Why Study Schizophyllum?

Carlene A. Raper  
*University of Vermont*

Thomas J. Fowler  
*University of Vermont*

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**Recommended Citation**

Raper, C. A., and T.J. Fowler (2004) "Why Study Schizophyllum?," *Fungal Genetics Reports*: Vol. 51, Article 12. https://doi.org/10.4148/1941-4765.1142

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Abstract
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.

This special paper is available in Fungal Genetics Reports: https://newprairiepress.org/fgr/vol51/iss1/12
Why Study Schizophyllum?

Carlene A. Raper and Thomas J. Fowler, Department of Microbiology and Molecular Genetics, Stafford Hall, University of Vermont, Burlington VT, 05405

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 recombinnable 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 mycelium 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; Vailancourt, 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.

**SELECTED PUBLICATIONS ON Schizophyllum commune**

Asgeirsdottir, S. A., Schuren, F. H. J. & Wessels, J. G. H. (1994). Assignment of genes to pulse-field separated chromosomes of *Schizophyllum commune*. Mycological research 98, 689-693.

Asgeirsdottir, S. A., van Wetter, M. A. & Wessels, J. G. H. (1995). Differential expression of genes under control of the mating-type genes in the secondary mycelium of *Schizophyllum commune*. Microbiology 141, 1281-1288.

Bray, M. R. & Clarke, A. J. (1995). The structure and function relationship of *Schizophyllum commune* xylanase A. In Carbohydrate bioengineering : proceedings of an international conference, Elsinore, Denmark, 23-26 April, 1995, pp. 147-163. Amsterdam ; New York: Elsevier.

Buzina, W., Lang-Loidolt, D., Braun, H., Freudenschuss, K. & Stammberger, H. (2001). Development of Molecular Methods for Identification of *Schizophyllum commune* from Clinical Samples. Journal of clinical microbiology 39, 2391-2396.

Carmi, P., Holm, P. B., Koltin, Y., Rasmusson, S., Sage, J. & Zickler, D. (1978). The pachytene karyotype of Schizophyllum commune analyzed by three dimensional reconstruction of synaptonemal complexes. Carlsberg Res. Commun. 43, 117-132.

Casselton, L. A. & Olesnicky, N. S. (1998). Molecular genetics of mating recognition in basidiomycete fungi. Micro. Mol. Biol. Rev. 62, 55-70.

Clarke, A. J. & Yaguchi, M. (1986). Difference spectrophotometric study on the interaction of cellulase from *Schizophyllum commune* with substrate and inhibitors. Biochimica et biophysica acta 870, 401-407.

deVries, O. M. H. & Wessels, J. G. H. (1973). Release of Protoplasts from *Schizophyllum commune* by Combined Action of Purified Alpha-1,3-Glucanase and Chitinase Derived from Trichoderma Viride. J Gen Microbiol 76, 319-330.

deVries, O. M. H. & Wessels, J. G. H. (1975). Chemical Analysis of Cell Wall Regeneration and Reversion of Protoplasts from *Schizophyllum commune* [Fungus]. Arch Mikrobiol 102, 209-218.

deVries, O. M. H., Fekkes, M. P., Wosten, H. A. B. & Wessels, J. G. H. (1993). Insoluble hydrophobin complexes in the walls of *Schizophyllum commune* and other filamentous fungi. Arch Microbiol 159, 330-335.
deVries, O. M. H., Hoge, J. H. C. & Wessels, J. G. (1980). Translation of RNA from *Schizophyllum commune* in a wheat germ and rabbit reticulocyte cell-free system. Biochim Biophys Acta 607, 373-378.

deVries, O. M. H., Hoge, J. H. C. & Wessels, J. G. H. (1980). Regulation of the pattern of protein synthesis in *Schizophyllum commune* by the incompatibility genes. Developmental Biology 74, 22-36.

Dons, J. J. M. & Wessels, J. G. (1980). Sequence organization of the nuclear DNA of *Schizophyllum commune*. Biochim Biophys Acta 607, 385-396.

Dons, J. J. M., deVries, O. M. H. & Wessels, J. G. H. (1979). Characterization of the genome of the basidiomycete *Schizophyllum commune*. Biochim Biophys Acta 563, 100-112.

Dubovoy, C. (1976). A Class of Genes Affecting B Factor-Regulated Development in *Schizophyllum commune* [Fungi]. Genetics 82, 423-428.

Ellingboe, A. H. & Raper, J. R. (1962). Somatic recombination in *Schizophyllum commune*. Genetics 47, 85-98.

Fowler, T. J. & Mitton, M. F. (2000). Scooter, a new active transposon in *Schizophyllum commune*, has disrupted two genes regulating signal transduction. Genetics 156, 1585-1594.

Fowler, T. J., Mitton, M. F. and Raper, C. A. (1998). Gene mutations affecting specificity of pheromone/receptor mating interactions in *Schizophyllum commune*. In Proceedings of the Fourth Meeting on the Genetics and Cellular Biology of Basidiomycetes, pp. 130-134. Edited by L. J. L. D. V. Griensven & J. Visser. Nimegen, The Netherlands: Mushroom Experiment Station: Horst, The Netherlands.

Fowler, T. J., Mitton, M. F., Rees, E. I. & Raper, C. A. (2004). Crossing the boundary between the B-alpha and B-beta mating-type loci in *Schizophyllum commune*. Fungal Genetics and Biology 41, 89-101.

Fowler, T. J., Mitton, M. F., Vaillancourt, L. J. & Raper, C. A. (2001). Changes in mate recognition through alterations of pheromones and receptors in the multisexual mushroom fungus *Schizophyllum commune*. Genetics 158, 1491-1503.

Fowler, T. J., DeSimone, S. M., Mitton, M. F., Kurjan, J. and Raper, C. A. (1999). Multiple sex pheromones and receptors of a mushroom-producing fungus elicit mating in yeast. Mol. Biol. Cell 10, 2559-2572.

Froeliger, E. H., Munoz-Rivas, A. M., Specht, C. A., Ullrich, R. C. & Novotny, C. P. (1987). The isolation of specific genes from the basidiomycete *Schizophyllum commune*. Current genetics 12, 547-554.

Giasson, L., Specht, C. A., Milgrim, C., Novotny, C. P. & Ullrich, R. C. (1989). Cloning and comparison of A alpha mating-type alleles of the Basidiomycete *Schizophyllum commune*. Molecular and general genetics 218, 72-77.

Gola, S., Hegner, J. & Kothe, E. (2000). Chimeric pheromone receptors in the basidiomycete *Schizophyllum commune*. Fungal genetics and biology 30, 191-196.

Gola, S. & Kothe, E. (2003). The little difference: in vivo analysis of pheromone discrimination in *Schizophyllum commune*. Current Genetics 42, 276-283.

Guetttler, S., Jackson, E. N., Lucchesse, S. A., Hanaas, L., Green, A., Hittinger, C. T., Tian, Y., Lilly, W. W. & Gathman, A. C. (2003). ESTs from the basidiomycete *Schizophyllum commune* grown on nitrogen-replete and nitrogen-limited media. Fungal Genetics and Biology 39, 191-198.

Hoffman, R. M. & Raper, J. R. (1972). Lowered Respiratory Response to Adenosine Diphosphate of Mitochondria Isolated from a Mutant B Strain of *Schizophyllum commune*. J Bacteriol 110, 780-781.

Horton, J. S., Palmer, G. E. & Smith, W. J. (1999). Regulation of dikaryon-expressed genes by FRT1 in the basidiomycete *Schizophyllum commune*. Fungal genetics and biology 26, 33-47.
James, T. Y., Porter, D., Hamrick, J. L. & Vilgalys, R. (1999). Evidence for limited intercontinental gene flow in the cosmopolitan mushroom, *Schizophyllum commune*. Evolution 53, 1665-1677.

Jersild, R. A., S. Mishkin and D. J. Niederpruem (1967). Origin and ultrastructure of complex septa in *Schizophyllum commune* development. Archives of microbiology 57, 20-32.

Kahmann, R., Romeis, T., Bolker, M. & Kamper, J. (1995). Control of mating and development in *Ustilago maydis*. Curr. Opin. Genet. Dev. 5, 559-564.

Kawai, G., Ikeda, Y. & Tubaki, K. (1985). Fruiting of *Schizophyllum commune* induced by certain ceramides and cerebrosides from *Penicillium funiculosum*. Agricultural and biological chemistry 49, 2137-2146.

Kniep, H. (1930). Uber Selektionswirkungen in fortlaufenden Massenaussaaten von Schizophyllum. Z. Bot. 23, 510-536.

Koltin, Y. (1969). The structure of the incompatibility factors of *Schizophyllum commune*. Mol Gen Genet 103, 380-384.

Koltin, Y. & Flexer, A. S. (1969). Alteration of Nuclear Distribution in B-Mutant Strains of *Schizophyllum commune*. J Cell Sci 4, 739-749.

Koltin, Y. & Raper, J. R. (1967). The genetic structure of the incompatibility factor of *Schizophyllum commune*: three functionally distinct classes of B factors. Proceedings of the National Academy of Sciences of the United States of America 58, 1220-1226.

Koltin, Y., Raper, J. R. & Simchen, G. (1967). Genetic structure of the incompatibility factors of *Schizophyllum commune*: the B factor. Proceedings of the National Academy of Sciences of the United States of America 47, 55-63.

Kothe, E. (1999). Mating types and pheromone recognition in the homobasidiomycete *Schizophyllum commune*. Fungal genetics and biology 27, 146-152.

Kothe, E., Gola, S. & Wendland, J. (2003). Evolution of multispecific mating-type alleles for pheromone perception in the homobasidiomycete fungi. Current Genetics 42, 268-275.

Kuhn, J. (1972). Protein-subunit aggregation model for self-incompatibility in higher fungi: *Schizophyllum commune*. J. Theor. Biol. 35, 77-91.

Latham, A. J. (1970). Development of Apple Fruit Rot and Basidiocarp Formation by *Schizophyllum commune*. Phytopathology 60, 596-598.

Leonard, T. J., Dick, S. & Deng, R. (1989). A new genetic element affecting somatic mnd recombination in *Schizophyllum commune*. Experimental mycology 13, 231-238.

Lilly, W. W., Wallweber, G. J. & Higgins, S. M. (1991). Proteolysis and amino acid recycling during nitrogen deprivation in *Schizophyllum commune*. Current microbiology 23, 27-32.

Magae, Y., Novotny, C. & Ullrich, R. (1995). Interaction of the A&alpha; Y and Z Mating-Type Homeodomain Proteins of *Schizophyllum commune* Detected by the Two-Hybrid System. Biochemical and Biophysical Research Communications 211, 1071-1076.

Marchant, R. & Wessels, J. G. H. (1974). An Ultrastructural Study of Septal Dissolution in *Schizophyllum commune*. Arch Mikrobiol 96, 175-182.

Muller, W. H., van Aelst, A. C., van der Krift, T. P. & Boekhout, T. (1994). Scanning electron microscopy of the septal pore cap of the basidiomycete *Schizophyllum commune*. Canadian journal of microbiology 40, 879-883.

Munoz-Rivas, A., Specht, C. A., Drummond, B. J., Froeliger, E., Novotny, C. P. & Ullrich, R. C. (1986). Transformation of the basidiomycete, *Schizophyllum commune*. M G G : Molecular and general genetics 205, 103-106.
Nguyen, T. T., Schloemer, R. H. & Niederpruem, D. J. (1987). Control of basidiospore germination in *Schizophyllum commune*. Mycologia 79, 399-404.

Niederpruem, D. J. (1971). Kinetic Studies of Septum Synthesis, Erosion and Nuclear Migration in a Growing B-Mutant of *Schizophyllum commune*. Arch Mikrobiol 75, 189-196.

Niederpruem, D. J., Jersild, R. A. & Lane, P. L. (1971). Direct Microscopic Studies of Clamp Connection Formation in Growing Hyphae of *Schizophyllum commune*. II. The a-Mutant Homokaryon and Pseudo-Clamp Connections. Arch Mikrobiol 80, 19-31.

Novotny, C. P., Stankis, M. M., Specht, C. A., Yang, H., Ullrich, R. C. & Giasson, L. (1991). The Aa mating type locus of *Schizophyllum commune*. More Gene Manipulations in Fungi, Bennett, J. W. and Lasure, L. L., eds., 234-257.

Oprea, M., Sesan, T. & Balan, V. (1995). *Schizophyllum commune*—Canker and Dieback Disease of Apricot Trees in Orchards of South-Eastern Rumania. Acta horticulturae, 384.

Papazian, H. P. (1950). Physiology of the incompatibility factors in *Schizophyllum commune*. Bot. Gaz. 112, 441-459.

Papazian, H. P. (1962). The incompatibility factors and related gene in *Schizophyllum commune*. Genetics 36, 441-459.

Parag, Y. (1962). Mutations in the B incompatibility factor of *Schizophyllum commune*. Proc. Natl. Acad. Sci. USA 48, 743-750.

Parag, Y. & Koltin, Y. (1971). The Structure of the Incompatibility Factors of *Schizophyllum commune*: Constitution of the Three Classes of B Factors. Mol Gen Genet 112, 43-48.

Perkins, J. H. & Gordon, S. A. (1969). Morphogenesis of *Schizophyllum commune*. II. Effects of Monochromatic Light. Plant Physiol 44, 1712-1716.

Radu, M., Steinlauf, R. & Koltin, Y. (1974). Meiosis in *Schizophyllum commune*: Chromosomal Behavior and the Synaptinemal Complex. Arch Mikrobiol 98, 301-310.

Raper, C. A. (1983). Controls for development and differentiation of the dikaryon in basidiomycetes. In Secondary Metabolism and Differentiation in Fungi, pp. 195-238. Edited by J. W. Bennett & A. Ciegler. New York: Marcel Dekker.

Raper, C. A. (1988). *Schizophyllum commune*, a model for genetic studies of the Basidiomycotina. In Advances in plant pathology: Genetics of plant pathogenic fungi, pp. 511-522. Edited by G. S. Sidhu. London: Academic Press.

Raper, C. A. & Raper, J. R. (1966). Mutations modifying sexual morphogenesis in *Schizophyllum commune*. Genetics 54, 1151-1168.

Raper, C. A. & Raper, J. R. (1973). Mutational analysis of a regulatory gene for morphogenesis in Schizophyllum. Proc. Natl. Acad. Sci. USA 69, 1426-1431.

Raper, J. R. (1966). Genetics of Sexuality in Higher Fungi. New York: Ronald Press.

Raper, J. R. & Hoffman, R. M. (1974). *Schizophyllum commune*. In Handbook of Genetics, pp. 597-626. Edited by R. C. King. New York: Plenum Press.

Raper, J. R. & Krongelb, G. S. (1958). Genetic and environmental aspects of fruiting in *Schizophyllum commune*. Mycologia 50, 707-740.

Raper, J. R. & Miles, P. G. (1958). The genetics of *Schizophyllum commune*. Genetics 43, 530-546.

Raper, J. R., Baxter, M. G. & Ellingboe, A. H. (1960). The genetic structure of the incompatibility factors of *Schizophyllum commune*: the A factor. Proc. Natl. Acad. Sci. USA 46, 833-842.
Raper, J. R., Baxter, M. G. & Middleton, R. B. (1958). The genetic structure of the incompatibility factors in *Schizophyllum commune*. Proceedings of the National Academy of Sciences of the United States of America 44, 889-900.

Raper, J. R., Boyd, D. H. & Raper, C. A. (1965). Primary and secondary mutation at the incompatibility loci in *Schizophyllum*. Proceedings of the National Academy of Sciences of the United States of America 53, 1324-1332.

Raper, J. R., Krongelb, G. S. & Baxter, M. G. (1958). The number and distribution of incompatibility factors in *Schizophyllum commune*. American Nat. 92, 221-232.

Raudaskoski, M. (1972). Occurrence of Microtubules in the Hyphae of *Schizophyllum commune* During Intercellular Nuclear Migration. Arch Mikrobiol 86, 91-100.

Raudaskoski, M., Mao, W. Z. & Yli-Mattila, T. (1994). Microtubule cytoskeleton in hyphal growth Response to nocodazole in a sensitive and a tolerant strain of the homobasidiomycete *Schizophyllum commune*. European journal of cell biology 64, 131-141.

Raudaskoski, M., Stamberg, J., Bawnik, N. & Koltin, Y. (1976). Mutational Analysis of Natural Alleles at the B Incompatibility Factor of [the Fungus] *Schizophyllum commune*: Alpha2 and Beta6. Genetics 83, 507-516.

Runeberg, P. & Raudaskoski, M. (1986). Cytoskeletal elements in the hyphae of the homobasidiomycete *Schizophyllum commune* visualized with indirect immunofluorescence and NBD-phallacidin. European journal of cell biology 41, 25-32.

Schuren, F. H. J., Asgeirsdottir, S. A., Kothe, E. M., Scheer, J. M. J. & Wessels, J. G. H. (1993). The Sc7/Sc14 gene family of *Schizophyllum commune* codes for extracellular proteins specifically expressed during fruit-body formation. The Journal of general microbiology 139, 2083-2090.

Sietisma, J. H. & Wessels, J. G. H. (1977). Chemical Analysis of the Hyphal Wall of *Schizophyllum commune* [Fungi]. Biochim Biophys Acta 496, 225-239.

Snider, P. J. (1963). Genetic evidence for nuclear migration in Basidiomycetes. Genetics 48, 47-55.

Snider, P. J. & Raper, J. R. (1958). Nuclear migration in the basidiomycete *Schizophyllum commune*. American Journal of Botany 45, 538-546.

Specht, C. A. (1995). Isolation of the B alpha and B beta mating-type loci of *Schizophyllum commune*. Current genetics 28, 374-379.

Specht, C. A., Munoz-Rivas, A., Novotny, C. P. & Ullrich, R. C. (1988). Transformation of *Schizophyllum commune*: an analysis of parameters for improving transformation frequencies. Experimental mycology 12, 357-366.

Specht, C. A., Novotny, C. P. & Ullrich, R. C. (1992). Mitochondrial DNA of *Schizophyllum commune*: restriction map, genetic map, and mode of inheritance. Current genetics 22, 129-134.

Specht, C. A., Stankis, M. M., Giasson, L., Novotny, C. P. & Ullrich, R. C. (1992). Functional analysis of the homeodomain-related proteins of the A-alpha locus of *Schizophyllum commune*. Proceedings of the National Academy of Sciences of the United States of America 89, 7174-7178.

Stamberg, J. & Koltin, Y. (1971). Selectively Recombining B Incompatibility Factors of *Schizophyllum commune*. Mol Gen Genet 113, 157-165.

Stamberg, J., Koltin, Y. & Tamarkin, A. (1977). Deletion Mapping of Wildtype and Mutant Alleles at the B Incompatibility Factor of *Schizophyllum* [Commune, Fungi]. Mol Gen Genet (Mgg) 157, 183-187.

Stankis, M. M., Specht, C. A. & Giasson, L. (1990). Sexual incompatibility in *Schizophyllum commune*: from classical genetics to a molecular view. In Seminars in developmental biology: Developmental systems in fungi, Vol.1(3), pp. 195-206. Edited by C. A. Raper & D. I. Johnson.
Tarkka, M. T., Vasara, R., Gorfer, M. & Raudaskoski, M. (2000). Molecular characterization of actin genes from homobasidiomycetes: Two different actin genes from *Schizophyllum commune* and *Suillus bovinus*. *Gene* 251, 27-35.

Ullrich, R. C., Specht, C. A., Stankis, M. M., Yang, H., Giasson, L. & Novotny, C. P. (1991). Molecular biology of mating-type determination in *Schizophyllum commune*. In *Genetic engineering: Principles and methods*, pp. 279-306. Edited by J. K. Setlow. New York, N.Y.: Plenum Press.

Vaillancourt, L. J., Raudaskoski, M., Specht, C. A. & Raper, C. A. (1997). Multiple genes encoding pheromones and a pheromone receptor define the B beta 1 mating-type specificity in *Schizophyllum commune*. *Genetics* 146, 541-551.

van der Valk, P., Marchant, R. & Wessels, J. G. H. (1977). Ultrastructural Localization of Polysaccharides in the Wall and Septum of the Basidiomycete *Schizophyllum commune* [Fungi]. *Exp. Mycol.* 1, 69-82.

van Wetter, M. A., Wosten, H. A. B. & Wessels, J. G. H. (2000). SC3 and SC4 hydrophobins have distinct roles in formation of aerial structures in dikaryons of *Schizophyllum commune*. *Molecular microbiology* 36, 201-210.

Wendland, J., Vaillancourt, L. J., Hegner, J., Lengeler, K. B., Laddison, K. J., Specht, C. A., Raper, C. A. & Kothe, E. (1995). The mating-type locus Bà1 of *Schizophyllum commune* contains a pheromone receptor gene and putative pheromone genes. *The EMBO journal* 14, 5271-5278.

Wessels, J. G. H. (1969). A Beta-1,6-glucan glucanohydrolase involved in hydrolysis of cell-wall glucan in *Schizophyllum commune*. *Biochim Biophys Acta* 178, 191-193.

Wessels, J. G. H. (2000). Hydrophobins, unique fungal proteins. *Mycologist* 14, 153-161.

Wessels, J. G. H. & Sietsma, J. H. (1979). Wall structure and growth in *Schizophyllum commune*. In *Fungal Walls and Hyphal Growth*, pp. 27-48. Edited by Burnett & Trinci. Cambridge: Cambridge University press.

Wessels, J. G. H. & deVries, O. M. H. (1973). *Wall Structure, Wall Degradation, Protoplast Liberation and Wall Regeneration in Schizophyllum commune*. In *Yeast, Mould, and Plant Protoplasts*, Proceedings of the 3rd International Symposium on Yeast Protoplasts, pp. 295-306. Edited by J. R. Villanueva, I. Garcia-Acha, S. Gascon & F. Uruburu. Salamanca, Spain.

Wessels, J. G. H., Hoeksema, H. L. & Stemmering, D. (1976). Reversion of Protoplasts from Dikaryotic Mycelium of *Schizophyllum commune* [Fungi, Morphology]. *Protoplasma* 89, 317-321.

Wessels, J. G. H., Sietsma, J. H. & Sonnenberg, A. S. M. (1983). Wall synthesis and assembly during hyphal morphogenesis in *Schizophyllum commune* Fungi. *The Journal of general microbiology* 129, 1607-1616.

Wosten, H. A. B., Richter, M. & Willey, J. M. (1999). Structural proteins involved in emergence of microbial aerial hyphae. *Fungal Genetics and Biology* 27, 153-160.