Phylogenetic revision of taxonomic concepts in the Hypocreales and other Ascomycota - A tribute to Gary J. Samuels

This volume of Studies in Mycology is something of a successor to another issue of the same journal published a decade ago, "Molecules, Morphology and Classification: Towards Monophyletic Genera in the Ascomycetes" (vol. 45, edited by Seifert, Gams, Crous & Samuels 2000). In that issue, the authors grappled with questions of integrating the new phylogenetic information derived from DNA sequencing into a classification system that was already complicated by the need to accommodate fungal pleomorphy. In the intervening time, mycologists have become less tentative about handling this complexity. The present volume continues the trend of applying multigene phylogenetics to generic and species concepts, extending the higher taxonomic level studies of the Assembling the Fungal Tree of Life project into a more finely resolved realm.

There is another controversy brewing in the consciousness of contemporary ascomycete taxonomists, namely the issue of dual nomenclature, the practise that allows (and in some minds demands) the use of two or more Latin binomials for one fungal species, one for the teleomorph, if known, and the other(s) for the anamorph(s). This has been the focus of passionate discussion and debate in special sessions at the last three International Mycological Congresses. When we initiated this collection of papers in 2008, we were not intending for a particular theme to arise. We knew the papers would focus on Ascomycete systematics, and pay homage to the craft of our honoree, Gary Samuels, i.e. an attention to quality illustrations, complete descriptions, anamorph-teleomorph connections, and species-level molecular phylogenetics. But along the way, in one way or another, most of the authors found themselves facing the concept of dual nomenclature, most of them trying to work around it in their own way.

Although there is disagreement among mycologists about the need for a single name nomenclatural system, most would probably agree with the following statements:

A. Taxonomists should try to minimise name changes.
B. If name changes are proposed, a stable nomenclature should result.
C. Classifications and nomenclature should reflect phylogeny to the extent that this is practical.
D. If classifications and the resulting nomenclature reflect phylogeny, taxonomic and nomenclatural stability will result.

The usual criticism of any taxonomic change, or change to nomenclatural rules, is that the changes will lead to chaos, with confusion among users and a loss of credibility for the taxonomic practise. The usual criticism of any taxonomic change, or change to nomenclatural rules, is that the changes will lead to chaos, with confusion among users and a loss of credibility for the taxonomic practise. This is disingenuous to suggest otherwise.

With Dual Nomenclature as the status quo, the authors of papers in this issue have adopted five different interpretations of One Fungus: One Name.

Option 1 – Strict priority. Strict application of priority of both generic names and species epithets, irrespective of whether these names were originally typified by anamorphic or teleomorph elements.

Following the lead primarily initiated by Lombard et al. (Stud. Mycol. 66, 2010), this approach was followed here by Gräfenhan et al. and Schroers et al. in their revisions of parts of Fusarium sensu Wollenweber and Acremonium by Summerbell et al.

Option 2 – Teleomorph priority with anamorphic species epithets. Transfer of anamorphic epithets to teleomorph genera for species that lack known teleomorphs. New teleomorph generic names are described when teleomorphs are discovered, irrespective of whether a previously described anamorphic generic name exists.

This option maintains the primacy of teleomorph names at both the genus and species rank. It was exercised in part by Chaverri et al. in their revision of Neonectria sensu lato, and the associated anamorph genera Cylindrocarpon and Campylocarpus.

Option 3 – Teleomorph priority with earlier anamorph species epithets not considered.

Teleomorph genus and species name are both given priority. No attempt is made to revise anamorph genus or species names to determine if older names exist.

In common with Option 2, this option also maintains the primacy of teleomorph names and both the genus and species rank, but discounts known or unknown anamorph names from consideration in the construction of binomials. This practise was followed by Hirooka et al. in their revision of Nectria cinnabarina, in parts of the revision of Neonectria by Chaverri et al., the revision of Plagiostoma by Meija et al. and the description of the new species Guignardia korthalsellae by Sultan et al. Disregarding of anamorph names, however, does not always indicate a rejection of anamorphic taxonomy per se; in the last example, there is no comprehensive revision of the anamorph genus Phyllosticta to enable the selection of possible earlier epithets for G. korthalsellae.

Option 4 – Teleotypification. Teleotypification of previously anamorphic names (genus or species) to holomorphic status.

This recently implemented provision of the ICBN in the Vienna Code (Art. 59.7) allows the status of an originally anamorphic name to be converted to holomorphic status by epitypification of its type specimen with a teleomorphic specimen. This provision cannot be used if an existing teleomorph is already named. As presently described in the ICBN, it is unclear whether this status is conveyed only to the species in question or to the generic name if the type species is teleotypified.

In this issue, this approach was followed by Réblová & Seifert, who changed the originally hypomycetous status of Sterigmatobotrys to holomorphic status by epitypification.

Option 5 – Single species names but allowing two genera per clade.

Teleomorph species are named in teleomorph genera and have only teleomorph-typified epithets; anamorphs are unnamed or referred to by their anamorph generic name. Anamorphic species are named in anamorph genera and have only anamorph-typified epithets. The result is that each species has a single name, but a monophyletic clade may have one teleomorph and one anamorph name associated with it. This has often been referred to as cross reference Nomenclature, where anamorph species epithets are dropped once the teleomorph is known, and anamorphs are then referred to only as Anamorph-genus-name of Teleomorph-genus species epithet.
This option is completely consistent with the requirements of the present Code. In this issue, Põldmaa followed this practice in her revision of tropical species of Hypocrean and related Cladobotryum anamorphs.

Which of these options, or practises derived from these, might ultimately be chosen to implement the concept of One Fungus: One Name remains for discussion amongst mycologists. We suggest that comparing options, including the maintenance of Dual Nomenclature, would be simplified if we could develop quantitative methods for evaluating each option objectively. **Nomenclatural Parsimony**, a measure of the number of name changes needed to implement any particular system, should be an easy concept to define and to apply to each approach to single name nomenclature. Developing an algorithm for **Nomenclatural Stability** will probably be much more challenging, but the ability to compare the relative stability of particular kinds of nomenclatural changes should be a critical aspect of these discussions.

**About this issue**

This issue is not about nomenclature, rather it is about the phylogeny and taxonomy of several groups of Ascomycetes. The papers are authored by collaborators and students of Gary Samuels, who has devoted his career to furthering the study of Ascomycetes all over the world. In parallel with his career, we have divided the papers into two groups. The larger set of papers focuses on the taxonomy of the Hypocreales, the order that Gary cut his teeth on as a graduate student and continued to study for his whole career. He couldn’t help dabbling though, and the second group of papers concern a diversity of Ascomycete orders and families, mirroring the many other papers that Gary has written.

The section on the Hypocreales includes four long papers revising generic and species concepts in the economically and biologically critical family, the Nectriaceae. The nominal genus Nectria is partly revised by Hirooka et al., with the well-known type species N. cinnabarina divided into four biological species, one of which is described as new. Chaverri et al. rework the Neonecctria clade, which includes important plant pathogens often referred to the anamorph generic name Cylindrocarpon, providing a framework with five monophyletic genera. Gräfenhan et al. and Schroers et al. provide a similar phylogeny-based taxonomic framework to the prevailing concept of Fusarium. They show that this concept is not monophyletic and propose a new single-named nomenclatural system that recognises several genera. The paper by Põldmaa describes several new species of the family Hypocreaceae collected from the tropics, following the model established for the taxonomy of temperate species of this family established by the papers on Hypomyces published by Clark Rogerson & Gary Samuels. The paper by Summerbell et al. deals with a plesiomorphic anamorph that is broadly distributed in the Ascomycetes, but particularly prevalent in the Hypocreales, the hyphomycete form-genus Acremonium. This paper presents the first comprehensive overview of these anamorphs, providing taxonomic solutions for some groups, and pointing out many groups with lingering problems awaiting satisfying solutions.

The second set of papers deals with other groups of Ascomycetes. Rébélová et al. determine that species of the anamorph genus Monilochaetis are phylogenetically diverse, although belonging primarily in the Sordariomycetidae. This revision results in the much-needed formal description of a new order for Glomerella and Colletotrichum. A teleomorph was discovered for the lignicolous Sterigmatobotrys macrocarpa, leading Rébélová & Seift to teleotypify this species. Huhndorff & Miller wrestle with the phylogeny of genera in the Chaetothyriales, describing a new species from New Zealand in the Helminthosphaeriales. Mejía et al. provide an account of the 25 accepted species of the genus Plagiostoma (Gnomoniaceae, Diaporthales) of which eight are new to science. Finally, Johnston et al. describe two new species on native New Zealand mistletoe in the dothideomycetous genera Guignardia and Rosenscheldiella.

**Reflections on the career of Gary Samuels**

Amy Rossmann: I have known Gary for over 35 years since we first met on a collecting expedition in 1971 led by Dick Korel along with Don Pfister, Don Reynolds, and Kent Dumont. Gary was an older student, two years ahead of me in graduate school, and he suggested that I tackle the long-spored Nectria-like fungi while he polished off those with short spores. Thus, I had a thesis project. Throughout his career Gary has influenced other scientists inspiring them as he did me to work in many different groups of fungi. In truth, I think he would like to study all fungi, at least all of the pyrenomycetes and their anamorphs.

Gary’s first job was in New Zealand where he relished the diversity of the many local undescribed fungi and set to work publishing on species ranging from the “bizzaro” discomycetes to his beloved Hypocreales. During this period in New Zealand he spent one-year with Emil Müller in Switzerland publishing on the connection of telemorphs with asexual states for many new and unusual species. Throughout his career Gary collected fungi on field trips especially in the Neotropics and New Zealand, later in Asia. From these fresh collections he would isolate single ascospores using a micromanipulator in order to grow the fungus in culture often producing the assexual state. These cultures have served as the basis for many projects undertaken by his students and associates. Gary’s philosophy was to collect everything and distribute his collections to specialists throughout the world.

One of Gary’s contributions to mycology was collaborating with Clark Rogerson ensuring that Clark’s extensive knowledge of Hymopomyces was published. Their series of papers on Hypomyces on discomycetes, boletes, polypores, and mushrooms laid the groundwork for the continuing studies currently undertaken by Kadri Põldmaa. Like Clark Rogerson, Gary collaborates with amateur mycologists; for his latest invitation to a foray, he developed a field guide to the fungicolous fungi. This is a small book with one species described and illustrated on each page—just the handy reference book one needs to identify these fungi. For this one occasion, he spent about three weeks developing this useful identification manual.

In 1989 Gary Samuels joined the Systematic Mycology & Microbiology Laboratory at USDA Agricultural Research Service in Beltsville, MD, to work on the systematics of biological control fungi. At ARS his main research focus has been on Hypocreal Trichoderma, a difficult group of fungi, and the most commonly used biological agents for controlling fungal diseases. His systematic knowledge of Trichoderma has resulted in the ability to distinguish species and to predict characteristics of unknown isolates. Working with David Farr, he developed an on-line system that provides descriptions and illustrations of the species of Trichoderma as well as a synoptic key that requires only minimal expertise to use. This was one of the first on-line identification systems for fungi. In addition, Gary has presented workshops on the identification of Trichoderma to plant pathologists in Cameroon, Peru, Thailand, and Vietnam, for which he developed a manual for the identification of Trichoderma especially for those working in biological control.
Gary and his graduate student Hans-Josef Schroers conducted research on the genus *Clonostachys*, asexual state of *Bionectria*, resulting in a major monograph of this genus. Invaluable to those developing these fungi as biological control agents, this research has resulted in their increased use in the control of diseases of greenhouse plants. Another real-life problem that Gary solved involved the confusion of a disease of cultivated mushrooms known as green mold with a biological control agent. Initially the cause of the mushroom disease was identified as *Trichoderma harzianum*, a species commonly used as a biological control agent. This resulted in a conflict between the cultivated mushroom growers who want to prevent the spread of green mold and growers using *T. harzianum* in their fields as a biological control agent of crop plant diseases. Gary carefully studied the green mold pathogen, compared it with the biocontrol fungus, and showed that these fungi were two different species. He also developed a reliable, straightforward technique for distinguishing them.

Throughout his career Gary has actively participated in the Mycological Society of America (MSA). Following Clark Rogerson’s influence about the importance of participation in the MSA, Gary served for over ten years as an Associate Editor of *Mycologia*, always giving each paper a fair and thorough review. This has included editing manuscripts written by non-English speakers so that they are acceptable, often spending days on one paper. Once he even sectioned and photographed a specimen so that an illustration of the teleomorph could be included - all this without any co-authorship. He has served on various MSA committees over the years including the one to review *Mycologia* when it first was increased in physical size with a new cover - this was considered very radical at the time. Gary was a willing participant in the rescue of the excess issues of *Mycologia* from the New York Botanical Garden and assemble of complete sets mailed to overseas mycological institutions. This involved lifting heavy boxes and putting them in order prior to assembling the sets, then packing them into new boxes all taking place in the dusty hot basement of our building.

Gary has greatly influenced the field of systematic mycology worldwide serving on the International Commission of the
Taxonomy of Fungi and on the editorial boards of three mycological journals, *Mycological Progress*, *Mycotaxon*, and *Sydowia*. He is widely known and well respected as evidenced by his frequent invitations to speak at national and international meetings. Gary was funded by the NSF Partnership in Enhancing Expertise in Taxonomy (PEET) programme through Pennsylvania State University where he trained three students and three research associates in the systematics of *Trichoderma* and related fungi. He is now a co-P.I. on a second PEET grant with one of the students (Priscila Chaverri) trained on the first grant. Numerous students and scientists from both inside and other the U.S. come each year to work with him usually for one to six months or longer. When they are here, he selflessly relinquishes his microscope system after patiently instructing them in its use while he does other work in the same room.

Gary is a world famous mycologist who has contributed enormously to the knowledge of the systematics of Ascomycetes. His research has resulted in monographs of important groups of fungi, mostly recently using multigene phylogenies to define species. His systematic research on biocontrol fungi has solved serious problems in agriculture in the U.S. and around the world. He has transferred that technology to plant pathologists through innovative web-based keys and through national and international workshops. Additionally, he has mentored a number of students and scientists who will provide a foundation for carrying on this important work into the future.

Gary is one of the people who enriched my career in mycology. We have not always agreed on such exciting topics as the generic circumscription of hypocrealean fungi or even which scientific names to apply to them but we have always respected each other’s ideas and have gained enormously by working together for many years.

**Keith Seifert:** At the 2008 meeting of the Mycological Society of America at the Pennsylvania State University, I had the chance to wear Gary Samuels’s name tag at the banquet. Apart from the comedy of little Keith parading around with tall Gary’s badge, which caused some double takes amongst our colleagues, I was proud to be so labelled for a time, even if it fooled no one. When Gary asked for his name tag back at the end of the evening, I refused to return it. It now sits as a prized possession in my collection of mycological memorabilia. I have interacted with Gary throughout my career, from my MSc on. His skills as a field mycologist, his attention to establishing teleomorph-anamorph connections and considering the whole fungus in his taxonomic decisions, and his adoption of molecular techniques, have placed him at the forefront of ascomycete taxonomy. At every meeting I have attended with him, there is a retinue of neophyte ascomycete taxonomists from different cultures, shyly asking him questions and looking for his help. His willingness to share specimens, cultures, and ideas, and the always impeccable quality of his own published work have made him a role model for me.

My first contact with Gary was in 1980, when I asked him to collect jelly fungi for me in New Zealand, which when revived yielded cultures essential for my research, and even now remain the only extant cultures of these *Dacrymyces* species. When I was looking for a PhD post in 1982, Gary was one of the people I turned to. With unusual honesty, he told me that going outside America or Europe would be "academic suicide." I ended up at CBS in Holland, and Gary became my covert collaborator, sharing many cultures and specimens that greatly enriched my research. After meeting him in person for the first time at the 3rd International Mycological Congress in Tokyo, he invited me to coauthor his symposium paper from that meeting. This was an amazing opportunity for a graduate student, and the resulting review about correlations between teleomorph and anamorph genera in the *Hypocreales* was central to our subsequent work. My PhD committee agreed that I should be the sole author on my thesis monograph; otherwise, Gary would have been a coauthor on the book that was so important to starting my career.

Gary returned to the United States at about the same time that I returned to Canada. Those were unsettled years for us both, but again at about the same time we achieved employment stability, he in Beltsville, me at Agriculture & Agri-Food Canada. We continued to correspond, and I was one of many colleagues welcomed at the Samuels home in Laurel (some visitors stayed for months…). During one visit (where he also introduced me to the concept of fine bourbon), Gary spent a whole evening going over a manuscript he was handling as an associate editor for *Mycologia*. He went far beyond the usual call of duty as an editor, doing so much more than selecting reviewers and collating reviews. He always ensured that the manuscripts he handled were rigorously reviewed, and then vigorously edited to ensure that the work was presented in the best light, especially for authors whose language was not English. Gary struggled with the adoption of molecular techniques to combine with his growing expertise in the anamorph genus *Trichoderma*. At the time he started this work, the enzymologists and biocontrol specialists who sought to exploit the species of this genus were using a nine species system published in 1968. My colleague John Bissett in Ottawa had applied a more refined morphological approach to the genus, but knowledge of its diversity was still very preliminary. At first Gary focused on isolating ascospores from the *Hypocreales* teleomorphs providing these strains to groups in several other labs who were exploring molecular markers. Continuing his fieldwork, he began accumulating anamorphic strains as well, including endophytic *Trichoderma* species from cacao - a complete surprise to those of us who dismissed this genus as a fast-growing, dirt-loving weed. About ten years ago, the pieces of the puzzle started to come together, resulting in a series of comprehensive monographs of many of the sections of this genus, involving many collaborators, with phylogenetic species concepts correlated with the
most detailed possible morphological observations on anamorphs and teleomorphs. He perfected a method of photographing the complexly branched conidiophores of Trichoderma species involving fluorescence microscopy; these illustrations were always accompanied by his characteristically precise line drawings.

Although Gary is mostly now known for his work on Trichoderma, his work on his beloved Hypocreales continued. This included his collaboration with his friend and colleague Amy Rossman, to produce the monographic revision on the Genera of the Hypocreales, and the identification guide to the Hypocreales of the southeastern United States (which we use almost daily in our lab). Gary has also worked on Fusarium, and, had I been more alert when I started my present job, I would have been working with him on this. With his knowledge of the teleomorphs, he has been a central figure in the development of a phylogenetic taxonomy in this genus, collaborating with David Geiser, Helgard Nirenberg, and Kerry O’Donnell in an ongoing attempt to settle issues of species concepts and nomenclature.

I cannot let a tribute to Gary go by without mentioning something else. He is interested in lots of things outside of science, and he is really a guy with a great sense of humour. Fans of James Trappe might disagree, but I think that Gary gave the funniest presentation in the history of the MSA. This happened in the late ’80s, and was a consequence of one of those friendly collaborations that Gary got himself into so easily. He was actually giving the presentation as a favour to someone else, and, after the title slide, the projector broke. Rather than waiting for it to be fixed, Gary continued his talk, swooping his arms around and gesturing as he vividly described what was on the invisible slides, giving a very detailed description of the methods used to isolate fungi from caterpillar guts. The crowd was in stitches, and Gary was horrified that no one had taken him seriously, feeling that he had poorly represented his collaborators. But how many talks do you remember from twenty years ago?

Gary always revered his mentor Clark Rogerson, who introduced him to the Hypocreales, and we must also remember Emil Müller, with whom Gary did a post doc in Switzerland before going to New Zealand. This mentoring line goes from Rogerson and Müller through Gary and then outward to Hans-Josef Schroers and David Brayford and David Geiser and Priscila Chaverri and Sabine Huhndorf and Kerry O’Donnell and Kadri Põldmaa and Pedro Crous and Irina Druzhinina to name those that come easily to mind. And me. Gary has never been a university professor, yet his influence and impact are all over the practitioners of ascomycete taxonomy. A GenBank search reveals close to 2 000 sequences in GenBank with GJS as part of their collection number; this does not count sequences derived from Gary’s cultures hidden under other numbers, such as the nearly 500 cultures that he has donated to the CBS culture collection.

Gary Samuels is a brilliant scientist, a generous mentor, a talented field mycologist, and a leader in our field. He is the mycologist’s mycologist, the taxonomist’s taxonomist. No hyperbole… he is my mycological hero.

The Editors

March 2011