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Review

Mucor: A Janus-faced fungal genus with human health impact and industrial applications

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ABSTRACT

The *Mucor* genus, a polyphyletic group pertaining to early diverging lineages of fungi, includes a high number of ubiquitous species. Some species have positive or negative impacts on human activities. Indeed, certain pathogenic *Mucor* species are a threat for animal and human health and identified more frequently as mycosis causative agents, especially in immunocompromised patients. On the contrary, a small number of *Mucor* species have been used for centuries in food manufacturing for cheese ripening or Asian fermented food production. Some species are also used as biotechnologically important microorganisms due to their high growth rates, dimorphism (for certain species) and their previously unsuspected potential for secondary metabolite production. Despite all these important roles played by *Mucor* spp., they have been less investigated than ascomycetous or basidiomycetous species and their taxonomy, metabolism and ecology are less documented when compared to their counterparts in the so-called higher fungi. Nevertheless, research focusing most often on the emblematic *Mucor circinelloides* species has led to increased knowledge on the biology of this genus, and overall on fungal biology. This is particularly documented for fungal dimorphism or light-induced gene regulation. The aim of this review is to give an overview of the current knowledge on *Mucor* morphology, taxonomy, ecology and genetics and of its importance regarding human health and industrial applications.

1. Introduction

Mucor is a fungal genus classified in the *Mucorales*, the most prominent order of zygospore-forming fungi that formerly constituted the *Zygomycota*, a phylum which is not currently accepted due to polyphyly. *Mucor* species, as well as other members of this now obsolete phylum, are early diverging fungi and basal in comparison to higher fungi (i.e. *Ascomycota* and *Basidiomycota* phyla). Members of this obsolete phylum constitute the most primitive terrestrial fungi (Krings *et al.*, 2013) with the oldest fossils originating from the Precambrian era, between 800 Ma to 1.2–1.4 Ga ago. According to Ainsworth

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(1965), the first microscopic observation of a *Mucor* specimen was done in 1665 by Robert Hooke. From this very first description until today, several hundreds of potential species have been reported. *Mucor* species, along with other members of the *Mucorales* order, are possibly the most studied species among the formerly classified "*Zygomycota*". However, the *Mucor* genus has received much less attention when compared to the emblematic *Ascomycota* and *Basidiomycota* genera. Still, there is growing interest for *Mucor* species due to some of their characteristic traits that have made them good models for genetic studies, but also for their importance as pathogens (including in humans), their contribution to fermented food production and their biotechnological abilities. This review aims to provide up-to-date information about *Mucor* and its impact on human health and activities.

2. A *Mucor* portrait

Systematics

Prior to 1969 and the description of the Fungi kingdom by Whittaker (1969), fungal organisms were classified in the Thallophyta subdivision within the Plant kingdom. Species producing cœnocytic hyphae were grouped in the Phycomycetes class that included fungi producing zygospores but also water molds forming oospores (Bessey, 1951; Bisby, 1945). After the Fungi kingdom was established, Phycomycetes were reclassified into Zygomycotina (for species without flagellated zoospores) and other series of new classes (Ainsworth *et al*., 1971). At the end of the twentieth century, fungi were classified into five phyla. The *Mucor* genus was placed within Zygomycota, a basal group when compared to the so- called higher fungi (Dikarya). With successive revisions of fungal systematics, the Zygomycota phylum has been considered as polyphyletic and subdivided into different phyla and subphyla defined on the basis of biological and molecular criteria (Hibbett *et al*., 2007; Humber, 2012; James *et al*., 2006; White *et al*., 2006). Today, based on 350 analysed whole genome sequences of early diverging fungal species, Spatafora *et al*. (2016) identified that zygomycete fungi actually correspond to two phyla: (i) Mucoromycota including Mucoromycotina, Mortierellomycotina and Glomeromycotina subphyla and (ii) Zoopagomycota including Zoopagomycotina, Kickxellomycotina and Entomophtoromycotina subphyla. The current classification for *Mucor* being Fungi, Mucoromycota, Mucoromycotina, Mucorales, Mucoraceae, *Mucor*. With a total of 58 currently accepted species (Walther *et al*., 2013), *Mucor* is the largest genus within the *Mucorales* order and the *Mucoraceae* family.

Molecular phylogenies based on multiple loci analyses, including the ribosomal desoxyribonucleic acid (rDNA) internal transcribed spacer (ITS) sequences and/or translation elongation factor EF-1α gene and/or actin gene sequences, concluded that *Mucor* cannot be considered as a monophyletic group (Álvarez *et al*., 2011; Budziszewska *et al*., 2010; O'Donnell *et al*., 2001; de Souza *et al*., 2012; Voigt and Wöstemeyer, 2001; Walther *et al*., 2013). In particular, the extensive study published by Walther *et al*. (2013), which included nearly 400 *Mucor* strains, placed *Mucor* species in different groups. Those groups were intermingled, within the 28S rDNA phylogeny proposed, with more than twenty genera such as *Chaetocladium*, *Helicostylum, Pilaira, Pirella, Thamnidium* or *Zygorhynchus* and even *Mycotypha* and *Choanoephora* that are not members of the *Mucoraceae* but belong to the Mycotyphaceae and Choanepheraceae, respectively. Noteworthy, the groups recently detected using molecular phylogenetics (Walther *et al*., 2013) are largely concordant with the species and species group delimitations yielded by the early extensive and detailed studies by Schipper (1967, 1973, 1976, 1978) and Schipper and van Wetenschappen (1975) based on morphological descriptions and mating tests. Those groups include *Mucor flavus*, *M. mucedo, M. hiemalis, M. racemosus, M. amphibiorum* and *M. recurvus*. Each one of these groups includes different species sharing some common morphological characters. However, some species delimited by Schipper (1967, 1976) (e.g. *M. circinelloides*, *M. hiemalis* and *M. flavus*) were not identified as monophyletic groups since their corresponding clades included other species that even belonged to other genera (Walther *et al*., 2013). Moreover, the latter authors identified several Molecular Operational Taxonomic Units (MOTUs) that may represent new *Mucor* species. Recently, *M. lanceolatus* was identified by a multilocus sequencing approach as a new species used for cheese ripening (Hermet *et al*., 2012). Hermet *et al*. (2012) also proposed *M. spinosus* and *M. brunneogriseus*, that are currently classified as two *M. plumbeus formae*, as two discrete species. Likewise, the different formae of *M. circinelloides*, i.e. formae *circinelloides, griseocyanus, lusitanicus* and *janssenii*, might correspond to discrete species (Álvarez *et al*., 2011). Multilocus phylogeny and the use of the gold standard of species criterion in fungi, the Genealogical Concordance – Phylogenetic Species Recognition criterion (GC-PSR) (Dettman *et al*., 2003; Giraud *et al*., 2008; Le Gac *et al*., 2007; Taylor *et al*., 2000) should be more broadly applied to detect hypothetical new species. Moreover, given the observed polyphylies both at the genus and family levels, these studies should rely on extensive samplings including representative strains from other genera such as *Backusella, Chaetocladium*, *Choanoephora, Helicostylum, Mycotypha, Pilaira, Pirella, Thamnidium* or *Zygorhynchus*. Such studies may lead to important taxonomic revisions within the *Mucorales* and yield to changes in the denomination of several species currently classified as non-*Mucor* species and to putative cryptic species and/or synonym identifications. Fig. 1 presents a current view of *Mucor* taxonomy and estimated phylogeny.

Since the *Mucor* genus has undergone, and will certainly still undergo, substantial changes, the literature reports a lot of erroneous species denominations. Among the most cited species, *Rhizomucor miehei* often appears as *Mucor miehei* and *Rhizomucor pusillus* has sometimes been named *Mucor pusillus*. These two species belong to the *Rhizomucor* genus that only comprises thermophilic species and does not include *Mucor endophyticus* anymore although it is often found in the literature as *Rhizomucor endophyticus*. Similarly, *Rhizopus arrhizus* var. *arrhizus* often appears as *Mucor rouxii* while it is definitely not included in the *Mucor* genus (see Hoffmann *et al*., 2013; Walther *et al*., 2013 for recent taxonomies).