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Aspergillus, its sexual states and the new International Code of Nomenclature

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Abstract: The newly adopted International Code of Nomenclature for algae, fungi and plants (ICN) demands that dimorphic fungi, in particular those with both sexual and asexual names, now bear a single name. Although priority is no longer associated with the mode of reproduction, the ICN requires justification for choosing an asexual name over an existing sexual one. The phylogenetic approach that made dual nomenclature for fungi obsolete can be used to help choose names for large groups of fungi that are best known by asexual names. Here we apply this approach to one of the largest and most diverse asexual genera, the genus *Aspergillus*. We find that existing sexual names may be given to well supported clades of fungi with distinct phenotypes, which include sexual morphology as well as physiological attributes associated with xerophily, thermophily and mycotoxin production. One group of species important to food production and food safety, *Aspergillus* subgen. *Circumdati*, lacks a well supported clade; here we propose that the name *Aspergillus* be retained for this group. Recognizing that nomenclature has economic and social implications, particularly for old, important genera, we discuss the consequences of various scenarios to implement the new ''one name for one fungus'' article in the ICN, showing that our approach requires the fewest appeals to the ICN while retaining the name *Aspergillus* for many of the most economically and socially important species.

Key words: *Aspergillus*, *Chaetosartorya*, *Emericella*, *Eurotium*, International Code of Nomenclature, *Neosartorya*, *Penicillium*, phylogeny

Introduction

The International Code of Nomenclature for algae, fungi and plants (ICN, McNeill et al. 2012) adopted at the Melbourne International Botanical Congress abolished dual nomenclature for the species of Ascomycota and Basidiomycota that bear separate names for their different asexual (anamorph) and sexual (teleomorph) states. Among the changes described in the ICN are two aimed at guiding mycologists as they choose one name from among the several possible asexual and sexual names. These are reproduced below:

> ''**Art. 59.1** *Note 2*. Previous editions of this *Code* provided for separate names for mitotic asexual morphs (anamorphs) of certain pleomorphic fungi and required that the name applicable to the whole fungus be typified by a meiotic sexual morph (teleomorph). Under the current *Code*, however, all legitimate fungal names are treated equally for the purposes of establishing priority, regardless of the life-history stage of the type (but see Art. 57.2; see also Art. 14.13).
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> ''**[Art.] 57.2**. In pleomorphic fungi (including lichenicolous fungi, but excluding lichen-forming fungi and those fungi traditionally associated with them taxonomically, e.g. *Mycocaliciaceae*), in cases where, prior to 1 January 2013, both teleomorph-typified and anamorph-typified names were widely used for a taxon, an anamorph-typified name that has priority is not to displace the teleomorph name(s) unless and until a proposal to reject the former under Art. 56.1 or 56.3 or to deal with the latter under Art. 14.1 or 14.13 has been submitted and rejected.''

These provisions of the ICN make it clear that although sexual names no longer have priority over asexual names, mycologists wishing to choose a widely used asexual name over a widely used sexual name first must convince the ICN General Committee of the wisdom of their action. For the majority of fungi, this decision will be uncomplicated. However, for fungi that are economically and socially important, with sexual and asexual names that both are old and well established, this decision may be difficult. Here, we examine this problem as it relates to one of the oldest established and most economically and socially important groups of fungi, those in the asexual genus *Aspergillus*, and the sexual generic names validly associated with it.

The genus *Aspergillus* was illustrated first by Micheli in 1729 and then by Link in 1809 as a fungal genus with a distinctive mop-like, vesiculate conidiophore resembling an aspergillum. This feature was used as the criterion for *Aspergillus* by later authors, including Thom and Church (1926), Thom and Raper (1945)

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TABLE I. Some phenotypes of the sexual genera associated with *Aspergillus*

Sexual genus	Type of cleistothecium	Physiology and ecology
Chaetosartorya	Pseudoparenchymatous, cream to buff, maturing rapidly; ascospores hyaline	Xerophilic, uncommon
Emericella	Pseudoparenchymatous, red, purple or black, surrounded by hülle cells, maturing rapidly at high water activities; ascospores purple	Moderately thermophilic, not xerophilic. Soil fungi, a few related species in indoor air, on food commodities
Eurotium	Pseudoparenchymatous, yellow, maturing only at reduced water activities; ascospores yellow	Xerophilic, growing more rapidly at reduced water activities. Decay fungi on dry and concentrated substrates of all kinds
Fennellia	Pseudoparenchymatous, thick walled, yellow; ascospores hyaline	Mesophilic; soil fungi, uncommon
Hemicarpenteles	Single in stroma, white to buff, maturing slowly; ascospores hyaline	Rare; dung or soil fungi
Neocarpenteles	Single in stroma, brown; ascospores hyaline	Rare; dung or soil fungi
Neopetromyces	One or more, pale sclerotial stroma; ascospores hyaline	Moderately xerophilic. Some related species decay fungi on dried materials or mycotoxin producers.
Neosartorya	Pseudoparenchymatous, white, maturing rapidly at high water activities; ascospores hyaline	Thermophilic, ascospores heat resistant, not xerophilic. Decay fungi on moist plant material. Some species pathogenic
Petromyces	Multiple, in sclerotial black stroma, maturing very slowly; ascospores yellow. Some species heterothallic	Moderately xerophilic. Some related species industrially important or mycotoxin producers
Sclerocleista	Pseudoparenchymatous, white becoming purple, maturing rapidly; ascospores pale brown	Mesophilic; soil fungi, uncommon
Warcupiella	Finely interwoven white hyphae; ascospores hyaline	Rare; soil fungi

and Raper and Fennell (1965). *Aspergillus* was more formally delimited from the closely related genus *Penicillium* by Pitt and Hocking (1985) who noted that ''the simultaneous production of phialides from a single [solitary] head on a well defined stipe … and the presence of a foot-cell are absolute criteria for *Aspergillus*.'' While no longer considered ''absolute'', this characteristic, asexual structure still provides the basis for the morphological recognition of *Aspergillus* species in the broadest sense.

Aspergillus has grown into a very large genus, currently comprising about 300 accepted species (ICPA, 2013). At the same time, the distinctive asexual fruiting structure characteristic of *Aspergillus* is known to be associated with no fewer than 11 sexual state genera reflecting variation in cleistothecial wall color, composition, decoration and the presence or absence of stroma of varying composition and colors. These sexual-state genera have been validly published at various times under the International Code of Botanical Nomenclature (Geiser 2009; TABLE I). In addition to varying in sexual morphology, these genera differ widely in physiology and ecology (e.g. xerophily, thermophily and mycotoxin production). Names in the more important of these sexual genera, *Eurotium*, *Neosartorya* and *Emericella*, have been widely used over the past 40 or more years. We estimate that about one-third of the accepted *Aspergillus* species have been validly described in one of the 11 sexual genera.

Houbraken and Samson (2011) used DNA sequences of four protein-coding genes (RPB1, RPB2, *Tsr1*, *Cct8*) to analyze phylogenetically many of the species in *Aspergillus*, *Penicillium* and other related genera, some as distant as *Talaromyces* and *Trichocoma*. Their analysis showed strong support for clades containing *Aspergillus* species with sexual names in the genera *Eurotium*, *Neosartorya*, *Chaetosartorya* and *Emericella* but weak support (< 50% ML bootstrap) for the clade embracing species in *Aspergillus* subgenus *Circumdati*, which includes species with the sexual names *Petromyces*, *Neopetromyces* and *Fennellia*. Their analysis also showed that the several clades of *Aspergillus* species were very closely related to species in *Penicillium* sensu stricto, such that the branch making *Aspergillus* monophyletic with respect to *Penicillium* sensu stricto had only 51% bootstrap support by maximum likelihood analysis.

Many phenotypic differences, both morphological and physiological, exist among the phylogenetically well supported clades that correspond to the sexual genera *Eurotium*, *Neosartorya*, *Emericella* and *Chaetosartorya*. Under Art. 57.2 of the ICN, acceptance of these genera is without complication and requires no

further action. *Aspergillus* species without known sexual states but phylogenetically related to one of these genera are almost all well supported, so publication of lists of species to be included in each of these genera, either with valid sexual names or by recombination from *Aspergillus*, is a similarly straightforward exercise.

To preserve the old and important name, *Aspergillus*, a case could be made to the ICN to apply that name to the phylogenetic grade, that is, the non-monophyletic group that, in this case, comprises *Aspergillus* subgenus *Circumdati*, which does include a few species with sexual states in the less well known genera *Petromyces*, *Neopetromyces* and *Fennellia*.

In this paper, we re-examine the phylogenetic analysis conducted by Houbraken and Samson (2011) by reducing the taxa to just those necessary to address support for clades of *Aspergillus* species and to address the monophyly of *Aspergillus* sensu lato compared to *Penicillium* sensu stricto.

MATERIALS AND METHODS

Phylogenetic analysis of DNA sequences rests on the assumption that the nucleotides in aligned positions are homologous, and this assumption is most likely to be true for closely related taxa where alignment of nucleotides is unambiguous. To maximize the proportion of homologous characters in a molecular phylogenetic analysis, the taxa in question should be reduced to the smallest group of closely related taxa needed to address the question. Therefore, to address the relationships among fungi with the asexual name *Aspergillus* we were guided by the phylogenetic analysis of Houbraken and Samson (2011), with the one salient difference that we limited our analysis to clades containing fungi that bear the asexual name, *Aspergillus*, fungi in the very closely related genus *Penicillium* sensu stricto, and, as the closest outgroup, species of *Thermoascus*. We removed the more distantly related species classified in *Talaromyces*, *Thermomyces*, *Sagenomella*, *Rasamsonia* and *Trichocoma*. Information about the sequences and strains, including their status as type specimens, can be found in Houbraken and Samson (2011).

Phylogenetic analysis of *Aspergillus* and related taxa was made with the DNA sequences of the four genes used by Houbraken and Samson (2011) (TABLE II): the RPB1 and RPB2 subunits of RNA polymerase II; Tsr1, a putative ribosome biogenesis protein; and Cct8, the theta subunit of the TCP-1 chaperonin complex. Sequences were aligned with MUSCLE (Goujon et al. 2010) and trimmed to equal lengths. For Bayesian phylogenetic analysis the alignment was put in Nexus format for MrBayes 3.2 (Ronquist et al. 2012) using concatenated sequences, a generalized time-reversible evolutionary model allowing for invariant sites and providing a gamma distribution of variable sites (lset nst = 6 rates = invgamma), with *Thermoascus aurantiacus* (Th_aur_396.78) as the outgroup based on Houbraken and Samson (2011). The alignment is deposited at TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S15611). Bayesian probabilities for each branch were calculated from samples taken every 1000 generations after discarding the first 25% as burn-in; after 10^6 generations the final average standard deviation of split frequencies was 0.007995. Maximum likelihood analysis of the same concatenated, aligned, trimmed sequences was by MEGA5 (Tamura et al. 2011) using converted fasta format and a discrete gamma distribution to model evolutionary rate differences among sites (five categories [+G, parameter = 0.5561]) while allowing for some sites to be evolutionarily invariable ([+I], 32.3809% sites). Maximum likelihood branch support is the percentage of 1000 bootstrap resampled datasets possessing the branch.

RESULTS

Our phylogenetic analysis (FIG. 1) shows strong support in terms of Bayesian posterior probabilities and maximum likelihood bootstrap percentages for four clades of species with *Aspergillus* asexual morphology that are associated with the sexual names *Eurotium*, *Neosartorya*, *Emericella* and *Chaetosartorya*. It also shows strong support for the clade of *Penicillium* species and for the clade of *Phialosimplex* and *Polypaecilum* species. One group of species with *Aspergillus* asexual morphology does not form a well-supported clade, and this grade is coincident with *Aspergillus* subgenus *Circumdati*. Based on the topology of the phylogeny, the placement of the *Thermoascus* outgroup, and the Bayesian posterior probabilities, the genera *Penicillium*, *Phialosimplex* and *Polypaecilum* make it impossible to define a monophyletic clade of all analyzed fungi with *Aspergillus* asexual states (FIG. 2). That is, to apply *Aspergillus* to all of the fungi with *Aspergillus* asexual states and maintain a monophyletic genus *Aspergillus*, species in the genera *Phialosimplex*, *Polypaecilum* and *Penicillium* would have to be given the name *Aspergillus*.

In recognition of the phylogenetic equivalence of the well-supported clades of *Penicillium*, *Eurotium*, *Neosartorya*, *Emericella* and *Chaetosartorya*, and the obvious morphological and physiological differences among these clades, we advocate adopting the sexual names for the species with *Aspergillus* asexual states, in accordance with the ICN. However, in the case of the clades lacking strong support that comprise the grade *Aspergillus* subgenus *Circumdati*, we advocate applying *Aspergillus* over *Petromyces*. Although this action would require appealing to the ICN, it can be justified by its preservation of the old, important name *Aspergillus*. In the discussion, we address the merits and impact of our recommendation as compared to the extreme alternatives of abandoning the name *Aspergillus* entirely, or applying it broadly.

TABLE II. Fungi, culture numbers and genes sequence accession numbers

Culture No.	FIG. 1 acronym[a]	Name in gene or genome databases	RPB1	RPB2	Tsr1	Cct8
CBS 172.66	As_acu_172.66	*Aspergillus aculeatus*	JN121590	JN121448	JN121755	JN121895
CBS 600.67	As_amy_600.67	*Aspergillus amylovorus*	JN121705	JN121538	JN121844	JN121931
CBS 463.65	As_are_463.65	*Aspergillus arenarius*	JN121684	JN121519[b]	JN121825	JN121916[b]
CBS 653.74	As_aur_653.74	*Aspergillus aureofulgens*	JN121712	JN121545	JN121851	JN121936
CBS 109.46	As_ave_109.46	*Aspergillus avenaceus*	JN121565	JN121424	JN121731	JN121878
CBS 468.65	As_bip_468.65	*Aspergillus biplanus*	JN121685	JN121520	JN121826	JN121917
CBS 707.71	As_bis_707.71	*Aspergillus bisporus*	JN121715	JN121548	JN121854	JN121939
CBS 127.61	As_bru_127.61	*Aspergillus brunneouniseriatus*	JN121583	JN121442	JN121749	JN121889
CBS 121611	As_cal_121611	*Aspergillus calidoustus*	JN121579	JN121438	JN121745	JN121887[b]
CBS 566.65	As_can_566.65	*Aspergillus candidus*	JN121702	JN121535	JN121841	JN121929
CBS 196.64	As_cer_196.64	*Aspergillus cervinus*	JN121595	JN121452	JN121759	JN121896
CBS 473.65	As_cla_473.65	*Aspergillus clavatoflavus*	JN121686	JN121521	JN121827	JN121918
CBS 513.65	As_cla_513.65	*Aspergillus clavatus genome*	XM_001268790.1	XM_001272354.1	XM_001275562.1	XM_001271852.1
CBS 476.65	As_con_476.65	*Aspergillus conjunctus*	JN121688	JN121523	JN121829	JN121920
CBS 553.77	As_cor_553.77	*Aspergillus coremiiformis*	JN121700	JN121533[b]	JN121839	JN121927[b]
CBS 656.73	As_egy_656.73	*Aspergillus egyptiacus*	JN121713	JN121546	JN121852	JN121937
CBS 128202/NRRL3357	As_fla_128202	*Aspergillus flavus genome*	XM_002374796.1	XM_002380626.1	XM_002379552.1	XM_002374044.1
CBS 260.73	As_fla_260.73	*Aspergillus flavipes*	JN121623	JN121475	JN121781	JN121901
Af293/CBS 101355	As_fum_Af293	*Aspergillus fumigatus genome*	XM_747744.1	XM_741647.1	XM_750526.1	XM_746759.1
CBS 116.56	As_fun_116.56	*Aspergillus funiculosus*	JN121572	JN121431	JN121738	JN121883
CBS 118.45	As_jan_118.45	*Aspergillus janus*	JN121576	JN121435	JN121742	JN121885
CBS 538.65	As_kan_538.65	*Aspergillus kanagawaensis*	JN121698	JN121531	JN121837	JN121925
CBS 151.66	As_lep_151.66	*Aspergillus leporis*	JN121588[b]	JN121446	JN121753	JN121893
CBS 513.88	As_nig_513.88	*Aspergillus niger genome*	XM_001389639.2	XM_001395124.2	XM_001399262.2	XM_001402058.2
CBS 101887	As_och_101887	*Aspergillus ochraceoroseus*	JN121557	JN121416	JN121723	JN121871
CBS 108.08	As_och_108.08	*Aspergillus ochraceus*	JN121562	JN121421	JN121728	JN121875
RIB40/ NBRC 100959	As_ory_RIB40	*Aspergillus oryzae genome*	XM_001819615.2	XM_001825417.2	XM_001821764.2	XM_001820276.2
CBS 130294/11C3	As_pen_11C3	*Aspergillus penicillioides*	JN121578	JN121437	JN121744	JN121886
CBS 622.67	As_pen_622.67	*Aspergillus penicilliformis*	JN121708	JN121542	JN121848	JN121934
CBS 578.65	As_pul_578.65	*Aspergillus pulvinus*	JN121703	JN121536	JN121842	JN121930
CBS 117.33	As_res_117.33	*Aspergillus restrictus*	JN121574	JN121433[b]	JN121740	JN121884
CBS 649.93	As_rob_649.93	*Aspergillus robustus*	JN121711	JN121544	JN121850	JN121935
CBS 139.61	As_spa_139.61	*Aspergillus sparsus*	JN121586	JN121444	JN121751	JN121891
CBS 112812	As_ste_112812	*Aspergillus steynii*	JN121569	JN121428	JN121735	JN121880
CBS 264.81	As_syd_264.81	*Aspergillus sydowii*	JN121624	JN121476	JN121782	JN121902
NIH 2624/FGSC A1156	As_ter_NIH2624	*Aspergillus terreus genome*	XM_001210766.1	XM_001209185	XM_001208611.1	XM_001210851.1
CBS 272.89	As_tog_272.89	*Aspergillus togoensis*	JN121627	JN121479[b]	JN121785	JN121904
CBS 245.65	As_ver_245.65	*Aspergillus versicolor*	JN121614	JN121468	JN121775	JN121899
CBS 104.07	As_wen_104.07	*Aspergillus wentii*	JN121559	JN121418	JN121725	JN121873

TABLE II. Continued

Culture No.	FIG. 1 acronym[a]	Name in gene or genome databases	RPB1	RPB2	Tsr1	Cct8
CBS 506.65	As_zon_506.65	*Aspergillus zonatus*	JN121691	JN121526	JN121832	JN121921
CBS 380.74	Ba_hal_380.74	*Basipetospora halophilica*	JN121666	JN121509	JN121815	JN121910
CBS 605.74	By_ver_605.74	*Byssochlamys verrucosa*	JN680311	JN121540	JN121846[b]	JN121932
CBS 132.31	Ch_ino_132.31	*Chrysosporium inops*	JN121584	JN121443	JN121750	JN121890
CBS 647.95	Ch_mal_647.95	*Chromocleista malachitea*	JN121710	JN121543	JN121849	JN121992[b]
CBS 525.83	Cr_arx_525.83	*Cristaspora arxii*	JN121695	JN121529	JN121835	JN121924
CBS 157.66	Di_cej_157.66	*Dichotomomyces cejpii*	JN121589	JN121447	JN121754	JN121894
CBS 231.61	El_sac_231.61	*Eladia saccula*	JN121607	JN121462	JN121769	JN121949
CBS112.46/FGSCA4	Em_nid_112.46	*Emericella nidulans genome*	XM_653321.1	XM_652833.1	XM_658778.1	XM_654363.1
CBS 352.67	Eu_cat_352.67	*Eupenicillium catenatum*	JN121659	JN121504	JN121810	JN121980
CBS 490.66	Eu_cin_490.66	*Eupenicillium cinnamopurpureum*	JN121690	JN121525	JN121831	JN121988
CBS 323.71	Eu_eug_323.71	*Eupenicillium euglaucum*	JN121644	JN121492	JN121798	JN121970
CBS 124.68	Eu_fra_124.68	*Eupenicillium fractum*	JN121582	JN121441	JN121748	JN121864
CBS 599.73	Eu_gra_599.73	*Eupenicillium gracilentum*	JN121704	JN121537	JN121843	JN121990
CBS 229.60	Eu_hir_229.60	*Eupenicillium hirayamae*	JN121604	JN121459	JN121766	JN121946
CBS 341.68	Eu_ida_341.68	*Eupenicillium idahoense*	JN121652	JN121499	JN121805	JN121976
CBS 351.67	Eu_inu_351.67	*Eupenicillium inusitatum*	JN121658	JN121503	JN121809	JN121979
CBS 341.48	Eu_jav_341.48	*Eupenicillium javanicum*	JN121651	JN121498	JN121804	JN121975
CBS 247.67	Eu_kat_247.67	*Eupenicillium katangense*	JN121618	JN121471	JN121777	JN121955
CBS 343.48	Eu_lap_343.48	*Eupenicillium lapidosum*	JN121653	JN121500	JN121806	JN121977
CBS 277.70	Eu_las_277.70	*Eupenicillium lassenii*	JN121630	JN121481	JN121787	JN121960
CBS 190.68	Eu_orn_190.68	*Eupenicillium ornatum*	JN121594	JN121451	JN121758	JN121867
CBS 290.48	Eu_she_290.48	*Eupenicillium shearii*	JN121631	JN121482	JN121788	JN121961
CBS 315.67	Eu_sto_315.67	*Eupenicillium stolkiae*	JN121640	JN121488	JN121794	JN121967
CBS 430.69	Eu_tul_430.69	*Eupenicillium tularense*	JN121681	JN121516	JN121822	JN121984
CBS 518.65	Eu_ams_518.65	*Eurotium amstelodami*	JN121694	JN121528	JN121834	JN121923
CBS 516.65	Eu_her_516.65	*Eurotium herbariorum*	JN121693	JN121527	JN121833	JN121922
CBS 295.48	Ha_ave_295.48	*Hamigera avellanea*	JN121632	JF417424	JF417391	JF417524
CBS 377.48	Ha_str_377.48	*Hamigera striata*	JN121665	JN121508	JN121814	JN121909
CBS 124.53	Sc_orn_124.53	*Hemicarpenteles ornatus*	JN121581	JN121440	JN121747	JN121888
CBS 527.65	He_par_527.65	*Hemicarpenteles paradoxus*	JN121696	JN121530	JN121836	JN121989
CBS 105.25	Sc_tha_105.25	*Hemicarpenteles thaxteri*	JN121560	JN121419	JN121726	JN121874
CBS 607.74	Le_ell_607.74	*Leiothecium ellipsoideum*	JN121707	JN121541	JN121847	JN121933
CBS 109402	Mo_arg_109402	*Monascus argentinensis*	JN121564	JN121423	JN121730	JN121877
CBS 113675	Mo_lun_113675	*Monascus lunisporas*	JN121570	JN121429	JN121736	JN121881
CBS 109.07	Mo_pur_109.07	*Monascus purpureus*	JN121563	JN121422	JN121729	JN121876
CBS 558.71	Ne_aca_558.71	*Neocarpenteles acanthosporum*	JN121701	JN121534	JN121840	JN121928
NRRL 181/CBS 544.65	Ne_fis_NRRL181	*Neosartorya fischeri genome*	XM_001264288.1	XM_001262828.1	XM_001260746.1	XM_001267038.1

TABLE II. Continued

Culture No.	FIG. 1 acronym[a]	Name in gene or genome databases	RPB1	RPB2	Tsr1	Cct8
CBS 761.68	Pe_cla_761.68	*Penicilliopsis clavariiformis*	JN121716	JN121549	JN121855	JN121940
CBS 209.28	Pe_ada_209.28	*Penicillium adametzii*	JN121598	JN121455	JN121762	JN121943[b]
CBS 220.66	Pe_are_220.66	*Penicillium arenicola*	JN121601	JN121457	JN121764	JN121897
CBS 300.48	Pe_can_300.48	*Penicillium canescens*	JN121636	JN121485	JN121791	JN121964
CBS 304.48	Pe_cha_304.48	*Penicillium charlesii*	JN121637	JN121486	JN121792	JN121965
CBS 306.48	Pe_chr_306.48	*Penicillium chrysogenum*	JN121638	JN121487	JN121793	JN121966
CBS 139.45	Pe_cit_139.45	*Penicillium citrinum*	JN121585	JF417416	JF417383	JF417516
CBS 258.29	Pe_cit_258.29	*Penicillium citreonigrum*	JN121622	JN121474	JN121780	JN121957
CBS 119387	Pe_cof_119387	*Penicillium coffeae*	JN121577	JN121436	JN121743	JN121862
CBS 271.89	Pe_cry_271.89	*Penicillium cryptum*	JN121626	JN121478	JN121784	JN121958
CBS 456.70	Pe_dim_456.70	*Penicillium dimorphosporum*	JN121682[b]	JN121517	JN121823	JN121985
CBS 325.48	Pe_exp_325.48	*Penicillium expansum*	JN121645	JF417427	JF417394	JF417527
CBS 125543	Pe_gla_125543	*Penicillium glabrum*	JN121717	JF417447	JF417413	JF417547
CBS 185.27	Pe_gri_185.27	*Penicillium griseofulvum*	JN121592	JN121449	JN121756	JN121865
CBS 277.58	Pe_gri_277.58	*Penicillium griseolum*	JN121629	JN121480	JN121786	JN121959
CBS 247.56	Pe_isa_247.56	*Penicillium isariiforme*	JN121616	JN121470	JN121720	JN121993
CBS 340.48	Pe_jan_340.48	*Penicillium janthinellum*	JN121650[b]	JN121497	JN121803	JN121974
CBS 185.65	Pe_lag_185.65	*Penicillium lagena*	JN121593	JN121450	JN121757	JN121866
CBS 106.11	Pe_lan_106.11	*Penicillium lanosum*	JN121561	JN121420	JN121727	JN121857
CBS 116871	Pe_mac_116871	*Penicillium macrosclerotiorum*	JN121573	JN121432	JN121739[b]	JN121860
CBS 256.55	Pe_meg_256.55	*Penicillium megasporum*	JN121621	JN121473	JN121779	JN121900
CBS 353.48	Pe_nam_353.48	*Penicillium namyslowskii*	JN121660	JF417430	JF417397	JF417530
CBS 489.66	Pe_och_489.66	*Penicillium ochrosalmoneum*	JN121689	JN121524	JN121830	JN121987
CBS 232.60	Pe_ols_232.60	*Penicillium olsonii*	JN121609	JN121464	JN121771	JN121951[b]
CBS 251.56	Pe_ram_251.56	*Penicillium ramusculum*	JN121619[b]	JN121472	JN121778	JN121956
CBS 372.48	Pe_sim_372.48	*Penicillium simplicissimum*	JN121663[b]	JN121507	JN121813	JN121982[b]
CBS 117503	Pe_thi_117503	*Penicillium thiersii*	JN121575	JN121434	JN121741	JN121861
CBS 430.64	Ph_mac_430.64	*Phialomyces macrosporus*	JN121680	JN121515	JN121821	JN121915
CBS 128032	Ph_can_128032	*Phialosimplex caninus*	JN121587	JN121445	JN121752	JN121892
CBS 109945	Ph_chl_109945	*Phialosimplex chlamydosporus*	JN121566	JN121425	JN121732	JN121879
CBS 366.77	Ph_scl_366.77	*Phialosimplex sclerotialis*	JN121661	JN121505	JN121811	JN121908
CBS 384.61	Po_ins_384.61	*Polypaecilum insolitum*	JN121667	JN121510	JN121816	JN121911
CBS 101166	Po_pis_101166	*Polypaecilum pisci*	JN121555	JN121415	JN121722	JN121870
CBS 396.78	Th_aur_396.78	*Thermoascus aurantiacus*	JN121671	JN121512	JN121818	JN121912
CBS 891.70	Th_aur_891.70	*Thermoascus aurantiacus*	JN121719	JF417444	JF417410	JF417544
CBS 528.71	Th_the_528.71	*Thermoascus thermophilus*	JN121697	JF417442	JF417408	JF417542
CBS 181.67	Th_cru_181.67	*Thermoascus crustaceus*	JN121591	JF417417	JF417384	JF417517
CBS 334.68	Th_can_334.68	*Thysanophora canadensis*	JN121646[b]	JN121493	JN121799	JN121971
CBS 206.57	Th_tax_206.57	*Thysanophora taxi*	JN121597	JN121454	JN121761	JN121942

TABLE II. Continued

Culture No.	FIG. 1 acronym[a]	Name in gene or genome databases	RPB1	RPB2	Tsr1	Cct8
CBS 512.65	Wa_spi_512.65	*Warcupiella spinulosa*	JN121692	JF417441	JF417407	JF417541
CBS 236.71	Xe_bis_236.71	*Xeromyces bisporus*	JN121612	JN121466	JN121773	JN121898

[a] Names used in FIG. 1 are those from the database. They are the same as those used by Houbraken and Samson (2011) except for differences in the use of sexual or asexual names for a few species. For the names *Hemicarpenteles ornatus* and *H. thaxteri* used in the database, the names *Sclerocleista ornatus* and *S. thaxteri* have been used in FIG. 1 in line with Houbraken and Samson (2011) because these genera are not related phylogenetically.

[b] Sequence identifying numbers are corrected from those published in Houbraken and Samson (2011).

DISCUSSION

The strongly supported clades for which we use sexual names also were well supported in the analysis of Houbraken and Samson (2011) (i.e. *Eurotium* = *Aspergillus* subgenus *Aspergillus*, *Neosartorya* = *Aspergillus* subgenus *Fumigati*, *Emericella* = *Aspergillus* subgenus *Nidulantes* and *Chaetosartorya* = *Aspergillus* section *Cremei*. Similar strong support was found in both studies for the *Penicillium* clade and the *Phialosimplex* and *Polypaecilum* clades. Weak support was found in both studies for the clades embracing the grade, *Aspergillus* subgenus *Circumdati*. Where the studies differ is in the relationship of *Penicillium* to the other clades. In the study by Houbraken and Samson (2011), *Penicillium* was sister to *Aspergillus* sensu lato. In our study, *Penicillium* is sister to *Eurotium*, both of which are the most deeply nested clades among species with *Aspergillus* asexual states. In Houbraken and Samson (2011), the one branch that unites *Aspergillus* clades with respect to *Penicillium* had insignificant maximum likelihood support (51%) and strong Bayesian support (1.0), while in our study the four branches that place *Penicillium* deeply within the clade of fungi having *Aspergillus* asexual morphology have strong Bayesian support (0.99–1.0) and weak (60% maximum) to insignificant maximum likelihood support. This difference in tree topology is likely due to the improved alignment obtained by omitting more distantly related taxa. Given that the deep branches are short and weakly supported, room exists for argument about the exact relationships among the clades named *Penicillium*, *Eurotium*, *Neosartorya*, *Emericella* and *Chaetosartorya*. However, no argument exists about their evolutionary equivalence in terms of age and variation in phenotypes of all sorts. Although the grade we name *Aspergillus* is not strongly supported phylogenetically, it is as old as the others and is as distinct as the others in sexual morphology and physiological phenotypes.

As noted in the INTRODUCTION, the abundant attention devoted to choosing names for species with *Aspergillus* asexual morphology is a consequence of their social and scientific importance. Here we consider the consequences of maintaining the sexual names. *Eurotium* species are xerophiles and are commercially important because many species are associated with spoilage, not only of food commodities but also of art and artefacts, paper, leather goods, textiles, timber, even lens of cameras, microscopes and binoculars. *Eurotium* is widely accepted among user groups, such that reintroduction of *Aspergillus* would cause widespread confusion, especially because many names would have to changed, as shown in Hubka et al. (2013).

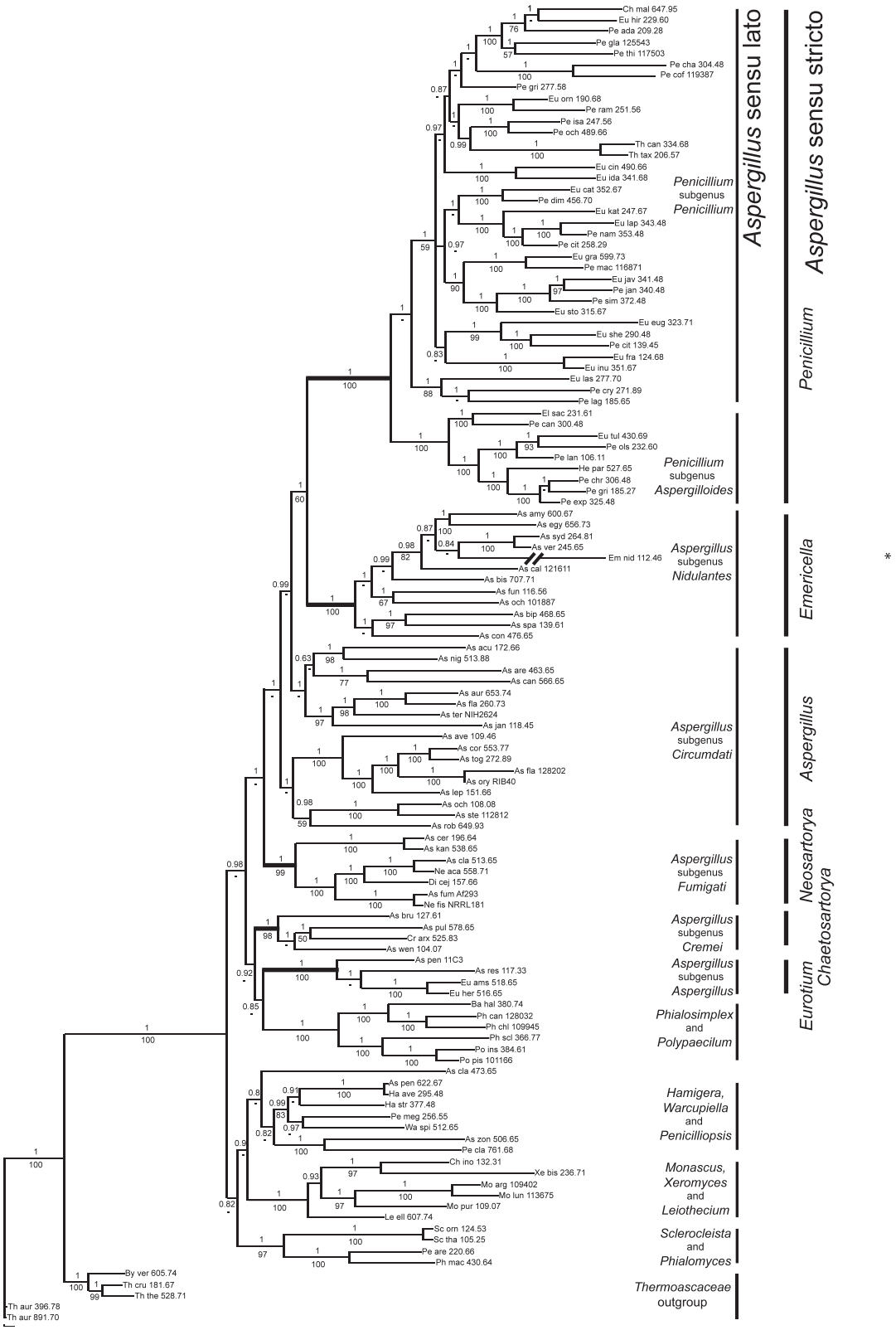

FIG. 1. Bayesian and maximum likelihood phylogenetic analyses of *Aspergillus* and related taxa made with four genes: the RPB1 and RPB2 subunits of RNA polymerase II, *Tsr1*, a putative ribosome biogenesis protein and *Cct8*, the putative chaperonin complex component, TCP-1. Numbers above internal branches are Bayesian probabilities; numbers below are maximum likelihood bootstrap percentages. Taxon names correlate with those in TABLE II. An asterisk marks the end of the

Neosartorya species are commercially and socially important because they are thermophiles. They affect commerce because their sexual spores resist pasteurization and initiate food spoilage and affect human and animal health because they grow at body temperatures. The food safety community is familiar with the name *Neosartorya* while the medical community is familiar with the name *Aspergillus* because *A. fumigatus* is the most important filamentous ascomycetous opportunistic human pathogen. The genus *Neosartorya* is more than 40 y old (Malloch and Cain 1972) and discovery of the sexual state of this species, *Neosartorya fumigata*, has been widely reported (O'Gorman et al. 2009). In our opinion, the medical mycology community is well organized with a strong history of continuing education, so *Neosartorya* will be accepted, particularly in light of the sound scientific basis for its usage. In fact, a large fraction of aspergillosis cases in neutorpenic patients are caused by species outside *Neosartorya* and these infections respond differently to treatment than *N. fumigata*. By emphasizing the different causes of aspergillosis, nomenclature proposed here may improve patient outcomes (Torres et al. 2003). The genus *Neocarpenteles* nests within *Neosartorya* and should be synonymized.

Emericella species are of little commercial importance but are commonly isolated from soils. We estimate that about 90 species are accepted in *Aspergillus* subgenus *Nidulantes* and 35 (40%) of these already have valid names in *Emericella*. One species, *E. nidulans*, is scientifically important as a model in genetic studies on filamentous ascomycetes. It is better known as *Aspergillus nidulans*, but acceptance of the valid sexual name has no fundamental issues and the academic research community can be counted on to endorse nomenclature based on the best available science.

Chaetosartorya species also are xerophiles but are not commercially important. Application of the name *Chaetosartorya* will not inconvenience any significant user group. The small sexual state genera *Warcupiella* and *Sclerocleista* include only species known by sexual names. Because their phylogenetic positions lie outside both *Aspergillus* and *Penicillium* sensu stricto, continued use will be consistent with the provisions of the ICN and not inconvenience any significant user group.

We emphasize that continued use of all of the sexual generic names described above is consistent with the provisions of the ICN and no nomenclatural issues need to be addressed other than preparation of lists of names with no known sexual state that must be recombined from *Aspergillus*.

The position of species currently classified in *Aspergillus* subgenus *Circumdati* is different. The name *Petromyces* could be applied to this grade, as encouraged by the ICN, and no nomenclatural argument exists against doing so. However, there are two arguments for using the old and important name, *Aspergillus*, in place of *Petromyces* for this grade. First, no more than five of the 100-plus species currently accepted in this grade possess a known sexual state in *Petromyces*. Second, several of these commonly occurring species are commercially important. *Aspergillus oryzae* has been in use for 1000 y in the production of Asian foods and, together with *A. niger*, is in widespread use as a source of food and industrial chemicals and enzymes. Equally, *A. flavus*, *A. parasiticus*, *A ochraceus* and *A. carbonarius* and a number of related species produce aflatoxins or ochratoxin A, mycotoxins of the greatest importance in human and animal health. The user base of the species that produce mycotoxins is both widespread and diffuse throughout both developed and developing countries. Applying the name *Aspergillus* to all fungi in this grade will be acceptable to almost all user groups with no inconvenience. Given that phylogenetic support for a *Petromyces* clade is wanting, we realize that additional research may resolve phylogenetic uncertainly in this grade and provide support for future nomenclatural activity. We think, however, that our answer to the problem posed by the new ICN is the one that most closely follows the ICN while also preserving the old and important name, *Aspergillus*. We chose *Aspergillus* subgenus *Circumdati* as the grade to bear the name *Aspergillus* based partly on its being a grade, rather than a well supported clade but also based on usage of names in scientific publications. Hawksworth (2012) has suggested that search engines may provide useful assistance in determining which of competing names are more widely used. To this end we searched major names of interest here in both Web of Science and Google Scholar. It can be seen (TABLE III) that *A. niger* is in much more frequent use in both databases than *A. fumigatus*. If

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exceptionally long terminal branch leading to *Emericella nidulans* 112.46. Clades are named for *Aspergillus* subgenera (left column) and for sexual genera (right column) as described in the text. Branch lengths are proportional to genetic distances among taxa. Details of phylogenetic analysis are in MATERIALS AND METHODS.

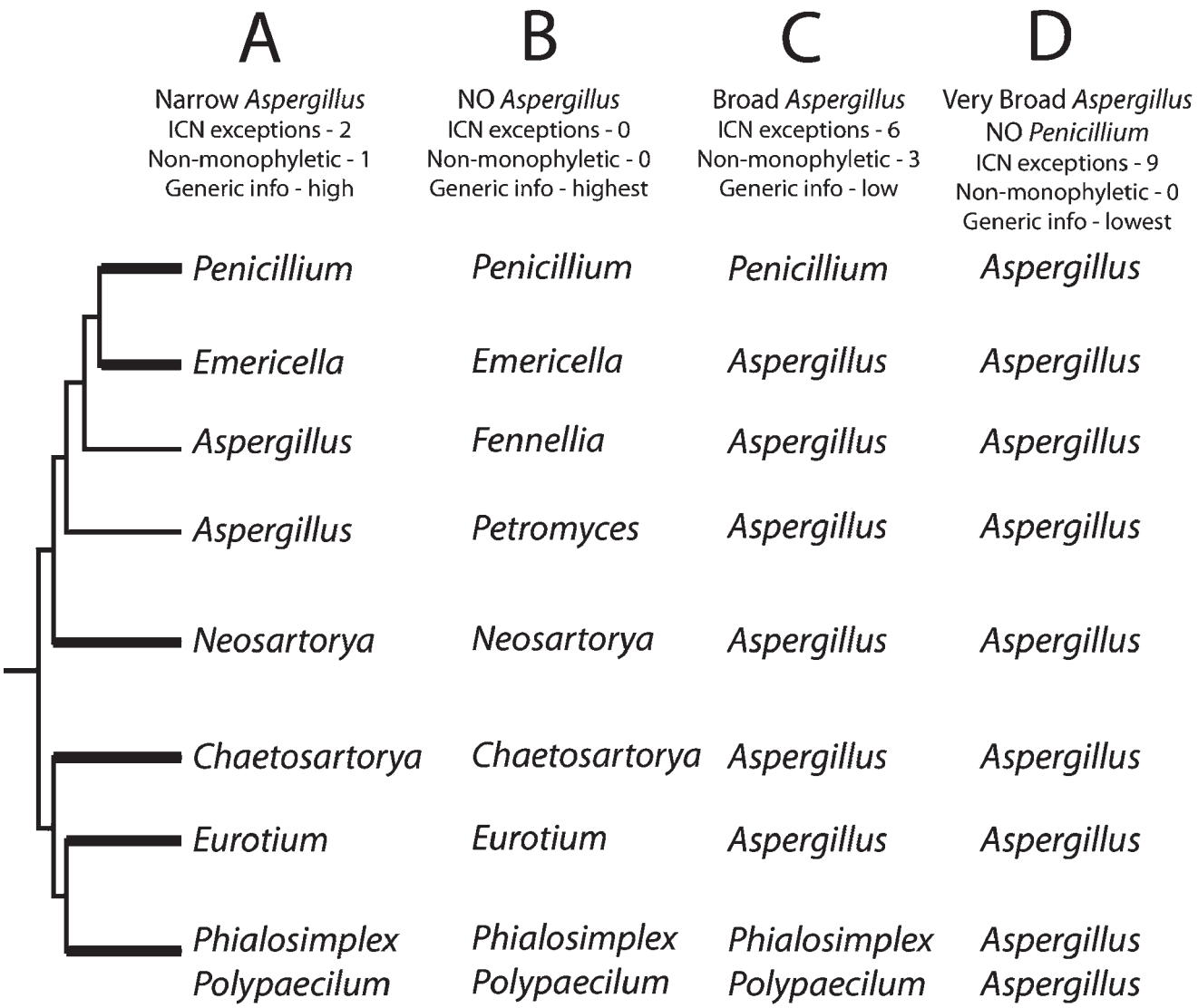

FIG. 2. Effect of the choice of teleomorph or anamorph names on appeals for exceptions to the ICN priority rule, non-monophyly of genera and information content of the generic names. Phylogenetic cartoon with strongly-supported branches thickened, based on the phylogeny presented in FIG 1. A. A narrowly defined genus *Aspergillus*. The ICN must be asked for approval to apply the name *Aspergillus* to the non-monophyletic grade embracing *Petromyces* and *Fennellia*. The information content of the genera would be high because each name embraces one monphyletic clade or, in the case of *Aspergillus*, a small grade. B. Abandon the genus *Aspergillus* by applying the teleopmorph name to every clade. This approach is fully compliant with the ICN, and all names would be applied to monophyletic clades. The information content would be high. However, the name *Aspergillus* would be lost to mycology. C. Apply the name *Aspergillus* broadly to all clades having *Aspergillus* anamorphs. Six exceptions to the ICN would be needed. *Aspergillus* would be made non-monophyletic by the inclusion of *Penicillium*, *Phialosimplex* and *Polypaecilum*. The information content of the name Aspergillus would be low due to the large phenotypc variation found among the six clades bearing the name *Aspergillus*. D. Make *Aspergillus* broad by applying the name to species in the genera *Penicillium*, *Phialosimplex* and *Polypaecilum*. Nine exceptions to the ICN would be needed, but *Aspergillus* would be monophyletic. The information content of the name *Aspergillus* would be low, due to the extreme phenotypic variation in the broad genus. The name *Penicillium* would be lost to mycology.

we add figures for *A. flavus* and *A. oryzae* to those of *A. niger*—a reasonable process because both are in common use and both also are classified within *Aspergillus* subgenus *Circumdati*—we find 2.5 times as many citations for these three species than *A. fumigatus* in Web of Science and only slightly less than 2.5 times in Google Scholar. Therefore, usage in the scientific literature and, by inference, size of the user group, support our choice to retain Aspergillus for *Aspergillus* subgenus *Circumdati* rather than the other

TABLE III. Results of a search of Web of Science and Google Scholar for the common species *A. fumigatus*, *A. niger*, *A. flavus* and *A. oryzae*[a]

Species	No. of hits in Web of Science	No. of hits in Google Scholar
Aspergillus fumigatus	9586	161 000
A. niger	15 397	250 000
A. flavus	6118	66 000
A. oryzae	4465	67 000

[a] Surveys carried out on 13 Feb 2014.

clade of socially-important species, *Neosartorya*. The same approach may be applied to the sexual names. Here *Neosarotrya* is the topic of far more articles than is *Petromyces* (i.e. 265–31 in Web of Science and 2820–488 in Google Scholar, that is 78–87% of the summed citations are for *Neosartorya*). The trend is increasing in favor of *Neosartorya*, which has seen a rise in citations from < 100 in 2004 to > 700 in 2013, whereas citations for *Petromyces* actually declined between 2012 and 2013, from 120 to 90. Again, usage in the scientific literature argues for retaining *Neosartorya* over *Petromyces*.

Our suggestion that the several clades of fungi with *Aspergillus* asexual morphology be recognized as independent genera equal in age, in genetic and in phenotypic diversity to each other and the related genus *Penicillium* stands in contrast to the suggestion that these fungi be recognized as one genus. As described above, lumping these very different fungi into one genus would hide phenotypic variation of significant scientific and social importance, not to mention ignoring the principle of taxonomic monophyly. In both the analysis of Houbraken and Samson (2011) and the analysis presented here the genera *Phialosimplex* and *Polypaecilum* make *Aspergillus* sensu lato non-monophyletic (FIG. 2). This situation could be rectified by renaming these genera as *Aspergillus*, but to do so would add two clades of fungi lacking the asexual spore producing aspergillum (*Phialosimplex* and *Polypaecilum*) to the already large phenotypic variation forced into *Aspergillus* sensu lato. In that case the name *Aspergillus* would not even carry the distinctive asexual morphology for which it was named. In the analysis presented here, the genus *Penicillium* also makes *Aspergillus* non-monophyletic. As noted above, the branches that enforce this non-monophyly are short and poorly supported by maximum likelihood analysis. However, any of the four branches strongly supported by Bayesian analysis would suffice to make *Aspergillus* non-monophyletic. As with the genera *Phialosimplex* and *Polypaecilum*, *Penicillium* could be renamed as *Aspergillus* to make *Aspergillus* sensu lato monophyletic. We think we are safe in assuming that renaming *Penicillium* to make an even larger, monophyletic *Aspergillus* would be rejected by the mycological community.

Proposal.—We advocate that sexual names be applied to the appropriate clades also known by subdivision of *Aspergillus* as follows: *Eurotium* = subgenus *Aspergillus*, *Neosartorya* = *Aspergillus* section *Fumigati*, *Emericella* = *Aspergillus* subgenus *Nidulantes*, and *Chaetosartorya* = *Aspergillus* section *Cremei*. Of the minor genera, *Neocarpenteles* is phylogenetically congeneric with *Neosartorya* while *Neopetromyces* and *Fennellia* nest within *Aspergillus* subgenus *Circumdati* and thus remain in *Aspergillus*. *Sclerocleista*, *Warcupiella* and *Hemicarpenteles* remain unaffected. We also advocate that *Aspergillus* be applied to the clade embracing species in *Aspergillus* subgenus *Circumdati*, a change that will require an application to the ICN and neotypification of the genus *Aspergillus* by *A. niger* in place of *A. glaucus*. The nomenclatural choices that we advocate are in accordance with the recommendations of the ICN, except for the use of *Aspergillus* in place of *Petromyces*. The genera *Penicillium*, *Phialosimplex* and *Polypaecilum* would remain unchanged. Our approach acknowledges the scientific reality of the distinctive morphological and physiological phenotypes associated with the several sexual genera and the evolutionary history of these fungi. Scientific advances based on genetic variation brought about the end of dual nomenclature for fungi (Taylor 2011). The same scientific advances should be used in implementing the new fungal nomenclature. To do otherwise would be unscientific and anti-intellectual.

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