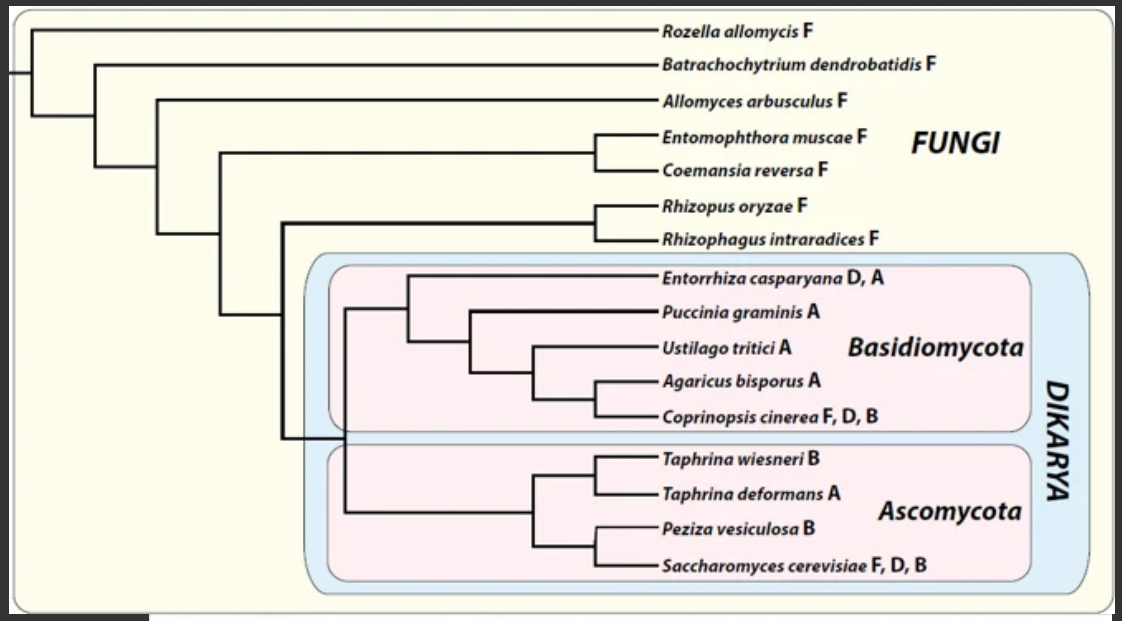
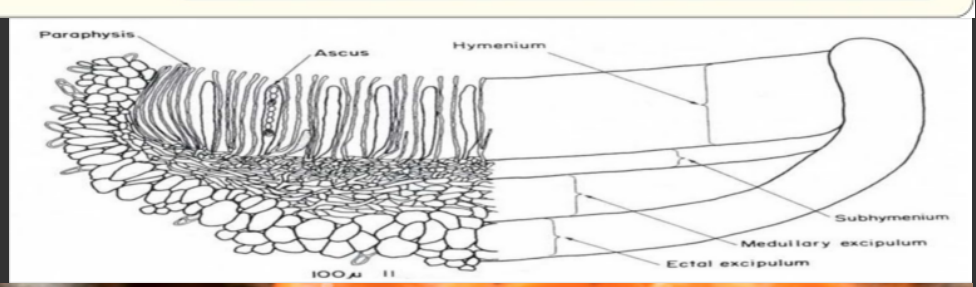
Ascomycetes and the limits of sex

Topics (just the very basics):

- Ascomycetes
  - Characters
  - Phylogeny and evolution
  - Major groups
  - Life cycles
  - Ecology
- The species concept in fungi
- Dikaryotism
- Closer look at several subgroups:
  - Saccharomycetales
  - Sordariales
  - Alternaria
  - Xylaria



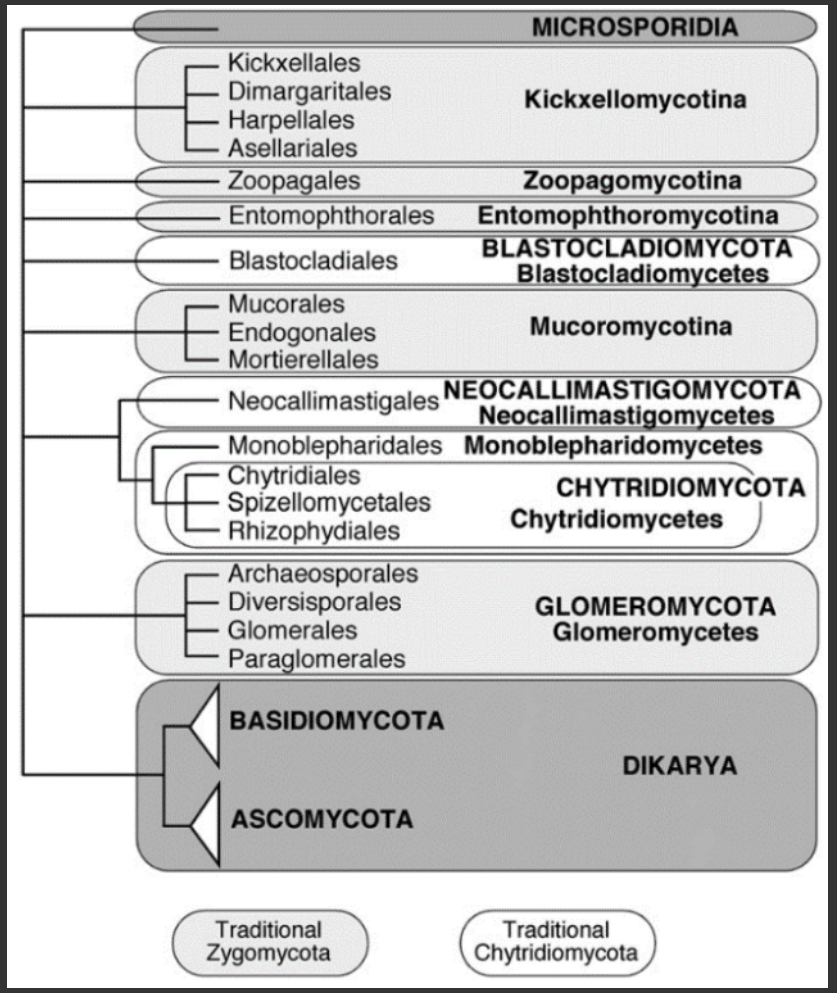


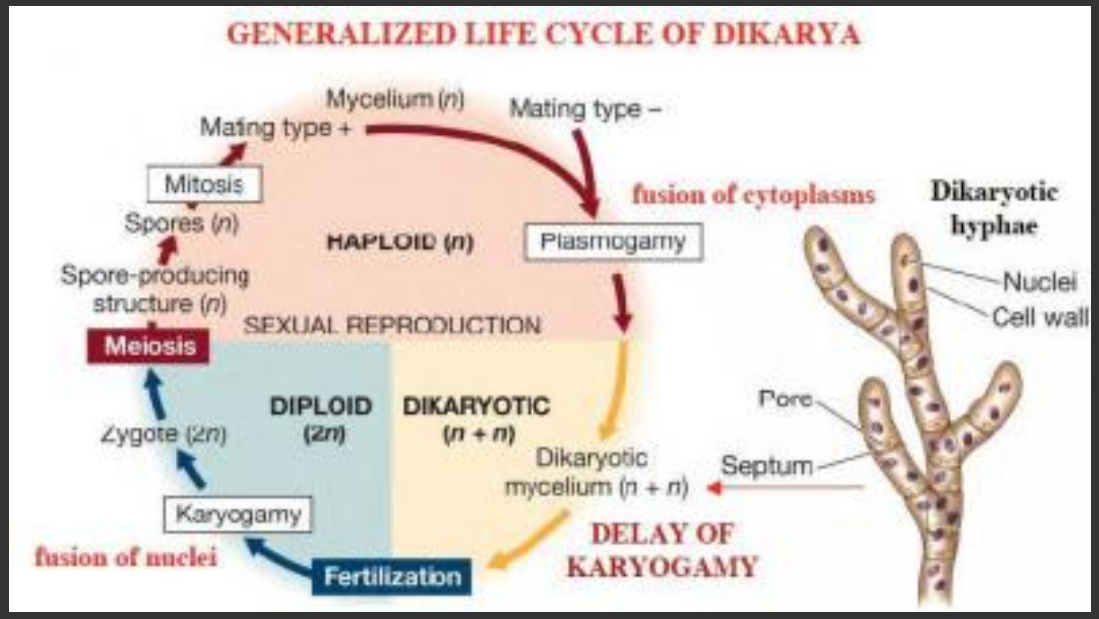
Dikarya

While there's still a degree of confusion about phylogenetic placement of the groups that tradiitionally have been known as Chytrids and Zygos, things are much more clear with the largest group of extant fungi known as Dikarya.

Dikarya:

- Composed of Ascomycetes and Basidiomycetes
- Named after "dikaryotic" genetic state (delayed karyogamy)
- Clearly monophyletic





Ascomycota (the sac fungi)

Largest fungal phylum
Morphologically defined by presence of ascus (Plural: "asci")

Ascus means "sac" and contains spores produced by sex/meiosis

Not ALL ascomycetes are known to undergo sexual reproduction, so asci haven't been observed in all species

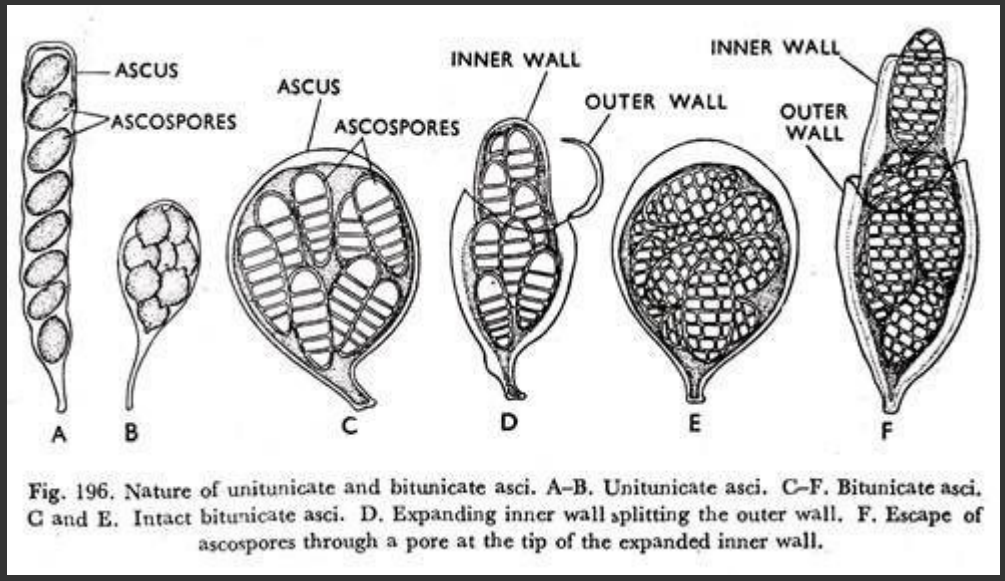
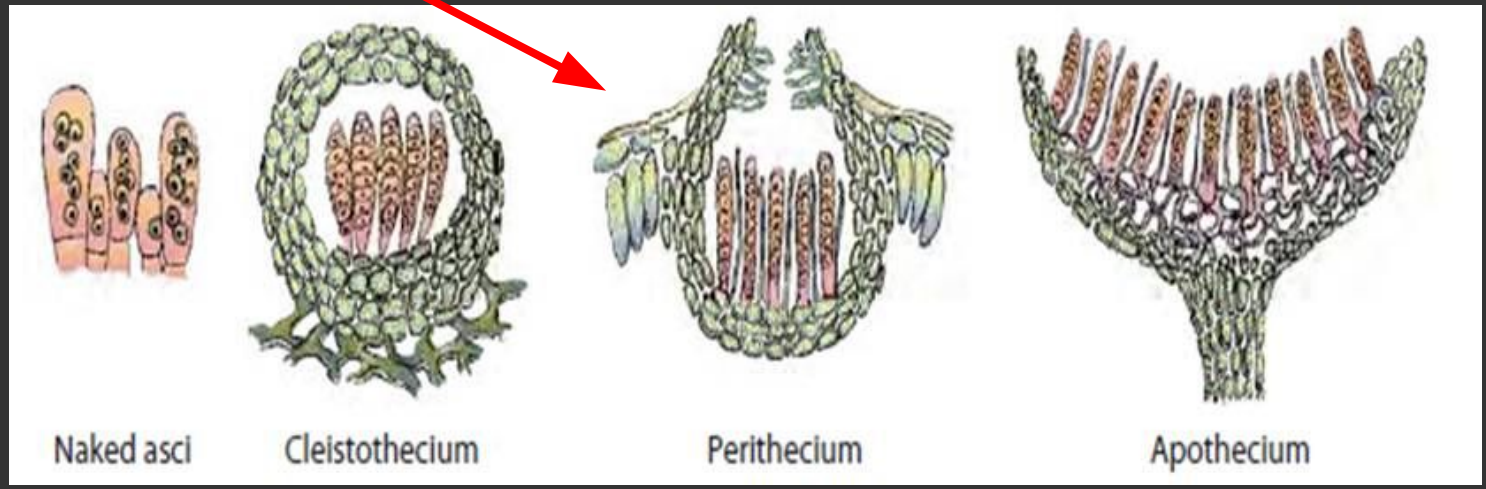
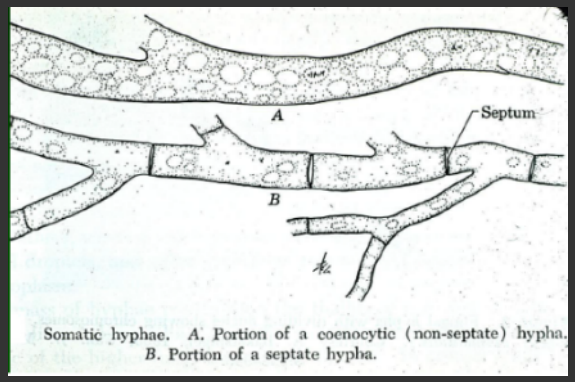


Fig. 196. Nature of unitunicate and bitunicate asci. A–B. Unitunicate asci. C–F. Bitunicate asci. C and E. Intact bitunicate asci. D. Expanding inner wall splitting the outer wall. F. Escape of ascospores through a pore at the tip of the expanded inner wall.

Diversity of sexual macrostructures that house asci



Septate hyphae



Somatic hyphae. A. Portion of a coenocytic (non-septate) hypha. B. Portion of a septate hypha.

Ascomycota life cycle

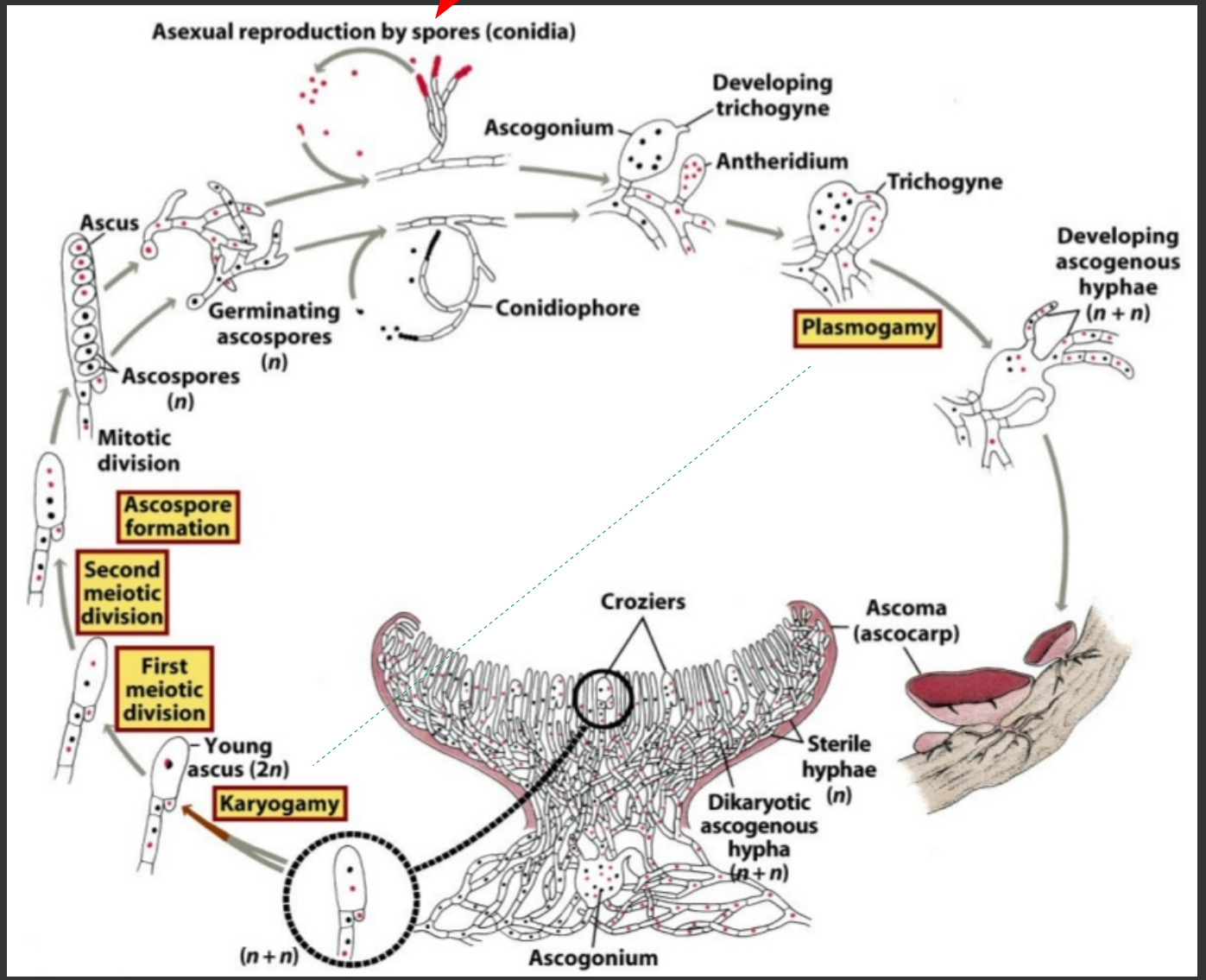
Vast majority of fungal life cycle is spent in asexual reproduction!

Let's look at the life cycle.
Pay attention, because things in dikarya do something a bit weird...

Note the huge delay between plasmogamy and karyogamy

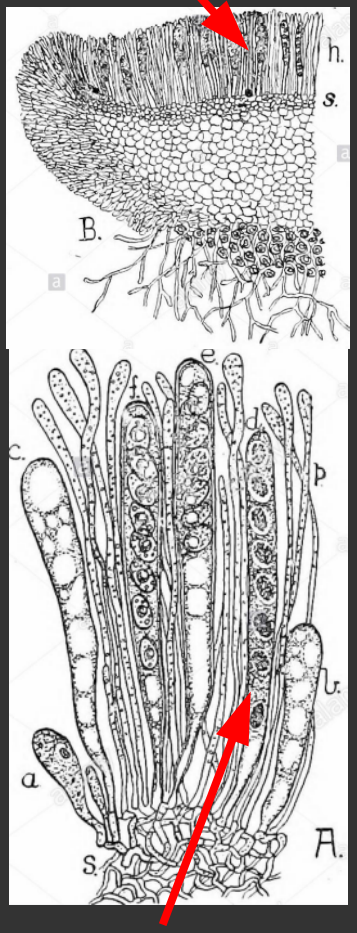
When two compatible nuclei are in the same cell, but do not fuse to become diploid, we call that "dikaryotic."
(n + n)

In dikarya, karyogamy only takes place RIGHT BEFORE meiosis.

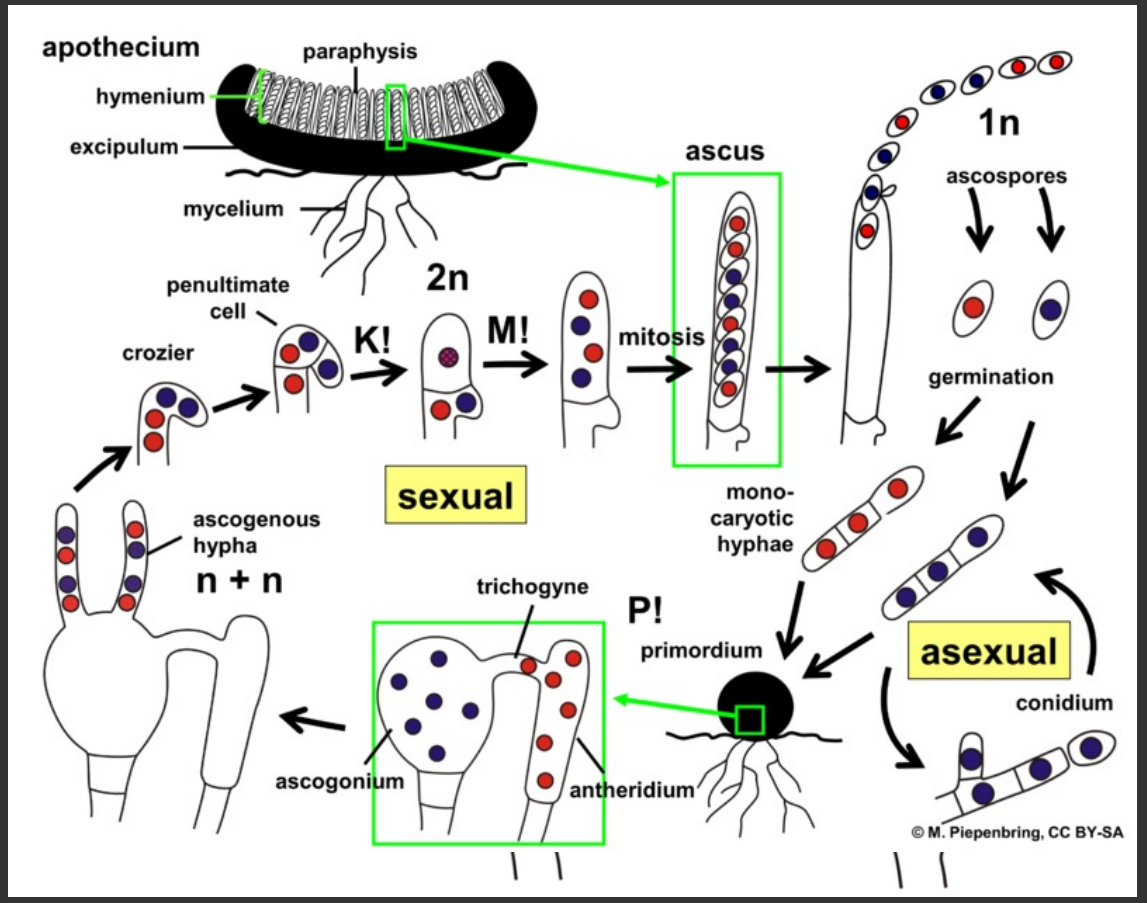


What goes on in an ascus?

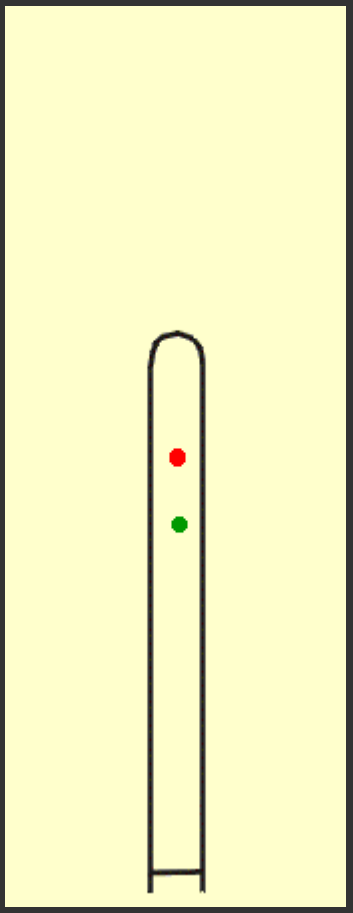
lots of asci



ascus, zoomed in

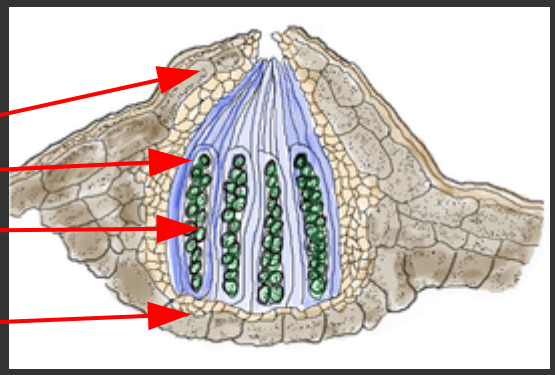


Can you find karyogamy and meiosis?



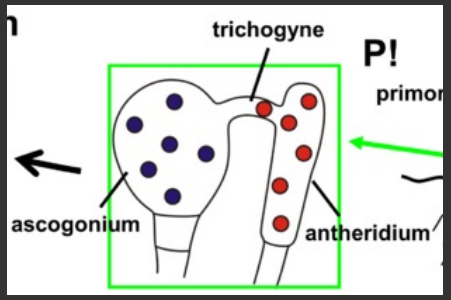
Terms so far:

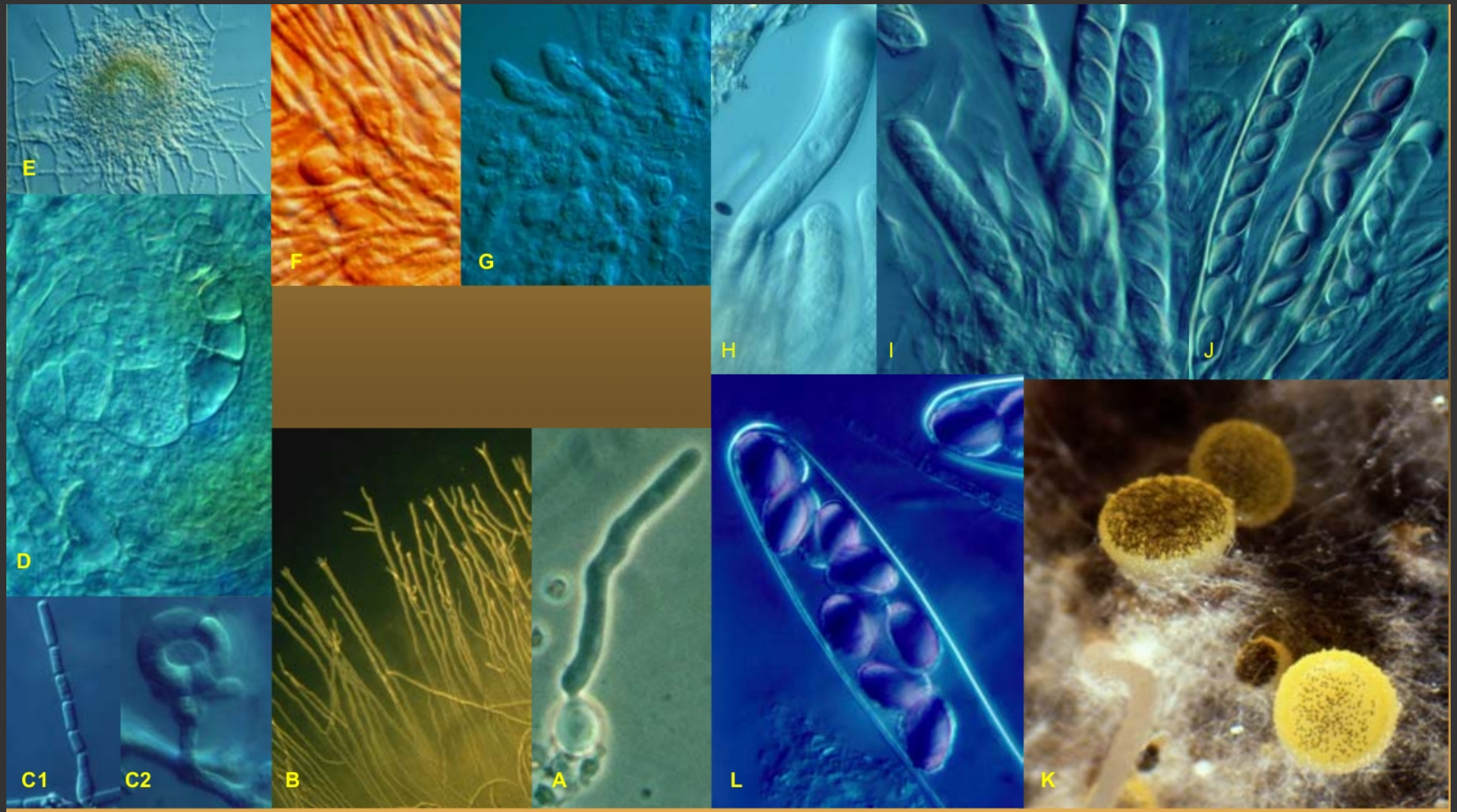
Ascocarp - Macrostructure that houses all the asci (fruiting body)
Ascus - Sac that houses sexually produced spores
Ascospore - Sexual spore in ascomycetes
Hymenium - The "fertile" surface of a fruiting structure and only place where asci are formed



When two compatible ascomycete hyphae come together for mating, one donates a nucleus and the other receives that nucleus...
Antheridium - The hyphal structure that donates a compatible nucleus
Ascogonium - The hyphal structure that receives a compatible nuclues

Conidium/Conidia - Asexually (via mitosis) produced spore(s)





A. Spore germination; B. Somatic haploid mycelium; C1. Antheridial elements (oidia); C2. Ascogonium; D. Fertilized ascogonium surrounded by investing hyphae in apothecial initial; E. Apothecial initial surrounding ascogonium; F. Ascogenous hyphae (*n* + *n*); G. Young asci (*n* + *n*); H. Zygote (2*n*) ascus; I, J. Developing asci; K. Mature apothecia; L. Mature ascus.

Ascomycete life cycle featuring real micrographs

Ascomycetes can be categorized into 3 major well-supported groups

Taphrinomycotina

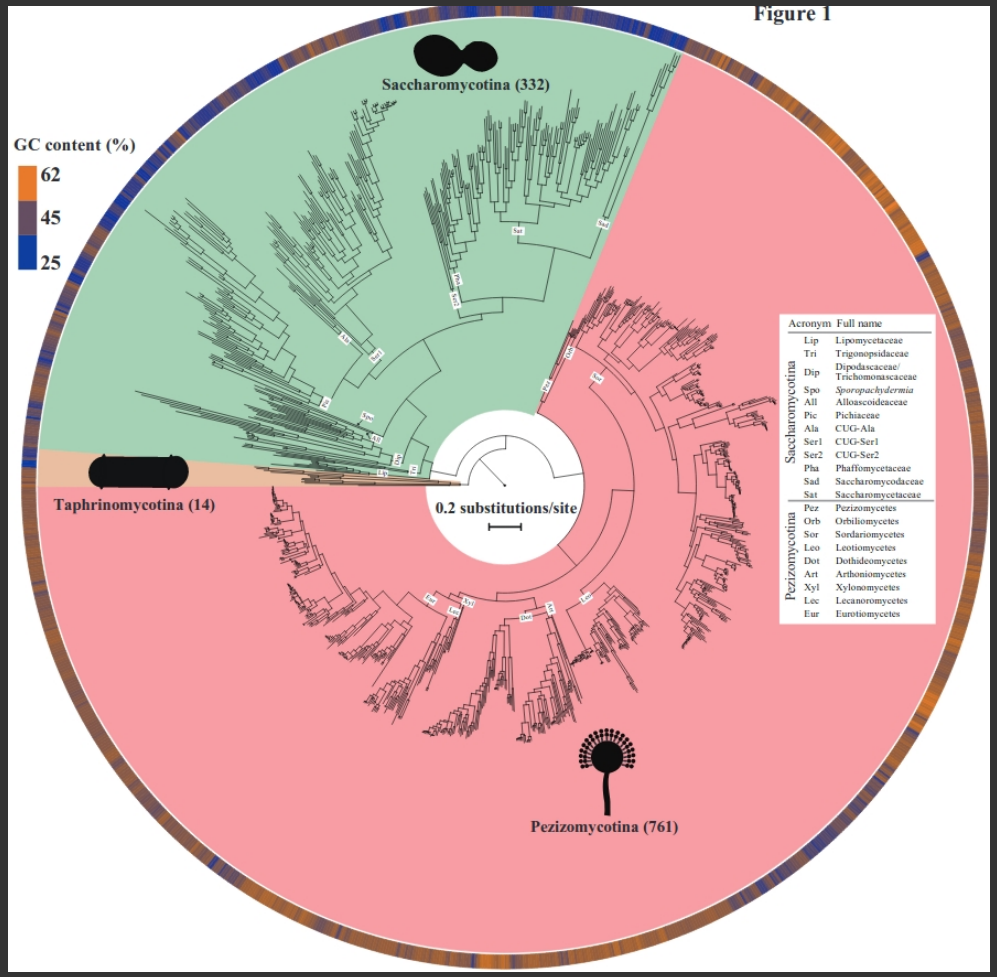
- Basal to the other 2 groups
- Used to be called Hemiascomycetes
- Contains "fizzion yeasts", weird dimorphic plant pathogens, and an important human pathogen

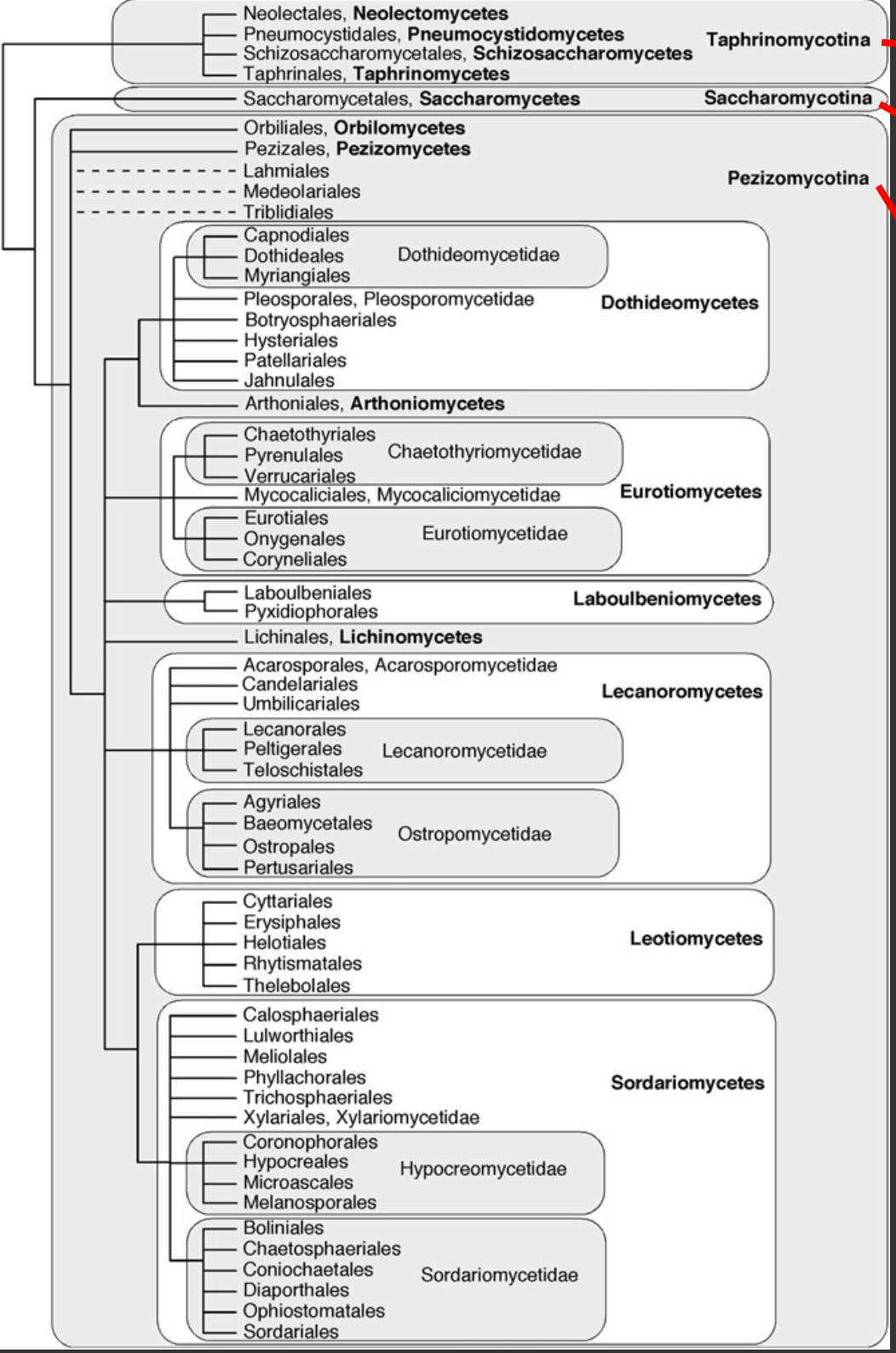
Saccharomycotina

- Contains most of the yeasts (budding)
- Many economically and environmentally important species
- Some basal species have retained hyphal growth

Pezizomycotina

- By far the largest ascomycete clade
- Almost all ascomycetes that make sporocarps are in this group
- Ecologically very diverse




Neolectales, Neolectomycetes
Pneumocystidales, Pneumocystidomycetes
Schizosaccharomycetales, Schizosaccharomycetes
Taphrinales, Taphrinomycetes
Taphrinomycotina
Saccharomycetales, Saccharomycetes
Saccharomycotina
Orbiliales, Orbilomycetes
Pezizales, Pezizomycetes
Lahmiales
Medeolariales
Triblidiales
Pezizomycotina
Capnodiales
Dothideales
Myriangiales
Dothideomycetidae
Pleosporales, Pleosporomycetidae
Botryosphaeriales
Hysteriales
Patellariales
Jahnulales
Dothideomycetes
Arthoniales, Arthoniomycetes
Chaetothyriales
Pyrenulales
Verrucariales
Chaetothyriomycetidae
Mycocaliciales, Mycocaliciomycetidae
Eurotiales
Onygenales
Coryneliales
Eurotiomycetidae
Eurotiomycetes
Laboulbeniales
Pyxidiophorales
Laboulbeniomycetes
Lichinales, Lichinomycetes
Acarosporales, Acarosporomycetidae
Candelariales
Umbilicariales
Lecanoromycetes
Lecanorales
Peltigerales
Teloschistales
Lecanoromycetidae
Agyriales
Baeomycetales
Ostropales
Pertusariales
Ostropomycetidae
Cyttariales
Erysiphales
Helotiales
Rhytismatales
Thelebolales
Leotiomycetes
Calosphaeriales
Lulworthiales
Meliolales
Phyllachorales
Trichosphaeriales
Xylariales, Xylariomycetidae
Sordariomycetes
Coronophorales
Hypocreales
Microascales
Melanosporales
Hypocreomycetidae
Boliniales
Chaetosphaeriales
Coniochaetales
Diaporthales
Ophiostomatales
Sordariales
Sordariomycetidae

How do ***YOU*** define a species?

Seriously. Think about it...
Think about it even more for a while.

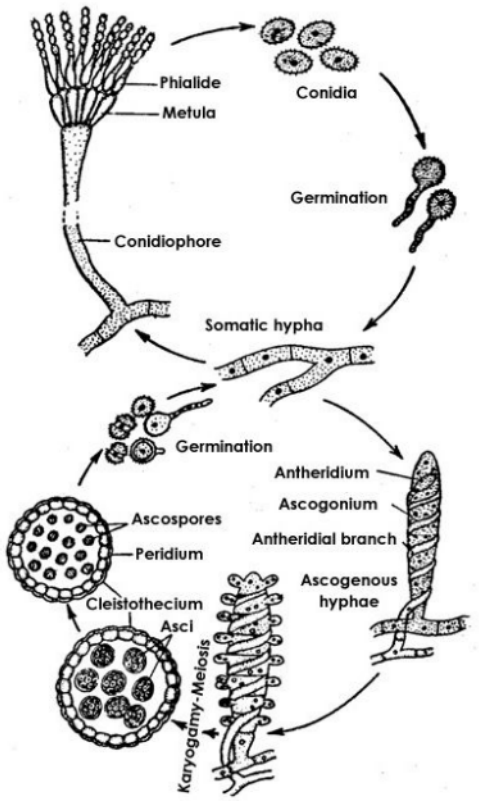
Table 15.1 The biological species concept and some recently proposed alternatives (Futuyma 1997)

BIOLOGICAL SPECIES CONCEPT	A species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents, or sterility of the hybrids, or both). (Dobzhansky 1935)
	Species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups. (Mayr 1942)
EVOLUTIONARY SPECIES CONCEPT	A species is a single lineage (an ancestral-descendant sequence) of populations or organisms that maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate. (Wiley 1978)
PHYLOGENETIC SPECIES CONCEPTS	A phylogenetic species is an irreducible (basal) cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent. (Cracraft 1989)
	A species is the smallest monophyletic group of common ancestry. (de Queiroz and Donoghue 1990)
RECOGNITION SPECIES CONCEPT	A species is the most inclusive population of individual biparental organisms that share a common fertilization system. (Paterson 1985)
COHESION SPECIES CONCEPT	A species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms. (Templeton 1989)
ECOLOGICAL SPECIES CONCEPT	A species is a lineage (or a closely related set of lineages) that 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 1976)
INTERNODAL SPECIES CONCEPT	Individual organisms are conspecific by virtue of their common membership in a part of the genealogical network between two permanent splitting events or between a permanent split and an extinction event. (Kornet 1993)

Source: Coyne (1994).

Aspergillus
(Anamorph)

Mitosporic State



Neosartorya
(Teleomorph)

Sexual State

How would you define a species in a group like ascomycetes?

Lots of them seem to have lost the ability to undergo sexual reproduction.

Those that still can do sex/meiosis, it's a rather rare occurrence.

In the life cycle on the left, 99% of the time, the fungus is in the top loop.

...so, mycologists saw that structure and gave a name to the genus (Aspergillus)

...many moons later they saw the structure on the bottom loop and gave it a new genus name (Neosartorya) because it was a totally new group, right?!

Well, turns out using morphology of reproductive structures to define taxa wasn't maybe the best idea, given that nobody really knew that all these molds just had two different-looking life cycle parts.
Now, we have teleomorph names and anamorph names....

Here's a small example of the problem.

Multiple names for the same species!

People are still working on cleaning up this mess, but it's propagated errors all over the place and makes research rather annoying at times.

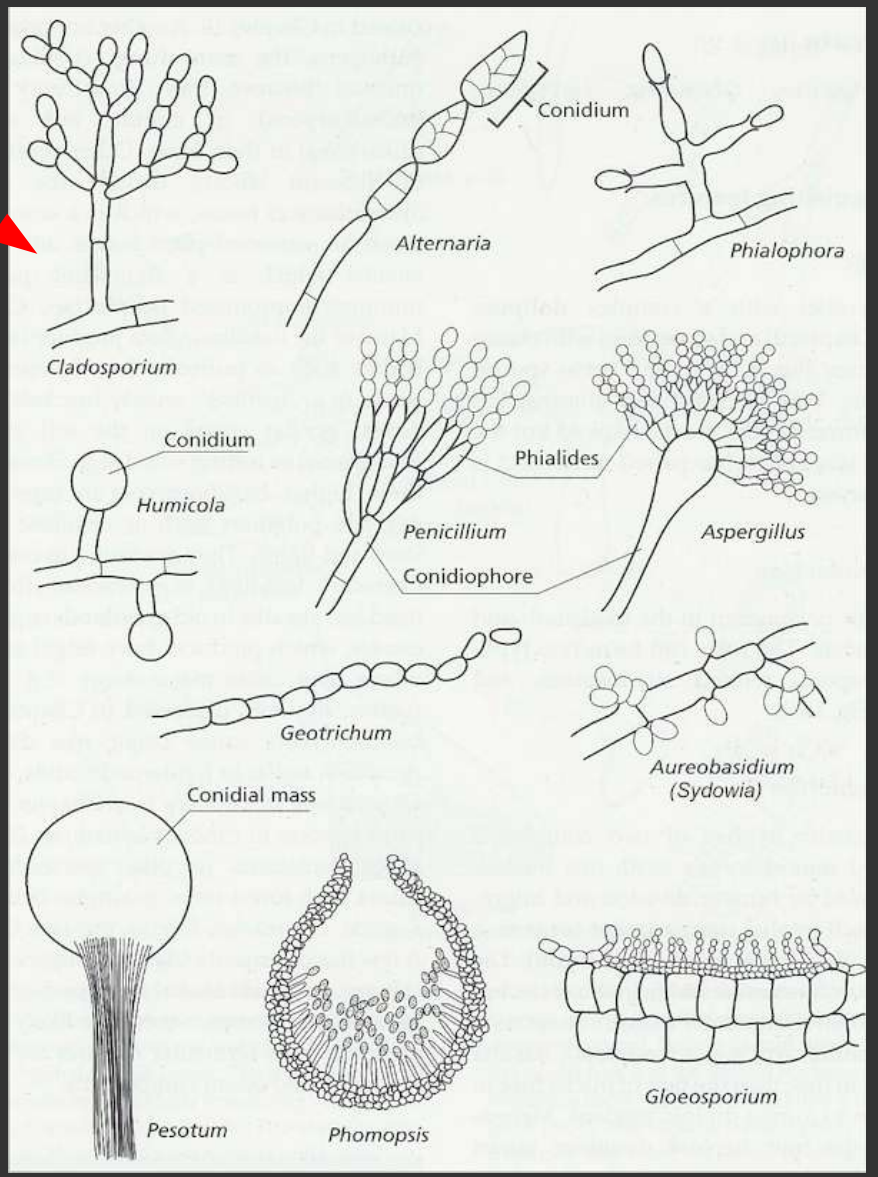
Table 12.1. Core groups of Pyrenomycetes as treated in this chapter. Species numbers (in brackets) are based mostly on Kirk *et al.* (2001).

Taxon	Examples of teleomorphs	Examples of anamorph
Sordariales (see p. 315)	*Sordaria* (14)	
	Podospora and *Schizothecium* (80)	
	Neurospora (12)	*Chrysonilia*
	Chaetomium (80)	
Xylariales (see p. 332)	*Daldinia* (13)	*Nodulisporium*
	Xylaria (100)	*Nodulisporium*
	Biscogniauxia (25)	*Nodulisporium*
	Hypoxylon (120)	*Nodulisporium*, *Geniculosporium*
	Kretzschmaria (5)	*Nodulisporium*
	Hypocopra (30)	
	Podosordaria (17)	*Lindquistia*
	Poronia (2)	
	Rosellinia (100)	*Dematophora*
Hypocreales (see p. 337)	*Hypocrea* (100)	*Trichoderma*
	Hypomyces (30)	*Cladobotryum*, *Verticillium*
	Nectria (28)	*Acremonium*, *Cylindrocarpon*, *Fusarium*
	Gibberella (10)	*Fusarium*
	Sphaerostilbella (4)	*Gliocladium*
Clavicipitales (see p. 348)	*Claviceps* (36)	*Sphacelia*
	Cordyceps (100)	*Beauveria*, *Metarhizium*, *Tolypocladium*
	Epichloe (8)	*Neotyphodium*
	Balansia (20)	*Ephelis*
Ophiostomatales (see p. 364)	*Ophiostoma* (100)	*Graphium*, *Leptographium*, *Sporothrix*, *Pesotum*
Microascales (see p. 368)	*Microascus* (13)	*Cephalotrichum*, *Scopulariopsis*, *Wardomyces*
	Ceratocystis (14)	*Thielaviopsis*
	Sphaeronaemella (5)	*Gabarnaudia*
Diaporthales (see p. 373)	*Diaporthe* (75)	*Phomopsis*
	Cryphonectria (6)	*Endothiella*
	Apiognomonia, *Gnomoniella* (18)	*Discula*
Magnaporthaceae (see p. 377)	*Magnaporthe* (4)	*Pyricularia*
	Gaeumannomyces (5)	*Phialophora*
Glomerellaceae (see p. 386)	*Glomerella* (5)	*Colletotrichum*

Thing is, not all ascomycetes have been discovered in a "teliomorph" state.

Sexual reproduction is ancestral to all extant eukaryotes, but a lot of ascomycetes have lost the ability (or they are just incredibly shy). So, we use molecular evidence and morphology of asexual structures to place them into the evolutionary tree.

Examples of asexual structures:



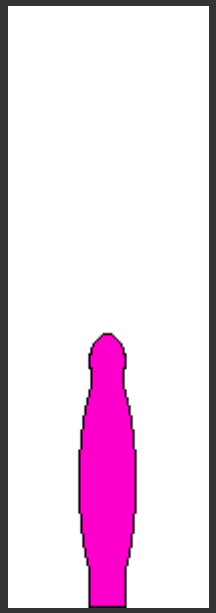
Examples of
conidial diversity:

Conidia

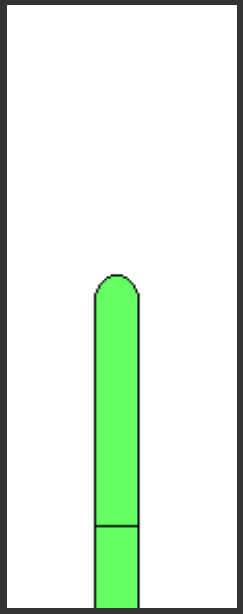
Products of "mitosporic" reproduction

Several ways to reproduce clonally if you are hyphal...just break off a piece of hypha, and you're done! Or, make tiny, resistant, peices of hyphae and squeeze them out.

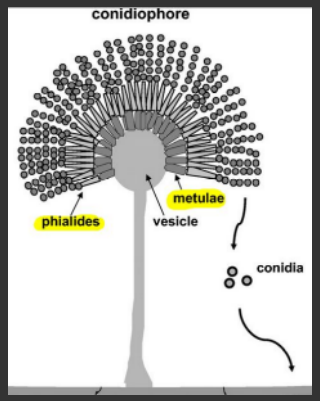
However you do it, it's just modified hyphae!

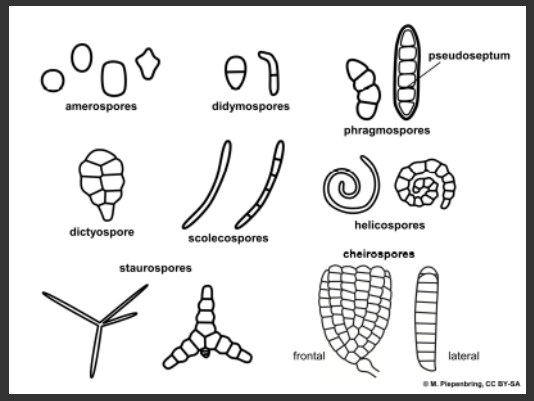


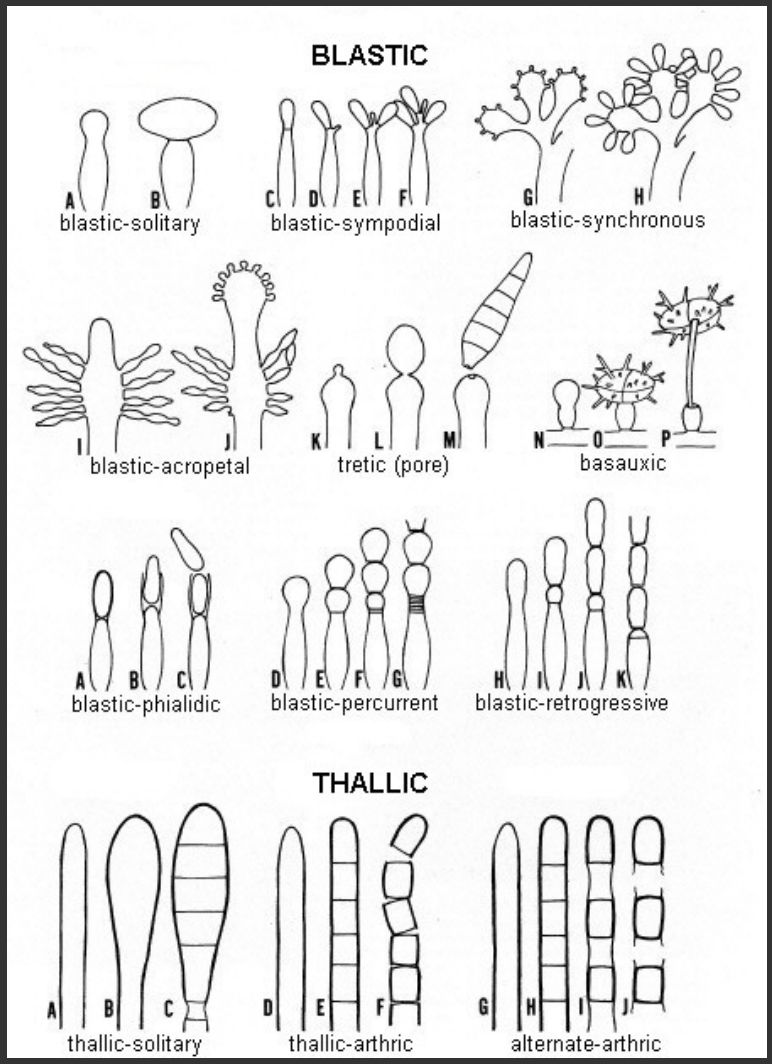
Blastic



Thallic





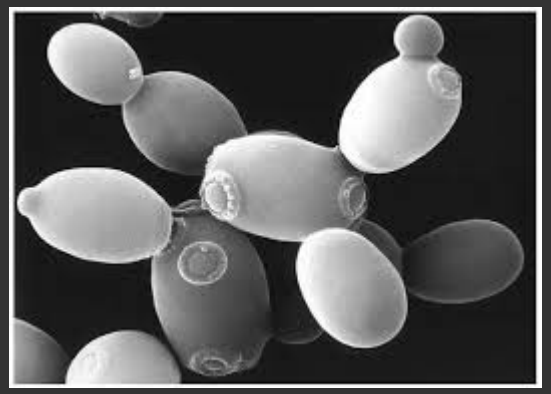


Asexual (clonal) reproduction is advantageous if conditions are favorable.

If you germinated somewhere and there's lots of food and moisture and you're happy, why would you want to roll the meiosis dice just to reproduce? Your offspring might very well not be happy there and then die. Better to just multiply yourself and enjoy life!

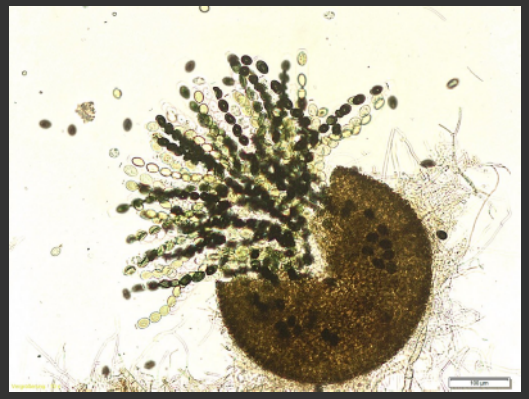
We're going to take a closer look at a few ascomycete groups and see how they fit into our concepts:

Saccharomyces



Alternaria

Sordaria



Xylaria

Saccharomyces cereviseae
(Brewer's/Baker's Yeast)

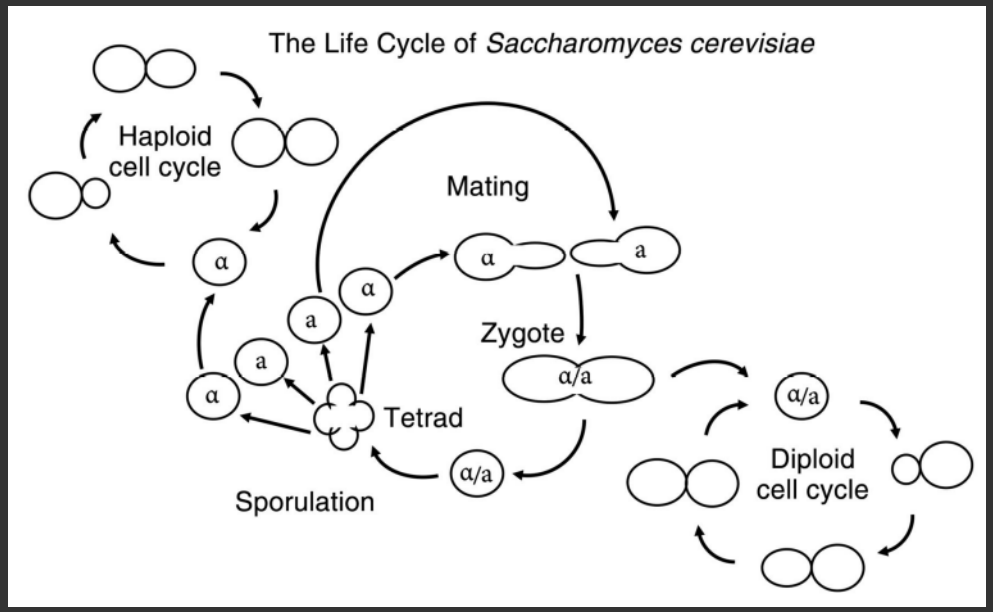
First domesticated microbe - responsible for civilization as we know it

First eukaryote to have a complete genome sequenced; main model organism for eukaryote genetics

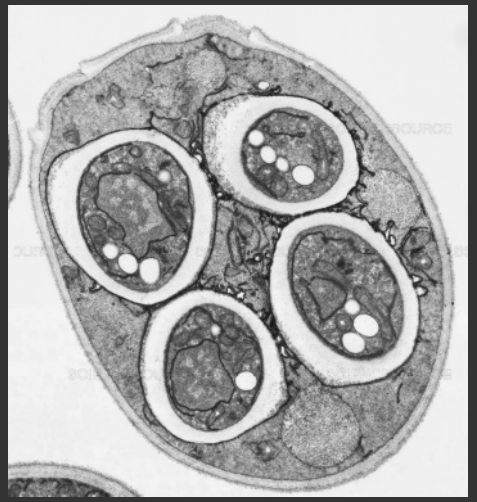
Facultative anaerobe... when oxygen is low, it ferments glucose to ethanol and CO_2

Often found in sugar-rich locations in nature

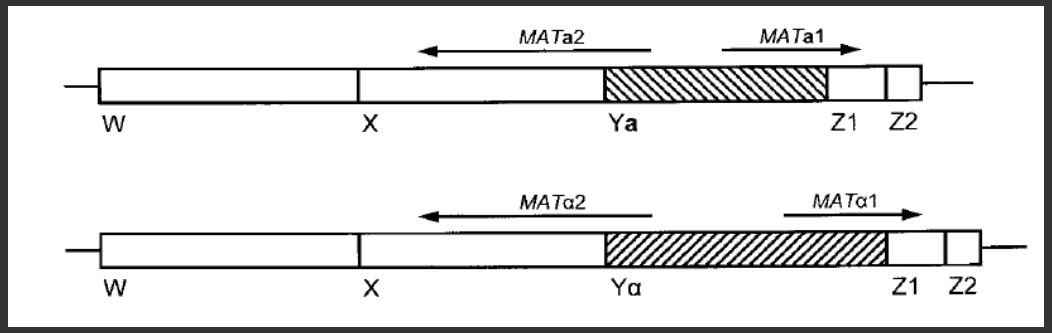
The dusty coating on every grape on Earth is *Saccharomyces* yeast



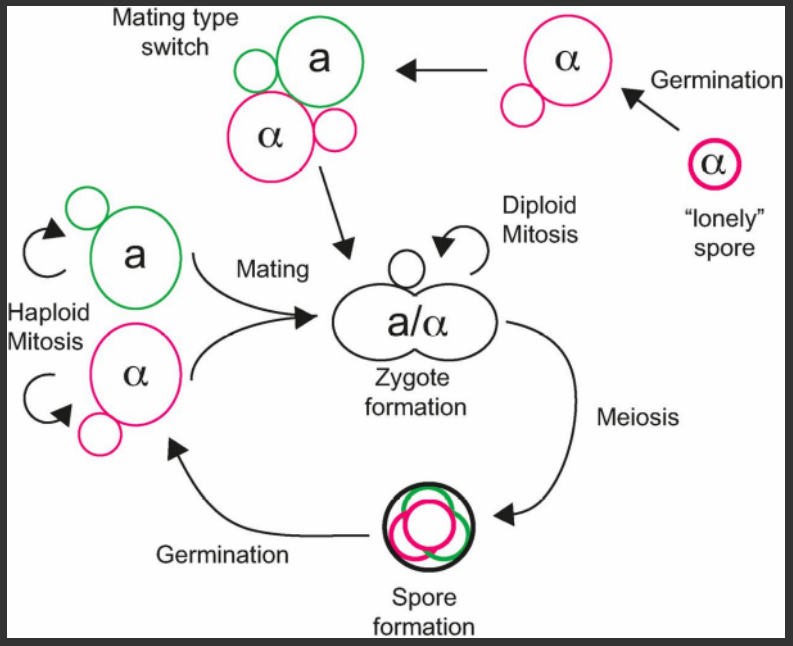
Ascus w/ 4 ascospores



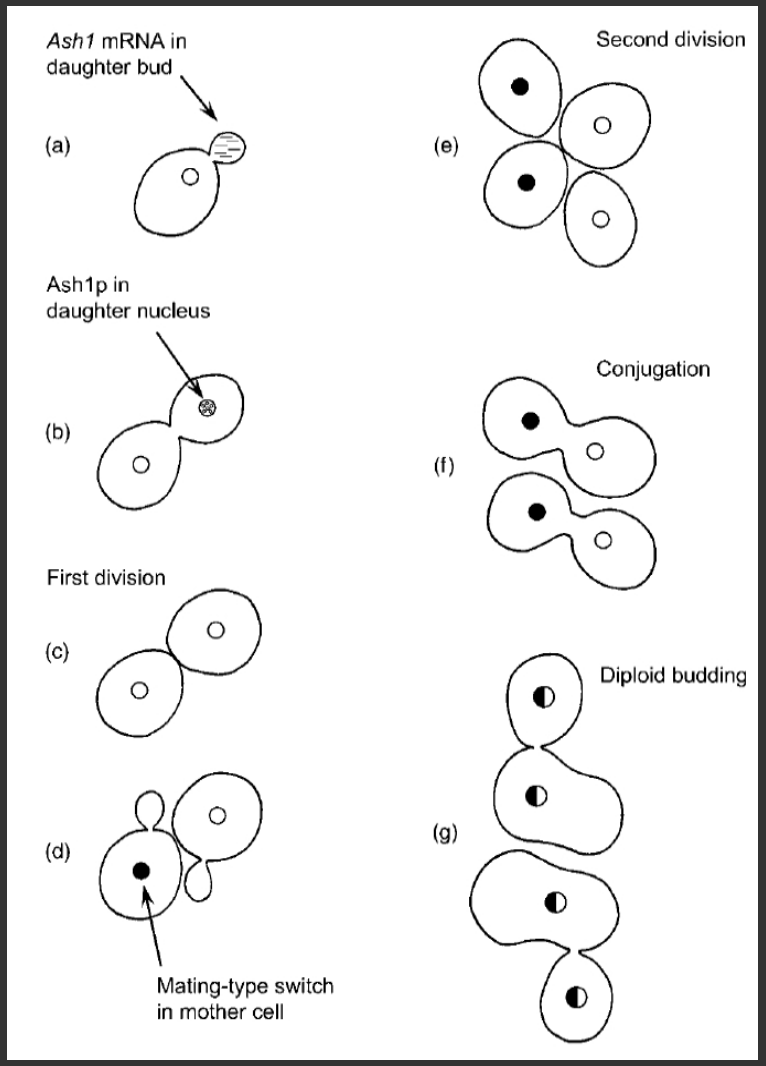
Single genetic locus controls mating type (a or α)



Like other dikarya, bulk of life history is hapoid



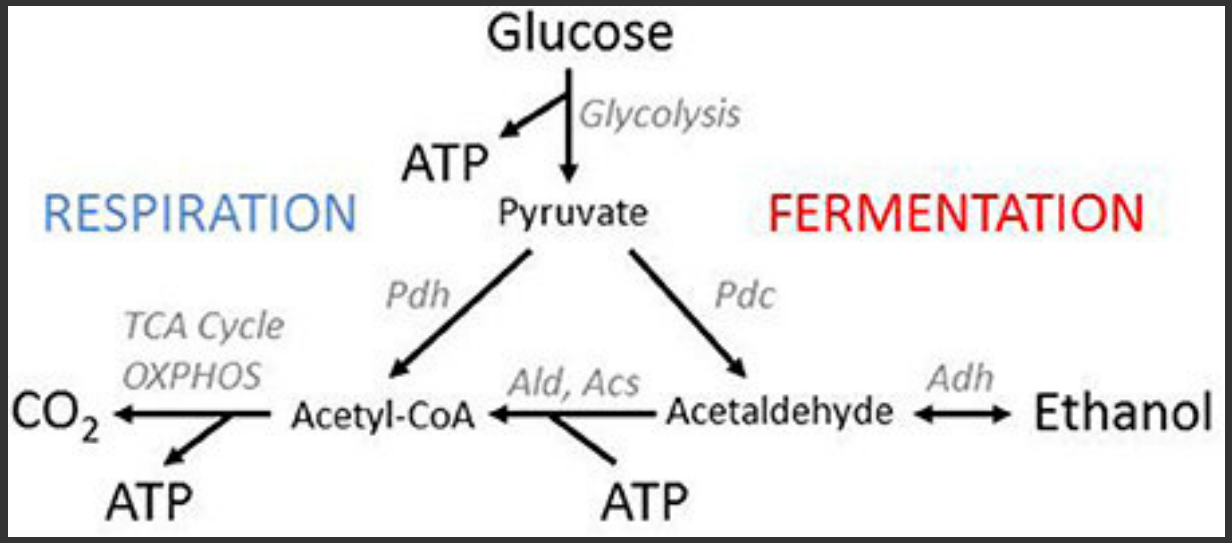
Cells can actually switch mating type!



Can actually remain diploid for some time unlike most dikaryotic fungi

S. cereviseae is used as a model organism to study....almost everything.
Here's one example:

Net=18 ATP



Net=2 ATP

S. cereviseae can do respiration and fermentation
In the presence of oxygen, it would make sense to only use the respiration pathway as it increases energy yield per molecule of glocose. But if glucose concentrations are high enough, this yeast will still "choose" to undergo fermentation. Why?

Cancer biologists are using Game Theory and this little yeast to better understand metabolic trade-off strategies of tumor cells

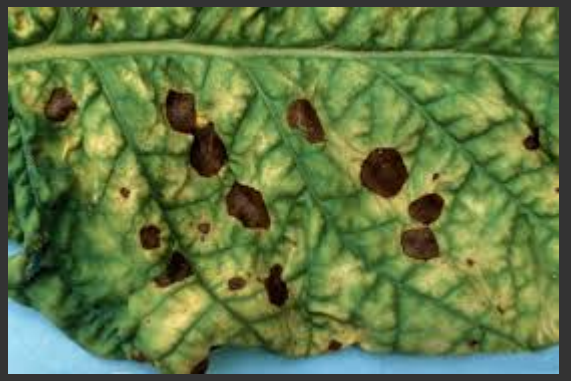
Alternaria

Three species of Alternaria not known to have sexual states, have mating type gene sequences.

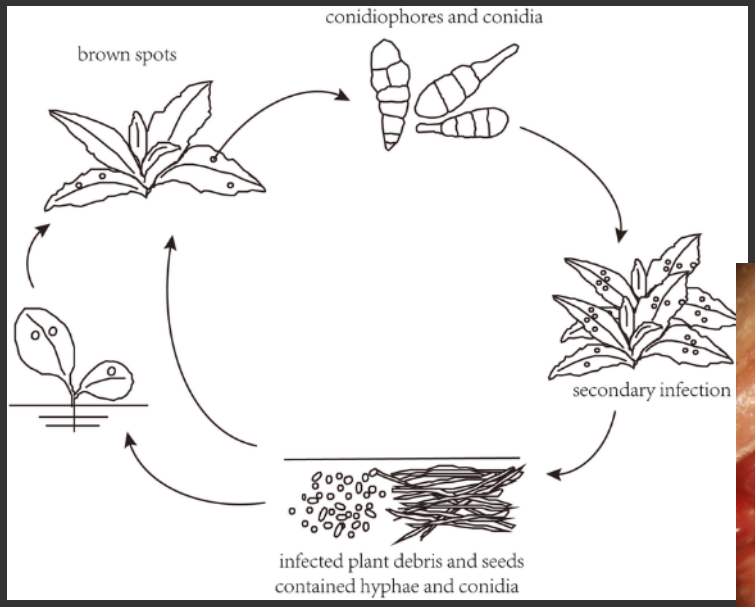
Species in this genus have diverse ecological roles: Animal Pathogens, Endophytes, Plant Pathogens, and Wood Saprotrophs

Typically, no known teleomorph stages, but *A. infectorium* (an opportunistic human pathogen) has well-known teleomorph identity in *Pleospora*

See this link



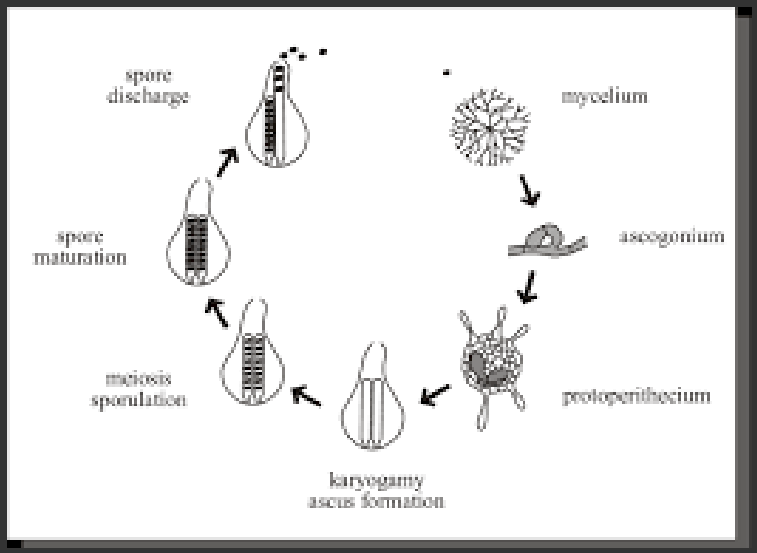
most commonly found as plant pathogens

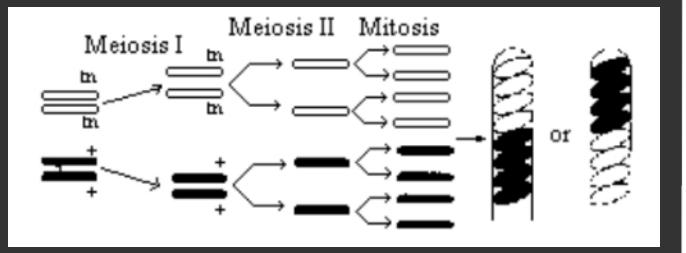


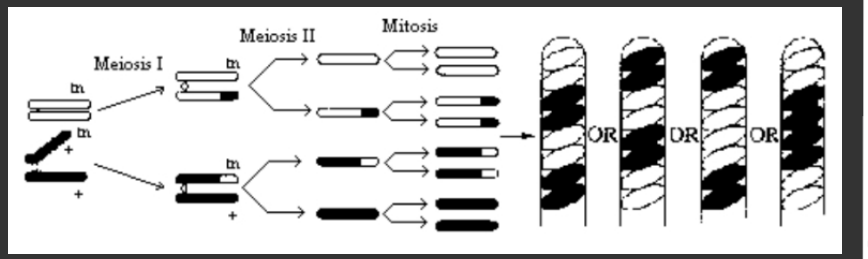
Sordaria

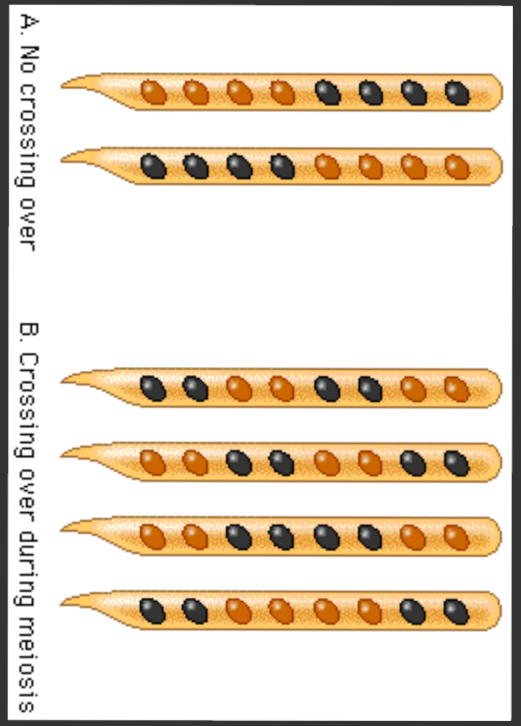
Used as a model of genetic crossing during meiosis and for mapping linked genes.

Asci with spore-color mutants



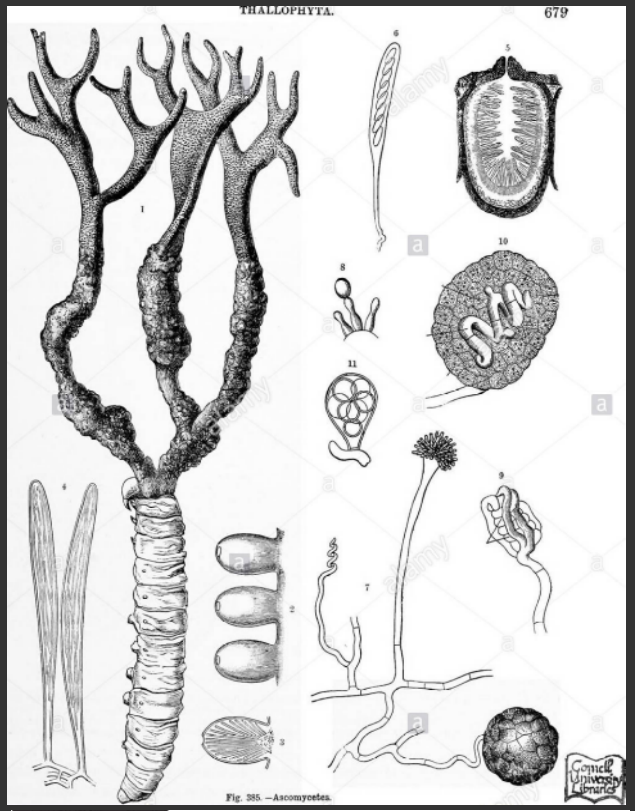


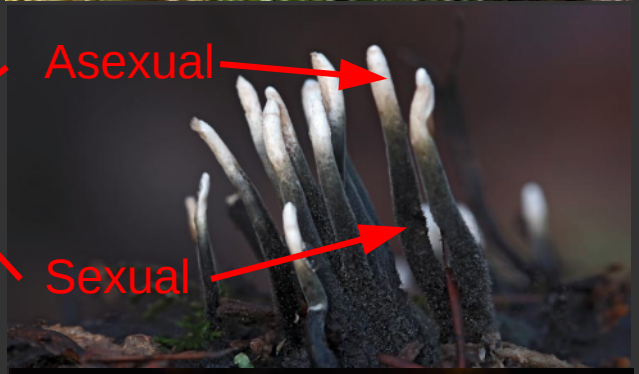




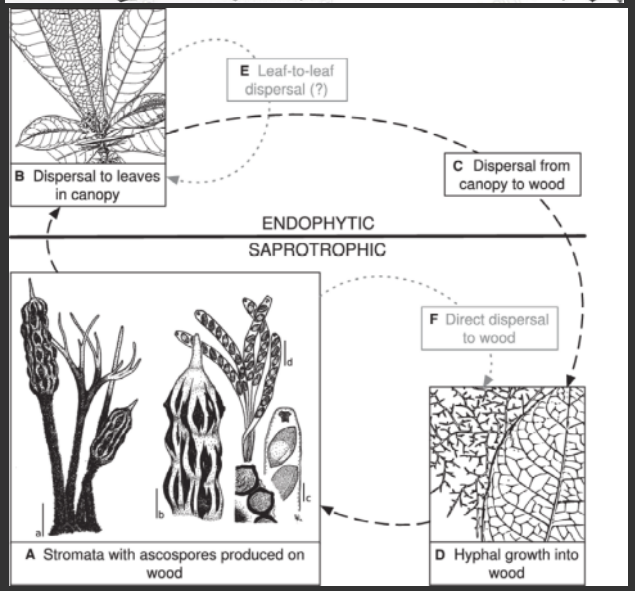
Perithecia on dead grass

Xylaria





typical anamorph



So, how do Ascomycetes fit into our picture of fungal evolution, morphology, physiology, diversity, and ecology?

Evolution -

Morphology -

Physiology -

Diversity -

Ecology -

Assignments

1. Read Webster & Weber, sections: 8, 10.2, 12.1, 12.2.1, 17.2.6
   - These cover an introduction to Ascomycetes and then closer looks at some specific groups

2. You will have a Canvas quiz on the assigned readings and will also have to participate in a Slack discussion about them.

3. Go through the website materials and try to get a feel for ascomycetes. This will help you get used to the terminology and gain an appreciation for the insane diversity of this group.

4. Using primary sources (peer-reviewed, not our old text book), answer the following question: How many Ascomycete species are there?
   Discuss your findings in 250-500 words. Include in-line citations. This will be turned in on Canvas next week.