

21st Century Guidebook to Fungi, Second Edition of the online version, by David Moore, Geoffrey D. Robson and Anthony P. J. Trinci

[URL: http://www.davidmoore.org.uk/21st_Century_Guidebook_to_Fungi_PLATINUM/]

Chapter 8: Sexual reproduction: the basis of diversity and taxonomy

Contents

Chapter 8: Sexual reproduction: the basis of diversity and taxonomy

8.1 The process of sexual reproduction

8.2 Mating in budding yeast

8.3 Mating type switching in budding yeast

8.4 Mating types of *Neurospora*

8.5 Mating types in Basidiomycota

8.6 Biology of mating type factors

8.7 Chapter 8 References and further reading

Chapter 8: Sexual reproduction: the basis of diversity and taxonomy

Sexual reproduction is a nearly universal feature of eukaryotes and its core features are conserved throughout each group within the eukaryotic tree of life. This is taken to imply that sexual reproduction evolved once only and was present in the Ekaryote Last Common Ancestor (ELCA; see [Fig. 2.11](#) and [Moore, 2013](#) [pp. 174 *et seq.*]). Studies of the fungal kingdom have revealed novel and unusual patterns of sexual reproduction, which we will discuss in this Chapter.

Fundamentally, sexual reproduction is the fusion of gametes (the differentiated sex cells) or their nuclei to form a diploid that can undergo meiosis. The overall summary ‘equation’ is:

$$\text{Plasmogamy} \rightarrow \text{Karyogamy} \rightarrow \text{Meiosis}$$

For most fungi, plasmogamy occurs when hyphal fusion (anastomosis) occurs, and is controlled by the incompatibility systems; growth of the resultant heterokaryon as an independent mycelium prolongs plasmogamy, in some cases indefinitely.

In this Chapter we describe the process of sexual reproduction in fungi. This includes description of mating and mating type switching in budding yeast, mating type factors of *Neurospora*, and the mating type factors of Basidiomycota. We finish with some thoughts about the biology of mating type factors.

8.1 The process of sexual reproduction

The core features of sexual reproduction are conserved throughout the eukaryotic tree of life, and are therefore thought to have evolved once and to have been a character of the Ekaryote Last Common Ancestor (ELCA; see [Fig. 2.11](#) and [Moore, 2013](#) [pp. 174 *et seq.*]). It follows that sexual reproduction in present day organisms displays a mixture of features that are ancient and ancestral, together with others that have arisen during the subsequent evolution of that organism. For example,

sexual reproduction in the great majority of eukaryotes alive today involves two contrasting sexes or mating types, so this *may* be considered an ancestral feature. Yet amongst the fungi there are species that indulge in unisexual reproduction, where a single mating type can undergo self-fertile (or homothallic) reproduction on its own, either with itself or with other members of the population of the same mating type.

Unisexual reproduction occurs in several different lineages and may therefore be interpreted as a **derived feature** that has arisen independently in those different lineages. On the other hand, the incredible variety of different types of sex (or mating type) determining mechanisms that can be observed in animals, plants, protists, and fungi of the present day *may* suggest that specification of sex (or mating type) is not the ancestral feature but is a derived trait; and if this is the case, then the original form of sexual reproduction *may* have been unisexual, onto which sexes were imposed independently in the different lineages as they evolved.

We do not know what ELCA was like, but the current belief is that our last common ancestor was a unicellular, aquatic, motile creature with one or two flagella (and really rather like the sort of thing that eventually became a chytrid fungus; see Moore, 2013). Of course, as the eukaryote's last common ancestor, ELCA certainly had a membrane-bound nucleus, mitochondria, secretory apparatus, the ability to regulate gene expression with interfering RNAs (RNAi), and the ability to reproduce both asexually and sexually (mitosis and meiosis are conserved processes throughout eukaryotes). So, when we settle down with a glass of wine and think about sex ... first evolving, we think it must have occurred first in an aqueous environment (probably in some primitive biofilm) and that it involved swimming cells, and changes in ploidy that needed a reduction division (meiosis) to correct.

Although cell-cell and nucleus-nucleus fusion are prominent in sexual reproduction today, there may have been a time in the distant past when internal replication cycles (endoreplication) caused the change in ploidy that needed to be corrected by a reduction division (meiosis) during ancestral attempts at sexual reproduction. This view predicts that cell-cell fusion may be ancient, but perhaps not as ancient as other features of sexual reproduction (Heitman, 2015).

It is the potential benefits of sexual reproduction that have given it the competitive edge and caused sex to be so pervasive in the eukaryotic tree of life. These benefits include that it provides a means to purge the genome of (vegetatively accumulated) deleterious mutations; and a means to shuffle the genome by means of chromosome reassortment and recombination to give rise to different gene arrangements among the meiotic progeny. Sex may also enable organisms to compete with pathogens, some of which may be internal, like transposons (see discussion and references in (Heitman, 2015).

The potential benefits of sex must be balanced against the costs of sexual reproduction: that only 50% of a parental genome is transmitted to any given progeny, the time and energy required to locate mates, and the reassortment of already adapted gene arrangements.

The core features of sexual reproduction are conserved in organisms as diverse as the model budding yeast *Saccharomyces cerevisiae* and humans, despite at least a billion years of evolution separating us from our last shared ancestor. These conserved features include:

- Regular changes in ploidy, from haploid to diploid to haploid, or from diploid to haploid to diploid.
- The process of meiosis that enables meiotic recombination and halves the ploidy of the genome.
- Cell-cell fusion (syngamy) between mating partners or their gametes.

The conservation of these core features of sexual reproduction across this enormous evolutionary time is what indicates the antiquity of the process (Billiard *et al.*, 2012; Heitman, 2015). Most fungi can undergo both asexual reproduction and sexual reproduction. The evolutionary persistence of

eukaryotes that rely on asexual reproduction alone is exceptional (see [Section 7.1](#)). Examples include rotifers, glomeromycotan fungi, some arthropods and some plants; but even these exceptional examples of asexuality are uncertain because molecular analyses show that genes required for the sexual cycle are maintained in their genomes, so it may simply be that their cryptic sexual stages have not yet been observed (Billiard *et al.*, 2012).

Eventually, for the majority of fungi of the present day, karyogamy and meiosis take place and the nuclear products of meiosis are packaged into sexual spores. In many fungi sexual spores have thickened walls; that is, they are resistant spores that are often dormant, and formed in relatively small numbers. In some cases the whole gametangium (the zygospores of zygomycetes would be a typical example [[CLICK HERE](#) for a reminder of the images]) develops into a resistant structure, in other cases the sexual spores (particularly ascospores) are resistant and have a period of obligate dormancy. However, in Basidiomycota, basidiospores are produced in large numbers and are dispersal spores, not dormant spores [[CLICK HERE](#) for a reminder of the appropriate section in Chapter 3].

As befits its use in traditional taxonomy there are numerous variations in sexual reproduction in fungi. The first of these variables is the presence or absence of incompatibility systems. For example, in the zygomycetes, *Mucor mucedo* is heterothallic (self-sterile), but its relative *Rhizopus sexualis* is homothallic (self-fertile).

There is then the matter of the morphology of the hyphal structures involved in the various stages and the manner in which the processes are carried out. For example, gametangia are morphologically alike in the true fungus (zygomycete) *Mucor mucedo*, but morphologically different in some of the Oomycota (kingdom Straminipila) like *Pythium*, which is an important pathogen causing damping-off of seedlings.

Similarly, the duration of the various stages of sexual reproduction may vary and some may be prolonged, for example **prolonged karyogamy** in diploid yeasts and, as indicated above, **prolonged plasmogamy** in the dikaryotic heterokaryon of Basidiomycota.

Hormones are probably involved in regulating sexual reproduction in most organisms, and fungi are no exception. Unfortunately, only a few of the active chemicals have been isolated from fungi; however, all of the major chemical classes of hormones identified in animals and plants are also known in fungi [[CLICK HERE](#) to view our **Resources Box** on pheromones in fungi]:

- **sterols** in the Oomycete *Achlya bisexualis*, female mycelium produces **antheridiol**, male produces **oogoniol** [[CLICK HERE](#) to see Section 3.10];
- the sesquiterpene hormone **sirenin** produced by female zoogametes of *Allomyces macrogynus* to attract male zoogametes [[CLICK HERE](#) to see Section 3.4];
- chemotropism to volatile precursors in the trisporic acid pathway that attracts heterothallic (self-sterile + and -) zygothores of *Mucor mucedo* to one another. On their own, neither strain can produce trisporic acid, but they ‘converse’, by exchanging a volatile precursor and collaborate in its biosynthesis (Lee & Heitman, 2014); [[CLICK HERE](#) to see our **Resources Box** on pheromones in fungi];
- **peptide pheromones** involved in yeast mating (see Section 8.2 below; [CLICK HERE](#) to see it now);
- **mating type pheromones** of filamentous Ascomycota and Basidiomycota that are part of a G-protein signalling pathway (see Section 8.5 below).

As in other eukaryotes, fungi have tightly regulated mechanisms that determine which haploid cells can fuse at syngamy; but fungi display a variety of life cycles and have additional possibilities for syngamy as compared to plants and animals. **Heterothallic** fungi require two compatible partners to produce sexual spores, whereas in **homothallic** fungi a single organism is capable of sexual reproduction. In fungi considered to be heterothallic, haploid selfing is prevented because they have