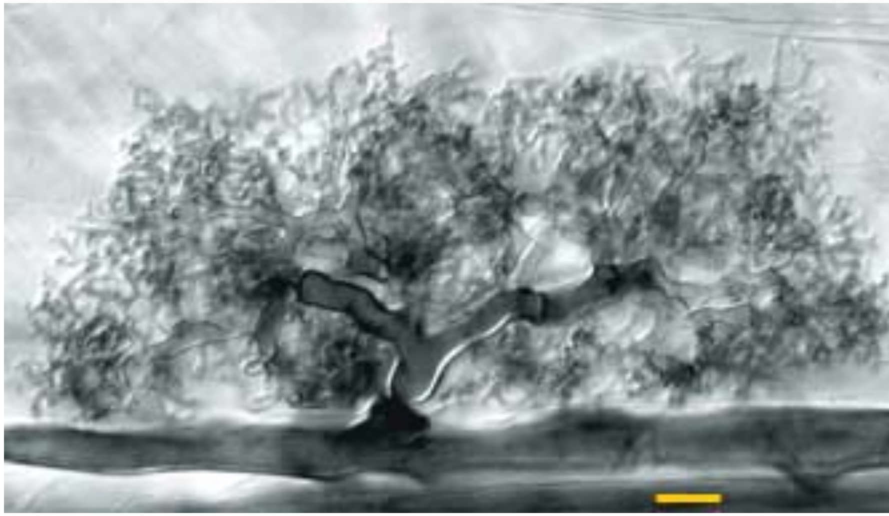
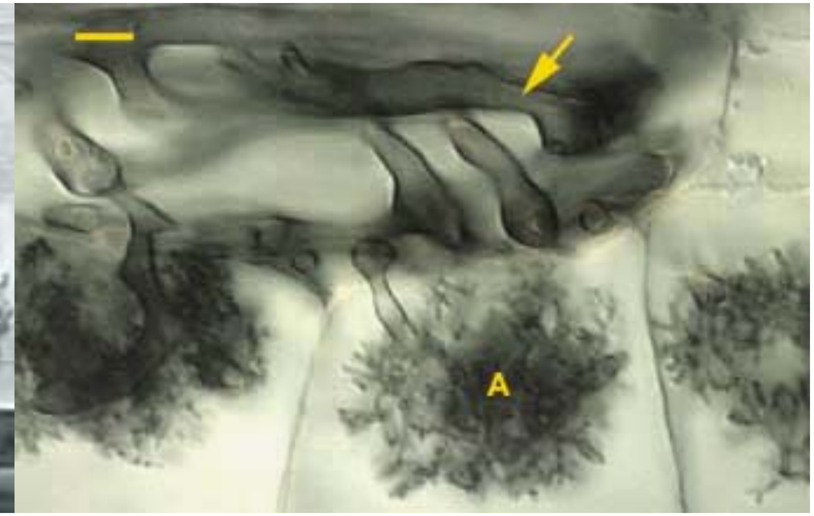
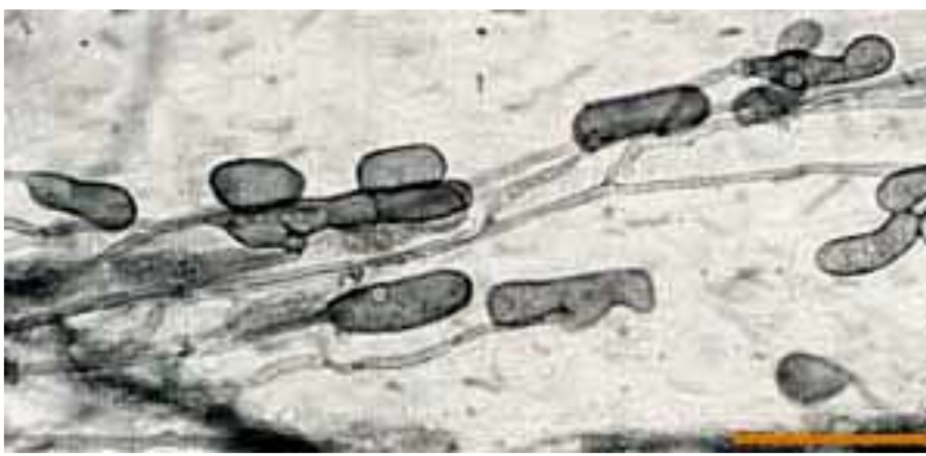
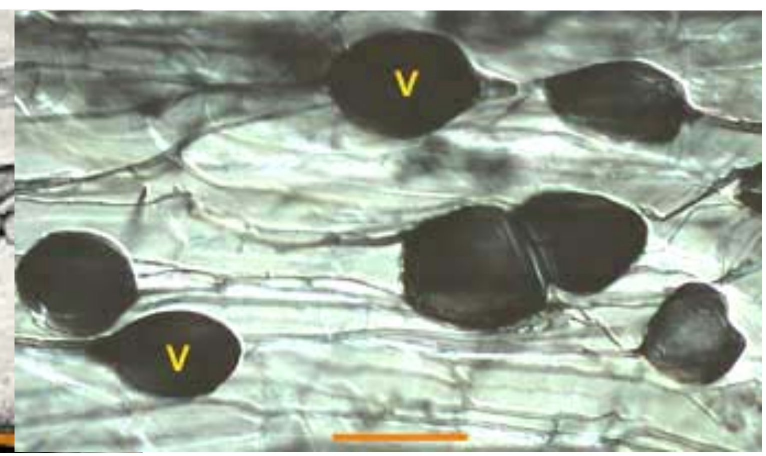




Glomeromycota: Glomerales
the arbuscular mycorrhizae



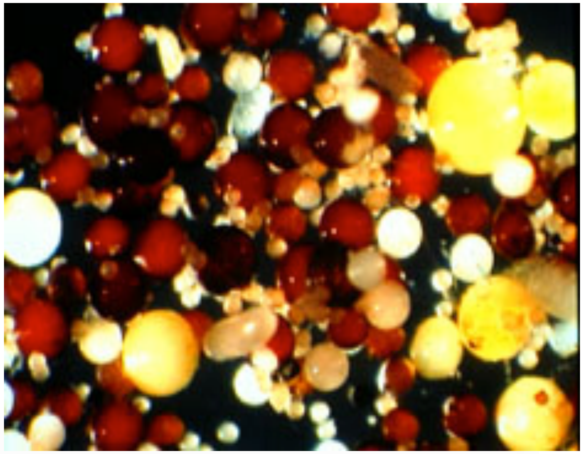


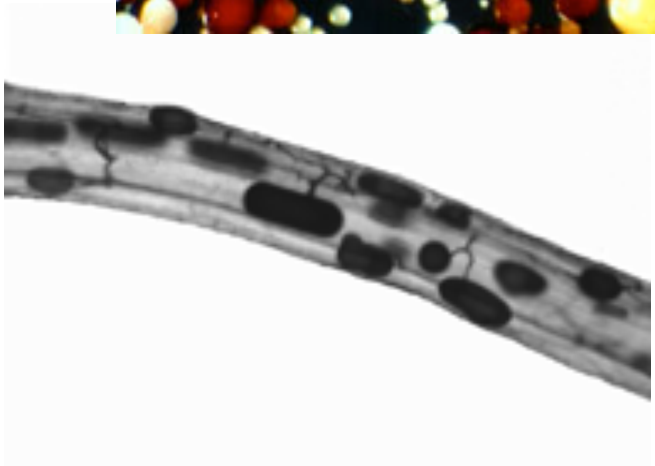
Classification based on limited morphology
now under revision due to molecular evidence

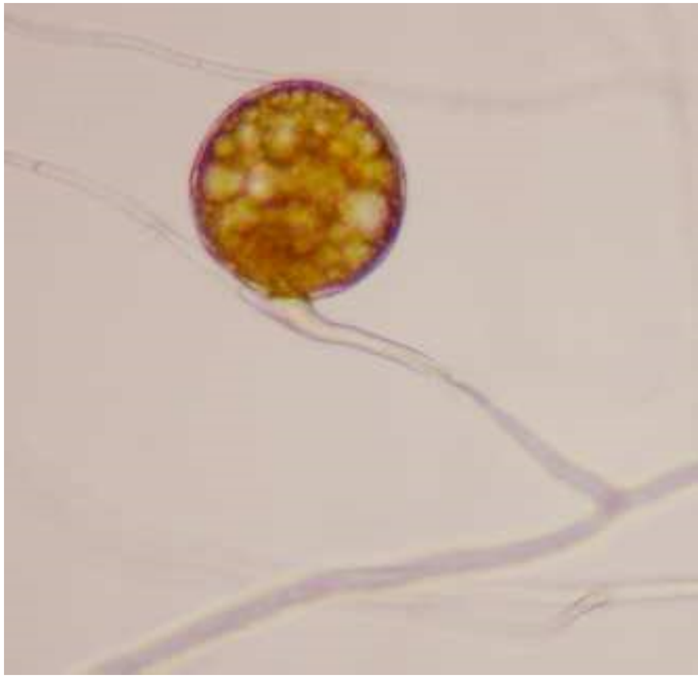
1 Order: Glomerales (=Glomales)

About 200 species, three families (based on morphology):

- Acaulosporaceae
- Gigasporaceae
- Glomaceae







Arbuscular mycorrhizae

The most common type of mycorrhizae
Widespread distribution, temperate, tropical
and widespread among plant families

Essential to ecosystem function, mineral nutrient uptake by plants

Apparently very many more plant species than AM fungal species
So AM fungi are thought to be generalists, not host specialized

BUT variation among AM fungi in P uptake ability and other effects, protection of roots against pathogens, etc still may indicate effects of AM diversity on plant community diversity

There may be multiple species of AM fungi present in a particular area even if one AM fungus species is capable of forming mycorrhizae with all of the plant species present

General characteristics

coenocytic hyphae, non septate
meiosis unknown
no evidence of sexual reproduction
lack fruiting structure of Basidiomycota & Ascomycota
no flagellated state in life cycle
obligate symbionts (?)
endomycorrhizae or vesicular-arbuscular mycorrhizae
(AM or VAM fungi)
or symbiosis with cyanobacteria (*Geosiphon* with *Nostoc*)

none has been grown in culture
very large (40 – 800 μm) asexual spores
multinucleate, hundreds to thousands of nuclei
layered walls
200 species probably an underestimate of true diversity

Glomeralean fungi structures

Hyphae

Within root (**intraradical**) and outside root (**extraradical**)

Arbuscules

Highly branched, thin-walled structures within host cell, short-lived, become digested by plant

Spores

Formed in soil or roots; asexual, variable in size and color between taxa, may contain hundreds of nuclei

Formed singly or in aggregations, spore balls

Vesicles

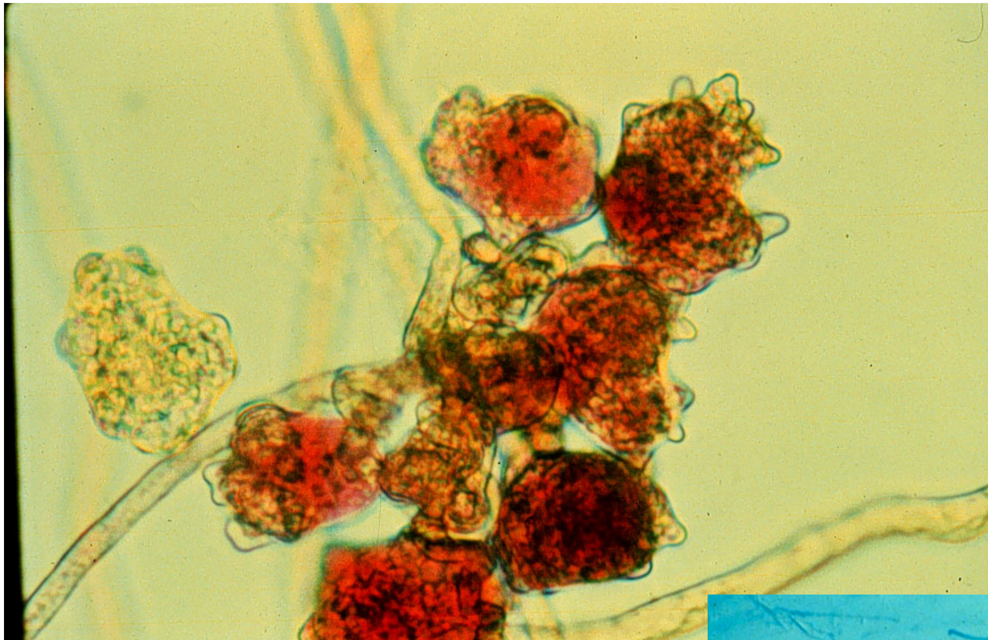
Ovoid, ellipsoid to irregular in shape, thin-walled, formed from hyphae in root cortex, storage organs

Only in suborder Glomineae (VAM)

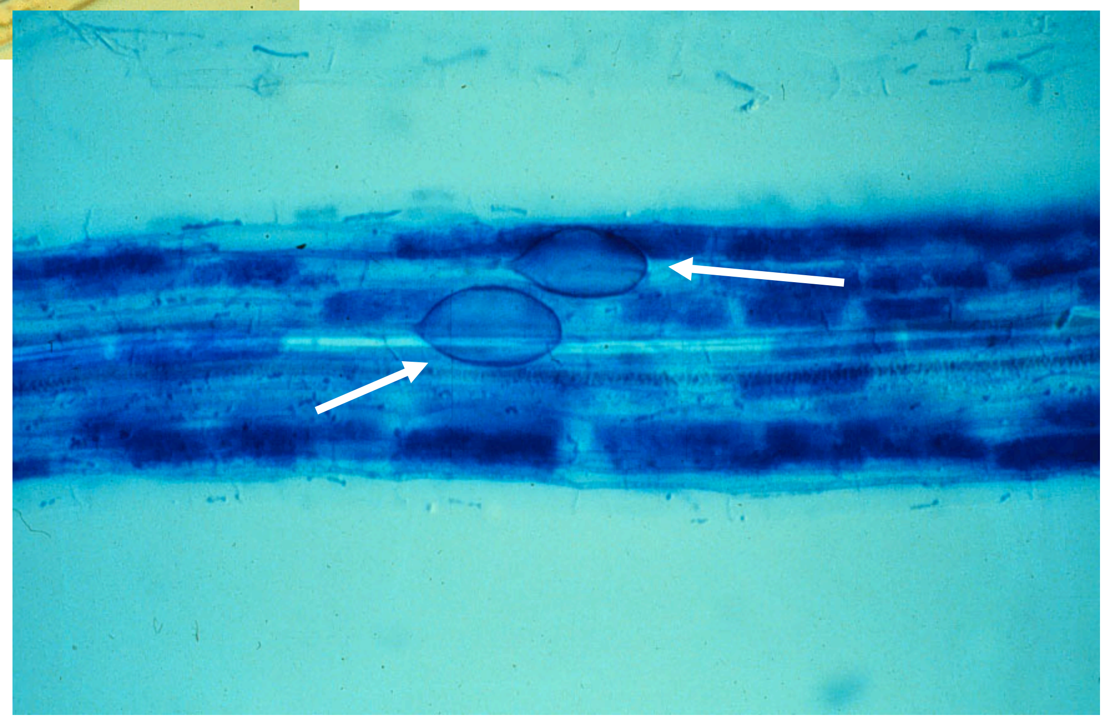
Auxiliary Cells

Clusters of thin-walled cells formed on hyphae outside the root

Only in suborder Gigasporinae (AM)



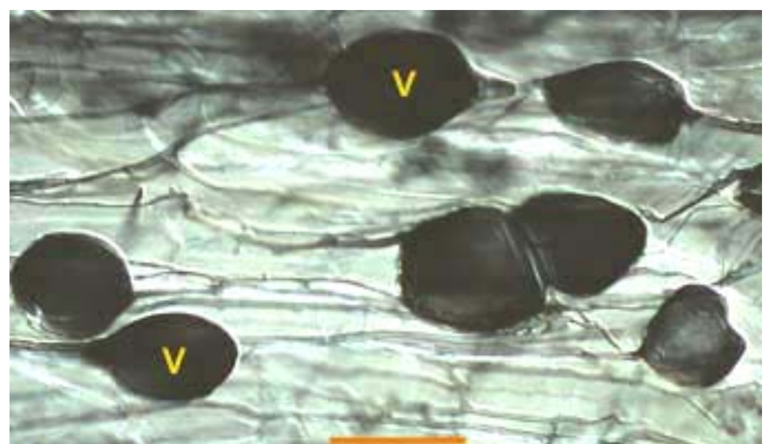
Auxiliary cells



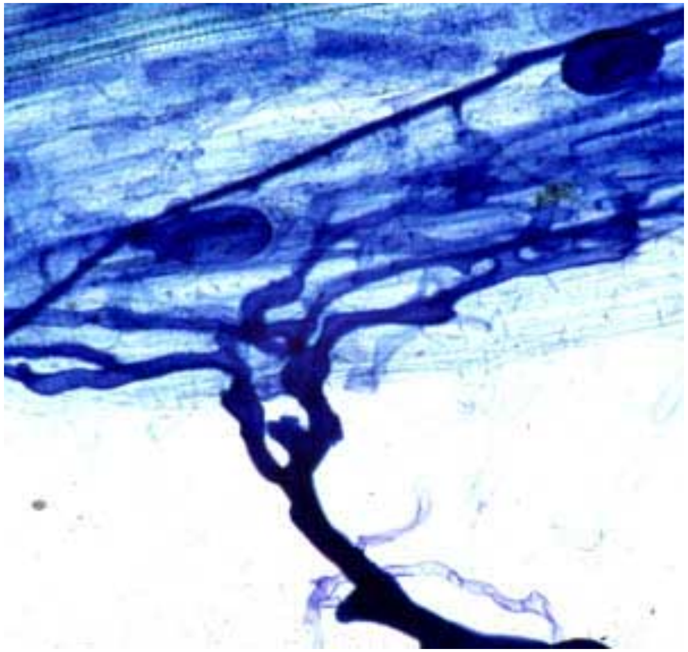
Vesicles in root

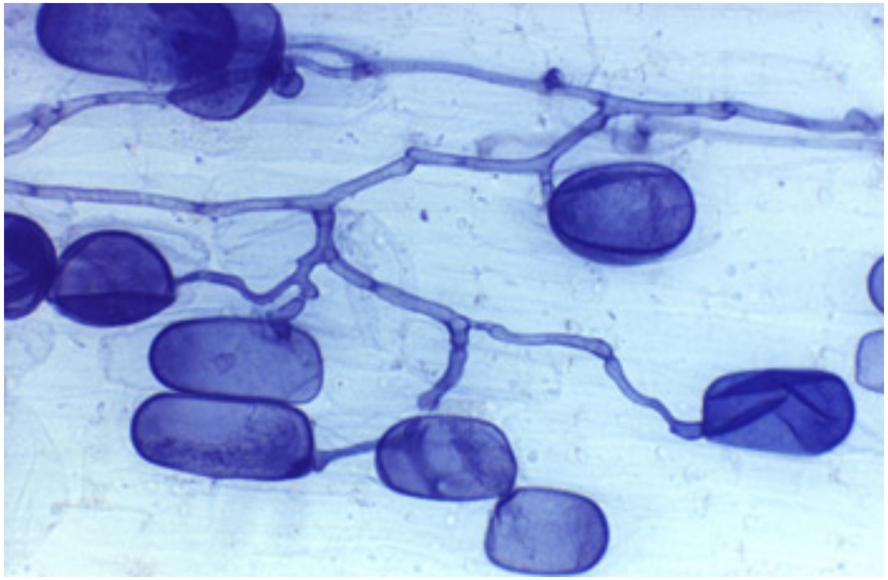
- **Arbuscules** - highly branched structures that are the site of nutrient transfer; they do not penetrate cell membrane; short-lived structures constantly being formed and degenerating

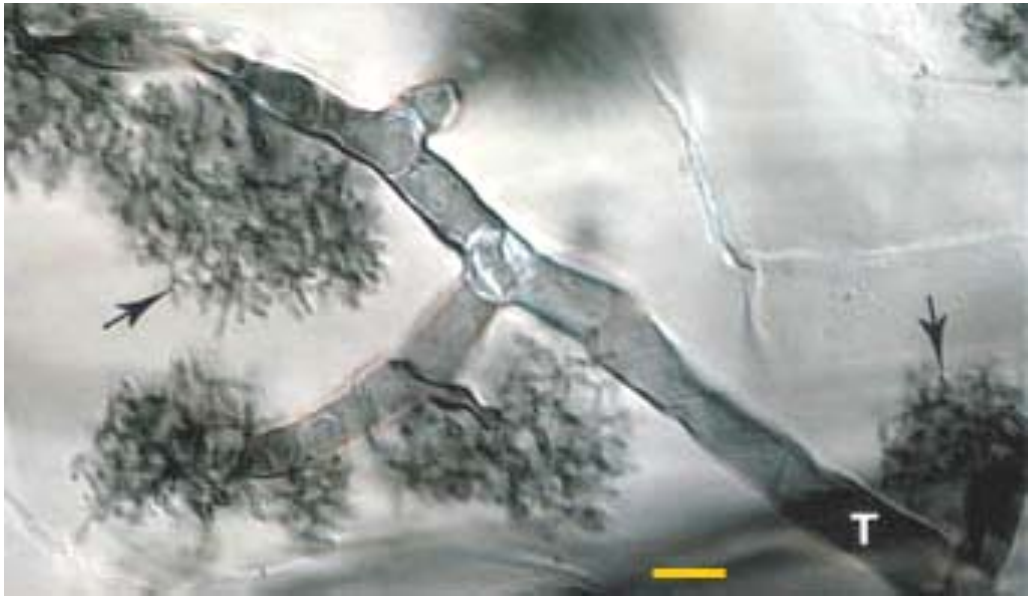
- **Vesicles** – oval or spherical, darkly staining structures that are thought to function as nutrient reservoirs



Vesicles and arbuscules







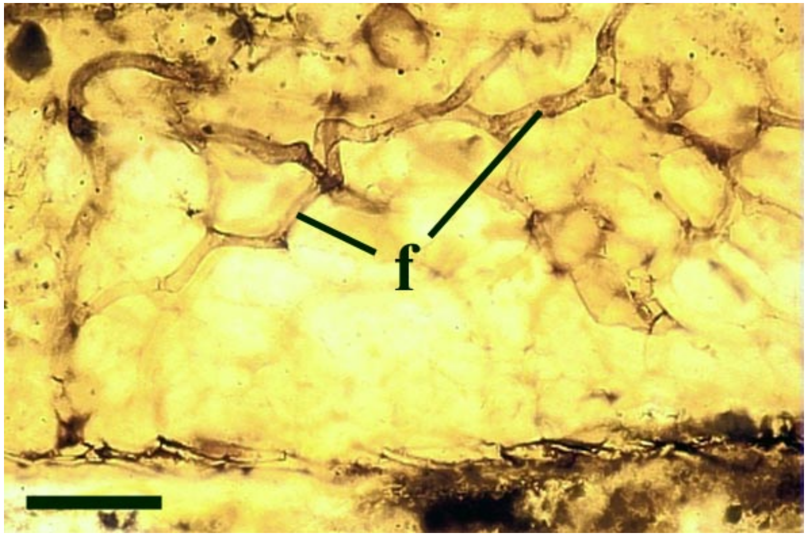
The oldest fossil Fungi?

Glomalean fungus from Ordovician, 460 MYA
Madison, WI
Redecker et al (2000). Science 289: 1920-21

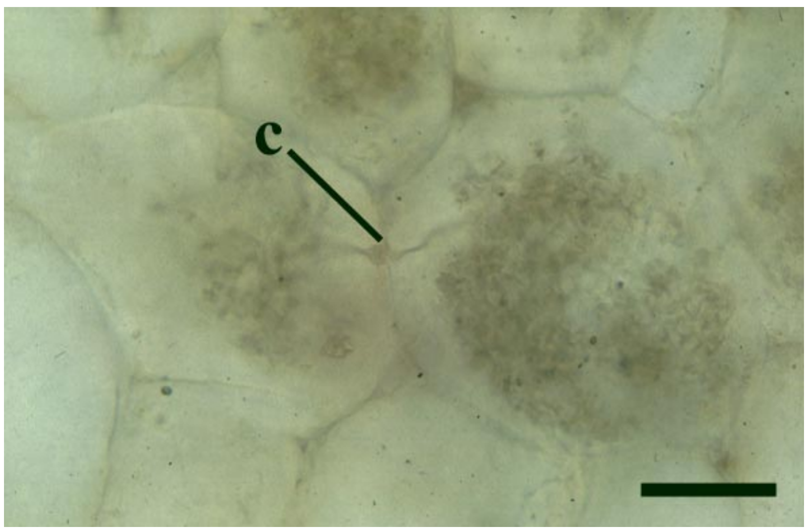
Evolutionary importance of mycorrhizae

- success of land plants?
- plants colonized land approx. 400-500 MYA
- fossils of Devonian land plants contain VAM fungi

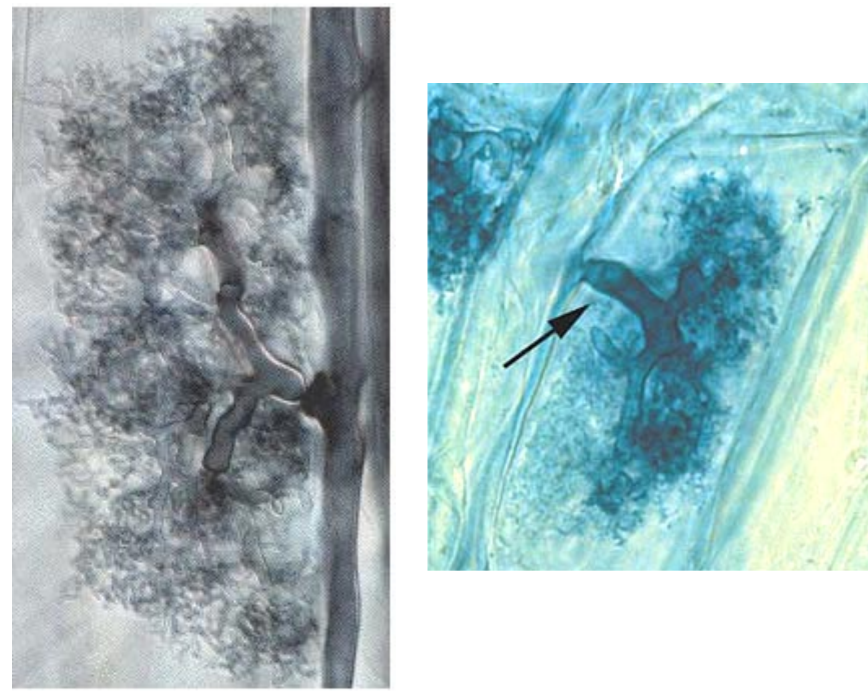
- 90% of all plant species are characterized as mycorrhizal
- Proteaceae - only nonmycorrhizal woody plant
- some herbaceous families nonmycorrhizal (e.g. Brassicaceae)



Glomites rhyniensis from Agalophyton, ca 410 MYA



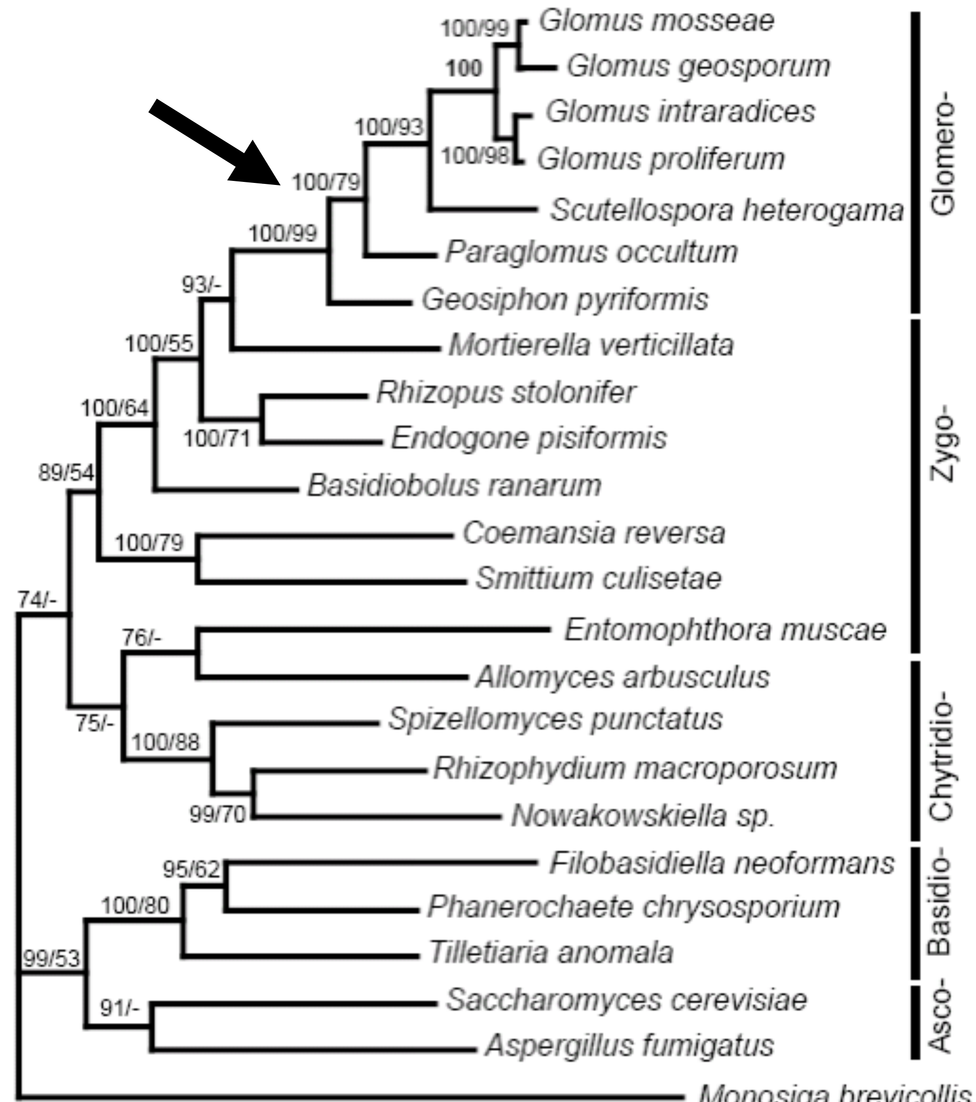
Fungal hyphae (**f**) and arbuscules penetrating the outer cortex of an *Aglaophyton major* stem (scale bar = 100μm)

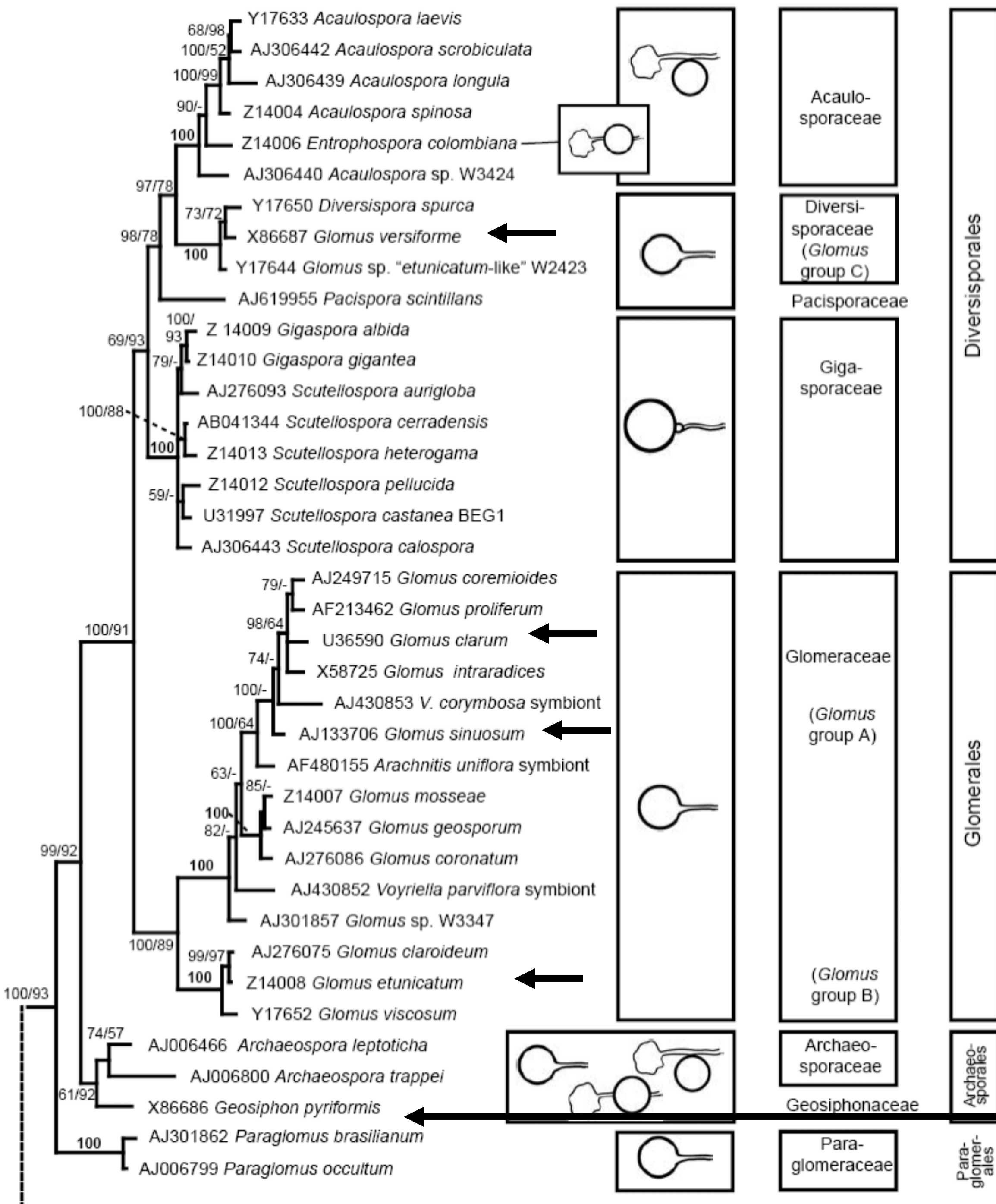


Arbuscules of modern AM (Glomeralean) fungi

Glomerales (=Glomales) formerly thought to be part of Zygomycota

Now considered a separate phylum based on molecular sequence studies





Now 4 Orders, 8 Families recognized based on molecular sequence data

The genus *Glomus* is not monophyletic!

Genus based on aspects of spore formation and germination, but these characters appear in different clades

Geosiphon

Glomeromycota

- often referred to as "VAM fungi" because some form both vesicles and arbuscules

- more recently referred to simply as “AM fungi”
  - not all species form vesicles

- a form of endomycorrhizae, fungal hyphae within root cells

- AM fungi can be found in about 70% of all plant families

- with most agronomically important angiosperms, e.g. grasses
  some gymnosperms (e.g., *Sequoia, Chamaecyparis*)
  some bryophytes and pteriodophytes

AM vs. Ectomycorrhizae (EcM)

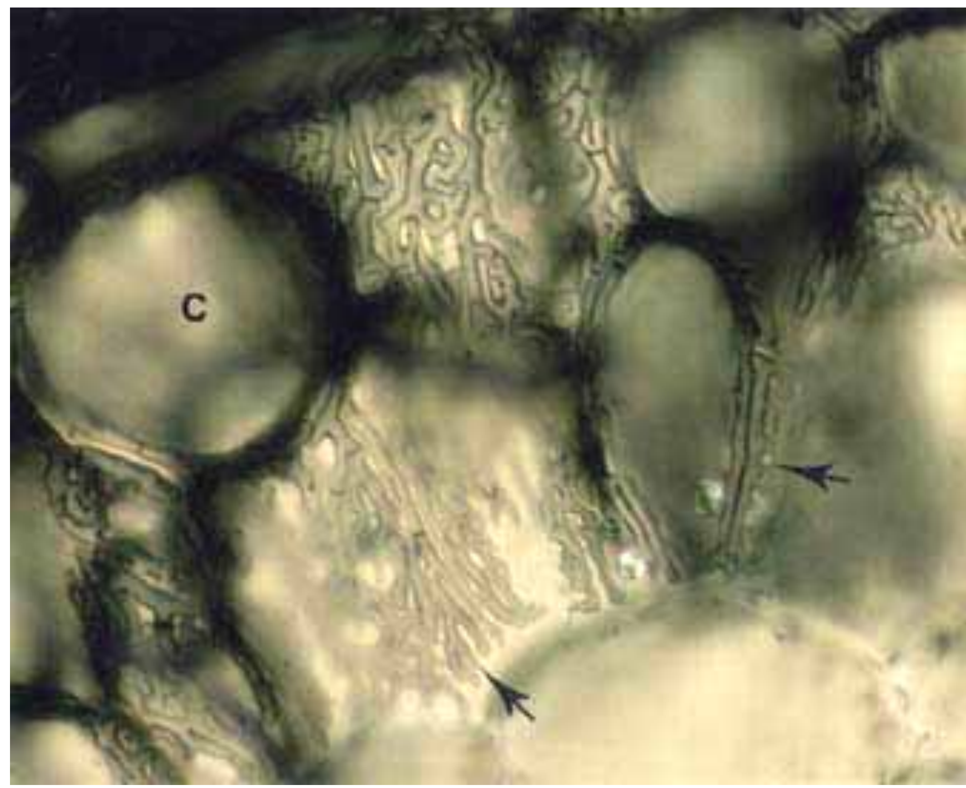
- both occur in the fine root system

- difference in penetration of cortex cells
    - AM fungal hyphae penetrate the cortex cells forming vesicles and arbuscules (endomycorrhizae)

    - EcM do not penetrate cell walls of cortex cell (ectomycorrhizae)
        - (except of course arbutoid, ericoid, orchid EcM)

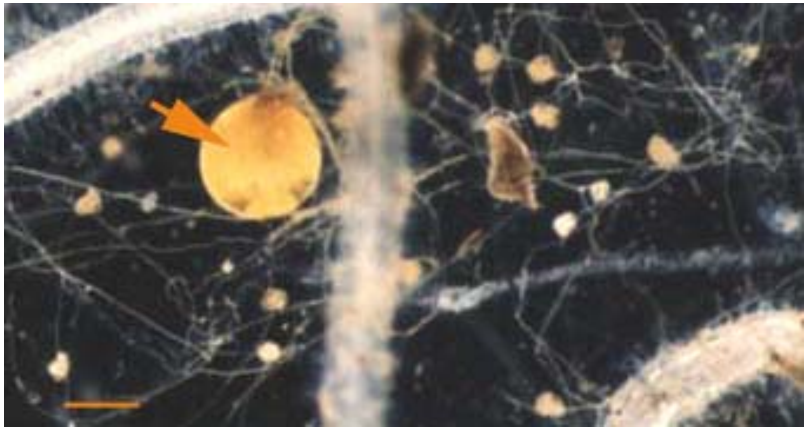
EcM do not penetrate cell walls of cortex cells

- EcM form a puzzled-shape covering of hyphae over the cortex cells called a Hartig net
- nutrient transfer across root cell wall and fungal cell walls
- relatively long-lived structures



Effect on root morphology

- VAM (AM) do not significantly alter root morphology
  - fine roots possess root hairs



- EcM alter root morphology; no root hairs; produce a mantle

Distribution

- estimated that >300,000 plant species have AM/VAM
  only ~200 spp. fungi participate (but true diversity may be greater)
- est. only ~2000 plant species have EcM
  - ~5000 fungi participate
- taxonomic distribution
  - VAM restricted to Glomeromycota
  - ectomycorrhiza in two (3?) phyla, >70 genera in 9 orders
    - Basidiomycota, Ascomycota, (Zygomycota?)
- host distribution
  - ectomycorrhiza mostly woody plants
    - Gymnosperms - e.g., Pinaceae
    - Angiosperms - e.g., Fagaceae, Betulaceae, Salicaceae, Dipterocarpoideae, Myrtaceae
  - (V)AM: woody & herbaceous plants
    - 90% of vascular plants normally assoc./w (V)AM fungi

(V)AM and EcM mycorrhizal symbioses

Fungus benefits

- carbohydrates (photosynthates, monosaccharides) that are converted to trehalose, mannitol, glycogen
- root exudates, necessary cofactors for spore germination

Plant benefits

- greater absorptive area
- uptake of P, N, Ca, K, Cu, Mb, Mg, Zn
- water
- protection against soil borne root pathogens

Ecosystem Distributions

(V)AM

- VAM, AM are common in most habitats
- Dominant mycorrhizae in <u>grasslands</u> and tropical forest ecosystems

EcM

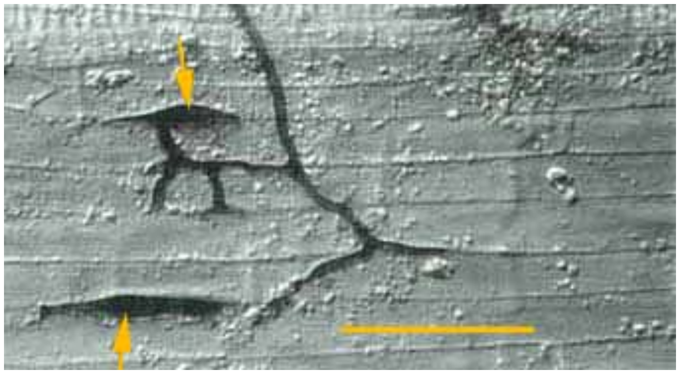
- dominant in coniferous forests, especially boreal or alpine regions
- common in many broad-leaved forests in temperate and mediterranean regions
- also occur in some tropical or subtropical savanna or rain forests habitats (Dipterocarp forests Malaysia, Eucalyptus forests)

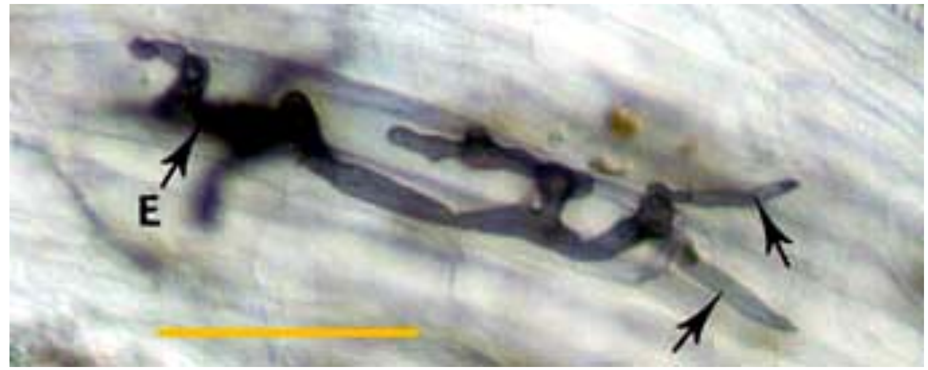
Nonmycorrhizal (NM) Plants

- most common in disturbed habitats, or sites with extreme environmental (high latitude or elevation) or soil conditions
- few families: Brassicaceae, Proteaceae, Juncaceae, Cyperaceae

Root colonization by Glomeromycota

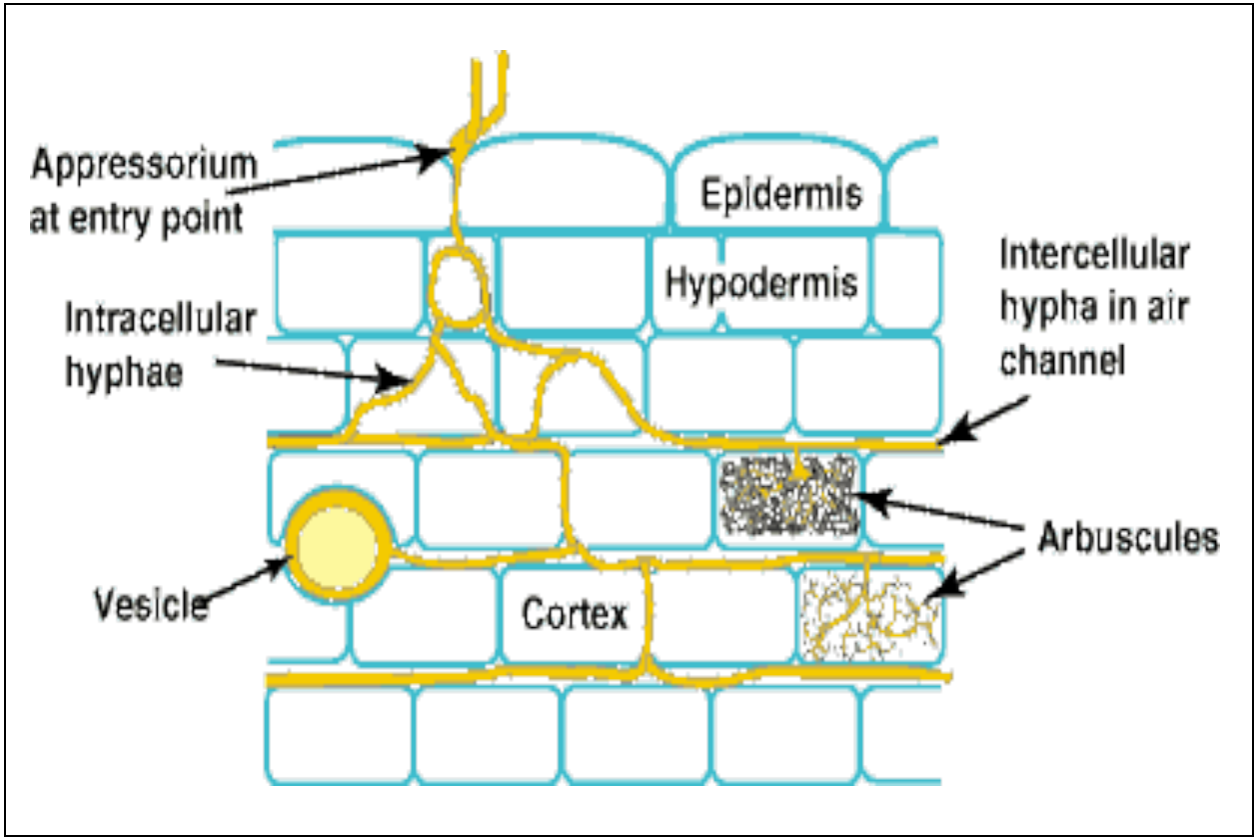
hyphae enter the root through root hairs or by forming appressoria between epidermal cells;





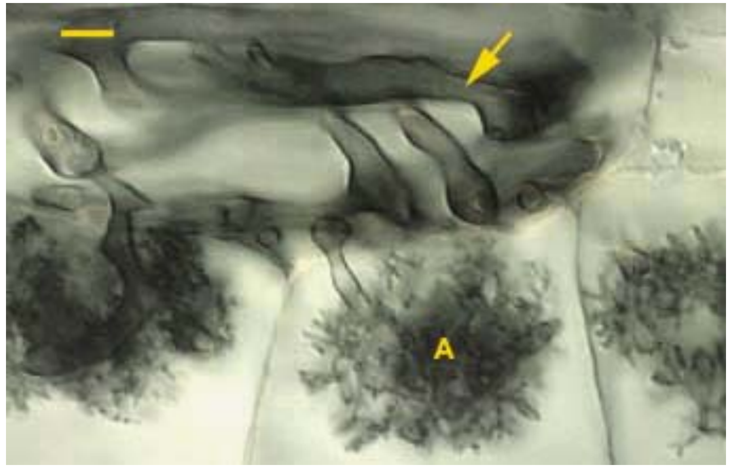
hypha grow intercellularly and also penetrate the cell walls of cortical cells, causing invagination of the plasma membrane

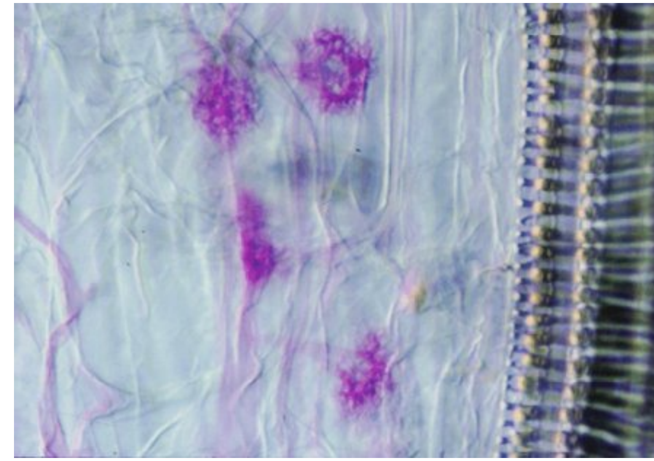
Root colonization by AM fungi



AM hyphae grow intercellularly, form arbuscules and, if produced by a species, vesicles

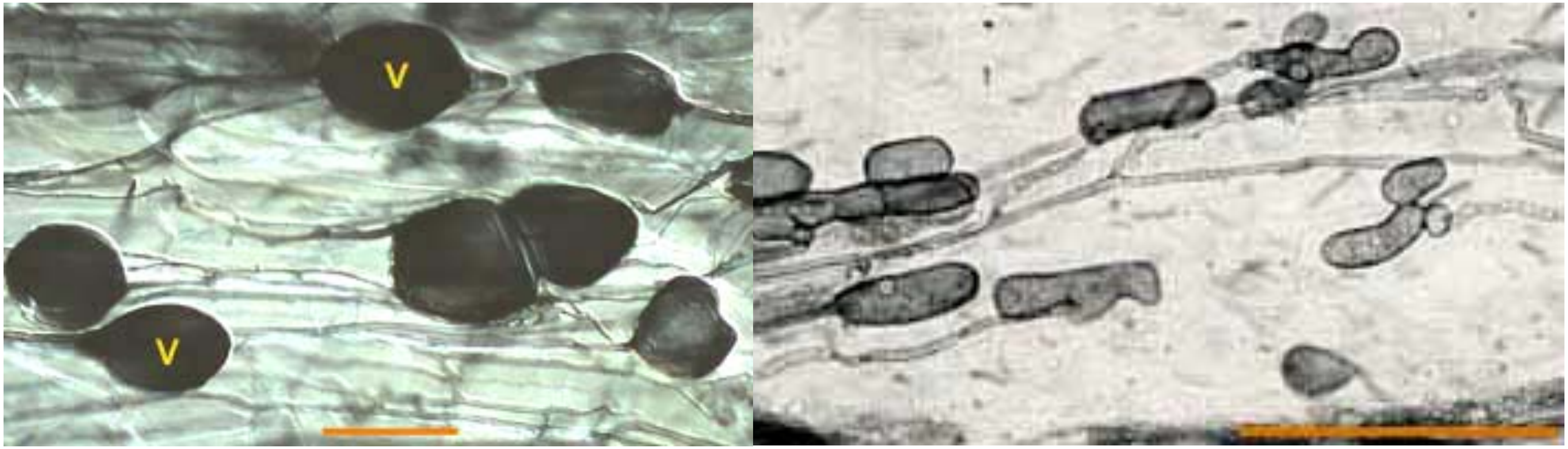
Arbuscules





- highly branched haustorium-like structures
- similar to haustoria, more highly branched, greater surface
- extend through the host cell wall, but not cell plasma membrane
- increased surface area between the fungus and the host cell plasma membrane
- sites of transfer of metabolites and nutrients between the two mycorrhizal partners
- short-lived: remains alive only for a few days before disintegrating and being digested by the cells of the plant
- in a healthy (V)AM mycorrhizal relationship there is a continuous sequence of development and disintegration of arbuscules


5 μm
Acaulospora delicata

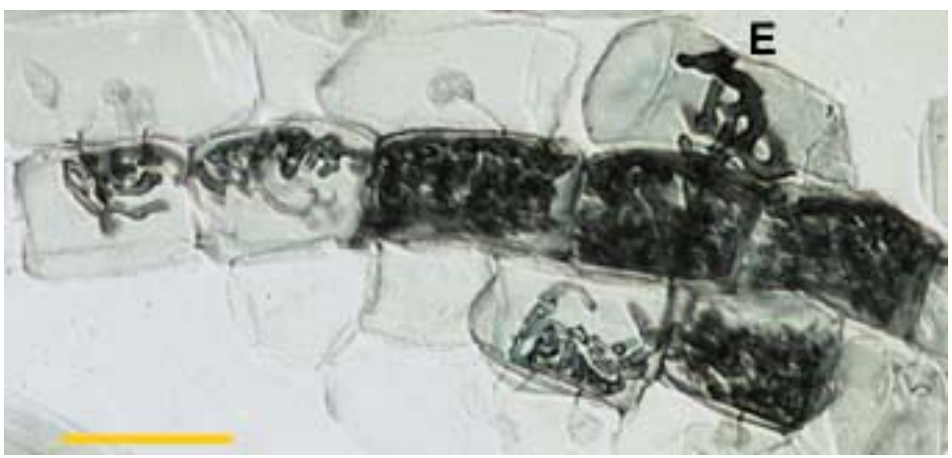


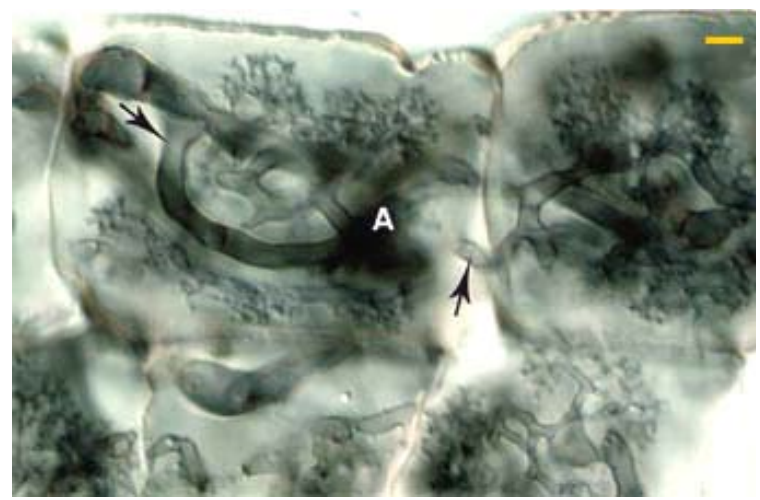
Vesicles

- terminal hyphal swellings; darkly staining
- not formed by all species of Glomeromycota
- formed either between or within host cell walls
- thought to function as energy stores for use by the fungus when the supply of host metabolites is low

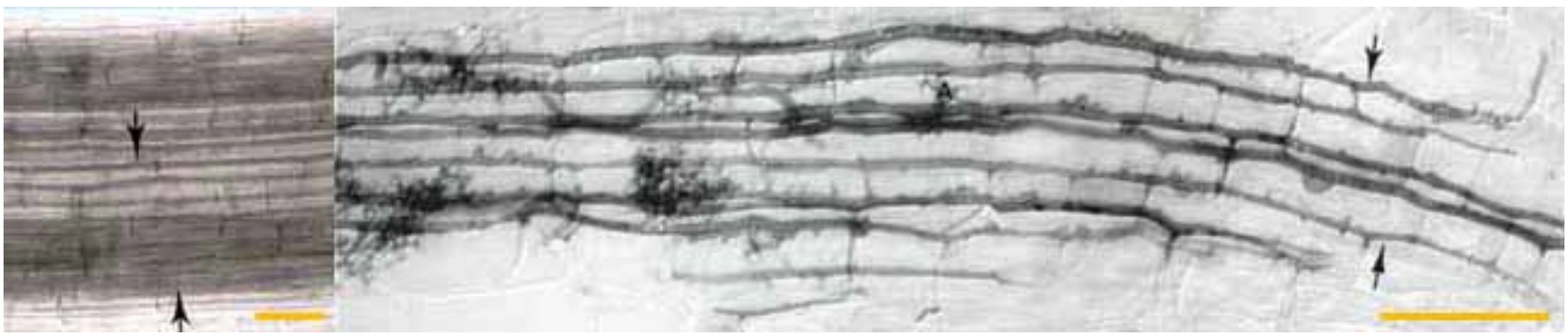
**Two types of arbuscular mycorrizal colonization:
Paris and Arum**

Paris type associations have hyphae that spread primarily by intracellular growth following a convoluted path through cortex cells. The resulting colonies of (V)AM fungi generally have a coiled appearance but may have more digitate branching patterns. Arbuscules may be restricted to a single layer of cells in the inner cortex.





Arum type associations have extensive growth of hyphae along longitudinal intercellular air channels between the walls of root cells. A relatively rapid parallel spread of intercellular hyphae may occur. The resulting colonies of (V)AM fungi have a linear appearance.



General characteristics of Glomeromycota

- traditional classification included two suborders, three families of six genera (but this is changing rapidly due to molecular data)

- meiosis is not confirmed in any member of the Glomerales

- somatic hyphae and arbuscles and vesicles (if present), are very similar in most taxa

- spores, vesicles, auxiliary cells have been used as criteria for differentiation of taxa (but shown to be unreliable based on molecular studies)

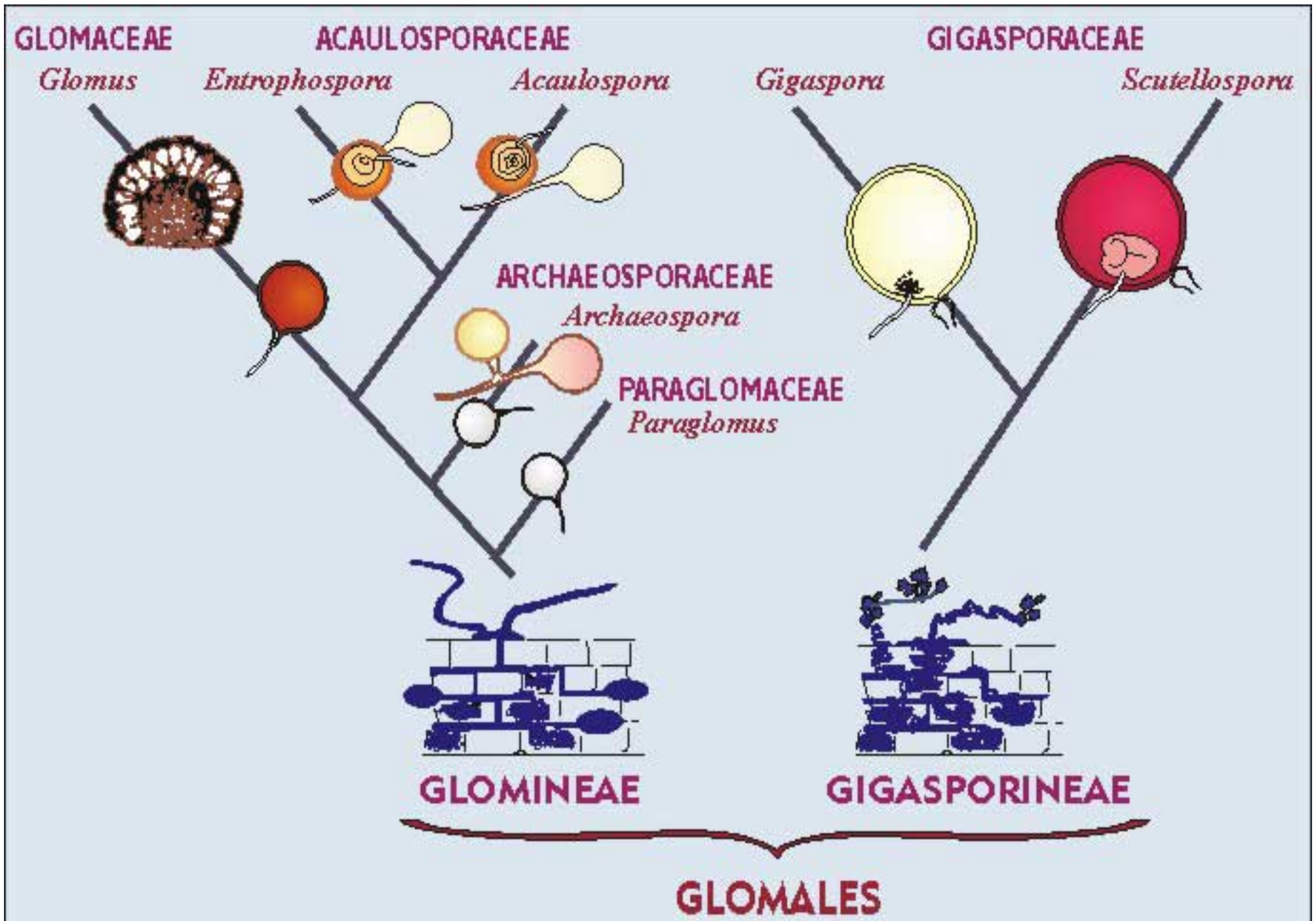
Traditional morphological classification: two suborders:

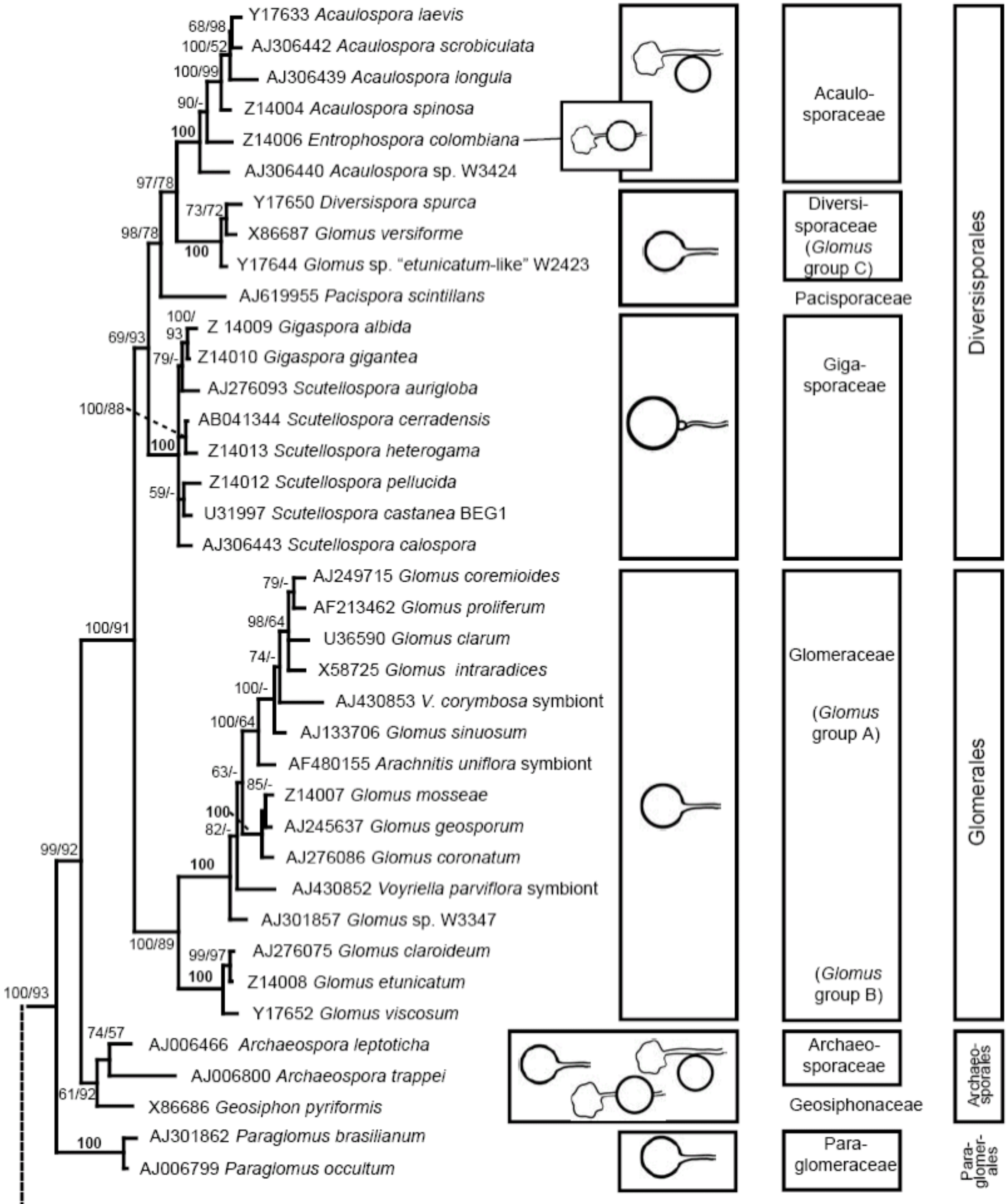
Glomineae—have intra-radical vesicles

Acaulosporaceae, Glomaceae

Gigasporinae— have auxiliary cells outside root

Gigasporaceae





But most recent molecular studies do not fully support this concept.

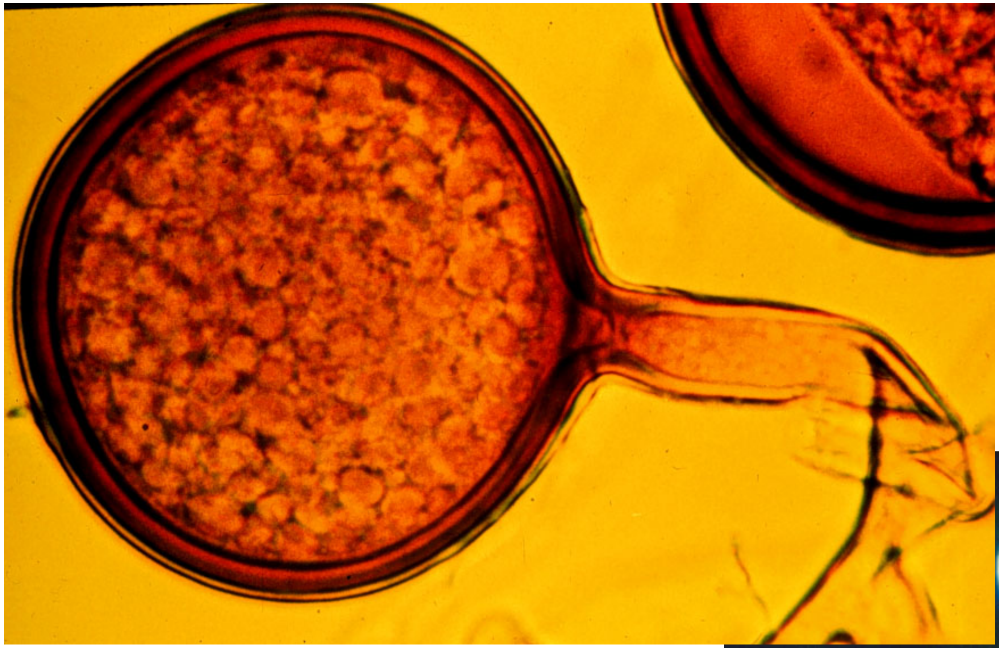
Glomeraceae

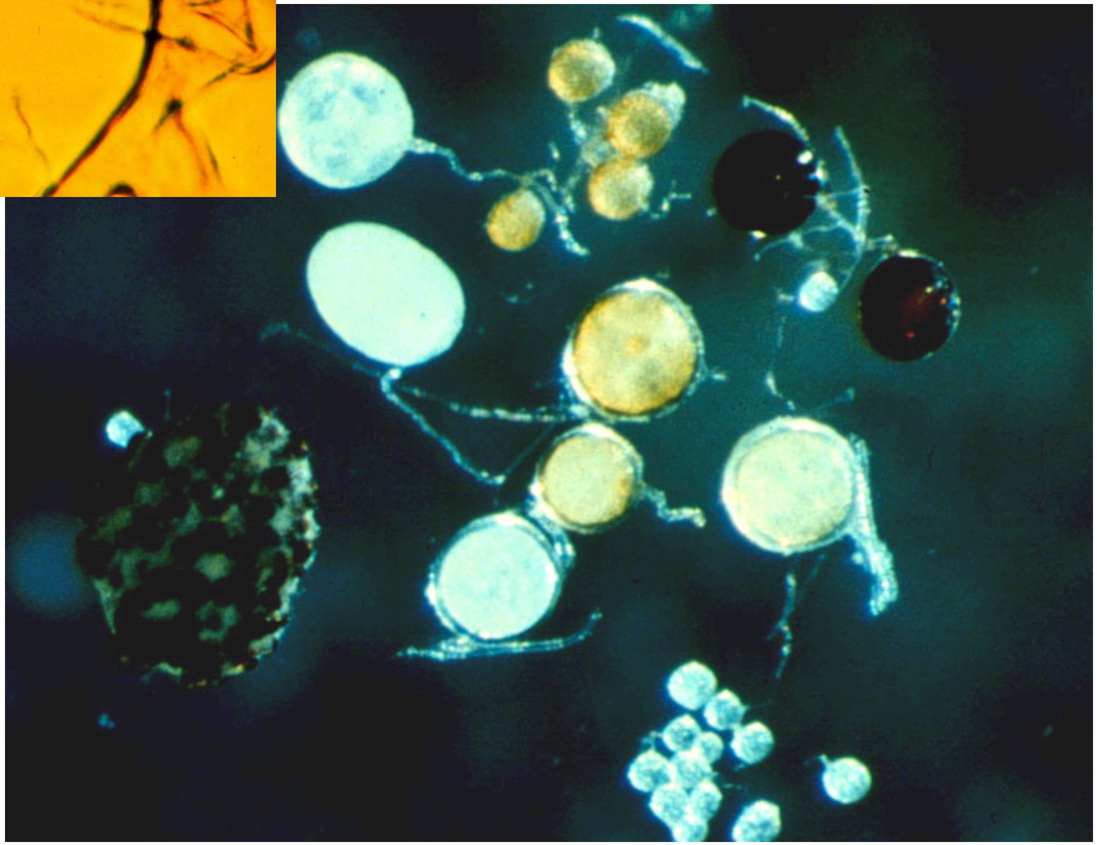
Glomus

"Sclerocystis"

- "chlamydospores" are borne <u>terminally</u> on fertile hyphae
- spores of most taxa are formed singly in the soil
- some species of *Glomus* and "*Sclerocystis*" form aggregates of spores, "spore balls" or sporocarps

Sclerocystis is now merged with *Glomus*



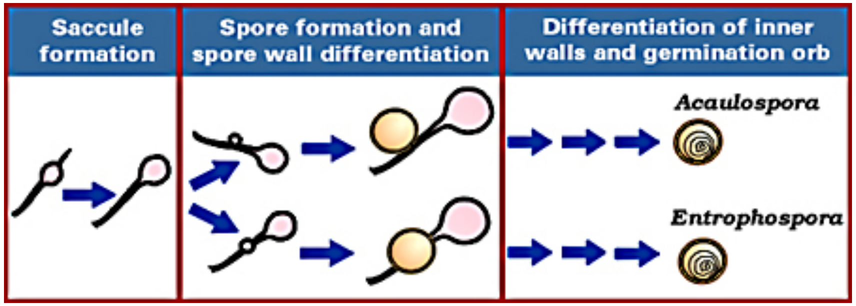


Spores of *Glomus* spp.

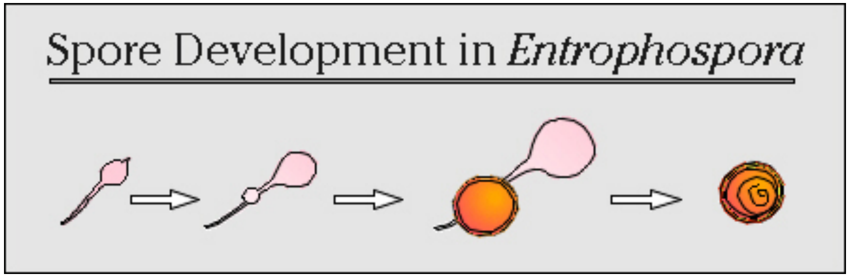
Acaulosporaceae

- vesicles and arbuscules present in roots
- produce "chlamydospores" in the soil either singly or in sporocarps.
- spores of both these genera arise from a hypha that subtends a swollen, sac-like structure; "sporiferous saccule"

Acaulospora the spore forms laterally on the subtending hypha

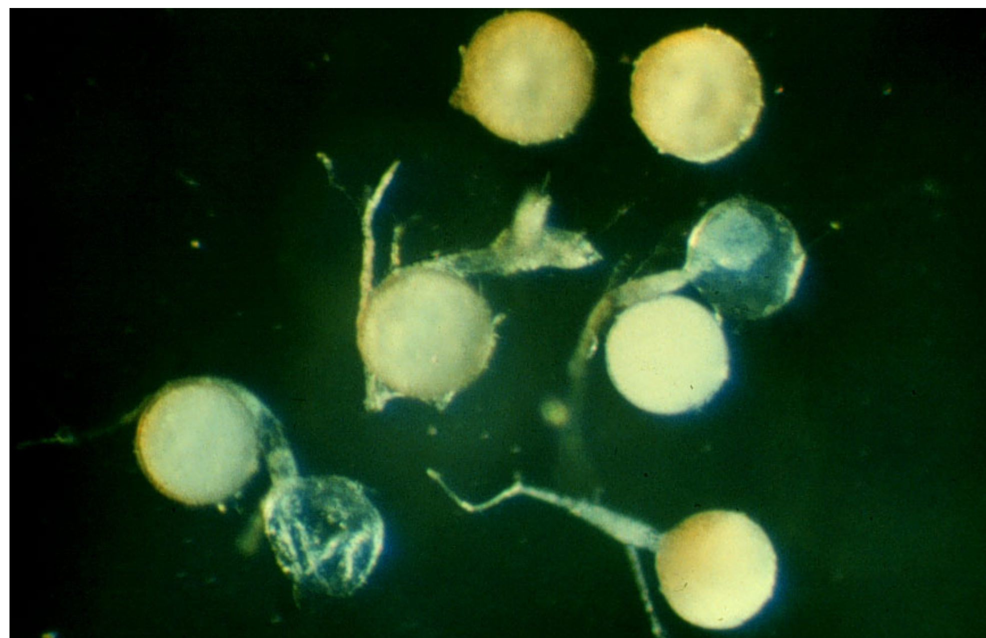


Entrophospora spore develops within the neck of the hypha



Intercalary spore of *Entrophospora* with terminal, empty sporiferous saccule

Lateral spores of *Acaulospora* with sporiferous saccules



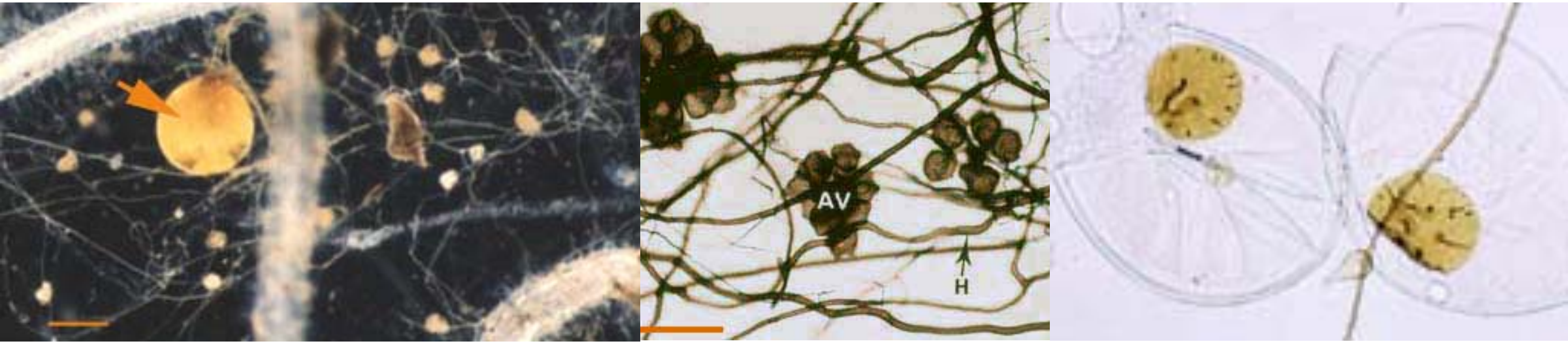
Gigasporaceae

Gigaspora and *Scutellospora*

only form arbuscules in the roots of their mycorrhizal partners

auxiliary cells (AV in image) are produced in the soil along with structures called "azygospores"

Function of auxiliary cells is unknown



- **azygospore** - term used for spores of that are produced on a hypha that resembles the gametangial hypha of some Zygomycota
- BUT, meiosis has never been documented in Glomerales

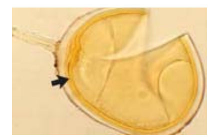
Recent molecular data do not support the strict morphological groupings. Classification of the Glomeromycota is under revision

Glomus morphology ancestral(?)

Glomerales

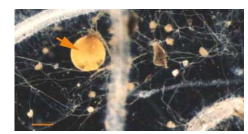
Glomeraceae – *Glomus group C*

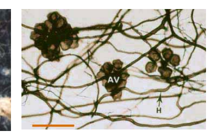
Diversisporales



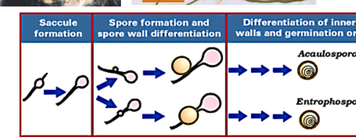
Diversisporaceae - *Glomus*

Gigasporaceae - *Gigaspora*, *Scutellospora*





Acaulosporaceae - *Acaulospora*, *Entrophospora*



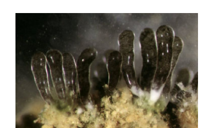
Paraglomerales

Paraglomeraceae - *Paraglomus*

Archaeosporales

Archaeosporaceae - *Archaeospora*

Geosiphonaceae - *Geosiphon*



Are mycorrhizae always beneficial?

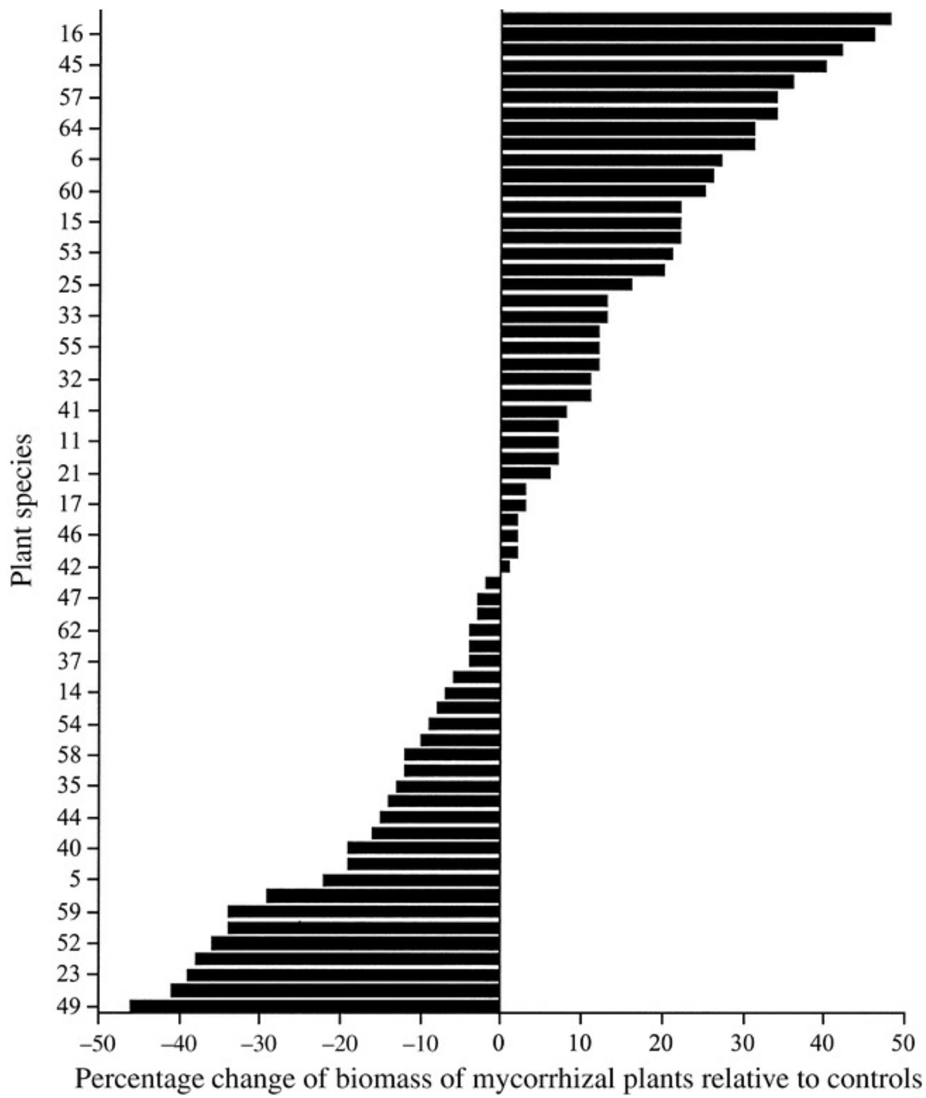
Because the external mycelium scavenges for P so effectively AM symbiosis frequently leads to higher P uptake and improved growth of AM plants compared with a nonmycorrhizal plant; the plants are said to show a positive mycorrhizal response.

However a great range in growth responses from strongly positive to negative can occur. Until recently it was generally thought that negative responses were due to experimental conditions such as low light. More recent research has emphasized a continuum in C-P exchange between plant and fungal symbionts.

Also, bear in mind Liebig's law of the minimum. The cost of mycorrhizal symbiosis in photosynthate lost to the fungus is only a good investment for the plant when P or another nutrient provided by the fungal partner is limiting. If the photosynthate provided to the fungus could have been invested in seeds, flowers, biomass etc. instead of a symbiont, the fungus has gained at the expense of the plant.

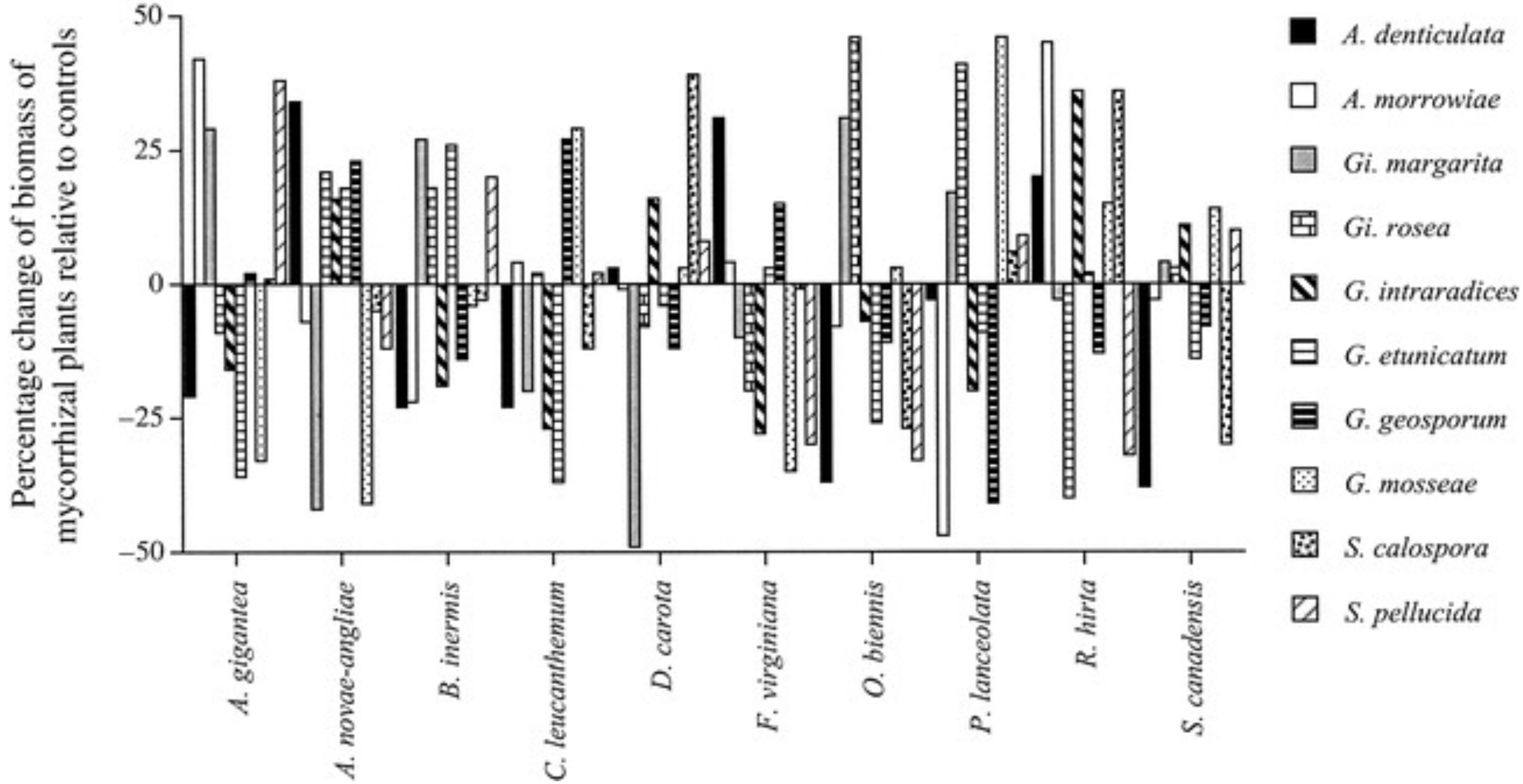
This may help explain why some groups of plants are nonmycorrhizal.

Growth responses of different host-AM fungus combinations



Klironomos 2003. Ecology 84:2292–2301

Klironomos (2003) compared growth responses of several plant species grown with a single AM mycorrhizal fungus, *Glomus etunicatum* vs. the same plants kept free of mycorrhizae. The results showed a wide range in growth response from positive to negative.



Klironomos 2003. Ecology 84:2292–2301

Klironomos (2003) also investigated the growth responses of several different plant species colonized by different AM fungi (bars) that commonly occur together in the same habitat. There was a range of growth responses depending on plant-AM fungus combination. No AM fungus or plant species was consistently associated with either positive or negative growth responses.

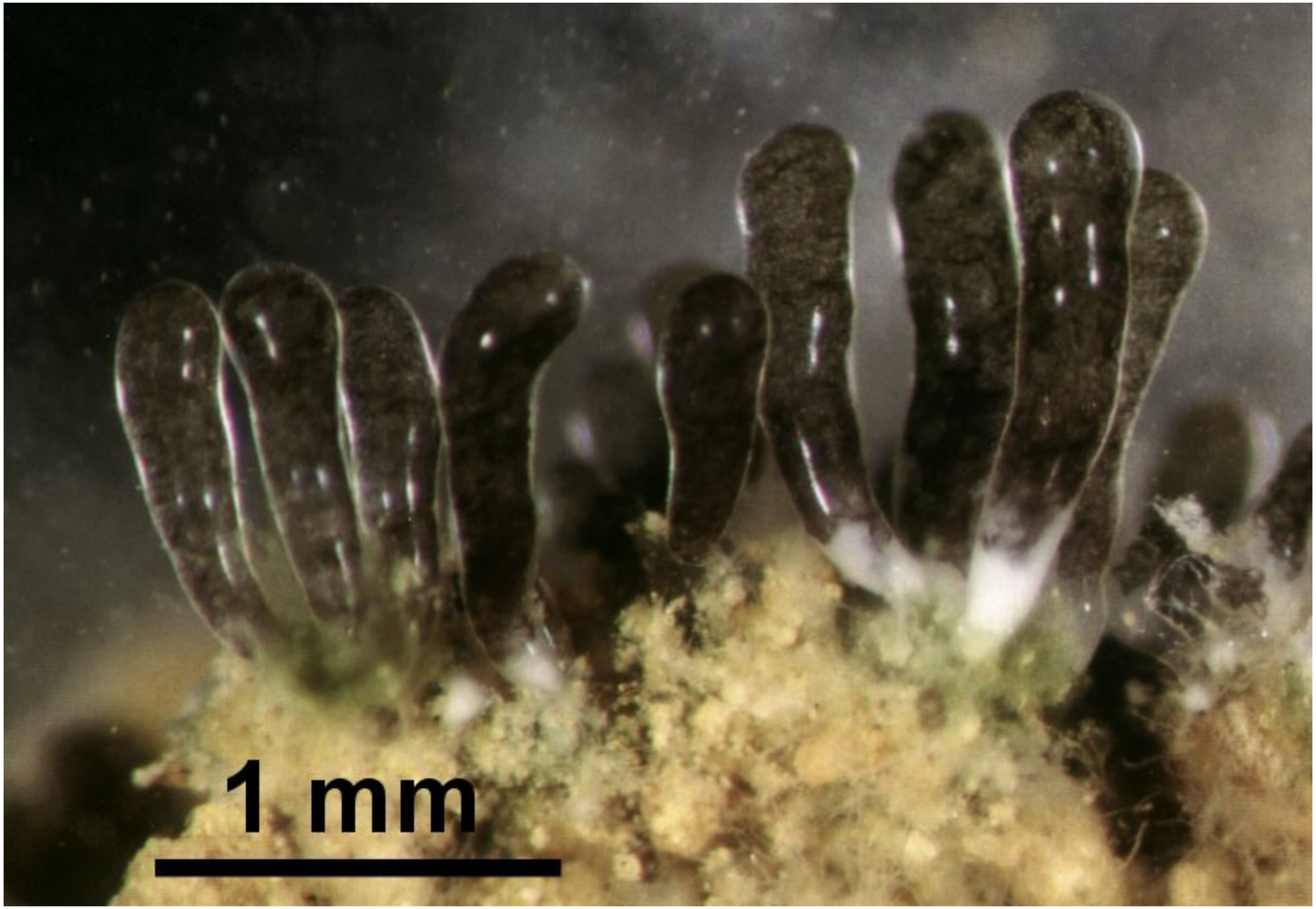
Takeaways: mycorrhizal symbiosis is complicated, not always mutualistic

Mycorrhizal symbiosis seems likely always to be beneficial for the AM or ECM fungi, but whether the plant always benefits depends on many factors. Are some mycorrhizal fungi ‘cheaters’ that take photosynthate but provide no P in return? The data from Klironomos (2003) don’t seem to support that idea. No single AM fungus consistently caused negative growth, as would be expected of a cheater strategy.

In addition, provision of P is not the only plant benefit attributed to mycorrhizal symbiosis. Improved drought tolerance, resistance to certain pathogens, and increased tolerance of some toxic substances such as arsenates have been reported as benefits of mycorrhizal colonization in plants.

Although mycorrhizal fungi are remarkably successful, ubiquitous components of plant root systems, contributing to nutrient uptake in the large majority of land plants and influencing higher level processes, such as plant competition and ecosystem stability, variable responses in different plants to colonization by different fungi may help explain how certain plant groups such as Brassicaceae can be successful without the help of mycorrhizal fungi.

Geosiphon



- Glomeromycotan fungus with endosymbiotic cyanobacterium (*Nostoc punctiforme*) in hyphal "bladders"

Geosiphon bladders and spores

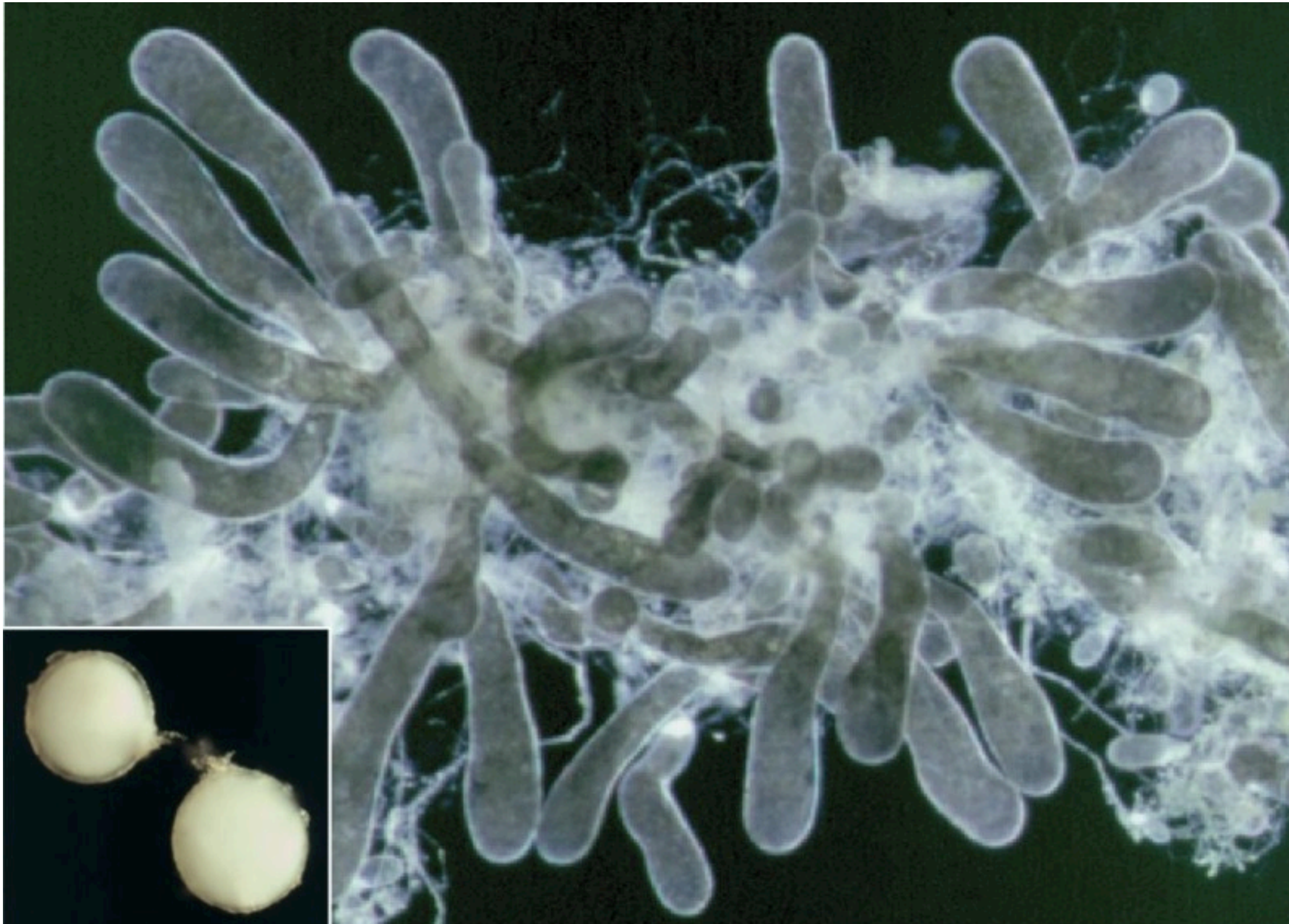
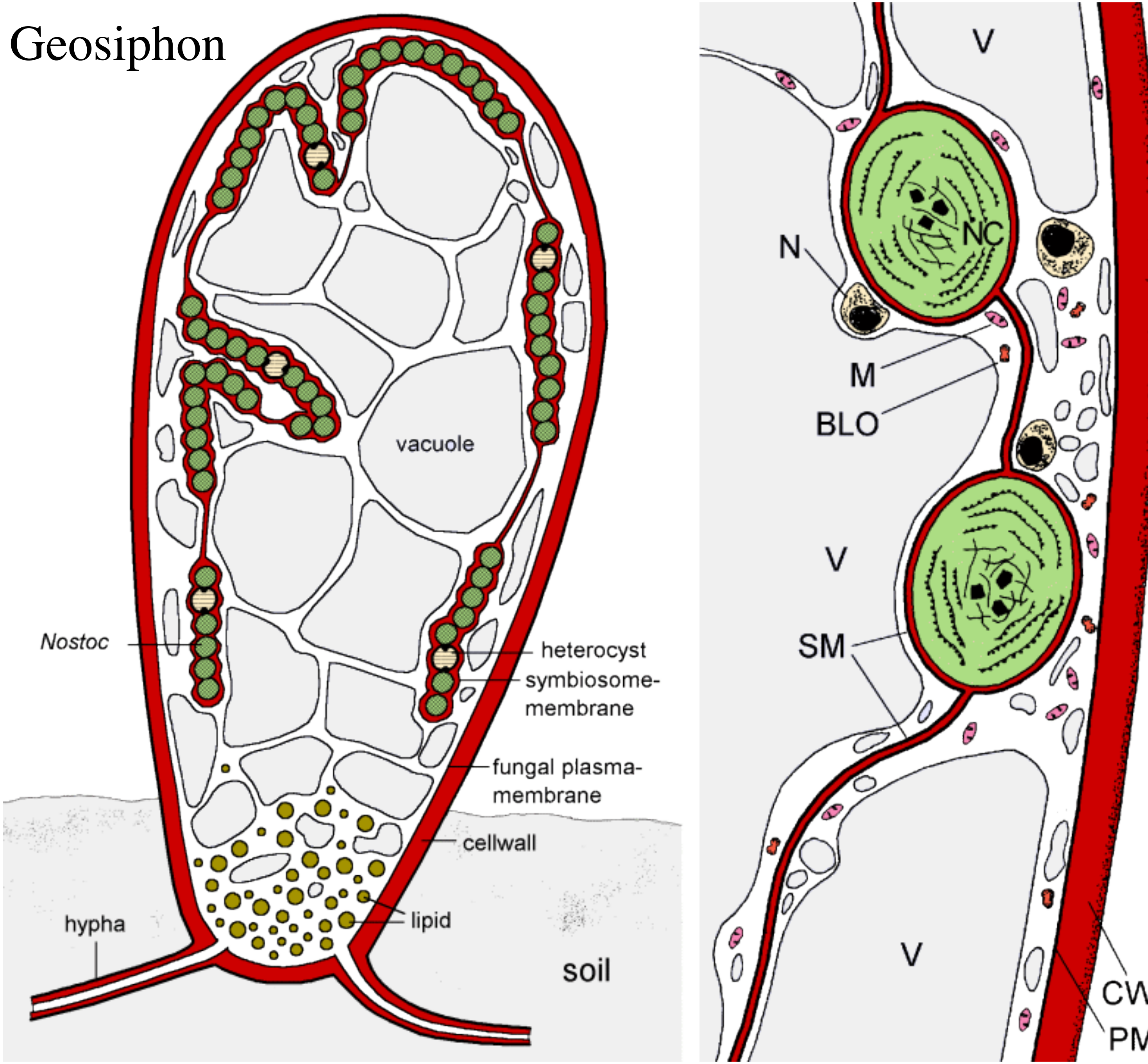


Diagram of Geosiphon



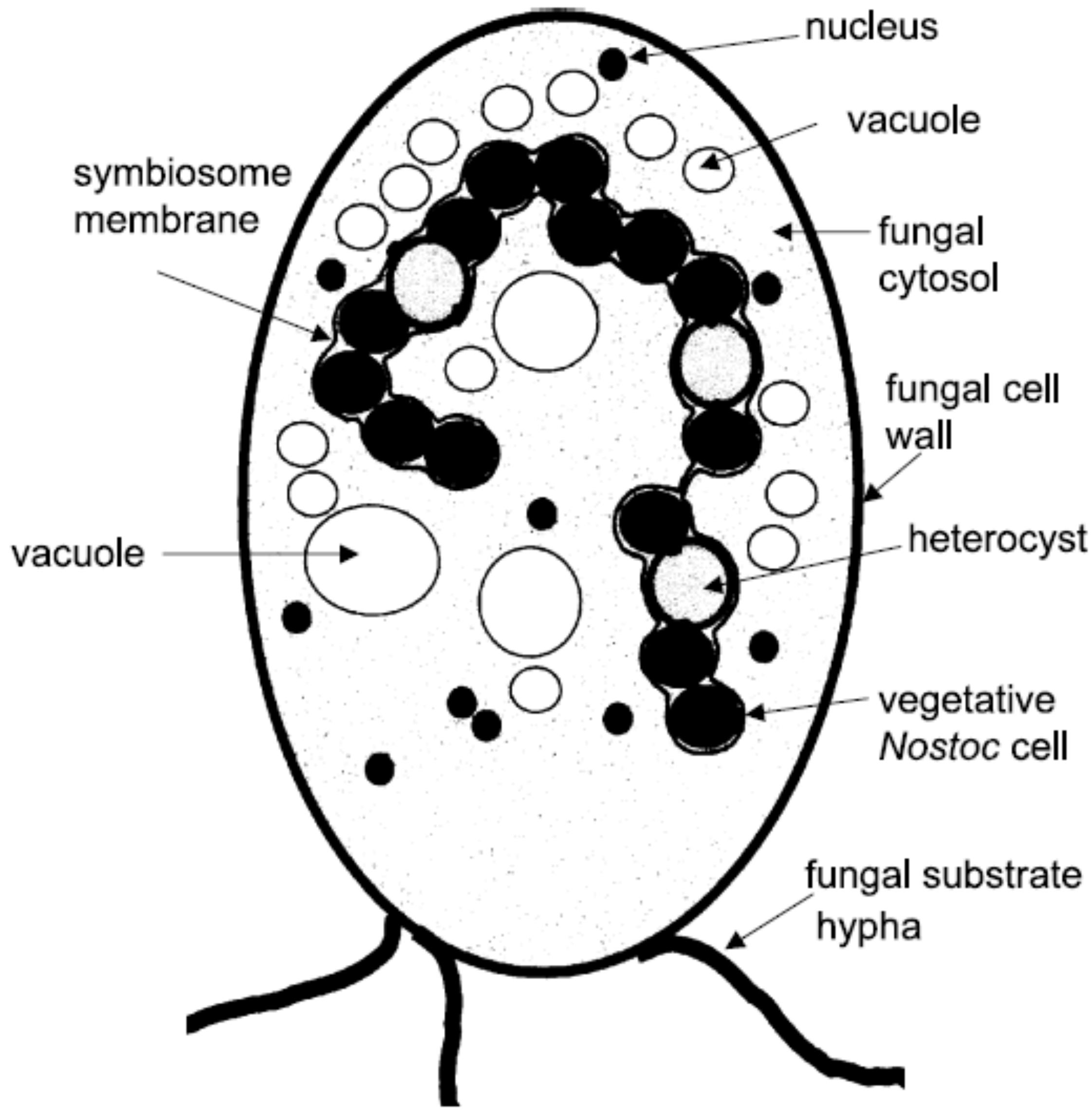


Fig. 1—Diagrammatic representation of the internal architecture of a mature bladder of *Geosiphon pyriformis*.