REVIEW

Corrections to recent changes in the taxonomy of the *Sordariales*

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Abstract

The classification of taxa belonging to the *Sordariales* has been problematic over the years. With the beginning of the DNA era, ascospore morphology, which was the main criterium for the delimitation of taxa in the *Sordariales*, was demonstrated to not be useful for inferring taxonomic relationships especially at the genus level. In the past decades, the combination of both morphological and molecular data allowed the reclassification of these taxa. Recently, a study of some often overlooked *Diaporthomycetidae* and *Sordariomycetidae* included a new taxonomic classification for members of the *Sordariales*, many of which were based on nomenclatural errors or which lacked sufficient data to support their hypotheses. The authors did not contribute any new DNA sequences, but instead relied on datasets generated by previous authors in their published phylogenetic studies. Surprisingly, different results were obtained contradicting these previous studies and, in an act of taxonomic vandalism, five new families were introduced without performing further molecular analyses to verify the incongruencies with these previous studies. Three of these new families, which we consider doubtful, are *Bombardiaceae*, *Lasiosphaeridaceae* and *Zygospermellaceae*. The family *Strattoniaceae* is here considered superfluous since it was introduced to accommodate only a single genus and delimited based on a species that is not the type species of *Strattonia*. The *Neoschizotheciaceae* was erected based on the new genus *Neoschizothecium*, which was introduced to accommodate members of *Schizothecium* since Huang et al. (2021) considered *Schizothecium* as a synonym of *Podospora* after misinterpreting their type species as the same. However, *Schizothecium* and *Podospora* have been two independent genera based on two different type species for half a century, making *Neoschizothecium* and *Neoschizotheciaceae* superfluous. Moreover, they proposed 32 new combinations, 16 of which are now superfluous or doubtful. Most of these taxonomic errors could have been avoided if a proper literature review had been performed. Two examples are the new superfluous combinations of *Triangularia tarvisina* and *Cladorrhinum olerum*, because the former is considered conspecific with *Triangularia setosa*, and the latter conspecific with *Cladorrhinum foecundissimum*, the anamorph of *Arnium olerum*. The focus of the current review is to provide a scientifically responsible alternative to the erroneous novelties proposed at the family, genus and species level in the recent classification of *Sordariales*.

Keywords Fungal classification · Integrative taxonomy · *Podospora* · *Schizothecium* · *Sordariales* · *Sordariomycetes*

Introduction

The order *Sordariales* is one of the most diverse groups in the *Sordariomycetes* and the classification of their members based solely on morphology has been problematic (Hawksworth and Eriksson 1986; Miller and Huhndorf 2004a, 2005; Huhndorf et al. 2004; Kruys et al. 2015). The taxonomic classification of taxa belonging to this order was traditionally based on ascospore morphology; however, Miller and Huhndorf (2005) demonstrated that this character is extremely homoplastic and not useful for inferring taxonomic relationships. Instead, the ascomatal wall morphology appears to be more phylogenetically informative, even though it has its limitation since not all taxa exhibit distinctive features in their ascomatal walls, and/or similar ascomatal wall characteristics are found in different monophyletic lineages.

For nearly two decades, extensive molecular studies have been combined with morphological data to delimit sordarialean taxa at the family, genus and species level (Miller and Huhndorf 2004a; Cai et al. 2005; Kruys et al. 2015; Wang

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et al. 2019a; Marin-Felix et al. 2020). Historically, the *Sordariales* has contained 7 to 14 families, depending on the authors' concepts (Hawksworth and Eriksson 1986; Eriksson et al. 2001). Huhndorf et al. (2004) restricted the order to 3 families, i.e. *Chaetomiaceae, Lasiosphaeriaceae* and *Sordariaceae,* the first two of which were considered polyphyletic based on molecular data. The *Chaetomiaceae* has been extensively studied in recent years based on a polyphasic approach combining morphological and molecular data, resulting in its delimitation as a monophyletic lineage (Wang et al. 2019a, b). However, the polyphyly of *Lasiosphaeriaceae,* which was the largest family of the order, remained problematic until it was recently partly resolved (Marin-Felix et al. 2020). Kruys et al. (2015) demonstrated the separation of the family into four different clades. Subsequently, Wang et al. (2019a) introduced the new family *Podosporaceae* to accommodate taxa belonging to clade IV in Kruys et al. (2015). Marin-Felix et al. (2020) delimited *Lasiosphaeriaceae* to clade III, which contained the type genus *Lasiosphaeria.* Moreover, the new families *Diplogelasinosporaceae, Naviculisporaceae* and *Schizotheciaceae* were introduced to accommodate three monophyletic lineages containing taxa resembling those in the *Lasiosphaeriaceae.* Once again, the morphological characters used to delimit these families turned out to be homoplastic and appeared independently in multiple lineages. Other lasiosphaeriaceous taxa were nested in an unsupported lineage (*Lasiosphaeriaceae* s. lat. I, Fig. 1), and therefore a new family was not introduced for this clade. Finally, another monophyletic lineage with two genera was shown as an unsupported sister group to *Schizotheciaceae* (*Lasiosphaeriaceae* s. lat. II, Fig. 1). However, a new family was not introduced until further studies including additional taxa and molecular data could be performed. Figure 1 shows the phylogenetic tree obtained from the study performed by Marin-Felix et al. (2020).

The genera belonging to this order have also been taxonomically challenging to delineate over the years. For example, the genera *Gelasinospora* and *Neurospora,* both in the *Sordariaceae,* were established based on different patterns of ascospore ornamentation. García et al. (2004) demonstrated that this character was not phylogenetically informative and synonymized *Gelasinospora* under *Neurospora.* This observation agreed with Miller and Huhndorf (2005), who found that ascospore morphology was a homoplastic character throughout the order. The largest genera in the *Chaetomiaceae* have also been recently refined, i.e. *Chaetomium, Humicola* and *Thielavia,* resulting in the introduction of 17 new genera and more than 70 new combinations to accommodate taxa not included in the molecular-based monophyletic lineages of these recircumscribed genera (Wang et al. 2016a, 2019a, b). Genera traditionally placed in *Lasiosphaeriaceae* are currently being studied. For example, Wang et al. (2019a)

delimitated *Cladorrhinum, Podospora* and *Triangularia,* whereas Marin-Felix et al. (2020) established 5 new genera, i.e. *Areotheca, Lundqvistomyces, Pseudoechria, Pseudoschizothecium* and *Rhypophila.* These taxonomic changes were done to accommodate taxa previously placed in *Cercophora, Podospora* and *Triangularia* based on morphology, but that no longer occurred in the more narrowly defined, DNA-based monophyletic lineages representing these genera.

Recently, Huang et al. (2021) performed a phylogenetic study based on ITS, LSU, *RPB2* and *TUB2* sequences already available in GenBank, without generating a single new sequence. As a result, they introduced 5 new families, 1 new genus and 32 new combinations in the order *Sordariales.* However, most of these taxonomic novelties are based on errors of interpretation or lack sufficient data for their creation (Table 1). In order to compare the contradictory results between the phylogenetic study of Huang et al. (2021) and previous studies (Kruys et al. 2015; Marin-Felix et al. 2020), we tried to reanalyze the original molecular alignments generated by Huang et al. (2021). However, these alignments are not available in TreeBase even though they stated in their publication that final alignments and trees were deposited in TreeBase. Therefore, we had to download all sequences from GenBank to perform a phylogenetic analysis that included all sequences previously used in Marin-Felix et al. (2020) and Huang et al. (2021).
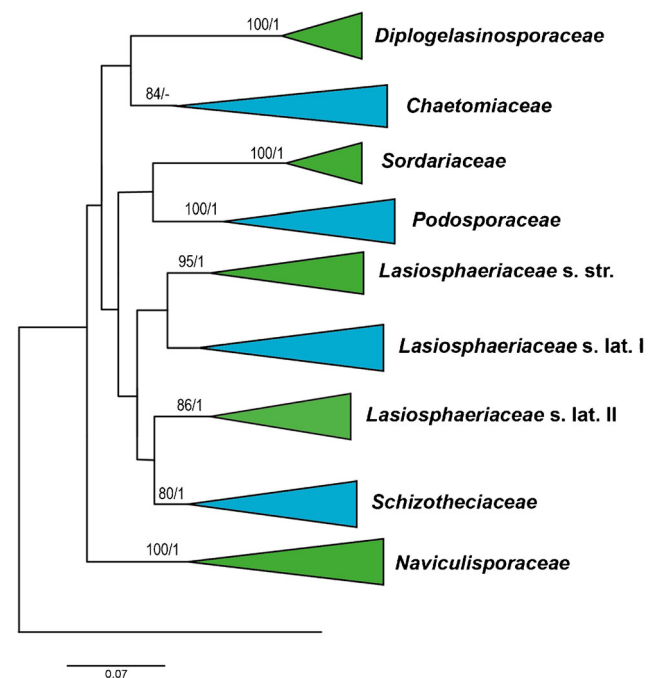
Fig. 1 Schematic RAxML phylogram based on ITS, LSU, *RPB2* and *TUB2* sequences obtained in the phylogenetic study performed by Marin-Felix et al. (2020) (adapted from Charria-Girón et al. 2022)

Table 1　Revised nomenclator for the *Sordariales* in alphabetical arrangement

This paper	Huang et al. (2021) with comment in brackets
Cladorrhinum brunnescens W. Gams, Mycotaxon 48: 435. 1993	[#]*Podospora brunnescens* (W. Gams) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 514. 2021 (premature new combination based on insufficient data and no molecular support)
Cladorrhinum foecundissimum Sacc. & Marchal, Bull. Soc. R. Bot. Belg. 24: 64. 1885	*Cladorrhinum olerum* (Fr.) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 512. 2021 (superfluous synonym. Synonymy performed by Marin-Felix et al. (2020))
Jugulospora rotula (Cooke) N. Lundq., Symb. bot. upsal. 20: 260. 1972	*Jugulospora minor* (N. Lundq.) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 537. 2021 (superfluous synonym supported by molecular data)
Lasiosphaeriaceae s. lato	[#]*Bombardiaceae* (insufficiently supported clade)
Lasiosphaeriaceae s. lato	[#]*Lasiosphaeridaceae* (premature new name based on insufficient data)
Lasiosphaeriaceae s. lato	[#]*Zygospermellaceae* (premature new name based on insufficient data)
Podospora minicauda Faurel & Locq.-Lin., Revue Mycol., Paris 42: 344. 1978	[#]*Neoschizothecium minicauda* (Faurel & Locq.-Lin.) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 540. 2021 (premature new combination based on insufficient data)
Podospora petrogale A.E. Bell, Muelleria 12: 236. 2000	[#]*Strattonia petrogale* (A.E. Bell) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 526. 2021 (premature new combination based on insufficient data)
Schizotheciaceae Y. Marin & Stchigel, Microorganisms 8: 1430, 24. 2020	*Neoschizotheciaceae* S.K. Huang & K.D. Hyde, Fungal Diversity 111: 529. 2021 (superfluous synonym)
Schizothecium Corda, Icon. fung. (Prague) 2: 29. 1838	*Neoschizothecium* S.K. Huang & K.D. Hyde, Fungal Diversity 111: 537. 2021 (superfluous synonym)
Schizothecium aloides (Fuckel) N. Lundq., Symb. bot. upsal. 20: 253. 1972	*Neoschizothecium aloides* (Fuckel) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 539. 2021 (superfluous synonym)
Schizothecium carpinicola (Mouch.) L. Cai, Fungal Diversity 19: 14. 2005	*Neoschizothecium carpinicola* (Mouch.) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 539. 2021 (superfluous synonym)
Schizothecium conicum (Fuckel) N. Lundq., Symb. bot. upsal. 20: 253. 1972	*Neoschizothecium conicum* (Fuckel) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 539. 2021 (superfluous synonym)
Schizothecium curvisporum (Cain) N. Lundq., Symb. bot. upsal. 20: 334. 1972	*Neoschizothecium curvisporum* (Cain) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 539. 2021 (superfluous synonym)
Schizothecium fimbriatum (A. Bayer) Barrasa & Soláns, Revta Ibér. Micol. 6: 3. 1989)	*Neoschizothecium fimbriatum* (A. Bayer) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 539. 2021 (superfluous synonym)
Schizothecium glutinans (Cain) N. Lundq., Symb. bot. upsal. 20: 254. 1972	*Neoschizothecium glutinans* (Cain) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 539. 2021 (superfluous synonym)
Schizothecium inaequale (Cain) N. Lundq., Symb. bot. upsal. 20: 334. 1972	*Neoschizothecium inaequale* (Cain) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 539. 2021 (superfluous synonym)
Schizothecium selenosporum (Stchigel, Guarro & M. Calduch) Y. Marín & Stchigel, Microorganisms 8: 1430, 34. 2020	*Neoschizothecium selenosporum* (Stchigel, Guarro & M. Calduch) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 540. 2021 (superfluous synonym)
Schizothecium tetrasporum (G. Winter) N. Lundq., Symb. bot. upsal. 20: 256. 1972	*Neoschizothecium tetrasporum* (G. Winter) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 539. 2021 (superfluous synonym)
Triangularia setosa (G. Winter) X. Wei Wang & Houbraken, Stud. Mycol. 93: 243. 2019	*Triangularia praecox* (Sacc.) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 515. 2021 (superfluous synonym supported by molecular data)
Triangularia setosa (G. Winter) X. Wei Wang & Houbraken, Stud. Mycol. 93: 243. 2019	*Triangularia tarvisina* (Sacc.) S.K. Huang & K.D. Hyde, Fungal Diversity 111: 515. 2021 (superfluous synonym. Synonymy performed by Lundqvist (1972))

*These 15 taxa are nomenclaturally invalid

[#] These six taxa are not accepted by the present authors due to insufficient data

No sequences in *Chaetomiaceae* were included since no novelties were proposed in this family (Table 2). The maximum likelihood (ML) and Bayesian inference (BI) analyses including the four loci were performed as described by Harms et al. (2021). The lengths of the individual alignments used in the combined dataset were 556 bp (ITS), 916 bp (LSU), 978 bp (*RPB2*) and 618 bp (*TUB2*), and the final combined alignment was 3068 bp. A poorly aligned ambiguous region was manually deleted from the ITS1 region. Figure 2 shows the most likely tree obtained from the RAxML analysis of the combined dataset generated in our study. It is identical in the topology of the 95% majority-rule consensus tree generated by the Bayesian analysis. It is unfortunate that Huang et al. (2021) did not indicate the GenBank accession numbers of the sequences they used to produce their trees, making it very difficult for

the scientific community to reproduce their results. It should have been mandatory to indicate which sequences were incorporated in their phylogenetic study, as well as to cite the underlying papers giving proper attribution to the authors that generated those data, as recommended in Aime et al. (2020), a recent ICTF-sponsored paper on best practices in taxonomy. Surprisingly, the second author of Huang et al. (2021) is also a co-author of the Aime et al. (2020) paper, yet he does not follow his own recommendation.

New families superfluously introduced or without sufficient evidence

The family *Schizotheciaceae* was recently introduced by Marin-Felix et al. (2020) to accommodate lasiosphaeriaceous taxa occurring in a well-supported monophyletic lineage phylogenetically distant from both the *Podosporaceae* and the clade containing the type genus *Lasiosphaeria*. However, Huang et al. (2021) erroneously changed its name to *Neoschizotheciaceae* based on taxonomic errors by Wang et al. (2019a). Both papers incorrectly assumed that the genera *Schizothecium* and *Podospora* shared the same type species, and thus, should be synonymized. Therefore, the new genus *Neoschizothecium* was introduced with *N. curvisporum* as its type species to accommodate species of *Schizothecium* outside the *Podosporaceae*. Huang et al. (2021) designated *Neoschizothecium* as type genus of their new family *Neoschizotheciaceae*.

The complex nomenclatural histories surrounding the type species of *Podospora* and *Schizothecium* have been discussed in detail (Lundqvist 1972; Ament-Velásquez et al. 2020; Vogan et al. 2021). Briefly, two distinct type specimens representing two distinct type species exist for each genus: the conserved non-original type specimen of *Podospora fimiseda* (Ces. & De Not.) Niessl. (in Hedwigia 22: 156. Oct 1883) and the lectotype illustration of *Schizothecium fimicola* Corda (in Icon. Fung. 2: 29, tab. 13, fig. 105, Jul 1838). This segregation, which was based on morphological data and discussed by Lundqvist (1972), was later supported by molecular data (Cai et al. 2005). Wang et al. (2019a) overlooked the conserved type of *Podospora* (i.e. *Sordaria fimiseda* Ces. & De Not.) and incorrectly cited *S. fimicola* Corda as type species. To further complicate matters, Wang et al. (2019a) designated an epitype specimen (CBS H-24048) for *S. fimicola* that was induced to produce fertile ascomata in culture (CBS 482.64), but this epitype represents *P. fimiseda*, not *S. fimicola*! We have examined the ex-epitype culture (CBS 482.64) and could not reproduce the fruiting of ascomata in culture. The epitype specimen was also examined, but no ascomata were found to study their morphology in detail, despite images of mature ascomata fruiting in culture provided in Wang et al. (2019a).

According to the pictures of the epitype shown by Wang et al. (2019a), this specimen produces hyphal-like ascomatal hairs surrounding the entire ascoma, which match *P. fimiseda* (Miller 2003). *Schizothecium fimicola* has swollen agglutinated ascomatal hairs only in the upper part of the ascomata. Thus, the type species of *Schizothecium* should be conserved as *S. fimicola* (typ. cons. pending). The ascomal wall of CBS 482.64 needs to be studied to verify that it is pseudobombardioid and matches the description of *P. fimiseda* (Miller 2003) and, therefore, it is a suitable epitype for this later species. If the conservation proposal to change the type species of *Podospora* from *P. fimiseda* to *P. anserina* (Vogan et al. 2021) is accepted, this would also bring additional resolution to the complicated and often confused nomenclatural history of these two genera. Since *Podospora* and *Schizothecium* are clearly not synonyms as Wang et al. (2019a) and Huang et al. (2021) believed, there was no reason to create a new family (i.e. *Neoschizotheciaceae*) for *Schizotheciaceae*. Thus, *Neoschizotheciaceae* is nomenclaturally illegitimate (Art. 14.3, Shenzhen Code) and a superfluous synonym of *Schizotheciaceae*.

It is worthwhile to mention that one should always attempt to make decisions that lead to as few taxonomic name changes and reduce the possibility of publishing taxonomically superfluous names, as recommended in the recent guidelines for publishing new fungal species or names, version 3.0 (Aime et al. 2020). This is especially important in this group of fungi, in which many names are not represented by DNA sequences of type material and many new combinations are possible. Therefore, the proposal to introduce a new genus with numerous subsequent new combinations for an established lineage should have never been accepted and was easily avoidable if a review of the literature was performed.

The new family *Strattoniaceae* was erected to accommodate the genus *Strattonia*. Surprisingly, the genus was redefined without the study of any material of the type species (*St. tetraspora*), but based only on the already available sequences of the type strain of another species, *St. oblecythiformis*. The redefinition was made only on morphological characters even though it has already been clearly demonstrated that taxonomists must be careful proposing any taxonomic reclassification of members of the *Sordariales* and that a polyphasic approach based on both morphological and molecular data is required (Miller and Huhndorf 2004a; Kruys et al. 2015; Marin-Felix et al. 2020). It is of note that no cultures of *St. tetraspora* are available in any recognized culture collection. Therefore, it is of upmost importance to recollect this species and include it in phylogenetic analyses to confirm the monophyly of *Strattonia*. Huang et al. (2021) argued that the characteristics of *Strattonia* should be reduced to those species producing ascospores with an upper cell surrounded by a gelatinous sheath. On the other hand, taxa that have no sheath have been demonstrated to belong to different genera, i.e. *Jugulospora*

Table 2 Isolates and reference strains of the order *Sordariales* included in the phylogenetic study. Taxa nomenclaturally invalid or not accepted by the present authors are indicated in brackets

Taxa	Strain	GenBank accession #				References
		LSU	ITS	*RPB2*	*TUB2*	
Amesia atrobrunnea	CBS 379.66^T	MH870470	MH858833	KX976798	-	Wang et al. (2016a), Vu et al. (2019)
*Anopodium ampullaceum**	MJR 40/07	KF557662	-	-	KF557701	Kruys et al. (2015)
	E00218015	KF557663	-	-	KF557702	Kruys et al. (2015)
*Apiosordaria microcarpa**	CBS 692.82^T	MK926841	MK926841	MK876803	-	Wang et al. (2019a)
Apodospora gotlandica	E00204952	KF557664	-	-	KF557703	Kruys et al. (2015)
Apodospora peruviana	CBS 118394	KF557665	EU573703	-	-	Kruys et al. (2015), Debuchy et al. (unpubl. data)
Apodospora simulans	Kruys 701	KF557666	-	-	KF557704	Kruys et al. (2015)
	n/a	KF557667	-	-	KF557705	Kruys et al. (2015)
Apodus deciduus	CBS 506.70^T	AY681165	AY681199			Cai et al. (2006)
*Apodus oryzae**	CBS 376.74	AY681166	AY681200	-	-	Cai et al. (2006)
Areotheca ambigua	CBS 215.60	AY999114	AY999137	-	-	Cai et al. (2005)
Areotheca areolata	UAMH 7495	AY587936	AY587911	AY600275	AY600252	Miller and Huhndorf (2004b)
*Arnium caballinum**	Lundqvist 7098-e	KF557672	-	-	-	Kruys et al. (2015)
*Arnium cirriferum**	CBS 120041	KF557673	-	-	KF557709	Kruys et al. (2015)
*Arnium japonense**	SANK 10273	KF557680	-	-	KF557713	Kruys et al. (2015)
*Arnium mendax**	Lundqvist 20874-c	KF557687	-	-	KF557716	Kruys et al. (2015)
	E00122117	KF557688	-	-	KF557717	Kruys et al. (2015)
*Bellojisia rhynchostoma**	CBS 118484	EU999217	-	-	-	Réblová (2008)
Bombardia bombarda	AR1903	AY780052	-	AY780152	AY780089	Miller and Huhndorf (2005)
	SMH 3391	AY346263	-	AY780153	AY780090	Huhndorf et al. (2004), Miller and Huhndorf (2005)
	SMH 4821	AY780053	-	AY780154	AY780091	Miller and Huhndorf (2005)
*Bombardioidea anartia**	HHB99-1	AY346264	-	AY780155	AY780092	Huhndorf et al. (2004), Miller and Huhndorf (2005)
Boothiella tetraspora	CBS 334.67^T	MH870684	MK926876	-	-	Vu et al. (2019), Wang et al. (2019a)
	CBS 887.97	MK926875	MK926875	-	-	Wang et al. (2019a)
Camarops amorpha	SMH 1450	AY780054	-	AY780156	AY780093	Miller and Huhndorf (2005), Miller (unpubl. data)
*Cercophora appalachianensis**	HKUCC 3711	AF132328	AF177155	-	-	Ranghoo et al. (unpubl. data)
*Cercophora aquatica**	JF 06314^T	JN673036	KX171947	-	-	Raja et al. (2011)
Cercophora mirabilis	CBS 120402	KP981429	MT784128	KP981611	KP981556	Marin-Felix et al. (2020)
*Cercophora newfieldiana**	SMH 3303	AY780062	-	AY780167	AY780106	Miller and Huhndorf (2005)
*Cercophora scortea**	GJS L556	AY780063	-	AY780168	AY780107	Miller and Huhndorf (2005)
*Cercophora sparsa**	JF 00229	AY587937	AY587912	-	AY600253	Miller and Huhndorf (2004b)
*Cercophora sulphurella**	SMH 2531	AY587938	AY587913	AY600276	AY600254	Miller and Huhndorf (2004b)
*Cercophora thailandica**	MFLUCC 12-0845^T	KU863127	KU940139	KU940176	-	Dai et al. (2017)
Chaetomium globosum	CBS 160.62^T	MH869713	KT214565	KT214666	-	Vu et al. (2019), Wang et al. (2016b)
*Cladorrhinum brunnescens** (*Podospora brunnescens*)	CBS 643.75A^T	FR692346	FM955446	-	-	Madrid et al. (2010, 2011)
Cladorrhinum coprophilum	SMH 3794	AY780058	-	AY780162	AY780102	Miller and Huhndorf (2005)
Cladorrhinum foecundissimum	CBS 180.66^T	MK926856	MK926856	MK876818	-	Wang et al. (2019a)
(*Cladorrhinum olerum*)	CBS 120012	KF557689	-	-	KF557718	Kruys et al. (2015)
Cladorrhinum globisporum	CGMCC 3.17921^T	KU746726	KU746680	KY883234	-	Zhang et al. (2017, 2018)
Cladorrhinum grandiusculum	CBS 120013	MT731524	GQ922544	MT731562	MT731530	Geydan et al. (2012), Ament-Velásquez et al. (2020)
Cladorrhinum hyalocarpum	CBS 322.70^T	MK926857	MK926857	MK876819	-	Wang et al. (2019a)
Cladorrhinum hyalocarpum	FMR 13412	KP981428	MT784129	KP981610	KP981555	Marin-Felix et al. (2020)
Cladorrhinum intermedium	CBS 433.96^T	MK926859	MK926859	MK876821	-	Wang et al. (2019a)
*Cladorrhinum leucotrichum**	CBS 463.61	MH869684	MH858107	-	-	Vu et al. (2019)
Cladorrhinum terricolum	ATCC 200395	AY780067		AY780170	AY780109	Miller and Huhndorf (2005)
Cladorrhinum tomentosum	Francoise Candoussau	KF557691	-	-	KF557720	Kruys et al. (2015)
*Corylomyces selenosporus**	CBS 113930^T	DQ327607	MT784130	KP981612	KP981557	Stchigel et al. (2006), Marin-Felix et al. (2020)
Corynascus sepedonium	CBS 111.69^T	MH871003	MH859271	FJ666394	-	Vu et al. (2019), Greif et al. (2009)
Dichotomopilus funicola	CBS 159.52^T	MH868497	MH856976	KX976856	-	Wang et al. (2016a), Vu et al. (2019)
Diplogelasinospora grovesii	CBS 340.73^T	MH872401	MH860693	-	-	Vu et al. (2019)
Diplogelasinospora inaequalis	CBS 436.74^T	AY681167	AY681201	-	-	Cai et al. (2006)

Table 2 (continued)

Taxa	Strain	LSU	ITS	RPB2	TUB2	References
Diplogelasinospora moalensis	CBS 136018[T]	KP981430	HG514152	KP981613	KP981558	Crous et al. (2014), Marin-Felix et al. (2020)
Diplogelasinospora princeps	FMR 13414	KP981431	MT784131	KP981614	KP981559	Marin-Felix et al. (2020)
	FMR 13415	KP981432	-	KP981615	KP981560	Marin-Felix et al. (2020)
Echria gigantospora	F77-1	KF557674	-	-	KF557710	Kruys et al. (2015)
Echria macrotheca	Lundqvist 2311	KF557684	-	-	KF557715	Kruys et al. (2015)
Episternus onthophagi	KRAM F58223[T]	KP903375	KP903374	-	-	Górz and Boroń (2018)
Fimetariella rabenhorstii	Lundqvist 20410-c	KF557694	-	-	KF557721	Kruys et al. (2015)
Immersiella caudata	SMH 3298	AY436407	-	AY780161	AY780101	Miller and Huhndorf (2004a, 2005)
Immersiella hirta	E00204950	KF557675	-	-	KF557711	Kruys et al. (2015)
	E00204487	KF557676	-	-	KF557712	Kruys et al. (2015)
Immersiella immersa	SMH 4104	AY436409	-	AY780181	AY780123	Miller and Huhndorf (2004a, 2005)
	SMH 2589	AY436408	-	-	-	Miller and Huhndorf (2004a)
Jugulospora antarctica	IMI 381338[T]	KP981433	-	KP981616	KP981561	Marin-Felix et al. (2020)
Jugulospora carbonaria	ATCC 34567	AY346302	-	AY780196	AY780141	Huhndorf et al. (2004), Miller and Huhndorf (2005)
Jugulospora rotula	ATCC 38359	AY346287	-	AY780178	AY780120	Huhndorf et al. (2004), Miller and Huhndorf (2005)
	CBS 110112	KP981434	-	KP981617	KP981562	Marin-Felix et al. (2020)
	CBS 110113	KP981435	-	KP981618	KP981563	Marin-Felix et al. (2020)
	FMR 12428	KP981436	MT784132	KP981619	KP981564	Marin-Felix et al. (2020)
	FMR 12690	KP981437	MT784133	KP981620	KP981565	Marin-Felix et al. (2020)
	FMR 12781	KP981438	MT784134	KP981621	KP981566	Marin-Felix et al. (2020)
(*Jugulospora minor*)	CBS 380.86 (type of *Strattonia minor*)	MH873659	MH861966	-	-	Vu et al. (2019)
Jugulospora vestita	CBS 135.91[T]	MT785872	MT784135	MT783824	MT783825	Marin-Felix et al. (2020)
Lasiosphaeria glabrata	TL 4529	AY436410	AY587914	AY600277	AY600255	Miller and Huhndorf (2004a, 2004b)
	SMH 4617	AY436411	AY587915	AY600278	AY600256	Miller and Huhndorf (2004a, 2004b)
Lasiosphaeria lanuginosa	SMH 3819	AY436412	AY587921	AY600283	AY600262	Miller and Huhndorf (2004a, 2004b)
Lasiosphaeria miniovina	SMH 2392[T]	MH700179	MH700179	-	-	Crous et al. (2018)
Lasiosphaeria ovina	SMH 1538	AF064643	AY587926	AY600287	AF466046	Fernández et al. 1999, 2006), Miller and Huhndorf (2004b)
	CBS 126299	MH875422	MH863967	-	-	Vu et al. (2019)
Lasiosphaeria rugulosa	SMH 1518	AY436414	AY587933	AY600294	AY600272	Miller and Huhndorf (2004a, 2004b)
Lasiosphaeria similisorbina	AR 1884[T]	MF806376	MF806376	-	-	Crous et al. (2017)
Lasiosphaeria sorbina	CBS 885.85	AY436416	AY587935	AY600296	AY600274	Miller and Huhndorf (2004a, 2004b)
Lasiosphaeris arenicola	ANM 1080	JN673037	JN673037	-	-	Raja et al. (2011)
Lasiosphaeris hirsuta	SMH 1543	AY436417	-	AY780179	AY780121	Miller and Huhndorf (2004a, 2005)
	JF 02183	AY436418	-	-	-	Miller and Huhndorf (2004a)
Lasiosphaeris hispida	SMH 3336	AY436419	-	AY780180	AY780122	Miller and Huhndorf (2004a, 2005)
	CBS 955.72	MH872327	AY681203	-	-	Cai et al. (2006), Vu et al. (2019)
Lundqvistomyces karachiensis	CBS 657.74	KP981447	MK926850	KP981630	KP981478	Wang et al. (2019a), Marin-Felix et al. (2020)
Lundqvistomyces tanzaniensis	TRTC 51981[T]	AY780081	MH862260	AY780197	AY780143	Miller and Huhndorf (2005), Vu et al. (2019)
Mammaria echinobotryoides	CBS 277.63	MH869889	MH858283	-	-	Vu et al. (2019)
	CBS 458.65	MH870308	MH858668	-	-	Vu et al. (2019)
	ANM 734	KX171943	KX171948	-	-	Miller (unpubl. data)
Morinagamyces vermicularis	CBS 303.81[T]	KP981427	MT904879	KP981609	KP981554	Harms et al. (2021)
Naviculispora terrestris	CBS 137295[T]	KP981439	MT784136	KP981622	KP981567	Marin-Felix et al. (2020)
Neurospora crassa	ICMP 6360	AY681158	AY681193	-	-	Cai et al. (2006)
Neurospora hispaniola	FGSC 8817[T]	FR774257	-	-	FR774329	Nygren et al. (2011)
Neurospora metzenbergii	FGSC 8847	FR774263	-	-	FR774330	Nygren et al. (2011)
Neurospora pannoica	TRTC 51327	AY780070	-	AY780185	AY780126	Miller and Huhndorf (2005)
Neurospora sitophila	CBS 112.19	MH866192	MH854676	-	-	Vu et al. (2019)
Neurospora tetrasperma	CBS 223.38	MH867446	MH855950	-	-	Vu et al. (2019)
*Podospora appendiculata**	CBS 212.97	AY780071	MH862644	AY780186	AY780129	Miller and Huhndorf (2005), Vu et al. (2019)
Podospora bulbillosa	CBS 304.90[T]	MK926861	MK926861	MK876823	-	Wang et al. (2019a)
*Podospora bullata**	CBS 115576[T]	MH874548	DQ166960	-	-	Bell et al. (2016), Vu et al. (2019)
*Podospora communis**	CBS 118393	MH874584	MH863031	-	-	Vu et al. (2019)
Podospora costariciensis	SMH 4021	AY780059	-	AY780163	AY780103	Miller and Huhndorf (2005)
Podospora cupiformis	CBS 246.71[T]	AY999102	AY999125	-	-	Cai et al. (2005)

Table 2 (continued)

Taxa	Strain	GenBank accession #				References
		LSU	ITS	*RPB2*	*TUB2*	
Podospora dacryoidea	INTA-AR 70[T]	KT312976	KT321062	-	-	Carmarán et al. ([2015])
*Podospora didyma**	CBS 232.78	AY999100	AY999127	-	-	Cai et al. ([2005])
*Podospora excentrica**	CBS 118392	MH874583	MH863030	-	-	Vu et al. ([2019])
*Podospora fabiformis**	CBS 112043[T]	MK926843	MK926843	MK876805	-	Wang et al. ([2019a])
*Podospora fibrinocaudata**	CBS 315.91[T]	MK926844	MK926844	MK876806	-	Wang et al. ([2019a])
	TRTC 48343	AY780074	-	AY780188	AY780131	Miller and Huhndorf ([2005])
Podospora fimiseda (*Podospora fimicola*)	CBS 482.64[ET]	KP981440	MK926862	KP981623	KP981568	Wang et al. ([2019a]), Marin-Felix et al. ([2020])
	CBS 990.96	MK926863	MK926863	-	-	Wang et al. ([2019a])
Podospora flexuosa	FMR 10415[T]	FN662477	FN662474	-	-	Madrid et al. ([2011])
Podospora hamata	CGMCC 3.15230[T]	KP878304	KP878306	-	-	Wu et al. ([2016])
Podospora inflatula	CBS 413.82	MH873254	MH861508	-	-	Vu et al. ([2019])
*Podospora intestinacea**	CBS 113106	AY999104	AY999121	-	-	Cai et al. ([2005])
Podospora jamaicensis	CBS 672.70[T]	MT731527	MH859895	MT731556	MT731534	Vu et al. ([2019]), Ament-Velásquez et al. ([2020])
*Podospora leporina**	CBS 365.69	MH871063	MH859324	-	-	Vu et al. ([2019])
Podospora macrospora	CBS 286.86[T]	MT731528	MH861958	MT731558	MT731532	Vu et al. ([2019]), Ament-Velásquez et al. ([2020])
*Podospora minicauda** (*Neoschizothecium minicauda*)	CBS 227.87	MH873757	MH862068	-	-	Vu et al. ([2019])
*Podospora petrogale** (*Strattonia petrogale*)	CBS 109409[T]	MH874419	AY071831			Bell ([1999]), Vu et al. ([2019])
*Podospora prethopodalis**	CBS 121128	MH874659	MH863103	-	-	Vu et al. ([2019])
Podospora sacchari	CBS 713.70[T]	KP981425	MH859915	KP981607	KP981552	Vu et al. ([2019]), Marin-Felix et al. ([2020])
*Podospora serotina**	CBS 252.71	MH871878	MH860102			Vu et al. ([2019])
Podospora spinosa	CBS 259.71[T]	MH877809	-	-	-	Vu et al. ([2019])
Podospora striatispora	CBS 154.77[T]	KP981426	MT784137	KP981608	KP981553	Marin-Felix et al. ([2020])
Pseudoechria curvicolla	IFO 8548	AY999099	AY999122	-	-	Cai et al. ([2005])
	CBS 259.69	MH871036	MH859302	-	-	Vu et al. ([2019])
Pseudoechria decidua	CBS 254.71[T]	MK926842	MK926842	MK876804	-	Wang et al. ([2019a])
Pseudoechria longicollis	CBS 368.52[T]	MK926847	MK926847	MK876809	-	Wang et al. ([2019a])
Pseudoechria. prolifica	CBS 250.71[T]	MK926848	MK926848	MK876810	-	Wang et al. ([2019a])
Pseudoneurospora amorphoporcata	CBS 626.80	FR774287	-	-	FR774294	Nygren et al. ([2011])
Pseudoneurospora canariensis	FMR 12156[T]	MH877580	-	-	HG423208	Crous et al. ([2014]), Vu et al. ([2019])
Pseudorhypophila mangenotii	CBS 419.67[T]	KP981444	MT784143	KP981627	KP981571	Marin-Felix et al. ([2020])
Pseudorhypophila marina	CBS 155.77[T]	MK926851	MK926851	MK876813	-	Wang et al. ([2019a])
	CBS 698.96	MK926853	MK926853	MK876815	-	Wang et al. ([2019a])
Pseudorhypophila pilifera	CBS 413.73[T]	MK926852	MK926852	MK876814	-	Wang et al. ([2019a])
Pseudoschizothecium atropurpureum	SMH 2961	AY780056	-	-	AY780099	Miller and Huhndorf ([2005])
	SMH 3073	AY780057	-	AY780160	AY780100	Miller and Huhndorf ([2005])
Ramophialophora globispora	CGMCC 3.17940	KU746745	KU746699	KY883252	-	Zhang et al. ([2017], [2018])
Ramophialophora humicola	FMR 9523[T]	FR692337	FM955449	-	-	Madrid et al. ([2010], [2011])
Ramophialophora petraea	CGMCC 3.17953	KU746747	KU746701	KY883254		Zhang et al. ([2017], [2018])
Ramophialophora vesiculosa	CBS 110629[T]	MH874452	MH862866	-	-	Vu et al. ([2019])
Rinaldiella pentagonospora	CBS 132344[T]	KP981442	MH866007	KP981625	KP981570	Vu et al. (2019), Marin-Felix et al. (2020)
Rhypophila cochleariformis	CBS 249.71	AY999098	AY999123	-	-	Cai et al. ([2005])
Rhypophila decipiens	CBS 258.69	AY780073	KX171946	AY780187	AY780130	Miller and Huhndorf ([2005]), Miller (unpubl. data)
Rhypophila myriaspora	TNM F17211	-	EF197083	-	-	Chang et al. ([2010])
Rhypophila pleiospora	TNM F16889	-	EF197084	-	-	Chang et al. ([2010])
Schizothecium aloides (*Neoschizothecium aloides*)	CBS 879.72	AY999097	AY999120	-	-	Cai et al. ([2005])
Schizothecium carpinicola (*Neoschizothecium carpinicola*)	CBS 228.87[T]	AY999095	AY999118	-	-	Cai et al. ([2005])
Schizothecium conicum (*Neoschizothecium conicum*)	CBS 434.50	MH868218	MH856702	-	-	Vu et al. ([2019])

Table 2 (continued)

Taxa	Strain	GenBank accession #				References
		LSU	ITS	*RPB2*	*TUB2*	
Schizothecium curvisporum	CBS 507.50	AY999096	AY999119	-	-	Cai et al. (2005)
(*Neoschizothecium curvisporum*)	ATCC 36709	AY346300	-	AY780192	AY780136	Huhndorf et al. (2004), Miller and Huhndorf (2005)
Schizothecium fimbriatum (*Neoschizothecium fimbriatum*)	CBS 144.54	AY780075	AY999115	AY780189	AY780132	Cai et al. (2005), Miller and Huhndorf (2005)
Schizothecium glutinans (*Neoschizothecium glutinans*)	CBS 134.83	AY999093	AY999116	-	-	Cai et al. (2005)
Schizothecium inaequale (*Neoschizothecium inaequale*)	CBS 356.49[T]	MK926846	MK926846	MK876808	-	Wang et al. (2019a)
Schizothecium selenosporum (*Neoschizothecium selenosporum*)	CBS 109403[T]	MK926849	MK926849	MK876811	-	Wang et al. (2019a)
Schizothecium tetrasporum (*Neoschizothecium tetrasporum*)	CBS 394.87	MH873776	MH862087	-	-	Vu et al. (2019)
Sordaria fimicola	SMH 4106	AY780079	-	AY780194	AY780138	Miller and Huhndorf (2005)
Sordaria islandica	CBS 512.77[T]	MH872859	MH861097	-	-	Vu et al. (2019)
Sordaria nodulifera	NBRC 32551[T]	LC146761	LC146761	-	-	Ban et al. (unpubl. data)
Sordaria tamaensis	NBRC 32552[T]	LC146762	LC146762	-	-	Ban et al. (unpubl. data)
*Strattonia oblecythiformis**	CBS 110350[T]	MH874449	MH862861	-	-	Vu et al. (2019)
Triangularia allahabadensis	CBS 724.68[T]	MK926865	MK926865	MK876827	-	Wang et al. (2019a)
Triangularia anserina	CBS 433.50	MK926864	MK926864	MK876826	-	Wang et al. (2019a)
Triangularia arizonensis	Santesson 18211-c	KF557668	-	-	KF557706	Kruys et al. (2015)
	Kruys 724	KF557669	-	-	KF557707	Kruys et al. (2015)
	E00204509	KF557670	-	-	KF557708	Kruys et al. (2015)
	CBS 120289	KU955584	-	-	-	Debuchy et al. (unpubl. Data)
Triangularia backusii	CBS 539.89[IsoT]	MK926866	MK926866	MK876828	-	Wang et al. (2019a)
Triangularia backusii	FMR 12439	KP981423	MT784138	KP981605	KP981550	Marin-Felix et al. (2020)
Triangularia backusii	FMR 13591	KP981424	MT784139	KP981606	KP981551	Marin-Felix et al. (2020)
Triangularia bambusae	CBS 352.33[T]	MK926868	MK926868	MK876830	-	Wang et al. (2019a)
Triangularia batistae	CBS 381.68[T]	KP981443	MT784140	KP981626	KP981577	Soil, Brazil
Triangularia longicaudata	CBS 252.57[T]	MK926871	MK926871	MK876833	-	Wang et al. (2019a)
	FMR 12365	KP981448	MT784141	KP981631	KP981474	Marin-Felix et al. (2020)
	FMR 12782	KP981449	MT784142	KP981632	KP981475	Marin-Felix et al. (2020)
Triangularia microsclerotigena	CBS 290.75[T]	FN662476	FN662475	-	-	Madrid et al. (2011)
*Triangularia nannopodalis**	CBS 113680	MH874504	MH862937	-	-	Vu et al. (2019)
Triangularia ovina	CBS 671.82[T]	MT731512	MH861539	MT731574	MT731553	Vu et al. (2019), Ament-Velásquez et al. (2020)
Triangularia pauciseta	CBS 451.62	MK926870	MK926870	MK876832	-	Wang et al. (2019a)
Triangularia phialophoroides	CBS 301.90[T]	MK926871	MK926871	MK876833	-	Wang et al. (2019a)
Triangularia samala	CBS 307.81[T]	MH873104	MH861345	-	-	Vu et al. (2019)
Triangularia setosa	FMR 12787	KP981441	MT784144	KP981624	KP981569	Marin-Felix et al. (2020)
	CBS 311.58	MK926872	MK926872	MK876834	-	Wang et al. (2019a)
(*Triangularia tarvisina*)	CBS 265.70	MT731516	MH859600	MT731573	MT731552	Vu et al. (2019), Ament-Velásquez et al. (2020)
(*Triangularia praecox*)	CBS 251.71 (type of *P. praecox*)	MH871877	MH860101	-	-	Vu et al. (2019)
Triangularia striata	SMH 3431	-	AY780065	AY780169	AY780108	Miller and Huhndorf (2005)
	SMH 4036	KX348038	AY780066	-	-	Miller and Huhndorf (2005), Miller (unpubl. data)
Triangularia tetraspora	CBS 245.71	MH860097	MH871873	-	-	Vu et al. (2019)
	FMR 5770	AY999130	AY999108	-	-	Cai et al. (unpubl. data)
Triangularia unicaudata	CBS 313.58[T]	MT731513	MH857799	MT731575	MT731554	Vu et al. (2019), Ament-Velásquez et al. (2020)
Triangularia verruculosa	CBS 148.77	MK926874	MK926874	MK876836	-	Wang et al. (2019a)
Triangularia yaeyamensis	NBRC 31170[T]	LC146720	LC146720	-	-	Ban et al. (unpubl. data)
*Zopfiella attenuata**	CBS 266.77[T]	KP981445	MH861060	KP981628	KP981572	Vu et al. (2019), Marin-Felix et al. (2020)
*Zopfiella erostrata**	CBS 255.71	AY999110	AY999133	-	-	Cai et al. (2005)
*Zopfiella latipes**	IFO 9826	AY999107	AY999129	-	-	Cai et al. (2005)

Table 2 (continued)

Taxa	Strain	GenBank accession #				References
		LSU	ITS	*RPB2*	*TUB2*	
Zopfiella pleuropora*	CBS 518.70[T]	KP981450	MT784145	KP981633	KP981476	Marin-Felix et al. (2020)
Zopfiella tabulata	CBS 230.78	MK926854	MK926854	MK876816	-	Wang et al. (2019a)
Zopfiella tardifaciens*	CBS 670.82[T]	MK926855	MK926855	MK876817	-	Wang et al. (2019a)
Zygopleurage zygospora	SMH 4219	AY346306	-	-	AY780147	Huhndorf et al. (2004), Miller and Huhndorf (2005)
Zygospermella insignis	Lundqvist 2444	KF557698	-	-	KF557722	Kruys et al. (2015)
Zygospermella insignis	E00204312	KF557699	-	-	KF557723	Kruys et al. (2015)

ATCC, American Type Culture Collection, VA, USA; CBS, Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; FMR, Facultat de Medicina, Reus, Spain; FGSC, Fungal Genetics Stock Center, University of Kansas Medical Center, Kansas City, USA; HKUCC, University of Hong Kong Culture Collection, Department of Ecology and Biodiversity, Hong Kong, China; IFO, Biological Resource Center, Chiba, Japan; IMI, International Mycological Institute, CABI-Bioscience, Egham, UK; KRAM, National Biodiversity Collection – Herbarium KRAM, Kraków, Poland; SANK, Research laboratories of the Daiichi Sanko Pharmaceutical Co., Ltd., Tokyo, Japan; TNM, Herbarium of National Museum of Natural Science, Taiwan; TRTC, Royal Ontario Museum, Toronto, Canada; UAMH, UAMH Center for Global Microfungal Biodiversity, University of Toronto, Canada; AR, Francoise Candoussau, GJS, JF, HHB, Kruys, Lundqvist, MJR, Santensoon, SMH, TL: personal collections of Amy Rossman, Francoise Candoussau, Gary J. Samuels, Jacques Fournier, Harold H. Burdsal, Åsa Kruys, Nils Lundqvist, Michael J. Richardson, Sweden R. Santesson, Sabine M. Huhndorf, Thomas Læssøe, respectively; n/a: not available. [ET, IsoT and T] indicate ex-epitype, ex-isotype and ex-type strains, respectively. *Taxa with generic names applied in the broad sense (sensu lato), not necessarily reflecting molecular phylogenetic relationships

and *Lundqvistomyces* (Marin-Felix et al. 2020). Therefore, the presence or absence of an ascospore sheath is polyphyletic and one cannot assume that all species with ascospores surrounded by a sheath are going to belong to the same monophyletic lineage. In fact, other species characterized by ascospores surrounded by a gelatinous sheath are placed in different genera, such as *Echria* (*Schizotheciaceae*), *Fimetariella* (*Lasiosphaeriaceae* s. lato) and *Sordaria* (*Sordariaceae*). This family is erected based on a clade containing only two species, *S. oblecythiformis* and the new combination *S. petrogale*, but both species only contain sequences from the internal transcribed spacer region (ITS) and the nuclear rDNA large subunit (LSU) from the study of Vu et al. (2019). For these reasons, we reject the family *Strattoniaceae* until additional taxa, including the type species, and additional genes (i.e. *RPB2* and *TUB2*) have been studied.

The families *Lasiosphaeridaceae* and *Zygospermellaceae*, erected for only one and two genera, respectively, are also points of contention since they were proposed based on limited taxon sampling and poor taxonomic practices. In the recent phylogenetic studies from Kruys et al. (2015) and Marin-Felix et al. (2020), both clades now considered independent families by Huang et al. (2021) were clustering together in a well-supported clade. Huang et al. (2021) prematurely introduced both families since they formed two independent lineages in their phylogenetic study. However, both families are included in the *Schizotheciaceae* clade in our Bayesian phylogenetic study (0.97 pp) (Fig. 2). More taxa and sequences should be incorporated in further phylogenetic

analyses to verify if the *Lasiosphaeridaceae* and *Zygospermellaceae* are two independent lineages or belong to the *Schizotheciaceae*. For these reasons, we reject these families until more data can be analysed and we refer to both lineages as *Lasiosphaeriaceae* s. lato.

In our phylogenetic study, the only family not supported is *Lasiosphaeriaceae* s. str. However, the conflicts may be caused by the high number of taxa in which only the ITS and LSU sequences are available, which most likely influences the backbone relationships and support for these phylogenetic relationships resulting in misleading higher-level classifications. Although most strains included in Huang et al. (2021) are available in the CBS collection, and therefore additional loci could have been sequenced, they chose not to generate these critical sequence data for their phylogenetic analyses.

Finally, the family *Bombardiaceae* was introduced by Huang et al. (2021), even though the ML bootstrap support was only 76% and there was no Bayesian inference support for this clade. Huang et al. (2021) explained that Marin-Felix et al. (2020) discussed the low support of this lineage, and for that reason no family was introduced to accommodate it. Nonetheless, they considered this lineage to be well-supported in their phylogenetic study, and therefore the new family *Bombardiaceae* was introduced to represent it. In our phylogenetic study (Fig. 2), which included the same sequences that Huang et al. (2021) used, the clade representing this family is not supported (42% bs/0.89 pp), so we do not accept the *Bombardiaceae* as a justifiable family.
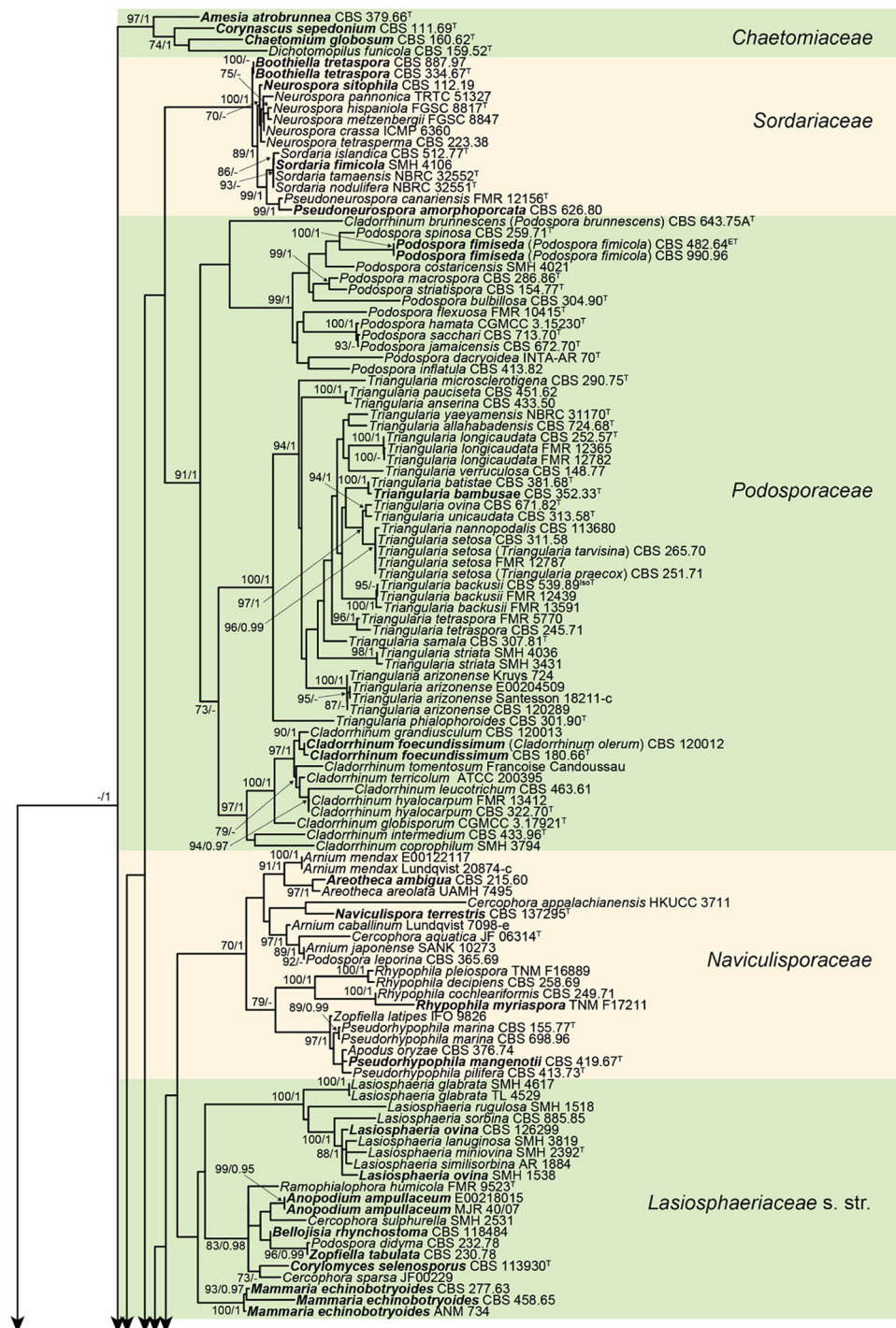
Fig. 2 RAxML phylogram obtained from the combined ITS, LSU, *RPB2* and *TUB2* sequences belonging to the families *Chaetomiaceae*, *Diplogelasinosporaceae*, *Lasiosphaeriaceae*, *Naviculisporaceae*, *Podosporaceae*, *Schizotheciaceae*, and *Sordariaceae*. *Camarops amorpha* SMH 1450 was used as an outgroup. Bootstrap support values ≥70/Bayesian posterior probability scores ≥0.95 are indicated along branches. Branch lengths are proportional to distance. Ex-epitype, ex-isotype and ex-type strains of the different species are indicated with ET, IsoT and T, respectively. Type species of the different genera are shown in bold. Alignment available in Supplementary Information
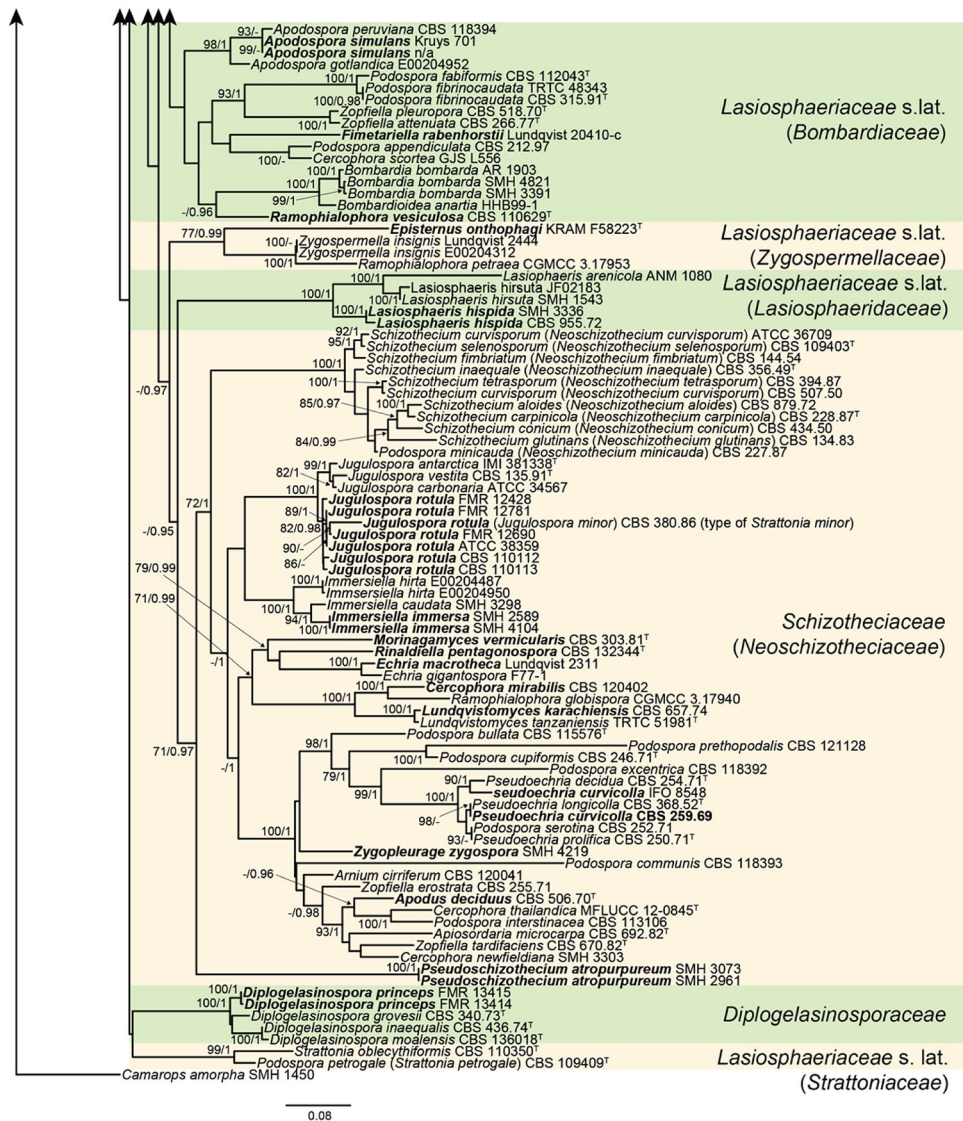
Fig. 2 (continued)

We take this opportunity to clarify that most of the outgroups used in Huang et al. (2021) do not belong to the family *Microascales* as they erroneously indicated, but rather to the *Coronophorales* (syn. *Melanosporales*) as in the case of all the *Microthecium* spp. included, as well as *Thielavia basicola*.

New genera superfluously introduced or redefined based on poor taxonomic practice

As mentioned above, *Neoschizothecium* is a superfluous genus based on misinterpretation of the type species of *Podospora* and *Schizothecium* so it is nomenclaturally illegitimate (Art. 14.3, Shenzhen Code) and thus, a superfluous

synonym under *Schizothecium*. The delimitation of *Strattonia* based on a single species is a poor taxonomic decision since the type species of the genus was not included in the study of Huang et al. (2021). Finally, the delimitation of *Cercophora* is also based on poor taxonomic practice since Huang et al. (2021) chose a dubious candidate to represent the type species of *C. mirabilis* in their analyses but thankfully, they did not designate an epitype. It is impossible to confirm the morphological identification of this strain (CBS 120402) because it does not sporulate in culture as mentioned by Marin-Felix et al. (2020). Therefore, it is not a suitable representative of the type species of *Cercophora* and a suitable epitype must be studied and designated before this genus can be properly delimited. The placement of *Cercophora* spp. in different lineages and families support the necessity of a detailed study of this genus and the careful designation of

an epitype for the type species in order to determine the proper taxonomic placement of *Cercophora* within the order.

New combinations superfluously introduced or failing to follow good taxonomic practice

The new combination of *Cladorrhinum olerum* proposed to accommodate *Arnium olerum* is superfluous because Marin-Felix et al. (2020) already synonymized this latter name under *Cl. foecundissimum*. The nucleotide similarity between both species is 99.81% for ITS, 100% for LSU, 98.60% for *RPB2* and 100% for *TUB2*, suggesting that these represent the asexual and sexual morphs of the same taxon.

The new combination *T. tarvisina* is superfluous since *P. tarvisina* has been considered a synonym of *T. setosa* for 50 years based on their morphological similarity (Lundqvist 1972). This is corroborated based on the high nucleotide similarity greater than 99.5% of the four loci (ITS, LSU, *RPB2* and *TUB2*) between both species according to a BLAST comparison. Therefore, this new combination was made in error due to the failure of a proper literature review by Huang et al. (2021). Likewise, the new combination *T. praecox* is also superfluous since this species shows morphological and molecular similarity also with *T. setosa*, and therefore *P. praecox* is here considered a synonym to this later species. The description of *T. setosa* is here emended to incorporate the sizes observed in *P. praecox* when it was introduced, which are similar to *T. setosa* except for the ascus dimensions (up to 190 μm wide in *P. praecox* vs. up to 60 μm in *T. setosa*) (Cailleux 1969; Lundqvist 1972; Wang et al. 2019a).

Triangularia setosa (G. Winter) X. Wei Wang & Houbraken, Stud. Mycol. 93: 243. 2019. emend. Y. Marin & A.N. Mill.
MB829894
Basionym: *Sordaria setosa* G. Winter, Abh. Naturf. Ges. Halle 13: 97. 1873.
Synonyms: *Philocopra setosa* (G. Winter) Sacc., Syll. Fung. 1: 249. 1882.
Podospora setosa (G. Winter) Niessl, Hedwigia 22: 156. 1883.
Pleurage setosa (G. Winter) Kuntze, Revis. Gen. Pl. 3: 505. 1898.
Cladochaete setosa (G. Winter) Sacc., Ann. Mycol. 10: 318. 1912.
Philocopra setosa subsp. *tarvisina* Sacc., Syll. Fung. (Abellini) 1: 250. 1882.
Philocopra setosa var. *tarvisina* (Sacc.) Traverso, Fl. Ital. Crypt. (Florence) 1: 437. 1907.
Philocopra tarvisina (Sacc.) J.H. Mirza & Cain, Can. J. Bot. 47: 2041. 1970.
Podospora tarvisina (Sacc.) J.H. Mirza & Cain, Can. J. Bot. 47: 2041. 1970.

Triangularia tarvisina (Sacc.) S.K. Huang & K.D. Hyde, Fungal Divers. 111: 515. 2021.
Podospora praecox Cailleux, Cahiers de La Maboké 7: 102. 1969.
Triangularia praecox (Cailleux) S.K. Huang & K.D. Hyde, Fungal Divers. 111: 515. 2021.

Ascomata superficial, mouse grey in reflected light, solitary, ovoid to ampulliform with a short, black beak, ostiolate, 230–900 μm high, 185–800 μm diam; ascomatal wall brown, opaque, of *textura intricata* or *epidermoidea* in surface view; ascomatal hairs arising mainly around the lower half, hyphal-like, erect or flexuous, brown, 1.5–3 μm diam near base. Asci fasciculate, fusiform or elongated fusiform, 170–430 × 25–60(–190) μm, without a conspicuous apical ring, stipitate, stipe 21.5–62 μm long, containing numerous irregularly- and densely-arranged ascospores, evanescent. Ascospores at first one-celled, hyaline, becoming transversely septate and two-celled; upper cell olivaceous brown to brown, ellipsoidal to broadly fusiform, equilateral, with an apical germ pore, (15–)17–21.5(–22) × (9–)10.5–13 μm; lower cell hyaline, clavate to cylindrical, 8–12 × 2–3 μm; apical and basal mucilaginous appendages mostly present, up to 120 μm long. Asexual morph not observed (adapted from Lundqvist 1972 and Wang et al. 2019a).

Huang et al. (2021) proposed the new combination *Jugulospora minor* to accommodate *Strattonia minor*. Even though we consider the transference of this species to *Jugulospora* necessary, Huang et al. (2021) did not demonstrate whether it is an independent species or if it should be synonymized with *J. rotula* as happened with *Apiosordaria globosa*, *A. hispanica* and *Rhexosporium terrestre* (Marin-Felix et al. 2020). *Strattonia minor* is similar to *J. rotula*, differing only by the size of the upper cell of the ascospores and the width of the asci (Lundqvist 1972; Marin-Felix et al. 2020). In our phylogenetic study (Fig. 2), the type strain of this species occurred in the moderately well-supported clade (82% bs/0.98 pp) representing *J. rotula*. Therefore, *J. minor* is here considered a synonym of *J. rotula*, whose description is here emended to incorporate the new sizes of asci and ascospores.

Jugulospora rotula (Cooke) N. Lundq. emend. Y. Marin & A.N. Mill.
MB315972
Basionym: *Sphaeria rotula* Cooke, Handb. British Fungi 2: no. 2598. 1871.
Synonyms: *Strattonia minor* N. Lundq., Symb. Bot. Upsal. 20: 271. 1972.
Jugulospora minor (N. Lundq.) S.K. Huang & K.D. Hyde, Fungal Divers. 111: 95. 2021.
Rhexosporium terrestre Udagawa & Furuya, Trans. Mycol. Soc. Japan 18: 303. 1977.

Apiosordaria globosa Dania García, Stchigel & Guarro, Mycologia 95: 137. 2003.

Apiosordaria hispanica Dania García, Stchigel & Guarro, Mycologia 95: 134. 2003.

Ascomata ostiolate, superficial or immersed, scattered to aggregated, pale brown to brown, pyriform, 350–770 × 200–540 μm, covered with pale brown, septate hyphal-like hairs, 1–5 μm diam; neck brown to dark brown, cylindrical to conical, papillate, 80–280 μm long, 90–250 μm wide; ascomatal wall membranaceous, semi-transparent, brownish-orange to brown, 3–9-layered, 15–45 μm thick; outer layers *textura angularis* and *textura intricata*; inner layers *textura epidermoidea*. Paraphyses and periphyses filiform, up to 2 μm in diam. Asci unitunicate, eight-spored, cylindrical, 145–250 × 8–28 μm, stipitate, with a thin apical ring, evanescent. Ascospores at first one-celled, hyaline, clavate, becoming transversely septate and two-celled; upper cell dark brown, obovoid to globose, truncate at the base, ornamented with warts arranged uniformly or forming longitudinal ridges or large spots, (12–)13–18(–29) × 6–27 μm, with an apical to lateral germ pore 0.5–3 μm in diam.; lower cell hyaline, conical, smooth-walled to slightly warted, 1–6 μm long, collapsing; gelatinous caudae absent. Asexual morph present. Conidia hyaline to pale-colored, almost smooth-walled, ovate to elongate, 2–6 × 1.5–2.5 μm, produced laterally or terminally on undifferentiated hyphae, solitary (adapted from Marin-Felix et al. 2020).

As mentioned above, the genus *Strattonia* is delimited based on the non-type species *S. oblecythiformis*, which should not be accepted due to the difficulty of delimiting genera in the *Sordariales* based on only morphological data (for further details, see section "New families superfluously introduced or without sufficient evidence"). For this reason, the new combination *S. petrogale* should not be taken up until further studies that include the type species confirm the correct taxonomic placement of the lineage representing *Strattonia*.

The nine new combinations in the newly erected genus *Neoschizothecium* proposed for accommodating the species previously belonging to *Schizothecium* are also here considered superfluous for the same reasons the family *Neoschizotheciaceae* is invalid. Moreover, *N. minicauda* was introduced to accommodate *P. minicauda*. However, the strain included in the phylogenetic study does not represent type material and its morphology was not studied. Therefore, the transfer of this species to *Schizothecium* should await further studies.

Cladorrhinum brunnescens is transferred to *Podospora* as *P. brunnescens*. However, in our phylogenetic study, this species is not placed in the well-supported clade (99% bs/1 pp) representing *Podospora*. Only ITS and LSU sequence data of the type strain are available. Therefore, the other two loci should be sequenced and additional analyses conducted before this combination is accepted.

Finally, two additional new combinations that followed poor taxonomic practices are *Cl. leucotrichum* and *T. nannopodalis*, which were proposed based on strains that do not represent type material and whose morphology was not studied.

Limitation in the morphological study

Huang et al. (2021) performed morphological studies of type material for several taxa belonging to the *Sordariales*, although they mostly repeated what can already be found in the literature without providing any new information while at the same time destroying irreplaceable type material. Examination of type material is important, but generating sequence data from types or designating epitypes with molecular data is a higher priority. No molecular data were generated in Huang et al. (2021). Due to the difficulty of delimiting species and genera of this order based only on morphology, it is much more important to generate sequences from these types of materials to incorporate in phylogenetic analyses instead of re-examining material that has previously been studied and well documented. This is the case of *Triangularia horridula*, a new combination proposed after a morphological and molecular study of the holotype from the fungarium of Saccardo (Forin et al. 2021). Using next-generation sequencing techniques, the generation of molecular data from type material is possible and essential to improve taxonomic classifications.

Conclusions and final remarks

In conclusion, it is clear that the authors of Huang et al. (2021) were not able to fully appreciate or understand the problems surrounding the reclassification of the order *Sordariales*, which has been studied using a combination of meticulous morphological and molecular analyses by various workers for more than a decade. Even in the last few years, chemotaxonomic data have been combined with morphological and molecular data to verify some taxonomic relationships. For example, Shao et al. (2020) demonstrated that different specimens and strains of *Jugulospora* produced the same xanthoquinodins compounds, corroborating the redefinition of the genus performed by Marin-Felix et al. (2020). Moreover, the new genus *Pseudorhypophila* was introduced based on the production of the same class of compounds, i.e. zopfinol and derivatives, by members of the same monophyletic lineage (Harms et al. 2021). In this later work, they observed that producers of sordarins, which are a class of natural antifungal agents, were all located in the *Naviculisporaceae*, supporting the introduction of this family based on molecular data by Marin-Felix et al. (2020). The taxonomy of the *Sordariales* should not be rearranged

following the results of a single phylogenetic study and numerous new family names should not be introduced without careful consideration. The study of Huang et al. (2021) is reminiscent of those of Raymond Hoser (Kaiser et al. 2013; Rhodin et al. 2015; Wüster et al. 2021) or Alexander Doweld (2001), who frequently practice taxonomic vandalism by formally naming clades based on the work of previous workers. The introduction of unnecessary families, genera and species for unstable and unsupported clades that will eventually change justifies the criticisms of other mycological disciplines. These claim fungal taxonomists only want to constantly change names and make systematic mycology a more difficult field. New scientific names will remain in databases forever even if they are proven to be invalid or superfluous and have the potential to be used by future careless workers and further populated in the literature making them appear as valid and accepted names. Therefore, the introduction of new taxa should be done responsibly by following the best taxonomic practices available, such as a thorough review of past literature, conducting polyphasic studies to corroborate initial hypotheses and collaborating with experts in the group of fungi under study (Aime et al. 2020; Lücking et al. 2020).

Furthermore, it is possible that DNA-based phylogenies can be misleading in the recognition of species just like morphological studies alone. Polymorphisms can interfere in species identification based only on morphology, but also the lack of loci or the use of loci inappropriate for the fungal taxa under study can also lead to the wrong conclusions (Lücking et al. 2020). This is the case for some of the new combinations proposed by Huang et al. (2021) based only on ITS and LSU sequences. Therefore, both phenotypic and molecular approaches should be combined for a more robust taxonomic classification.

It is worthy to mention that according to the recent guidelines for publishing a new fungal species or name provided by Aime et al. (2020), it is strongly recommended to examine the types of the basionyms before making changes and include notes on how to differentiate the new recombined species from other similar species in that genus. Even though one of the co-authors of this guideline was also one of the authors of all new combinations proposed, none of these recommendations were followed in any of the new combinations performed by Huang et al. (2021).

Declarations

Conflict of interest The authors declare no competing interests.

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