Genomes and the Evolution of the Zygomycetes

Subjects: Mycology

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The first genome sequence of a zygomycete fungus was from a clinical strain of *Rhizopus delemar* that was isolated from a patient with mucormycosis—a highly destructive and lethal infection that is typically seen in immunocompromised hosts. Sequencing of the *R. delemar* genome was driven from the clinical perspective, but it also provided the first genome of a fungus outside of the *Dikarya.*

fungal evolution ecological relevance pathogens model organisms

1. Mucoromycota

Mucoromycota comprises many ubiquitous soil saprotrophs, among them critically important plant symbionts, including the arbuscular mycorrhizal fungi (*Glomeromycotina*) [1], *Endogonales* (*Mucoromycotina*) [2], “fine root endophytes” (*Mucoromycotina*) [3], and putative root endophytic species including *Mortierella* (*Mortierellomycotina*) [4], *Pygmaeomycetaceae* (*Mucoromycotina*) [5], and *Umbelopsis* (*Mucoromycotina*) [6]. On the other hand, many fungi within this group are also noted plant pathogens (e.g., *Rhizopus microsporus*, which causes rice seedling blight, and various *Choanephora*, *Gilbertella*, and *Mucor* species that cause post-harvest rots) as well as numerous species (*Actinomucor*, *Apophysomyces*, *Cokeromyces*, *Cunninghamella*, *Lichtheimia*, *Mucor*, *Rhizomucor*, *Rhizopus*, *Saksenea*, *Syncephalastrum*) that can cause the disease mucormycosis in humans and other animals [7].

Most zygomycete genomes are of species within *Mucoromycota*; as a result, much of what resesarchers know about genome evolution among early-diverging fungi comes from this phylum. Genome duplication appears to have played a significant role in their evolution, as first described for *Rhizopus delemar* and *Mucor circinelloides* [8][9]. Genome sequencing has also revealed a diversity of endobacteria that may be found as symbionts in the *Mucoromycota*, e.g., in *Rhizopus microsporus* and *Endogone pisiformis* (*Mucoromycotina*), *Linnemannia elongata* and *Mortierella alpina* (*Mortierellomycotina*), and *Rhizophagus irregularis* (*Glomeromycotina*) [10][11][12][13][14][15]. Many plant-associated fungal lineages contain endobacteria, but the potential role of these symbionts in the land colonization process remain to be characterized. “Foreign” DNA in the form of diverse mycoviruses has also been frequently detected during genome sequencing of zygomycetes [16][17]. Genomics enabled the systematic study of genome architecture [18][19][20], genetic manipulations [21], and intra-isolate genomic variations [22]. Genome-wide searches and comparisons have also detected evidence for transposon spread through genomes [23][24][25] and uniquely high 6-methyladenine DNA modifications in zygomycete fungi as compared to *Dikarya* [26]. Studies on metabolic patterns across the fungal kingdom, the search for the mating gene loci and protein families [27][28][29], and the phylogenies of certain taxonomic groups [30][31] have also been conducted using-whole genome sequencing data. Genome-based research has also provided insights into the trophic modes of zygomycete fungi, including the evolution of mycorrhizae [2][32] and commonalities in the pathogenicity of Mucoralean fungi [33][34].

2. Mucoromycotina

Genome sequencing of this subphylum has been the most comprehensive among all the basal fungal lineages although genomes are still unavailable for several genera, including species of *Siepmannia*, *Chlamydoabsidia*, and *Utharomyces*, as well as for two new root-associated species of *Pygmaeomyces* of the new genus and family *Pygmaeomycetaceae* [5]. Furthermore, the plant-associated order *Endogonales* remains highly undersampled despite recent advances [2][35]. Some of its “fine root endophytes” colonize early-diverging plants, and sometimes co-occur with AMF [36][37]. The average genome size in *Mucoromycotina* species ranges from 35 to 50 Mbp, with species of *Umbelopsis* at the low end of the spectrum (22–30 Mbp) and *Endogonales* such as *Jimgerdemannia* species at the higher end (240 Mbp). For some genera, several hundred genomes have already been sequenced. For example, there are >220 genomes available for species of *Rhizopus*, mostly of *R. arrhizus* (syn. *R. oryzae*) and its varieties and synonyms, and of *R. microsporus*, *R. delemar*, and *R. stolonifer*. *Rhizopus* is increasingly studied as a model organism thanks to its availability in culture collections and its important role in biotechnology and human health. Genomic information might be helpful for future studies of pathogenicity in *Rhizopus* species since infections by members of this genus are the leading cause of human mucormycosis [30][33]. Phylogenomic data suggest that species of *Rhizopus* are part of a well-resolved monophyletic group. However, this is in stark contrast to the situation among members of the genus *Mucor* (>150 genomes), which is incredibly diverse and is likely polyphyletic (**Figure 1**). The additional *Mucoromycotina* genomes consist mostly of saprotrophic species that are relevant to human health (species of *Lichtheimia* and *Cunninghamella*) and biotechnology (*Phycomyces blakesleeanus*) [38][39][40]. Genomes of *Endogonales* (as well as *Glomeromycotina*) contain effectors to facilitate plant–fungus interactions, which apparently aided in the terrestrialization of Earth by early land plants. Genome information helped to describe and clarify the phylogenetic placement of new lineages and species, such as *Bifiguratus* [41] and *Calcarisporiella* [42].

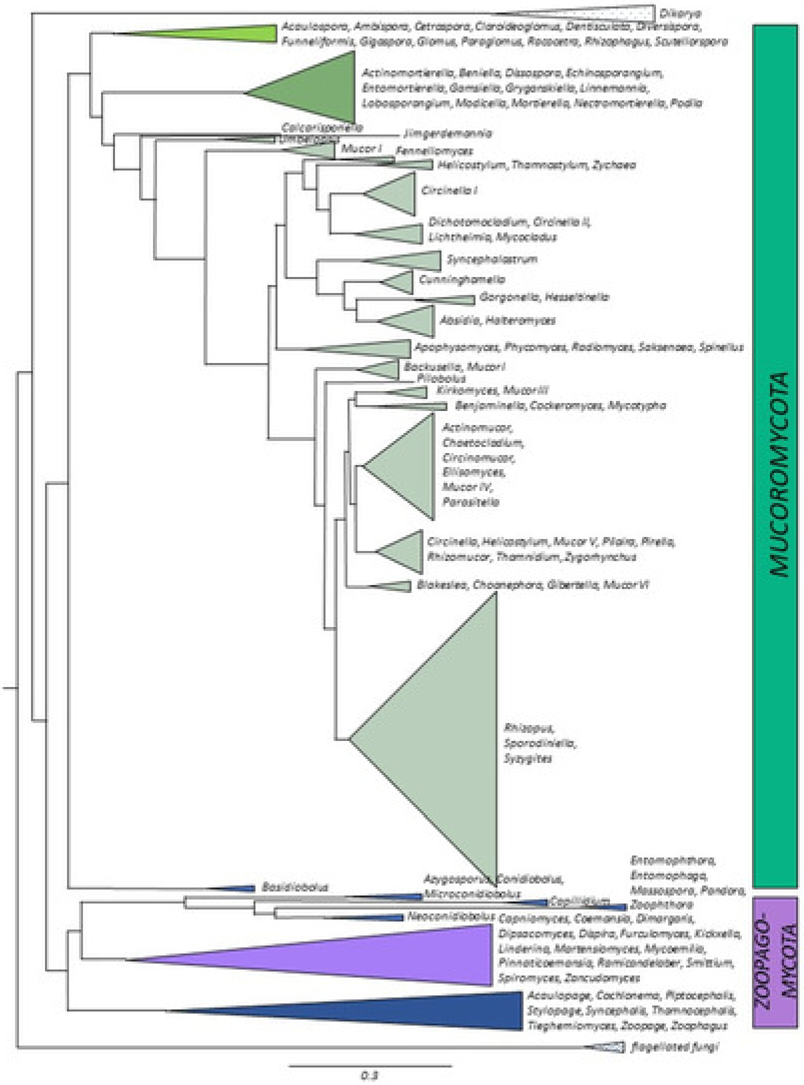

Figure 1. Distributions of the number of genomes sequenced imposed onto phylogenetic tree. Different shades of green and brown—*Mucoromycota*, purple and blue—*Zoopagomycota*.

3. Mortierellomycotina

This subphylum contains an estimated 170 species [43] and was recently circumscribed into 13 monophyletic genera using multi-locus and low-coverage genome sequencing [44]. Reference genome sequences of both low quality and high quality are now available for representatives for most genera, including *Actinomortierella*, *Benniella*, *Dissophora*, *Entomortierella*, *Gamsiella*, *Gryganskiella*, *Linnemannia*, *Lobosporangium*, *Lunasporangiospora*, *Mortierella*, *Necromortierella*, *Podila*, and the sporocarpic genus *Modicella* [44][45]. A high diversity of *Mortierellomycotina* species can be isolated from soil, but it appears that genera may differ in their ecological roles. For example, *Necromortierella* species appear to be necrotrophic, whereas *Actinomortierella* spp. are often associated with millipedes, and *Entomortierella* spp. are often associated with arthropods [46]. Many genera, such as *Linnemannia* and *Podila*, have been recovered as rhizosphere associates and endophytes of plant roots [47][48], and they appear to improve plant growth and impact flower and seed production [49]. Several species such as *Mortierella alpina* have been sequenced due to their use in industry and biotechnology for lipid production [50].

4. Glomeromycotina

Arbuscular mycorrhizal fungi (AMFs) are arguably the most common and oldest symbionts of terrestrial plants [1], credited with their role in the facilitation of plant transition to the terrestrial habitat [51]. AMFs supply their plant hosts with mineral nutrients translocated from the soil in return for plant-assimilated carbon [52]. Yet, there are not many genomic sequences of these organisms available due to historical impediments hampering sequencing projects, including multinucleate spores with different genotypes, obligate biotrophy of AMFs, and the initial uncertainty concerning their genome sizes, with conflicting size estimates in *Rhizophagus irregularis* ranging from 14.1 [53] to 154.8 Mb [54]. Once these obstacles were surmounted, genomic data confirmed that AMFs have unusually large genomes, ranging from 153 Mb in *R. irregularis* [55] to 773.1 Mb in *Gigaspora margarita* [56]. This size enhancement relative to other *Mucoromycota* is driven by lineage-specific expansions of gene families and massive proliferation of transposable elements [32][55][56]. Genomic data also revealed that AMFs display several other features that differentiate them not only from *Mucoromycota* but also from other fungi. For example, despite the lack of morphological evidence of sexual reproduction, the *R. irregularis* genome harbors a candidate mating-type locus with two genes encoding homeodomain-like transcription factors [57]. If these homeodomain-like genes indeed control sex, then regulation of the reproductive processes in AMFs would resemble mating in *Dikarya* rather than in *Mucoromycota*, which rely on HMG domain proteins for sex determination [58]. *Rhizophagus irregularis* differs also from other fungi in the organization of its rRNA operons. Instead of being tandemly arrayed as they are in other fungi, the rRNA operons in *Glomeromycotina* are dispersed individually across the genome [55]. This important discovery put an end to a long-lasting debate on whether intraindividual rRNA gene variation typical for AMFs is distributed among dissimilar nuclei [59] or contained in each nucleus [60], supporting the latter scenario. Lastly, genome-based inferences of metabolic capacity revealed that AMFs lack the gene encoding fatty acid synthase [61][62][63], which makes them obligately dependent on plant hosts for lipids [64][65][66][67]. As in other fastidious organisms, this information is important for devising cultivation strategies that complement fatty acid auxotrophy of AMF [68][69]. Even though accumulation of genomic data for AMF has lagged behind other *Mucoromycota*, the insights gathered so far have been critical for resolving several puzzles in the biology of these unique organisms. PacBio HiFi and Hi-C sequencing of all available AMF heterokaryons helped to discover the two sets of coexisting homologous chromosomes in one heterokaryon. Genes required for plant colonization were found in gene-sparse, repeat-reach compartments [70]. Another important question that remains to be addressed is which genomic features of AMFs contribute to superior yield outcomes in agronomic crop species, as AMFs do not universally benefit all plant hosts.

5. Zoopagomycota

In contrast to *Mucoromycota*, most species of *Zoopagomycota* are parasites or pathogens of animals and fungi. This includes the insect pathogenic group *Entomophthoromycotina* (some members of which exhibit behavioral control over their hosts) [71], the *Kickxellomycotina* which includes a mixture of ecologies (including commensalistic arthropods gut fungi) [72], and *Zoopagomycotina*, which are parasites of fungi (mainly in *Mucoromycota*) and microinvertebrates (e.g., amoebae, nematodes, rotifers) [73]. There are also opportunistic human pathogens in this phylum, including species of *Basidiobolus* and *Conidiobolus* [74]. Axenic culturing of some fungi in *Zoopagomycota* is possible [75][76] but extracting high-quality genomic DNA from many species remains difficult. Sometimes there is a need to extract the genomic material of the parasite together with the host (often another fungus or insect) and separate their genomes during assembly, which creates additional challenges. Small amounts of available DNA have necessitated the use of single-cell DNA extraction in some cases, especially in species with dramatically reduced vegetative mycelial structures. Much greater success has been achieved for putative saprotrophic fungi such as dung-inhabiting species of *Kickxellales*. Genomes and transcriptomes have been used primarily to resolve various evolutionary questions, including the monophyletic origin of *Zoopagales* [73], the evolution of ploidy from a diploid ancestral stage [77], and loss of a large number of pectinases and other plant cell-wall-degrading enzymes in *Zoopagomycota* [78]. Genome data were also successfully used to resolve evolutionary relationships within particular taxonomic groups, such as *Massospora* [46], to track other evolutionary events such as horizontal gene transfer events in gut fungi [79], and to reveal the genetic toolbox in insect symbionts [80]. These studies help researchers to understand the evolutionary trajectories of genome size, namely, a dramatic increase in genome size for the insect pathogens and insect endosymbionts as compared to the genome size in the saprobes and mycoparasites. Genome data have also helped to clarify fundamental differences among *Zoopagomycota* lineages in their production of secondary metabolites [81], as well as metabolic pathways in general [77]. Mating genetics in this phylum is still not well understood, and that is a question that remains to be addressed with genomic data.

6. Kickxellomycotina

This subphylum contains an interesting mix of mycoparasites (*Dimargaritales*), putative saprotrophs (*Kickxellales*), and obligate insect endobionts (*Asselariales*, *Barbatosporales*, *Harpellales*, and *Orphellales*). The *Dimargaritales* are similar to mycoparasites in the *Zoopagales* in that they form penetration hyphae (haustoria) and mostly attack similar host species in the *Mucoromycota*. In contrast to the *Zoopagales* mycoparasites, species of *Dimargaritales* appear to be rare in the environment and have mostly been isolated from dung rather than soil. Recent genomic analyses have also highlighted that members of the *Dimargaritales* that have larger genomes and more predicted secondary metabolite genes compared to their close relatives [72][81]. Furthermore, single-cell genome data have suggested that *Dimargaris cristalligena* may be nonhaploid and missing certain enzymes from metabolic pathways (e.g., thiamine biosynthesis and biotin metabolism) [77]. Identifying such genomic features of symbiotic species can provide targets for further experimental tests to understand the molecular interactions between hosts and parasites.

On the other hand, the *Kickxellales* is the only group of *Zoopagomycota* containing mostly saprotrophic species, and many appear to be rare in the environment, having only been reported in the literature one or a few times. An exception is the genus *Coemansia*, the species of which are commonly isolated from soil and dung samples [82][83]. Genome sequencing efforts have demonstrated that *Kickxellales* species have small genomes (less than 40 MB) and variability in their predicted secondary metabolite genes, with *Coemansia* and *Linderina*, along with more polyketide synthases than other *Kickxellales* and *D. cristalligena* having more nonribosomal peptide synthetases than other *Kickxellales* [81]. A preliminary rDNA phylogeny showed polyphyly among *Kickxellales* [83], and a large-scale sequencing project that utilized low-coverage genome data from >100 isolates to test these hypotheses, as well as explore the diversity of *Coemansia* species, resolved many of these relationships [72].

The gut fungi (*Trichomycetes*) include arthropod symbionts for which several draft genomes have been available since 2016 [84]. These fungi are distinct from the saprotrophic and coprophilic relatives (i.e., *Kickxellales*) and belong to four distinct phylogenetic lineages—*Asellariales*, Barbatosporales, *Harpellales*, and *Orphellales* [85]. *Asellariales* are associated with isopods and springtails (*Collembola*) [86]. Species within the three genera (*Asellaria*, *Baltomyces*, and *Orchesellaria*) have been recovered from both terrestrial and aquatic hosts [86], but their phylogenetic relationships remain unclear, as sequence data have only been obtained from *Asellaria* [85], and no cultures are available for this group.

Harpellales species are usually found in lower *Diptera* insect larvae and have coevolved with their hosts for over 200 million years [87]. Species of *Orphellales* are stonefly nymph symbionts with unusual morphological characters (i.e., asexual and sexual spore shapes, and thalli protruding beyond the anus of insect hosts) [88], which cluster together with other *Trichomycetes* and the *Spiromycetales* for a sister clade to *Kickxellales* [72]. *Smittium* is a well-studied genus within *Harpellales* with approximately 100 described species [89]. However, there are only nine whole-genome sequences available for these insect gut-dwelling fungi, and all were made from culturable *Harpellales* species, with the best assembly—*Capniomyces stellatus*—having 72 scaffolds [84]. *Barbatosporales* are monotypic, and the single species (*Barbatospora ambicaudata*) has only been recorded from black fly larvae collected in the Great Smoky Mountains National Park in Tennessee, obtained in axenic culture [90].

Although researchers only have a handful of *Harpellales* genomes, they have already expanded the knowledge and understanding of these enigmatic microbial fungi in multiple ways. For example, a mosquito-like polyubiquitin gene has been identified in *Zancudomyces culisetae* (*Harpellales*), which was presumably acquired via a horizontal gene transfer event [79]. Comparative genomics revealed a fungus–insect symbiotic core gene toolbox (FISCoG) that is shared among the insect-associated fungi (e.g., *Harpellales*, *Basidiobolus*, and *Conidiobolus*) and higher-ranked *Hypocreales* (*Ascomycota*). However, the insect pathogens (*Hypocreales* and *Entomophthoromycotina* members) tend to have genomes enriched in genes that are useful for pathogenic processes such as the platelet-activating factor acetyl-hydrolase coding genes, whereas the gut commensals have genomes enriched in cell adhesion genes for a successful gut-dwelling lifestyle [80]. In addition, *Harpellales* genomes also facilitated a kingdom-wide study to confirm the production of selenoproteins in early-diverging fungal lineages [91]. As a major group of early-diverging fungi, representing seven of the nine fungal species that utilize selenoproteins, *Harpellales* may take the advantages of selenocysteine over cysteine for specific oxidoreductase functions.

Unfortunately, no efforts have been successful in obtaining genome information of the *Asellariales*, *Barbatosporales*, and *Orphellales*, which colonize different host types. However, multigene analyses incorporating low-coverage genome data (along with data from *Asellariales* and *Orphellales*) suggested an alternate hypothesis for the evolution of fungal–insect associations. Contrary to previous topologies that suggested multiple events [85], the larger dataset showed a possible single origin of gut fungi [72]. Further evolutionary evidence may be identified with the help of their genome sequences to understand how these gut-dwelling microbial fungi interact with various aquatic insect hosts and evaluate the origins of the symbiosis.

7. Zoopagomycotina

Zoopagomycotina species are fascinating, partially due to their cryptic ecological niches and ability to parasitize various hosts such as amoebae, nematodes, rotifers, and other fungi. It is still challenging to culture most of the *Zoopagomycotina* isolates. Thus, it is not surprising to see that *Zoopagomycotina* has the lowest number of available genomes, the qualities of which are not comparable to other lineages, especially the well-sequenced *Mucoromycotina*. Recently developed single-cell genomic techniques have provided an alternative, culture-independent method to obtain their genomic information [77]. On the basis of single-cell or multiple-cell libraries, the completeness of genome assemblies can be as high as 89.6% (*Piptocephalis tieghemiana* RSA 1565) [73]. The assembled *Zoopagomycotina* genomes indicate that this clade of fungi is characterized by small genome size, but the numbers of protein-coding genes are not necessarily low. Some of the genomes can encode close to 10,000 genes (e.g., *Zoophagus insidians*, a predator of rotifers and nematodes. It seems likely that these completely microscopic fungi are capable of more complicated and yet-to-be-identified interactions with their animal and/or fungal hosts, but more work will be needed to explore these interactions.

Two additional *Zoopagales* have remarkably small genomes: a species of *Acaulopage* (11 Mbp) and a species of *Zoopage* (14 Mbp). No genomes have yet been published for the following genera: *Amoebophilus*, *Aplectosoma*, *Bdellospora*, *Brachymyces*, *Cystopage*, *Endocochlus*, *Euryancale*, *Helicocephalum*, *Reticulocephalis*, and *Sigmoideomyces*.

8. Entomophthoromycotina

This lineage remains the most insufficiently sequenced fungal group at the subphylum level. Despite many genomes from the genus *Conidiobolus*, there are only a few other species (all from the key family *Entomophthoraceae*) for which genomes are available. The genus *Conidiobolus* is a polyphyletic assemblage of multiple lineages. This group of *Conidiobolus*-like fungi was recently phylogenetically divided into three new families, using a combined multi-gene and phylogenomic approach, revealing that the ballistic conidia arose prior to their transition to a parasitic lifestyle [31][92]. Difficulties with culturing and, therefore, obtaining enough high-molecular-weight genomic DNA represent a reason why some species only have transcriptomes available. Alternatively, in some cases, the fungal pathogen is sequenced together with its host, and then the reads are separated bioinformatically. Aside from the polyphyletic genus *Conidiobolus* and entomophthoroid-like *Basidiobolus*, genome or transcriptome data are available only for a few species of *Entomophaga*, *Entomophthora*, *Massospora*, *Pandora*, and *Zoophthora*. No genomes yet exist for *Ancylistes*, *Apterivorax*, *Batkoa*, *Erynia*, *Eryniopsis*, *Furia*, *Macrobiotophthora*, *Meristacrum*, *Neozygites*, *Orthomyces*, *Tabanomyces*, *Thaxterosporium*, *Schizangiella*, and *Strongwellsea*. The largest genomes recovered are over 2000 Mbp in *Massospora* and 650 Mbp in *Zoophthora*, with possibly similar genome sizes in *Entomophthora* and *Entomophaga*. A phylogenetic analysis recently demonstrated that *Basidiobolus*, a genus of amphibian gut-dwelling fungi, does not belong to *Entomophthorales*, where it was traditionally placed, mostly on the basis of its production of forcibly discharged conidia that are morphologically similar to those in other entomophthoralean fungi [93]. The genus was difficult to place with rDNA data [94], but was inferred either as a separate clade sister to the *Mucoromycota* [95] or as the earliest diverging lineage within *Zoopagomycota* [80], on the basis of phylogenomic data. The ballistic spore dispersal mechanism, which differs structurally from that found in the *Entomophthorales*, is likely an example of convergent evolution among fungi that appear to be similar but are distantly related. In addition to being evolutionarily enigmatic, the genomes of *B. meristosporus* and *B. heterosporus* are larger than most other basal fungi and contained a much higher proportion of secondary metabolite-encoding genes than other *Zoopagomycota* species that have been studied thus far. Furthermore, *Basidiobolus* genomes contain numerous genes that putatively originated from horizontal gene transfer events from bacteria [81].

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