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Changes in fungal taxonomy: mycological rationale and clinical implications

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SUMMARY Numerous fungal species of medical importance have been recently subjected to and will likely continue to undergo nomenclatural changes as a result of the application of molecular approaches to fungal classification together with abandonment of dual nomenclature. Here, we summarize those changes affecting key groups of fungi of medical importance, explaining the mycological (taxonomic) rationale that underpinned the changes and the clinical relevance/importance (where such exists) of the key nomenclatural revisions. Potential mechanisms to mitigate unnecessary taxonomic instability are suggested, together with approaches to raise awareness of important changes to minimize potential clinical confusion.

KEYWORDS fungal taxonomy, nomenclature, clinical impact, name changes, phylogenetics, molecular identification, medically important fungi

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INTRODUCTION

Kingdom *Fungi* is an enormous and diverse collection of predominantly ubiquitous organisms. Of the estimated 1.5 to >5 million fungal species in the Kingdom, only approximately 150,000 species (<10%) have been formally described (1–6). The Kingdom includes many species capable of infecting humans, other animals, wild and cultivated plants, and other fungi (7, 8). Indeed, the annual burden of human disease was recently proposed to exceed 1 billion infections, with >150 million people suffering from serious fungal disease (7–9). While the majority of fungal infections are caused by a handful of key human pathogenic species that have long been recognized as opportunistic agents of human disease (7, 9), the potential clinical significance of hitherto undiscovered species is unknown (5).

The number of novel fungi reported from human infections continues to grow rapidly, with a 10-fold increase in reports of new fungal pathogens of humans, animals, and plants between 1995 and 2012 (5, 10). Indeed, 136 novel taxa isolated from human clinical samples have been published since 2012, with 110 of those being the agents of confirmed cases of human infection (11–14) and previously recognized fungi have been newly associated with local, national, or worldwide outbreaks of human disease (15–22). In parallel, human activity (alteration of natural environments, global warming, increased global trade and travel, widespread environmental antifungal usage, increased use of aggressive immunosuppressive strategies in medicine and hematology in particular, viral pandemics) is driving the emergence of new opportunistic fungal pathogens and providing more susceptible hosts for existing pathogens (7, 10, 23–28). It is, therefore, inevitable that the number of fungal species recognized as etiological agents of human disease and the numbers of human infections caused by such fungi will continue to grow.

Since it is well established that different fungal species have wildly variable antifungal susceptibility profiles (29–36), the correct identification of the etiological agents of human infections coupled with accurate and unambiguous reporting to the treating physician is paramount to optimizing clinical outcomes in patients with invasive fungal disease. Historically, fungal identification was achieved by careful examination of morphological and phenotypic traits, which also allowed fungal taxonomists to classify fungi on the basis of shared traits (37–41). In medical mycology, this approach to identification and classification has become increasingly complicated due to the incredible diversity of the fungal Kingdom and the ever-increasing number of fungi capable of causing human infection. As more of the Kingdom was described and more human pathogenic fungi were discovered, new classifications and changes to existing nomenclature have become commonplace (5, 11–14, 21). More recently, the speed of taxonomic upheaval has been dramatically increased by the adoption of molecular methods for fungal identification and polyphasic approaches to species boundary delineation (11–14, 42–47). This review examines in detail (i) the drivers and rationale for changes in fungal taxonomy and nomenclature, (ii) the key genera and species of medical importance that have been and (iii) are likely to continue to be affected, (iv) the potential clinical implications of widespread nomenclatural change, and (v) potential mitigators to limit clinical confusion.

THE DRIVERS OF NOMENCLATURAL CHANGE

Molecular phylogenetic approaches to fungal identification

As alluded to above, traditional identification methods for fungi of medical importance that were based on meticulous examination of morphological and phenotypic characters (including analyses of carbohydrate assimilation/fermentation and/or biochemical profiling) are fraught with limitations. For filamentous fungi (molds), microscopic and macroscopic features often are not produced constitutively, can be dependent on growth substrate, and frequently differ between the sexual (teleomorph) and asexual (anamorph) states (42, 48, 49). Additionally, numerous genera are known to exhibit

dimorphism or pleomorphism (20, 49–51). Conventional (morphological) identification approaches are further complicated by convergent evolution of unrelated taxa (52, 53), divergent evolution of genetically related organisms (54), and hybridization (55). Faced with the above conundra, the medical mycology field enthusiastically adopted molecular approaches to fungal identification, typically based around PCR amplification and sequencing of segments of the fungal genome and comparison of the sequences with those present in public nucleotide sequence databases (42, 43, 56). When such approaches are extended to include multiple genes/genome fragments and phylogenetic comparisons with well-characterized extant taxa (phylogenetic species recognition), they can also be used to discover, delineate, and describe novel fungal organisms (44, 45).

The principal advantages of molecular approaches to identification and taxonomy are that related fungi are grouped together regardless of growth form or morphological characteristics and that fungi that remain sterile in the laboratory can be identified in the absence of any notable morphological characters, allowing predictions to be made regarding potential clinical significance and likely antifungal susceptibility patterns (5, 29, 35, 42, 43, 48, 57). At the simplest level, notwithstanding the many issues with sequence database integrity (3, 58–60), medical mycologists can now accurately identify the vast majority of fungi that they encounter and flag novelties that have not previously been encountered or at least subjected to sequencing (20, 51, 56, 61, 62). An immediate effect of implementation of molecular identification approaches was the description of innumerable, often hitherto unsuspected, cryptic fungal species (those that can only be discriminated by molecular approaches) in many well-studied morpho-species of established human pathogenic fungi (43, 55, 63–75). This recently discovered molecular diversity has resulted in an incredible increase in the number of clinically relevant fungi and associated novel names together with an increase in our understanding of the diversity and possible size of Kingdom *Fungi*.

The Amsterdam declaration

Historically, dual nomenclature was permitted across Kingdom *Fungi*, as different scientific names had been separately and independently assigned to the teleomorph and anamorph states which often bore little morphological resemblance (11–14, 76). Since both growth forms are identical at the genetic level and molecular methods can now be employed to prove this relatedness, this system was clearly impractical, and the Amsterdam Declaration of Fungal Nomenclature agreed that dual nomenclature should be prohibited by abolition of Article 59 in the Code of Botanical Nomenclature (77). Since 1 January 2013, not only was dual nomenclature banned, the practice of assigning precedence to the teleomorph name over any anamorph alternative(s) was also abandoned. The International Code of Nomenclature for algae, fungi, and plants (ICN) recommended that any one of the legitimately published names (whether for the anamorph or teleomorph form) for a given species can now be proposed as the correct name for that species. In cases where a sexual name has historical priority over the asexual one(s), the final decision would require the majority support by the mycological community. This amendment thus has profound implications for fungal nomenclature since all established fungal names (plus disease names where these are linked to genera, e.g., candidosis, aspergillosis) are potentially in jeopardy, as mycologists are forced to choose a single name for each fungus (78). In general, the majority of nomenclatural questions addressed to date have been easily resolved for many fungal genera (79–82), but complications have arisen for a number of medically, economically, and socially important fungi that have well-established sexual and asexual names, including *Fusarium* (where a consensus from the mycological community is proving harder to reach) and *Cryptococcus* (for which there was initial resistance). These will be discussed in detail later.

KINGDOM- AND PHYLUM-WIDE TAXONOMIC RE-ORGANISATIONS

Although the ability to apply molecular approaches to fungal identification and classification has allowed the correct placement of thousands of sterile fungi (organisms historically classified in the false phylum *Deuteromycota*) in the fungal Kingdom, the single most significant impact of such approaches was the Kingdom-wide restructuring of the fungal tree of life (45, 83). The fungal Kingdom is now known to encompass either eight or nine phyla (instead of the original three), dependent on whether *Glomeromycota* is recognized as a phylum or rather as the subphylum *Glomeromycotina* (45, 83–85). Dramatically, although the *Ascomycota* and *Basidiomycota* are retained and now constitute the sub-Kingdom *Dikarya*, the phylum *Zygomycota* was disbanded based upon molecular approaches that demonstrated definitively that it was polyphyletic (83–85). *Fungi* previously classified in *Zygomycota* are now dispersed between the phyla *Mucoromycota* and *Zoopagomycota* (Table 1), with most of the medically important members contained in the order *Mucorales*, sub-phylum *Mucoromycotina*, within *Mucoromycota* (86).

The phylum *Ascomycota* currently contains three subphyla (Table 1): (i) subphylum *Taphrinomycotina*, contains a single medically important genus, *Pneumocystis*, which is formally subsumed into Kingdom *Fungi*; (ii) subphylum *Saccharomycotina* contains a single medically important order *Saccharomycetales*, which encompasses most pathogenic ascomycetous yeasts, including *Candida* and many related teleomorph genera; (iii) subphylum *Pezizomycotina* contains the remainder of the medically important Ascomycete genera, distributed among the 14 different orders which are listed in Table 1 (83–85, 87). Even with the advent of molecular phylogenetic approaches, some medically important Ascomycetous genera (*Neoscytalidium*, *Geomyces*, and *Pseudogymnoascus*) remain *incertae sedis* (unknown position), pending analyses of more of the fungal Kingdom. Finally, the phylum Basidiomycota contains three subphyla (*Pucciniomycotina*, *Ustilaginomycotina*, and *Agaricomycotina*) and at least 46 orders (83–85, 87), only a handful of which include the ~20 Basidiomycete genera that have been formally associated with human infections (Table 1).

KEY FUNGI OF MEDICAL IMPORTANCE SUBJECT TO RECENT TAXONOMIC REVISIONS AT THE GENUS LEVEL

The delineation of species boundaries traditionally depended upon sexual compatibility and the ability to produce viable progeny after mating (88). Today, such boundaries can generally be tested with molecular approaches by Genealogical Concordance Phylogenetic Species Recognition (88, 89), However, all taxonomic categories above species are intrinsically arbitrary in nature, since genera were historically erected to encompass collections of species that shared similar phenotypic and/or morphological traits. Similarly to more traditional identification and classification methods, there are currently no accepted molecular criteria that can be used to define and delimit a genus, although phylogenetic distance and clustering of species in well-delimited clades are the most common parameters used in current taxonomic practice [reviewed in reference (76)]. Given the above, it was inevitable that many genera circumscribed based on shared morphological characters would prove to be polyphyletic using molecular approaches, with the result that a number of well-established human fungal pathogens might be subject to nomenclatural revision (6, 12–14, 45, 57, 76).

Candida and allied ascomycete yeast genera

Asexual yeasts that divide by multilateral budding with no other distinctive morphological features have traditionally been ascribed to the anamorphic ascomycetous yeast genus *Candida*, with the result that this genus has continued to grow disproportionately in size [reviewed in reference (90)]. However, DNA-based studies have clearly shown that the classification of asexually producing yeasts based on phenotypic characteristics is often discordant with well-established and apparently stable molecular phylogenies (91,

TABLE 1 Revised taxonomy of the fungal Kingdom, indicating the positions of key medically relevant genera

Phylum	Subphylum	Order	Genera
Ascomycota	*Taphrinomycotina*	*Pneumocystidiales*	*Pneumocystis*
	Saccharomycotina	*Saccharomycetales*	*Candida*
			Clavispora
			Cyberlindnera
			Debaryomyces
			Diutina
			Hanseniaspora
			Issatchenkia
			Kazachstania
			Kluyveromyces
			Lodderomyces
			Metschnikowia
			Meyerozyma
			Nakaseomyces
			Pichia
			Saccharomyces
			Wickerhamiella
			Yarrowia
			Wickerhamomyces
			Zygosaccharomyces
	Pezizomycotina	*Capnodiales*	*Cladosporium*
			Hortaea
			Piedraia
		Dothideales	*Aureobasidium*
		Pleosporales	*Alternaria*
			Curvularia
			Emarellia
			Exserohilum
			Falciformispora
			Medicopsis
			Neotestudina
			Nigrograna
			Parathyridaria
			Phoma
			Trematosphaeria
			Ulocladium
		Chaetothyriales	*Cladophialophora*
			Exophiala
			Fonsecaea
			Phialophora
			Ramichloridium
			Rhinocladiella
		Eurotiales	*Aspergillus*
			Monascus
			Paecilomyces
			Penicillium
			Rasamsonia
			Talaromyces
			Thermoascus
		Onygenales	*Aphanoascus*
			Arthroderma

(*Continued on next page*)

TABLE 1 Revised taxonomy of the fungal Kingdom, indicating the positions of key medically relevant genera (*Continued*)

Phylum	Subphylum	Order	Genera
			Chrysosporium
			Blastomyces
			Coccidioides
			Emergomyces
			Emmonsia
			Epidermophyton
			Histoplasma
			Lacazia
			Lophophyton
			Microsporum
			Myceliophthora
			Nannizzia
			Nannizziopsis
			Paracoccidioides
			Paraphyton
			Trichophyton
		Hypocreales	*Acremonium*
			Fusarium
			Nectria
			Purpureocillium
			Sarocladium
		Microascales	*Lomentospora*
			Pseudallescheria
			Scedosporium
			Scopulariopsis
		Sordariales	*Chaetomium*
			Madurella
			Phialemonium
		Calosphaeriales	*Pleurostoma*
		Patellariales	*Rhytidhysteron*
		Coniochaetiales	*Lecythophora*
		Ophiostomatales	*Sporothrix*
		Diaporthales	*Phaeoacremonium*
Basidiomycota	*Pucciniomycotina*	*Sporidiales*	*Rhodotorula*
			Sporobolomyces
	Ustilagiomycotina	*Malasseziales*	*Malassezia*
	Agaricomycotina	*Cystofilobasidiales*	*Cystobasidium*
		Filobasidiales	*Naganishia*
			Filobasidium
		Tremellales	*Cryptococcus*
			Papiliotrema
		Trichosporonales	*Trichosporon*
			Cutaneotrichosporon
			Apiotrichum
		Agaricales	*Bjerkandera*
			Coprinus
			Hormographiella
			Schizophyllum
			Sporotrichum
Mucoromycota	*Mucormycotina*	*Mucorales*	*Apophysomyces*
			Cokeromyces

(*Continued on next page*)

TABLE 1 Revised taxonomy of the fungal Kingdom, indicating the positions of key medically relevant genera (*Continued*)

Phylum	Subphylum	Order	Genera
			Cunninghamella
			Lichtheimia
			Mucor
			Rhizomucor
			Rhizopus
			Saksenaea
		Mortierellales	*Mortierella*
Zoopagomycota	*Entomopthoromycotina*	*Entomophthorales*	*Conidiobolus*
		Basidiobolales	*Basidiobolus*
	Kickxellomycotina	*Kickxellales*	*Kickxella*

92). Indeed, for several decades, it has been accepted that *Candida* is polyphyletic: the medically relevant species among the >400 currently recognized *Candida* species are distributed among at least 13 teleomorph genera in the order Saccharomycetales [Table 1; (90–94)]. Under the rules of the new Code that require fungal species to have a single valid name (77), many of the current species of *Candida* and other asexual yeast genera must undergo nomenclatural revision so that genus membership reflects phylogenetic affinities.

The type species of *Candida*, *C. vulgaris* (a synonym of *C. tropicalis*), forms a well-supported monophyletic group within the family *Debaryomycetaceae* that contains a limited number of other medically important *Candida* spp., including members of the *C. albicans* complex (*C. albicans*, *C. dubliniensis*, and *C. africana*) and the *C. parapsilosis* complex (*C. parapsilosis*, *C. metapsilosis*, and *C. orthopsilosis*) (90). Given that *C. albicans* is the most widely recognized species medically and that the use of the *Candida* genus name for this clade has precedence, it makes sense to retain the anamorph genus name for this group of organisms. Many of the *Candida* species that sit outside this group form well-circumscribed phylogenetic clades with members of other recognized teleomorph genera and their transfer to those teleomorph genera is thus theoretically relatively straightforward. Key, medically important species affected include members of the *Candida glabrata* complex (*C. glabrata*, *C. nivariensis*, and *C. bracarensis*), which sit in the *Nakaseomyces* clade (95); *Candida krusei*, *C. norvegensis*, and *C. inconspicua* which have *Pichia* teleomorphs (90, 92, 94); *Candida guilliermondii* and *Candida fermentati* with *Meyerozyma* teleomorphs (96, 97); members of the *C. rugosa* complex (*C. rugosa*, *Candida pseudorugosa*, *Candida pararugosa*, *Candida mesorugosa*, and *Candida neorugosa*) plus *C. catenulata*, which all have *Diutina* teleomorphs (98); *Candida kefyr* [teleomorph *Kluyveromyces marxianus* (99)]; *Candida lipolytica* [teleomorph *Yarrowia lipolytica* (100)]; *Candida lusitaniae* [teleomorph *Clavispora lusitaniae* (101)]; *Candida pelliculosa* [teleomorph *Wickerhamomyces anomalus* (102)]; and *Candida utilis* [teleomorph *Cyberlindnera jadinii* (103)]. A list of the most commonly encountered *Candida* species subject to nomenclatural changes is provided in Table 2 and references (13, 94). All of the alternative names listed above are legitimate according to the new Code and have been registered with Mycobank.

Basidiomycetous yeast genera

A number of recent phylogenetic studies have resulted in the revision of the taxonomy of those *Cryptococcus* species that frequently cause human and animal disease (*C. neoformans* and *C. gattii* complexes), together with the reorganization of those species in the genus *Cryptococcus* that are rarely associated with human disease. The species complexes previously designated *Cryptococcus neoformans* and *C. gattii*, after some initial resistance, are now accepted to encompass at least seven species, including five species in the *C. gattii* complex (55). In parallel, the vast majority of the non-*C. neoformans*/*gattii* species that have been anecdotally reported as possible agents of mammalian infection

TABLE 2 Taxonomic revisions affecting basidiomycete and ascomycete yeasts of medical importance

Previous name	Revised name	Order	Family	Reference
Candida bracarensis	*Nakaseomyces bracarensis*	*Saccharomycetales*	*Saccharomycetaceae*	104
Candida catenulata	*Diutina catenulata*	*Saccharomycetales*	*Metschnikowiaceae*	105
Candida fabianii	*Cyberlindnera fabianii*	*Saccharomycetales*	*Phaffomycetaceae*	103
Candida famata	*Debaryomyces hansenii*	*Saccharomycetales*	*Debaryomycetaceae*	106
Candida fermentati	*Meyerozyma caribbica*	*Saccharomycetales*	*Debaryomycetaceae*	97
Candida glabrata	*Nakaseomyces glabratus*	*Saccharomycetales*	*Saccharomycetaceae*	104
Candida haemulonii group II	*Candida duobushaemulonii*	*Saccharomycetales*	*Metschnikowiaceae*	107
Candida inconspicua	*Pichia cactophila*	*Saccharomycetales*	*Pichiaceae*	108
Candida infanticola	*Wickerhamiella infanticola*	*Saccharomycetales*	*Trichomonascaceae*	109
Candida kefyr	*Kluyveromyces marxianus*	*Saccharomycetales*	*Saccharomycetaceae*	99
Candida krusei	*Pichia kudriavzevii*	*Saccharomycetales*	*Pichiaceae*	110
Candida guilliermondii	*Meyerozyma guilliermondii*	*Saccharomycetales*	*Debaryomycetaceae*	97
Candida lambica	*Pichia fermentans*	*Saccharomycetales*	*Pichiaceae*	111
Candida lipolytica	*Yarrowia lipolytica*	*Saccharomycetales*	*Dipodascaceae*	100
Candida lusitaniae	*Clavispora lusitaniae*	*Saccharomycetales*	*Metschnikowiaceae*	101
Candida nivariensis	*Nakaseomyces nivariensis*	*Saccharomycetales*	*Saccharomycetaceae*	104
Candida norvegensis	*Pichia norvegensis*	*Saccharomycetales*	*Pichiaceae*	112
Candida pararugosa	*Wickerhamiella pararugosa*	*Saccharomycetales*	*Trichomonascaceae*	109
Candida pelliculosa	*Wickerhamomyces anomalus*	*Saccharomycetales*	*Phaffomycetaceae*	102
Candida pintolopesii	*Kazachstania telluris*	*Saccharomycetales*	*Saccharomycetaceae*	113
Candida pulcherrima	*Metschnikowia pulcherrima*	*Saccharomycetales*	*Metschnikowiaceae*	114
Candida utilis	*Cyberlindnera jadinii*	*Saccharomycetales*	*Phaffomycetaceae*	103
Cryptococcus albidus	*Naganishia albida*	*Filobasidiales*	*Filobasidiaceae*	115
Cryptococcus curvatus	*Cutaneotrichosporon curvatum*	*Trichosporonales*	*Trichosporonaceae*	115
Cryptococcus diffluens	*Naganishia diffluens*	*Filobasidiales*	*Filobasidiaceae*	115
Rhodotorula minuta	*Cystobasidium minutum*	*Cystobasidiales*	*Cystobasidiaceae*	116
Rhodotorula slooffiae	*Cystobasidium slooffiae*	*Cystobasidiales*	*Cystobasidiaceae*	116
Stephanoascus ciferrii	*Trichomonascus ciferrii*	*Saccharomycetales*	*Trichomonascaceae*	117
Trichosporon cutaneum	*Cutaneotrichosporon cutaneum*	*Trichosporonales*	*Trichosporonaceae*	115
Trichosporon loubieri	*Apiotrichum loubieri*	*Trichosporonales*	*Trichosporonaceae*	115
Trichosporon mucoides	*Cutaneotrichosporon mucoides*	*Trichosporonales*	*Trichosporonaceae*	115
Trichosporon mycotoxinivorans	*Apiotrichum mycotoxinivorans*	*Trichosporonales*	*Trichosporonaceae*	115

have been renamed, including *Cryptococcus adeliensis*, *Cryptococcus albidus*, *Cryptococcus curvatus*, *Cryptococcus diffluens*, *Cryptococcus flavescens*, *Cryptococcus luteolus*, *Cryptococcus laurentii*, *Cryptococcus liquefaciens*, *Cryptococcus terreus*, and *Cryptococcus uniguttulatus* (*Filobasidium uniguttulatum*). Many of these species are only distantly related to the seven species in the *Cryptococcus neoformans*/*C. gattii* species complexes, and for this reason, they are among the >100 ex-*Cryptococcus* spp. that have recently been correctly reassigned to alternative *Tremellomycete* genera, including *Naganishia* (*C. adeliensis*, *C. albidus*, *C. diffluens*, and *C. liquefaciens*), *Hannaella* (*C. luteolus*), *Solicoccozyma* (*C. terreus*), and *Papiliotrema* (*C. laurentii* and *C. flavescens*) (115).

The genus *Trichosporon*, which previously contained in excess of 30 validly described species, is also now known to be polyphyletic (115). *Trichosporon asahii*, *Trichosporon asteroides*, *Trichosporon cutaneum*, *Trichosporon dermatis*, *Trichosporon inkin*, *Trichosporon jirovecii*, *Trichosporon loubieri*, *Trichosporon mucoides*, *Trichosporon mycotoxinivorans*, and *Trichosporon ovoides* have all been reported from human infections (118). *T. asahii*, *T. asteroides*, and *T. ovoides* have been retained in *Trichosporon*; *T. loubieri* and *T. mycotoxinivorans* are reclassified in *Apiotrichum*; and *T. cutaneum*, *T. mucoides*, *T. dermatis*, and *T. jirovecii* have been assigned to the novel genus *Cutaneotrichosporon* (115). Similarly, although more than 60 species of *Rhodotorula* were originally listed in the Mycobank database, the genus is now known to be polyphyletic (119). The major clinically

relevant species are *Rhodotorula mucilaginosa*, *Rhodotorula minuta*, *Rhodotorula glutinis*, *Rhodotorula slooffiae*, and *Rhodotorula dairenensis*. *R. mucilaginosa*, *R. dairenensis*, and *R. glutinis* are retained in *Rhodotorula*; *R. minuta* and *R. slooffiae* have been reclassified in *Cystobasidium* (119). We believe that these nomenclatural corrections to the less common *Cryptococcus* spp. and to the outlier *Rhodotorula* spp., which are well supported by the available DNA data, are welcome as they reflect that most of these organisms are unlikely or very rare human pathogens and are more commonly encountered in the clinical laboratory as either contaminants or common (frequently skin) commensal organisms (120–123).

Dermatophytes and their relatives

It has been known for some time that the three historical genera of dermatophytes (*Microsporum*, *Trichophyton*, and *Epidermophyton*) as delineated by conventional morphological criteria were only partly concordant with phylogenetic analyses based on limited data sets that included the nuclear rRNA genes (124, 125). In particular, *Trichophyton* was clearly polyphyletic in most studies, with the strictly anthropophilic organisms and those geophilic members of the genus that rarely cause human infections clustering separately in molecularly stable trees (124, 126). This was confirmed more recently via an MLST approach targeting five loci and a large panel of type and reference strains of the *Arthrodermataceae* (127). Tree topologies were remarkably similar to those earlier phylogenies, indicating that the phylogenetic representation of the dermatophytes and their relatives had reached a level of stability not influenced by taxon bias or sampling errors.

Under the auspices of these new phylogenetic analyses, the main anthropophilic dermatophytes and those zoophilic organisms regularly associated with human infections were almost all retained in *Trichophyton*, *Microsporum*, and *Epidermophyton* and the geophilic species, and additional zoophilic organisms that are rare human pathogens were re-distributed between *Arthroderma*, *Nannizzia*, and *Lophophyton* (Table 3). Under that newly proposed taxonomy, *Arthroderma* contained 21 species; *Trichophyton*, 16; *Nannizzia*, 9; *Microsporum* and *Paraphyton* were restricted to 3 species each; and *Lophophyton* and *Epidermophyton*, 1 species each (127). In that study, it was recognized that the numbers of zoophilic and particularly geophilic species were still likely to grow as these organisms were likely under-sampled compared to their anthropophilic counterparts (127). Indeed, in a little over 6 years, the numbers of *Arthroderma*, *Trichophyton*, and *Nannizzia* spp. have risen to 27, 22, and 13, respectively [reviewed in reference (128) and references therein].

Dimorphic fungal pathogens of humans and animals in the family *Ajellomycetaceae*

For almost a century, four main genera of systemic, dimorphic fungal pathogens of humans were recognized (*Histoplasma*, *Coccidioides*, *Blastomyces*, and *Paracoccidioides*), with each genus containing at most one or two species [reviewed in references (147–150)]. Additional dimorphic fungi which resided in the genus *Emmonsia* are the etiological agents of the pulmonary disease adiaspiromycosis which is principally encountered in small burrowing mammals [*Emmonsia crescens* and *Emmonsia parva* (151–153)] or occasionally disseminated infections in immunocompromised hosts [*Emmonsia pasteuriana* (154, 155)].

This historical taxonomy was recently challenged by the description of a number of novel thermally dimorphic human fungal pathogens which was coupled with detailed MLST and whole genome analyses of new and extant members of the *Onygenales* (51, 133, 156–158). As a result, five existing or novel *Emmonsia*-like fungi (including *Emmonsia pasteuriana*, now *Emergomyces pasteurianus*) were placed in a newly erected Onygenalean genus *Emergomyces*, which includes *Emergomyces africanus*, the most common dimorphic fungal pathogen encountered in immunocompromised patients in Southern Africa (156). Additionally, *Emmonsia parva* and *Emmonsia helica* were

TABLE 3 List of revised taxa of key human pathogenic filamentous fungi (molds)

Previous species name(s)	Revised species name	Order	Reference
Absidia corymbifera	*Lichtheimia corymbifera*	*Mucorales*	129
Acremonium kiliense	*Sarocladium kiliense*	*Hypocreales*	130
Acremonium strictum	*Sarocladium strictum*	*Hypocreales*	130
Aspergillus amoenus	*Aspergillus versicolor*	*Eurotiales*	131
Aspergillus austroafricanus	*Aspergillus versicolor*	*Eurotiales*	131
Aspergillus cvetkovicii	*Aspergillus creber*	*Eurotiales*	131
Aspergillus fructus	*Aspergillus versicolor*	*Eurotiales*	131
Aspergillus griseoaurantiacus	*Aspergillus versicolor*	*Eurotiales*	131
Aspergillus hongkongensis	*Aspergillus versicolor*	*Eurotiales*	131
Aspergillus jensenii	*Aspergillus creber*	*Eurotiales*	131
Aspergillus pepii	*Aspergillus versicolor*	*Eurotiales*	131
Aspergillus protruberus	*Aspergillus versicolor*	*Eurotiales*	131
Aspergillus puulaaueensis	*Aspergillus creber*	*Eurotiales*	131
Aspergillus tabacinus	*Aspergillus versicolor*	*Eurotiales*	131
Aspergillus tennesseensis	*Aspergillus creber*	*Eurotiales*	131
Aspergillus venenatus	*Aspergillus creber*	*Eurotiales*	131
Bipolaris australiensis	*Curvularia australiensis*	*Pleosporales*	132
Bipolaris hawaiiensis	*Curvularia hawaiiensis*	*Pleosporales*	132
Bipolaris spicifera	*Curvularia spicifera*	*Pleosporales*	132
Emmonsia helica	*Blastomyces helicus*	*Onygenales*	133
Emmonsia parva	*Blastomyces parvus*	*Onygenales*	133
Emmonsia pasteuriana	*Emergomyces pasteurianus*	*Onygenales*	51
Geosmithia argillacea	*Rasamsonia argillacea*	*Eurotiales*	134
Lecythophora hoffmannii	*Coniochaeta hoffmannii*	*Coniochaetales*	135
Lecythophora mutabilis	*Coniochaeta mutabilis*	*Coniochaetales*	135
Leptosphaeria senegalensis	*Falciformispora senegalensis*	*Pleosporales*	136
Leptosphaeria tomkinsii	*Falciformispora tomkinsii*	*Pleosporales*	136
Madurella grisea	*Trematosphaeria grisea*	*Pleosporales*	136
Microsporum cookei	*Paraphyton cookei*	*Onygenales*	127
Microsporum fulvum	*Nannizzia fulva*	*Onygenales*	127
Microsporum gallinae	*Lophophyton gallinae*	*Onygenales*	127
Microsporum gypseum	*Nannizzia gypsea*	*Onygenales*	127
Microsporum nanum	*Nannizzia nana*	*Onygenales*	127
Microsporum persicolor	*Nannizzia persicolor*	*Onygenales*	127
Ochroconis gallopava	*Verruconis gallopava*	*Venturiales*	137
Paecilomyces lilacinus	*Purpureocillium lilacinum*	*Hypocreales*	53
Penicillium marneffei	*Talaromyces marneffei*	*Eurotiales*	138
Phialemonium curvatum	*Thyridium curvatum*	*Sordariales*	139
Phoma versabilis	*Sclerotiophoma versabilis*	*Pleosporales*	140
Pleurostomophora ochracea	*Pleurostoma ochraceum*	*Calosphaeriales*	141
Pleurostomophora richardsiae	*Pleurostoma richardsiae*	*Calosphaeriales*	141
Pleurostomophora repens	*Pleurostoma repens*	*Calosphaeriales*	141
Pseudallescheria boydii	*Scedosporium boydii*	*Microascales*	142
Pyrenochaeta mackinnonii	*Nigrograna mackinnonii*	*Pleosporales*	143
Pyrenochaeta romeroi	*Medicopsis romeroi*	*Pleosporales*	144
Sarcopodium oculorum	*Thyridium oculorum*	*Sordariales*	139
Scedosporium prolificans	*Lomentospora prolificans*	*Microascales*	142
Trichophyton benhamiae[a]	*Trichophyton africanum*	*Onygenales*	145
Trichophyton benhamiae[b]	*Trichophyton europaeum*	*Onygenales*	145
Trichophyton benhamiae[c]	*Trichophyton japonicum*	*Onygenales*	145
Trichophyton terrestre	*Arthroderma terrestre*	*Onygenales*	146

[a]African race.
[b]European race, predominates in guinea pigs.
[c]East Asia strains, found in rabbits and guinea pigs.

reassigned to *Blastomyces* as *B. parvus* and *B. helicus*, respectively [Table 3; (51, 133)]. Currently, *Emergomyces* encompasses five distinct species some of which are potentially geographically restricted (*Es. pasteurianus*, *Es. africanus*, *Es. canadensis*, *Es. europaeus*, and *Es. orientalis*), and *Blastomyces* has been expanded to include seven species (*B. dermatitidis*, *B. gilchristii*, *B. parvus*, *B. silverae*, *B. percursus*, *B. emzantsi*, and *B. helicus*). While the genus *Emmonsia* has been preserved (it was originally typified by *E. parva*), it is now limited to two species, *E. crescens* (the cause of adiaspiromycosis worldwide and designated new type species) and *E. soli* (currently represented by a single isolate).

Individual genera of fungi of medical interest

Aside the examples of extensive revisions of the large genera listed above, a significant number of other individual medically important pathogenic fungi have undergone recent taxonomic and nomenclatural changes. The dimorphic fungal pathogen endemic to parts of Asia formerly known as *Penicillium marneffei* (159, 160) was shown to be unrelated to most of the other, principally saprobic, *Penicillium* species, and was moved, together with most other biverticillate "*Penicillium*" species into the teleomorph genus *Talaromyces* (as *Talaromyces marneffei*), which better reflects its pathogenic potential (138).

In a similar vein, the emerging fungal pathogen originally described as *Paecilomyces lilacinus* was shown by MLST to be unrelated to other *Paecilomyces* spp., and the novel genus *Purpureocillium* was erected to accommodate it, as *Purpureocillium lilacinum* (53). The recognition that *P. lilacinum* (*Hypocreales*) was genetically unrelated to *Paecilomyces variotii* (its previous sister species; *Eurotiales*) also helped explain the very different antifungal susceptibility profiles of these two pathogens: *P. lilacinum* isolates are routinely resistant to amphotericin B *in vitro* but have low MICs with the triazole antifungal drugs itraconazole, posaconazole, and voriconazole, whereas isolates of *Paecilomyces variotii* are generally susceptible to amphotericin B but resistant to voriconazole (35). Phylogenetic analyses of additional organisms contained in Hypocreales similarly demonstrated that species classified as *Acremonium* formed two major, distantly related clades, with the two principal, medically important species *A. kiliense* and *A. strictum* found in a cluster containing the type species of the genus *Sarocladium*, which justified their reassignment to this genus and the new combinations of *Sarocladium kiliense* and *S. strictum*, respectively (130).

Many of the agents of dark grain eumycetoma were historically classified in the umbrella genus *Madurella* (*Sordariales*) which contained two sister species *M. mycetomatis* and *M. grisea* (161–163). Since many of these fungi fail to sporulate in culture, identification was based on colonial morphology and clinical presentation [reviewed in references (48, 164)]. More recently, molecular approaches have demonstrated that although *M. mycetomatis* is a homogeneous species, albeit with additional mainly cryptic sibling species (*M. pseudomycetomatis*, *M. tropicana*, and *M. fahalii*) (165), "*M. grisea*" is clearly polyphyletic (48, 164). Indeed, organisms conforming to the historical concept of *Madurella grisea*, the majority of which are actually classified in *Pleosporales*, are entirely unrelated to the type species of the genus (*M. mycetomatis; Sordariales*) (162). Such molecular phylogenetic approaches have resulted in the transfer of historical isolates of "*M. grisea*" to other genera, both extant and novel, including *Trematosphaeria* [*T. grisea* (136)] *Emarellia* [*E. grisea* and *E. paragrisea* (48)] and *Nigrograna* [*N. mackinnonii* (143)]. Additional pleosporalean agents of eumycetoma that were also subjected to taxonomic revisions using the same approaches included *Leptosphaeria senegalensis* and *L. tompkinsii* which were transferred to *Falciformispora* [*F. senegalensis* and *F. tomkinsii*, respectively (136)] and *Pyrenochaeta romeroi* which was renamed as *Medicopsis romeroi* (144).

The genus *Scedosporium* represents another group of medically important fungi that has been the subject of recent and major taxonomic revisions. Phylogenetic analyses revealed that *Scedosporium apiospermum* and *Pseudallescheria boydii* were distinct species rather than the anamorph-teleomorph forms of the same fungus and

also identified a number of additional species within this complex many of which were indistinguishable morphologically (142, 166, 167). The "*Scedopsorium apiospermum*" complex thus comprises *S. apiospermum* and *S. boydii*, with the two *Pseudallescheria* species *Ps. angusta and Ps. ellipsoidea* included in the broadest sense of the complex. The additional species *S. aurantiacum*, *S. dehoogii*, and *Ps. minutispora* are more phylogenetically distant from this core *S. apiospermum* complex and exhibit phenotypic differences, including in antifungal susceptibility profiles and virulence, which merit their differentiation (168–171). *Scedosporium prolificans*, which is phylogenetically and clinically very different to all other *Scedosporium* species, including the high resistance it exhibits to all currently available antifungal drug classes, was renamed as *Lomentospora prolificans* (142).

Finally, nomenclatural revisions affecting fungi that are less frequent human pathogens include: (i) transfer of the species of *Bipolaris* reported as occasional human pathogens (*B. australiensis*, *B. hawaiiensis*, and *B. spicifera*) to the alternative anamorph genus *Curvularia* based on phylogenetic analyses of these organisms with overlapping morphological traits (132); (ii) reassignment of the emerging pathogen of patients with cystic fibrosis *Geosmithia argillacea* (172) to the newly erected genus *Rasamsonia* (as *R. argillacea*) together with other related thermotolerant *Geosmithia* and *Talaromyces* spp. (134); (iii) transfer of *Lecythophora hoffmannii* and *L. mutabilis* to the teleomorph genus *Coniochaeta* (as *C. hoffmannii* and *C. mutabilis*, respectively) following phylogenetic evidence of genus-level synonymy and nomenclatural priority/precedence (135); (iv) *Pleurostomophora ochracea*, *Pleurostomophora repens*, and *Pleurostomophora richardsiae* were transferred to *Pleurostoma* (with the species epithets *ochraceum*, *repens*, and *richardsiae*, respectively) also for reasons of anamorph-teleomorph synonymy and the principle of priority (141); (v) the thermophilic fungal pathogen associated with human brain infections *Ochroconis gallopava* (173, 174) was moved to a new genus *Verruconis* (as *V. gallopava*) to distinguish it from the mainly mesophilic *Ochroconis* spp. (137); transfer of *Phoma versabilis* to the novel genus *Sclerotiophoma* (with epithet retained) following a large-scale multi-locus phylogenetic evaluation of the polyphyletic genus *Phoma* (140).

CRYPTIC SIBLING SPECIES IN KEY FUNGAL MORPHOSPECIES

As alluded to earlier in this review, another key impact of molecular phylogenetic approaches to fungal identification and classification was the discovery of innumerable sibling species in key morphospecies of human pathogenic fungi (5, 6, 11–14, 21, 175). In many cases, these cryptic species could only reliably be identified by DNA sequence analyses, often involving multiple, artificially concatenated barcoding sequences or sometimes by using proteomic approaches such as matrix-assisted laser desorption/ionization-time of flight (MALDI-TOF MS) (5, 6, 11–14, 21, 64, 175). For the more common ascomycetous yeasts of medical importance, closely related sibling species have been described in *Candida albicans* (175–179), *Candida parapsilosis* (64, 180), and *Nakaseomyces* (*Candida*) *glabratus* (95, 181–183). At least some of the novel cryptic siblings have been associated with altered antifungal susceptibility patterns, clinical presentations, and/or virulence (177, 178). In many respects, the situation is equally if not more complex with regard to cryptic species in filamentous fungi (molds). The presence of cryptic species within *Scedosporium* and the distinction of the *S. apiospermum* complex from other recently described *Scedosporium* sister species have been alluded to above and will not be discussed further. Other key genera/families of filamentous fungi will be discussed in detail separately below.

Cryptic species in the dimorphic fungal pathogens

Closely related molecular siblings have been extensively reported in the *Ajellomycetaceae* (51, 133, 157, 158), with cryptic sister species identified up to a century after the initial descriptions of *Coccidioides immitis* [sister species *C. posadasii* (184)], *Blastomyces dermatitidis* [*B. gilchristii* (185)], and *Paracoccidioides brasiliensis* [*P. lutzii* (186)].

As explained previously, the genus *Blastomyces* has been further expanded by the additional, predominantly cryptic, species *B. emzantsi* (157), *B. percusus* (51), and *B. silverae* (133) and the transfer to the genus from *Emmonsia* of *B. helicus* and *B. parvus* (133). For *Paracoccidioides*, the novel species *Paracoccidioides ceti* was erected to accommodate the uncultivated pathogen of dolphins, with *P. loboi* (ex *Lacazia loboi*) reserved for the agent of similar disease in humans (187). The additional species *P. restrepoana*, *P. americana*, and *P. venezuelensis* have been separately proposed to accommodate three additional cryptic species in the *P. brasiliensis* complex (188) but together with *P. lutzii* are currently invalid under article 40.7 (Schenzhen) of the Code (a single herbarium, collection, or institution in which the type strain is conserved was not specified in the description).

The historical concept of *Histoplasma* entailed three varieties of a single etiological agent (*H. capsulatum*) based on differences in clinical disease presentation and geographical distribution: (i) the widely dispersed human pathogen causative of classical pulmonary histoplasmosis, *H. capsulatum* var. *capsulatum*; (ii) the old world pathogen *H. capsulatum* var. *duboisii*, the causative agent of African histoplasmosis, a disease typified by skin/bone involvement; and (iii) *H. capsulatum* var. *farciminosum*, the causative agent of equine epizootic lymphangitis endemic in parts of Africa [reviewed in reference (189)]. Phylogeographical studies spanning nearly two decades have indicated that *Histoplasma* encompasses far more genetic variation than can be accommodated in this historical concept of the genus, with at least eight clades recognized across seven phylogenetic lineages/species (190–193). More recently, several of these independently evolving lineages were elevated to species level: alongside *H. capsulatum sensu stricto* (retained for the Panamanian lineage) and *H. capsulatum* var. *duboisii*, *H. mississippiense*, *H. ohiense*, and *H. suramericanum* were proposed for the *H. capsulatum* lineages previously known as Nam1, Nam2, and LAmA, respectively (193), although all three are listed as invalidly described in MycoBank and Index Fungorum. However, a recent multi-locus evaluation of *Histoplasma* isolates from Brazil where considerable genetic diversity parallels geographical origin (189), together with similar analyses of isolates from cases of histoplasmosis in India (194), suggests that the genus might contain significantly more diversity than can be accounted for in the recently proposed concept of *Histoplasma* (193). Regardless of the final numbers of cryptic species and the status of those proposed or accepted to date, it is clear that numerous novel sibling species exist in *Blastomyces*, *Histoplasma*, *Coccidioides*, and *Paracoccidioides* and that at least a proportion of them exhibit particular geographical distributions, are associated with different disease presentations, or have measurable differences in virulence in animal or invertebrate models of infection (157, 184, 185, 187, 189, 195).

Sporothrix schenckii, the sole recognized dimorphic agent of human sporotrichosis for over a century, is also now recognized to be a complex of a number of individual cryptic species (196), with the clinically relevant species *S. brasiliensis*, *S. globosa*, and *S. mexicana* described in addition to *S. schenckii sensu stricto* following extensive phenotypic and phylogenetic studies (197). *S. schenckii* has worldwide distribution and remains the principal agent of cutaneous human sporotrichosis following traumatic inoculation involving vegetation (196, 198), *S. brasiliensis* is the principal agent of zoonotic (feline) sporotrichosis in Brazil (199), whereas *S. globosa* has been reported from isolated human infections in Europe but appears endemic in Northeast China where it is acquired from contact with certain plants (200, 201). *S. mexicana* is principally environmental and has only rarely been reported from human disease (197). Recently, *S. schenckii* var. *luriei* has also been proposed to be a distinct species (*S. luriei*) on the basis of multilocus sequence analyses, but this again is a rare human pathogen (196, 202). The major human pathogens *S. schenckii*, *S. brasiliensis*, *S. globosa*, and *S. luriei* are recovered in a clinical clade coined the *Sporothrix* pathogenic clade, which is more distantly related to the *Sporothrix pallida* complex containing those *Sporothrix* species that have either reduced pathogenicity in mammalian models and/or are principally environmental saprobes (*S. pallida*, *S. chilensis*, and *S. mexicana*) (203).

Cryptic species in *Aspergillus*, *Cladosporium*, *Fusarium*, and *Trichophyton*

Since early reports of cryptic speciation in *Aspergillus flavus* (204) and the description of *Aspergillus lentulus* as a new sibling species of *A. fumigatus* with potentially reduced antifungal susceptibility (63), clinically relevant cryptic species have been described across the entire genus, to the extent that *Aspergillus* is now arranged into six sub-genera and 27 sections that accommodate species complexes of well-known morphospecies and their relatives (82), with the species encountered in the clinical laboratory distributed across the sections *Aspergillus*, *Candidi*, *Circumdati*, *Clavati*, *Flavi*, *Flavipedes*, *Fumigati*, *Nidulantes*, *Nigri*, *Polypaecilum*, *Restricti*, *Tannerorum*, *Terrei*, and *Usti*. For example, *Aspergillus* section *Fumigati*, which contains the most common cause of invasive aspergillosis [*A. fumigatus* (205)] contains in excess of 60 phylogenetically distinct species, of which approximately 20 have been reported from human and animal infections (5, 206). Although some of these species are distinguishable phenotypically, e.g., on the basis of electrolyte profiles (207), these are not tests that are available in routine mycology/microbiology laboratories, and these species are thus effectively cryptic in the clinical setting. Similarly, *Aspergillus* section *Nidulantes* series *Versicolores* has been proposed to contain 18 (mainly cryptic) species that are ubiquitous and preponderant in indoor air, many of which are opportunistic pathogens (208), and similar complexity has been reported for sections *Nigri* and *Flavi* (209, 210). Several surveillance studies have suggested that a significant proportion of *Aspergillus* isolates encountered in the clinical setting are cryptic (211–213), with frequencies of 11% and 14.5% reported, respectively, from the TRANSNET (USA) and FILPOP (Spain) studies (212, 213). Moreover, a growing body of evidence supports the contention that at least some cryptic species are associated with different disease presentations (210, 214, 215) and altered antifungal susceptibility profiles and disease outcome (63, 209, 210, 214–217).

Cladosporium spp., while being rare causes of invasive human disease, are often encountered in the clinical laboratory as *Cladosporium* spores are ubiquitous in indoor environments and are thus often recovered as plate contaminants (218). While the number of *Cladosporium* species associated with clinical cases was originally believed to be restricted to four (*C. cladosporioides*, *C. herbarum*, *C. oxysporum*, and C. *sphaerospermum*), *C. cladosporioides*, *C. herbarum*, and C. *sphaerospermum* have been shown to be species complexes (219–221). Indeed, a phylogenetic revision of *Cladosporium* from 2012 already recognized 7, 21, and 39 named sibling species in *C. sphaerospermum*, *C. herbarum*, and *C. cladosporioides*, respectively (222), and a later study of *C. cladosporioides* listed 54 sibling species, many of which have been recovered from clinical materials (223).

The genus *Fusarium* comprises a large number of human and plant pathogenic fungi that were originally segregated into relatively vague morphological sections based on increasingly complicated phenotypic characters (224, 225), many of which sections later proved to be polyphyletic and/or encompass complexes of numerous cryptic sibling species. Clinically relevant *Fusarium* species are now grouped in at least eight distinct species complexes: *Fusarium solani* species complex, *Fusarium oxysporum* species complex, *Fusarium dimerum* species complex, *Fusarium fujikuroi* species complex, *Fusarium chlamydosporum* species complex, *Fusarium incarnatum-equiseti* species complex, *Fusarium sambucinum* species complex, and *Fusarium tricinctum* species complex (226). The *F. fujikuroi* species complex was recently expanded to contain at least 74 phylogenetic sibling species (227), and over 60 distinct species are encompassed in the *F. solani* species complex (228). For the latter, a proportion of species have received formal species epithets, while most are identified by haplotype based on multilocus sequencing of housekeeping genes (229, 230).

Complexes of closely related but distinguishable genotypes are also known to exist in certain species of the dermatophyte genera *Trichophyton* and *Arthroderma*. The *Trichophyton mentagrophytes* species complex, which was originally a zoophilic species associated with rodents and other small mammals, contains a number of clonal lineages [nine genotypes to date based on sequences of the ITS1 region (231, 232)], several

of which are now commonly found in humans. These include the now anthropophilic *T. interdigitale* (genotypes I and II) and genotype VIII which has recently emerged as a highly virulent and often terbinafine-resistant cause of tinea corporis first in India and now with outbreaks worldwide (231–233). Given the specific clinical manifestations associated with genotype VIII infections (predominantly recalcitrant tinea cruris), greater virulence and reduced susceptibility to several antifungal drugs as compared to other members of the complex, and the rapid clonal expansion/outbreak potential of genotype VIII, it has been proposed to be practical and clinically useful to specifically elevate this genotype to species level under the name *Trichophyton indotineae* (234, 235). Additional species complexes in the dermatophytes and their relatives include *Trichophyton terrestre* and *T. benhamiae* complexes. *Trichophyton terrestre* was historically a mitosporic, geophilic dermatophyte relative referable to three closely related, but distinct sexual species in *Arthroderma* (*A. lenticularum*, *A. quadrifidum*, and *A. insingulare*) but conspecific with none of them [discussed in reference (236)]. Recent phylogenetic studies employing three genes supported the transfer of *T. terrestre* to the genus *Arthroderma* (as *A. terrestre*), with their close relatives grouped in five distinct clades (146). Members of this complex are geophilic (or less commonly zoophilic) and, as such, are rare pathogens of humans (146, 236).

Historically, the *T. benhamiae* complex encompassed several closely related zoophilic dermatophyte species (*T. benhamiae*, *T. erinacei*, *T. eriotrephon*, and *T. verrucosum*) plus the anthropophilic species *T. concentricum* (127). Originally described as *Arthroderma benhamiae* and considered to be the perfect state of *T. mentagrophytes* (237), *Trichophyton benhamiae* is an emerging pathogen in humans, causing highly inflammatory tinea corporis and tinea capitis, with the guinea pig as predominant animal host (238–240). *T. benhamiae* exists as two independent geographically constrained races, an African race and an Americano-European race which are genetically distinct (241), and two different phenotypic groups (yellow and white phenotypes) among the Americano-European strains (242). Recent polyphasic approaches that included phylogenetic analyses of four separate loci demonstrated that isolates of the white phenotype contain three independent taxa and supported the creation of the novel species *T. africanum* (African race, known strains mostly from humans so animal host unknown), *T. europaeum* (widely distributed in guinea pigs in Europe), and *T. japonicum* (widely distributed in Japan in rabbits and less commonly in guinea pigs, less common in Europe where the natural host is more often guinea pigs than rabbits) and the varieties *T. benhamiae* var. *luteum* (yellow form, widely distributed but predominant in Europe, animal host mainly guinea pigs) and *T. benhamiae* var. *benhamiae* (animal hosts dogs, cats, chinchillas, North American porcupines) (145). These delineations were supported in subsequent independent polyphasic studies that also included proteomic analyses (243).

RESOLVED AND UNRESOLVED ISSUES OF CONTENTION

For certain species that have been or should be renamed, additional problems and conflicts exist. Currently, these chiefly concern the large traditional anamorph genera *Aspergillus* and *Fusarium*, where no operational molecular criteria have been established to delimit the fungal genus and the existing groupings currently encompass multiple teleomorph genera. For both of these genera, different approaches have been proposed that would result either in fragmentation of the genus or merging of smaller more distantly related genera to maintain *Aspergillus* and *Fusarium* in their classical sense. For the genus *Cryptococcus*, initial disputes concerning the recognition of seven distinct species in *C. neoformans/C. gattii* have been fully resolved. Each will be discussed separately below.

Aspergillus

The ascomycete anamorph genus *Aspergillus* is huge compared to many other fungal genera and contains numerous clades that are organized into sections and series

each containing complexes of related species (81, 82). The genetic distances between these clades are much larger than those seen in many other fungal genera (81, 82). Additionally, *Aspergillus* encompasses at least 10 teleomorph genera that are more narrowly delimited than the anamorph genus (81, 82, 244, 245). Theoretically, these teleomorph names could be proposed for retention as the accepted name(s) for the various *Aspergillus* species after the abolition of dual nomenclature (244, 245). If this approach were adopted, since the type species of *Aspergillus* is *A. glaucus (Aspergillus* section *Aspergillus*; teleomorph *Eurotium*), many other *Aspergillus* species of medical, agricultural, and biotechnological importance would be removed from the genus and placed in one of the known teleomorph genera [reviewed in reference (81)]. The alternative suggestion to conserve the genus *Aspergillus* with a different type species (e.g., *A. fumigatus* as the most clinically relevant or *A. niger* as the predominant species of biotechnological importance) would provoke equal debate and would not resolve issues around nomenclatural stability since again all *Aspergillus* spp. with different teleomorphs from *A. fumigatus* (teleomorph *Neosartorya*) or *A. niger* (teleomorph *Eurotium*) would require renaming (246, 247). Several recent analyses of the phylogenetic relationships of *Aspergillus* and related fungi in *Penicillium* have supported the monophyly of both of these genera in their widest senses, albeit with numerous sub-genera or clades (81, 82, 244, 247–250). On the basis of those studies showing that *Aspergillus* is monophyletic and in the absence of precise criteria for the genetic delimitation of the genus in Kingdom Fungi, the working solution that is currently in place is the retention of the genus *Aspergillus* in its widest sense (with all teleomorph genera absumed), a solution that has received the support of the International Commission of *Penicillium* and *Aspergillus* as it maintains the prevailing, broad concept of *Aspergillus* (81, 247–250).

Fusarium

The large genus *Fusarium* presents an equally complex nomenclatural conundrum for similar reasons to those discussed for *Aspergillus* above, namely, the presence of a single, large anamorph genus of medical and agricultural interest that encompasses numerous individual teleomorph genera. Since the type species for *Fusarium* is *F. sambucinum* which has a *Gibberella* teleomorph, the genus name must be retained at least for all species with *Gibberella* teleomorphs, which is not disputed (251–253). However, the genetic delineation of the genus remains hotly disputed, with different groups of authors proposing distinctly different nodes in the phylogenetic trees of the *Nectriaceae* to serve as the terminal *Fusarium* clade (TFC) and thus delimit the genus. Simplistically, a (large) subset of the *Fusarium* community argue that the TFC should be reserved for *Fusarium sensu stricto* (i.e., the *Gibberella* clade, the F3 node), which is highly supported in all MLST phylogenies as monophyletic (251, 252) and which would exclude *Fusarium solani* species complex (teleomorph *Neocosmospora*) and *Fusarium dimerum* species complex (253) among others. Based upon those analyses, a modern revision was published for *Neocosmospora* to encompass 68 species including *Fusarium solani* species complex (254), and the novel genus *Bisifusarium* was proposed for members of the *Fusarium dimerum* complex (253). The arguments for a broader concept for *Fusarium* centre around the selection of "upstream" nodes in phylogenetic analyses to represent the TFC or the broader *Fusarium* clade, with the nodes F1 (all *Fusarium* spp. including *F. dimerum* complex) or F2 (includes *F. solani* complex but excludes *F. dimerum* clade) proposed (252, 255, 256). Counter arguments against the latter proposals, which would result ultimately in less nomenclatural change, are that the nodes F1 and F2 are less well supported by the existing multi-gene phylogenies (with phylogenetic support skewed by insufficient sampling of clades upstream of node F1) and that the resulting *Fusarium* genus would be polyphyletic (253, 254, 257) with 10 and 9 distinct genera delimited by the F1 and F2 nodes, respectively. This situation has not been definitively resolved.

Cryptococcus

Even after removal of basidiomycetous yeasts that are only distantly related to *Cryptococcus* to the alternative *Tremellomycete* genera *Naganishia* and *Papiliotrema* (115) as discussed previously, it has long been apparent that the remaining genetic diversity in the medically important *Cryptococcus neoformans/gattii* species complex far exceeds the number of currently accepted species (55, 258, 259). Based on a phylogenetic analysis of 11 loci and a panel of 115 isolates in this complex, Hagen and colleagues proposed the recognition of seven species (55). *Cryptococcus neoformans* was retained to describe species formerly referred to as *Cryptococcus neoformans* var. *grubii*, *Cryptococcus deneoformans* was erected to encompass serotype D isolates (formerly *C. neoformans* var. *neoformans*) as proposed at the International Conference on Cryptococcus and Cryptococcosis in 2011 and embraced by the audience at the time and at least five cryptic species were described in the *C. gattii* species complex. These included *C. gattii*, *Cryptococcus deuterogattii*, *Cryptococcus tetragattii*, *Cryptococcus decagattii*, and *Cryptococcus bacillisporus*. These new species differ in prevalence, pathogenicity, and antifungal susceptibility and are represented as distinct lineages in most recent molecular analyses (260–263). However, this proposal was initially criticized by some workers (259) who argued that insufficient numbers of strains had been examined with insufficiently sampled loci/chromosomes to fully capture the diversity of the complex and that identification of the seven species would require MLST phylogenetic approaches that would likely be difficult to instigate in routine clinical laboratories. On this basis, they argued that the erection of the seven proposed taxa was premature and proposed the continued use of *C. neoformans* species complex and *C. gattii* species complex for reporting of such isolates in clinical laboratories (259). The arguments against the recognition of the seven species were subsequently thoroughly refuted in detail (263): the individual species are readily distinguishable by sequencing of the ITS1 region or by MALDI-TOF MS approaches, the original loci and methods used for species delineation have been widely used for species delineation in both sexual and asexual fungi and the vast majority of prior and subsequent studies employing whole genome sequencing revealed the same well-demarcated and supported clades (263).

MYCOLOGICAL AND CLINICAL IMPACTS OF TAXONOMIC REVISIONS

Nomenclatural changes are neither new nor unique to fungi. However, due to the increasingly widespread application of molecular phylogenetic approaches to fungal taxonomy over the last three decades, the pace of nomenclatural change and the number of fungal organisms recognized as threats to human health have significantly increased (5, 6, 11–14, 21–23, 29, 42, 43, 48, 51, 53, 55–57, 63–76, 264). Since phylogenetic relationships are highly subject to sampling bias, it is inevitable that many existing phylogenies will be subject to considerable change when additional, more diverse taxa are sampled (57, 265). Thus, the species *Sarcopodium oculorum* which was newly described as an opportunistic agent of keratitis in 2002 (266) was transferred together with *Phialemonium curvatum* (267) into a newly created genus *Phialemoniopsis* in 2013 (268) only for this genus to be synonymized with the historical genus *Thyridium* in 2022 (139). Similarly, *Lichtheimia corymbifera*, which was originally described as *Mucor corymbifer* in 1884 (269), was transferred to the genus *Lichtheimia* in 1903 (270), transferred again in 1912 to the genus *Absidia* as *A. corymbifera* (271) where it remained until 1991 when it was removed to the genus *Mycocladus* (272). Since the type of *Mycocladus* has since been shown to likely be a co-culture with elements that appear to be conspecific with *Absidia*, the oldest available name for the fungus is *Lichtheimia corymbifera* which it has now regained (129, 273).

The potential issues of instability will be exaggerated for phyla that have been delineated using only the conventional rDNA fungal barcode regions ITS and LSU, as they perform poorly at taxonomic classifications above species level and neither locus adequately classified fungi at the generic level (46, 274, 275). Moreover, ITS as

the universal barcode has limited utility for some medically important species due to extensive gene flow between sub-lineages (276). Thus, continued revisions of the fungal Kingdom at the generic level will likely be necessary in the future.

Accelerated taxonomic change has led to serious concerns in parts of the medical mycology community with vocal reticence to implement such nomenclatural advances (277–280). The arguments raised included (i) disruption of molecular databases and lack of continuity of historical literature sources, (ii) loss of traceability of epidemiological and antifungal susceptibility data, (iii) confusion caused by clinical reporting of unfamiliar pathogen names, and even (iv) ensuing patient harm if clinicians dismiss old pathogens reported with new names either as contaminants or colonizers (277, 278, 280). The latter two fears concerning clinical confusion, while genuine, are surmountable and will be discussed in the remainder of this review under "Avoiding unnecessary instability," and "Managing nomenclatural change in medical mycology."

The first two concerns, while theoretically valid, are largely unwarranted. Since all the principal databases (including those of the National Center for Biotechnology Information) rely on standardized taxonomic databases that cross-reference novel and obsolete names, key searches will retrieve all relevant historical records (281, 282). Similarly, the publicly available databases/resources at MycoBank (www.mycobank.org; curated by Konstanze Bensch at the Westerdijk Fungal Biodiversity Institute, The Netherlands) and Index Fungorum (www.indexfungorum.org; curated by Paul Kirk, Royal Botanic Gardens Kew, United Kingdom) are regularly updated with nomenclatural changes and are thus an invaluable and usually highly accurate record of the status of a fungal name, together with links to obsolete names and their associated literature. In rare cases, there are discrepancies between the accepted current names listed in MycoBank and Index Fungorum. In such instances, a list of additional useful taxonomy/nomenclature resources (with links) is available in Table 3 of reference (6) which is usually helpful to clarify any confusion. If these fail to resolve the conflicting taxonomic positions, consultation with a regional or national mycology reference center is advisable.

AVOIDING UNNECESSARY INSTABILITY

The instability described above can be partially mitigated going forward via the use of multi-locus approaches to phylogenetic inference and also the increasing availability of completely sequenced fungal genomes which produce robust scaffolds with improved taxonomic resolution (47, 51, 62, 131). However, genome scale assemblies often do not include the ribosomal RNA cistron which is necessary to allow comparability with data sets generated by DNA barcoding (283). Taxonomic instability can further be lessened by delaying the implementation of changes that involve closely related species until the underlying taxonomy has been confirmed by independent authors, preferably employing or obtained via multiple phylogenetic inference methods and wide taxon sampling.

When multilocus phylogenetic methods were combined with multispecies coalescence model-based approaches to analyze a large collection of strains of *Aspergillus* series *Versicolores*, all methods consistently supported only four species (*A. creber*, *A. versicolor*, *A. sydowii*, and *A. subversicolor*), with a broad species concept, rather than the 17 species that had been previously accepted, 13 of which have now been returned to synonymy with either *A. versicolor* or *A. creber* (284; Table 3). Recent similar approaches with isolates of *Aspergillus* series *Nigri* supported the reduction in the number of recognized species from 14 to at most six [see reference (285) for taxonomic details]. In both cases, the significantly reduced species numbers better correlated with intraspecific variation previously reported for other aspergilli and were better recognized by proteomic or DNA-sequence-based laboratory identification methods (284, 285).

MANAGING NOMENCLATURAL CHANGES IN MEDICAL MYCOLOGY

The "species complex" for closely related collections of siblings

A number of groups have suggested that name changes to fungi of medical importance are more easily accepted by the clinical community when they are phylogenetically convincing and clinically relevant, i.e., when they are underpinned by significant evolutionary distances that are likely to or known to affect their behavior in terms of virulence, pathogenicity, and resistance to antifungal drugs (5, 11–14, 21, 73, 76, 127, 277, 279, 280). For complexes of cryptic species described as a result of molecular phylogenetic approaches, it is seldom initially apparent whether the novel taxa exhibit clinically significant differences or indeed whether such differences are universally applicable. In such instances, it has been proposed that the use of "species complex," although not clearly defined taxonomically, be employed for groups of closely related sibling species that share clinically similar properties (5, 11–14, 57, 76, 280). This has been seamlessly implemented across many major fungal species including the *Candida parapsilosis* (64, 180), *C. albicans* (177–179), *Rasamsonia argillacea* (74), and *Scedosporium apiospermum* (166, 169) species complexes and also the large complexes of cryptic species in many of the medically important morphospecies in *Aspergillus* (65, 286) and *Fusarium* (228).

Managing major nomenclatural shifts by education and re-iteration

Aside from the issues of closely related siblings and the treatment of hitherto unsuspected diversity in common morphospecies discussed above, many of the nomenclatural changes alluded to in this review represent genuine revisions of fungal taxonomy/phylogeny that accurately recognize the unrelatedness of organisms previously grouped together in historical genera. As such, they absolutely fulfil the criteria proposed for nomenclatural revision of medically important fungi (5, 11–14, 21, 73, 76, 127, 277, 279, 280): (i) they are phylogenetically compelling and (ii) recognition of this amended taxonomy is clinically important as it impacts fundamental behavior (virulence, pathogenicity, thermostability, and antifungal drug susceptibility) and thus potentially patient management.

Numerous examples of recent nomenclatural revisions that have met with little resistance from the medical mycology community exist (5, 11, 12, 57, 76) including (i) the separation *Purpureocillium lilacinum* (53), a species uniformly resistant to amphotericin B (35), from its historical sister species *Paecilomyces variotii* (264) which is amphotericin B susceptible but resistant to voriconazole (35); (ii) recognition that the dimorphic human fungal pathogen *Talaromyces marneffei* is only distantly related to principally saprobic *Penicillium* species (138); (iii) assignment of the pan-resistant fungus *Scedosporium prolificans* to the genus *Lomentospora* to distinguish it from the other members of the *Scedosporium/Pseudallescheria* complex (142); (iv) large-scale re-arrangements of the genera *Blastomyces* and *Emmonsia* (51, 133); (v) re-assignment of the principally zoophilic and geophilic dermatophyte relatives from *Trichophyton* and *Microsporum* to *Arthroderma* and *Nannizzia*, respectively (127); (vi) removal of many of the distant relatives of *Cryptococcus* that are extremely rare human pathogens to allied basidiomycete genera (26); (vii) renaming of many of the agents of dark-grain eumycetoma based on phylogenetic analyses (48, 136, 143, 144). A common feature to these accepted taxonomic reassignments, aside from the clinical relevance, is that, for the most part, they involve fungi that are relatively rarely encountered in the medical microbiology laboratory and changes have been introduced sporadically as data became available. In addition, these transitions were facilitated by retention of the same species epithet for the former and new names, after appropriate minor adjustments to conform to the requirements of Latin declension.

The arguments for the re-assignment of many species previously grouped in the polyphyletic anamorph genus *Candida* are equally if not more compelling. The phylogenetic distances (as measured by amino acid substitutions/site) between

members of the *Nakaseomyces glabratus* (ex-*Candida glabrata*) species complex (104) and *C. albicans* are more than double those that separate humans and pythons (287). In addition, isolates of the clinically relevant members of *N. glabratus* species complex (*N. glabratus*, *N. nivariensis*, and *N. bracarensis*; Table 2) exhibit significantly higher MICs with fluconazole than *C. albicans* (33, 288) and marked differences as compared to *C. albicans* in virulence (289), biofilm formation (290), and other pathogenicity traits that have been acquired independently of *C. albicans* (291). Similarly, and as discussed previously (13, 278), recognition that *Candida krusei* belongs to the genus *Pichia* (as *Pichia kudriavzevii*) (76) explains the "unusual" innate resistance of the former to fluconazole: all isolates of *Pichia* species exhibit high fluconazole and flucytosine MICs (33). Despite overwhelming evidence that recognition of the correct taxonomic standing of many species in "*Candida*" has genuine clinical relevance, recent reviews that summarized the current taxonomic anomalies and suggested revision (13) were met with widespread criticism with concerns that clinicians would not recognize or act appropriately to if old pathogenic "*Candida*" species were reported under their new identities [discussed in references (277–281)].

As we and others have pointed out previously (277, 278), name changes have been successfully applied to common "*Candida*" species in the past, and these changes reached global acceptance. Prior to 1923, *Candida albicans* was known successively as *Oidium albicans* and then *Monilia albicans* (292, 293), and *Nakaseomyces glabratus* was transferred from the genus *Torulopsis*, where it had resided for 40 years (294), to *Candida* as late as 1978 (295). Critical to the successful implementation of those past changes and to assimilation of continued taxonomic revisions going forward is the education of both laboratory and medical staff which we believe is best achieved by modifications to the way that clinical mycology laboratories convey results. The approach that we advocate (13, 278) and indeed have implemented at the UK National Mycology Reference laboratory is the one shared by Wiederhold and Gibas (5) and Kidd and colleagues (277, 279, 280). We report the new (accurate) nomenclature together with the most recent, previous name(s) that is most commonly encountered in the literature: "Isolate identified as *Pichia kudriavzevii* (previously known as *Candida krusei*)," in this way allowing clinicians to access the wealth of historical data concerning treatment options and patient management. The intention is to persist with this system until the novel nomenclature has been widely assimilated.

In the UK, this approach has been met with limited resistance (Borman and Johnson, personal observation), and recent surveys of Australasian clinicians and laboratory staff showed these proposals to be well supported (279). Many commercial fungal identification systems have adopted at least partially updated nomenclature for fungi of medical importance. We would strongly encourage the manufacturers of such databases to continue to provide the previous names for those "*Candida*" species that have been assigned to alternative genera in a similar manner to that which we have suggested above, which should also aid implementation of current nomenclature, reduce resistance to change, and limit clinician confusion [discussed in reference (280)]. Similarly, acceptance and increased clinical awareness of nomenclatural changes would also be facilitated if groups such as the Clinical Laboratories Standards Institute and the European Committee on Antimicrobial Susceptibility Testing were to employ both novel and previous names in their documents and standards. As discussed previously, avoiding unnecessary and transient name changes is central to the acceptance of the concept that nomenclatural change may be beneficial. In this respect, we certainly support many of the suggestions in the recent opinion piece by Yurkov and colleagues (296) that are intended to limit unnecessary nomenclatural changes that result from invalid description of novel fungal taxa. Finally, publication of regular update articles listing the latest (accepted) nomenclatural changes and explaining the mycological and/or clinical rationale behind them will aid in the continued education of both the laboratory worker and the clinician and also hopefully increase the speed of acceptance of changes (5, 11, 12, 57, 76, 280).

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