Lecture 5

Basidiomycota I

- Major characteristics

- Major evolutionary groups

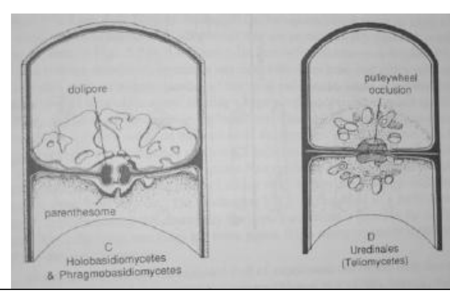
Basidiomycota: major characteristics

- Very successful group; approx. 30,000 known species out of the ca. 75,000 known

- Vegetative growth:
---- mostly filamentous, but yeast forms are also produced;
---- hyphal cords (including rhizomorphs) and sclerotia not uncommon;
---- asexual reproduction from chlamydospores or arthrospores can occur (no conidiospores!).

- Cell wall:
---- **multi-layered** (EM observation); (two-layered in the Ascomycetes);

- Mycelium:
---- **Regularly septate** hyphae:
-------- **dolipore** with parenthesome:
(typical of Basidiomycota, see L1);
-------- or **simple septate** with occlusion
(e.g., smuts and rusts)
---- **clamp connections** often present;
---- **dikaryotic**;



Experimentation, and reflections on evolutionary consequences of being a basidiomycetous dikaryon.

Travis A. Clark, T.A & J.B. Anderson. 2004. Dikaryons of the Basidiomycete Fungus *Schizophyllum commune*: Evolution in Long-Term Culture. Genetics 167: 1663–1675

ABSTRACT

The **impact of ploidy on adaptation** is a central issue in evolutionary biology. While many eukaryotic organisms exist as diploids, with two sets of gametic genomes residing in the same nucleus, **most basidiomycete fungi exist as dikaryons in which the two genomes exist in separate nuclei** that are physically paired and that divide in a coordinated manner during hyphal extension. To determine if haploid monokaryotic and dikaryotic mycelia adapt to novel environments under natural selection, we serially transferred replicate populations of each ploidy state on minimal medium for 18 months (ca. 13,000 generations). **Dikaryotic mycelia responded to selection with increases in growth rate, while haploid monokaryotic mycelia did not.** To determine if the haploid components of the dikaryon adapt reciprocally to one another's presence over time, we recovered the intact haploid components of dikaryotic mycelia at different time points (without meiosis) and mated them with nuclei of different evolutionary histories. **We found evidence for coadaptation between nuclei in one dikaryotic line**, in which a dominant deleterious mutation in one nucleus was followed by a compensatory mutation in the other nucleus; the mutant nuclei that evolved together had the best overall fitness. In other lines, nuclei had equal or higher fitness when paired with nuclei of other histories, indicating **a heterozygote advantage**. To determine if genetic exchange occurs between the two nuclei of a dikaryon, we developed a 24-locus genotyping system based on single nucleotide polymorphisms to monitor somatic exchange. **We observed genetic exchange and recombination between the nuclei of several different dikaryons, resulting in genotypic variation in these mitotic cell lineages.**

Basidiomycota: major characteristics

- Reproductive structures:
--- many species form large **basidiomata** (= basidiocarps, fructifications, or fruiting bodies; e.g., mushrooms)
====> includes the bulk of the edible fungal species;
--- some taxa (e.g., rusts and smuts) do not produce basidiomata.

- Three **major ecological roles**:

--- **saprobic**: (=decomposer of organic matter),
-------- e.g. white-rot (= lignin-degrading) and brown-rot of wood;
====> Carbon cycling;

--- **symbiotic**:
-------- with plants: mycorrhiza (mostly ecto-) with trees and shrubs, sometimes with grassy plants e.g. orchids;
-------- with insects: fungal gardens of ants and termites; scale insects;
-------- with algae: a few basidiolichens exist.

--- parasites / pathogenic:
-------- mostly on plants (e.g., rusts and smuts);
-------- also in animals including humans (e.g., *Cryptococcus*)

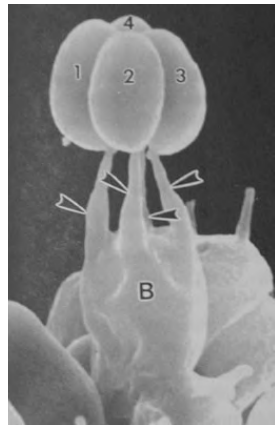
The basidium (plural = basidia) - definitions

Basidiospores: sexual spores (result of karyogamy and meiosis).
Basidium: cell bearing basidiospores on its sterigmata;
--- that cell is called “probasidium” when karyogamy occurs, and “metabasidium” when meiosis occurs; sterigmata are formed following meiosis, as nuclei migrates ‘outside’ the cell into basidiospores ---

Holobasidium: a non-septate basidium; single-celled, typically club-shaped, and bearing sterigmata (usually four)
--- chiastobasidium: a holobasidium in which, during meioisis, the nuclear spindles / microtubules are oriented perpendicular to the long axis of the basidium, and at the same level.
--- stichobasidium: during meiosis the nuclear spindles / microtubules are oriented parallel to the long axis of the basidium (are not at the same level).

Heterobasidium: any type of basidium that differ from a typical holobasidium

Phragmobasidium: a septate basidium (a phragmobasidium is an heterobasidium)



B: Holobasidium; **1-4:** basidiospores;
Arrows: sterigmata (SEM, from Alexopoulos)

Development of a 4-spored basidium

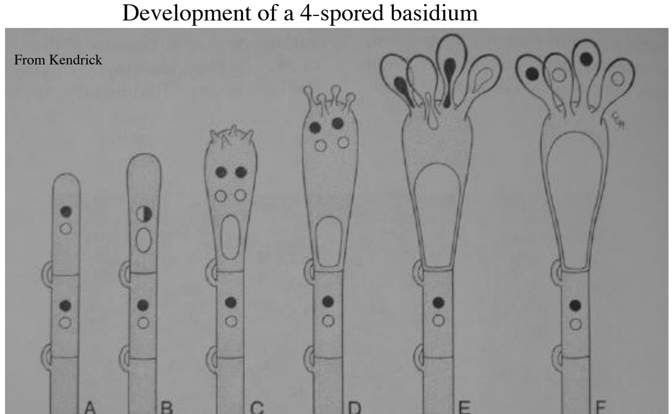


Figure 16-6 Successive stages in development of a basidium and basidiospores. (A) Binucleate hyphal tip. (B) Uninucleate, diploid basidium following karyogamy. (C) Postmeiotic basidium with four haploid nuclei. Sterigmata have begun to develop. (D) Basidiospore initials on sterigmata and nuclei preparing to migrate into the spore initials. (E) Migration of nuclei into basidiospore initials. (F) Highly vacuolate, maturing basidium bearing four young uninucleate basidiospores. (Drawing by Carol Gubbins Hahn.)

- Basidiospores are haploid, and generally uninucleate; binucleate basidiospores are sometimes formed, when a mitosis follows the meiosis (either in the basidium or in the spore).
- 2-spored and 8-spored basidia are sometimes formed (rare).

Basidiomycota: types of basidia

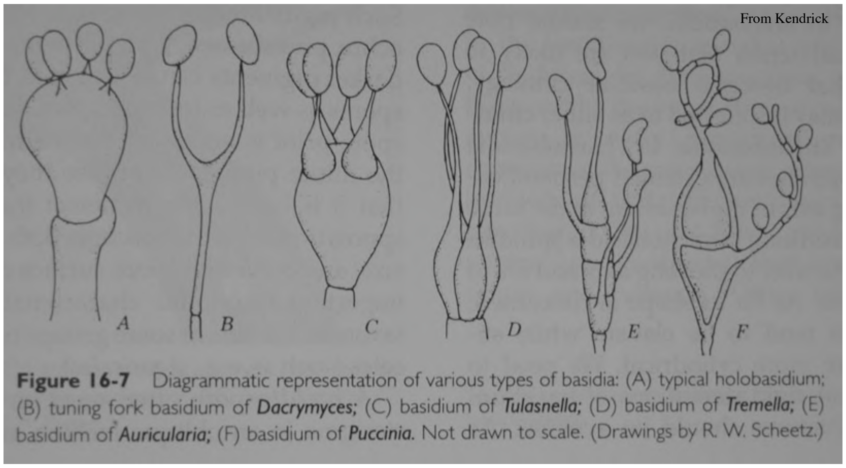


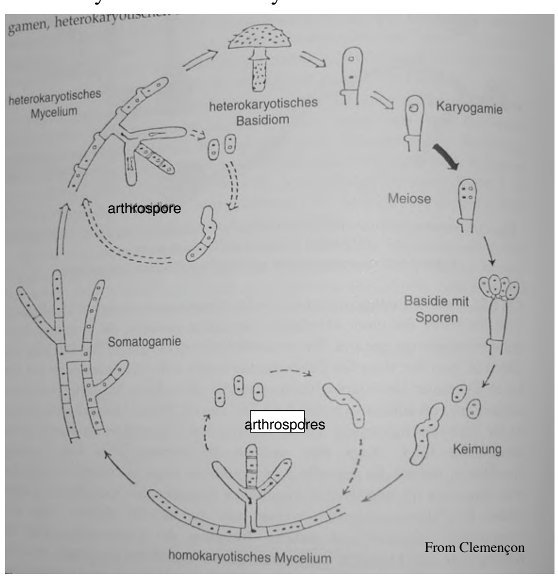
Figure 16-7 Diagrammatic representation of various types of basidia: (A) typical holobasidium; (B) tuning fork basidium of ***Dacrymyces;*** (C) basidium of ***Tulasnella;*** (D) basidium of ***Tremella;*** (E) basidium of ***Auricularia;*** (F) basidium of ***Puccinia.*** Not drawn to scale. (Drawings by R. W. Scheetz.)

A: holobasidium; B-F: heterobasidia; C-F: phragmobasidia
F: basidia of rusts germinating from a teliospore.

Life-cycle of a basidiomycotes mushroom

Formation of a secondary mycelium (dikaryon / heterokaryon)
-- generally the longest living stage

Fusion between two primary mycelia (somatogamy)



meiosis immediately follows karyogamy

Binucleate basidiospores in this example (basidiospores are generally unicleate)

Basidiospore germination ==> Primary mycelium (haploid nuclei / homokaryon)

Formation of arthrospores or chlamydospores is possible for asexual reproduction /genet dssemination

Sexual Reproduction in Basidiomycota

Two steps:
(1) hyphal fusion and exchange of nuclei (somatogamy via anastomosis, and nuclear migration)
(2) nuclear fusion (karyogamy) and meiosis

Homothallic: a single strain can undertake sexual reproduction (self-compatibility)
-- Advantages? Disadvantages?
-- strictly homothallic species do not have a mating type system.

Heterothallic: two different but genetically compatible strains undergo sexual reproduction;
-- The majority of Basidiomycota species are heterothallic.

Mating systems of heterothallic species are either **unifactorial** (bipolar), or **bifactorial** (tetrapolar)
-- In Basidiomycota, ~25% of heterothallic species are unifactorial; ~75% are bifactorial

Unifactorial (bipolar) mating type:
-- one locus (= factor) controls the mating;
-- different alleles at that locus are required for compatibility of nuclei;
----- A Basidiomycota species can have from a few to several hundred alleles at the mating type locus;
----- A1 X A2 (karyogamy) ===> A1A2 (meiosis) ===> A1 + A2 (spores)
===> 50% incompatibility (compatibility) in **sibling pairing** of spores
(sibling pairing = pairing of spores from the same basidiocarp progeny)

Sexual Reproduction in Basidiomycota

Bifactorial (tetrapolar) mating type:
-- two loci (= factors) control the mating (they are typically labeled A and B factors); these two loci are generally located on different chromosomes.
-- different alleles required at both loci for mating compatibility;
---- Numerous alleles per locus exist within a specie;
---- A1B1 X A2B2 (karyogamy) ===> A1B1A2B2 (meiosis) ====> A1B1, A2B2 (if no crossingover), or
A1B1, A2B2, A1B2, A2B1 if crossingover.
===> 75% incompatibility or 25% compatibility in sibling pairing of spores

Function of A & B alleles discerned via partial compatibility crosses: ex. in *Schizophullum commune* (Raper, 1966)
- cross between A1B1 X A1B2 (identical A alleles)
===> no clamp connections observed: **somatic incompatibility**
- fusion between A1B1 X A2B1 (identical B alleles)
===> clamp connections formed but no migration of nuclei: **zygotic (nuclear) incompatibility**

The realty is slightly more complex than the A/B factorial system proposed by Raper, but in practice that system generally works well to interpret the results of mating compatibility tests on a genetic basis.

UNIFACTORIAL MATING SYSTEM

Spores from the same progeny (e.g., from the same basidiocarp) carry either the Ai or Aj mating allele (there are n alleles in an interbreeding population / species)

Within the same progeny, chance of mating is 50%

	Ai	Aj
Ai	-	+
Aj	+	-

BIFACTORIAL MATING SYSTEM

Spores from the same progeny (e.g., from a same basidiocarp) carry either the Ai-By or Aj-Bx mating alleles.

Within the same progeny, chance of:

+ successful mating is 25%

~ partial compatibility (i.e., somatic fusion possible but no nuclear migration / karyogamy) is 25%

- complete incompatibility is 50%

	AiBy	AjBy	AiBx	AjBx
AiBy	-	~	-	+
AjBy		-	+	-
AiBx			-	~
AjBx				-

How to conduct a mating compatibility experiment - Example from the agarics

strain 1 strain 2

Prepare single spore isolates (= monokayons, which don't have clamp connections) on agar

Conduct intra-strain crosses to determine the strain's mating type (i.e, uni- or bifactorial); identify and isolate all possible allelic type (2 if uni-, and 4 if bifactorial)

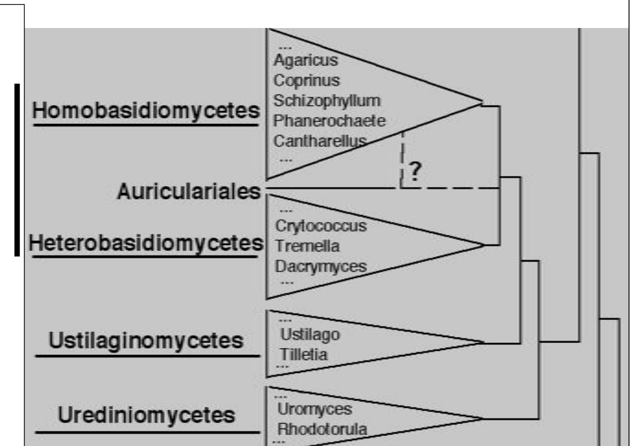
Conduct inter-strain crosses in all possible pairwise combinations of the identified allelic types of each strain

Basidiomycota: major evolutionary groups

Agaricomycotina
Macrofungi (mostly)

Ustilaginomycotina
smuts

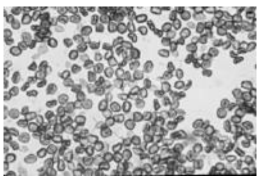
Pucciniomycotina
rusts

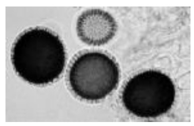


Classification following Hibbett et al., 2007

Ustilaginomycotina

smuts

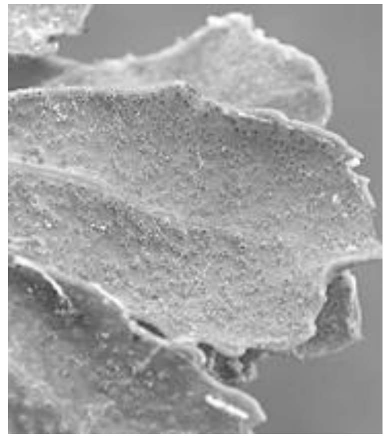




http://plantpath.caes.uga.edu/extension/Fungi/smutfungi.html
http://www.ars.usda.gov/Research/docs.htm?docid=9419

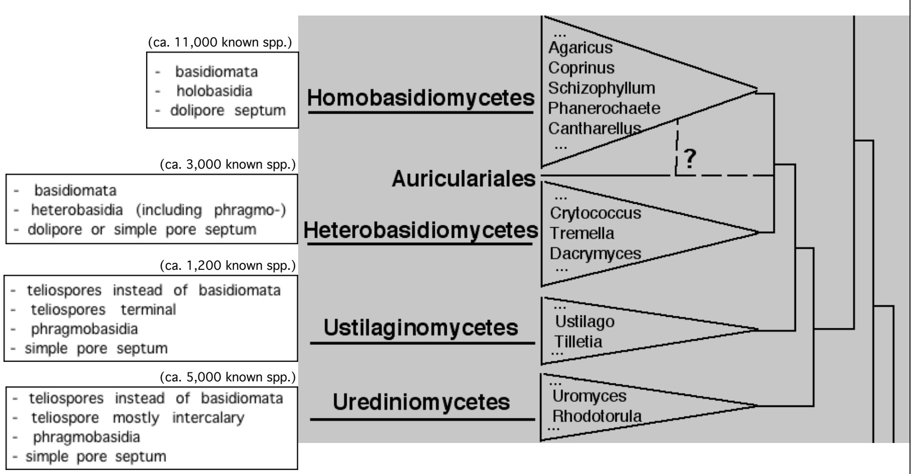
Pucciniomycotina

rusts



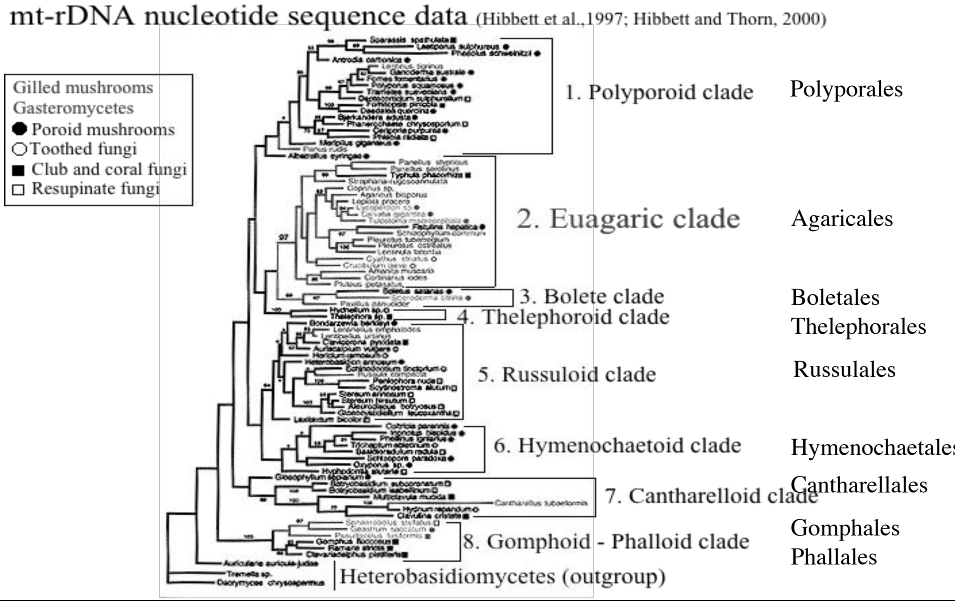
http://www.csiro.au/science/BoneseedBiocontrol.html

Basidiomycota: major evolutionary groups



Urediniomycetes and Ustilaginomycetes are characterized by the formation of **teliospores**, which directly produce phragmobasidia and basidiospores (more later) ; they fungi are also referred as **Teliomycetes.**

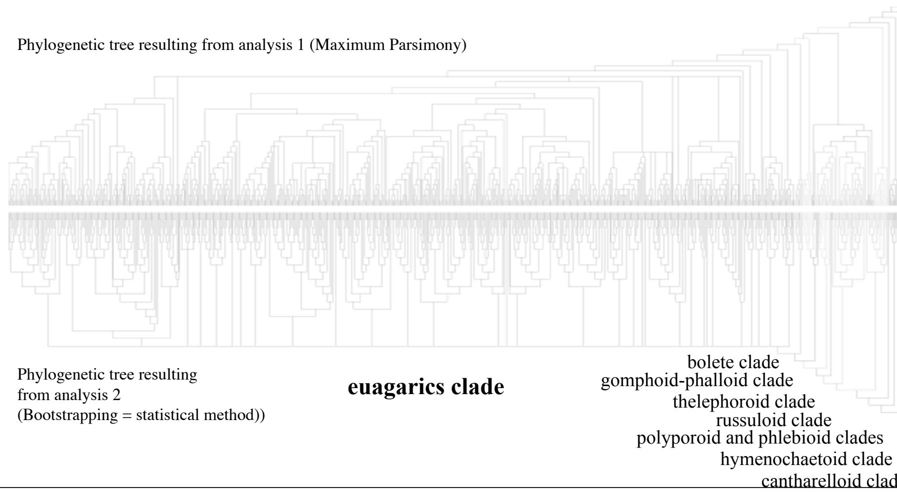
Homobasidiomycetes Phylogeny based on18S nuc-rDNA and 12S mt-rDNA nucleotide sequence data (Hibbett et al.,1997; Hibbett and Thorn, 2000)



The Agaricales

Recent progress toward a phylogenetic classification of the agaric fungi

- Moncalvo et al., 2002, *Mol. Phylogenet. Evol.* 23:357-400.
- 877 taxa (ca. 1/10th of the known species in the group); 117 clades resolved with confidence.



Agaricales

The Agaricales is by far the largest order of Basidiomycota: ca. 8,500 known species

- includes the **core group of gilled fungi**
--- roughly corresponds to the traditional Agaricales, which were originally restricted to include all gilled fungi ("Friesian system")
--- **not all gilled fungi** belong to the Agaricales
--- **many non-gilled fungi** belong to the Agaricales
--- many traditional groups, particulaly genera (e.g., *Amanita, Inocybe*,...) are natural, but many are not, particularly families (e.g., Tricholomataceae, Cortinariacae,...)

- mostly macromycetes;
- includes most of the edible mushrooms;
- mycorrhizal (mostly ecto-), saprobic, some wood pathogens (e.g. *Armillaria*)

Agaricales

Major characters that are shared by natural groups of Agaricales
(many natural groups correspond to traditional "genera", but many do not...):

- **spore print color**;

- **basidiospore** shape and ultrastructure;

- **ontogeny** (basidiocarp development)**?** (not enough species studied but seems consistent within a genus);

- particular tissues: e.g., type of lamellar (gill) trama, gelification, etc.

- **ecology**; e.g., mycorrhizal, saprophytes (primary vs.late decomposers), bryophyte associated, etc.;

- **biochemistry** and **physiology**; e.g., secondary metabolites, nutritional modes, etc.

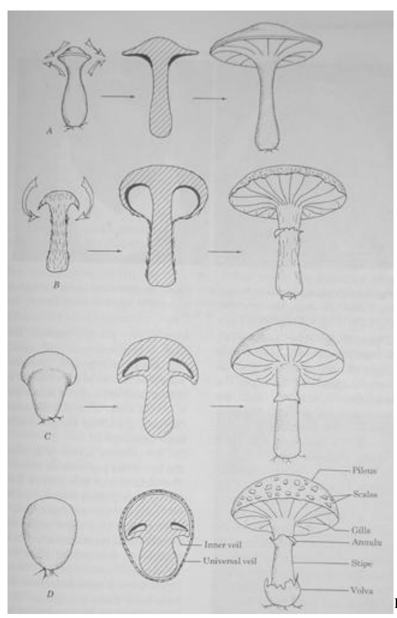
Basidiocarp development (ontogenesis)

A. Gymnocarpic

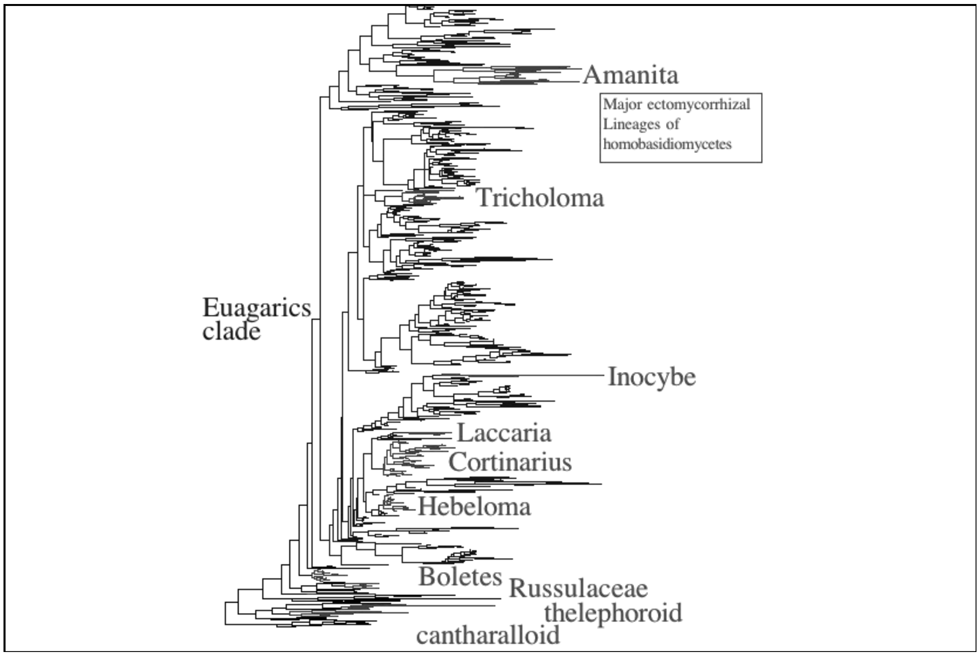
B. Pseudoangiocarpic
Note the **secondary** formation of a **veil**, which sometimes leaves fugaceous remnants on the stipe ("ring"), or elsewhere on the cap (e.g., at the margin) - e.g., *Cortinarius*

C. Hemiangiocarpic
Note the **primary** formation of a veil, which often leaves solid remnants on the stipe (ring) - e.g., *Agaricus*

D. Biveliangiocarpic
Note the **primary** formation of two veils (inner veil and universal veil), which often leave solid remnants on the stipe (ring, volva) and/or cap (scales) - e.g., *Amanita*



From Alexopoulos


Amanita
Major ectomycorrhizal
Lineages of
homobasidiomycetes
Tricholoma
Euagarics
clade
Inocybe
Laccaria
Cortinarius
Hebeloma
Boletes
Russulaceae
thelephoroid
cantharalloid