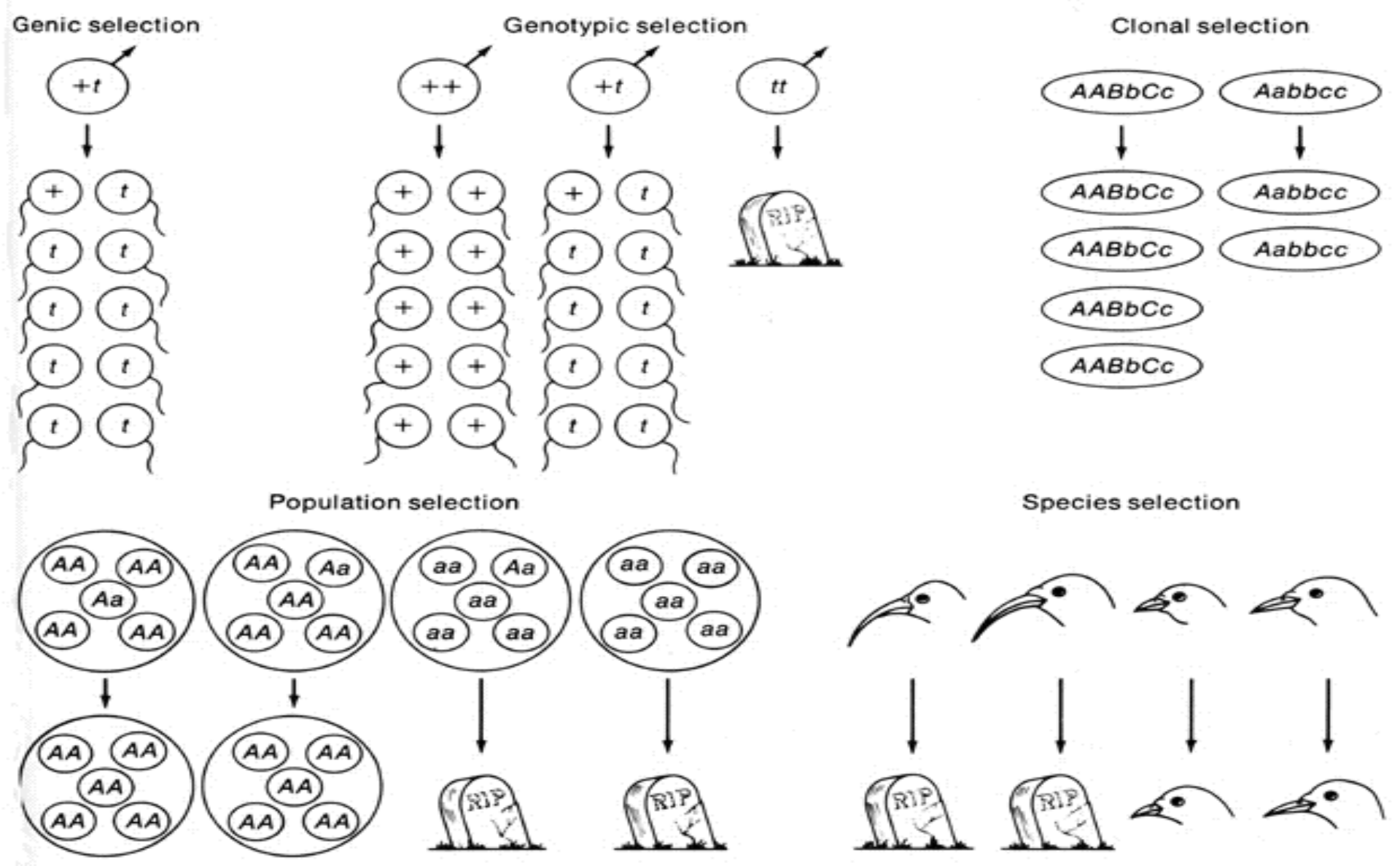


Fig. 9.14. Distribution in the British Isles of variants of *Spergula arvensis* with smooth and papillate seed-coats. (From New, 1958.)

Valiku tasemed

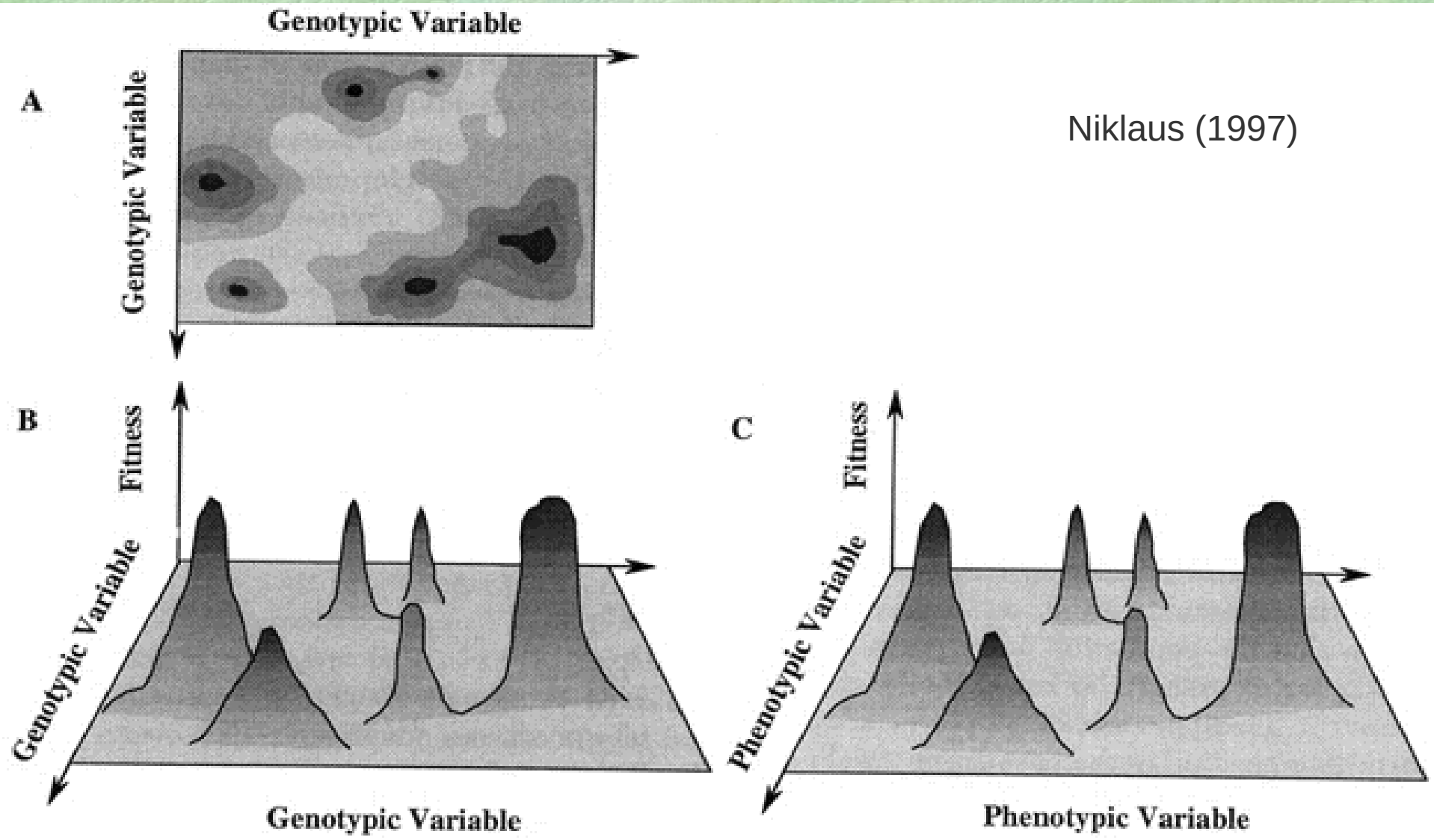


Valiku eriliigid

- **Rühmavalik**
- **Perekondlik valik**
- **Sagedusest sõltuv valik**
- **Suguline valik**

Organismid on selektsioonilised “mosaiigid”

Adaptiivne “kohasuse maastik”



Niklaus (1997)

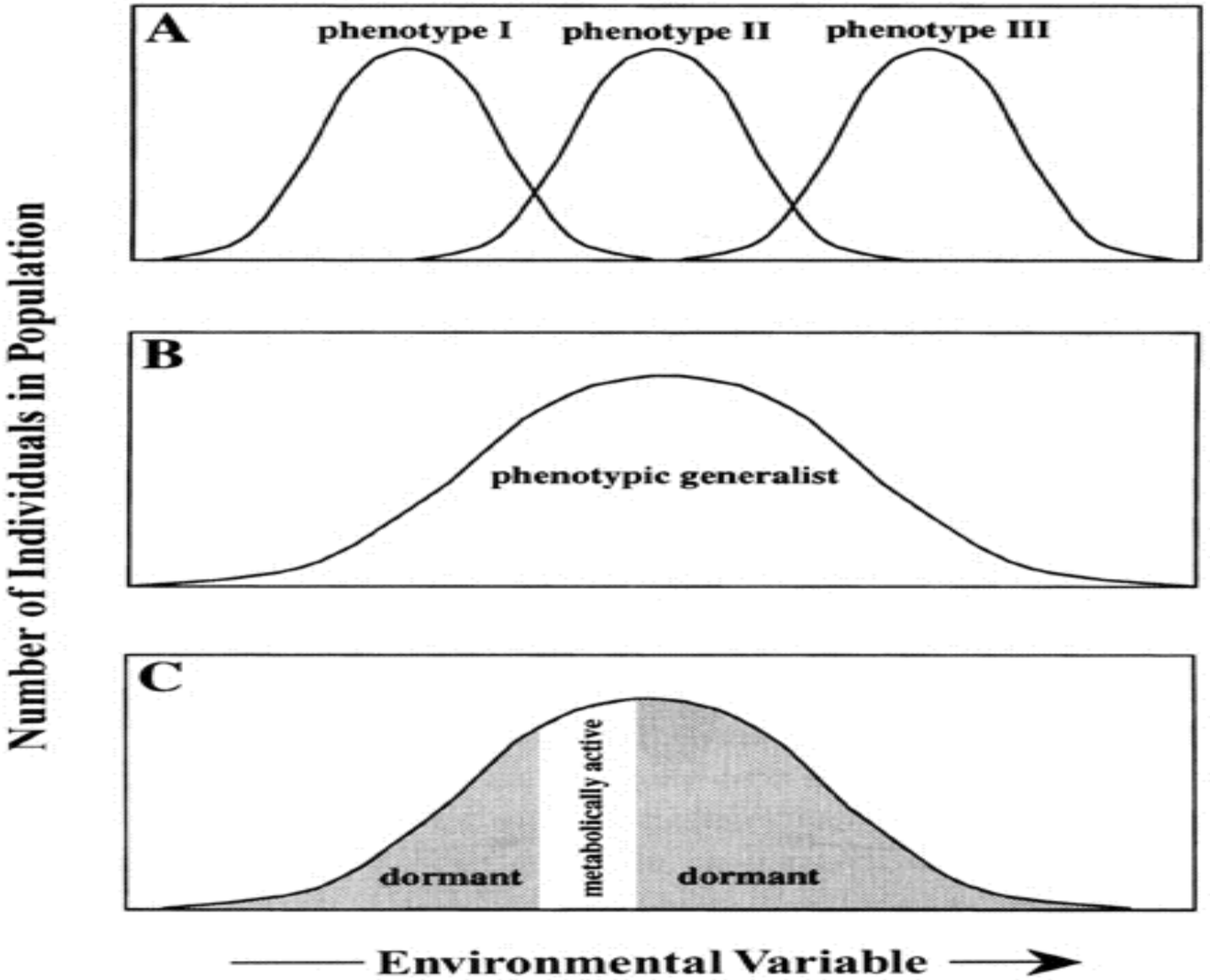


Figure 1.14. Alternative adaptive phenotypic responses to a changing environmental variable illustrated by plotting the frequency distribution of phenotypes against an environmental variable critical to [illegible] reproductive success. (A) A population may consist of individuals with different [illegible] capable of survival over a narrow range of the environmental variable; (B) population may consist of a phenotype capable of survival and reproductive success across a broad range of the environmental variable; (C) individuals may suspend metabolic activity [illegible] environmental variable exceeds a critical threshold.

Vastused valikule (muutuv keskkond)

Homöostaa
Geneetiline assimilee-rumine
Kanalisee-rumine

Adaptatsioon

- Protsess ja pärilik tunnus/tunnuste kompleks, mis võimaldab organismil ellu jääda ja/või muudab ta edukamaks (kohasemaks) antud keskkonnatingimustes
- **Aptatsioon -** struktuur, mis tõstab kohasust
- Adaptatsioon *s.s.* - aptatsioon, mis on kujunenud praeguseks otstarbeks
- **Eksaptatsioon ja**
- **Preadaptatsioon -** struktuurid või funktsioonid, mis arenesid ühes kontekstis, hiljem hakkasid täitma (lisaks või ainult) teist funktsiooni
- Üksiktunnused ja kompleksid – **adaptiivsed sündroomid**

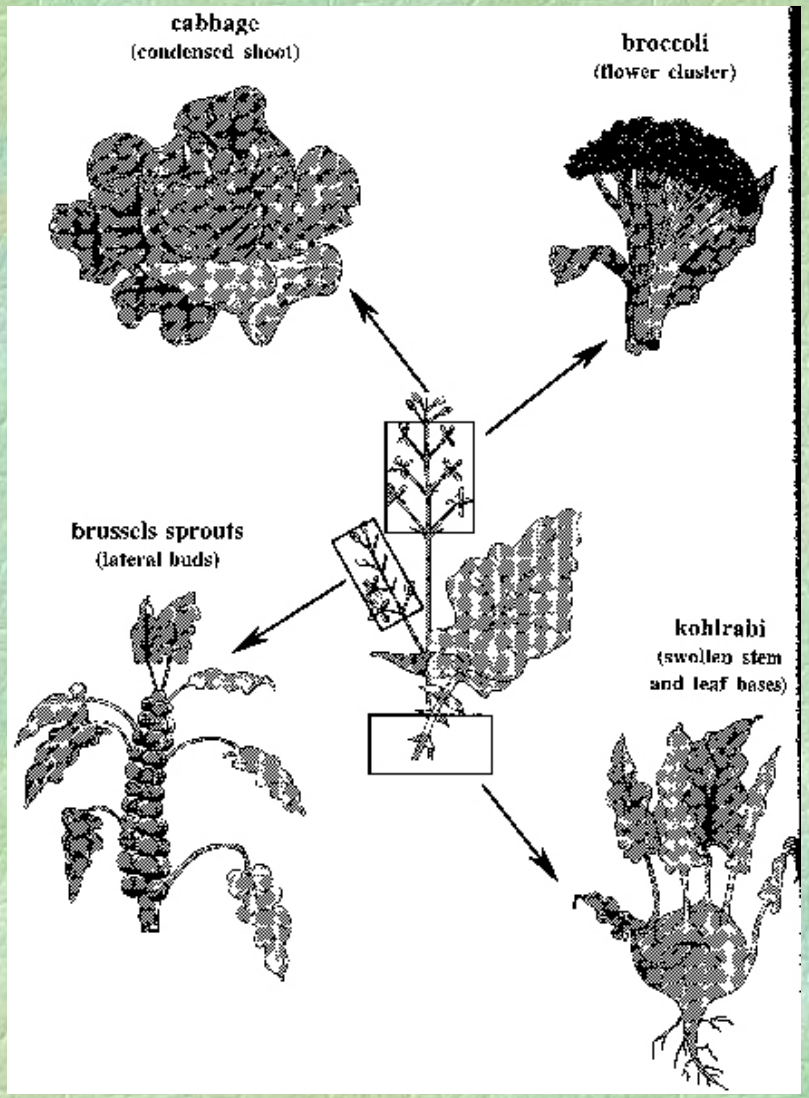
Analoogia ja homoloogia
Parallelism ja konvergents

Cypripedium calceolus

Helianthus maximiliani

Bromus catharticus

Figure 1.1. Plants adapted to living in arid deserts. From left to right: a North American cactus; the Madagascar *Pachypodium lealii* (subspecies *saundersii*); and the African *Aloe dichotoma*. All three store water in succulent stems. The cactus retains its spiny leaves; *P. lealii* and *A. dichotoma* drop their large foliage leaves in times of drought. *A. dichotoma* amputates branches and terminal crowns of foliage leaves during times of extreme water deprivation.



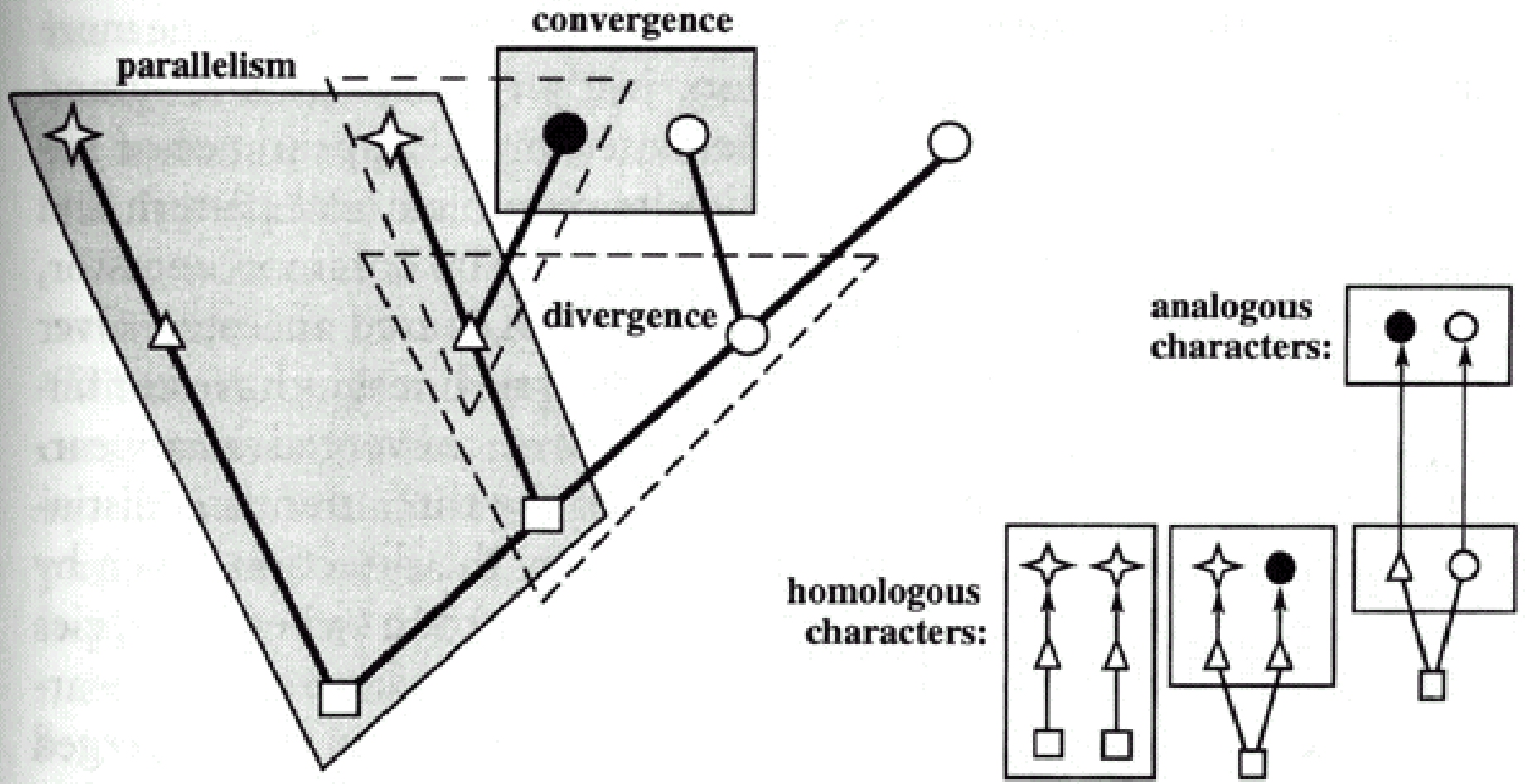


Figure 7.1. Evolutionary parallelism, divergence, and convergence diagrammed in terms of a hypothetical cladogram for eleven phyletically related taxa. Symbols denote different states of a single phenotypic trait. Arrows connecting symbols show character transformations among the states of the trait. Homologous character states are those that are derived directly from the same previous character states, are comparable parts of the same character transformation series, or are identical with that of the last common ancestor. Analogous characters appear to be similar because they serve the same function, but they are derived from different character states.

Vastuolud

- **Adaptatsionistid**
- **Neutraalse evolutsiooni** teooria
- Kompromiss nn **sünteetiline evolutsiooniteooria**

Evolutsioon – kuidas ikkagi?

- **Evolutsiooni kiirus**
- Füleetiline gradualism, muutuste aeglane kogunemine
- Katkestatud tasakaal, “plahvatused”
- **Evolutsiooni-liigitekke mudelid**
- Jagunemine
- Füleetiline
- Kvantliigiteke

Uudsuste tekkimine

- Uudsused - vanade tunnuste modifikatsioonid
- Juhuslikult tekkinud uudsus võib esile kutsuda diversifikatsiooni
- Geneetiline assimileerimine
- Spetsialiseerumine
- Makromutatsioonid
- **Suur roll ka mutatsioonide juhuslikul tekkel ja fikseerumisel**

Makroevolutsioon

- **Evolutsiooniline “radiatsioon” ehk diversifikatsioon-** ekstensiivne, kiire divergeerumine ja liigiteke, mis viib terve uue liikide grupi tekkele, oluline **adaptatiivsete uudsuste** teke

- **Adaptiivne radiatsioon. Kuidas?**
- Eri niššide hõlvamine, uus areaal
- Liikide vastastikune mõju
- Parallelismid, koevolutsioon, arengukonversioonid, suguline valik
- Arenguline radiatsioon

Mitteadaptiivne radiatsioon ehk difuusne evolutsioon

•Evolution abhors a vacuum—whenever possible, organisms will evolve by chance into and come to occupy all regions in the domain of theoretically possible phenotypes that permit survival and reproductive success" (Niklaus)

Divergeerumise uurimine

- Vähe korralikult uuritud rühmi (pisut enam saartel)
- Molekulaarsüstemaatika töid saab kasutada difuusse evolutsiooni uurimiseks
- Ringpõhjendused
- Fenotüüpsete tunnuste kasutamine fülogeneesi koostamiseks viib tsüklilisele põhjendamisele
- Molekulaarne fülogenees aluseks
- Selle baasil saab uurida morfoloogiat, ökoloogiat jm

Näide: Brocchinia (Bromeliaceae)

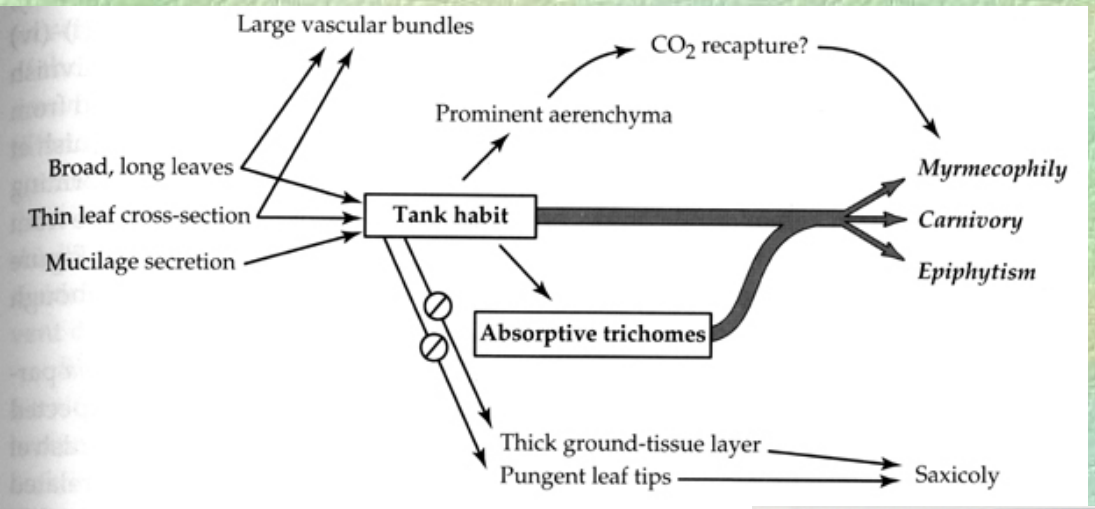
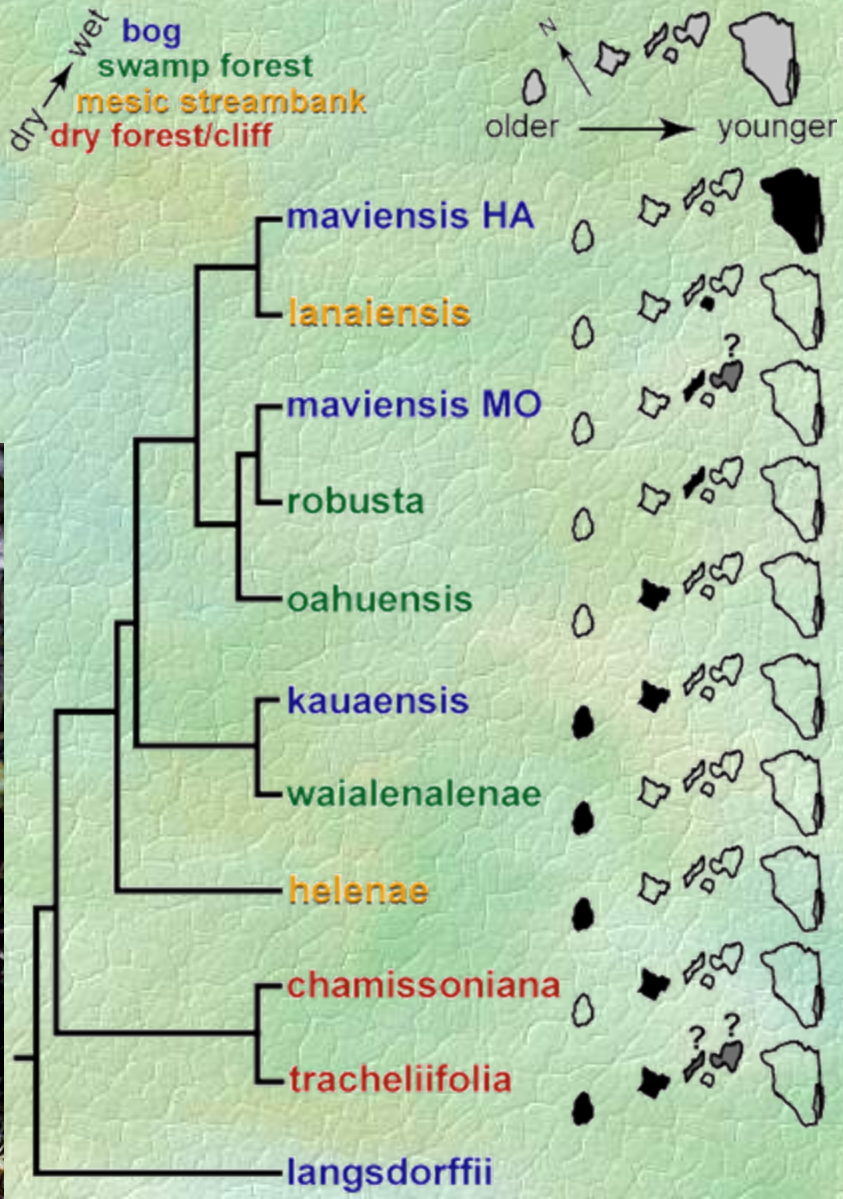


Figure 8.13. Tank habit as a key innovation in *Brocchinia,* showing entrain phological traits and the evolutionary path leading to specialized mecha subsequent ecological dominance and widespread distribution.

Givnish et al. (1997)

Plate 1. Adaptive radiation in *Brocchinia* (see Chapter 8).

Näide: Hawai Viola



Paljunemisviisid ja nende osa taimede evolutsioonis

- **Bell (1982)** "**Sex** is the queen of problems in evolutionary biology. Perhaps no other natural phenomenon has aroused so much interest; certainly none has sowed as

Millest koosneb suguline paljunemine?

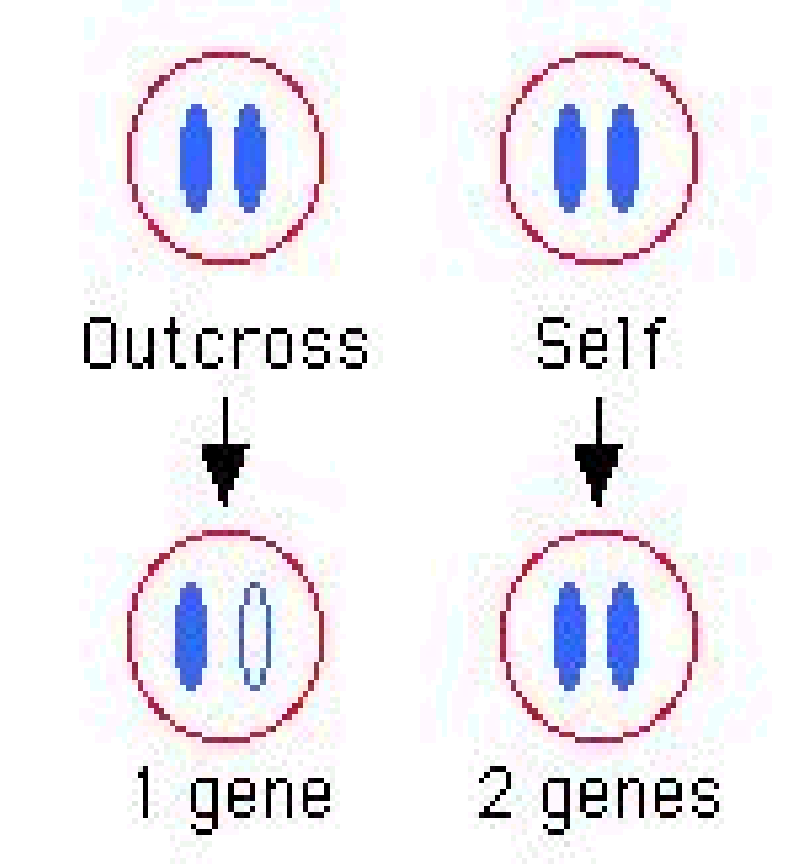
- rekombinatsioon
- segregatsioon
- süngaamia
- uute genotüüpide teke

Seksi hind ehk miks mitte seksida?

- Rekombinatsioon lõhub edukad geenikombinatsioonid - evolutsioon aeglustub
- Osa järglasi on madala kohasusega
- Meioos ja süngaamia on aeganõudvamad kui mitoos
- Kõrgematel organismidel võib seks olla seotud riskiga
- Toimub gameetide “raiskamine” ja seksuaalne dimorfism “maksab”
- Madala asustustiheduse korral on paaritumine raskendatud

Seksi hind ehk miks mitte seksida?

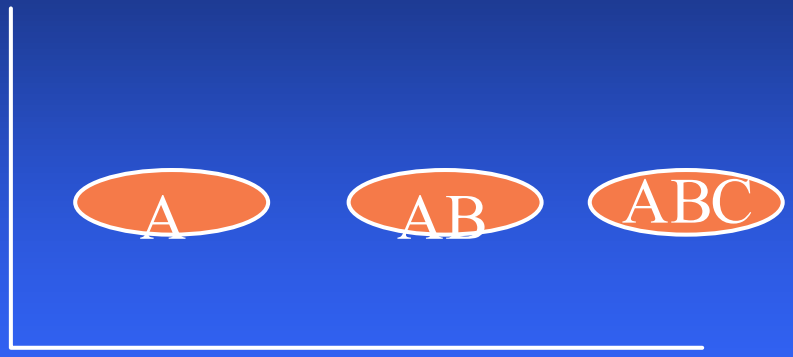
- Olulisim: **sugulised emased saavad sama kuluga edas anda vaid 50% om geenidest**



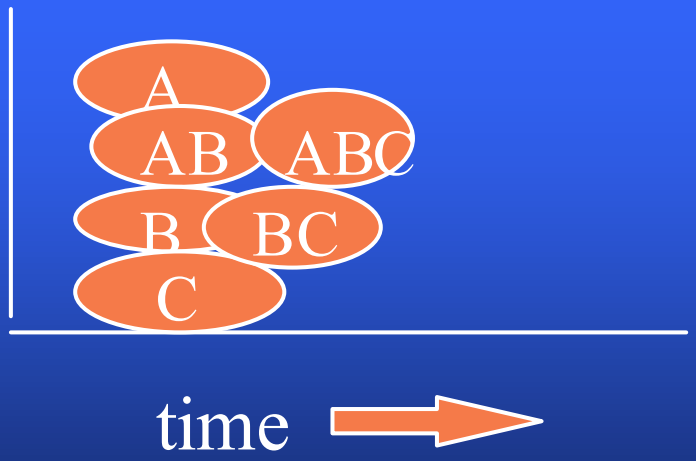
Miks ikkagi seks?

- **Loob varieeruvust, samas ka ühtlustab**
- **DNA parandamise hüpotees**: krossingover
- **Mulleri "hammasratas"** - aseksuaalsetes kloonides kuhjuvad kahjulikud mutatsioonid, rekombinatsioon elimineerib need
- **Fisher-Mulleri hüpotees -** rekombinatsioon loob uusi alleelikombinatsioone, võimaldab kasulikul mutatsioonil avalduda
- **Loob evolutsiooni "materjali"** kiiresti muutuvas keskkonnas

Asexual



Sexual



Segiaetud panga hüpotees

- **Bell 1982, Felsenstein 1988**
- ruumiline heterogeensus
- osad genotüübid edukad ühtedes tingimustes, ebaedukad teistes, teised *vice versa*
- suguliselt paljunevad rühmad suudavad hõlmata rohkem nišše kui piiratud arv partenogeneetilisi kloone

Punase emanda hüpotees

- eelmisega sarnane, rõhutab keskkonna heterogeensust ja muutlikkust

- Viimased hüpoteesid on kooskõlas sellega, et **stabiilsetes tingimustes**, kus on suur konkurents, on **seksuaalne paljunemine levinum**

Taimepopulatsioonid looduses

- Paljud liigid esinevad **valdavalt** väikeste populatsioonidena
- Populatsioonid on fragmenteeritud ja isoleeritud
- Paljudel liikidel piiratud levikuvõime
- Sugulusristumine on tavaline

Taimede kõrvalekalded panmiksisest

- risttolmlemine naabertaimede vahel (vitsinism)
- isetolmlemine (autogaamia)
- vegetatiivne paljunemine
- agamospermia

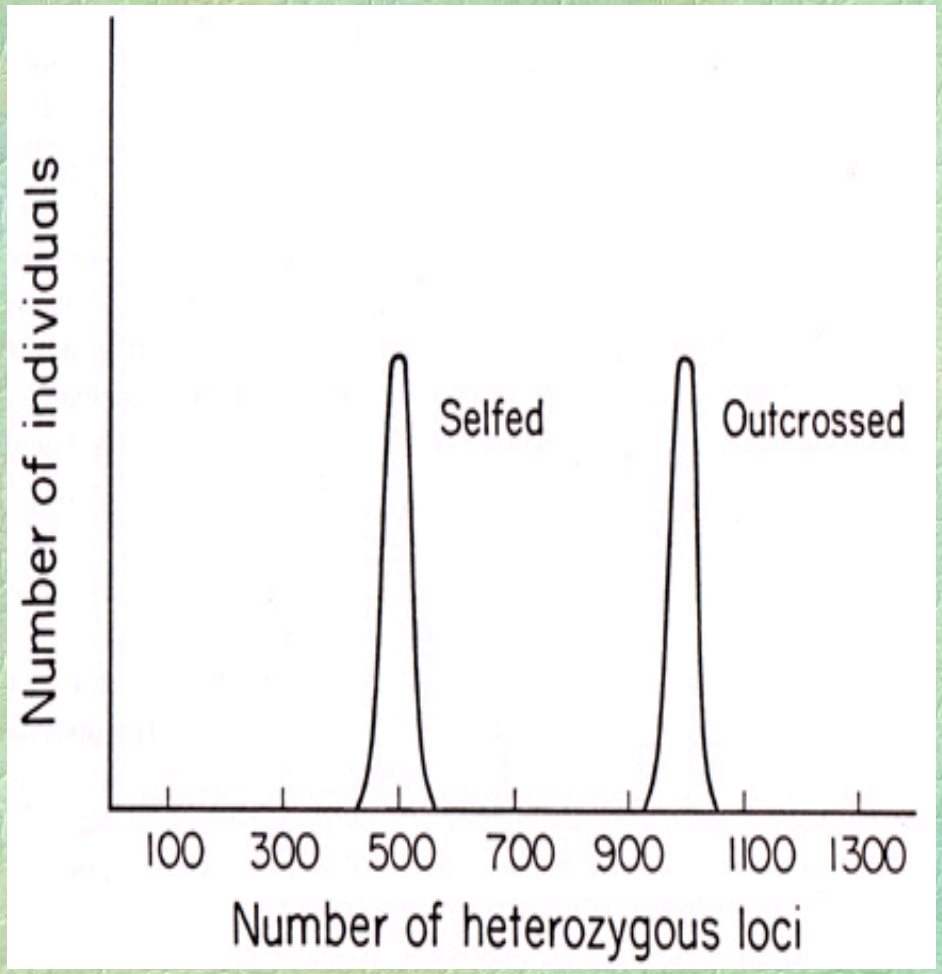
- Kolm äärmuslikku **strateegiat**
  - **panmiksis**
  - **autogaamia**
  - **aseksuaalsus**
- Praktikas sageli **segastrateegia**

Inbriiding

- Igasuguse mittejuhusliku paljunemise tagajärg
- Koefitsient F
  - F-->0 panmiksis
  - F-->1 inbriiding

Inbriiding

- Rohkem homosügoote, vähem heterosügoote
- Ei muuda allelisagedusi
- Genotüübiline ja fenotüübiline varieeruvus väheneb populatsiooni sees, suureneb populatsioonide vahel
- Inbriidingudepressioon



Populatsioonidevaheline geneetiline erinevus

Soltis & Soltis 1989

Kõrge	Madal
Isetolmlemine	Risttolmlemine
Hermafrodiidid	Ühe- ja kahekojalised
Gravitatsiooniline seemnelevi	Tuul- ja loomlevi
Üheaastane	Mitmeaastane
Monokarpne	Polükarpne
Suktsessioonis varane	Suktsessioonis hiline

Tolmlemine ja viljastumine

- Risttolmlemine ehk **allogaamia**
  - **ksenogaamia**
    - anemofiilia
    - hüdrofiilia
    - zoofiilia
  - **geitonogaamia**
- Isetolmlemine ehk **autogaamia**

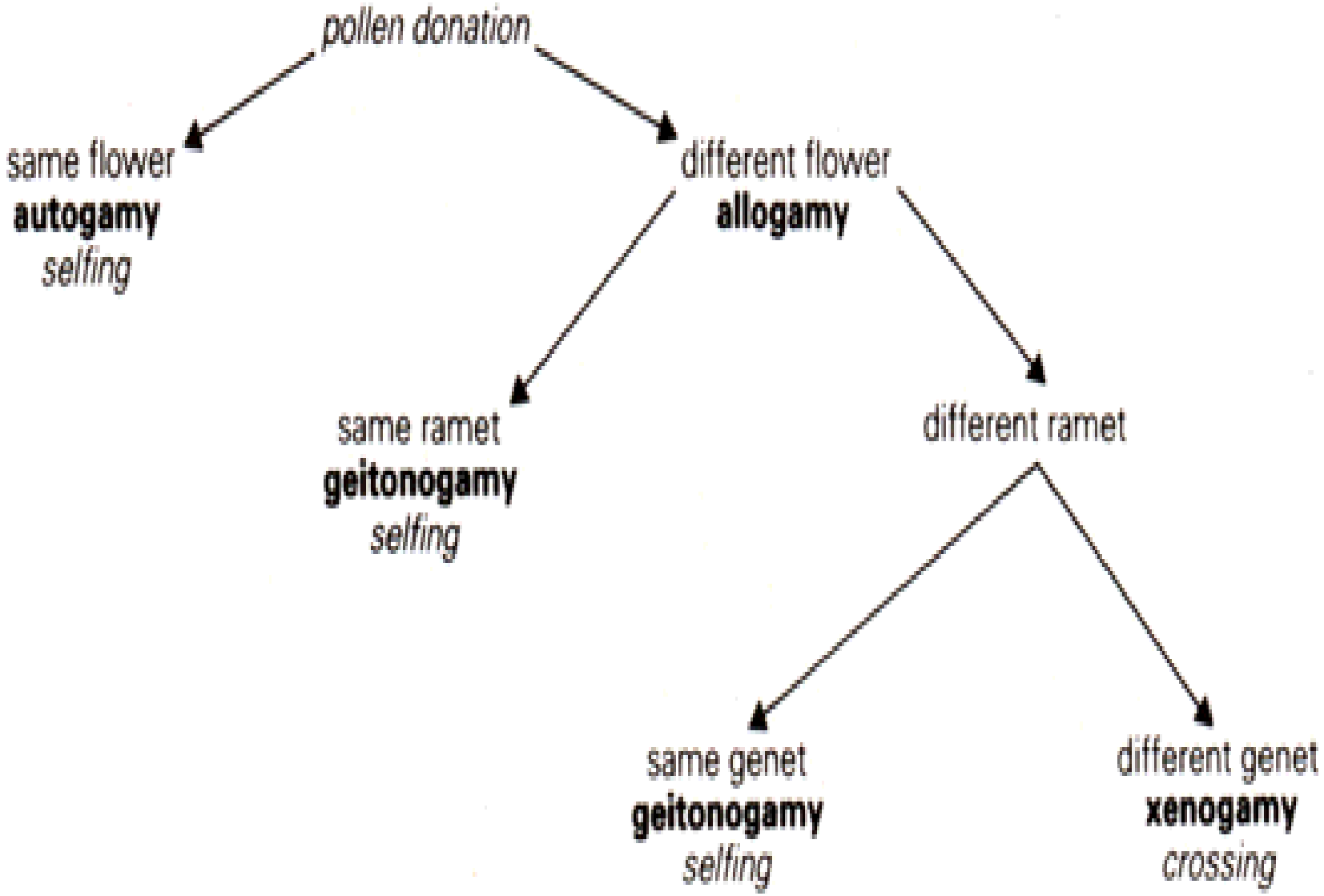


FIGURE 22.4 Patterns of pollen transfer within and between flowers and plants. (From Richards 1986:3)

Ristolmlemise tagamise mehhanismid - lahksugulisus

TABLE 22.2 Common Types of Sex Distribution Within and Between Flowers and Genets of Angiosperms. (From Richards 1986: 4)

Name	*Distribution of sex organs*		*Breeding system*	*Angiosperm species (%)*
	within a flower	*within a plant*		
dioecy	♂ or ♀	♂ or ♀	xenogamous (outcrossing)	4
gynodioecy	☿, ♂ or ♀	☿ or ♀	xenogamous, geitonogamous, autogamous	7
monoecy	♂ or ♀	☿	allogamous, some selfing, some crossing	5
gynomonoecy	☿ or ♀	☿	allogamous and autogamous	3
hermaphrodity	☿	☿	allogamous and autogamous	72
(other)				9
				100

Risttolmlemise tagamise mehhanismid

Dihhogaamia

- proterandria
- proterogüünia

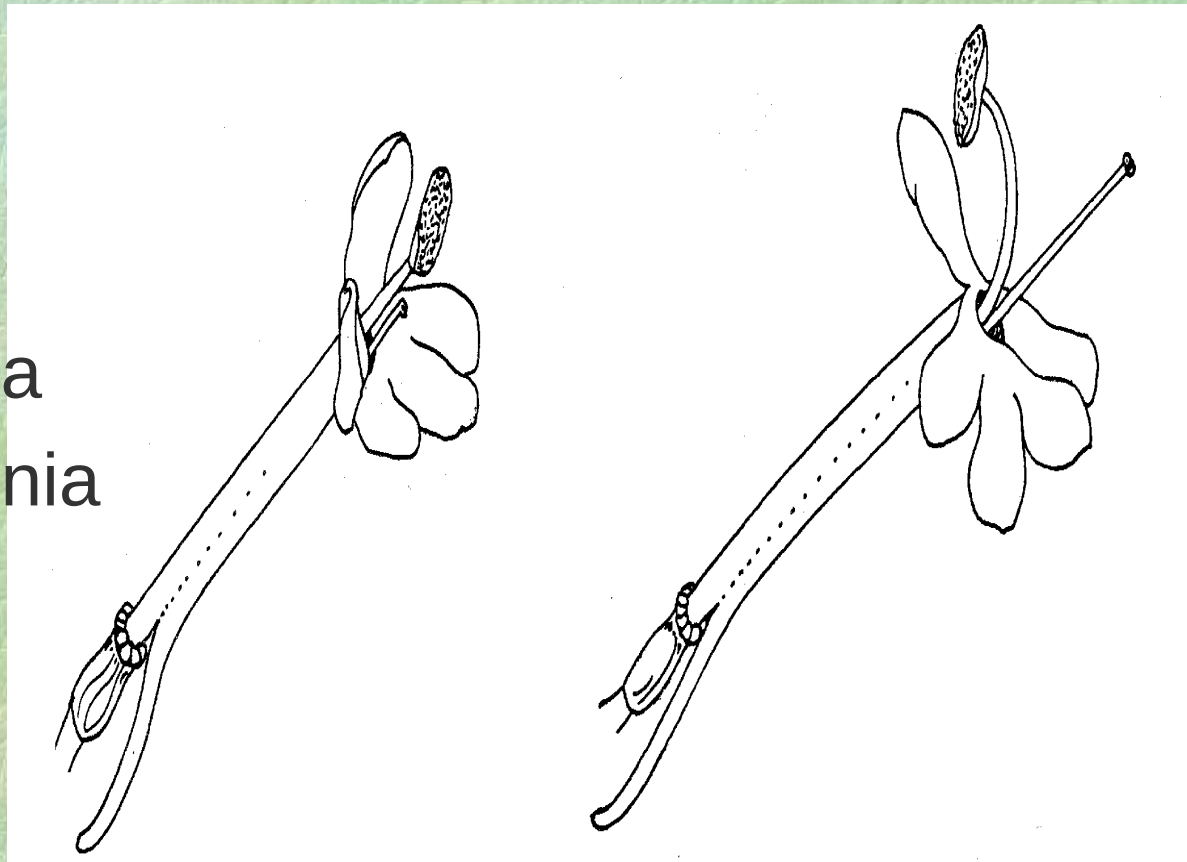


Figure 22. Two flowering stages in red valerian (*Centranthus ruber*). The stamen, which ripens before the stigma, moves out of the way when the latter reaches maturity. This is intended to prevent self-pollination.

mehhanismid: herkogaamia ehk heterostüülia

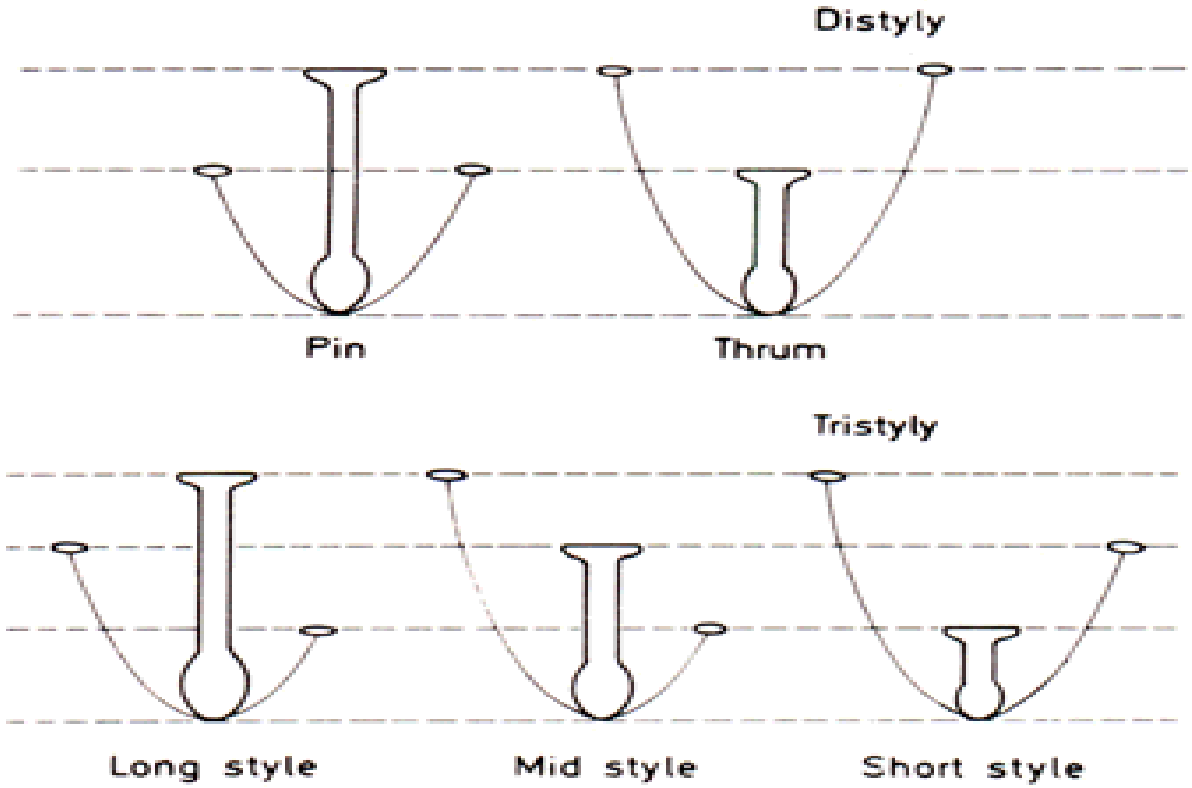


Fig. 7.3. Symbolic representation of distyly and tristyly. In each system, the compatible pollinations only involve anthers and styles at the same level, and therefore the following are incompatible combinations: pin × pin, thrum × thrum, long × long, mid × mid, and short × short. (From De Nettancourt, 1977.) Darwin (1877) listed 14 families in which heterostyly had been confirmed. This list has now been extended to *c.* 25 families (Barrett, 1992).

Risttolmlemise tagamise mehhanismid: gametofüütne isesobimatus

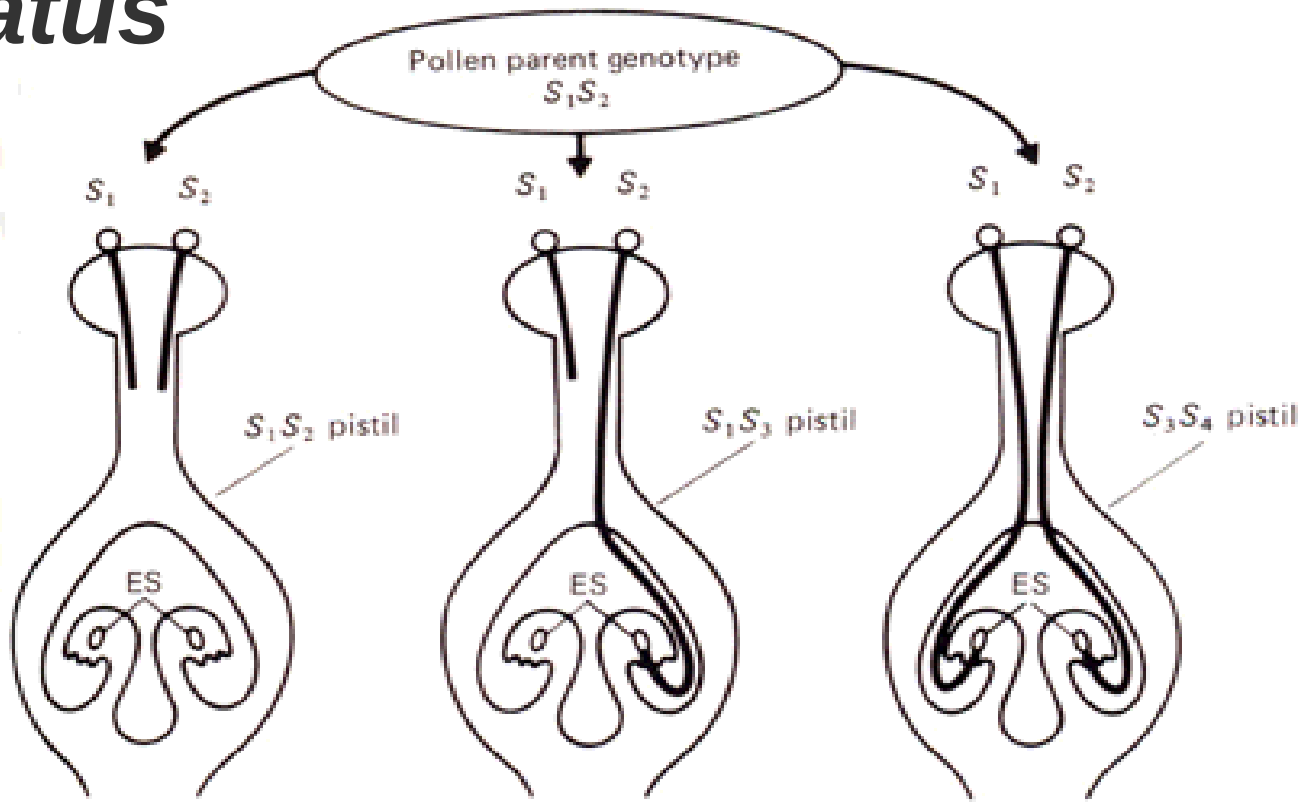
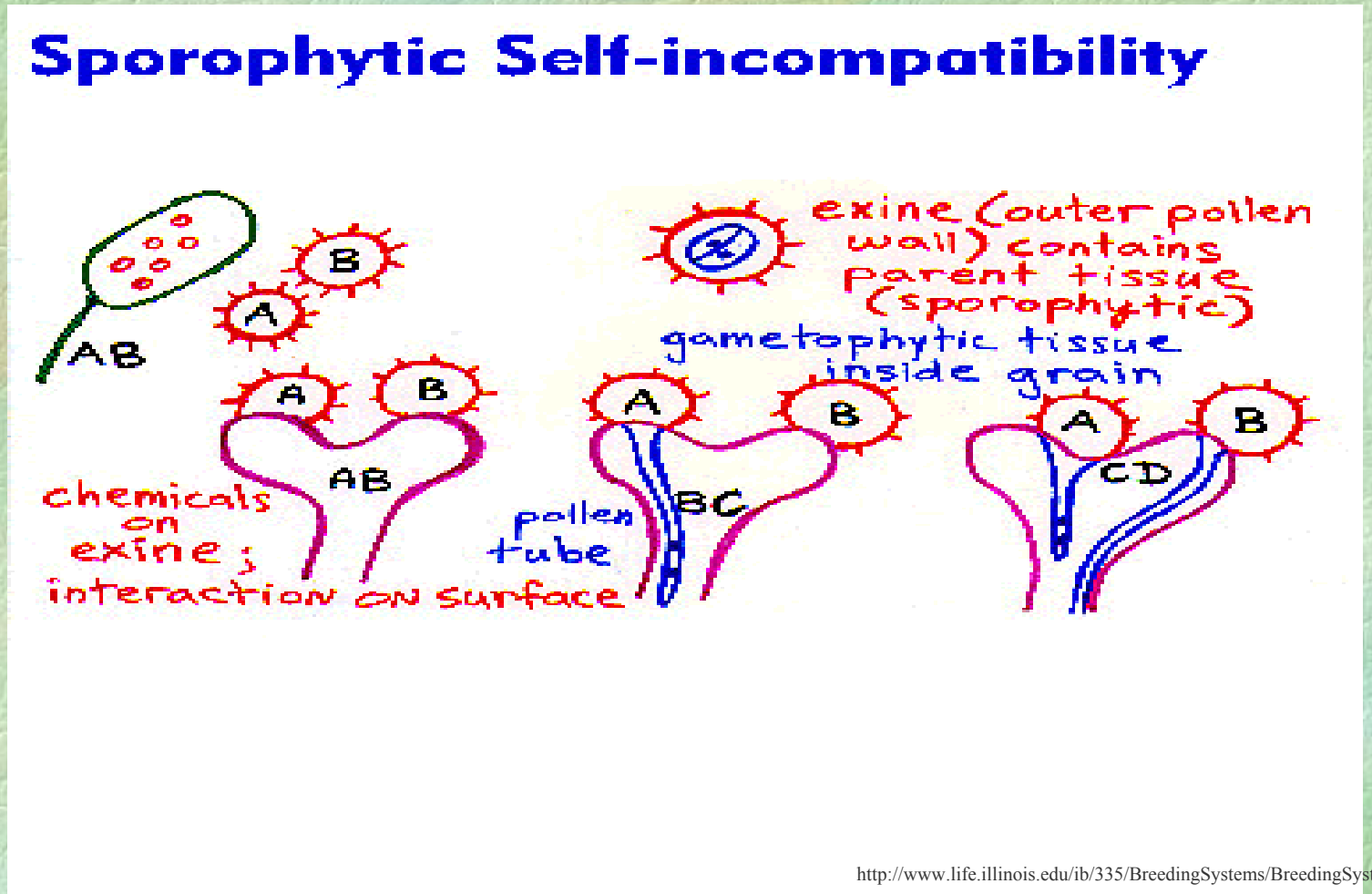


Fig. 7.1. Gametophytic self-incompatibility. A pollen parent of genotype S_1S_2 will be infertile, semi-fertile or fully fertile according to the genotype of the female plant. In most species with this system, incompatible pollen tubes are inhibited in the style. ES = embryo-sac. (From Heslop-Harrison, 1978). Note that in some families gametophytic self-incompatibility is more complex genetically, being controlled by two or more loci (De Nettancourt, 1977).

Ristlõmlemise tagamise mehhanismid: sporofüütne isesobimatus



Isesobimatus

stigma tüüp	**stigma eksudaat**	**papillide kutiikula**	**õietolmu hüdratatsioon**	**õietolmu sisenemine**	**isesobimatuse tüüp**
märg	olemas	mitte-pidev	väline	inter-tsellu-laarne	**gametofüütne**
kuiv	puudub	pidev	sisemine	intra-tsellu-laarne	**sporofüütne**

Isetolmlemine

- Isesobivus
- Struktuursed mehhanismid (kleisotgaamia)
- Obligaatsed ja fakultatiivsed

Aseksuaalne paljunemine= apomiksis s.l.

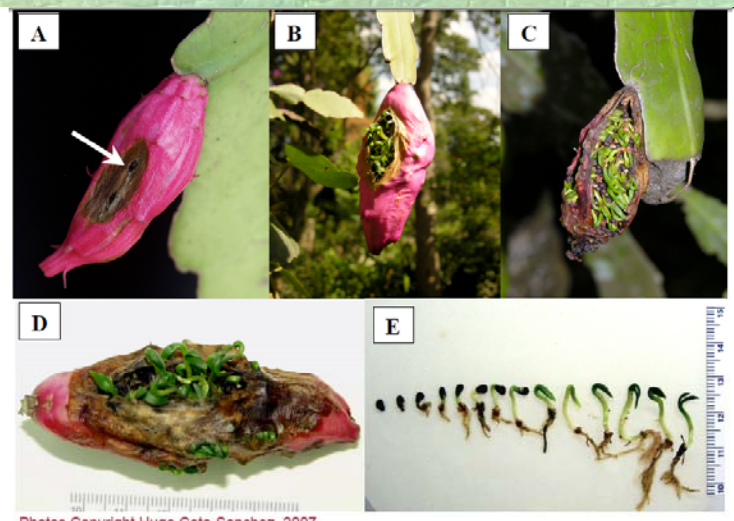
- **Vegetatiivne paljunemine**
  - Taimefragmendid
  - Spetsiaalsed struktu
  - **Vivipaaria**:

  tõeline ja

  pseudo
- **Agamospermia ehk apomiksis *s.s.***

Cryptovivipary

The embryo grows to break through the seed coat but not the fruit wall before it splits open



Photos Copyright Hugo Cota-Sanchez, 2007

Figure showing different stages of vivipary in fruits and offspring of *Epiphyllum phyllanthus*. **A.** Mature, four-week-old fruit showing the area of dehiscence (arrow), region through which the viviparous seedlings emerge upon germination. **B.** Six-week-old fruit on mother plant showing the emergence of viviparous seedlings through pericarp. **C.** A seven-week-old fruit on mother plant with viviparous offspring. **D.** Close-up of a six-week-old viviparous fruit. **E.** Developmental series of viviparous seedlings harvested from the fruit in the previous picture. Scale: 1 bar = 1 mm. From: Cota-Sánchez, J. H. & D. D. Abreu. (2007). Vivipary and offspring survival in the epiphytic cactus *Epiphyllum phyllanthus* (Cactaceae). Journal of Experimental Botany 58: 3865-3873 (doi: 10.1093/jxb/erm232).

Agamospermia

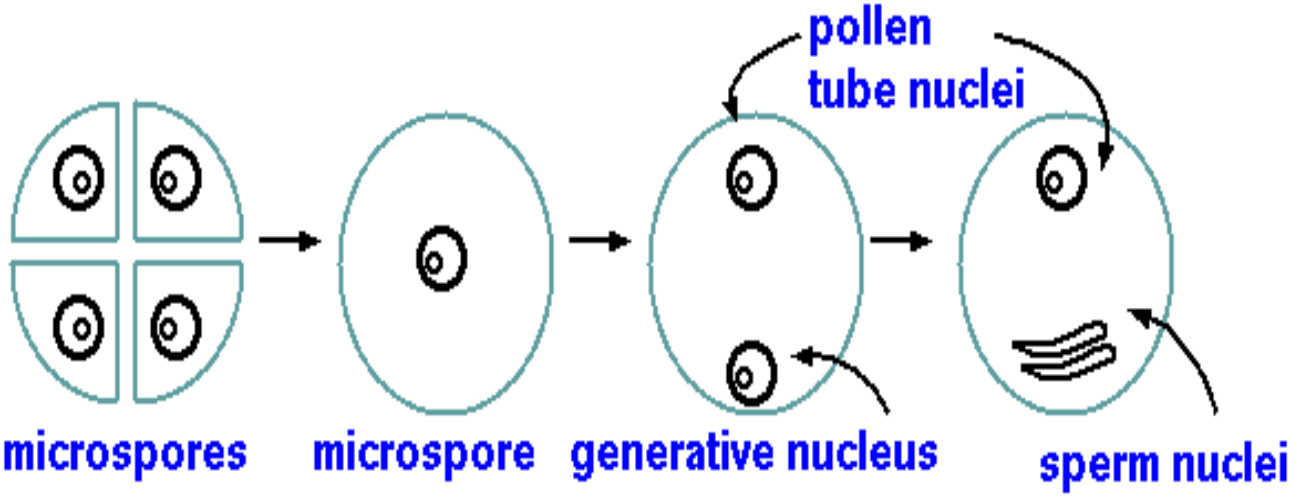
- fertiilsete seemnete aseksuaalne, viljastumiseta moodustumine

http://et.wikipedia.org/wiki/Pilt:36_Taraxacum_officinale.jpg

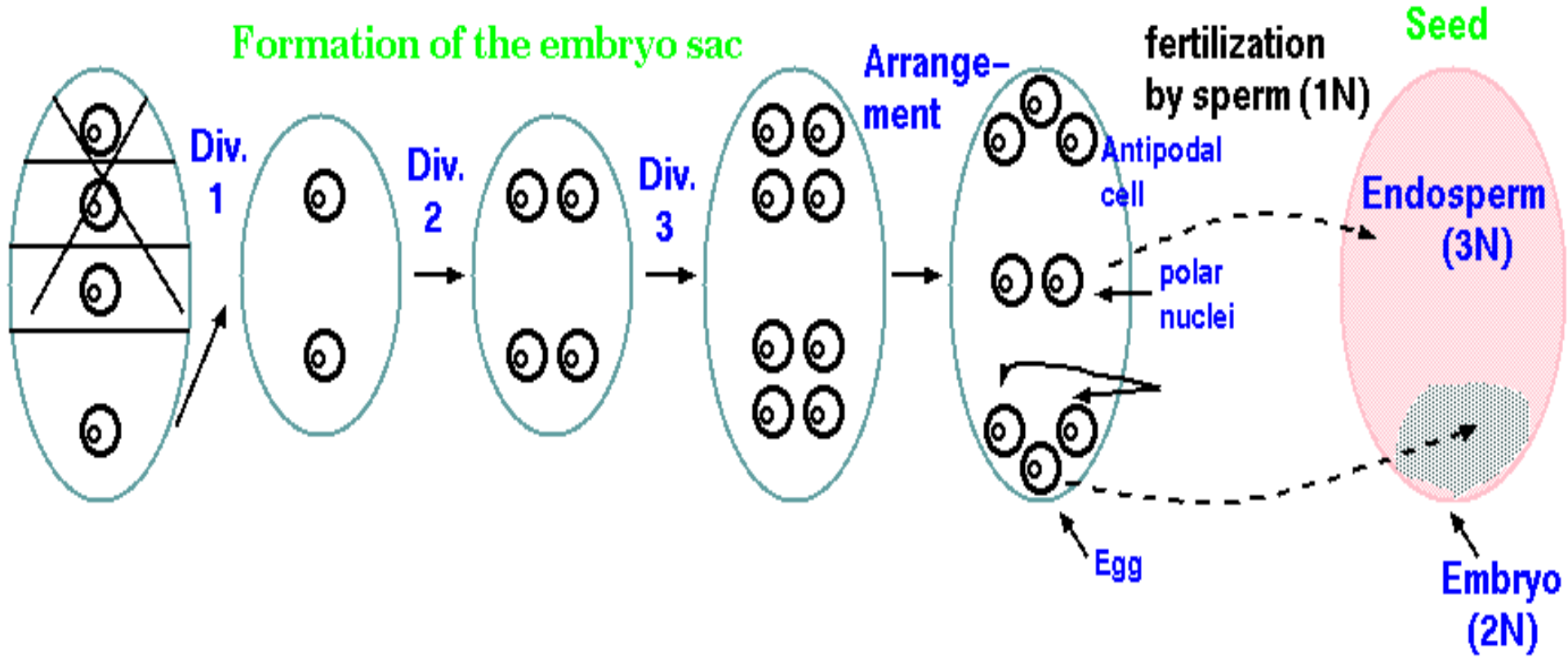
Emasgameetide areng ja viljastamine õistaimedel

- 1. arhesporogenees
- sporofüüdi seemnealgme nutselli rakud ⇒ arhespoori rakk
- 2. sporogenees
- arhespoor ⇒ meioos ⇒ 4 makrospoori ⇒ ühest megagametofüüdi emarakk
- 3. megagametogenees
- emarakk ⇒ 3 mitoosi ⇒ 8-tuumaline lootekott (emasgametofüüt)
- 4. gametogenees
- lootekoti diferentseerumine 7 rakuks: munarakk, 2 sünergiidi, 3 antipoodi ja 2 polaartuuma ühinemisel moodustunud teistuum
- 5. sügotogenees
- kaheliviljastamine ja sügoodi areng

Formation of pollen grains



Formation of the embryo sac



Agamospermia liigid

- **1. adventiivne embrüoonia** ehk sporofüütne agamospermia
- embrüo tekib nutselli somaatilistest rakkudest, lootekott puudub
- koos normaalse sugulise sigimisega
- **2. apogaamia**

lootekott tekib gametofüüdi 1n rakkudest süngaamia teel

- **3. gametofüütne agamospermia** (=partenogenees s.s., autonoomne embrüoonia) meioosi ei toimu
- **2A. apospooria**

lootekott tekib nutselli vm 2n somaatilistest rakkudest,

- **2C. diplospooria**

lootekott kujuneb 2n megaspoori emarakust

Agamospermia liigid

- **I. autonoomne agamospermia**
- seemned arenevad sõltumata tolmeldamisest, lootekoti teistuum muutub partenogeneetiliselt endospermiks

- **II. pseudogaamia**
- embrüo hakkab arenema enne tolmeldamist, kuid endospermi moodustumiseks on vajalik teistuuma viljastamine

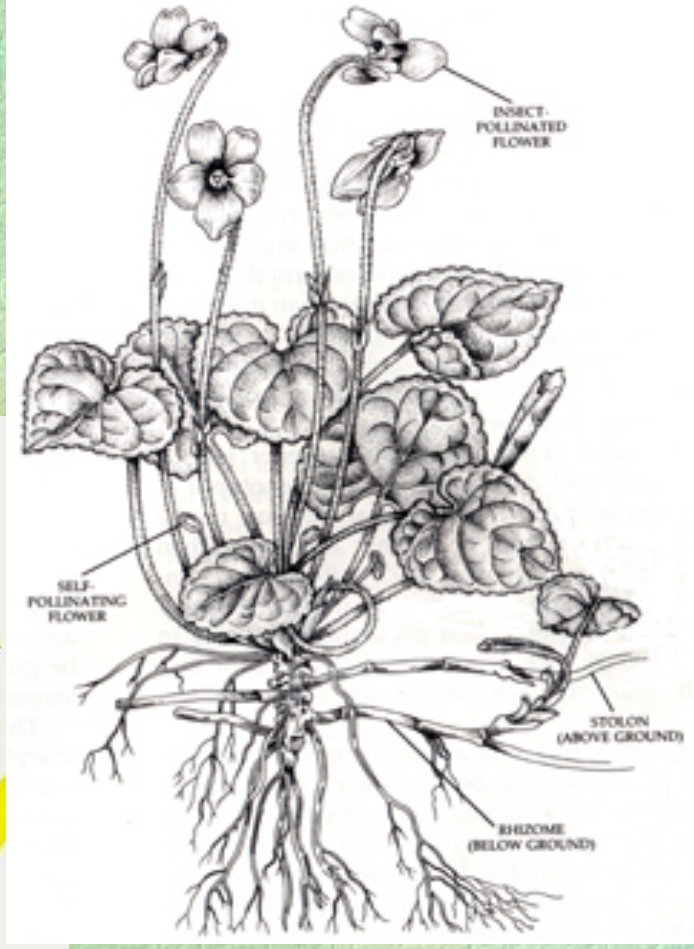
- **Obligaatne ja fakultatiivne**

Asteraceae, Poaceae, Rosaceae

Evolutsiooniline potentsiaal

- \+
  - heteroosi fikseerumine
  - hübriididel pääs steriilsusest
  - tugev heterosügootsus
  - sõltumatus tolmlemisest
  - võimaldab uute alade hõlvamist üksikisendi järeltulijatega
  - diaspooride edukas kauglevi
  - kokkuhoid seksi hinnalt
- \-
  - puudub kasulike mutatsioonide rekombinatsioon $\Rightarrow$
  - varieeruvuse puudumine $\Rightarrow$
  - üks genotüüp, ebaedukad muutuvas keskkonnas
  - kasututе mutatsioonide kuhjumine

Segastrateegia näiteid



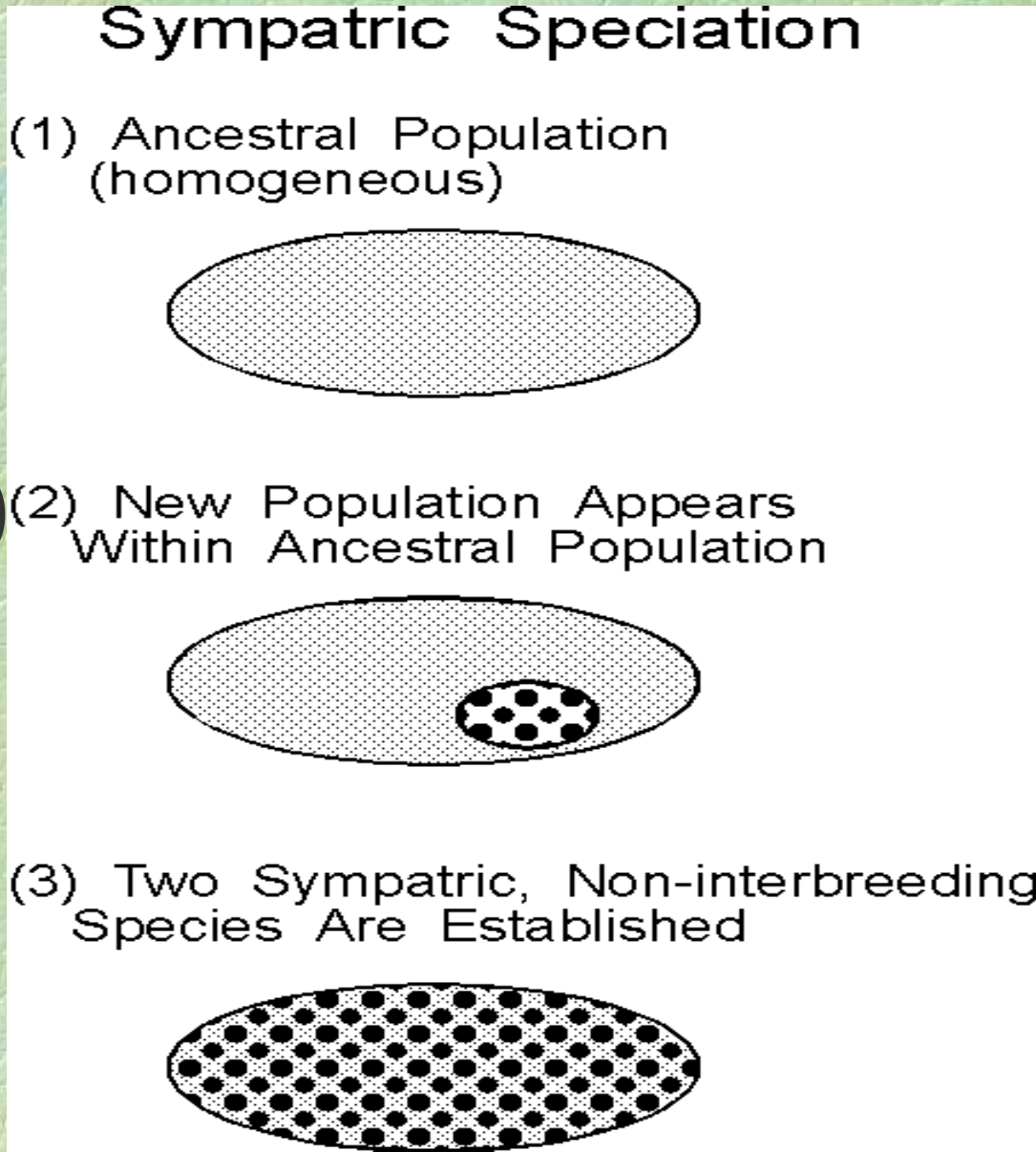
http://et.wikipedia.org/wiki/Ristik

http://et.wikipedia.org/wiki/Pilt:36_Taraxacum_officinale.jpg

Liikide tekkimine

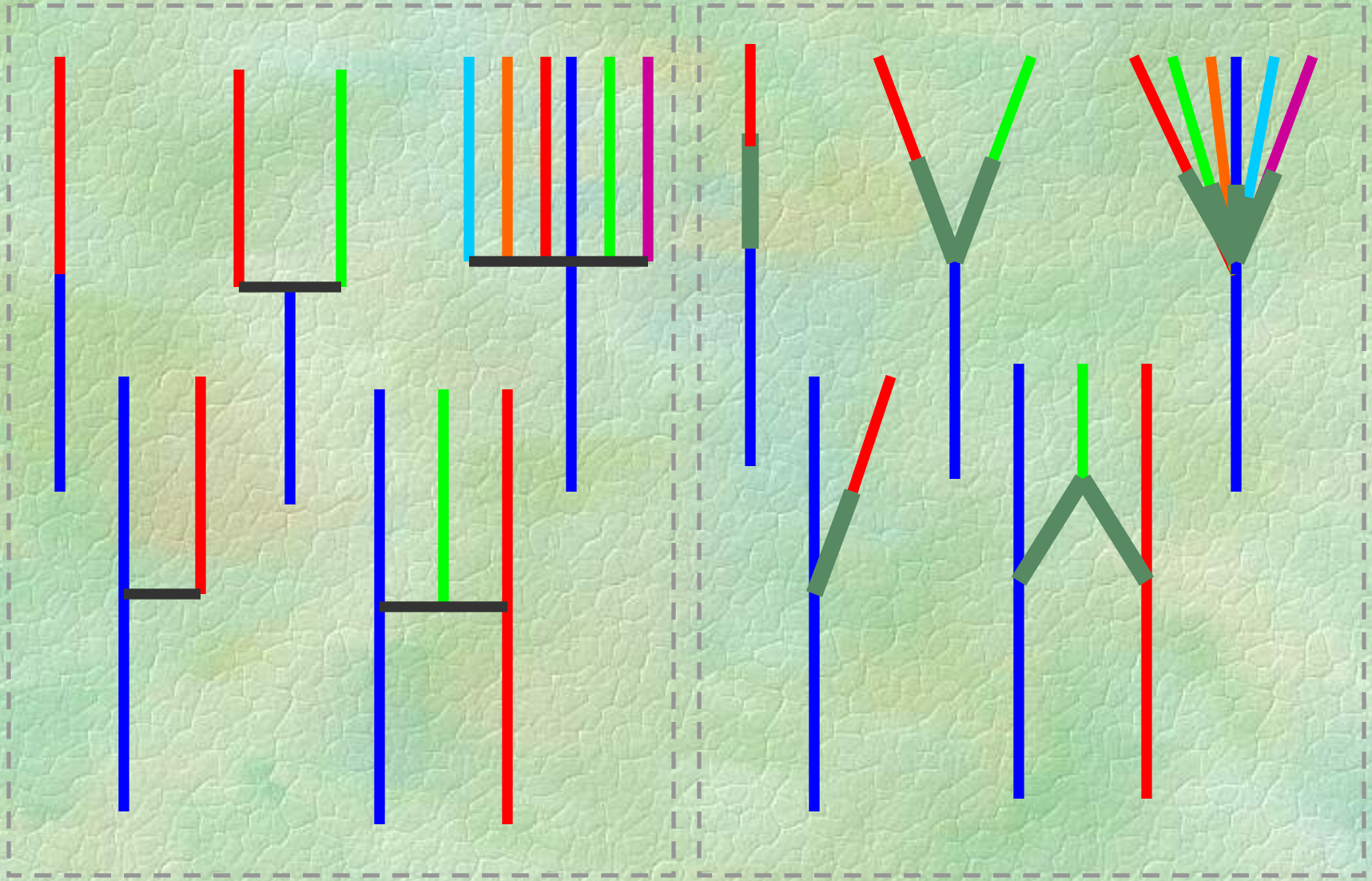
Liigitekke viisid

- allopatriline
- sümpatriline
- (parapatriline)



Punctuated

Gradual

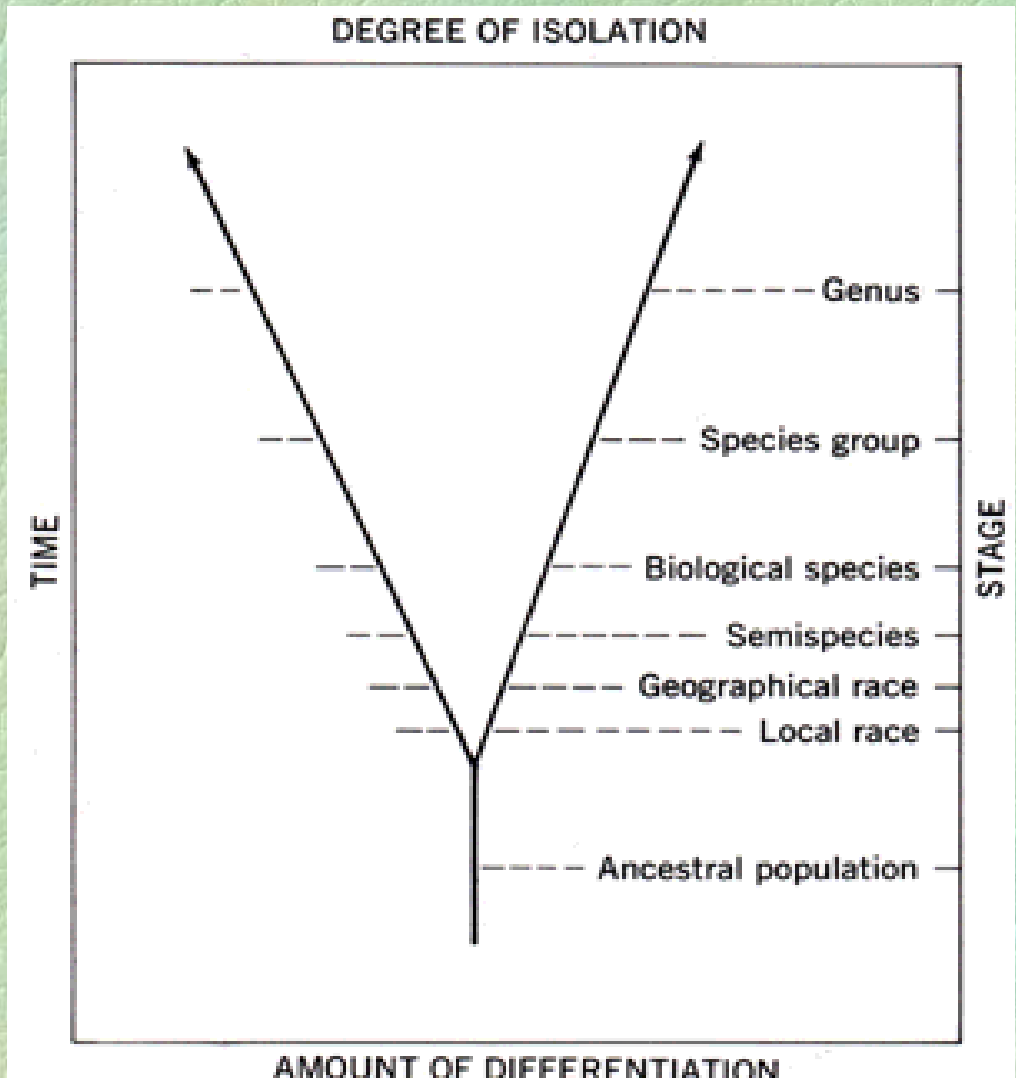


Liigitekke viisid

- geograafiline
- polüploidne
- kromosomaalne
- ökoloogiline
- aseksuaalne
- hübriidne
- jne

Geograafiline liigiteke

- geograafiline kaugus, mis väldib või piirab ristumist
- tavalisim nii taimedel kui loomadel
- palju tõendeid



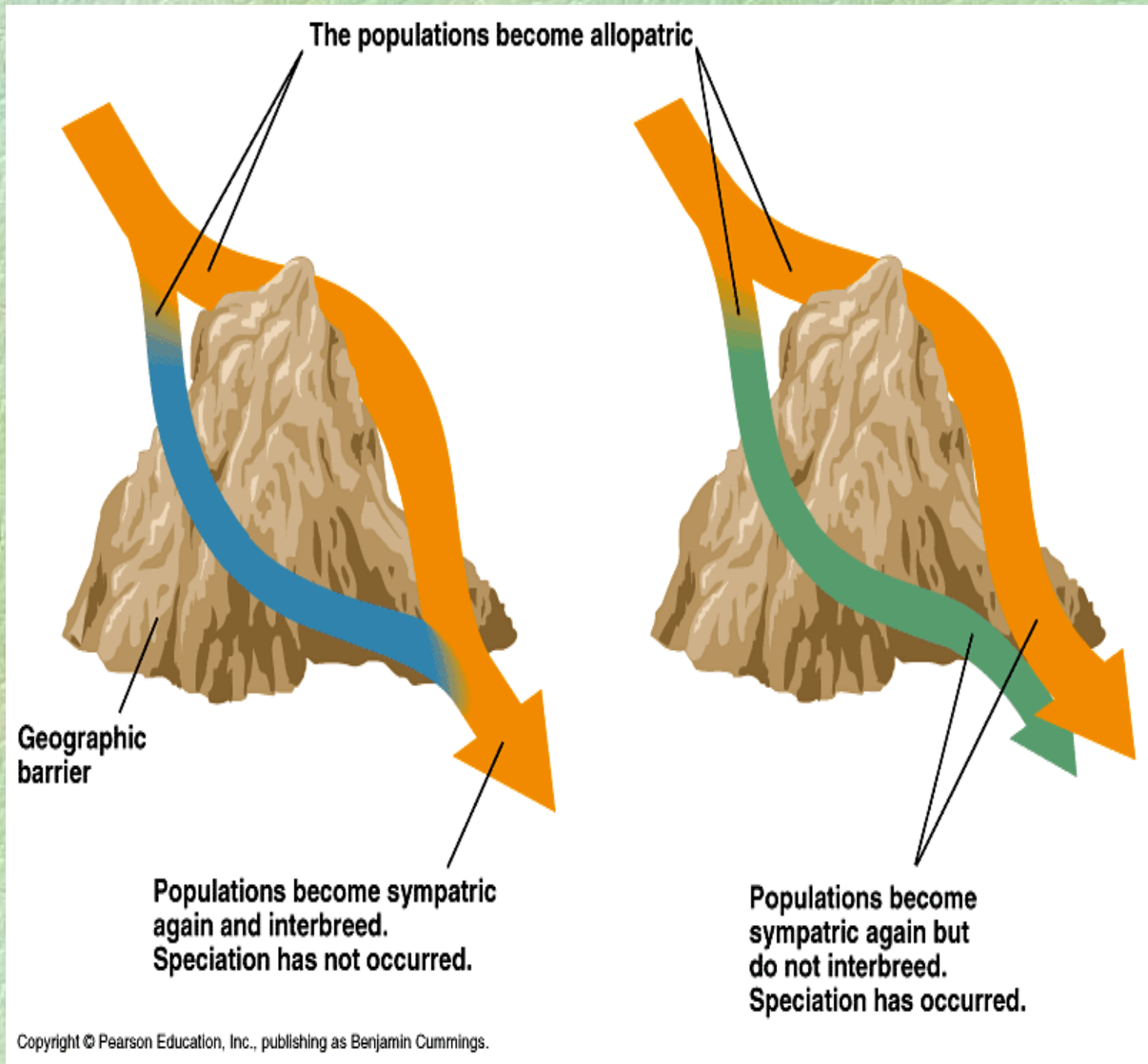
http://www.plant.siu.edu/PLB479/Lectures%20PLB479/SpeciationProcess.html

Võimalikud barjäärid

- Mäeahelikud
- Meri, mageveekogud
- Maa (veeliikidele)
- Jää, liustikud
- Orud

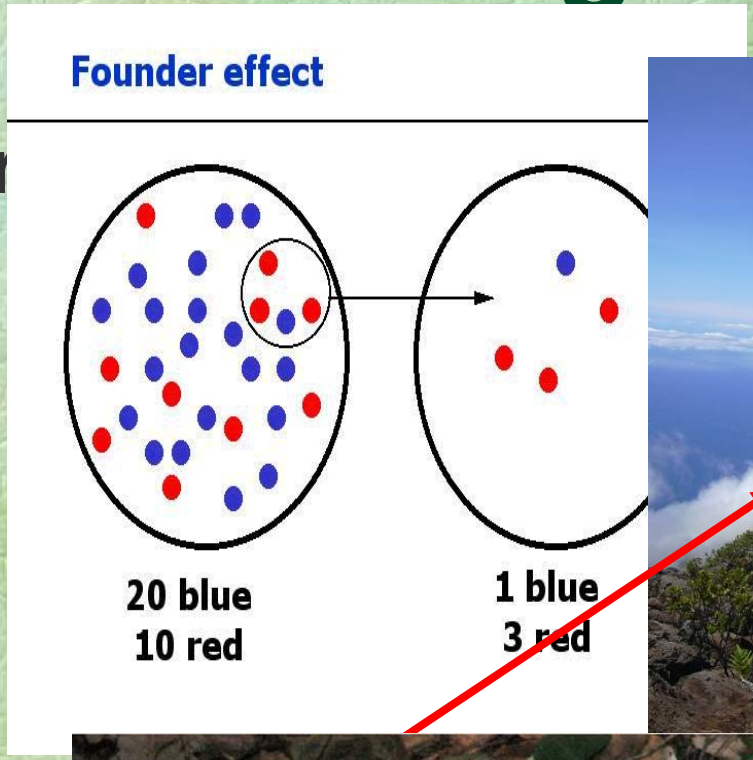
Geograafiline liigiteke Mudelid

- klassikaline allopatriline mudel s.s.



Geograafiline liigiteke

- pioneeriefekti mudel (founder effect)
- perifeersete isolaatide mudel



silverswords in Hawaii,

tarweeds in California

Polüploidne liigiteke

- Polüploidid enamasti diploididega ei ristu
- Paralleelselt erinevates kohtades
- Kiire, spontaanne
- Maismaataimed iidsed polüploidid
- **Sümpatriline**
- Enamasti **allopolüploidne**, harvem **autopolüploidne**

Autopolüploidne liigiteke

- Kromosoomistiku duplikatsioon
- Allopatriline või sümpatriline
- Füsioloogilised erinevused
- Duplikaatsetes lookustes allelide vaigistamine
- Harv

Kromosomaalne liigiteke

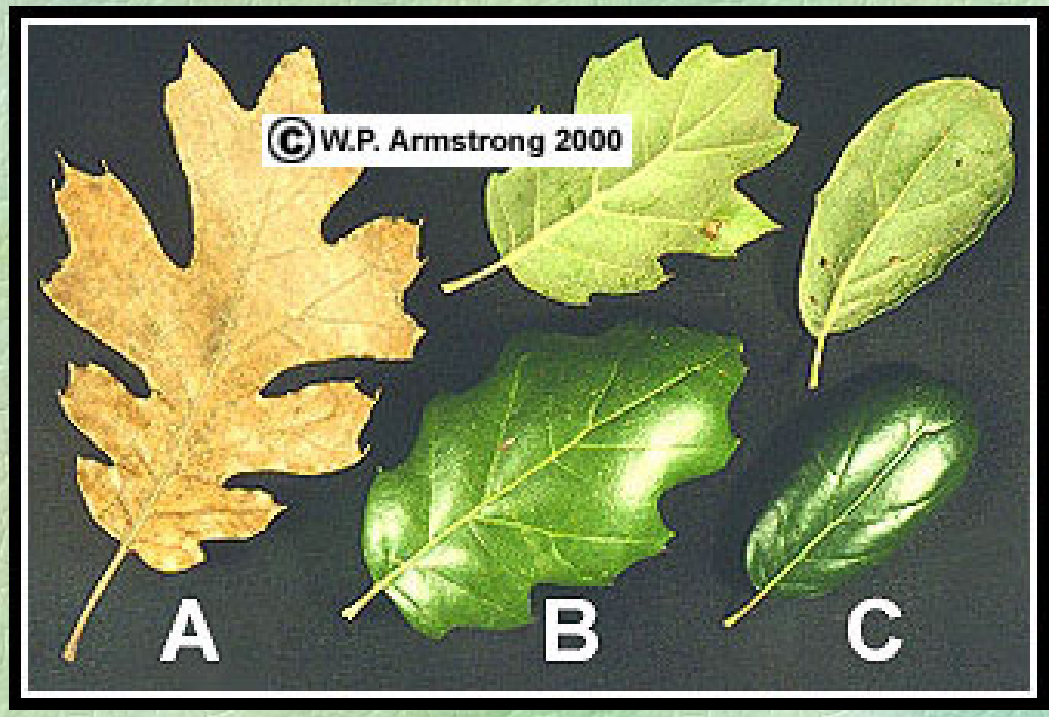
- **Sümpatriline**
- Kiire
- Väikestes populatsioonides
- Valik ja adaptatsioon ei mängi rolli
- **Homoploidne hübriidne liigiteke**
- **Kvant-liigiteke**
- **Stasipatriline liigiteke**

Kvant-liigiteke

Clarkia

Ökoloogiline liigiteke

- populatsioonid adapteeruvad järkjärgult erinevatele niššidele
- **sümpatriline** või parapatriline
- sõsarliigid

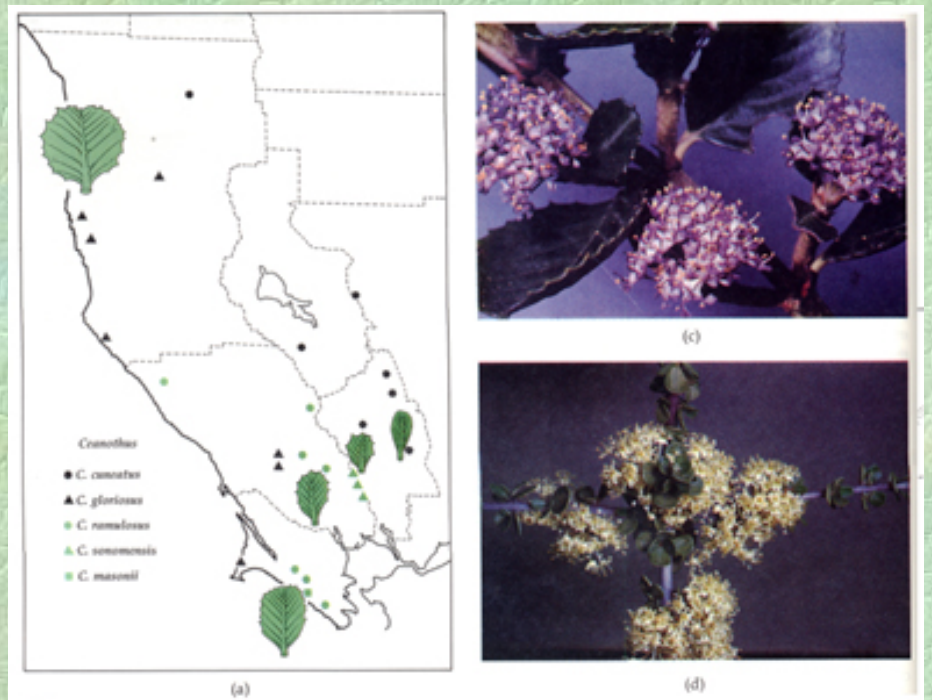


Aseksuaalne liigiteke

- klonaalsetel, partenogeneetilistel organismidel
- mutatsioonide akumuleerumine
- ristumiste-klonaalsete perioodide vaheldumine
- mikroliigid, taksonoomilised probleemid

Hübridisatsioon

- *s.l.* Igasugune erinevate genotüüpide ristviljastumine, nii liigisisene kui liikidevaheline
- *s.s.*
- Seotud teiste protsessidega
- Geograafilised ja ökoloogilised rassid



9-10
The establishment of hybrid populations is an important evolutionary mechanism in many groups of woody plants, including the mountain lilacs, Ceanothus, shown here. (a) Map showing a portion of central California (with county lines; note San Francisco Bay at the bottom), a geologically complex region. Two relatively widespread and distinct species of mountain lilac, the coastal C. gloriosus and the interior C. cuneatus (which ranges far to the east out of the area depicted), have produced three series of hybrid populations; each is variable but stabilized and is able to grow better than either parent in the areas in which they occur together. Leaves from representative populations are shown on the map. (b) Segregation of the extremes in the progeny of an artificial cross between the parental species. In habit, some of the intermediates resemble the named intermediate species of hybrid origin shown on the map to the left. (c) Flowering branch of C. gloriosus. (d) Flowering branch of C. cuneatus.

Hübriidid

- Vahepealsed
- Mitte alati
- Uued tunnused
- Sageli tavalised
- Vahel kaugel vanemliikidest
- Taimedel väga tavalised
- Materjal valikule

Introgressioon

- Tagasiristumine
- Ühe- või kahesuunaline
- Sarnasus ühe vanemaga
- Laiem ökoloogiline amplituud

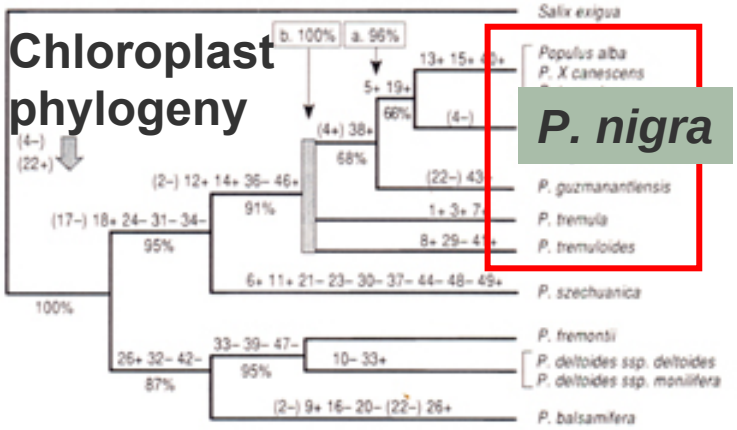


Fig. 1. The shortest Wagner parsimony tree of 54 steps using 49 chloroplast DNA restriction site mutations. Gray area represents the unresolved trichotomy. Mutations are numbered according to Table 2. Gains and losses of sites are indicated by + and −, respectively. Parentheses indicate convergences. A large number of other site mutations (many of which could not be precisely inferred in side-by-side comparisons) separated *Salix exigua* from all other *Populus* species and are not shown at the base of the tree. Two convergent site mutations occur between *Salix* and specific lineages within *Populus*. These mutations are arbitrarily ordered relative to *Salix*. Confidence levels for each lineage from bootstrap analysis are shown as percents. This Wagner tree is topologically congruent to the shortest Dollo tree.

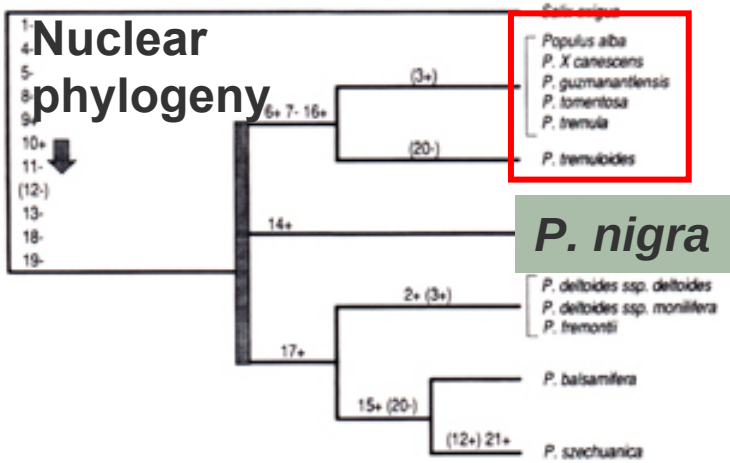


Fig. 4. The shortest Wagner parsimony tree of 24 steps using 21 nuclear rDNA restriction site mutations. Gray area represents the unresolved trichotomy. Mutations are numbered according to Table 4. Gains and losses of sites are indicated by + and −, respectively. Parentheses indicate convergences. Eleven site changes separating *Salix exigua* and all species of *Populus* are arbitrarily ordered relative to *Salix*. The consensus tree of three equally short Dollo trees places the lineage of *P. balsamifera* and *P. szechuanica* as a fourth radiation from the unresolved polychotomy.

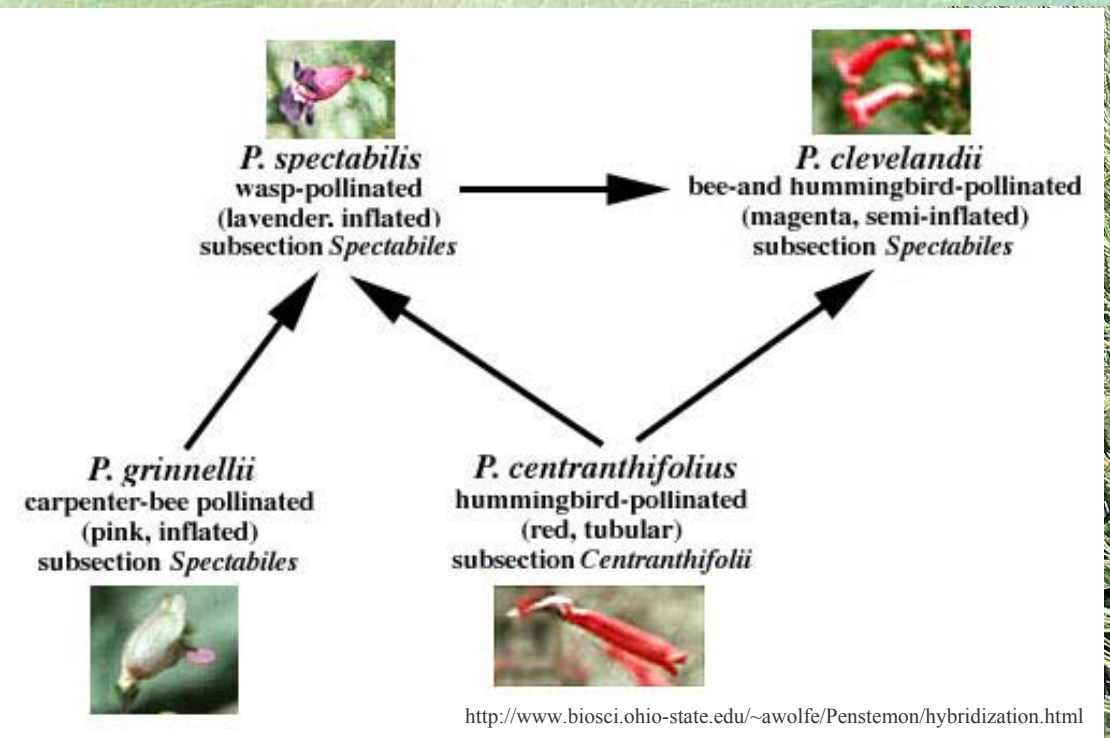
Smith & Sytsma (1990)

Hübriidne liigiteke

- Homoploidne hübriidne liigiteke

Peekerlill *Penstemon*

Elymus



http://www.biosci.ohio-state.edu/~awolfe/Penstemon/hybridization.html

Rekombinatsiooniline liigiteke

Ökoloogiline
liigiteke
algse
hübridisatsiooniga

Allopolüploidne liigiteke

- 47% õistaimi ja 97% sõnajalgu hübriidid

http://www.florafinder.com/Species/Asplenium_trichomanes_ssp_trichomanes.php

Süngameon

Looduses

- Ühe liigi teket võib seletada mitu mudelit
- **Liik loetakse tekkinuks, kui populatsioonid uuesti kontakteerudes enam ei ristu**

(Reproduktiivse) isolatsiooni mehhanismid

Piiravad geenisiiret divergentsete populatsioonide vahel

Ruumiline ehk geograafiline isolatsioon

- Lihtne, rassidel ja alamliikidel
- Võib olla liigitekke algus
- Varaseim, ajutine
- Ei ole geneetiliselt määratud, väline mehhanism

Keskkonnaline ehk ökoloogiline isolatsioon

- Kohastumus erinevatele keskkonna-tingimustele
- Väline, kuid geneetiliselt määratud

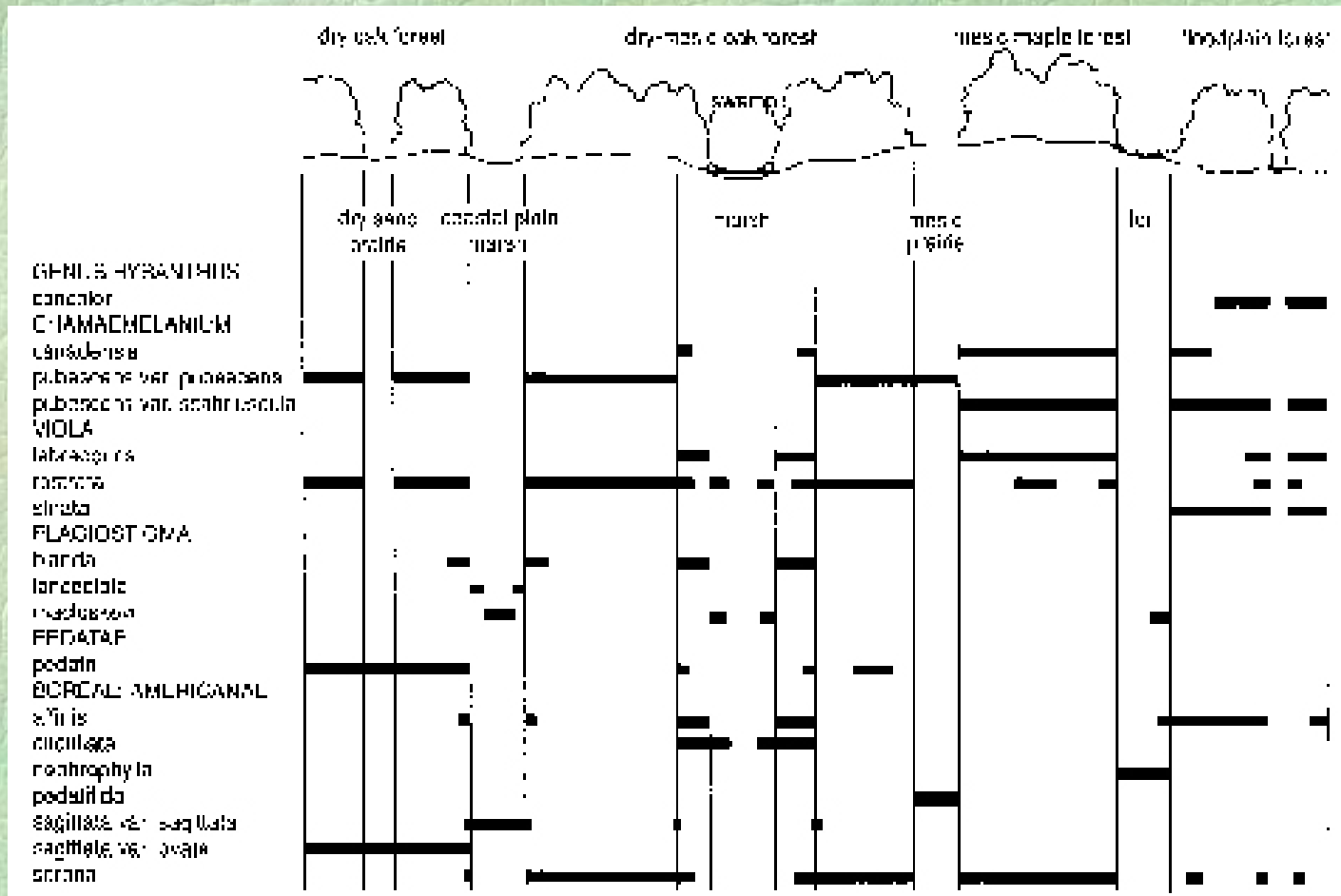


FIGURE 5 Characteristic distributions of Michigan species along an imaginary transect bisecting normal communities of the southern Lower Peninsula (see text for further details). Taxa are grouped together as in the TAXON DISCUSSIONS for comparative purposes.

Reproduktiivne isolatsioon s.s. Presügootsed mehhanismid

- Väldib õietolmu sattumise emakasuudmele
- **Ajaline**
  - aastaajaline
  - ööpäevane

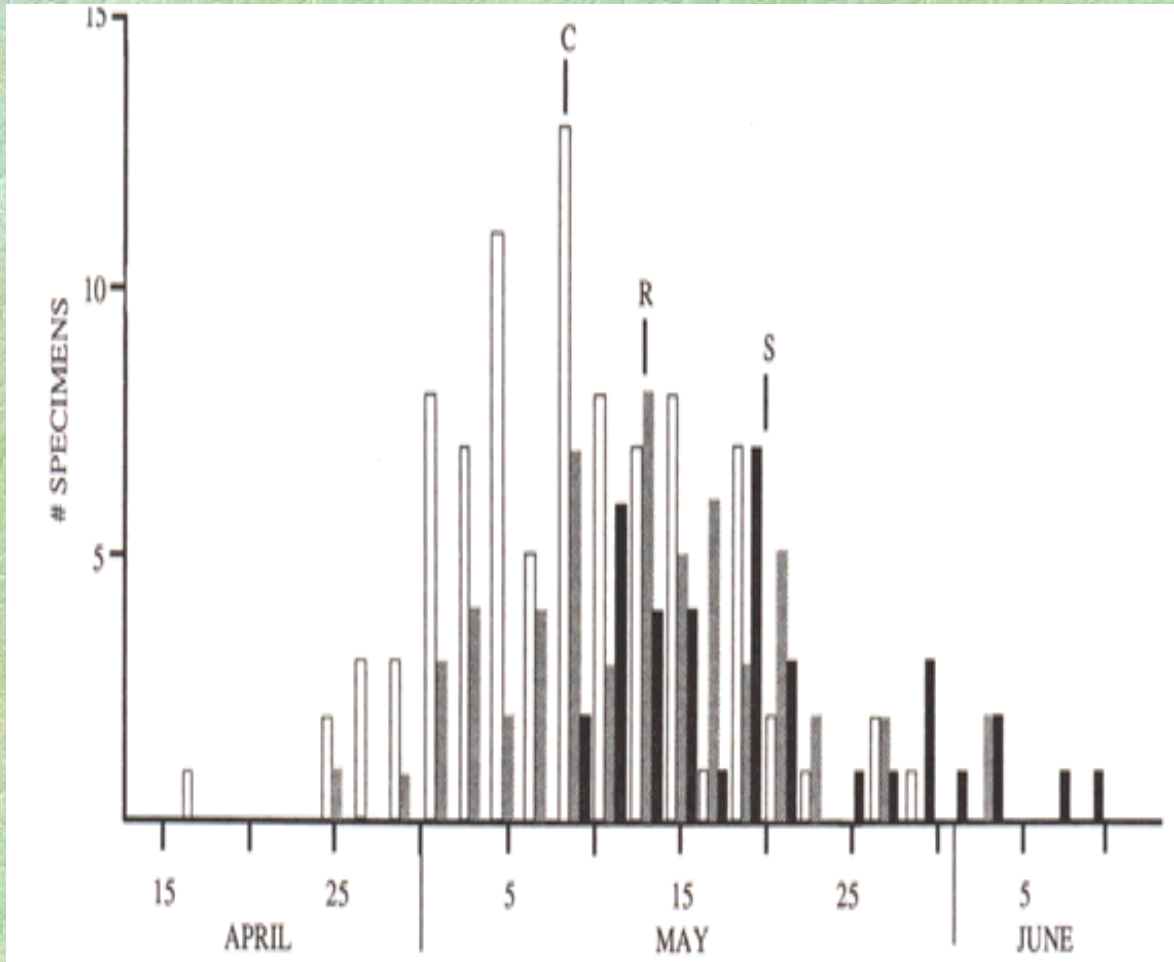
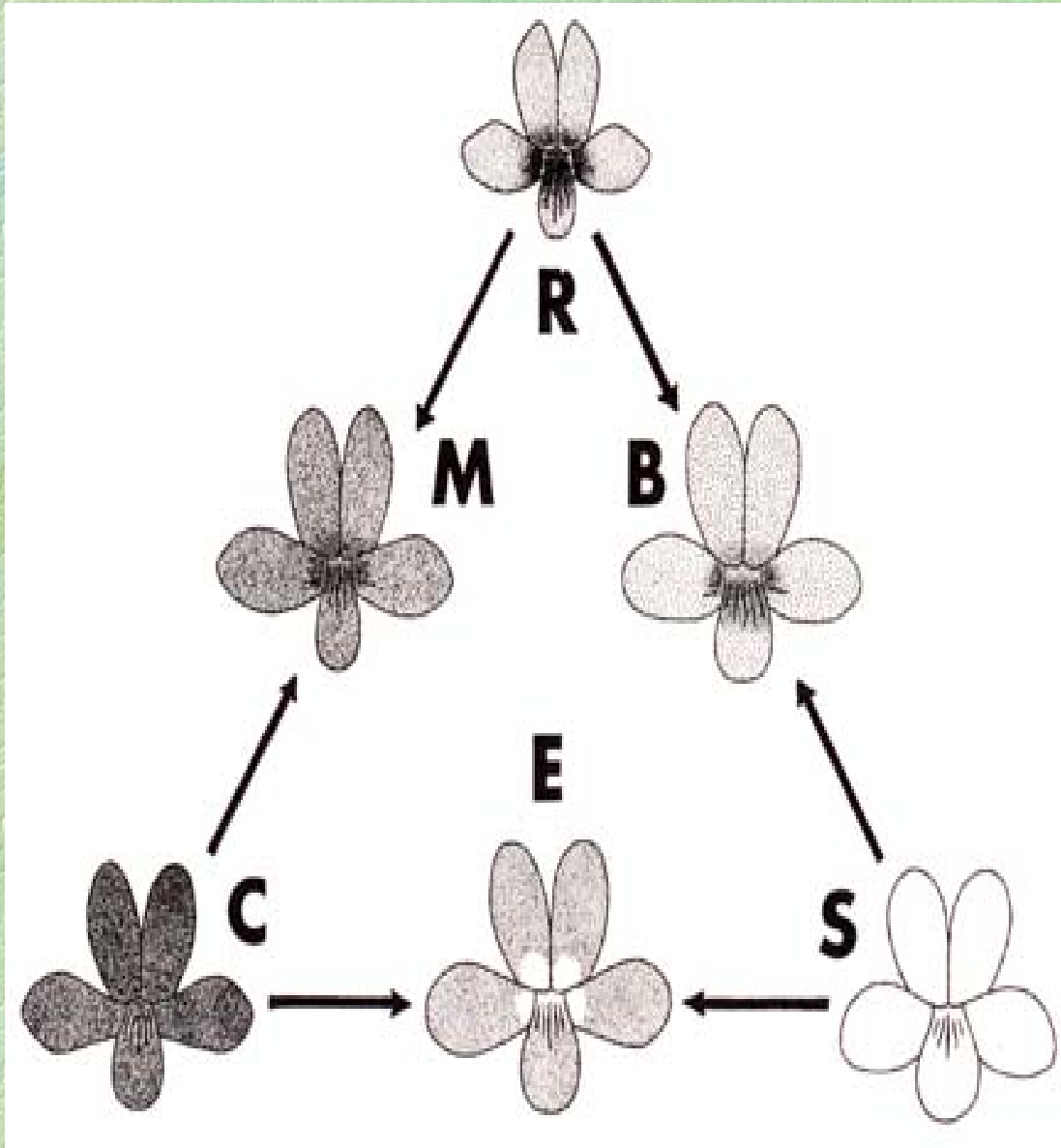


FIGURE 4. Phenology of *V. conspersa* (white), *V. rostrata* (gray), and *V. striata* (black) based on specimens at MICH from south-central Michigan; initials of specific epithets indicate means of collection dates for each species.

Presügootsed mehhanismid

- **Etoloogiline**
  - õiestruktuuride erinev areng, muster
  - erinevad tolmeldajad



Presügootsed mehhanismid

- **Mehhaaniline**
  - õite erinevad struktuurid
  - sama tolmeldaja
- **Gameetne**
  - isesobimatus

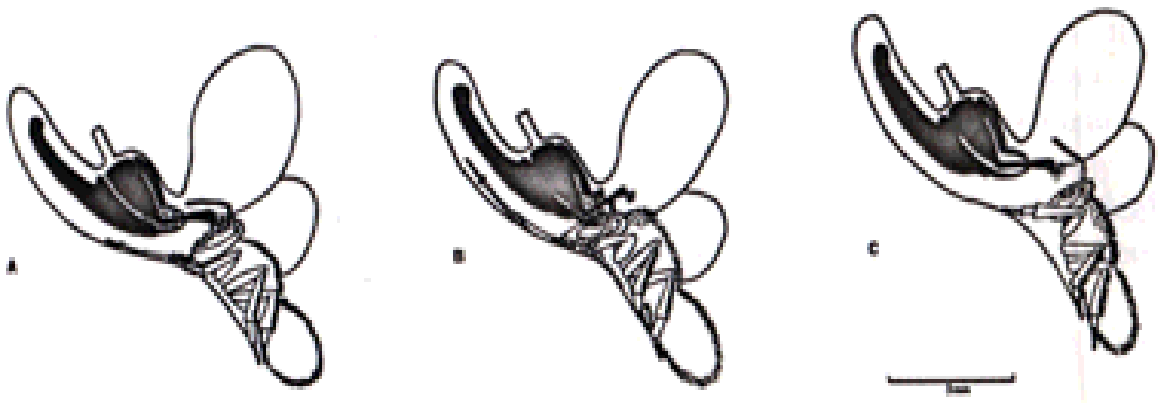


FIGURE 2. Diagram to show nototribic pollination in *Viola*.—A. Proboscis inserted into petal spur; pollen from another flower contacts opening of stigmatic cavity.—B. Proboscis penetrates to nectar; style raised and pollen released.—C. Proboscis withdrawn with new pollen load, style back to resting position.

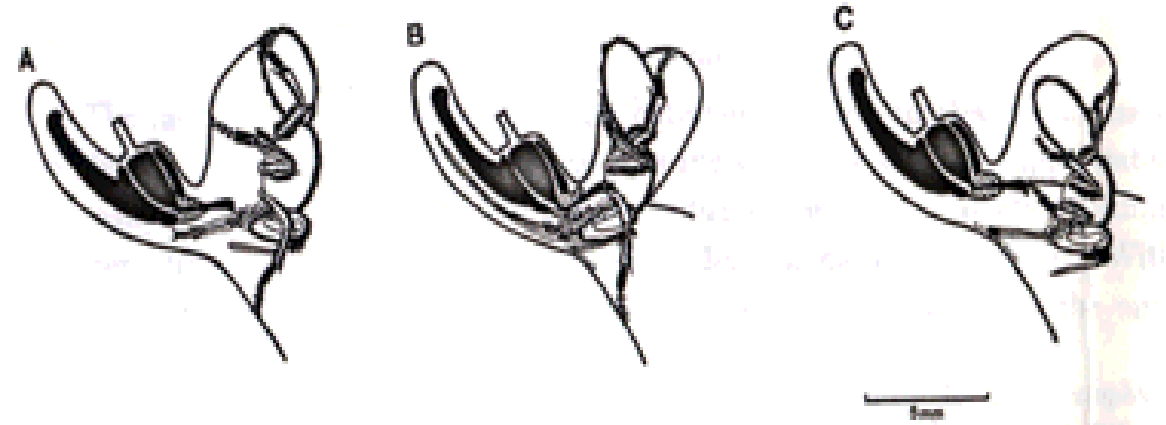


FIGURE 3. Diagram to show sternotribic pollination in *Viola*.—A. Proboscis inserted into petal spur; pollen from another flower contacts opening of stigmatic cavity.—B. Proboscis penetrates to nectar; style raised and pollen released.—C. Proboscis withdrawn with new pollen load, style back to resting position.

Reproduktiivne isolatsioon s.s. Postsügootsed mehhanismid

- **Postsügootne isesobimatus**
  - embrüo sureb enne seemne valmimist või ei ole idanemisvõimeline
- **Hübriidide eluvõimetus**
  - F1 ei saavuta sugukküpsuse iga
- **Hübriidide alakohasus**
  - F2 nõrgad, haigustundlikud jms

Postsügootsed mehhanismid

- **Hübriidide steriilsus**
  - geenne
  - kromosomaalne
  - tsütoplasmaatiline

Looduses

- Üks mehhanism domineerib, lisaks teised
- Tugevamad hiljuti divergeerunud, sõsarliikidel

Liik, süstemaatika ja evolutsioon

Liigikontseptsioonid

- **Morfoloogiline**
  - “Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means.” **(A. Cronquist)**
- **Bioloogiline**
  - “Species is a group of interbreeding populations which are reproductively isolated from other such groups.” (**E. Mayr**)

Liigikontseptsioonid

- **Fülogeneetiline (*s./.*)**
  - monofüleetilisus
  - sünapomorfsed tunnused
- **Evolutsiooniline**
- “An evolutionary species is a lineage (an ancestral-descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies.” (**G. Simpson**)

Liigikontseptsioonid

- **Ökoloogiline**

"A species is a linegae (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range." (**Van Valen**)

- **Piiratud kasutusega:** feneetiline, geneetiline, paleontoloogiline

Kolm vaatepunkti

- Taksonoomia
- Evolutsioon
- Kladistika
- **Vastuolud**
- Ükski kontsepstioon ei hõlma kogu varieeruvust
- Süstemaatika eesmärk on praktiline klassifikatsioon, aga morfoloogiline kontseptsioon alahindab varieeruvust
- Evolutsiooni käiku on väga raske tuvastada
- Evolutsioon ei kulge sugugi alati monofüleetiliselt ja parsimoonselt
- Aseksuaalsus, autogaamia, polüploidia, hübridisatsioon jm

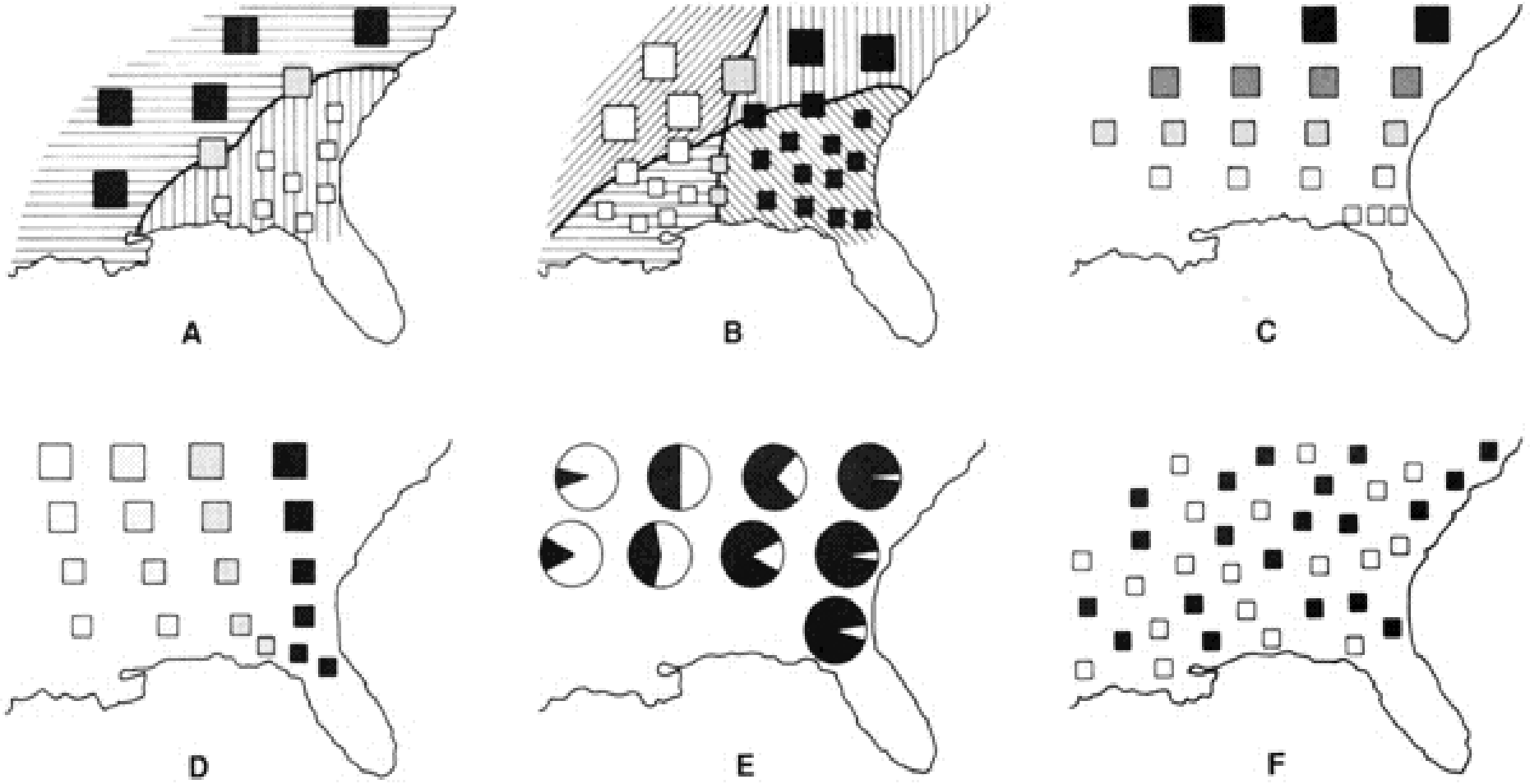
Miks liigid eksisteerivad?

- stabiilsed mittepideva mateeria seisundid
- adaptatsioonid diskreetsetele ökoniššidele
- reproduktiivne isolatsioon põhjustab hiaatusi ja sõltumatut evolutsiooni

Liigisisene varieeruvus

- **diskreetne**
- **pidev**

- **Populatsioonisisene**
- **Geograafiline**
  - klinaalne ühe tunnuse suhtes
  - klinaalne mitme tunnuse suhtes
  - mosaiikne
- **Ökotüüpne**
  - keerukas mitmetunnuseline varieeruvus
  - geneetiliselt määratud tunnused adapteerunud kohalikule keskkonnale
  - Turesson



Highly diagrammatic representations of some common patterns of geographic variation. (A) Two classical subspecies that interbreed along a narrow border. Size and color are correlated. (B) Abrupt transition in each of two characters that have discordant distributions. (C) Concordant clines in each of two characters. (D) Discordant clines in each of two characters. (E) An east-west cline in the frequency of black and white individuals; each "pie diagram" represents proportions in a sample from a single locality. (F) A mosaic distribution of two phenotypes, as might be observed if one (black) were a wetland ecotype and the other (white) an upland ecotype.

Liigisisene varieeruvus

- **kromosomaalne**
  - autopolüploidid
  - translokatsioonid, inversioonid jms
- **Molekulaarne geograafiline**
  - ei ole sageli kooskõlas morfoloogilise varieeruvusega

Fig. 12.4. Variants of *Polypodium vulgare*. (*a*) Diploid (2*n* = 2*x* = 74) from Cheddar, England. (*b*) The triploid hybrid (2*n* = 3*x* = 111) between diploid and tetraploid from Roches, Switzerland. (*c*) Tetraploid (2*n* = 4*x* = 148) from North Wales. (*d*) The pentaploid (2*n* = 5*x* = 185) hybrid from Bolton Abbey, Yorkshire, England. (*e*) Hexaploid (2*n* = 6*x* = 222) from Ireland. (*f*) The tetraploid (2*n* = 4*x* = 148) hybrid between diploid and hexaploid from Istanbul, Turkey. (Fronds × 0.2.) ((*a*)–(*e*) from Manton, 1950; (*f*) from Shivas, 1961*a*.)

Liigisisesed taksonoomilised ühikud

- **vorm**
  - nt albiino
- **varieteet**
  - nõrgalt morfoloogiliselt ja ökoloogiliselt eristunud, geograafiliselt enamasti mitte
- **alamliik**
  - morfoloogiliselt ja geograafiliselt eristunud populatsioonide kogumik