What are Fungi?

Fungi in the Tree of Life

- Living organisms on earth first arose about 3.5 billion years ago
  - Prokaryotic
  - Anaerobic
- Oldest fossils of fungi are about 460 million years old
- Coincides with the rapid expansion of multi-cellular organisms
- Major multicellular eukaryotes are divided into Kingdoms
  - Animals
  - Plants
  - Fungi
- Each of these three kingdoms differ in their basic cellular structure and mode of nutrition (defined by Whittaker, 1969)
  - Plants - photosynthetic, cellulosic cell walls
  - Animals - digestive systems, wall-less cells
  - Fungi - absorptive nutrition, chitinous walls
- The estimates for the expansion of multicellular organisms are based upon phylogenetic analyses of Carl Woese
  - Examined ribosomal RNA (rRNA)
    - Present in prokaryotes and eukaryotes
    - Relatively stable, but changes occur over time; thereby acting as a chronometer
  - Distinguished three separate groups (Domains) of living organisms
- Domains - rRNA sequence differences correlate with differences in cellular structure and physiology
  - Bacteria - “true bacteria”
  - Archaea - “ancient prokaryotes”
  - Eucarya - eukaryotes
- Taxonomic grouping of “Kingdom” lies beneath that of “Domain”
- Though the fossil evidence suggests fungi were present on earth about 450 million years ago, aquatic fungi (Phylum Chytridiomycota) most likely were present about a million years before this time

- About 354 - 417 million years ago, fungi evolved with primitive land plants
- These plant-associated fungi probably helped their photosynthetic partners gather nutrients from the harsh soils of the time
- These fungi were the early ancestors of the present day phylum Glomeromycota
- Despite plant-fungus co-evolution, fungi are more closely related to animals

Defining the Fungal Kingdom

- Mycology is the study of fungi
  - *Myco-* = fungi
  - *-ology* = the study of
- Mycology originally arose as a branch of botany because fungi were once believed to be "achlorophyllic" plants

Why Study the Fungi?

- There are over 100,000 species of ***known*** fungi and probably 15 times that many that have yet to be discovered
- Fungi are an extremely important part of the ecosystem
  - Recycling of minerals and carbon
  - Source of food, medicines, and chemicals
  - Important models in scientific research
  - Cause plant and animal diseases

Defining the Fungal Kingdom

- Fungi are simple, eukaryotic microbes
  - Many are microscopic
  - Studies typically employ standard microbiological techniques
- Mycologists (fungal biologists) have traditionally studied not only the true fungi (e.g., mildew), but also fungus-like organisms (e.g., slime molds)
- The kingdom Mycota is comprised of the true fungi
- True fungi have the following features:
  - Eukaryotic
  - Typically grow as filaments, termed hyphae (sing., hypha) via apical growth [the latter differs from the growth of other filamentous organisms]

  - Fungal hyphae repeatedly branch to form a network of filaments termed a mycelium (sing., mycelia)
  - Some fungi grow as a single-celled entity, termed a yeast, that grows either by a budding process or via binary fission
  - Some fungi can switch growth forms between a hyphal phase and a yeast phase, a property known as dimorphism
    - Typically induced by environmental conditions
    - A number of such fungi are disease-causing agents of humans and animals
  - Heterotrophic (chemo-organotrophs) - require preformed organic compounds
  - Absorb nutrients after degradation by exogenously released enzymes
  - Unique cell wall components
    - Chitin
    - Glucans
    - Rare instances of cellulose, but definitely fungal cell walls are not as rich in this polymer as are plants
  - Typically have haploid nuclei
    - Hyphae often have a number of haploid nuclei present in each cell
    - Some yeasts have a single diploid nucleus
  - Reproduce both sexually and asexually, typically through the production of spores
  - Other differences between fungi and animals and plants include:
    - Histone types
    - Sensitivity of microtubules to inhibitors
    - Manner of lysine biosynthesis
    - Membrane sterols
    - Organellar structure/morphology

Major Activities of Fungi

- Plant parasites
  - Irish potato blight of the 1840s
  - Dutch elm disease
  - Disappearance of frogs in Costa Rica
- Plant symbionts
  - Lichens (can also form with cyanobacteria)
  - Mycorrhiza

- Human pathogens
  - About 200 known species of fungi are known to infect humans
  - Diverse diseases including:
    - Dandruff
    - “ring worm”
    - *Pneumocystis* infection of HIV-infected persons
    - Candidiasis (mucocutaneous and systemic)
- Biological control agents
  - Mycoparasites (other fungi)
  - Entomopathogens (insects)
  - Nematophagous (nematodes)
- Decomposition
  - Cellulose (plant material)
  - Rumen fungi in cows
  - Dry rot
- Toxin production (mycotoxins)
  - Aflatoxins (peanuts and grains)
  - Mushroom poisoning

Fungi in Biotechnology

- Foods and flavorings
  - Edible mushrooms
    - 5 million tons produced worth $14 billion (1994)
    - Diverse types now widely available in supermarkets
  - Alcoholic beverages
  - Breads, cheeses, soy sauce
  - Quorn mycoprotein

- Fungal metabolites
  - Two categories
    - Primary - intermediates or end products of common metabolic pathways essential for normal cellular function
    - Secondary - diverse range of compounds formed by specific pathways of a given organism and not essential for growth (but may provide some selection advantage)
  - Examples of primary metabolites
    - Citric acid (estimated 200,000 tons produced in the year 2000) [soft drinks]
    - Gluconic acid (estimated annual production of 100,000 tons) [food additive]
    - Itaconic acid (estimated annual production of 80,000 tons) [paint and adhesive manufacture]
  - Examples of secondary metabolites
    - β-lactam antibiotics, e.g., penicillins and cephalosporins
    - Non-β-lactam antibiotics, e.g., griseofulvin, gliotoxin, ciclosporins
    - Pullulan - film-wrap for food in Japan
    - Chitosan - sewage clarification, plant defense initiator
- Enzymes and enzymic conversions
  - Extracellular enzymes
  - Commercially valuable roles
    - Food industry
    - Bioconversions
- Heterologous gene products - expression of foreign proteins by fungi having medical/industrial applications

Terms You Should Understand

- ‘Fungus’ (pl., fungi) is a taxonomic term and does not refer to morphology
- ‘Mold’ (sometimes spelled ‘mould’) is a morphological term referring to a filamentous (multicellular) condition
- ‘Mildew’ is a term that refers to a particular type of mold
- ‘Yeast’ is a morphological term referring to a unicellular condition

Special Lecture Notes on Fungal Taxonomy

- Fungal taxonomy is constantly in flux
- Not one taxonomic scheme will be agreed upon by all mycologists
- Classical fungal taxonomy was based primarily upon morphological features
- Contemporary fungal taxonomy is based upon phylogenetic relationships

Fungi in a Broad Sense

- Mycologists have traditionally studied a diverse number of organisms, many not true fungi, but fungal-like in their appearance, physiology, or life style
- At one point, these fungal-like microbes included the Actinomycetes, due to their filamentous growth patterns, but today are known as Gram-positive bacteria
- The types of organisms mycologists have traditionally studied are now divided based upon phylogenetic relationships
- These relationships are:
  – Kingdom Fungi - true fungi
  – Kingdom Straminipila - “water molds”
  – Kingdom Mycetozoa - “slime molds”
- Kingdom Fungi (Mycota)
  – Phylum: Chytridiomycota
  – Phylum: Zygomycota
  – Phylum: Glomeromycota
  – Phylum: Ascomycota
  – Phylum: Basidiomycota
  – Form-Phylum: Deuteromycota (Fungi Imperfecti)
- Kingdom Straminipila (Chromista)
  – Phylum: Oomycota
  – Phylum: Hyphochytridiomycota
  – Phylum: Labyrinthulomycota
- Kingdom Mycetozoa
  – Phylum: Myxomycota
  – Phylum: Dictyosteliomycota
  – Phylum: Acrasiomycota
  – Phylum: Plasmodiophoromycota

The Mycetozoa (Slime Molds)

- Kingdom Mycetozoa is comprised of four phyla containing three different groups of organisms that differ in their trophic (feeding) stages
  - Myxogastrids - plasmodial
  - Dictyostelids and acrasids - amoeboid
  - Protostelids - obligate parasites having two plasmodial stages
- Phylum Dictyosteliomycota
  - Monophyletic group of cellular slime molds
  - Best example: *Dictyostelium discoideum*
  - Grow and divides as unicellular, haploid amoebae
  - Swarming amoeba respond to gradients of cAMP
  - Feed on bacteria via phagocytosis
- Phylum Acrasiomyctoa
  - Polyphylogenetic group of cellular slime molds
  - Best example: *Acrasis rosea*
  - Feeds on bacteria by phagocytosis
  - Do not respond to cAMP; chemotactic factor is unknown
- Phylum Myxomycota
  - Plasmodial slime molds
  - Best example: *Physarum polycephalum*
  - Prominent feature is the multinuclear network of protoplasm that exhibits rhythmic streaming
  - Feeds by phagocytosis of bacteria
  - A mature plasmodium can form either:
    - A sclerotium under adverse conditions that can then regenerate as a plasmodium; or
    - A sporangium that bears haploid spores
- Phylum Plasmodiophoromycota
  - Obligate intracellular parasites of plants, algae, or fungi
  - Best example: “club foot” of plant roots caused by *Plasmodiophora brassicae*

The Chromistans

- The term 'Chromistan Fungi' is oxymoronic in that:
  - Chromists are a broadly diverse of protists containing stramenopiles (also spelled straminiples), but not true fungi
  - Phylogenetic evidence suggests a monophyletic origin quite distinct from the true fungi, most likely a red algal ancestor
- Chromists seem to share a common ancestry with alveolates (ciliates, sporozoans, dinoflagellates)

The Stramenopiles

- Stramenopiles are also known as heterokonts, referring to two types of flagella found in this group
  - Smooth (whiplash) flagellum
  - "Tinsillated" (or tinsel) flagellum
    - Contains stiff lateral hairs (mastigonemes)
    - Pulls, doesn't push, cell through the medium
- Number/kind of flagella varies among the different groups of organisms
- Stramenopiles include diatoms and kelps in addition to fungus-like microbes
- Kingdom Straminipila
  - Comprised of three fungal-like phyla
    - Hyphochytridiomycota
    - Oomycota
    - Labyrinthulomycota
  - Phylum Hyphochytridiomycota
    - Very similar in many ways to the Phylum Chytridiomycota (Kingdom Fungi [Eumycota])
    - Motile spores (zoospore) possess a single, anterior tinsel flagellum [distinguishes the hyphochytrids from the chytrids]
    - No sexual reproduction yet observed among the hyphochytrids
    - Best example: *Rhizidiomyces apophysatus* - parasite water mold oogonia
  - Phylum Oomycota
    - Economically important fungus-like organisms that have extremely significant environmental roles in agriculture

- Causes of the following plant/fish diseases:
  - Potato blight (*Phytophthora infestans*)
  - Sudden oak death (*Phytophthora ramorum*)
  - “Decline” diseases (*Pythium* spp.)
  - Downy mildews (*Peronospora* spp.)
  - Water molds/fish pathogens (*Saprolegnia* spp.)
- Greatly mimic the true fungi in many ways probably due to convergent evolution
- Possess the following plant-like features:
  - Glucan and cellulose-like cell walls (not chitin)
  - Diploid nuclei (most fungi tend to be haploid)
  - Membranes contain plant sterols (not ergosterol)
- Key features
  - Zoospores have two flagella - a forward directed tinsel type and a backward directed whiplash type
  - Sexual reproduction is oogamous, i.e., the zygote develops into a thick-walled oospore that can persist in the environment [Note: oogamy can also occur in some chytrids (Eumycota)]
- Features of a oomycetous life cycle is typified by that of *Phytophthora infestans*

– Phylum Labyrinthulomycota

- Commonly referred to as “net slime molds”
- Characterized by a network of branch, anastomosing (fusing), wall-less filaments held together by a secreted polysaccharide sheath
- Produce biflagellated zoospores
  - Anteriorly directed tinsel type
  - Posteriorly directed whiplash type
- Most members are marine parasites

The Mycota (True Fungi)

- Traditionally, differentiated by their mode of sexual reproduction, though not exclusively
- Generally confirmed by phylogenetic analysis

- Kingdom Fungi (Mycota)
  - Phylum: Chytridiomycota (motile zoospores)
  - Phylum: Zygomycota (zygospores)
  - Phylum: Glomeromycota (typically asexual)
  - Phylum: Ascomycota (ascospores)
  - Phylum: Basidiomycota (basidiospores)
  - Form-Phylum: Deuteromycota (Fungi Imperfecti)

The Chytridiomycota

- 'Chytrids' are considered the earliest branch of the true fungi (Eumycota)
- Cell walls contain chitin and glucan
- Only true fungi that produce motile, flagellated zoospores
  - Usually single, posterior whiplash type
  - Some rumen species have multiple flagella
- Zoospore ultrastructure is taxonomically important within this phylum
- Commonly found in soils or aquatic environments, chytrids have a significant role in degrading organics
- Exhibit many of the same thallus structure types and arrangements as hyphochytrids (e.g., eucarpic; rhizoidal; endobiotic; etc.)
- A few are obligate intracellular parasites of plants, algae, and small animals (e.g., frogs)
- Very few economically important species (*Synchytrium endobioticum* causes potato wart disease)
- More important (and fascinating) as biological models (e.g, *Allomyces*)

The Zygomycota

- Five features of Phylum Zygomycota
  - Cell walls contain chitin, chitosan, and polyglucuronic acid
  - Some members typically bear multinucleate, coenocytic hyphae, i.e., without cross walls (septa; sing., septum)
    - When present, septa are simple partitions
    - Some Orders have regular septations that are flared having a centrally plugged pore
  - Produce zygospores (meiospore) via sexual reproduction (gametangial fusion)

  - Asexual spores (mitospores), termed sporangiospores, form through cytoplasmic cleavage within a sac-like structure termed a sporangium
  - Haploid genome
- Importance of the zygomycetous fungi
  - Organic degraders/recyclers
  - Useful in foodstuffs/fermentations
  - Pathogens of insects/other animals
- Generalized life cycle
  - Asexual stage (anamorphic; imperfect)
    - Hyphae develop erect branches termed sporangiophores
    - A thin-walled sac (sporangium) is walled off at the tip and fills with cytoplasm containing multiple nuclei (with collumella underneath sac)
    - Cytoplasmic cleavage and separation of nuclei into walled units produces sporangiospores
    - Thin sporangial wall (peridium) breaks releasing sporangiospores
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    - Sporangiospores germinate to repeat the asexual life cycle
- The zygospore represents the teleomorphic phase (sexual; perfect form) of this phylum
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  - Results from the fusion of gametangia of heterothallic (two different mating types; designated “+” and “-”) or homothallic (self fertile) strains
  - Acts as a thick-walled resting spore
    - Zygosporangium becomes thick walled to form the zygospore
    - Hyphae to the sides become empty appendages (suspensor cells)
    - Zygospore often forms ornate appendages
    - Zygospore is constitutively dormant for a time, but then germinates to produce a sporangium containing haploid sporangiospores

The Glomeromycota

- These fungi were originally placed within the Phlyum Zygomycota
  - ***Do not*** produce zygospores
  - Live as obligate, mutualisitic symbionts in >90% of all higher plants - known at arbusular mycorrhizas (AM; endomycorrrhiza)
- Will not grow axenically
- Produce large, thick-walled spores in soils that germinate in the presence of a plant root
- Develop non-septate hyphae that invade the root, then form a branch, tree-like arbuscules within the root
- Help plants thrive in nutrient poor soils, especially phosphorous

The Ascomycota

- This phylum contains 75% of all fungi described to date
- Most diverse phylum being significant:
  - Decomposers
  - Agricultural pests (e.g., Dutch elm disease, powdery mildews of crops)
  - Pathogens of humans and animals
- Asexual spores (mitospores)
  - Variety of types
  - Usually not used for taxonomic purposes
  - Generally referred to as conidia
  - Tend to be haploid and dormant
- Key feature is the ascus (pl., asci) - sexual reproductive cell containing meiotic products termed ascospores
- Another significant structural feature - a simple septum with a central pore surrounded by Woronin bodies
- The fruiting body of these fungi, termed an ascocarp, takes on diverse forms
  - Flasked shaped - perithecium
  - Cup-shaped - apothecium
  - Closed structure - cleistothecium
  - Embedded structure - pseudothecium
  - Some ascospores are borne singly or not enclosed in a fruiting structure

- Some ascomycetous fungi grow as yeasts
  - Either budding or fission
  - Both types are capable of sexual reproduction under the appropriate conditions

The Basidiomycota

- This phylum contains 30,000 different species or about 37% of all true fungi
- Most often recognized as mushrooms and toadstools, as well as other types of fruiting bodies in nature
- Very important for their ecological and agricultural impact
- Majority are terrestrial, although some can be found in marine or freshwater environments
- Oldest confirmed basidiomycete fossil is about 290 millions years old
- Some are molds, some are yeasts, and some are dimorphic
- Features similar to those of the Ascomycota
  - Haploid somatic hyphae
  - Septate hyphae
  - Potential for hyphal anastomosis
  - Production of complex fruiting structures
  - Presence of a dikaryotic life cycle phase
  - Production of a conidial anamorph
- Key differences
  - Cell wall
    - Ascomycetes - two layered
    - Basidiomycetes - multilayered
  - Septa
    - Ascomycetes
      - Hyphal forms - simple with central pore surrounded by Woronin bodies
      - Yeast forms - simple with micropores
    - Basidiomycetes - dolipore septum
  - Basidiomycetes also form a clamp connection at each septum of a dikaryotic hypha
  - Meiospore production - meiosis occurs within a specialized cell termed a basidium (pl., basidia), but the spores are borne ***exogenously*** on tapering outgrowths termed sterigmata (sing., sterigma)

- Sterigmata form on the surface of the basidium
- Haploid nuclei migrate into the sterigmata as the basidiospore develops
- Mature basidiospore in many fungi released through a ballistic-like method involving a hylar (or hilar) drop
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The Mitosporic Fungi

- Many ascomycetous fungi produce asexual (mitotic) spores (anamorphic phase), but their teleomorph phase (sexual reproduction) is absent
- Taxonomically, such fungi are placed in an artificial category variously termed Deuteromycota (or Deuteromycotina) or Fungi Imperfecti
- Due to the absence of a teleomorph, these fungi are often given a provisional name termed a “form” genus/species
- If the teleomorph is discovered, the fungus renamed
- Example of teleomorph/anamorph dichotomy of names:
  - Anamorph - *Aspergillus nidulans* - forms mitosporically-derived conidia, therefore classified within the form-phylum Deuteromycota
  - Teleomorph - *Emerciella nidulans* - forms a cleistothecium containing ascospores, therefore classified within the Phylum Ascomycota
- Conidia are produced in a variety of ways, but never by cytoplasmic cleavage as in the Zygomycota
- Two main types of conidium development are the basis for the production for all types of conidia
  - Thallic - fragmentation process
  - Blastic - swelling process
- Most conidia are blastic in origin and are borne in various ways:
  - Budding
  - Extrusion of flask shaped cells termed phialides
  - Aggregation of condiophores in stalks termed synnema or coremium
  - On a pad-like surface (acervulus)
  - Within a flask-shaped structure (pycnidium)

- Taxonomic divisions of the Fungi Imperfecti - truly an artificial classification scheme based solely on conidial structures
  – Hyphomycetes - conidia borne on conidiophores
  – Coelomycetes - conidia borne on an acervulus or within a pycnidium
  – Agonomycetes - “Mycelia Sterilia” - no conidia; sometimes sclerotia