PERSPECTIVES

ESSAY

Fungal systematics: is a new age of enlightenment at hand?

David S. Hibbett and John W. Taylor

Abstract | Fungal taxonomists pursue a seemingly impossible quest: to discover and give names to all of the world's mushrooms, moulds and yeasts. Taxonomists have a reputation for being traditionalists, but as we outline here, the community has recently embraced the modernization of its nomenclatural rules by discarding the requirement for Latin descriptions, endorsing electronic publication and ending the dual system of nomenclature, which used different names for the sexual and asexual phases of pleomorphic species. The next, and more difficult, step will be to develop community standards for sequence-based classification.

Taxonomists create the language of biodiversity, enabling communication about different organisms among basic and applied scientists, educators, students and the general public. This essential work is particularly challenging in hyperdiverse and morphologically cryptic groups, such as the kingdom Fungi. Roughly 100,000 species of fungi are accepted in the current taxonomy[1], but more than 400,000 fungal species names — including numerous synonyms — are recorded in the literature, and it is likely that millions of new species[2] still await description. Thus, the challenge for modern fungal taxonomy is to weed out redundant published names while accelerating the naming of newly discovered species. To regulate the naming of fungi, mycologists adhere to the *International Code of Botanical Nomenclature*[3]. The code provides stability to a potentially chaotic discipline, but it is updated only once every 7 years and only at meetings of the Nomenclature Section during the International Botanical Congress (IBC), which makes the code slow to adapt to modern practices in systematics. The fungal elements of the code that have been criticized as archaic include the dual system of nomenclature[4], which creates different names for the anamorphs (asexual forms) and teleomorphs (sexual forms) of the same species (FIG. 1), and the requirement for physical type specimens, which complicates efforts to classify taxa that are discovered through metagenomics[5].

In the lead-up to the last IBC in July 2011, a vocal and well-organized group of mycologists launched a 'One fungus, one name' campaign aimed at ending the system of dual nomenclature. The movement culminated in the publication of 'The Amsterdam declaration on fungal nomenclature' (by 88 co-authors from 26 countries)[4], which suggested that if dual nomenclature were retained in the botanical code, it might be necessary to create a separate MycoCode for the kingdom Fungi[6]. Independently, some mycologists had already begun to publish new fungal names that ignored reproductive morphology, putting sexual and asexual species in the same genus and thus deliberately disregarding the code[7–9]. Facing nomenclatural disobedience and the threat of secession, the Nomenclature Section of the 2011 IBC voted to abolish the dual system of fungal nomenclature[10,11]. At the same time, and in response to pressure from other activists, the Nomenclature Section also voted to eliminate Latin descriptions (English will now suffice), to allow the publication of new names in online-only journals (previously, print was required) and to require registration of new fungal names in a publically accessible database such as Index Fungorum or MycoBank[10]. Finally, the code itself was renamed the *International Code of Nomenclature for Algae, Fungi, and Plants* (ICN). To many scientists, these may seem like overdue, common-sense measures, but to some fungal taxonomists, the changes were seismic[11].

In the long run, a unitary nomenclature system for pleomorphic fungi, along with the other changes, will promote effective communication. In the short term, however, the abandonment of dual nomenclature will require mycologists to work together to resolve the correct names for large numbers of fungi, including many economically important pathogens and industrial organisms. Here, we consider the opportunities and challenges posed by the repeal of dual nomenclature and the parallels and contrasts between nomenclatural practices for fungi and prokaryotes. We also explore the options for fungal taxonomy based on environmental sequences and ask whether sequence-based taxonomy can be reconciled with the ICN.

One name, one fungus

The dual nomenclature system for pleomorphic fungal species arose in the nineteenth century, influenced by the use of sexual morphology in the Linnaean classification of plants[12,13]. Despite the fact that is illogical to assign multiple names to one species, the dual nomenclature system persisted, in part because the morphology of sexual reproductive structures was assumed to be superior to that of asexual forms for inferring the evolutionary relationships of fungi[14]. However, sexual characteristics lost their pre-eminence for classifying fungi in the late 1980s, when PCR made DNA variation accessible to systematic mycologists. More than 20 years later, the dual nomenclature system was finally abolished.

As is always the case, the hard work begins after the revolution. For mycologists, this means choosing names for thousands of pleomorphic fungal species. Some choices will be difficult. For example, the anamorphic genus *Penicillium* (with teleomorphic genera *Eupenicillium* and *Talaromyces*) contains fungi as important as *Penicillium rubens* (the original source of penicillin), *Penicillium marneffei* (the causative agent of an AIDS-defining disease in Thailand),

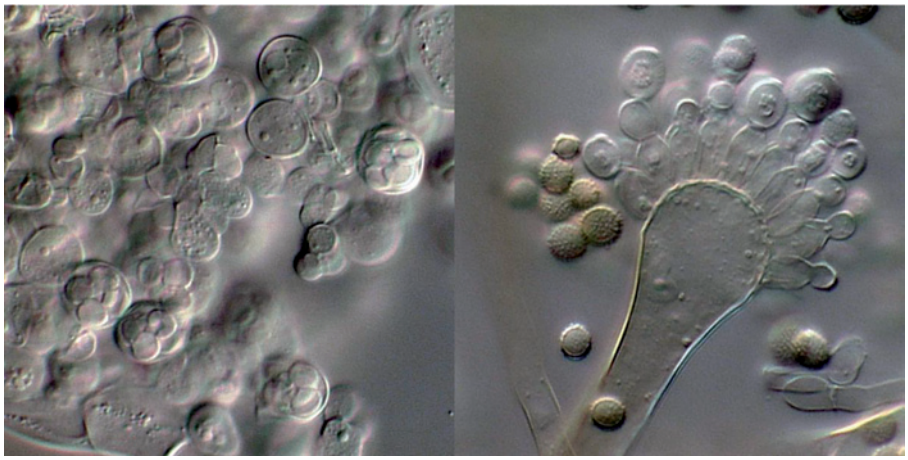

Figure 1 | **Two names, one fungus.** *Eurotium herbariorum* is a pleomorphic fungus that has a sexual phase, reproducing by ascospores (the teleomorphic form; left), as well as a conidium-producing asexual phase (the anamorphic form; right) that has been named *Aspergillus glaucus*. Images courtesy of Paul F. Cannon, Royal Botanical Gardens, Kew, London, UK, and the Centre for Agricultural Bioscience International (CABI).

and *Penicillium camemberti* and *Penicillium roqueforti* (used to make Camembert and Brie, and Roquefort cheeses, respectively). However, *Penicillium* spp., as traditionally delimited, are paraphyletic as well as pleomorphic, so these well-known species cannot all remain in this historic genus[15].

Under the revised code, any of the existing valid names for a species can be selected as its correct name, with preference given to the oldest name. However, this libertarian view is tempered by two additional revisions, both involving review by the General Committee (GC) of the ICN, which is empowered to vote on proposals to conserve or reject names of fungal taxa, as well as to modify the ICN itself[3]. First, in situations in which both the anamorph and teleomorph names for the same taxon are widely used — for example, *Fusarium* (anamorph) and *Gibberella* (teleomorph) at the genus level — the teleomorph name can be chosen without approval of the GC, but selection of the anamorph name, even if it is the older name, requires approval. Apparently, it is hard for systematists to abandon the primacy of sexual characteristics. Second, the GC has the authority to approve lists of names, which presumably will be generated by committees of mycologists with expertise in particular taxonomic groups. However, mycologists have retained the right to appeal any decision about names through the established process of conservation of names.

No one has had a chance to choose a name for a pleomorphic fungal species under the new code, which only came into effect on 1 January 2013, but the nomenclatural changes mentioned above illustrate what might lie ahead. Another example is the work of Gräfenhan *et al.*[9] on the taxonomy of the anamorphic genus *Fusarium*, one of the largest genera of fungi, containing nearly 1,500 species, subspecies, varieties and formae speciales. *Fusarium* spp. include important plant and animal pathogens and mycotoxin producers and have been linked to as many as seven teleomorph genera. On the basis of sequence analyses for RNA polymerase II and ATP citrate lyase genes, Gräfenhan *et al.*[9] identified 15 clades with *Fusarium*-like asexual forms and gave six of them names based on anamorphs, although five of these six have known teleomorphic forms. The reclassification of *Fusarium* by Gräfenhan *et al.* is based on robust phylogenies and would be nomenclaturally valid under the forthcoming ICN. Nevertheless, name changes in the genus *Fusarium sensu lato* might confuse and inconvenience user communities and regulatory bodies in agriculture and medicine, and it remains to be seen how these constituencies will react to the new taxonomy.

The complex nomenclatural history of many groups of pleomorphic fungi, coupled with phylogenetic uncertainty and the sometimes passionate opinions of stakeholders, presents a very challenging taxonomic problem. The code provides guidance, but many decisions about names cannot be reduced to 'legal' algorithms. As a follow-up to the 'One fungus, one name' movement that led to the repeal of dual nomenclature, a 'One fungus, which name?' conference was held in Amsterdam in April 2012 (REF. 16). This time, the goal was to begin working through the myriad options for the classification of pleomorphic fungi in light of the new rules. Similar meetings and workshops on the taxonomy of the genus *Fusarium*, the order Hypocreales and other groups were held in association with meetings of the Mycological Society of Japan (May 2012), the Mycological Society of America (July 2012) and the Mycological Society of China (August, 2012).

Classification of environmental sequences

Now that dual nomenclature has been abolished, the next major challenge for fungal taxonomy is to develop strategies for classifying environmental sequences (FIG. 2). Nobody knows how many unnamed species have already been detected through metagenomic studies (and this fact alone indicates the need for a centralized database of species that are based on environmental sequences), but as early as 2007 the number of clusters of closely related rRNA genes being discovered with Sanger chemistry approached the number of species being described from specimens[5], and the rate of molecular species discovery has surely increased with the application of next-generation sequencing in metagenomics.

Environmental studies have revealed not only individual species, but also major clades of fungi, such as the class Archaeorhizomycetes[17], containing a diverse group of soil-inhabiting fungi from the phylum Ascomycota. Sequences of Archaeorhizomycetes members have been reported in more than 50 independent studies, and they can be grouped into more than 100 species-level entities[17]. Nevertheless, only one species, *Archaeorhizomyces finlayi*, has been formally described, based on a culture that was obtained from conifer roots. A similar example is provided by the phylum Rozellomycota[18] (also known as Cryptomycota[19]), a large clade of aquatic and soil-inhabiting fungi that is known almost entirely from environmental sequences. The phylum Rozellomycota has been shown to contain the previously described chytrid genus *Rozella*[19], but most of the diversity of this phylum is in groups that are known only from environmental sequences and have not been named. These examples, and many others from fungal molecular ecology, illustrate the profound disconnect that now exists between formal taxonomy and species discovery through environmental sequences. Barriers to the naming of such species include a perceived conflict with the code, and errors and

Figure 2 | **Unnamed diversity.** A demonstration of the problem posed by unnamed fungi that are known only from environmental DNA sequences. When a new environmental sequence (the bottom-most operational taxonomic unit, gi|22497358; blue box) was used in a BLAST search of the GenBank database and the result displayed using the BLAST distance tree tool, only two of the 35 most closely related sequences were from cultured organisms (green boxes), and only one was named (*Fibulobasidium murrhardtense*). Without names, the information content of this tree leaves much to be desired. ITS, internal transcribed spacer; PS, partial sequence.

incomplete taxon sampling in reference sequence databases.

The perceived incompatibility of the code with sequence-based taxonomy is a consequence of the requirement for type specimens. However, the code places no restrictions on the form of type specimens, which need not be complete or representative; all that is required of a type specimen is that it should be a physical specimen. In principle, an aliquot of DNA extracted from an environmental sample, or a portion of the substrate from which the DNA was isolated, can serve as a legitimate type specimen. To prove this point, Kirk *et al.*[20] recently described a new species of rumen chytrid, *Piromyces cryptodigmaticus*, based on sequence data, and typified it with a sample from the fermenter from which the DNA was extracted. The new taxon name was validly published, even though the fungus was never directly observed. In the future, if purely sequence-based taxonomy is incorporated into the code, it may be possible to forego the deposition of physical type materials altogether. In the meantime, the publication of *P. cryptodigmaticus* provides a model for environmental molecular biologists who would like to formalize their discoveries through code-compliant taxonomic names.

Errors and incomplete taxonomic sampling in sequence databases, such as GenBank, present a psychological barrier to naming environmental sequences; if an environmental sequence has no match in GenBank, it could still represent a described but unsequenced species. Faced with such uncertainty, fungal taxonomists might be reluctant to describe new species based on environmental sequences. They should not be; current estimates of the actual diversity in the kingdom Fungi range from as few as 500,000 species to millions of species[2], suggesting that most unmatched environmental sequences probably do represent new species[5]. Even if some environmental species prove to be redundant, taxonomists are accustomed to resolving synonymy based on the principle of priority. Finally, the solution to the GenBank problem is conceptually straightforward — that is, generate well-documented reference sequences[21] — and is already being pursued through the fungal bar-coding initiative[22] and the creation of custom-curated databases of well-documented reference sequences, such as the RefSeq collection within GenBank, and the UNITE database for mycorrhizal fungi[23].

Lessons from prokaryotic taxonomy

Many of the taxonomic challenges faced by mycologists parallel those faced by researchers studying prokaryotes, but the nomenclatural practices adopted by the two groups are often divergent. For example, the expanded power of the GC to rule on the legitimacy of choices among existing names under the forthcoming ICN might worry some mycologists, who could fear a loss of taxonomic freedom, but the new system for fungi might seem familiar to prokaryote taxonomists, who have long used a Judicial Commission to accept or reject newly proposed names[24,25]. Another key difference between the nomenclatural codes for prokaryotes[26] and fungi[3] is that

the prokaryotic code specifies the technical means to recognize new species, and all new species are recorded in the *International Journal of Systematic and Evolutionary Microbiology*, whereas the ICN specifies no particular technique for the recognition of fungal species, which can be published in diverse venues. Under the ICN, acceptance of fungal species is left to the mycology community; new names are picked up by other mycologists and appear in the literature, or they are simply ignored. The highly regulated system for prokaryotes promotes uniformity in the species recognition criteria and preserves the stability of names, but it can also limit the rate of species description. By contrast, the laissez-faire system for fungi results in non-uniform species recognition criteria (for example, many new species descriptions lack supporting molecular data[5]), extensive synonymy, an ongoing challenge in compiling new names (although the new requirement for name registration will solve this problem) and frequent changes in species-level classifications. At the same time, the fungal system promotes rapid taxonomic updates to reflect new discoveries and advances in phylogenetic reconstruction.

Changes in fungal species classifications often occur when evidence for genetic diversity is discovered within morphological taxa. For example, it might have surprised readers to learn that Alexander Fleming's *Penicillium* species, *Penicillium chrysogenum*, is now known as *P. rubens*[27], but the change was necessitated when phylogenetic and population genetics data showed that the *P. chrysogenum* of old harboured several genetically isolated species[28]. Older mycologists may grumble about having to learn a new name, but the new classification reflects the current state of knowledge, and new students will not be bothered by the change. By contrast, the archaeon *Sulfolobus islandicus* was shown to comprise several genetically isolated species according to population genetics techniques, which showed genetic isolation by distance[29] and also evidence of ecological speciation[30], but these species were left unnamed, in part because the now passé technique of DNA–DNA hybridization would have been required for formal species descriptions[24]. Admittedly, there are huge challenges in determining species limits in bacteria and archaea, particularly in the face of extensive horizontal gene transfer[31]. Nonetheless, the differences in nomenclatural practices for bacteria and archaea versus fungi may be part of the reason why the number of new species described per year is about twice as many for fungi as it is for prokaryotes[5,32]. The ICN will increase the centralization of taxonomic authority for fungi, although the basic criteria for fungal species recognition will remain unrestricted. It is important that as the new rules of the ICN are implemented, the GC acts with restraint and does nothing to impede progress in fungal species description.

Mycologists can also learn from the experience of bacterial and archaeal researchers with regard to the classification of environmental sequences. The requirement for a living type culture for describing bacterial or archaeal species[26] is comparable to the requirement for a physical type specimen for naming fungal species. To enable the naming of bacteria that lack cultures but are known by "more than a mere sequence" (REF. 33), Murray and Schleifer[34] suggested that the prefix *Candidatus* be used, indicating that the name is provisional. This recommendation has been appended to the bacterial code[25], but fewer than 400 bacteria and archaea have been described as *Candidatus* species[35]. If mycologists wish to adopt a new category similar to *Candidatus* to accommodate the huge numbers of species discovered through environmental sequences, as has been suggested[5], they will need to find ways to facilitate high-throughput taxonomy, almost certainly involving automated work flows.

The future of fungal taxonomy

Twenty-five years after the first description of PCR, species-level fungal taxonomy is finally catching up with the molecular revolution. Change has come slowly and has been prompted by the actions of radicals, who flouted and subverted the code by naming taxa based on anamorphs[7,8] or environmental sequences[20]. Such individual acts of rebellion illuminate the way forward, but ultimately fungal taxonomy is a group enterprise that can succeed only with the support and participation of the broad community of mycologists. Proponents of unitary taxonomy worked effectively as a community to repeal dual nomenclature and are now organizing themselves to resolve the correct names of scores of pleomorphic fungal species. Supporters of sequence-based taxonomy have not been so unified, however. The publication of *P. cryptodigmaticus* demonstrates that it is 'legally' possible, under the code, to describe new species based on sequences (as long as a nominal type is deposited somewhere), but community effort will be needed to develop the broadly accepted protocols required for a mass movement towards sequence-based taxonomy.

At least one difficult issue appears to have been resolved: the internal transcribed spacer (ITS) region of the nuclear rRNA gene has been proposed as the fungal barcode locus[22] and is being used for sequence-based species delimitation in environmental surveys for many groups of fungi. However, other key issues remain problematic. Longer reads that provide sequences for the ITS and the phylogenetically tractable large subunit (LSU) rRNA cannot be obtained until there are improvements in next-generation sequencing. The gold standard for species delimitation in fungi is the genealogical concordance method, which uses multiple genetic loci to assess the limits of recombination[36]. Such approaches are not applicable in environmental data sets, which usually use single loci amplified from pooled DNAs. Moreover, in order to carry out species delimitation in environmental samples, the consequences of intragenomic heterogeneity in multicopy rRNA genes, as well as error owing to gene tree versus species tree conflict, will have to be determined empirically in relation to multigene data sets. The names of species known only from environmental sequences might require a new taxonomic category comparable to the *Candidatus* status for bacteria and archaea[5], or an identifying suffix (for example, ENAS (environmental nucleic acid sequence) or eMOTU (environmental molecular operational taxonomic unit))[6]. The reality of sequencing errors might prevent naming until the same sequence is found a second time and by a different research group. Finally, mycological databases such as MycoBank must prepare for a massive influx of new species, especially if automated work flows are developed to describe fungi from environmental nucleic acid sequences. Given the rate of species discovery, mycologists do not have another 25 years to ponder the problem.

David S. Hibbett is at The Biology Department, Clark University, Worcester, Massachusetts 01610, USA.

John W. Taylor is at The Department of Plant and Microbial Biology, University of California, Berkeley, California 94720, USA.

Correspondence to D.S.H.
e-mail: dhibbett@clarku.edu

doi:10.1038/nrmicro2942
Published online 3 January 2013

1. Kirk, P. *et al*. (eds) *Dictionary of the Fungi* 10th edn (CABI, 2008).
2. Bass, D. & Richards, T. A. Three reasons to re-evaluate fungal diversity "on Earth and in the ocean". *Fungal Biol. Rev.* **25**, 159–164 (2011).

3. McNeill, J. *et al.* (eds) *International Code of Botanical Nomenclature (Vienna Code)* (Gantner, 2006).
4. Hawksworth, D. L. *et al.* The Amsterdam declaration on fungal nomenclature. *IMA Fungus* **2**, 105–112 (2011).
5. Hibbett, D. S. *et al.* Progress in molecular and morphological taxon discovery in Fungi and options for formal classification of environmental sequences. *Fungal Biol. Rev.* **25**, 38–47 (2011).
6. Taylor, J. W. One fungus = one name: DNA and fungal nomenclature twenty years after PCR. *IMA Fungus* **2**, 113–120 (2011).
7. Houbraken, J., Frisvad, J. C. & Samson, R. A. Taxonomy of *Penicillium citrinum* and related species. *Fungal Divers.* **44**, 117–133 (2010).
8. Crous, P. W. *et al.* Phylogenetic lineages in the *Botryosphaeriaceae. Stud. Mycol.* **55**, 235–253 (2006).
9. Gräfenhan, T., Schroers, H.-J., Nirenberg, H. I. & Seifert, K. A. An overview of the taxonomy, phylogeny, and typification of nectriaceous fungi in *Cosmospora, Acremonium, Fusarium, Stilbella,* and *Volutella. Stud. Mycol.* **68**, 79–113 (2011).
10. Norvell, L. L. Fungal nomenclature. 1. Melbourne approves a new Code. *Mycotaxon* **116**, 481–490 (2011).
11. Hawksworth, D. A new dawn for the naming of fungi: impacts of decisions made in Melbourne in July 2011 on the future publication and regulation of fungal names. *IMA Fungus* **2**, 155–162 (2011).
12. Weresub, L. K. & Pirozynski, K. A. in *The Whole Fungus: The Sexual-Asexual Synthesis* (ed. Kendrick, B.) 17–30 (National Museum of Natural Sciences and National Museums of Canada, 1979).
13. Tulasne, L.-R. & Tulasne, C. *Selecta Fungorum Carpologia.* Vol. 1 (Imperial Typographer, 1861).
14. Kendrick, B. (ed.) *The Whole Fungus: The Sexual-Asexual Synthesis.* (National Museum of Natural Sciences and National Museums of Canada, 1979).
15. Houbraken, J. & Samson, R. A. Phylogeny of *Penicillium* and the segregation of Trichocomaceae into three families. *Stud. Mycol.* **70**, 1–51 (2011).
16. Hawksworth, D. L. & Taylor, J. W. One fungus = which name? *IMA Fungus* **3**, 10–14 (2012).
17. Rosling, A. *et al.* Archaeorhizomycetes: unearthing an ancient class of ubiquitous soil fungi. *Science* **333**, 876–879 (2011).
18. James, T. Y. & Berbee, M. L. No jacket required – new fungal lineage defies dress code: recently described zoosporic fungi lack a cell wall during trophic phase. *Bioessays* **34**, 94–102 (2012).
19. Jones, M. D. *et al.* Discovery of novel intermediate forms redefines the fungal tree of life. *Nature* **474**, 200–203 (2011).
20. Kirk, P. M. Index Fungorum no. 2. *Index Fungorum* [online] http://www.indexfungorum.org/Publications/Index%20Fungorum%20no.2.pdf (2012).
21. Bidartondo, M. I. Preserving accuracy in GenBank. *Science* **319**, 1616 (2008).
22. Schoch, C. L. *et al.* Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proc. Natl Acad. Sci. USA* **109**, 6241–6246 (2012).
23. Abarenkov, K. *et al.* The UNITE database for molecular identification of fungi – recent updates and future perspectives. *New Phytol.* **186**, 281–285 (2010).
24. Tindall, B. J., Rossello-Mora, R., Busse, H. J., Ludwig, W. & Kampfer, P. Notes on the characterization of prokaryote strains for taxonomic purposes. *Int. J. Syst. Evol. Microbiol.* **60**, 249–266 (2010).
25. De Vos, P., Trüper, H. G. & Tindall, B. J. Judicial Commission of the International Committee on Systematics of Prokaryotes; Xth International (IUMS) Congress of Bacteriology and Applied Microbiology; Minutes of the meetings, 28, 29 and 31 July and 1 August 2002, Paris, France. *Int. J. Syst. Evol. Microbiol.* **55**, 525–532 (2005).
26. Lapage, S. *et al.* (eds) *International Code Of Nomenclature Of Bacteria.* (American Society for Microbiology, 1992).
27. Houbraken, J., Frisvad, J. C. & Samson, R. A. Fleming's penicillin producing strain is not *Penicillium chrysogenum* but *P. rubens. IMA Fungus* **2**, 87–95 (2011).
28. Henk, D. A. *et al.* Speciation despite globally overlapping distributions in *Penicillium chrysogenum*: the population genetics of Alexander Fleming's lucky fungus. *Mol. Ecol.* **20**, 4288–4301 (2011).
29. Whitaker, R. J., Grogan, D. W. & Taylor, J. W. Geographic barriers isolate endemic populations of hyperthermophilic archaea. *Science* **301**, 976–978 (2003).
30. Cadillo-Quiroz, H. *et al.* Patterns of gene flow define species of thermophilic Archaea. *PLoS Biol.* **10,** e1001265 (2012).
31. Gevers, D. *et al.* Re-evaluating prokaryotic species. *Nature Rev. Microbiol.* **3**, 733–739 (2005).
32. Rainey, F. A. & Oren, A. in *Methods in Microbiology.* Vol. 38 (eds Rainey, F. & Oren, A.) 1–5 (Academic, 2011).
33. Murray, R. G. E. & Stackebrandt, E. Taxonomic note: implementation of the provisional status *Candidatus* for incompletely described procaryotes. *Int. J. Syst. Bacteriol.* **45**, 186–187 (1995).
34. Murray, R. G. E. & Schleifer, K. H. Taxonomic notes: a proposal for recording the properties of putative taxa of procaryotes. *Int. J. Syst. Bacteriol.* **44**, 174–176 (1994).
35. Euzéby, J. P. Some names included in the category *Candidatus. List of Prokaryotic Names with Standing in Nomenclature* [online], http://www.bacterio.cict.fr/candidatus.html (2012).
36. Taylor, J. *et al.* Phylogenetic species recognition and species concepts in fungi. *Fungal Genet. Biol.* **31**, 21–32 (2000).

Acknowledgments
The authors thank their colleagues and members of their laboratories for discussions on the principles of fungal taxonomy, and the International Mycological Association and the Centraalbureau voor Schimmelcultures for hosting meetings addressing the revolution in fungal nomenclature. Research in the authors' laboratories is supported by the Open Tree of Life Project (http://opentreeoflife.org/), the US National Science Foundation (grant DEB-1208719 to D.S.H.), the US National Institutes of Health (grant U54-AI65359 to J.T.W.) and the Energy Biosciences Institute (grant EBI 001J09 to J.W.T.).

Competing interests statement
The authors declare no competing financial interests.

FURTHER INFORMATION
David S. Hibbett's homepage: http://www.clarku.edu/faculty/dhibbett/
John W. Taylor's homepage: http://taylorlab.berkeley.edu/
GenBank: http://www.ncbi.nlm.nih.gov/genbank/
IndexFungorum: http://www.indexfungorum.org/
MycoBank: http://www.mycobank.org/
RefSeq: http://www.ncbi.nlm.nih.gov/RefSeq/
UNITE: http://unite.ut.ee/

ALL LINKS ARE ACTIVE IN THE ONLINE PDF