



An updated taxonomic framework of *Hymenochaetales* (*Agaricomycetes*, *Basidiomycota*)

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Abstract

Hymenochaetales is one of the fungal orders being mainly composed of wood-inhabiting macrofungi within *Agaricomycetes*, *Basidiomycota*. While the species diversity has been well explored, the classification of *Hymenochaetales* at the family level is still contrary and not fully resolved. In this study, the taxonomic framework of *Hymenochaetales* is updated with the help of phylogenetic and molecular clock analyses based on six to seven gene regions. Compared with previous papers, the concepts of *Hyphodontiaceae* and *Schizoporaceae* are unchanged, while six additional families are emended: the circumscription of the monotypic family *Chaetoporellaceae* is enlarged by including *Echinoporia* in this family; a larger concept of *Hymenochaetaceae* is formally proposed to accommodate members originally in the families *Hymenochaetaceae*, *Neoantrodiaellaceae* and *Nigrofomitaceae*, and the genera *Basidioradulum* and *Trichaptum*; *Repetobasidiaceae* and *Tubulicrinaceae* are reinstated as two monotypic families; the circumscription of *Rickenellaceae* is reduced to be a monotypic family; and the family name *Rigidoporaceae* is resurrected to replace its later synonym *Oxyporaceae*. Besides these eight previously known families, *Odonticiaceae* is newly erected for *Leifia* and *Odonticium*, while five additional monotypic families are also newly erected to make as many genera as possible accommodated at the family level. In addition, *Botryodontia*, *Neoantrodiaella* and *Skvortzoviella* are considered to be later synonyms of *Rigidoporus*, *Cyanotrama* and *Schizocorticium*, respectively, and species sampled from these three genera in the current phylogenetic analyses are accordingly transferred. Eventually, a total of 14 families, viz. *Chaetoporellaceae*, *Hymenochaetaceae*, *Hyphodontiaceae*, *Odonticiaceae*, *Peniophorellaceae*, *Repetobasidiaceae*, *Resiniaceae*, *Rickenellaceae*, *Rigidoporaceae*, *Schizocorticiaceae*, *Schizoporaceae*, *Sideraceae*, *Skvortzoviaceae* and *Tubulicrinaceae* accommodating 64 genera, and 19 independent genera are accepted in *Hymenochaetales*. In conclusion, a more natural taxonomic system of *Hymenochaetales* is achieved, which is a crucial basis for further exploring species diversity, resource utilization and trait evolution of this fungal order.

Keywords – 11 new taxa – *Hymenochaetaceae* – molecular clock – six new families – wood-inhabiting fungi

Introduction

Hymenochaetales is one of the fungal orders being mainly composed of wood-inhabiting

macrofungi within *Agaricomycetes*, *Basidiomycota* (James et al. 2020, Wang et al. 2021). This order was erected with the type family *Hymenochaetaceae* (Frey et al. 1977). Later, several additional families were successively added to *Hymenochaetales* (Fig. 1).

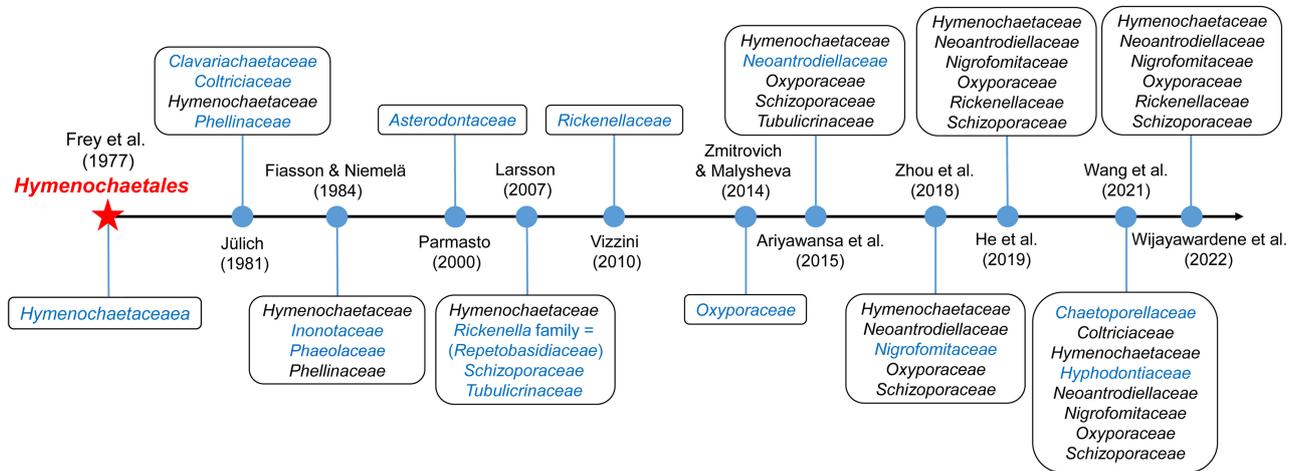


Figure 1 – The development track of taxonomic revisions on *Hymenochaetales* at the family level. Newly added families are in blue. “=” means that *Rickenella* family was equivalent to *Repetobasidiaceae*, as its type genus *Repetobasidium* was included in *Rickenella* family.

Besides *Hymenochaetaceae*, Jülich (1981) added three newly introduced families, viz. *Clavariachaetaceae*, *Coltriciaceae* and *Phellinaceae* to *Hymenochaetales*. Taking morphological characters and unpublished nLSU-based phylogenetic analyses into consideration, Parmasto (2010) indicated *Clavariachaetaceae* is closely related to *Hymenochaetaceae*. Morphologically, Miettinen et al. (2019) also considered *Clavariachaetaceae* to be a synonym of *Hymenochaetaceae*. Similarly, *Coltriciaceae* was treated as a synonym of *Hymenochaetaceae* in most papers (He et al. 2019, Wu et al. 2022), whereas a few phylogenetic analyses on the basis of two or three genes did recover *Coltriciaceae* as a separated clade from *Hymenochaetaceae* (Larsson et al. 2006, Wang et al. 2021). Therefore, the independence of *Coltriciaceae* is still debated. *Phellinaceae* Jülich is an illegitimate family name due to being a later homonym (Art. 53.1; Turland et al. 2018). Moreover, *Phellinus* the type genus of *Phellinaceae* is widely accepted to be a member of *Hymenochaetaceae* (Wu et al. 2022).

Fiasson & Niemelä (1984) erected a new family *Inonotaceae* and also accepted three additional families, viz. *Hymenochaetaceae*, *Phaeolaceae* and *Phellinaceae* in *Hymenochaetales*. Although *Inonotaceae* was accepted by some papers, its monophyly was first rejected by Wagner & Fischer (2001), which was confirmed by later phylogenetic analyses (e.g., Zhou 2015, Wu et al. 2022). In addition, *Inonotus* the type genus of *Inonotaceae* is widely accepted to be a member of *Hymenochaetaceae* (Wu et al. 2022), which makes *Inonotaceae* a later synonym of *Hymenochaetaceae*. *Phaeolaceae* was originally erected in *Phaeolales* by Jülich (1981). Although the type genus *Phaeolus* shares certain morphological characters and chemical compounds with members of *Hymenochaetales*, the substance causing brown rot of wood makes it distinct from others (Fiasson & Niemelä 1984). More importantly, Wagner & Fischer (2001) for the first time revealed the separation of *Phaeolus* from *Hymenochaetales* from the phylogenetic perspective, and thus *Phaeolaceae* was excluded from *Hymenochaetales*.

Asterodontaceae was erected according to the distinct morphological characters of its type genus *Asterodon* in *Hymenochaetales* (Parmasto 2000); however, later phylogenetic analysis

rejected the separation of *Asterodon* from its original family *Hymenochaetaceae* (Larsson et al. 2006) and thus *Asterodontaceae* is accepted to be a synonym of *Hymenochaetaceae*.

Repetobasidiaceae, *Schizoporaceae* and *Tubulicrinaceae* are three additional families newly introduced by Jülich (1981), who placed them outside *Hymenochaetales*. When revisiting the classification of corticioid fungi, besides *Hymenochaetaceae*, Larsson (2007b) accepted *Schizoporaceae* and *Tubulicrinaceae* in *Hymenochaetales*. In addition, *Repetobasidium* the type genus of *Repetobasidiaceae* was treated as a member of the so-called *Rickenella* family in *Hymenochaetales* (Larsson 2007b). This treatment means to place *Repetobasidiaceae* being equivalent to the *Rickenella* family in *Hymenochaetales*, even though not clearly stated (Larsson 2007b). Maybe due to the misleading treatment of *Repetobasidiaceae* by Larsson (2007b), Vizzini (2010) formally erected a new family *Rickenellaceae* equivalent to the *Rickenella* family sensu Larsson (2007b), which makes *Rickenellaceae* as a superfluous name in the case that its circumscription inappropriately includes *Repetobasidium* the type genus of a prior family name *Repetobasidiaceae* (Art. 52.4; Turland et al. 2018). Until recently, *Repetobasidium* was excluded from the *Rickenella* family sensu Larsson (2007b), and thus both *Repetobasidiaceae* and *Rickenellaceae* should be independent families within *Hymenochaetales* (Olariaga et al. 2020).

Zmitrovich & Malysheva (2014) erected a new family *Oxyporaceae* in *Hymenochaetales*, which was widely adopted by subsequent papers referring to *Hymenochaetales* (Ariyawansa et al. 2015, Zhou et al. 2018, He et al. 2019, Wang et al. 2021, Wijayawardene et al. 2022). Of these papers, Ariyawansa et al. (2015) erected a new family *Neoantrodidiellaceae* in *Hymenochaetales*, and also accepted *Hymenochaetaceae*, *Oxyporaceae*, *Schizoporaceae* and *Tubulicrinaceae* as families in *Hymenochaetales*. Zhou et al. (2018) further moved *Nigrofomitaceae* from *Polyporales* to *Hymenochaetales*, but omitted *Tubulicrinaceae* compared with Ariyawansa et al. (2015). He et al. (2019) also omitted *Tubulicrinaceae*, and accepted six families, viz. *Hymenochaetaceae*, *Neoantrodidiellaceae*, *Nigrofomitaceae*, *Oxyporaceae*, *Schizoporaceae* and *Rickenellaceae* in *Hymenochaetales*. According to multilocus-based phylogenetic analyses with a biased sampling to *Schizoporaceae*, Wang et al. (2021) segregated *Chaetoporellaceae* originally erected by Jülich (1981) and a new family *Hyphodontiaceae* from *Schizoporaceae*, and also accepted the independence of *Coltriciaceae* from *Hymenochaetaceae*. Besides, *Neoantrodidiellaceae*, *Nigrofomitaceae* and *Oxyporaceae* were also accepted in *Hymenochaetales* by Wang et al. (2021). The latest outline of *Fungi* and fungus-like taxa (Wijayawardene et al. 2022), following He et al. (2019) and obviously omitting the taxonomic changes of *Hymenochaetales* proposed by Wang et al. (2021), gathered *Hymenochaetaceae*, *Neoantrodidiellaceae*, *Nigrofomitaceae*, *Oxyporaceae*, *Schizoporaceae* and *Rickenellaceae* in *Hymenochaetales*.

In summary, at the family level the classification of *Hymenochaetales* has been continually emended especially in the past fifteen years and a total of 14 family names have been successively applied in this order (Fig. 1). However, for now, the families being accommodated by *Hymenochaetales* are still contrary in different papers (Fig. 1). In addition, the delimitations of certain families are not fully resolved. For example, the monophyly of *Neoantrodidiellaceae* accommodating four genera, viz. *Cyanotrampa*, *Fibricium*, *Neoantrodidiella* and *Poriodontia* sensu Ariyawansa et al. (2015) was rejected in the phylogeny of Wang et al. (2021), and was also not accepted by He et al. (2019); even if excluding *Repetobasidium*, the monophyly of *Rickenellaceae* sensu He et al. (2019) is still never well confirmed (Korotkin et al. 2018, Olariaga et al. 2020, Wang et al. 2021); whether *Oxyporaceae* should be a monotypic family as stated when its erection (Zmitrovich & Malysheva 2014) and accepted by He et al. (2019), or also accommodate *Leucophellinus* as indicated in the phylogeny of Ariyawansa et al. (2015) and *Bridgeoporus* as that in Wang et al. (2021) needs to be further determined; and whether *Tubulicrinaceae* should be an independent family in *Hymenochaetales* (Larsson 2007b, Ariyawansa et al. 2015) or its type genus *Tubulicrinis* be treated as a member of *Hymenochaetaceae* (He et al. 2019) needs to be clarified.

At the genus level, about 20 genera have never been placed in any family in *Hymenochaetales* (He et al. 2019, Wu et al. 2021, Yu et al. 2021). Whether these genera can be

placed in known families, newly erected families or uncertain positions at the family level in *Hymenochaetales* also needs to be determined.

In this study, the taxonomic framework of *Hymenochaetales* is updated with the help of phylogenetic and molecular clock analyses based on six to seven gene regions. In addition, the taxonomic status of certain genera is accordingly clarified.

Materials & Methods

Vouchers and morphology

Specimens studied are preserved at the Fungarium, Institute of Microbiology, Chinese Academy of Sciences (HMAS), Beijing, China. To assist species identification, macromorphological and micromorphological characters were examined with the help of a Leica M 125 stereomicroscope (Wetzlar, Germany) at magnifications up to 100× and an Olympus BX43 light microscope (Tokyo, Japan) at magnifications up to 1000×, respectively, following Wang et al. (2020).

Molecular sequencing

Crude DNA was extracted from basidiomes of dry specimens using FH Plant DNA Kit (Beijing Demeter Biotech Co., Ltd., Beijing, China), and then directly used as template for PCR amplifications. The primer pairs PNS1/NS41 (Hibbett 1996), ITS1F/ITS4 (Gardes & Bruns 1993), LR0R/LR7 (Vilgalys & Hester 1990), MS1/MS2 (White et al. 1990), EF1-526F/EF1-1567R and EF1-983F/EF1-1953R (Rehner & Buckley 2005, Matheny et al. 2007), RPB1-Af/RPB1-Cr (Matheny et al. 2002), and fRPB2-5F/fRPB2-7cR (Liu et al. 1999) and bRPB2-6F/bRPB2-7.1R (Matheny 2005) were selected for amplifying nSSU, ITS, nLSU, mt-SSU, *tefla*, *rpb1* and *rpb2* regions, respectively. The PCR procedures were as follows: for nSSU and mt-SSU regions, initial denaturation at 94 °C for 3 min, followed by 34 cycles at 94 °C for 40 s, 55 °C for 45 s and 72 °C for 1 min, and a final extension at 72 °C for 10 min; for ITS region, initial denaturation at 95 °C for 3 min, followed by 34 cycles at 94 °C for 40 s, 57.2 °C for 45 s and 72 °C for 1 min, and a final extension at 72 °C for 10 min; for nLSU region, initial denaturation at 94 °C for 1 min, followed by 34 cycles at 94 °C for 30 s, 47.2 °C for 1 min and 72 °C for 1.5 min, and a final extension at 72 °C for 10 min; for *tefla*, *rpb1* and *rpb2* regions, initial denaturation at 94 °C for 2 min, followed by 9 cycles at 94 °C for 40 s, 60 °C for 40 s and 72 °C for 2 min and 36 cycles at 94 °C for 45 s, 55 °C for 1.5 min and 72 °C for 2 min, and a final extension at 72 °C for 10 min. The PCR products were sequenced with the same primers in PCR amplifications at the Beijing Genomics Institute, Beijing, China. All newly generated sequences were deposited in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>; Table 1).

Phylogenetic analysis

Besides the newly generated sequences for this study, additional related sequences downloaded from GenBank (Table 1) were also incorporated in four datasets for phylogenetic analyses.

Dataset 1 with a combination of nSSU, ITS, nLSU, *tefla*, *rpb1* and *rpb2* regions was used to determine the monophyly of *Hymenochaetales* within *Agaricomycetes*. The representative taxa from all main lineages in *Hymenochaetales* and other main orders in *Agaricomycetes* listed in Table 1 were included as ingroup taxa. *Calocera cornea* and *Dacryopinax spathularia* from *Dacrymycetes* were also included as additional ingroup taxa, while *Bullera alba* and *Dioszegia antarctica* from *Tremellomycetes* were selected as outgroup taxa following He et al. (2019).

Dataset 2 with a combination of nSSU, ITS, nLSU, mt-SSU, *tefla*, *rpb1* and *rpb2* regions was used to explore the phylogenetic relationships among members in *Hymenochaetales* at the family and genus levels. All taxa in *Hymenochaetales* listed in Table 1 (but only holotypes for *Schizocortium magnosporum*, *S. mediosporum* and *S. parvisporum*) were included as ingroup taxa. *Fomitopsis pinicola* and *Grifola frondosa* from *Polyporales* were also included as additional

ingroup taxa, while *Boletopsis leucomelaena* and *Thelephora ganbajun* from *Thelephorales* were selected as outgroup taxa following Hibbett et al. (2007). Considering the uneven availability of *tefla*, *rpb1* and *rpb2* regions among different taxa in this dataset, the sub-dataset 2.1 excluding these three gene regions was chosen to further verify the accuracy of topology resulting from dataset 2. Moreover, the ITS and nLSU regions, commonly treated as fungal barcoding sequences, were also, respectively, used as sub-datasets 2.2 and 2.3 to test the topology robustness.

Dataset 3 with a combination of ITS, nLSU and *tefla* regions was used to explore the species identity in *Schizocorticium* and *Skvortzoviella*. All taxa in these two genera listed in Table 1 were included as ingroup taxa, while *Xylodon heterocystidiatus* was selected as an outgroup taxon following Wu et al. (2021).

Dataset 4 with a combination of nSSU, ITS, nLSU, *tefla*, *rpb1* and *rpb2* regions was used for estimating divergence times of taxa within *Hymenochaetales*. The representative taxa from all main lineages in *Hymenochaetales* and other main orders in *Agaricomycetes* listed in Table 1, were included as ingroup taxa. *Calocera cornea* and *Dacryopinax spathularia* from *Dacrymycetes* were also included as additional ingroup taxa, while *Neurospora crassa* from *Ascomycota* was selected as an outgroup taxon following Wang et al. (2021).

Each gene region in these datasets was separately aligned using MAFFT v.7.110 (Katoh & Standley 2013) under the “G-INS-i” option (Katoh et al. 2005). All gaps were reserved as the fifth character due to their critical role in delimiting taxa at the higher taxonomic level. Then, corresponding to the datasets the alignments were concatenated as four combined alignments (Supplementary files 1–4). In addition, the alignment of the sub-dataset 2.1 was also concatenated for phylogenetic analyses along with alignments of the other two sub-datasets (Supplementary files 2.1–2.3). jModelTest v.2.1.10 (Darriba et al. 2012, Guindon & Gascuel 2003) with calculation under Akaike information criterion was used to estimate the best-fit evolutionary model for each alignment resulting from datasets 1–4 and sub-datasets 2.1–2.3. Maximum likelihood (ML) and Bayesian inference (BI) algorithms were utilized for phylogenetic analyses of the alignments resulting from datasets 1–3 and sub-datasets 2.1–2.3. The ML algorithm was performed using raxmlGUI v.1.2 (Silvestro & Michalak 2012, Stamatakis 2006) with the calculation of bootstrap (BS) replicates under the auto FC option (Pattengale et al. 2010). The BI algorithm was performed using MrBayes v.3.2 (Ronquist et al. 2012). Two independent runs were employed, each run including four chains and starting from random trees. Trees were sampled every 1,000th generation, and the first 25% of the sampled trees were removed, while the other 75% were retained for constructing a 50% majority consensus tree and calculating Bayesian posterior probabilities (BPPs). Tracer v.1.5 (<http://tree.bio.ed.ac.uk/software/tracer/>) was used to judge whether chains converged.

BEAST v2.6.0 (Bouckaert et al. 2019) was used to perform molecular clock analysis for the combined alignment resulted from dataset 4. The lognormal relaxed molecular clock model and the Yule speciation prior were selected to evaluate the divergence times and their corresponding credibility intervals. Three time points were set for calibration: (1) the offset age with a Gamma distribution prior (scale = 20, shape = 1) for *Agaricales*: 90 million years ago (Mya) indicated by the minimum age of *Archaeomarasmius leggetti*, a fossil agaricoid species preserved in Dominican amber (Hibbett et al. 1995, 1997); (2) the mean age with a normal distribution prior (standard deviation [SD] = 1) for *Agaricomycetes*: 290 Mya indicated by the mean age of *Agaricomycetes* from genome analyses (Floudas et al. 2012); and (3) the offset age with a Gamma distribution prior (scale = 20, shape = 1) for *Basidiomycota*: 400 Mya indicated by the divergence time between *Ascomycota* and *Basidiomycota* from *Paleopyrenomycites devonicus*, a fossil fungus found in Great Britain (Berbee & Taylor 2010, Floudas et al. 2012). Trees were sampled every 1,000th generation from a total of 200 million generations with the first 10% of the sampled trees as burn-in. The resulting log file was used to judge whether chains converged using Tracer v.1.5.

Table 1 Information of taxa used in phylogenetic and molecular clock analyses.

Phylum/Class/Order/Family	Species	Voucher	nSSU	ITS	nLSU	mt-SSU	<i>tefla</i>	<i>rpb1</i>	<i>rpb2</i>
Ascomycota/Sordariomycetes/ Sordariales/Sordariaceae	<i>Neurospora crassa</i>	OR74A		HQ271348	AF286411		XM959775		AF107789
Basidiomycota/Agaricomycetes/ Agaricales/Hymenogastraceae	<i>Gymnopilus picreus</i>	ZRL2015011	KY418948	LT716066	KY418882		KY419077	KY418980	KY419027
-/-/Lyophyllaceae	<i>Asterophora lycoperdoides</i>	CBS 170.86	DQ367417	AF357037	AF223190		DQ367424	EF421021	DQ367431
-/-/Marasmiaceae	<i>Marasmius oreades</i>	ZRL2015086	KY418930	LT716048	KY418864		KY419066	KY418972	KY419010
-/-/Psathyrellaceae	<i>Psathyrella candolleana</i>	ZRL20151400	KY418945	LT716063	KY418879		KY419075	KY418978	KY419024
-/-/Amylocorticiales/ Amylocorticiaceae	<i>Amylocorticium cebennense</i>	HHB-2808	GU187612	GU187505	GU187561		GU187675	GU187439	GU187770
	<i>Anomoloma myceliosum</i>	MJL-4413	GU187614	GU187500	GU187559		GU187677	GU187441	GU187766
	<i>Podoserpula ailaoshanensis</i>	ZJL2015015	KU324491	KU324484	KU324487		KU324494		
-/-/Atheliales/Atheliaceae	<i>Athelia arachnoidea</i>	CBS 418.72	GU187616	GU187504	GU187557		GU187672	GU187436	GU187769
	<i>Leptosporomyces raunkiaerii</i>	HHB-7628	GU187640	GU187528	GU187588		GU187471	GU187791	GU187791
	<i>Piloderma fallax</i>	S-12	GU187644	GU187535	GU187591		GU187738		GU187797
-/-/Auriculariales/ Auriculariaceae	<i>Auricularia heimuer</i>	Xiaoheimao		LT716074	KY418890		KY419083		KY419035
	<i>Exidia sp.</i>	PBM2527		DQ241774	AY700191		DQ408144		
-/-/Boletales/Coniophoraceae	<i>Coniophora arida</i>	FP104367	GU187622	GU187510	GU187573		GU187684	GU187445	GU187775
-/-/Gomphidiaceae	<i>Gomphidius roseus</i>	MB 95-038	DQ534682	DQ534570	DQ534669		GU187702	GU187459	GU187818
-/-/Hygrophoropsidaceae	<i>Leucogyrophana lichenicola</i>	DAOM194172	GU187638	GU187531	GU187583		GU187715	GU187467	GU187789
-/-/Serpulaceae	<i>Serpula lacrymans</i>	REG-383	GU187649	GU187542	GU187596		GU187752	GU187485	GU187809
-/-/Cantharellales/Hydniaceae	<i>Multiclavula mucida</i>	AFTOL 1130	DQ521416	DQ521417	AY885163				
	<i>Hydnum albomagnum</i>	AFTOL 471	AY665777	DQ218305	AY700199		DQ234568	DQ234570	DQ234553
	<i>Sistotrema coronilla</i>	AFTOL 618	AY757259	DQ397337	DQ457641				DQ381838
-/-/Corticiales/Corticiaceae	<i>Corticium roseum</i>	MG 46		GU590877	AY463401				
	<i>Erythricium laetum</i>	MG 73		GU590874	GU590879				
-/-/Punctulariaceae	<i>Punctularia strigosozonata</i>	AFTOL 1248	AF518586	DQ398958	AF518642		DQ408147	DQ831031	DQ381843
-/-/Geastrales/Geastraceae	<i>Schenella pityophilus</i>	OSC59743			DQ218519	DQ218694	DQ219232		DQ219057
	<i>Geasteroides taylorii</i>	OSC59760			DQ218520		DQ219235		DQ219060

Table 1 Continued.

Phylum/Class/Order/Family	Species	Voucher	nSSU	ITS	nLSU	mt-SSU	<i>tefla</i>	<i>rpb1</i>	<i>rpb2</i>
-/-/Gloeophyllales/ Gloeophyllaceae	<i>Gloeophyllum</i> <i>trabeum</i>	1320	HM536068	HM536094	HM536067		HM536113		HM536112
	<i>Osmoporus</i> <i>protractum</i>	H-80	HM536060	HM536090	HM536059		HM536108		HM536107
-/-/Jaapiaceae -/-/Incertae sedis	<i>Jaapia argillacea</i>	CBS 252.74	AF518581	GU187524	GU187581		GU187711	GU187463	GU187788
	<i>Paratrichaptum</i> <i>accuratum</i>	GC 1708-180	LC473736	LC473732	LC473734		LC473742	LC473738	LC473740
-/-/Gomphales/ Clavariadelphaceae	<i>Clavariadelphus</i> <i>truncatus</i>	OSC67280			AY574649		DQ219240		DQ219064
	<i>Kavinia alboviridis</i>	O102140			AY574692		DQ219250		DQ219073
-/-/Lentariaceae -/-/Hymenochaetales/ Chaetoporellaceae	<i>Echinoporia</i> <i>hydnohpora</i>	LWZ 20150802- 9	ON063768	ON063639	ON063838	ON063707		ON100735	
	<i>Kneiffiella</i> <i>eucalypticola</i>	LWZ 20180509- 11		MT319410	MT319142	MT326421			
	<i>Kneiffiella subglobosa</i>	LWZ 20180416- 6		MT319413	MT319145	MT326422			
	<i>Basidioradulum mayi</i>	LWZ 20180510- 18	ON427363	MN017785	MN017792	ON463756		ON456063	ON456070
-/-/Hymenochaetaceae	<i>Basidioradulum</i> <i>radula</i>	LWZ 20201017- 62	ON063814	ON063684	ON063884	ON063747	ON089691	ON100770	ON100713
	<i>Coltricia abieticola</i>	Cui 10321	KY693761	KX364785	KX364804	KY693823	KY693911	KX364828	KX364876
	<i>Coltricia perennis</i>	AFTOL-447		DQ234559	AF287854		AY885147		AY218526
	<i>Coltricia weii</i>	LWZ 20190811- 1b		ON063641	ON063840	ON063709	ON089689	ON100737	ON100684
	<i>Coltricia</i> sp.	LWZ 20210626- 3b	ON063770	ON063642	ON063841	ON063710	ON089688	ON100738	
	<i>Coniferiporia</i> <i>qilianensis</i>	Dai 13320		MT420707	MT416471	MT386051	MT470372	MT376013	
	<i>Coniferiporia</i> <i>sulphurascens</i>	FP-134848-SP		MT420687	MT416462	MT386065	MT470375	MT376016	
	<i>Coniferiporia weirii</i>	FP-134599-SP		MT420695	MT416461	MT386053	MT470379	MT376001	
	<i>Coniferiporia</i> <i>uzbekistanensis</i>	LWZ 20160909- 7		MT420709	MT416472	MT386049	MT470377		
	<i>Cyanotrampa gypsea</i>	Cui 10372			KT203290	MT319396	MT326567		KT210367
<i>Cyanotrampa rimosa</i>	MG56			GU566010	GU566003				
<i>Cyanotrampa thujae</i>	Dai 5065			KT203293	MT319397	MT326568		KT210368	

Table 1 Continued.

Phylum/Class/Order/Family	Species	Voucher	nSSU	ITS	nLSU	mt-SSU	<i>tefla</i>	<i>rpb1</i>	<i>rpb2</i>
	<i>Cyanotrampa</i> sp.	LWZ 20180906-5	ON427364	ON427469	ON427351	ON463757			ON456071
	<i>Cyanotrampa</i> sp.	LWZ 20180906-6	ON427365	ON427470	ON427352	ON463758		ON456064	ON456072
	<i>Fibricium rude</i>	CBS 339.66		MH858815	MH870454				
	<i>Fomitiporia aethiopica</i>	MUCL 44777		GU478341	AY618204		GU461893		JQ087956
	<i>Fomitiporia gabonensis</i>	MUCL 47576		GU461971	GU461990		GU461923		JQ087972
	<i>Fomitiporia mediterranea</i>	AFTOL-688		AY854080	AY684157		AY885149		AY803748
	<i>Fomitiporia rhamnoides</i>	LWZ 20180905-15		ON063643	ON063842	ON063711	ON089672	ON100739	
	<i>Fomitiporia sonora</i>	MUCL 47689		JQ087893	JQ087920		JQ087947		JQ088006
	<i>Fulvoderma australe</i>	LWZ 20190809-39b	ON063771	ON063644	ON063843	ON063712		ON100740	ON100686
	<i>Fulvoderma scaurum</i>	LWZ 20170816-31		ON063645	ON063844	ON063713			
	<i>Fulvoderma</i> sp.	LWZ 20210626-12b	ON063772	ON063646	ON063845	ON063714	ON089673	ON100741	ON100687
	<i>Fuscoporia acutimarginata</i>	Dai 15137		MH050751	MH050765		MN848821		MN159384
	<i>Fuscoporia ferruginosa</i>	LWZ 20180927-2	ON063774		ON063847	ON063716		ON100743	ON100689
	<i>Fuscoporia gilva</i>	LWZ 20190814-19b	ON063775	ON063648	ON063848	ON063717	ON089686	ON100744	ON100734
	<i>Fuscoporia sinica</i>	LWZ 20190816-19a	ON063776	ON063649	ON427358	ON063719		ON100746	ON100691
	<i>Hydnoporia laricicola</i>	Dai 13458		NR_166380	NG_068765				
	<i>Hydnoporia olivacea</i>	CLA 02-003	AY293134		AY293185	AY293229			
	<i>Hydnoporia tabacina</i>	LWZ 20210924-26a	ON063778	ON063651	ON063851	ON063720	ON089676	ON100747	ON100685
	<i>Hydnoporia tabacinoides</i>	LWZ 20190814-29b	ON063779	ON063652	ON063852	ON063721		ON100748	
	<i>Hymenochaete corrugata</i>	LWZ 20180921-5	ON063780	ON063653	ON063853	ON063722	ON089677	ON100749	

Table 1 Continued.

Phylum/Class/Order/Family	Species	Voucher	nSSU	ITS	nLSU	mt-SSU	<i>tef1a</i>	<i>rpb1</i>	<i>rpb2</i>
	<i>Hymenochaete rubiginosa</i>	LWZ 20201017-32	ON063782	ON063655		ON063724	ON089678	ON100751	ON100698
	<i>Hymenochaete sphaericola</i>	LWZ 20190808-2b	ON063783	ON063656	ON063855	ON063725	ON089679		ON100700
	<i>Hymenochaete xerantica</i>	LWZ 20190814-13b	ON063784	ON063657	ON063856	ON063726	ON089680	ON100752	ON100699
	<i>Inonotus hispidus</i>	LWZ 20180703-1	ON063785	ON063659	ON063858	ON063727	ON089681	ON100753	ON100692
	<i>Nigrofomes melanoporus</i>	JV 1704/39		MF629835	MF629831				
	<i>Nigrofomes sinomelanoporus</i>	Cui 5277		MF629836	MF629832				
	<i>Ochrosporellus puerensis</i>	Dai 12241		OL583991	OL583985				
	<i>Onnia kesiya</i>	Dai 18415		MG397042	MG397043				
	<i>Onnia tomentosa</i>	Cui 10048		MT332141	MT319387	MT326561			
	<i>Phellinopsis conchata</i>	L-7601		KU139188	KU139257		KU139377		KU139315
	<i>Phellinopsis tibetica</i>	LWZ 20190808-31a	ON063788	ON063660	ON063859	ON063730			
	<i>Phellinus piceicola</i>	LWZ 20190921-5	ON063790	ON063662	ON063862	ON063731		ON100754	ON100695
	<i>Phellinus pomaceus</i>	LWZ 20160908-1	ON063792	ON063663	ON063863	ON063732			
	<i>Phylloporia oreophila</i>	LWZ 20190811-27a	ON063793	ON063665	ON063865	ON063733	ON089684		ON100694
	<i>Phylloporia radiata</i>	LWZ 20141122-6	ON063794	ON063666	ON063866		ON089685		
	<i>Phylloporia</i> sp.	LWZ 20171014-13	ON063791	ON063664	ON427359		ON089683		
	<i>Poriodontia subvinosa</i>	Dai 11781		KT203306	KT203327				
	<i>Porodaedalea himalayensis</i>	LWZ 20180903-21	ON063795	ON063667	ON063867	ON063734		ON100755	
	<i>Porodaedalea laricis</i>	LWZ 20190724-9	ON063796	ON063668	ON063868	ON063735		ON100756	ON100693

Table 1 Continued.

Phylum/Class/Order/Family	Species	Voucher	nSSU	ITS	nLSU	mt-SSU	<i>tef1a</i>	<i>rpb1</i>	<i>rpb2</i>
	<i>Sanghuangporus baumii</i>	LWZ 20190722-18	ON063798	ON063670					ON100696
	<i>Sanghuangporus quercicola</i>	LWZ 20170821-18	ON063797	ON063669	ON063869				
	<i>Sanghuangporus weigela</i>	LWZ 20210623-2a	ON063799	ON063671	ON063870	ON063736	ON089687		ON100697
	<i>Trichaptum bifforme</i>	LWZ 20210919-32a	ON063832	ON063701	ON063901	ON063764	ON089702		ON100730
	<i>Trichaptum durum</i>	LWZ 20140622-7	ON063831	ON063700	ON063900				
	<i>Trichaptum fumosoavellaneum</i>	LWZ 20191108-44	ON063833	ON063702	ON063902				ON100731
	<i>Trichaptum fuscoviolaceum</i>	LWZ 20210918-5b	ON063834	ON063703	ON063903	ON063765		ON100784	ON100732
-/-/Hyphodontiaceae	<i>Hyphodontia pachyspora</i>	LWZ 20170908-5		MT319426	MT319160	MT326431		MT326350	MT326261
	<i>Hyphodontia zhixiangii</i>	LWZ 20170818-13		MT319420	MT319151	MT326424	MT326397	MT326361	MT326270
	<i>Hyphodontia</i> sp.	LWZ 20170814-15		MT319417	MT319148	MT326423			MT326269
-/-/Odonticiaceae	<i>Leifia brevispora</i>	LWZ 20170820-48	ON427367	MK343470	MK343474	ON463759			
	<i>Leifia flabelliradiata</i>	KG Nilsson 36270		DQ873635	DQ873635				
	<i>Leifia</i> sp.	LWZ 20171015-38	ON427368	ON427471	ON427354	ON463760			
	<i>Odonticium romellii</i>	KHL s. n.		DQ873639	DQ873639				
-/-/Peniophorellaceae	<i>Peniophorella crystallifera</i>	LWZ 20210626-4a	ON063815	ON063685	ON063885	ON063748		ON100771	
	<i>Peniophorella praetermissa</i>	LWZ 20180903-14	ON063816	ON063686	ON063886	ON063749	ON089699		ON100714
	<i>Peniophorella pubera</i>	LWZ 20210624-16b	ON063817	ON063687	ON063887	ON063750		ON100772	ON100715
	<i>Peniophorella rude</i>	LWZ 20171026-7	ON063818	ON063688	ON063888	ON063751	ON089692	ON100773	ON100716

Table 1 Continued.

Phylum/Class/Order/Family	Species	Voucher	nSSU	ITS	nLSU	mt-SSU	<i>tef1a</i>	<i>rpb1</i>	<i>rpb2</i>
-/-/Repetobasidiaceae	<i>Peniophorella subpraetermissa</i>	LWZ 20190816-3b	ON063819	ON063689	ON063889	ON063752		ON100774	ON100717
	<i>Repetobasidium conicum</i>	KHL 12338	DQ873646	DQ873647	DQ873647				
	<i>Repetobasidium mirificum</i>	FP-133558-sp	AY293155		AY293208	AY293243			
-/-/Resiniaceae	<i>Resinicium austroasianum</i>	LWZ 20191208-11	ON063821	ON063691	ON063891	ON063753	ON089694	ON100776	ON100720
	<i>Resinicium bicolor</i>	AFTOL-810		DQ218310	AF393061		DQ061277		DQ457635
	<i>Resinicium friabile</i>	LWZ 20210923-23a	ON063822	ON063692	ON427362	ON063754	ON089695	ON100777	ON100719
-/-/Rickenellaceae	<i>Rickenella danxiashanensis</i>	GDGM45513	ON063823	MF326424		ON063755	ON089700		ON100721
	<i>Rickenella fibula</i>	PBM 2503	MF319021	DQ241782	MF318953		DQ435794	DQ832204	DQ408115
-/-/Rigidoporaceae	<i>Bridgeoporus sinensis</i>	Cui 10013		KY131832	KY131891				
	<i>Leucophellinus hobsonii</i>	Cui 6468		KT203288	KT203309	KT203330			KT210365
	<i>Leucophellinus irpicoides</i>	Yuan 2690		KT203289	KT203310	KT203331			KT210366
	<i>Rigidoporus cirratus</i>	LWZ 20170818-16	ON427369	ON427472	ON427355	ON463761		ON456065	ON456073
	<i>Rigidoporus corticola</i>	LWZ 20190819-3b	ON063801	ON063673	ON063872	ON063738			
	<i>Rigidoporus cuneatus</i>	LWZ 20190819-5a	ON063802		ON063873	ON063739		ON100758	ON100701
	<i>Rigidoporus ginkgonis</i>	Cui 5555		KT203295	KT203316	KT203336			KT210371
	<i>Rigidoporus millavensis</i>	Wei 1622		KT203300	KT203321	KT203340			KT210375
	<i>Rigidoporus populinus</i>	LWZ 20190811-39a	ON063803	ON063674	ON063874	ON063740		ON100759	ON100702
	<i>Rigidoporus</i> sp.	LWZ 20170815-52	ON427370	ON427473	ON427356	ON463762	ON456060	ON456066	ON456074
-/-/Schizocorticiaceae	<i>Schizocorticium lenis</i>	LWZ 20180921-7	ON063827	ON063696	ON063896	ON063760		ON100782	ON100726

Table 1 Continued.

Phylum/Class/Order/Family	Species	Voucher	nSSU	ITS	nLSU	mt-SSU	<i>tefla</i>	<i>rpb1</i>	<i>rpb2</i>
		LWZ 20180921-17	ON427371	MW414522	MW414468	ON463763		ON456067	ON456075
		LWZ 20180921-25	ON427372	MW414523	MW414469			ON456068	ON456076
		LWZ 20180921-32	ON427373	MW414524	MW414470		ON456061		ON456077
		LWZ 20180922-39	ON427374	MW414525	MW414471	ON463764	ON456062	ON456069	ON456078
		LWZ 20180922-61	ON063829	ON063698	ON063898	ON063762		ON100781	ON100728
		LWZ 20191203-1	ON063830	ON063699	ON063899	ON063763			ON100729
		LWZ 20210919-37a	ON063828	ON063697	ON063897	ON063761	ON089701	ON100783	ON100727
	<i>Schizocorticium magnosporum</i>	GC 1703-9		MK405352	MK405338		LC567449		
		Wu 1510-32		MK405353	MK405339		LC567448		
		Wu 1510-34		MK405351	MK405337		LC567450		
	<i>Schizocorticium mediosporum</i>	Chen 2229		MK405356	MK405342		LC567438		
		Chen 2373		MK405357	MK405343		LC567439		
		Chen 2421		MK405355	MK405341		LC567440		
		Chen 2456		MK405359	MK405345		LC567441		
		Chen 2488		MK405354	MK405340		LC567442		
		Chen 2583		MK405358	MK405344		LC567443		
		Chen 2922		MK405360	MK405346		LC567444		
	<i>Schizocorticium parvisporum</i>	GC 1508-127		MK405361	MK405347		LC567445		
		GC 1609-16		MK405362	MK405348		LC567446		
		WEI 16-282		MK405363	MK405349		LC567447		
		MSK-F 7245a		MK575201	MK598734				
-/-/Schizoporaceae	<i>Fasciodontia brasiliensis</i>								
	<i>Fasciodontia yunnanensis</i>	LWZ 20190811-50a	ON063804	ON063675	ON427360	ON063741		ON100760	ON100704
	<i>Fasciodontia</i> sp.	LWZ 20201011-37	ON063805	ON063676	ON427361	ON063742	ON089690	ON100761	ON100705

Table 1 Continued.

Phylum/Class/Order/Family	Species	Voucher	nSSU	ITS	nLSU	mt-SSU	<i>tefla</i>	<i>rpb1</i>	<i>rpb2</i>
	<i>Fasciodontia</i> sp.	KUC 20121109-15		KJ668516	KJ668368				
	<i>Lyomyces crustosus</i>	LWZ 20170815-23		MT319465	MT319201	MT326446	MT326400	MT326313	MT326275
	<i>Lyomyces leptocystidiatus</i>	LWZ 20170814-14		MT319429	MT319163	MT326512	MT326395	MT326341	MT326256
	<i>Lyomyces sambuci</i>	LWZ 20180905-1	ON063807	MT319444	MT319178	MT326438	MT326391	ON100763	MT326291
	<i>Lyomyces</i> sp.	LWZ 20180906-20	ON063808	ON063678	ON063878	ON063743		ON100764	ON100707
	<i>Xylodon heterocystidiatus</i>	WEI 17-314		MT731753	MT731754		LC567451		
	<i>Xylodon nesporii</i>	LWZ 20190814-17a	ON063809	ON063679	ON063879			ON100765	ON100708
	<i>Xylodon ovisporus</i>	LWZ 20190817-6b	ON063810	ON063680	ON063880	ON063744		ON100766	ON100709
	<i>Xylodon rimosissimus</i>	LWZ 20180904-28	ON063812	ON063682	ON063882	ON063745		ON100768	ON100711
	<i>Xylodon serpentiformis</i>	LWZ 20190816-12a	ON063813	ON063683	ON063883	ON063746		ON100769	ON100712
-/-/Sideraceae	<i>Sidera lenis</i>	Miettinen 11036		FN907914	FN907914				
	<i>Sidera minutipora</i>	Cui 16720	MW418078	MN621349	MN621348	MW424986	MW446248	MW526261	MW505865
	<i>Sidera srilankensis</i>	Dai 19654	MW418087	MN621344	MN621346	MW424989	MW427602		MW505868
	<i>Sidera tenuis</i>	Dai 18697	MW418083	MK331865	MK331867	MW424988	MW427600	MW526264	MW505866
	<i>Sidera vulgaris</i>	Dai 21057	MW418090	MW198484	MW192009	MW424987	MW427603		MW505869
-/-/Skvortzoviaceae	<i>Skvortzovia dabieshanensis</i>	LWZ 20210918-15b	ON063825	ON063694	ON063894	ON063757	ON089696	ON100779	ON100723
	<i>Skvortzovia pinicola</i>	LWZ 20210623-18b	ON063826	ON063695	ON063895	ON063758		ON100780	ON100724
	<i>Skvortzovia qilianensis</i>	LWZ 20180904-20	ON063824	ON063693	ON063893	ON063756		ON100778	ON100722
	<i>Skvortzovia yunnanensis</i>	CLZhao 16084		MW472754	MW473473	ON063759	ON089697		ON100725
-/-/Tubulicrinaceae	<i>Tubulicrinis calothrix</i>	LWZ 20210919-1b	ON063835	ON063704	ON063904	ON063766			ON100733

Table 1 Continued.

Phylum/Class/Order/Family	Species	Voucher	nSSU	ITS	nLSU	mt-SSU	<i>tef1a</i>	<i>rpb1</i>	<i>rpb2</i>
	<i>Tubulicrinis glebulosus</i>	LWZ 20180903-13	ON063836	ON063705	ON063905		ON089698	ON100785	
	<i>Tubulicrinis subulatus</i>	LWZ 20190914-7	ON063837	ON063706	ON063906	ON063767			
-/-/Incertae sedis	<i>Alloclavaria purpurea</i>	M. Korhonen 10305	MF318986	MF319044	MF318895				
	<i>Atheloderma mirabile</i>	TAA 169235		DQ873592	DQ873592				
	<i>Blasiphalia pseudogrisella</i>	P. Joijer 4118	MF318989	MF319047	MF318898				
	<i>Bryopistillaria sagittiformis</i>	IO.14.164		MT232349	MT232303				MT242333
	<i>Cantharellopsis prescotii</i>	H6059300	MF318993	MF319051	MF318903				MF288855
	<i>Contumyces rosellus</i>	MGW 1462	MF319001	MF319059	MF318912				MF288859
	<i>Contumyces vesuvianus</i>	203608	MF319002		MF318913				MF288860
	<i>Cotylidia</i> sp.	AFTOL-700	AY705958	AY854079	AY629317	FJ436111	AY885148	AY864868	AY883422
	<i>Ginnsia viticola</i>	Wu 0010-29		MN123802	GQ470670				
	<i>Globulicium hiemale</i>	Hjm 19007		DQ873595	DQ873595				
	<i>Gyroflexus brevibasidiata</i>	IO.14.230		MT232351	MT232305				MT242335
	<i>Hastodontia halonata</i>	HHB-17058		MK575207	MK598738				
	<i>Hastodontia hastata</i>	KHL 14646		MH638232	MH638232				
	<i>Lawrynomyces capitatus</i>	KHL 8464		DQ677491	DQ677491				
	<i>Loreleia marchantiae</i>	Lutzoni 930826-1		U66432	U66432				
	<i>Lyoathelia laxa</i>	Spirin 8810a		MT305998	MT305998				
	<i>Muscinupta laevis</i>	V. Haikonen 19745	MF319004	MF319066	MF318921				MF288861
	<i>Sphaerobasidium minutum</i>	KHL 11714		DQ873652	DQ873653				
	<i>Tsugacorticium kenaicum</i>	CFMR HHB17347	JN368234		JN368221	JN368203			
-/-/Hysterangiales/ Hysterangiaceae	<i>Aroramyces gelatinosporus</i>	H4010			DQ218524		DQ219118		DQ218941

Table 1 Continued.

Phylum/Class/Order/Family	Species	Voucher	nSSU	ITS	nLSU	mt-SSU	<i>tefla</i>	<i>rpb1</i>	<i>rpb2</i>
-/-/Mesophelliaceae	<i>Chondrogaster pachysporus</i>	OSC49298			DQ218538		DQ219136		DQ218958
-/-/Phallales/Claustulaceae	<i>Gelopellis</i> sp.	H4397			DQ218630		DQ219269		DQ219090
-/-/Phallaceae	<i>Phallus hadriani</i>	AFTOL 683	AY771601	DQ404385	AY885165		DQ435792		DQ408114
-/-/Polyporales/Polyporaceae	<i>Polyporus squamosus</i>	Cui 10595	KU189840	KU189778	KU189809		KU189925	KU189892	KU189988
-/-/Fomitopsidaceae	<i>Fomitopsis pinicola</i>	AFTOL 770	AY705967	AY854083	AY684164		AY885152	AY864874	AY786056
-/-/Grifolaceae	<i>Grifola frondosa</i>	AFTOL 701	AY705960	AY854084	AY629318		AY885153	AY864876	AY786057
-/-/Meruliaceae	<i>Climacodon septentrionalis</i>	ZW	AY705964	AY854082	AY684165		AY885151	AY864872	AY780941
-/-/Russulales/Bondarzewiaceae	<i>Heterobasidion annosum</i>	06129/6		KJ583211	KJ583225		KX252741	KF033133	KF006499
-/-/Echinodontiaceae	<i>Echinodontium tinctorium</i>	DAOM16666		AY854088	AF393056		AY885157	AY864882	AY218482
-/-/Sebacinales/Sebacinaceae	<i>Sebacina</i> sp.	AFTOL 1517	DQ521413	DQ911617	DQ521412				
	<i>Tremellodendron pallidum</i>	AFTOL 699	AY766081	DQ411526	AY745701		DQ029196		DQ408132
-/-/Thelephorales/Bankeraceae	<i>Boletopsis leucomelaena</i>	PBM2678	DQ435797	DQ484064	DQ154112		GU187763	GU187494	GU187820
-/-/Thelephoraceae	<i>Thelephora ganbajun</i>	ZRL20151295	KY418962	LT716082	KY418908		KY419093	KY418987	KY419043
	<i>Tomentella</i> sp.	AFTOL 1016	DQ092920	DQ835998	DQ835997				DQ835999
-/- /Trechisporales/Hydnodontaceae	<i>Subulicystidium daii</i>	LWZ 20170820-35		OM523399	OM339224				
	<i>Trechispora alnicola</i>	AFTOL 665	AY657012	DQ411529	AY635768		DQ059052		DQ408135
-/Dacrymycetes/Dacrymycetales/ Dacrymycetaceae	<i>Calocera cornea</i>	AFTOL 438	AY771610	AY789083	AY701526		AY881019	AY857980	AY536286
	<i>Dacryopinax spathularia</i>	AFTOL 454	AY771603	AY854070	AY701525		AY881020	AY857981	
-/Tremellomycetes/ Tremellales/Bulleraceae	<i>Bullera alba</i>	CBS 501	X60179	AF444368	AF075500		KF037016	KF036334	KF036745
-/-/Cryptococcaceae	<i>Dioszegia antarctica</i>	CBS 10920	KF036667	DQ402529	FJ640575		KF037129	KF036444	KF036858

The newly generated sequences are in boldface.

Results

Molecular phylogeny

A total of 74 specimens from species belonging to *Hymenochaetales* were newly examined and sequenced. From these specimens, 393 new sequences being composed of 70 nSSU, 63 ITS, 63 nLSU, 63 mt-SSU, 30 *tefla*, 50 *rpb1* and 54 *rpb2* sequences were generated (Table 1).

Dataset 1 included 135 collections and resulted in a combined alignment of 8504 characters. The best-fit evolutionary model for this alignment was estimated as GTR + I + G. The ML search for this alignment stopped after 150 BS replicates. In the BI algorithm, all chains converged after 15 million generations with an average standard deviation of split frequencies of 0.004587, which was indicated by the effective sample sizes (ESSs) of all parameters above 4870 and the potential scale reduction factors (PSRFs) of all parameters equal to 1.000. ML and BI algorithms generated congruent topologies in main lineages. Therefore, the tree generated by the ML algorithm was presented along with BS values above 50% and BPPs above 0.7 at the nodes (Fig. 2). All main lineages at the family and genus level in *Hymenochaetales* closely grouped together as an independent order (BS = 99%, BPP = 1) from other orders within *Agaricomycetes* (BS = 99%, BPP = 1).

Dataset 2 included 149 collections and resulted in a combined alignment of 8248 characters. The best-fit evolutionary model for this alignment was estimated as GTR + I + G. The ML search for this alignment stopped after 150 BS replicates. In the BI algorithm, all chains converged after 15 million generations with an average standard deviation of split frequencies of 0.004951, which was indicated by the ESSs of all parameters above 4660 and the PSRFs of all parameters equal to 1.000. ML and BI algorithms generated congruent topologies in main lineages. Therefore, the tree generated by the ML algorithm was presented along with BS values above 50% and BPPs above 0.7 at the nodes (Fig. 3). Within the strongly supported clade of *Hymenochaetales* (BS = 100%, BPP = 1), eight previously known families, viz. *Chaetoporellaceae*, *Hymenochaetaceae*, *Hyphodontiaceae*, *Repetobasidiaceae*, *Rickenellaceae*, *Rigidoporaceae*, *Schizoporaceae* and *Tubulicrinaceae* were recovered. Except for *Hyphodontiaceae* and *Schizoporaceae*, the circumscriptions of six additional families were revised. Moreover, *Leifia*, *Odonticium*, *Peniophorella*, *Resinicium*, *Schizocorticium*, *Sidera* and *Skvortzovia* were placed in six newly erected families, while 17 additional sampled genera were independent from the 14 families. The delimitations of the 14 families and 17 genera also corresponded to the phylogeny inferred from dataset 1 (Fig. 2).

The sub-dataset 2.1 included 149 collections and resulted in a combined alignment of 3623 characters. The best-fit evolutionary model for this alignment was estimated as GTR + I + G. The ML search for this alignment stopped after 250 BS replicates. In the BI algorithm, all chains converged after 15 million generations with an average standard deviation of split frequencies of 0.007433, which was indicated by the ESSs of all parameters above 3279 and the PSRFs of all parameters equal to 1.000. ML and BI algorithms generated congruent topologies in main lineages (Supplementary files 2.4–2.5). The sub-dataset 2.2 included 143 collections and resulted in a combined alignment of 1233 characters. The best-fit evolutionary model for this alignment was estimated as GTR + I + G. The ML search for this alignment stopped after 400 BS replicates. In BI algorithm, all chains converged after 15 million generations with an average standard deviation of split frequencies of 0.029331, which was indicated by the ESSs of all parameters above 2181 and the PSRFs of all parameters close to 1.000. ML and BI algorithms generated congruent topologies in main lineages (Supplementary files 2.6–2.7). The sub-dataset 2.3 included 145 collections and resulted in a combined alignment of 960 characters. The best-fit evolutionary model for this alignment was estimated as GTR + I + G. The ML search for this alignment stopped after 350 BS replicates. In the BI algorithm, all chains converged after 15 million generations with an average standard deviation of split frequencies of 0.010820, which was indicated by the ESSs of all parameters above 1471 and the PSRFs of all parameters equal to 1.000. ML and BI algorithms generated congruent topologies in main lineages (Supplementary files 2.8–2.9). The topologies

generated from the alignments of the sub-datasets 2.1–2.3 were not contrary to that generated from the alignment of dataset 2 in main lineages, but sometimes presented low statistical values (Supplementary files 2.4–2.9).

Dataset 3 included 22 collections and resulted in a combined alignment of 2305 characters. The best-fit evolutionary model for this alignment was estimated as GTR + I. The ML search for this alignment stopped after 300 BS replicates. In the BI algorithm, all chains converged after one million generations with an average standard deviation of split frequencies of 0.008654, which was indicated by the ESSs of all parameters above 1030 and the PSRFs of all parameters close to 1.000. ML and BI algorithms generated congruent topologies in main lineages. Therefore, the tree generated by the ML algorithm was presented along with BS values above 50% and BPPs above 0.7 at the nodes (Fig. 4). While *Schizocorticium magnosporum* occupied a distinct position, the collections of *Skvortzoviella lenis* merged into the clade being composed of *Schizocorticium mediosporum* and *S. parvisporum* (BS = 100%, BPP = 1), and were scattered in the lineages of *S. mediosporum* (BS = 100%, BPP = 1) and *S. parvisporum* (BS = 89%, BPP = 0.78).

Dataset 4 included 124 collections, of which 95 belonged to *Hymenochaetales*. This dataset resulted in a concatenated alignment of 7081 characters with GTR + I + G as the best-fit evolutionary model. Chain convergence was indicated by the ESSs of all parameters above 310. Corresponding to the circumscriptions of families in Fig. 3, the divergence times for the 14 families in *Hymenochaetales* were estimated (Fig. 5). All these times fit well with the range of families in *Basidiomycota* (27–178 Mya, He et al. 2019).

Taxonomy

Hymenochaetales Oberw., in Frey, Hurka & Oberwinkler, Beitr. Biol. Pfl.: 89 (1977).

Type family – *Hymenochaetaceae* Donk, Bull. bot. Gdns Buitenz. 17(4): 474 (1948).

Type genus – *Hymenochaete* Lév., Anns Sci. Nat., Bot., sér. 3 5: 150 (1846).

Type species – *Hymenochaete rubiginosa* (Dicks.) Lév., Anns Sci. Nat., Bot., sér. 3 5: 150 (1846).

Families accepted in this order – *Chaetoporellaceae*, *Hymenochaetaceae*, *Hyphodontiaceae*, *Odonticiaceae*, *Peniophorellaceae*, *Repetobasidiaceae*, *Resiniaceae*, *Rickenellaceae*, *Rigidoporaceae*, *Schizocorticiaceae*, *Schizoporaceae*, *Sideraceae*, *Skvortzoviaceae* and *Tubulicrinaceae*.

Notes – *Hymenochaetales* was originally erected for a single family *Hymenochaetaceae* (Frey et al. 1977). Additional families and genera were successively added to this order (e.g., Jülich 1981, Parmasto 2000, Larsson 2007b, Ghobad-Nejhad & Dai 2010, Vizzini 2010, Miettinen & Larsson 2011, Zmitrovich & Malysheva 2014, Ariyawansa et al. 2015, Zhou et al. 2018, He et al. 2019, Wang et al. 2020, 2021, Wu et al. 2021, Yu et al. 2021, Lima et al. 2022). According to the current molecular evidence (Figs 2–5), the taxonomic framework of *Hymenochaetales* is updated and the status of new and previously known families as well as genera without a certain position at the family level is summarized below.

Families accepted in *Hymenochaetales*

Chaetoporellaceae Jülich, Bibliotheca Mycol. 85: 359 (1982) [1981].

Type genus – *Chaetoporellus* Bondartsev & Singer, in Singer, Mycologia 36(1): 66 (1944).

= *Kneiffiella* P. Karst., Bidr. Känn. Finl. Nat. Folk 48: 371 (1889).

Type species – *Chaetoporellus latitans* (Bourdot & Galzin) Bondartsev & Singer, in Singer, Mycologia 36(1): 66 (1944).

= *Kneiffiella abdita* Riebesehl & Langer, Mycol. Progr. 16(6): 647 (2017).

Description – *Basidiomes* annual, resupinate, effused. *Hymenophore* smooth, grandinioid, odontoid, irpicoid to hydroid, white to yellowish, buff, brown. *Hyphal system* monomitic to pseudodimitic; generative hyphae with clamp connections. *Cystidia* tubular, thick-walled. *Basidia*

barreled, clavate, cylindrical or utriform, with median constriction, with four sterigmata. *Basidiospores* allantoid, cylindrical or ellipsoid, smooth, thin-walled or slightly thick-walled, hyaline, inamyloid, acyanophilous.

Genera accepted in this family – *Echinoporia* and *Kneiffiella*.

Notes – The independence of *Kneiffiella* at the family level in *Hymenochaetales* was determined recently (Wang et al. 2021). In the case that *Kneiffiella* is the prior synonym over *Chaetoporellus*, a previously existing family name *Chaetoporellaceae* (Jülich 1981) was resurrected for *Kneiffiella* (Wang et al. 2021). The current phylogenetic and molecular clock analyses further recover *Echinoporia* in this family (Figs 3, 5). Morphologically, species in *Echinoporia* may produce pileate basidiomes and poroid hymenophores (Ryvarden & Johansen 1980, Motato-Vásquez et al. 2015), which make *Echinoporia* distinctly different from *Kneiffiella* (Wang et al. 2021). However, these morphological differences will not be the taxonomic obstacle to delimiting families, as we can find that the different hymenophoral configurations sometimes exist even in the same genera in *Hymenochaetales* (e.g. *Hymenochaete* & *Xylodon*) and also in other basidiomycetous orders (e.g. *Heteroradulum* in *Auriculariales*, Li et al. 2022; *Trechispora* in *Trechisporales*, Liu et al. 2022a). Moreover, *Echinoporia* was indeed considered to resemble certain corticioid genera (Wu 2001). Therefore, *Echinoporia* is placed in the family *Chaetoporellaceae* together with *Kneiffiella*, and the concept of this family is thus adjusted accordingly.

Hymenochaetaceae Donk, Bull. bot. Gdns Buitenz. 17(4): 474 (1948).

= *Clavariachaetaceae* Jülich, Bibliothca Mycol. 85: 360 (1982) [1981].

= *Coltriciaceae* Jülich, Bibliothca Mycol. 85: 361 (1982) [1981].

= *Nigrofomitaceae* Jülich, Bibliothca Mycol. 85: 381 (1982) [1981].

= *Inotaceae* Fiasson & Niemelä, Karstenia 24(1): 23 (1984).

= *Asterodontaceae* Parmasto, Folia cryptog. Estonica 37: 55 (2001) [2000].

= *Neoantrodidiellaceae* Y.C. Dai, B.K. Cui, Jia J. Chen & H.S. Yuan, in Ariyawansa et al., Fungal Diversity 75: 228 (2015).

Type genus – *Hymenochaete* Lév., Annl. Sci. Nat., Bot., sér. 3 5: 150 (1846).

Type species – *Hymenochaete rubiginosa* (Dicks.) Lév., Annl. Sci. Nat., Bot., sér. 3 5: 150 (1846).

Description – *Basidiomes* annual to perennial, resupinate to pileate. *Pileus* if present, yellowish, rusty brown, grey to black, tomentose to glabrous. *Hymenophore* smooth, grandinoid, hydroid, irpicoid to poroid, cream, yellowish, ochraceous to brownish. *Hyphal system* monomitic, dimitic or trimitic; generative hyphae with simple septa, hyaline to pale yellow; skeletal hyphae thick-walled, hyaline, pale yellowish to rusty brown. *Hymenial setae* and *tramal setae* present or absent. *Basidia* clavate to tubular, thin-walled, with four sterigmata. *Basidiospores* globose, ellipsoid to cylindrical, hyaline to rusty brown, smooth, thin to thick-walled, amyloid or inamyloid, cyanophilous or acyanophilous.

Genera accepted in this family – *Asterodon*, *Basidioradulum*, *Clavariachaete*, *Coltricia*, *Coniferiporia*, *Cyanotrampa* (= *Neoantrodidiella*), *Cylindrosporus*, *Fibricium*, *Flaviporellus*, *Fomitiporella*, *Fomitiporia*, *Fulvifomes*, *Fulvoderma*, *Fuscoporia*, *Hydnoporia*, *Hymenochaete*, *Inocutis*, *Inonotopsis*, *Inonotus*, *Meganotus*, *Mensularia*, *Neomensularia*, *Neophellinus*, *Nigrofomes*, *Nothonotus*, *Nothophellinus*, *Ochrosporellus*, *Onnia*, *Pachynotus*, *Perenninotus*, *Phellinidium*, *Phellinopsis*, *Phellinus*, *Phellopilus*, *Phylloporia*, *Poriodontia*, *Porodaedalea*, *Pseudoinonotus*, *Pseudophylloporia*, *Pyrrhoderma*, *Rigidonotus*, *Sanguangporus*, *Sclerotus*, *Trichaptum* and *Tropicoporus*.

Cyanotrampa gypsea (Yasuda) L.W. Zhou, comb. nov.

Index Fungorum number: IF 900249; Facesoffungi number: FoF 14020

Basionym – *Polystictus gypseus* Yasuda, Bot. Mag., Tokyo 32: (249) (1918).

≡ *Antrodidiella gypsea* (Yasuda) T. Hatt. & Ryvarden, Mycotaxon 50: 35 (1994).

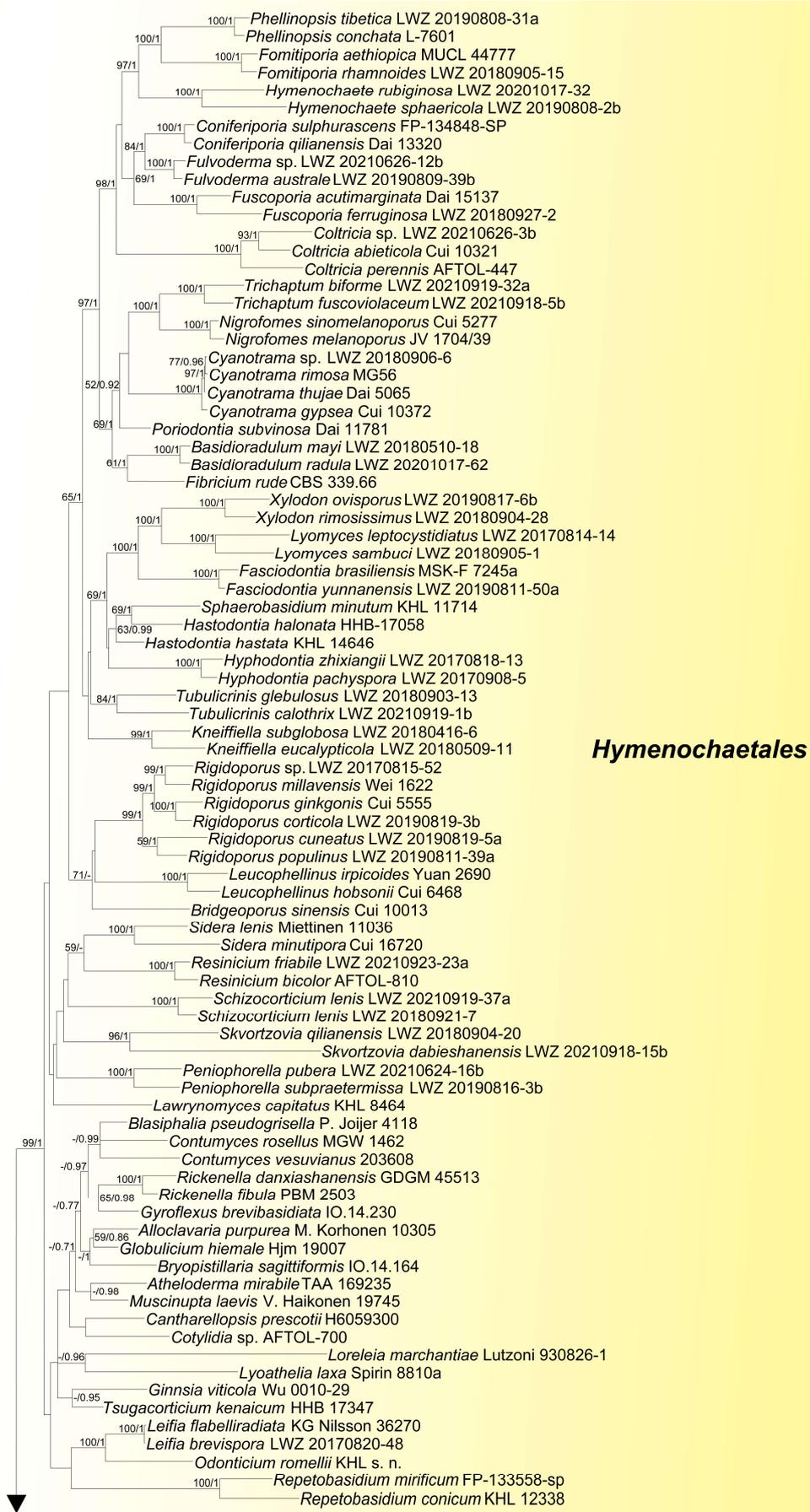


Figure 2 – Phylogenetic position of *Hymenochaetales* within *Agaricomycetes* inferred from the combined dataset of nSSU, ITS, nLSU, *tefla*, *rpb1* and *rpb2* regions. The topology is generated by

the maximum likelihood algorithm. Bootstrap values and Bayesian posterior probabilities, when simultaneously above 50% and 0.7, respectively, are labelled at the nodes.

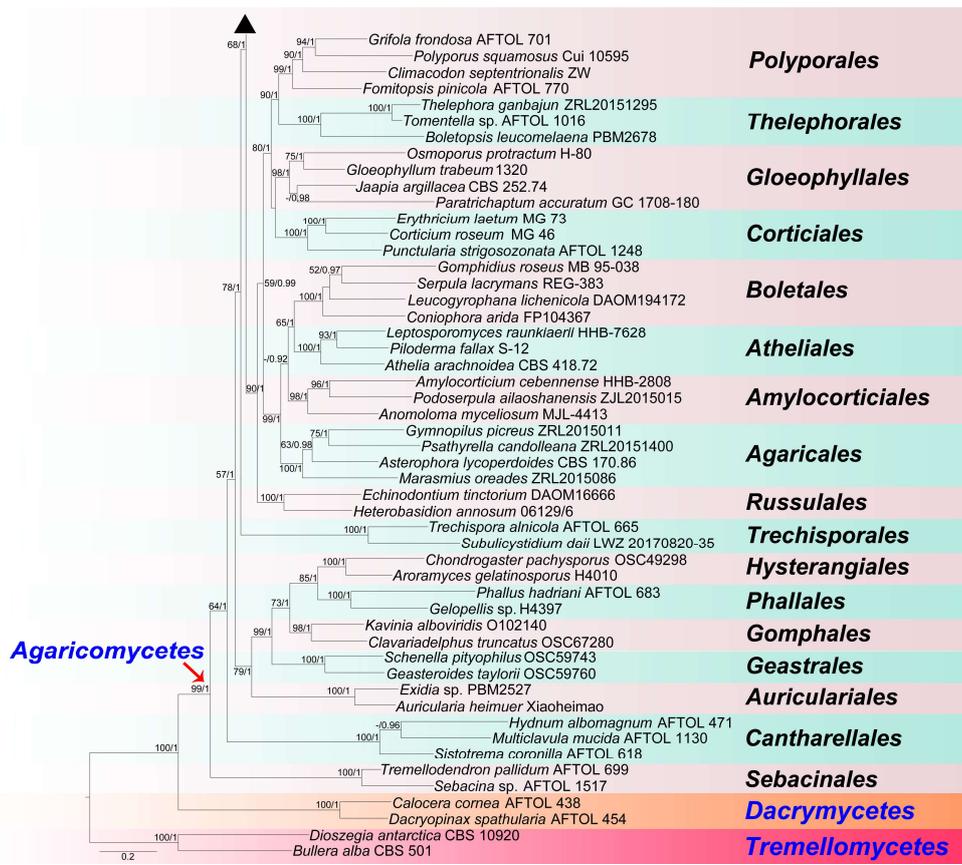


Figure 2 – Continued.

≡ *Neoantrodiaella gypsea* (Yasuda) Y.C. Dai, B.K. Cui, Jia J. Chen & H.S. Yuan, in Ariyawansa et al., Fungal Diversity 75: 228 (2015).

Cyanotrampa thujae (Y.C. Dai & H.S. Yuan) L.W. Zhou, comb. nov.

Index Fungorum number: IF 900250; Facesoffungi number: FoF 14021

Basionym – *Antrodiaella thujae* Y.C. Dai & H.S. Yuan, in Dai, Cui & Yuan, Cryptog. Mycol. 28(3): 179 (2007).

≡ *Neoantrodiaella thujae* (Y.C. Dai & H.S. Yuan) Y.C. Dai, B.K. Cui, Jia J. Chen & H.S. Yuan, in Ariyawansa et al., Fungal Diversity 75: 228 (2015).

Notes – *Clavariachaetaceae* was originally erected for a single genus *Clavariachaete* (Jülich 1981). In addition, another genus *Dichochoaete* was newly erected and added to this family (Parmasto 2000). However, *Dichochoaete* was later treated as a synonym of *Hymenochaete* by the same author (Parmasto et al. 2014), while *Clavariachaete* was morphologically placed in *Hymenochaetaceae* (Miettinen et al. 2019). Similarly, *Asterodon* was moved from *Hymenochaetaceae* to *Asterodontaceae* due to its distinct morphological characters (Parmasto 2000). However, later phylogenetic analysis placed *Asterodon* in the *Hymenochaetaceae* clade (Larsson 2007b). This taxonomic placement was widely followed (Larsson 2007b, Dai 2010, He et al. 2019). Given above, even though *Asterodon* (ITS and nLSU available, but from different collections), *Clavariachaete* (unavailable) and *Dichochoaete* (nLSU available) are not included in the current phylogenetic analyses due to the limits of available gene regions, *Asterodontaceae* and *Clavariachaetaceae* are accepted to be later synonyms of *Hymenochaetaceae* following previous papers.

The independence of *Coltriciaceae* is doubtful as the relationship of *Coltricia* its type genus with genera in *Hymenochaetaceae* was contrary in different papers (Larsson et al. 2006, He et al. 2019, Wang et al. 2021, Wu et al. 2022). Based on phylogenetic and molecular clock analyses, Wang et al. (2021) indicated a larger concept of *Hymenochaetaceae* that also accommodates *Neoantrodiaellaceae*, *Nigrofomitaceae* and additional genera, besides *Coltriciaceae*. However, in the case of sampling bias focusing mainly on *Hyphodontia* sensu lato, Wang et al. (2021) did not propose any formal taxonomic changes. Comparatively, the current study has a balanced sampling and includes more gene regions, both phylogenies (Figs 2, 3) and divergence time of 161.9 Mya (Fig. 5) falling in the range of additional families in *Basidiomycota* (27–178 Mya, He et al. 2019) support the larger concept of *Hymenochaetaceae* suggested by Wang et al. (2021). Therefore, we formally propose *Coltriciaceae*, *Neoantrodiaellaceae* and *Nigrofomitaceae* as the synonyms of *Hymenochaetaceae*, and place *Basidioradulum* and *Trichaptum* in *Hymenochaetaceae*.

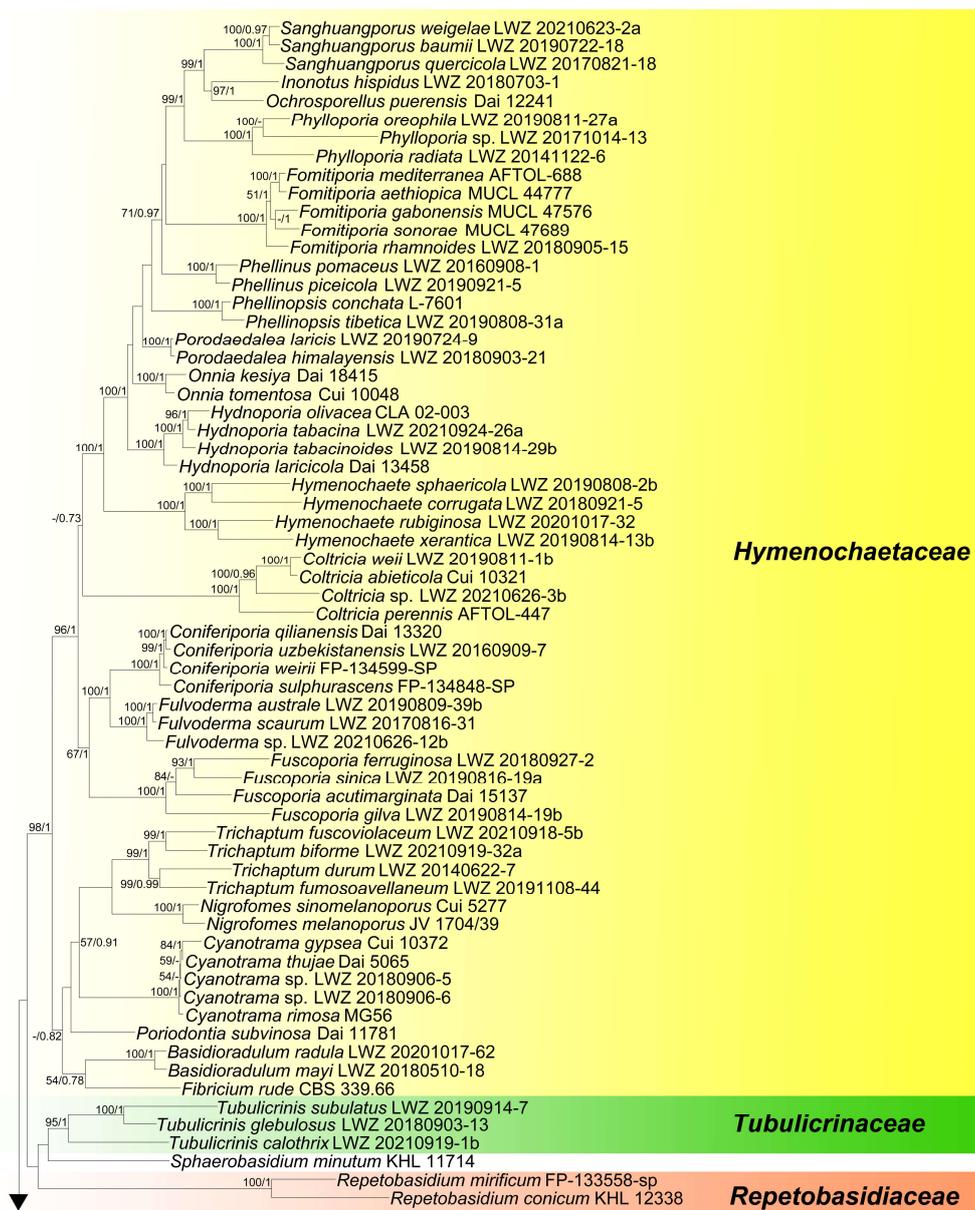


Figure 3 – Phylogenetic relationship among families and genera within *Hymenochaetales* inferred from the combined dataset of nSSU, ITS, nLSU, mt-SSU, *tefla*, *rpb1* and *rpb2* regions. The topology is generated by the maximum likelihood algorithm. Bootstrap values and Bayesian posterior probabilities, when simultaneously above 50% and 0.7, respectively, are labelled at the nodes.

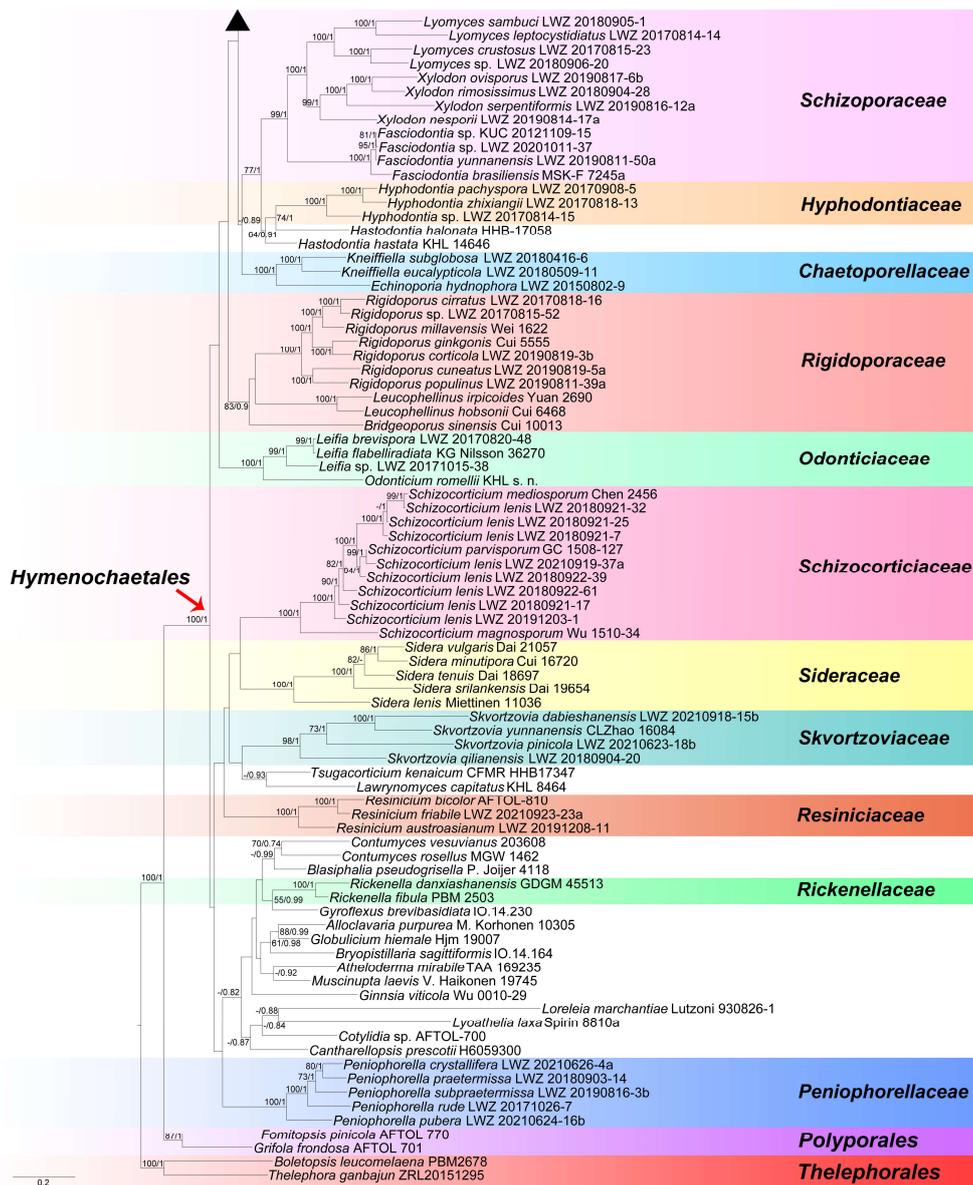


Figure 3 – Continued.

Neoantrodidiellaceae was originally erected for a new genus *Neoantrodidiella* and three previously known genera, viz. *Cyanotrama*, *Fabricium* and *Poriodontia*; however, the phylogeny inferred from ITS and nLSU regions across the whole *Hymenochaetales* did not well support the clade comprising these four genera (Ariyawansa et al. 2015). Indeed, these two gene regions are normally not robust enough to solve the phylogenetic relationships among genera and families across a fungal order. In the current phylogenetic analyses, *Fabricium* is actually closer to *Basidioradulum* than three additional genera originally placed in *Neoantrodidiellaceae* (Ariyawansa et al. 2015), while the monophyly of these three genera is also not well supported (Figs 2, 3). On the contrary, the relationship between *Cyanotrama* and *Neoantrodidiella* is too close to be separated. *Cyanotrama* was erected as a monotypic genus with *C. rimosa* as the generic type by Ghobad-Nejhad & Dai (2010), who also mentioned the morphological similarity between *C. rimosa* and *Antrodidiella thujae* (= *Neoantrodidiella thujae*). *Neoantrodidiella* was erected for *N. gypsea* and *N. thujae* (Ariyawansa et al. 2015). The morphological affinity of the two species of *Neoantrodidiella* with *Cyanotrama rimosa* was earlier noticed by Miettinen (2011), who informally proposed two combinations of *C. gypsea* and *C. thujae*. The current phylogenies (Figs 2, 3) undoubtedly merge *Cyanotrama rimosa*, *Neoantrodidiella gypsea* and *N. thujae* in a strongly supported clade. Therefore, from both morphological and phylogenetic perspectives, *Cyanotrama* and *Neoantrodidiella* should be

congeneric with the former prior over the latter. Accordingly, two combinations *Cyanotrampa gypsea* and *C. thujae* are formally proposed above. Although the circumscription of *Neoantrodiellaceae* sensu Ariyawansa et al. (2015) is polyphyletic, its genera, viz. *Cyanotrampa*, *Fibricium* and *Poriodontia* are all accepted in *Hymenochaetales*.

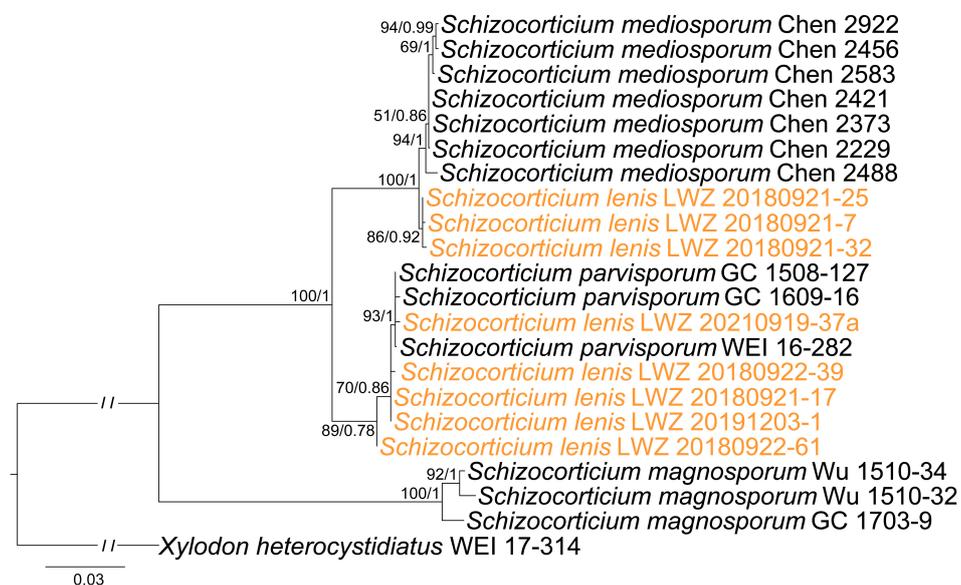


Figure 4 – Phylogenetic relationship among species of *Schizocorticium* and *Skvortzoviella* inferred from the combined dataset of ITS, nLSU and *tefla* regions. The topology is generated by the maximum likelihood algorithm. Bootstrap values and Bayesian posterior probabilities, when simultaneously above 50% and 0.7, respectively, are labelled at the nodes.

Hyphodontiaceae Xue W. Wang & L.W. Zhou, in Wang, May, Liu & Zhou, Journal of Fungi 7(no. 478): 24 (2021).

Type genus – *Hyphodontia* J. Erikss., Symb. bot. upsal. 16(no. 1): 101 (1958).

Type species – *Hyphodontia pallidula* (Bres.) J. Erikss., Symb. bot. upsal. 16(no. 1): 104 (1958).

Description – *Basidiomes* annual, resupinate, effused, adnate. *Hymenophore* smooth, grandinoid, odontoid or poroid, whitish to yellowish, buff, tawny olive or buckthorn brown. *Hyphal system* monomitic to pseudodimitic; generative hyphae with clamp connections. *Cystidia* of one or two types: lagenocystidia, apically strongly encrusted; capitate cystidia, often apically encrusted, sometimes septate. *Basidia* clavate, capitate, subcylindrical or utriform, with four sterigmata. *Basidiospores* ellipsoid, cylindrical, ovoid or subglobose, smooth, thin-walled or slightly thick-walled, hyaline, inamyloid, acyanophilous.

Genus accepted in this family – *Hyphodontia*.

Notes – *Hyphodontiaceae* was recently erected for *Hyphodontia*, which was separated from all additional genera formerly belonging to *Hyphodontia* sensu lato (Wang et al. 2021). The current molecular evidence confirms *Hyphodontiaceae* as an independent monotypic family in *Hymenochaetales* (Figs 2, 3, 5).

Odonticiaceae L.W. Zhou & Xue W. Wang, fam. nov.

Index Fungorum number: IF 900251; Facesoffungi number: FoF 14025

Etymology – *Odonticiaceae* (Lat.), refers to the type genus *Odonticium*.

Type genus – *Odonticium* Parmasto, Consp. System. Corticiac. (Tartu): 126 (1968).

Type species – *Odonticium romellii* (S. Lundell) Parmasto, Consp. System. Corticiac. (Tartu): 126 (1968).

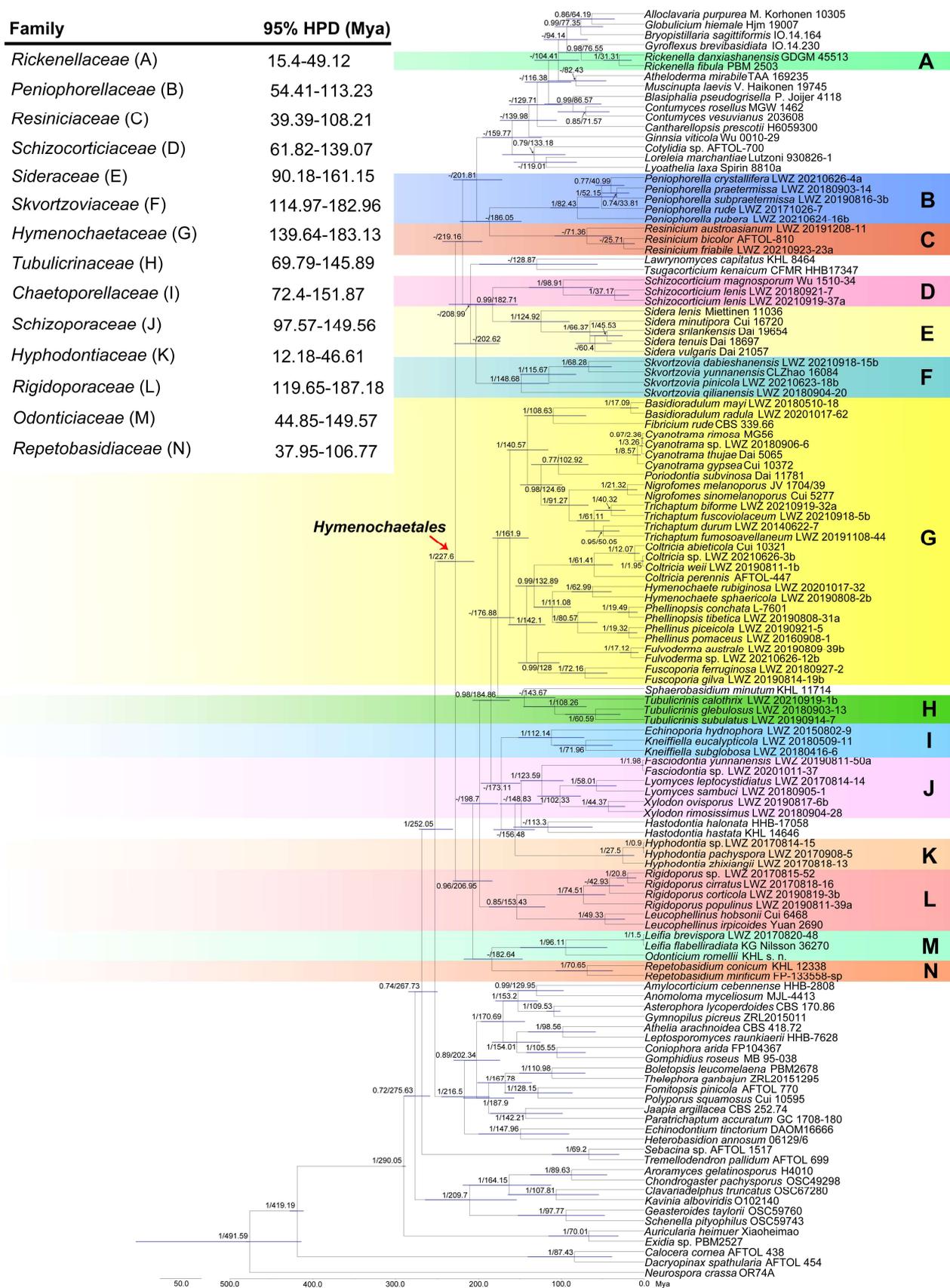


Figure 5 – Maximum-clade-credibility chronogram and estimated divergence times of families within *Hymenochaetales* inferred from the combined dataset of nSSU, ITS, nLSU, *tefla*, *rpb1* and *rpb2* regions. The estimated divergence times of 95% highest posterior density were indicated as node bars for all clades and were also provided in the upper-left of the tree as exact numbers for families within *Hymenochaetales*. The Bayesian posterior probabilities above 0.7 and the mean

divergence times of clades (crown ages) were labeled before and after the slashes, respectively, at the nodes.

Description – *Basidiomes* annual, resupinate, effused. *Hymenophore* grandinioid, odontoid to hydroid, cream to yellowish. *Hyphal system* monomitic to pseudodimitic, generative hyphae with simple septa. *Cystidia* present or absent, cylindrical, thin to thick-walled, hyaline, smooth or encrusted. *Basidia* clavate, with four sterigmata. *Basidiospores* ellipsoid to cylindrical, thin-walled, hyaline, inamyloid, acyanophilous.

Genera accepted in this family – *Leifia* and *Odonticium*.

Notes – *Odonticium* was erected with *O. romellii* as the generic type (Parmasto 1968). Ten species are accommodated in *Odonticium* according to the Index Fungorum (<http://www.indexfungorum.org/>, access on April 24 2022), but this genus is not well studied from the phylogenetic perspective. For example, *Odonticium romellii* was placed in *Hymenochaetales* (Larsson et al. 2006, Miettinen & Larsson 2011, Liu et al. 2019), while *O. laxum* was in *Polyporales* (Miettinen et al. 2012). Following the phylogenetic position of the generic type, *Odonticium* is accepted in *Hymenochaetales*. Although *Odonticium* was placed in *Chaetoporellaceae* morphologically (Jülich 1981), all related phylogenetic analyses rejected this taxonomic placement at the family level (Larsson et al. 2006, Miettinen & Larsson 2011, Liu et al. 2019).

Leifia typified by *L. flabelliradiata* was erected to replace the later homonym *Granulocystis* Hjortstam (Ginns 1998). Later, the monotypic genus was treated as a synonym of *Odonticium* (Zmitrovich 2001). Larsson et al. (2006) noticed that *Leifia flabelliradiata* has a close relationship with *Odonticium romellii* the generic type of *Odonticium* in *Hymenochaetales*, but doubted that *Leifia* and *Odonticium* are the congeneric due to morphological heterogeneity. Recently, besides newly described *Leifia brevispora*, Liu et al. (2019) reinstated *Leifia* as an independent genus in *Hymenochaetales*.

In the current phylogenies, *Leifia* and *Odonticium* form a strongly supported clade that is independent from all named families in *Hymenochaetales* (Figs 2, 3). In addition, the divergence time of this clade (96.11 Mya, Fig. 5) fits well with the range of families in *Basidiomycota* (27–178 Mya, He et al. 2019). Given above, a new family *Odonticiaceae* is proposed to accommodate *Leifia* and *Odonticium*.

Peniophorellaceae L.W. Zhou, Xue W. Wang & S.L. Liu, fam. nov.

Index Fungorum number: IF 900252; Facesoffungi number: FoF 14026

Etymology – *Peniophorellaceae* (Lat.), refers to the type genus *Peniophorella*.

Type genus – *Peniophorella* P. Karst., Bidr. Känn. Finl. Nat. Folk 48: 427 (1889).

Type species – *Peniophorella pubera* (Fr.) P. Karst., Bidr. Känn. Finl. Nat. Folk 48: 427 (1889).

Description – *Basidiomes* annual, resupinate, effused, adnate, thin, ceraceous. *Hymenophore* smooth to tuberculate, white to yellowish. *Hyphal system* monomitic; generative hyphae with clamp connections, hyaline, thin-walled. *Cystidia* present, of different kinds, metuloids, gloeocystidia or leptocystidia, echinulate cells usually present. *Basidia* narrowly to broadly clavate, with four sterigmata. *Basidiospores* ellipsoid, cylindrical or allantoid, hyaline, thin-walled, smooth, with oily contents, inamyloid, acyanophilous.

Genus accepted in this family – *Peniophorella*.

Notes – *Peniophorella* was erected as a monotypic genus for *P. pubera* (Karsten 1889). Since the erection of *Peniophorella*, this genus has not been widely used. Furthermore, Donk (1962) questioned the exact circumscription of *Peniophorella*. Until Larsson (2007a) emended the definition of *Peniophorella* and transferred 19 additional species to this genus, *Peniophorella* was widely accepted in *Hymenochaetales*. Later, 13 additional species were transferred to or newly described in this genus (Hallenberg et al. 2007, Hjortstam & Ryvarden 2009, Duhem & Buyck 2011, Duhem 2012, Nakasone 2012, Telleria et al. 2012, Prasher 2015, Guan et al. 2020, Xu et al.

2020, Yurchenko et al. 2020). For now, a total of 33 species are accepted in *Peniophorella*, although the species identify in *P. praetermissa* species complex needs to be further explored (Hallenberg et al. 2007) and the phylogenetic placement of certain species even if being sequenced is not reliable in this genus, like *P. cremea* (Xu et al. 2020).

At the family level, several papers placed *Peniophorella* in the *Rickenella* family (Larsson 2007b, Liu et al. 2019) or directly in *Rickenellaceae* (He et al. 2019, Olariaga et al. 2020) in *Hymenochaetales*, but no comprehensive phylogeny focusing on this genus really recovers this taxonomic placement. In the current phylogenies, *Peniophorella* occupies an independent position from other known genera and families in *Hymenochaetales* (Figs 2, 3). In addition, the divergence time of this genus (82.43 Mya, Fig. 5) is not contrary with the range of families in *Basidiomycota* (27–178 Mya, He et al. 2019). Therefore, a new family *Peniophorellaceae* is proposed for *Peniophorella*.

Repetobasidiaceae Jülich, *Bibliotheca Mycol.* 85: 388 (1982) [1981].

Type genus – *Repetobasidium* J. Erikss., *Symb. bot. upsal.* 16(no. 1): 67 (1958).

Type species – *Repetobasidium vile* (Bourdot & Galzin) J. Erikss., *Symb. bot. upsal.* 16(no. 1): 67 (1958).

Description – *Basidiomes* annual, resupinate, effused, adnate, very thin, ceraceous. *Hymenophore* smooth, white, pale yellowish to greyish. *Hyphal system* monomitic; generative hyphae with clamp connections, thin-walled. *Cystidia* cylindrical or conical, with capitate or subulate apex, thin-walled. *Basidia* subglobose to pyriform, produced by internal repetition from old basidia, with four sterigmata. *Basidiospores* ellipsoid or subfusiform, smooth, thin-walled, inamyloid, acyanophilous.

Genus accepted in this family – *Repetobasidium*.

Notes – *Repetobasidiaceae* was originally erected to accommodate *Repetobasidium* and *Sphaerobasidium* in *Sistotrematales* (Jülich 1981). Although these two genera have long been included in *Hymenochaetales* (Binder et al. 2005, Larsson et al. 2006, Larsson 2007b), *Repetobasidiaceae* seems to be buried in oblivion (Larsson et al. 2006, Larsson 2007b, Vizzini 2010, Nakasone & Burdsall 2012) and is never formally accepted as an independent family in *Hymenochaetales* (Fig. 1). Instead, *Repetobasidiaceae* was treated as a synonym of *Hydnaceae* in *Cantharellales* (= *Sistotrematales*), while *Sphaerobasidium* was placed in *Hydnodontaceae*, *Trechisporales* (He et al. 2019). Although the generic type of *Repetobasidium vile*, is unavailable for phylogenetic analyses, we cannot see any reason to place *Repetobasidium* in *Hydnaceae*. Similarly, to our knowledge, there is no reason to place *Sphaerobasidium* in *Trechisporales* (Liu et al. 2022a). The current phylogenies confirm *Repetobasidium* and *Sphaerobasidium* as members of *Hymenochaetales* but do not support their close relationship (Figs 2, 3). Therefore, we tentatively accept *Repetobasidiaceae* as a monotypic family in *Hymenochaetales*.

Resiniciaceae L.W. Zhou & Xue W. Wang, fam. nov.

Index Fungorum number: IF 900253; Facesoffungi number: FoF 14027

Etymology – *Resiniciaceae* (Lat.), refers to the type genus *Resinicium*.

Type genus – *Resinicium* Parmasto, *Consp. System. Corticiac.* (Tartu): 97 (1968).

Type species – *Resinicium bicolor* (Alb. & Schwein.) Parmasto, *Consp. System. Corticiac.* (Tartu): 98 (1968).

Description – *Basidiomes* annual, resupinate, effused, adnate. *Hymenophore* smooth, grandinoid, odontoid to hydroid; white to yellowish. *Hyphal system* monomitic; generative hyphae usually with clamp connections, thin-walled. *Cystidia* of two types: halocystidia, cylindrical with a capitate apex; astrocystidia, at apex a stellate cluster of hyaline crystals. *Basidia* clavate, with four sterigmata. *Basidiospores* ellipsoid to cylindrical, smooth, thin-walled, hyaline, inamyloid, acyanophilous.

Genus accepted in this family – *Resinicium*.

Notes – *Resinicium* typified by *R. bicolor* morphologically accommodates species similar to *Mycoacia* and *Phlebia* in *Polyporales* (Parmasto 1968, Eriksson et al. 1981). However, phylogenetic analyses indicated the generic type and several other species of *Resinicium* in *Hymenochaetales* (Hibbett & Binder 2002, Larsson et al. 2004, 2006, Binder et al. 2005). Later, Nakasone (2007) firstly performed a comprehensive taxonomic revision on *Resinicium* from both morphological and phylogenetic perspectives. With this taxonomic system as an important foundation, the species diversity and generic circumscription of *Resinicium* were further explored, and a total of 12 species are accepted in this genus (Telleria et al. 2008, Gruhn et al. 2017, Yu et al. 2021). Although certain papers placed *Resinicium* in the *Rickenella* clade (Larsson et al. 2006) or directly in *Rickenellaceae* (He et al. 2019, Olariaga et al. 2020), the phylogenies in some other papers cannot recover *Resinicium* and *Rickenella* the type genus of *Rickenellaceae* in a single clade at all (Larsson 2007b, Miettinen & Larsson 2011, Korotkin et al. 2018, Yu et al. 2021). In the current phylogenies (Figs 2, 3), *Resinicium* occupies an independent position from other genera and known families in *Hymenochaetales*. Moreover, the divergence time of *Resinicium* (71.36 Mya, Fig. 5) also fits with the range of families in *Basidiomycota* (27–178 Mya, He et al. 2019). Therefore, a new monotypic family *Resiniciaceae* is proposed for *Resinicium*.

Rickenellaceae Vizzini, Micol. Veg. Medit. 25(2): 144 (2010).

Type genus – *Rickenella* Raithelh., Metrodiana 4(4): 67 (1973).

Type species – *Rickenella fibula* (Bull.) Raithelh., Metrodiana 4: 67 (1973).

Description – *Basidiomes* annual, small, omphalinoid, surface yellow to brownish orange. *Lamellae* decurrent, white to yellowish white. *Stipe* central, cylindrical to subcylindrical, equal or slightly tapered downwards, cartilaginous, solid, white to yellowish white. *Hyphal system* monomitic; generative hyphae with clamp connections, thin-walled. *Caulocystidia*, cheilocystidia, pileocystidia and pleurocystidia present, narrowly lageniform to obclavate often with subcapitate apex, hyaline, thin-walled. *Basidia* clavate, with four sterigmata. *Basidiospores* ellipsoid to cylindrical, smooth, thin-walled, hyaline, inamyloid, acyanophilous.

Genus accepted in this family – *Rickenella*.

Notes – *Rickenellaceae* was erected to accommodate all genera in the *Rickenella* clade sensu Larsson et al. (2006) and the *Rickenella* family sensu Larsson (2007b) (Vizzini 2010). However, due to the inclusion of *Repetobasidium*, the type genus of *Repetobasidiaceae*, in *Rickenellaceae* (Vizzini 2010), *Repetobasidiaceae* should be adopted as the formal family name of the *Rickenella* clade and the *Rickenella* family. Therefore, *Rickenellaceae* was actually a superfluous name (Art. 52.4; Turland et al. 2018). Until recently, *Repetobasidium* was excluded from *Rickenellaceae* (Olariaga et al. 2020), which makes *Rickenellaceae* as the correct name for the *Rickenella* clade and the *Rickenella* family. However, even though excluding *Repetobasidium*, additional genera accommodated in *Rickenellaceae* sensu Vizzini (2010) have never fully recovered as a well-supported clade in previous phylogenetic analyses (Larsson et al. 2006, Larsson 2007b, Korotkin et al. 2018, Olariaga et al. 2020, Wang et al. 2021). The current phylogenies also support the separation of *Repetobasidium* and *Rickenellaceae*, and moreover, group *Rickenella* together with *Alloclavaria*, *Atheloderma*, *Blasiphalia*, *Bryopistillaria*, *Cantharellopsis*, *Contumyces*, *Cotylidia*, *Ginnsia*, *Globulicium*, *Gyroflexus*, *Loreleia*, *Lyoathelia* and *Muscinupta* (separated in Fig. 3) in *Hymenochaetales* but without reliable statistical support (Figs 2, 3). Moreover, species in these genera produce highly diverse morphological traits of basidiomes. In addition, the divergence time of *Rickenella* (31.31 Mya, Fig. 5) also falls within the range of families in *Basidiomycota* (27–178 Mya, He et al. 2019). Given above, *Rickenellaceae* is tentatively restricted for the type genus *Rickenella* in *Hymenochaetales*. The relationship of *Rickenellaceae* with the above mentioned 13 additional genera producing highly diverse morphological traits of basidiomes needs to be further clarified.

Rigidoporaceae Jülich, Bibliothca Mycol. 85: 388 (1982) [1981].

= *Oxyporaceae* Zmitr. & Malysheva, Mikol. Fitopatol. 48(3): 169 (2014).

Type genus – *Rigidoporus* Murrill, Bull. Torrey bot. Club 32(9): 478 (1905).

= *Botryodontia* (Hjortstam & Ryvarde) Hjortstam, Mycotaxon 28(1): 20 (1987).

Type species – *Rigidoporus microporus* (Sw.) Overeem, Icon. Fung. Malay. 5: 1 (1924).

Description – *Basidiomes* annual to perennial, resupinate to pileate. *Pileus* tomentose to glabrous, usually zonate, reddish orange to pinkish, isabelline or ochraceous. *Hymenophore* poroid, pore surface concolorous. *Hyphal system* monomitic to dimitic; generative hyphae with simple septa; skeletal hyphae thick-walled to solid. *Encrusted cystidia* present or absent. *Basidia* clavate, with four sterigmata. *Basidiospores* ovoid to globose, hyaline, smooth, thin-walled, inamyloid, acyanophilous.

Genera accepted in this family – *Bridgeoporus*, *Leucophellinus* and *Rigidoporus* (= *Botryodontia*).

Rigidoporus cirratus (Hjortstam & Ryvarde) L.W. Zhou, comb. nov.

Index Fungorum number: IF 900254; Facesoffungi number: FoF 14022

Basionym – *Candelabrochaete cirrata* Hjortstam & Ryvarde, Mycotaxon 25(2): 545 (1986).

≡ *Botryodontia cirrata* (Hjortstam & Ryvarde) Hjortstam, Mycotaxon 28(1): 20 (1987).

Rigidoporus millavensis (Bourdot & Galzin) L.W. Zhou, comb. nov.

Index Fungorum number: IF 900255; Facesoffungi number: FoF 14023

Basionym – *Poria mucida* subsp. *millavensis* Bourdot & Galzin, Bull. trimest. Soc. mycol. Fr. 41(2): 238 (1925).

≡ *Botryodontia millavensis* (Bourdot & Galzin) Duhem & H. Michel, Bull. Soc. mycol. Fr. 121(1): 43 (2006) [2005].

≡ *Chaetoporus philadelphi* Parmasto, Botanicheskie Materialy 12: 237 (1959).

≡ *Rigidoporus philadelphi* (Parmasto) Pouzar, Folia geobot. phytotax. bohemoslov. 1(4): 368 (1966).

Notes – This family is known as *Oxyporaceae*, which was erected with *Oxyporus* as the family type (Zmitrovich & Malysheva 2014). Besides *Oxyporus*, *Leucophellinus* was also accepted as a member of *Oxyporaceae* (Ariyawansa et al. 2015). Later, *Oxyporus* was treated as a later synonym of *Rigidoporus* (Wu et al. 2017). Recently, Wang et al. (2021) further included *Bridgeoporus* in *Oxyporaceae*. The current phylogenies confirmed the close relationship among these three genera with moderate statistical support (Figs 2, 3).

Botryodontia was erected with *Botryodontia cirrata* as the generic type in the earlier concept of *Corticaceae* (Hjortstam 1987). Larsson (2007b) hypothesized that *Botryodontia* may be close to *Hymenochaetales*, which was later phylogenetically confirmed by Sell et al. (2014). Besides, Sell et al. (2014) also indicated a closely morphological and phylogenetic relationship between *Botryodontia* and *Oxyporus* (= *Rigidoporus*), and treated *Botryodontia millavensis* and *Oxyporus philadelphi* (= *Rigidoporus philadelphi*) to be conspecific. In the current phylogenies the Chinese specimens morphologically identified to the generic type *B. cirrata* also fall within the clade of *Rigidoporus* (Figs 2, 3). Therefore, *Botryodontia* is treated as a later synonym of *Rigidoporus*. *Botryodontia cirrata* and *B. millavensis* are accordingly transferred to *Rigidoporus*, while the phylogenetic position of non-sequenced species originally placed in *Botryodontia* is still left to be open.

Noteworthy, when being treated as synonyms, *Oxyporus* and *Rigidoporus* actually belong to a single family. Although being omitted (Zhou et al. 2018, He et al. 2019, Wang et al. 2021), a previous family name *Rigidoporaceae* on the basis of *Rigidoporus* actually exists (Jülich 1981). Therefore, we accept *Rigidoporaceae* as the prior family name over *Oxyporaceae* to accommodate *Bridgeoporus*, *Leucophellinus* and *Rigidoporus*.

Rigidoporaceae originally accommodated three additional genera, viz. *Ceriporia*, *Henningsia* and *Macrohyporia* (Jülich 1981). However, *Ceriporia* that has been extensively studied especially in China undoubtedly belongs to *Polyporales* (Jia et al. 2014); *Henningsia* was indicated to belong to *Polyporales* by the only sequenced specimen representing *H. resupinata* from this genus (Crous

et al. 2018); *Macrohyporia* was also evidenced to belong to *Polyporales* according to the ITS- and nLSU-based phylogeny including its generic type *M. dictyopora* (Permpornsakul et al. 2016). Therefore, at this stage, these three genera are not accepted in the current circumscription of *Rigidoporaceae*.

Schizocorticiaceae L.W. Zhou & Xue W. Wang, fam. nov.

Index Fungorum number: IF 900256; Facesoffungi number: FoF 14028

Etymology – *Schizocorticiaceae* (Lat.), refers to the type genus *Schizocorticium*.

Type genus – *Schizocorticium* Sheng H. Wu, in Wu, Wei, Chen, Chen & Chen, Mycol. Progr. 20(6): 774 (2021) [published June 7 2021].

= *Skvortzoviella* Jia Yu, Xue W. Wang, S.L. Liu & L.W. Zhou, in Yu, Wang, Liu, Shen & Zhou, IMA Fungus 12(no. 19): 12 (2021) [published July 19 2021].

Type species – *Schizocorticium magnosporum* Sheng H. Wu & C.L. Wei, in Wu, Wei, Chen, Chen & Chen, Mycol. Progr. 20(6): 774 (2021).

Description – *Basidiomes* annual, widely effused, not easily separable, thin, membranous. *Hymenophore* smooth or irregular, cream to pale yellow, more or less cracked. *Hyphal system* monomitic; generative hyphae with clamp connections, hyaline, thin-walled. *Leptocystidia* tubular with obtuse apex, hyaline, thin-walled. *Basidia* cylindrical, often with a median constriction, four sterigmata. *Basidiospores* ellipsoid, hyaline, smooth, thin-walled, inamyloid, acyanophilous.

Genus accepted in this family – *Schizocorticium* (= *Skvortzoviella*).

Schizocorticium lenis (Jia Yu, Xue W. Wang, S.L. Liu & L.W. Zhou) L.W. Zhou, comb. nov.

Index Fungorum number: IF 900257; Facesoffungi number: FoF 14024

Basionym – *Skvortzoviella lenis* Jia Yu, Xue W. Wang, S.L. Liu & L.W. Zhou, in Yu, Wang, Liu, Shen & Zhou, IMA Fungus 12(no. 19): 13 (2021).

Notes – *Schizocorticium* was recently erected for three new species in *Hymenochaetales* (Wu et al. 2021). Of these three species, *S. mediosporum* and *S. parvisporum* presented closer phylogenetic relationship than each with *S. magnosporum* (Wu et al. 2021). Actually, in the current species circumscription, *S. mediosporum* and *S. parvisporum* can be well distinguished by the phylogeny inferred from *tefla* region but not that from ITS and nLSU regions (Wu et al. 2021). About one month later after the erection of *Schizocorticium*, a monotypic genus *Skvortzoviella* was newly introduced in *Hymenochaetales* (Yu et al. 2021). In the current phylogeny inferred from ITS, nLSU and *tefla* regions, the generic type *Skvortzoviella lenis* is found to be merged into the clade being composed of *S. mediosporum* and *S. parvisporum*: the holotype LWZ 20180921-17 and four additional specimens of *S. lenis* seems to be conspecific with *S. parvisporum* but without strong statistical support, while three specimens of *S. lenis*, viz. LWZ 20180921-7, LWZ 20180921-25 and LWZ 20180921-32 can be distinguished as an independent lineage from *S. mediosporum* (Fig. 4). Moreover, more independent lineages are revealed from the clade being composed of *S. lenis*, *S. mediosporum* and *S. parvisporum* in the phylogeny inferred from seven gene regions (Fig. 3). Morphologically, *S. mediosporum* and *S. parvisporum* are different mainly in the size of basidiospores, while the basidiospores in *S. lenis* also differs from the former two species; however, the sizes of basidiospores in these three species are consecutive (Wu et al. 2021, Yu et al. 2021). Given above, *S. lenis*, *S. mediosporum* and *S. parvisporum* can be treated to be conspecific with certain intraspecies variations; alternatively, subtler circumscription should be delimited to explore the species diversity in this species complex. This taxonomic issue at the species level is beyond the scope of the current study, but it is obvious that *Schizocorticium* is the prior synonym of *Skvortzoviella*. Therefore, a combination of *Skvortzoviella lenis* to *Schizocorticium lenis* is tentatively proposed. In the current phylogenies (Figs 2, 3), *Schizocorticium* stands an independent position from known families and genera in *Hymenochaetales*. In association of the divergence time of *Schizocorticium* (98.91 Mya, Fig. 5) falling in the range of families in *Basidiomycota* (27–178 Mya, He et al. 2019), a new monotypic family *Schizocorticiaceae* is proposed for *Schizocorticium*.

Schizoporaceae Jülich, *Bibliotheca Mycol.* 85: 389 (1982) [1981].

Type genus – *Schizopora* Velen., *České Houby (Praze)* 4-5: 638 (1922).

= *Xylodon* (Pers.) Gray, *Nat. Arr. Brit. Pl.* (London) 1: 649 (1821).

Type species – *Schizopora paradoxa* (Schrad.) Donk, *Persoonia* 5(1): 76 (1967).

= *Xylodon paradoxus* (Schrad.) Chevall., *Fl. gén. env. Paris* (Paris) 1: 274 (1826).

Description – *Basidiomes* annual, resupinate or pileate. *Hymenophore* smooth, tuberculate, grandinioid, odontoid, coralloid, irpicoid or poroid, white to yellowish, buff to ochraceous. *Hyphal system* monomitic, dimitic or trimitic; generative hyphae with clamp connections. *Cystidia* present or absent, different types: capitate to subcapitate, cylindrical to subcylindrical, fusiform, subulate, bladder-like, bottle-shaped, clavate, moniliform to submoniliform, pyriform, astro-, gloeo- or leptocystidia, lecythiform, rarely lagenocystidia and snake-like sinuous tramacystidia. *Basidia* barrel-shaped, clavate to subclavate, cylindrical to subcylindrical, pyriform, utriform, with two or four sterigmata. *Basidiospores* ellipsoid or subellipsoid, cylindrical to subcylindrical, ovoid, allantoid, globose or subglobose, smooth, thin to thick-walled, hyaline, inamyloid, acyanophilous or slightly cyanophilous.

Genera accepted in this family – *Fasciodontia*, *Lyomyces* and *Xylodon*.

Notes – Three genera formerly belonging to *Hyphodontia* sensu lato, viz. *Fasciodontia*, *Lyomyces* and *Xylodon* formed a strongly supported clade that stood an independent position at the family level in *Hymenochaetales* (Wang et al. 2021). In the case that *Xylodon* is a prior synonym over *Schizopora*, the previous family name *Schizoporaceae* typified by *Schizopora* (Jülich 1981) was adopted to accommodate *Fasciodontia*, *Lyomyces* and *Xylodon* (Wang et al. 2021). This arrangement is confirmed by the current phylogenies (Figs 2, 3).

Sideraceae L.W. Zhou & Xue W. Wang, fam. nov.

Index Fungorum number: IF 900258; Facesoffungi number: FoF 14029

Etymology – *Sideraceae* (Lat.), refers to the type genus *Sidera*.

Type genus – *Sidera* Miettinen & K.H. Larss., *Mycol. Progr.* 10(2): 136 (2011).

Type species – *Sidera lenis* (P. Karst.) Miettinen, in Miettinen & Larsson, *Mycol. Progr.* 10(2): 136 (2011).

Description – *Basidiomes* annual to perennial, resupinate. *Hymenophore* hydroid or poroid, white to yellowish. *Hyphal system* monomitic or dimitic, crystals usually abundant in subiculum and sometimes in trama; generative hyphae with clamp connections, thin-walled; skeletal hyphae relatively loosely arranged, straight and without branches. *Cystidia* absent; cystidioles present, thin-walled. *Basidia* clavate to cylindrical, with four sterigmata. *Basidiospores* ellipsoid to cylindrical, smooth, thin-walled, hyaline, inamyloid, acyanophilous.

Genus accepted in this family – *Sidera*.

Notes – *Sidera* typified by *S. lenis* was newly erected in the circumscription of the *Rickenella* clade that was actually paraphyletic in *Hymenochaetales* (Miettinen & Larsson 2011). A total of 16 species are accommodated in this genus (Liu et al. 2022b). In the current multilocus-based phylogenetic analyses, *Sidera* is clearly separated from *Rickenellaceae* and additional known families and genera in *Hymenochaetales* (Figs 2, 3). Moreover, the divergence time of *Sidera* (124.92 Mya, Fig. 5) is not out of the range of additional families in *Basidiomycota* (27–178 Mya, He et al. 2019). Therefore, a new monotypic family *Sideraceae* is proposed for *Sidera*.

Skvortzoviaceae L.W. Zhou & Xue W. Wang, fam. nov.

Index Fungorum number: IF 900259; Facesoffungi number: FoF 14030

Etymology – *Skvortzoviaceae* (Lat.), refers to the type genus *Skvortzovia*.

Type genus – *Skvortzovia* Bononi & Hjortstam, in Hjortstam & Bononi, *Mycotaxon* 28(1): 12 (1987).

Type species – *Skvortzovia furfurella* (Bres.) Bononi & Hjortstam, in Hjortstam & Bononi, *Mycotaxon* 28(1): 12 (1987).

Description – *Basidiomes* annual, resupinate, effused. *Hymenophore* smooth, grandinioid, odontoid, cream to yellowish. *Hyphal system* monomitic; generative hyphae usually with clamp connections, thin-walled. *Cystidia* tubular with obtuse apex, hyaline, thin-walled. *Basidia* clavate to cylindrical, with four sterigmata. *Basidiospores* cylindrical or allantoid, smooth, thin-walled, hyaline, inamyloid, acyanophilous.

Genus accepted in this family – *Skvortzovia*.

Notes – *Skvortzovia* was erected as a monotypic genus for *S. furfurella* (Hjortstam & Bononi 1987). This generic type *S. furfurella* was earlier known as *Resinicium furfurellum* as one of the two species in *Resinicium* when its erection (Parmasto 1968). When revising the taxonomy of *Resinicium*, Nakasone (2007) excluded *R. furfurellum* from *Resinicium sensu stricto* and treated this species as a member of *Resinicium sensu lato*. Besides *R. furfurellum*, three additional species, viz. *R. furfuraceum*, *R. meridionale* and *R. pinicola* were also accepted as members of *Resinicium sensu lato* by Nakasone (2007). Recently, these three species and *Phlebia georgica* were formally transferred to *Skvortzovia* (Gruhn & Hallenberg 2018). More recently, three new species of *Skvortzovia* were described (Dong et al. 2021, Yu et al. 2021), which brings the species number of this genus to eight. Regarding the higher-level taxonomic rank, *Skvortzovia* was placed in the *Rickenella* clade (Larsson et al. 2006) or directly in *Rickenellaceae* (Olariaga et al. 2020) in *Hymenochaetales*, whereas He et al. (2019) treated this genus with an uncertain family position in *Hymenochaetales*. Indeed, the phylogenies in most papers cannot recover *Skvortzovia* and *Rickenella* the type genus of *Rickenellaceae* in a single clade at all (Larsson 2007b, Miettinen & Larsson 2011, Korotkin et al. 2018, Yu et al. 2021), and Yu et al. (2021) stated that the family position of *Skvortzovia* in *Hymenochaetales* needs to be explored with the help of more gene regions than ITS and nLSU. In the current phylogenies inferred from six to seven gene regions (Figs 2, 3), *Skvortzovia* is separated from other genera and known families in *Hymenochaetales*. Taking the divergence time of *Skvortzovia* (148.68 Mya, Fig. 5) within the range of additional families in *Basidiomycota* (27–178 Mya, He et al. 2019) into consideration together, a new monotypic family *Skvortzoviaceae* is proposed for *Skvortzovia*.

Tubulicrinaceae Jülich, *Bibliotheca Mycol.* 85: 392 (1982) [1981].

Type genus – *Tubulicrinis* Donk, *Fungus*, Wageningen 26(1-4): 13 (1956).

Type species – *Tubulicrinis glebulosus* (Fr.) Donk [as '*glebulosa*'], *Fungus*, Wageningen 26(1-4): 14 (1956).

Description – *Basidiomes* annual, resupinate, effused, firmly adnate. *Hymenophore* smooth, pruinose to porulose, white, cream to pale ochraceous. *Hyphal system* monomitic; generative hyphae with clamp connections. *Cystidia* cylindrical or conical, with capitate or subulate apex, generally bi- or multi-radiculate. *Basidia* clavate, thin-walled, with four sterigmata. *Basidiospores* subglobose, ellipsoid, cylindrical or allantoid, smooth, thin-walled, hyaline, inamyloid, acyanophilous.

Genus accepted in this family – *Tubulicrinis*.

Notes – *Tubulicrinaceae* was erected to accommodate *Tubulicium* and the family type genus *Tubulicrinis* in *Tubulicrinales* (Jülich 1981). Of these two genera, *Tubulicium* was phylogenetically evidenced to belong in the trechisporoid clade (Larsson et al. 2004) and later placed in *Trechisporales* (Larsson 2007b), while *Tubulicrinis* was in the hymenochaetoid clade (Larsson et al. 2004) and later placed in *Hymenochaetales* (Larsson et al. 2006, Larsson 2007b). Both Larsson (2007b) and Ariyawansa (2015) accepted *Tubulicrinis* in the independent family *Tubulicrinaceae*. However, for unknown reasons, He et al. (2019) placed *Tubulicrinis* in *Hymenochaetaceae*, which actually treated *Tubulicrinaceae* as a later synonym of *Hymenochaetaceae*. Recently, Wang et al. (2021) did not accept *Tubulicrinaceae*, because the sampled species failed to be grouped in a strongly supported clade in the phylogeny inferred from ITS, nLSU and mt-SSU regions. The current phylogenies based on both nuclear and protein-encoding gene regions strongly support the sampled species of *Tubulicrinis* including the generic type *T. glebulosus* in an independent clade from other known families and genera in *Hymenochaetales* (BS = 84%, BPP = 1 in Fig. 2; BS =

95%, BPP = 1 in Fig. 3). In association of the divergence time (108.26 Mya, Fig. 5) falling within the range of additional families in *Basidiomycota* (27–178 Mya, He et al. 2019), *Tubulicrinaceae* is accepted as a monotypic family for *Tubulicrinis* in *Hymenochaetales*.

Genera incertae sedis at the family level in *Hymenochaetales*

Alloclavaria Dentinger & D.J. McLaughlin, *Mycologia* 98(5): 757 (2007) [2006].

Type species – *Alloclavaria purpurea* (O.F. Müll.) Dentinger & D.J. McLaughlin, *Mycologia* 98(5): 757 (2007) [2006].

Notes – Among species of *Clavaria*, *C. purpurea* was found to occupy a separated phylogenetic position in *Hymenochaetales* from *C. vermicularis* a synonym of the generic type *C. fragilis* in the family *Clavariaceae* in *Agaricales* (Dentinger & McLaughlin 2006). Therefore, a monotypic genus *Alloclavaria* was erected for *C. purpurea* in *Hymenochaetales* (Dentinger & McLaughlin 2006). The current phylogenies confirm the placement of *Alloclavaria* in *Hymenochaetales* (Figs 2, 3).

Atheloderma Parmasto, *Consp. System. Corticiac.* (Tartu): 73 (1968).

Type species – *Atheloderma mirabile* Parmasto, *Consp. System. Corticiac.* (Tartu): 200 (1968).

Notes – *Atheloderma* was erected for *A. mirabile* as the generic type and *A. orientale* (Parmasto 1968). This genus was treated as a subgenus of *Athelia* in *Atheliaceae*, *Atheliales* (Zmitrovich 2004). However, from the phylogenetic perspective, *Atheloderma mirabile* was proved to belong to *Hymenochaetales* (Larsson et al. 2006), which is also recovered in the current phylogenies (Figs 2, 3). Therefore, *Atheloderma* is accepted as an independent genus in *Hymenochaetales*.

Blasiphalia Redhead, in Larsson, Parmasto, Fischer, Langer, Nakasone & Redhead, *Mycologia* 98(6): 934 (2007) [2006].

Type species – *Blasiphalia pseudogrisella* (A.H. Sm.) Redhead, in Larsson, Parmasto, Fischer, Langer, Nakasone & Redhead, *Mycologia* 98(6): 934 (2007) [2006].

Notes – *Blasiphalia pseudogrisella* the generic type of *Blasiphalia* is an omphalinoid species and was previously placed in *Rickenella*. Larsson et al. (2006) revealed this species in an independent lineage from *Rickenella* and other genera in *Hymenochaetales*, and thus erected a monotypic genus *Blasiphalia* for this species in *Hymenochaetales* (Larsson et al. 2006). This phylogenetic placement was confirmed by later phylogenetic analyses (Korotkin et al. 2018, Olariaga et al. 2020, Salcedo et al. 2020) and the current phylogenies (Figs 2, 3).

Bryopistillaria Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, *Stud. Mycol.* 96: 177 (2020).

Type species – *Bryopistillaria sagittiformis* (Pat.) Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen, *Stud. Mycol.* 96: 177 (2020).

Notes – *Bryopistillaria sagittiformis* the generic type of *Bryopistillaria* was well known in *Ceratellopsis* as *C. sagittiformis*. Olariaga et al. (2020) were preparing to propose the conservation of *Ceratellopsis* with *C. acuminata* as the conserved type in *Clavariaceae*, *Agaricales* that has recently been formally published (Olariaga et al. 2022), and thus erected a new genus *Bryopistillaria* for the single separated species with bryophilous, reduced clavarioid basidiomes in *Rickenellaceae*, *Hymenochaetales*. The current phylogenies confirm *Bryopistillaria* in *Hymenochaetales* but not closely related to *Rickenella* (Figs 2, 3). Therefore, *Bryopistillaria* is accepted as an independent genus from other genera and families in *Hymenochaetales*.

Cantharellopsis Kuyper, in Borghi (Ed.), *La Famiglia delle Tricholomataceae*, *Atti del Convegno Internazionale del 10-15 Settembre 1984*, Borgo Val di Taro, Italy (Borgo Val di Taro): 99 (1986).

Type species – *Cantharellopsis prescottii* (Weinm.) Kuyper, La Famiglia delle Tricholomataceae, Atti del Convegno Internazionale del 10-15 Settembre 1984, Borgo Val di Taro, Italy (Borgo Val di Taro) 6: 99 (1986).

Notes – *Cantharellopsis* was erected for an omphalinoid species *C. prescottii* (Kuyper 1986). Moncalvo et al. (2002) placed this monotypic genus in the hymenochaetoid clade (equal to *Hymenochaetales*). This placement was confirmed by later phylogenetic analyses (Redhead et al. 2002, Larsson et al. 2006, Olariaga et al. 2020) and the current phylogenies (Figs 2, 3).

Contumyces Redhead, Moncalvo, Vilgalys & Lutzoni, Mycotaxon 82: 161 (2002).

Type species – *Contumyces rosellus* (M.M. Moser) Redhead, Moncalvo, Vilgalys & Lutzoni [as ‘*rosella*’], Mycotaxon 82: 161 (2002).

Notes – *Contumyces* was erected to replace the later homonym *Jacobia* Contu and accommodates *C. brunneolilacinus*, *C. rosellus* the generic type and *C. vesuvianus* in *Hymenochaetales* (Redhead et al. 2002). This phylogenetic placement was confirmed by later papers (Larsson et al. 2006, Zhou et al. 2018) and the current phylogenies (Figs 2, 3). Recently, without any explanation, *Contumyces* was proposed to be a subgenus of *Loreleia* as *Loreleia* subgen. *Contumyces* and the generic type *C. rosellus* was transferred to *Loreleia* (Redhead 2019). In the original phylogenetic analysis supporting the erection of *Contumyces*, the only two sampled species from *Contumyces* and *Loreleia*, viz. *C. rosellus* and *L. marchantiae* was separated from each other (Redhead et al. 2002). This separation was later confirmed by Larsson et al. (2006). Similarly, the current phylogenies separate all two sampled species of *Contumyces*, viz. *C. rosellus* and *C. vesuvianus* even not grouping as a well-supported clade from *L. marchantiae* (Figs 2, 3). In the case that molecular sequence from *Loreleia postii* the generic type of *Loreleia* is not available, it seems no reason to merge *Contumyces* into *Loreleia*. Therefore, *Contumyces* is still accepted to be an independent genus from other known genera in *Hymenochaetales*.

Cotylidia P. Karst. [as ‘*Cotilydia*’], Revue mycol., Toulouse 3(no. 9): 22 (1881).

Type species – *Cotylidia undulata* (Fr.) P. Karst. [as ‘*Cotilydi*’], Revue mycol., Toulouse 3(no. 9): 22 (1881).

Notes – *Cotylidia* comprises 11 species with stipitate stereoid basidiomes and smooth hymenophores (Yang et al. 2021). According to morphological characters, this genus was successively placed in *Thelephoraceae* (Welden 1958) and *Podoscyphaceae* (Reid 1965). Moncalvo et al. (2002) for the first time phylogenetically placed species of *Cotylidia* in the hymenochaetoid clade (equal to *Hymenochaetales*). This placement was repeated by later phylogenetic analyses (Redhead et al. 2002, Larsson et al. 2006). However, maybe due to lack of the generic type in previous phylogenetic analyses, the phylogenetic placement of *Cotylidia* in *Hymenochaetales* was not accepted by Welden (2010), who instead placed this genus in *Aphelariaceae*, *Cantharellales*. Later, Sjökvist et al. (2012) included the generic type *Cotylidia undulata* in the phylogenetic analysis on the basis of ITS and nLSU regions, and recovered this genus in *Hymenochaetales*. To sample more gene regions in the current phylogenetic analyses, sequences from an unnamed species of *Cotylidia* that was evidenced to be close to the generic type *C. undulata* (Olariaga et al. 2020) are selected. The resulted phylogenies recover *Cotylidia* as an independent genus from other known genera and families in *Hymenochaetales* (Figs 2, 3).

Ginnsia Sheng H. Wu & Hallenb., in Wu, Nilsson, Chen, Yu & Hallenberg, Fungal Diversity 42(1): 114 (2010).

Type species – *Ginnsia viticola* (Schwein.) Sheng H. Wu & Hallenb., in Wu, Nilsson, Chen, Yu & Hallenberg, Fungal Diversity 42(1): 116 (2010).

Notes – When exploring the taxonomic delimitation of *Phanerochaete*, Wu et al. (2010) found that *Phanerochaete* was polyphyletic and one species *P. viticola* separated from others fell within *Hymenochaetales*. Therefore, a new monotypic genus *Ginnsia* was erected for this species (Wu et al. 2010). The placement of *G. viticola* in *Hymenochaetales* was confirmed by later

phylogenetic analyses (Ghobad-Nejhad et al. 2015, Wu et al. 2021) and the current phylogenies (Figs 2, 3).

Globulicium Hjortstam, Svensk bot. Tidskr. 67(2): 108 (1973).

Type species – *Globulicium hiemale* (Laurila) Hjortstam, Svensk bot. Tidskr. 67(2): 108 (1973).

Notes – *Globulicium* a monotypic genus erected by Hjortstam (1973) was placed in the *Rickenella* clade of *Hymenochaetales* by Larsson et al. (2006), which was accepted by later phylogenetic analyses (Larsson 2007b, Miettinen & Larsson 2011, Olariaga et al. 2020). However, the monophyly of the *Rickenella* clade was never fully resolved as indicated by the current phylogenies (Figs 2, 3). So, *Globulicium* is treated as an independent genus from other known genera and families in *Hymenochaetales*.

Gyroflexus Raithelh., Die Gattung Clitocybe (Stuttgart) 1: 17 (1981).

= *Sphagnomphalia* Redhead, Moncalvo, Vilgalys & Lutzoni, Mycotaxon 82: 162 (2002).

Type species – *Gyroflexus brevibasidiatus* (Singer) Raithelh. [as ‘brevibasidiatum’], Die Gattung Clitocybe (Stuttgart) 1: 17 (1981).

Notes – The monotypic genus *Gyroflexus* was erected with *G. brevibasidiatus* as the generic type (Raithelhuber 1981). Later, on the basis of the same species, another monotypic genus *Sphagnomphalia* was erected in *Hymenochaetales* with the omission of *Gyroflexus* (Redhead et al. 2002). This taxonomic placement at the order level was confirmed by Larsson et al. (2006) and the current phylogenies (Figs 2, 3). Given above, *Gyroflexus* and *Sphagnomphalia* are obligate synonyms, and *Gyroflexus* has a priority over *Sphagnomphalia* as an independent genus in *Hymenochaetales*.

Hastodontia (Parmasto) Hjortstam & Ryvarden, Syn. Fung. (Oslo) 26: 49 (2009).

Type species – *Hastodontia halonata* (J. Erikss. & Hjortstam) Hjortstam & Ryvarden, Syn. Fung. (Oslo) 26: 50 (2009).

Notes – As one of the six genera belonging to *Hyphodontia* sensu lato, the phylogenetic position of *Hastodontia* was proved to be separated from another five genera that are accommodated in three families, viz. *Chaetoporellaceae*, *Hyphodontiaceae* and *Schizoporaceae* in *Hymenochaetales* (Wang et al. 2021). Moreover, the monophyly of *Hastodontia* was also not recovered (Wang et al. 2021). The phylogenetic position of *Hastodontia* in the current phylogenies (Figs 2, 3) is consistent with that in Wang et al. (2021). Therefore, *Hastodontia* is accepted to be an independent genus in *Hymenochaetales*.

Kurtia Karasiński, Index Fungorum 141: 1 (2014).

Type species – *Kurtia argillacea* (Bres.) Karasiński, Index Fungorum 141: 1 (2014).

Notes – Larsson (2007a, b) found nLSU region-based phylogenetic analyses cannot clarify the taxonomic position of *Hyphoderma argillaceum* and its morphologically similar species in *Hyphoderma*. With this species as the generic type, a new genus *Kurtia* was erected to also accommodate another two species previously in *Hyphoderma* (Karasiński 2014). Later, via the identity of nLSU gene region, an ericoid mycorrhizal fungus was linked to *Kurtia argillacea*, and moreover, the phylogenies inferred from the datasets of *tefla* and *rpb2* gene regions, and mt-SSU gene region supported this species in *Hymenochaetales* (Kolařík & Vohník 2018). However, we found that the same gene regions from various collections of *K. argillacea* used in the phylogenetic analyses of Kolařík & Vohník (2018) have distinct variations. Then, we selected one of these collections of *K. argillacea* with the availability of multiple gene sequences for phylogenetic analyses, which indicated *Kurtia* outside from *Hymenochaetales* (data not shown). Taken together, the accuracy of sequences generated from the two cultures of ericoid mycorrhizae instead of basidiomes is questionable. Fortunately, the whole genome of *K. argillacea* sequenced from a polysporic culture originated from basidiomes is available from Joint Genome Institute (JGI;

<https://mycocosm.jgi.doe.gov/Kurarg1/Kurarg1.home.html>), which indicated this species close to *Rickenella* within *Hymenochaetales* (<https://mycocosm.jgi.doe.gov/mycocosm/species-tree/tree;6MGD8G?organism=agaricomycetes>). So, we tentatively place *Kurtia* in *Hymenochaetales* with undefined taxonomic positions at the family level.

Lawrynomycetes Karasiński, Acta Mycologica, Warszawa 48(1): 6 (2013).

Type species – *Lawrynomycetes capitatus* (J. Erikss. & Å. Strid) Karasiński, Acta Mycologica, Warszawa 48(1): 6 (2013).

Notes – *Hyphoderma capitatum* was indicated to occupy a distinct phylogenetic position from *Hyphoderma* and other known genera in *Hymenochaetales* (Larsson et al. 2006, Larsson 2007a). In association of morphological distinctives, a monotypic genus *Lawrynomycetes* was erected for this species (Karasiński 2013). Later, another species was transferred from *Hyphoderma* to this genus as *L. etrusiae*, and meanwhile, the phylogenetic position of *Lawrynomycetes* in *Hymenochaetales* was further confirmed (Salcedo et al. 2020). However, even though *L. capitatus* and *L. etrusiae* were recovered in a strongly supported clade in *Hymenochaetales* (Salcedo et al. 2020), the ITS sequence itself of *L. etrusiae* (MT875014) used in Salcedo et al. (2020) seems to be a chimera (indicated by its cover range from BLAST search). With the exclusion of this ITS sequence, only nLSU gene region is available from *L. etrusiae*. Therefore, this species is not included in the current phylogenetic analyses that confirms *L. capitatus* as an independent lineage in *Hymenochaetales* (Figs 2, 3). The nLSU sequence of *L. etrusiae* (MT875015) indicates this species in *Hymenochaetales* but not having a close relationship with *L. capitatus* and other species via BLAST search. Given above, *Lawrynomycetes* is accepted to be a monotypic genus for *L. capitatus* in *Hymenochaetales*, while the taxonomic position of *L. etrusiae* at the genus level in *Hymenochaetales* needs to be further clarified.

Loreleia Redhead, Moncalvo, Vilgalys & Lutzoni, Mycotaxon 82: 162 (2002).

Type species – *Loreleia postii* (Fr.) Redhead, Moncalvo, Vilgalys & Lutzoni, Mycotaxon 82: 162 (2002).

Notes – When determining the phylogenetic position of several bryophilous omphalinoid species in *Hymenochaetales*, *Loreleia* was newly erected to accommodate *L. marchantiae*, *L. postii* the generic type and *L. roseopallida* (Redhead et al. 2002). Later phylogenetic analyses confirmed *Loreleia* represented by *L. marchantiae* as an independent genus in *Hymenochaetales* (Larsson et al. 2006, Liu et al. 2019). The current phylogenies also recover *L. marchantiae* as an independent lineage in *Hymenochaetales* (Figs 2, 3). Therefore, although the generic type is unavailable for phylogenetic analyses, *Loreleia* is tentatively accepted to be an independent genus in *Hymenochaetales*.

Lyoathelia Hjortstam & Ryvar den, Syn. Fung. (Oslo) 18: 10 (2004).

Type species – *Lyoathelia laxa* (Burt) Hjortstam & Ryvar den, Syn. Fung. (Oslo) 18: 11 (2004).

Notes – *Lyoathelia* was erected as a monotypic genus to accommodate *L. laxa* that was successively placed in *Peniophora*, *Athelia* and *Hyphodontia* (Hjortstam & Ryvar den 2004). Morphologically, *Lyoathelia* was doubtfully placed in *Atheliaceae*, *Atheliales* (Larsson 2007b). This taxonomic opinion was recently accepted by He et al. (2019). However, Sulistyo et al. (2021) for the first time generated molecular sequences from *L. laxa* and phylogenetically placed it in *Hymenochaetales*. The current phylogenies (Figs 2, 3) are consistent with that in Sulistyo et al. (2021). Therefore, *Lyoathelia* is accepted in *Hymenochaetales*.

Musciniupta Redhead, Lücking & Lawrey, Mycol. Res. 113(10): 1167 (2009).

Type species – *Musciniupta laevis* (Fr.) Redhead, Lücking & Lawrey, Mycol. Res. 113(10): 1167 (2009).

Notes – *Muscinipta laevis* was previously well known as *Cyphellostereum laeve* in *Hymenochaetales* (Larsson et al. 2006). However, *Cyphellostereum pusiolum* the generic type of *Cyphellostereum* was found to occupy a distant position in *Hygrophoraceae*, *Agaricales* (Lawrey et al. 2009). Therefore, a monotypic genus *Muscinipta* was newly proposed for *C. laeve* in *Hymenochaetales* (Lawrey et al. 2009). This taxonomic proposal is confirmed in the current phylogenies (Figs 2, 3).

Sphaerobasidium Oberw., Sydowia 19(1-6): 57 (1966) [1965].

Type species – *Sphaerobasidium minutum* (J. Erikss.) Oberw. ex Jülich, Persoonia 10(3): 335 (1979).

Notes – *Sphaerobasidium* was placed in *Repetobasidiaceae* (Jülich 1981) and later doubtfully in *Tubulicrinaceae* (Larsson 2007b). However, the placement of this genus at the family level was contrary in previous phylogenetic analyses (Binder et al. 2005, Larsson et al. 2006). Likewise, the current phylogenies also do not reliably support *Sphaerobasidium* together with *Repetobasidium* or *Tubulicrinis* in *Hymenochaetales* (Figs 2, 3). Therefore, *Sphaerobasidium* is treated as an independent genus from other known genera and families in *Hymenochaetales*.

Subulicium Hjortstam & Ryvar den, Mycotaxon 9(2): 511 (1979).

Type species – *Subulicium lautum* (H.S. Jacks.) Hjortstam & Ryvar den, Mycotaxon 9(2): 513 (1979).

Notes – *Subulicium* accommodating three species is not a well-studied genus from the phylogenetic perspective. The only available molecular data of this genus is a nLSU sequence from an unnamed species of *Subulicium*, which indicated its phylogenetic position in *Hymenochaetales* (Redhead et al. 2002, Binder et al. 2005). Even though this genus is not included in the current phylogenetic analyses due to that only a nLSU sequence is available, the phylogenetic evidence from previous papers (Redhead et al. 2002, Binder et al. 2005) is solid enough to place *Subulicium* in *Hymenochaetales*. The phylogenetic relationship of *Subulicium* with other known genera and families in *Hymenochaetales* needs to be further determined by sampling more gene regions from more taxa of *Subulicium* in phylogenetic analyses.

Tsugacorticium Nakasone & Burds., N. Amer. Fung. 7(1): 3 (2012).

Type species – *Tsugacorticium kenaicum* Nakasone & Burds., N. Amer. Fung. 7(1): 6 (2012).

Notes – The monotypic genus *Tsugacorticium* and its generic type *T. kenaicum* were described from Alaskan specimens (Nakasone & Burdsall 2012) that were earlier misidentified to *Dendrothele incrustans* by Volk et al. (1994). The original phylogenetic analysis indicated *T. kenaicum* in *Hymenochaetales* and weakly related to members of *Rickenellaceae*, although lack of close morphological similarity (Nakasone & Burdsall 2012). Later papers confirmed the phylogenetic position of *T. kenaicum* at the order but not family level (Kolařík & Vohník 2018, Korotkin et al. 2018, Wu et al. 2021) that is consistent to the current phylogenies (Figs 2, 3). Therefore, *Tsugacorticium* is accepted to be an independent genus from other known genera and families in *Hymenochaetales*.

Discussion

The taxonomic frame of *Hymenochaetales* is updated based on multilocus phylogenetic and molecular clock analyses. Eventually, a total of 14 families, viz. *Chaetoporellaceae*, *Hymenochaetaceae*, *Hyphodontiaceae*, *Odonticiaceae*, *Peniophorellaceae*, *Repetobasidiaceae*, *Resiniaceae*, *Rickenellaceae*, *Rigidoporaceae*, *Schizocorticaceae*, *Schizoporaceae*, *Sideraceae*, *Skvortzoviaceae* and *Tubulicrinaceae* are accepted in *Hymenochaetales*. Moreover, 19 genera are considered to have uncertain taxonomic position at the family level in *Hymenochaetales*. In addition, *Botryodontia*, *Neoantrodiella* and *Skvortzoviella* are considered to be later synonyms of *Rigidoporus*, *Cyanotrama* and *Schizocorticium*, respectively.

All the 14 families accepted in *Hymenochaetales* under the current circumscription are monophyletic (Figs 2, 3) and their divergence times fit well with the range of basidiomycetous families estimated previously (He et al. 2019, Fig. 5). These molecular analyses are more and more considered to be the crucial basis to delimit taxonomic circumscriptions at and above the family level (e.g., Larsson et al. 2004, Dentinger & McLaughlin 2006, Hibbett et al. 2007, Larsson 2007b, Olariaga et al. 2020, Sulistyo et al. 2021, Liu et al. 2022a). In addition, the macromorphological characters of these families are relatively uniform, except for the enlarged *Hymenochaetaceae*. However, even under the original circumscription, *Hymenochaetaceae* is composed of species producing stipitate, sessile, resupinate and clavarioid basidiomes with poroid, odontoid, lamellate and smooth hymenophoral configurations (Miettinen et al. 2019, Wu et al. 2022).

Of the 14 families accepted in *Hymenochaetales*, eight family names are previously known. The concepts of *Hyphodontiaceae* and *Schizoporaceae* are, respectively, adopted from the recent erection and emendation by Wang et al. (2021), while those of another six families are emended. The circumscription of *Chaetoporellaceae* is enlarged by adding *Echinoporia* in this family comparing with the reinstatement of this monotypic family by Wang et al. (2021). A larger concept of *Hymenochaetaceae* firstly indicated by Wang et al. (2021) is formally proposed to accommodate members originally in the families *Coltriciaceae*, *Hymenochaetaceae*, *Neoantrodiellaceae* and *Nigrofomitaceae*, and the genera *Basidioradulum* and *Trichaptum*. *Repetobasidiaceae* and *Tubulicrinaceae* that were not accepted by He et al. (2019) and Wang et al. (2021) are reinstated as two monotypic families. The circumscription of *Rickenellaceae* is reduced to be a monotypic family comparing with Vizzini (2010) and Olariaga et al. (2020). The family name *Rigidoporaceae* is resurrected to replace its later synonym *Oxyporaceae* that was inaccurately used in recent papers (Zhou et al. 2018, He et al. 2019, Wang et al. 2021). It is noteworthy that the clade of *Rigidoporaceae* is not strongly supported (Figs 2, 3, 5). Therefore, the circumscription of this family needs to be further clarified.

Besides the above-mentioned previously known families, six new families are erected to make as many genera as possible being accommodated at the family level. Of the six families, five are monotypic families, viz. *Peniophorellaceae*, *Resiniciaceae*, *Schizocorticiaceae*, *Sideraceae* and *Skvortzoviaceae*, while *Odonticiaceae* accommodates *Leifia* and *Odonticum*. Although these families are small-sized at the genus level, their independences at the family level in *Hymenochaetales* are strongly supported (Figs 2, 3). Moreover, species diversity of the genera within each family has been recently explored in association of morphological and phylogenetic evidence (Liu et al. 2019, Yurchenko et al. 2020, Wu et al. 2021, Yu et al. 2021, Liu et al. 2022b). Therefore, it is reasonable to provide definite taxonomic position at the family level for these genera at this stage. In future, more genera may be included in these families like the phenomenon of *Chaetoporellaceae* from a monotypic family when reinstatement (Wang et al. 2021) to adding one more genus *Echinoporia* here.

Although we aim to place each genus accepted in *Hymenochaetales* in a proper family, the family positions of 19 genera are still not determined. Of these genera, *Hastodontia*, *Lawryomyces*, *Sphaerobasidium* and *Tsugacorticium* are clearly independent from other genera and known families in *Hymenochaetales* (Figs 2, 3), and likewise, *Kurtia* and *Subulicium* were also proved to be separated genera in the phylogenomics backbone in JGI (<https://mycocosm.jgi.doe.gov/mycocosm/species-tree/tree;6MGD8G?organism=agaricomycetes>) and the previous phylogenetic analyses (Redhead et al. 2002, Binder et al. 2005, Kolařík & Vohník 2018). This phenomenon indicates that new families need to be erected for these six corticioid fungal genera. However, we prefer to refrain from formally proposing any taxonomic changes until more samples and gene regions from these six genera can be included in phylogenetic analyses. Regarding other 13 genera, viz. *Alloclavaria*, *Atheloderma*, *Blasiphalia*, *Bryopistillaria*, *Cantharelloopsis*, *Contumyces*, *Cotylidia*, *Ginnsia*, *Globulicium*, *Gyroflexus*, *Loreleia*, *Lyoathelia* and *Musciniupta*, they all group together with *Rickenella* without reliable statistical support in the current phylogenetic analyses (Figs 2, 3). *Lyoathelia* was recently moved to *Hymenochaetales* from *Atheliales* (Sulistyo et al. 2021), while the other 12 genera were previously accepted in

Rickenellaceae (Olariaga et al. 2020). Although the clade comprising these 13 genera and *Rickenella* is not well supported, its monophyly cannot be rejected (Figs 2, 3). Therefore, to avoid creating superfluous family names, the family positions of these 13 genera have to be left open at this stage. Of these 13 genera, *Alloclavaria*, *Bryopistillaria* and *Musciniupta* were newly erected for species originally placed in *Agaricales* (Dentinger & McLaughlin 2006, Lawrey et al. 2009, Olariaga et al. 2020), while *Atheloderma* and *Lyoathelia* were moved from *Atheliales* (Larsson et al. 2006, Sulistyo et al. 2021) and *Cotyldia* from *Cantharellales* (Sjökqvist et al. 2012); moreover, *Alloclavaria*, *Blasiphalia*, *Bryopistillaria*, *Cantharellopsis*, *Ginnsia*, *Globulicium*, *Gyroflexus*, *Lyoathelia* and *Musciniupta* are monotypic genera. Therefore, the species diversity of these poorly studied genera also needs to be further explored in association with species currently placed outside *Hymenochaetales*, which, as well as including more gene regions in phylogenetic analyses, may be helpful to clarify the phylogenetic relationship among these genera and then their taxonomic positions at the family level.

At the species level, some potential new species are revealed from the genera *Coltricia*, *Fulvoderma*, *Hyphodontia*, *Lyomyces* and *Rigidoporus*, while species complexes are found in *Cyanotrampa*, *Fasciodontia* and *Schizocorticium* (Fig. 3). It is expected that more new species await to be discovered, which is beyond the current scope focusing on taxonomic framework and will be dealt with in separated works.

Since the erection of *Hymenochaetales*, some more genera than above-mentioned were included in this fungal order, but the placements of these genera are not reliable or even inaccurate and thus are not accepted as independent genera in *Hymenochaetales* for various reasons as exemplified below.

Caeruleomyces was erected to accommodate the later homonym *Sporotrichum azureum* J.E. Wright & Arx and was placed in *Hymenochaetales* (Staplers 2000); however, its taxonomic placement at the order level is arbitrary due to the simple anamorphic morphological characters and lack of molecular evidence. Moreover, the taxonomic position of *Caeruleomyces* in *Hymenochaetales* is also not followed by MycoBank (MB 28445, MB 467629, access on April 24, 2022).

Erythromyces was erected as a monotypic genus for *E. crocicreas* that was segregated from *Hymenochaete* due to its distinct morphological characters (Hjortstam & Tellería 1990). Maybe for the segregation from the type genus of *Hymenochaetales*, *Erythromyces* was placed in *Hymenochaetales* (He et al. 2019), although its taxonomic position at the order level was earlier considered to be uncertain by Larsson (2007b). Actually, a previous phylogeny in Yuan & Wan (2012) that was also cited by He et al. (2019) clearly indicated that *Erythromyces* fell within the clade being composed of genera in *Polyporales*.

Physodontia was doubtfully placed in *Hymenochaetales* by Larsson (2007b). This taxonomic placement was followed by He et al. (2019). However, the only available molecular sequence from this monotypic genus (KJ140741 in GenBank) indicates its position in *Polyporales* via BLAST search. This ITS sequence was resulted from Brazeo et al. (2014) that was also mentioned by He et al. (2019).

Paratrachaptum was placed in *Hymenochaetales* without molecular evidence by He et al. (2019). However, later phylogenetic analysis indicated this genus as the basal lineage of *Gloeophyllales* (Chen et al. 2020).

Odontiopsis was proposed to be a later synonym of *Xylodon* by recent phylogenetic analysis (Riebesehl et al. 2019).

It is aware that the whole genome sequences are available from about two dozen species of *Hymenochaetales* in National Center for Biotechnology Information (<https://www.ncbi.nlm.nih.gov/data-hub/genome/?taxon=139380>) and JGI (<https://mycocosm.jgi.doe.gov/Hymenochaetales/Hymenochaetales.info.html>). Comparing with the high species diversity of *Hymenochaetales*, the number of available genomes that mostly concentrate in *Hymenochaetaceae* is quite low. This makes it impossible to achieve a comprehensive phylogenetic relationship of *Hymenochaetales* with the help of phylogenomic

analyses. Therefore, molecular analyses using multiple gene sequences are still the best way towards the taxonomic framework of *Hymenochaetales*. Moreover, the current framework is not conflict with the topology generated from the phylogenomics of *Hymenochaetales* indicated in JGI (<https://mycocosm.jgi.doe.gov/mycocosm/species-tree/tree;6MGD8G?organism=agaricomycetes>). In future, genomic data from more species in *Hymenochaetales* will help determine the current taxonomic framework.

In conclusion, a more natural taxonomic system of *Hymenochaetales* is achieved, and 14 families and 83 genera are accepted in this fungal order. This system is a crucial basis for further exploring species diversity, resource utilization and evolutionary trends in *Hymenochaetales*, on which we have been focusing.

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Supplementary materials

Supplementary File 1 Alignment resulted from the dataset 1.

[Supplementary File 1](#)

Supplementary File 2 Alignment resulted from the dataset 2.

[Supplementary File 2](#)

Supplementary File 2.1 Alignment resulted from the sub-dataset 2.1.

[Supplementary File 2.1](#)

Supplementary File 2.2 Alignment resulted from the sub-dataset 2.2.

[Supplementary File 2.2](#)

Supplementary File 2.3 Alignment resulted from the sub-dataset 2.3.

[Supplementary File 2.3](#)

Supplementary File 2.4 Phylogenetic tree generated from the sub-dataset 2.1 by the maximum likelihood algorithm.

[Supplementary File 2.4](#)

Supplementary File 2.5 Phylogenetic tree generated from the sub-dataset 2.1 by the Bayesian inference algorithm.

[Supplementary File 2.5](#)

Supplementary File 2.6 Phylogenetic tree generated from the sub-dataset 2.2 by the maximum likelihood algorithm.

[Supplementary File 2.6](#)

Supplementary File 2.7 Phylogenetic tree generated from the sub-dataset 2.2 by the Bayesian inference algorithm.

[Supplementary File 2.7](#)

Supplementary File 2.8 Phylogenetic tree generated from the sub-dataset 2.3 by the maximum likelihood algorithm.

[Supplementary File 2.8](#)

Supplementary File 2.9 Phylogenetic tree generated from the sub-dataset 2.3 by the Bayesian inference algorithm.

[Supplementary File 2.9](#)

Supplementary File 3 Alignment resulted from the dataset 3.

[Supplementary File 3](#)

Supplementary File 4 Alignment resulted from the dataset 4.

[Supplementary File 4](#)