Lecture 3: Fungal structures and propagules

Propagules in fungi

Two basic types of reproductive propagules are found in the fungi:

1. Sexual propagules are produced by the fusion of two nuclei that then generally undergo meiosis. Sexual methods of reproduction involve plasmogamy (cytoplasmic fusion of two cells), karyogamy (fusion of two nuclei), genetic recombination and meiosis. The resulting haploid spore is said to be a sexual spore, e.g. zygospores, ascospores and basidiospores. If a sexual spore is produced only by fusion of a nucleus of one mating type with a nucleus of another mating type (+ and - strains), the fungus is said to be heterothallic. In contrast, homothallic moulds produce sexual spores following the fusion of two nuclei from the same strain.
2. Asexual propagules are termed either spores or conidia depending on their mode of production, and which arise following mitosis of a parent nucleus. Conidia arise either by budding off conidiogenous hyphae or by differentiation of preformed hyphae. Asexual spores are commonly formed by consecutive cleavages of a sporangium. Asexual forms of reproduction represent the major method for the maintenance and dissemination of many fungi.

Reproduction in fungi

The fungal life cycle of the fungi has two main types of reproduction: sexual and asexual. Some fungi show only one known reproduction type. Asexual forms (anamorph) were previously often described separately and given different names than the sexual form (teleomoph). The complete form having both reproductive forms is called a holomorph. Fungi known only as anamorphs were previously grouped into the form-group Deuteromycetes (Fungi Imperfecti). This group is not used anymore, because with molecular phylogenetic techniques the systematic position of a fungus can be determined even if the sexual structures are not known.

Sexual reproduction

Meiotic development of haploid nuclei, their fusion, and the emerging diploid nuclei or zygote are the key-steps of sexual reproduction. If a diploid nucleus/cell undergoes further mitotic divisions, we consider that as the diploid phase of the life cycle. The haploid nuclei/cells arise from the meiosis of the diploid nuclei, and if the haploid cells go through mitotic cell divisions, that is the haploid phase of the life cycle. A life cycle is considered as haplo-diploid if both phases exist. Generally a phase exists if mitotic cell divisions happen in that nuclear-state. If the first division of the diploid zygote/nucleus is meiotic, the nuclei return to the haploid state immediately and the life cycle is haploid. The life cycle is diploid when only the haploid cells/nuclei represent the haploid state and fuse after they arise from a meiosis. Both Ascomycota and Basidiomycota have a special phase in their life cycle, the dikaryotic phase, when two haploid nuclei are in one hyphal segment. These dikaryotic hyphae develop when two monokaryotic cells or hyphae fuse (somatogamy or plasmogamy) but their nuclei do not.

When a monokaryotic haploid stage is represented by distinct cells that fuse, we term them gametes and the fusion is called gametogamy. The gametes can develop in special structures termed a gametangium.

The differences necessary for successful sexual reproduction of fungi are represented by mating types. Homothallic fungi can sexually reproduce even if only one strain originating from the same meiospore/hypha is present, whereas heterothallic fungi require two different compatible mating types to complete sexual reproduction. Mating types are determined by mating loci (MAT loci). Homothallism has several modes, the simplest being when one version of the MAT locus and the strains/cells containing it are compatible and can undergo sexual reproduction. The main modes of heterothallism are grouped according to the number of MAT loci. The simplest version has one MAT locus with two types (alleles) and two strains/cells with different MAT loci can successfully complete sexual reproduction. This type is the bipolar heterothallism. In tetrapolar heterothallism two MAT loci with at least two alleles determine the mating type. Two strains/cells can complete sexual reproduction only if both MAT loci are different. Several genes can function as MAT loci; often they code pheromones and their receptors or regulate genes coding such products.

Sexual reproduction and its structures

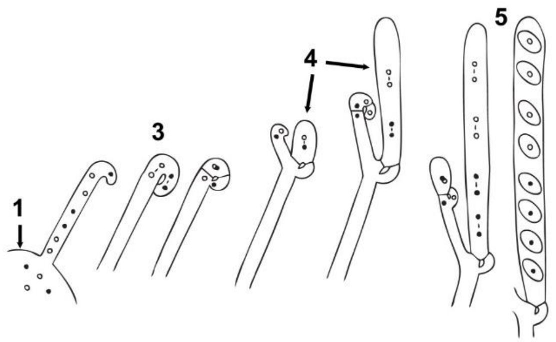
Names of the main groups of fungi were coined according to the structures developed during their sexual reproduction. Sexual reproduction of the main fungal groups differs significantly between each other and even within those groups.

Oomycetes (Protists) produce gametangia. The oogonium contains haploid oocytes produced by meioses. Beside the oogonium, antheridia develop and produce haploid nuclei via meioses. These nuclei migrate to oogonia across a fertilization tube developed by the oogonium to fertilize an oocyte. Their fusion produces diploid oospores that germinate and produce coenocytic non-septate hyphae with many nuclei. This life cycle is diploid. Differences in lifecycles occur within the group: different numbers of oocytes develop in the oogonia, and the oospores can produce not only coenocytic hyphae but also sporangium-producing zoospores. Both the oogonia and the antheridia can produce hormones that reciprocally stimulate and regulate their development.

Chytrids (the primitive fungi) have several different types of sexual reproduction. Some have gametes which fuse (gametogamy). They can be similar in size (izogamy) or different (anyzogamy). Moreover, a bigger, non-motile oocyte sometimes develops and is fertilized by a motile gamete (oogamy). In some chytrids the gametangia fuse (gametangiogamy) and in others gametes fertilize gametangia. Somatogamy can also happen when thalli of chitrids fuse.

Gametangia develop during the sexual reproduction of zygomycetes. Compatible coenocytic hyphae with haploid nuclei develop gametangia, generally opposite to each other, and these gametangia fuse (real gametangiogamy). Afterwards, the nuclei also fuse (karyogamy) and a thick walled, generally spherical zygospore develops. Homothallic zygomycetes do not need two gametangia for sexual reproduction and consequently could produce azygospores. Zygospores are held by suspensors which develop from the remaining parts of the two opposing hyphal outgrowths. The name of the Zygomycota originated from the Greek name of yoke (“zygos”), as the opposing gametangia and the zygospore held by two suspensors resemble this structure. The zygospore, strictly speaking, is not a spore but a resting zygote. After karyogamy the diploid nucleus undergoes meiosis, in some cases during spore development, in others during germination of the zygospores. This life cycle is haploid. When the zygospore germinates, a sporangium developed from the hypha produces endogenous haploid mitospores.

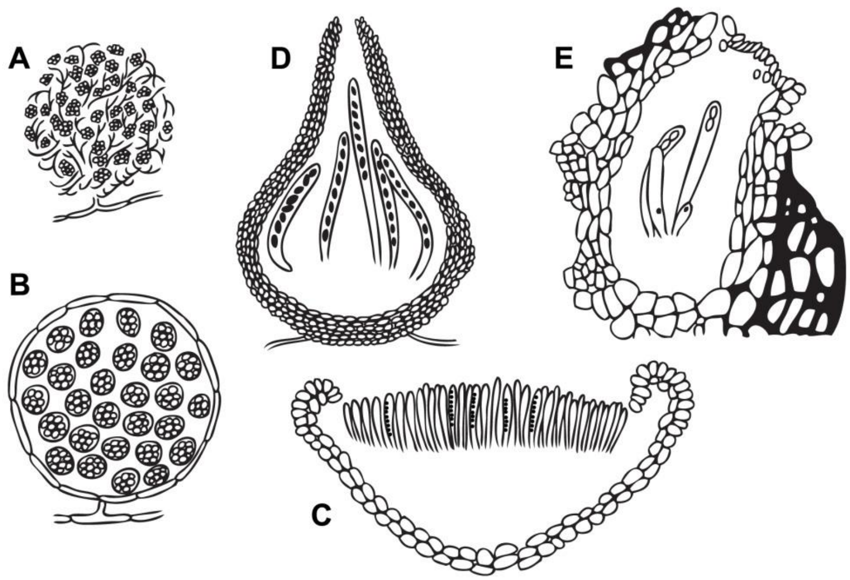
The name of the Ascomycota refers to the sac-like structure (ascus) in which the meiospores (ascospores) develop. The reproductive features discussed below refer to the hyphal taxa of the Pezizomycotina. An ascogonium develops with haploid nuclei and produces a trichogyn, a fertilization tube to the antheridium developed from a compatible monokaryotic hypha nearby. The haploid nucleus migrates from the antheridium to the ascogonium, from which dikaryotic hyphae with two nuclei of different origin will develop in each segment. The dikaryotic hyphae form crosiers which enable proper segregation of the two different nuclei after mitotic cell division.



Development of an ascus. 1: ascogonium, 2: ascogenous hyphae; 3: crozier; 4: ascus initial; 5: ascus with ascospores.

These dikariotic hyphae can participate in ascoma development. During ascus development the two nuclei of the terminal cell of an ascogenous hypha fuse (karyogamy). The diploid nucleus undergoes meiosis, and a post meiotic mitosis of the haploid nuclei will result the general eight nuclei of the eight ascospores. The life cycle of hyphal ascomycetes is dominated by the haploid phase; the dikaryotic phase is relatively short and a diploid nucleus is present only during karyogamy, followed immediately by a meiosis. The characteristics of the asci (shape, number of ascospores, organization of spores, chemical reactions of ascus wall, ascus wall layers etc.) are important features in the taxonomy of these fungi. Ascospores vary in shape and in size from a few microns to a couple of hundred microns. Both unicellular and septate spores can be found with few (e.g. *Lewia*) or many (e.g. *Cordyceps*) segments. The numbers of nuclei in ascospores can differ, e.g. the Morchellaceae (Pezizales) the ascospores have many nuclei. Ornamentation of spores can serve as an important taxonomic character.

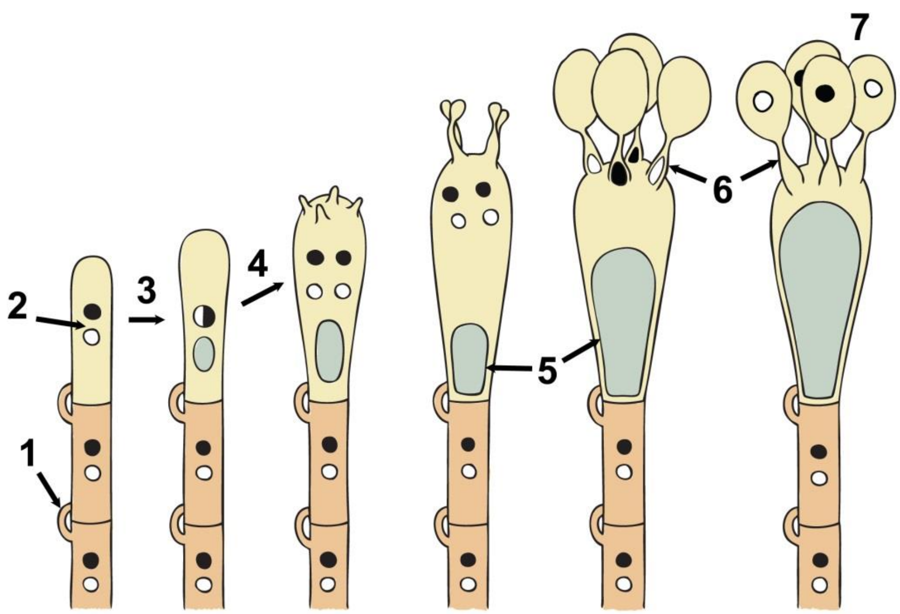
The asci of hyphal ascomycetes may develop in different types of ascomata.



Types of ascomata. A: gymnothecium; B: cleistothecium; C: apothecium; D: perithecium; E: pseudothecium.

The asci are surrounded by a loose hyphal net in gymnothecia. In cleistithecia the asci develop in a closed spherical ascoma with no definite operculum. A chasmothecium is a special type of cleistothecium wherein the asci form in a single basal fascicle; this ascoma is characteristic of the powdery mildews (Erysiphales). The perithecium is a flask-shaped ascoma in which the asci form in a palisade termed a hymenium. The perithecium has an aperture (ostiolum) where the spores can emerge. Perithecia can develop singly (e.g. *Sordaria*) or sometimes are embedded in a compact mycelial structure called a perithecial stroma (e.g. ergot, *Claviceps pupurea*). In a pseudothecium the asci develop in cavities of a compact hyphal aggregate (ascostroma). The apothecium is a cup-like open ascoma and the asci with sterile cells (parahpyses) among them develop in a layer (hymenium) on the open side. The apothecia could have stipes as do the mushroom-form morels or can form closed hypogeous ascomata characteristic of the truffles.

In the general life cycle of hyphal basidiomycetes the monokaryotic phase is relatively short, the hyphae developing from haploid basidiospores fuse (somatogamy) and produce dikarytic hyphae. This dikaryotic phase dominates the life cycle of the basidiomycetes. During the sexual reproductive phase the final cells of generative hyphae develop into a basidium. The nuclei fuse (karyogamy), and the diploid nucleus undergoes meiotic division. The four haploid nuclei migrate into the developing basidiospores across the spore-holding sterigma.



Development of a holobasidium and basidiospores. 1: clamp; 2: nuclei; 3 karyogamy; 4: meiosis; 5: vacuole; 6: sterigma; 7: basidiospore.

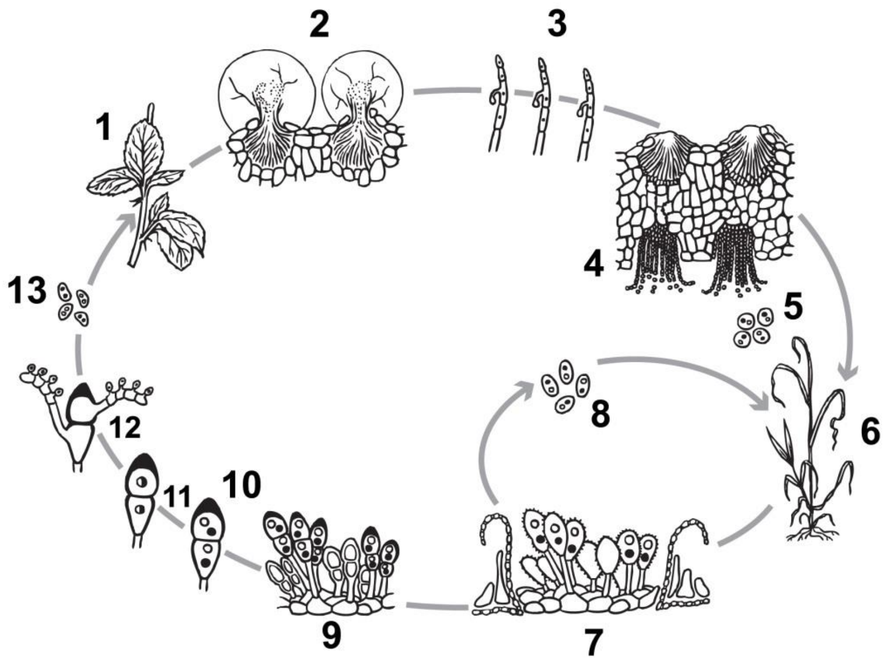
In chiastobasidia the second division of the meiosis is parallel with the axis of the basidium, in stichobasidia this division is perpendicular with the axis. A probasidium is where karyogamy happens, and a metabasidium is the place of the meiosis. In some species where a postmeiotic mitosis happens, the faith of the four additional nuclei is characteristic of the species.

Basidia may be grouped by several features. Holobasidia are not divided by walls, whereas fragmobasidia are segmented. When a fungus has heterobasidia, its basidiospores can produce secondary spores, while the basidiospores of fungi with homobasidia germinate with hyphae.

Basidia generally produce four exogenous basidiospores, but some species with less (e.g. two: *Agaricus bisporus*) or more (e.g. up to nine: *Phallus*) spores per basidium. The size, shape, and ornamentation of the basidiospores can be characteristic of the taxa, as are the number of nuclei in the spores or the dispersal type (active vs. passive) of the basidiospores.

The dikaryotic hyphae of hyphal Agaricomycotina produce sporocarps (basidiocarps or basidiomata) where basidia and basidiospores develop. To expand the surface for spore production the trama employ variable anatomies (gills, pores, etc.). Basidiomata have two main types according to the spore producing tissue. In the hymenial type the basidia develop in a layer (hymenium). Mushrooms with cap (pileus) and stem (stipe) generally produce the basidia in a hymenium. The basidioma can develop with its hymenium exposed throughout its development (gymnocarpic). In hemiangiocarpic basidiomycetes the young basidioma is completely covered by a sheath (universal veil) which breaks during development of the basidioma, and its remnants form a cup (volva) at the base of the stem and often leave fragments on the cap surface. Another veil covers the hymenium (partial veil) which also breaks, the remaining parts form web-like structures or flaps at the margin of the cap and a ring (annulus) on the stem. In other taxa basidia can form not only in a hymenium but in a tissue mass called the gleba, that is enclosed by an outer skin or peridium. Many gastroid fungi (e.g. puffballs) have such basidiomata which can open with pores (angiocarp basidioma) or the peridium breaks (cleistocarpic basidioma).

Complexity life cycles in fungi

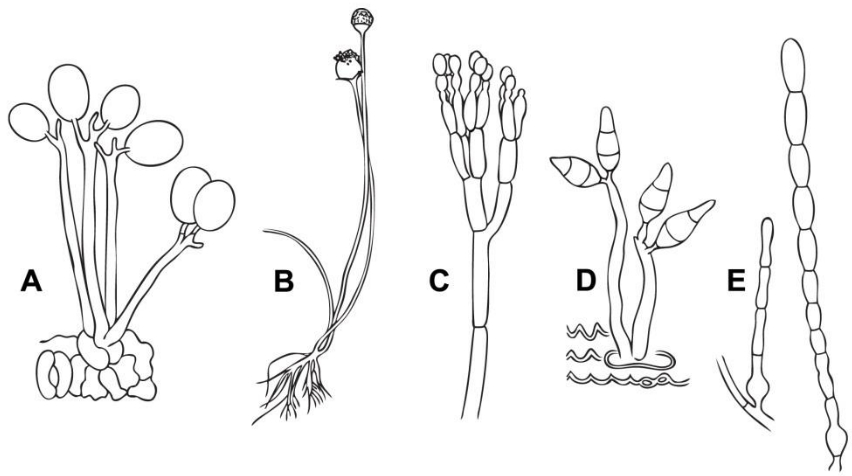


Life cycle of the stem rust (*Puccinia graminis*). 1: Berberis; 2: spermogonium (pycnium), with nectar, monokaryotic hyphae and spermatia (pycniospores); 3: plasmogamy, fusion of spermatia and flexuous hyphae; 4: aecium; 5: aeciospores; 6: gramineous host; 7: uredinium; 8: urediniospores; 9: telium; 10: teliospores; 11: karyogamy; 12: meiosis, basidium and basidiospore formation; 13: basidiospores.

It has two hosts to complete its life cycle: such rusts are called heteroecious (autoecious rusts complete their life cycle on one host). The stem rust is macrocyclic, as its life cycle contains all the five possible spore forms. Rusts form haustoria in both monokariotic and dikaryotic phase (M- and D-haustorium, respectively) during their life cycle.

Asexual reproduction of fungi

A great diversity of structures and forms aid asexual reproduction of fungi. The most important probably are the asexual mitospores that can develop in closed sporangia, or the internal or terminal parts of hyphae that develop into resting spores (chlamydospores). Conidia are asexual non-motile spores produced exogenously. Conidia play fundamental roles in dispersal of many fungi and can even be the exclusive dispersal structures of anamorphic fungi.



Asexual reproductive structures of some fungi. A: Sporangiophores with zoosporangia of Plasmopara (Oomycota). B: Sporangiophores with a opened and closed sporagia of Rhizopus (Zygomycota). C: Conidiophore and conidia of Penicillium (Ascomycota). D: Conidiophore and multicellular conidia of Magnaporthe (Ascomycota). E: Juvenile and mature conidiophore of Blumeria (Ascomycota).

The development of conidia (conidiogenesis) has two main types. During blastic conidiogenesis the conidium initial enlarges, and emerges from a hyphal tip. In thallic conidiogenesis a septum delimits the conidium initial from the end segment of the hypha. Several sub-types of both versions occur according to e.g. the manner of delimitation and mode of septum/cell wall development.

Asexual reproduction in the main fungal groups

The asexual dispersing structures of the oomycetes are either flagellate motile zoospores (e.g. in water molds) or sporangia in which those zoospores develop. The dispersing zoosporangia can either release the zoospores or germinate and develop coenocytic hyphae upon arrival on an appropriate surface. Some species undergo both processes depending, for example, on the temperature of the environment.

In chtyrids the mitotic zoospores represent the asexual reproductive phase. The arbuscular mycorrhizal fungi (Glomeromycota) have no sexual life cycle, they produce asexual chlamydospores generally in the soil but in some species chlamydospores can develop in colonized roots as well. Hyphal fragments and colonized root segments can also serve as propagules of Glomeromycota.

The zygomycetes develop sporangia in which mitospores are produced endogenously. There is an interesting tendency within the group: the number of the meiospores within a sporangium decreases and the number of sporangia on one sporangiophore increases. In some species the sporangia can disperse as well, these structures resembling conidiophores and conidia.

Asexual reproduction of ascomycetes is very diverse from both structural and functional points of view. The most important and general is production of conidia, but chlamydospores are also frequently produced. The diverse conidia and conidiophores sometimes develop in asexual sporocarps with different characteristics (e.g. aecervulus, pycnidium, sporodochium).

Asexual reproduction, especially asexual spore production is less important in Basidiomycota than in Ascomycota. However, the various spore types excluding basidiospores of rust and smut fungi could be considered as asexual spores which have great importance in the effective spread of those pathogens.

References of this lecture:

1- Introduction to fungi, by John Webster, 2010.
2- Medical Mycology by Rippon, J.W. (3rd. edition), 1988