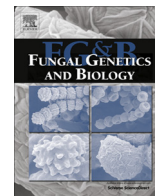




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In Memoriam

Tribute to Lorna Casselton (1938–2014)



Professor Lorna Casselton, CBE, MA, DSc, FRS, and Queen of mating-type recognition in *Coprinopsis cinerea*, died on Valentine's Day, 2014, in Oxford, England. Beyond the prestigious professional tags (Commander of the Order of the British Empire, Fellow of the Royal Society), Lorna was special in other special ways. Born Lorna Smith, she obtained her doctorate from University College London in 1964 and began her career in lecturing and research at Royal Holloway College. She moved to Queen Mary University of London where she advanced to Professor of Genetics, taking up the gauntlets of her doctoral supervisor, Professor Dan Lewis, and colleague, Dr. Peter Day, to study the fascinating multiple mating-type system of the mushroom fungus then called *Coprinus lagopus*.



Lorna had the courage to resign her secure position at Queen Mary in 1991 to seek another venue where she could concentrate full time on her research. She received funding from Britain's Biological Sciences Research Council and Agricultural Food

Research Council and Biotechnology, and moved to St Cross College, Oxford where she became a Fellow in 1993 progressing to Professor of Fungal Genetics in 1997.

Lorna married Peter Casselton in 1961. As was common before full development of the Women's Movement, she adopted her husband's last name. She and Peter were divorced in 1978, but, having by then achieved prominence in her field of science, Lorna kept the Casselton name for professional reasons. She married a handsome airplane pilot, William Joseph Dennis Tollett, in 1981. That marriage lasted happily until Lorna's recent death.

As those before her (Hans Kneip, Mathilde Bensaude, Daniel Lewis, Haig Papazian, John Raper, Peter Day), Lorna Casselton became utterly fascinated by mushroom bearing fungi with multiple sexes. She devoted a life-time career studying the genes and molecules regulating the promiscuous life style of the fungus first named *Coprinus fimetarius*, (in Bensaude's day) *Coprinus lagopus* (in Lewis's and Day's day) and, more recently renamed *Corinopsis cinerea*. Lorna's doctoral advisor, Dan Lewis introduced her to this fungus in the early nineteen sixties and she remained irredeemably hooked the rest of her life.

She and her students unveiled the secrets of how *Corinopsis* distinguishes compatible partners among 11,000 different mating types in the world-wide population. Meanwhile John Raper and associates were working on the wood-rotting fungus *Schizophyllum commune*, a mushroom of comparable promiscuity with 20,000 sexes. The two studies fortified one another, ultimately determining similar controls for mating-type recognition in both Basidiomycetes. While *S. commune* chomps on wood, *C. cinerea* relishes horse dung. Both are easily collected and cultivated in the laboratory. The basic research on these two organisms laid the groundwork for comparable studies in other fungi.

Over a span of years, Lorna took the lead to define the parameters of mating-type recognition in *Coprinopsis*. She and

her students identified the genes contained within the two mating-type loci, called A and B, which reside on two different chromosomes. They discovered that each locus consists of three closely linked sub loci and each sub locus contains more than one gene. Using molecular techniques, they revealed the A loci to contain two genes each, encoding specific homeodomain proteins that heterodimerize in compatible matings to produce a transcription factor regulating part of the sexual pathway towards meiosis. Each of the three B loci contains multiple genes encoding specific pheromones and a single gene for a G-protein-coupled receptor that, when titillated by a compatible pheromone, activates a complementing part of the sexual pathway. The molecules encoded by the mating-type genes of each type, A and B, are specifically different to effect binding (compatibility) or no binding (incompatibility) in the mating process. Successful interaction between the encoded molecules of the A genes *and* between encoded molecules of the B genes is required to activate the entire mating pathway leading to meiosis. No haploid homokaryotic individual is capable of activating self. Each must find a compatible partner to accomplish the entire pathway to sexual reproduction.

Coprinopsis cinerea and *Schizophyllum commune* function comparably at the molecular level. They differ in that *Schizophyllum* has only two linked sub loci at the non-linked A and B mating-type loci respectively.

Lorna was honored by election to fellowship in the Royal Society of London in 1999. She became a member of its council in 2002 and was elected vice president and foreign secretary in 2006. While Foreign Secretary, she traveled on behalf of the Society to 27 countries over a period of several years, advising scientific societies, promoting discussions of specific issues such as climate change, and sponsoring University Research Fellows. With her captivating smile, she described her role recently as follows: “According to my brief from the 1663 charter of the Society, Fellows must go out and have affairs with all manner of Foreigners. Well, it’s been a very good job for the past five years!”

My personal recollection of Lorna started in the early nineteen seventies when she came to the John Raper lab at Harvard to learn something about our research on the genetics of mating in *S. commune*. She sat opposite me at the lab bench while we taught our methods of researching our organism. Lorna, was a quick learner, yet, having brought her own dissecting tools, she evidenced a twist of independence by insisting on using *hers* instead of *ours*. As an assertive and talented scientist, she nonetheless possessed an inherent modesty, accompanied by an ever present smile and a sense of astonishment—not quite believing she could do what she did.

We soon became friends, and after my husband’s death in 1974, she and I shared many adventures: vacationing together at my summer place on Lake Champlain, taking walking tours in Britain, rooming together at scientific meetings. Once, while driving together to a Gordon Conference on Fungal Biology, I introduced Lorna to a typical New England flea market in the backwaters of New Hampshire. Fascinated, she poked around in a vast mess of things and found a perfectly atrocious centerpiece of colorful plastic mushrooms. We shared the three dollar purchase price, brought it to the conference, and, with proper ceremony, presented it in gratitude to the conference co-chairs who gladly passed it on to several successive co-chairs until the trophy and the chairs couldn’t take it anymore.

I shall always treasure Lorna’s inscribed sentiments written on the frontispiece of *Sex in Fungi: Molecular Determination and Evolutionary Implications*, ASM Press, for which she was an Editor along with Joseph Heitman, James Kronstad, and John Taylor.

She wrote: “Dear Cardy, Sex keeps us young! Love, Lorna”.

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