



Aleurodiscus bicornis and *A. formosanus* spp. nov. (Basidiomycota) with smooth basidiospores, and redescription of *A. parvisporus*

Sheng-Hua Wu¹ · Chia-Ling Wei¹ · Chiung-Chih Chang²

Received: 8 March 2021 / Revised: 28 May 2021 / Accepted: 14 July 2021
© German Mycological Society and Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

Three species of *Aleurodiscus* s.l. characterized in having effused basidiomata, clamped generative hyphae and quasi-binding hyphae, sulphuric positive reaction of gloeocystidia, hyphidia, acanthophyses, and smooth basidiospores are described. They are *A. bicornis* sp. nov., *A. formosanus* sp. nov., and *A. parvisporus*. *Aleurodiscus bicornis* was found from the high mountains of northwestern Yunnan Province of southwestern China, and grew on branches of *Picea* sp. *Aleurodiscus formosanus* was found from high mountains of central Taiwan, and grew on branches of gymnosperm. *Aleurodiscus parvisporus* was previously only reported once from Japan and once from Sichuan Province of China, and is reported in this study from Jilin Province of China. Phylogenetic relationships of these three species were inferred from analyses of a combined dataset consisting of three genetic markers, viz. 28S, nuc rDNA ITS1-5.8S-ITS2 (ITS), and a portion of the translation elongation factor 1-alpha gene, *TEF1*. The studied three species are phylogenetically closely related with significant support, and this relationship corresponds with resemblance of their morphological features.

Keywords China · Corticioid fungi · Taiwan · Taxonomy · Wood-decaying fungi

Introduction

The genus *Aleurodiscus* Rabenh. ex J. Schröt. belongs to the Stereaceae Pilát of the Russulales. *Aleurodiscus* s.l. is characterized by cupulate, effused or effused-reflexed basidiocarps, a monomitic or dimitic hyphal system with simple-septate or clamped generative hyphae, smooth or ornamented amyloid basidiospores, and sterile organs such as acanthophyses, gloeocystidia, hyphidia, and dendrohyphidia may be present (Núñez and Ryvarden 1997; Wu et al. 2001). However, it has long been a complicated and unsettled problem as how to delimit the segregated genera among *Aleurodiscus* s.l. (Núñez and Ryvarden 1997; Wu et al. 2001, 2010, 2019; Larsson and Larsson 2003; Miller et al. 2006; Larsson 2007), due to highly variable diagnostic characters

among species. The characteristics combined for separating segregated genera within *Aleurodiscus* s.l. (*Acanthobasidium* Oberw., *Acanthofungus* Sheng H. Wu et al., *Acanthophysellum* Parmasto, *Aleurobotrys* Boidin, *Aleurodiscus* s.s., *Aleurocystidiellum* P.A. Lemke, *Gloeosoma* Bres., and *Neoeurodiscus* Sheng H. Wu) as well as *Stereum* Hill ex Pers. and *Xylobolus* P. Karst. were provided by Wu et al. (2001, Table 1) and Wu et al. (2010, Table 1). Currently, 187 names are recorded under *Aleurodiscus*, of which about 90 taxa are generally accepted (Feb. 2021, <http://www.indexfungorum.org/>). In the recent decade, new species of *Aleurodiscus* s.l. have been proposed by Ryvarden et al. (2012), Gorjón et al. (2013), Maninder et al. (2014), Dai and He (2016, 2017), Dai et al. (2017a, b), Ghobad-Nejhad and Langer (2018), Tian et al. (2018), and Wu et al. (2019). Since the phylogenetic relationships of the taxa in *Aleurodiscus* s.l., together with the family Stereaceae it belongs to, are not resolved, we adopt a broad and inclusive generic concept of *Aleurodiscus* for the studied taxa presented in this study.

During an ongoing survey of corticioid fungi from mainland China and Taiwan, we noted two un-described and an uncommon *Aleurodiscus* sp. They are peculiar in sharing some morphological characteristics: effused basidiomata, clamped generative hyphae and quasi-binding hyphae,

Section Editor: Yu-Cheng Dai

✉ Sheng-Hua Wu
shwu@mail.nmns.edu.tw

¹ Department of Biology, National Museum of Natural Science, Taichung 40453, Taiwan

² Biodiversity Research Center, Academia Sinica, Taipei 11529, Taiwan

Table 1 List of species, specimens, and sequences used in this study. Sequences generated in this study are shown in boldface

Fungal species	Specimen or strain no	DDBJ/GenBank/EMBL accession no		
		ITS	28S	<i>TEF1</i>
<i>Acanthobasidium bambusicola</i>	He 2357*	KU559343	KU574833	–
<i>Acanthofungus rimosus</i> #	Wu 9601–1*	MF043521	AY039333	–
<i>Acanthophysellum cerussatum</i>	He 20120920–3	KU559339	KU574830	KU992716
<i>Aleurobotryis botryosus</i> #	He 2712	KX306877	KY450788	–
<i>Aleurocystidiellum disciforme</i>	He 3159	KU559340	KU574831	KU992721
<i>Aleurocystidiellum subcruentatum</i> #	He 2886	KU559341	KU574847	KU992720
<i>Aleurodiscus alpinus</i>	Wu 1407–59	MF043522	MF043527	–
<i>Aleurodiscus alpinus</i>	Wu 1407–55*	–	MF043526	LC269190
<i>Aleurodiscus alpinus</i>	Wu 1407–61	MF043523	MF043528	–
<i>Aleurodiscus amorphus</i> #	Ghobad-Nejhad-2464	KU559342	KU574832	KU992717
<i>Aleurodiscus amorphus</i> #	KHL 4240	AF506397	AF506397	–
<i>Aleurodiscus bambusinus</i>	He 4261*	KY706207	KY706219	LC430911
<i>Aleurodiscus bicornis</i>	Wu 1308–101	LC433893	LC433900	LC433907
<i>Aleurodiscus bicornis</i>	Wu 1308–125*	LC433899	LC433906	LC433912
<i>Aleurodiscus canadensis</i>	Wu 1207–90	KY706203	KY706225	–
<i>Aleurodiscus dextrinoideocerussatus</i>	EL25-97	AF506401	AF506401	–
<i>Aleurodiscus dextrinoideophyses</i>	He 4105	MH109050	KY450784	–
<i>Aleurodiscus effusus</i>	He 2261*	KU559344	KU574834	KU992719
<i>Aleurodiscus formosanus</i>	Chen 2736*	LC433894	LC433901	LC433908
<i>Aleurodiscus formosanus</i>	Chen 2748	LC433895	LC433902	LC433909
<i>Aleurodiscus formosanus</i>	Chen 2739	LC433896	LC433903	–
<i>Aleurodiscus formosanus</i>	WEI 19–274	LC514405	LC514406	–
<i>Aleurodiscus gigasporus</i>	Wu 0108–15	KY706205	KY706213	–
<i>Aleurodiscus grantii</i>	HHB-14417	KU559363	KU574821	KU992708
<i>Aleurodiscus grantii</i>	HHB-14418	KU559364	KU574822	–
<i>Aleurodiscus isabellinus</i>	He 5283	MH109052	MH109046	LC430912
<i>Aleurodiscus mesaverdense</i>	FP-120155	KU559359	KU574817	–
<i>Aleurodiscus mirabilis</i>	Dai 13281	KU559350	KU574839	KU992711
<i>Aleurodiscus oakesii</i>	He 2243	KU559352	KU574840	–
<i>Aleurodiscus oakesii</i>	HHB11890-A-sp	KU559365	KU574823	–
<i>Aleurodiscus parvisporus</i>	Wu 1307–84	LC433897	LC433904	LC433910
<i>Aleurodiscus parvisporus</i>	Wu 1307–88	LC433898	LC433905	LC433911
<i>Aleurodiscus pinicola</i>	Wu 1106–16	MF043524	MF043529	–
<i>Aleurodiscus pinicola</i>	Wu 1308–54*	MF043525	MF043530	LC269191
<i>Aleurodiscus senticosus</i>	Wu 1209–7*	MH596849	MF043531	LC271169
<i>Aleurodiscus senticosus</i>	Wu 1209–9	MH596850	MF043533	LC269192
<i>Aleurodiscus senticosus</i>	Wu 9610–1	MH596851	MF043532	LC269193
<i>Aleurodiscus sichuanensis</i>	Wu 0010–18*	MH596852	MF043534	LC269194
<i>Aleurodiscus sichuanensis</i>	He 4935	LC430904	LC430907	–
<i>Aleurodiscus subroseus</i>	He 4807*	MH109054	MH109048	–
<i>Aleurodiscus subroseus</i>	He 4895	LC430903	LC430910	LC430913
<i>Aleurodiscus tenuissimus</i>	He3575*	KX306880	KX842529	–
<i>Aleurodiscus thailandicus</i>	He 4099*	KY450781	KY450782	–
<i>Aleurodiscus tropicus</i>	He 3830*	KX553875	KX578720	LC269195
<i>Aleurodiscus verrucosporus</i>	He 4491*	KY450786	KY450790	–
<i>Aleurodiscus wakefieldiae</i>	He 2580	KU559353	KU574841	KU992710
<i>Boidinia macrospora</i>	Wu 9202–21*	AF506377	AF506377	–
<i>Conferticum heimii</i>	CBS321.66	AF506381	AF506381	–

Table 1 (Continued)

Fungal species	Specimen or strain no	DDBJ/GenBank/EMBL accession no		
		ITS	28S	<i>TEF1</i>
<i>Conferticium ravum</i>	NH13291	AF506382	AF506382	–
<i>Gloeocystidiellum aspellum</i>	LIN 625	AF506432	AF506432	–
<i>Gloeocystidiellum porosum</i> #	Wu 1608–176	LC430905	LC430908	–
<i>Gloeocystidiopsis cryptacanthus</i>	KHL10334	AF506442	AF506442	–
<i>Gloeocystidiopsis flammea</i> #	CBS324.66	AF506437	AF506437	–
<i>Heterobasidion parviporum</i>	91605	KJ651503	KJ651561	KU985089
<i>Megalocystidium chelidonium</i>	LodgeSJ110.1	AF506441	AF506441	–
<i>Megalocystidium leucoxanthum</i> #	HK9808	AF506420	AF506420	–
<i>Megalocystidium wakullum</i>	Oslo-930107	AF506443	AF506443	–
<i>Neoaleurodiscus fujii</i> #	He 2921	KU559357	KU574845	KU992709
<i>Stereum complicatum</i>	He 2234	KU559368	KU574828	KU992706
<i>Stereum hirsutum</i> #	Wu 1109–127	LC430906	LC430909	–
<i>Stereum ostrea</i>	He 2067	KU559366	KU574826	KU992703
<i>Stereum sanguinolentum</i>	He 2111	KU559367	KU574827	KU992705
<i>Xylobolus frustulatus</i> #	He 2231	KU881905	KU574825	KU992704

* Holotype

Generic type

sulphuric positive reaction of gloeocystidia, hyphidia, acanthophyses, and smooth basidiospores. These morphologically resembling species were also detected in this study as phylogenetically closely related within *Aleurodiscus* s.l. Hence, we conducted a taxonomic study for these three species that have some peculiar morphological features.

Materials and methods

Morphological study

Specimens used in this study are deposited in the herbarium of the National Museum of Natural Science of ROC (TNM; Taichung City, Taiwan). Macroscopic and microscopic studies were based on dried specimens. Color names from Rayner (1970) are capitalized. Thin free-hand sections of basidiocarps were prepared for microscopic study. For observations and measurements of microscopic characters, sections were mounted in 5% KOH to ensure rehydration. A blue-black color change with Melzer's reagent (IKI) indicates an amyloid reaction. Cotton blue (CB) was used as a mounting medium to determine cyanophily. Sulphoaldehyde (SA) was used to detect a sulphuric reaction of gloeocystidia; a bluish black color change with SA indicates a positive reaction. The following abbreviations are used for basidiospore measurements: L, mean spore length with standard

deviation; W, mean spore width with standard deviation; Q, variation in L/W ratio; and n, number of spores measured from each specimen. Apiculi were excluded in spore measurements. Living mycelia were isolated from the woody substratum beneath the basidiocarps, and were cultured on 1.5% malt extract agar (MEA).

DNA extraction and sequencing

Dried specimens or the mycelial colonies cultured on MEA were used for DNA extraction, carried out with a Plant Genomic DNA Extraction Miniprep System (Viogene-Biotek Corp., New Taipei City, Taiwan). Liquid N and TissueLyser II (Qiagen, Hilden, Germany) were used to disrupt and homogenize the fungal tissues before DNA extraction process. The primer pairs ITS1/ITS4 or ITS1F/LR22 were used for the ITS region (White et al. 1990; Gardes and Bruns 1993), and LR0R/LR3 and LR0R/LR5 were used for the 28S region (Vilgalys and Hester 1990). Efd1/1953R and 983F/2218R were used to amplify a portion of the *TEF1* gene (Rehner and Buckley 2005; Matheny et al. 2007). The PCR protocol followed Chen et al. (2018). PCR products were purified and directly sequenced by MB Mission Biotech Company (Taipei City, Taiwan). We examined the technical quality of the newly obtained sequences by comparison to entries in GenBank (Benson et al. 2018). Sequences were assembled using BioEdit v7.2.5 (Hall 1999). Newly obtained sequences (Table 1) were submitted to DNA Data Bank of Japan (DDBJ) (Mashima et al. 2016).

Phylogenetic analyses

The selection of strains and sequences consulted Dai and He (2016) and Wu et al. (2019). MAFFT 7 was used to align sequences with Q-INS-i strategy for ITS dataset, and FFT-NS-i for both 28S and *TEF1* datasets. Three final alignments were manually adjusted, when necessary, in Bioedit (Hall 1999) before being combined. Phylogenetic trees were inferred from Maximum Likelihood (ML) and Bayesian inference (BI) methods using RaxML Black Box (Stamatakis 2014) and MrBayes v. 3. 2. 6. (Ronquist et al. 2012) on CIPRES (<http://www.phylo.org/>), respectively. The best fit model of each dataset for BI analyses was estimated by jModelTest 2 (Darriba et al. 2012) based on the Bayesian Information Criterion (BIC). The BI analysis was conducted with ten million generations, sampled every 1000 generations, and resulted in ten thousand trees. The first 2500 trees were discarded as the burn-in. The posterior probabilities (PP) were calculated. In ML analysis, the bootstrap values were calculated with 1000 replicates. Only phylogram inferred from BI analyses was shown since both ML and BI analyses resulted in similar topologies. Statistic supports were shown on nodes of BI tree when BP value ≥ 70 and PP value ≥ 0.7 . The final alignment and phylogenetic trees were submitted to TreeBASE (TBS: S27713; www.treebase.org).

Results

Phylogeny

The 3-gene dataset was composed of 63 taxa and 2923 sites including gaps, 1420 for 28S, 932 for ITS, and 571 for *TEF1*. The absent gene sequences were treated as missing data. GTR+G+I model was fit for ML analysis. For BI analysis, partition model was selected: GTR+I+G for 28S, GTR+G for ITS, GTR+I+G+I for *TEF1*. Average standard deviation of split frequencies fell to 0.008016 after 10 million generations. For all parameters, PSRFs approached 1.0. The BI tree of the 3-gene dataset (Fig. 1) showed that strains of *Aleurodiscus bicornis*, *A. formosanus*, and *A. parvisporus* formed separate monophyletic lineages with significant statistical support (PP:1, BP:93–99). *Aleurodiscus formosanus* was sister to *A. bicornis* with significant supports (PP:1, BP:96), while *A. parvisporus* resolved as sister to them with poor statistical supports (PP:0.75, BP<70).

Taxonomy

Aleurodiscus bicornis Sheng H. Wu, sp. nov. (Figs. 2A and 3).
Mycobank: MB 839874.

Etymology. From *bicornis* (=two-horned), referring to the 2-sterigmate basidia.

Holotype. China, Yunnan Province, Lichiang, near Astronomy Observatory, alt. 3150 m, on branch of *Picea* sp., coll. S.H. Wu, 31-VIII-2013, *Wu 1308–125* (TNM F27227).

Basidiomata resupinate, effused, adnate, membranaceous, 80–300- μ m thick in section. Hymenial surface Buff, smooth, occasionally cracked and exposing white subiculum; margin white, thinning, arachnoid-pruinose.

Hyphal system dimitic; generative hyphae nodose-septate. Subiculum bi-layered, basal layer up to ca. 40- μ m thick, sometimes indistinct, intermediate layer with somewhat loose to fairly dense texture, 20–100- μ m thick; hyphae interwoven. Subicular generative hyphae moderately ramified, colorless, 2–5- μ m diam, with 0.3–1.2- μ m-thick walls, with abundant small oily drops, anastomoses rather frequent; quasi-binding hyphae richly ramified, colorless, 1–3- μ m diam, walls almost solid. Hymenial layer thickening, subhymenium differentiated, with dense texture, 50–200- μ m thick; hyphae \pm vertical, irregularly swollen, full of small oily drops, 2.2–6.5- μ m diam. thin- to slightly thick-walled. Crystal masses scattered throughout section. Gloeocystidia numerous, immersed or slightly projecting, cylindrical, usually moniliform toward apices or with a schizopapillate constriction, occasionally with stalked bases or a lateral branch, colorless, usually with several big oily drops, 40–120 \times 7–13 μ m, thin- to slightly thick-walled, SA+. Acanthophyses numerous, colorless, cylindrical, ventricose, subclavate or broadly clavate, apices with numerous aculei, occasionally with adventitious septa, 25–70 \times 4–17 μ m, thin- to thick-walled, usually thick-walled toward aculei parts, adventitious septa occasionally occur, aculei 1–4 \times 1 μ m. Hyphidia numerous, 20–55 \times 3–5.5 μ m, sometimes branched. Basidia subclavate, \pm flexuous, 45–76 \times 14–19 μ m, 2-sterigmate. Basidiospores broadly ellipsoid, adaxially slightly concave, smooth, with a distinct apiculus, colorless, thin-walled, with several very small oily drops or homogeneous, IKI bluish black, CB-, generally 19–22 \times 12.5–15 μ m.

Statistic measurements of basidiospores. (18.4-)19.2–21.5 (-22.6) \times (11.7-)13.3–14.9(-16) μ m, L = 20.10 \pm 1.00 μ m, W = 14.00 \pm 0.80 μ m, Q = 1.44 (n = 30) (*Wu 1308–125*). (18.7-)20.1–22.6(-23.2) \times (11-)12.1–14.8(-15.7) μ m, L = 21.01 \pm 1.13 μ m, W = 13.42 \pm 1.14 μ m, Q = 1.57 (n = 30) (*Wu 1308–101*). (19.2-)20.2–22.1(-24) \times (12.8-)13.4–15.6 (-16.2) μ m, L = 21.19 \pm 0.96 μ m, W = 14.64 \pm 0.94 μ m, Q = 1.45 (n = 30) (*Wu 1308–108*).

Additional specimens (paratypes) examined. China, Yunnan Province, Lichiang, near Astronomy Observatory, alt. 3150 m, on branch of *Picea* sp., coll. S.H. Wu, 31-VIII-2013, *Wu 1308–101* (TNM F27210), *Wu 1308–108* (TNM F27214).

Distribution. Known from northwestern Yunnan Province, southwestern China.

Aleurodiscus formosanus Sheng H. Wu, sp. nov. (Figs. 2B and 4).



Fig. 1 BI tree of *Aleurodiscus* and related genera of Stereaceae inferred from the 28S-ITS-*TEF1* markers. ML bootstrap values $\geq 70\%$ and PP ≥ 0.7 from the Bayesian analysis are indicated at internodes. The target studied species are shown in boldface type

Mycobank: MB 839875.

Etymology. From formosanus, relating to Formosa (Taiwan).

Holotype. Taiwan, Nantou County, Hsinyi Township, Tatachia, 23°29'N, 120°53'E, alt. 2450 m, on branch of gymnosperm, coll. S.Z. Chen, W.C. Chen & C.C. Chen, 30-VIII-2014, *Chen 2736* (TNM F28401).

Basidiomata resupinate, effused, adnate, membranaceous, 50–200- μm thick in section. Hymenial surface Light Buff, Pale Luteous, smooth, occasionally cracked; margin concolorous or white, thinning or fairly determinate, arachnoid-pruinose or shortly filamentous.

Hyphal system dimitic; generative hyphae nodose-septate. Subiculum fairly uniform, with somewhat loose



Fig. 2 Basidiomata. (A) *Aleurodiscus bicornis* (holotype, Wu 1308–125). (B) *A. formosanus* (holotype, Chen 2736). (C) *A. parvisporus* (holotype, Wu 1307–84)

to dense texture, 15–80- μm thick, sometimes indistinct; hyphae usually horizontal near substrate, \pm vertical near hymenial layer. Generative hyphae colorless, fairly straight, moderately ramified, 2–5.2- μm diam, walls up to 1- μm thick, with several small oily drops, anastomoses occasional; quasi-binding hyphae few in deep subiculum, richly ramified, colorless, 1–2.5- μm diam, walls almost solid. Hymenial layer thickening, subhymenium differentiated, with dense texture, 50–150- μm thick; hyphae \pm vertical, colorless, 2–4.6- μm diam, thin- to slightly thick-walled. Crystal masses scattered throughout section. Gloeocystidia numerous, immersed or projecting, cylindrical to tubular, usually moniliform towards apices, usually with swollen bases and narrow apices, colorless, with several big oily drops, 45–115 \times 7–16 μm , walls up to 1- μm thick, SA +. Acanthophyses numerous, subglobose, fusiform or cylindrical, usually with stalked base, usually

with an apical projection provided with \pm dextrinoid aculei, colorless, 18–35 \times 4–17 μm , walls up to 0.8- μm thick. Hyphidia numerous, \pm flexuous, 18–40 \times 2–4 μm . Basidia broadly clavate, usually with stalked bases, 45–76 \times 14–19 μm , usually with a lateral aculeate branch up to 25- μm long, walls up to 1- μm thick, 4-sterigmate, occasionally 2-sterigmate. Basidiospores narrowly ellipsoid to broadly ellipsoid, adaxially flatten, smooth, colorless, thin-walled, with small oily drops or homogeneous, IKI bluish black, CB-, generally 14–16 \times 7.5–10.5 μm .

Statistic measurements of basidiospores. (14-)14.5–15.8 (-16.5) \times (7.2-)8–10.2(-11.8) μm , L = 15.14 \pm 0.71 μm , W = 9.02 \pm 1.07 μm , Q = 1.70 (n = 30) (Chen 2736). (13-)13.5–15(-16) \times (7.2-)8–9.8(-11.2) μm , L = 14.29 \pm 0.74 μm , W = 8.99 \pm 0.86 μm , Q = 1.60 (n = 30) (Chen 2748).

Additional specimens (paratypes) examined. Taiwan, Nantou County, Hsinyi Township, Lulinshan, 23°28'N, 120°52'E, alt. 2600 m, on branch of *Pinus taiwanensis*, coll. S.H. Wu, 5-X-1992, Wu 9210–4 (TNM F00388); Hsinyi Township, Tatchia, 23°29'N, 120°53'E, alt. 2450 m, on branch of gymnosperm, coll. S.Z. Chen, W.C. Chen & C.C. Chen, 30-VIII-2014, Chen 2739 (TNM F28404), Chen 2748 (TNM F28411).

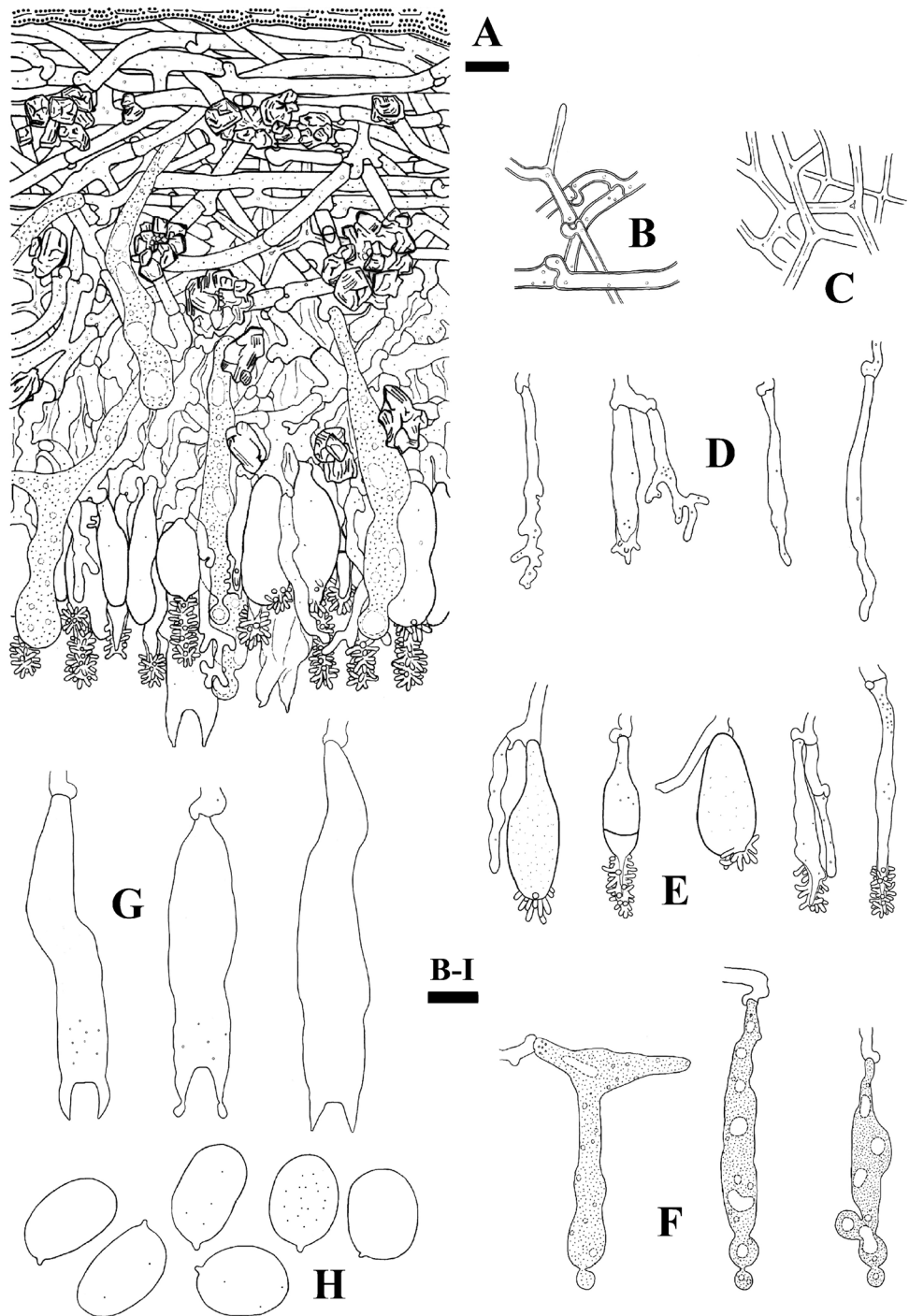
Distribution. Known from temperate high mountains of Taiwan.

Aleurodiscus parvisporus Núñez & Ryvardeen, Synopsis Fungorum 12: 117 (1997) (Figs. 2C and 5).

Basidiomata resupinate, effused, adnate, membranaceous, 90–300- μm thick in section. Hymenial surface Pale Buff or Buff when young, Pale Luteus when old, smooth to \pm tuberculate, extensively cracked and exposing white subiculum; margin concolorous, thinning, pruinose.

Hyphal system dimitic; generative hyphae nodose-septate. Subiculum mostly embedded in woody substrate, with dense to compact texture, hyphae interwoven; generative hyphae moderately ramified, colorless, 2–7.5- μm diam, with walls up to ca. 1- μm thick, usually with small oily drops; quasi-binding hyphae embedded in woody substrate, richly ramified, colorless, 1.2–3.2- μm diam, walls almost solid. Hymenial layer thickening, with compact texture, 90–300- μm thick; generative hyphae \pm vertical, irregularly swollen, with small oily drops, colorless, 2–4.5- μm diam. Lumpy crystals scattered in section. Gloeocystidia numerous, immersed or slightly projecting, irregularly cylindrical or tubular, \pm flexuous, usually moniliform toward apices or with a schizopapillate constriction, sometimes laterally or apically protruding, usually with several big oily drops, colorless, (25-)40–120 \times 4.5–15 μm , thin- to slightly thick-walled, walls up to ca. 1- μm thick, SA +. Acanthophyses numerous, cylindrical, colorless, with numerous aculei towards apices, 25–55 \times 2–3.5 μm , usually slightly thick-walled toward apices; aculei subcolorless when young,

Fig. 3 *Aleurodiscus bicornis* (Wu 1308–125). (A) Basidiocarp section. (B) Generative hyphae. (C) Quasi-binding hyphae. (D) hyphidia. (E) Acanthophyses. (F) Gloeocystidia. (G) Basidia. (H) Basidiospores (scale bar = 10 μm)

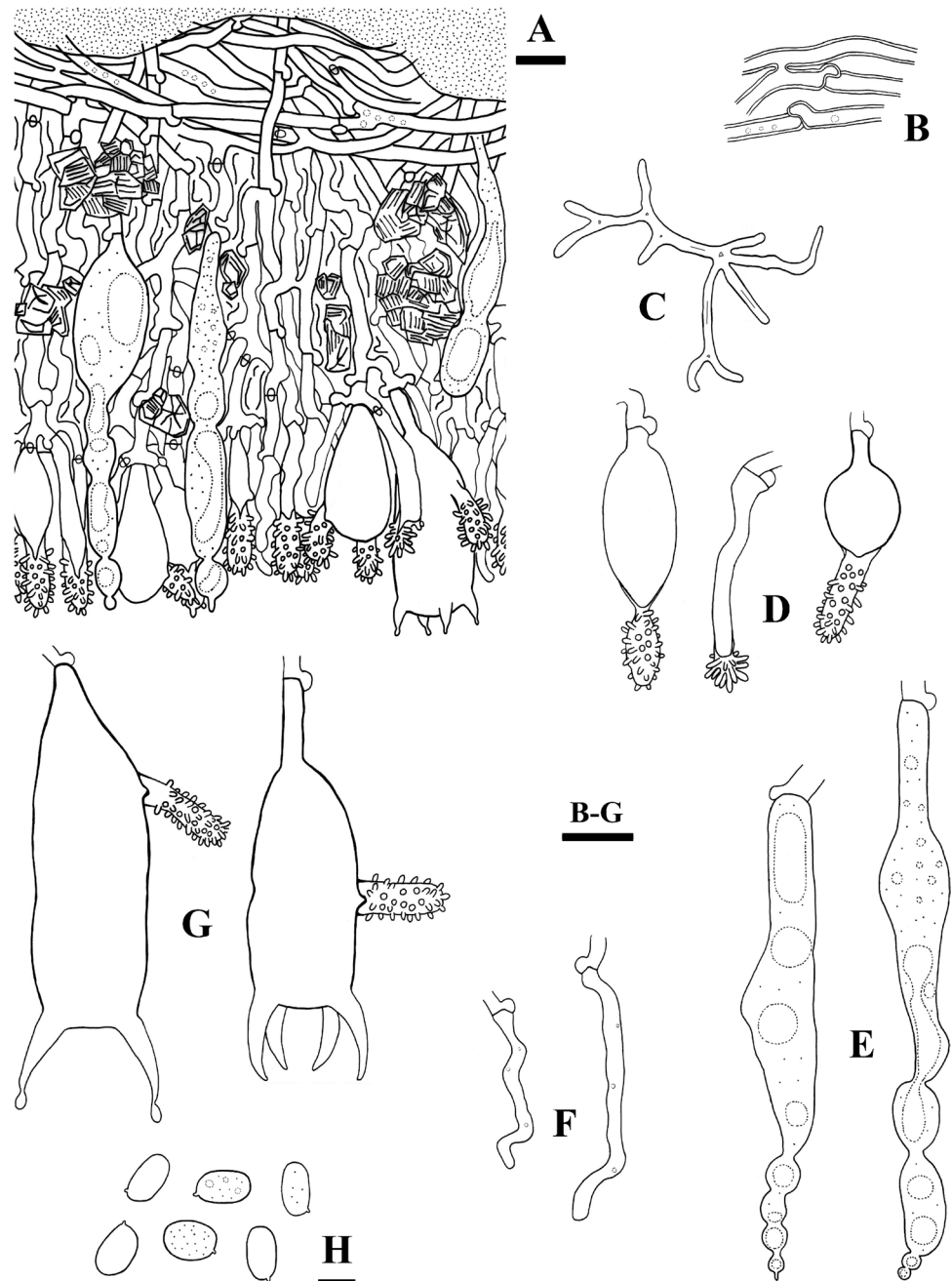


slightly brownish when old, $2\text{--}4(-10)\times 0.8\text{--}1\ \mu\text{m}$. Hyphidia numerous, $20\text{--}40\times 2\text{--}4.5\ \mu\text{m}$, sometimes branched. Basidia clavate to narrowly clavate, \pm flexuous, usually laterally with several aculei, \pm guttulate, $25\text{--}40\times 4\text{--}5.5\ \mu\text{m}$, 4-sterigmate. Basidiospores broadly ellipsoid to ellipsoid, adaxially flattened or slightly concave, smooth, with a minute apiculus, colorless, thin-walled, with several minute oily drops, IKI bluish black, CB-, generally $5.7\text{--}6.3\times 3.5\text{--}4.2\ \mu\text{m}$.

Statistic measurements of basidiospores. $(5.6\text{--})5.8\text{--}6.2(-6.6)\times (3.3\text{--})3.5\text{--}4.1(-4.3)\ \mu\text{m}$, $L = 5.96 \pm 0.23\ \mu\text{m}$, $W = 3.78 \pm 0.30\ \mu\text{m}$, $Q = 1.58$ ($n = 30$) (Wu 1307–84). $(5.5\text{--})5.7\text{--}6.2(-6.5)\times (3.4\text{--})3.6\text{--}4.2(-4.5)\ \mu\text{m}$, $L = 5.95 \pm 0.27\ \mu\text{m}$, $W = 3.94 \pm 0.25\ \mu\text{m}$, $Q = 1.51$ ($n = 30$) (Wu 1307–88).

Specimens examined. China, Jilin Province, Fusong County, Touxi Protection Station, $42^{\circ}18'N$, $127^{\circ}50'E$, alt. 1025 m, on branch of *Synga reticulata* var. *mandshurica*,

Fig. 4 *Aleurodiscus formosanus* (Chen 2736). (A) Basidiocarp section. (B) Generative hyphae. (C) Quasi-binding hyphae. (D) Acanthophyses. (E) Gloeocystidia. (F) Hyphidia. (G) Basidia. (H) Basidiospores (scale bar = 10 μ m)



coll. S.H. Wu, 13-VII-2013, Wu 1307–84 (TNM F27616), on branch of *Lonicera* sp., Wu 1307–88 (TNM F27617).

Distribution. Known from Japan (type locality), Sichuan (Maekawa et al. 2002) and Jilin Province of China (this study).

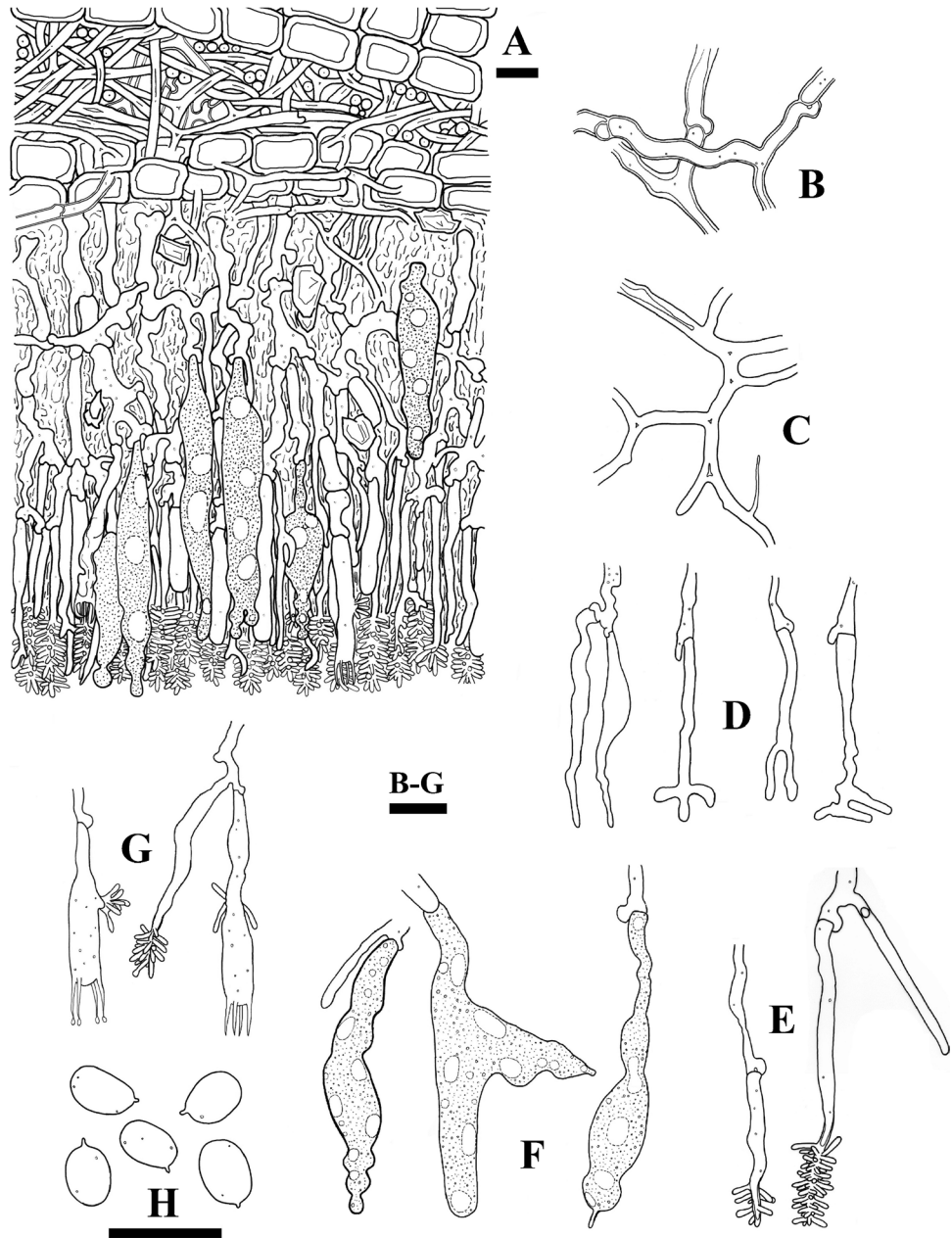
Discussion

Aleurodiscus bicornis and *A. formosanus*, presented here as new species, are phylogenetically most closely related in the present study (Fig. 1). These two species

grow on gymnosperm branches, distribute in temperate climatic regions, and have similar basidiome morphology and color. Microscopically, *Aleurodiscus bicornis* differs from *A. formosanus* in having 2-sterigmate basidia and distinctly larger basidiospores. A lateral aculeate branch developed from the basidium of *A. formosanus*, is not present in *A. bicornis*.

Aleurodiscus canadensis Skolko resembles *A. bicornis* in having whitish hymenial surface, clamped hyphae, acanthophyses, and smooth basidiospores, especially 2-sterigmate basidia; but differs from the latter in having smaller basidiospores (10–18 \times 7–13 μ m, Núñez and Ryvarden

Fig. 5 *Aleurodiscus parvisporus* (Wu 1307–84). (A) Basidiocarp section. (B) Generative hyphae. (C) Quasi-binding hyphae. (D) Hyphidia. (E) Acanthophyses. (F) Gloeocystidia. (G) Basidia. (H) Basidiospores (scale bar = 10 μ m)



1997). Moreover, *Aleurodiscus canadensis* has basidia with protuberances in the middle parts, which are lacking in basidia of *A. bicornis*. *Aleurodiscus canadensis* is distributed in North America and grows on *Picea* and other gymnosperms (Núñez and Ryvar den 1997). *Aleurodiscus canadensis* is phylogenetically closely related to the three studied species (Fig. 1).

Aleurodiscus dextrinoideocerussatus Manjón, M.N. Blanco & G. Moreno is distributed in Spain and Italy, resembles *A. formosanus* in having similar morphological characteristics including acanthophyses with dextroid apical protuberances; but differs from the latter in having smaller basidiospores (7–10 \times 4–7 μ m,

Núñez and Ryvar den 1997). In addition, the lateral aculeate branch of basidia in *A. formosanus* is not present in *A. dextrinoideocerussatus*. *Aleurodiscus dextrinoideocerussatus* is phylogenetically closely related to the presented three new species (Fig. 1).

Aleurodiscus parvisporus was originally reported based on the holotype collected from Niigata Prefecture of Japan (Núñez and Ryvar den 1997). The second specimen of this species was reported from high mountain (3890 m) of Sichuan Province in China (Maekawa et al. 2002). The present study reports two specimens of this species collected from NE China in 2013. All of these four collections were made from branches of angiosperms. Recognition of

two specimens (*Wu 1307–84* & *Wu 1307–88*) collected from NE China as *A. parvisporus* is based on resemblance of some diagnostic features described from the holotype (Núñez and Ryvarden 1997): effused basidiomata with similar color of hymenial surfaces, thin subiculum and thick hymenial layer, clamped generative hyphae, gloeocystidia, narrow acanthophyses, and smooth basidiospores which are distinctly small in *Aleurodiscus* s.l. It is hard to have different species to share these characteristics. Moreover, the collecting site of these two specimens in Jilin Province of China is geographically close to the holotype collected from Niigata Prefecture of Japan; additionally, both collecting sites are temperate climatic regions, and all the collections were made from angiosperm branches. However, the characteristics of hyphidia and basidia with lateral aculei present in the specimens (*Wu 1307–84* & *Wu 1307–88*) were not mentioned for the holotype of *A. parvisporus*. Nevertheless, the hyphidia could be neglected in study, and good basidia may be not found in the holotype as drawing of this structure was lacking in the protologue (Núñez and Ryvarden 1997). This study first reports DNA sequences of *A. parvisporus*.

The studied three *Aleurodiscus* species share some important morphological characteristics, i.e. effused basidiomata, clamped generative hyphae and quasi-binding hyphae, sulphuric positive reaction of gloeocystidia, hyphidia, acanthophyses, and smooth basidiospores. These three species are phylogenetically closely related with significant support (Fig. 1), which corresponds with resemblance of their morphological features. An independent generic taxon separate from *Aleurodiscus* s.s., to accommodate these three new species, should be proposed. However, it needs further studies by advanced phylogenetical analysis based on a comprehensive survey of *Aleurodiscus* s.l.

Author contribution Conceptualization: Sheng-Hua Wu. Methodology: Sheng-Hua Wu, Chiung-Chih Chang. Formal analysis and investigation: Sheng-Hua Wu, Chia-Ling Wei, Chiung-Chih Chang. Writing—original draft preparation: Sheng-Hua Wu, Chia-Ling Wei, Chiung-Chih Chang. Writing—review and editing: Sheng-Hua Wu. Funding acquisition: Sheng-Hua Wu. Supervision: Sheng-Hua Wu.

Funding This study was financed by the Ministry of Science and Technology of ROC (Taiwan) (Grant no 107–2621-B-178–002-MY3).

Data availability All the authors make sure that all data and materials as well as software application or custom code support our published claims and comply with field standards.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

- Benson DA, Cavanaugh M, Clark K, Karsch-Mizrachi I, Ostell J, Pruitt KD, Sayers EW (2018) GenBank. *Nucleic Acids Res* 46(D1):D41–D46. <https://doi.org/10.1093/nar/gkx1094>
- Chen CC, Wu SH, Chen CY (2018) *Hydnophanerochaete* and *Odon-toefibula*, two new genera of phanerochaetoid fungi (Polyporales, Basidiomycota) from East Asia. *Mycospora* 39:75–96. <https://doi.org/10.3897/mycokeys.39.28010>
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nat Methods* 9:772–772. <https://doi.org/10.1038/nmeth.2109>
- Dai LD, He SH (2016) New species and new records of *Aleurodiscus* s.l. (Basidiomycota) in China. *Mycol Prog* 15:717–730. <https://doi.org/10.1007/s11557-016-1202-z>
- Dai LD, He SH (2017) A new species and a new combination of *Aleurodiscus* s.l. (Russulales, Basidiomycota). *Mycosphere* 8:908–916. <https://doi.org/10.5943/mycosphere/8/7/7>
- Dai LD, Wu SH, Nakasone KK, Burdsall HH, He SH (2017a) Two new species of *Aleurodiscus* s.l. (Russulales, Basidiomycota) on bamboo from tropics. *Mycoscience* 58:213–220. <https://doi.org/10.1016/j.myc.2017.02.001>
- Dai LD, Zhao Y, He SH (2017b) Three new species of *Aleurodiscus* s.l. (Russulales, Basidiomycota) on bamboos from East Asia. *Cryptogamie Mycologie* 38:227–239. <https://doi.org/10.7872/crym/v38.iss2.2017.227>
- Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. *Mol Ecol* 2:113–118. <https://doi.org/10.1111/j.1365-294X.1993.tb00005.x>
- Ghobad-Nejhad M, Langer E (2018) A new species in *Aleurodiscus* s.l. (Stereaceae, Russulales) from Iran. *Phytotaxa* 351:264–272. <https://doi.org/10.11646/phytotaxa.351.4.2>
- Gorjón SP, Greslebin AG, Rajchenberg M (2013) The genus *Aleurodiscus* s.l. (Stereaceae, Russulales) in the Patagonian Andes. *Mycol Prog* 12:91–108. <https://doi.org/10.1007/s11557-012-0820-3>
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp Ser* 41:95–98
- Larsson KH (2007) Re-thinking the classification of corticioid fungi. *Mycol Res* 111:1040–1063. <https://doi.org/10.1016/j.mycres.2007.08.001>
- Larsson E, Larsson KH (2003) Phylogenetic relationships of russuloid basidiomycetes with emphasis on aphyllorhalean taxa. *Mycologia* 95:1037–1065. <https://doi.org/10.2307/3761912>
- Maekawa N, Yang ZL, Zang M (2002) Corticioid fungi (Basidiomycetes) collected in Sichuan Province, China. *Mycotaxon* 83:81–95
- Maninder K, Avneet PS, Dhingra GS, Ryvarden L (2014) *Aleurodiscus himalaicus* (Agaricomycetes) sp. nov. from India. *Synopsis Fungorum* 32:5–7
- Matheny BP, Wang Z, Binder M, Curtis JM, Lim YW, Nilsson RH, Hughes KW, Hofstetter V, Ammirati JF, Schoch CL, Langer E, Langer G, McLaughlin DJ, Wilson AW, Frøslev T, Ge Z-W, Kerrigan RW, Slot JC, Yang ZL, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vauras J, Hibbett DS (2007) Contributions of rpb2 and tef1 to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Mol Phylogenet Evol* 43:430–451. <https://doi.org/10.1016/j.ympev.2006.08.024>
- Mashima J, Kodama Y, Kosuge T, Fujisawa T, Katayama T, Nagasaki H, Okuda Y, Kaminuma E, Ogasawara O, Okubo K, Nakamura Y, Takagi T (2016) DNA data bank of Japan (DDBJ) progress report. *Nucleic Acids Res* 44:D51–D57. <https://doi.org/10.1093/nar/gkv1105>

- Miller SL, Larsson E, Larsson K-H, Verbeken A, Nuytinck J (2006) Perspectives in the new Russulales. *Mycologia* 98:960–970. <https://doi.org/10.1080/15572536.2006.11832625>
- Núñez M, Ryvarden L (1997) The genus *Aleurodiscus* (Basidiomycotina). *Synopsis Fungorum* 12:1–164
- Rayner RW (1970) *A mycological colour chart*. Kew: Commonwealth Mycological Institute & British Mycological Society, p 34
- Rehner SA, Buckley E (2005) A *Beauveria* phylogeny inferred from nuclear ITS and EF1- α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97:84–98. <https://doi.org/10.1080/15572536.2006.11832842>
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst Biol* 61:539–542. <https://doi.org/10.1093/sysbio/sys029>
- Ryvarden L, Sanyal SK, Dhingra GS (2012) *Aleurodiscus indicus* (Agaricomycetes) sp. nov. from India. *Synopsis Fungorum* 30:14–16
- Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Tian Y, Ghobad-Nejhad M, He SH, Dai YC (2018) Three new species of *Aleurodiscus* s.l. (Russulales, Basidiomycota) from southern China. *MycKeys* 37:93–107. <https://doi.org/10.3897/mycokeys.37.25901>
- Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *J Bacteriol* 172:4238–4246. <https://doi.org/10.1128/jb.172.8.4238-4246.1990>
- White TJ, Bruns TD, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) *PCR protocols, a guide to methods and applications*. Academic, San Diego, pp 315–322. <https://doi.org/10.1016/b978-0-12-372180-8.50042-1>
- Wu SH, Hibbett DS, Binder M (2001) Phylogenetic analyses of *Aleurodiscus* s.l. and allied genera. *Mycologia* 93:720–731. <https://doi.org/10.2307/3761826>
- Wu SH, Wang DM, Yu SY (2010) *Neoeurodiscus fujii*, a new genus and new species found at the timberline in Japan. *Mycologia* 102:217–223. <https://doi.org/10.3852/09-052>
- Wu SH, Wei CL, Lin YT, Chang CC, He SH (2019) Four new East Asian species of *Aleurodiscus* with echinulate basidiospores. *MycKeys* 52:71–87. <https://doi.org/10.3897/mycokeys.52.34066>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.