Why Study Schizophyllum?

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For its fascinating sex life, of course! The German mycologist Hans Kniep (1930) was the first to discover that the wood-rotting basidiomycete, *Schizophyllum commune*, recombines its genome regularly and propagates effectively by consorting with any one of many compatible mates through a system known as tetrapolar sexuality, a term describing the meiotic segregation of four different mating types

The process of mating, fertilization, fruiting, meiosis and spore formation is regulated by two kinds of genetic factors residing at the A and B mating-type loci, earlier called incompatibility factors A and B. Over the eight decades since Kniep's discovery, revelations about the genetic, biochemical and molecular underpinnings of this bizarre system have made an exciting story (see list of selected references, below). While other interesting aspects of Schizophyllum have been explored, notably the hydrophobins of Wessels and associates (reviewed in Wessels, 2000), a principal focus over the years has been on mating compatibility and sexual development. Although *Schizophyllum commune*'s main role in nature is to recycle carbon by breaking down cellulose and xylans in fallen wood (Clarke and Yaguchi, 1986; Bray and Clarke, 1995), it has been documented occasionally as a pathogen in fruit orchards (Latham, 1970; Oprea, *et al*, 1995) and also in immunologically compromised humans (Buzina *et al*, 2001).

Haig Papazian , a graduate student in John (Red) Raper's lab at the University of Chicago in the early 1950's was the first to extend Kniep's findings. Against Red Raper's better judgment, Haig persisted in studying the mating system of Schizophyllum for his doctoral thesis, (Raper was working on sex hormones in the water mold, Achlya at the time.) Haig's stubbornness paid off. He showed that the A incompatibility factor resides in two linked loci and that the B incompatibility factor, assorting independently, regulates a depressed phenotype, called "flat" that is commensurate with nuclear migration and fertilization (Papazian, 1950; 1962).

Haig eventually defected to yeast and Raper, acknowledging his faulty first judgment, took up the gauntlet. Thus began many successive decades of revelations about how Schizophyllum manages its copious sex life. Red Raper, marveling at the variety of sexual mechanisms extant among the fungi, claimed it was as if nature had used the fungi as a testing ground for all the different ways in which to accomplish sex. His fascination for Schizophyllum was fired by a strong curiosity to figure out how such an organism can have thousands of sexes and manage to keep them all straight.

After moving from the University of Chicago to Harvard in the mid fifties, Red led an effort to determine the number and distribution of mating types in this species by assembling a large collection of specimens from all over the world and analyzing each for mating-type specificity (Raper, Krongelb and Baxter, 1958). Recombination within the B factor showed that B, as well as A, consisted of two linked loci (Koltin, Raper and Simchen, 1967; Koltin and Raper, 1967; Parag and Koltin, 1971; Stamberg and Koltin, 1972). The loci of the A factor were designated A alpha, A beta, and the loci of the B factor were designated B alpha, B beta.

On the basis of their survey Raper and associates estimated that the world-wide population of *Schizophyllum commune* contains nine different versions of A alpha, 32 A betas and nine each of B alpha and B beta (Raper, J.R. 1966). Compatibility between any two mates requires a minimal difference between either A alpha or A beta AND either B alpha or B beta. Thus the alphas and betas of each factor function redundantly but are recombinable to generate non-parental mating types by the thousands. Every individual is haploid and self-sterile. Cross fertility among siblings is restricted to 25-30 percent but outbreeding is possible up to 98 percent. The B factor regulates nuclear migration to accomplish a process of reciprocal fertilization in which the nuclei of one mate migrates into and throughout the mycelieum of the other and vice versa. The A factor regulates establishment and maintenance of the dikaryon in which two compatible haploid nuclei of opposite mating type pair within each cell, divide conjugately and are maintained as a genetically complementing pair in every newly formed cell. The dikaryon can be propagated indefinitely; it is the only entity normally capable of forming fruiting bodies commonly known as mushrooms. (For reviews, see Raper, J.R. and Miles 1958; Raper, J.R. 1966; Raper, C.A. 1983.)

Studies since Red Raper's death in 1974 have revealed the genetic components and molecular products of the A and B factors (reviewed in Stankis, *et al*, 1990; Ullrich *et al*, 1991; Vaillancourt and Raper, C.A. 1996; Kothe, 1999). The cloning and characterization of these mating-type genes became possible through development of the methods of protoplast formation and regeneration (De Vries and Wessels, 1972) and DNA-mediated transformation (Specht *et al*, 1988). As Red had always believed, they turn out to be of fundamental interest.

Robert Ullrich, Charles Novotny, and associates showed that the A loci contain genes encoding homeodomain proteins, thought to be transcriptional regulators (Giasson *et al*, 1989; Specht *et al*, 1992, 1994; Magae *et al*, 1995), and Charles Specht, Erika Kothe, Marjatta Raudaskoski, Carlene Raper, Thomas Fowler, and associates showed that the B loci contain numerous genes encoding G protein binding pheromone receptors and lipopeptide pheromones (Specht, 1995; Wendland *et al*, 1995; Vaillancourt, *et al*, 1997; Fowler *et al*, 2001, 2004). The receptors belong to a class of molecules used for various sensory processes throughout the biological world. [Comparable studies by Lorna Casselton and associates in the related homobasidiomycete, *Coprinus cinereus* (for review, see Casselton and Olesnicky, 1998) and by Regina Kahmann and associates in the hemibasidiomycete, *Ustilago maydis* (Kahmann *et al* , 1995) also identified homeodomain proteins, pheromones and receptors as mating-type molecules with different arrangements of the encoding gene clusters.]

Current studies are aimed towards understanding Red Raper's original query. How does this mushroom fungus keep all its sexes straight? More specifically, how does a multitude of pheromones (an estimated one hundred or more) discriminate among some eighteen receptors to activate certain ones and not others? And, for the future, how does one homeodomain protein actively engage another to perform its job as transcriptional regulator and what are the regulated genes? Ultimately how do all these regulating molecules relate to one another in the grand scheme of things? Answers to such questions may extend beyond the fungi and contribute significantly to an understanding of comparable processes elsewhere in the biological world.
Red Raper's original collection and many of its derivatives representing all the predicted B mating-type variants and most of the A mating-type variants were deposited at the Fungal Genetics Stock Center in 2003 (Accession numbers 9098 through 9350). They include many auxotrophs, mutants that modify sexual development, and specific mutants of the mating-type genes themselves. These stocks are now available to the public from the FGSC for teaching and research. A list of 559 publications on *Schizophyllum commune* (a subset is given below) as well as selected reprints, are on file at FGSC. The preparation and transfer of this material was supported by the National Science Foundation as a supplement to a grant to Jack Kinsey, P.I. and director of the FGSC at the University of Kansas.

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