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George N. Bistis
Drew University

David D. Perkins
Stanford University

Nick D. Read
University of Edinburgh

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Abstract

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Different cell types in *Neurospora crassa*

George N. Bistis[1], David D. Perkins[2], and Nick D. Read[3]
[1]Department of Biology, Drew University, Madison, NJ 07940, [2]Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020, [3]Department of Cell and Molecular Biology, University of Edinburgh, Rutherford Building, Edinburgh EH8 9QU, U.K.

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Neurospora possesses more cell types than are commonly recognized. We have been able to identify 28 morphologically distinct types. Having the cell types clearly defined will be important for genome annotation, describing new mutant phenotypes, and determining sites of gene expression.

Neurospora is a morphologically complex multicellular organism with many more cell types than the unicellular yeast Saccharomyces. Most workers are familiar with mycelia, macroconidia, perithecia, asci, and ascospores, but the diversity of cell types produced by Neurospora may not be fully appreciated. Now that the products of specific genes can be localized using GFP and other fluorescent proteins, attention will be focused increasingly on particular cell types that differ in morphology, physiology, or developmental origin. Distinguishing different cell types is also important for genome annotation.

For convenience, we need to use the terms 'cell' and 'cell type' rather loosely to cover both cellular elements such as hyphae and discrete cells such as spores (see discussion by Read, 1994). The basic undifferentiated, totipotent cellular element is the compartmentalized vegetative hypha at the colony periphery (the leader hypha). Certain other cell types are comprised of differentiated hyphae (e.g., fusion hyphae, ascogonia, trichogynes, ascogenous hyphae, asci, paraphyses, and periphyses). At the other extreme are highly differentiated nonhyphal cells such as ascospores, microconidia, and the different wall cells of protoperithecia and perithecia.

Twenty-eight morphologically distinct cell types are listed and described below. Designation of protoperithecia and microconidia as vegetative or sexual is arbitrary. Additional types or subtypes will no doubt be revealed.

Vegetative phase

Leader (leading) hypha. This is a wide, fast-growing hypha located at the colony periphery. It consists of an apical, tip-growing hyphal compartment interconnected with subapical compartments separated by perforated septa that provide continuity by allowing the passage of nuclei, other organelles, and cytoplasm. The leader hyphae undergo subapical branching and their growth contributes to the increase in colony diameter (Robertson 1965).

Trunk hypha. This is located in the colony interior. It is wide and composed of hyphal compartments that typically become highly vacuolate. These hyphal compartments are typically shorter than those of leader hyphae because of the greater frequency of septa. The septal pores of trunk hyphae are frequently occluded.

Fusion hypha. This is typically a narrow, dichotomously branching hypha that arises from a trunk hypha. It exhibits positive tropisms, homing towards other fusion or trunk hyphae and anastomosing with them (Hickey *et al.*, 2002).

Aerial hyphae. In contrast to the hyphae described above which grow in or on the surface of solid or liquid media, aerial hyphae grow away from the medium surface into the air. This is believed to be a result of forming hydrophobic hydrophobin proteins on their surfaces (Sietsma and Wessels, 1994).

Macroconidiophore. The specialized hypha that gives rise to macroconidia (Springer and Yanofsky, 1989).

Macroconidium (blastoconidium). Large, multinucleate (typically 3-6 nuclei) asexual spore that grows and develops by repeated budding of the apical cell of the conidiophore (Springer and Yanofsky, 1989). Important as a dispersal agent and as a male fertilizing agent.

Macroconidium (arthroconidium). Large asexual, multinucleate (typically 3-6 nuclei) spore that arises by fragmentation of the conidiophore (Springer and Yanofsky, 1989). Important as a dispersal agent and as a male fertilizing agent.

Macroconidial germ tube. Specialized hypha that emerges from the macroconidium and subsequently undergoes branching and differentiates into the vegetative hyphae of the young colony.

Macroconidial (conidial) anastomosis tube. Specialized hypha that emerges from the macroconidium but which is narrower than the germ tube. It grows only a short distance and exhibits positive tropisms to other conidial anastomosis tubes with which it fuses (M.G. Roca and Read, unpubl.).

Microconidiophore. The specialized hypha that gives rise to microconidia (Maheshwari, 1999).

Microconidium. Small, uninucleate spore that primarily functions as a male fertilizing agent (Maheshwari, 1999).

Microconidial germ tube. Specialized hypha that emerges from a microconidium but exhibits only limited growth (Maheshwari, 1999).

Ascospore germ tube. Specialized hypha that emerges from an ascospore (usually one at each end) and subsequently undergoes branching and differentiates into the vegetative hyphae of the young colony.

Sexual phase

Ascogonium. A wide, coiled septate hypha that arises as a specialized branch of a trunk hypha (Read, 1983). It acts as the 'female organ' during fertilization.

Enveloping (or ascogonial investing) hyphae. Slender and highly branched hyphae that arise from the ascogonium or surrounding vegetative hyphae, and which envelope and interweave around the ascogonium (Read, 1983). The fused enveloping hyphae develop into the different cells of the protoperithecial wall (Read, 1994).

Trichogyne. Specialized narrow and often branched hypha that emerges from hyphal compartments of the ascogonium. It exhibits a positive tropism toward cells of opposite mating type, with which it fuses and obtains fertilizing nuclei (Bistis, 1981).

Ascogenous hyphae. Specialized hyphae that arise from the ascogonium and contain nuclei of both mating types. These hyphae generate asci from specialized cells within their croziers (Read and Beckett, 1995; Raju, 1980, 1992).

Terminal (apical) crozier cell. Specialized apical compartment of the hook-shaped crozier. This cell, which is haploid and uninucleate, grows around toward the basal crozier cell with which it fuses to recover the dikaryotic state (Read and Beckett, 1996; Raju, 1980, 1992).

Basal (stalk) crozier cell. Specialized third compartment of a crozier. This cell, which is haploid and uninucleate, fuses with the terminal crozier cell to recover the dikaryotic state (Beckett and Read, 1996; Raju, 1980, 1992).

Penultimate crozier cell (ascus mother cell). Second compartment of a crozier. This cell is initially dikaryotic and haploid. It then becomes diploid after karyogamy has occurred, and develops into the ascus (Read and Beckett, 1996; Raju, 1980, 1992).

Ascus. The specialized unbranched nonseptate hypha within which eight ascospores develop. Its nucleus is initially diploid but subsequently undergoes meiosis and an extra mitotic division to produce eight haploid nuclei. Each nucleus becomes enclosed within an ascospore wall (Read and Beckett, 1996; Raju, 1980, 1992).

Ascospore. A thick-walled, pigmented spore with characteristic longitudinal ribs on its surface. Formed in the ascus following meiosis. Initially uninucleate but later multinucleate. Haploid, with nuclei derived from one of the products of meiosis (Raju, 1980, 1992).

Paraphyses. Specialized multinucleate and branched hyphae possessing thin walls and interspersed between asci within the perithecium. They arise from centrum pseudoparenchyma cells and from in between asci (Read and Beckett, 1985).

Centrum pseudoparenchymal cells. Pseudoparenchymal cells derived from the fusion of the innermost layer of enveloping hyphae. These thin-walled cells are initially very swollen in the protoperithecium but subsequently become flattened and form the innermost layer of the two layered perithecial wall (Read and Beckett, 1986; Read, 1994).

Outer protoperithecial and perithecial wall cells (not neck). Thick-walled, pseudoparenchymatous cells with that are derived from the fusion of the outer layer of enveloping hyphae (Read and Beckett, 1985; Read, 1994).

Fringe hyphae (hair cells). Slender, sometimes branched, hyphae that extend outward from protoperithecial and perithecial wall cells (Read, 1983). Typically shorter than trichogynes

Periphyses. Specialized short, slender and branched hyphae which line the neck canal. They possess multiple, multinucleate hyphal compartments, and their tips bend towards the centre of the neck canal. They differentiate into the pseudoparenchymatous neck wall cells around of rim of the ostiolar pore (Read and Beckett, 1985).

Wall cell of perithecial neck. Pseudoparenchymatous cells which, being derived from periphyses, are distinct from wall cells of the lower bulbous region of the perithecium (Read and Beckett, 1985).

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