Terrestriporiaceae fam. nov., a new family of Russulales (Basidiomycota)

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Abstract

A new family of Russulales, Terrestriporiaceae fam. nov. is proposed based on the combination of molecular and morphological data, and it is typified by *Terrestriporia* gen. nov. The phylogenetic analyses inferred from the combined dataset of five genes, including ITS, nLSU, RPB1, RPB2 and TEF1, show that *Terrestriporia alba* sp. nov. forms a monophyletic lineage within Russulales. The Bayesian evolutionary analysis on two datasets of RPB1 and RPB2 sequences indicate an ancient divergence of the new family from Albatrellaceae during the Cretaceous (124.68±0.39 Mya). The new family is characterized by annual and resupinate basidioma, poroid hymenophore, a monomitic hyphal structure, and generative hyphae mostly simple septate, but occasionally having clamp connections, the presence of gloeoplerous hyphae and cystidioles, thin-walled, hyaline, smooth, amyloid and acyanophilous basidiospores.

Key words – phylogeny – polypore – taxonomy – wood-inhabiting fungi

Introduction

The Russulales Kreisel ex P.M. Kirk, P.F. Cannon & J.C. David is a highly diverse group of Agaricomycetes including around 2000 described species in 83 genera and 13 families (Kirk et al. 2008, Chen et al. 2016, Hyde et al. 2017, Wang 2018, Caboñet al. 2019, Vidal et al. 2019). It contains not only the lamellate species like *Russula* Pers. and *Lactarius* Pers. (Herrera et al. 2018, Caboñ et al. 2019), but also the poroid, hydroid and corticioid representatives like *Heterobasidion* Bref., *Herichium* Pers. and *Asterostroma* Masee (Chen et al. 2015, Liu et al. 2017). Russulales is a very important group of basidiomycetes because of the ectomycorrhizal, saprobic and pathogenic species (Henkel et al. 2000, Chen et al. 2016). However, the phylogeny among many taxa in the order is not well demonstrated (Larsson et al. 2004, Chen et al. 2016, Liu et al. 2017, Leal-Dutra et al. 2018, Vizzini et al. 2018).

During a field trip to Malaysia, four samples were collected on soil in a tropical forest. These samples have resupinate basidiocarps with poroid hymenophore, and the ecology and macro-morphology are similar to those of *Byssoporia terrestris* (DC.) M.J. Larsen & Zak. After further laboratory examination we found these samples have thin-walled and amyloid basidiospores, while *Byssoporia terrestris* has thick-walled non-amyloid basidiospores. The multi-locus phylogenetic analysis on these samples and related taxa was carried out, the Malaysian samples form a

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monophyletic lineage within Russulales, and no existing family fits them, so we described a new species for these samples. A new genus and a new family are proposed for accommodating the new species. In addition, based on RPB1 and RPB2 sequences the Bayesian evolutionary analysis is carried out to indicate divergence time of the new family.

Materials & Methods

Morphological studies

The studied specimens are deposited in the herbarium of the Institute of Microbiology, Beijing Forestry University (BJFC), Royal Botanic Gardens Victoria (MEL), and the private herbarium of Josef Vlasák (JV) which will be sent to National Museum Prague (PRM). Morphological descriptions are based on field notes and herbarium specimens. Microscopic analyses follow Song & Cui (2017). In the description: KOH = 5% potassium hydroxide, CB– = acyanophilous in Cotton Blue, IKI– = neither amyloid nor dextrinoid in Melzer's reagent. The microscopical measurements and drawings were made from slide preparations stained with Cotton Blue, L = arithmetic average of all spore length, W = arithmetic average of all spore width, Q = L/W ratios, n = number of spores/measured from given number of specimens. Special color terms are cited from Anonymous (1969) and Petersen (1996).

DNA extraction, PCR and sequencing

A CTAB rapid plant genome extraction kit (Aidlab Biotechnologies, Beijing) was used to obtain PCR products from dried specimens, according to the manufacturer's instructions with some modifications (Chen et al. 2016). The DNA was amplified with the primers: ITS5 and ITS4 for ITS (White et al. 1990), LR0R and LR7 for nLSU (Vilgalys & Hester 1990), RPB1-Af and RPB1-Cr for RPB1 (Matheny et al. 2002), bRPB2-6F and bRPB2-7R for RPB2 (Matheny 2005), and EF1-983F and EF1-1567R for TEF1 (Rehner 2001). The PCR procedure for ITS and TEF1 was as follows: initial denaturation at 95°C for 3 min, followed by 35 cycles at 94°C for 40 s, 54°C for 45 s and 72°C for 1 min, and a final extension of 72°C for 10 min. The PCR procedure for nLSU was as follows: initial denaturation at 94°C for 1 min, followed by 35 cycles at 94°C for 30 s, 50°C for 1 min and 72°C for 1.5 min, and a final extension of 72°C for 10 min. The PCR procedure for RPB1 and RPB2 included an initial denaturation at 94°C for 2 min, followed by 10 cycles at 94°C for 40 s, 60°C for 40 s and 72°C for 2 min, then followed by 37 cycles at 94°C for 45 s, 53–58°C for 1.5 min and 72°C for 2 min, and a final extension of 72°C for 10 min. The PCR products were purified and sequenced in Beijing Genomics Institute, China with the same primers.

Phylogenetic analyses

New sequences, deposited in GenBank (Table 1), were aligned with additional sequences retrieved from GenBank (Table 1) using BioEdit (Vilgalys & Hester 1990) and ClustalX (Thompson et al. 1997). *Calocera cornea* (Batsch) Fr. and *Dacryopinax spathularia* (Schwein.) G.W. Martin were used as outgroups. Prior to phylogenetic analysis, ambiguous regions at the start and the end of the alignment were deleted and gaps were manually adjusted to optimize the alignment. The edited alignment was deposited at TreeBase (Treebase No. 25791).

Table 1 A list of species, specimens and GenBank accession number of sequences used in this study

Species	Specimen Number	ITS	LSU	RPB1	RPB2	TEF1
<i>Albatrellus avellaneus</i>	Dai20805	–	–	MW290309	MW290302	–
<i>Albatrellus avellaneus</i>	Dai20806	MW269672	MW269684	MW290310	MW290303	MW290319
<i>Albatrellus ellisii</i>	PKSR12	KJ411956		KJ411963	KJ411971	–
<i>Albatrellus ovinus</i>	PS11795	MW269673	MW269685	–	MW290304	MW290320

Table 1 Continued.

Species	Specimen Number	ITS	LSU	RPB1	RPB2	TEF1
<i>Aleurocystidiellum disciforme</i>	NH 13003	AF506402	AF506402	–	–	–
<i>Aleurocystidiellum subcruentatum</i>	He2886	KU559341	KU574847	–	–	KU992720
<i>Aleurodiscus bambusinus</i>	He4361	KY706207	KY706219	–	–	LC430911
<i>Aleurodiscus wakefieldiae</i>	He2580	KU559353	KU574841	KX577720	KX577723	KU992710
<i>Amylostereum laevigatum</i>	olrim409	AY781246	AF287843	–	AY218469	–
<i>Amylostereumchailletii</i>	B1387	KM821143	–	–	KM882973	KM981422
<i>Auricularia tibetica</i>	Cui12267	KT152106	KT152122	MW290311	KT152139	MW290321
<i>Auriscalpium</i> sp.	HKAS86980	KY485962	KY485989	–	KY495306	–
<i>Auriscalpium vulgare</i>	HKAS93484	MK211170	KY485984	–	KY495319	KY474614
<i>Boletus edulis</i>	HMJAU4637	JN563894	KF112455	KF112586	KF112704	KF112202
<i>Bondarzewia berkeleyi</i>	Dai 12759	KJ583202	KJ583216	KX066152	KX066162	KX066138
<i>Bondarzewia dickinsii</i>	Dai 13413	KJ583210	KJ583224	KX066151	KX066161	KX066137
<i>Bondarzewia occidentalis</i>	HHB 14803	KM243329	KM243332	KX066156	KX066163	KX066142
<i>Bondarzewia podocarpi</i>	Cui 6380	KJ583206	KJ583220	KX577718	KX577721	KX252745
<i>Bondarzewia tibetica</i>	Yu 56	KT693203	KT693205	KX066158	KX066165	KX066148
<i>Byssoporia terrestris</i>	Hjm18172	DQ389664	DQ389664	–	–	–
<i>Calocera cornea</i>	AFTOL-ID 438	AY789083	AY701526	AY857980	AY536286	AY881019
<i>Dacryopinax spathularia</i>	AFTOL-ID 454	AY854070	AY701525	AY857981	AY786054	AY881020
<i>Echinodontium tinctorium</i>	AFTOL-ID 455	AY854088	AF393056	AY864882	AY218482	AY885157
<i>Exidia glandulosa</i>	Wu265	MN850376	MN850356	MW290312	MN819812	MN819834
<i>Fomitiporia hartigii</i>	Dai 11766	KT203287	KT203308	KJ651628	KJ651721	–
<i>Fomitiporia mediterranea</i>	AFTOL-ID 688	AY854080	AY684157	AY864869	AY803748	AY885149
<i>Gloeophyllum sepiarium</i>	CFMR Wilcox-3BB	NR_119869	NG_060630	–	HM536109	HM536110
<i>Gloeophyllum trabeum</i>	isolate 1320	HM536094	HM536067	–	HM536112	HM536113
<i>Heterobasidion annosum</i>	06129/6	KJ583211	KJ583225	KF033133	KF006499	KX252741
<i>Heterobasidion parviporum</i>	voucher 091605	KJ651503	KJ651561	KJ651657	KJ651750	KX252742
<i>Lactarius crocatus</i>	KVP08034	HQ318243	HQ318151	JN389145	HQ328888	–
<i>Lactarius deceptivus</i>	AFTOL-ID 682	AY854089	AY631899	AY864883	AY803749	AY885158
<i>Lactarius sulphosmus</i>	HMAS 276808	NR_160503	LT602948	KX442536	KX442559	KX442513
<i>Lactifluus</i> sp.	HMAS 276798	LT602968	LT602945	KX442533	KX442556	KX442510
<i>Malassezia globosa</i>	CBS 7966			KF706493	KF706518	
<i>Marasmius rotula</i>	AFTOL-ID 1505	–	–	DQ447922	DQ474118	–
<i>Mycena amabilissima</i>	AFTOL-ID 1686	–	–	DQ447926	DQ474121	–
<i>Mycena aurantiidisca</i>	AFTOL-ID 1685	–	–	DQ447927	DQ474122	–
<i>Neurospora crassa</i>	OR74A			XM959004	AF107789	
<i>Peniophora nuda</i>	AFTOL-ID 660	DQ411533	–	–	DQ408129	DQ435788

Table 1 Continued.

Species	Specimen Number	ITS	LSU	RPB1	RPB2	TEF1
<i>Perplexostereum endocrocinum</i>	Dai15998	KY172899	KY172915	–	–	–
<i>Phylloporia gutta</i>	Dai16070	MH151183	MH165863	MW290313	MH161215	MH167423
<i>Picipes tibeticus</i>	Cui12215	KU189755	KX196787	KU189879	KU189975	KU189902
<i>Polyporus squamosus</i>	Cui10595	KU189778	KU189809	KU189892	KU189988	KU189925
<i>Pseudowrightoporia japonica</i>	Dai12086	KJ513293	KM107883	KX577719	KX577722	–
<i>Russula blennia</i>	569/BB08.066	MH545687	KU237556	KU237701	KU237842	KU237987
<i>Russula pseudociliata</i>	545/BB08.061	MH545688	KU237537	KU237686	KU237823	KU237967
<i>Serpula lacrymans</i>	REG 383	–	–	GU187485	GU187809	–
<i>Rhizopus stolonifer</i>	AFTOL-ID 632			AFTOL database	AFTOL database	
<i>Schizosaccharomyces pombe</i>	972h			NM001021568	NM001018498	
<i>Stereum hirsutum</i>	AFTOL-ID 492	AY854063	–	AY864885	AY218520	AY885159
<i>Suillus pictus</i>	AFTOL-ID 717	–	–	AY858965	AY786066	–
<i>Terrestriporia alba</i>	Dai 18546	MT068558	MT068562	MW290314	MW290305	MW290322
<i>Terrestriporia alba</i>	Dai 18547	MT068559	MT068563	MW290315	MW290306	MW290323
<i>Terrestriporia alba</i>	Dai 18548	MT068560	MT068564	MW290316	MW290307	MW290324
<i>Terrestriporia alba</i>	Dai 18556	MT068561	MT068565	MW290317	MW290308	MW290325
<i>Trametes suaveolens</i>	Cui10697	KC848280	KC848365	KX880839	KX880866	KX880933
<i>Ustilago maydis</i>	AFTOL-ID 505			AFTOL database	AY485636	
<i>Vararia abortiphysa</i>	CBS 630.81	KR364005	KR364133	–	KR364266	–
<i>Wrightoporia srilankensis</i>	Dai 19667	MN688692	MN688685	MW290318	–	MW290326
<i>Wrightoporia lenta</i>	Dai 10462	KJ513291	KJ807082	–	–	–
<i>Wrightoporia subavellanea</i>	Dai 11488	KJ513296	KJ807086	–	–	–
<i>Xerocomus sp.</i>	HKAS52557	KC215207	KC215220	KC215225	KC215234	KC215243

Note: New sequences are in **bold**.

Maximum parsimony (MP) analysis was also applied to the combined ITS+nLSU+RPB1+RPB2+TEF1 dataset. Tree construction was performed in PAUP* version 4.0b10 (Swofford 2002). All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1000 random sequence additions. Max-trees were set to 5000, branches of zero length were collapsed and all parsimonious trees were saved. Clade robustness was assessed using a bootstrap (BT) analysis with 1000 replicates (Felsenstein 1985). Descriptive tree statistics tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each maximum parsimonious tree (MPT) generated. Phylogenetic trees were visualized using Treeview (Page 1996).

Maximum likelihood (ML) and Bayesian inference (BI) analysis were applied to the combined dataset too. Substitution models suitable for each partition in the dataset were determined using Akaike Information Criterion (AIC) implemented in MrModeltest2.3 (Nylander 2004). The GTR+I+G model was estimated as the best-fit evolution models for all partition in the combined dataset. BI was calculated with MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) with GTR+I+G model of DNA substitution and an invgamma distribution rate variation across sites. Four Markov chains were run for 2 runs from random starting trees for 6 million generations of the combined dataset and sampled every 100 generations. The burn-in was set to discard the first 25% of the trees.

A majority rule consensus tree of all remaining trees was calculated. ML tree was done applying raxmlGUI 1.2 (Stamatakis 2006, Silvestro & Michalak 2012) with the model GTR + I + G and the option of auto FC (Pattengale et al. 2010) in BS (bootstrap) replicates. Branches that received bootstrap support values for MP and ML greater than or equal to 70% and BPP greater than or equal to 0.95 were considered as significantly supported.

Divergence time estimation

The BEAST 1.8.0 software package was used to estimate divergence times (Drummond & Rambaut 2007). Internal calibration to determine the divergence time between Ascomycota and Basidiomycota, 582 Mya, with the 400-million-years-old fossil *Paleopyrenomycites devonicus* Taylor et al. was used in present study. A normal distribution was applied by setting the mean and the standard deviation to 582.5 and 50.15 (Taylor et al. 2004). Two fossils for comparison were used, i: *Archaeomarasmius leggetti* Hibbett et al., an agaricoid fruiting body preserved in 90 Ma Dominican amber (Hibbett et al. 1997) as representative of the minimum age of Agaricales, ii: *Quatsinoporites cranhamii* S.Y. Sm. et al., a poroid fruiting body from Apple Bay on Vancouver Island from 113 Ma (Smith et al. 2004) as representative of the minimum age of Hymenochaetales. An XML file with BEAUTI v1.8.4 with a combined RPB1 and RPB2 alignment was constructed. For both partitions, the GTR model was chosen as the best substitution model by MrModelTest, and a relaxed lognormal model was employed for molecular clock analysis (Drummond & Rambaut 2007). The tree prior was set to Yule speciation. For each analysis, two independent runs were conducted for 5000 million generations. Log files of the two runs were combined using LogCombiner by setting the first 10% of the logs as burn-ins and then analyzed in Tracer 1.5 (<http://tree.bio.ed.ac.uk/software/figtree/tracer>). The resulting trees were also combined, interpreted in TreeAnnotator, and viewed in FigTree 1.4.0.

Results

Phylogenetic analysis with the combined dataset

The combined dataset included sequences from 52 fungal collections representing 49 species. The dataset had an aligned length of 4587 characters, of which 1635 characters are constant, 568 are variable and parsimony-uninformative, and 2384 are parsimony-informative. MP analysis yielded one equally parsimonious trees (TL = 16245, CI = 0.356, RI = 0.538, RC = 0.191, HI = 0.644). The best model for the combined dataset estimated and applied in the BI was GTR+I+G. BI resulted in a similar topology with an average standard deviation of split frequencies = 0.006471 to MP and ML analysis, and thus only the BI tree was provided. The phylogenetic tree inferred from the combined dataset (Fig. 1) shows that the newly sequence specimen formed a distinct lineage within Russulales.

The resulting phylogenetic tree was overall consistent with the previous reports (Larsson 2007, Chen et al. 2016). The phylogenetic analyses based on the combined dataset produced a well-resolved phylogeny, and twelve major clades of Russulales were identified (Fig. 1). *Terrestriporia alba* formed a distinct lineage with strong support in the Russulales clade, and was close to Albatrellaceae Nuss (Fig. 1).

Divergence of Terrestriporiaceae

The alignment of the two datasets (RPB1 and RPB2) are 668 and 1137 bp in length respectively, consisted of 40 taxa. Analyses calibrated by *Paleopyrenomycites devonicus* (Fig. 2), 582 Mya between Ascomycota and Basidiomycota estimate the divergence time of Hymenochaetales at 176.11 ± 0.64 Mya (120.03–234.73 Mya, 95% HPD) and the divergence time of Agaricales at 137.19 ± 0.5 Mya (98.66–177.98 Mya, 95% HPD), that meet the minimum age of Hymenochaetales and Agaricales at 113 Mya and 90 Mya. The initial diversification between Terrestriporiaceae and Albatrellaceae at 124.68 ± 0.39 Mya (91.47–159.17 Mya, 95% HPD). The estimated divergence times for other nodes are summarized in Fig. 2.

Figure 1 – BI tree illustrating the phylogeny of *Terrestriporia alba*, and related species in Agaricomycetes based on the combined ITS+nLSU+RPB1+RPB2+TEF1 dataset. Branches are labelled with maximum parsimony and maximum likelihood bootstrap proportions higher than 75% and Bayesian posterior probabilities more than 0.95 respectively.

Figure 2 – Chronogram and estimated divergence times of Terrestriporiaceae generated by molecular clock analysis using the RPB1 and RPB2 dataset. The chronogram was obtained using the Ascomycota–Basidiomycota divergence time of 582 Mya as the calibration point. The calibration point and objects of this study are marked in the chronogram. The geological time scale is in millions of years ago (Mya).

Taxonomy

Terrestriporiaceae Y.C. Dai, B.K. Cui, F. Wu, Y. Yuan & Jia J. Chen, fam. nov.

Mycobank number: MB 834539; Facesoffungi number: FoF 09499

Type genus – *Terrestriporia* Y.C. Dai, B.K. Cui, F. Wu, Y. Yuan & Jia J. Chen

Habitat – grows on soil.

Rotting type – unknown.

Basidioma annual, resupinate, hymenophore poroid, hyphal structure monomitic, generative hyphae mostly simple septate, but occasionally having clamp connections, gloeoplerous hyphae present, basidiospores hyaline, thin-walled, smooth, amyloid.

Notes – The family Terrestriporiaceae is established to accommodate the genera *Terrestriporia* in the order Russulales based on its distinct lineage in the phylogenetic analysis. The combined phylogeny of five genes data (Fig. 1) demonstrates that Terrestriporiaceae is related to Albatrellaceae but shows no affinity to the other families of Russulales. The family Albatrellaceae includes mostly stipitate and mycorrhizal species. Hence a new family Terrestriporiaceae is established.

Terrestriporia Y.C. Dai, B.K. Cui, F. Wu, Y. Yuan & Jia J. Chen, gen. nov.

Mycobank number: MB 834540; Facesoffungi number: FoF 09501

Etymology – *Terrestriporia* (Lat.): referring to the species in the genus growing on ground.

Type species – *Terrestriporia alba* Y.C. Dai, B.K. Cui, F. Wu & Jia J. Chen, sp. nov.

Habitat – grows on soil.

Rotting type – unknown.

Basidioma annual, resupinate, hymenophore poroid and white, hyphal structure monomitic, generative hyphae mostly simple septate, but occasionally with clamp connections, gloeoplerous hyphae and gloecystidioles present, basidiospores hyaline, thin-walled, smooth, amyloid, acyanophilous.

Terrestriporia alba Y.C. Dai, B.K. Cui, F. Wu, Y. Yuan & Jia J. Chen, sp. nov.

Figs 3-5

Mycobank number: MB 834545; Facesoffungi number: FoF 09502

Diagnosis – Differs from other poroid species of Russulales by its annual and resupinate habit, a monomitic hyphal structure with both simple septa and clamp connections, the presence of both gloeoplerous hyphae and gloecystidioles, ellipsoid, hyaline, thin-walled, smooth basidiospores.

Type – MALAYSIA, Kuala Lumpur, Forest Eco-Park, on ground of a slope with some fine roots in the soil, 14 April 2018, *Dai 18548* (BJFC026837, holotype).

Etymology – *Alba* (Lat.): referring to the species having white pores.

Fruiting body – Basidioma annual, resupinate, inseparable from substrate, soft and without odour or taste when fresh, soft corky when dry. Pore surface white when fresh, becoming buff when dry; margin distinct, fimbriate, concolorous with pore surface, up to 3 mm wide, thinning out; pores round to angular, 2–3 per mm; dissepiment thick, entire to slightly lacerate, cottony. Subiculum concolorous with pores, cottony to soft corky, up to 0.4 mm thick. Tubes concolorous with hymenophore, soft corky, up to 0.7 mm long.

Hyphal structure – Hyphal system monomitic; generative hyphae mostly simple septate, occasionally bearing clamp connections; all hyphae IKI–, CB–, frequently encrusted by fine crystals; tissues unchanged in KOH.

Subiculum – Generative hyphae hyaline, thin-walled with a wide lumen, frequently branched and simple septate, rarely bearing clamp connections, mostly smooth, rarely bearing crystals, interwoven, 3.5–5 µm in diam.; gloeoplerous hyphae present, almost the same size as generative hyphae.

Tubes – Generative hyphae hyaline, thin-walled with a wide lumen, frequently branched and simple septate, occasionally bearing clamp connections, frequently bearing fine crystals, interwoven, 2.5–4.5 µm in diam.; gloeoplerous hyphae present, almost the same size as generative hyphae; gloecystidioles present, fusoid, 17–40 × 4–7 µm; fusoid cystidioles present, hyaline, thin-walled,

almost the same size as gloeocystidioles; basidia clavate to barrel-shaped, bearing four sterigmata and a basal simple septum, $18\text{--}27 \times 5\text{--}8\ \mu\text{m}$; basidioles in shape similar to basidia, but slightly smaller.

Figure 3 – Basidioma of *Terrestriporia alba*. Scale bar = 4 cm (Dai 18548, holotype).

Figure 4 – Basidioma of *Terrestriporia alba*. Scale bar = 4 cm (Dai 18547, paratype).

Spores – Basidiospores ellipsoid, hyaline, thin-walled, smooth, IKI+, CB–, $(4.1\text{--}4.2\text{--}6(-7.2) \times (2.8\text{--}3\text{--}3.6(-3.8) \mu\text{m}$, $L = 5.08 \mu\text{m}$, $W = 3.11 \mu\text{m}$, $Q = 1.5\text{--}1.69$ ($n = 90/3$).

Specimens examined (paratypes) – MALAYSIA, Kuala Lumpur, Forest Eco-Park, on ground of a slope with some fine roots in the soil, 14 April 2018, *Dai 18546* (BJFC026835), *Dai 18547* (BJFC026836) & *Dai 18556* (BJFC026845).

Figure 5 – Microscopic structures of *Terrestriporia alba* (drawn from the holotype). a Basidiospores. b Basidia and basidioles. c Cystidioles. d Gloeocystidioles. e Hyphae from subiculum. f Hyphae from trama.

Discussion

Morphologically, *Terrestriporia alba* is similar to *Byssoporia terrestris* (DC.) M.J. Larsen & Zak by annual, resupinate basidioma with fimbriate margin, a monomitric hyphal structure with both simple septa and clamp connections, and growing on ground (Ryvarden & Melo 2014). However, the latter species lacks gloeoplerous hyphae and gloeocystidioles, and its basidiospores are slightly thick-walled, negative in Melzer's reagent. In addition, *Byssoporia* M.J. Larsen & Zak is closely related to *Albatrellus* Gray which is a stipitate genus belonging to Albatrellaceae (Fig. 1).

Terrestriporia resembles *Anomoporia* Pouzar and *Anomoloma* Niemelä & K.H. Larss. by sharing annual and resupinate basidioma, a monomitic hyphal structure, and hyaline, thin-walled, smooth and amyloid basidiospores (Ryvarden & Melo 2014), but the latter two genera have clamp connections only, lack gloeoplerous hyphae and cystidioles, and belong to Amylocorticiales.

Terrestriporia alba occupies similar ecological habitat growing on ground with some fine roots in the soil as some species in *Rhizochaete* Gresl., Nakasone & Rajchenb. and *Sebacina* Tul. & C. Tul. (e.g. *Rhizochaete radicata* (Henn.) Gresl., Nakasone & Rajchenb. and *Sebacina epigaea* (Berk. & Broome) Bourdot & Galzin), but the latter two genera have smooth or tuberculate hymenophores, and they belong to Sebaciniales and Polyporales, respectively (Breitenbach & Kränlin 1988, Greslebin et al. 2004).

Among species in Russulales, the DNA sequences of the ITS regions of *Terrestriporia alba* are more similar to *Perplexostereum endocrocinum* (Berk.) Ryvarden & Tutka, but the latter has perennial, pileate and hard basidioma with smooth hymenophore, a dimitic hyphal structure with clamp connections only, distinctly ornamented basidiospores, and growing on wood of *Juniperus* (Ryvarden & Tutka 2014). It is therefore both species have completely different morphology and ecology. In addition, the familial placement for *Perplexostereum* Ryvarden & Tutka is still unresolved and it has been referred to *incertae sedis*.

Divergence times have been used in ranking taxa (especially in higher taxa ranking) in different fungal groups (Divakar et al. 2017, Hongsanan et al. 2017, Zhao et al. 2017, Zhang et al. 2019). The divergence time of Terrestriporiaceae is also estimated and its divergence time from Albatrellaceae is 124.68 ± 0.39 Mya, which supports recent study of ranking a family with divergence time estimates (Zhao et al. 2017, Zhang et al. 2019).

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