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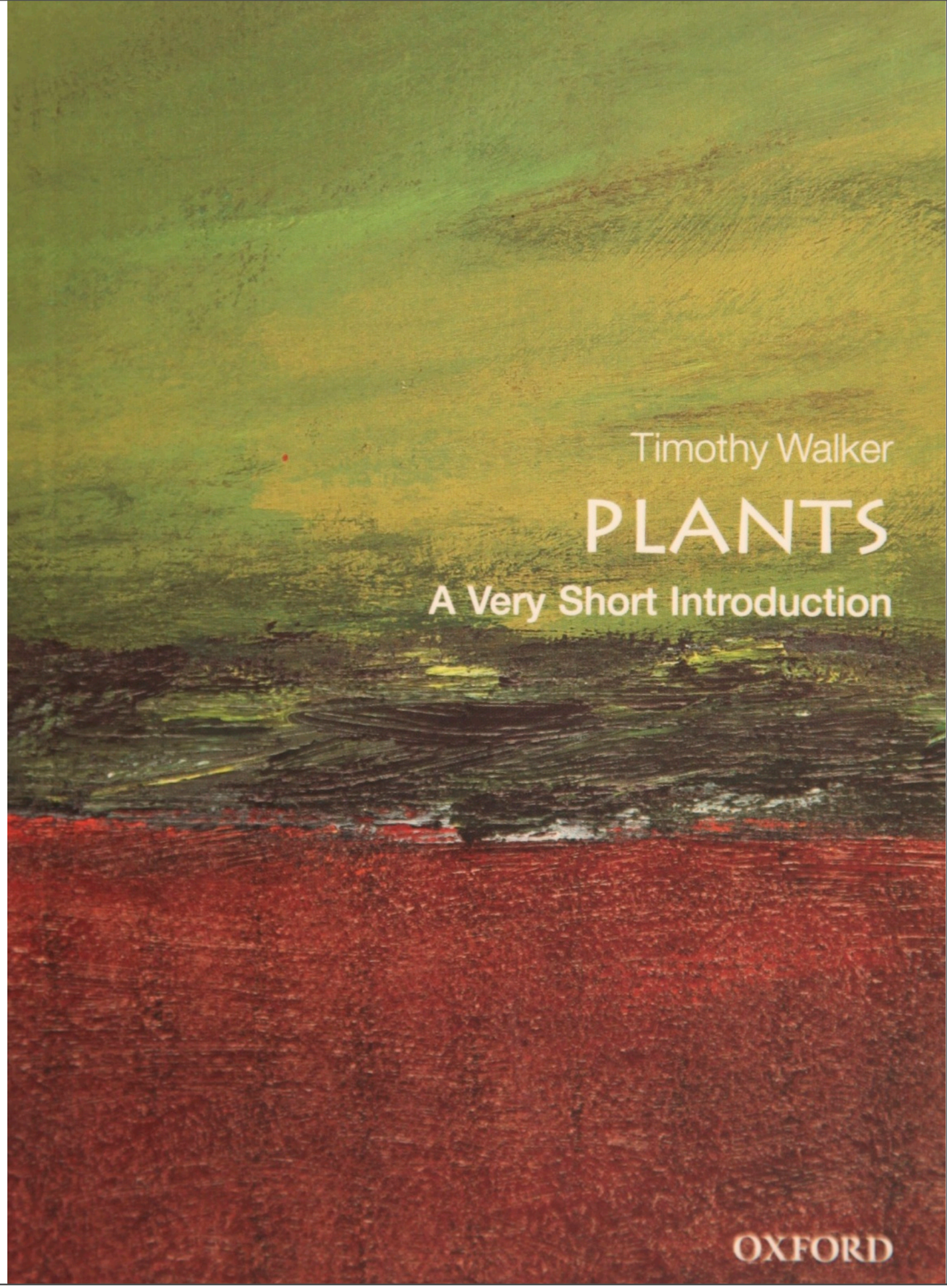


Natural selection cannot possibly produce any modification in any one species exclusively for the good of another species; though throughout nature one species incessantly takes advantage of, and profits by, the structure of another.

Charles Darwin (**1859**) *The Origin of Species*

8th Week Hilary Term

Organisms

timothy.walker@obg.ox.ac.uk

IT'S ALL ABOUT **SEEDS**

Natural selection will produce nothing in one species **for the exclusive good or injury of another**; though it may well produce parts, organs, and excretions highly useful or even indispensable, or highly injurious to another species, **but in all cases at the same time useful to the owner**.

Charles Darwin (**1859**) The Origin of Species

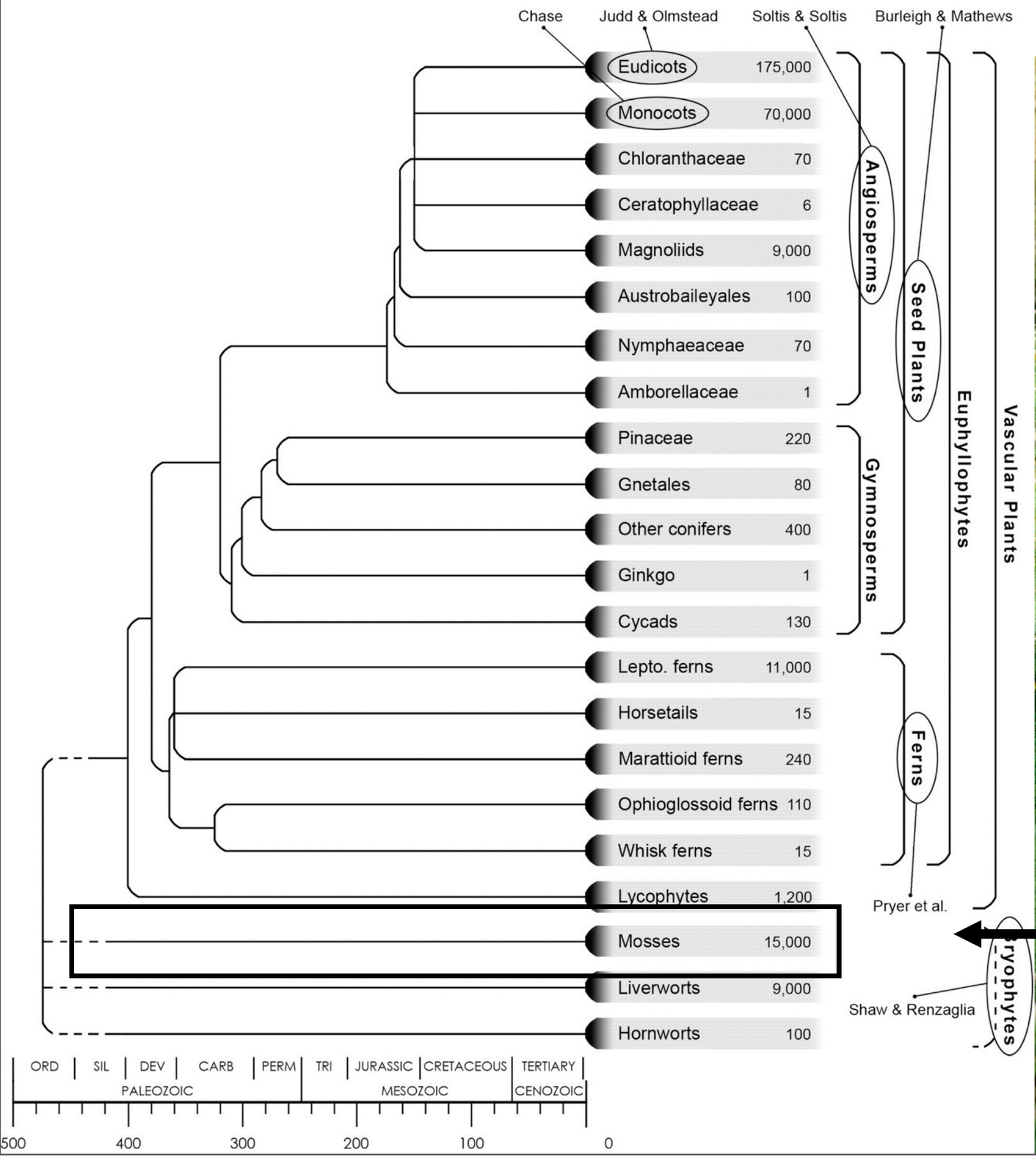
Seed plants now dominate the land partly because of the positive advantage that seeds gave their parent plants, **but some land plants still survive without them**.

23,000 species of bryophytes and 11,000 species of ferns have done very nicely without seeds for 450,000,000 years. How?

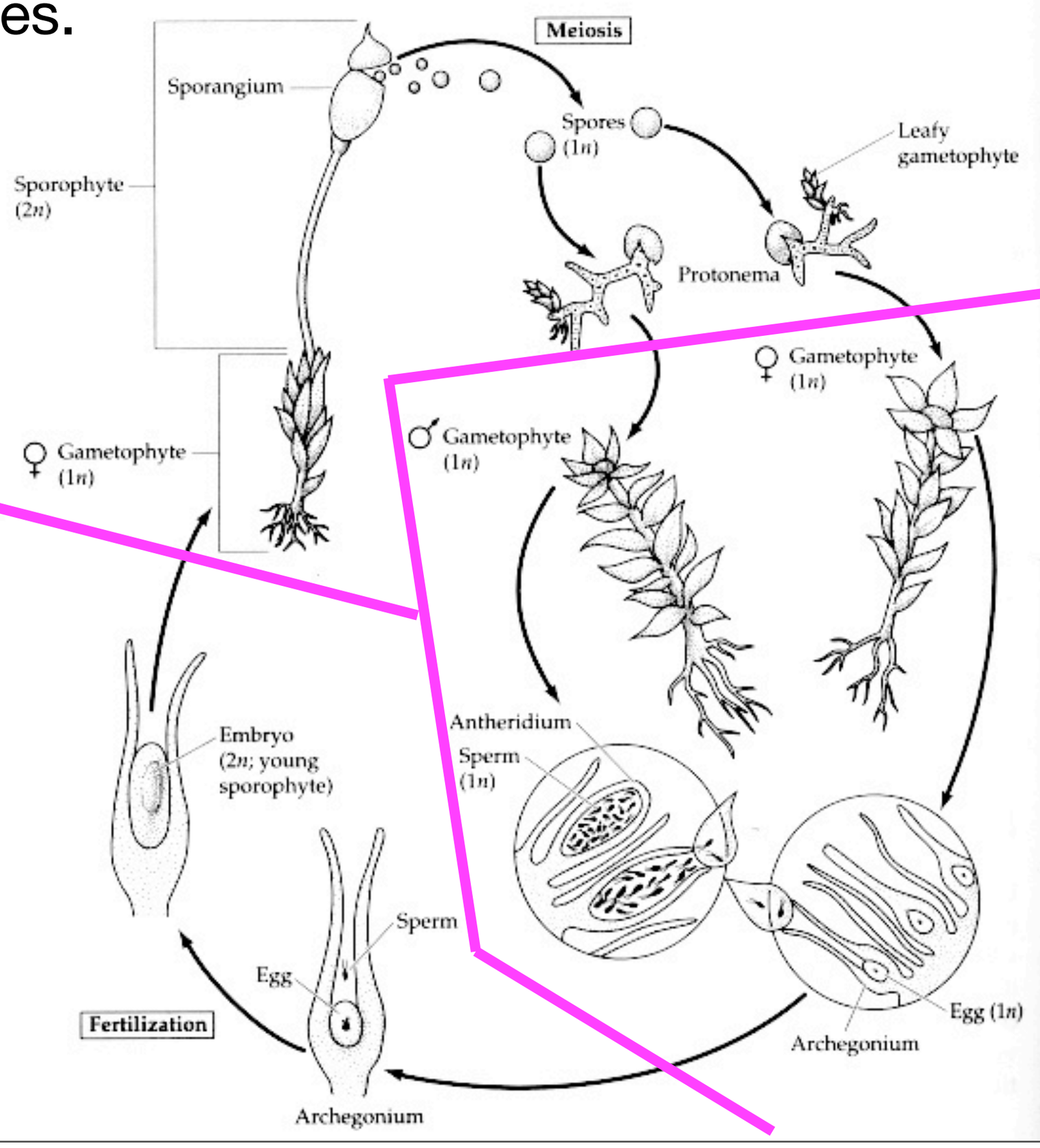
By having their embryos developing next to the means of support for the new sporophyte.

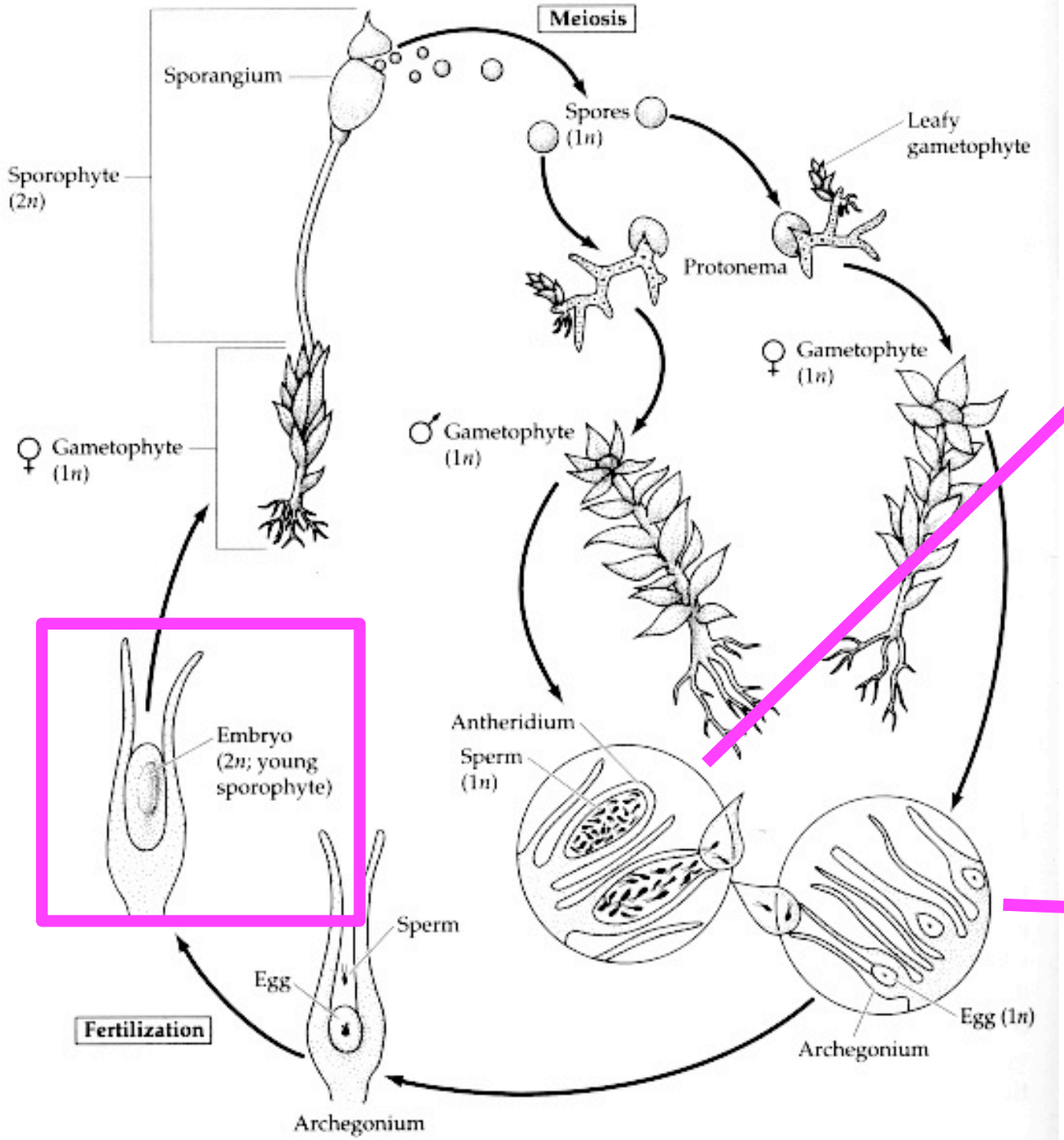
In the case of bryophytes this is from the female gametophyte and in the ferns the support comes initially from the female gametophyte and then it becomes free-living.

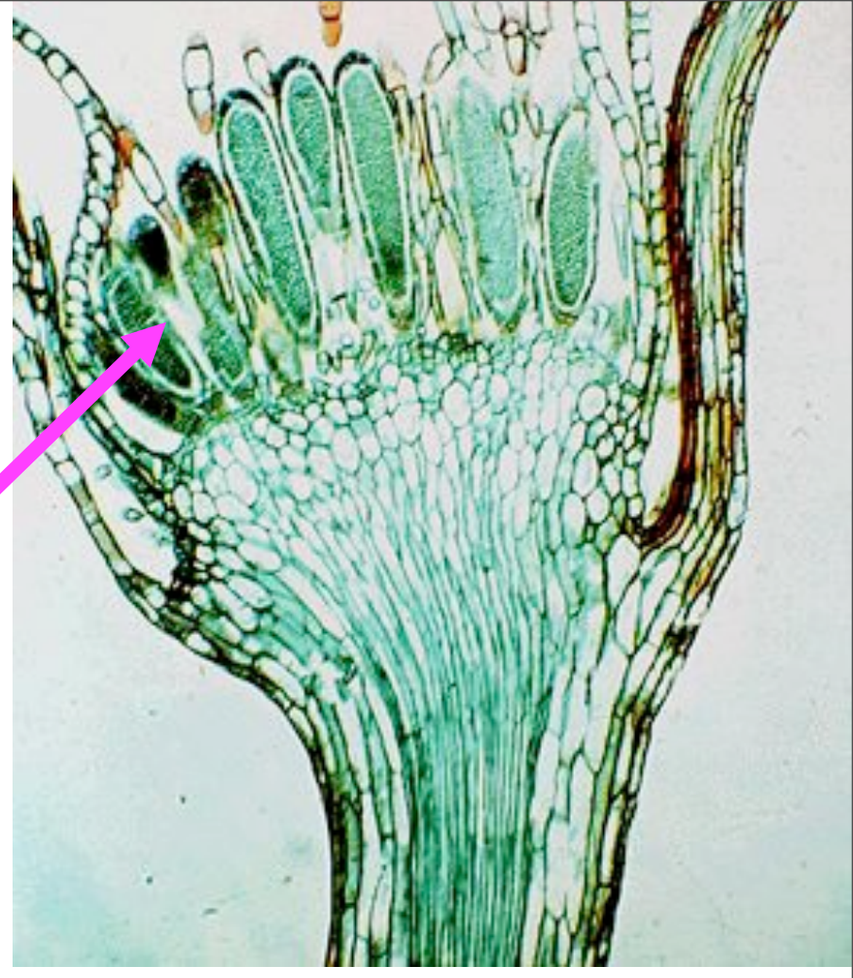
Extant land plants on the phylogeny: MOSSES

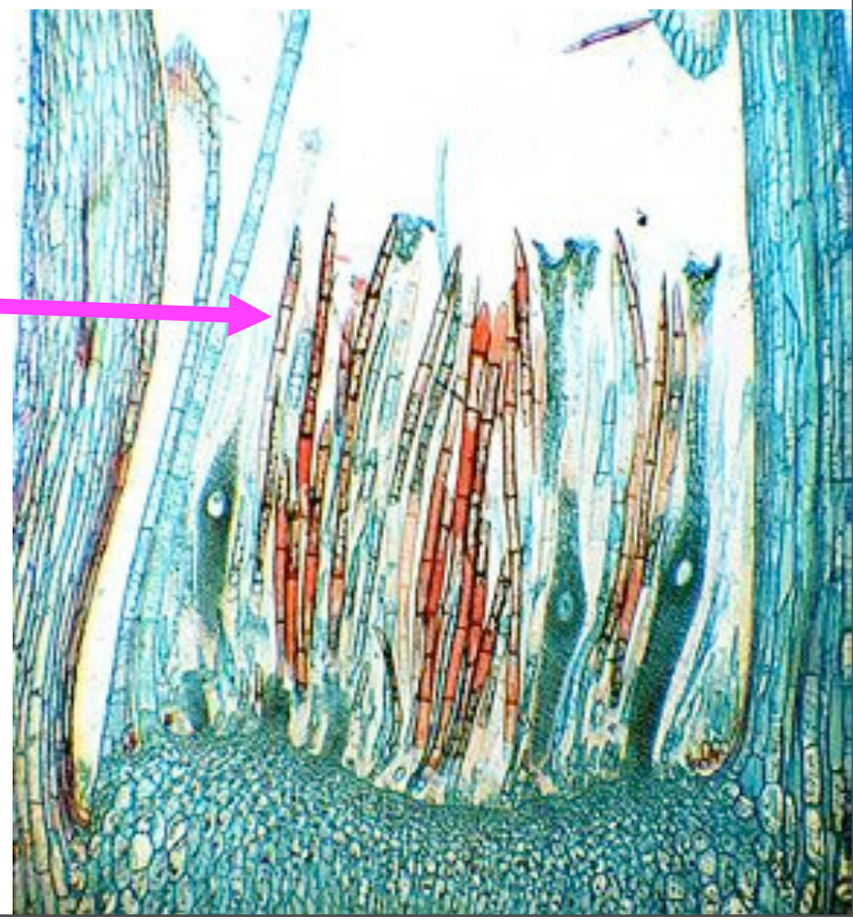


HAPLOID POLYTRICHUM **MOSS GAMETOPHYTE**. In the tips of the ‘leafy’ shoots the archegonia or archegonia form. These produce the haploid gametes.



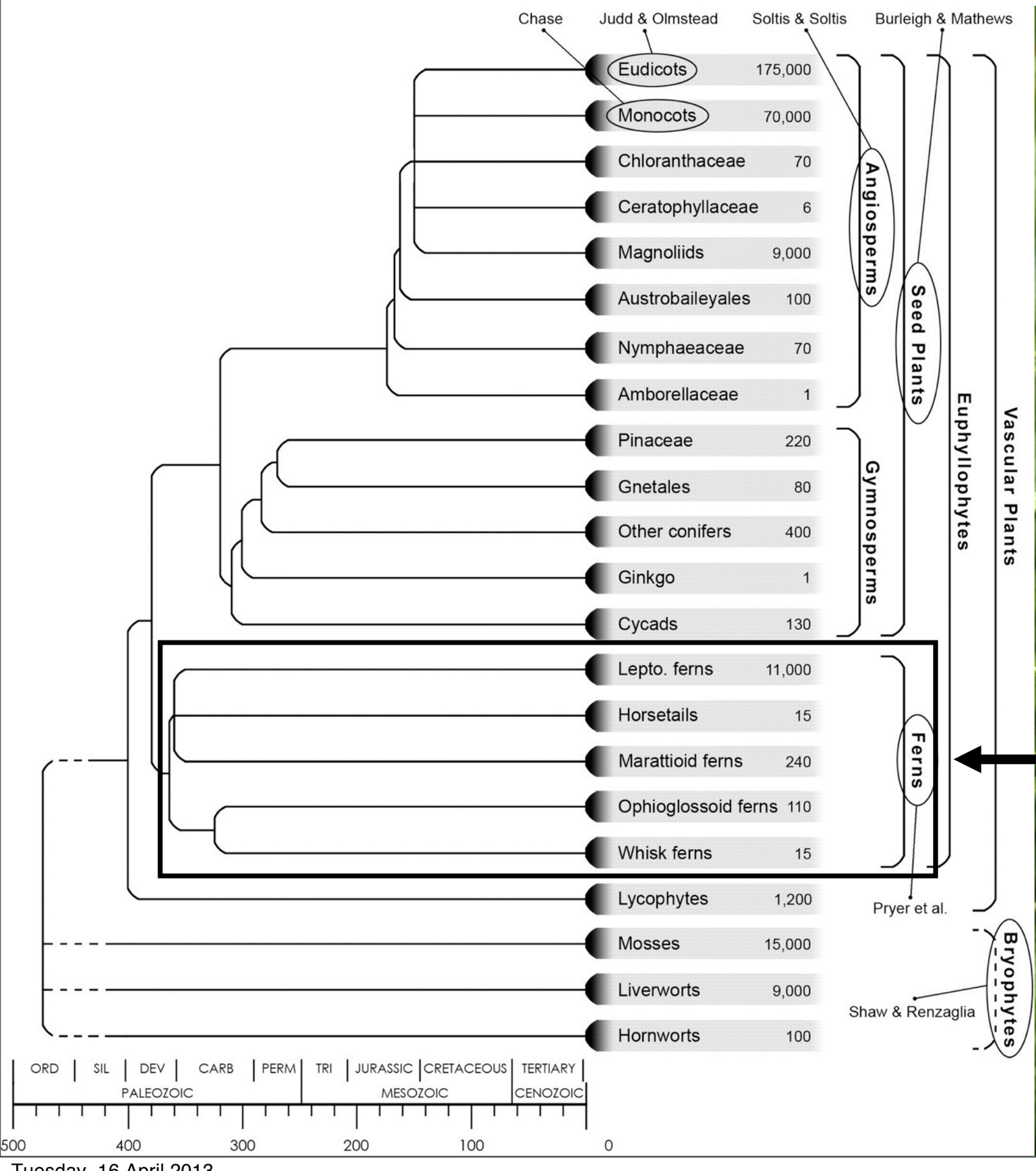




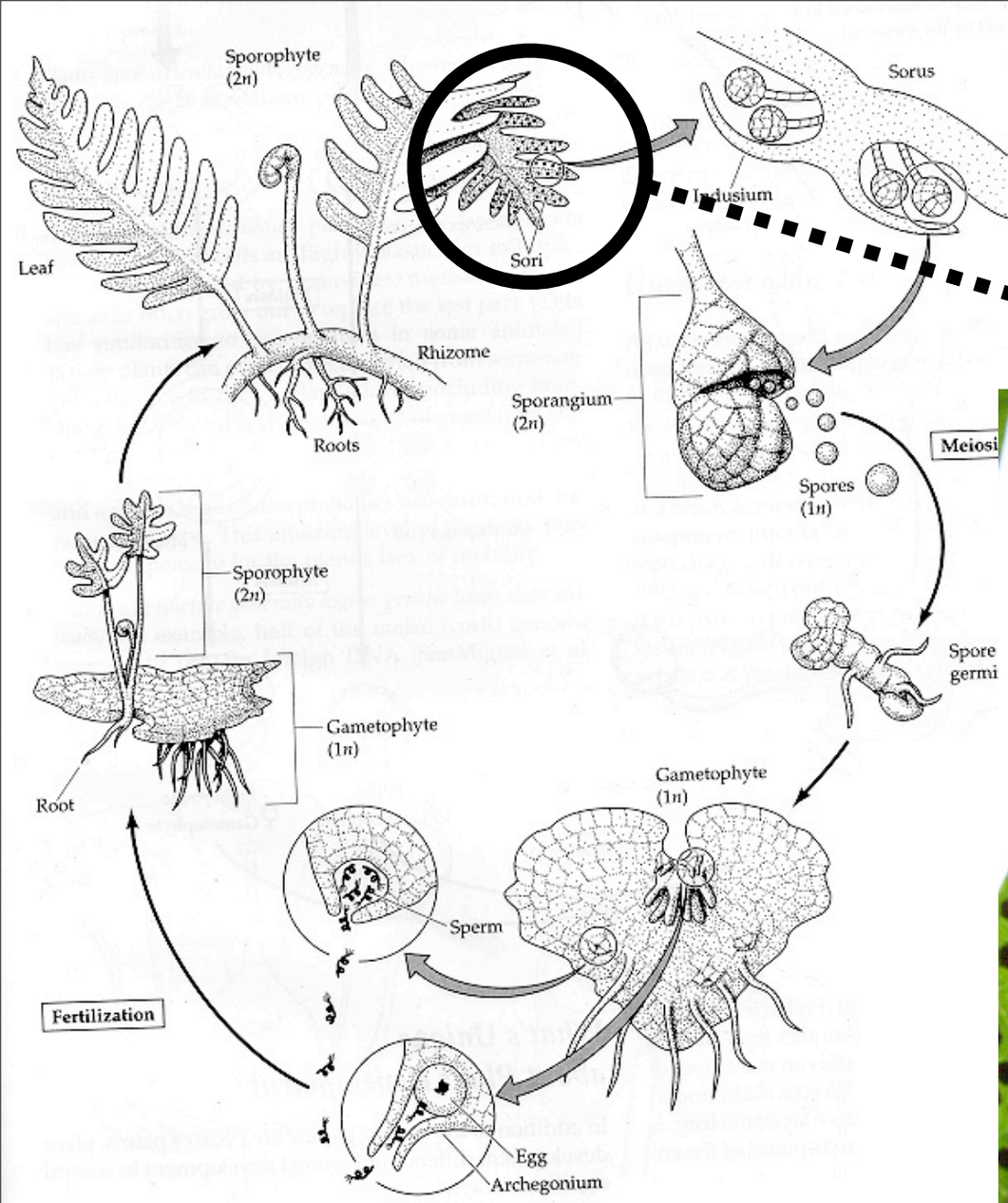


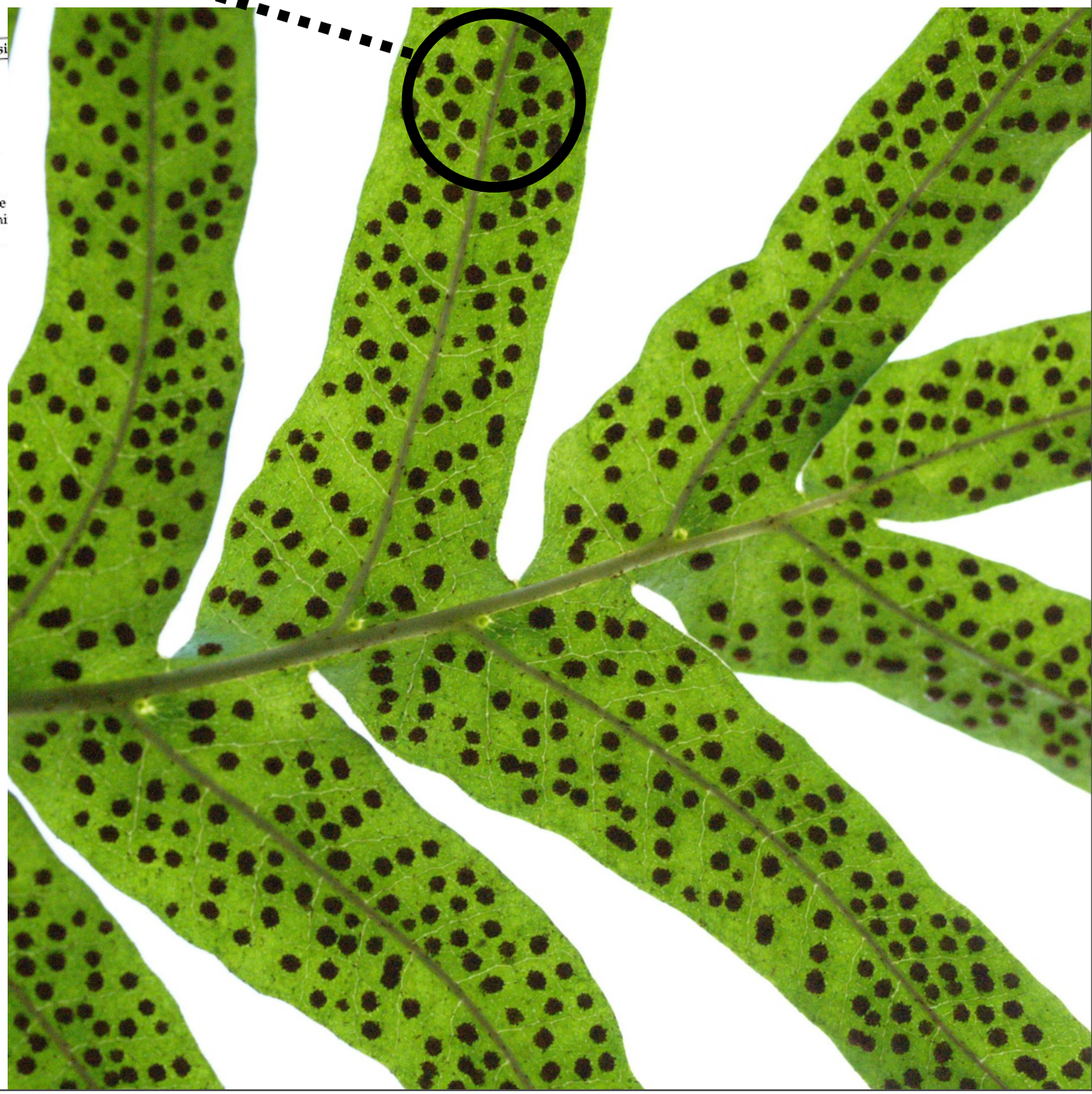
Moss life cycle

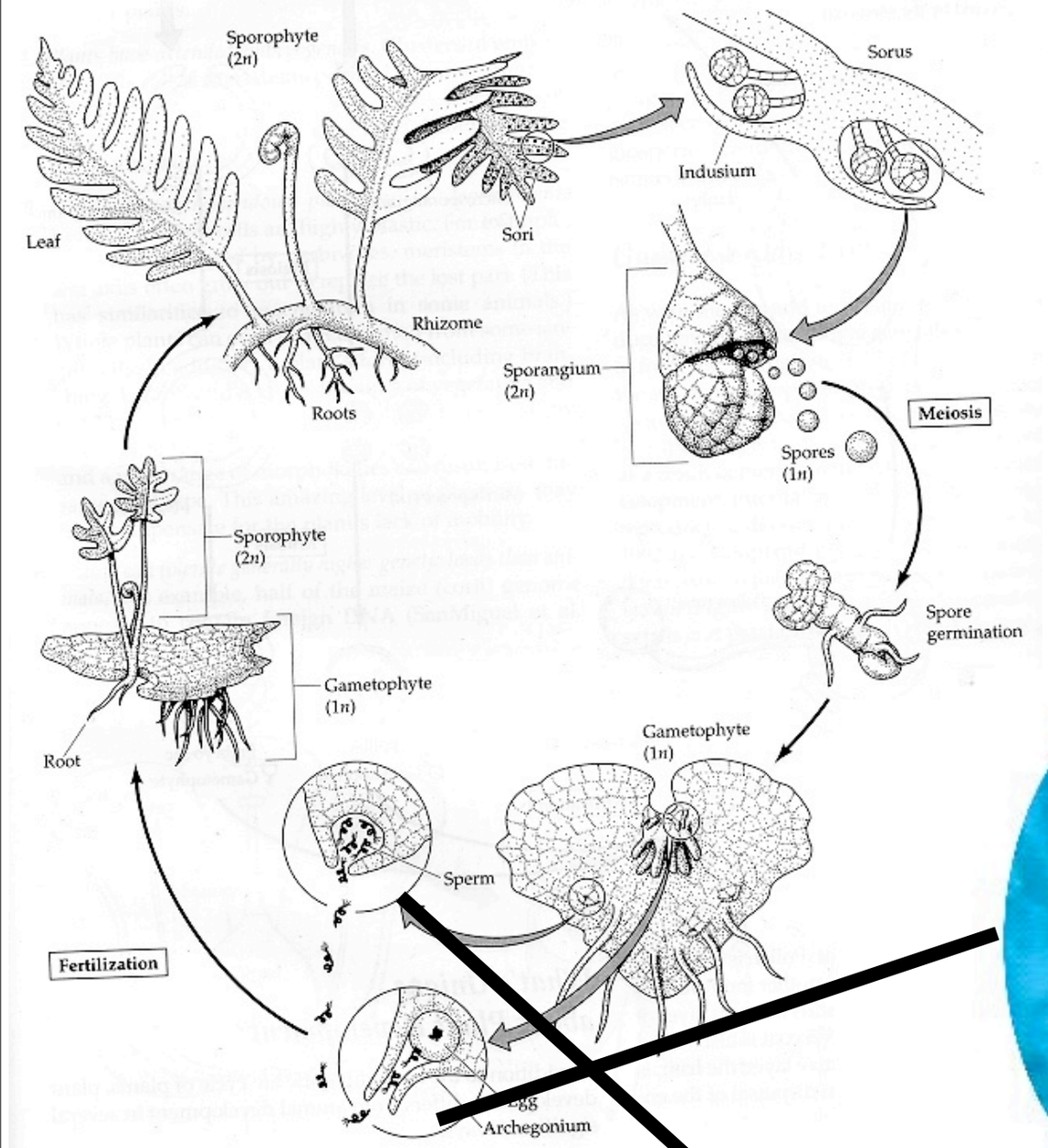
Extant land plants on the phylogeny: FERNS

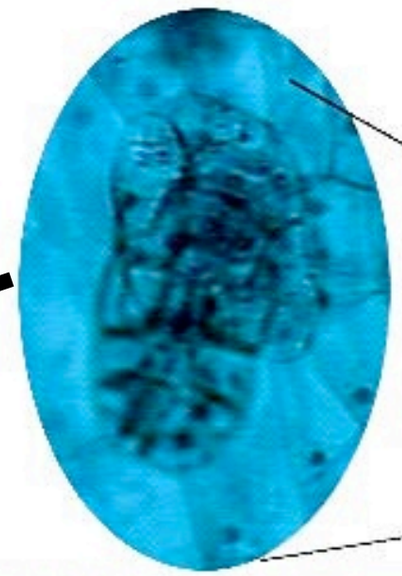


Fern sporangia



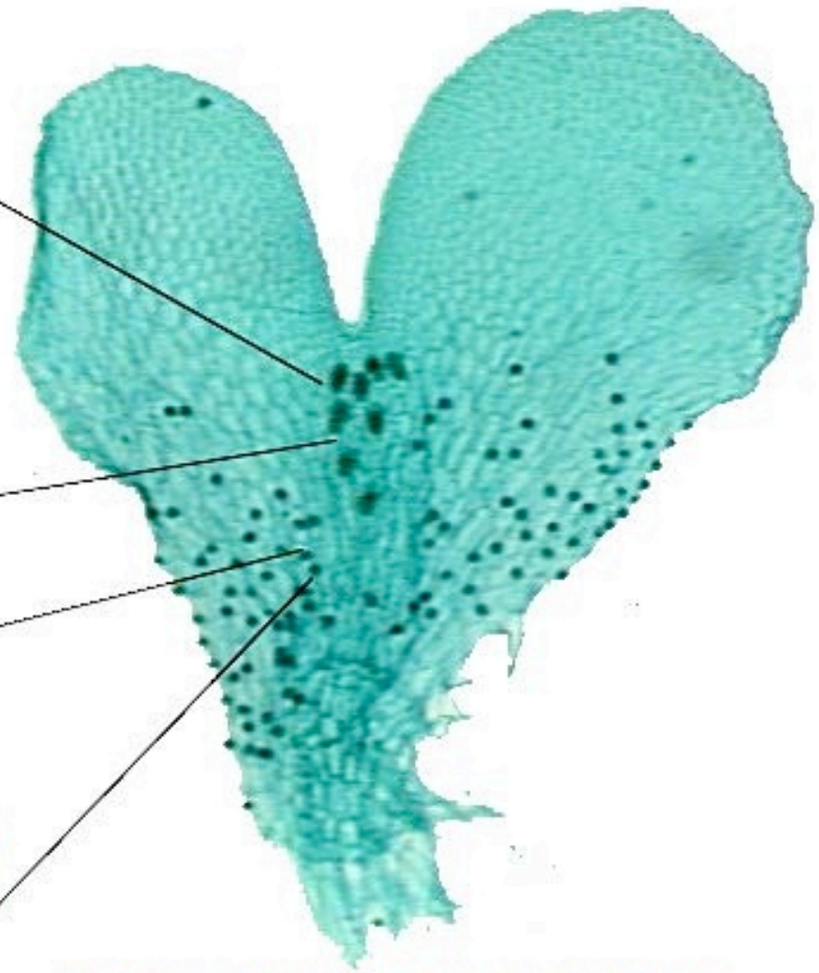




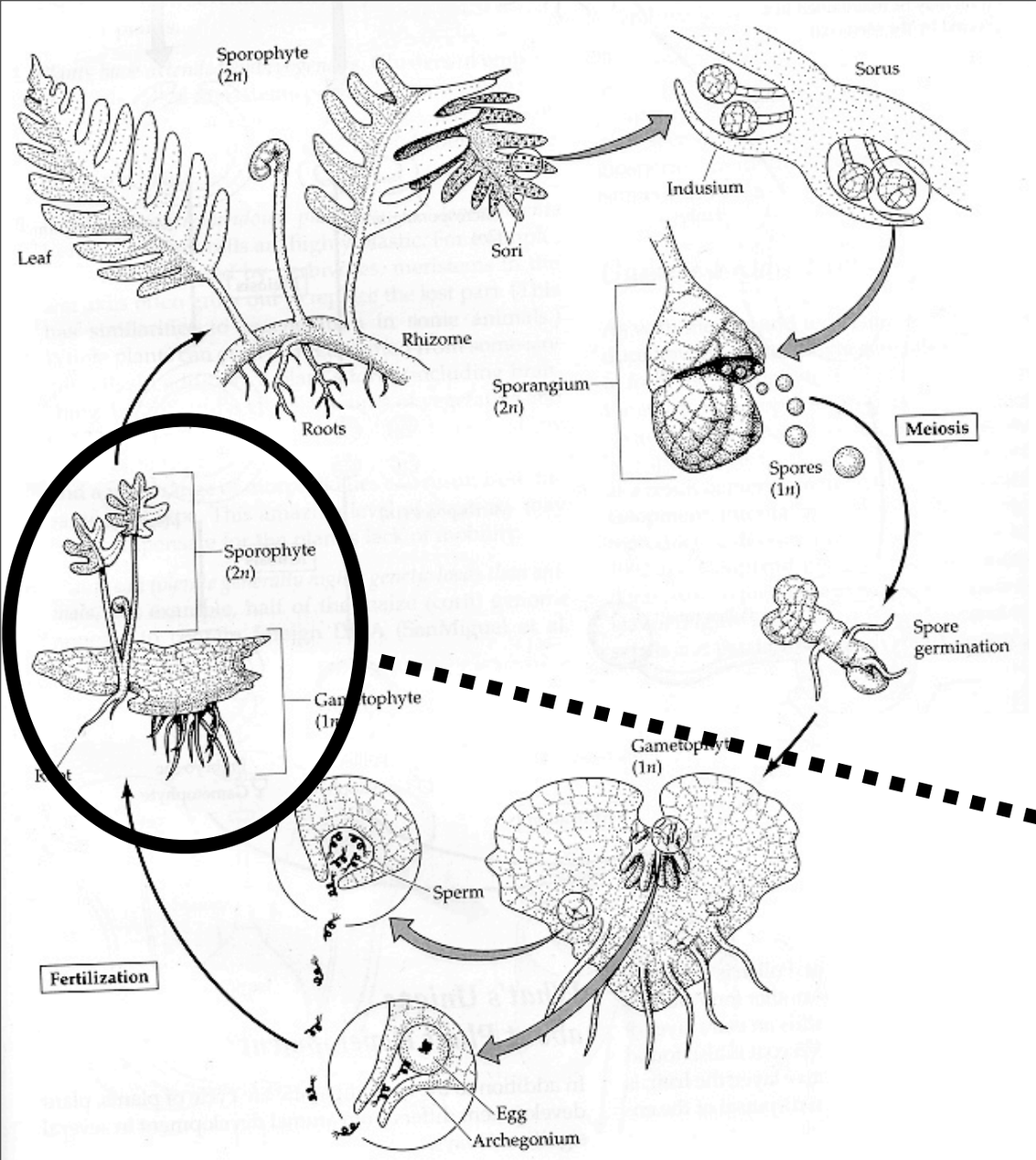


archegonium

antheridia



Fern Gametophyte


Sporophyte
(2n)
Sorus
Indusium
Sori
Leaf
Rhizome
Roots
Sporangium
(2n)
Meiosis
Spores
(1n)
Spore
germination
Sporophyte
(2n)
Gametophyte
(1n)
Gametophyte
(1n)
Sperm
Fertilization
Egg
Archegonium

In all the seed-less plants the **embryo develops at the location where it will grow into the next sporophyte generation** (generally at ground level)

But then came the seed plants where **the development of the embryo is halted. It is given an overcoat** (the integuments) **and a meal for the journey** (the female gametophyte in the earliest seed plants, endosperm in flowering plants) **and it is sent out into the World.**

When did seeds first appear?

Gymnosperms

Angiosperms

Cenozoic

Quaternary

Tertiary

65

Mesozoic Era

Cretaceous

144

Jurassic

206

Triassic

248

Paleozoic Era

Permian

290

Carboniferous

354

Devonian

417

Pinopsida / Coniferopsida

Megagame-tophyte (n)

Gnetopsida

Ginkgopsida

Cycadopsida

Pentoxyles

Bennettitales

Caytoniales

Magnolilds

Basal angiosperms

Monocots

Eudicots

Rosids

Asterids

Caryophyllids

Basal eudicots

Endosperm (3n)

Voltziales

Cordaitales

Lyginopteridopsida

Gloss.

Gigan.

Gigantopterids

"Progymnosperms"

Aneurophytales

Archaeopteridales

Extinct gymnosperms and seed ferns

Seed plant phylogenetic tree considering major gymnosperm and angiosperm clades. Note that the precise evolutionary connections between the different gymnosperm groups are unknown and that the ancestors of angiosperms are unknown. Typical seed types visualize steps in the evolution of the seed. Extinct gymnosperm groups (fossils): Lyginopteridopsida (seed ferns, "Samenfarne", includes Devonian/Carboniferous Lyginopterids and Carboniferous/ Permian Medullosans and other subgroups), Cordaitales, Voltziales, Pentoxylales. Bennettitales (cycadeoids), Caytoniales, Glossopteridales (glossopterids), Gigantopteridales (gigantoperids). Extant gymnosperm groups: Pinopsida/Coniferopsida (conifers, "Nadelbäume"), Ginkgopsida (ginkgos), Cycadopsida (cycads, "Palmfarne"), Gnetopsida (gnetophytes: Ephedridae, Gnetidae, Welwitschiidae). Angiosperms (flowering plants): Most important groups depicted. Time scale: Geological eras, periods, time in MYBP (million years before present). © 2007 G. Leubner, "The Seed Biology Place", http://www.seedbiology.de

Gymnosperms

Angiosperms

Cenozoic

Quaternary

Tertiary

65

Mesozoic Era

Cretaceous

144

Jurassic

206

Triassic

248

Paleozoic Era

Permian

290

Carboniferous

354

Devonian

417

Pinopsida / Coniferopsida

Megagame-tophyte (n)

Gnetopsida

Ginkgopsida

Cycadopsida

Pentoxyales

Voltziales

Cordaitales

Lyginopteridopsida

Gloss.

Gigan.

Bennettitales

Caytoniales

Magnolilids

Basal angiosperms

Monocots

Eudicots

Rosids

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Endosperm (3n)

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However, it seems reasonable to speculate that the first seeds were produced at ground level. In this scenario the male and female gametophytes were **either** close enough for the sperm to swim to the egg **or** where there was a chance that the male gametophytes could be passively brought close enough to the female for the sperm to be delivered close enough to the egg.

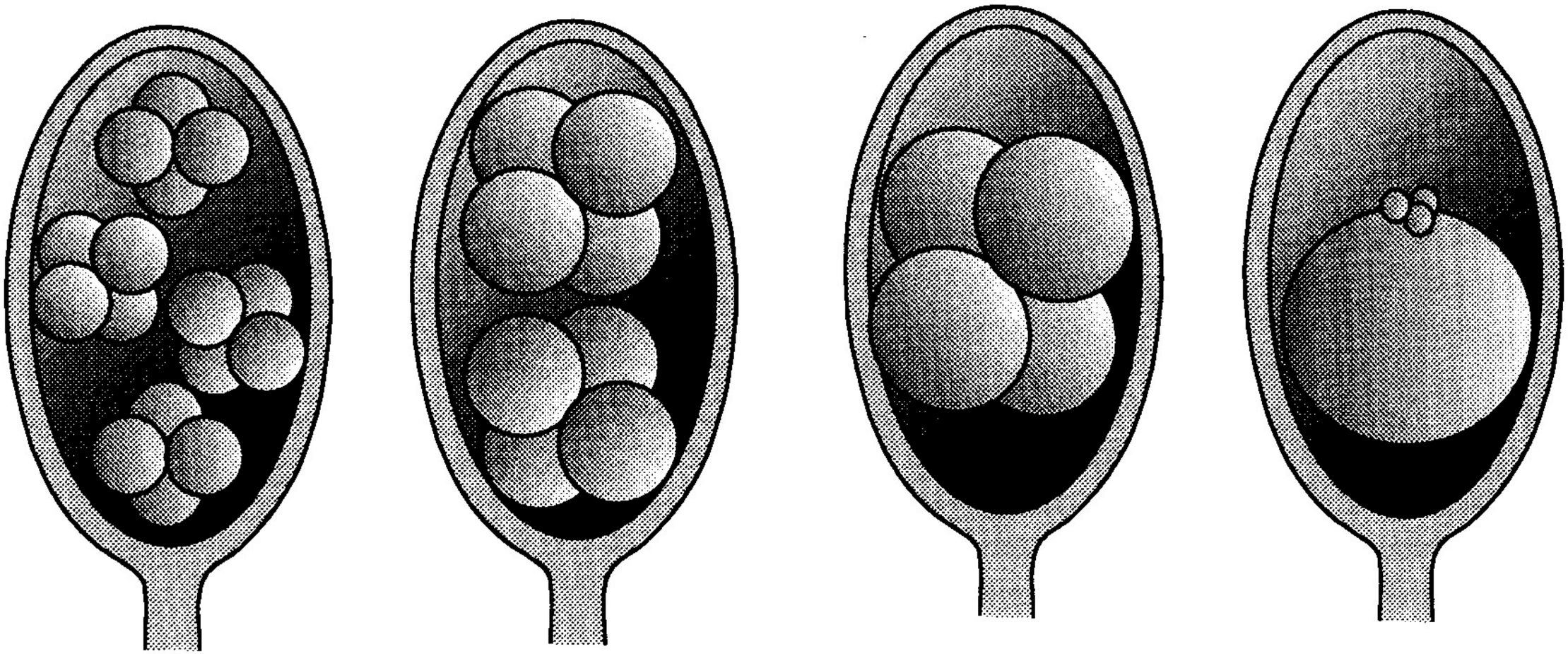
Seed ferns such as *Neuropteris*

What are seeds?

Microspores –

always many

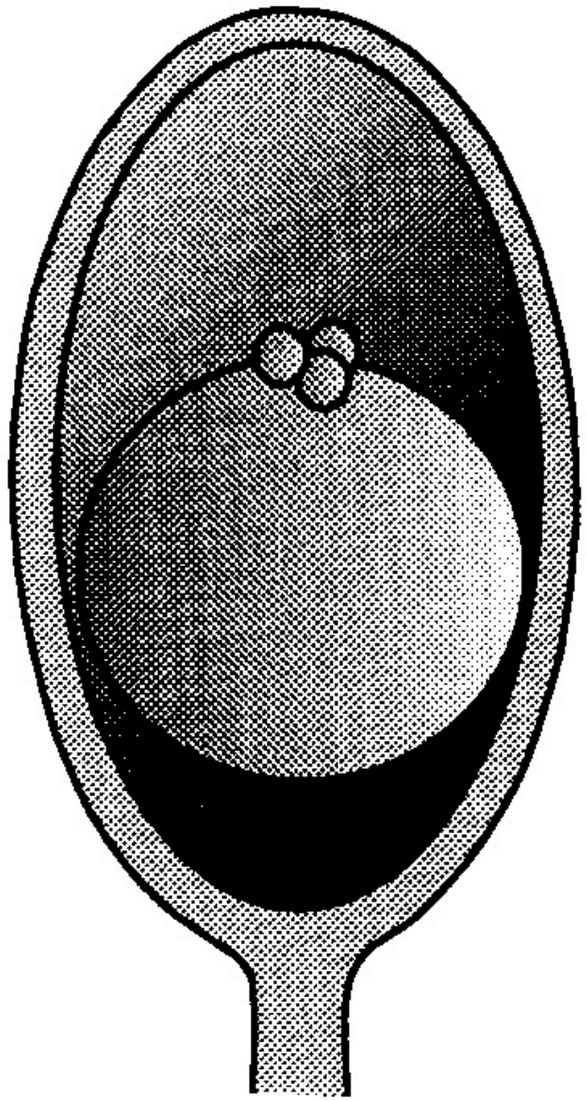
Megaspores (in megasporangia) reduced in number to just one in the seed plants

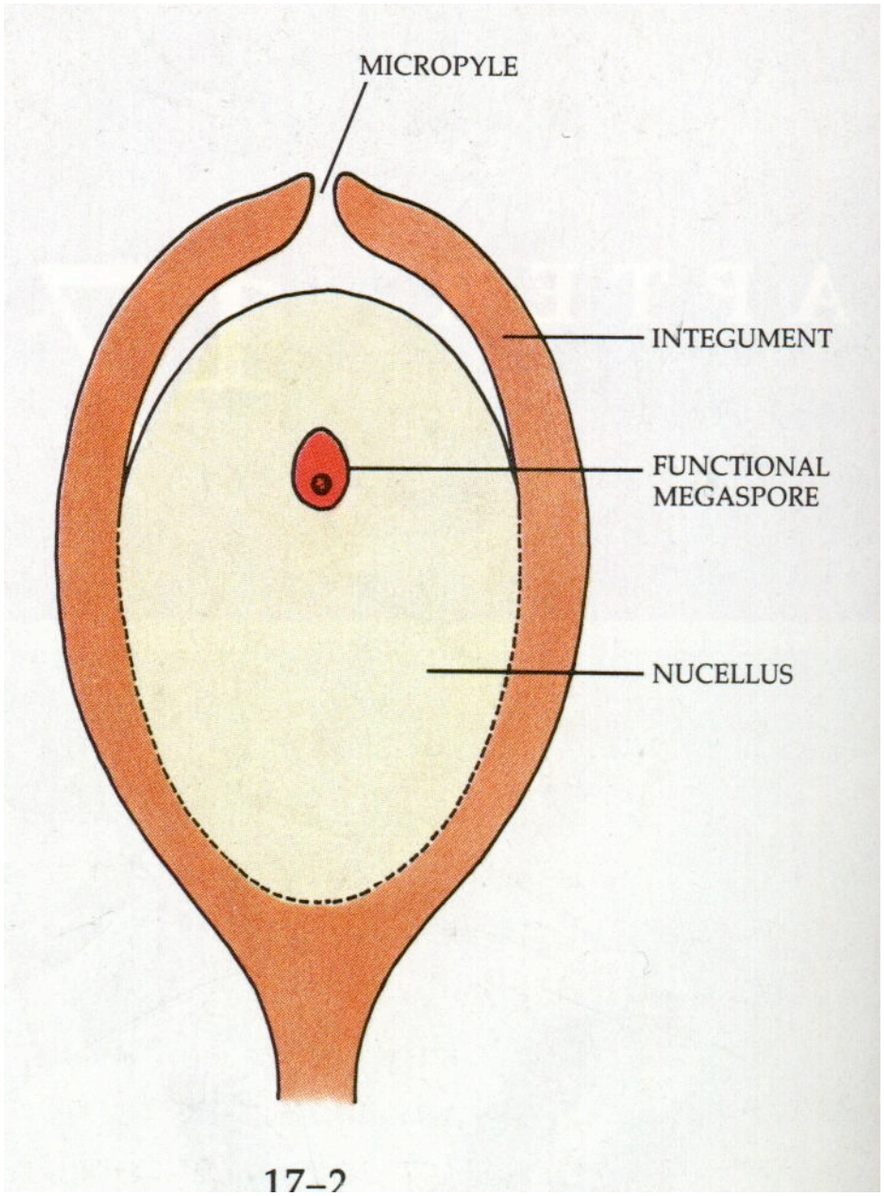


Microsporangia

Megasporangia

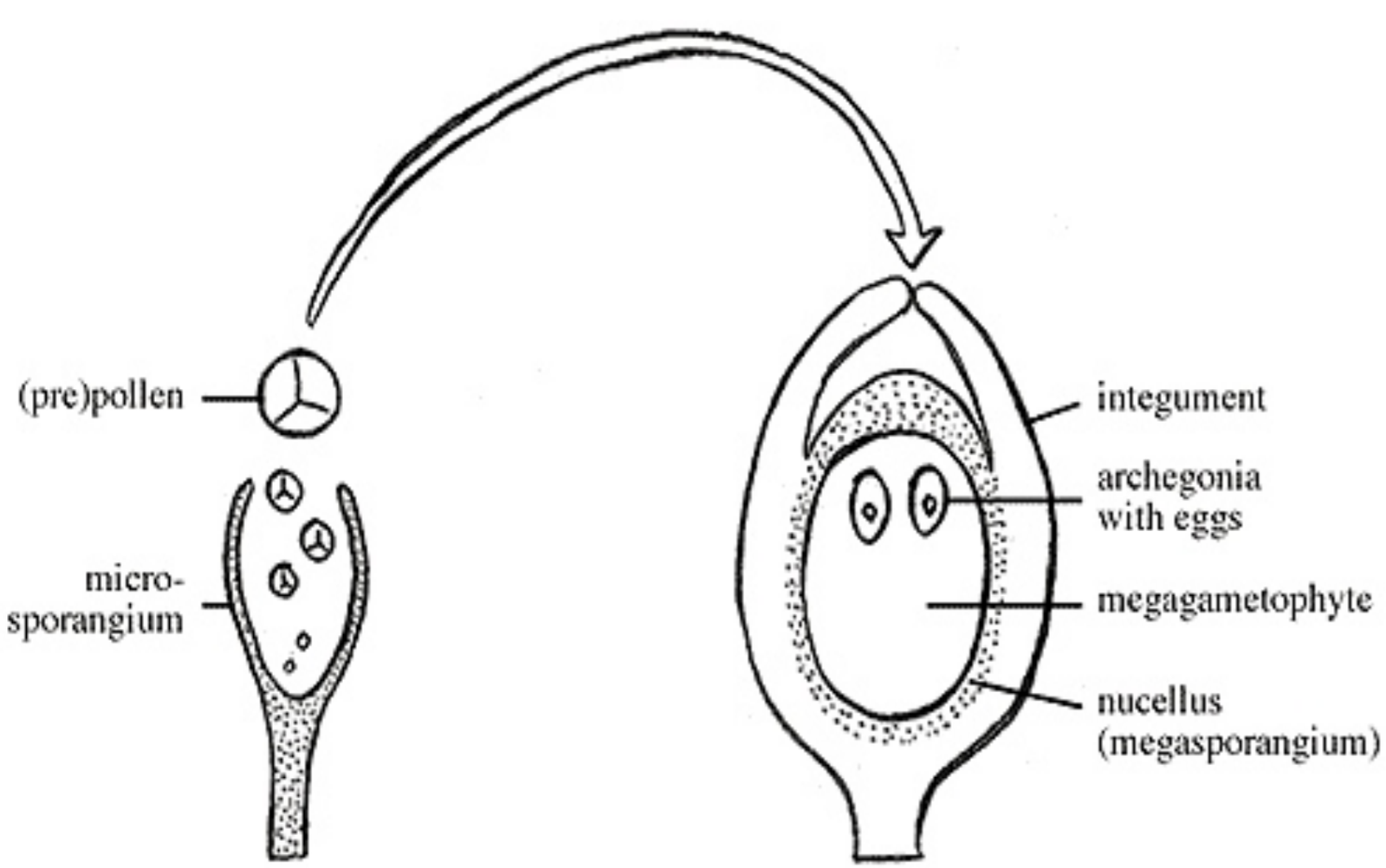
The one remaining megaspore is retained on the sporophyte where it is protected by the integuments provided by the sporophyte

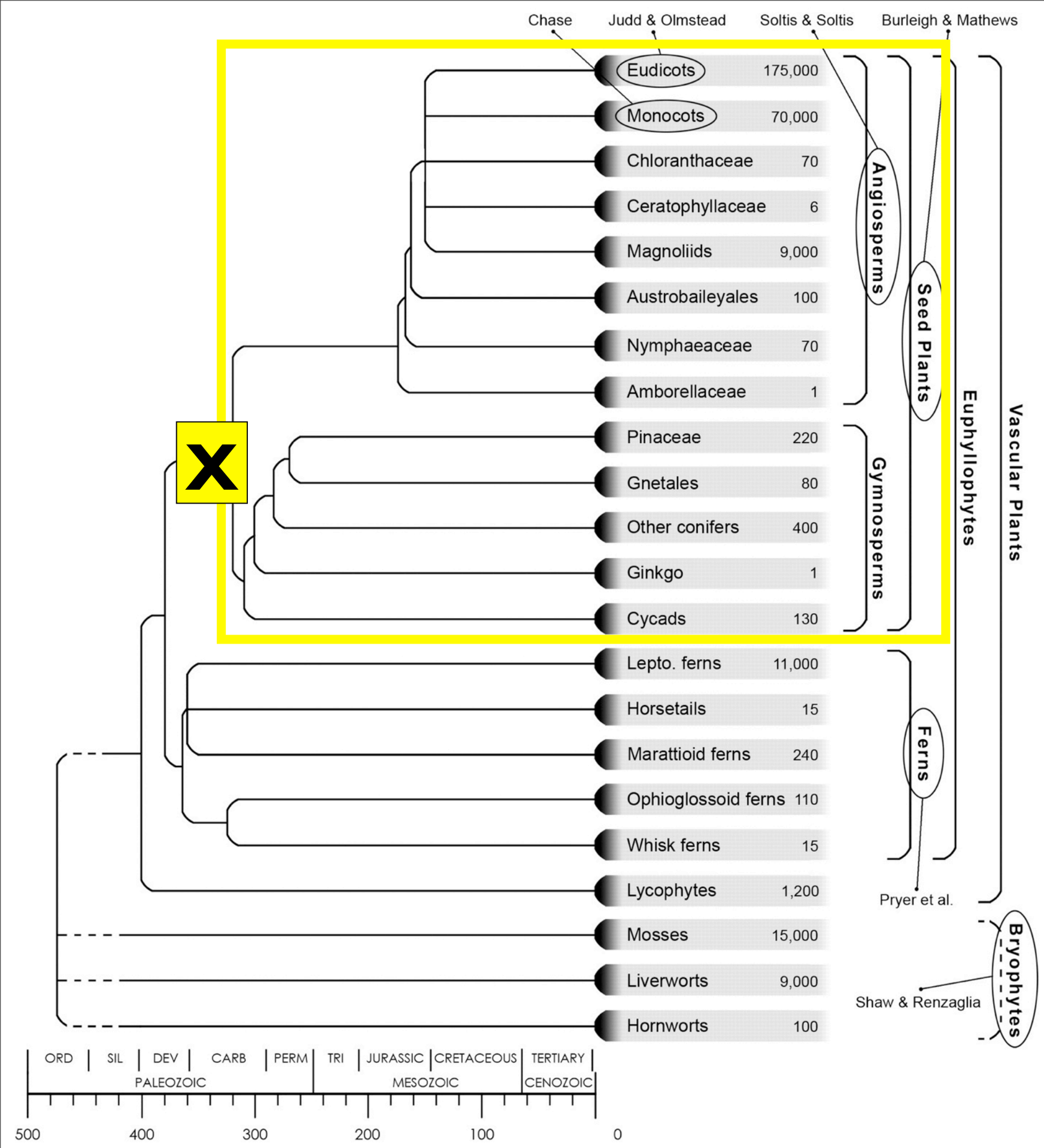




17–2

In the first seed plants the immature male gametophyte (pre-pollen) made its way to the immobile female gametophyte that had developed from the retained megaspore. The eggs were produced by the female gametophyte in archegonia just like the extant bryophytes, ferns and gymnosperms





Chronogram showing estimates of phylogenetic relationships and divergence times of the major groups of land plants & X is where the seed plants emerged

(Palmer et al. (2004))

SEED PLANTS – a few facts (1/2)

1. Seed plants may have evolved during the Carboniferous period from the Cordaitales, plants that had

- strap-shaped leaves in spirals at the shoot tip
- pithy stems
- vascular cambium
- secondary xylem
- cone-like structures

2. Seed plants are all heterosporous and so have two types of gametophyte – big & immobile (female) megagametophyte and small & mobile (male) microgametophyte and they need to be brought together by pollination [today's & tomorrow's lecture]

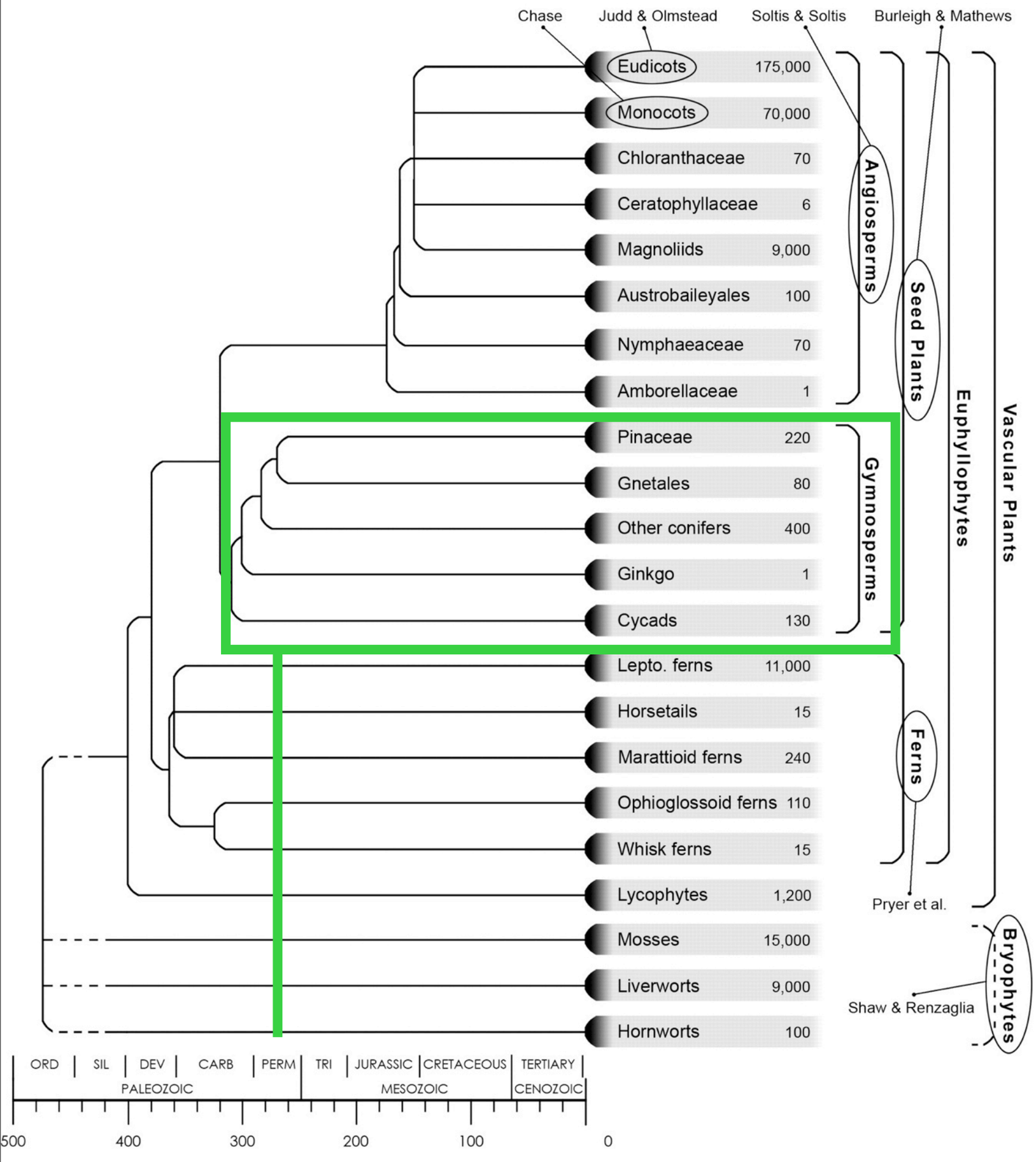
SEED PLANTS – a few facts (2/2)

3. Seeds are survival capsules – other analogous survival capsules have evolved e.g. the sporocarps of the aquatic heterosporous ferns

4. Seed dormancy & dispersal have helped plants to survive short & medium-term changes

5. Seeds have played a very important role in animal & human evolution as well as plant evolution [Thursday's lecture]

6) The world would be very different without seed plants and so we need to understand how they live and work so that we can plan for the future [Friday's Lecture]



The gymnosperms became dominant in the Permian (290-245 mya) as continents drifted to cooler places

The Gymnosperms have survived several mass extinction events – except this one?

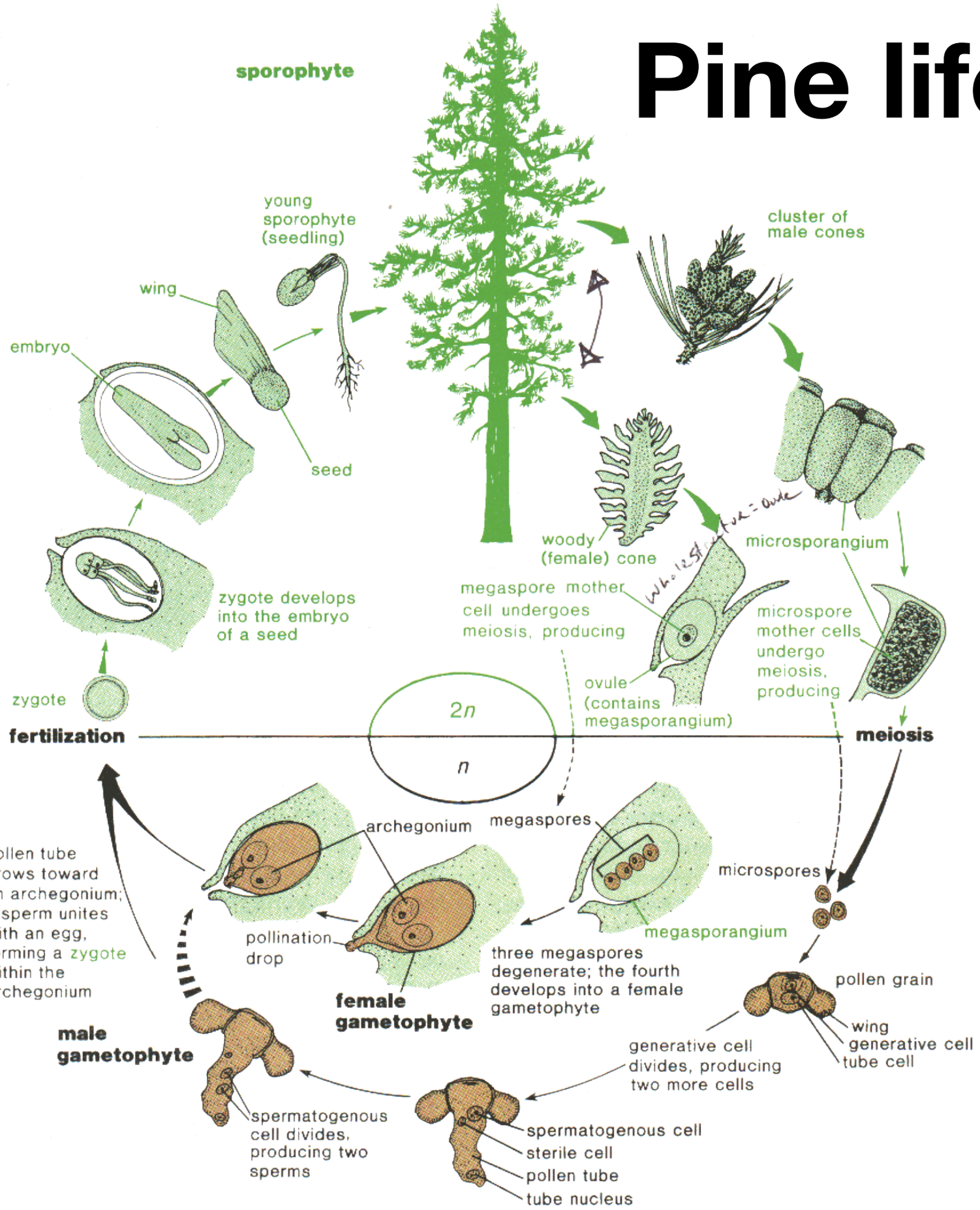
Along the Appalachian Way spruce trees (*Abies*) are dying – both mature plants and seedlings.

There is no clear reason but it is suggested that changes in climate have altered the severity of adelgid infestations.

Gymnosperms still dominate large areas of land and are economically very important such as the Pacific north-west of USA …

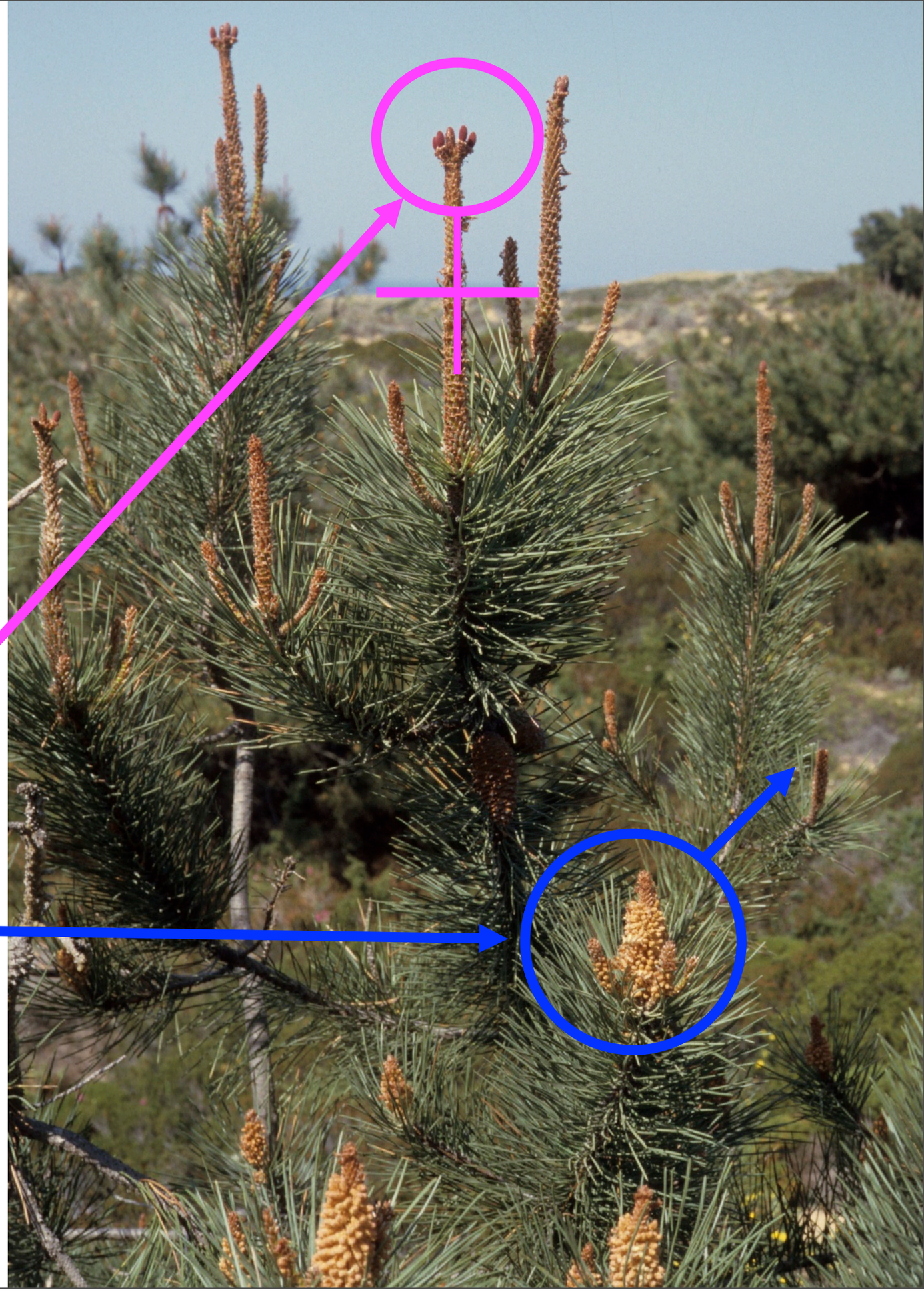
but are being harvested unsustainably in Washington State

Pine life cycle



PINES AS THE EXAMPLE FOR THE GYMNOSPERMS:

All gymnosperms are heterosporous so they have megasporangia in the **female** cones and microsporangia in the **male** cones

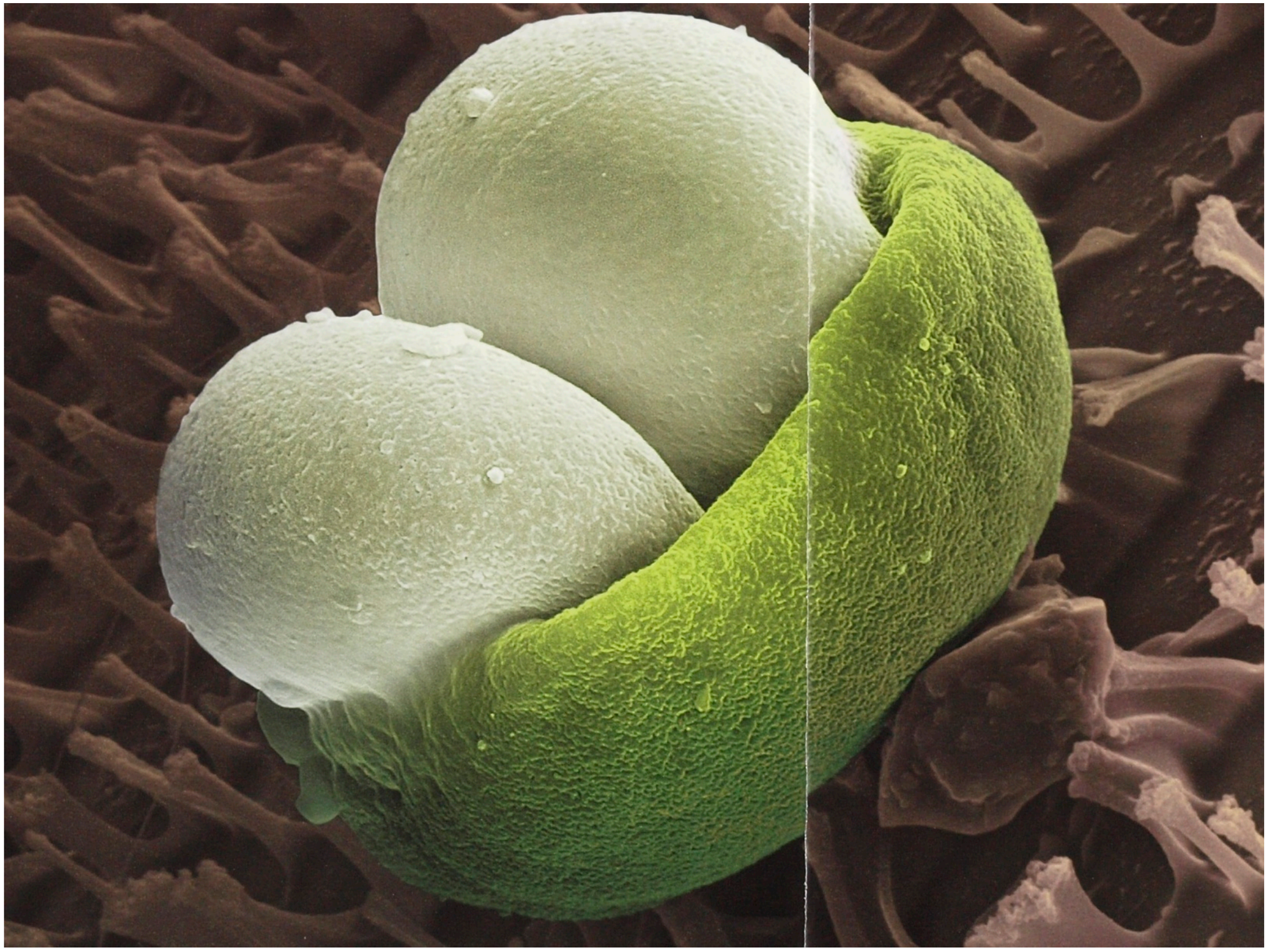


THE MALE CONE OF A PINE has microsporangia in the axils of microsporophylls. The haploid microspores develop into POLLEN grains that are immature male gametophytes. No antheridia are formed

If we admire the several ingenious contrivances, by which the flowers of the orchids and of many other plants are fertilised through insect agency, **can we consider as equally perfect the elaboration by our fir-trees of dense clouds of pollen**, in order that a few granules may be wafted by a chance breeze on to the ovules?

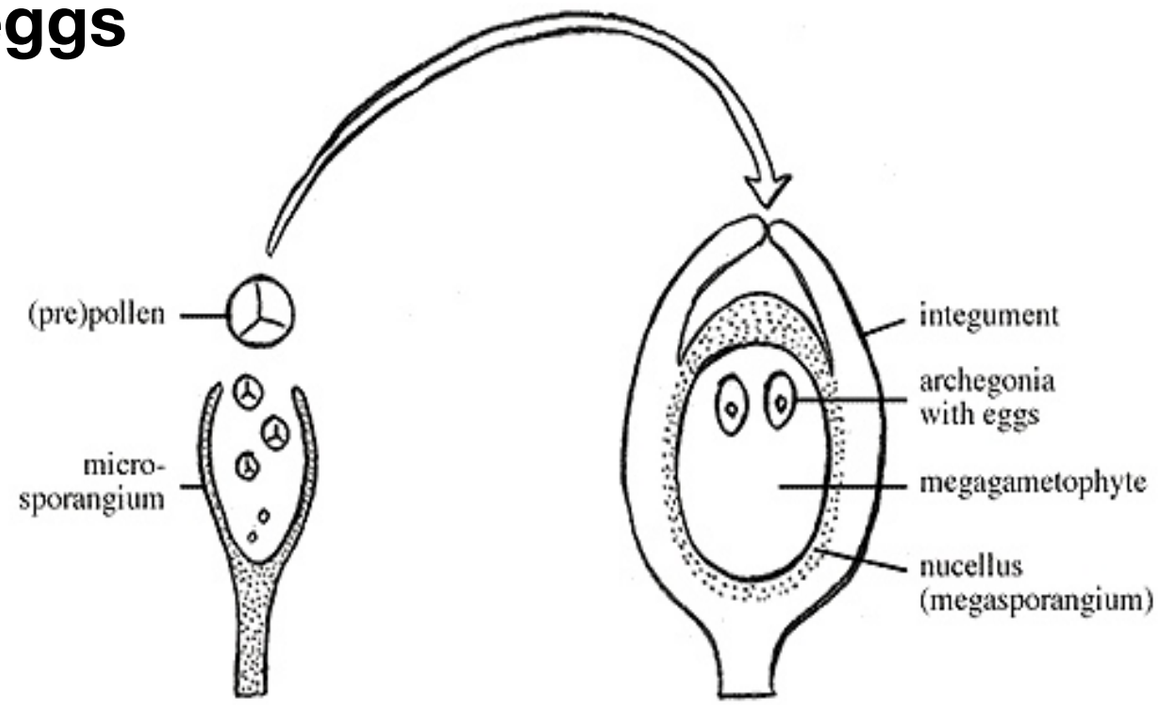
Charles Darwin (**1859**) The Origin of Species

MALE GAMETOPHYTE OF PINES The pollen has two air sacs to aid dispersal in the wind and it contains 2 gametes. The pollen must germinate close to the female gametophyte in the female cone.

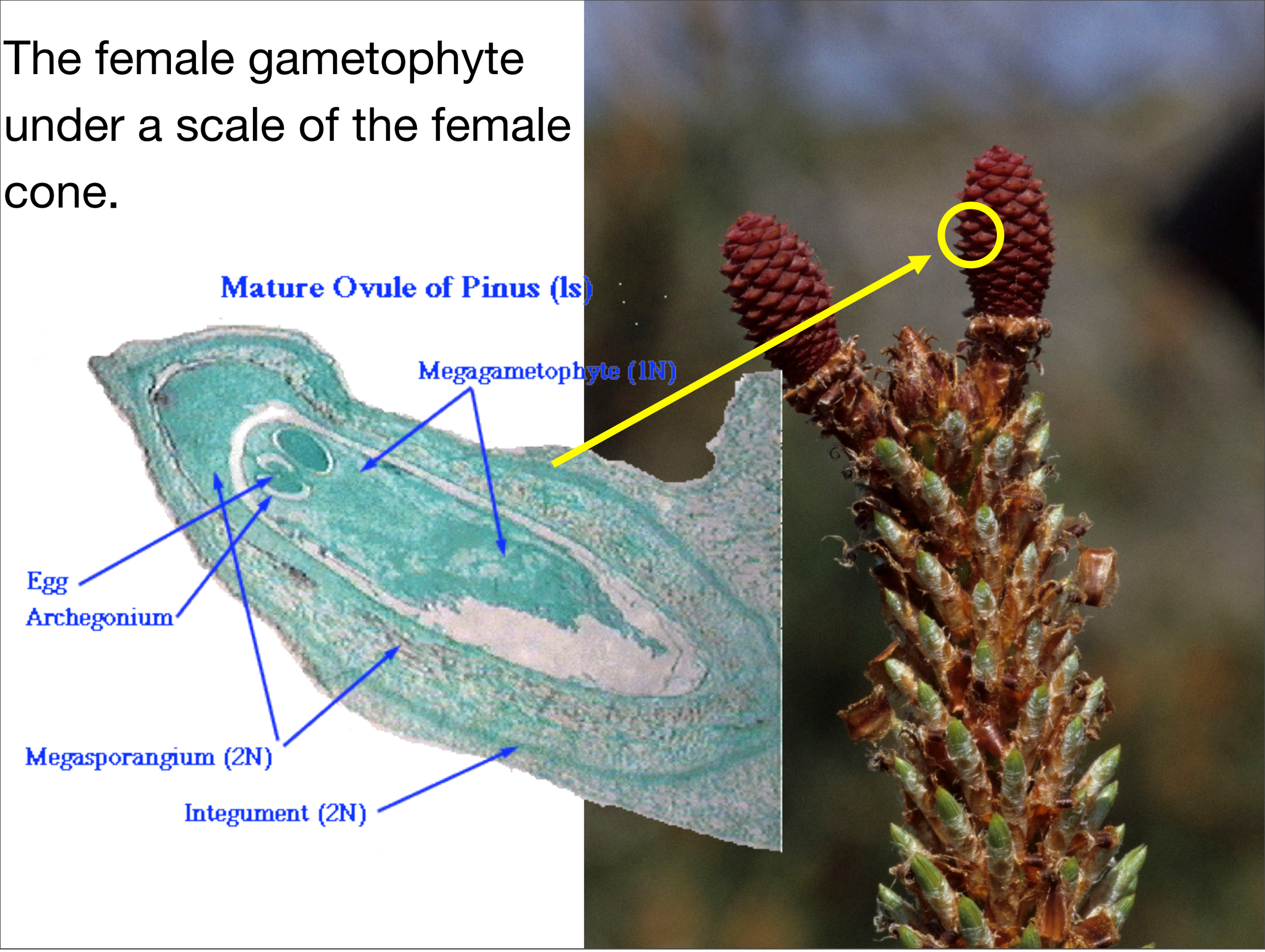


THE FEMALE CONE OF A PINE

has megasporangia in the axils of megasporophylls. The megasporangium is also known as the nucellus. This is almost entirely surrounded by integuments. The small opening is filled with the pollen drop. The pollen must land on the pollen drop close to the female (mega)gametophyte produced in the nucellus. **The female gametophyte consists of c.2,000 cells on which grows 2 archegonia in which are the 2 eggs**



The female gametophyte under a scale of the female cone.



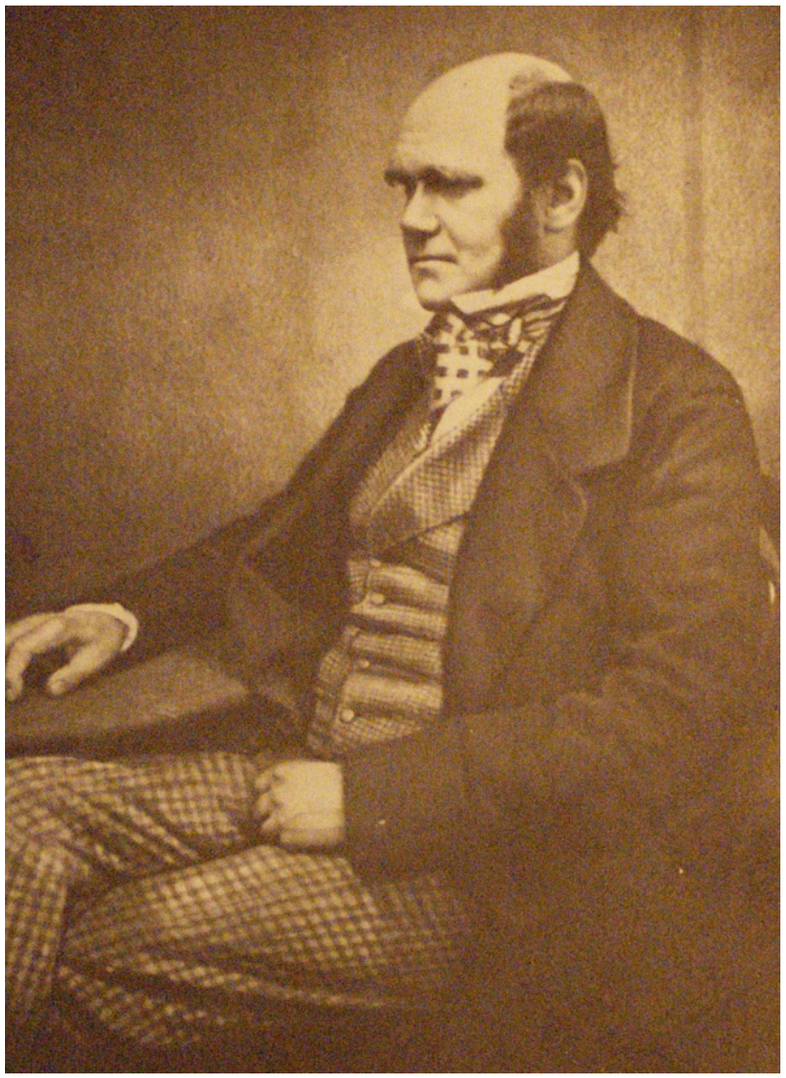
The pollen germinates in the pollen drop and grows towards the archegonium & its egg. Gametes are released and one fertilises the egg to form a zygote that grows into an embryo. BUT the embryo is a long way from the soil. This is not the case in the liverworts, mosses & ferns where the embryo is already at ground level. The seed enables the sporophyte to drop its embryo to the ground. Genetically the **coat** is ♀♀, the **food** supply is ♀ (the female gametophyte) and the **embryo** is ♀♂.

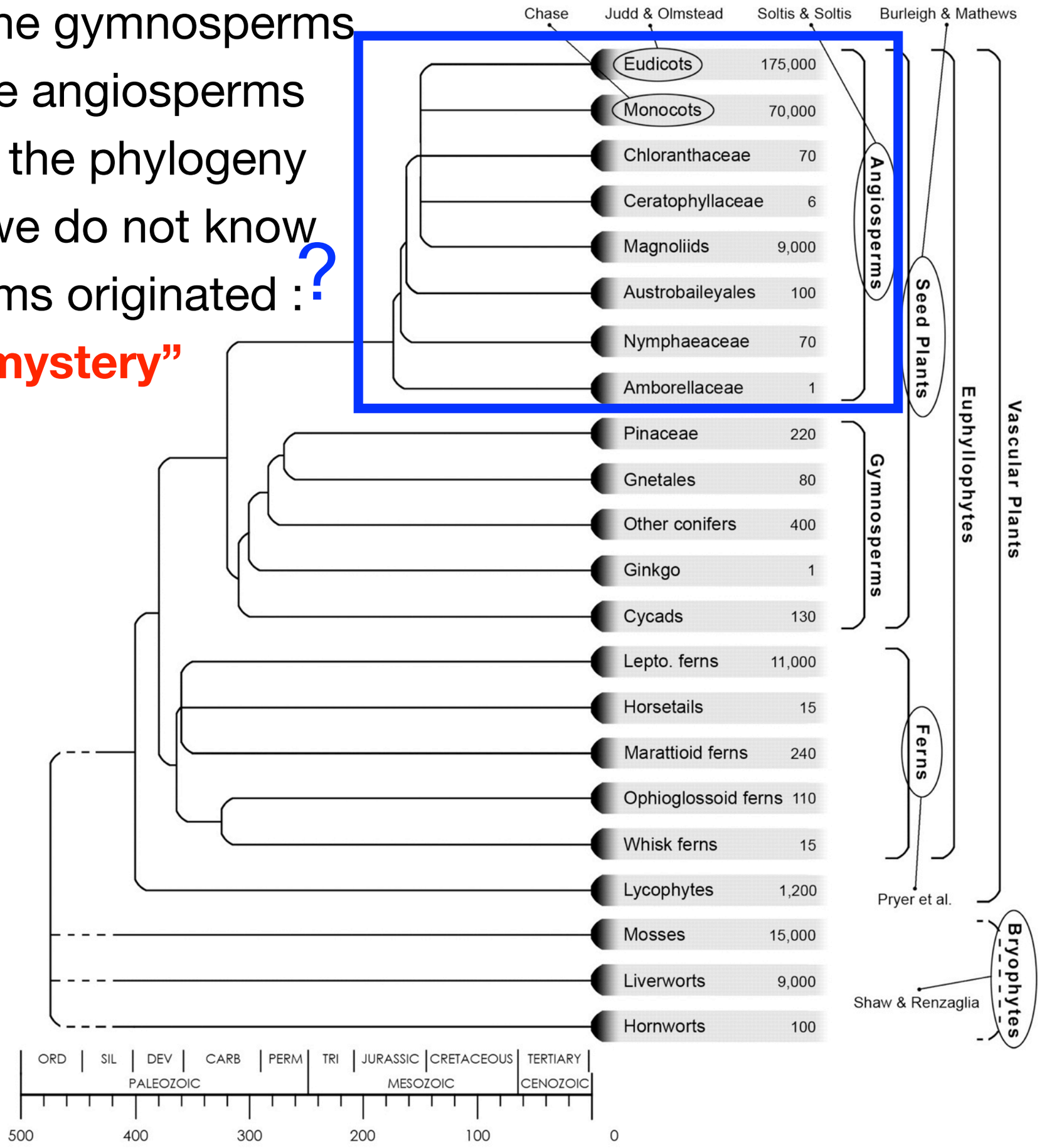
MATURE CONE
and SEEDS of
Pinus sylvatica

Although we know that the gymnosperms are the sister group of the angiosperms and we know a lot about the phylogeny within the angiosperms we do not know from what the angiosperms originated : ?

Darwin's "abominable mystery"

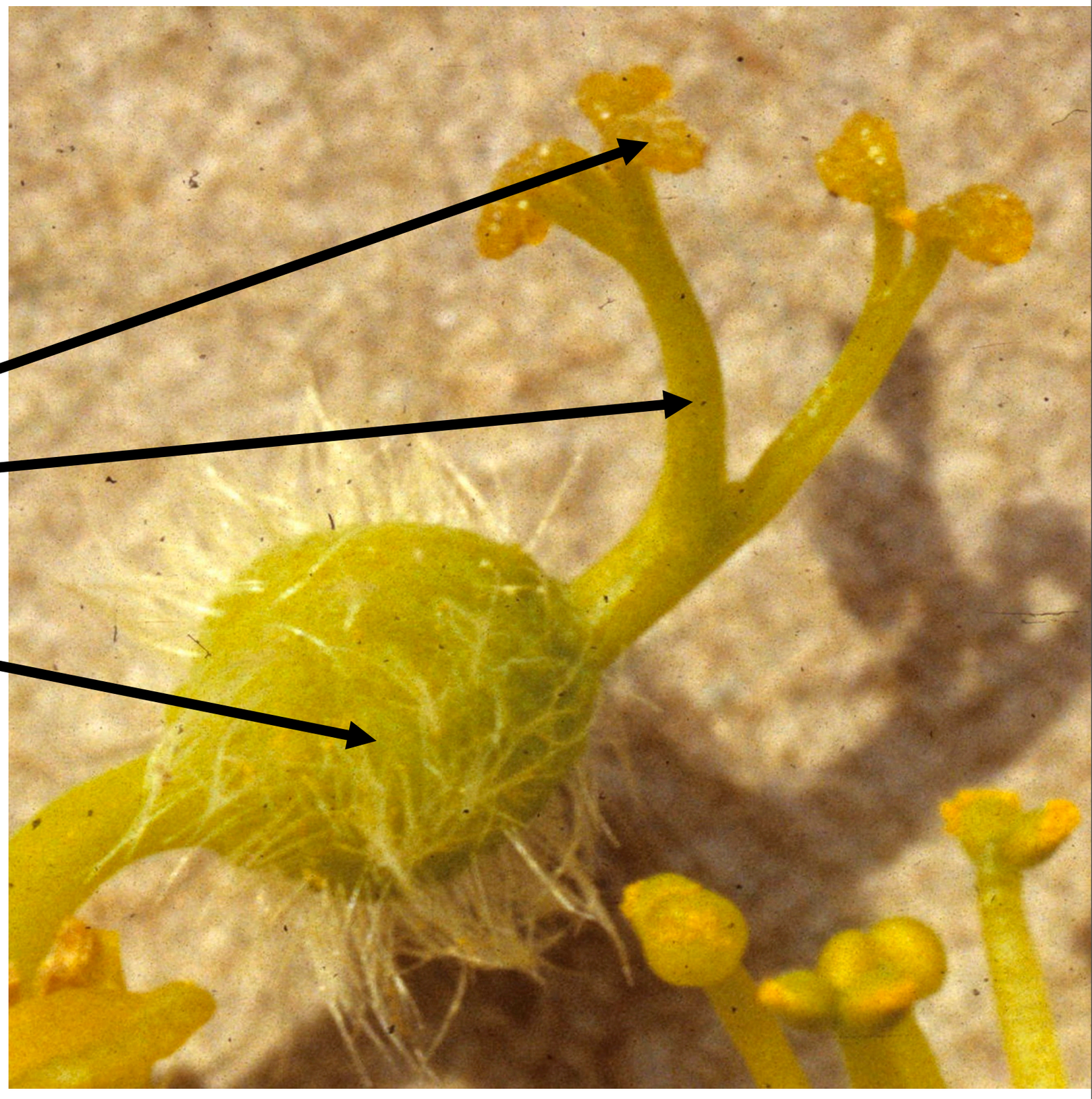
[Frollich & Chase (2007)]





New characters found in the angiosperms include the **CARPEL.** This consists of a **stigmatic surface**, a **style** and an **ovary**

There may be just one carpel or several fused together for all or part of their length.



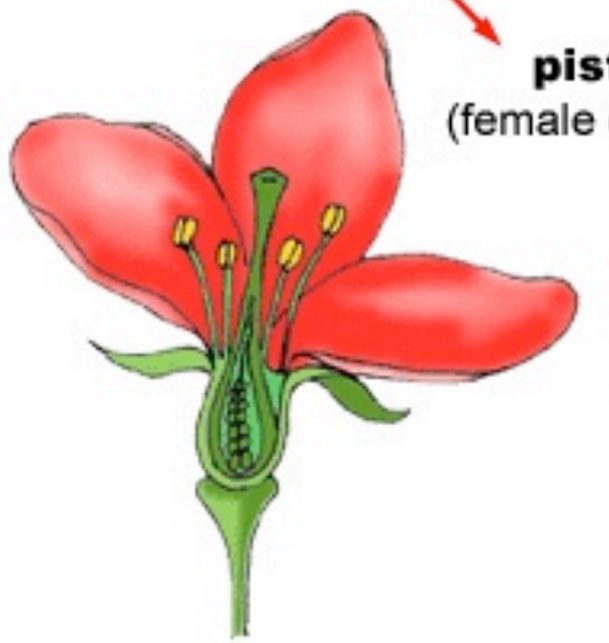
The carpels are located in the flower. In bisexual flowers the stamens are situated close to the carpels. Pollen has to be moved from the stamens to the stigmatic surface <u>preferably on a different plant</u>. Many plants have strategies to avoid or prevent self pollination

The **microsporangia** of angiosperms are situated in the stamens. The **megasporangia** are in the ovules in the ovaries at the base of the style. The pollen tube has to grow down the style to the female gametophyte in the ovary

flower
(bisexual)

stamen
(male organ)

mature plant
with stem, roots
and leaves



pistil
(female organ)

embryo
(inside seed)

ovule
(containing a
megaspore
mother cell)

anther
(containing
microspore
mother cells)

zygote

sporophyte (2n)

MEIOSIS

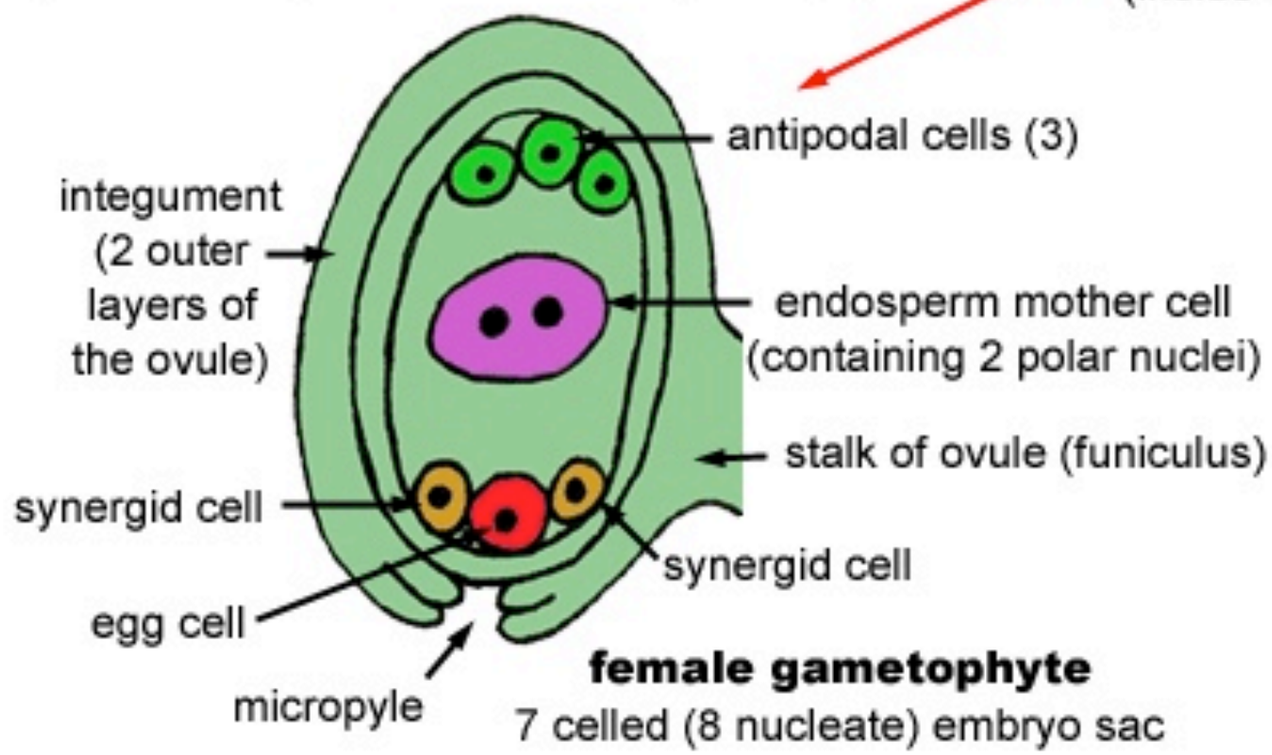
FERTILIZATION

gametophyte (n)

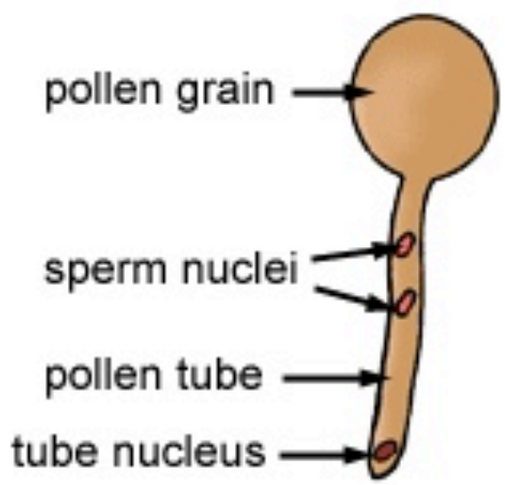
sperm #1 + egg = zygote (2n)
sperm #2 + 2 polar nuclei = endosperm (3n)

one functional
megaspore
(inside ovule)

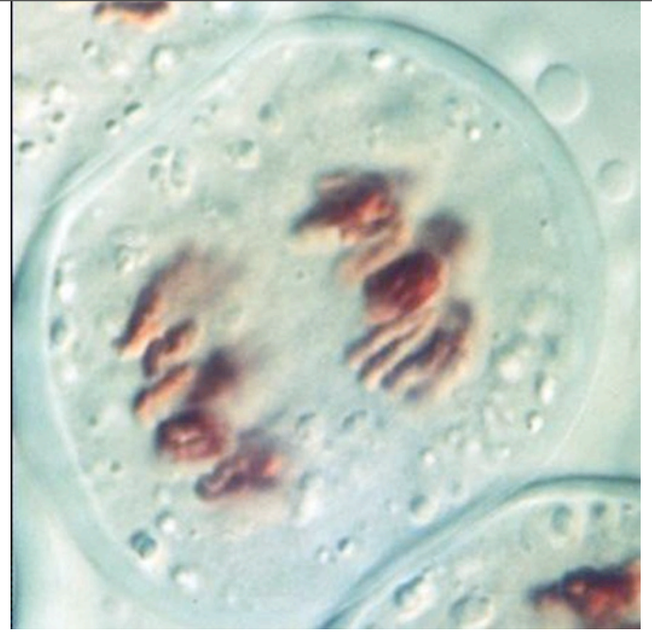
microspore
(pollen grain)

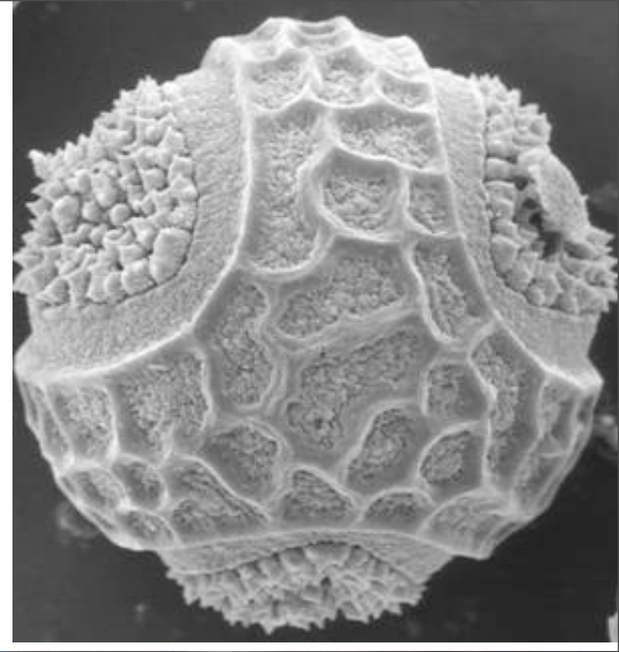


female gametophyte
7 celled (8 nucleate) embryo sac

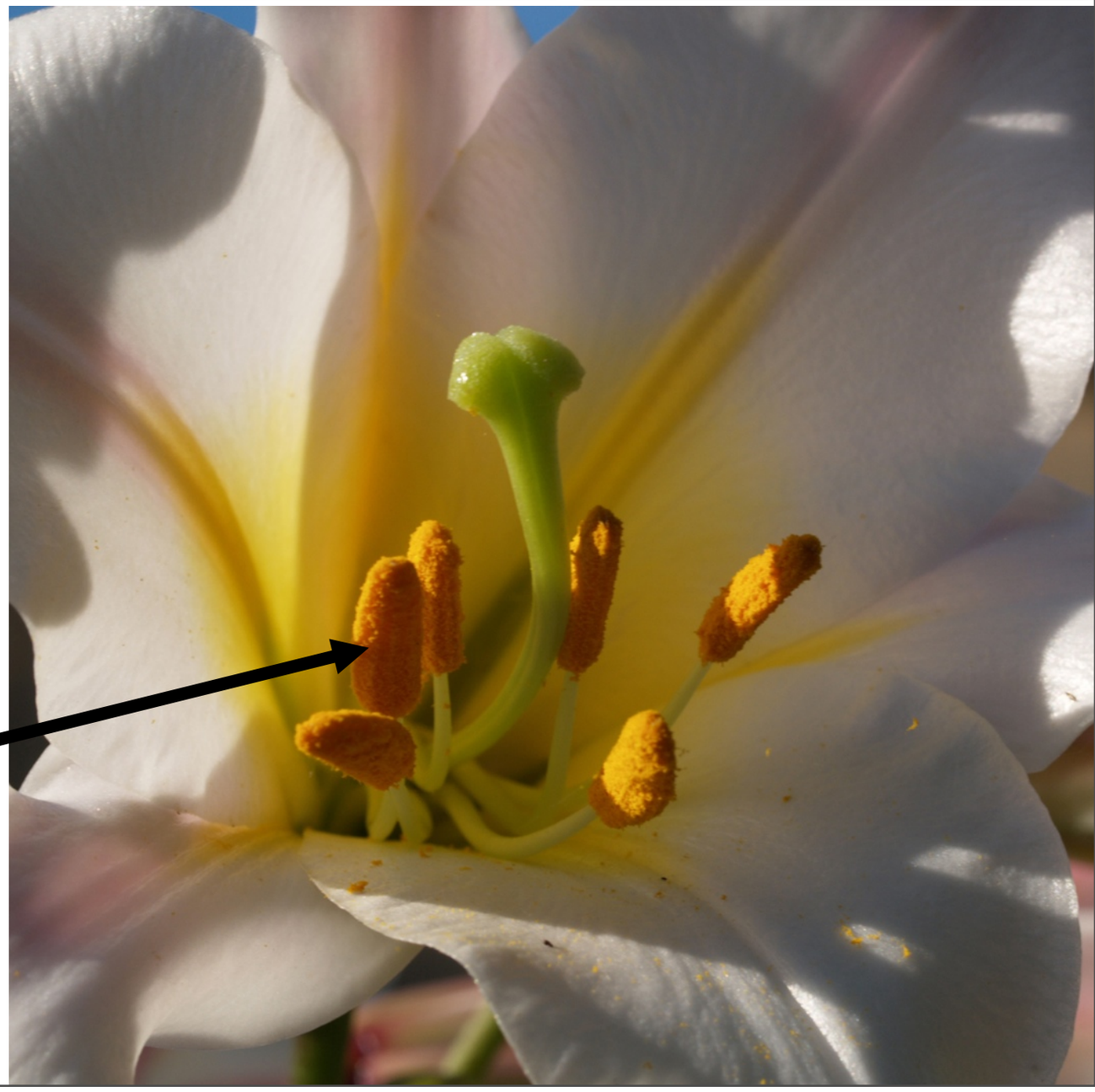


male gametophyte





Pollen grains (immature male gametophytes) are produced in fours (tetrads) in the microsporangia in the anthers



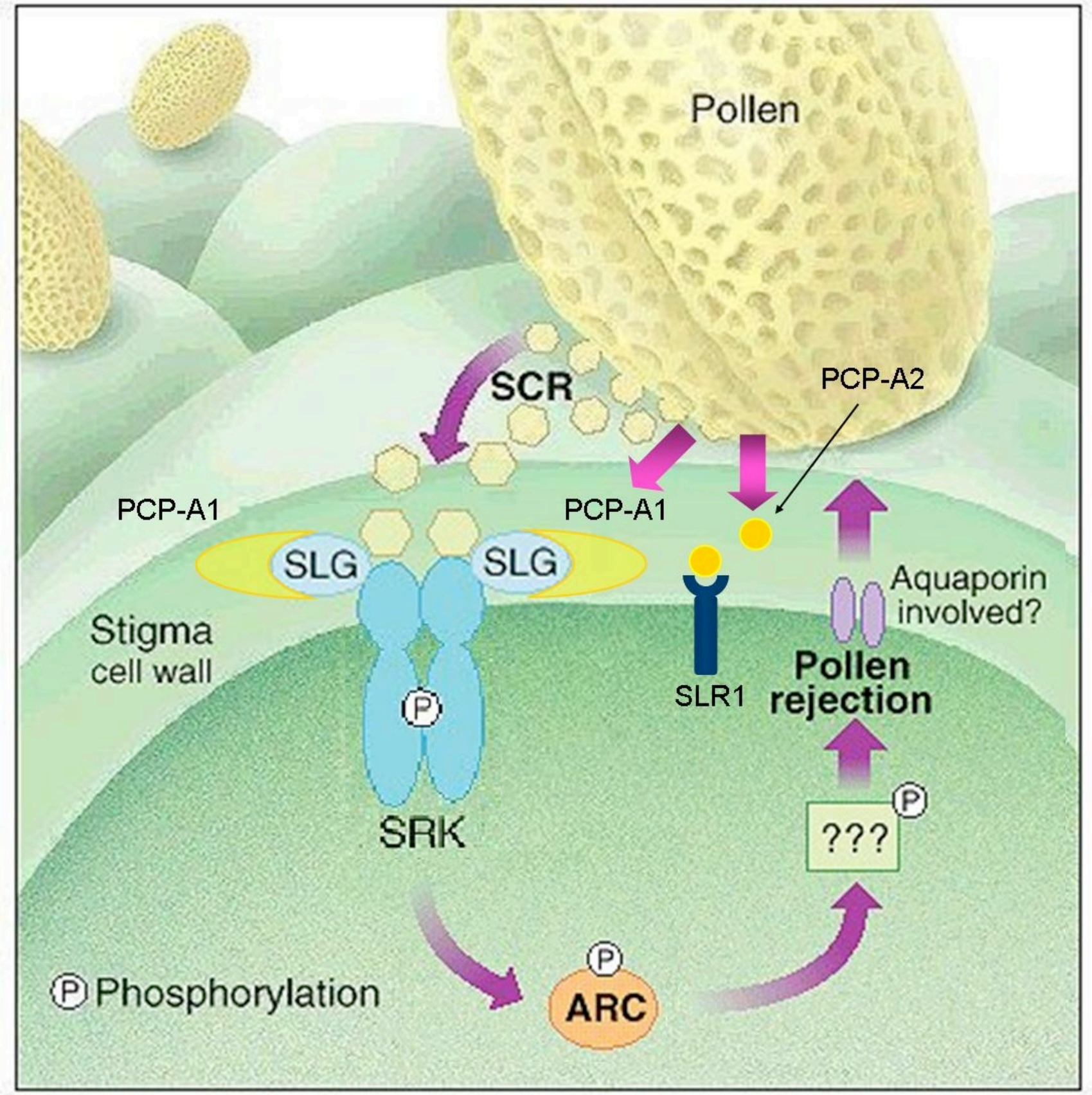
Once the pollen is on the stigma then it can be allowed to germinate by water being made available through the stigmatic surface. Or it may be rejected because it is from an unrelated species or from the same plant.

This may have contributed to the diversity & success of the angiosperms over the gymnosperms

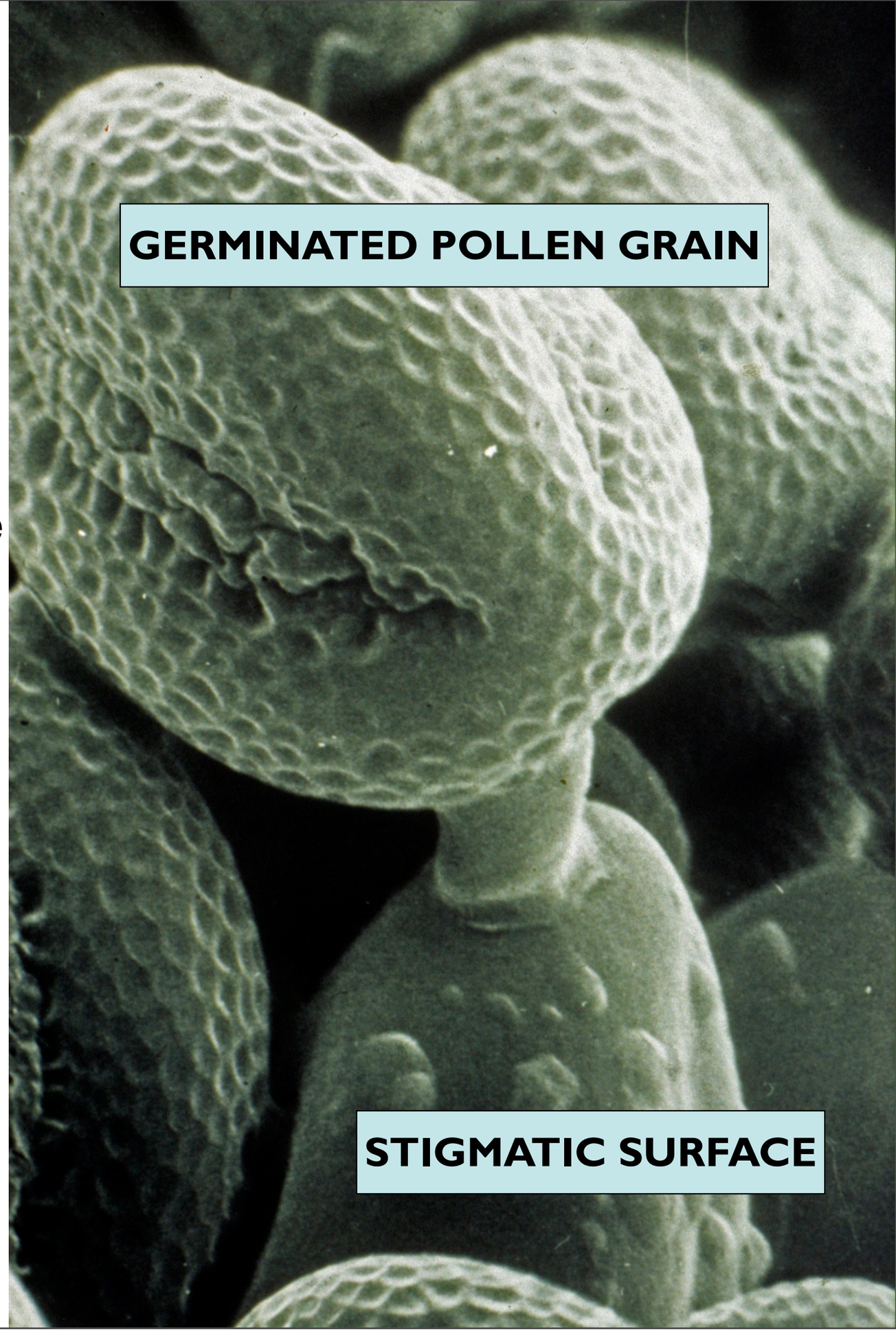
It has also been observed that when pollen of one species is placed on the stigma of a distantly allied species, though the pollen tubes protrude, they do not penetrate the stigmatic surface.

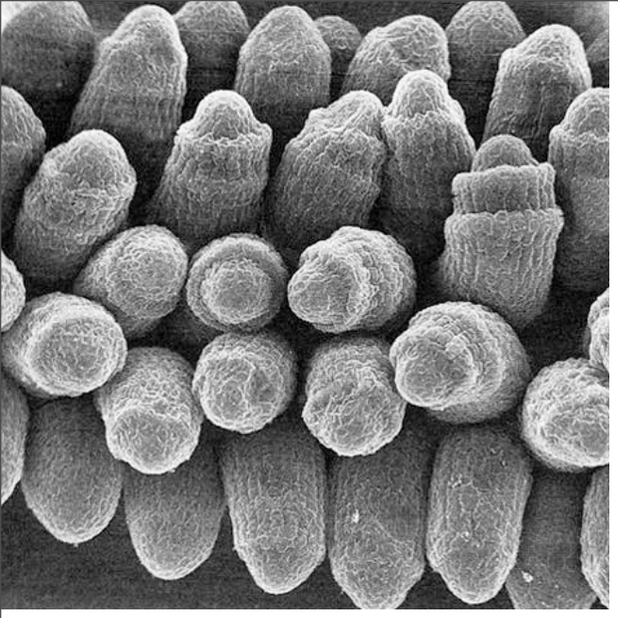
Darwin (**1859**) in The Origin of Species

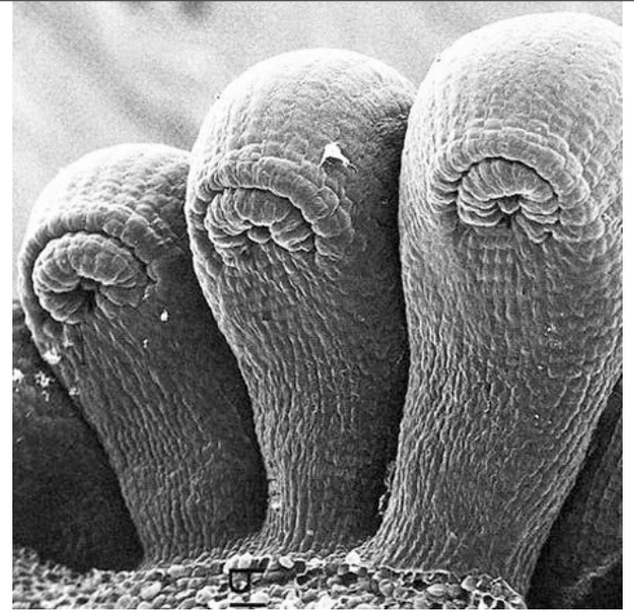
Understanding the conversation between the pollen & stigma is very important for plant breeding but it is not dealt with here.

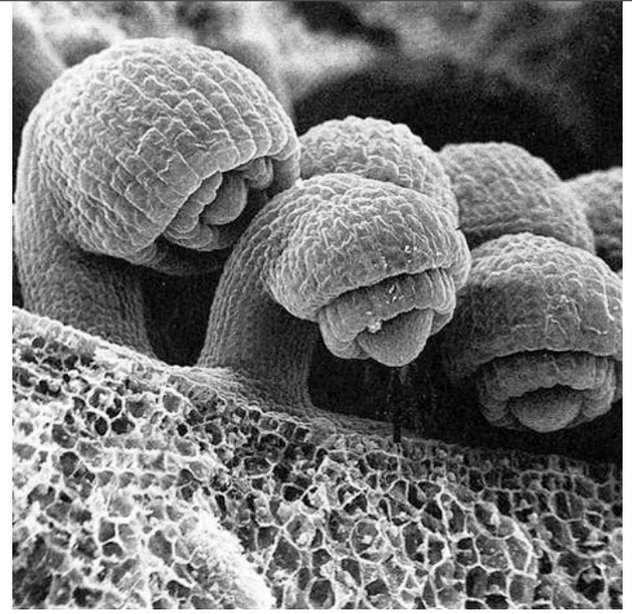


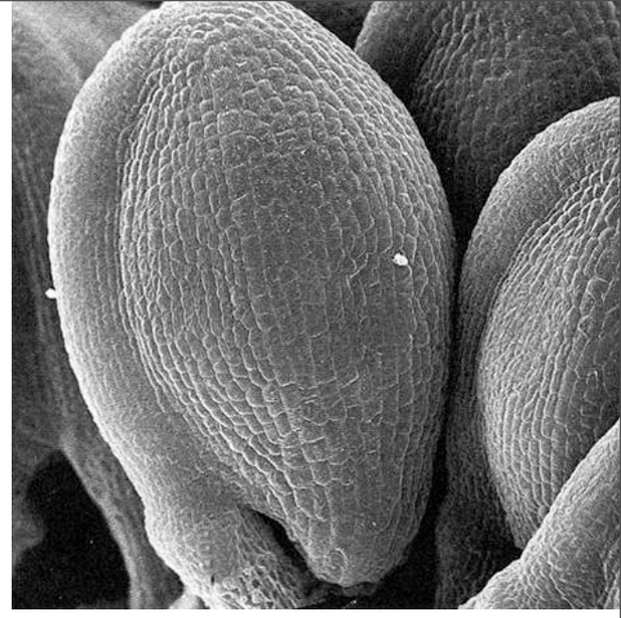
In the angiosperms there are neither antheridia nor archegonia on the male & female gametophytes respectively. The mature male, microgametophyte has 1 cell that contains two gametes. The female, megagametophyte has just 7 cells. The megagametophyte is retained inside the ovule. The pollen tube grows to the ovule & releases its 2 gametes. One fertilises the egg cell giving the zygote. The other gamete fertilises the di-haploid central cell to give the triploid endosperm that is the food supply for the young diploid embryo in the seed. This is **double fertilisation**. (electron micrograph by Hugh Dickinson)

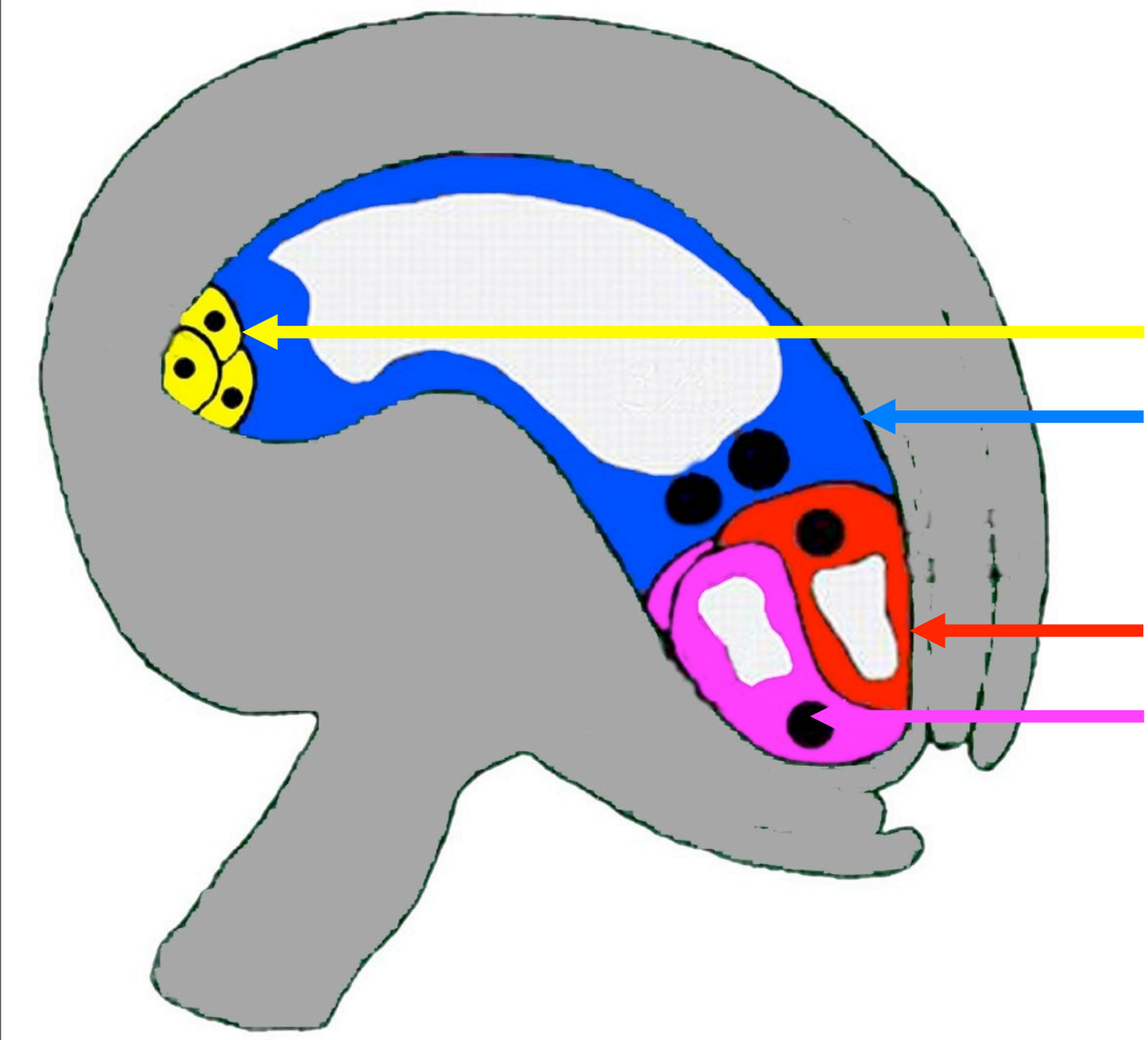








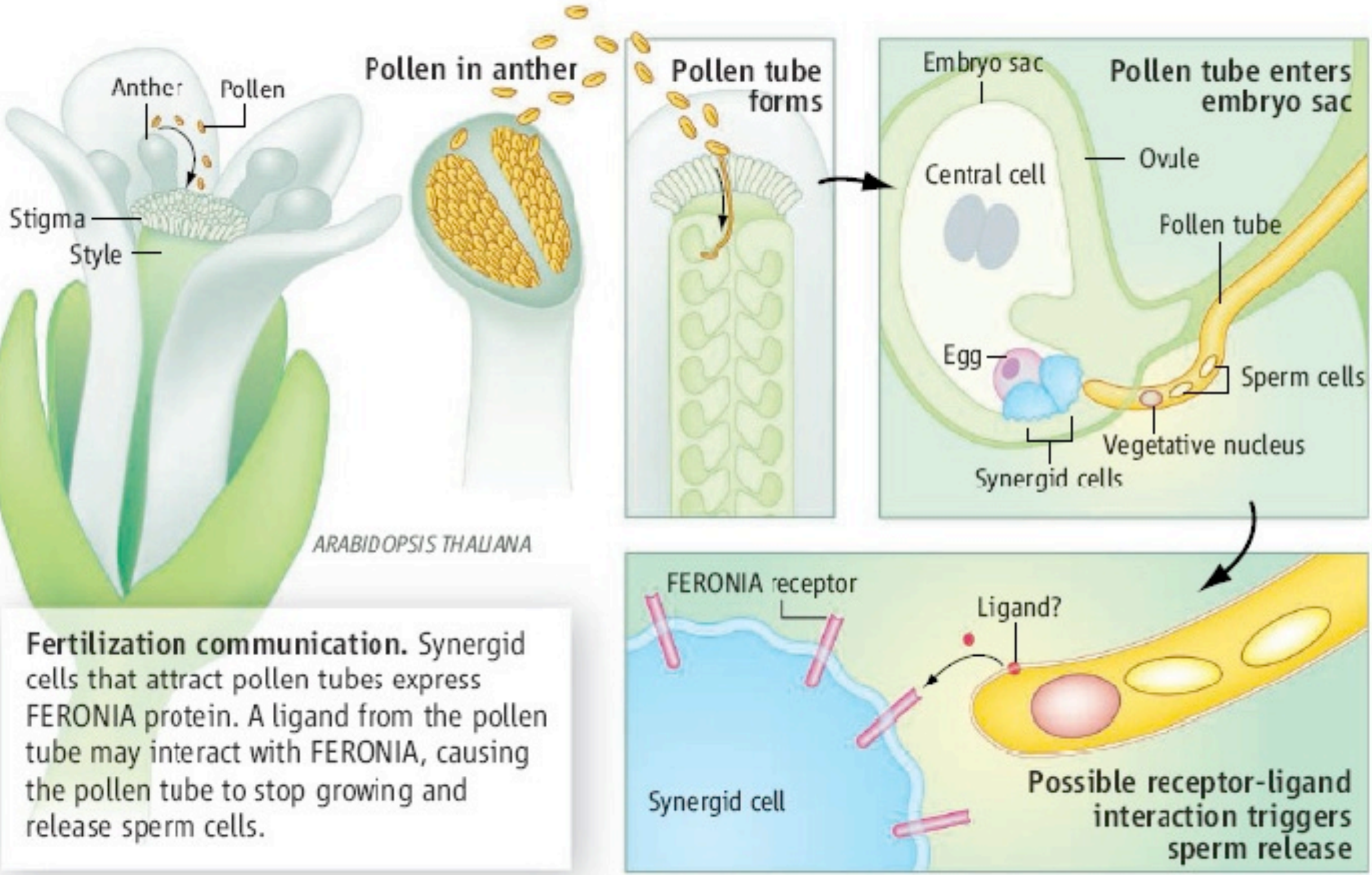




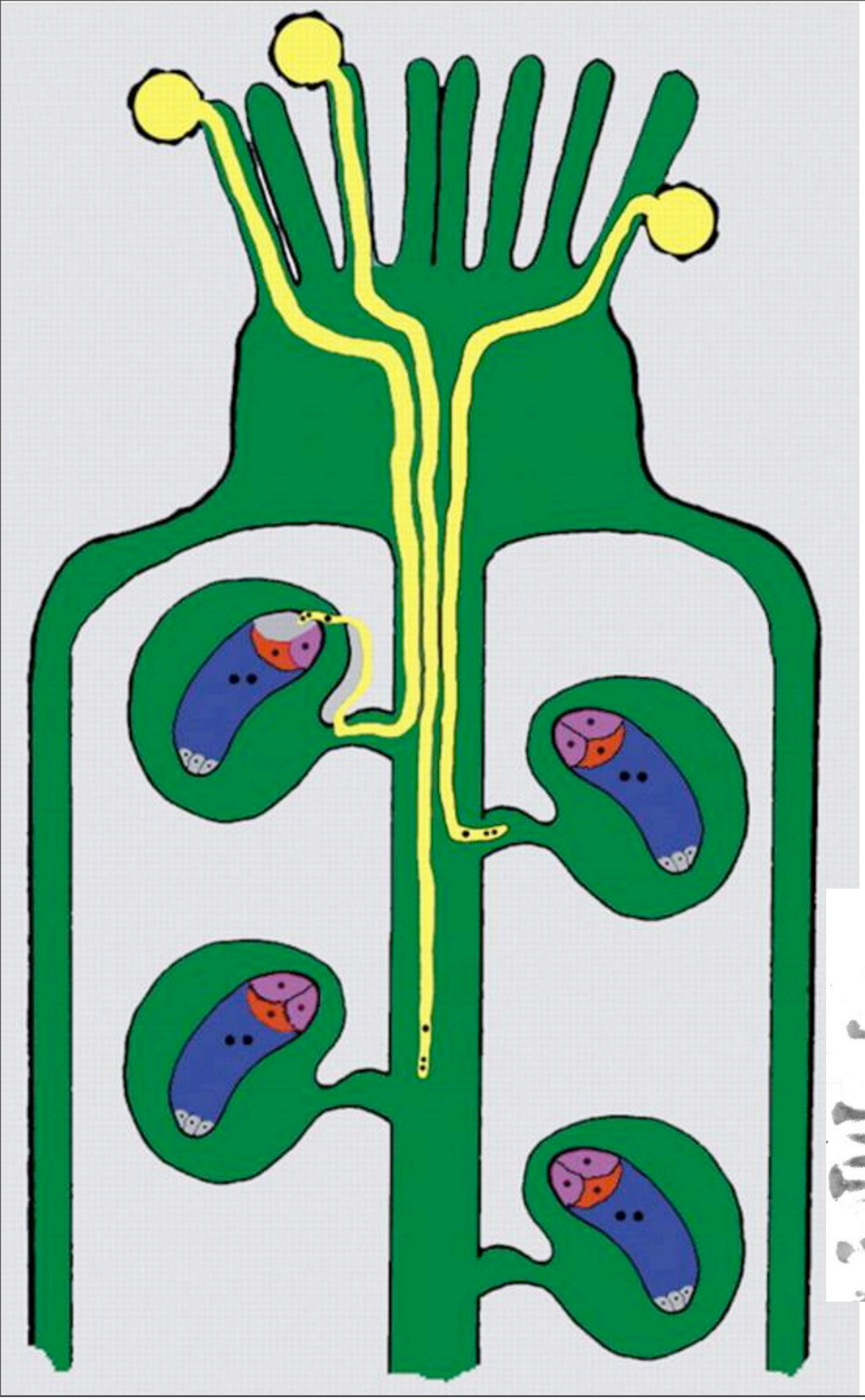
The embryo sac (female gametophyte) develops inside the ovaries. There are 3 antipodal cells, one central cell (with 2 haploid nuclei), one egg cell and 2 synergids.

Lilium female gametophyte – 7 cells & 8 nuclei

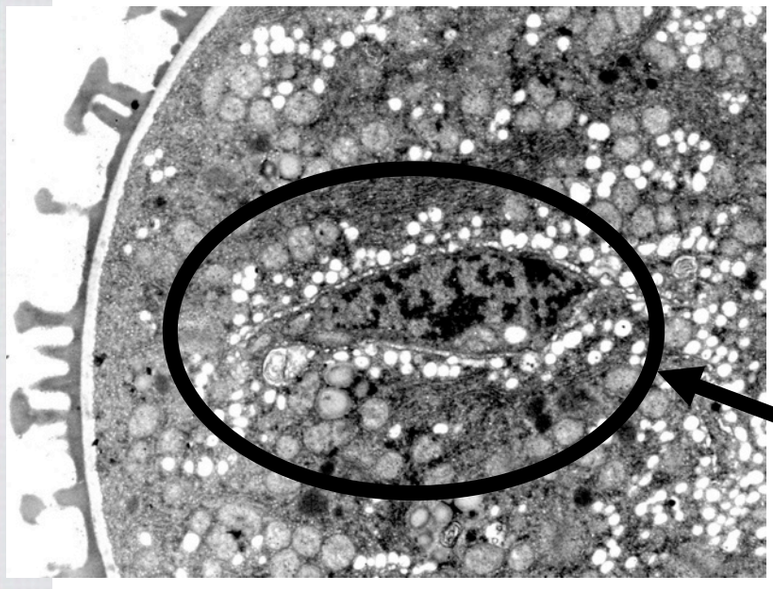
Angiosperm gametophyte interaction

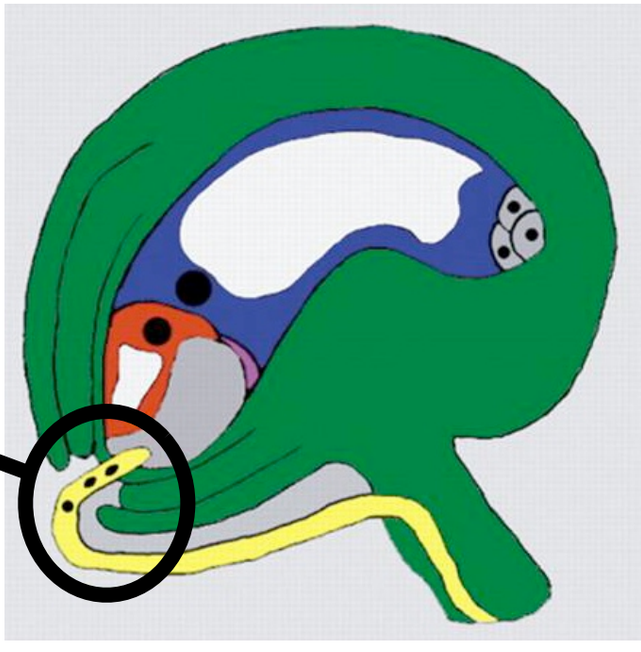


Fertilization communication. Synergid cells that attract pollen tubes express FERONIA protein. A ligand from the pollen tube may interact with FERONIA, causing the pollen tube to stop growing and release sperm cells.



In the angiosperms two fertilisations are required for the development of each seed (**double fertilisation**). One sperm fuses with the haploid egg cell to give the diploid embryo. The other sperm fuses with the di-haploid central cell to give the triploid endosperm. The endosperm is the food supply for the embryo in the seed as well as the major food source for *Homo sapiens*.





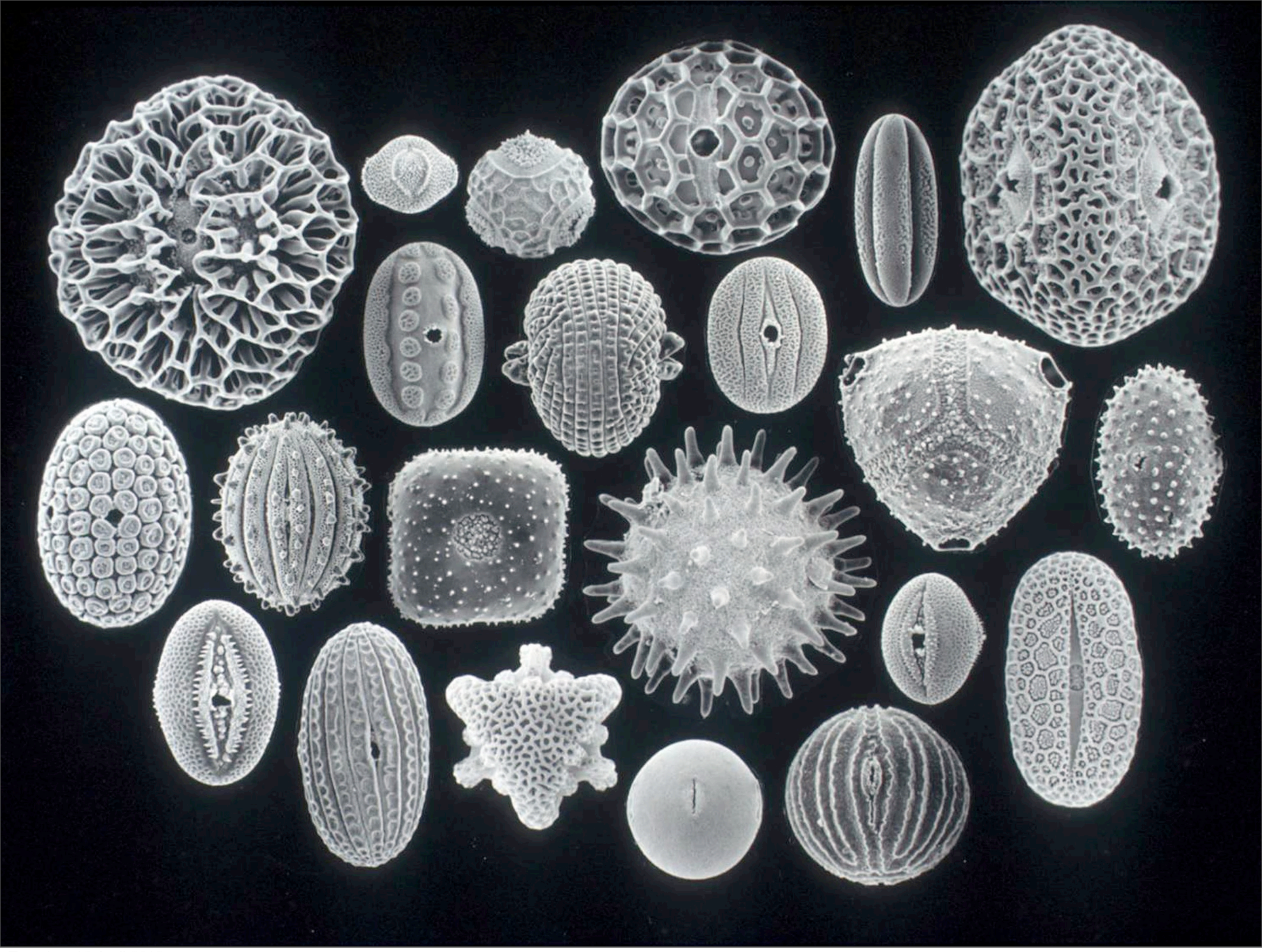
The ovule develops into a seed. Genetically the seed coat is ♀♀, the food supply is ♀♀♂ (the triploid endosperm) and the embryo is ♀♂.

In liverworts, mosses (right) & ferns long distance dispersal is by spores. At the same time gametophytes are brought (passively) together

In seed plants (left) gametophytes are brought together by a range of agents. This is **POLLINATION**.

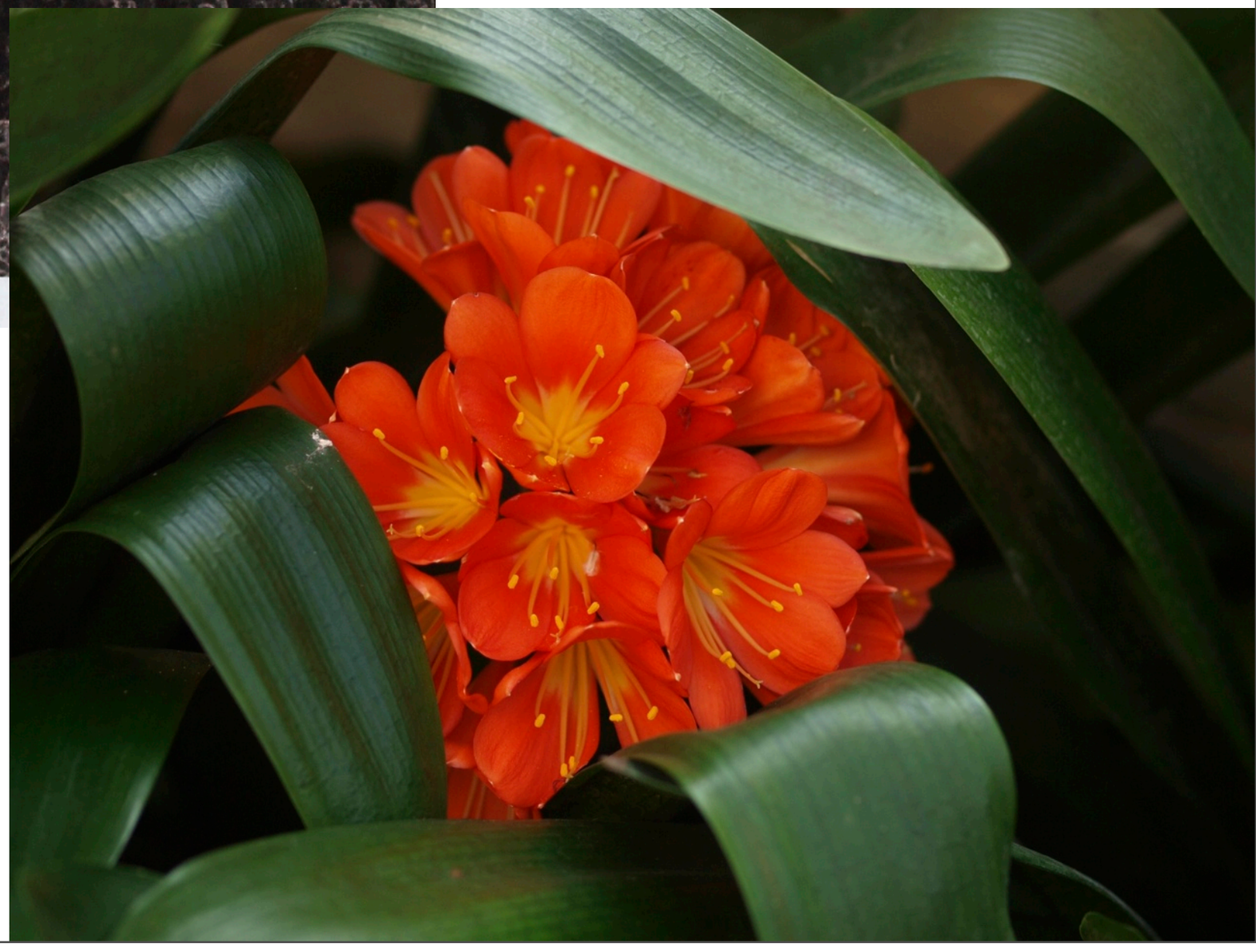
Pollination –

a tale of sex, lies and putrefaction



Tuesday, 16 April 2013

Poison bulb *CRINUM JAPONICUM*



Finding the right stigmatic surface

Some plants produce up 3,000,000 pollen grains for every ovule and trust their fate to the wind.

Others use visual, olfactory & taste stimuli to attract an animal intermediary.

In the process the plants employ a mixture of rewards and deceit.

Tuesday, 16 April 2013

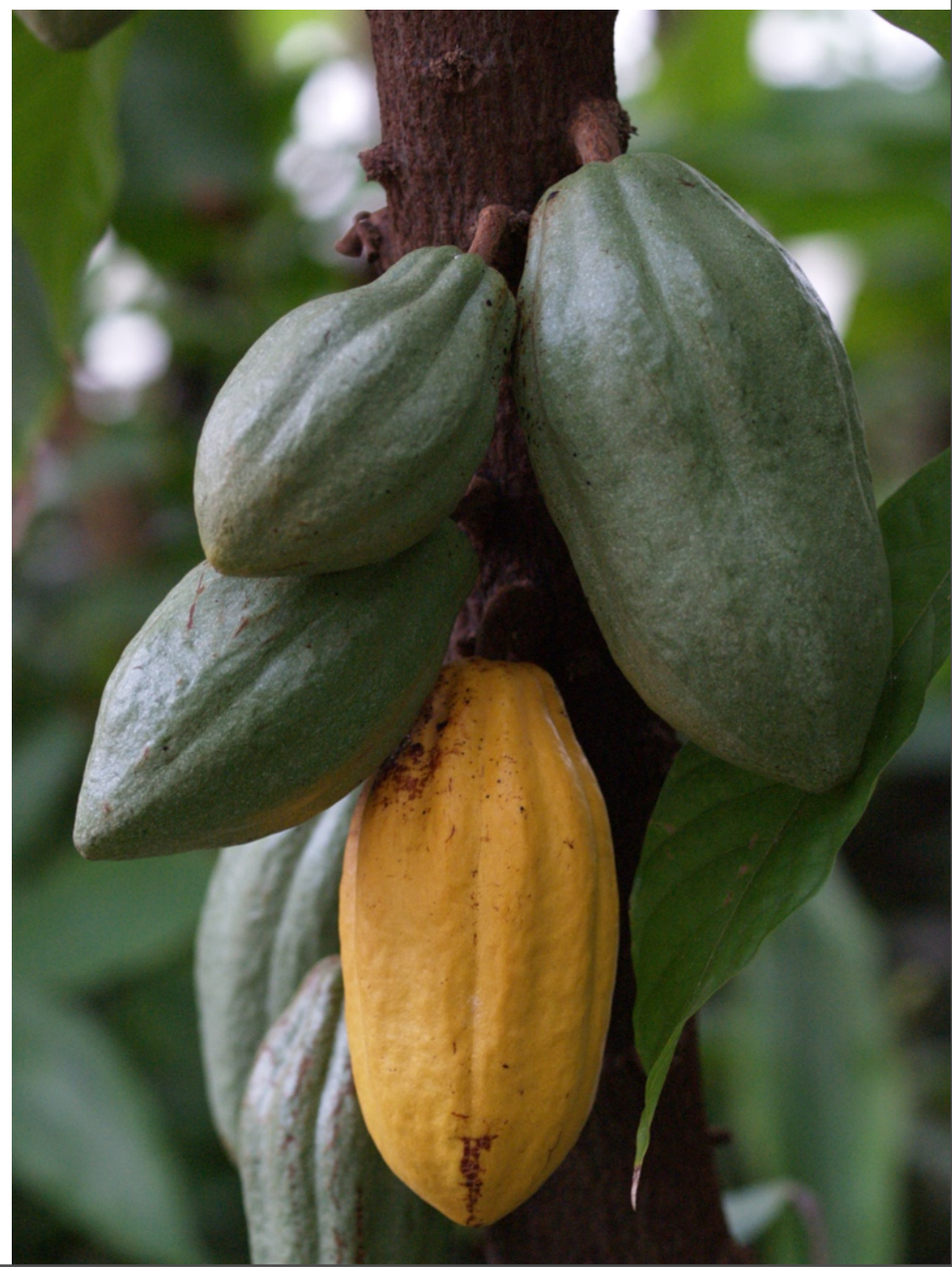
Tuesday, 16 April 2013

Biting midges -
Ceratopogonidae

Biting midges -
Ceratopogonidae

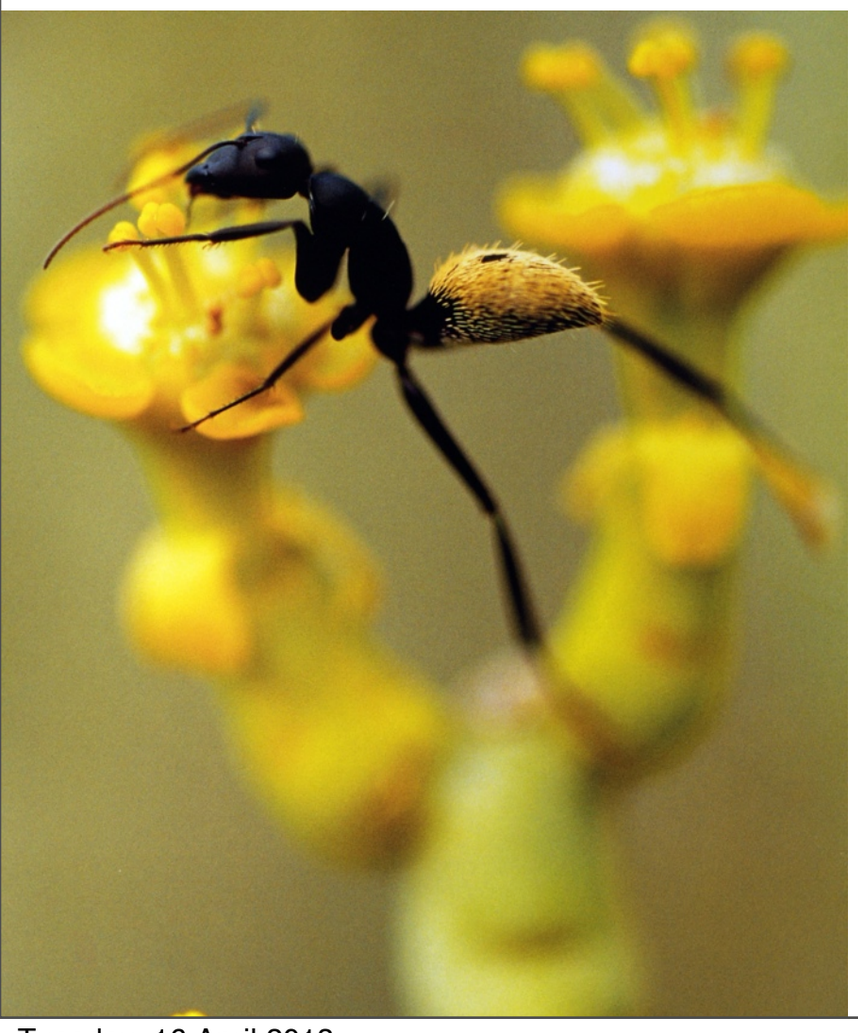
Biting midges -
Ceratopogonidae

Biting midges – Ceratopogonidae pollinate *Theobroma cacao*



Pollination syndromes in the genus *Euphorbia*.

(clockwise from top left) flies, birds, snails, wasps & ants



Pollination syndromes are rarely phylogenetically important. For example tropical oak species are insect pollinated while temperate species are wind pollinated.

NON-BIOLOGICAL POLLINATION

i.e. wind & water

Wind pollination has evolved many times and is the most common pollination syndrome.

It is **neither a primitive nor an advanced trait**. Pollen of wind pollinated species tends to be small (20-30μm), dry, smooth and non-adhesive. *Artemisia* species that live at alpine altitudes have lost the sticky pollen surface of their relatives.

Wind pollinated grasses & plantains (*Plantago* sp) – convergent evolution

Tuesday, 16 April 2013

Castor oil (*Ricinus communis*) forcibly ejects its pollen into the wind

Pollen grains of *Cornus canadensis* are ejected with a force equal to an acceleration of 2,300 gravities

Catkins of male flowers on *Quercus coccifera* in Portugal.

All British timber trees, e.g. hornbeam (*Carpinus betulus*) are pollinated by wind

Male *Pinus* cones

Female *Pinus* cones

Pistachios

This year’s male catkins and last year’s female “cones” on alder (*Alnus* sp)

Tuesday, 16 April 2013

Hazel (*Corylus*) flowers:
Tiny female flower
with red stigma

Catkins of male flowers

3 million pollen grains are
produced for each female
flower

(Statisticians have proved that 9 times
out of 10, million to 1 chances
actually happen (Pratchett 1995))

Birch (*Betula*) catkins have flaps that prevents the pollen from falling out of the catkin due to gravity. The pollen must be actively blown from the flowers by strong wind.

Wind pollination is a common trait of early colonisers such as these alders at Mt St Helens

Grasses are all wind pollinated including the major crops such as rice, wheat & maize

The pollen of maize (sweet corn) has the aerodynamics of a house brick so it is always planted in square blocks & not thin rectangles

Stipa gigantea
flowers at
Cape St Vincent,
southwest Portugal

The grass flower spikelet

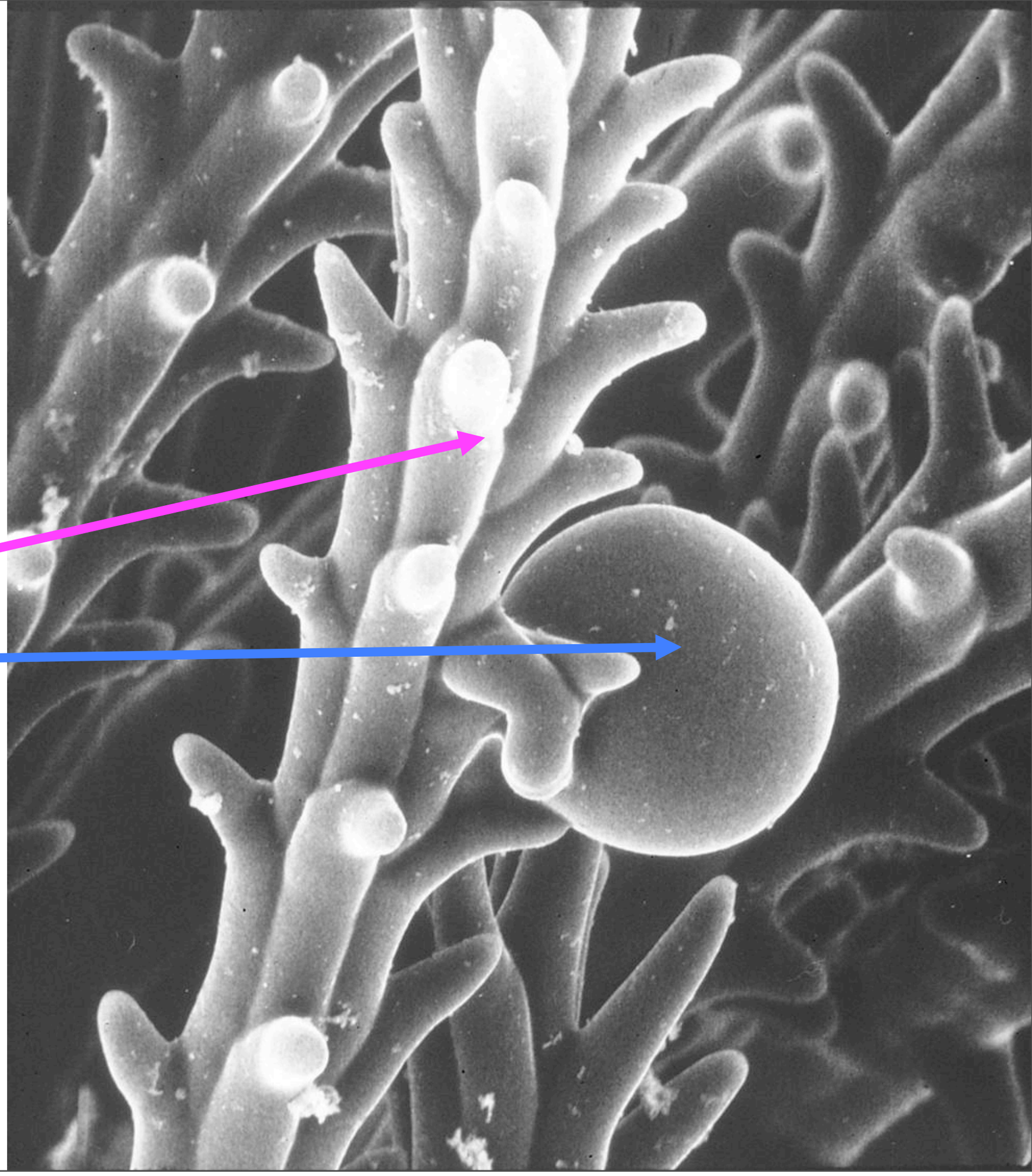
Feathery female stigma

Three male anthers

The grass flower:

Female stigma

Male pollen

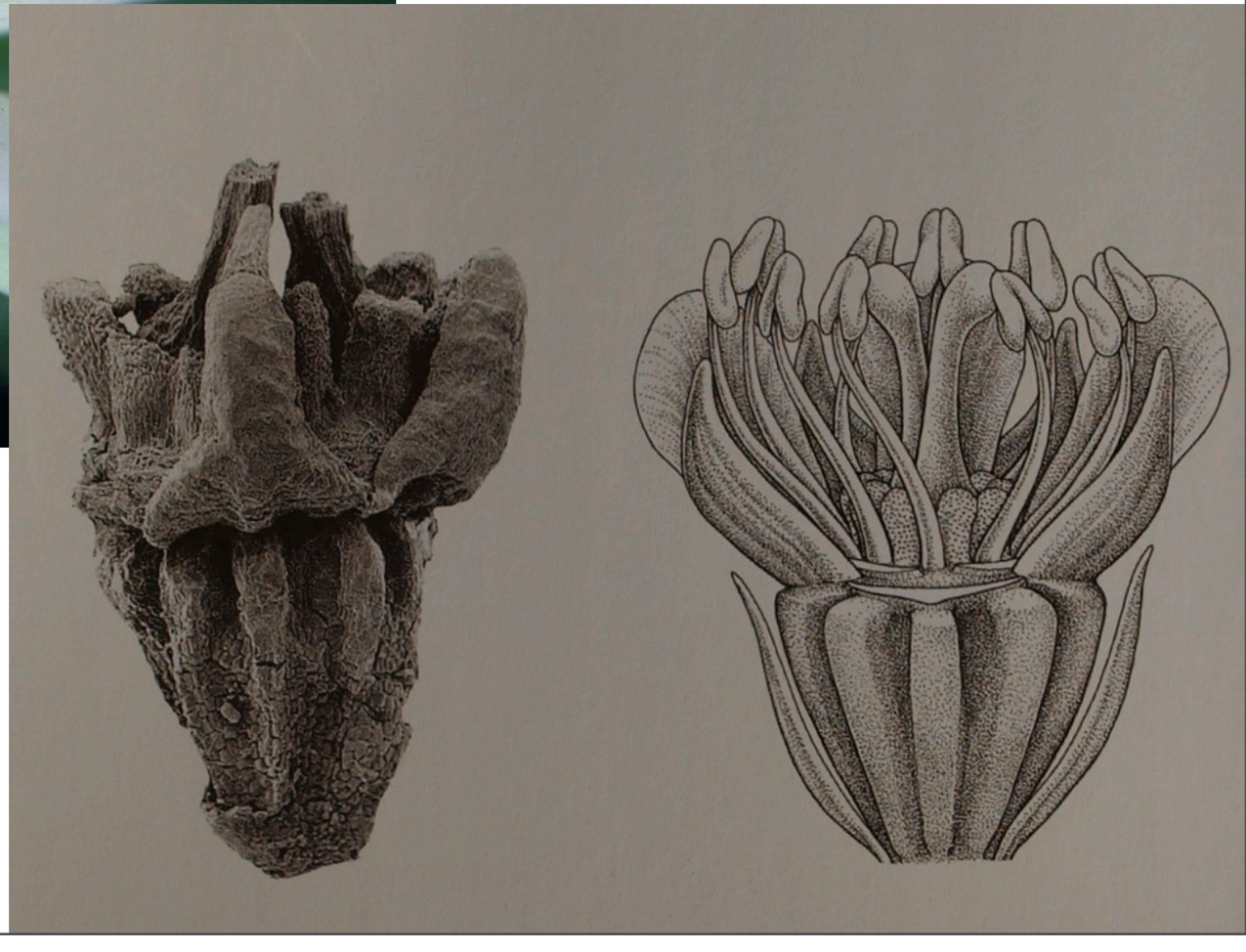


The MG5 meadow at the Harcourt Arboretum, Nuneham Courtenay where not all the plants are wind pollinated

Not all meadow plants are wind pollinated

Tuesday, 16 April 2013

Aquatic plants are rarely pollinated by water. *Nymphaea* flowers are beetle pollinated; evidence of their ancient ancestry?



Elodea (Canadian pond weed) releases pollen onto the water surface. It drifts on to the stigmatic surface that is held at the surface of the water.

Valisneria – male flowers float to the surface & open like a raft with 3 anthers around the edge. Female flowers floating on the water surface have protruding sticky stigma & these “rescue” the pollen off the anthers.

BIOLOGICAL POLLINATION

i.e. animals