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NEWS AND VIEWS

Cryptomycota: the missing link

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Fungi have been well studied for 150 years and it was thought that there was a good understanding of the major evolutionary groups, but new findings by UK researchers from the University of Exeter have radically changed this perception. From a local pond near the Exeter University, UK, they discovered a diverse and deep evolutionary branch of fungi named Cryptomycota (Greek: crypto, hidden; mycota, fungi) that has now doubled our knowledge of fungal diversity. The surprising unique feature of this branch was revealed by co-staining with cell wall markers and demonstrated that Cryptomycota differ from all previously known fungi by lacking a chitin cell wall (Jones et al., 2011).

Since our current understanding of fungal evolutionary diversity is based upon species amenable to growth in culture, and these typically yeast or filamentous forms are bound by a rigid cell wall, evolution of this body plan is thought critical for the success of the fungi, enabling them to adapt to heterogeneous habitats and live by osmotrophy.

Chitin, the same substance that makes the exoskeleton of arthropods, is the main component of the fungal cell wall. In plants and among protists and algae, the cell wall is made of cellulose whereas in bacteria, the cell wall is made of peptidoglycans. The chitin polymers of the fungal cell wall are also linked to other components including β-1,3 glucan microfibrils with chitosan polymers made of glucosamine, with a surface of antigenic glycoproteins, agglutinans and adhesion compounds playing a major role in tensile strength and structural integrity (Bowman and Free, 2006). The fungal cell walls enclose the cell plasma membrane, and the lower and middle glucans layers and outer glycoprotein layers are interwoven fibrillar polymers held together by covalent bonds. The wall matrix itself contains gel-like mannoproteins, polysaccharides and melanin pigments providing coloration and chitin polymer chains are present throughout the cell wall, helping to maintain its structural morphology. Fungal cell walls are distinctive in three ways. Their synthesis involves the combined action of an exceptionally large number of chitin synthases; they are continuously remodeled to permit active growth; and they surround fungal cells that are actively taking up nutrients (Bulawa, 1993; Munro and Gow, 2001; Ruiz-Herrera et al., 2002). Chitin synthases are widely distributed among opisthokonts[1] and the gene duplications that gave rise to the oldest of the fungal chitin synthases are more ancient than the divergences of the fungi themselves which may explain the complexity and distinctive characteristics of the fungal cell wall.

Cryptomycota were first detected as DNA sequences detected by van-Hannen et al. (1999) and showed only a distant match with any of the known sequences at the time. Relatives of the group, named after one of the clones, LKM11, were discovered in many environmental DNA surveys of freshwater aquatic ecosystems as well as terrestrial and marine systems. These observations suggested that LKM11, like fungi in Chytridiomycota (chytrids), reproduce with motile spores, but because no member had ever been isolated, the group remained an enigma (James and Berbee, 2011).

The first breakthrough on the placement of the LKM11 clade was the demonstration of a robust phylogenetic relationship to the aquatic genus Rozella (Lara et al., 2010). Rozella is an internal parasite, primarily of water molds (Held, 1981), that diverged to form the primary (basal-most) branch on the fungal tree retaining ancestral protistan characteristics (Lara et al., 2010). Their life cycle comprises a uniflagellate motile stage that allows them to disperse in search of a new host, and a trophic wall-less intracellular stage, which develops inside a host cell (Held, 1981). At this point, the parasite is amoeboid and phagocytoses the organelles of the host (Powell, 1984); no filamentous growth (formation of hyphae/rhizoid) has been observed in this genus. Subsequently, the parasite eventually induces the host to create a cell wall that will surround the parasite's future sporangium; the para-

[1] Greek: opísthios = "rear, posterior"; kontós = "pole." i.e. "flagellum" or "Fungi/Metazoa group" is a broad group of eukaryotes, including both the animal and fungus kingdoms, together with the eukaryotic microorganisms.

site never builds its own cell wall. Flagellated cells are produced within these walled sporangia (Held, 1980). Jones et al. (2011) opened the door to a broader view of the environmental clade by adapting state-of-the-art cytological and nucleic acid probing techniques designed by Not et al. (2002) to directly observe cryptomycota cells. Tyramide signal amplification coupled with group-specific fluorescence in situ hybridization (TSA-FISH) reveals that the cryptomycota cells appeared ovoid shape and 3–5 micrometers across, capable of forming a microtubule-based flagellum, which they use to swim. Cryptomycota was coined for the group, to highlight its cryptic nature and its characters, which like Lara et al. (2010) interpreted, as intermediate between fungi and ancestral protists. The wide phylogenetic distribution of chitin synthases together with evidence of a wall in Rozella's young spores suggests that cryptomycota, or their recent ancestors, have or had a chitinous wall at some stage in their life history. Because cryptomycota are currently uncultured, we rely on environmental observations alone to understand their biology; it is therefore likely that several aspects of their life cycle have not yet been observed, and key cellular apparatuses may remain undetected, such as germ tubes, filter-feeding structures, rhizoids, hyphae, sporangia and cell division characteristics. What cryptomycota have taught us is that while chitin alone cannot define fungi, the presence of division 2 chitin synthases, and especially chitin synthases with a myosin domain, along with transport of chitosomes along the cytoskeleton, may be unifying characters for most of Kingdom Fungi. The diversity of the cryptomycota shows they have been evolutionarily successful.

"Whatever job they do, they've probably been doing it for almost a billion years, so it's likely to be useful." —Meredith D. M. Jones, Natural History Museum, London.

Now that these 'living fossils' have been discovered, researchers are hard at work picking apart their importance in natural ecosystems, how they feed, reproduce and grow while lacking what was thought to be a crucial part of anatomy.

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