Biology of Fungi

The Diversity of Fungi and Fungus-Like Organisms

The Kingdom Fungi

- Kingdom Fungi (Mycota)
  - Phylum: Chytridiomycota
  - Phylum: Zygomycota
  - Phylum: Glomeromycota
  - Phylum: Ascomycota
  - Phylum: Basidiomycota
  - 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

The Chytridiomycota (cont.)

- Zoospore ultrastructure is taxonomically important within this phylum
- Ultrastructure of chytrid zoospores. Source: Kendrick, 2003
- 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.)

The Chytridiomycota (cont.)

- A few are obligate intracellular parasites of plants, algae, and small animals (e.g., frogs)
- Unstained specimen showing a number of oval-shaped chytrids (arrow) infecting the skin of a frog. Source: www.jcu.edu.au/school/phtm/PHTM/frogs/anzcarrt.htm
The Chytridiomycota (cont.)
- Very few economically important species (Synchytrium endobioticum causes potato wart disease)
- More important (and fascinating) as biological models (e.g., Allomyces)

Isolation of chytrids is not easy
- Requires 'baiting' techniques
- Appears to be species-substrate specificity/preference presumably due to specific receptor molecules on the zoospore surface membrane

Five orders within the chytrids, based largely on zoospore ultrastructure
- Chytridiales and Spizellomycetales
  - Similar to one another
    - Spizellomycetales live in soil
    - Chytridiales live in aquatic environments
  - These Orders do not produce hyphae
  - Unique to the chytrids, Spizellomycetales zoospores exhibit amoeboid movement

Blastocladiales
- Produces true hyphae and narrow rhizoids
- Some species (e.g., Allomyces) exhibit alternation of generations (i.e., rotating from haploid and diploid phases)
  - Haploid thalli of Allomyces produce gametes in specialized gametangia
  - Diploid thalli of Allomyces produce flagellated zoospores and resting sporangia
- Allomyces also exhibits anisogamy - two different sizes of gametes (small, highly mobile ['male'] and larger, less mobile ['female'])

Life cycle of Allomyces. Source: www.bio.utexas.edu/faculty/laclaire/bot321/handouts/AllomyLH.jpg
Gametophyte stage of Allomyces (right) and the sporophyte stage (left). Source: www2.una.edu/pdavis/kingdom_fungi.htm
The Chytridiomycota (cont.)

- **Monoblepharidales**
  - Unique among the true fungi for its means of sexual reproduction via oogamy
  - Not of economic importance

![Image of Monoblepharella sp.](source: www.bsu.edu/classes/ruch/msa/barr.html)

The Chytridiomycota (cont.)

- **Neocallimastigales**
  - Obligate anaerobes
  - No mitochondria, but instead produce energy via a hydrogenosome
  - Often found in animal rumens; highly cellulytic
  - Multiflagellated zoospores

![Image of Neocallimastix](source: www.bsu.edu/classes/ruch/msa/wubah.html)

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

![Diagram of coenocytic and septated hypha](source: www.apsnet.org/education/IllustratedGlossary/PhotosA-D/coenocytic.htm and www-micro.msb.le.ac.uk/MBChB/6a.htm)

The Zygomycota (cont.)

- 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

![Image of zygospore](source: www-micro.msb.le.ac.uk/MBChB/6a.htm)

The Zygomycota (cont.)

- Importance of the zygomycetous fungi
  - Organic degraders/recyclers
  - Useful in foodstuffs/fermentations
  - Pathogens of insects/other animals

![Diagram of zygomycete fungi](source: www-micro.msb.le.ac.uk/MBChB/6a.htm)
The Zygomycota (cont.)
- Generalized life cycle
  - Asexual stage (anamorphic; imperfect)
    - Hyphae develop erect branches termed sporangiophores

The Zygomycota (cont.)
- Asexual stage (cont.)
  - A thin-walled sac (sporangium) is walled off at the tip and fills with cytoplasm containing multiple nuclei (with collumella underneath sac)

The Zygomycota (cont.)
- Asexual stage (cont.)
  - Cytoplasmic cleavage and separation of nuclei into walled units produces sporangiospores
  - Thin sporangial wall (peridium) breaks releasing sporangiospores

The Zygomycota (cont.)
- The zygospore represents the teleomorphic phase (sexual; perfect form) of this phylum

Development of asexual sporangiophores
- Source: Kendrick, 2003

Mature sporangia (left image) and a visible collumella (right image).
- Source: Kendrick, 2003

Diagrammatic representation of sporangiospore development and release.
- Source: www.unex.es/botanica/LHB/anima/mucor2.htm

Ruptured peridium and underlying sporangiospores (left image) and remaining collumella following complete spore dispersal (right image).
- Source: Kendrick, 2003

Diagrammatic representation of sporangiospore development and release.
- Source: www.unex.es/botanica/LHB/anima/mucor2.htm

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Mating of Phycomyces in culture (left image) showing a line of darkly-pigmented zygospores (right image). The zygospores are highly ornate (left image).
- Source: Kendrick, 2003

Generalized life cycle of a zygomycetous fungus.
- Source: Kendrick, 2003

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The Zygomycota (cont.)

- The 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 Zygomycota (cont.)

- Phylum Zygomycota - two Classes

  - Class Zygomycetes - six orders
    - Order Mucorales
      - Typical globose mitosporangium containing hundreds of non-motile asexual spores.
      - Contains saprobes and the common 'black bread molds' - Mucor, Rhizopus, Absidia.
    - Order Entomophthorales - insect pathogens.
    - Order Kickxellales - atypical zygomycete having regularly septate hyphae.
    - Order Zoopagales - mycoparasites.
  - Class Trichomycetes - four Orders
    - Live nearly exclusively in the guts of arthropods.
    - Does not produce sporangiospores, but instead trichospores.
    - Unusual zygospore structure.
**The Glomeromycota**

- These fungi were originally placed within the Phylum Zygomycota
  - *Do not* produce zygospores
  - Live as obligate, mutualistic symbionts in >90% of all higher plants - known as arbuscular mycorrhizas (AM; endomycorrhiza)
- Will not grow axenically

**The Glomeromycota (cont.)**

- Produce large, thick-walled spores in soils that germinate in the presence of a plant root

**The Glomeromycota (cont.)**

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 Glomeromycota (cont.)**

- Phylogenetics of the Glomeromycota
  - Based upon RNA sequences, this phylum is monophyletic

**The Glomeromycota (cont.)**

- Fossil hyphae and spores (A and B) compared with a spore (C) of a present-day Glomus species (arbuscular mycorrhizal fungus). Source: Deacon, 2006

**The Glomeromycota (cont.)**

Phylogenetic tree of Glomeromycota showing the monophyletic group. Source: Schussler et al., 2001.
The Glomeromycota (cont.)
- Phyllogenetics of the Glomeromycota
  - Based upon RNA sequences, this phylum is monophyletic
  - Morphologically distinct from other fungi
  - Probably had same ancestor as the phyla Ascomycota and Basidiomycota

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

The Ascomycota (cont.)
- Asexual spores (mitosporic)
  - Variety of types
  - Usually not used for taxonomic purposes
  - Generally referred to as conidia
  - Tend to be haploid and dormant

The Ascomycota (cont.)
- Key feature is the ascus (pl., asci) - sexual reproductive cell containing meiotic products termed ascospores

The Ascomycota (cont.)
- Another significant structural feature - a simple septum with a central pore surrounded by Woronin bodies
The Ascomycota (cont.)

- The fruiting body of these fungi, termed an ascocarp, takes on diverse forms:
  - Flasks shaped - perithecium
  - Cup-shaped - apothecium
  - Closed structure - cleistothecium
  - Embedded structure - pseudothecium

- Asci also vary in structure:
  - Unitunicate-operculate - single wall with lid/opening (operculum), found only in apothecial ascomata (fruiting body tissue)
  - Unitunicate-inoperculate - operculum replaced with an elastic ring; found in perithecial and some apothecial
The Ascomycota (cont.)

- Protunicate - no active spore shooting mechanism; ascus dissolves to release spores; characteristically produced by fungi that form cleistothecia


The Ascomycota (cont.)

- Bitunicate - double-walled ascus in which outer wall breaks down, inner wall swells through water uptake, then expels spores

Diagram (left image) and a photomicrograph (right image) of a bitunicate ascus with ascospores. Source: Kendrick, 2003

The Ascomycota (cont.)

- Ascomycetes differ from zygomycetes in both their basic anamorphic and teleomorphic characteristics:
  - Anamorph - mitospores (conidia) of ascomycetes are typically derived from modified bits of hyphae, whereas zygospores result from the cleavage of a multinucleated cytoplasm within a sporangium

The Ascomycota (cont.)

- Teleomorph - in zygomycetes, the anamorph and teleomorph often occur together and share the same nomenclature; in ascomycetes, anamorphs can be completely separated from the teleomorph and are often given different binomials
  - For the Ascomycota, anamorph + teleomorph = holomorph

The Ascomycota (cont.)

- Life cycle of most ascomycetes typified by Neurospora
  - Conidia/ascospores give rise to hyphae
  - Hyphae may continue to grow and produce conidia
  - Sexual reproduction begins with the differentiation of female hyphae into a trichogyne

Diagrammatic overview of the life cycle of Neurospora. Source: Deacon, 2006
The Ascomycota (cont.)
- Trichogyne is fertilized by a conidium or by an antheridium (male reproductive structure)
- Plasmogamy occurs without karyogamy, i.e., cytoplasmic fusion without nuclear fusion, producing heterokaryotic hyphae (presence of two different nuclei in the same cytoplasm)
- The heterokaryotic hyphae undergo crozier formation

The Ascomycota (cont.)
- Nuclear division continues followed by septation of the crozier to produce an ascus initial cell that contains one nucleus of each mating type, i.e., a dikaryotic state
- Karyogamy occurs to form a diploid nucleus that then undergoes meiosis
- Haploid nuclei are then walled off to form ascospores - typically there are 4-8 meiotic products

The Basidiomycota
- 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
The Basidiomycota (cont.)

- 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

The Basidiomycota (cont.)

- 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 type septum surrounded by a parenthosome
      - Central pore blocked by a pulleywheel occlusion
      - Dolipore-like, but parenthosome is absent

The Basidiomycota (cont.)

- Septa
  - Ascomycetes
    - Hyphal forms - simple with central pore surrounded by Woronin bodies
    - Yeast forms - simple with micropores
  - Basidiomycetes

- Dolipore septum in the hypha of the basidiomycetous fungus Coprinus psychromorbidus.
The Basidiomycota (cont.)

- **Dikaryophase**
  - Ascomycetes
    - Restricted to ascogenous tissue
    - Nuclear fusion and subsequent meiosis involve the formation of a crozier

![Diagrammatic representation of ascosporogenesis.](source: www.unex.es/botanica/LHB/an/asca2.gif)

The Basidiomycota (cont.)

- **Basidiomycetes**
  - Heterokaryotic nuclei (2 per cell)
  - Not restricted to a tissue phase and may continue indefinitely
  - Perpetuated by the formation of a clamp connection at each septum of a dikaryotic hypha

![Diagrammatic representation of clamp cell formation in a basidiomyceteous fungus.](source: www.unex.es/botanica/LHB/an/fibula0.gif)

The Basidiomycota (cont.)

- **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**)

![Clamp connection (left image) and the its dolipore-type septum (right image).](source: www.apsnet.org/education/IllustratedGlossary/PhotosS-V/septum.jpg and Kendrick, 2003)

The Basidiomycota (cont.)

- Very complex life cycles that vary among the different classes/species
- Generalized life cycle:
  - Haploid basidiospores germinate to form hyphae with a single nucleus per cell (monokaryotic phase)
  - Monokaryons can produce **oidia** (= conidia)
The Basidiomycota (cont.)

- Monokaryons of different mating types fuse or an odium attracts monokaryon of compatible mating type, then fuses
- Fusion (plasmogamy) results in dikaryotic hyphae (two nuclei per cell; heterokaryotic)
- Fruiting body forms containing dikaryotic basidia
- Nuclear (karyogamy) fusion occurs followed by meiosis

The Basidiomycota (cont.)

- Sterigmata form on the surface of the basidium
- Haploid nuclei migrate into the sterigmata as the basidiospore develops

The Basidiomycota (cont.)

- Mature basidiospore in many fungi released through a ballistic-like method involving a hylar (or hilar) drop (see Chapter 1 in Money’s book for historical and descriptive details about this mechanism)
The Basidiomycota (cont.)

- Phylogenetics
  - rDNA analysis has separated the Phylum Basidiomycota into three separate sub-groups (clades)
    - Hymenomycetes - typical mushroom, toadstools, and "jelly fungi"
    - Urediniomycetes - "rusts"
    - Ustilaginomycetes - "smuts"
  - Phylogenetic relationships between and within the sub-groups remains unclear

The Basidiomycota (cont.)

- Taxonomy
  - Urediniomycetes
    - Agriculturally significant "rusts"
    - Example Puccinia graminis - causes black stem of wheat
  - Ustilaginomycetes
    - Agriculturally significant "smuts"
    - Example Ustilago maydis - corn smut fungus

The Basidiomycota (cont.)

- Selected differences between 'rusts' and 'smuts' (adapted from Table 5.1 in Kendrick):

<table>
<thead>
<tr>
<th>Urediniomycetes</th>
<th>Ustilaginomycetes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Terminal teliospores</td>
<td>Intercalary teliospores</td>
</tr>
<tr>
<td>No clamp connections</td>
<td>Clamp connections present</td>
</tr>
<tr>
<td>Requires 2 hosts</td>
<td>Does not require 2 hosts</td>
</tr>
<tr>
<td>Infections are localized</td>
<td>Infections are systemic</td>
</tr>
<tr>
<td>Obligate biotroph</td>
<td>Facultative biotroph</td>
</tr>
</tbody>
</table>

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

The Mitosporic Fungi (cont.)

- 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
The Mitosporic Fungi (cont.)

- 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

Thallic vs. Blastic

- Most conidia are blastic in origin and are borne in various ways:
  - Budding
The Mitosporic Fungi (cont.)

- Extrusion of flask shaped cells termed phialides

The Mitosporic Fungi (cont.)

- Aggregation of conidiophores in stalks termed synnema or coremium

The Mitosporic Fungi (cont.)

- On a pad-like surface (acervulus)
- Within a flask-shaped structure (pycnidium)

The Mitosporic Fungi (cont.)

- 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