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Evidence of natural hybridization among homothallic members of the basidiomycete *Armillaria mellea sensu stricto*

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ABSTRACT

Populations of *Armillaria mellea* (Basidiomycota, Agaricales) across much of its range are heterothallic; homothallic populations occur only in Africa (*A. mellea* ssp. *africana*), China (China Biological Species CBS G), and Japan (*A. mellea* ssp. *nipponica*). Monosporous isolates of heterothallic *A. mellea* are haploid and their mating behaviour is consistent with the requirement of two different alleles at two mating-type loci (tetrapolar mating system) to create a diploid individual. In contrast, monosporous isolates of homothallic *A. mellea* are putatively diploid; they bypass the haploid phase by undergoing karyogamy in the basidium (a unique type of secondary homothallism/pseudohomothallism). In order to determine the genetic origin of this homothallism, we analyzed genetic variation of 47 heterothallic isolates from China, Europe, and North America, and 14 homothallic isolates from Africa, China, and Japan. Gene trees and mutational networks were constructed for partial mitochondrial gene ATP synthase subunit 6 (ATP6) and for the following nuclear genes: actin (ACTIN), elongation factor subunit 1-alpha (EFA), glyceraldehyde 3-phosphate dehydrogenase (GPD), and the RNA polymerase subunit II (RPB2). Homothallic isolates from Africa and Japan shared a common mitochondrial ATP6 haplotype with homothallic isolates from China, and are likely introductions. Homothallic isolates from China that shared a common mitochondrial haplotype with all European isolates did not share European nuclear haplotypes, as revealed by median-joining networks, but instead clustered with haplotypes from China or were intermediate between those of China and Europe. Such mitochondrial–nuclear discordance in homothallic isolates from China is indicative of hybridization between lineages originating from China and Europe.

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Introduction

Fungi exhibit a diverse range of life cycles associated with different reproductive modes, including homothallism (self-compatible gametes on the same thallus) and heterothallism (compatible gametes from different thalli). At the genome level, comparative studies between closely-related homothallic and heterothallic species show that chromosomal characteristics of the former (e.g., more frequent protein substitutions and chromosome repetitive elements) are consistent with the theory that suppressed recombination and small effective population sizes result in a disproportionately strong influence of genetic drift, relative to selection (Whittle et al. 2011). For example, the mating-type locus of most homothallic *Neurospora* species has a high proportion of stop codons or frameshift mutations, and such genomic degradation may be associated with the relatively unimportant role of the mating system in reproduction of a homothallic species (Wik et al. 2008).

In Basidiomycete study systems, with fewer genomic studies than Ascomycetes, we can only surmise that such chromosomal and protein differences exist between homothallic and heterothallic species. Nonetheless, there are some similar patterns between Ascomycetes and Basidiomycetes in homothallic versus heterothallic isolates, particularly with respect to reproductive isolation, and differences in virulence or host specificity. For example, the homothallic and heterothallic biotypes of the pathogen *Moniliophthora perniciosa* (Agaricales, Marasmiaceae; syn. *Crinipellis perniciosa*) are not inter-fertile, presumably because genetic barriers have evolved since the biotypes diverged (Griffith & Hedger 1994b). The homothallic C-biotype of *M. perniciosa* causes one of the most damaging diseases of *Theobroma cacao* (cocoa). In contrast, the heterothallic L-biotype colonizes an unrelated host, *Arrabidaea verrucosa* (liana), and is far less aggressive (Griffith & Hedger 1994a). Another relationship between reproductive mode and aggressiveness in Basidiomycetes that exhibit both heterothallic and homothallic life cycles (i.e., they are amphithallic) is also reported for the human pathogen *Cryptococcus gattii* (teleomorph *Filobasidiella bacillispora*; Tremellales, Tremellaceae), homothallic isolates of which were associated with an outbreak of cryptococcosis after introduction to western North America (Fraser et al. 2005). Therefore, the presence of both homothallic and heterothallic populations may correspond to differences in aggressiveness or potential host shifts, depending on the reproductive mode of a given isolate.

Armillaria (Agaricales, Physalacriaceae) is an interesting case study with respect to reproductive modes in the Fungal Kingdom. This is a Basidiomycete genus of economic significance, namely with respect to the species that cause Armillaria root disease of horticultural crops, timber trees, and ornamentals (Baumgartner et al. 2011). Of ecological significance is the fact that *Armillaria* species are white-rot fungi, which degrade lignin, hemicelluloses, and thus have an important role in carbon cycling. The only spore stage produced is the basidiospore; *Armillaria* does not have an asexual spore stage, but an individual genotype can spread from one infected tree to the root system of a neighbouring tree, by subterranean mycelial growth. Most species are heterothallic and

have a tetrapolar mating system (Ullrich & Anderson 1978), with a few exceptions. *Armillaria fuscipes* [formerly *Armillaria heimii* (Coetzee et al. 2005a)] has a bipolar mating system (Abomo-Ndongo et al. 1997). Another exception is *Armillaria mellea*, which has both homothallic and heterothallic populations. A comprehensive phylogeny of all *Armillaria* species known worldwide has not been published, and so it is difficult to test hypotheses on the evolution of reproductive modes and mating systems at the genus level. Therefore, we focus on *A. mellea* because it is a holarctic species with populations that are either homothallic or heterothallic (Baumgartner et al. 2011; Coetzee et al. 2011).

Populations of *A. mellea* in Europe and North America are heterothallic (Guillaumin et al. 1991), and are primarily outcrossing (Baumgartner et al. 2010b). Populations in Africa (Ethiopia, Kenya, Tanzania, and Sao Tome) and Japan are homothallic (Abomo-Ndongo et al. 1997; Ota et al. 1998), and are recognized as subspecies *A. mellea* ssp. *africana* (Kile et al. 1994) and *A. mellea* ssp. *nipponica* (Cha & Igarashi 1995), respectively. China is the only locale where both heterothallic and homothallic *A. mellea* are known to occur (Qin et al. 2007). The latter is recognized as the biological species CBS G. Homothallism in *A. mellea* appears to be a unique type of secondary homothallism and has, thus, been referred to as 'nonheterothallic' by other authors (Ota et al. 1998).

The ploidy of monosporous isolates and their mating behaviour varies between heterothallic and homothallic isolates. In heterothallic *A. mellea*, the diploid nucleus undergoes meiosis in the basidium, and then the four resulting haploid nuclei migrate to four basidiospores (Hintikka 1973). These progeny of heterothallic isolates are haploid, and mating between two haploid progeny (controlled by a tetrapolar mating system) is required for spore production (Ullrich & Anderson 1978). In homothallic *A. mellea*, basidiospore development most closely resembles some stages of secondary homothallic (syn. pseudohomothallic) Basidiomycetes, such as *Microbotryum* (Giraud 2004) and *Stereum* (Calderoni et al. 2003). In the basidium of homothallic *A. mellea*, the four haploid products of meiosis fuse into two pairs (intratetrad mating), and the two resulting diploid nuclei migrate to two of four basidiospores (Abomo-Ndongo et al. 1997; Ota et al. 1998). In the two occupied basidiospores, the diploid nuclei undergo post-meiotic mitosis and, because of occasional back-migration of one nucleus to the basidium, basidiospores are either uninucleate, binucleate, or anucleate. These progeny of homothallic isolates are diploid and are fertile. As such, spore production by a homothallic isolate, and subsequent spread of *Armillaria* root disease to distant hosts, does not require another isolate.

Phylogenetic analyses demonstrate that heterothallic populations of *A. mellea* have undergone genetic divergence as a byproduct of geographic isolation (Coetzee et al. 2000; Maphosa et al. 2006). Despite geographic limitations to intercontinental spore dispersal, the inadvertent transfer of infected plants and/or soil is a potential means of inter- as well as cross-continental migration of *A. mellea*. Introductions of heterothallic isolates to ornamental gardens of Africa were linked to European populations, based on the presence of shared nrDNA internal transcribed spacer region (ITS) and itergenic spacer (IGS)

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