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On the ontogeny of the fungus spore

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Abstract

Fungus spores can be borne endogenously in sporangia, gametangia or asci, or exogenously on basidia, conidiophores or sporogenic cells. Exogenous spores can be produced by sprouting (blastospores), by fission (arthrospores) or by an intermediate manner (sprouting followed by fission). This has to be considered especially in the classification of the imperfect fungi.

The most typical feature of the fungi is undoubtedly the mycelium, consisting of hyphae or filaments. These can be coenocytic or septate, hyaline or dark, simple or united into strands. Besides the vegetative mycelium the fruit bodies often are composed of hyphae or hyphal elements. In Basidiomycetes especially, several types of hyphae can be distinguished. Therefore the hyphae can be an important character for the identification of a fungus. In the yeasts they are, however, mostly absent.

Likewise, the spores are a typical feature of the fungi. These reproductive structures serve for multiplication, dispersal and survival. Their morphological character and especially their manner of development represent the most important feature for the identification of a fungus. Some fungi cannot be identified in pure culture because they lose their sporulating capacity.

The following types of spores are distinguishable. Fungus spores can be motile (planospores, swarm cells, zoospores) or non-motile (aplanospores). Planospores move in water by means of flagella. Fungi with planospores are mostly water moulds or occur under humid conditions as soil saprophytes or plant parasites. Planospores are known especially in Myxomycetes, Chytridiomycetes and Oomycetes, but do not occur in the Mycota (Eu-Mycota).

Aplanospores for dispersal are dependent on air currents, streaming water or animals, especially insects. Many spores are violently discharged or show other adaptations for dispersal (Ingold, 1953).

In the ontogeny of spores two main types can be distinguished: spores can be borne endogenously in cells or exogenously either on or from cells.

Endogenous spores mostly are borne in specialized cells, the sporangia; zoospores are borne in zoosporangia and sex cells (gametes) in gametangia. Sporangia (many-spored) and sporangiola (one- or few-spored) are typical of the Mucorales. The asci of the ascomycetes are specialized sporangia, in which, after meiosis, a constant number of aplanospores is usually produced, for instance 8 or 4. In typical ascomycetes the asci arise on dicaryotic hyphae in fruiting bodies called ascomata.

Endogenous spores can also be formed in hyphal cells or in sporogenic yeasts in sprout cells. In hyphal cells these spores are often arranged in a row. In sprout cells the number of endospores is limited to one or a few. Often such endospores have a thick wall and function as resting spores. Spores may also be formed endogenously in the meristematic zone of a specialized sporogenous cell in basipetal succession and then freed through an opening (e.g. phialospores, and arthrospores).

Exogenous spores can be produced by sprouting or by the formation of a cross wall followed by fission. Sprouting cells are called blastospores, fission cells are arthrospores (or aleuriospores).

There are intermediates between blastospores with a small base and arthrospores with a cross wall without any constriction between the mother and daughter cell. A spore may arise as a blown-out end of a cell by budding with a broad base and moderate constriction, and the final separation of two cells takes place by the formation of a cross wall. Such a spore may be considered as a blastospore with a broad base or as an arthrospore with a constriction.

Blastospores with a narrow and with a broad base and arthrospores are known in yeasts (Lodder and Kreger-van Rij, 1952). Species of the genus *Saccharomyces* form blastospores with a small base. In this genus the sporulation is multipolar all over the surface. In *Schizosaccharomyces* the multiplication takes place by fission. Blastospores with a broad base followed by the formation of a septum are typical in genera such as *Nadsonia* or *Saccharomycodes*. In this case the formation of daughter cells takes place only at the ends of the mother cells (bipolar) and can repeat itself by a meristematic growth of the apical region. A number of daughter cells can be produced in basipetal succession as blown-out ends or by proliferation through the scars of previous daughter cells. In some cases a collarette-like sheath may surround the scar.

Blastospores of different kinds can be distinguished in the Deuteromycetes (Fungi Imperfecti). Blastospores with a narrow base may be borne simultaneously all over the surface of a sporogenous cell. Or the spores are borne in succession direct on the hypha or on short, denticulate outgrowths. The conidiophore may form successive new growing points to one side of the previous conidium. The conidiophore, therefore, either increases in length or becomes apically thickened and covered with denticles. Blastospores with a narrow base may be separated from the sporogenous cell by a total constriction of the small lumen of the canal between sporogenous cell and conidium fills up with cell-wall substances.

Blastospores with a broader base also may be borne acropetally on conidiophores which increase by growing sympodially at one side, becoming geniculate (Radulasporae, Sympodulosporae).

Blastospores with a narrow or broad base can produce a new blastospore at the apex, thus forming acropetal chains of conidia, which may be simple or branched. In chains of blastospores the points of attachment are usually broad allowing the transport of nutrients. In fully grown chains thickened cross walls with or without disjunctors often develop between the conidia (compare *Cladosporium* or *Monilia*).The conidia in this type are mostly comparable with bipolar multiplication in some yeasts.

Blastospores with a narrow or a broad base can also be borne in basipetal succession on a specialized sporogenous cell. Such a cell develops one or more open ends

from which the conidia arise. If the opening is narrow and the conidia have a small, rounded base, the sporogenous cell is called a phialide and the conidia are phialospores. The phialide may be attenuated towards the opening in the tip, which may or may not possess a collarette (e.g. *Phialophora*). If the meristematic zone is broad, conidia develop by successive proliferation through the scars of previous conidia. In such cases the sporogenous cell may elongate and become annellate, and is called an annellophore. Blastospores with a broad base may also be borne on a sporogenous cell with an apical collarette-like sheath. In this case the sporogenous cell does not elongate (compare the conidial states of *Monascus* or *Eremascus*).

Porospores are blastospores borne singly through pores of thick-walled conidiophores. Porospores are mostly dark and thick-walled and may occur in acropetal chains. There are intermediate forms to genera such as *Cladosporium* with chains of blastospores with thickened scars of attachment.

Basidiospores are borne in the same manner as blastospores with mostly a narrow base. They arise after meiosis on spicula-like processes (pedicels) of a specialized cell, the basidium. The pedicels are called sterigmata; they mostly develop in a constant number of 4 (rarely 2 or 8), depending on the number of haploid daughter nuclei. Basidiospores are mostly asymmetrical, have a hilum (a lateral mark at the point of attachment), and are forcibly discharged when mature (ballistospores). A similar mechanism of forced discharge occurs in *Sporobolomyces*, *Tilletiopsis* and other imperfect, mostly yeast-like fungi where the ballistospores arise on vegetative cells or on hyphae. Spores borne on sterigmata always develop singly and never in succession.

Arthrospores develop by a simultaneous or basipetal septation (fragmentation) of sporogenous hyphae or conidiophores and are arranged in simple or branched chains. Such spores may also arise endogenously by the formation of cylindrical spores within sporogenous hyphae. They become free by histolysis or breaking up of the outer wall of the sporogenous hyphae. Such spores occasionally were described as ascospores in *Endomyces* (*Geotrichum*) and related genera. In *Thielaviopsis* and related genera cylindrical conidia arise endogenously in basipetal succession by fragmentation of the protoplasm in a meristematic zone and are liberated in chains through an apical opening.

Aleuriospores or chlamydospores are usually thick-walled; they arise as a terminal, lateral or intercalary swelling of a conidiophore or a hypha and are separated from the mother cell by one or two septa. Aleuriospores mostly are persistent and function as resting spores. In other cases aleuriospores may arise as a terminal swelling of a tapering conidiophore. They are freed easily by the formation of a separating cell or a disjunctor. Blastospores with a broad base and borne in basipetal succession are often characterized as aleuriospores.

In the imperfect fungi, especially in the Moniliales, Hughes (1953), Tubaki (1958), Subramanian (1962) and Barron (1968) distinguished eight or more sections by the manner in which conidia are formed and by the structure of the conidia-bearing apparatus. This classification is preferable to the classification given by Saccardo (1886) and based on conidium morphology. The classifications given by the four authors mentioned above differ in some respects. The preferable arrangement seems

to be that given by Barron, because he distinguishes clearly between aleuriospores and blastospores with a broad base (called annellosporae). But in general, the distinction between blastospores with a narrow and blastospores with a broad base, is only applied in yeast taxonomy. Therefore in the taxonomy of Moniliales closely related genera such as e.g. *Spilocaea* and *Fusicladium* are usually classified in different sections although both genera have blastospores with a broad base.

So much for the mechanisms of spore formation. The spores themselves can be divided into Xerosporae and Gloiosporae. Xerosporae are formed in dry masses and then are often arranged in rows or chains or represent dusty masses (Wakefield and Bisby, 1941; Mason, 1937), which are dispersed by air currents. Gloiosporae form wet, slimy or viscous droplets or masses and are dispersed by water, especially by rain, or by insects. In one and the same species, the spores can be wet or dry and taxonomically this character is mostly of no value.

Spores can be non-septate (amerosporae) or septate. In the latter case we distinguish between didymosporae (2-celled), phragmosporae (with 2 or more transverse septa), dictyosporae (with transverse and longitudinal septa), scolecosporae (filiform or vermiform), staurosporae (radiate or stellate), and helicosporae (coiled). Spores can be colourless, (Hyalosporae) or pigmented mostly brown or blackish (Phaeosporae). These characters were used by Saccardo (1886) in his arrangement of Hyphomycetes and other fungi. But in one and the same species, spores can be 1-celled or septate, hyaline or coloured. Therefore the system of Saccardo is not even of practical use; colour and cell number of spores is considered by modern taxonomists as being of minor value. Nevertheless these characters and the shape and size of the spores have to be used frequently in distinguishing genera or species.

Samenvatting

Sporevorming bij schimmels

Schimmelsporen kunnen zowel endogeen als exogeen ontstaan. Cellen met een endogene sporevorming heten sporangia. Wanneer aan de sporevorming een reductiedeling vooraf gaat, worden de sporogene cellen asci genoemd. Exogene sporevorming geschiedt door afgrenzing door middel van een celwand (arthrosporen en aleuriosporen) of door knopvorming of wel spruiting (blastosporen).

Hiertussen komen overgangen voor: na een knopvorming kan het knopgedeelte zich van de moedercel afgrenzen door een dwarswand. Er wordt voorgesteld bij de indeling van de imperfecte fungi met dergelijke tussenvormen rekening te houden, zoals dit bij de indeling van de gisten geschiedt. Basidiosporen zijn blastosporen die na een reductiedeling op een gespecialiseerde moedercel ontstaan.

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