NOMENCLATURE

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Choosing one name for pleomorphic fungi: The example of *Aspergillus* versus *Eurotium*, *Neosartorya* and *Emericella*

John W. Taylor,[1] Markus Göker[2] & John I. Pitt[3]

1 *Department of Plant and Microbial Biology, University of California, Berkeley, California 94720-3102, U.S.A.*
2 *Leibniz Institute DSMZ – German Collection of Microorganisms and Cell Cultures, Braunschweig 38124, Germany*
3 *CSIRO Food and Nutrition, North Ryde, New South Wales 2113, Australia*
Author for correspondence: *John W. Taylor, jtaylor@berkeley.edu*
ORCID JWT, http://orcid.org/0000-0002-5794-7700; MG, http://orcid.org/0000-0002-5144-6200; JIP, http://orcid.org/0000-0002-6646-6829

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Abstract With the termination of dual nomenclature, each fungus may have only one name. Now mycologists must choose between genus names formerly applied to taxa with either asexual or sexual reproductive modes, a choice that often influences the breadth of genotypic and phenotypic diversity in a genus, and even its monophyly. We use the asexual genus *Aspergillus* to examine the problems involved in such choices because (a) 11 sexual generic names are associated with it and (b) phenotypic variation and genetic divergence within sexual genera are low but between sexual genera are high. As a result, in the case of *Aspergillus*, applying the asexual name to the many sexual genera masks information now conveyed by the genus names and would lead to taxonomic inconsistency in the Eurotiales because this large *Aspergillus* would then embrace more genetic divergence than neighboring clades comprised of two or more genera. Two proposals have been published concerning this problem as it relates to *Aspergillus*: one advocates a broad concept, referred to here as "Wide Aspergillus", which embraces as many *Aspergillus* species as possible while maintaining *Penicillium* as a separate genus; the other, referred to here as "Narrow Aspergillus", preserves this genus for a much smaller group of closely related species and retains many of the sexual genera. Phylogenetic analyses detailed here show that, to be monophyletic, Wide Aspergillus must embrace several genera morphologically discordant with *Aspergillus*, including *Penicillium*, *Phialosimplex* and *Polypaecilum*. Likelihood ratio tests reject a Wide Aspergillus that excludes *Phialosimplex* and *Polypaecilum*. Phylogenetic Rank Boundary Optimization, which employs the genetic divergence measure, maximum subtree height, to assess inconsistency in the ranking of genera and species, shows that Narrow Aspergillus provides a more consistent taxonomy than Wide Aspergillus. Adopting Narrow Aspergillus and retaining sexual names instead of adopting Wide Aspergillus will result in genera that convey precise morphological and physiological information, that are monophyletic, and that are taxonomically consistent.

Keywords anamorph; generic concept; one-fungus-one-name; pleomorphic fungi; phylogeny; taxonomy; teleomorph

Supplementary Material DNA sequence alignment is available from TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S18596).

■ INTRODUCTION

Among the significant changes to botanical nomenclature following the International Botanical Congress in Melbourne was the abandonment of dual nomenclature for pleomorphic fungi. Previously, the sexual (teleomorphic) and asexual (anamorphic) states of ascomycetous fungi (except lichens) and some basidiomycetous fungi could be given separate names. However, the abandonment of this practice in the latest *International Code of Nomenclature for algae, fungi and plants* (*ICN*, McNeill & al., 2012) requires that each fungal species have only one name. This change poses a dilemma for fungal taxonomists, as many fungi are pleomorphic, having one or more generic names for sexual states associated with one or more asexual states. Guidance has been provided to mycologists in the form of a preference for sexual names and a consideration by the Nomenclature Committee for Fungi of lists of preferred names created and submitted by working groups of specialists. Here, to explore this general problem we focus on the asexual genus *Aspergillus* P.Micheli ex Haller because it is one of the oldest names applied to any fungus, and because species of *Aspergillus* impact the fields of industry (in both the creation and preservation of products), medicine and basic scientific research. This genus is characterized by a well-defined asexual fruiting structure, but is very broad in concept, as it is associated with 11 sexual state genera that reflect variations in morphology, physiology (especially temperature and water relations), enzymology, and toxicology (Geiser, 2009; Houbraken & Samson, 2011).

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Two proposals have been advanced for applying one name to the fungi with *Aspergillus* asexual morphology. One begins by identifying the largest monophyletic clade containing a majority of species with the asexual, reproductive morphology characteristic of *Aspergillus* that does not also include members of the genus *Penicillium* Link, which is as least as well known and important as *Aspergillus*. Species of *Penicillium* make the famous antibiotic, penicillin, and are essential to the production of many cheeses and sausages, but they also produce toxins and cause spoilage in food and animal feeds. Under this proposal, the name *Aspergillus* would be applied to all of the species in that clade (Houbraken & Samson, 2011). This circumscription we will refer to as "Wide Aspergillus". The second proposal advocates recognizing the diversity in morphological and physiological phenotypes among these fungi, by maintaining the sexual names in some of these clades, and restricting the name *Aspergillus* to one or more closely related clades, at the same time preserving *Aspergillus* for many important species names (Pitt & Taylor, 2014). This circumscription we will refer to as "Narrow Aspergillus". Both proposals can be seen in Figs. 1 and 2 below.

Although Wide Aspergillus has the natural appeal of preserving a large, important genus, phylogenetic problems exist, concerning both exclusion of fungi with *Aspergillus* morphology and inclusion of other fungi that lack it. In terms of exclusion, several taxa that possess *Aspergillus* anamorphs (the sexually defined genus *Sclerocleista* Subram. and the species *A. clavatoflavus* Raper & Fennell, *A. zonatus* Kwon-Chung & Fennell, and *A. penicilliformis* Kamyschko) must be left outside Wide Aspergillus because including them would require also including *Penicillium*. In terms of inclusion, some taxa that lack the *Aspergillus* anamorph (the genera *Polypaecilum* G.Sm. and *Phialosimplex* Sigler & al. and the species *Basipetospora halophila* (J.F.H.Beyma) Pitt & A.D.Hocking) must be included in Wide Aspergillus to maintain monophyly. Also in terms of inclusion, some widely accepted, sexual genera, based on distinct sexual and physiological phenotypes associated with socially important attributes of spoilage, disease and research, i.e., *Eurotium* (F.H.Wigg.) Link, *Neosartorya* Malloch & Cain and *Emericella* Berk., lie inside Wide Aspergillus.

In pursuit of a nomenclature that supports a large and diverse genus *Aspergillus*, a taxonomy has recently been proposed that ignores these biological and socially important differences (Samson & al., 2014). As we show here, in doing so, the normal process of using biological data to inform taxonomy, and then establishing a nomenclature to reflect taxonomy, has been inverted, resulting in a single, overly large genus that hides variation in sexual morphology and physiology and that is rendered inconsistent by embracing an excess of genetic variation.

Alternatives to the Wide Aspergillus circumscription are available in the form of valid names based on sexual morphology, which, if recognized rather than synonymized, would better reflect the phenotypic diversity of these fungi. Simply maintaining this existing nomenclature would implement a taxonomy based on sound biological characters, but would result in the loss of the name *Aspergillus*. More particularly, because the type of *Aspergillus* resides in the *Eurotium* clade, a sexual genus with distinctive morphology, physiology and social importance (Pitt & Taylor, 2014), both generic names cannot validly be maintained without a nomenclatural change. If the type of *Aspergillus* were moved from *Eurotium* to another biologically defined clade, it would be possible to achieve a nomenclature that reflects a sound biological taxonomy and also preserves *Aspergillus*. Such a change would be readily accomplished by conservation. Based on phylogenetic analysis and social importance, *Aspergillus* subg. *Circumdati* W.Gams & al. is the logical clade, and *A. niger* Teigh. the logical species to serve as a conserved type (Pitt & Taylor, 2014). This change is proposed in a companion paper (Pitt & Taylor, 2016). It is important to note that the proposed change in typification of *Aspergillus* does not affect the debate between Wide and Narrow Aspergillus, because both proposals for redefining *Aspergillus* would be compatible with the change in type.

■ MATERIALS AND METHODS

DNA sequences analyzed included the *RPB1* and *RPB2* genes coding for subunits of RNA polymerase II; *tsr1*, coding for a putative ribosome biogenesis protein; and *cct8*, coding for the theta subunit of the TCP-1 chaperonin complex, all of which have been used for phylogenetic analysis of *Aspergillus* and related taxa (Table 1—Houbraken & Samson, 2011; Table 2—Pitt & Taylor, 2014). Taxon sampling is identical to that of Pitt & Taylor (2014). Sequences for two species were updated with new sequences from GenBank, *Aspergillus flavus* Link (*tsr1* HM802990.1) and *Emericella nidulans* (Eidam) Vuill. (*cct8* XM_654363.1, *RPB1* XM_653321.1, *RPB2* XM_677297.1, *tsr1* XM_658778.1).

Alignment of concatenated DNA sequences of the four genes was initiated with EMBL-EBI web-based MUSCLE (http://www.ebi.ac.uk/Tools/msa/muscle/; Edgar, 2004), optimized manually, and trimmed to make sequences of equal length. The alignment is deposited at TreeBASE (submission ID:18596).

Maximum likelihood, phylogenetic analysis of the alignment was performed using RAxML-HPC2 on XSEDE (v.8.1.11) (Stamatakis, 2006) as implemented in CIPRES v.3.3 (https://www.phylo.org/) using RAxML-HPC2 on XSEDE for nucleotide data with 25 distinct rate categories. For bootstrapping, a GTRCAT evolution model was used with 1000 iterations. Maximum likelihood analysis of constrained phylogenies (Tables 1, 2) used constraint trees in Newick format that were uploaded using Constraint (-g) in RAxML. The unconstrained tree (Fig. 3) was plotted with Dendroscope v.3.2.10 (Huson & Scornavacca, 2012).

The Shimodaira Approximately Unbiased Test (Shimodaira, 2002) was applied using PAUP v.4.0a145 (http://paup.csit.fsu.edu/) with the RAxML alignment converted to NEXUS format and a file composed of the best trees from each constrained RAxML analysis using the following likelihood settings: substitution rates as GTR estimated, nucleotide frequency as HKY 1985 empirical, variation across sites as a gamma distribution

with 4 categories and none invariable, and as default, starting values, optimization and "other".

For Phylogenetic Rank Boundary Optimization (PRBO), we have developed an implementation based on the "APE" (Paradis & Strimmer, 2004) and "rpart" (Therneau & al., 2015) packages for the statistical computing environment R (R Development Core Team, 2015). PRBO (Liu & al., 2015) is a variant of clustering optimization (Göker & al., 2009) that is based on rooted phylogenies. PRBO employs maximum subtree height (MaSH), which is the only divergence measure that guarantees, even in non-ultrametric trees, that the divergence of each progeny clade is no larger than the divergence of its immediate parent clade. MaSH is to some degree comparable to pairwise distances because the length of the stem branch is not counted in order to obtain a measure that is, in the case of ultrametric phylogenies, equal to half the maximum patristic distance within each subtree (Scheuner & al., 2014).

A classification is found to be inconsistent regarding its ranks if there exists a taxon of a certain rank whose clade has a higher MaSH than a clade that contains more than a single taxon of the same rank. This situation can be observed in phylogenies that contain *Aspergillus* and related genera of Onygenales, where the depth of branching among *Aspergillus* species exceeds that of clades that comprise multiple genera as distinct as *Histoplasma* Darling, *Blastomyces* Costantin & Rolland and *Emmonsia* Cif. & Montemart. or as distinct as *Coccidioides* G.W.Stiles and *Uncinocarpus* Sigler & G.F.Orr (Fig. 4). To document such inconsistencies in a quantitative manner, an optimal upper MaSH boundary can be determined for each rank, which also serves as the lower MaSH boundary of the next higher rank. Using an existing classification as a template, these MaSH ranges for each rank are chosen so as to minimize the number of taxa whose MaSH is outside the MaSH range of their respective rank (Liu & al., 2015). The remaining inconsistent taxa can be improved by revising their circumscription to include more or fewer species, until their MaSH values indicate an absence of inconsistencies.

■ RESULTS AND DISCUSSION

It is an axiom that taxonomy should be based on the best biology, both genetic and phenotypic, and that both should advise nomenclature. Recent phylogenetic analyses of fungi with *Aspergillus* anamorphs have resulted in two topologies, one published by Houbraken & Samson (2011) (Fig. 1), and the other by Pitt & Taylor (2014) (Fig. 2). In both topologies the backbone is weakly supported, although support for individual clades is often strong. The phylogenetic trees shown diagrammatically in Figs. 1 and 2 were developed using the same data, originally obtained in a broad investigation of the Aspergillaceae (Houbraken & Samson, 2011). To focus on *Aspergillus*, Pitt & Taylor (2014) reduced the taxon sampling to clades populated only by species with *Aspergillus* morphology together with the nearest outgroup, *Thermoascus* Miehe and allies.

Likelihood ratio testing using the Shimodaira Approximately Unbiased Test (Shimodaira, 2002) was used with the sequence data studied in Houbraken & Samson (2011) and Pitt & Taylor (2014) to assess the size and inclusiveness of *Aspergillus* under the two proposed circumscriptions, and to compare the topologies shown in Figs. 1 and 2. The first test involved the widest possible circumscription of the genus *Aspergillus*, which included all species having an *Aspergillus* anamorph, i.e., of all white clades in Figs. 1 and 2. Comparison of the most likely phylogenetic tree with no constraints with one where all *Aspergillus* species are constrained into one monophyletic branch resulted in rejection of the constrained, widest possible

Table 1. Likelihood ratio tests with all taxa, clades 1–7.

Tree	−ln *L*	Diff. −ln *L*	Shimodaira Approximately Unbiased
1	130838.63840	(best)	
2	131517.01639	678.37799	~0*
3	131489.20977	650.57137	~0*
4	131385.49278	546.85438	~0*
5	130936.80186	98.16346	0.0076*
6	130884.12206	45.48365	0.0691

Values for the Shimodaira Approximately Unbiased test are *P* values for null hypothesis of no difference between trees.
* $P < 0.05$, indicating a significant difference between unconstrained Tree 1 and constrained Trees 2–6.
Tree 1. No constraints. This is the tree for which the data are most probable.
Tree 2. Constraint to make monophyletic all clades possessing species with *Aspergillus* anamorphs (2A, 2B, 2C, 2D, 2E, 2F, 3A, 4B, 4C, 7).
Tree 3. Constraint as in Tree 2 excluding *Sclerocleista* (7) from the monophyletic group (2A, 2B, 2C, 2D, 2E, 2F, 3A, 4B, 4C).
Tree 4. Constraint as in Tree 3 retaining only *A. penicilliformis* (3A) in addition to Wide Aspergillus (2A, 2B, 2C, 2D, 2E, 2F, 3A).
Tree 5. Constraint as in Tree 3 retaining only *A. zonatus* (4B) in addition to Wide Aspergillus (2A, 2B, 2C, 2D, 2E, 2F, 4B).
Tree 6. Constraint as in Tree 3 retaining only *A. clavatoflavus* (4C) in addition to Wide Aspergillus (2A, 2B, 2C, 2D, 2E, 2F, 4C).
Number of bootstrap replicates = 10,000.

Table 2. Likelihood ratio tests with taxa in clades 1 and 2.

Tree	−ln *L*	Diff −ln *L*	Shimadaira Approximately Unbiased
1	106903.77264	(best)	
2	106950.17747	46.40484	0.0475*
3	106903.85140	0.07876	0.5838

*$P < 0.05$, indicating a significant difference between unconstrained Tree 1 and constrained Trees 2–3.
Tree 1. No constraints. This is the tree for which the data are most likely.
Tree 2. Constraint to make monophyletic all taxa in clade 2 possessing species with *Aspergillus* anamorphs (2A, 2B, 2C, 2E, 2F).
Tree 3. Constraint to make monophyletic all taxa in clade 2, including species lacking *Aspergillus* anamorphs, i.e., *Phialosimplex* and *Polypaecilum* (2D) (2A, 2B, 2C, 2D, 2E, 2F).

Aspergillus phylogeny (Table 1). To determine if the rejection was due to the inclusion of *Sclerocleista*, the earliest diverging clade with *Aspergillus* morphology in Fig. 1, *Sclerocleista* was excluded from a subsequent test. Again, the widest possible *Aspergillus* phylogeny was rejected (Table 1). Similarly, rejection resulted if *A. zonatus* or *A. penicilliformis* (but not *A. clavatoflavus*), was included in the widest possible *Aspergillus* (Table 1). Thus, it is not possible to recognize a monophyletic genus *Aspergillus* that includes all of the species, and only those species, possessing *Aspergillus* morphology.

The second test involved Wide Aspergillus and its inclusion of taxa lacking *Aspergillus* morphology (i.e., *Phialosimplex* and *Polypaecilum*). When Wide Aspergillus was constrained to include only species with *Aspergillus* morphology by excluding *Phialosimplex* and *Polypaecilum*, the Shimadaira Approximately Unbiased Test rejected the resulting phylogeny as significantly less likely than the unconstrained tree (Table 2), which also included *Penicillium* species.

The third test involved Wide Aspergillus and the inclusion of *Penicillium*, as shown in Fig. 2. When Wide Aspergillus was constrained to exclude *Penicillium* species, the resulting tree was less likely than the most likely unconstrained tree, but it was not significantly less likely.

To summarize the results of likelihood ratio testing, attempts to bring together all of the species with *Aspergillus* morphology to make the widest possible, truly inclusive genus *Aspergillus*, are rejected. Similarly, attempts to create a Wide Aspergillus that excludes taxa lacking the *Aspergillus* morphology, that is, *Phialosimplex* and *Polypaecilum*, are rejected. Finally a Wide Aspergillus that includes *Phialosimplex* and *Polypaecilum* but excludes *Penicillium* is not rejected. The most likely phylogeny is reflected in Fig. 2, where Wide Aspergillus is rendered non-monophyletic by the inclusion of *Phialosimplex* and *Polypaecilum* as well as *Penicillium*.

Recently, Samson and colleagues (Samson & al., 2014) addressed these problems of non-monophyly of Wide Aspergillus.

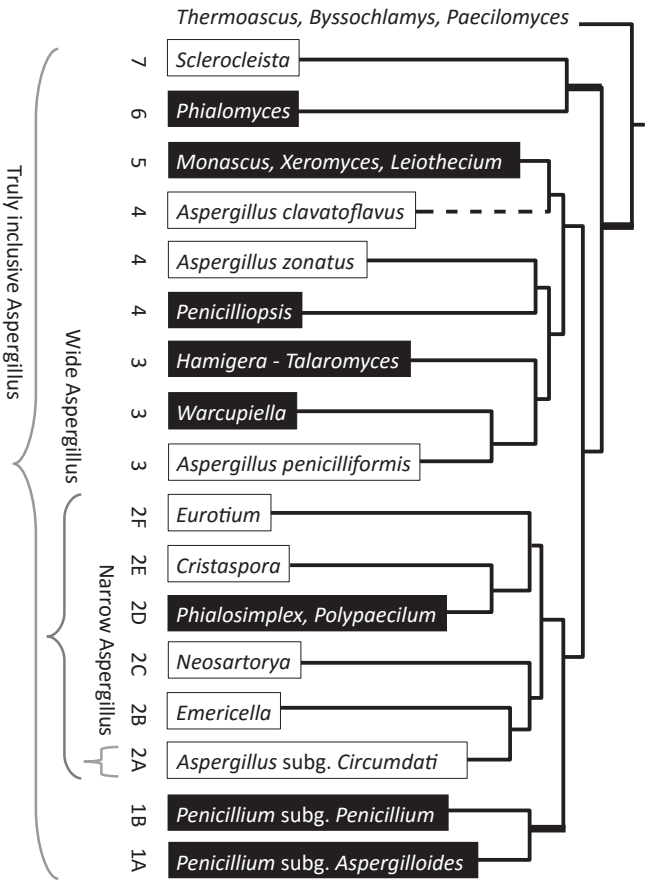

Fig. 1. The *Aspergillus* problem in black and white. Tree topology presented as a diagram based on the phylogenetic analyses of Houbraken & Samson (2011). White clades have *Aspergillus* asexual morphology, black do not. The genus *Aspergillus* as "Narrow Aspergillus" encompasses just clade 2A, *Aspergillus* subg. *Circumdati* (Pitt & Taylor, 2014); as "Wide Aspergillus", it encompasses clades 2A–2F (Houbraken & Samson, 2011); and if to be inclusive of all species with *Aspergillus* anamorphs, it would need to encompass clades 1–7. Bold branches are strongly supported (Bayesian probabilities of 1 and ML bootstrap support ≥95).

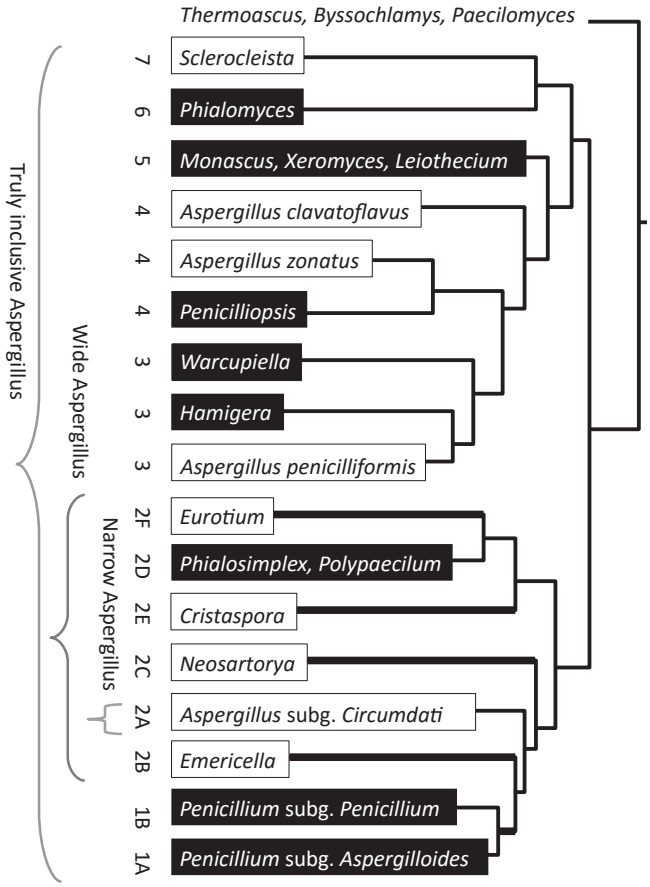

Fig. 2. The *Aspergillus* problem in black and white. Tree topology presented as a diagram based on the phylogenetic analyses of Pitt & Taylor (2014). White clades have *Aspergillus* asexual morphology, black do not. The genus *Aspergillus* as "Narrow Aspergillus" encompasses just clade 2A, *Aspergillus* subg. *Circumdati* (Pitt & Taylor, 2014); as "Wide Aspergillus", it encompasses clades 2A–2F (Houbraken & Samson, 2011); and if to be inclusive of all species with *Aspergillus* anamorphs, it would need to encompass clades 1–7. Bold branches are strongly supported (Bayesian probabilities of 1 and ML bootstrap support ≥95).

To solve the non-monophyly due to the inclusion of two genera lacking *Aspergillus* morphology, *Phialosimplex* and *Polypaecilum*, they simply applied the name *Aspergillus* broadly to include these fungi. Thus, Wide Aspergillus was enlarged to embrace fungi that lacked the defining morphology of *Aspergillus*. This approach could not be applied to the non-monophyly caused by *Penicillium*, because nothing would be gained by preserving the name *Aspergillus* at the cost of losing the name *Penicillium*. The phylogenies presented in support of Wide Aspergillus (Fig. 1; Houbraken & Samson, 2011; Samson & al., 2014) show Wide Aspergillus and *Penicillium* to be reciprocally monophyletic, whereas the phylogeny presented here (Fig. 3) and in Pitt & Taylor (2014) do not. Initially we expected that differences in alignment were responsible for this incongruence. There are two regions in *tsr1* where alignment is ambiguous and these regions comprise less than 2% of the alignment of all four gene regions. However, when we excluded these regions, we still found Wide Aspergillus to be non-monophyletic due to the inclusion of *Penicillium*. As such, we are at a loss to explain the differences in phylogenies. Albeit, as noted at the outset, branch support is weak for all of the basal branches (Fig. 3).

A frequently noted shortcoming of Linnaean classification germane to the problem of whether to recognize a Narrow Aspergillus versus Wide Aspergillus is that Linnaean taxa

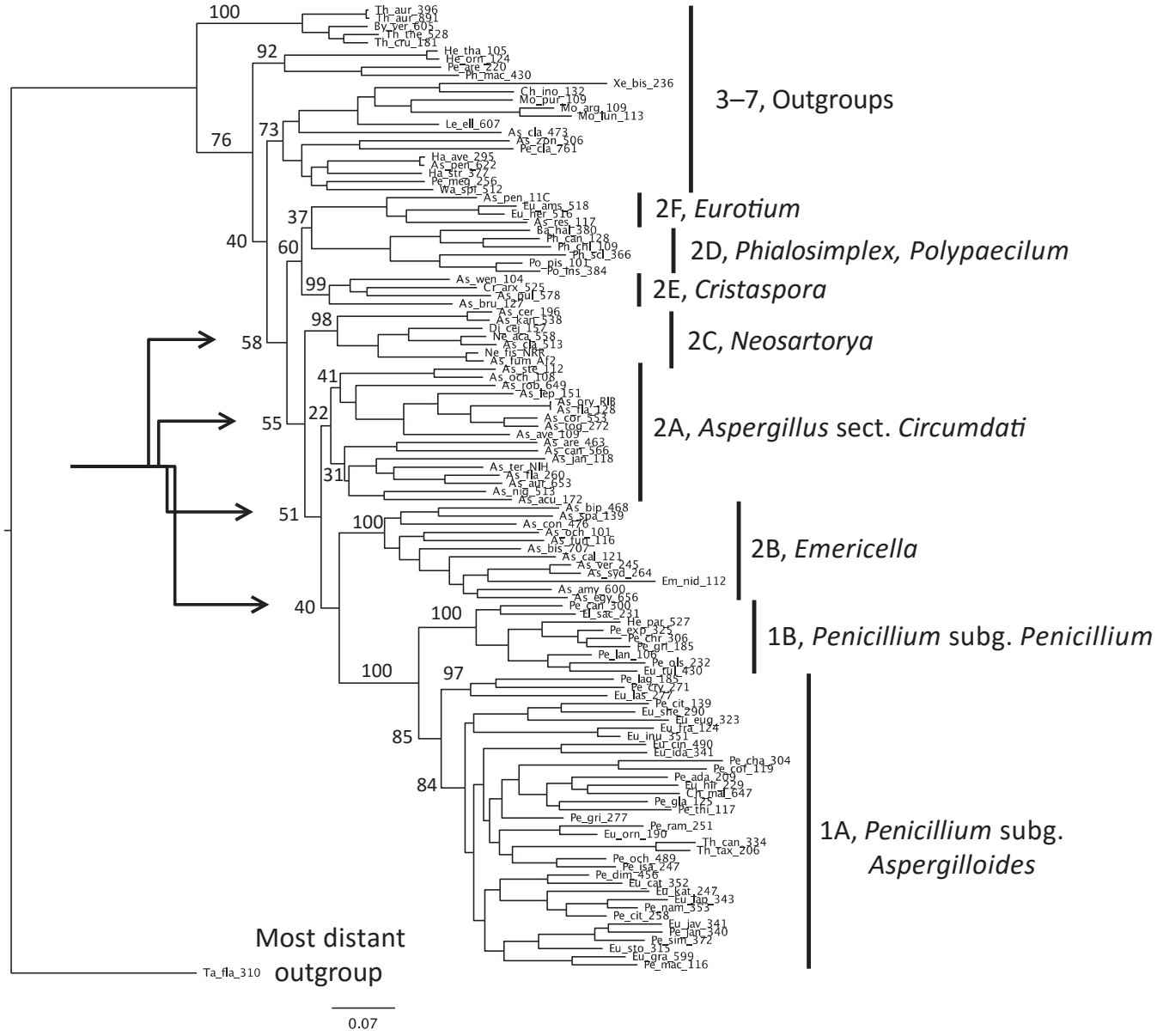

Fig. 3. Maximum likelihood phylogeny (RAxML) of four gene regions showing the most likely tree based on all taxa (clades 1–7 and the outgroup). Outgroup selection from Houbraken & Samson (2011). Note four, albeit weakly supported, branches (arrows) make Wide Aspergillus non-monophyletic by uniting clades with *Aspergillus* morphology with *Penicillium* (arrow). Bootstrap numbers at branches are percentages of 1000 maximum likelihood RAxML phylogenies possessing that branch based on 1000 resampled datasets.

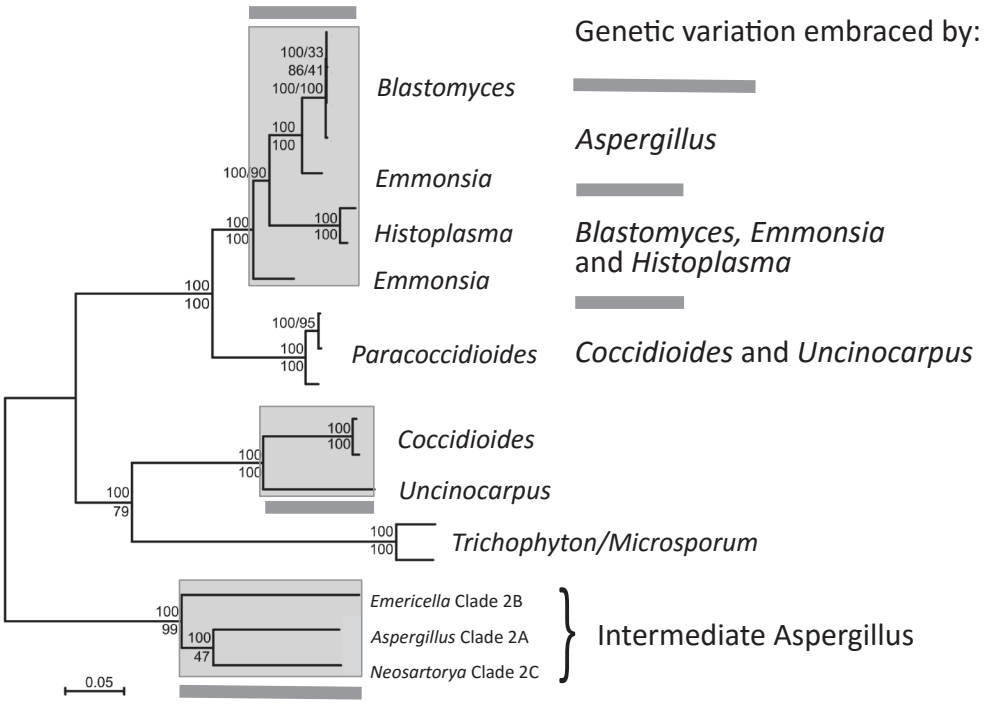

Fig. 4. Graphic demonstration of taxonomic inconsistency. Thick gray bars mark genetic variation and show that more genetic variation (MaSH = 0.150) is contained in just three species with *Aspergillus* asexual morphology (Intermediate Aspergillus, clades 2A, 2B, 2C in Figs. 1 and 2), than is contained in other monophyletic clades that harbor several genera (i.e., *Blastomyces*, *Emmonsia* and *Histoplasma*, MaSH = 0.121; or *Coccidioides* and *Uncinocarpus*, MaSH = 0.094). The inconsistency would be greater for Wide Aspergillus. This phylogeny was based on 2062 core genes and has been redrawn from Muñoz & al. (2015).

of the same rank are not normally quantitatively comparable, which can cause taxonomic inconsistency (Zachos, 2011). A taxonomic classification can be judged to be inconsistent regarding its ranks if it contains a taxon that is more divergent than a taxon of higher rank, for example, a genus with more divergence than a family, or if a single taxon is more divergent than neighboring clades embracing more than one taxon of the same rank (Fig. 4). To avoid taxonomic inconsistency, microbiologists have used thresholds for pairwise distances or similarities to assign taxonomic ranks (Schloss & Handelsman, 2004). However, threshold-based sequence clustering, like all clustering approaches that group according to increased similarity, is fundamentally distinct from phylogenetic inference, as more similar organisms are not necessarily more closely related. To guarantee that a set of organisms located within a certain maximum distance from each other, or from an organism acting as a type, formed a monophyletic group, their sequences would need to have evolved under a molecular clock (Felsenstein, 2004; Göker & al., 2009; Wiley & Lieberman, 2011). Moreover, it is not logical to cluster sequences when a phylogenetic tree is already present that contains all groupings of potential interest. Temporal banding has been suggested as a phylogenetic approach to achieve consistency (Avise & Johns, 1999; Holt & Jønsson, 2014), but it is not generally applicable because it requires molecular clocks, too, as well as phylogenetic dating. Here we instead employ PRBO (Liu & al., 2015), which is the phylogenetic variant of clustering optimization (Göker & al., 2009).

Six hypothetical classifications were tested for inconsistencies regarding the divergences of their genera. Due to the partial lack of resolution at the backbone of the unconstrained trees (Figs. 1, 2), and because monophyly has been treated above, here a phylogeny was inferred by simultaneously constraining for the monophyly of all alternative hypothetical genera. Given the large difference between Wide Aspergillus, which would combine six clades (2A through 2F) and Narrow Aspergillus, which is limited to clade 2A, we also examined a third taxonomic possibility, Intermediate Aspergillus, in which the genus *Aspergillus* would comprise clades 2A, 2B and 2C. As shown in Table 3, experiment 1 tested Narrow Aspergillus with separate genera for clades 2A, 2B, 2C, 2D, 2E and 2F, as well as a single genus *Penicillium* combining clade 1A and clade 1B; experiment 2 tested Intermediate Aspergillus (like experiment 1 but combining clades 2A, 2B and 2C); and experiment 3 tested Wide Aspergillus (like experiment 1 but unifying clades 2A to 2F). Experiments 4–6 paralleled 1–3, but treated clade 1A and clade 1B as separate genera. A second series of experiments (7–12) was conducted that used the same classification as in experiments 1–6, but, for each experiment, enforced only the monophyly of its specific set of hypothetical genera. In all six experiments, the monophyly of the appropriate outgroup was enforced, which in different experiments consisted of a group comprising both clade 6 and clade 7, clade 5, or both clade 3 and clade 4. Experiments 7–12 nevertheless yielded six distinct topologies.

Of the 12 experiments, the three most germane to consideration of the appropriate size of the genus *Aspergillus* are those that maintain one genus for *Penicillium* and that use an input phylogeny inferred by simultaneously constraining for the monophyly of all alternative hypothetical genera, that is, experiments 1 (Narrow Aspergillus), 2 (Intermediate Aspergillus) and 3 (Wide Aspergillus) (Table 3).

Examining the results of experiments in Table 3, it can be seen that Intermediate Aspergillus could be made

taxonomically consistent by merging *Eurotium*, *Cristaspora* Fort & Guarro, *Phialosimplex* and *Polypaecilum* into one genus, and also merging clades 3 through 7 into a second genus, which would include *Warcupiella* Subram., *Hamigera* Stolk & Samson, *Penicilliopsis* Solms, *Monascus* Tiegh., *Xeromyces* L.R.Fraser, *Leiothecium* Samson & Mouch., *Phialomyces* P.C. Misra & P.H.B.Talbot and *Sclerocleista*. Wide Aspergillus could be made taxonomically consistent by merging clades 3 through 7 into one genus, which would include *Warcupiella*, *Hamigera*, *Penicilliopsis*, *Monascus*, *Xeromyces*, *Leiothecium*, *Phialomyces* and *Sclerocleista*, keeping in mind that Wide Aspergillus already includes *Eurotium*, *Cristaspora*, *Phialosimplex* and *Polypaecilum*. Narrow Aspergillus could be made taxonomically consistent by merging *Eurotium*, *Cristaspora*, *Phialosimplex* and *Polypaecilum* into one genus.

The type of *Cristaspora*, *C. arxii* Fort & Guarro, belongs in the same clade as *Aspergillus wentii* Wehmer (Houbraken & Samson, 2011), which belongs in the same clade as the sexual genus *Chaetosartorya* (Peterson, 2000). *Cristospora* is thus a synonym of *Chaetosartorya*.

Table 3. Divergence tests with taxa in clades 1 and 2

Exp.	Thresh.	Merge	Split
1	0.348	2D, 2E, 2F	-
2	0.395	2D, 2E, 2F, 3 & 4, 5, 6 & 7	-
3	0.421	3 & 4, 5, 6 & 7	-
4	0.321	2D, 2E, 2F	-
5	0.283	-	1A1, 1A2, 2A, 2B, 2C
6	0.321	-	2A, 2B, 2C, 2D & 2E & 2F
7	0.341	2D, 2E, 2F	-
8	0.415	3 & 4, 5, 6 & 7	-
9	0.421	3 & 4, 5	-
10	0.317	2D, 2E, 2F	-
11	0.320	-	2A, 2B, 2C
12	0.424	1A, 1B, 3 & 4, 5	-

Experiments (Exp.):
1. Containing Narrow Aspergillus and one genus for *Penicillium*
2. Containing Intermediate Aspergillus and one genus for *Penicillium*
3. Containing Wide Aspergillus and one genus for *Penicillium*
4. Containing Narrow Aspergillus and two genera for *Penicillium*
5. Containing Intermediate Aspergillus and two genera for *Penicillium*
6. Containing Wide Aspergillus and two genera for *Penicillium*
7–12. Like 1–6, respectively, but distinct trees inferred with a constraint involving only the genera from the specific hypothetical classification

Threshold (Thresh.): Upper threshold of intraclade divergence to achieve taxonomic consistency.

Merge: Clades that would need to be merged into a single genus to obtain a classification consistent in terms of the divergences of the genera.

Split: Clades that would need to be retained as discrete genera to obtain a classification consistent in terms of the divergences of the genera.

A clear result from the PRBO analysis is that Narrow Aspergillus provides the most consistent taxonomy compared to both Intermediate and Wide Aspergillus and the one that would require the fewest taxonomic rearrangement to achieve consistency. Here, our focus is on *Aspergillus*, so we will not address combining *Eurotium*, *Cristaspora* (= *Chaetosartorya*), *Phialosimplex* and *Polypaecilum* into one genus.

■ TAXONOMY AND NOMENCLATURE

Having presented the biological information, which supports Narrow Aspergillus over Wide Aspergillus in terms of phylogeny as tested by maximum likelihood analysis, likelihood ratio testing and taxonomic consistency, we now consider taxonomy and nomenclature. The monophyletic group comprising clades 2D, 2E and 2F (Figs. 1, 2), cannot be included in Wide Aspergillus due to the presence of species of *Phialosimplex* and *Polypaecilum* (clade 2D in Figs. 1 and 2), and those generic and species names should continue to be used. Excluding these genera also removes from Wide Aspergillus species in the teleomorph genera *Cristaspora* (= *Chaetosartorya*, see above) (2E) and *Eurotium* (2F). Species in *Eurotium* and the few other species in the current *Aspergillus* subg. *Aspergilloides* (Gams & al., 1985; Houbraken & Samson, 2011) therefore should continue to be known by *Eurotium*, their well established, widely used, teleomorph name. Names in *Chaetosartorya* should also continue to be used.

The remaining clades with *Aspergillus* anamorphs, 2A, 2B and 2C, form a monophyletic group in Fig. 1 and might comprise the aforementioned Intermediate Aspergillus. Thus constituted, the genus would embrace industrially important species (*A. niger*, *A. oryzae* (Ahlb.) Cohn), toxigenic species (*A. flavus* Link, *A. parasiticus* Speare, *A. ochraceus* K.Wilh., *A. carbonarius* (Bainier) Thom), medically important species (*A. fumigatus* Fresen.), and scientific models (*A. nidulans* (Eidam) G.Winter), any of which could be selected as the conserved type of *Aspergillus*. However, the new phylogenetic analyses presented here reveal that, in the most likely phylogeny, *Penicillium* prevents these clades from forming a monophyletic group (Table 2; Figs. 2, 3). Therefore, only one of the clades 2A, 2B or 2C can be named *Aspergillus*. The justification for choosing *A. niger* as the conserved type, in the clade representing *Aspergillus* subg. *Circumdati*, rests on the importance of this and closely related species in the subgenus to human society in terms of industrial microbiology, food toxicology and research activity (Pitt & Taylor, 2014).

Narrow Aspergillus is favored over Wide Aspergillus in three ways: (1) by genotype, as measured by phylogenetic analysis; (2) by phenotype, as evidenced by the names based on distinct sexual morphologies, which reflect equally distinct physiological attributes; and (3) by PBRO analysis, which shows that Narrow Aspergillus provides a more consistent taxonomy than either Intermediate or Wide Aspergillus and, as shown in Table 3, would require the fewest taxonomic rearrangements to achieve consistency. In other words, Narrow Aspergillus results in genera that convey more precise morphological and

physiological information, that are monophyletic, and that come closer to taxonomic consistency.

In our opinion, based on the information presented here, the advantages of Narrow Aspergillus are so numerous and compelling that Wide Aspergillus might never be adopted under the normal processes of nomenclature. However, in the wake of the revision of the rules of fungal nomenclature, which necessitates large-scale changes of names, the normal nomenclatural processes were altered, also necessarily, in the name of expediency under *ICN* Art. 56.3. This article encourages subcommittees to develop lists of names for rejection by the Nomenclature Committee for Fungi (NCF) and, although not specifically mentioned, has also resulted in the generation of lists of names for approval by NCF. In replacing the normal process of publication of taxonomic hypotheses followed by community acceptance or rejection with the opinion of a subcommittee, there is a danger that science could be supplanted by politics. Therefore, it will be important (1) that the membership of subcommittees be representative of the breadth of mycological thought; (2) that debate is encouraged about generic concepts and specific lists; and (3) that normal nomenclatural processes are resumed once the current large-scale changes of names are accomplished. To ensure that the lists and the biological and taxonomic principles underlying their creation be widely circulated and open to discussion and amendment, we advocate their submission to the International Committee on Taxonomy of Fungi, a committee under NCF.

We believe that our example of *Aspergillus* demonstrates how phylogenetics combined with tests of topology and genetic divergence can be used to apply one name to one fungal genus in a scientific manner. We hope that our approach will be considered as mycologists grapple with the need to choose one name for fungal genera, particularly those that are too large to be taxonomically consistent.

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