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Short Communication

How many fungi make sclerotia?

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ABSTRACT

Most fungi produce some type of durable microscopic structure such as a spore that is important for dispersal and/or survival under adverse conditions, but many species also produce dense aggregations of tissue called sclerotia. These structures help fungi to survive challenging conditions such as freezing, desiccation, microbial attack, or the absence of a host. During studies of hypogeous fungi we encountered morphologically distinct sclerotia in nature that were not linked with a known fungus. These observations suggested that many unrelated fungi with diverse trophic modes may form sclerotia, but that these structures have been overlooked. To identify the phylogenetic affiliations and trophic modes of sclerotium-forming fungi, we conducted a literature review and sequenced DNA from fresh sclerotium collections. We found that sclerotium-forming fungi are ecologically diverse and phylogenetically dispersed among 85 genera in 20 orders of Dikarya, suggesting that the ability to form sclerotia probably evolved ≥14 different times in fungi.

Fungi are among the most diverse lineages of eukaryotes with an estimated 5.1 million species (Blackwell, 2011). They are the principle saprotrophs in most terrestrial biomes and play important ecological and economic roles as plant pathogens and mutualists. Fungi are found in all terrestrial ecosystems and they use a variety of strategies to colonize appropriate substrata and survive unfavorable conditions (Blackwell, 2011). They have significant impacts on the biology of plants because they are the most economically significant plant pathogens, serve as mycorrhizal and endophytic symbionts, and act as key players in nutrient cycles (Schumann, 1991; Rodriguez et al., 2009; Hobbie and Hogberg, 2012). Two fungal phyla, Basidiomycota and Ascomycota, comprise the subkingdom Dikarya, a diverse group with ca. 100,000 described species (James et al., 2006). Most Dikarya share key features such as a hyphal thallus, non-flagellated cells, and the production of spores (Stajich et al., 2009). However, because of their cryptic lifestyles within environments such as plants and soil, the ecology and evolutionary history of many fungi remains poorly understood.

Almost all fungi produce some type of durable, quiescent microscopic structure such as a spore that is important for dispersal and/or survival under adverse conditions (Stajich et al., 2009). However, some fungi also produce dense aggregations of fungal tissue called sclerotia (Willetts, 1971). These persistent structures help fungi to survive challenging conditions such as freezing temperatures, desiccation, microbial attack, or the long-term absence of a host (Townsend and Willetts, 1954; Coley-Smith and Cooke, 1971). Sclerotia are highly variable in their morphology (Fig 1). Some have a hard,

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Fig 1 – Morphologically variable sclerotia found in soil, leaf litter, and decayed wood in natural forest habitats of North and South America: (A) *Ceriporia* sp. (MES 332; Polyporales) from decayed wood on the forest floor in Pigsah National Forest, North Carolina, USA; (B) *Entoloma* sp. (MES 347; Agaricales) from soil in a tropical rainforest dominated by leguminous ectomycorrhizal trees, Guyana; (C) *Cheilymenia* sp. (MES 313; Pezizales) from soil in mixed woods near Cherryfield, Maine, USA; (D) unknown species of Amylocorticiales (MCA 3949) from soil and leaf litter in a tropical rainforest in Guyana; (E) *Boletus* sp. (MES 260; Boletales) from soil and leaf litter in angiosperm-dominated forest in Lexington, Massachusetts, USA. Identities of illustrated sclerotia were determined based on ribosomal DNA sequence comparisons with GenBank. Scale bars = approximately 10 mm.

melanized rind enclosing compact, undifferentiated hyphae while others lack a rind (Willetts, 1971). Some species make round, determinate sclerotia but others have indeterminate forms where the shape and size are influenced by resources and environmental conditions (Chet and Henis, 1975). Some sclerotia are produced inside of host tissues; *Claviceps purpurea* produces sclerotia in grass florets after it has destroyed the plant cells (Douhan et al., 2008) and *Ophiocordyceps sinensis* colonizes caterpillars and transforms their tissues into a sclerotium (Xing and Guo, 2008). In contrast, some fungi make sclerotia that are spatially separated from hosts (e.g. *Phymatotrichopsis omnivora* forms sclerotia deep in soil – Lyda, 1984). Sclerotia also range in size from "microsclerotia" <1 mm across, as in the plant pathogen *Macrophominia phaseolina* (Short and Wyllie, 1978), to the massive sclerotia of *Polyporus mylittae* that reach over 40 cm in diameter (Macfarlane et al., 1978). Sclerotia putatively serve a resource-storage and survival role in all sclerotium-forming fungi. However, some fungi such as *Sclerotinia sclerotiorum* produce sexual fruiting structures directly on sclerotia (Bolton et al., 2006) whereas others such as *Pteromyces flavus* (=*Aspergillus flavus*) produce fruiting bodies within sclerotia (Horn et al., 2009). Still others, such as *Boletus rubropunctus*, produce fruit bodies and sclerotia at different times or in different places (Smith and Pfister, 2009).

Although sclerotia have been documented in several fungal lineages, sclerotium formation is primarily recognized as a key life history trait in several necrotrophic plant pathogens (e.g. *Sclerotium rolfsii*, *Rhizoctonia solani*, *M. phaseolina*, *P. omnivora*, *S. sclerotiorum*). Collectively, these devastating host generalist pathogens are responsible for hundreds of millions of dollars in global crop losses annually (Aycock, 1966; Parmeter, 1971; Purdy, 1979; Mulrean et al., 1984). For example, *S. sclerotiorum* and *S. rolfsii* each attack >400 plant species, including major crops such as peanuts, potatoes, and soybeans, and can cause up to 100 % yield losses (Jenkins and Averre, 1986;