The evolution of maize and other grasses

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http://katiehutchison.squarespace.com/display/ShowJournal?moduleId=1186140&categoryId=117050&currentPage=8

Just like an old house, every organism is the product of its history.

A note on graphics

Historical information can be presented in multiple ways:

- Venn diagrams
- Unrooted trees (phylogenies)
- Rooted trees

Venn diagram (ovals not to scale).

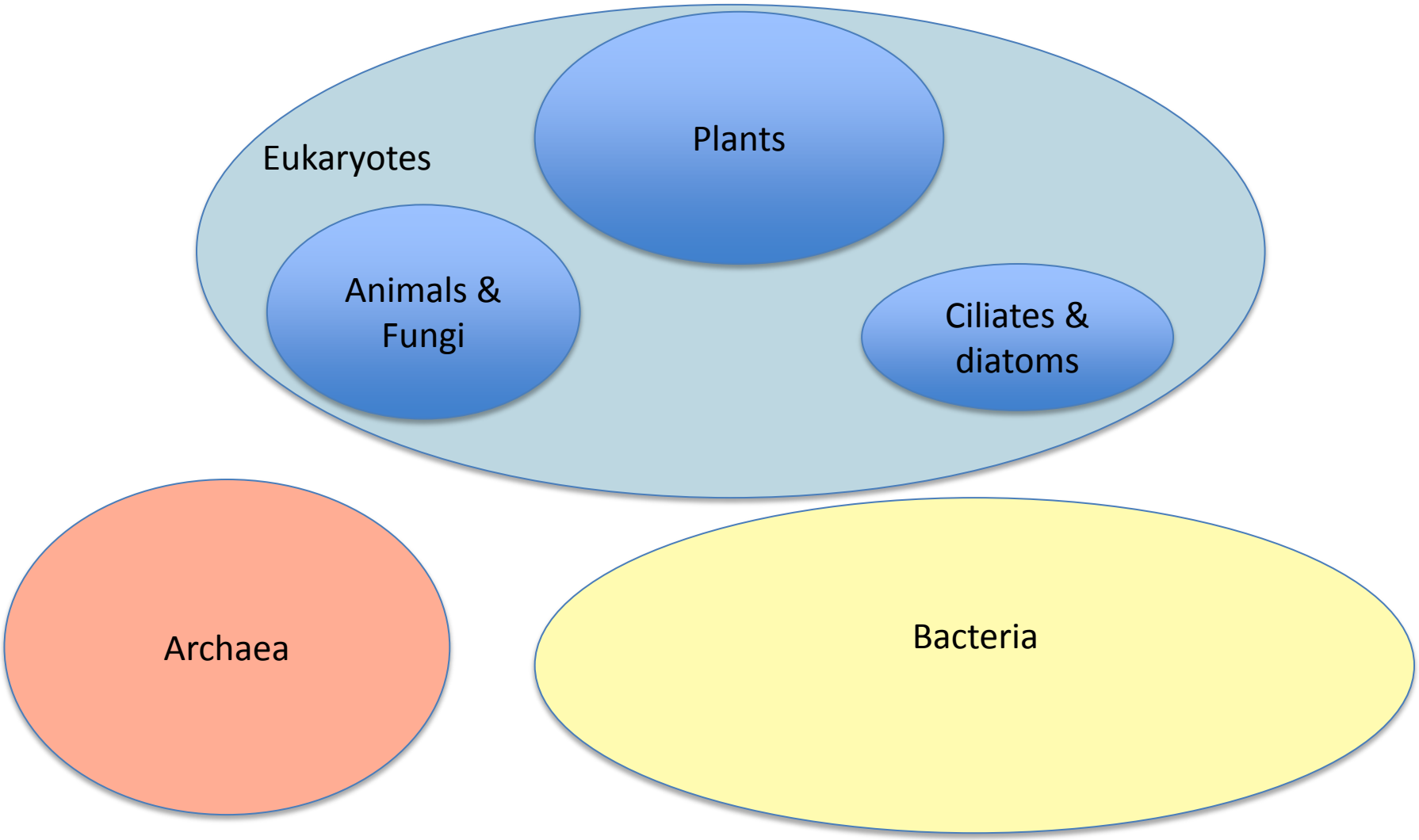
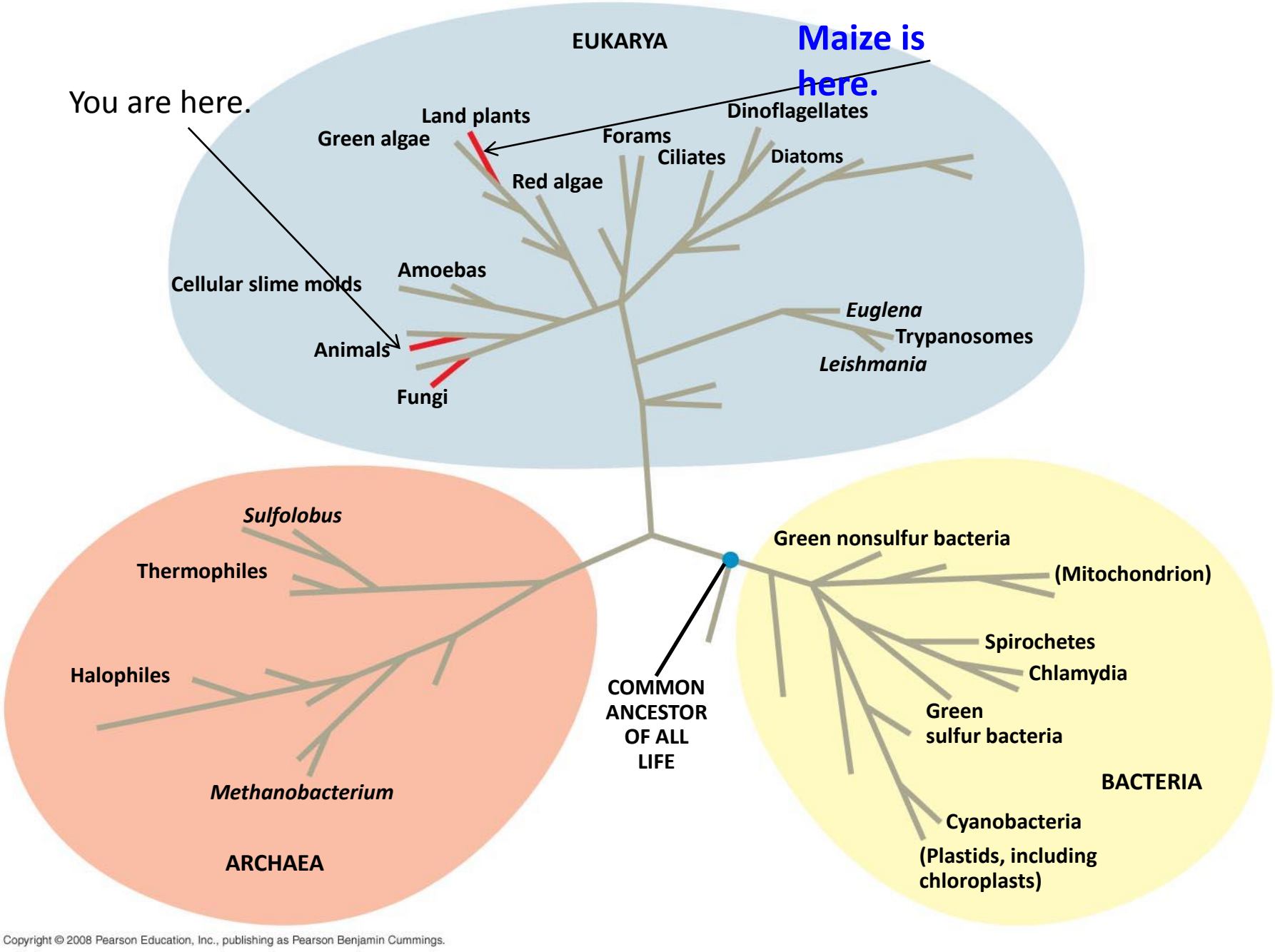
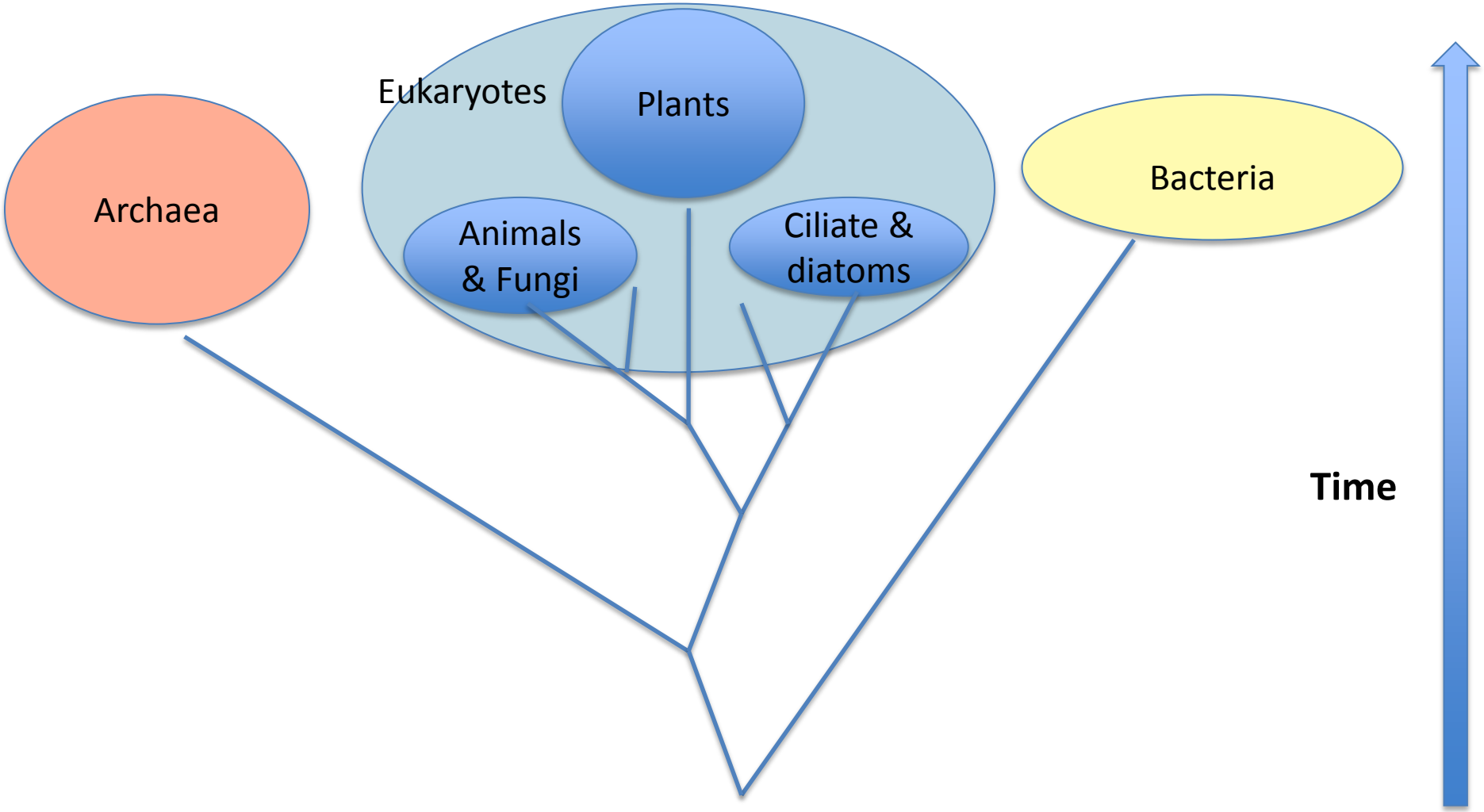


Fig. 26-21



Rooted tree


Eukaryotes
Plants
Archaea
Animals & Fungi
Ciliate & diatoms
Bacteria
Time

A phylogeny is described as though it were a real tree, with nodes and internodes.

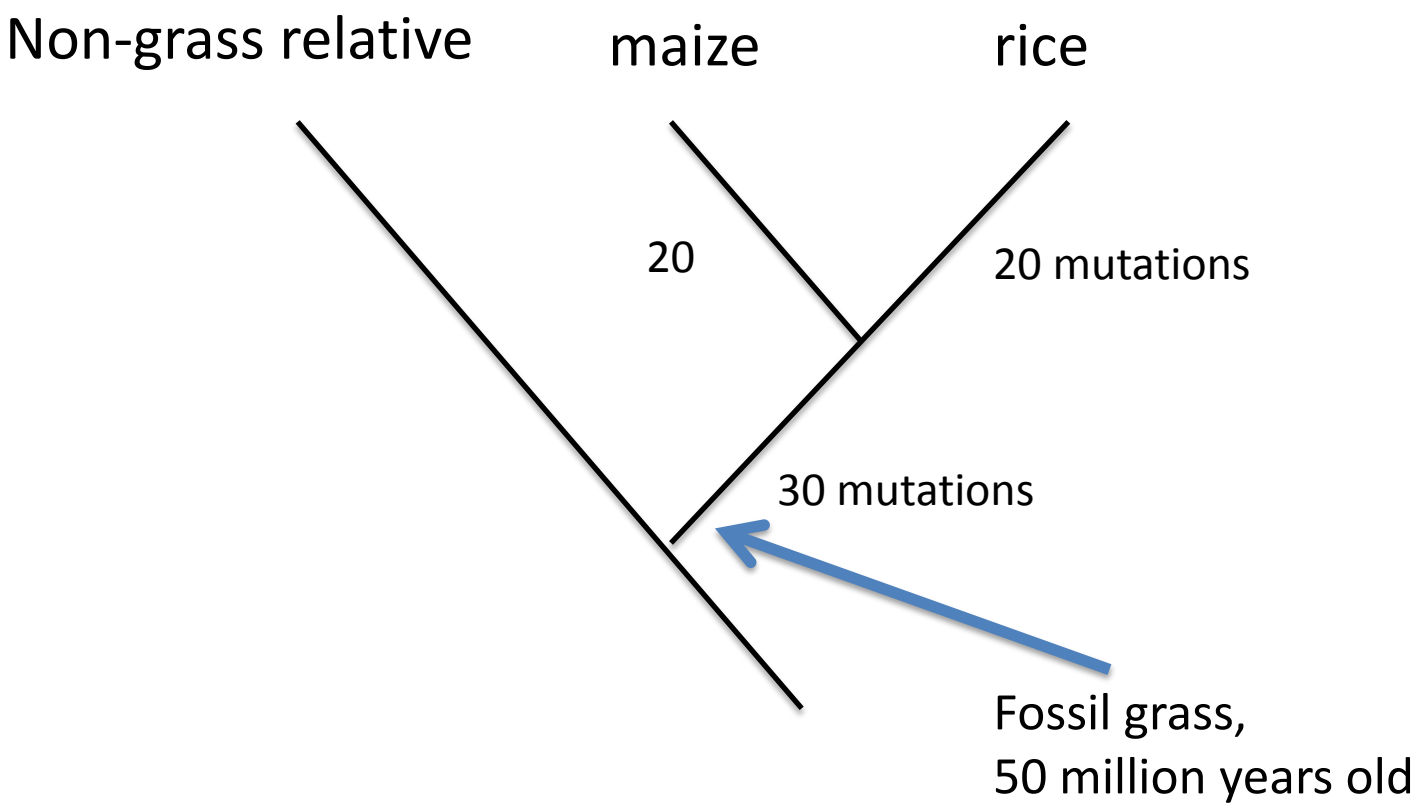
Some of the nodes may bear names, with the name referring to all descendants of that common ancestor.

A named group is monophyletic = all descendants of a common ancestor.

These are defined with reference to a phylogeny.

How can we estimate dates?

- Create a phylogeny using DNA sequence data.
- Calculate the estimated number of mutations along each branch.
- Branch length (BL) = substitution rate (sr) x time (t)
- Therefore $sr = BL / t$
- Calibrate the phylogeny with a fossil.

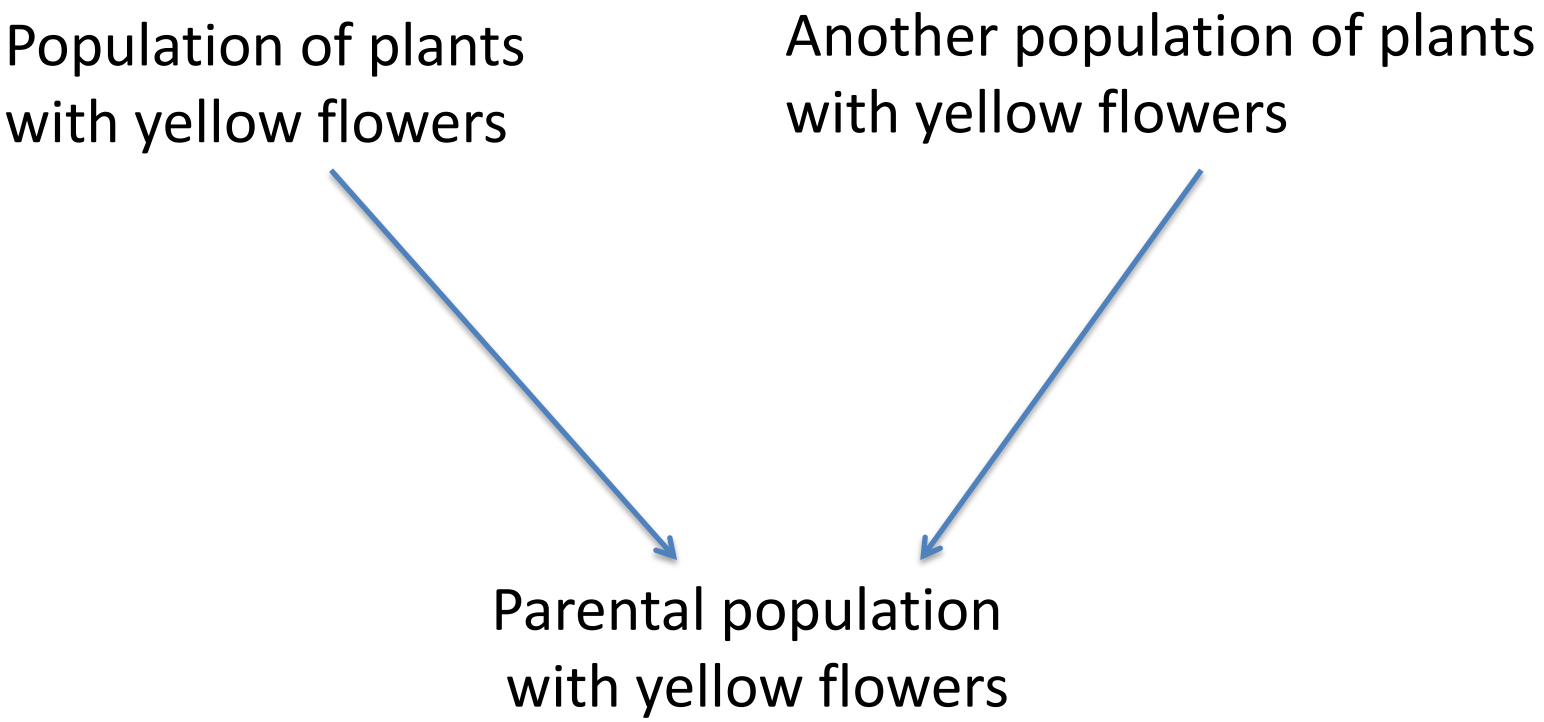


Substitution rate = 50 mutations/50 million years
= 1 mutation/million years

The phylogeny also lets us make an intelligent guess about what the common ancestor looked like.

How do we do this?

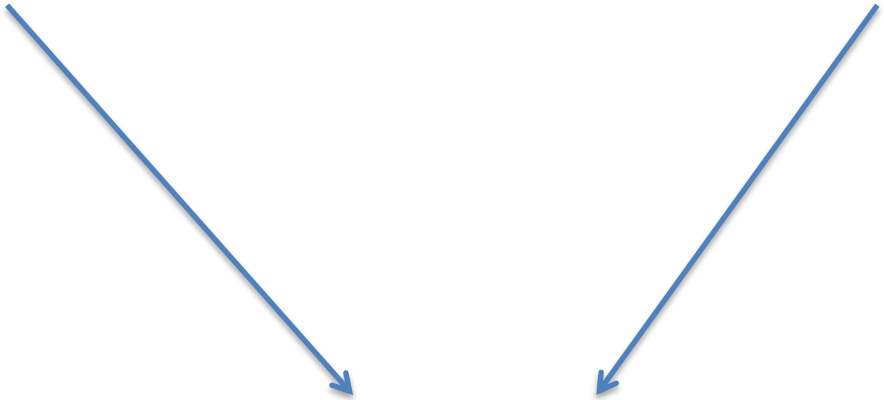
Sometimes this is obvious:



Sometimes this is obvious:

Maize undergoes
Double fertilization

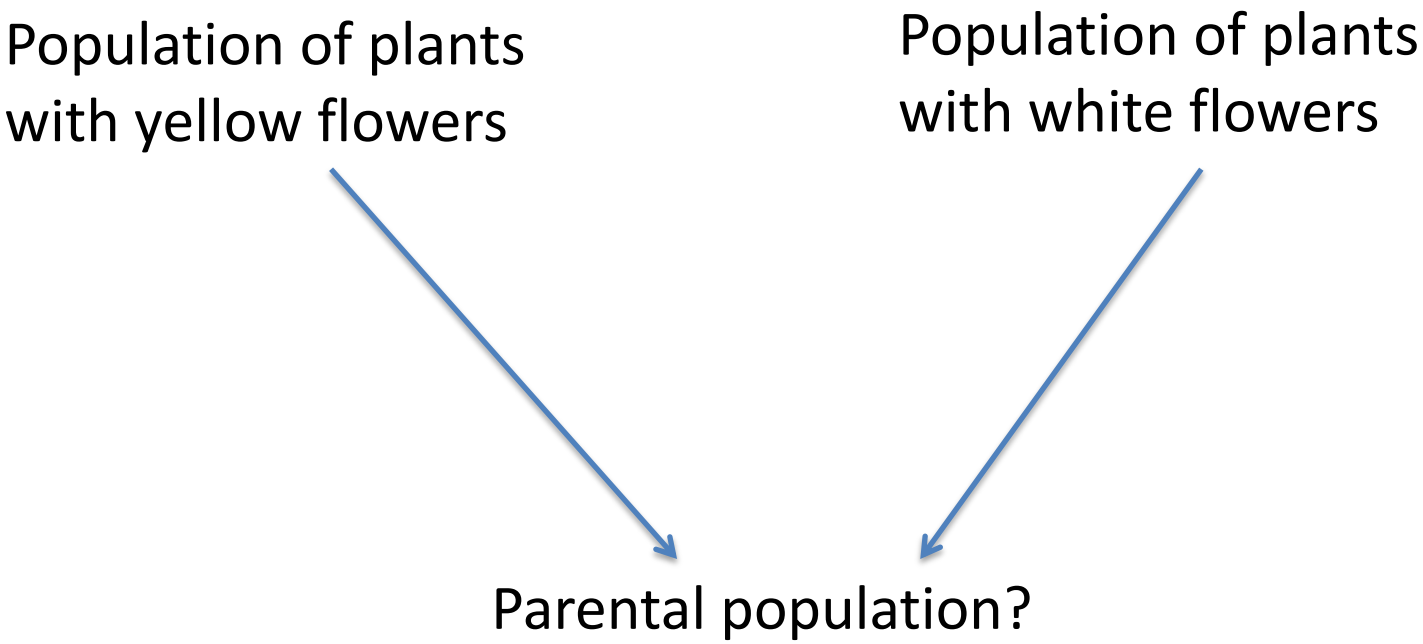
Arabidopsis undergoes
Double fertilization



The common ancestor of maize and
Arabidopsis and all its descendants
Undergo double fertilization.

Obviously this inference is stronger as more and more descendants are Considered.

Sometimes an inference is impossible:



So far:

- Venn diagrams and phylogenetic trees; I'll use Venn diagrams when I don't want to bother with the details of a tree.

- How to infer the date of an ancestor; I'll just cite these, but be aware that they are all anchored in imperfect fossil data.

- How we might infer the characters of ancestors; I'll try to stick to characters where the inference is strong.

How was the maize plant assembled over evolutionary time?

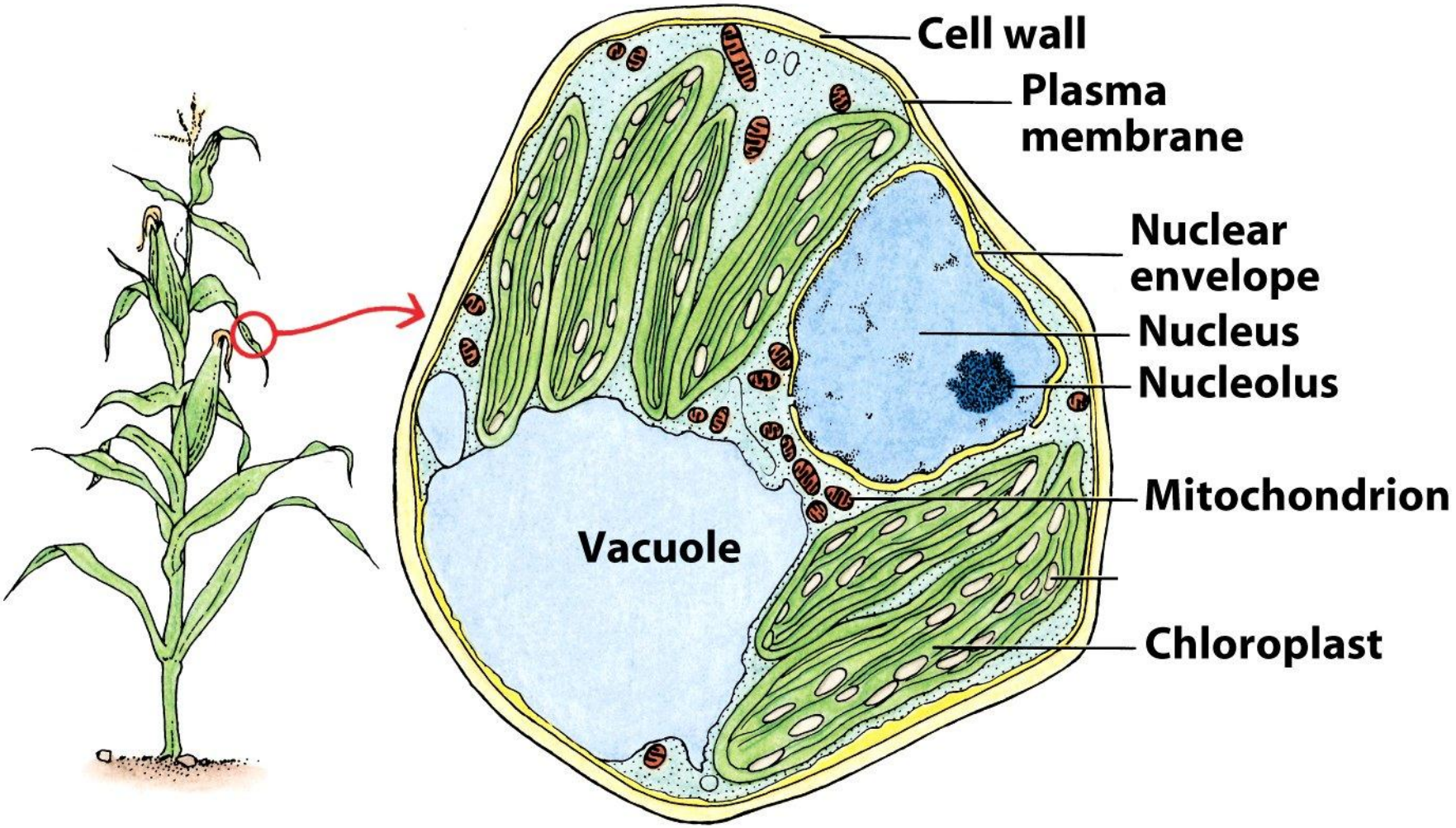
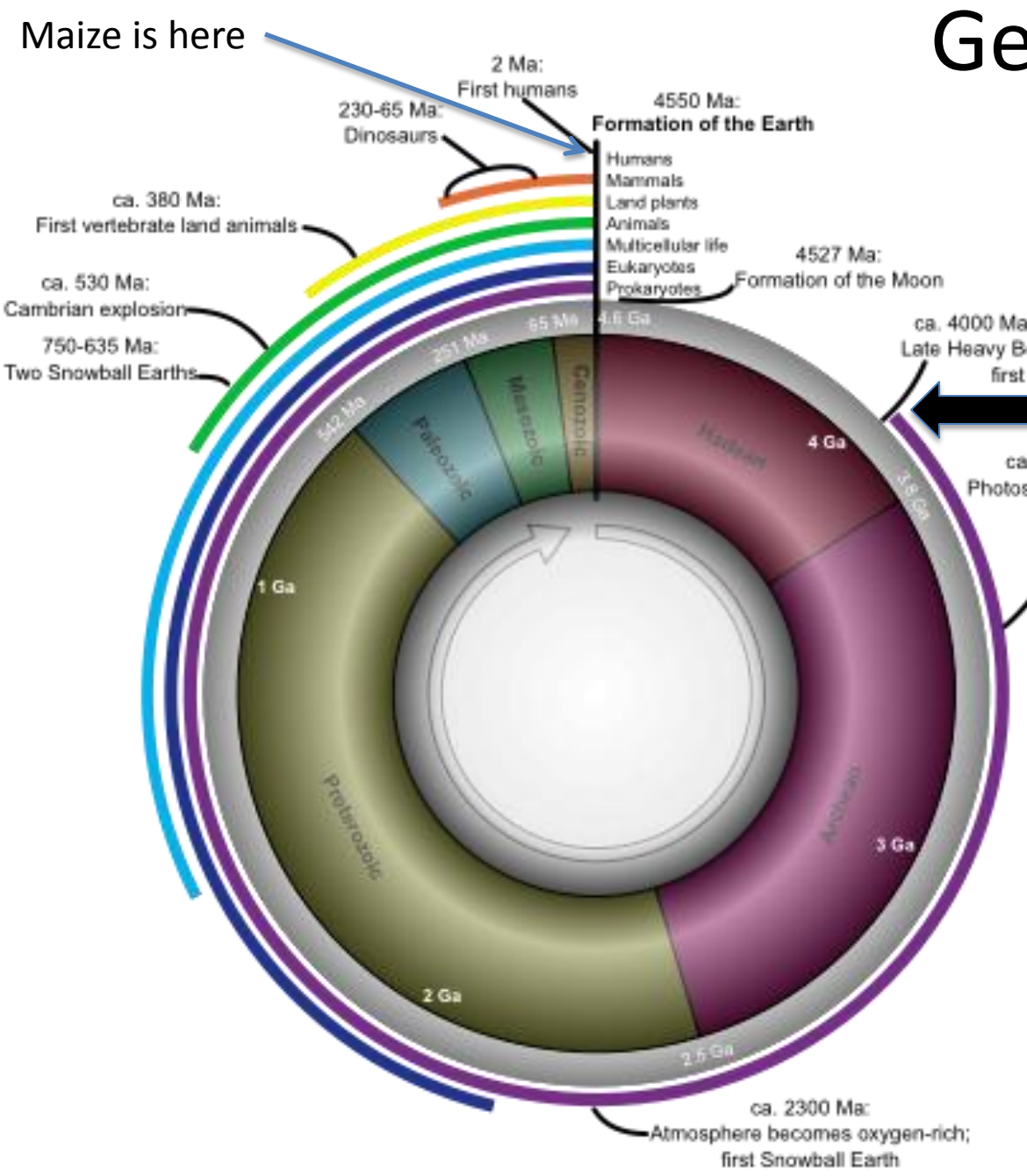


Figure 3-3 part 1
Biology of Plants, Seventh Edition

The challenge with such a talk is deciding how far back in time to go.

I figured a good starting point would be the origin of life on earth.

Geological clock



First life

4,000,000,000 years ago

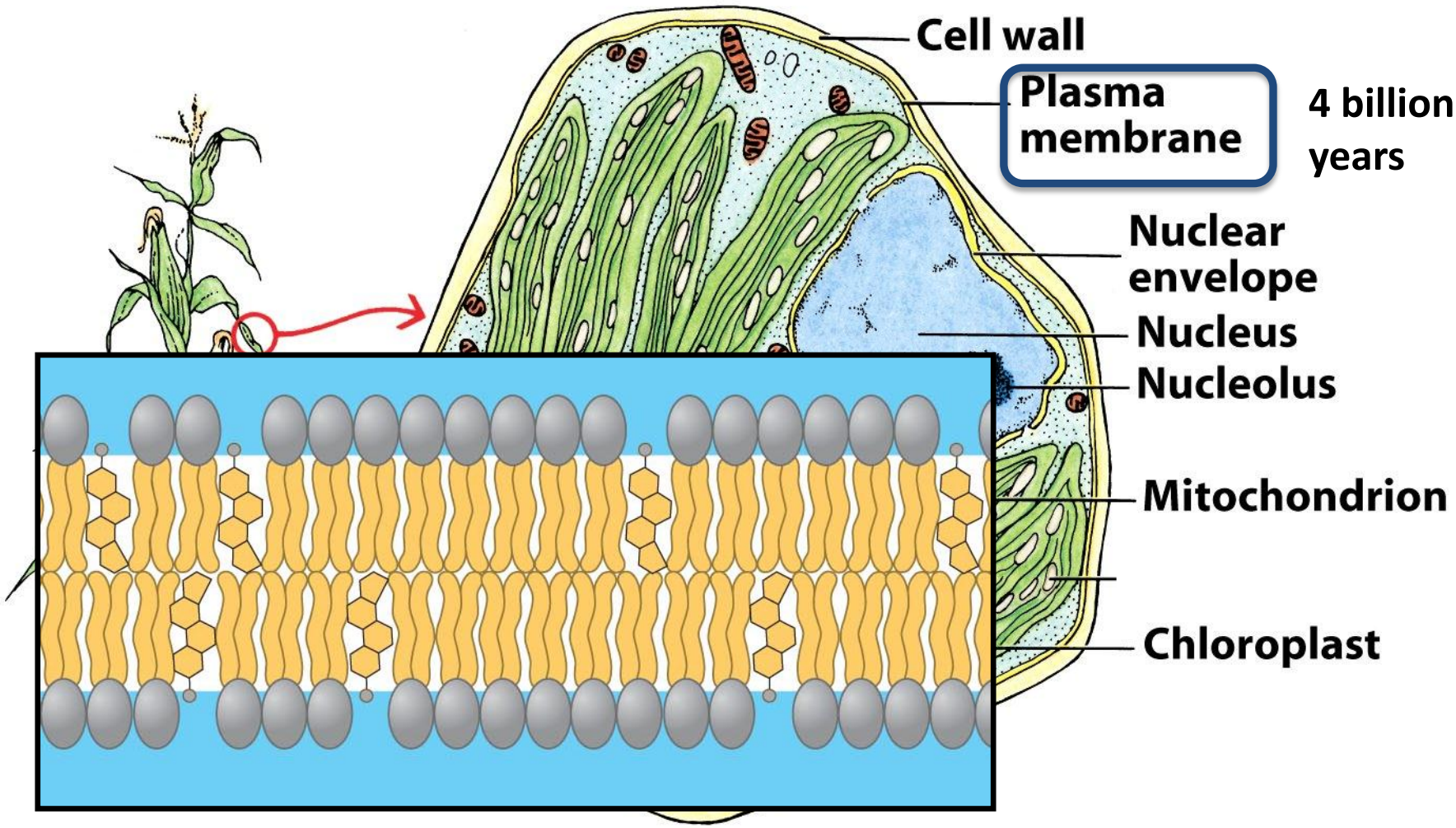


Figure 3-3 part 1
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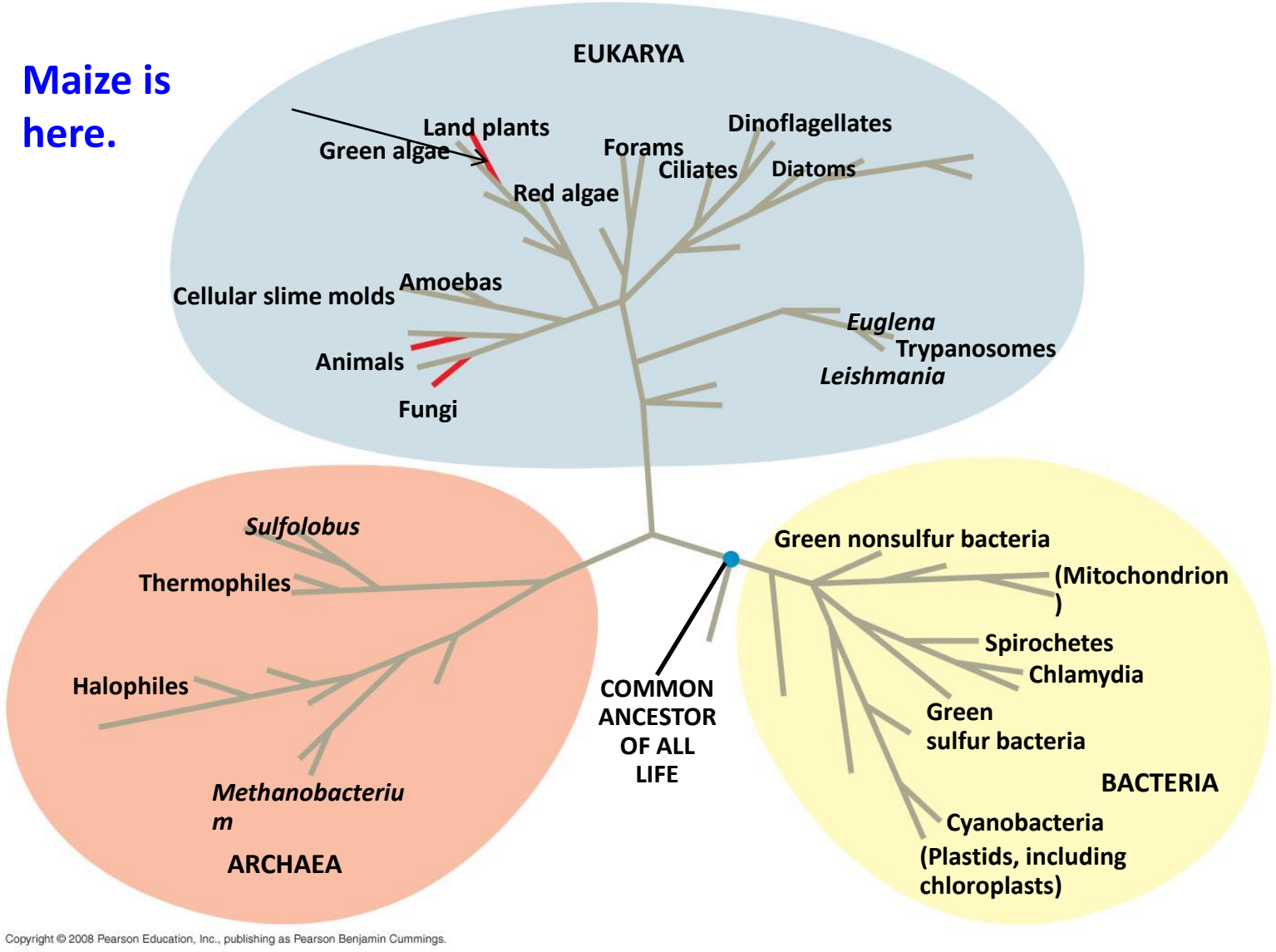
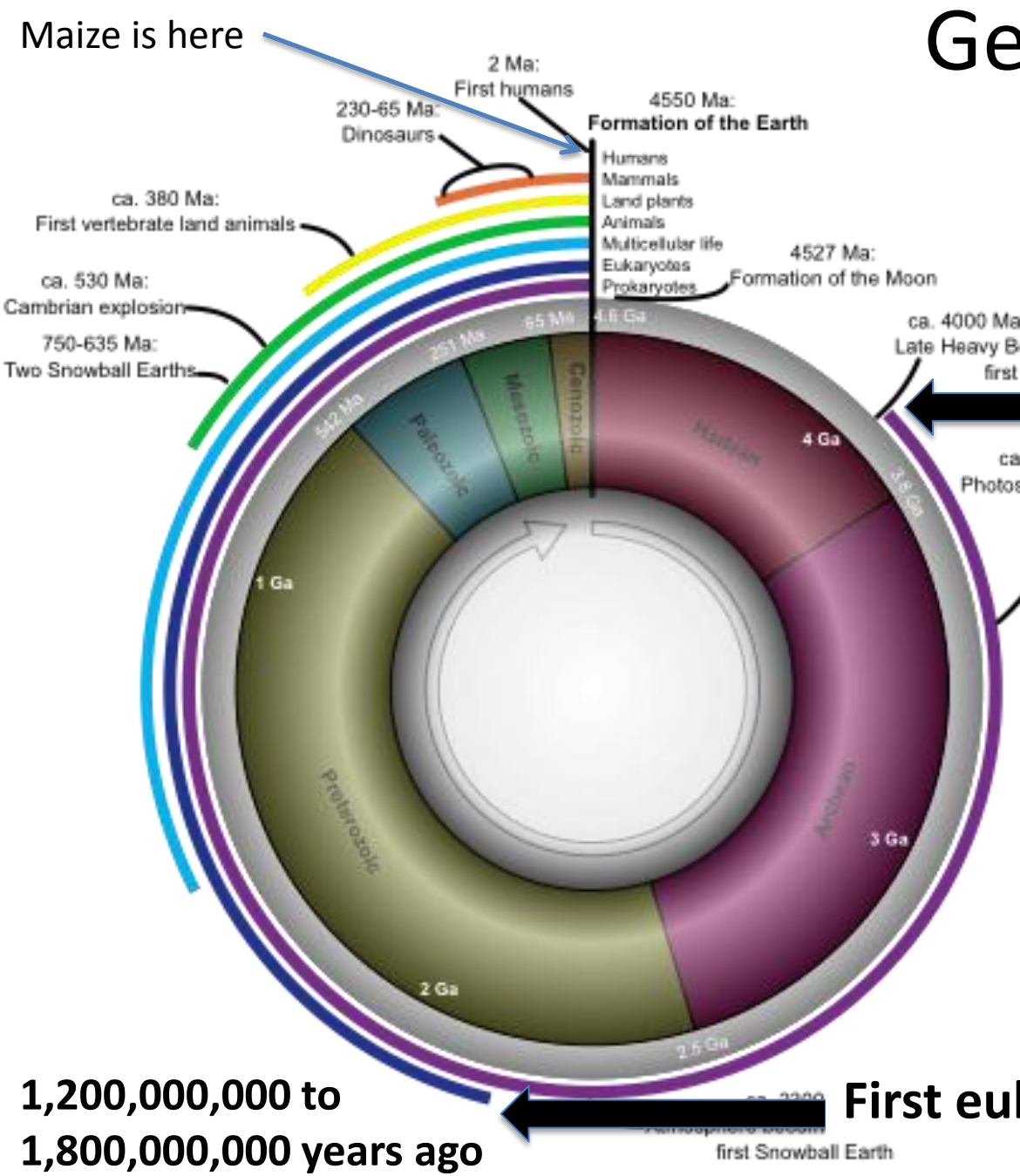
Ribosomes and DNA are equally ancient

Maize shares a plasma membrane, DNA, and ribosomes with all living things.



Geological clock



First life

4,000,000,000 years ago

First eukaryotes

1,200,000,000 to 1,800,000,000 years ago

Inherited from the common ancestor of the Eukarya

- Nucleus
- Endomembrane system
  - Endoplasmic reticulum
  - Golgi apparatus

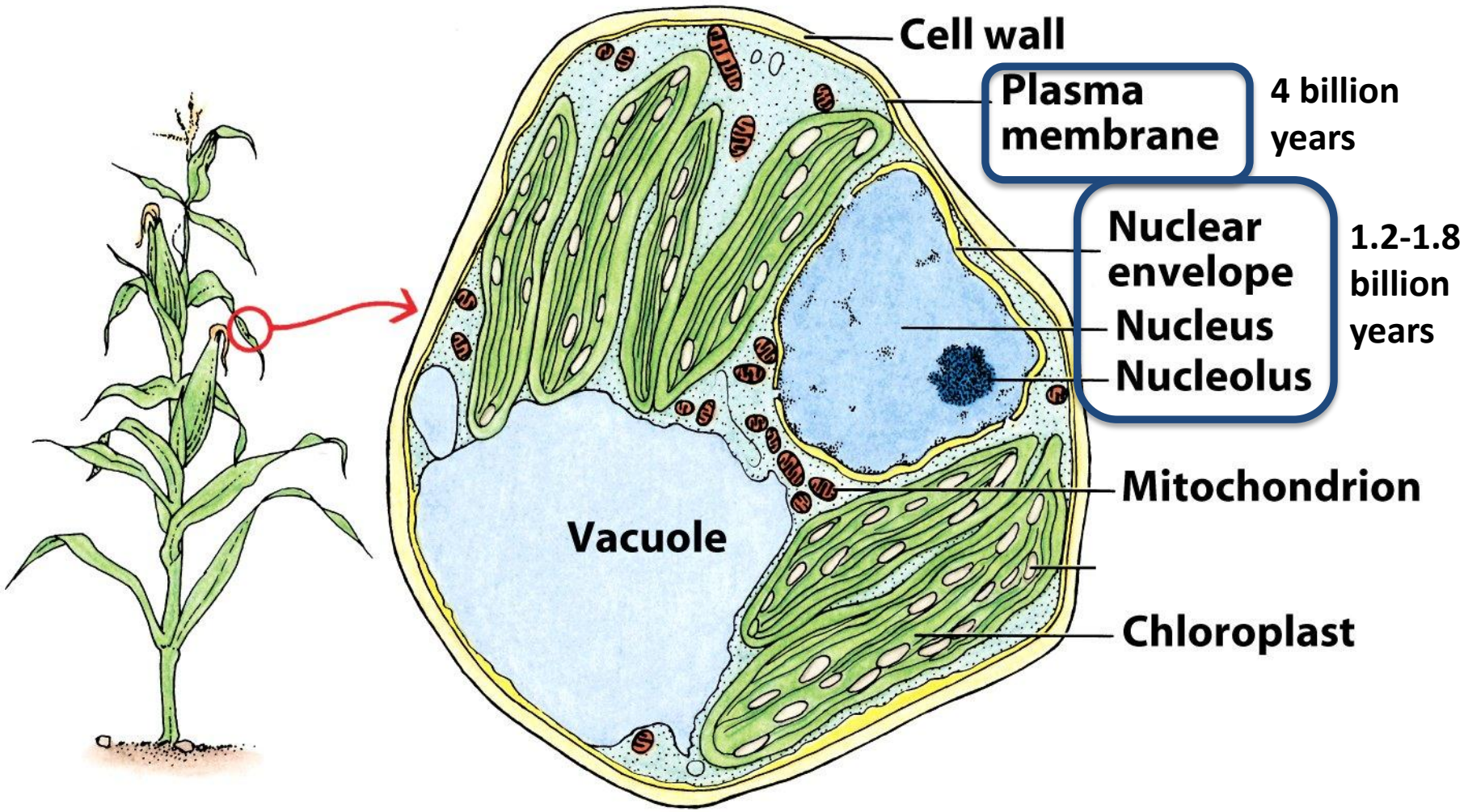


Figure 3-3 part 1
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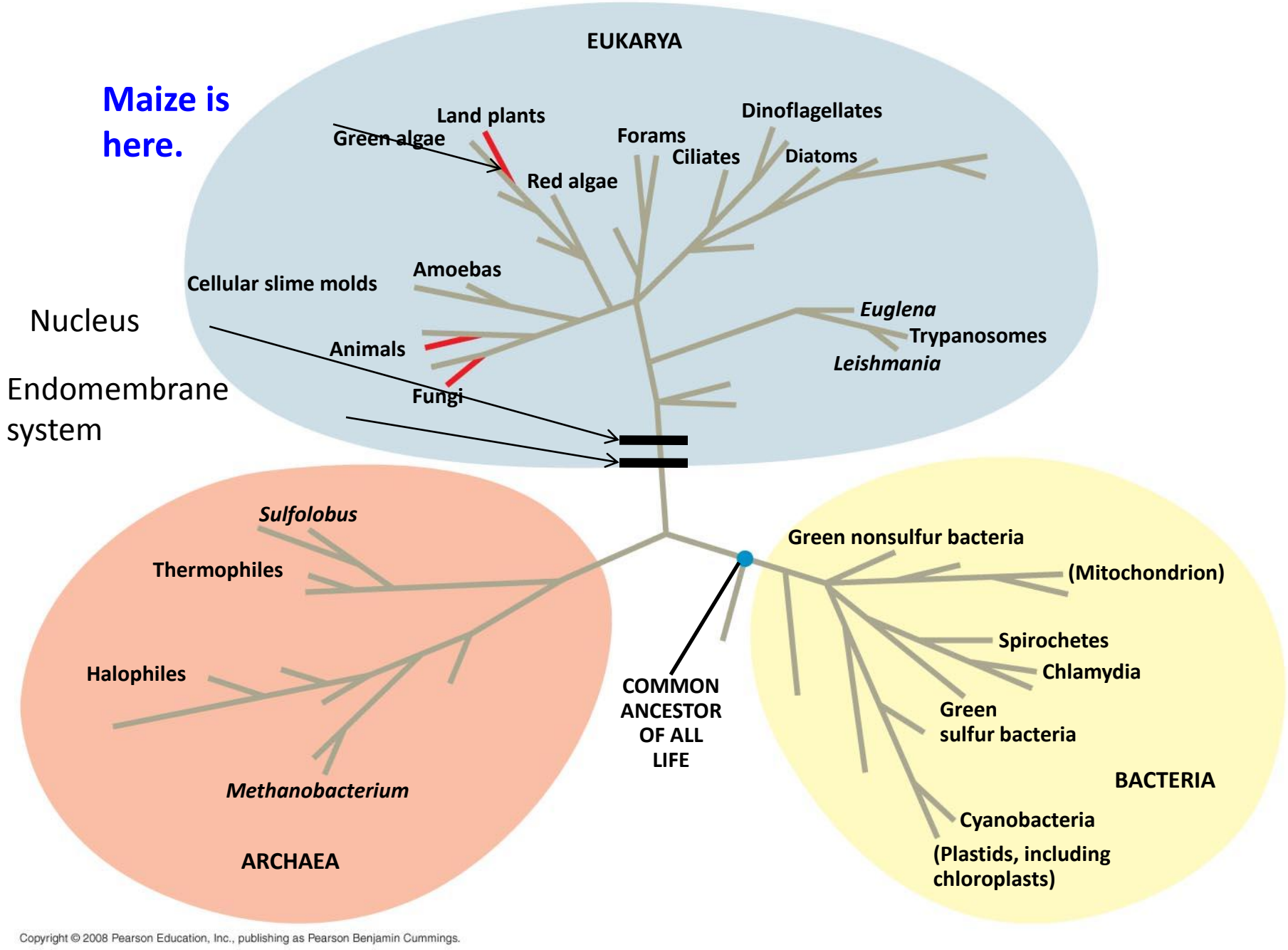
Fig. 26-21



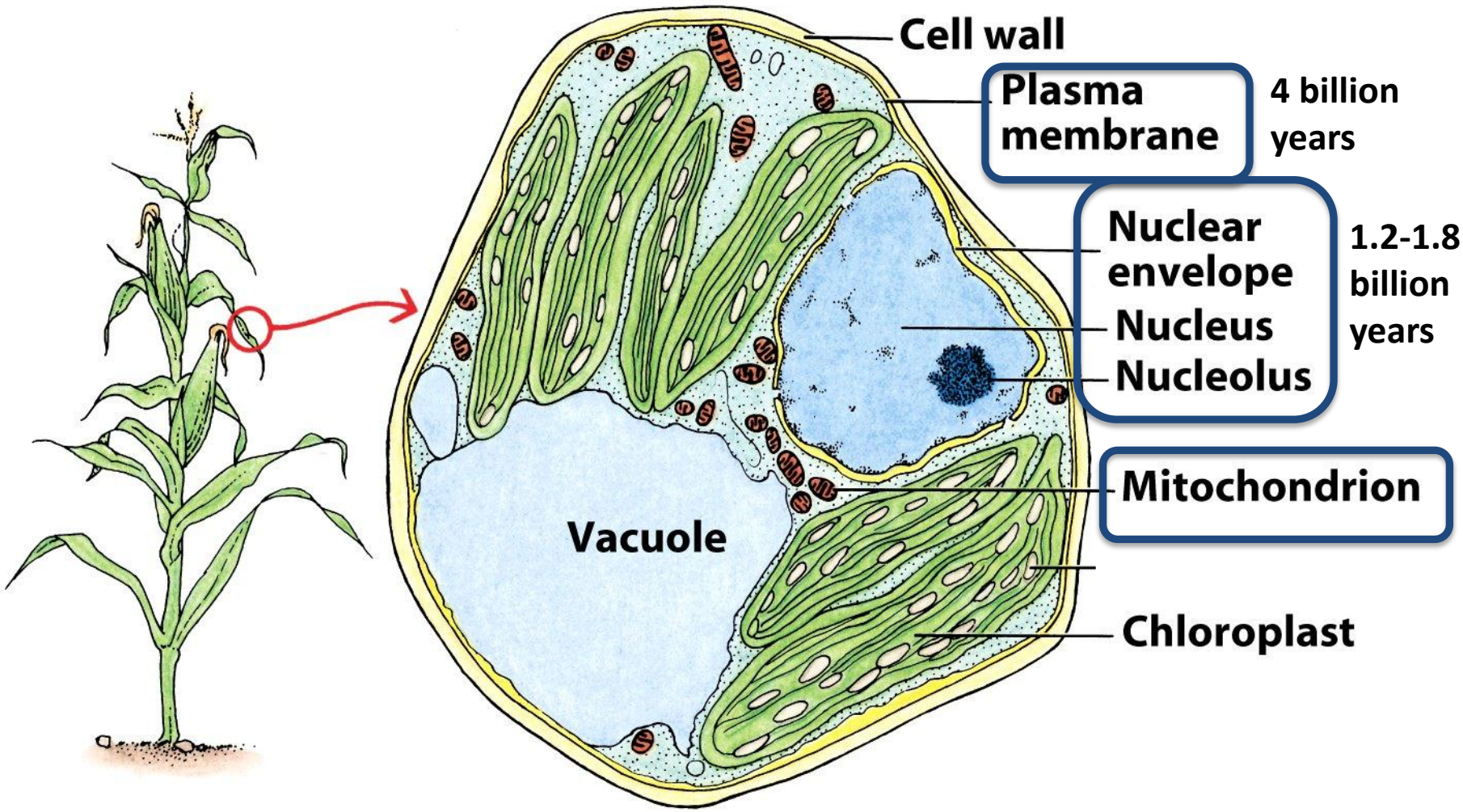


Figure 3-3 part 1
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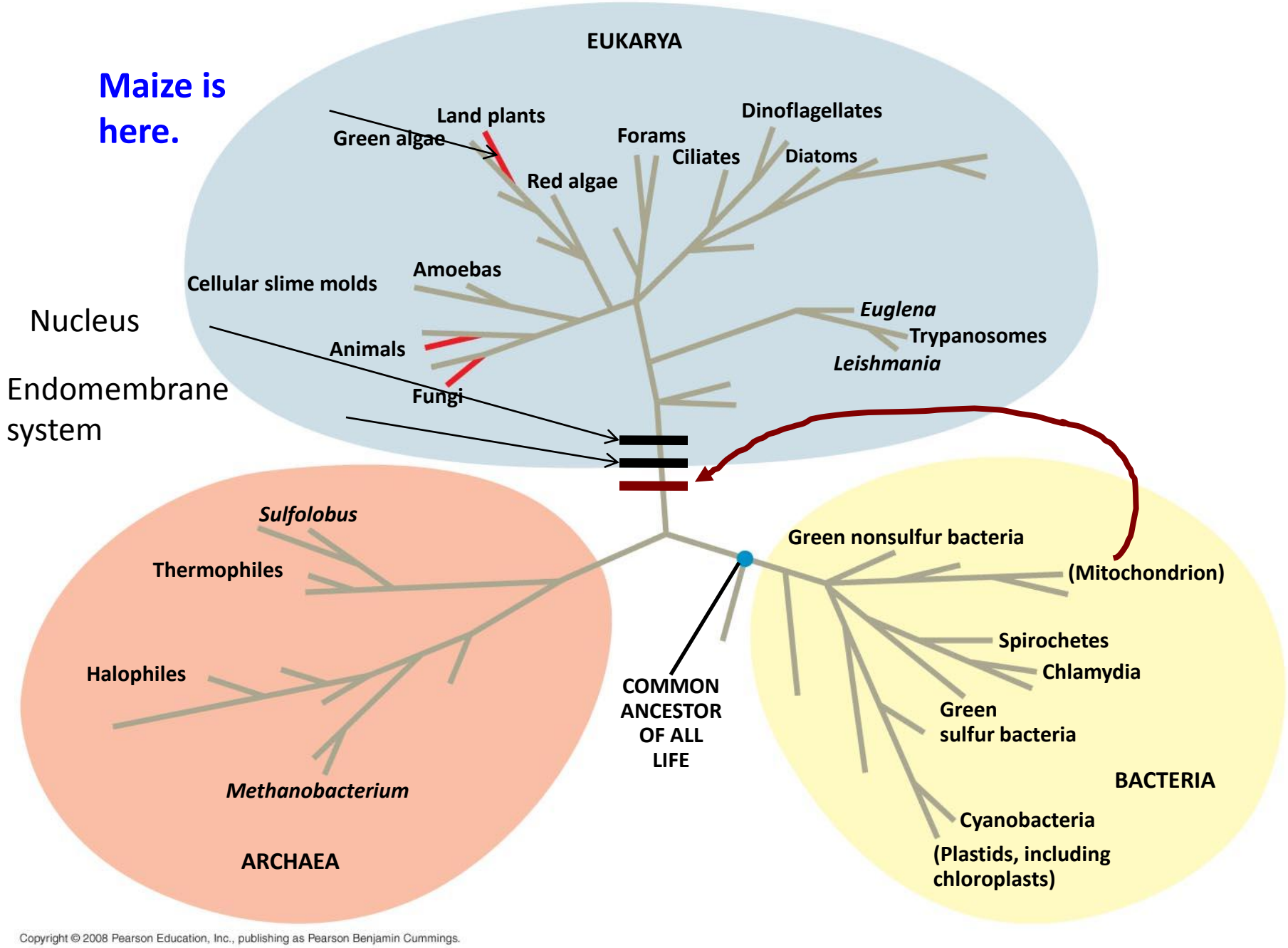
Fig. 26-21



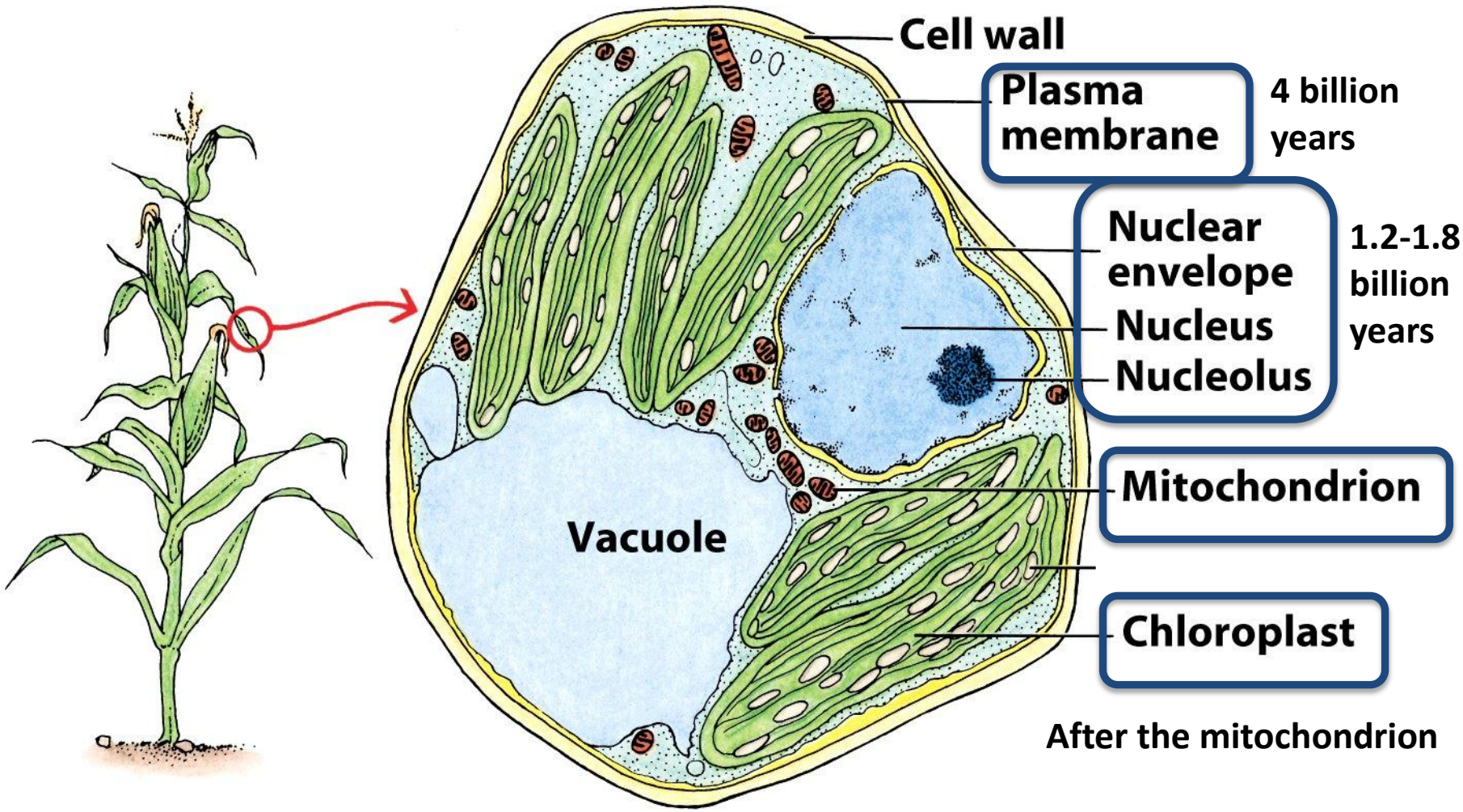


Figure 3-3 part 1
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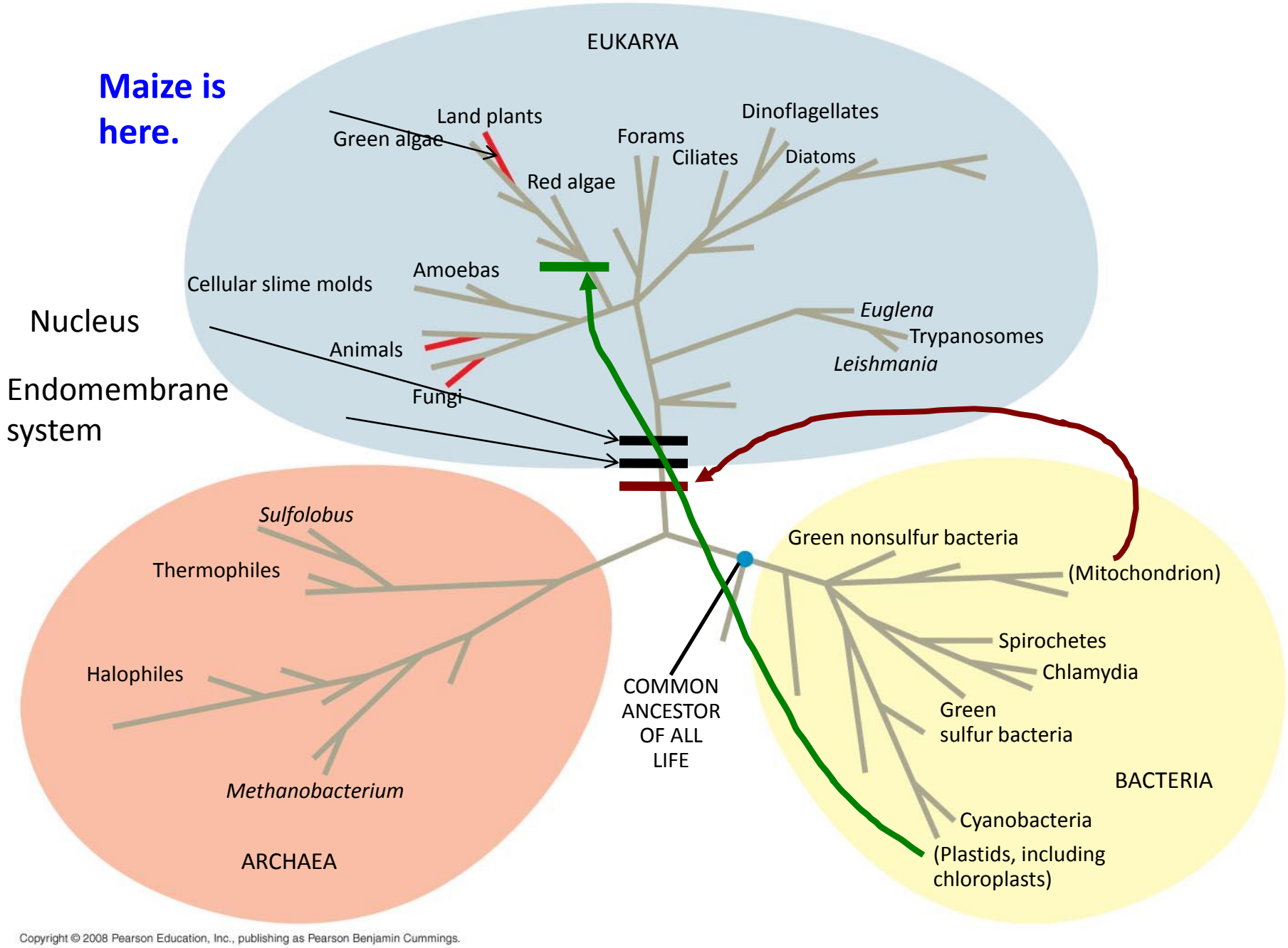
Fig. 26-21



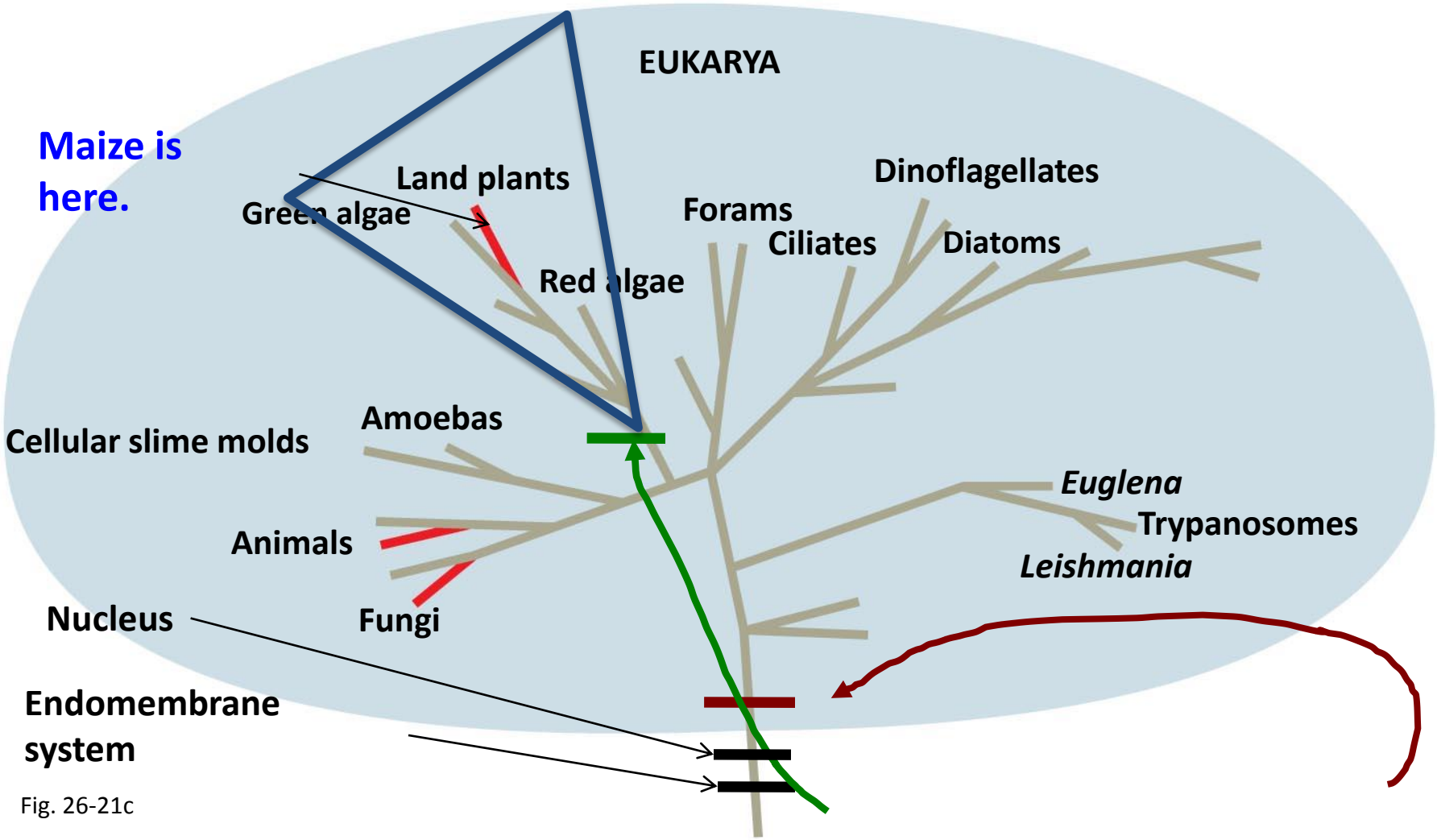
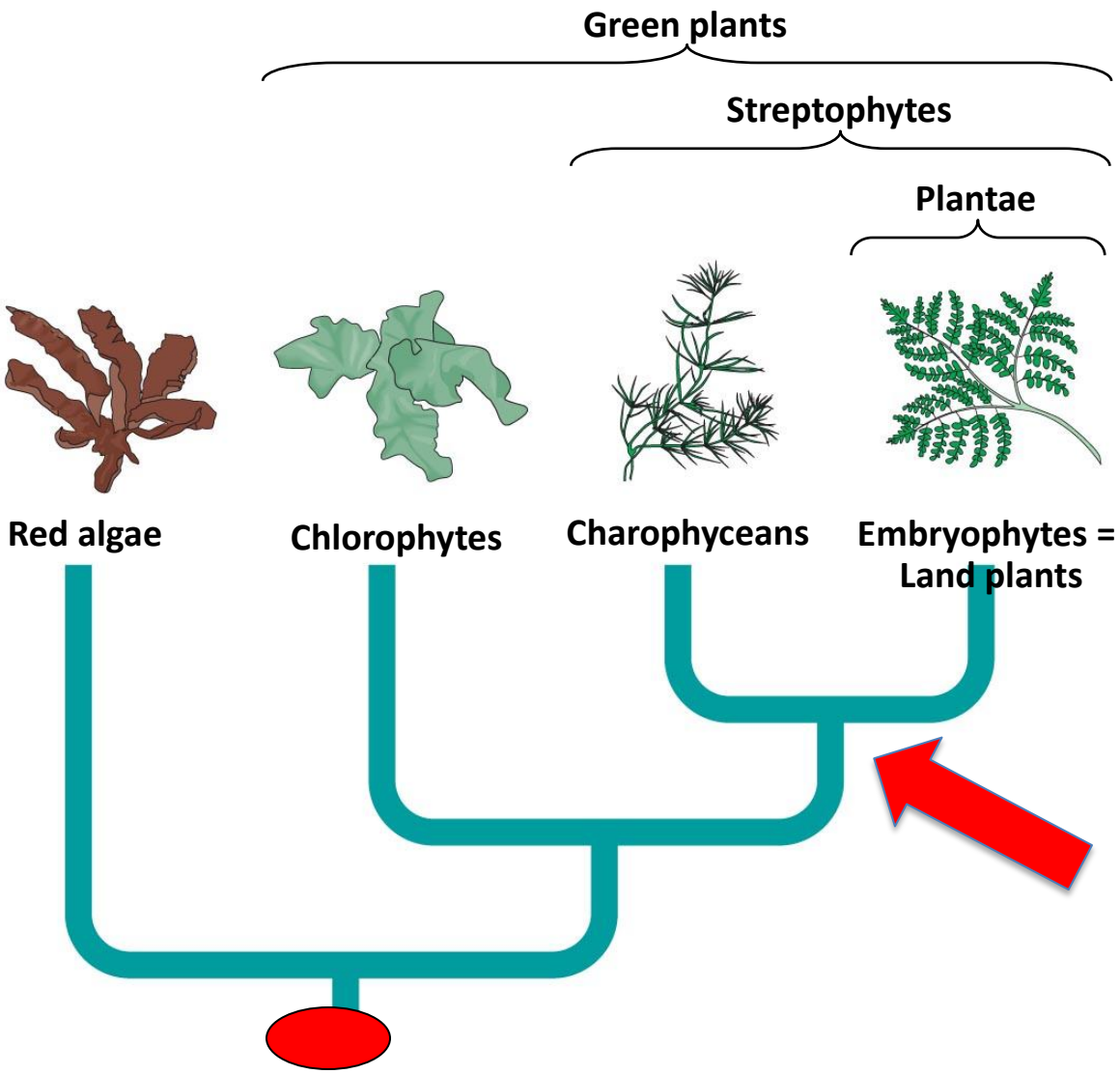


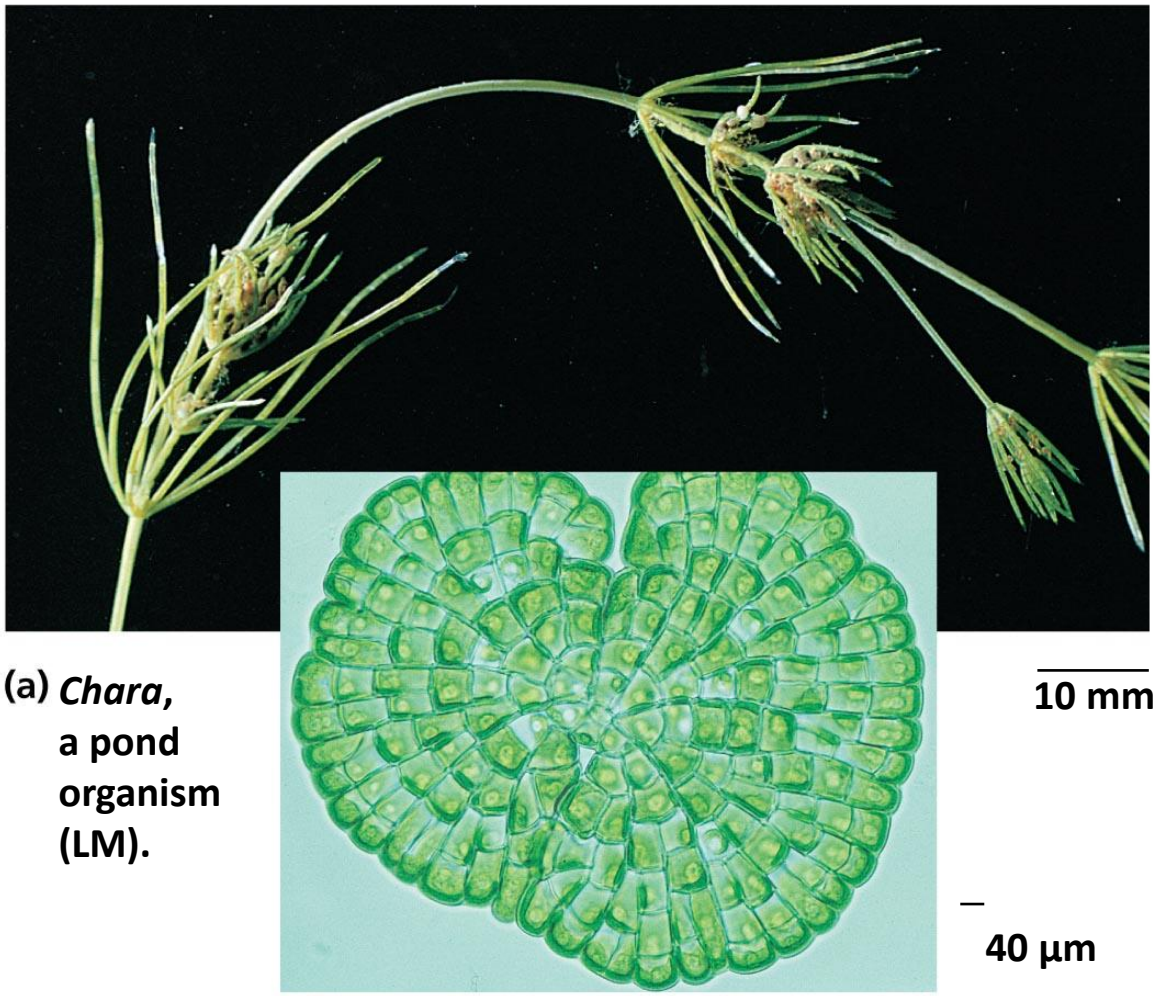
Fig. 26-21c



Eukaryotic cell with primary endosymbiont
(I.e., a chloroplast derived from a cyanobacterium)

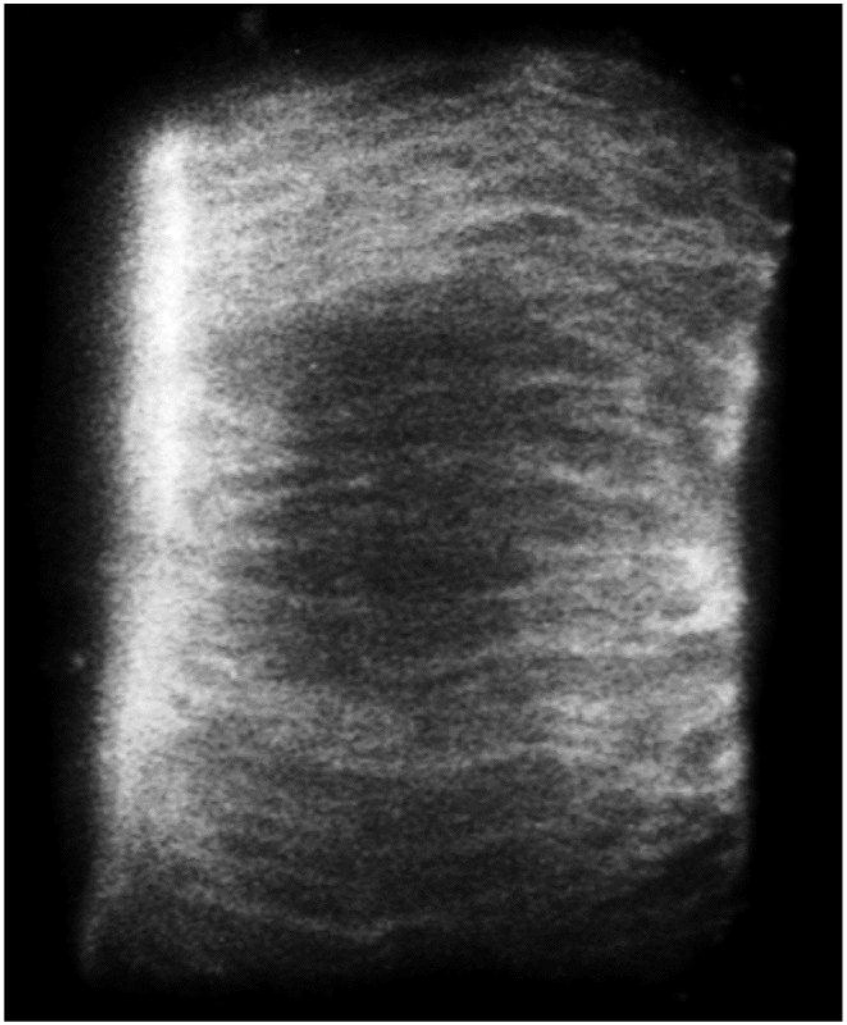
Charophycean algae

LE 29-3

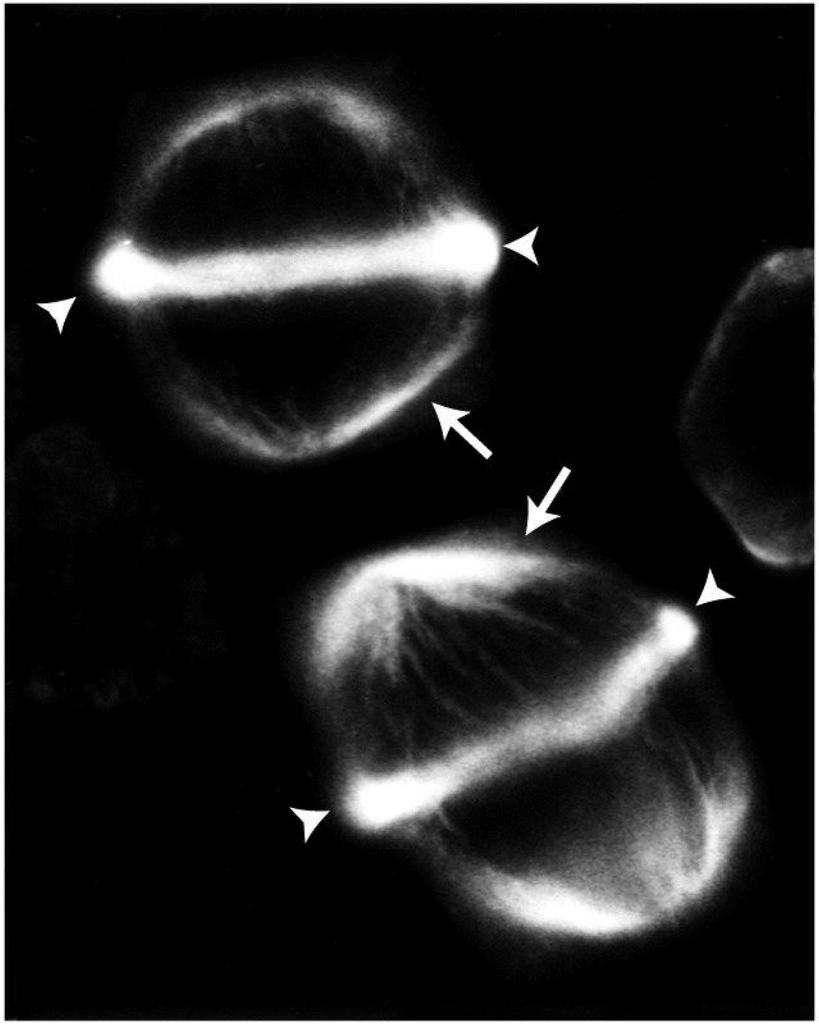


(a) *Chara*, a pond organism (LM).

(b) *Coleochaete orbicularis*, a disk-shaped charophycean (LM).



Interphase



Preprophase band and spindle

Figure 3-45 part 1
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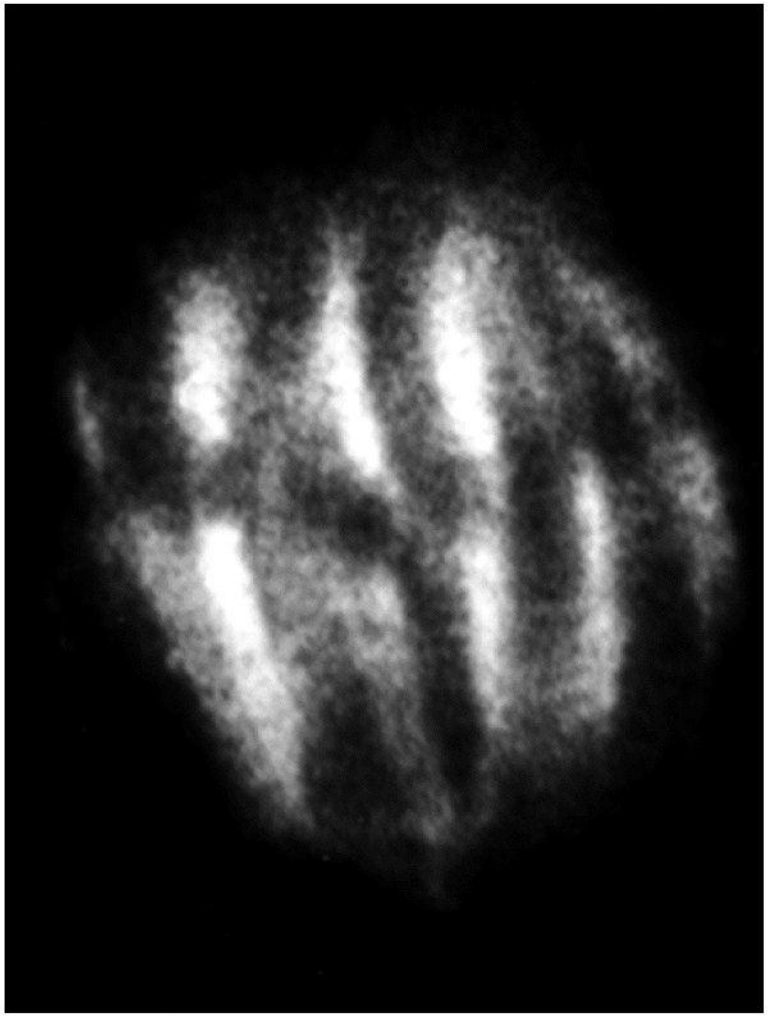
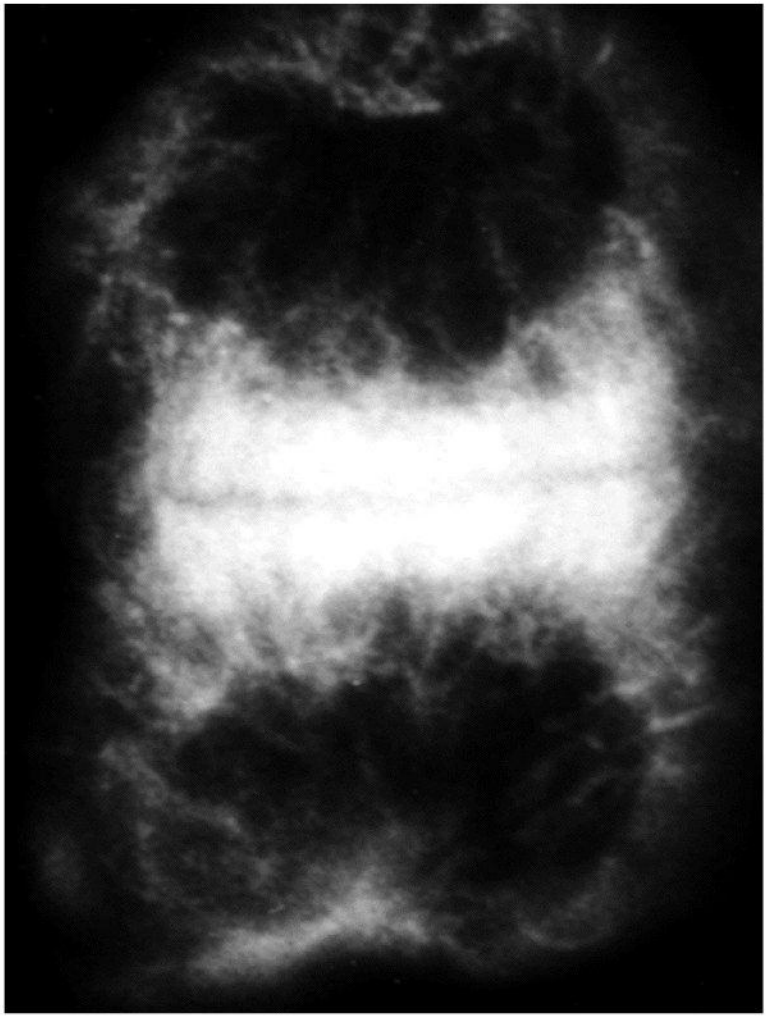


Mitotic spindle at metaphase



Phragmoplast at telophase

Figure 3-45 part 2
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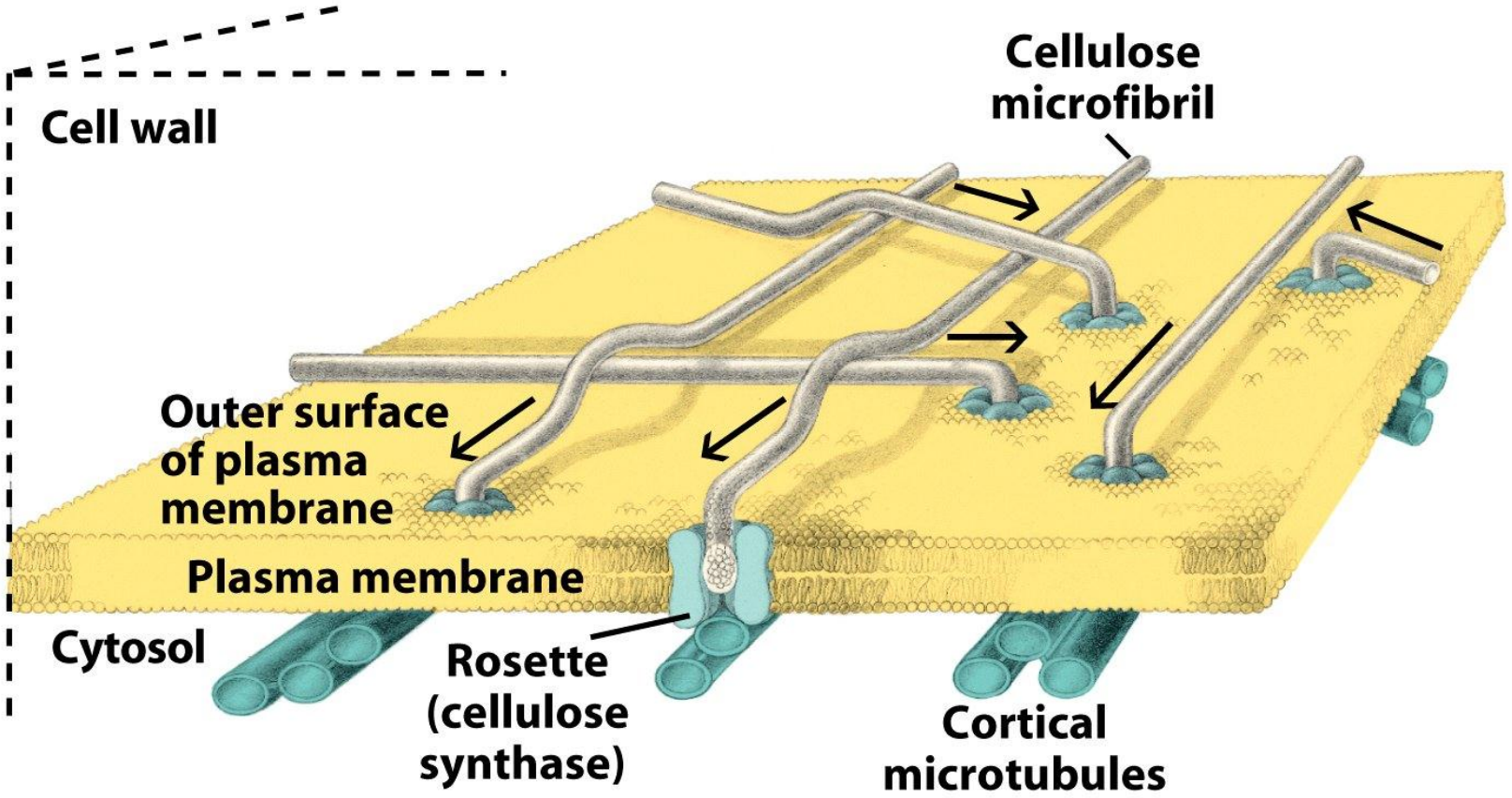

Figure 3-33b
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Orientation of microtubules controls orientation of cellulose Microfibrils.

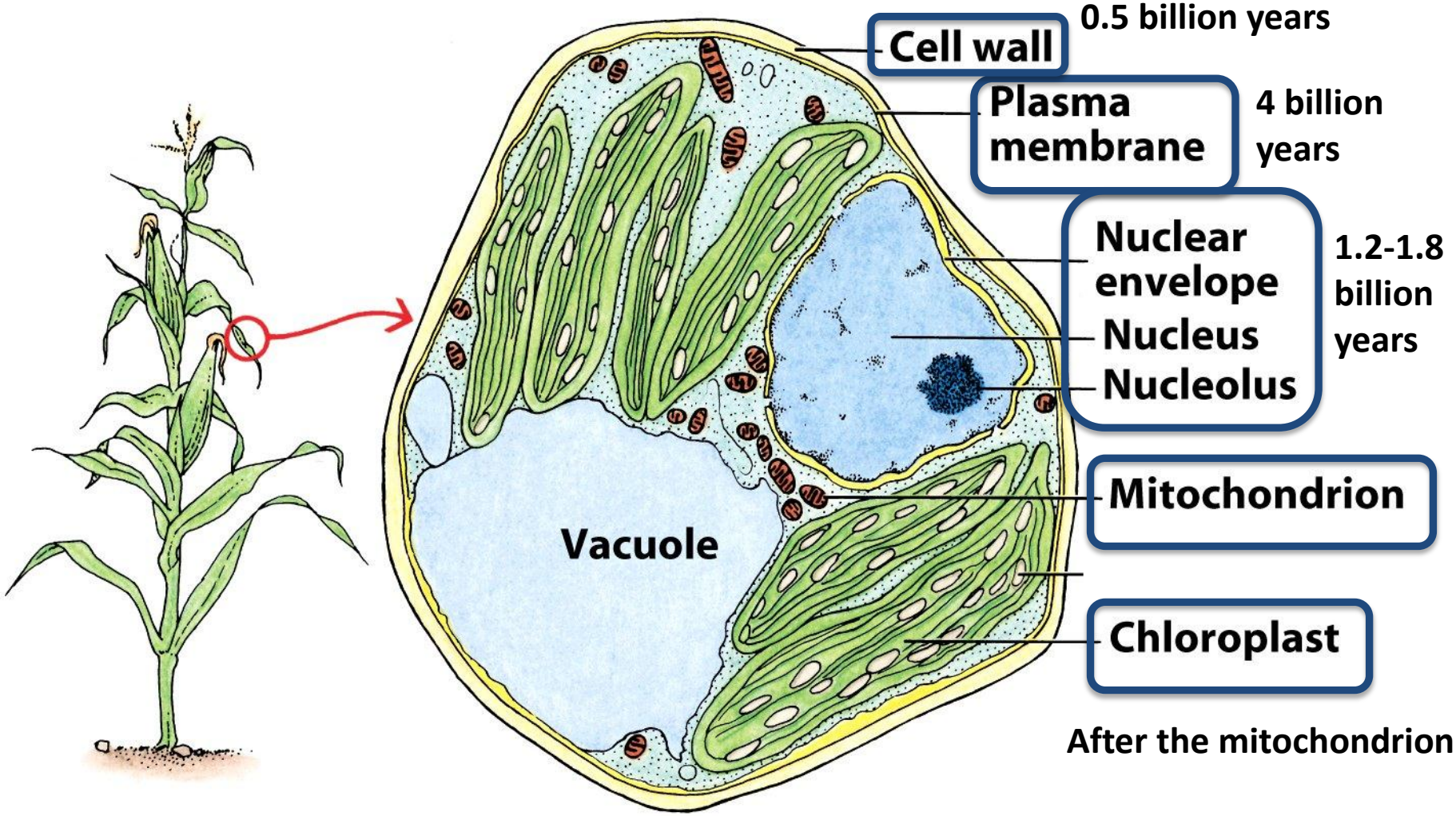

Figure 3-3 part 1
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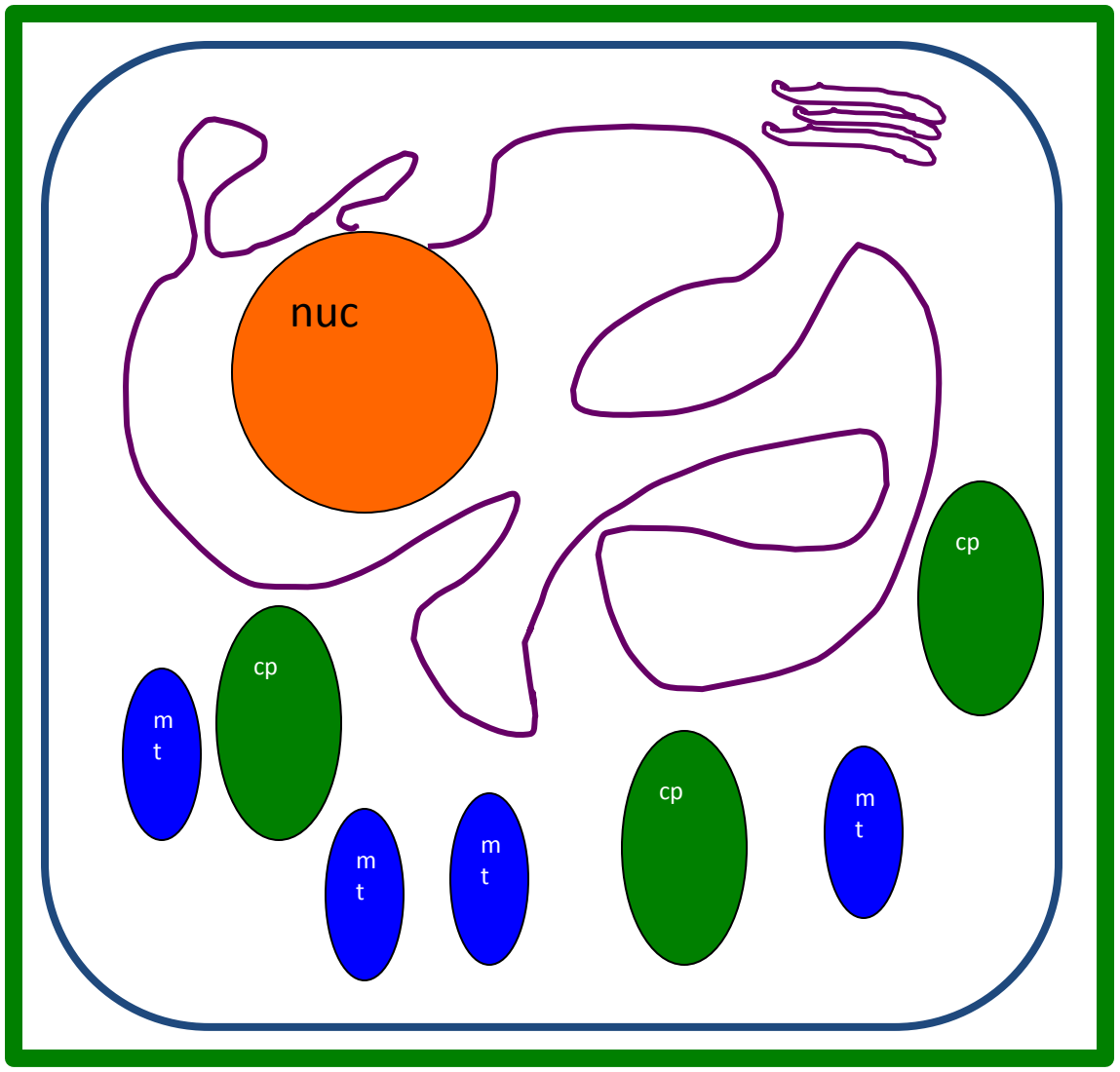
Nucleus from ancestor of Eukarya

Mitochondria from Bacteria

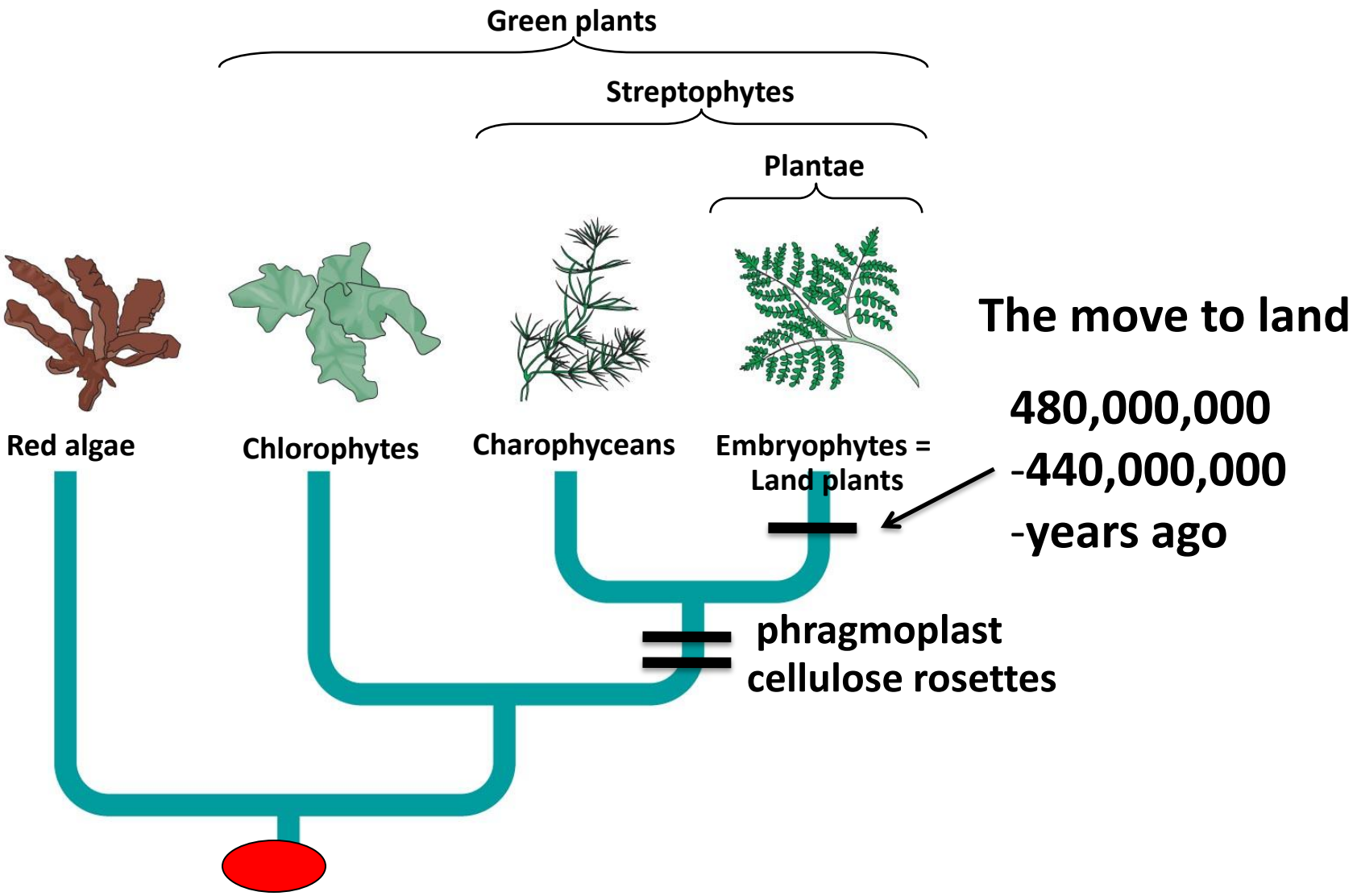
ER and Golgi probably about the same time as nucleus



Chloroplasts from Cyanobac-teria

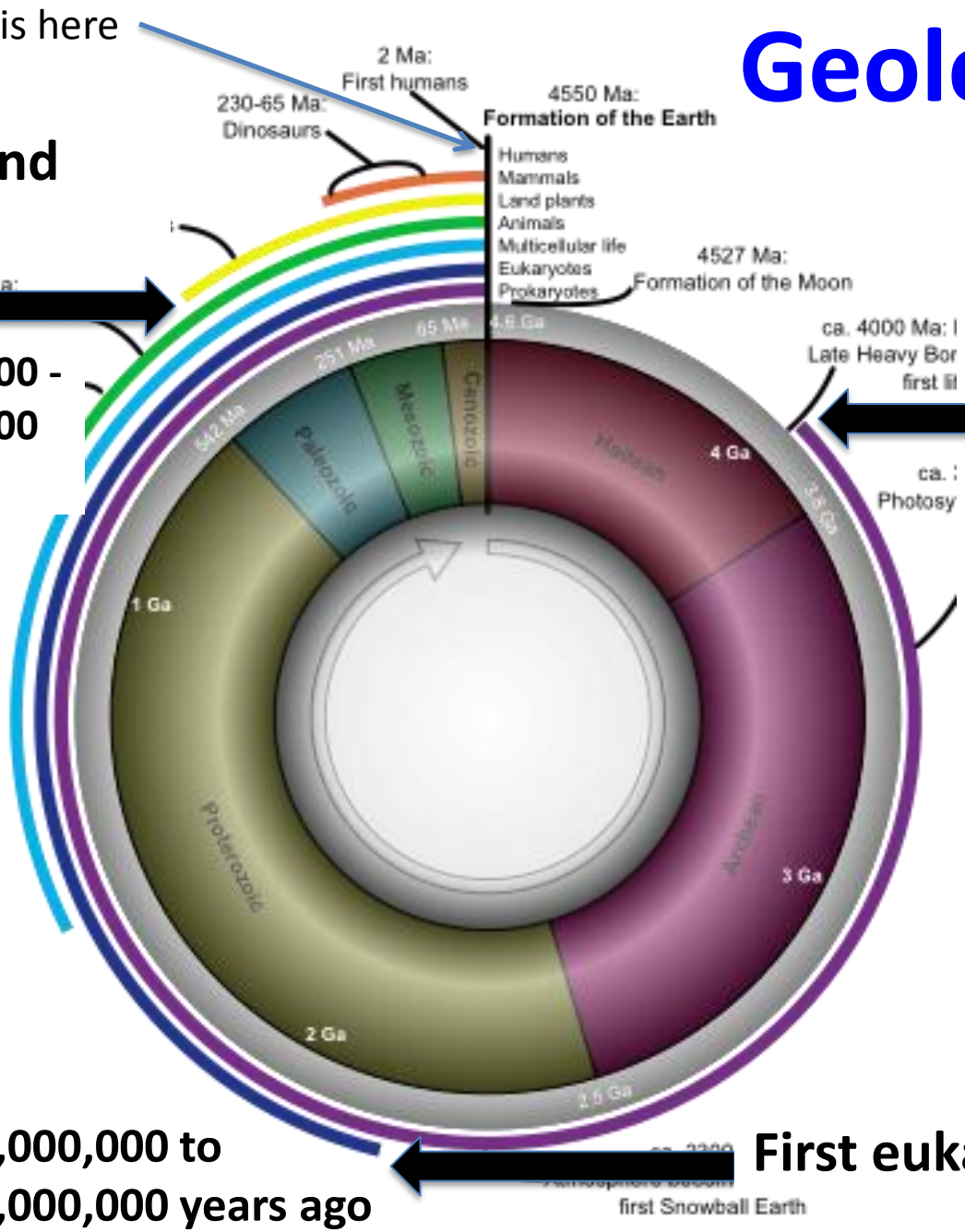
Unique cell wall structure from common ancestor of land plants and Charophy-ceans

Plasma membrane
4 billion years old – shared with all of life



Eukaryotic cell with primary endosymbiont
(I.e., a chloroplast derived from a cyanobacterium)

Geological clock



First land plants

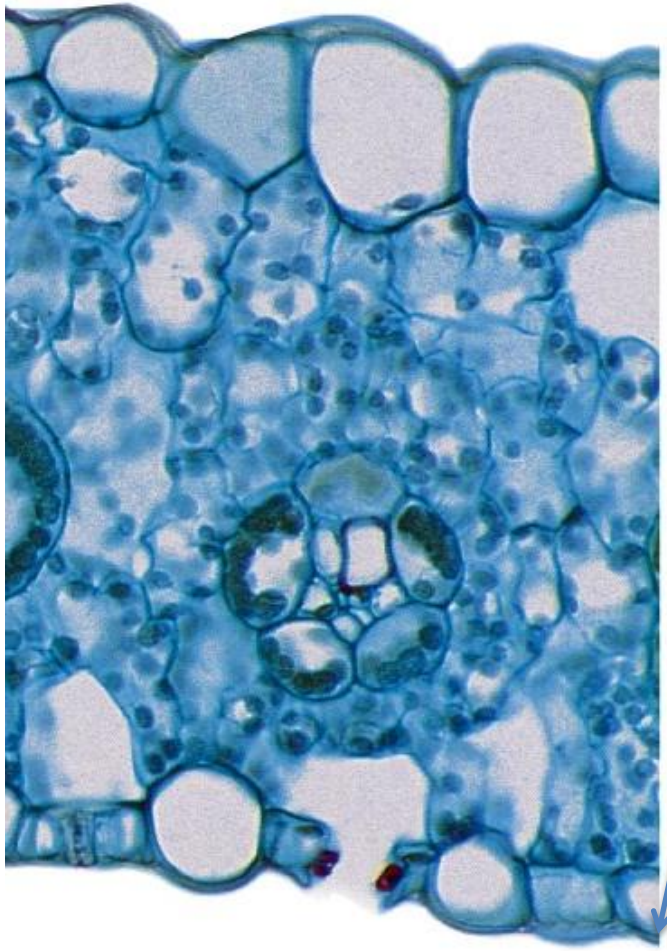
480,000,000 - 440,000,000 years ago

First life

4,000,000,000 years ago

1,200,000,000 to 1,800,000,000 years ago

First eukaryotes

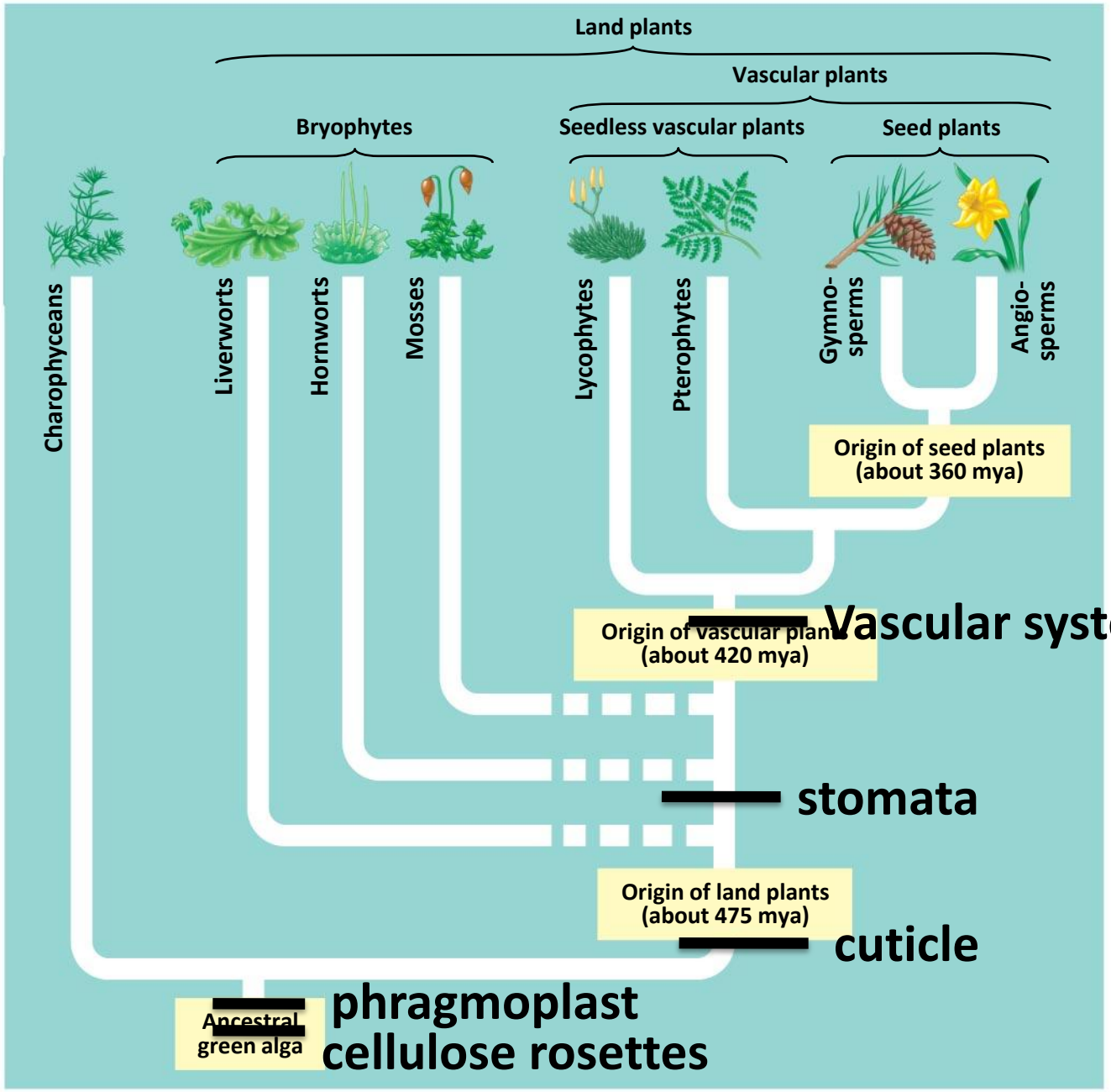


Cuticle

480,000,000- 440,000,000 years ago

Stomata
– somewhat after the cuticle

LE 29-7



The maize vascular system
Originated with the vascular plants, ca. 420,000,000 years ago

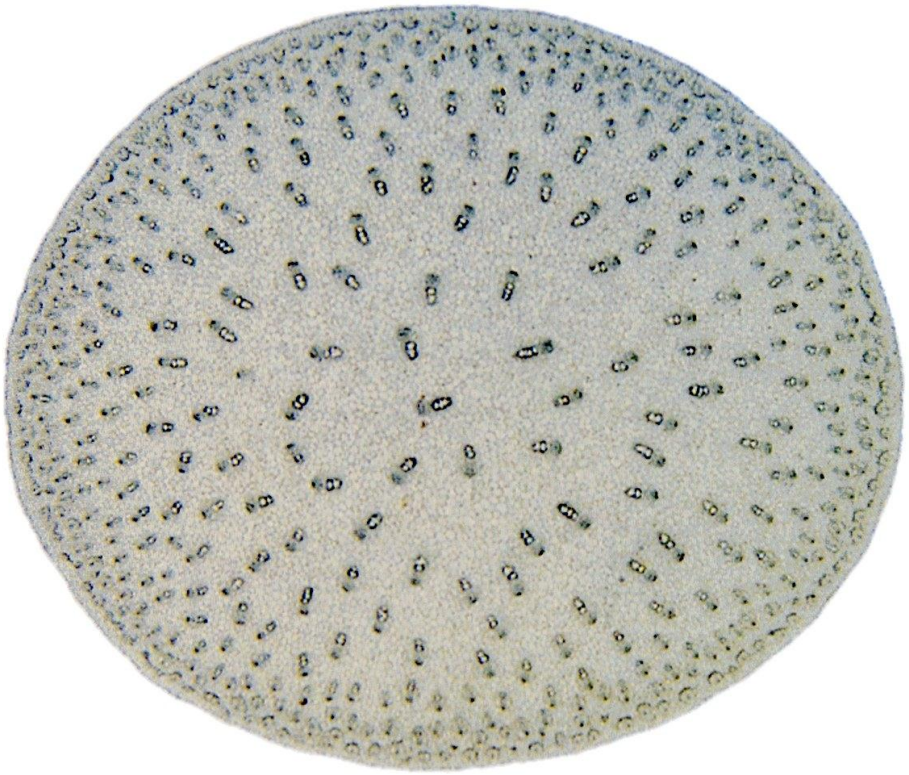


Figure 25-12a
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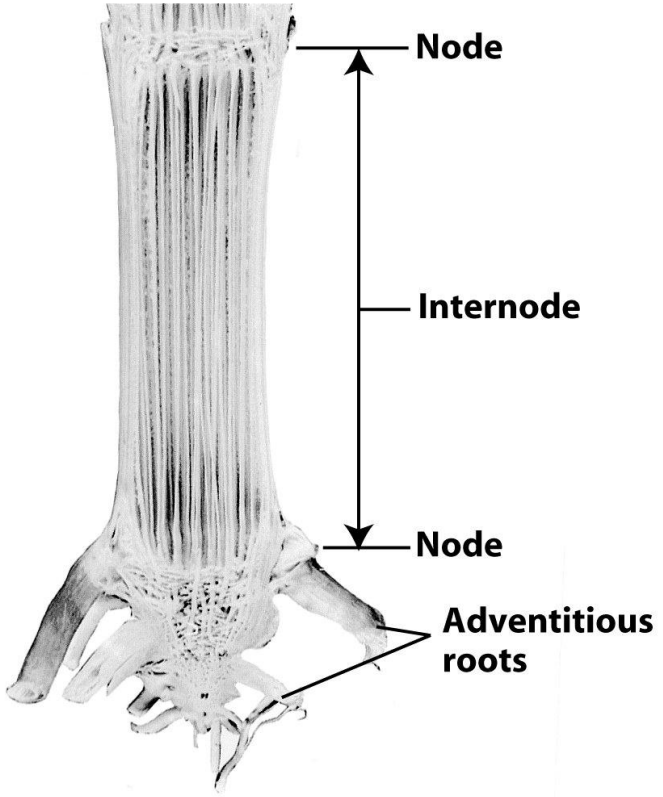
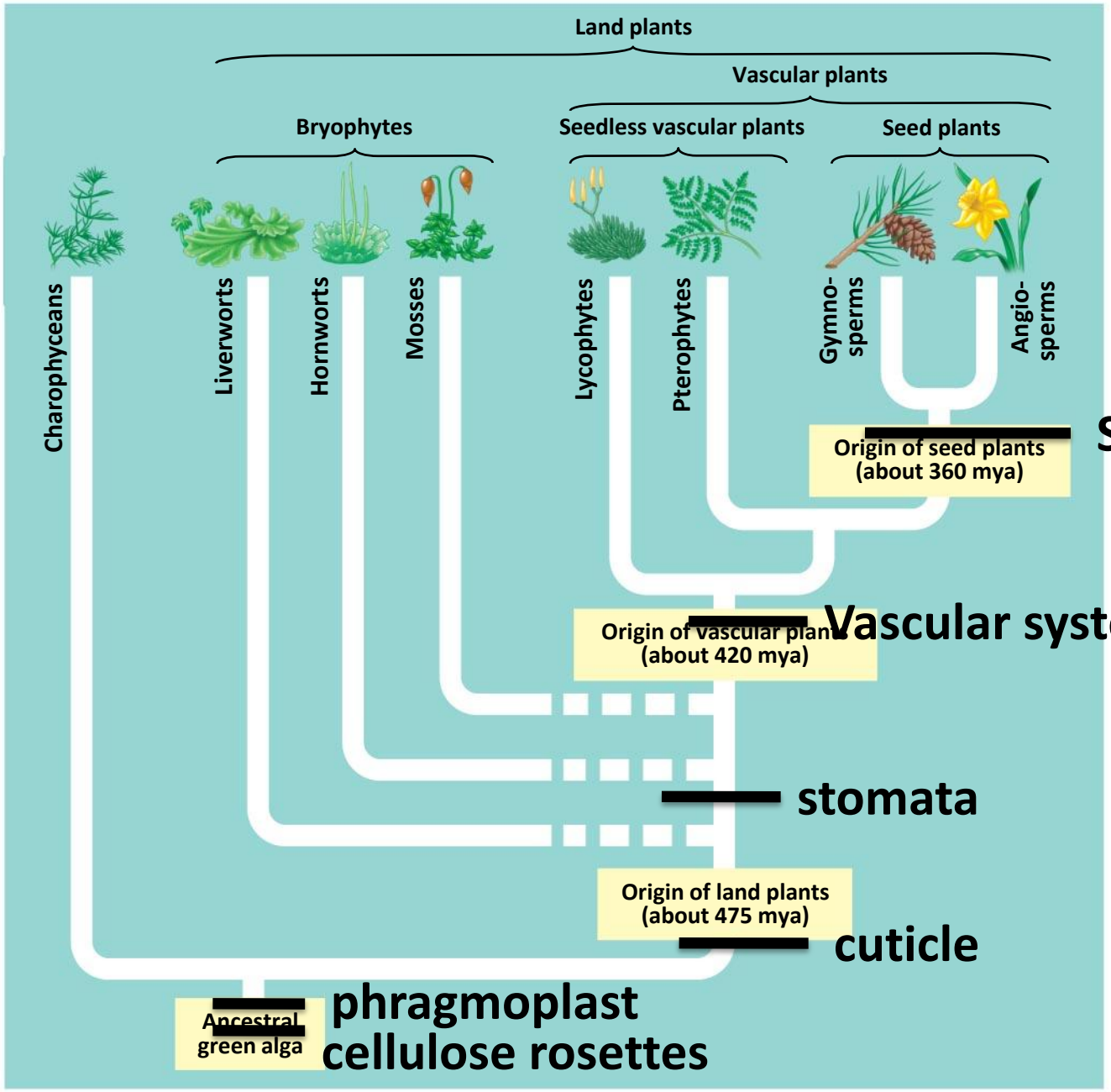


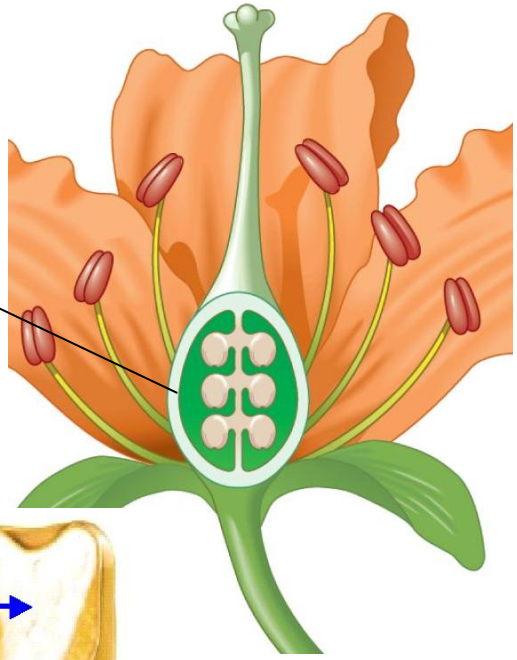
Figure 25-12c
Biology of Plants, Seventh Edition

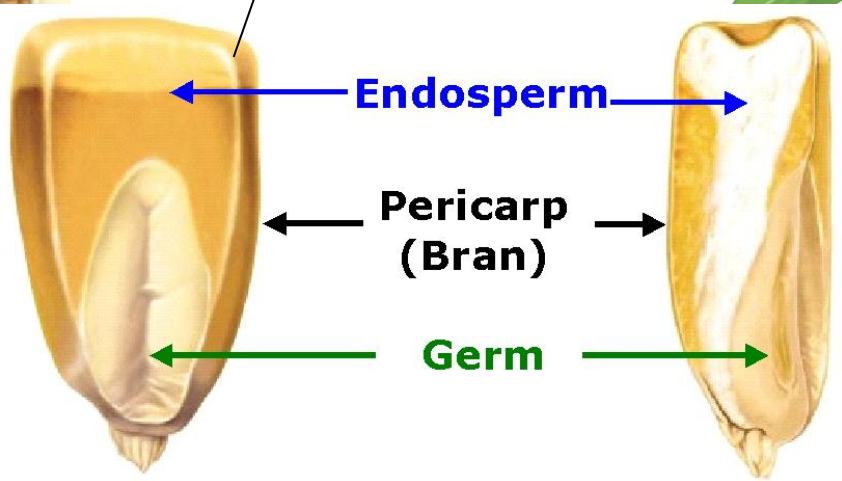
LE 29-7



The seed is a mature ovule, which is an integumented megasporangium. The megagametophyte of seed plants is always dependent on the sporophyte.

(inside here and here)



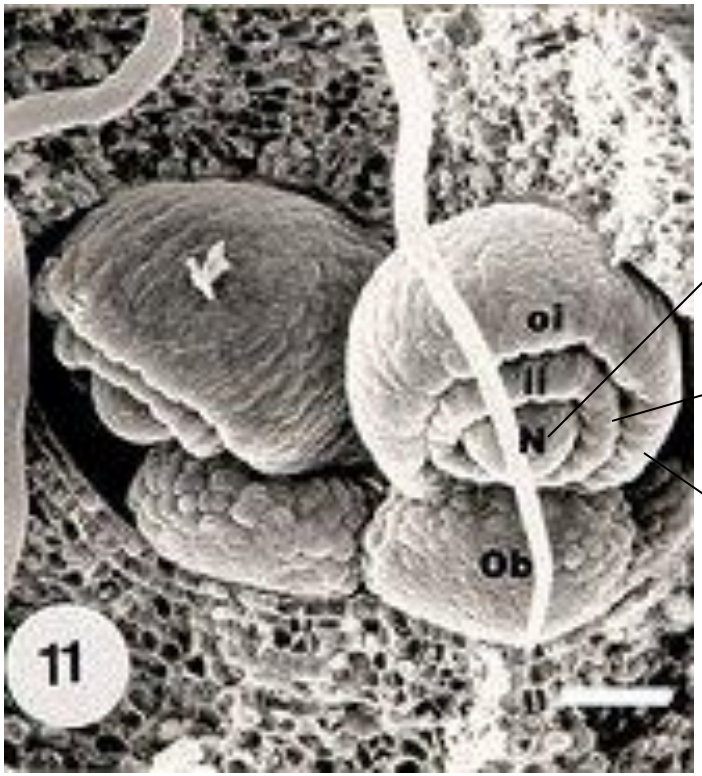


Angiosperms = flowering plants

275-141 million years ago
(i.e., we don't have a clue when they originated)

- Enclosed ovary
- Double fertilization
- Outer integument
- Rapid pollen tube growth

The female gametophyte is wrapped in sporophyte tissue.

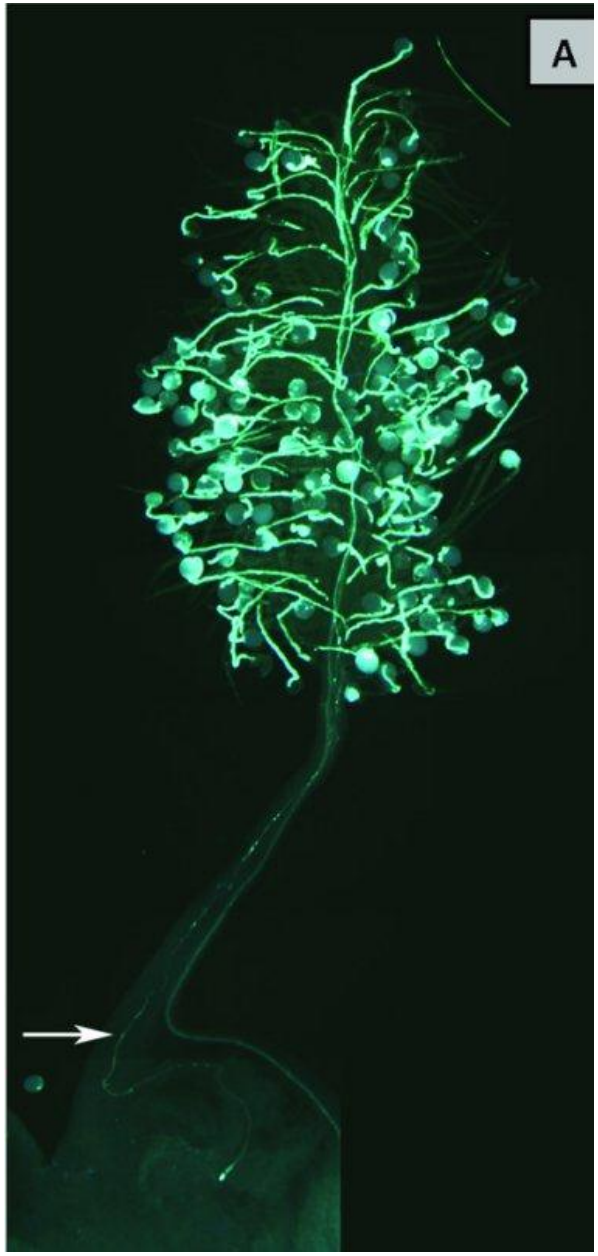


Megagametophyte forms in here.

It is surrounded by an inner integument.

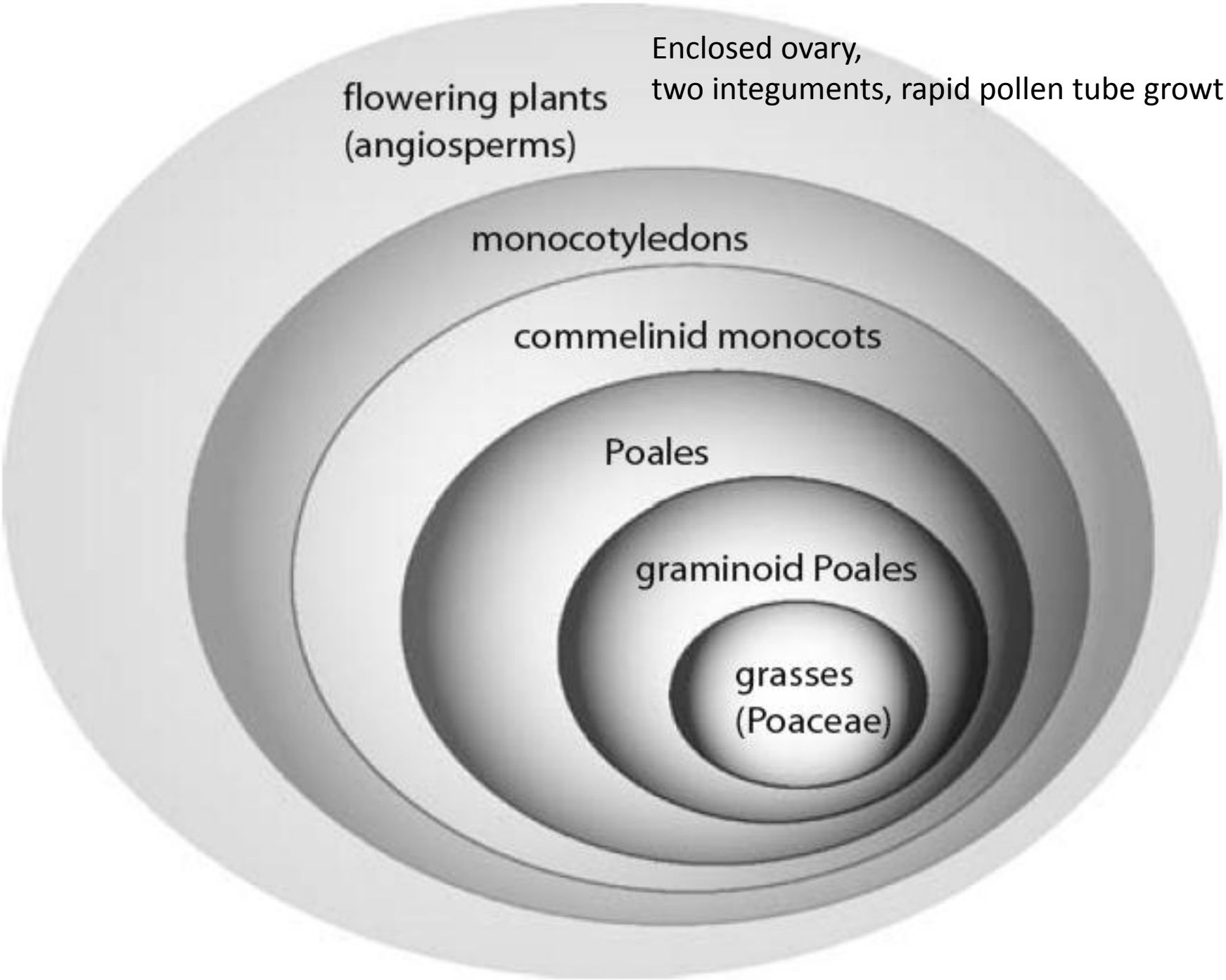
Angiosperms also have an outer integument.

http://www.botany.utoronto.ca/faculty/dickinson/rosaceaeevolution/floral.html



Kuhlman & Rooney 2010

https://www.crops.org/publications/jpr/articles/5/1/133

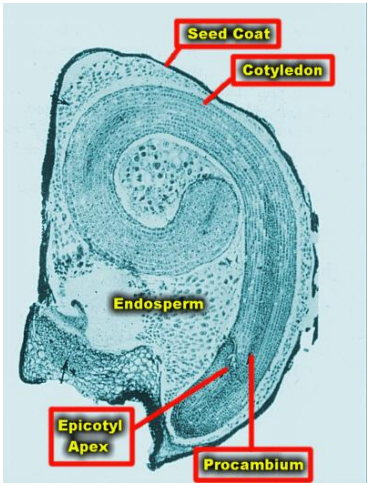

Enclosed ovary,
two integuments, rapid pollen tube growth
flowering plants
(angiosperms)
monocotyledons
commelinid monocots
Poales
graminoid Poales
grasses
(Poaceae)

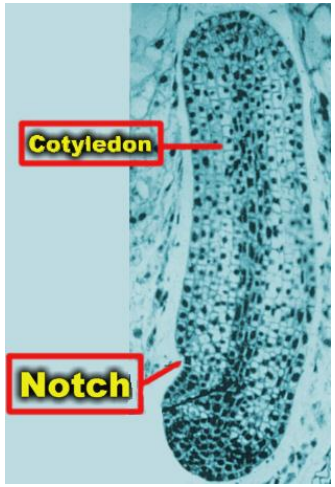
Monocots

191-137 million years ago

- One cotyledon
- Single adaxial prophyll
- Meristem with 1-layered tunica corpus construction
- Leaf venation parallel

Embryos



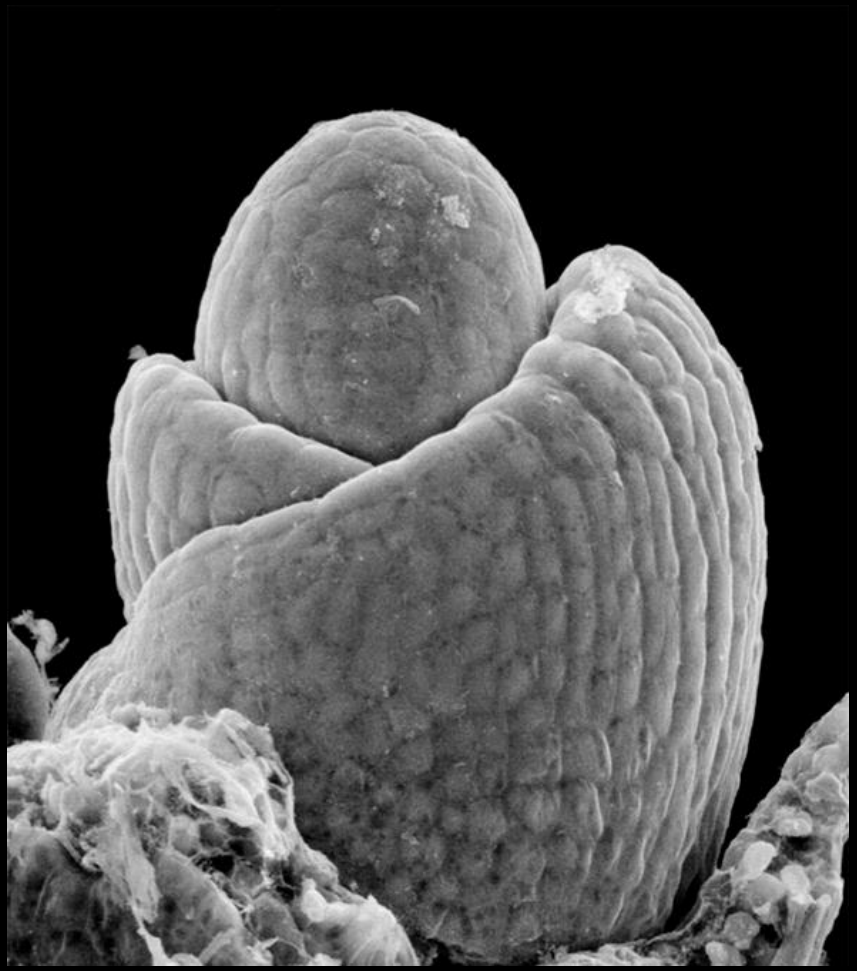


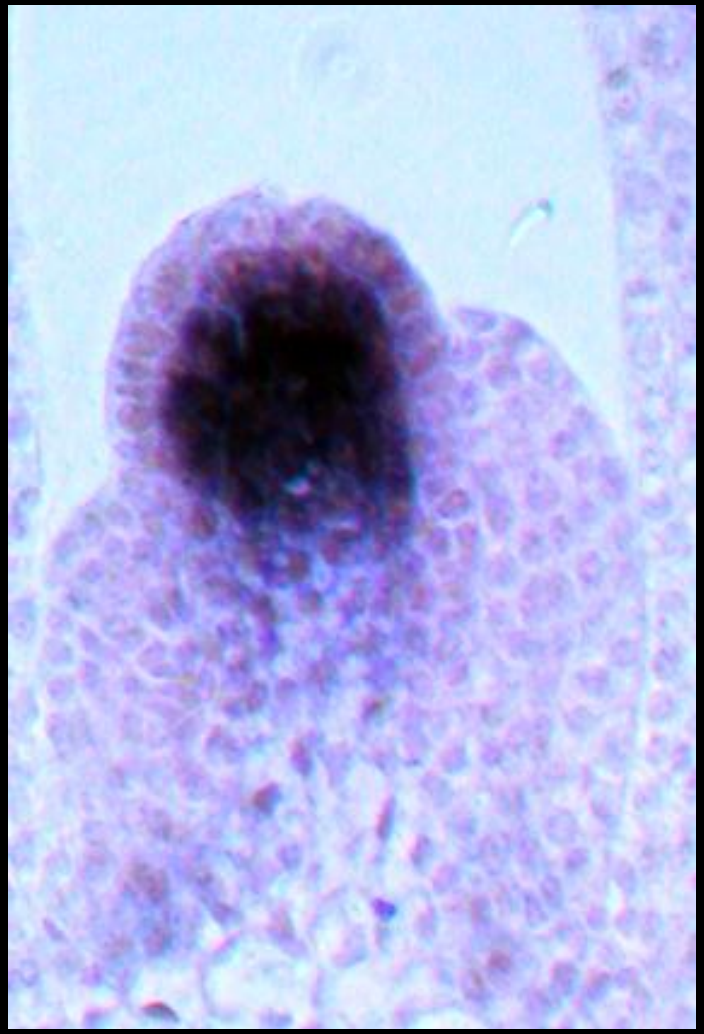
onion

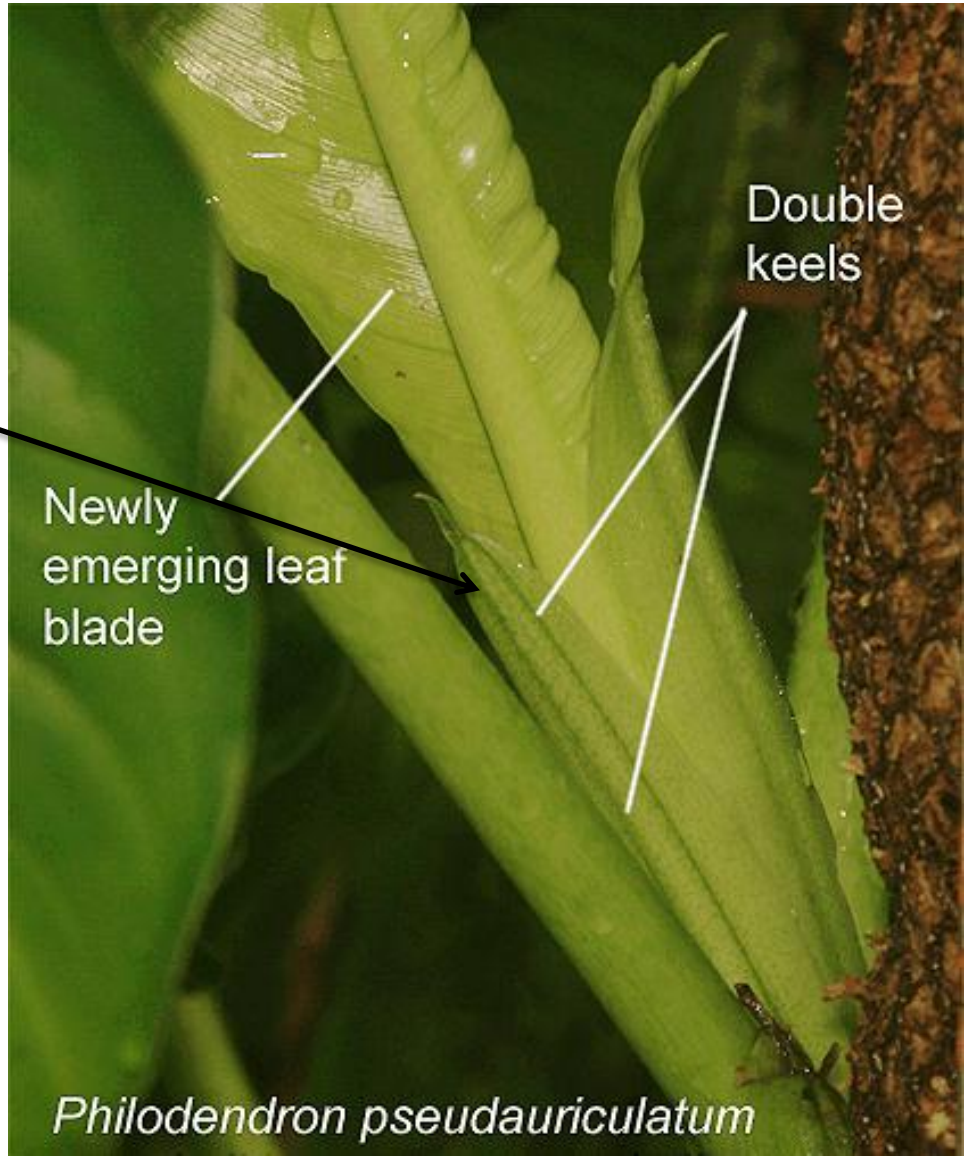
Grass embryo

www.botany.hawaii.edu/faculty/webb/

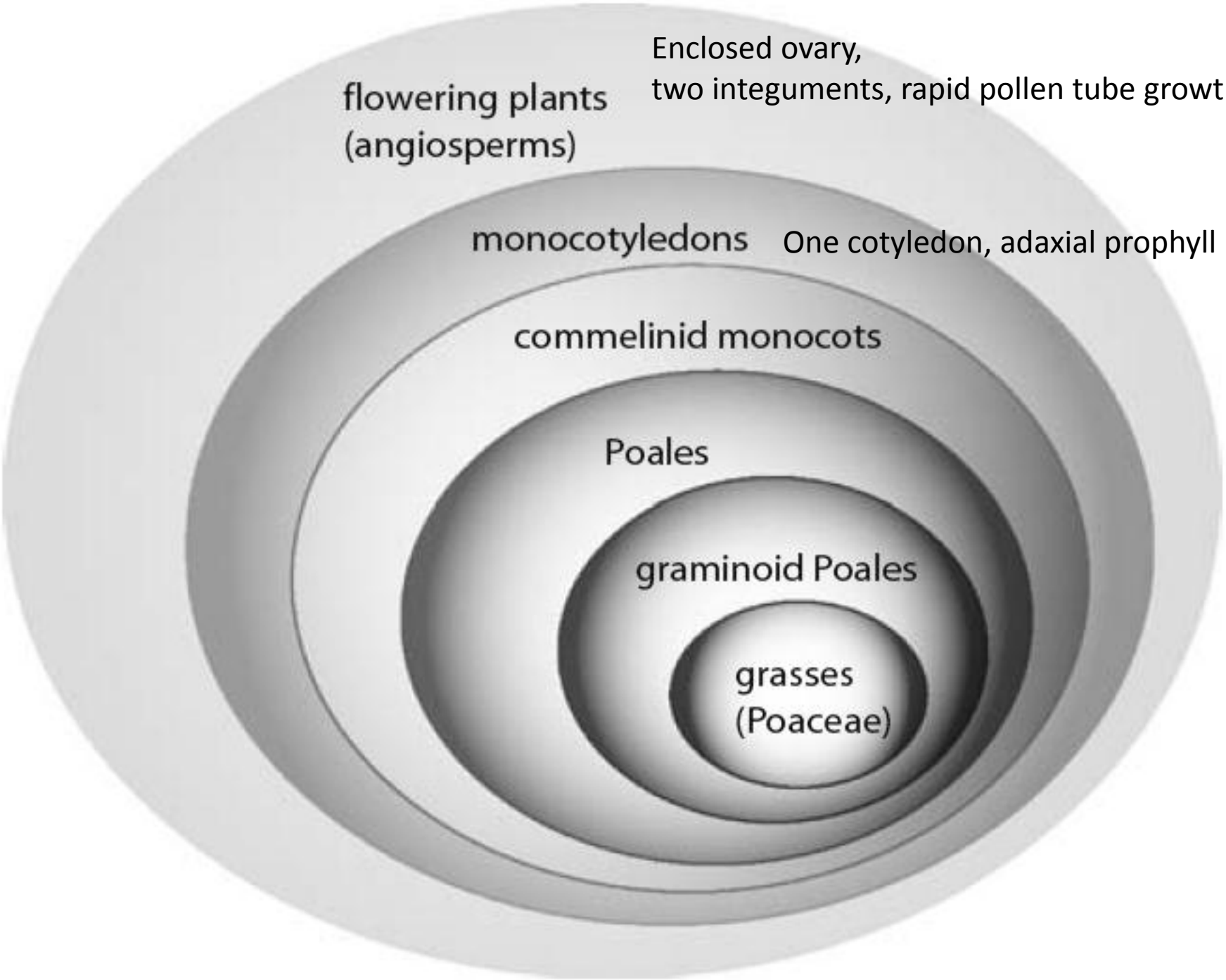
KNOTTED1 expression in *Setaria viridis*







http://www.exoticrainforest.com/Philodendron%20pseudauriculatum.html


flowering plants
(angiosperms)
Enclosed ovary,
two integuments, rapid pollen tube growth
monocotyledons
One cotyledon, adaxial prophyll
commelinid monocots
Poales
graminoid Poales
grasses
(Poaceae)

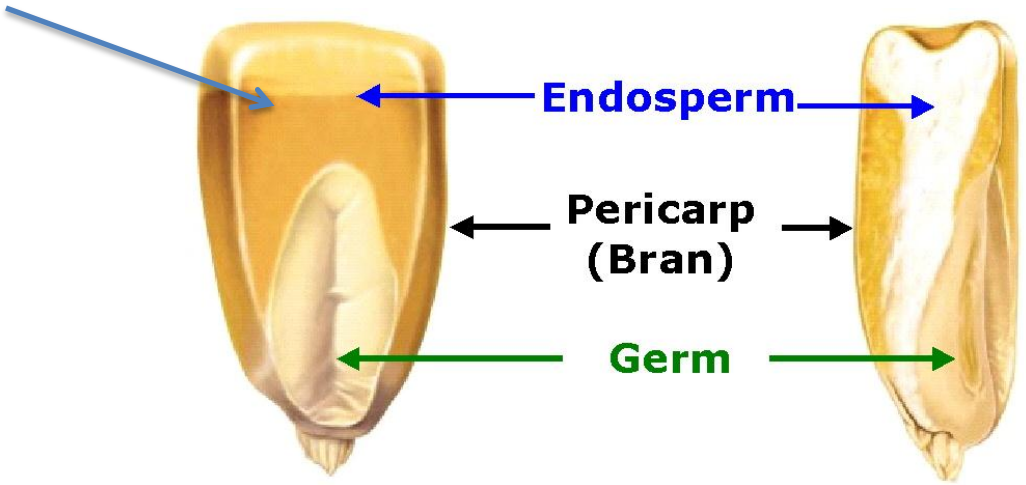
Commelinid monocots

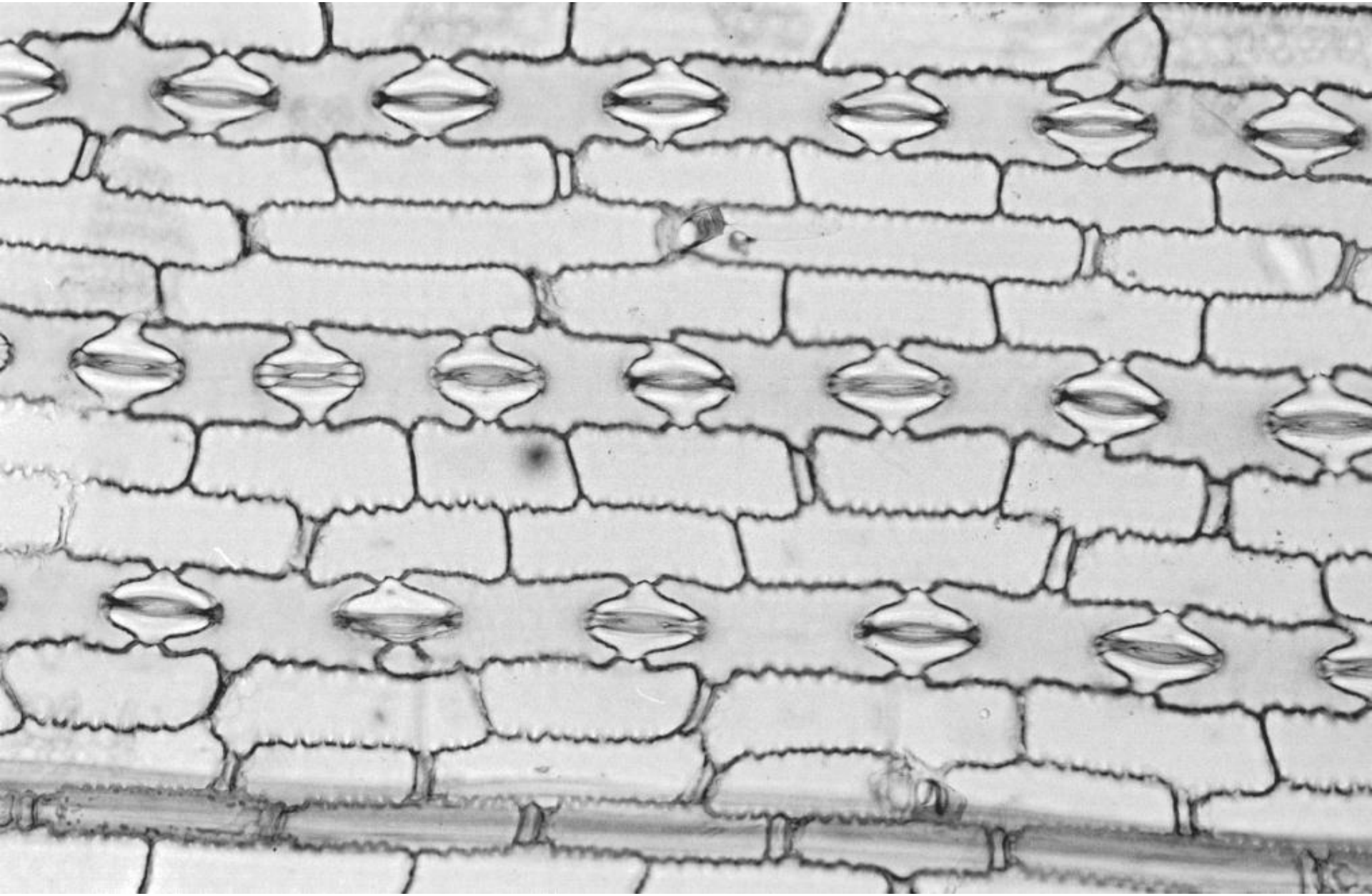
(124,000,000 -100,000,000 years ago)

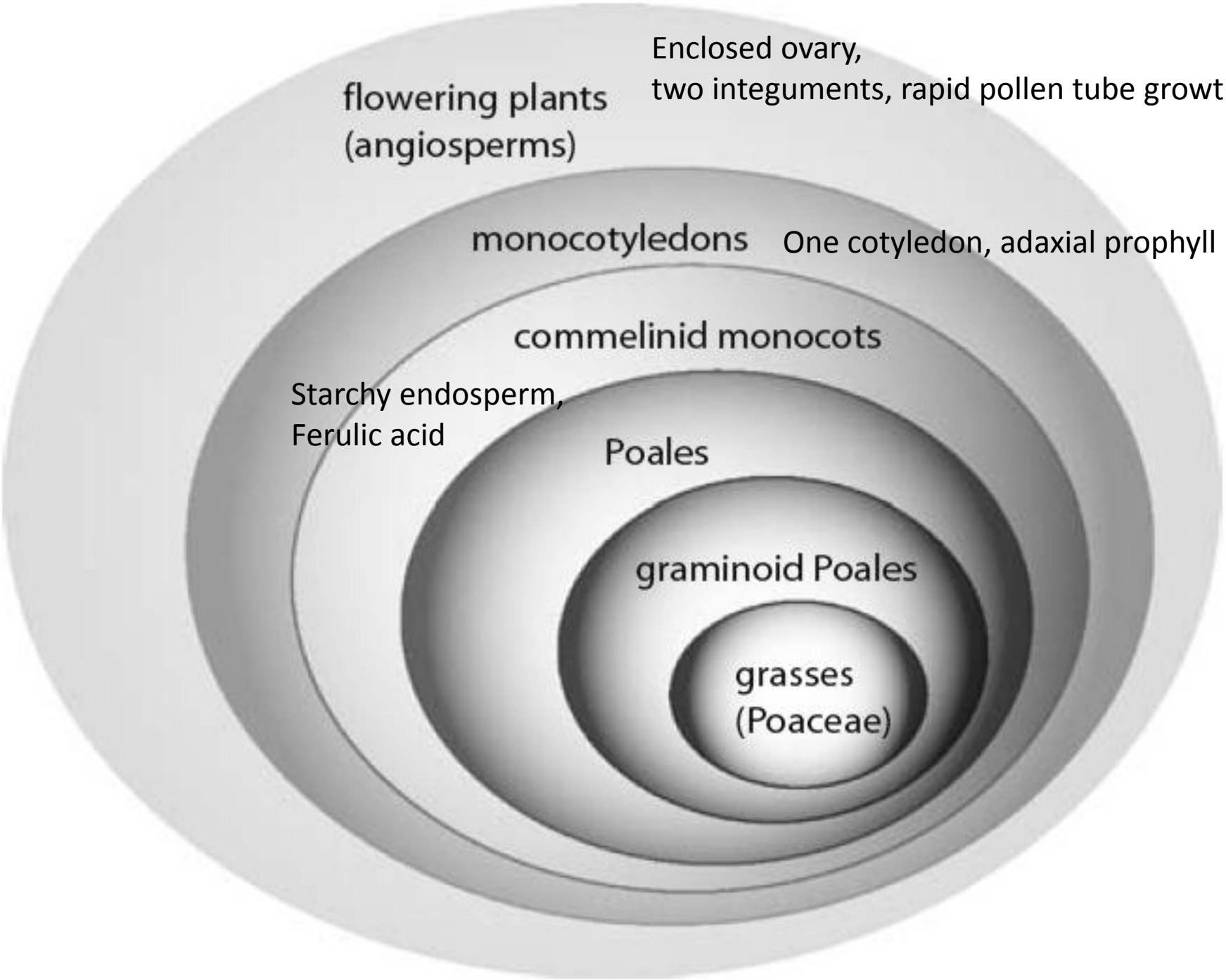
- Arecaceae (Palmae)
- Commelinales
- Zingiberales
- Poales

Commelinid monocots

- Ferulic acid in the cell walls
- Silica bodies in the leaves
- Paracytic stomata
- Starchy endosperm (in all but the palms)





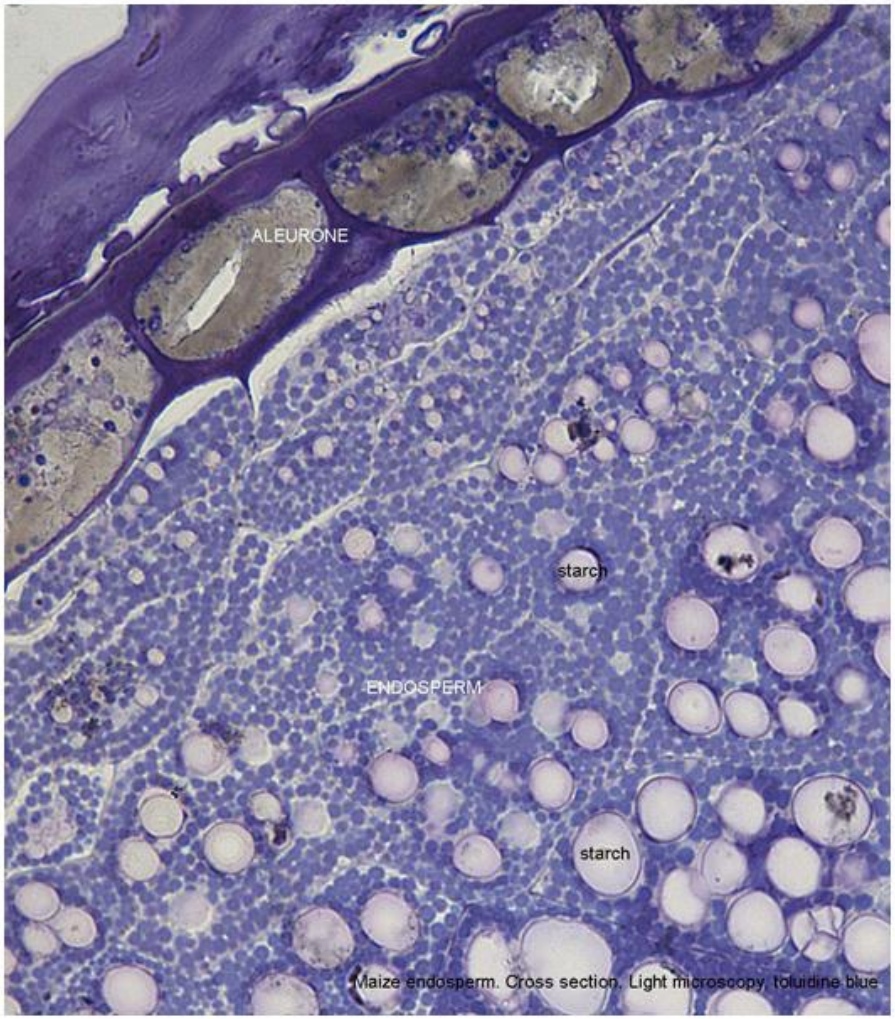

flowering plants
(angiosperms)
Enclosed ovary,
two integuments, rapid pollen tube growth
monocotyledons
One cotyledon, adaxial prophyll
commelinid monocots
Starchy endosperm,
Ferulic acid
Poales
graminoid Poales
grasses
(Poaceae)

Poales

- Typhaceae – cattails
- Bromeliaceae – pineapples
- Cyperaceae – sedges
- Juncaceae – rushes
- Graminoid poales

Poales

- Silica bodies in the epidermis
- Endosperm nuclear



Maize endosperm. Cross section. Light microscopy, toluidine blue

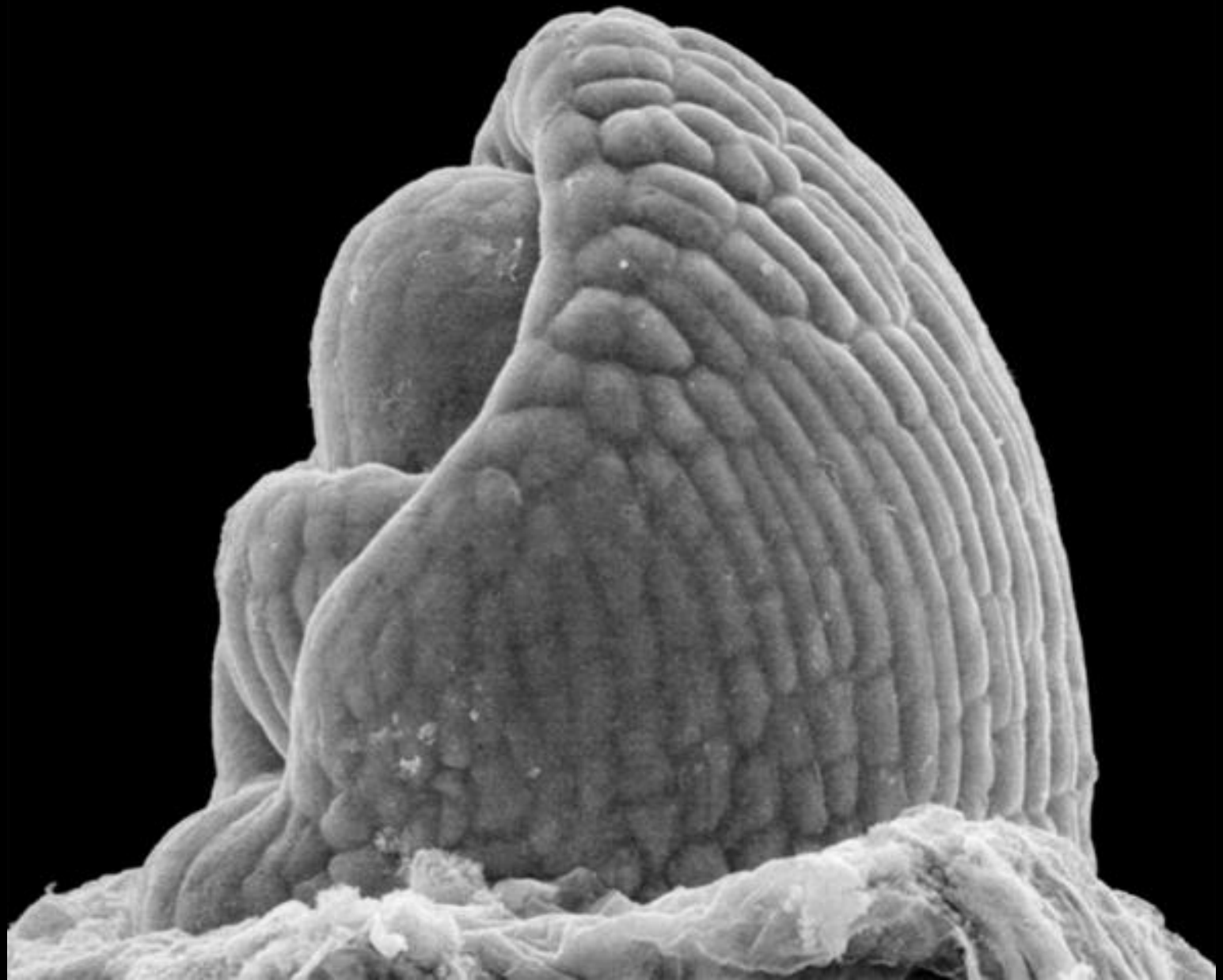
http://www.dagz.boku.ac.at/fileadmin/_/H94/H941/bilder/Stoeger_Mitarbeiter_AG/Bilder/Light_Microscopy/GR_Maize_endosperm._Cross_section._Light_microscopy__toluidine_blue._gr.jpg

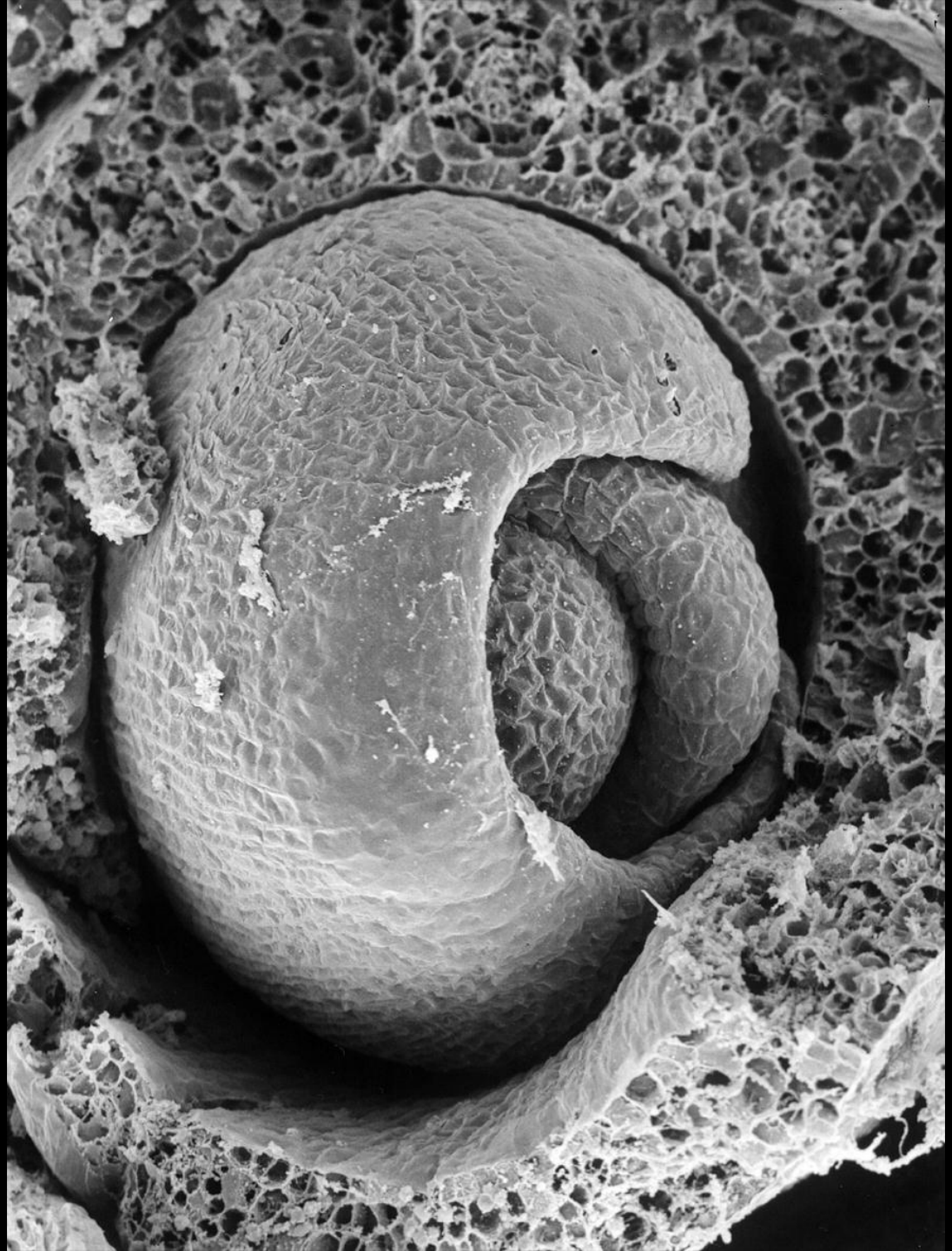
Graminoid Poales

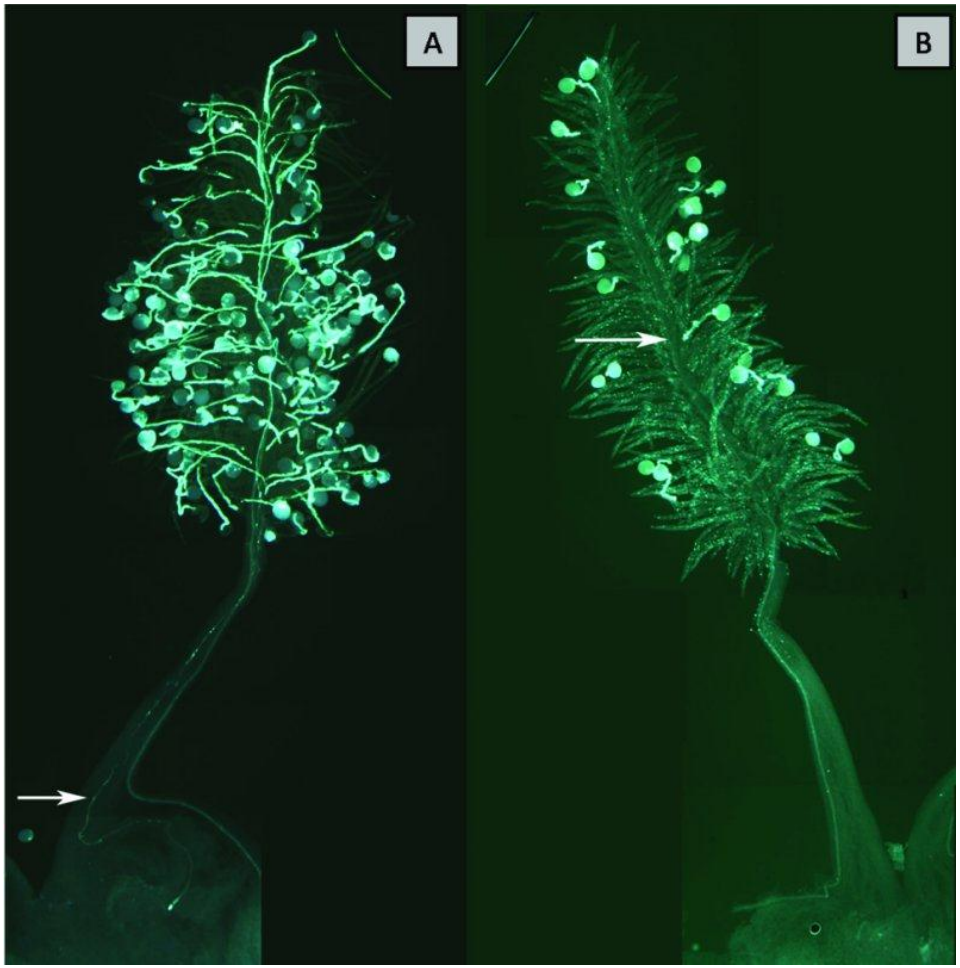
- Centrolepidaceae
- Restionaceae
- Flagellariaceae
- Joinvilleaceae
- Ecdeiocoleaceae
  - Ecdeiocolea
  - Georgeantha
- **Poaceae**

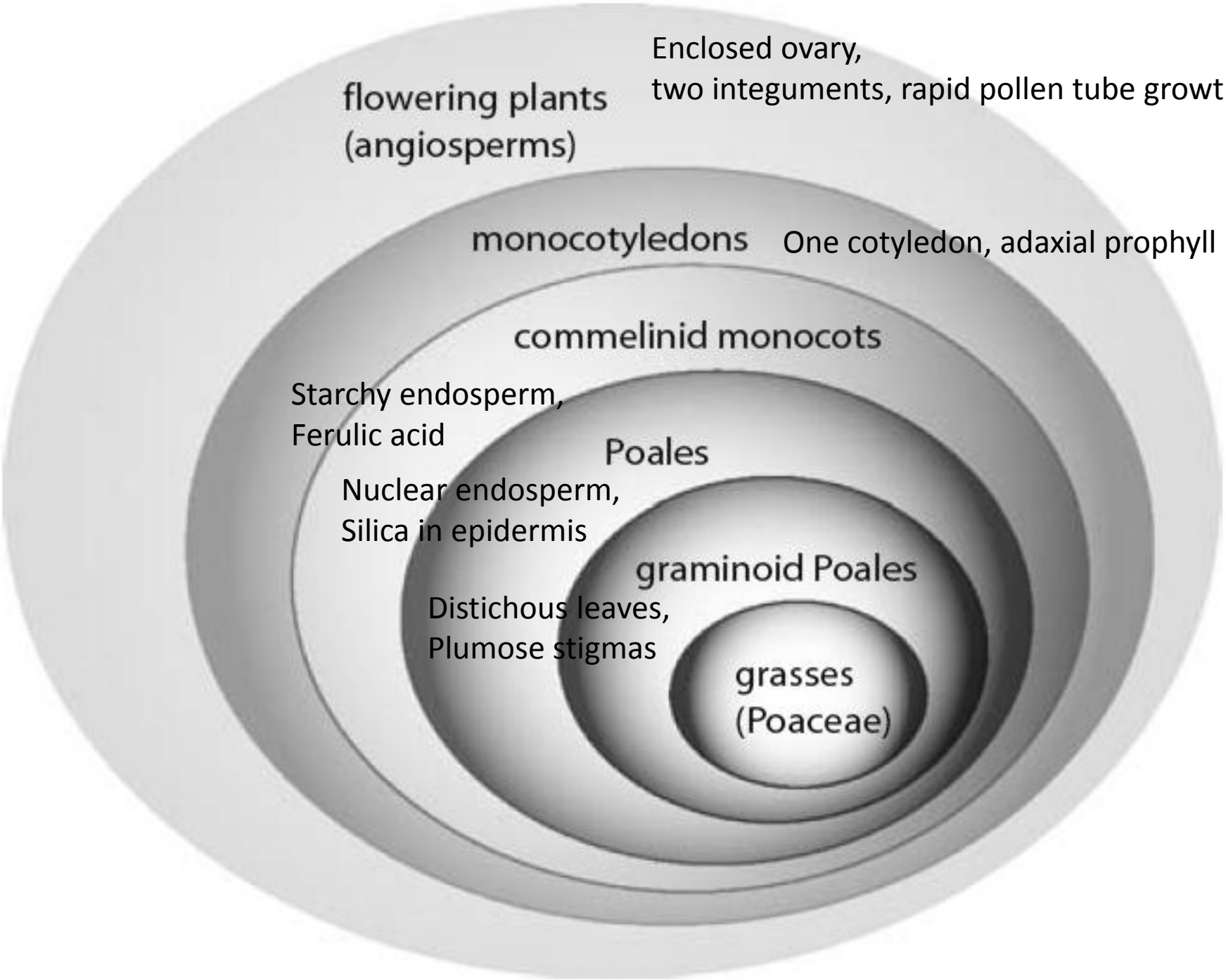
Graminoid Poales

- Leaves distichous, with a sheath
- Stigmas plumose





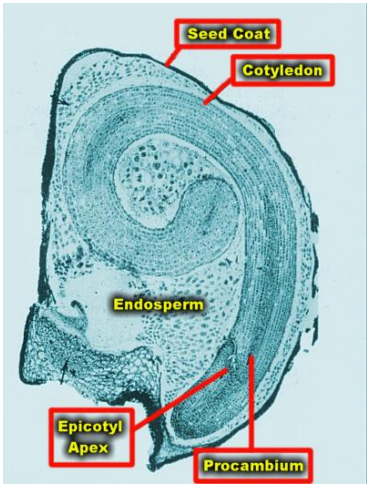

A
B

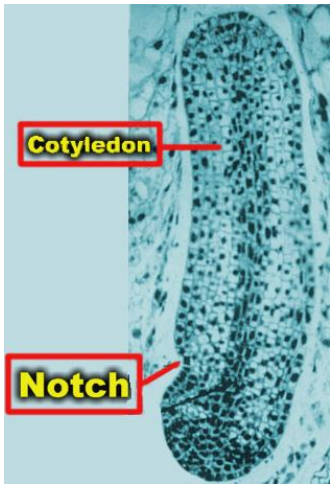

flowering plants
(angiosperms)
Enclosed ovary,
two integuments, rapid pollen tube growth
monocotyledons
One cotyledon, adaxial prophyll
commelinid monocots
Starchy endosperm,
Ferulic acid
Poales
Nuclear endosperm,
Silica in epidermis
graminoid Poales
Distichous leaves,
Plumose stigmas
grasses
(Poaceae)

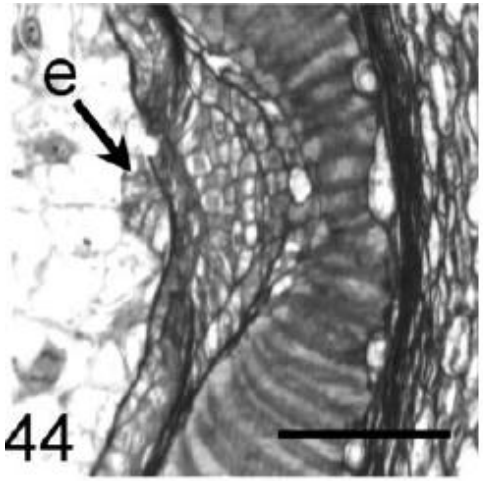
Poaceae
71,000,000 years ± 9,000,000

- Outer integument fused to ovary wall (fruit a caryopsis)
- Embryo highly differentiated
- Whole genome duplication
- Proliferation of antipodal cells
- Subsidiary cells triangular or dome shaped
- Bicellular microhairs

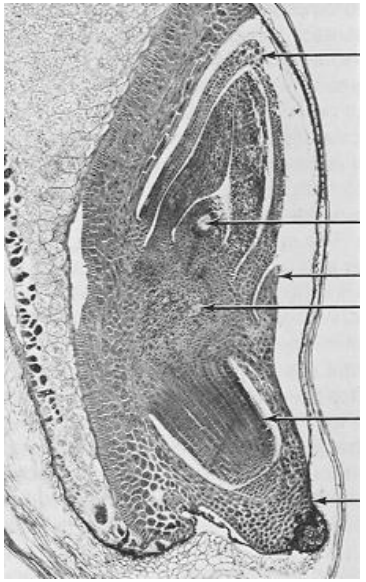
Embryos







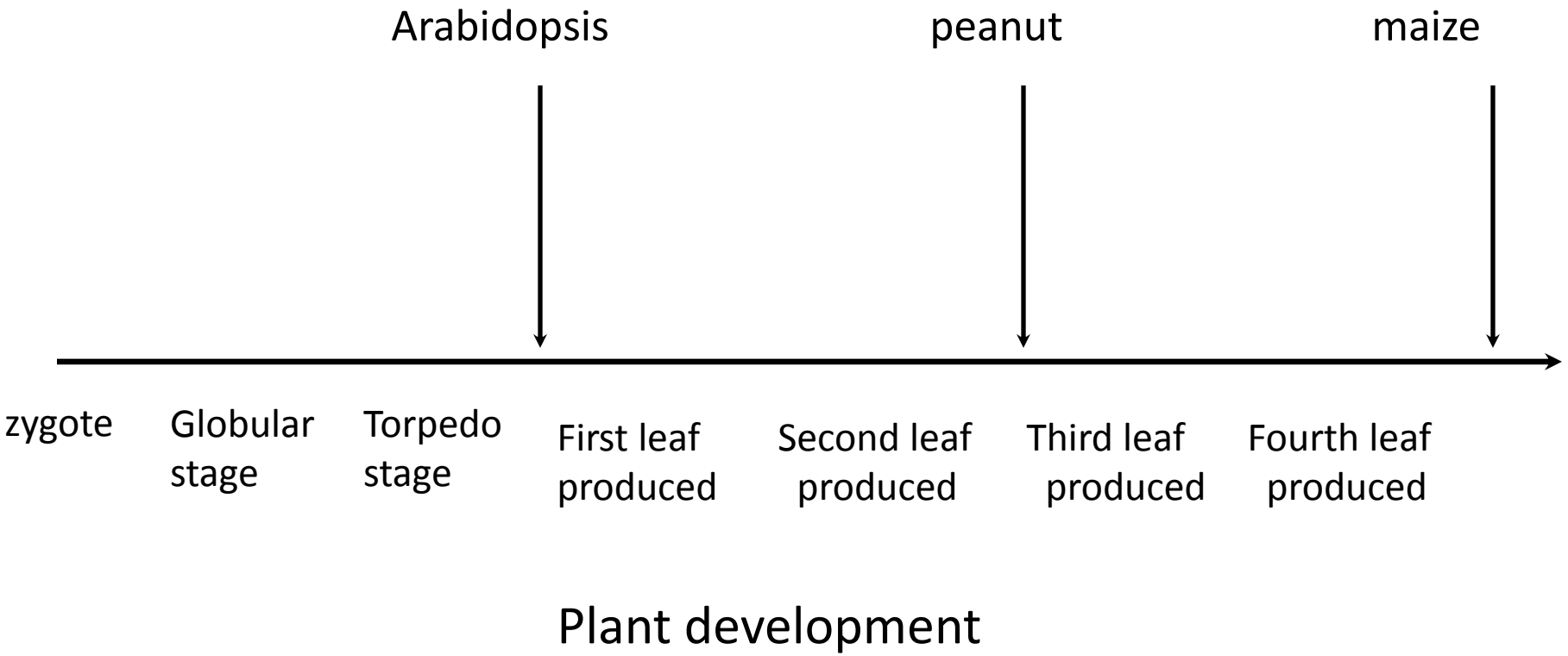
Ecdeiocolea



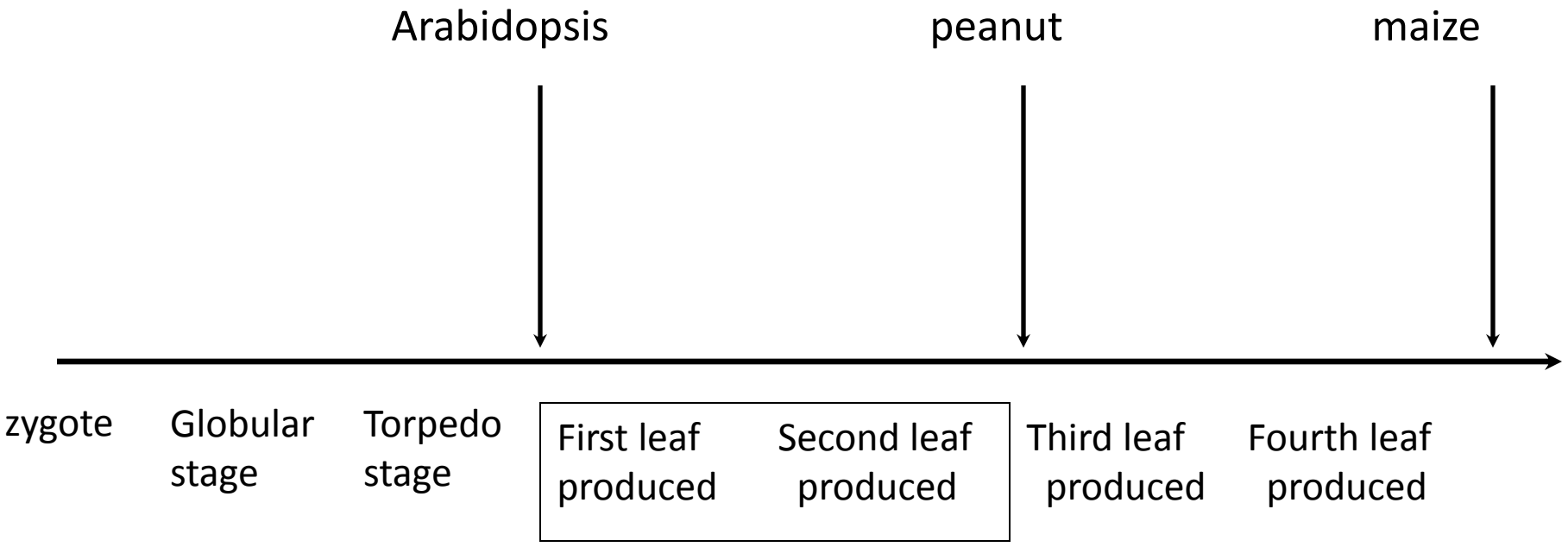
Grass embryo

www.botany.hawaii.edu/faculty/webb/

Seed maturation (dessication, accumulation of LEA proteins, burst of ABA, etc.)

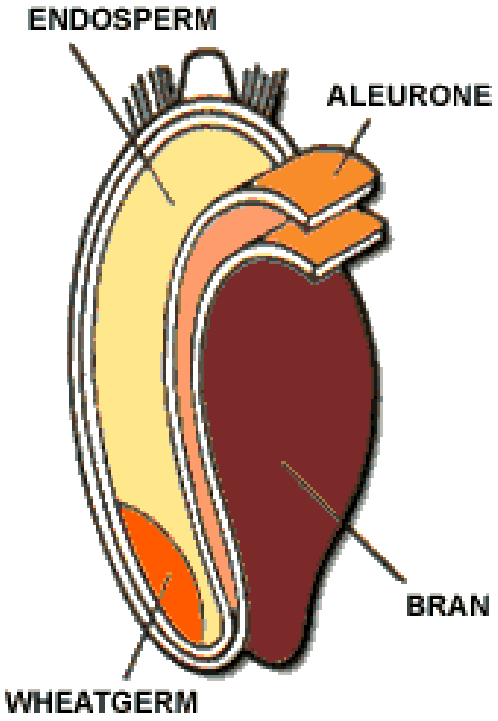


Seed maturation (dessication, accumulation of LEA proteins, burst of ABA, etc.)



Seedling leaves in Arabidopsis
Embryonic leaves in legumes, grasses

Grain/caryopsis/kernel



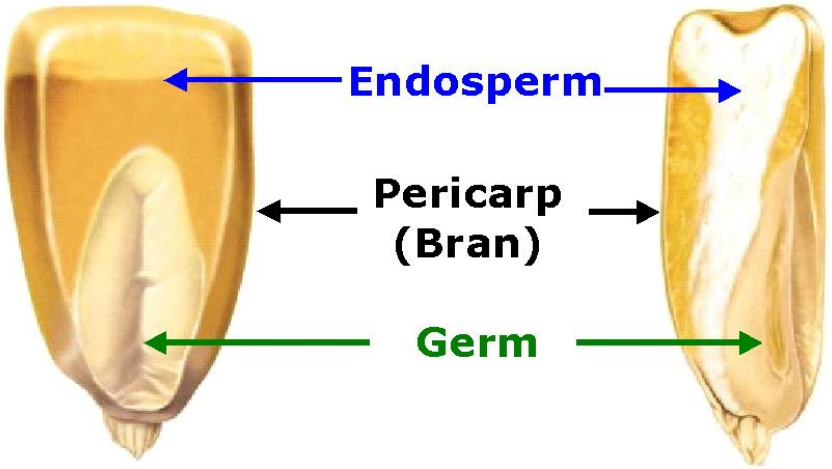
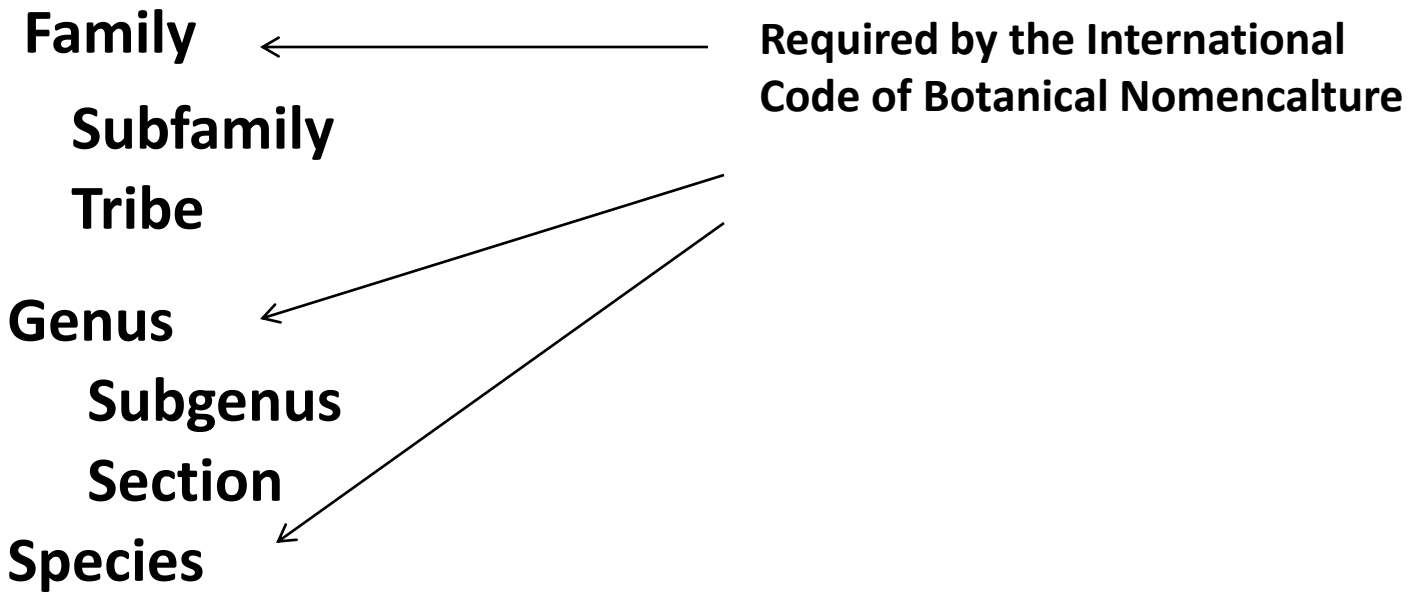


Diagram from
www.baking911.com/seed.gif

www.cerealprocess.com/html/fractionation.html

Taxonomic ranks



http://ibot.sav.sk/icbn/main.htm

Taxonomic ranks

Each rank above genus based on a generic name (8 exceptions)

Family - <genus name>aceae

Subfamily - <genus name>oideae

Tribe - <genus name>eae

Genus

Subgenus

Section

Species

Taxonomic ranks

Each rank above genus based on a generic name (8 exceptions)

Family - POAaceae

Subfamily - POoideae

Tribe - POeae

Genus - Poa

Subgenus - Pratenses

Section - none

Species - Poa pratensis

Taxonomic ranks

Each rank above genus based on a generic name (8 exceptions)

Family - POAaceae = Gramineae (1 of the exceptions)

Subfamily - POoideae

Tribe - POeae

Genus - Poa

Subgenus - Pratenses

Section - none

Species - Poa pratensis

Classification of maize

Family - Poaceae = Gramineae

Subfamily - Panicoideae

Tribe - Andropogoneae

Genus - *Zea*

Subgenus – [rank not used]

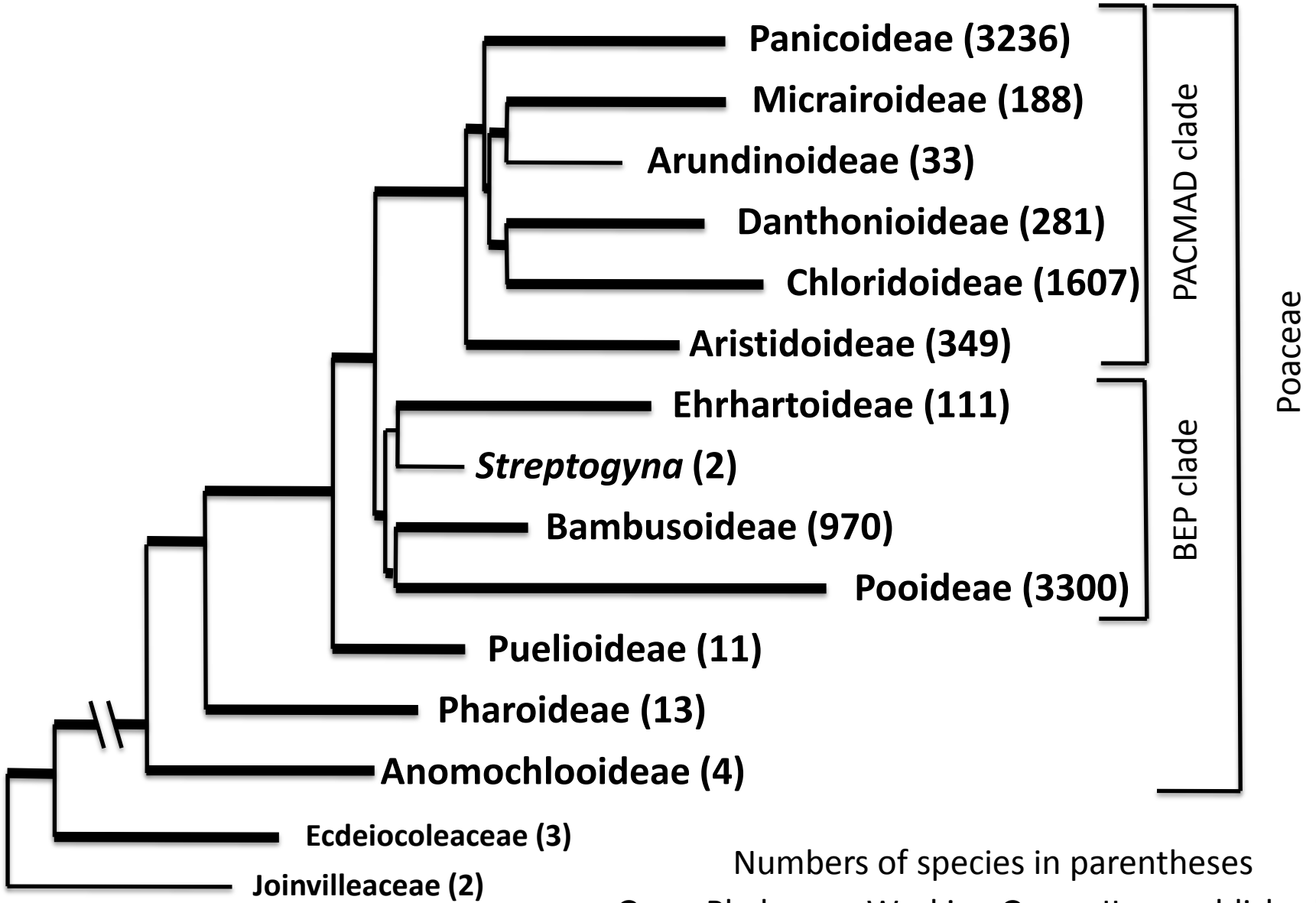
Section - *Zea*

Species – *Zea mays*

Subspecies – *Zea mays* subspecies *mays*

Overview of grass phylogeny

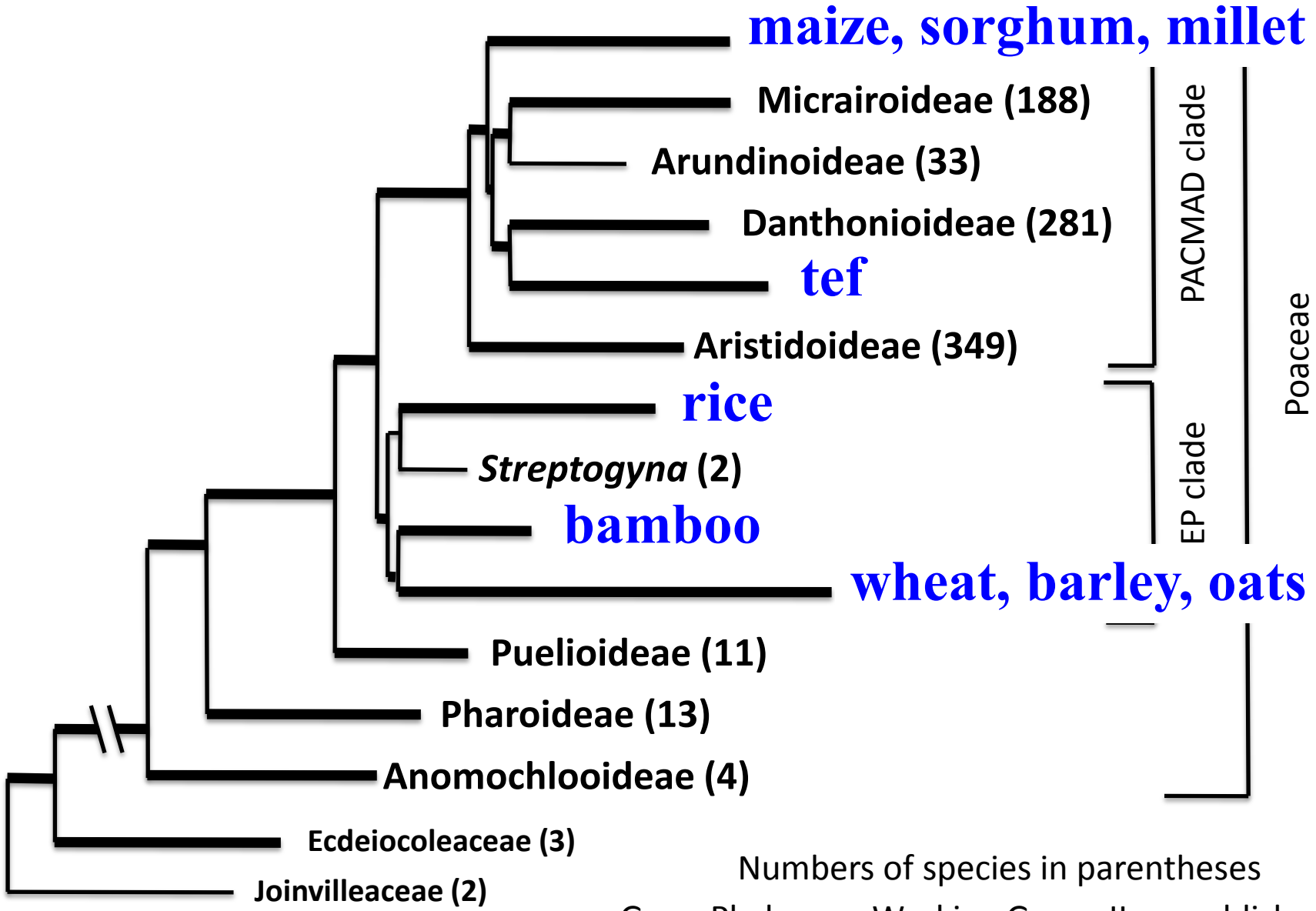
Phylogeny and classification of the grass family



Numbers of species in parentheses

Grass Phylogeny Working Group II, unpublished

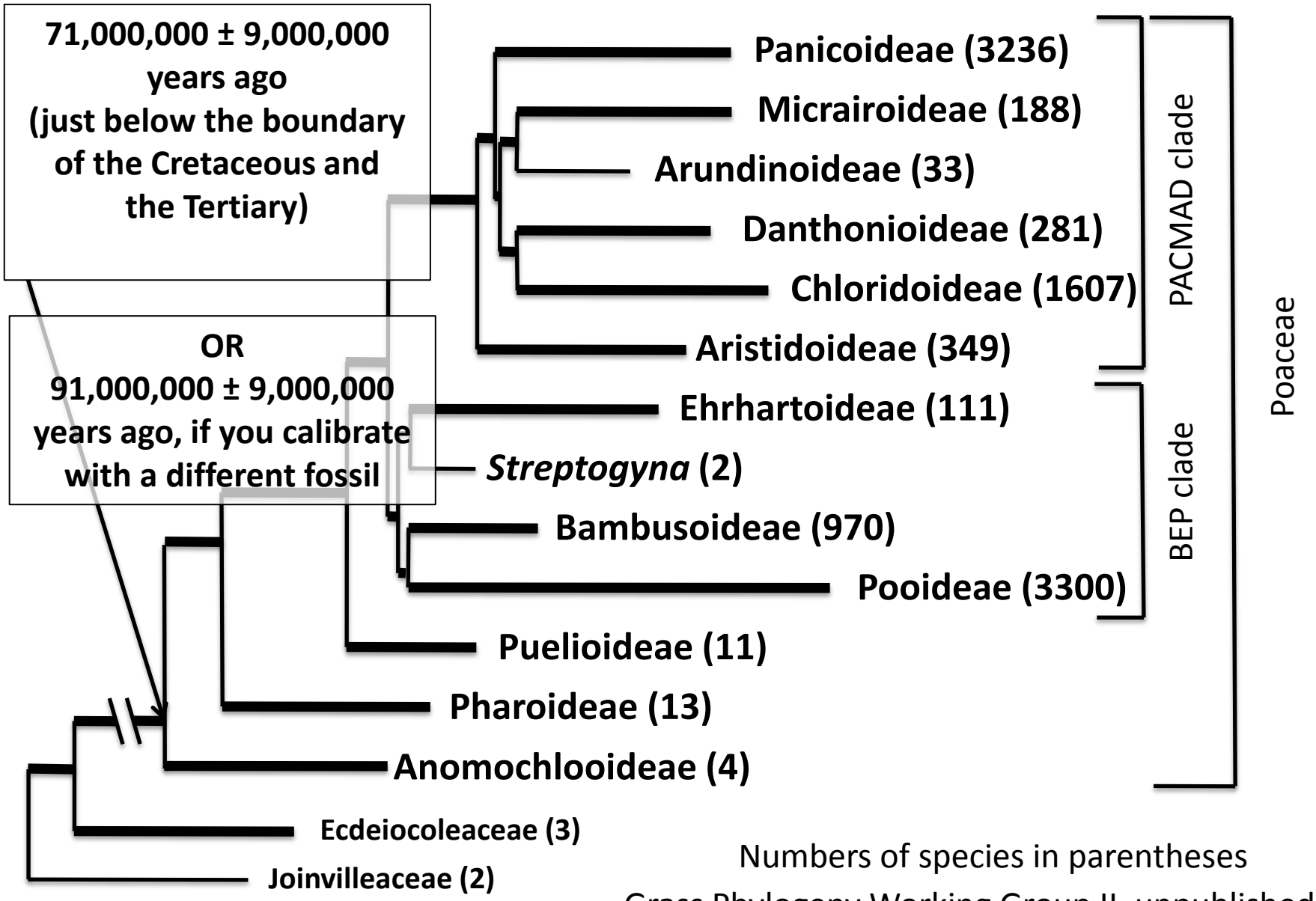
Phylogeny and classification of the grass family



Numbers of species in parentheses

Grass Phylogeny Working Group II, unpublished

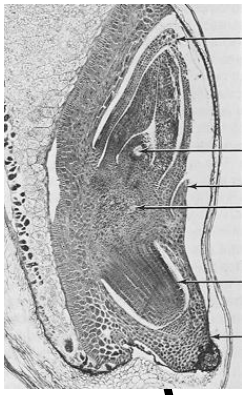
Dating the origin of the grass family



Numbers of species in parentheses

Grass Phylogeny Working Group II, unpublished

Phylogeny and classification of the grass family



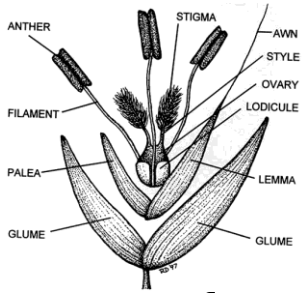
Unique embryo, caryopsis

Panicoideae (3236)
Micrairoideae (188)
Arundinoideae (33)
Danthonioideae (281)
Chloridoideae (1607)
Aristidoideae (349)
Ehrhartoideae (111)
Streptogyna (2)
Bambusoideae (970)
Pooideae (3300)
Puelioideae (11)
Pharoideae (13)
Anomochlooideae (4)
Ecdeiocoleaceae (3)
Joinvilleaceae (2)

PACMAD clade
BEP clade
Poaceae

Numbers of species in parentheses
Grass Phylogeny Working Group II, unpublished

Phylogeny and classification of the grass family



Spikelet

Unique embryo, caryopsis

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Anomochlooideae (4)
Ecdeiocoleaceae (3)
Joinvilleaceae (2)

PACMAD clade
BEP clade
Poaceae

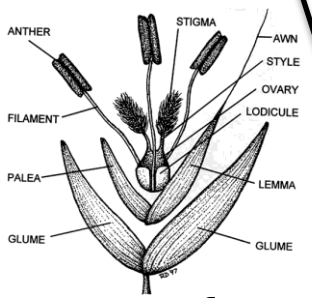
Numbers of species in parentheses
Grass Phylogeny Working Group II, unpublished

The spikelet clade

- All but four species of grasses have their flowers arranged in spikelets. (Spikelet = little spike.)
- The oldest fossil spikelet is dated to about 55,000,000 years ago.
- Most spikelets have two glumes, although one or both are lost in some species.
- All spikelets have at least one flower (floret).
- There is enormous variation in the morphology of the glumes and the number of florets.

Phylogeny and classification of the grass family

Spikelets with multiple florets



Spikelet

Unique embryo, caryopsis

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Puelioideae (11)
Pharoideae (13)
Anomochlooideae (4)
Ecdeiocoleaceae (3)
Joinvilleaceae (2)

PACMAD clade
BEP clade
Poaceae

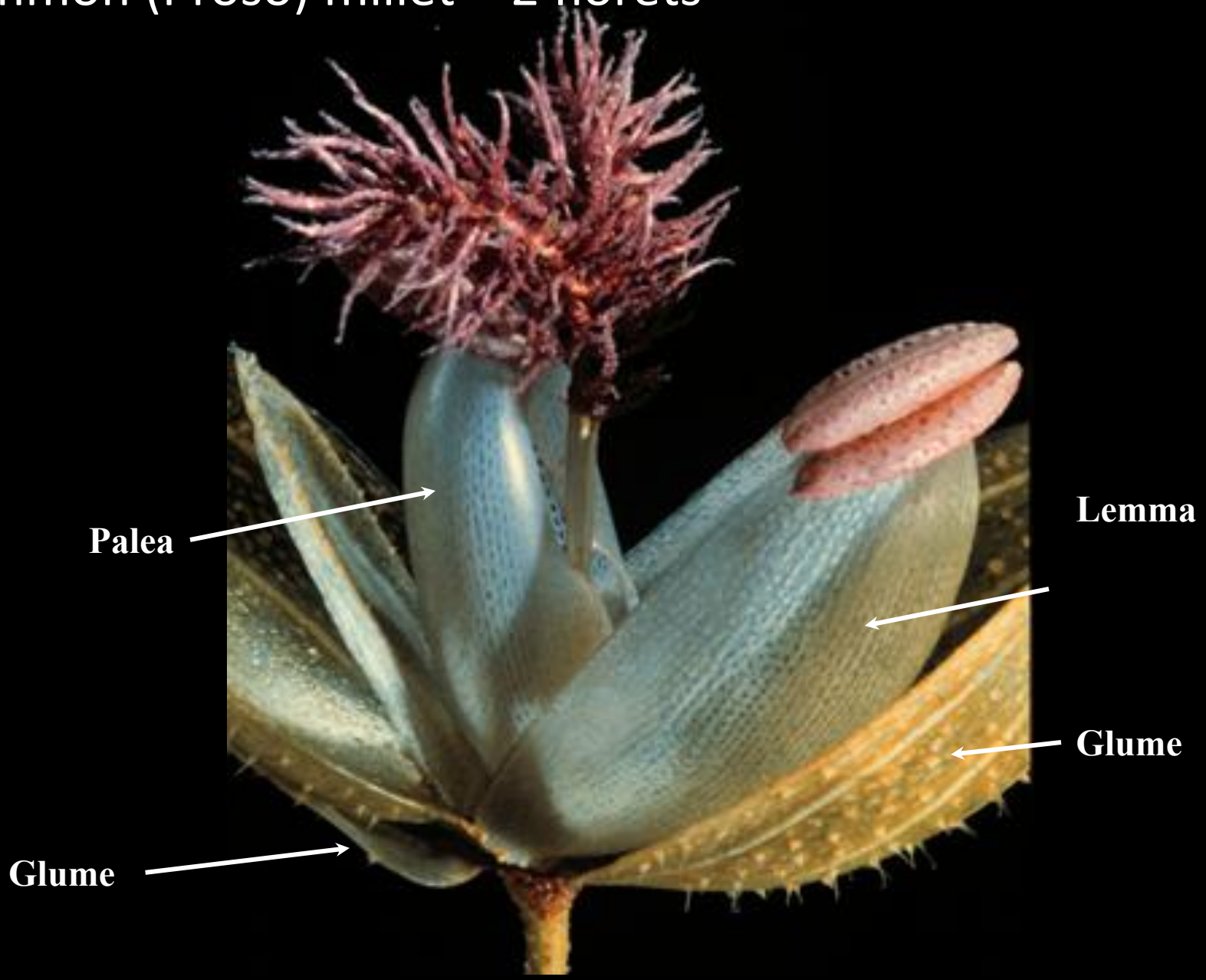
Numbers of species in parentheses
Grass Phylogeny Working Group II, unpublished

Wheat spikelet – 5 florets

http://www.ksre.ksu.edu/aawf/May/may_4.htm

Inland sea oats – 13+ florets

Common (Proso) millet – 2 florets

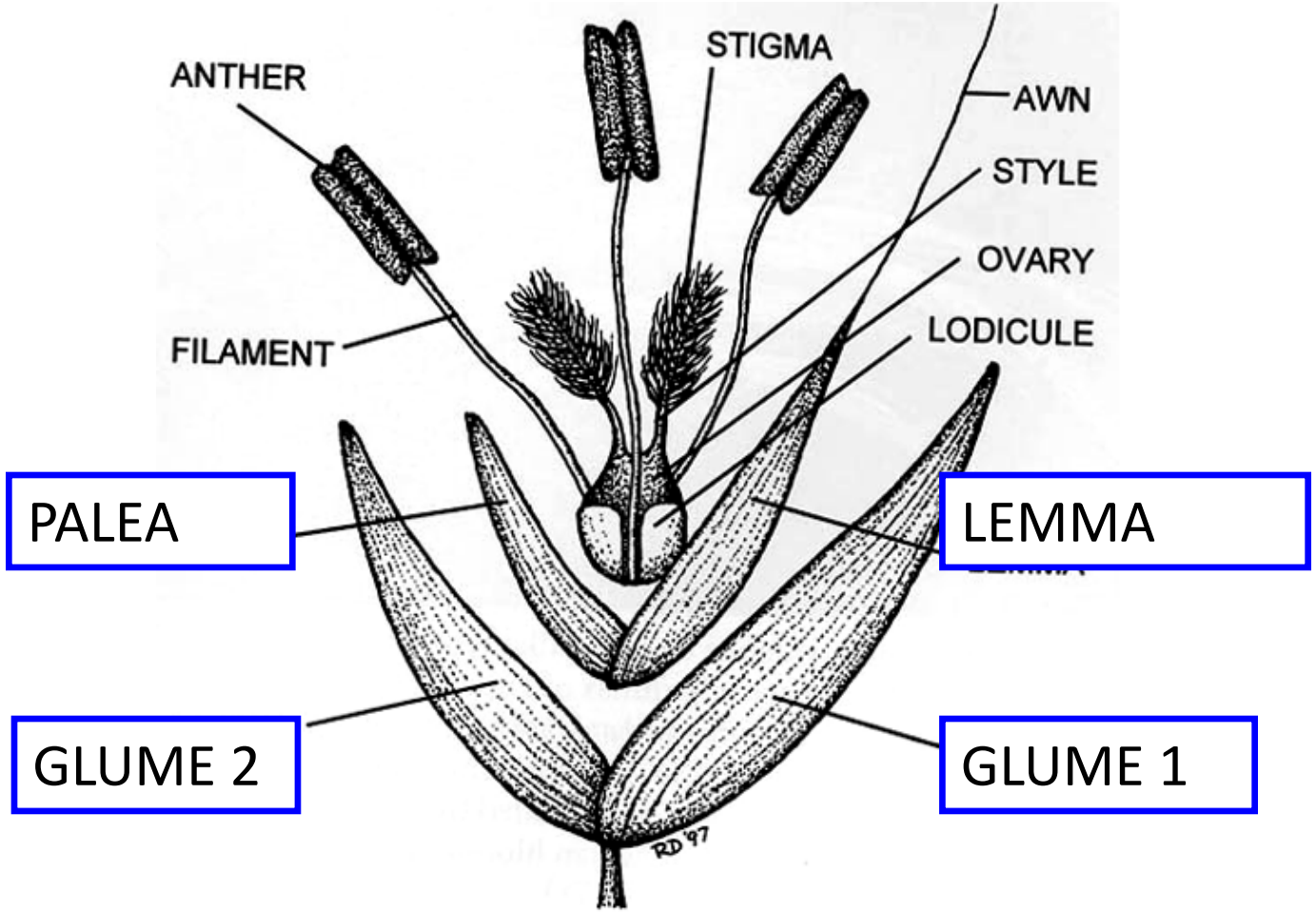


rice

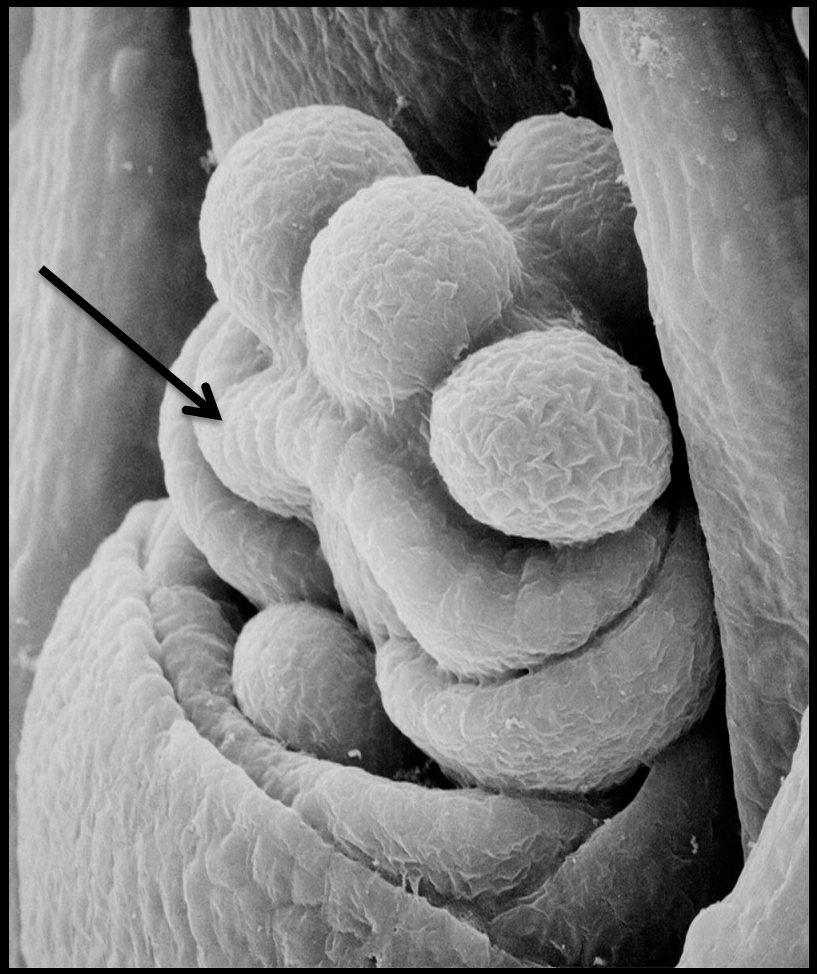
maize

sorghum

A closer look at the floret



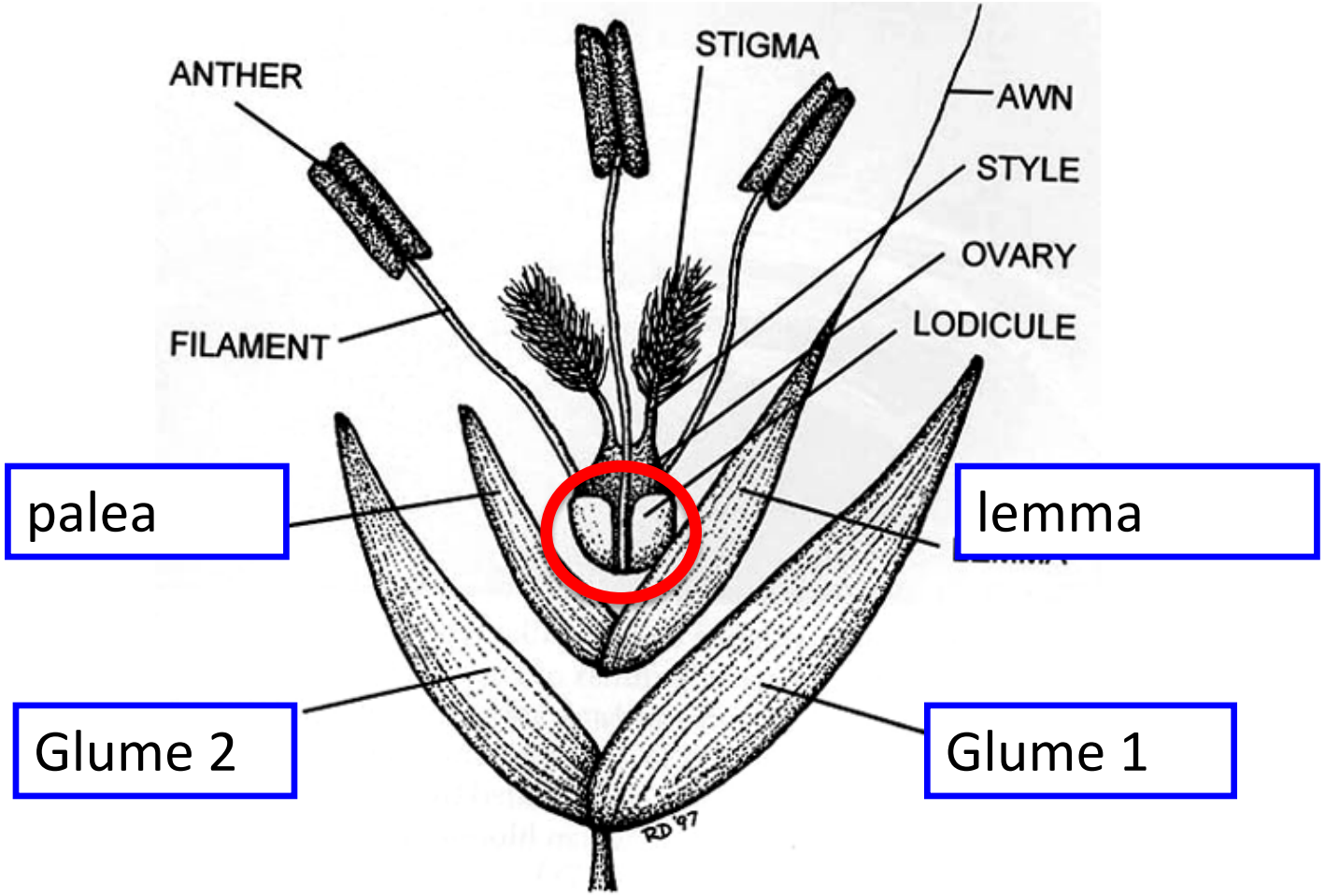
Palea

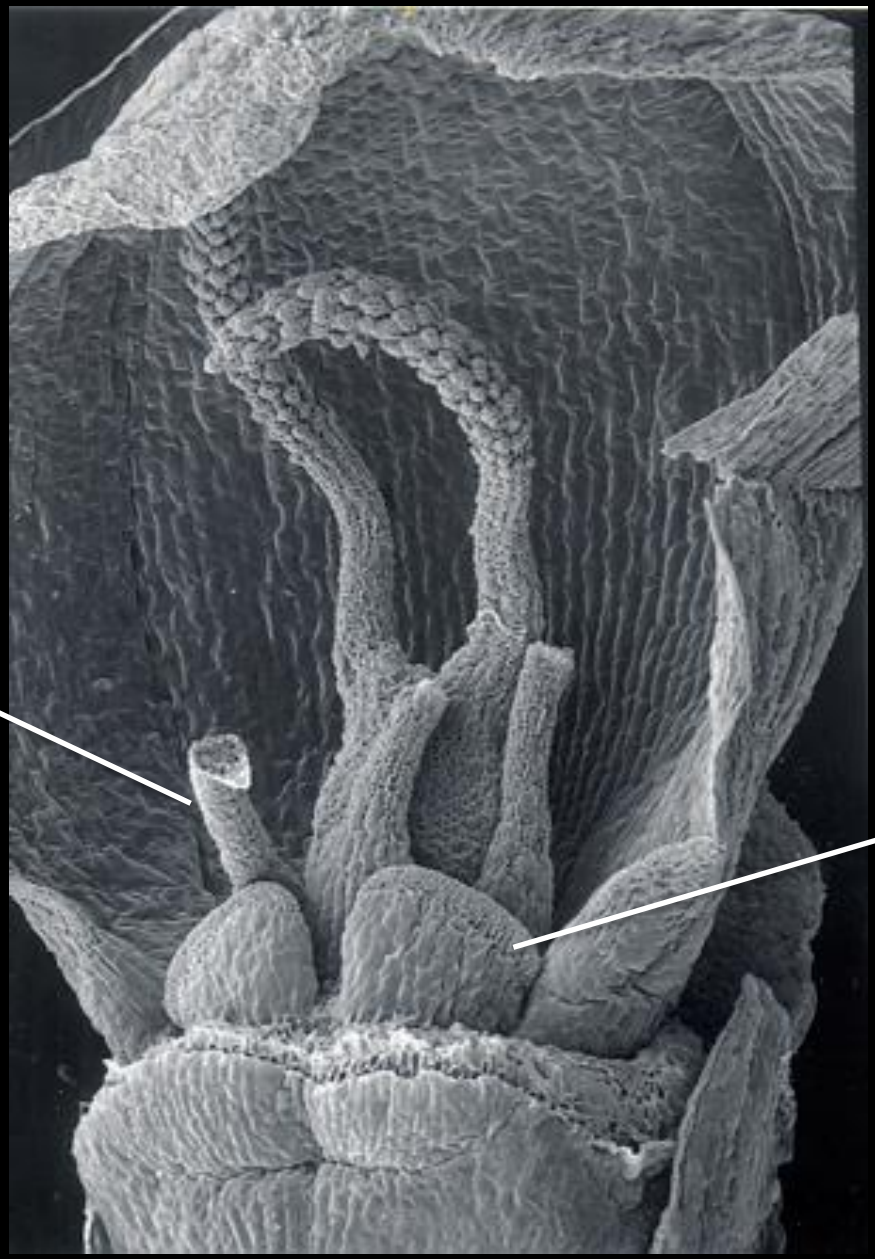


Doust photo

Kellogg photo

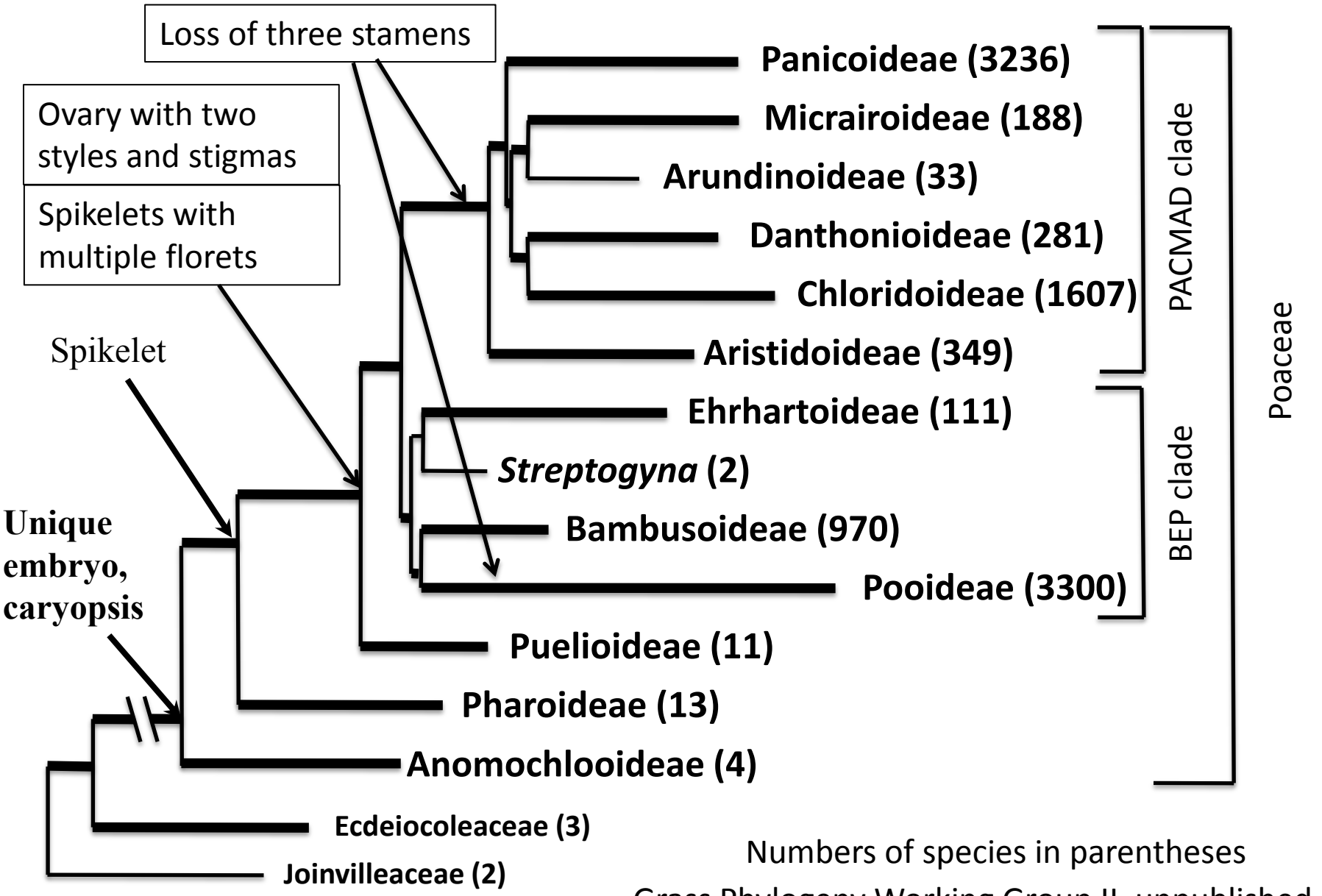
Lodicules – highly modified petals





LeRoux photo

Phylogeny and classification of the grass family

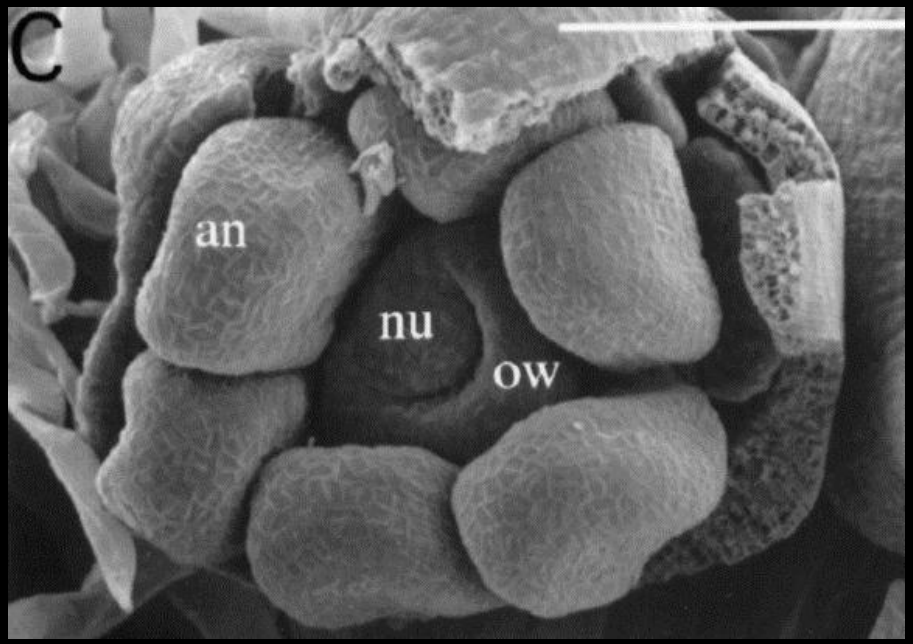


Numbers of species in parentheses

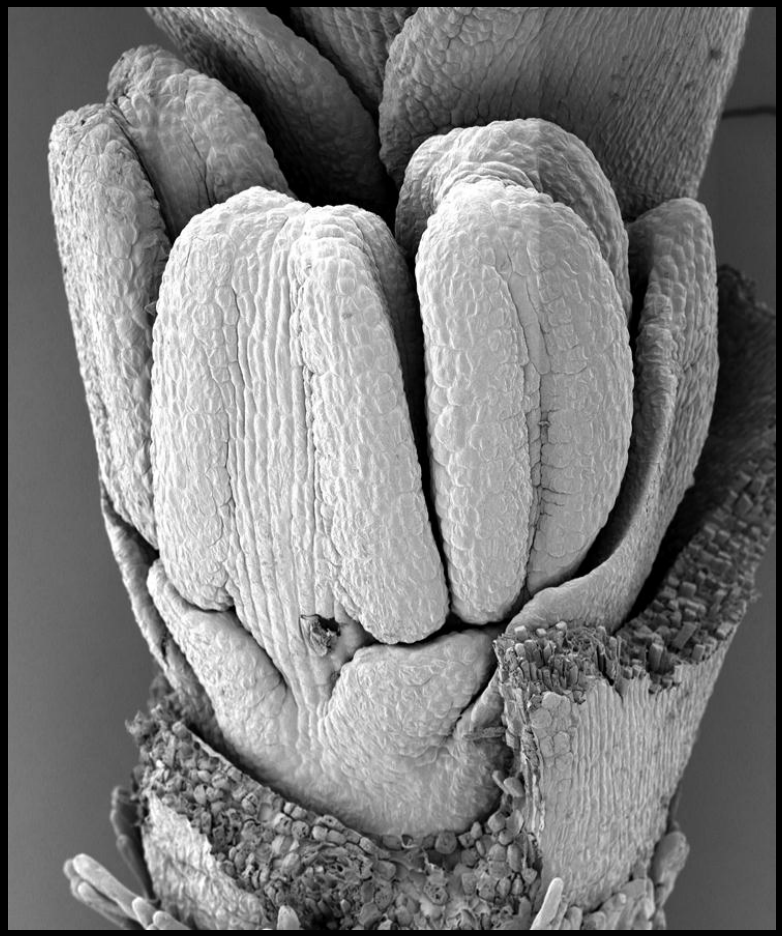
Grass Phylogeny Working Group II, unpublished

Ancestral carpel number = 3

Ancestral stamen number = 6

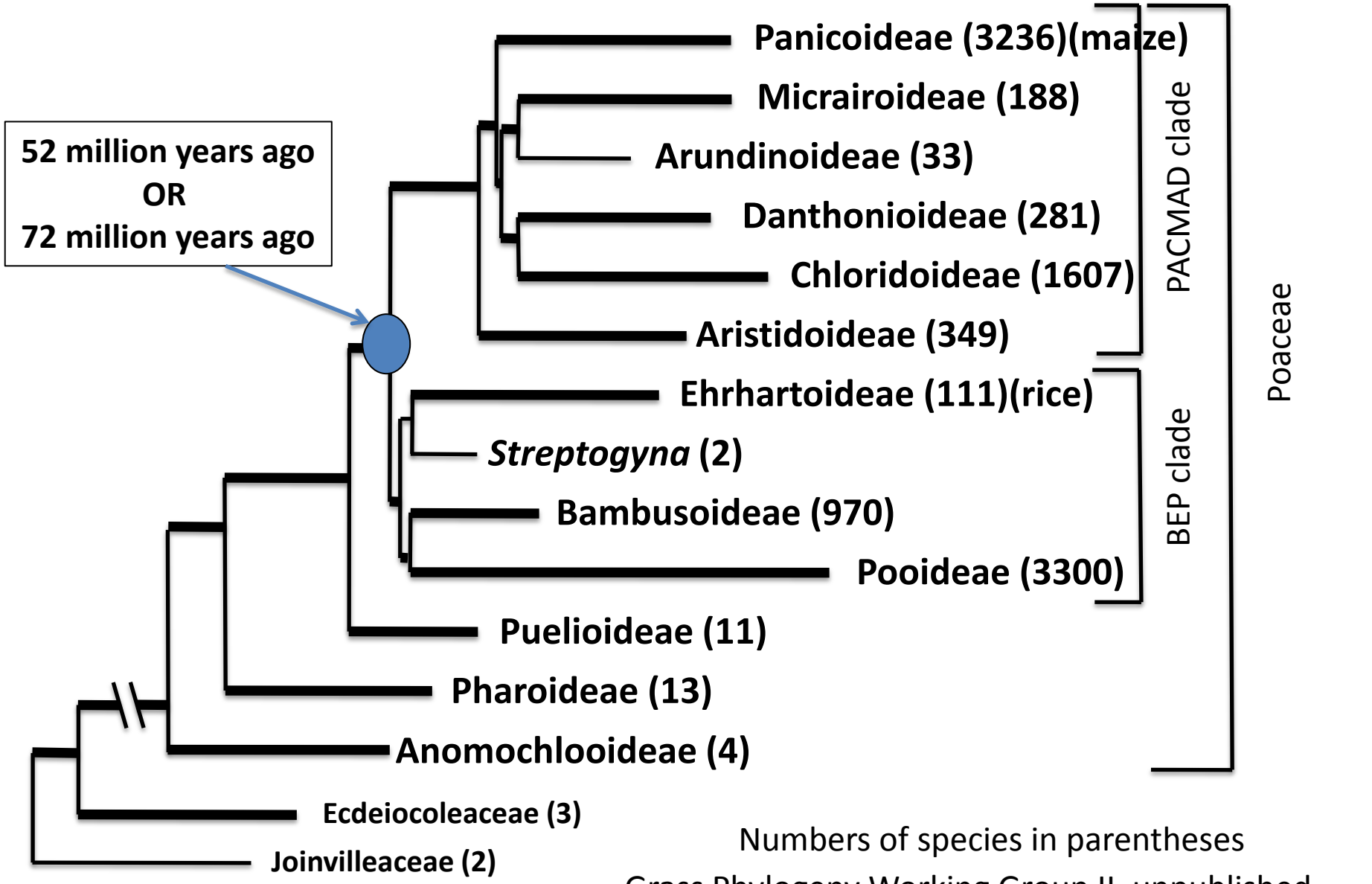


Zaitchik, Le Roux and Kellogg, 1998



Kellogg photo

Most species in the family are descended from the common ancestor of maize and rice.



Numbers of species in parentheses

Grass Phylogeny Working Group II, unpublished

PACMAD

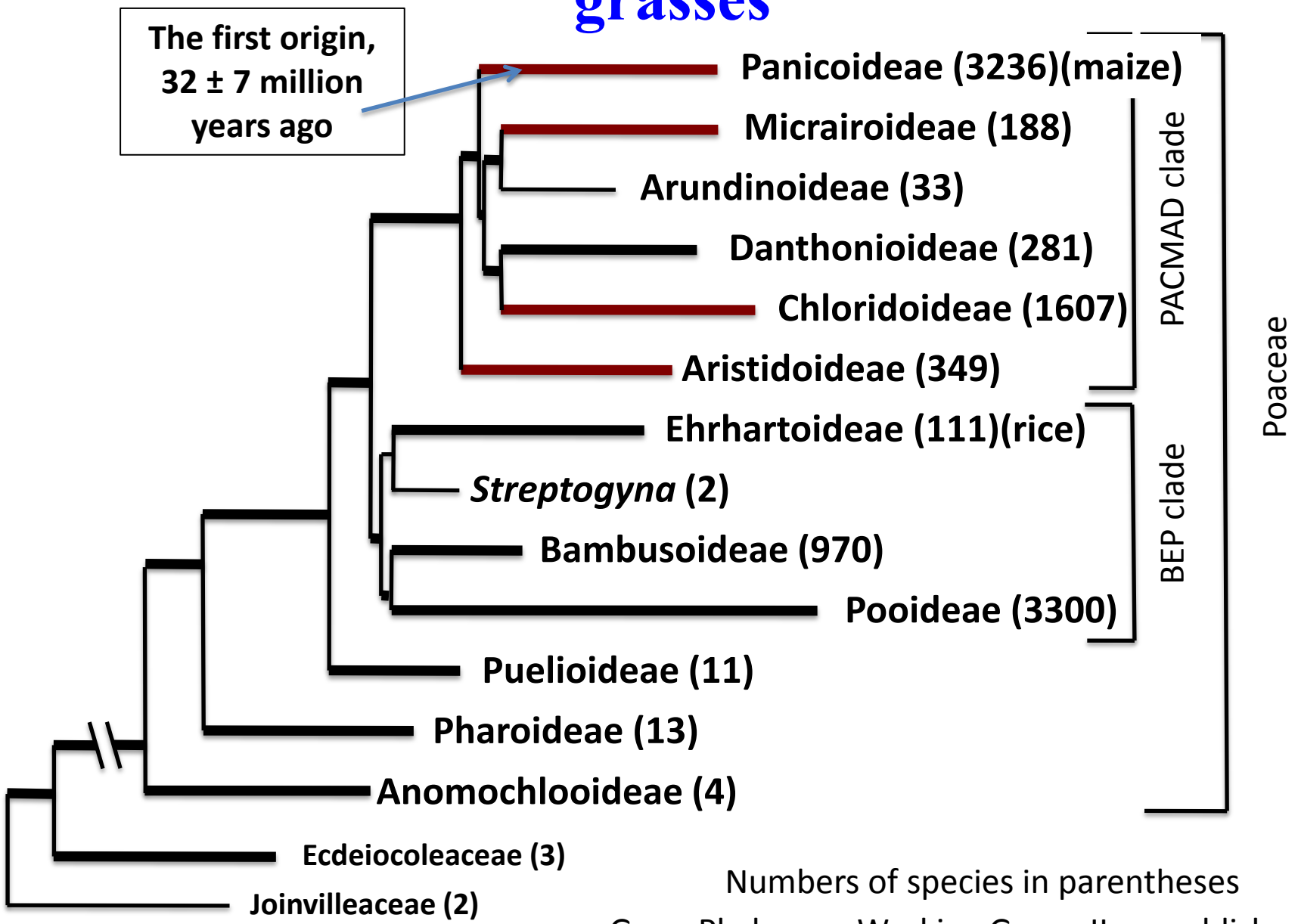
- **Panicoideae** – maize is here, along with sorghum and most kinds of millet
- Arundinoideae
- Chloridoideae
- Micrairoideae
- Aristidoideae
- Danthonioideae

PACMAD

includes all origins of C_4 photosynthesis

- Panicoideae – multiple C_4 origins
- Arundinoideae
- Chloridoideae – one or two C_4 origins
- Micrairoideae – one C_4 origins
- Aristidoideae - two C_4 origins
- Danthonioideae

C_4 photosynthesis originated at least 17 times in the grasses



Numbers of species in parentheses

Grass Phylogeny Working Group II, unpublished

C_4 anatomy

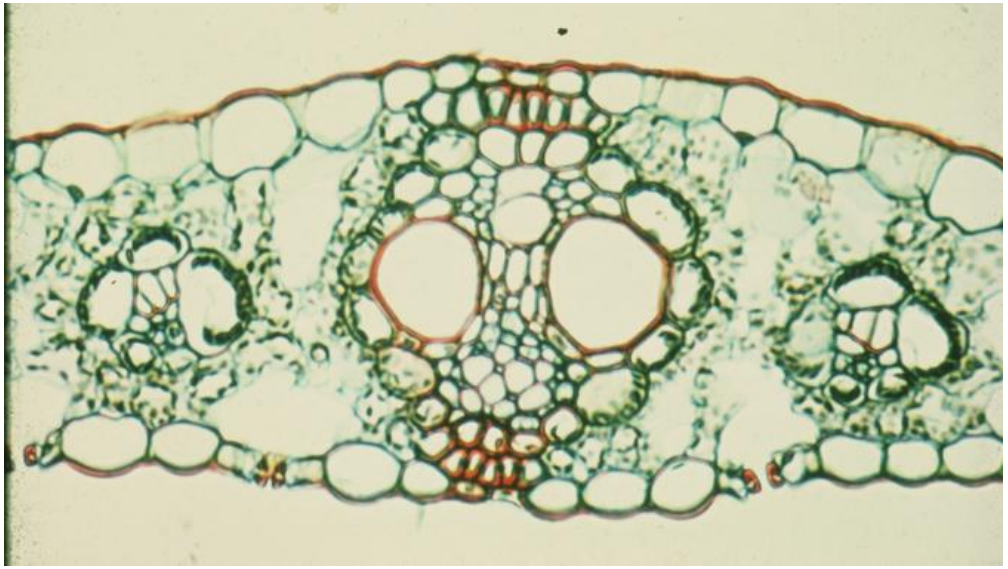
To make C_4 work, every mesophyll cell must be close to a bundle sheath cell.

The veins in C_4 plants are closer together than in C_3 plants.

C_3
Many mesophyll
Cells between veins

Maize

C_4
Two mesophyll
cells between veins



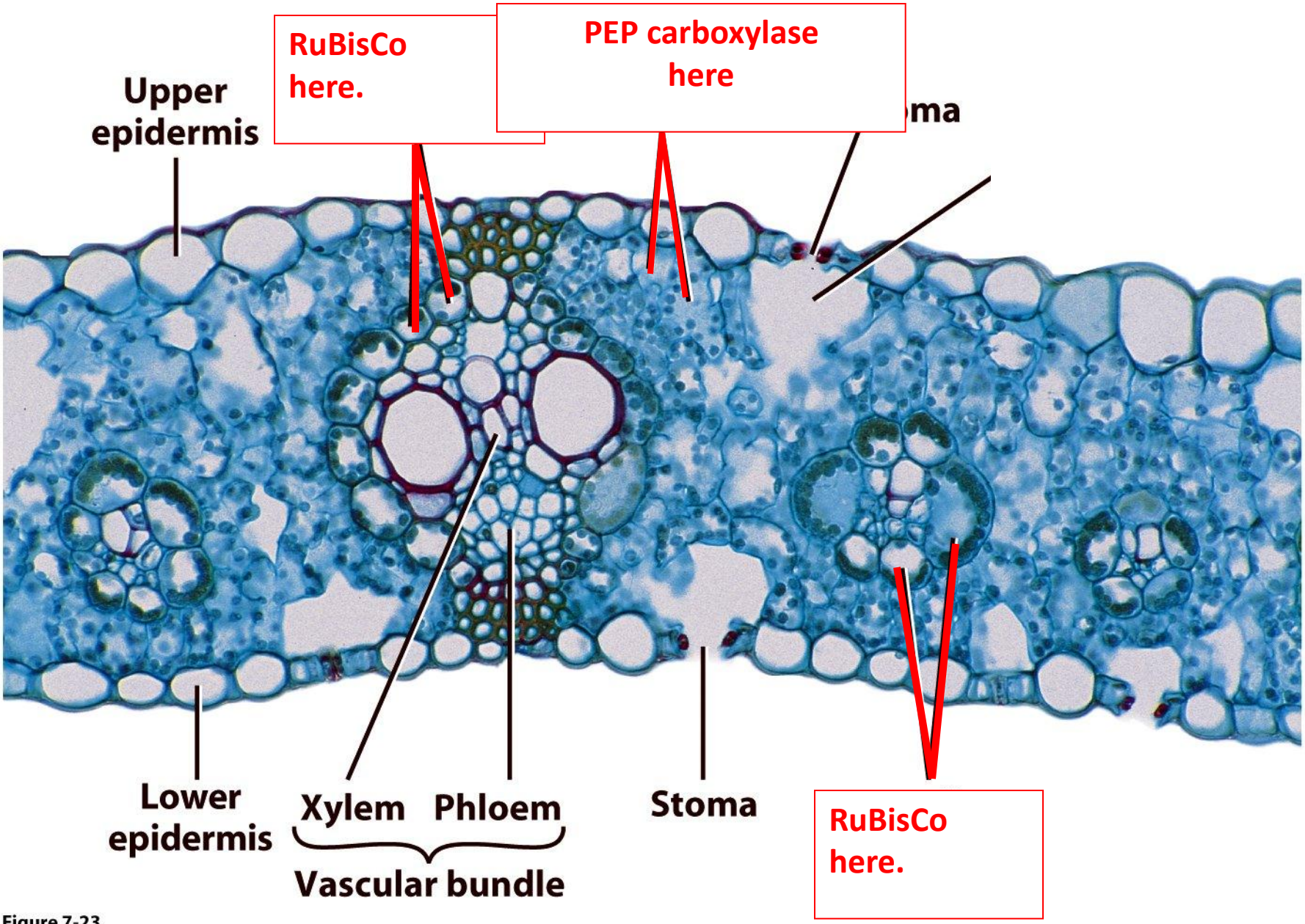
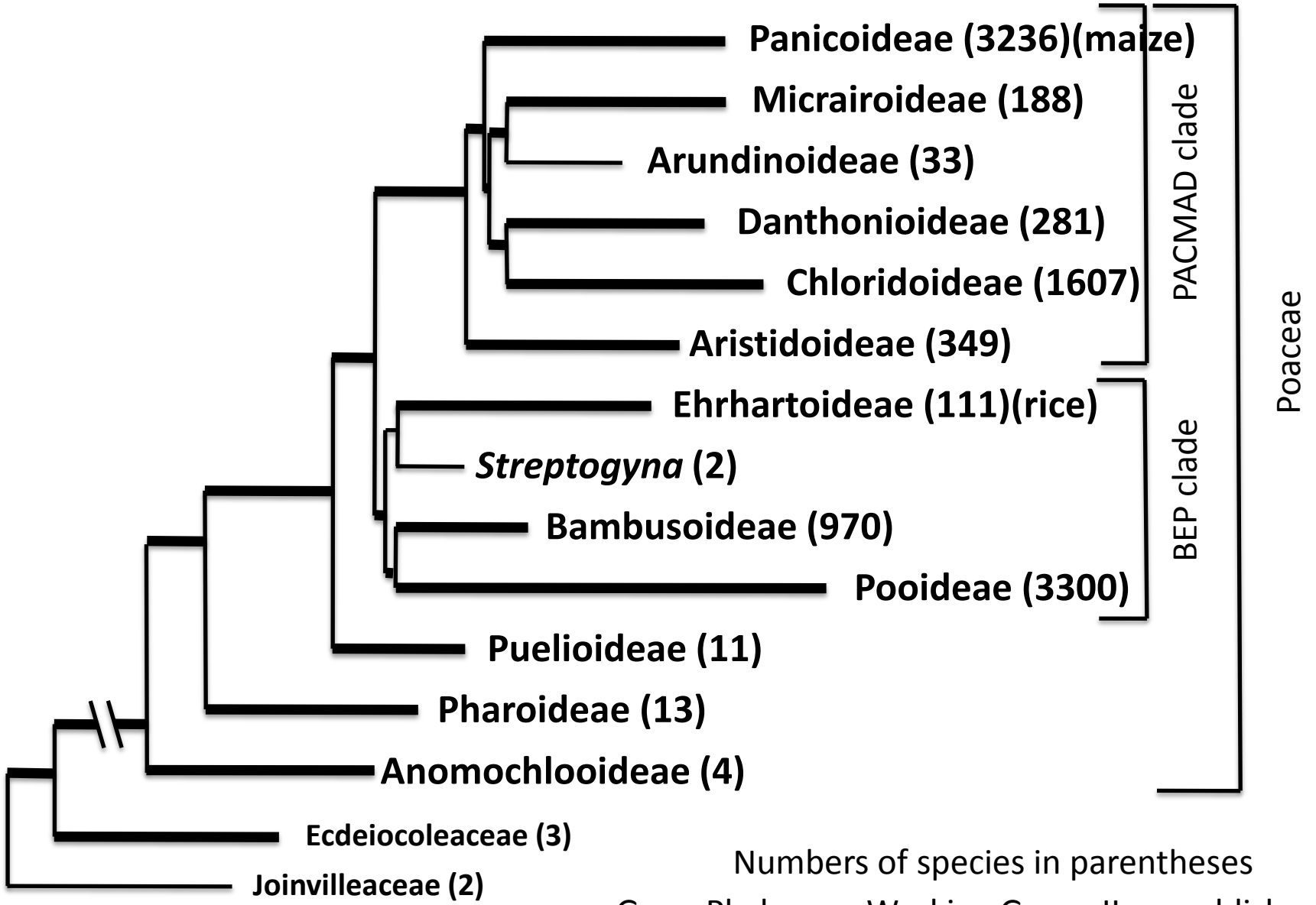


Figure 7-23
Biology of Plants, Seventh Edition

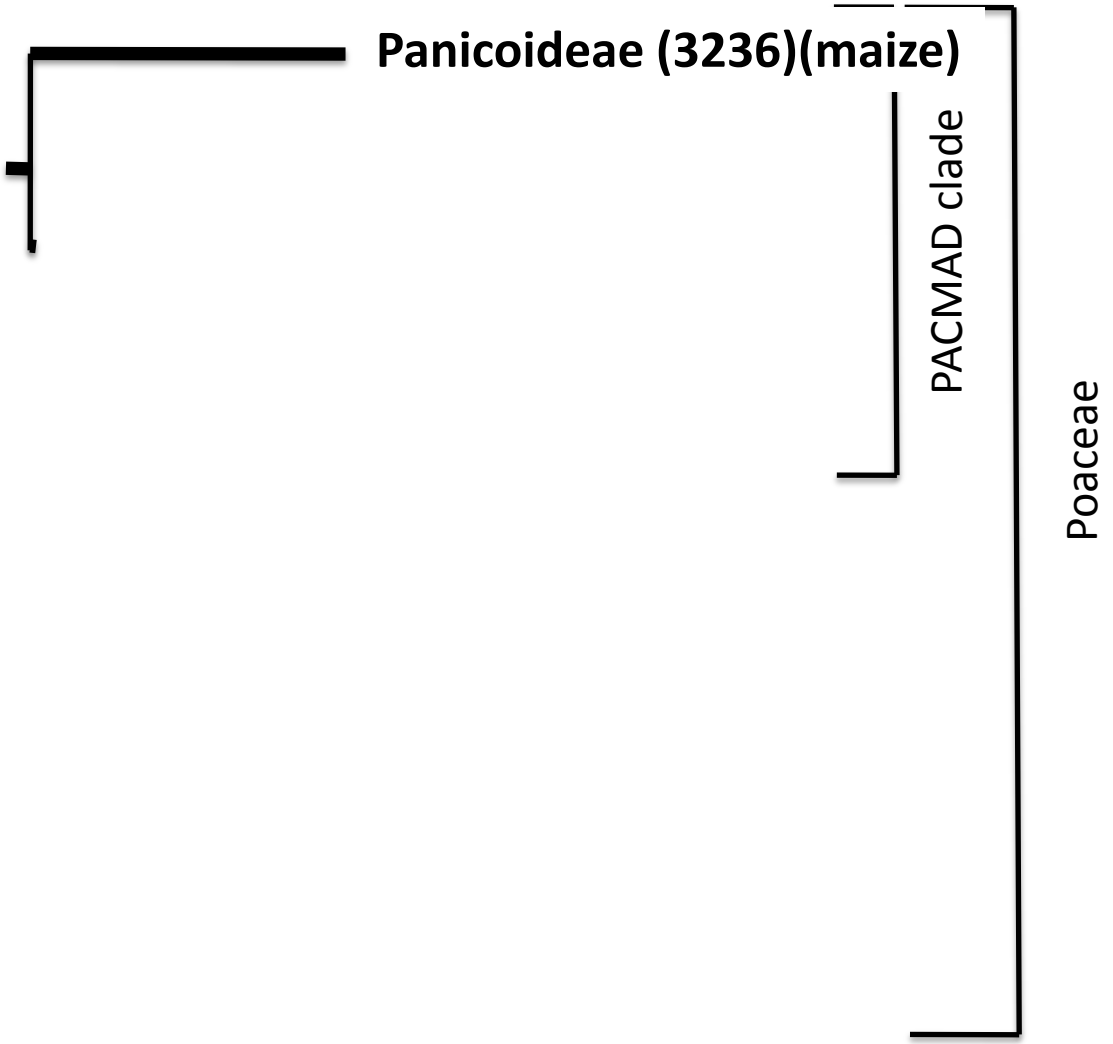
Grass phylogeny



Numbers of species in parentheses

Grass Phylogeny Working Group II, unpublished

Grass phylogeny

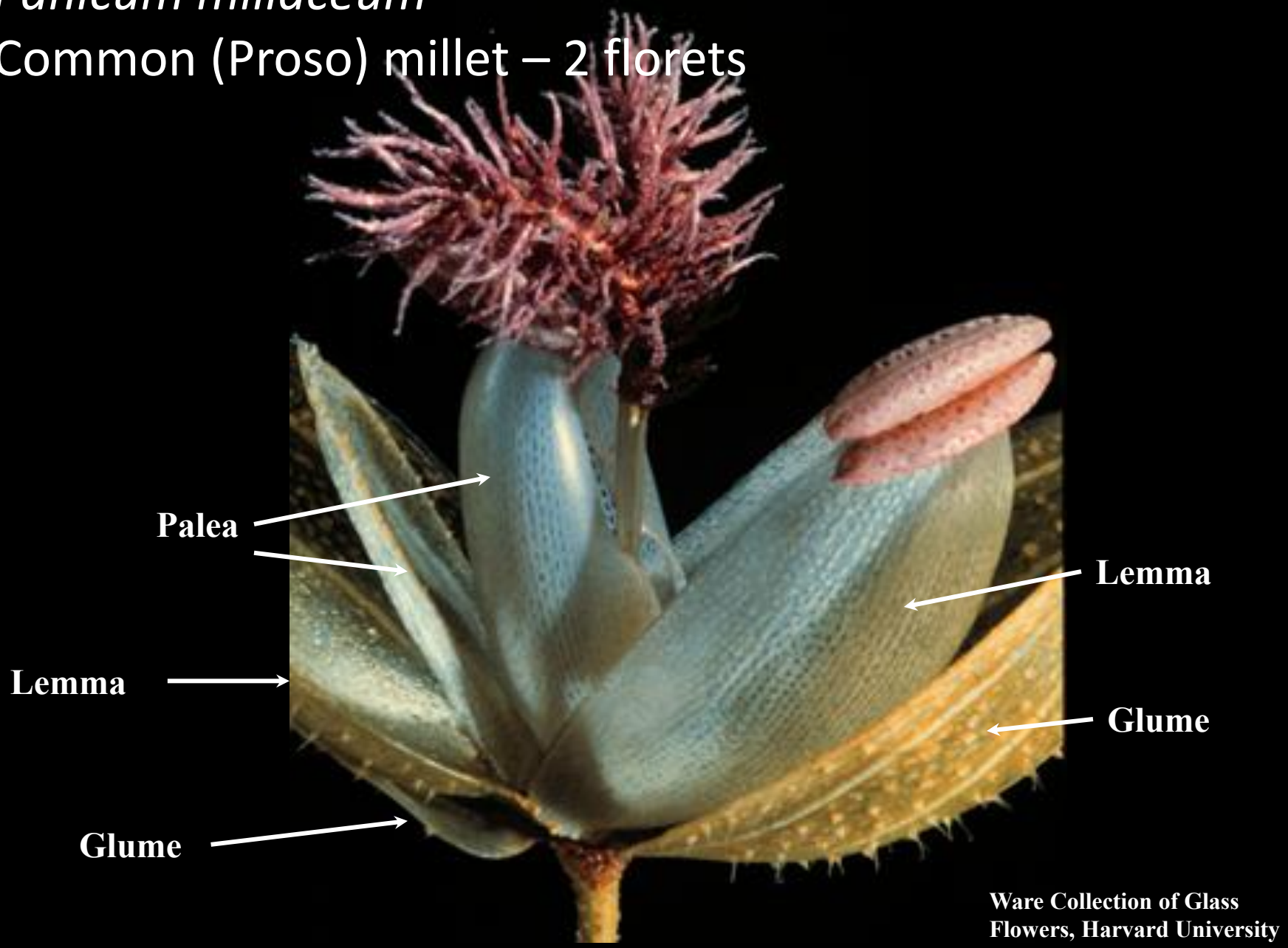


Panicoideae

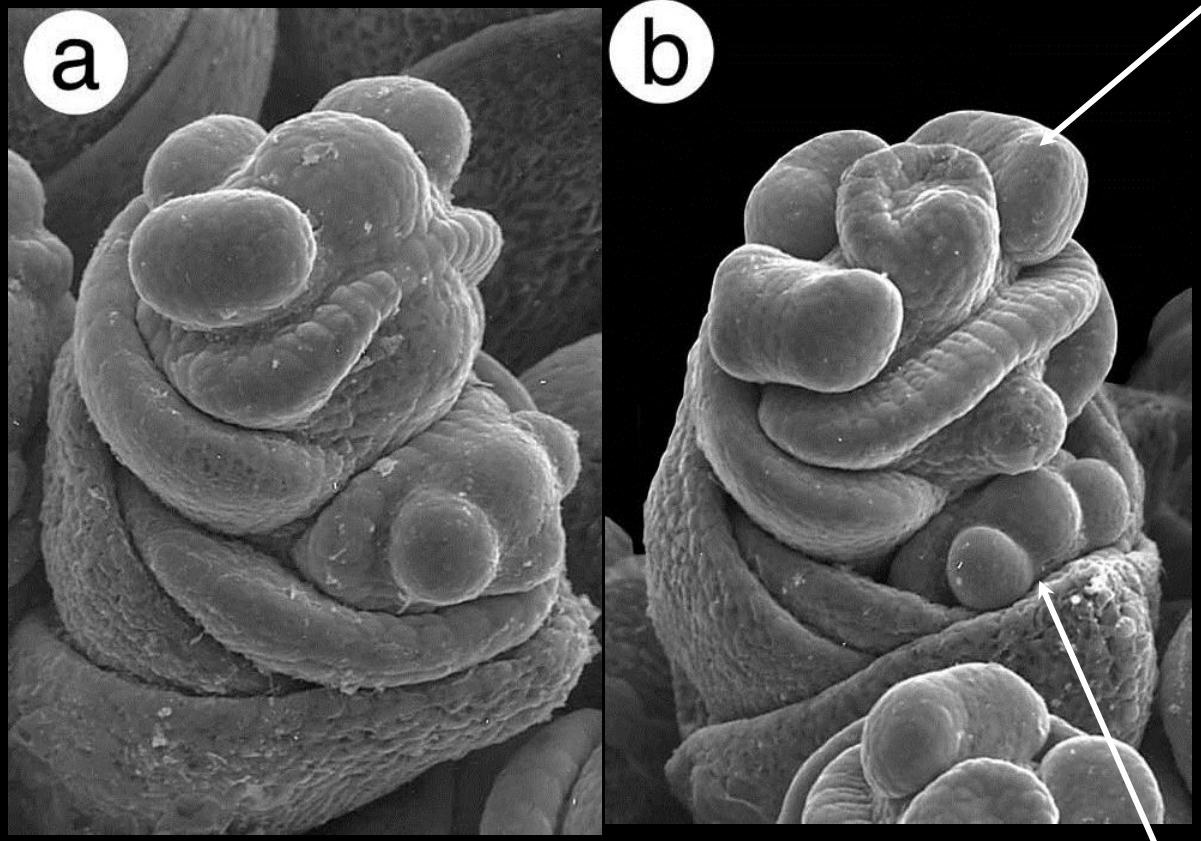
- Ca. 1/3 of grass species (ca. 3300)
- C_3 and C_4
- Two-flowered spikelets, development basipetal
- 34,000,000 ± 6,000,000 years (or 56 million)

Panicum miliaceum

Common (Proso) millet – 2 florets



Ware Collection of Glass Flowers, Harvard University



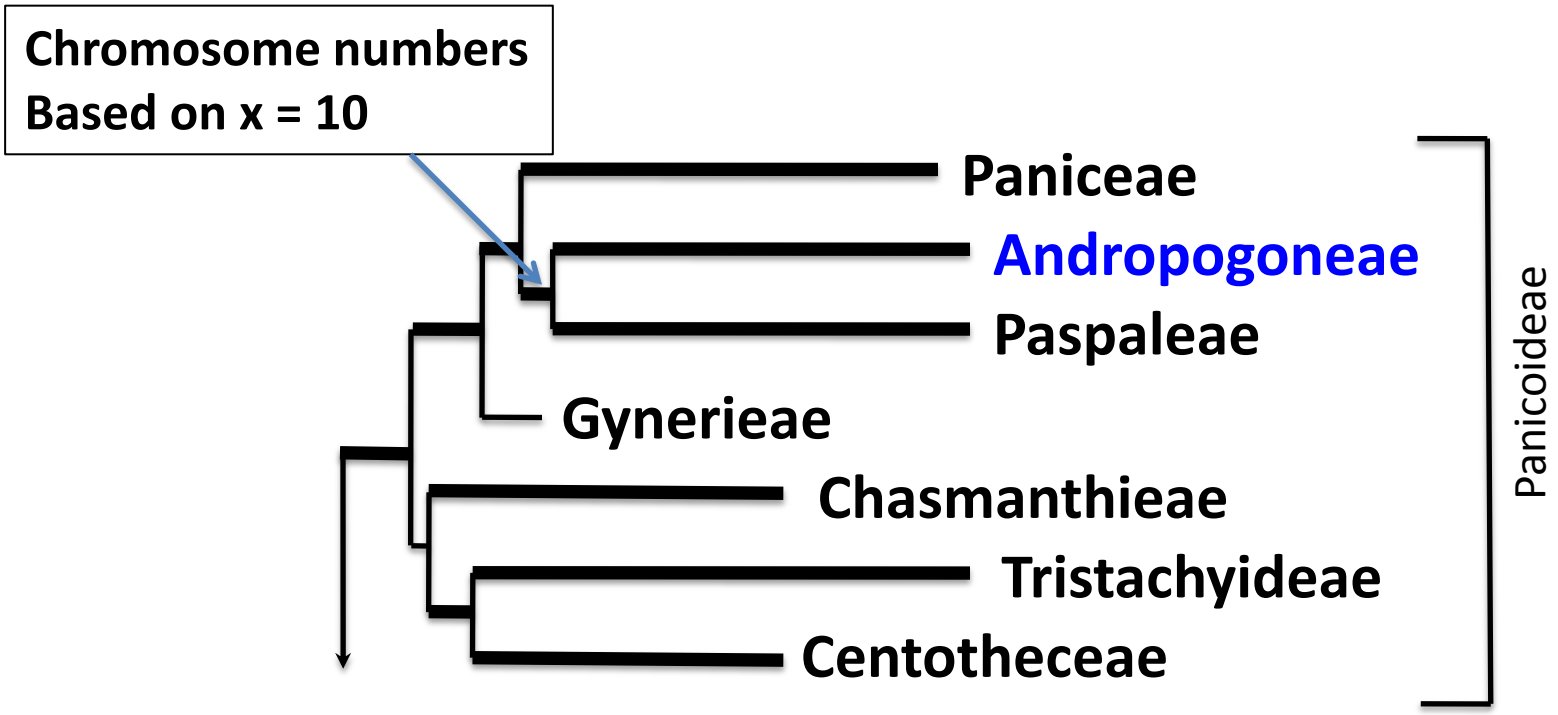
Top flower

developing ahead of the

Bottom flower

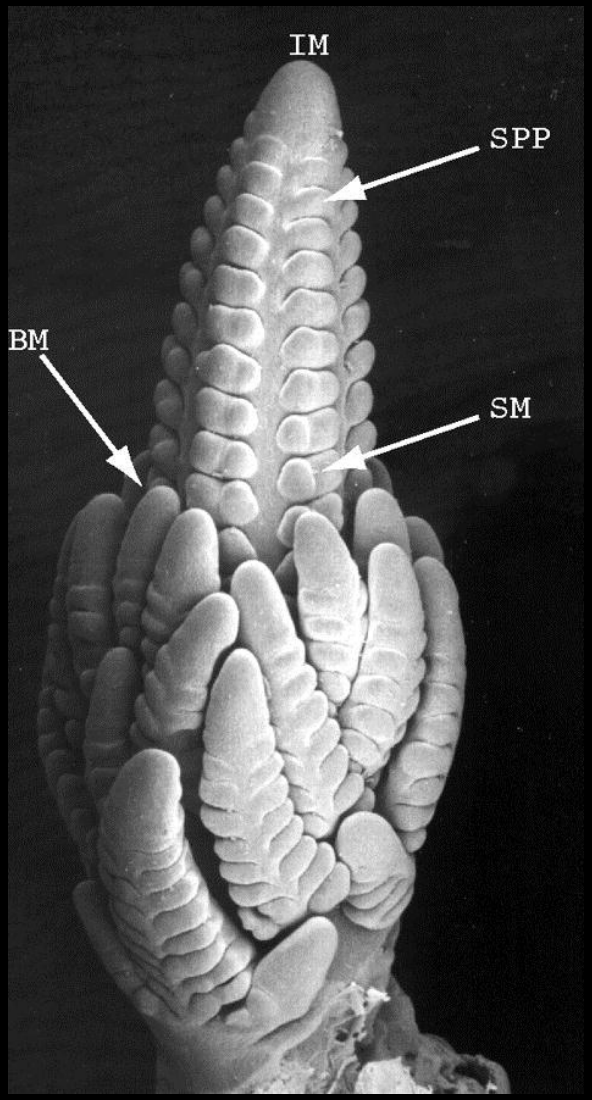
Bess, Doust, and Kellogg, 2005

Relationships within subfamily Panicoideae



Andropogoneae

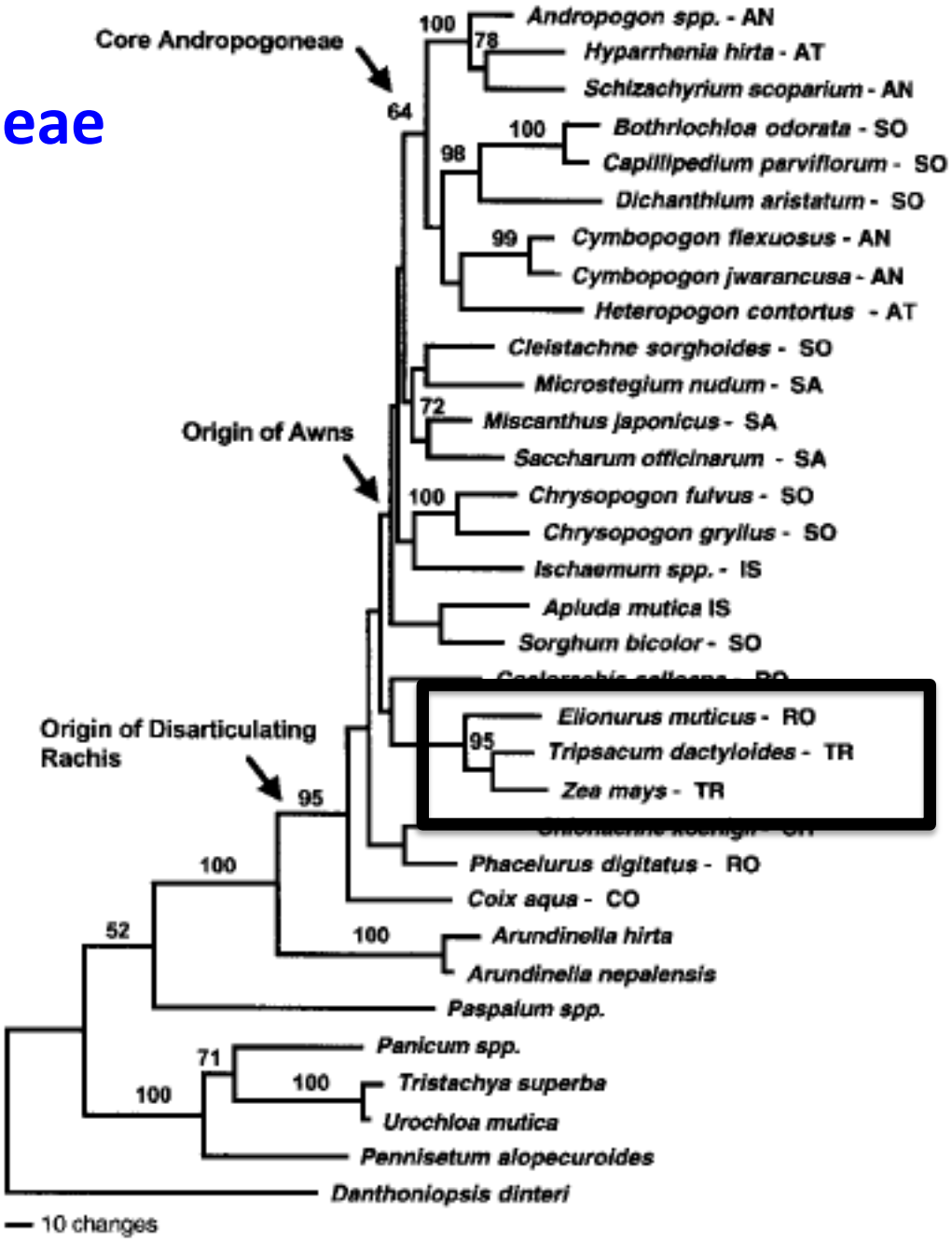
- Maize, sugar cane, sorghum
- Spikelet pairs
- 19,000,000 ± 4,000,000 (or 31 million)

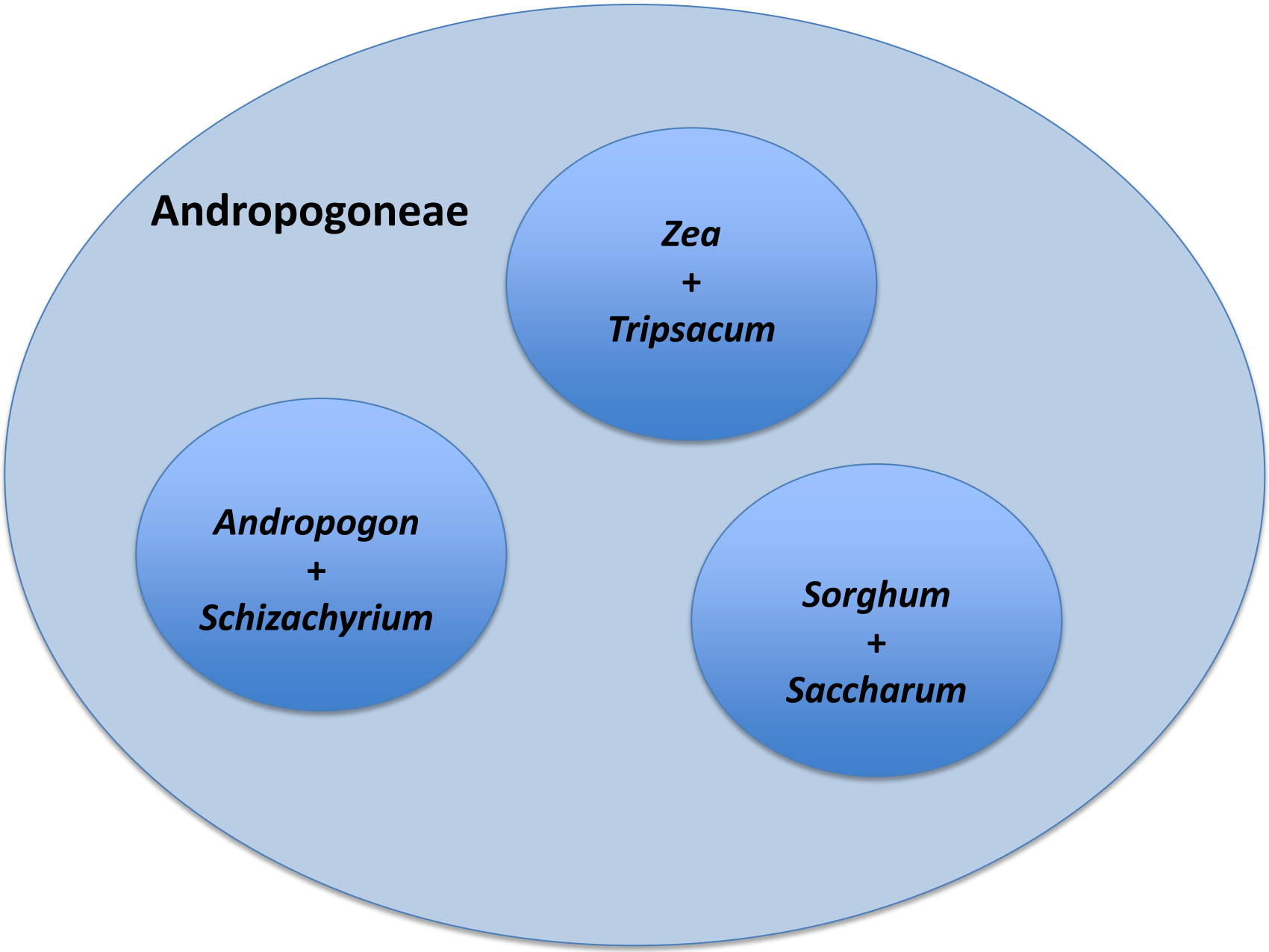


Maize

Ritter et al., Amer. J. Bot., 2002

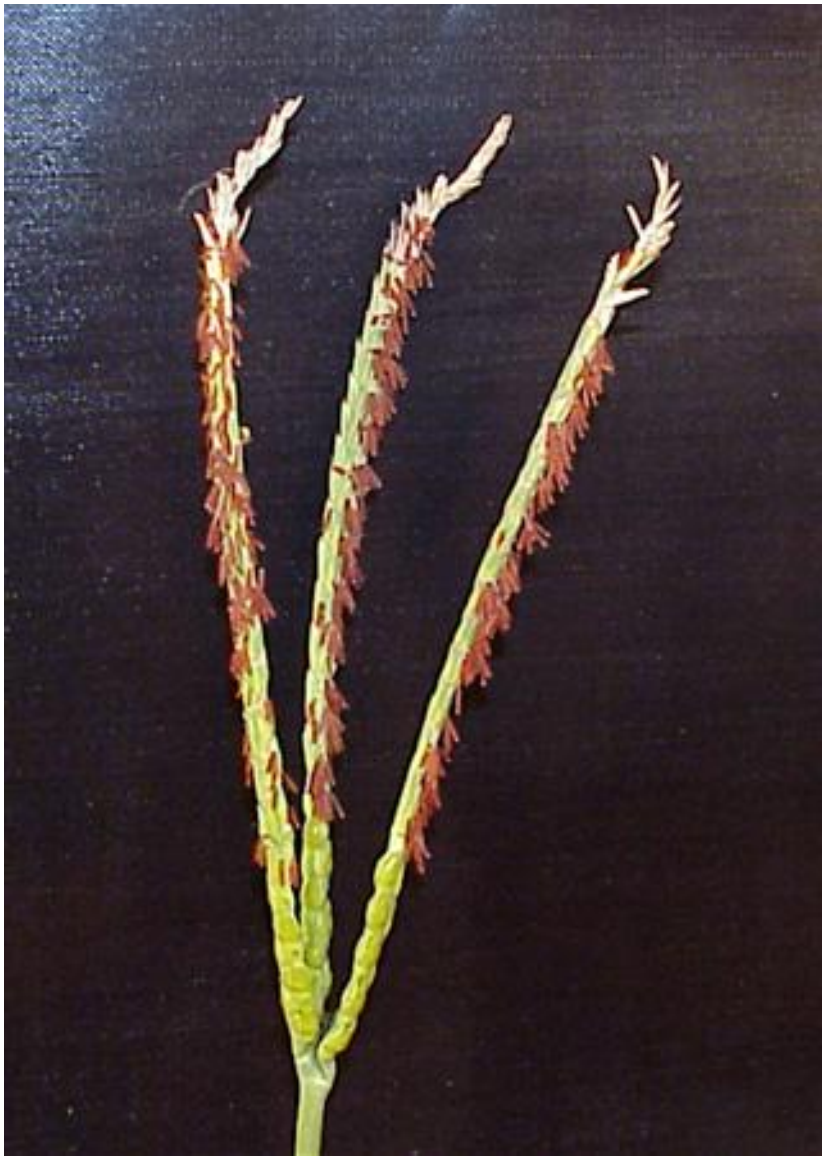
Andropogoneae phylogeny




Andropogoneae
Zea
+
Tripsacum
Andropogon
+
Schizachyrium
Sorghum
+
Saccharum

Zea plus *Tripsacum*

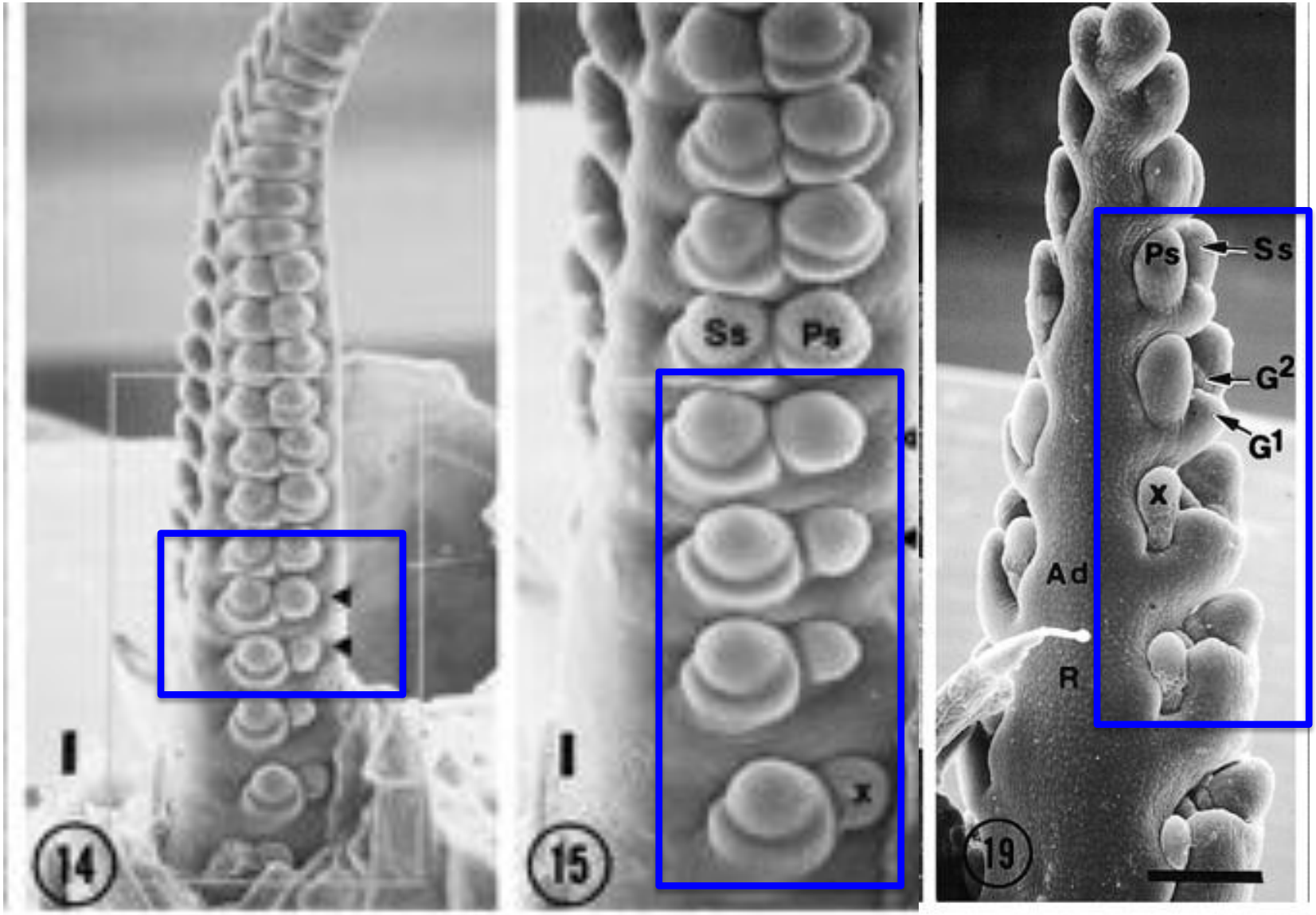
- Origin of monoecy – male and female florets in separate spikelets
- Female spikelets unpaired by suppression of the pedicellate spikelet
- Estimates of the dates of divergence of the two genera vary wildly: 9,000,000 ± 3,000,000 or 5 million, or 1.2 million years



Tripsacum

Teosinte

(photo by H. Iltis)



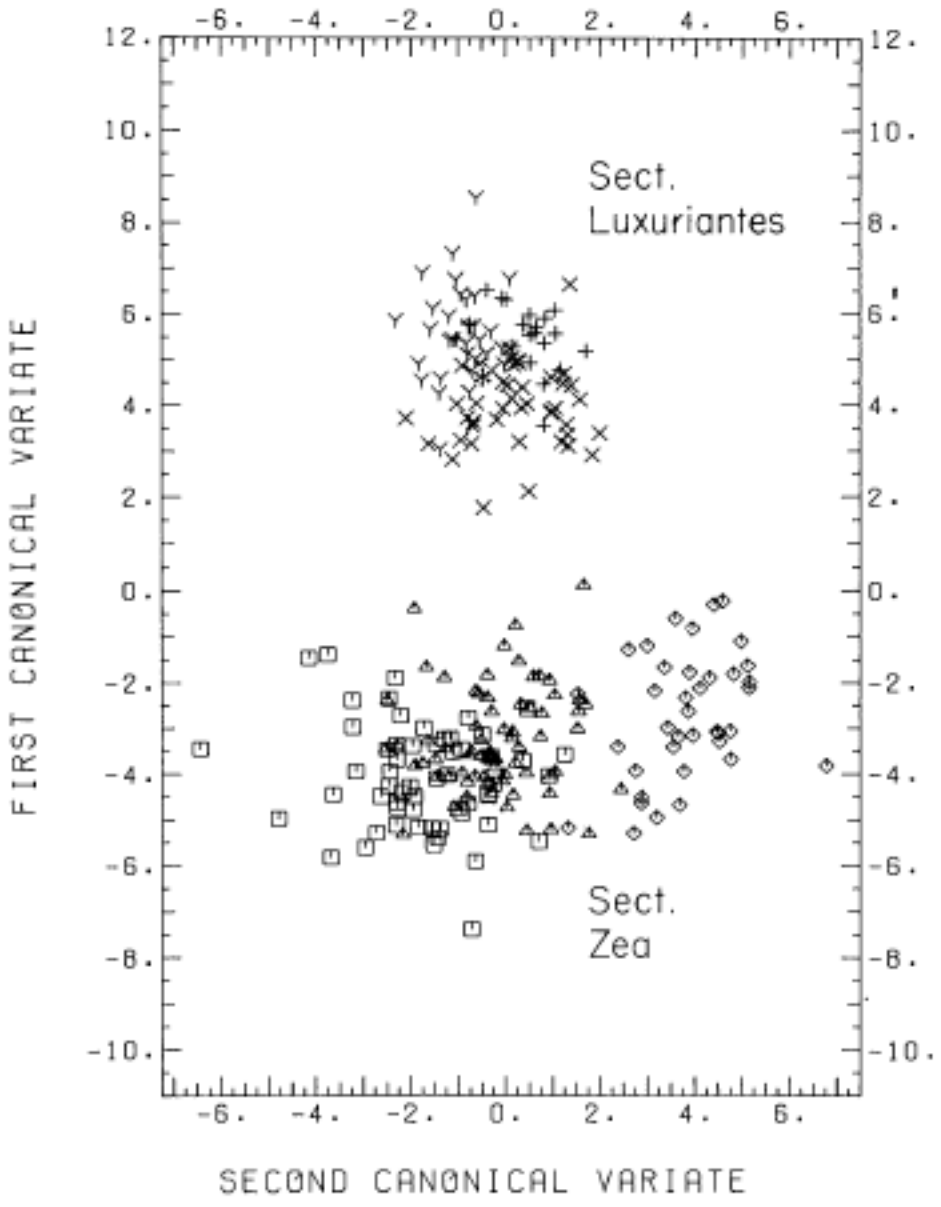
Tripsacum *Tripsacum* *Zea mays* ssp. *mexicana*

Orr et al., 2001, Amer. J. Bot.

Orr et al., 2002, Amer. J. Bot.

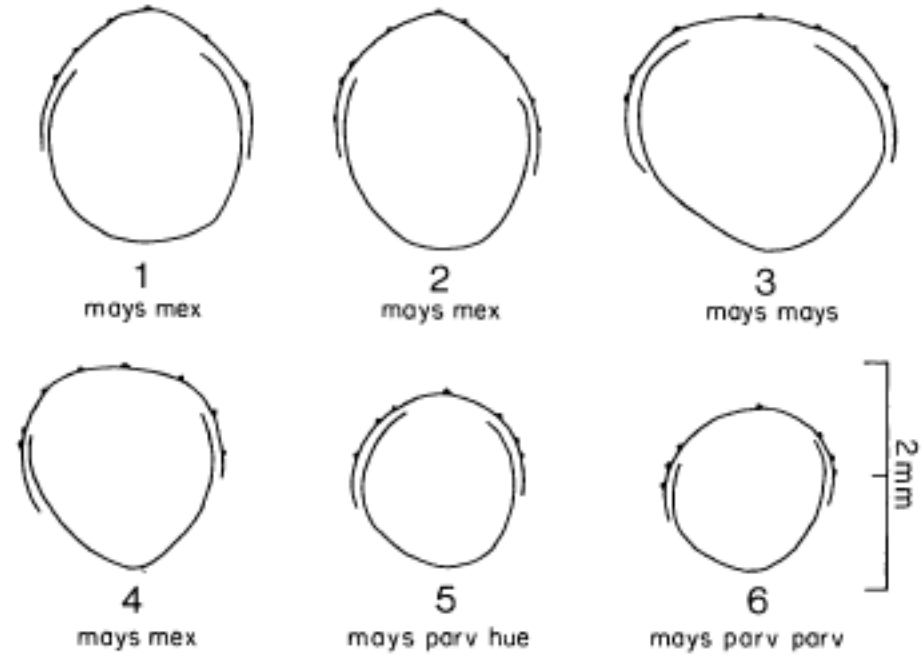
The genus *Zea*

- Male and female spikelets generally in separate inflorescences.
- Five species in two sections: Luxuriantes and Zea.
- Diversification estimated at 100,000-300,000 years ago.

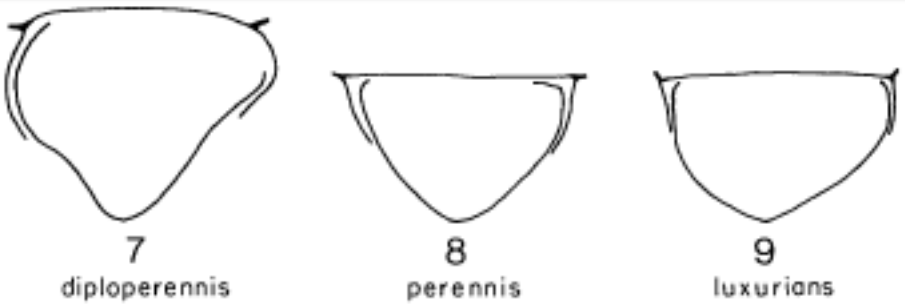


Doebley & Iltis, 1980,
American Journal of Botany

Tassel spikelet cross sections, showing differences in glume structure.



Zea* sect. *Zea



Zea* sect. *Luxuriantes

Doebley & Iltis, 1980,
American Journal of Botany

Zea mays ssp. *mays*

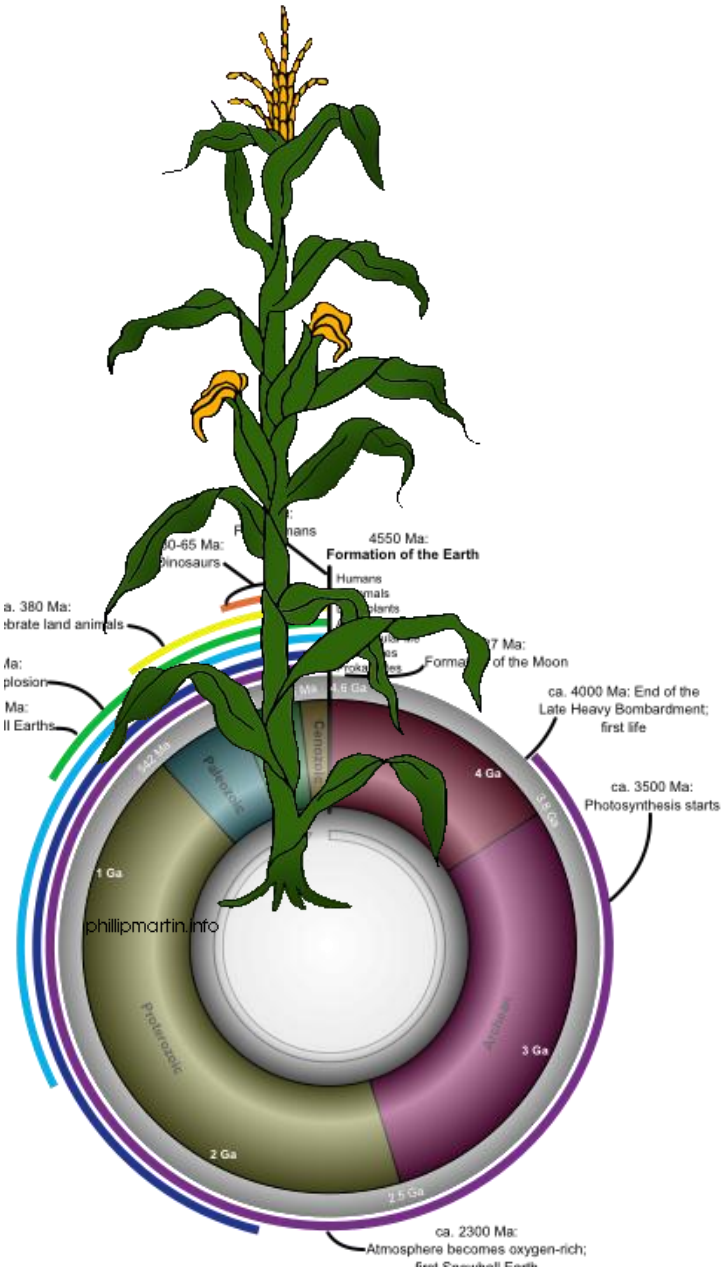
- Highly modified female inflorescence.
- Recent – within human history.

In summary

- The components of the maize cell are shared with other land plants and have been assembled over 3+ billion years of evolution.
- The structure and cell types of the maize stem and leaf are shared with other vascular plants and have been assembled over 300+ million years.
- The maize seedling, endosperm, and cell walls are shared with other commelinid monocots, and have been assembled over 120 million years.

- The maize spikelet is almost as old as the grasses, but the flower number and developmental pattern are panicoid, ca. 34 million years old.
- C_4 photosynthesis is ca. 32 million years old and shared with other members of Panicoideae.
- The paired spikelets are shared with other Andropogoneae and have been around for 19 million years.
- The structure of the ear is recent – less than 10,000 years old.

http://katiehutchison.squarespace.com/display/ShowJournal?moduleId=1186140&categoryId=117050&currentPage=8



http://plants.phillipmartin.info/plants_corn_plant.htm