

One Fungus = One Name: DNA and fungal nomenclature twenty years after PCR

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Abstract: Some fungi with pleomorphic life-cycles still bear two names despite more than 20 years of molecular phylogenetics that have shown how to merge the two systems of classification, the asexual “Deuteromycota” and the sexual “Eumycota”. Mycologists have begun to flout nomenclatorial regulations and use just one name for one fungus. The International Code of Botanical Nomenclature (ICBN) must change to accommodate current practice or become irrelevant. The fundamental difference in the size of fungi and plants had a role in the origin of dual nomenclature and continues to hinder the development of an ICBN that fully accommodates microscopic fungi. A nomenclatorial crisis also looms due to environmental sequencing, which suggests that most fungi will have to be named without a physical specimen. Mycology may need to break from the ICBN and create a MycoCode to account for fungi known only from environmental nucleic acid sequence (i.e. ENAS fungi).

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INTRODUCTION

It has been a bit over two decades since the polymerase chain reaction (PCR) changed evolutionary biology in general and fungal systematics in particular. Even before PCR became generally available, mycologists realized that the evolutionary record contained in the nucleic acid sequence of every fungus could be used to merge two systems of nomenclature that had been employed in most fungi, i. e. one for the “Eumycota” based on sexual morphology and the “Deuteromycota” based on all other morphologies (Berbee & Taylor 1992, Bruns *et al.* 1991, Guadet *et al.* 1989, Reynolds & Taylor 1992). Why, then, has it taken more than two decades for nomenclature to catch up with biology, and why is the possibility of nomenclatorial rapprochement now being taken seriously? These questions, and three others posed to the participants in this symposium will be the subject of this contribution: Does DNA sequencing make dual nomenclature superfluous? Can the International Code of Botanical Nomenclature (ICBN) (McNeill *et al.* 2006) be modified to enable this process, or would a MycoCode be more effective? How can the mycological community get rid of the legacy of dual nomenclature and Article 59 without nomenclatural chaos?

Two examples illustrate the practical problems raised by dual nomenclature. First, this year, while serving as a member of a governmental committee researching the use of mycoherbicides to eradicate drug crops, it fell to me to explain the nomenclature of two poppy pathogens that are sister species, one named as a teleomorph *Crivellia*

papaveracea and the other as an anamorph, *Brachycladium papaveris* (Inderbitzin *et al.* 2006) (Fig. 1). The fifteen other members of the committee, eleven academics and four very knowledgeable staff, stared at me in disbelief when I said that sister species could have different generic names. Second, together with Tom Bruns, I have been directing research about fungi that naturally decay plants proposed as sources of lignocellulose for the production of biofuels. In the course of this work, we have sequenced ITS using DNA isolated from the decaying grasses and compared the sequences to those deposited in GenBank. Often, a single sequence will be attached to two names; you guessed it, it's the same fungus with some GenBank sequences having been deposited under the teleomorph name and others under the anamorph name. Perpetuation of dual nomenclature when we have the means to abandon it is hindering mycology, both scientifically and socially.

Dual nomenclature has persisted for the past 20 years because few mycologists are deeply interested in both molecular phylogenetics and nomenclature. One Fungus = One Name has gained momentum, as evidenced by this conference, because mycologists who are studying the

Dedication: Dedicated to Don Reynolds, mycological iconoclast, whose sabbatical visit to Berkeley from the Los Angeles County Museum of Natural History more than 20 years ago stimulated thought about One Fungus = One Name.

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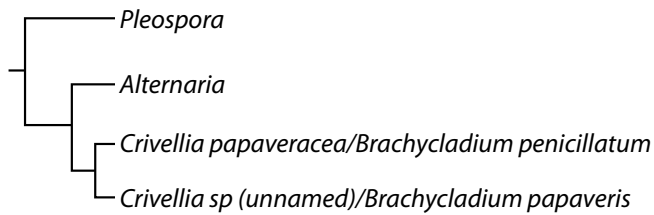


Fig. 1. Phylogenetic relationships of the sister species *Crivellia papaveracea* and *Brachycladium papaveris*, the former named as teleomorphic and the latter as an anamorphic fungus. The *Crivellia* state of *B. papaveris* remains unnamed due to a lack of suitable material to serve as a nomenclatural type (Inderbitzen *et al.* 2006).

molecular phylogenetics of economically important fungal groups have begun naming newly recognized genus-level clades with just one *Ascomycota* name, whether or not the fungus exhibits sexual reproduction. The first thorough exploration of this practice was provided by Crous *et al.* (2006), whose revision of the *Botryosphaeriaceae* includes this sentence, “Separate teleomorph and anamorph names are not provided for newly introduced genera, even where both morphs are known.” Where a teleomorph name was available, as in the case of *Botryosphaeria*, the authors used it. Where only anamorph names were available, they were used, e.g. *Macrophomina* or *Neoscytalidium*. Where a new clade was segregated from an existing teleomorph genus, and best distinguished by the anamorphic morphology, the new name reflected the anamorph, e.g. *Neofusicoccum*.

Matters were taken further in a study of *Penicillium* species by Houbraken *et al.* (2010). As they put it, “Using this approach and applying the concept of one name for one fungus (Reynolds & Taylor 1992), we have chosen to describe these two species under [their] anamorphic name.” That is, Houbraken *et al.* described new species that have both anamorphic and teleomorphic states as species in the anamorph-typified genus *Penicillium* and ignored the existing teleomorphic generic name, *Eupenicillium*. These actions are clearly outside the ICBN and constitute a social rebellion. Though smaller and far less important than social rebellions concerning, for example, women’s rights, the rights of African Americans, or those of homosexuals, this mycological rebellion is similar to the others in that activism has outpaced the law and the law must now change or become irrelevant.

Dual nomenclature has a long history. The choice made by Houbraken *et al.* (2010) to use the anamorph name *Penicillium* over the teleomorph name *Eupenicillium* for one of the most economically important fungi echoes the choice made more than 40 years earlier by Raper & Fennel (1965) when they applied the anamorphic name *Aspergillus* to all members of that genus whether or not the species also produced a sexual structure. Forty years are not enough to understand the origins of dual nomenclature, to do that we have to go all the way back to Linnaeus and the beginning of botanical nomenclature. In this tour back through time, our guides will be Weresub & Pirozynski through their excellent article on the history of fungi that produce both meiotic

and mitotic spores, that is, pleomorphic fungi (Weresub & Pirozynski 1979) and the opening chapters of *Selecta Fungorum Carpologia*, the monumental work of Louis-René Tulasne and Charles Tulasne (Fig. 2) (Tulasne & Tulasne 1861).

The Tulasne’s point out that Linnaeus based his plant taxonomy on floral morphology and that he could demonstrate that each plant had but one type of flower. At a time when fungi were considered to be plants, and fungal spores were equated with seeds, Linnaeus extended his taxonomic concept to fungi. The Tulasne brothers then argue that Linnaeus had such an influence over his mycological contemporaries, Fries foremost among them, that these mycologists were in denial about pleomorphy, despite their being able to see more than one type of “seed” through their lenses.

“In the Mucedinei [Fries] sees the conidia . . . but everywhere he flatly denies that there occur “two kinds of sporidia on the same plant”, exactly as if he had heard, sounding in his ears, the loud voice of Linnaeus, crying “It would be a remarkable doctrine – that there could exist races differing in fructification, but possessing one and the same nature and power; that one and he same race could have different fructifications; for the basis of fructification, which is also the basis of all botanical science, would thereby be destroyed, and the natural classes of plants would be broken up” (Tulasne & Tulasne 1861: 48’). The brothers go on to chide Linnaeus, adding “But since the illustrious author always completely abjured the use of magnifying glasses, and therefore scarcely ever tried to describe accurately either conidia or spores, we fear (may he pardon the statement) that he really knew very few seeds of either kind” (Tulasne & Tulasne 1861: 48-49). The influence that the size of an organism has on its systematics can be profound (Taylor *et al.* 2006). The fact that the overwhelming majority of plants are macroscopic while the overwhelming majority of fungi are microscopic still affects nomenclature and will be revisited near the end of this article.

Louis René and Charles Tulasne went on to argue against mycological denial of pleomorphy when they wrote, “The fungus upon which we are now touching [*Pleospora*] is not only almost the commonest of all belonging to its order, but also affords a wonderful proof of our doctrine concerning the multiple nature of the seeds of species of fungi” (Tulasne & Tulasne 1861: 248). One cannot help wondering if the brothers guessed not only that their work was controversial, but that the mycological world was heading toward dual nomenclature, when they wrote, “As today we have seen the various members of the same species now unwisely torn from one another against the laws of nature . . .” (Tulasne & Tulasne 1861: 189).

Alas, when the most useful characters that could be used for classification were meiosporic, and when many fungi did not exhibit them, there were not many options and the one that prevailed was dual nomenclature. Fuckel, a retired

¹ The English translations are from the 1931 Clarendon Press (Oxford) edition, and were prepared by W B Grove and edited by A H R Buller and C L Shear.



Fig. 2. Louis Renè Tulasne (l) and Charles Tulasne (r). Photo: courtesy of the National Museum of Natural History, Paris.

pharmacist, got the ball rolling (Fuckel 1870) and Saccardo did the heavy lifting with his *Sylloge Fungorum* beginning in 1882 (Saccardo 1882). By 1910, the International Rules of Botanical Nomenclature (Briquet 1912) contained a section of Article 49, Art 49^{bis} (the precursor of the current Article 59), that forbade “botanical” names for any but the sexual stage of pleomorphic fungi and that is where matters rest with the current ICBN.

Saccardo’s use of mature anamorph morphology is wonderfully convenient for classification and identification but, obviously, it is not based on evolutionary relationships. The hope that study of mitospore development would lead to a separate systematics based on evolutionary relationships began with Vuillemin (1910a, b) and Mason (1933, 1937) and led to the work of Hughes (1953), Tubaki (1958) and Barron (1968). Elegant microscopic studies of mitospore development followed (Cole & Samson 1979) and the movement reached its zenith at the second Kananaskis conference (Kendrick 1979). Just as these studies of development were peaking, two events occurred in the realms of evolution and systematics that promised the irresistible appeal of a new approach and a seemingly endless supply of characters – cladistic analysis (Hennig 1966) and access to nucleic acid variation.

The first applications of nucleic acid variation to fungal systematics involved DNA-DNA hybridization of yeasts (Kurtzman 1980) and then sequencing of nucleic acids. Pioneering work with painfully difficult RNA sequencing modeled on the work of bacteriologists (Walker & Doolittle 1982, 1983) was followed by DNA sequencing (Gottschalk & Blanz 1984, Guadet *et al.* 1989, Gueho *et al.* 1989). But

it was the discovery of the polymerase chain reaction (PCR) (Rabinow 1996, Saiki *et al.* 1988) that made possible the broad studies we now take for granted.

The first application of PCR amplified DNA sequence to fungal phylogenetics demonstrated the evolution of hypogeous fungi from mushroom ancestors (Bruns *et al.* 1989; Fig. 3). This work relied on the development of primers designed to amplify regions of both mitochondrial and nuclear rDNA including the nuclear small subunit, large subunit and internal transcribed spacer (ITS), which were published the following year and have been cited a bit more often than once-a-day since then (White *et al.* 1990; Fig. 4).

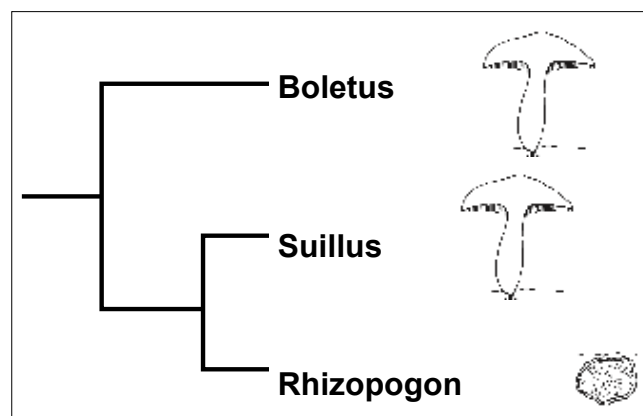


Fig. 3. Phylogenetic analysis of PCR amplified rDNA showing the evolution of hypogeous Basidiomycota in the genus *Rhizopogon*, from mushroom ancestors in the genus *Suillus* (Bruns *et al.* 1989). Adapted from Bruns *et al.* (1989).



Fig. 4. Authors of the publication of PCR primers for the amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Left to right: Tom Bruns, Tom White, Steve Lee, and John Taylor. Photo: taken in 2010, 20 years after the publication of White *et al.* (1990).

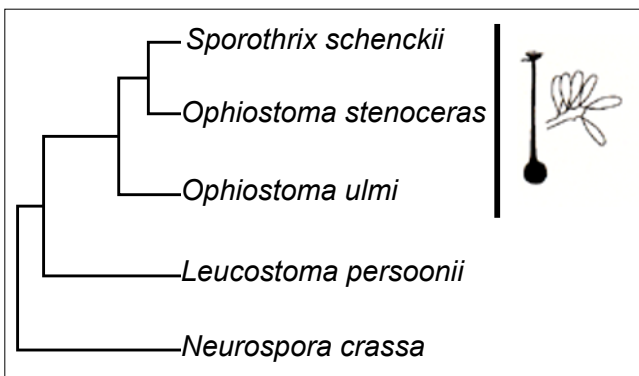


Fig. 5. Phylogenetic analysis of PCR amplified rDNA showing the anamorphic *Sporothrix schenckii* nestled within the teleomorphic genus *Ophiostoma* (Berbee & Taylor 1992).

Within a few years, analysis of PCR amplified rDNA showed that the anamorphic *Sporothrix schenckii* nested within the teleomorph genus *Ophiostoma* (Berbee & Taylor 1992; Fig. 5). This work demonstrated the integration of anamorphic and teleomorphic fungi based on DNA variation, as had earlier work on *Fusarium* (Guadet *et al.* 1989). These studies showed a separate classification for “Deuteromycota” to be superfluous.

That same year, Reynolds & Taylor (1992) addressed the nomenclatural implications of using DNA variation to assess the phylogenetic relationships of fungi, writing, “The use of nucleic acid sequence allows systematists to demonstrate the phylogenetic relatedness of fungi possessing and lacking meiotically produced spores. . . . This demonstration presents a serious challenge to the separate classification of these two types of fungi and undermines the elevated position that characters associated with sexual reproduction have held in the classification of higher fungi. . . . We believe that all fungi should be classified in one system and that characters associated with sexual reproduction should be given the same weight as other characters. . . . By the broad interpretation [of Article 59] in current use, the potential for pleomorphy is assumed of all fungi and the Article is applied to all fungi. . . . With an alternative and strict interpretation however, Article 59 would apply only to fungal species that have been actually demonstrated to be pleomorphic. Under the latter interpretation, sexual, asexual, and pleomorphic fungi would be classified together and form taxa would not be necessary.”

Following the Fungal Holomorph Symposium in Newport (OR, USA) to discuss nucleic acid variation and the integration of anamorphic and teleomorphic classifications (Reynolds & Taylor 1993), there have been presentations and discussions on the topic at every International Mycological Congress from

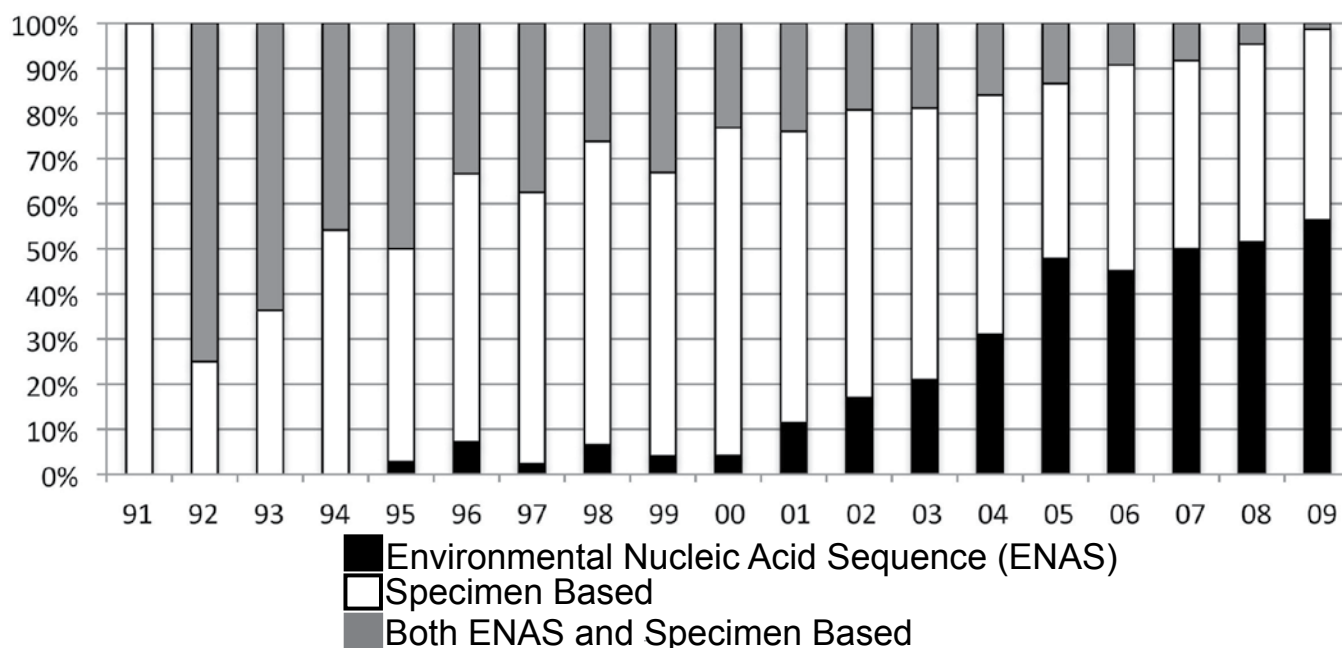


Fig. 6. Graph of the Operational Taxonomic Units (OTUs) added to GenBank from 1991 to 2009 showing the increasing proportion of OTUs based only on environmental nucleic acid sequence (ENAS). Adapted from Hibbett *et al.* (2011).

Vancouver (1994; Taylor 1995) to Edinburgh (2010; Norvell *et al.* 2010), leading up to the present One Fungus = One Name conference and the Amsterdam Declaration (Hawksworth *et al.* 2011).

Nucleic acid variability has proved to be useful in other areas of fungal systematics and classification related to mitotic fungi. Beginning with the mitosporic human pathogen *Coccidioides immitis*, DNA variation has been used to show that anamorphic fungi recombine in nature (Burt *et al.* 1996), that they speciate (Koufopanou *et al.* 1997), and that, based only on DNA variation, they can be described in the system for *Ascomycota* (Fisher *et al.* 2002). As Fisher *et al.* wrote when they described a new *Coccidioides* species as an ascomycete, "*Coccidioides posadasii* is morphologically indistinguishable from *Coccidioides immitis*. *C. posadasii* is diagnosed by the following nucleotide characters (given as the gene, the nucleotide position in the gene, and parenthetically, the nucleotide fixed in *C. posadasii*) showing reciprocal fixation between *C. immitis* and *C. posadasii*: Chitin synthase positions 192 (A), 288 (T); Dioxygenase positions 872 (C), 1005 (C), 1020 (G), 1179 (C), 1272 (T); etc." Of course, description is not the same as acceptance. In the case of *Coccidioides posadasii*, acceptance for this "Select Agent" came from an unexpected quarter, the United States Congress (Federal Register 2005).

Another point made soon after PCR became available was that DNA, or even a DNA sequence, could act as the type element in a species description (Reynolds & Taylor 1991). This observation has gained importance due to the advent of environmental sequencing, where mycologists use PCR primers for rDNA to amplify variable regions from DNA isolated from soil or plants. Environmental sequencing has begun to produce large numbers of rDNA sequences that

document the existence of fungi for which there is neither a specimen nor a culture. Most importantly, ecological studies have shown that the number of these DNA-only fungi, or "Environmental Nucleic Acid Sequences" (ENAS) can exceed the number of fungi for which there is a culture or specimen (Jumpponen & Jones 2009, 2010). This imbalance poses a challenge to fungal classification and nomenclature that may dwarf the challenge of integrating anamorphic and teleomorphic fungi.

David Hibbett, in his plenary presentation at IMC9 (Hibbett *et al.* 2011), noted that the number of fungal OTUs added each year to GenBank that are based only on rDNA sequences (ENAS fungi) is now exceeding the number from fungi with cultures or specimens (Fig. 6). Ecologists face the prospect that most of the fungal species dwelling in their favourite environment can neither be cultivated nor collected; as a result they are going to have to rely on ENAS to assess the true fungal diversity. Each of these ecological studies may add hundreds or thousands of ENAS to GenBank. Already, searches of GenBank using a new ENAS mostly recover previously deposited ENASs, which are identified not by names but by numbers. Imagine two ecological studies, one where each new ENAS in tables or figures is associated with a numbered, existing ENAS and the other where the existing ENASs have been named – the reader would come away with ignorance on the one hand and understanding on the other. Fungal classification and nomenclature must respond to this challenge by developing a means of associating ENASs with names and the response must be timely.

As discussed by Hibbett *et al.* (2011), fungi known only as ENAS can be named by comparison to named fungi already in GenBank. It seems important that this name be identified as attached to an ENAS rather than a culture or specimen,

perhaps by appending ENAS as a suffix. Several essential issues will have to be addressed before ENAS naming can begin, among them the problems of sequencing errors, variation in rDNA sequence within an individual, and accommodation of all these new ENAS fungi in MycoBank (Hawksworth *et al.* 2010). Perhaps most unsettlingly, the naming will have to be automated in some way because no one can possibly name the thousands of new sequences that will arise in each new environmental study.

At this point, a reader might fairly ask, if separate “Deuteromycota” and “Eumycota” nomenclatural systems still remain separate 20 years after their merger became intellectually obvious, how could anyone possibly entertain thoughts about the acceptance of the automated description of fungi based only on DNA sequence? I see two steps to acceptance of ENAS fungi. The first step would be a published demonstration of the naming of ENAS fungi, echoing the aforementioned social activism already in play for One Fungus = One Name (Crous *et al.* 2006, Houbraken *et al.* 2010). The second step, acceptance of named ENAS fungi by the ICBN, is the tougher problem and is unlikely to occur quickly enough to satisfy the pressing needs of fungal ecologists. Here, social activism alone is not going to be sufficient largely due to the problem of organismal size, mentioned above, which is as old as Linnaeus. Mycologists cannot expect botanists to fully appreciate the problems created by working with microscopic organisms that can neither be routinely collected nor cultured. Mycology, to free itself from the legacy of botanical nomenclature, needs a nomenclatorial revolution.

It is time for mycologists, who best understand the nomenclatorial needs peculiar to fungi, to design a nomenclatorial code for fungi. The timing could not be better because over the past two decades one of our own, David Hawksworth, has been helping to guide the development of the BioCode (Greuter *et al.* 2011, Hawksworth 2011). Modification of the draft BioCode to enable One Fungus = One Name and to accommodate ENAS fungi could produce a MycoCode that would be fully compatible with the BioCode. In considering microscopic organisms, a newly created MycoCode could also inspire those working on *Bacteria*, *Archaea* and other microscopic *Eukarya*. We mycologists have the need and, in the nomenclatorial committees of the International Mycological Association² and the Mycological Section of the International Union of Microbiological Societies, the means to accomplish this task. All that mycologists now lack is an excuse to do nothing.

² Including the Nomenclature Committee for Fungi, which it is proposed be elected at International Mycological Congresses rather than at International Botanical Congresses as at present (Hawksworth *et al.* 2009, Norvell *et al.* 2010), and the International Commission on the Taxonomy of Fungi (a joint Commission with IUMS).

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