

Chytridiomycota

Blastocladiomycota

Neocallimastigomycota

About 1000 species in six (+) orders:

Blastocladales

Chytridiales

Monoblepharidales

Neocallimastigales

Spizellomyceteales

Rhizophydiales

**All have motile zoospores with posterior whiplash flagellae
most are monoflagellate, a few spp are polyflagellate
flagellae are always the whiplash type**

Only group of true fungi that has a motile cell stage (zoospores and gametes)

most primitive group of true fungi

Ecology

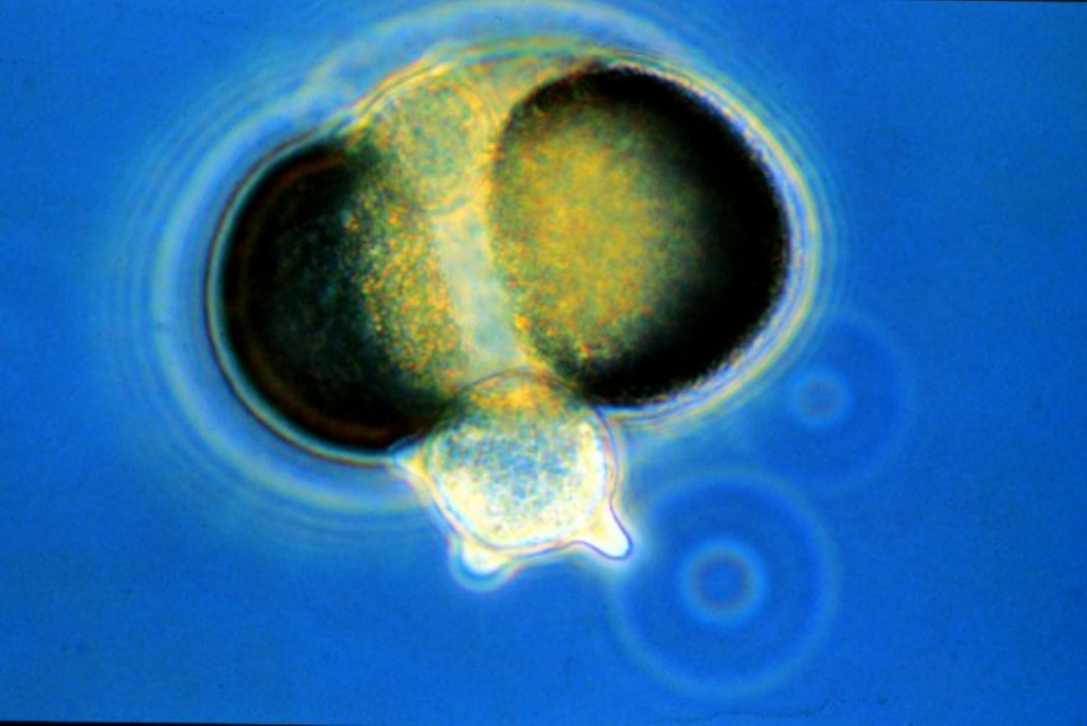
**Most chytrid species are saprobes in aquatic habitats and soils, grow on decaying plant matter, pollen
A few marine spp**

**A few are pathogens of plants, animals, and fungi:
e.g. chytridiomycosis of amphibians
parasites/pathogens of vascular plants, mosses
algae and phytoplankton
fungal parasites of vesicular-arbuscular mycorrhizal
fungi, basidiomycetes, and other chytrids
animal parasites of nematodes, rotifers,
tardigrades, and insects**

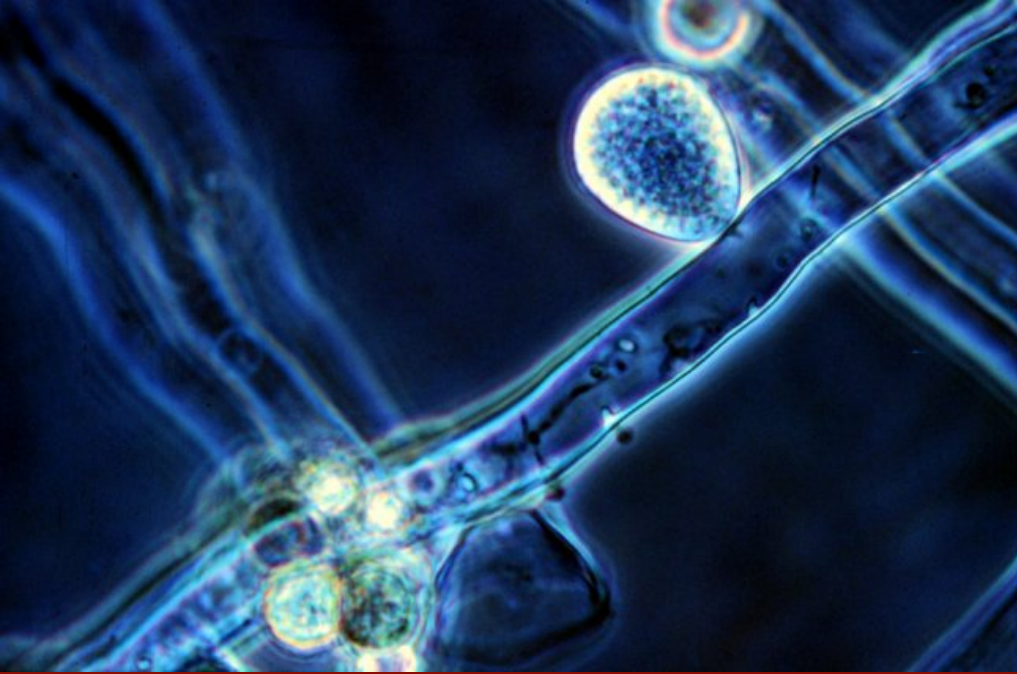
**Only true anaerobes, Neocallimasticales, live in rumen
of herbivores, contribute to animal nutrition**



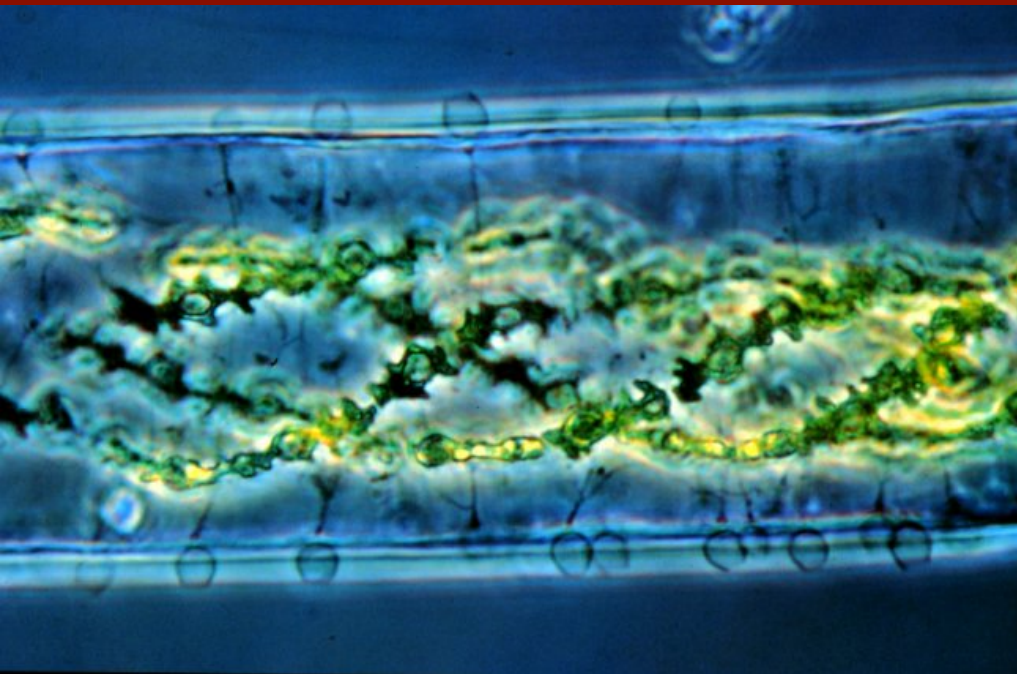
Pollen, a primary substrate used by aquatic chytrids



Chytrids growing on pollen grains



Chytrids growing on algae



Chytridiomycetes are true fungi, Eumycota

Based on rDNA sequences a part of the same lineage that includes zygomycetes, ascomycetes and basidiomycetes

The only true Fungi with flagellated stage, zoospores

Cell walls contain chitin and glucan (cellulose, however, has been detected recently in one species)

mitochondrial cristae are flat (vs. tubular type in oomycetes)

nuclear condition is predominantly haploid, like other true Fungi

Endobiotic forms: most simple thallus structure
live entirely within the cells of their hosts

Epibiotic forms: produce reproductive structures on
either the surface of the living host or organic
matter, absorptive hyphae are immersed in the
substrate

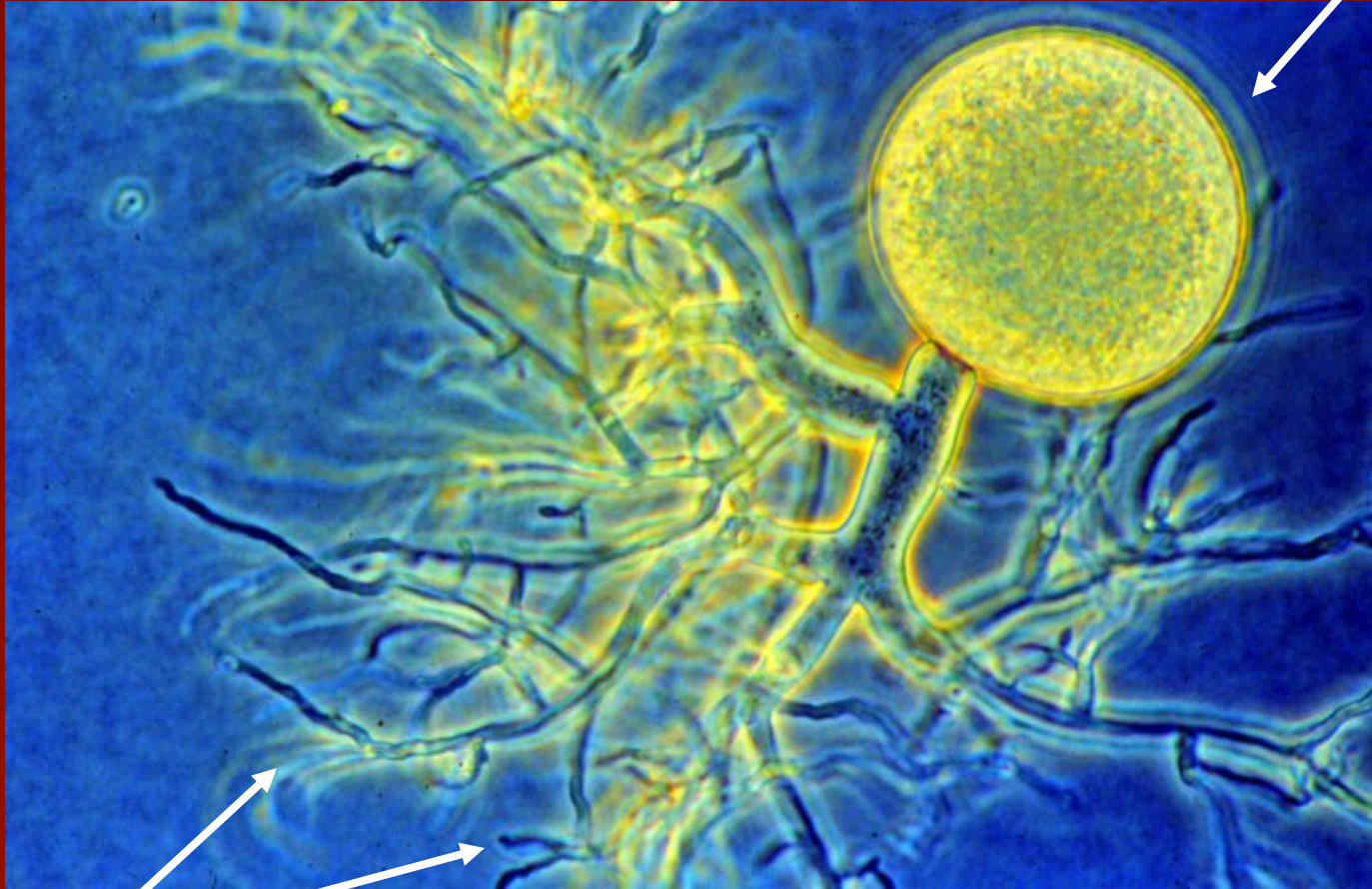
Holocarpic: The entire thallus is converted into one or
more reproductive structures (sporangia, gametangia)

Eucarpic: The reproductive structures arise from only a
part of the thallus, the rhizoids are not incorporated.

Rhizoids of eucarpic chytrids are fine hyphae that
contain cytoplasm but no nuclei

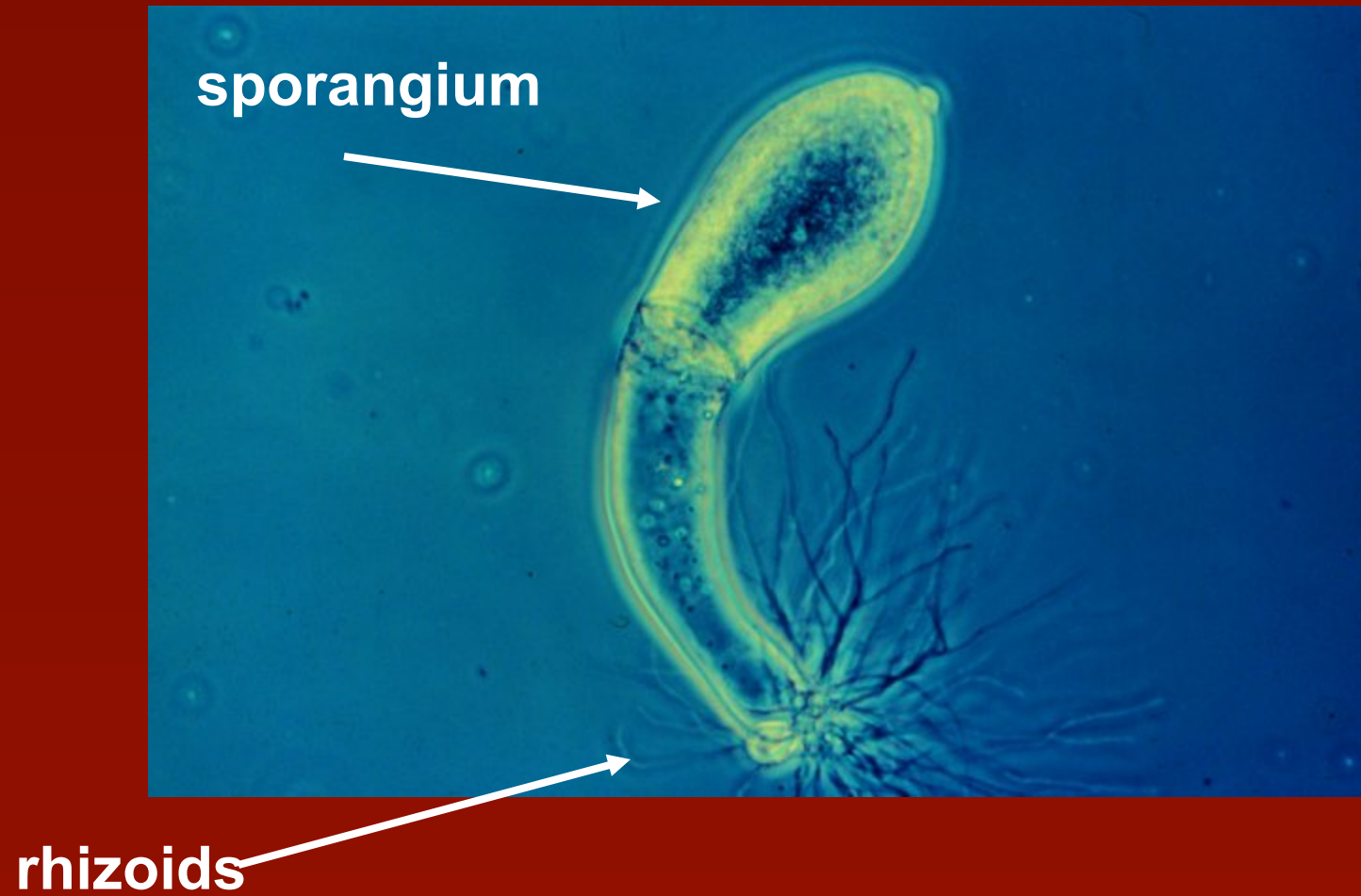
A Eucarpic Chytrid

sporangium



rhizoids

Another Eucarpic Chytrid



holocarpic: thallus reduced, no vegetative structures, entire thallus consists of reproductive structures (sporangia, gametangia). *Olpidium*, *Synchytrium*

**eucarpic: thallus has both vegetative (rhizoids, rhizomycelium) and reproductive structures
*Physoderma***

**endobiotic: entire thallus within host tissue.
Olpidium, *Synchytrium***

epibiotic: reproductive structures produced on the surface of host plant. *Physoderma*.

Reproduction

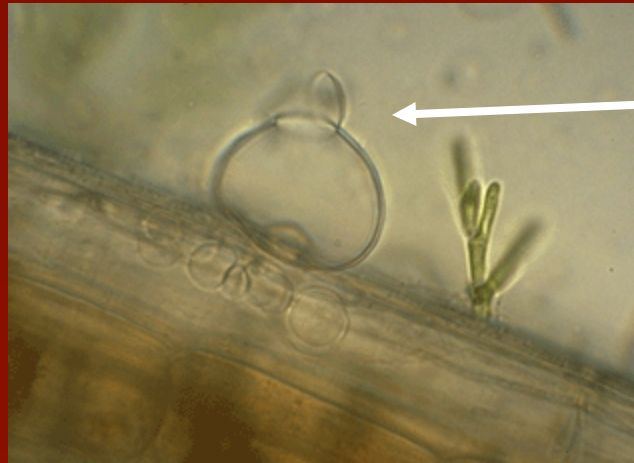
Asexual reproduction by motile zoospores produced in sporangia

zoosporangia initially contain multinucleate cytoplasm that undergoes cleavage into numerous uninucleate sections that develop into posteriorly flagellated zoospores



When the sporangium matures one or multiple a discharge papillae form in the sporangium wall

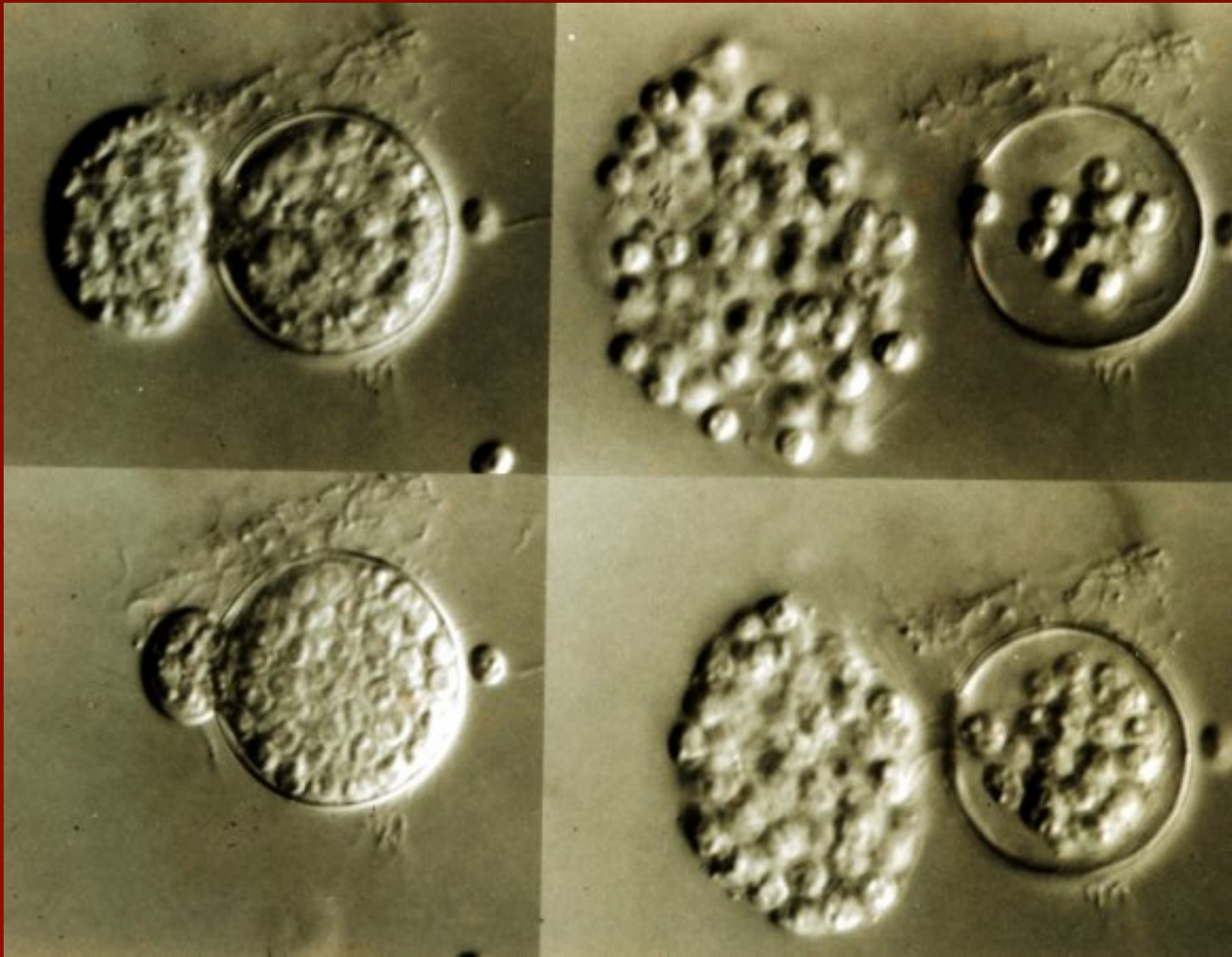
Papillae may be operculate or inoperculate



operculum

After emergence, zoospores swim to find a suitable substrate, forms a cyst, germinates

Zoospore release



Zoospore structure

Zoospores contain a single nucleus, its position and shape vary according to Chytrid Order

There are two kinetosomes associated with the flagella but only one is functional

Non functional kinetosome is called a basal body

At least one mitochondrion, microbodies, strands of ER, lipid bodies

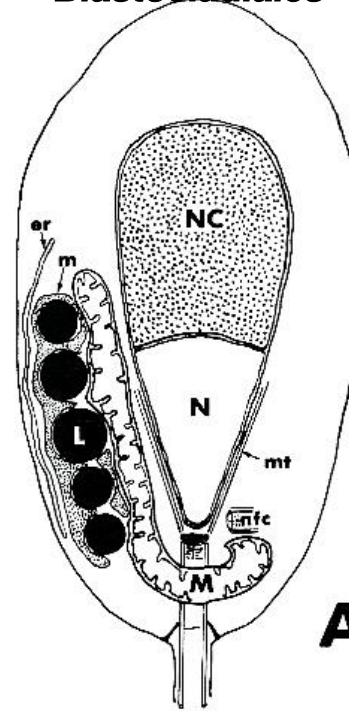
Microbodies and lipid bodies closely associated in the microbody-lipid globule complex (MLC)

Ribosomes either dispersed in cytoplasm (Spizellomyces type) or clustered in a ribosomal aggregation or nuclear cap (Blastocladales)

Current ordinal taxonomy of the Chytridiomycota is based on zoospore ultrastructure.

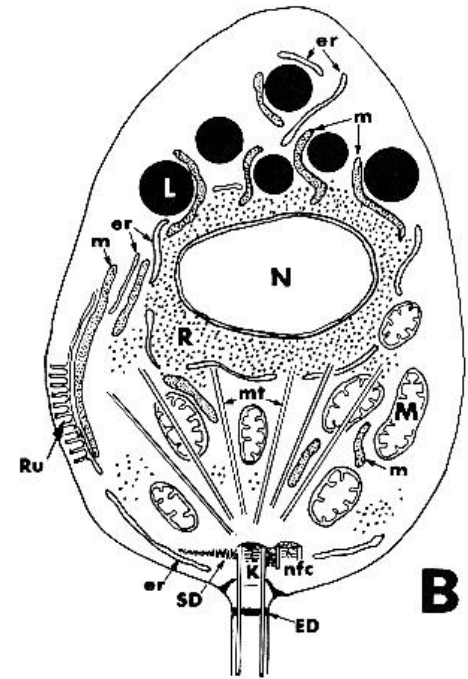
The more diffuse organization of the Spizellomycetales appears to have been derived more than once.

Blastocladales



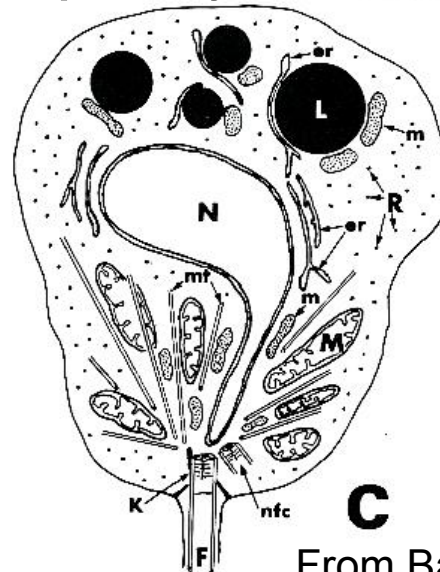
A

Monoblepharidales



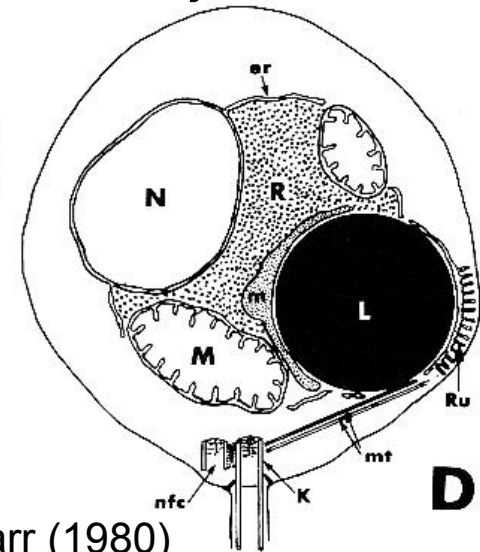
B

Spizellomycetales $1 \mu\text{m}$



C

Chytridiales

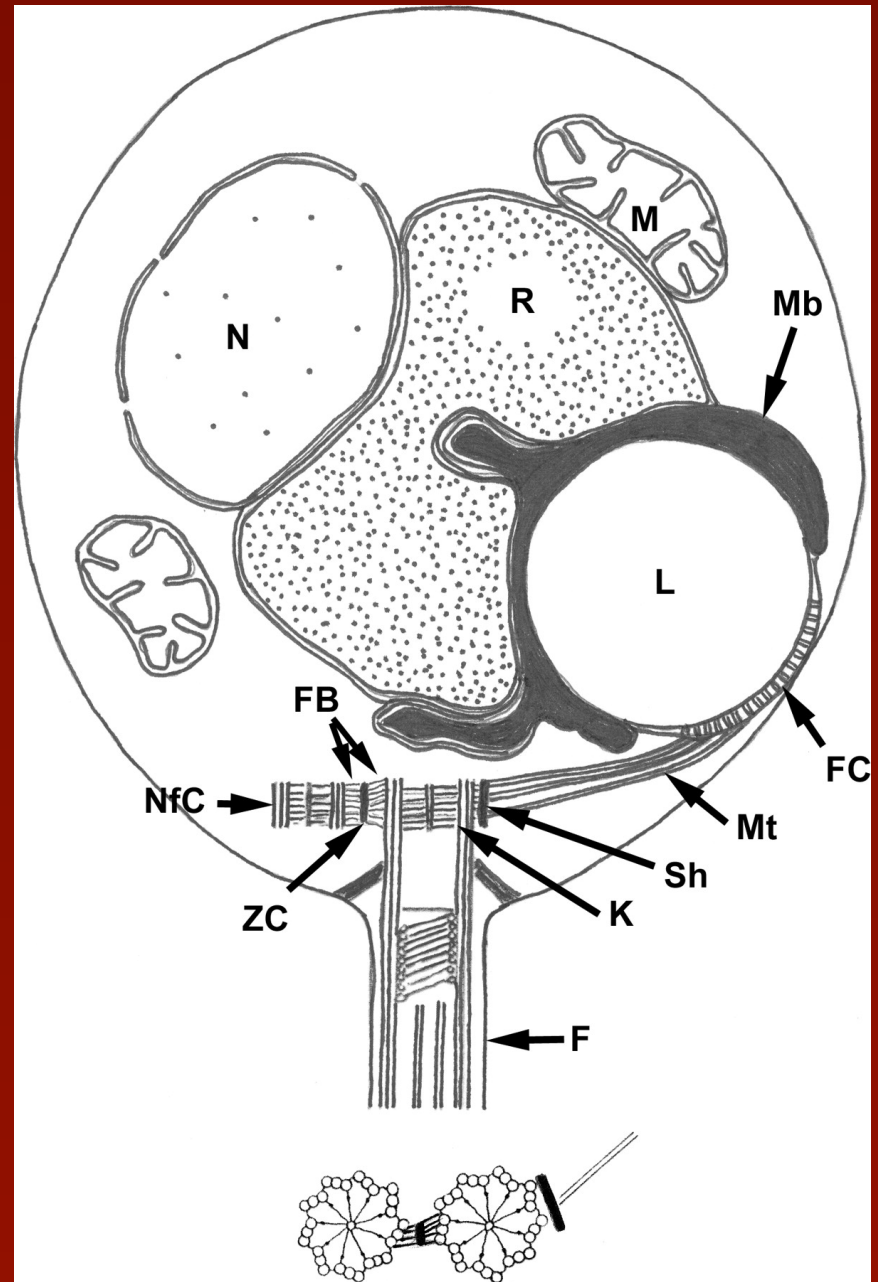


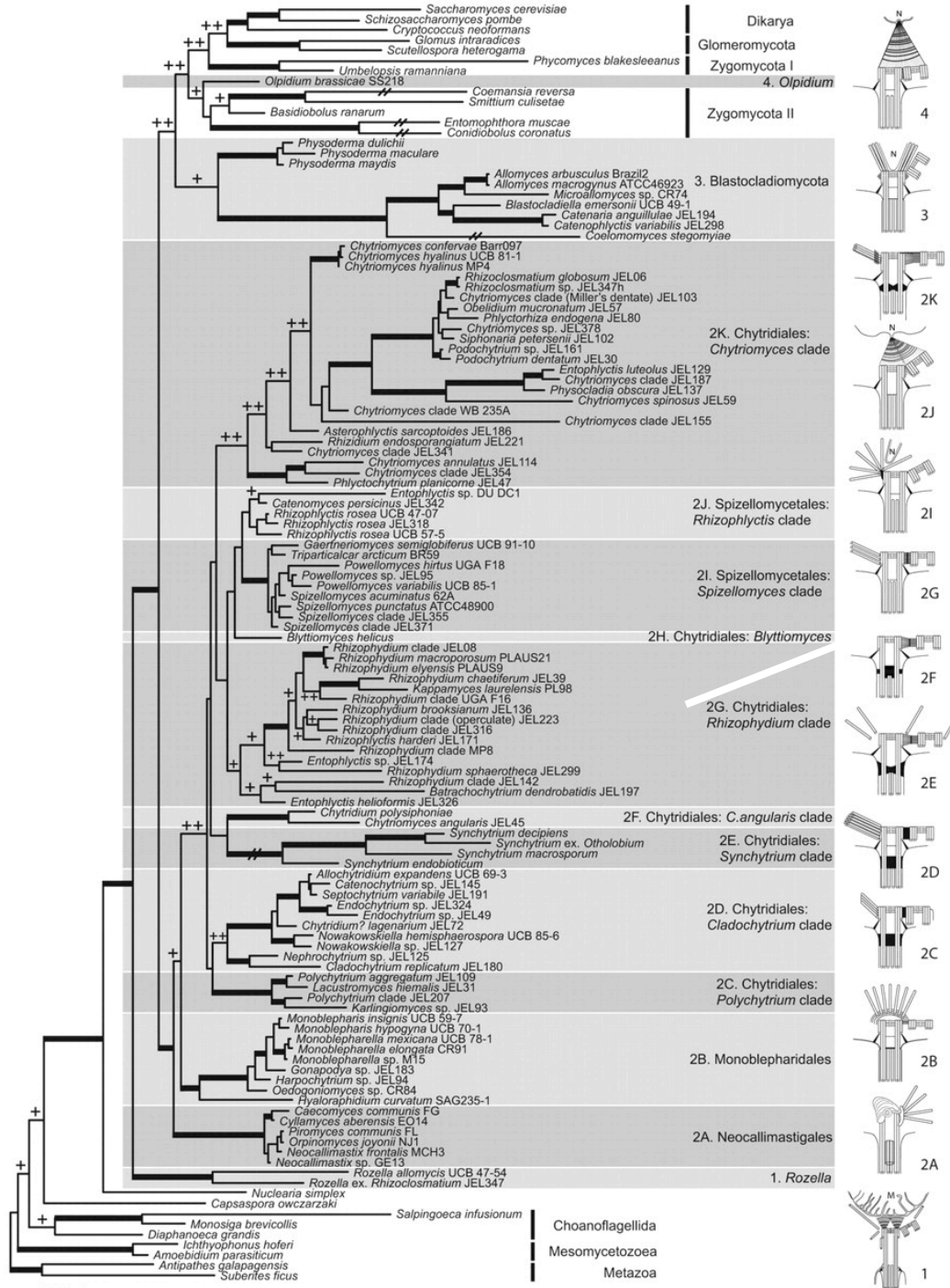
D

From Barr (1980)

A new order, Rhizophydiales was introduced in 2006.

This order now includes the amphibian pathogen *Batrachochytrium dendrobatidis*





Blastocladiomycota

Chytridiales is polyphyletic

Rhizophydiales

Chytridiomycota

structure of the kinetosome has been used as a character for classifying chytrid fungi

Sexual reproduction

Sexual reproduction is unknown in several chytrid genera, but is well documented in others

1. Planogametic copulation

- a. isogametic conjugation; two swimming gametes similar, fuse to form a motile zygote
- b. anisogamous conjugation: one gamete is much larger, gametes fuse to form a motile zygote
- c. nonmotile egg fertilized by motile male gamete (antherozoid): motile male gametes swim to female gametangia (oogonia) with one female gamete (egg). Male zoospore enters the oogonium and unites with the egg.

2. Gametangial copulation: contents of one gametangium transferred to the other

3. Somatogamy: fusion of rhizoids precedes formation of a resting spore

Gametes, gametic fusion

Gametes and gametic fusion vary in the different Chytrid groups:

**Isogamous gametes, i.e. of similar size and appearance,
Fusion of the two flagellate gametes results in a biflagellate zygote**

Anisogamous gametes

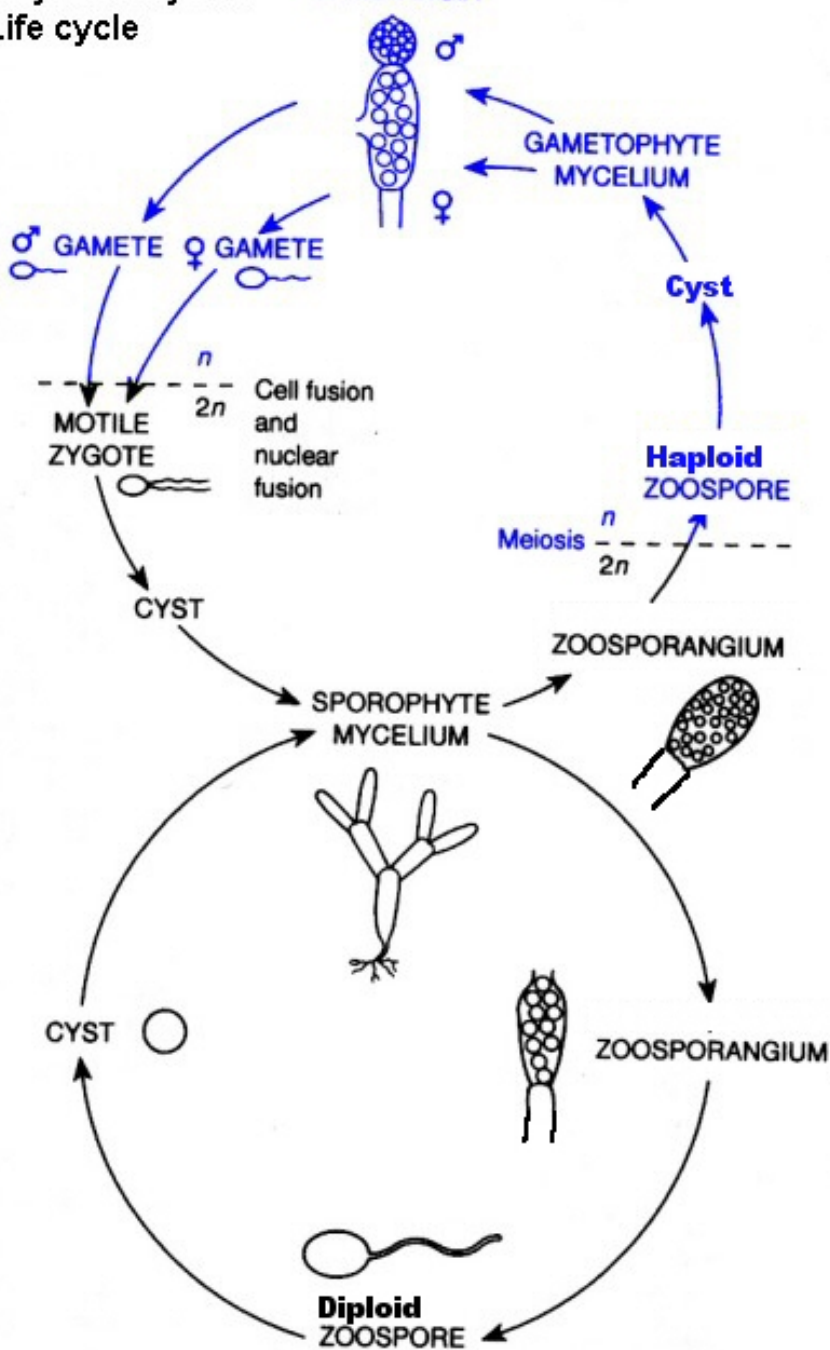
**fusion results in a biflagellate zygote
or one may be nonmotile (designated female by convention) and
remains in the female gametangium (oogonium), swimming male
gametes fuse with the female gametes in the female gametangium
(Monoblepharis)**

**Taxis of male gametes to female gametes and gametangia is directed
by a pheromone, sirenin**

A second pheromone attractive to female gametes, parisin

Chytridiomycete
Life cycle

GAMETANGIA



Alternation of generations:

Alternation of haploid and diploid generations in *Allomyces*

Haploid thalli produce gametes in differentiated gametangia

Gametes fuse (conjugate) to produce a zygote that gives rise to the diploid thallus (plasmogamy + karyogamy),

sporangia produce diploid zoospores

Classification

Spizellomycetales

Order recognized based on zoospore structure, appears to be polyphyletic based on molecular evidence

Ribosomes in zoospore are dispersed

scattered lipid droplets with associated microbodies

nucleus near kinetosome

sexual reproduction unknown in the entire Order

Parasites of other fungi, including the chytrid genus

Allomyces

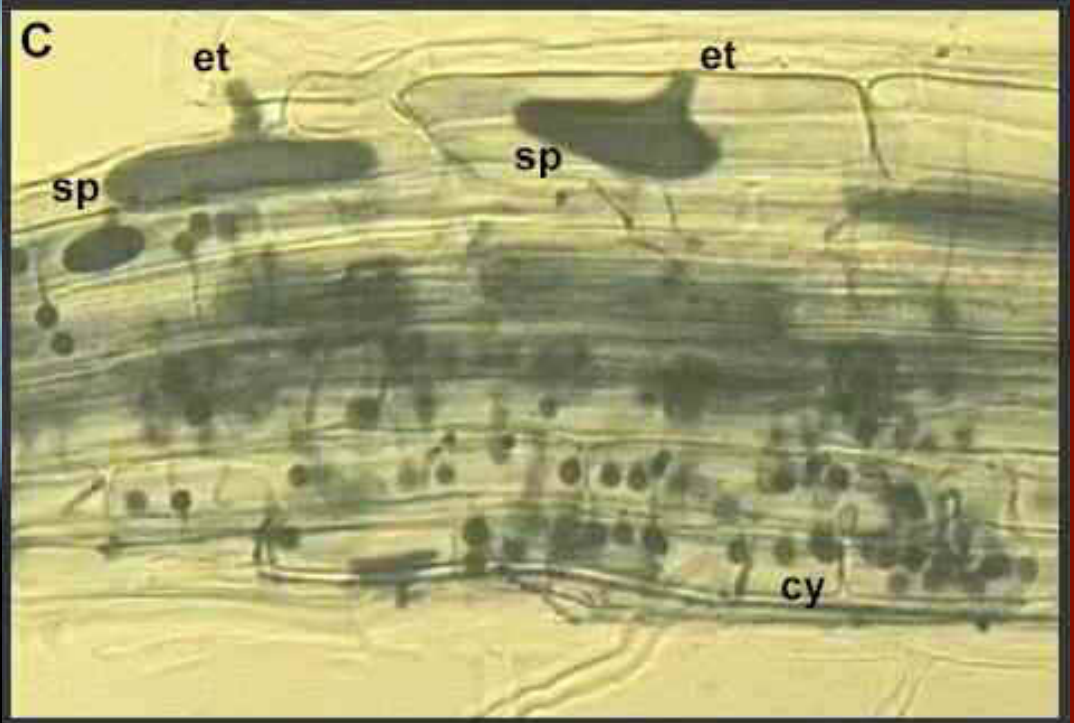
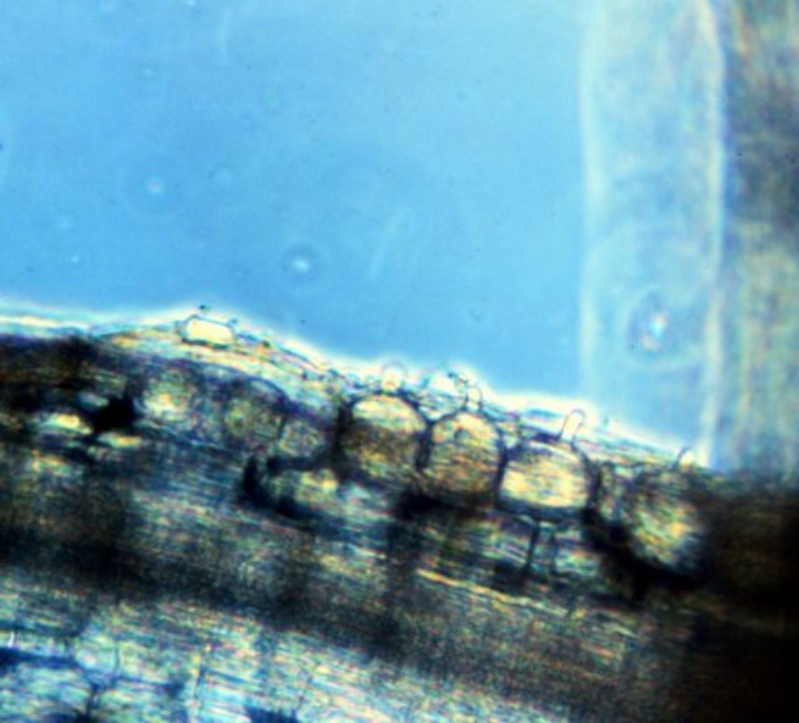
Plant pathogens: *Urophlyctis alfalfae*, crown wart disease of alfalfa

Olpidium 35 spp

Olpidium brassicae

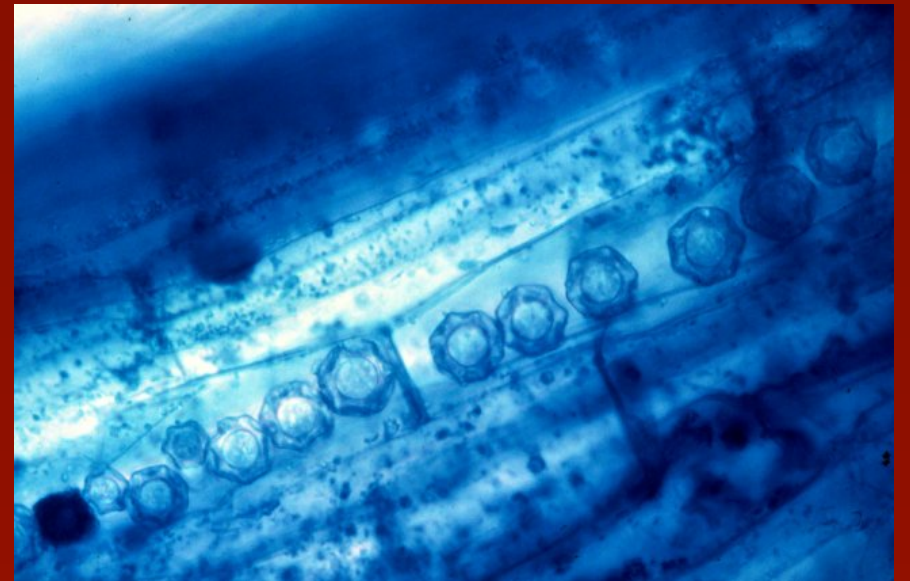
O. trifolii

Inconsequential, except as vectors of plant viruses



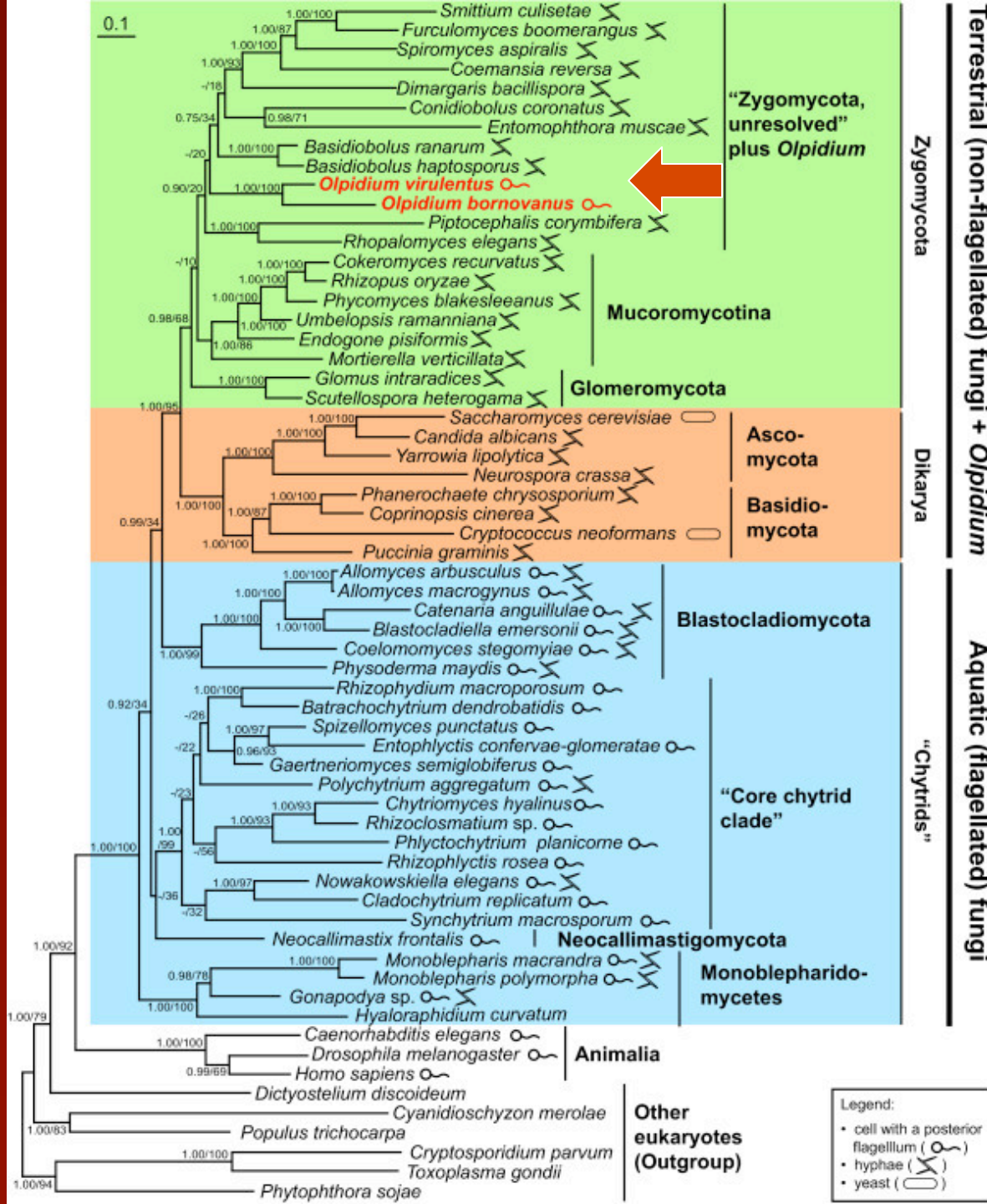
Olpidium

whoops! Olpidium now groups
in the Zygomycota!



Olpidium

This study provides strong support for *Olpidium* as the closest living flagellated relative of the terrestrial fungi. Appearing nested among hyphal fungi, *Olpidium*'s unicellular thallus may have been derived from ancestral hyphae. Early in their evolution, terrestrial hyphal fungi may have reproduced with zoospores.





Symptoms of lettuce big vein virus, vectored by *Olpidium brassicae*

Neocallimastigomycota, Neocallimasticales

All anaerobic, inhabit the rumen and caecum of herbivores

The only known obligately anaerobic fungi

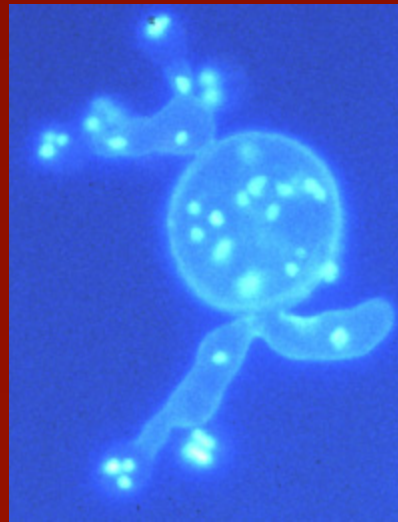
Degrade cellulose but have fermentative metabolism

Some polyflagellate (10+ flagella) species

Zoospores lack mitochondria

Able to break down cellulosic plant material in the rumen and contribute to animal nutrition

Break down material that would otherwise pass through digestive tract



Neocallimastix

Order Chytridiales

Based on zoospore structure

One or several mitochondria associated with MLC

Ribosomes aggregated and separated from cytoplasm by membrane

Water or soil inhabiting, parasitic on algae, water molds, parasites of microscopic eggs of nematodes and protozoa

Rhizophydiales (new order in Chytridiomycota)

Batrachochytrium dendrobatidis cause of worldwide amphibian decline

Blastocladales zoospore

Chytridiales zoospore

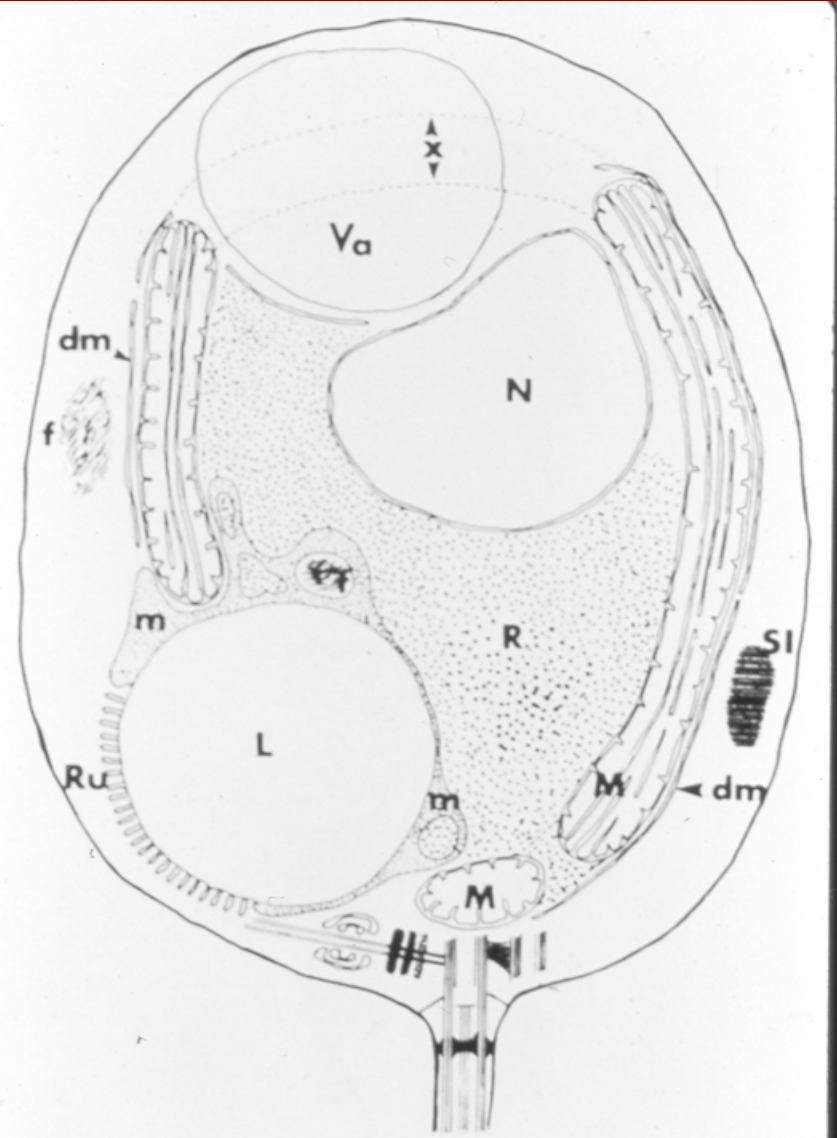
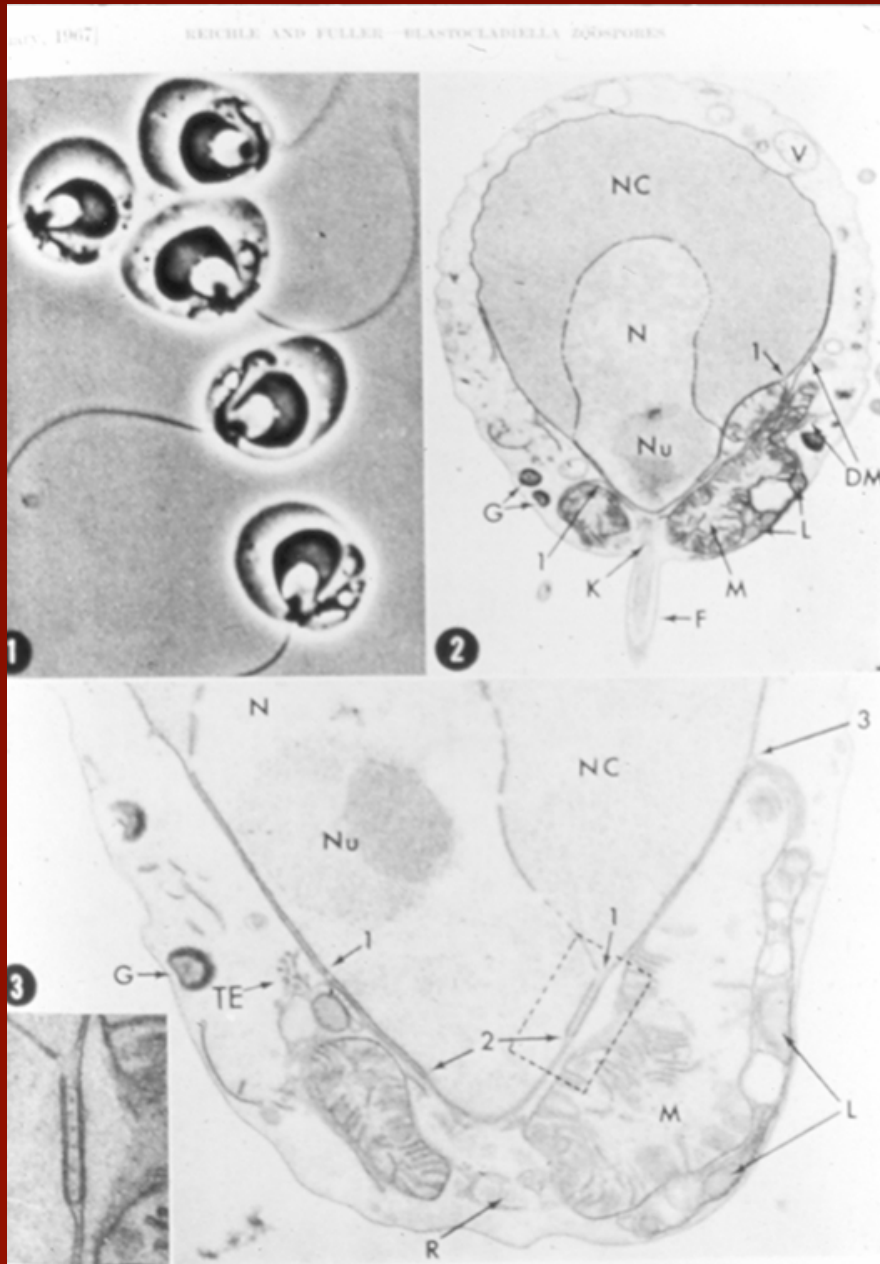


FIG. 4. Schematic drawing of *Rhizoclosmatium globosum* zoospores in longitudinal section. Continuity of the mitochondrion is shown by the dotted lines at X.

Chytridiales, various plant pathogens

Synchytrium 120 spp

Synchytrium aureum: galls of various hosts (~200 host spp.)

**S. desmodii: wart disease or false rust of Desmodium ovalifolium
(Fabaceae)**

S. decipiens: false rust of Amphicarpaea (Fabaceae)

**S. endobioticum: potato wart
long life cycle**

S. lagenariae: galls of cucurbits, Luffa

**S. macrosporum: galls of various hosts, mainly ornamentals
short life cycle, resting spores but no summer sporangia**

**S. phaseoli: pustules on leaves, pods of Phaseolus
short life cycle, summer sporangia no resting spores**

**S. phaseoli-radiati: galls on stems and leaves of Phaseolus
short life cycle, resting spores, no summer sporangia**

**S. psophocarpi: false rust of winged bean
short cycle, summer sporangia, no resting spores**

Synchytrium endobioticum life cycle

Holoarpic, endobiotic
motile cells functions as either zoospores or gametes
depends on the availability of water during development
early season more zoospores produced

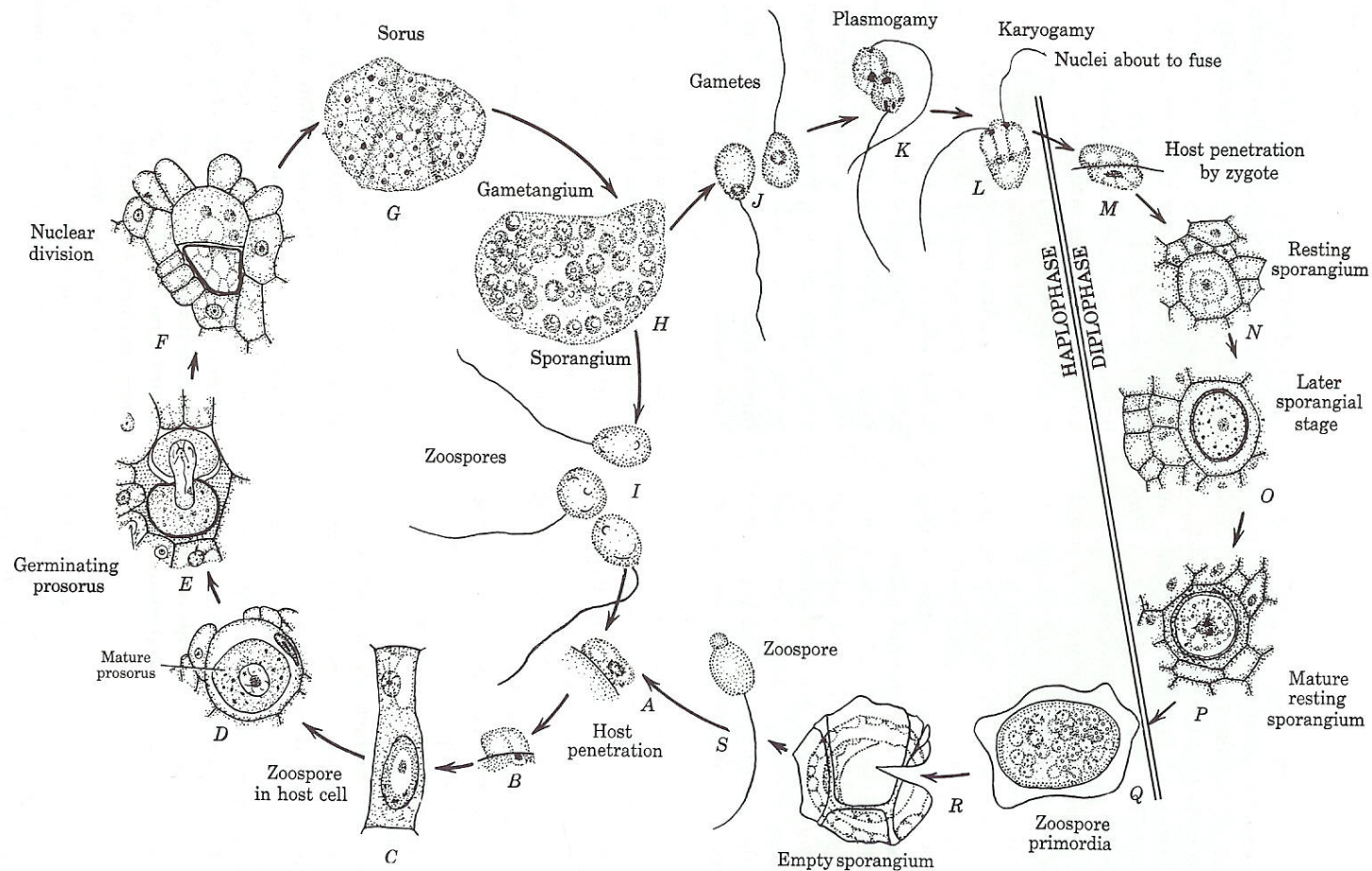


Figure 4-11 Life cycle of *Synchytrium endobioticum*. [Redrawn from Curtis (1921). By permission of the Royal Society of London.]

Potato wart disease

Synchytrium endobioticum



Resting spores of *S. endobioticum* can persist in soil for >40 years



Origin of potato wart disease

widespread in South America, particularly Peru and thought to be endemic there

also found on wild potatoes in Mexico, but unknown whether native or introduced there, however, others have concluded that the pathogen is native to Europe (England or Russia)

May have been introduced to Europe from S America during genetic improvement projects following the potato late blight epidemics of 1840-50. This timing agrees with the first detections of the disease in the UK, 1876.

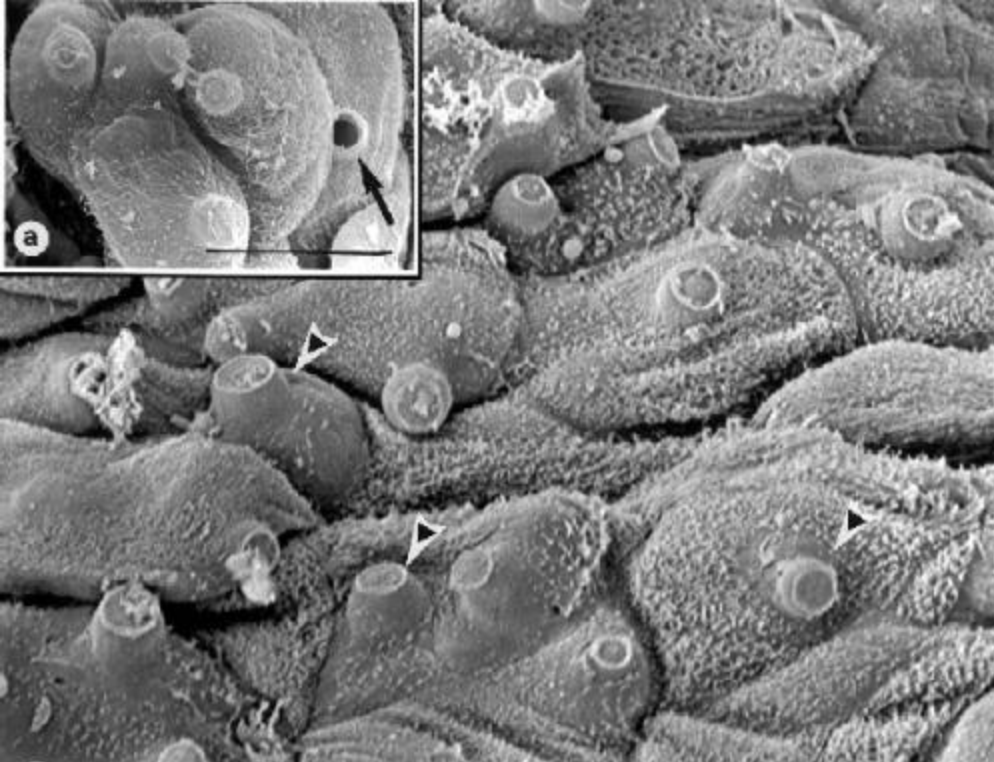
Disease was established in Newfoundland by 1908, believed to have been introduced from the UK

Chytridiomycota, Rhizophydiales



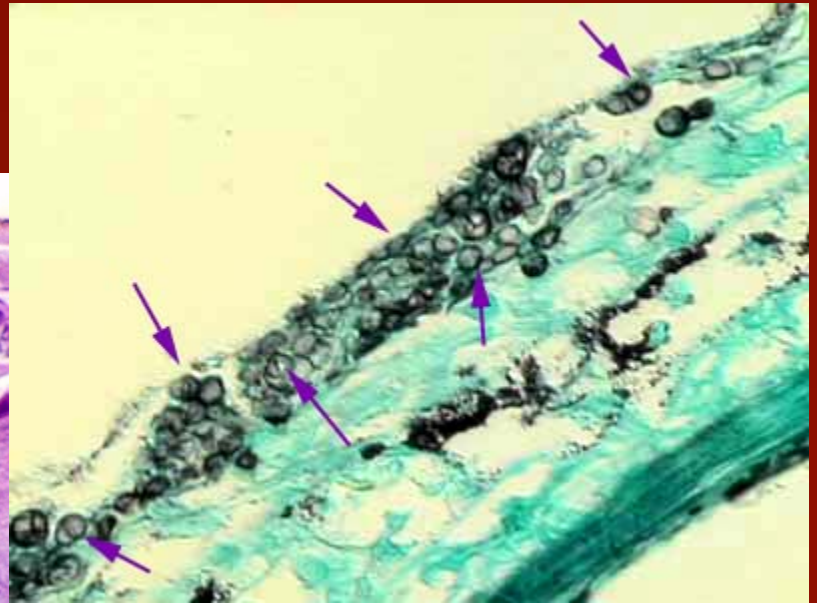
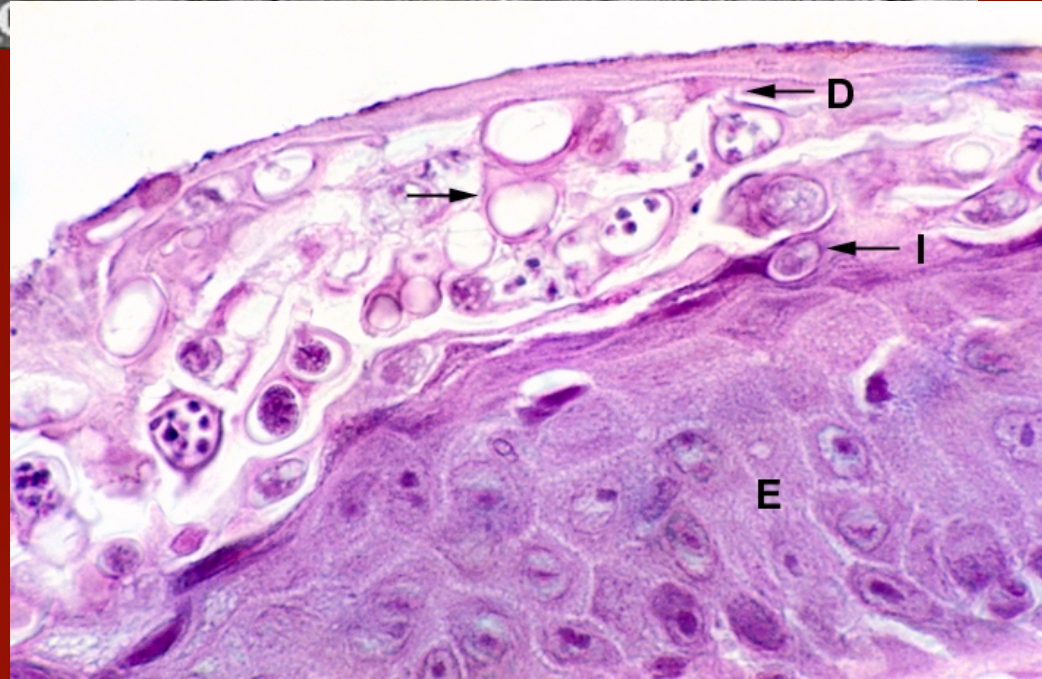
Amphibian decline caused by *Batrachochytrium dendrobatidis* was first reported in 1998. Found in Australia, Panama, now found affecting Amphibians world wide.





B. dendrobatidis affects the skin of amphibians, impairs their exchange with the atmosphere and electrolytes

Affects keratinized portions of amphibian skin





Early effects of chytridiomycosis appear on keratinized tadpole mouthparts

Bd infection inhibits Na absorption, disrupts electrolyte transport

Fig. 2 Electrophysiological measurements of electrolyte transport across ventral skin samples from *L. caerulea* infected with *B. dendrobatidis*.

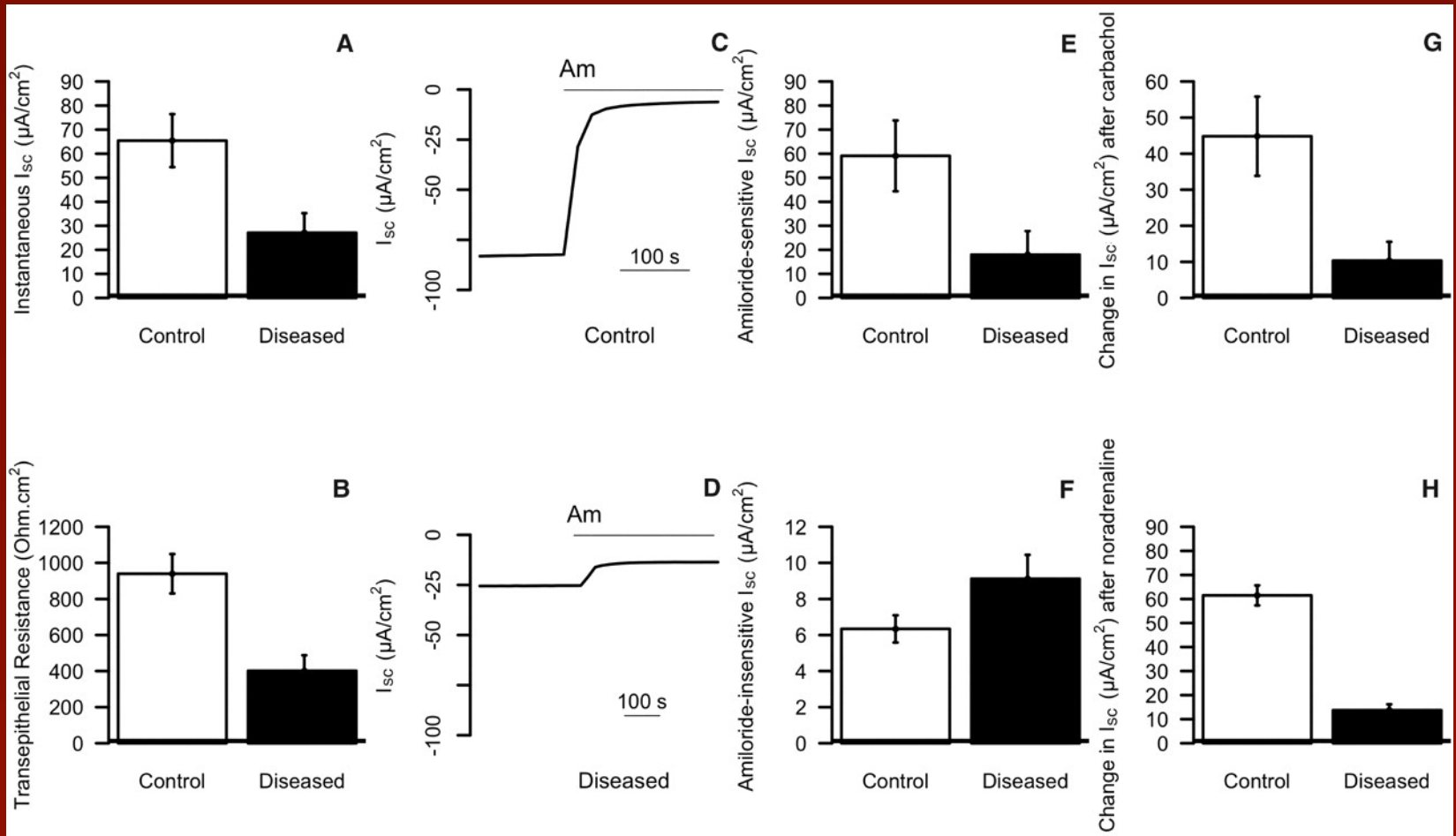
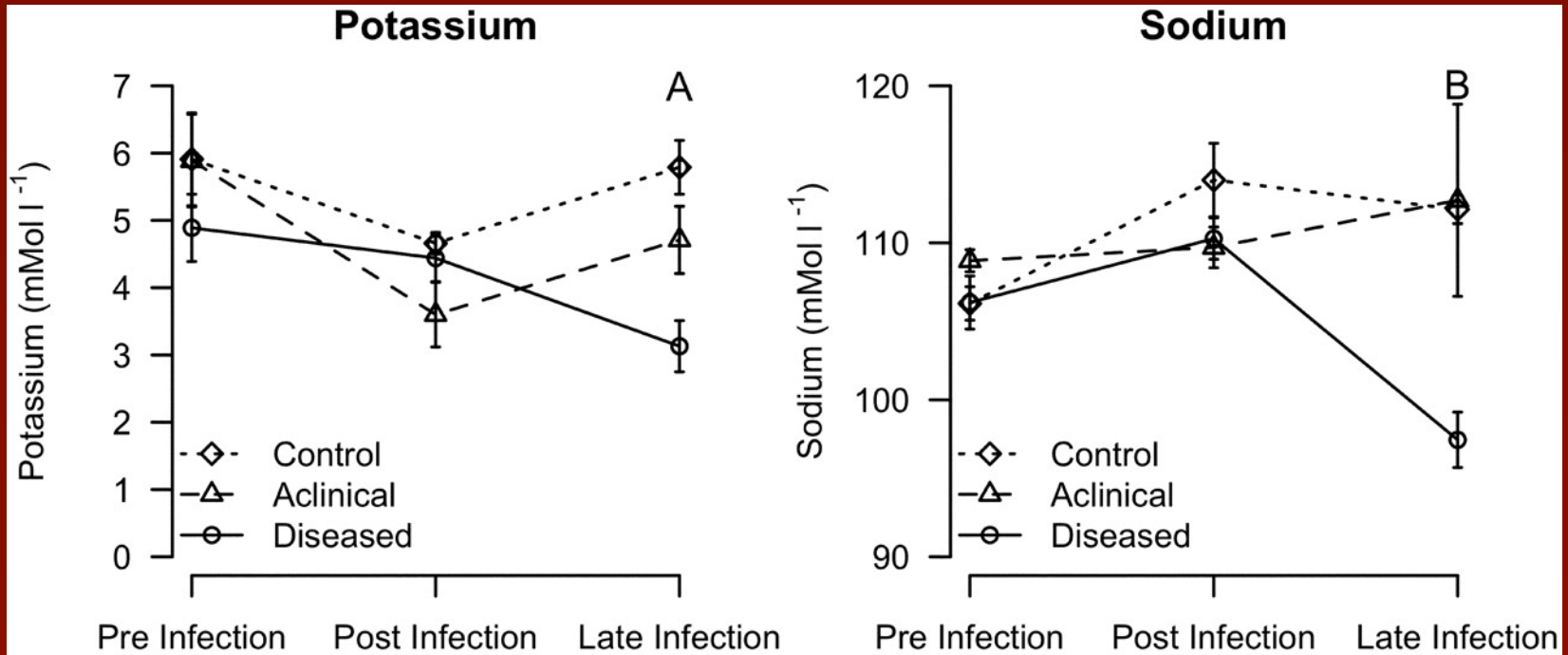
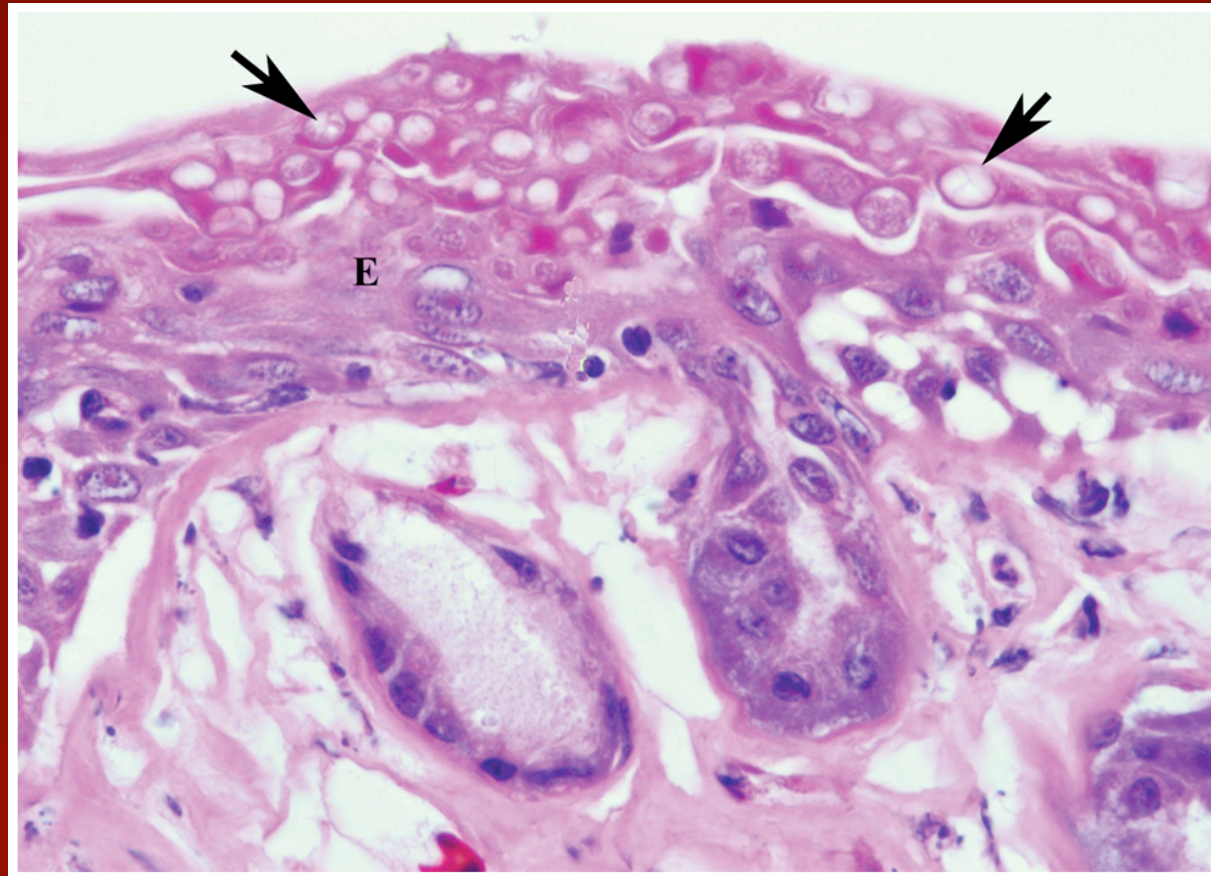


Fig. 3 Blood plasma potassium and sodium concentrations in *L. caerulea*.



Blood plasma potassium and sodium concentrations in *L. caerulea*. Blood samples were collected from infected *L. caerulea* (acclinal, N = 7; clinically diseased, N = 11; uninfected control, N = 7) on three sample occasions: 20 days before exposure (Pre Infection), 30 days after exposure (Post Infection), and 60 to 123 days after exposure when clinical signs of disease were obvious (Late Infection). (A and B) Data show mean (\pm SEM) concentrations of plasma potassium and plasma sodium.

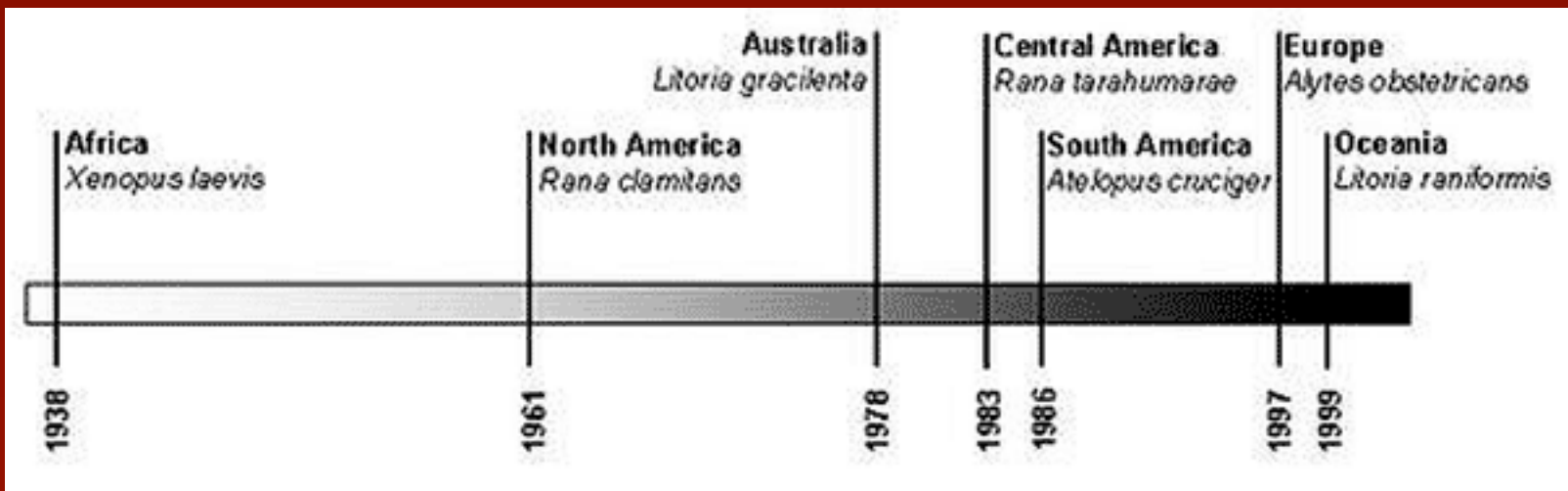
“Our results support the epidermal dysfunction hypothesis, which suggests that Bd disrupts cutaneous osmoregulatory function, leading to electrolyte imbalance and death. The ability of Bd to compromise the epidermis explains how a superficial skin fungus can be fatal to many species of amphibians; their existence depends on the physiological interactions of the skin with the external environment”



Oldest *B. dendrobatidis* found in preserved *Xenopus laevis* in South Africa

Thought to have been spread worldwide by use of *X. laevis* in pregnancy testing

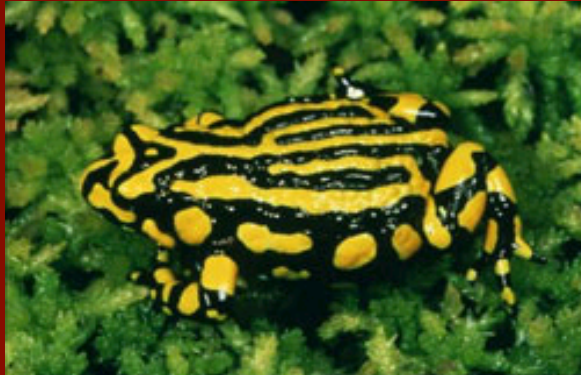
Amphibian declines caused by this fungus have been reported from the Boreal toad in Colorado, the Wyoming toad in Wyoming, the mountain yellow leg frog in the Sierra of California and numerous additional species in Central America.



Amphibians in six continents, Africa, South America, Central America, North America, Europe, Australia, and Oceania have been reported as infected by the amphibian chytrid. The earliest record is from North America in *Rana pipiens* collected in 1974.

Currently a total of 2 amphibian orders (Anura and Caudata), 14 families and 93 species have been diagnosed infected with *Batrachochytrium dendrobatidis*. Australia has the most species infected (46) of any country. All of the records from Germany, except for a report in one species in the wild, are in imported amphibians or amphibians in the pet trade, illustrating the importance of the global movement of amphibians in disseminating chytridiomycosis.

Various amphibians worldwide are now threatened with extinction due to Batrachochytrium



Southern corroboree frog, Australia



Litoria raniformis, New Zealand



Could amphibian chytrid fungus disease cause some of our native frogs to become extinct?

Amphibian chytrid fungus disease is a deadly pathogen that is spreading rapidly across the world, threatening the survival of many native frog species. Scientists are working to understand how the disease spreads and how to prevent it from spreading further.

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And now another species of *Batrachochytrium*

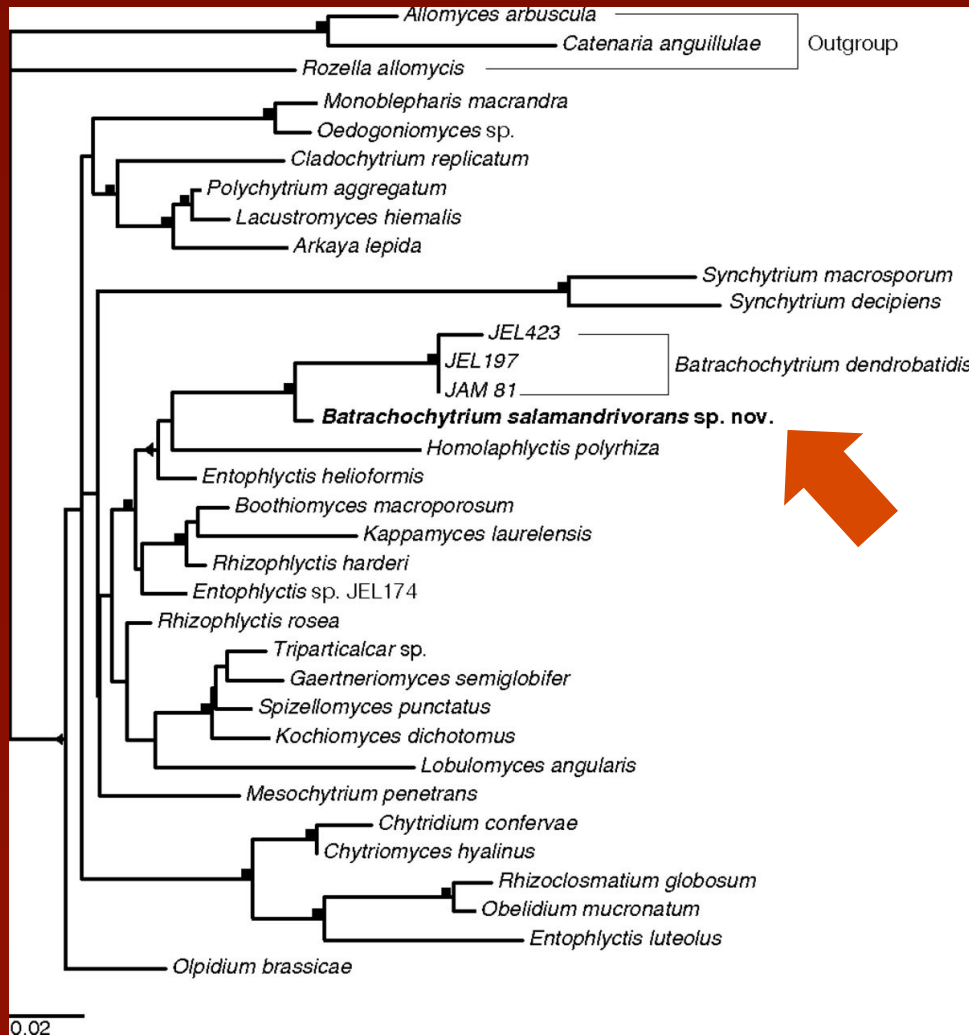
Endangered populations of fire salamanders in Europe have succumbed to a new fungus.



E Stokstad *Science* 2014;346:530-531



Maximum likelihood tree ($-\ln L = 9,562.04266$) for the analysis of a 1,513-bp data matrix of partial 18S + 28S rRNA genes.



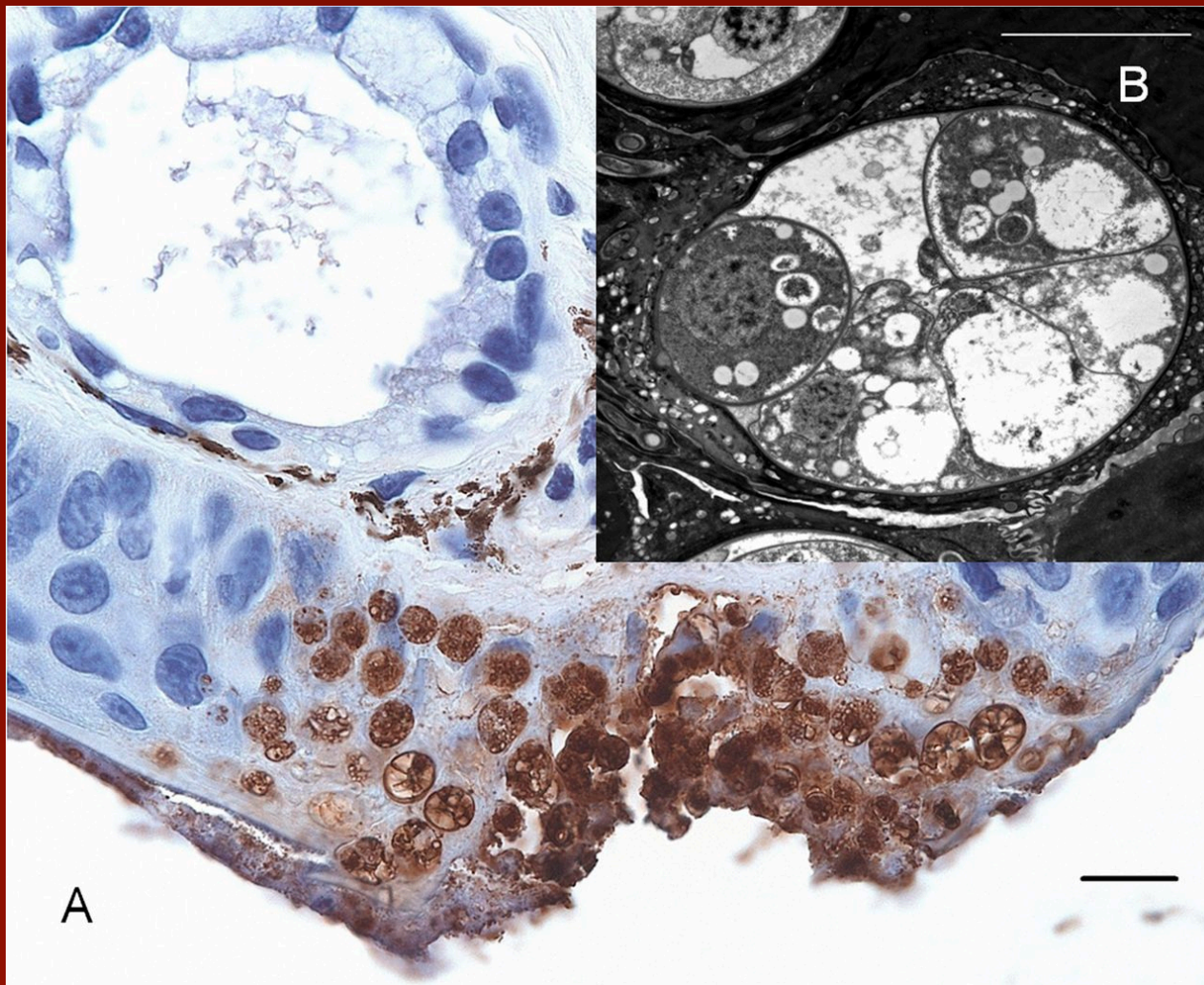
First described from diseased fire salamanders in the Netherlands.

Probably native to South Asia, lethal to most European and North American salamanders

“Chytridiomycosis in amphibians can no longer be attributed to a single species of chytrid, but can be caused by either *B. dendrobatidis* or *B. salamandrivorans*.”

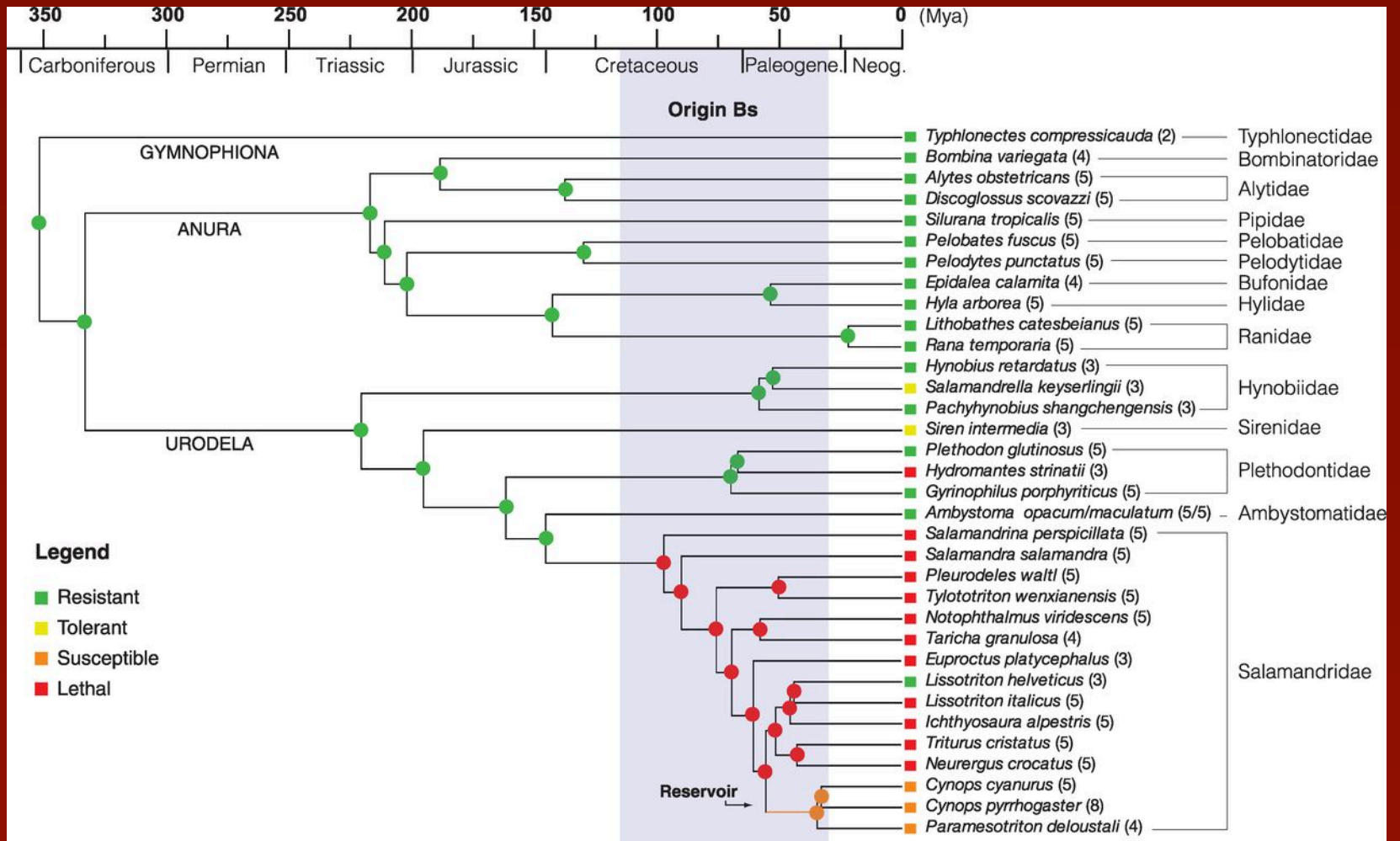
Martel A et al. PNAS 2013;110:15325-15329

Microscopy of the skin of a fire salamander that died due to infection with *B. salamandrivorans*.



Martel A et al. PNAS 2013;110:15325-15329

Fig. 1 Amphibian susceptibility to *Batrachochytrium salamandrivorans* (Bs) through time. Molecular time scale (millions of years ago) for 34 species; rectangles indicate the species category based on the experimental infection tests.



A Martel et al. Science 2014;346:630-631



Species loss and rediscovery in Costa Rica. The fungal pathogen *Batrachochytrium dendrobatidis* (Bd) has been linked to the decline and extinction of amphibians worldwide.



Amphibian populations in Costa Rica experienced substantial declines, with 20 of the 199 species feared extinct, after Bd moved through the country from the mid-1980s to the early 1990s. However, 11 of the 23 species have been rediscovered. Holdridge's toad (*Incilus holdridgei*), a species endemic to a single volcano, vanished during the declines and was declared extinct in 2007 but was rediscovered in 2008. Today, relict populations persist in areas where Bd once contributed to their demise.

B A Minteer et al. Science 2014;344:260-261



Order Blastocladales Now in phylum Blastocladiomycota

Mainly soil and water inhabitants

Form thick-walled resting sporangia

Zoospores have prominent nuclear cap, ribosomes

Allomyces, Physoderma, Catenaria, Coelomomyces

Allomyces hormones: females make Sirenin, males make parisin

Mechanism of sexual differentiation is unknown

Chytrid plant pathogens

Blastocladales

Physoderma ~ 50 spp.

Physoderma alfalae: crown wart of alfalfa

P. citri: citrus blight

P. leproides: galls of sugar beet

P. maydis: brown spot of maize

P. pulposum: galls of Chenopodiaceae

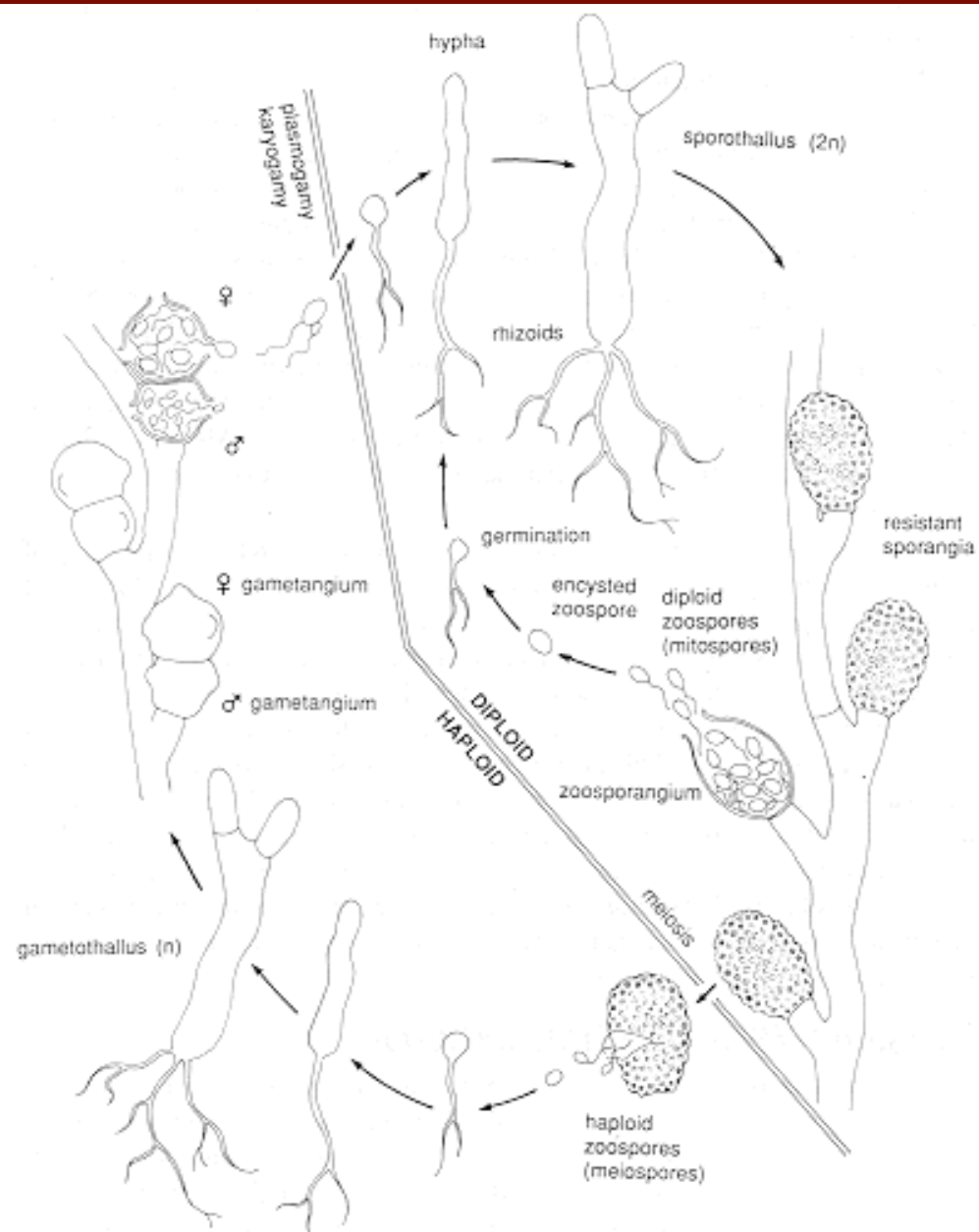


Fig. 2.7 Blastocladales: life cycle of *Allomyces arbusculus*.

Allomyces

male gametangium



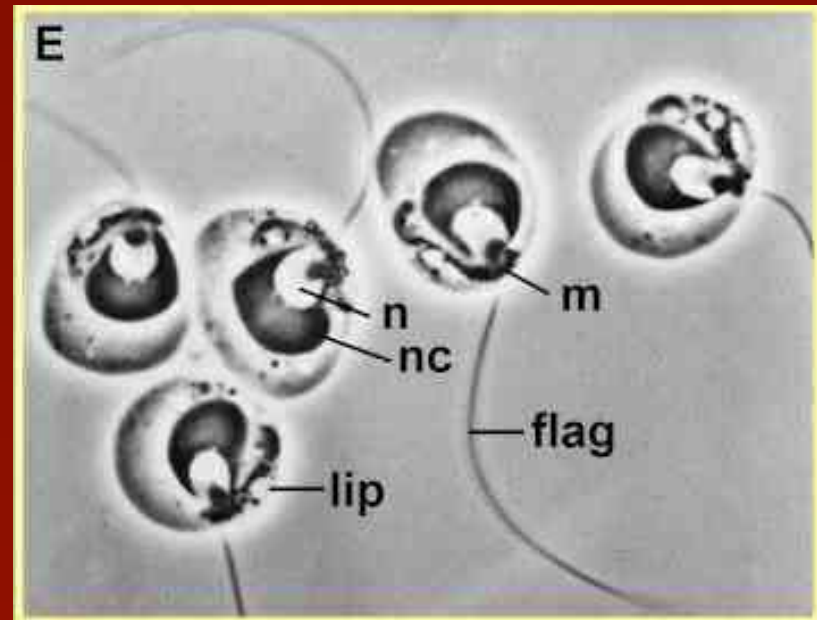
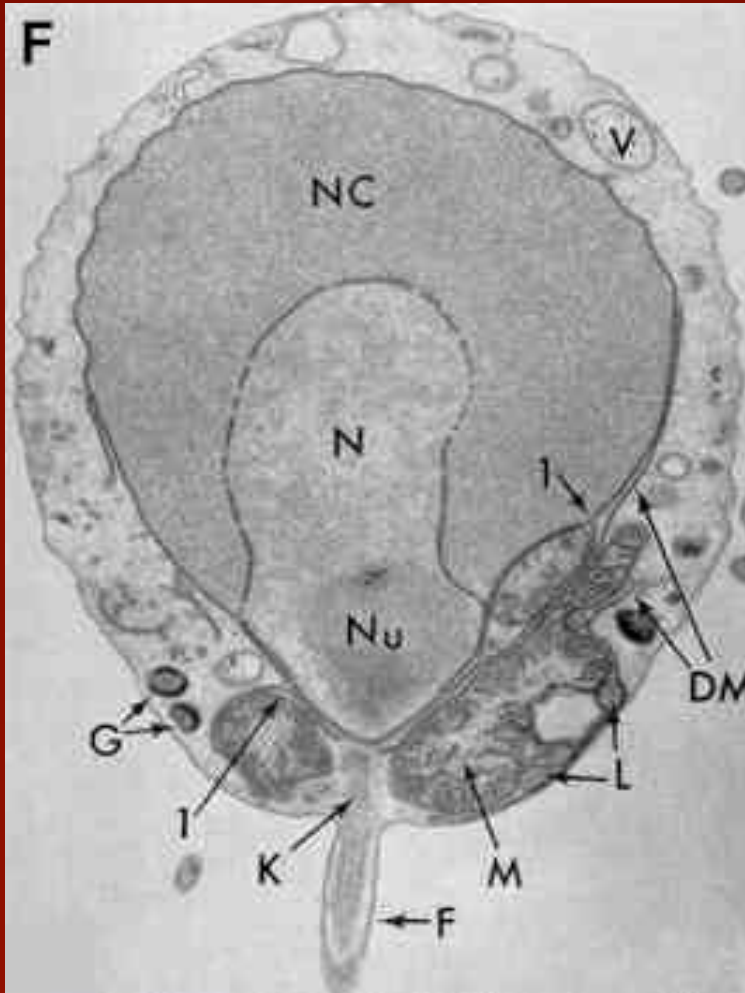
female gametangium

Allomyces sporangia (diploid)



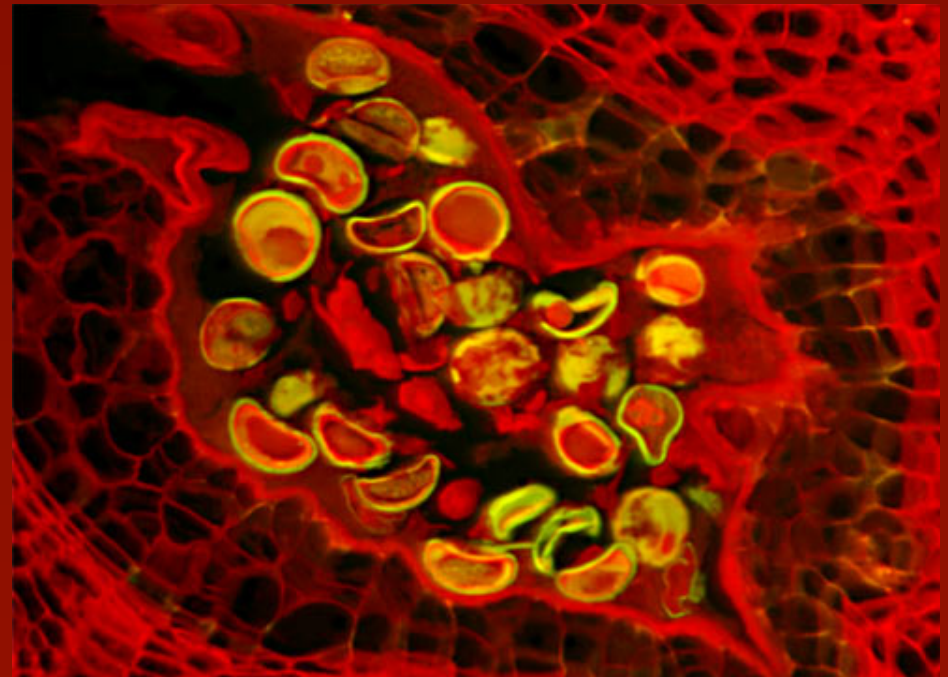
Zoospores of Blastocladiales

Have a distinct nuclear cap:
ribosomes aggregated near
nucleus, not dispersed

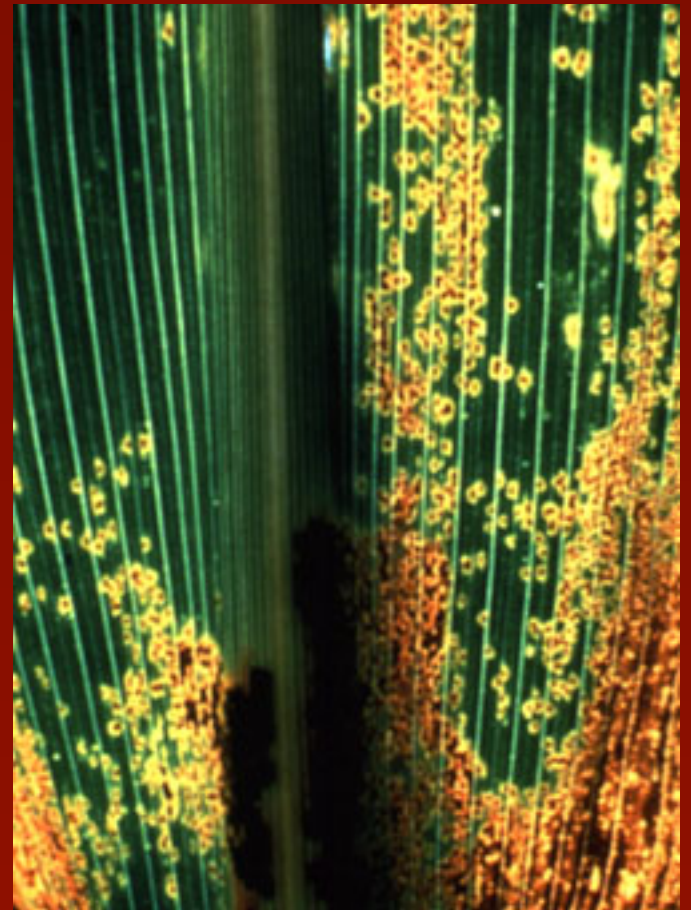


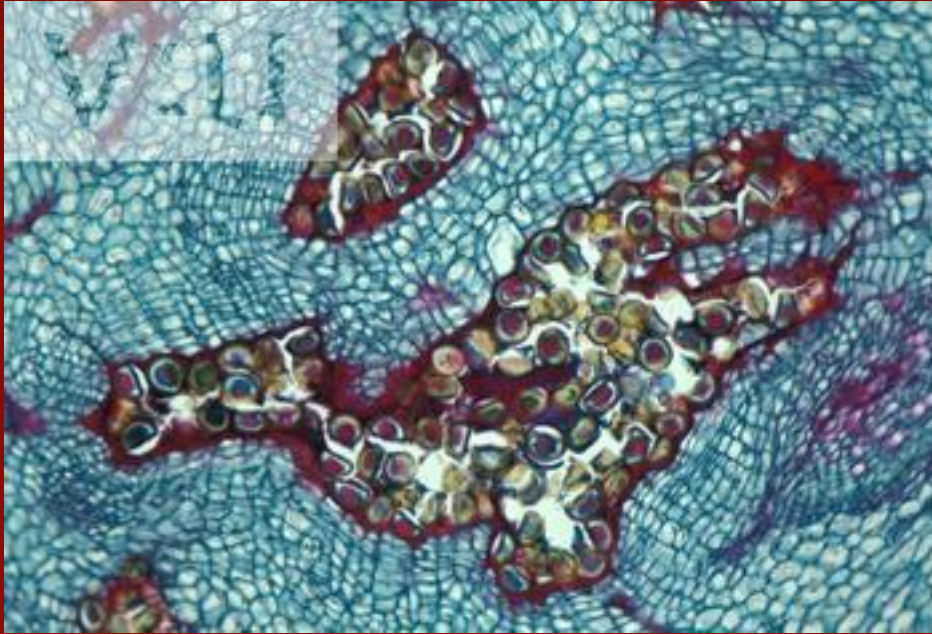
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Crown wart of alfalfa caused by *Physoderma alfalfae*

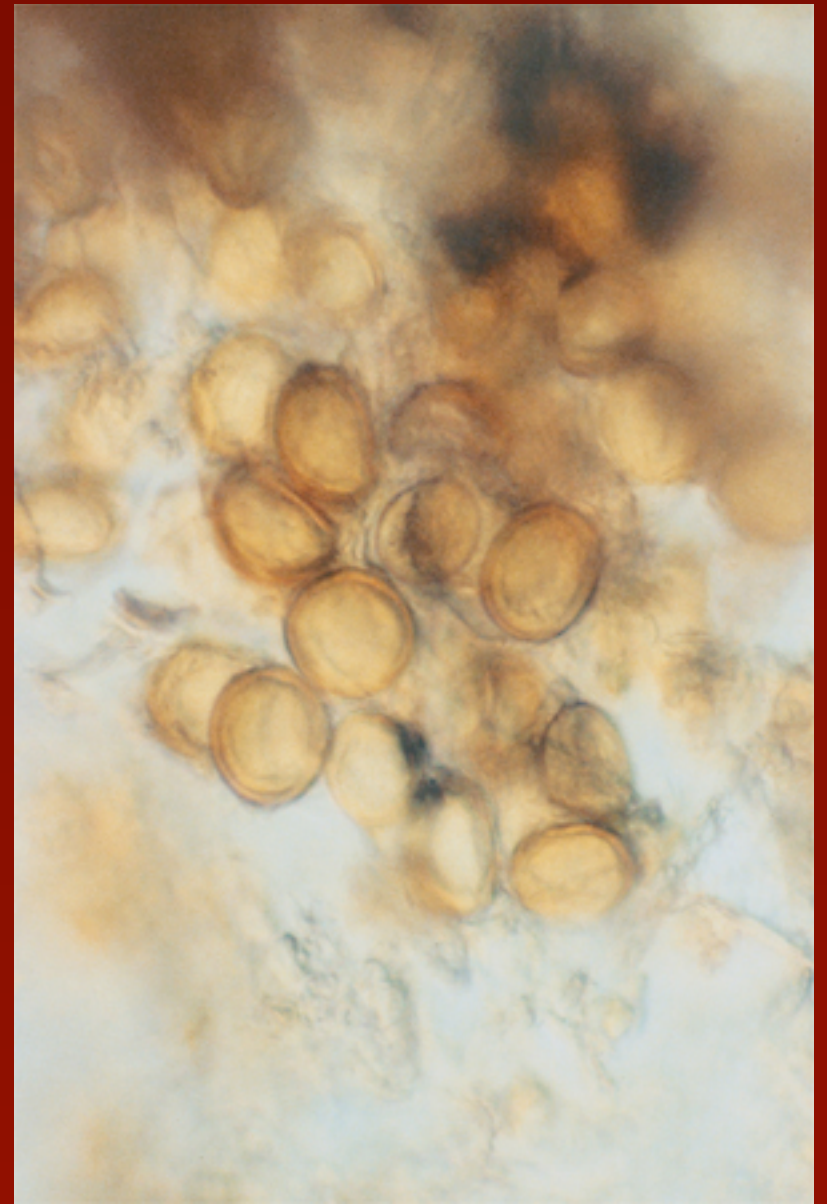


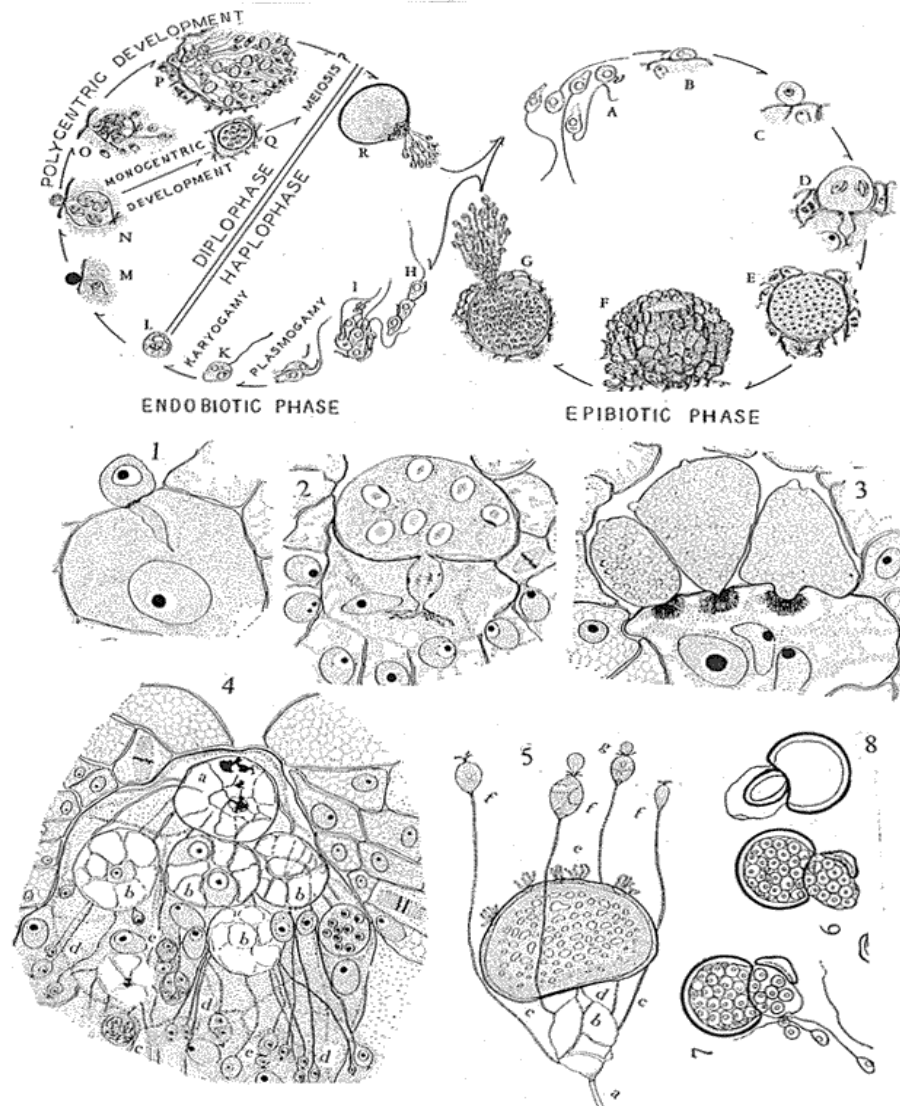
Physoderma maydis brown spot symptoms





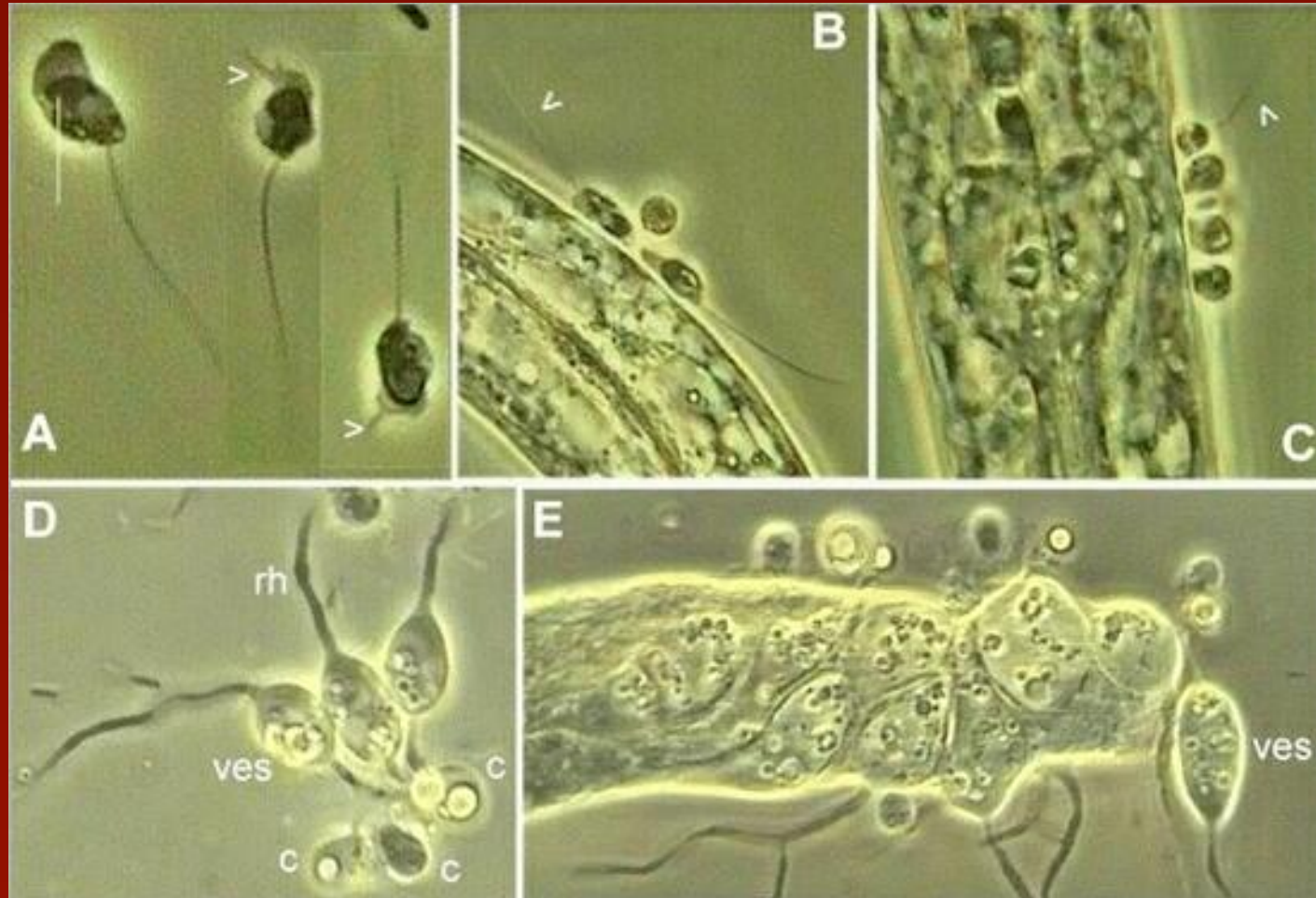
**Physoderma
endobiotic resting sporangia**





Physoderma pulposum (Walr.) Karling on *Chenopodium album* L. Life-cycle. Fig. A-G. Stages in the development of Epibiotic phase. Fig. A. Planospores (zoospores, gametes). B. Attachment of a planospore to an epidermal cell. C. An early stage of infection. D. Incipient epibiotic sporangium. E-F. It's maturation and germination. G-L. Some zoospores functioning as gametes, copulate, & result in zygote. M-N. Zygotes Infect the host cell. O-P. Development of the rhizomycelium (Endobiotic phase). R. Germinating Resting sporangium. 1. Infection of an epidermal cell by a planospore. 2. An early stage in the development of epibiotic sporangium. 3. Three mature epibiotic sporangia developing on an epidermal host cell. 4. Eight days-old rhizomycelium ; with empty, primary (a), secondary (b), & tertiary ©, turbinate organs. (Fig.5). 6 & 7. Stages in germination of resting sporangia of *P. corcori*, Lingappa. Notice the difference between germination processes between Fig. R & 6-7. Fig. 8. Empty resting sporangium.

Catenaria, an endobiotic parasite of nematodes and nematode eggs



Catenaria



Coelomomyces

About 70 species

parasites of aquatic insects (Diptera), mosquito larvae

proposed as biocontrol by Couch (the *Septobasidium* guy)

Actually a heteroecious fungus, the only non-rust heteroecious fungus known

Alternation of generations, gametophyte (haploid) stage produced on Copepods (Crustacea)

Sporophyte (diploid) produced on mosquito larvae

Used as a biocontrol agent for mosquito control
effective but difficult to mass produce

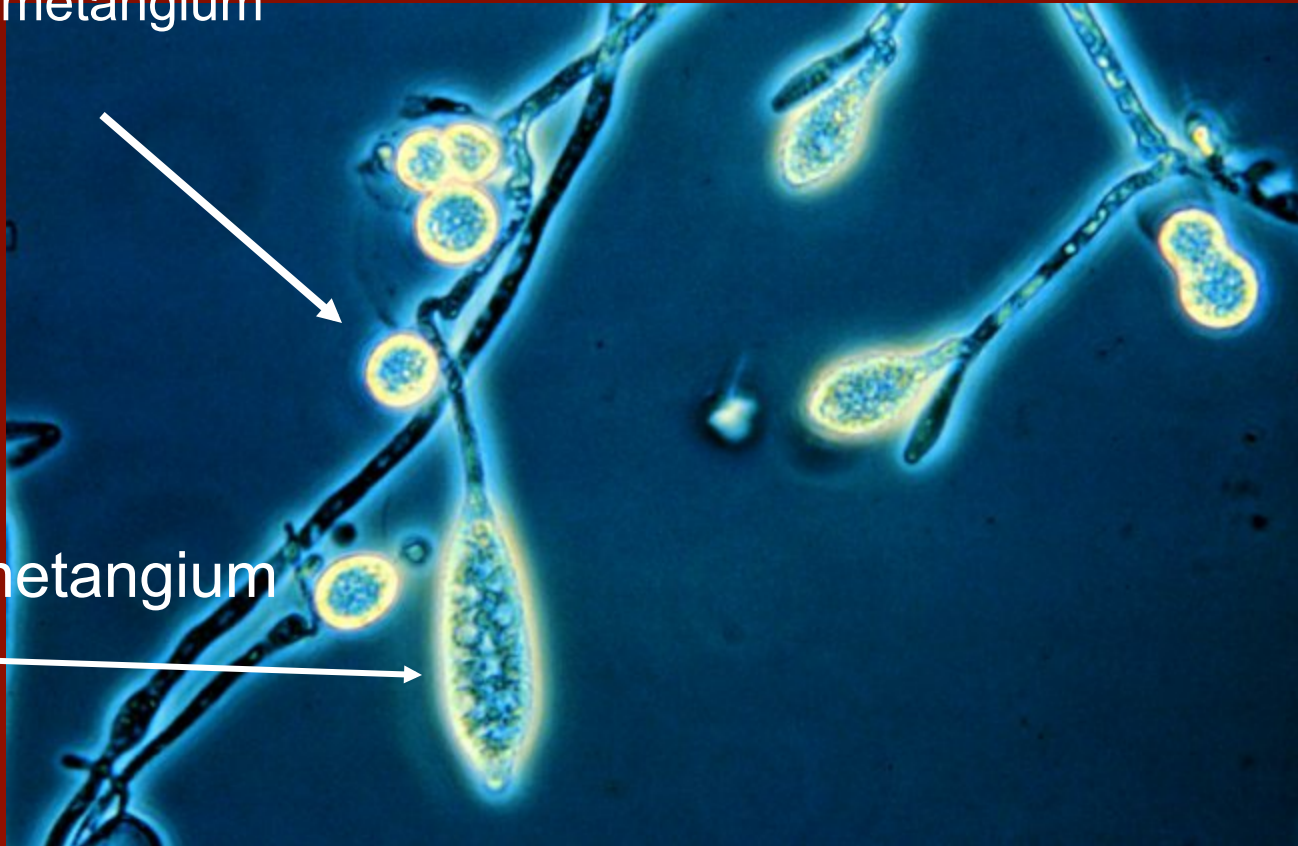
Life cycle of Coelomomyces, alternation between mosquito larva and copepod



Monoblepharidales (now Monoblepharidomycetes)

Reproduction by fertilization of nonmotile female gamete by a motile male gamete

female gametangium



male gametangium

Saprobies in freshwater environments