Aleurodiscus Bicornis and A. Formosanus Spp. Nov. (Basidiomycota) With Smooth Basidiospores, and Description of A. Parvisporus From NE China

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Research Article

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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 high mountains of NW Yunnan Province of SW China, grew on branch of *Picea* sp. *Aleurodiscus formosanus* was found from high mountains of central Taiwan, grew on branch of gymnosperm. *Aleurodiscus parvisporus* was previously reported only once from Japan and Sichuan Province of China respectively, 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, corresponds with resemblance of their morphological features.

Introduction

The genus *Aleurodiscus* Rabenh. ex J. Schröt. belongs to the Stereaceae Pilát of the Russulales Kreisel ex P.M. Kirk, P.F. Cannon & J.C. David. *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 dendorhyphidia 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 segregate genera among *Aleurodiscus* s.l. (Núñez and Ryvarden 1997; Wu et al. 2001; Larsson and Larsson 2003; Miller et al. 2006; Larsson 2007; Wu et al. 2010; Wu et al. 2019), due to highly variable diagnostic characters among species. The characteristics combined for separating segregate 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 *Neoaleurodiscus* 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 (http://www.indexfungorum.org/). In the recent decade, new species of *Aleurodiscus* s.l. have been proposed by Ryvarden et al. (2012), Gorrón 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, 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 undescribed and an uncommon *Aleurodiscus* sp. with effused basidiomata, clamped generative hyphae and quasi-binding hyphae, sulphuric positive reaction of gloeocystidia, hyphidia, acanthophyses and smooth basidiospores. These morphologically resembling species are also phylogenetically closely related.
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 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 and ornamentation 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). Edf/1953R and 983F/2218R were used to amplify a portion of the TEF1 gene (Rehner & Buckley 2005; Matheny et al. 2007). 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 (Mashima et al. 2016). Sequences were assembled using BioEdit v7.2.5 (Hall 1999). Newly obtained sequences (Supplementary Table 1) were submitted to DNA Data Bank of Japan (DDBJ) (Benson et al. 2018).

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 EF1 datasets. Three final alignments were manually adjusted, when necessary, in Bioedit (Hall 1999) before 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. (Fig. 2A and 3)

MycoBank: MB xxxxxx

*Etymology*. From bicornis (= two-homed), 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-Ⅴ-2013, *Wu 1308-125* (TNM F27227)

Basidiomata resupinate, effused, adnate, membranaceous, 80–300 μm 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 μm thick, sometimes indistinct, intermediate layer with somewhat loose to fairy dense texture, 20–100 μm thick; hyphae interwoven. Subicular generative hyphae moderately ramified, colorless, 2–5 μm diam., with 0.3–1.2 μm thick walls, with abundant small oily drops, anastomoses rather frequent; quasi-binding hyphae richly ramified, colorless, 1–3 μm diam, walls almost solid. Hymenial layer thickening, subhymenium differentiated, with dense texture, 50–200 μm thick; hyphae ± vertical, irregularly swollen, full of small oily drops, 2.2–6.5 μm 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\(\times\)120 \(\times\) 7\(\times\)13 \(\mu\)m, thin- to slightly thick-walled, SA\(\frac{1}{2}\). Acanthophyses numerous, cylindrical, colorless, ventricose, subclavate or broadly clavate, apices with numerous aculei, occasionally with adventitious septa, 25\(\times\)70 \(\times\) 4\(\times\)17 \(\mu\)m, thin- to thick-walled, usually thick-walled toward aculei parts, adventitious septa occasionally occur, aculei 1\(\times\)4 \(\times\) 1 \(\mu\)m.

Hyphidia numerous, 20\(\times\)55 \(\times\) 3\(\times\)5.5 \(\mu\)m, sometimes branched. Basidia subclavate, \(\pm\) flexuous, 45\(\times\)76 \(\times\) 14\(\times\)19 \(\mu\)m, 2-sterigmate. Basidiospores broadly ellipsoid, adaxially slightly concave, smooth, with a distinct apiculus, with several very small oily drops or homogeneous, IKI bluish black, CB\(\frac{1}{2}\), generally 19\(\times\)22 \(\times\) 12.5 \(\times\) 15 \(\mu\)m.

Statistic measurements of basidiospores. (18.4\(\times\))19.2\(\times\)21.5\(\times\)22.6 \(\times\) (11.7\(\times\))13.3\(\times\)14.9\(\times\)116 \(\mu\)m, L = 20.10\(\pm\)1.00 \(\mu\)m, W = 14.00\(\pm\)0.80 \(\mu\)m, Q = 1.44 (n = 30) (Wu 1308-125). (18.7\(\times\))20.1\(\times\)22.6\(\times\)23.2 \(\times\) (11\(\times\))12.1\(\times\)14.8\(\times\)15.7 \(\mu\)m, L = 21.01\(\pm\)1.13 \(\mu\)m, W = 13.42\(\pm\)1.14 \(\mu\)m, Q = 1.57 (n = 30) (Wu 1308-107). (19.2\(\times\))20.2\(\times\)22.1\(\times\)24 \(\times\) (12.8\(\times\))13.4\(\times\)15.6\(\times\)16.2 \(\mu\)m, L = 21.19\(\pm\)0.96 \(\mu\)m, W = 14.64\(\pm\)0.94 \(\mu\)m, Q = 1.45 (n = 30) (Wu 1308-108).

**Additional specimens (paratypes) examined.** China, Yunnan Province, Lichiang, near Astronomy Observatory, alt. 3,150 m, on branch of *Picea* sp., coll. S.H. Wu, 31-\(\frac{1}{2}\)-2013, Wu 1308-101 (TNM F27210), Wu 1308-108 (TNM F27214).

**Distribution.** Known from SW China (NW Yunnan Province).

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

MycoBank: MB xxxxxx

**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-\(\frac{1}{2}\)-2014, Chen 2736 (TNM F28401).

Basidiomata resupinate, effused, adnate, membranaceous, 50\(\times\)200 \(\mu\)m thick in section. Hymenial surface Light Buff, Pale Luteous, 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 to dense texture, 15\(\times\)80 \(\mu\)m thick, sometimes indistinct; hyphae usually horizontal near substrate, \(\pm\) vertical near hymenial layer. Generative hyphae colorless, fairly straight, moderately ramified, 2\(\times\)5.2 \(\mu\)m diam, walls up to 1 \(\mu\)m thick, with several small oily drops, anastomoses occasional; quasi-binding hyphae few in deep subiculum, richly ramified, colorless, 1\(\times\)2.5 \(\mu\)m diam, walls almost solid. Hymenial layer thickening, subhymenium differentiated, with dense texture, 50\(\times\)150 \(\mu\)m thick; hyphae \(\pm\) vertical, colorless, 2\(\times\)4.6 \(\mu\)m 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\(\times\)115 \(\times\) 7\(\times\)
16\,\mu m, walls up to 1\,\mu m thick, SA. Acanthophyses numerous, subglobose, fusiform or cylindrical, usually with stalked base, usually with an apical projection provided with ± dextrinoid aculei, colorless, 18-35 \times 4-17\,\mu m, walls up to 0.8\,\mu m thick. Hyphidia numerous, ± flexuous, 18-40 \times 2-4\,\mu m. Basidia broadly clavate, usually with stalked bases, 45-76 \times 14-19\,\mu m, usually with a lateral aculeate branch up to 25\,\mu m long, walls up to 1\,\mu m thick, 4-sterigate. Basidiospores narrowly ellipsoid to broadly ellipsoid, adaxially attened, smooth, with small oily drops or homogeneous, IKI bluish black, CB, generally 14-16 \times 7.5-10.5\,\mu m.

**Statistic measurements of basidiospores.** (14)14.5\pm15.8(\pm16.5) \times (7.2)8\pm10.2(\pm11.8)\,\mu m, L = 15.14\pm0.71\,\mu m, W = 9.02\pm1.07\,\mu m, Q = 1.70 (n = 30) (Chen 2736). (13)13.5\pm15(\pm16) \times (7.2)8\pm9.8(\pm11.2)\,\mu m, L = 14.29\pm0.74\,\mu m, W = 8.99\pm0.86\,\mu m, 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, Tatachia, 23°29'N, 120°53'E, alt. 2450 m, on branch of gymnosperm, coll. S.Z. Chen, W.C. Chen & C.C. Chen, 30-1-2014, Chen 2739 (TNM F28404), Chen2748 (TNM F28411).

**Distribution.** Known from temperate high mountains of Taiwan.

**Aleurodiscus parvisporus** Núñez & Ryvarden, Synopsis Fungorum 12: 117 (1997) (Fig. 2C and 5)

Basidiomata resupinate, effused, adnate, membranaceous, 90-300\,\mu m thick in section. Hymenial surface Pale Buff or Buff when young, Pale Luteus when old, smooth to ± 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\,\mu m diam, with walls up to ca. 1\,\mu m thick, usually with small oily drops; quasi-binding hyphae embedded in woody substrate, richly ramified, colorless, 1.2-3.2\,\mu m diam, walls almost solid. Hymenial layer thickening, with compact texture, 90-300\,\mu m thick; generative hyphae ± vertical, irregularly swollen, with small oily drops, colorless, 2-4.5\,\mu m diam. Lumpy crystals scattered in section. Gloeocystidia numerous, immersed or slightly projecting, irregularly cylindrical or tubular, ± 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\,\mu m, thin- to slightly thick-walled, walls up to ca. 1\,\mu m thick, SA. Acanthophyses numerous, cylindrical, colorless, with numerous aculei towards apices, 25-55 \times 2-3.5\,\mu m, usually slightly thick-walled toward apices; aculei subcolorless when young, slightly brownish when old, 2-4(\pm10) \times 0.8-1\,\mu m. Hyphidia numerous, 20-40 \times 2-4.5\,\mu m, sometimes branched. Basidia clavate to narrowly clavate, ± flexuous, usually laterally with several aculei, ± guttulate, 25-40 \times 4-5.5\,\mu m, 4-sterigate. Basidiospores broadly ellipsoid to ellipsoid, adaxially flattened or slightly concave, smooth, with a minute apiculus, with several minute oily drops, IKI bluish black, CB, generally 5.7-6.3 \times 3.5-4.2\,\mu m.
Statistic measurements of basidiospores. (5.6±5.8±6.2(6.6) × (3.3±3.5±4.1(4.3) μm, L = 5.96±0.23 μm, W = 3.78±0.30 μm, Q = 1.58 (n = 30) (Wu 1307-84). (5.5±5.7±6.2(6.5) × (3.4±3.6±4.2(4.5) μm, L = 5.95±0.27 μm, W = 3.94±0.25 μm, Q = 1.51 (n = 30) (Wu 1307-88).

Specimens examined. China, Jilin Province, Fusong County, Touxi Protection Station, 42°18’N, 127°50’E, alt. 1025 m, on branch of Syringa reticulate var. mandshurica, coll. S.H. Wu, 13-⅔-2013, 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

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), 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.

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 × 7±13 μm, Núñez and Ryvarden 1997). Moreover, Aleurodiscus canadensis have 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 Ryvarden 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 dextnoid apical protuberances; but differs from the latter in having smaller basidiospores (7±10 × 4±7 μm, Núñez and Ryvarden 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 Ryvarden 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 hardly 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. 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*.

**Declarations**

The authors declare that they have no conflict of interest.

**Availability of data and materials (data transparency)**

All 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.

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Authors' contributions -

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

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**References**

1. Benson DA, Cavanaugh M, Clark K, Karsch-Mizrachi I, Ostell J, Pruitt KD, Sayers EW (2018) GenBank. Nucleic Acids Research 46 (D1):D41–D46. https://doi.org/1093/nar/gkx1094

2. Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9:772–772. https://doi.org/1038/nmeth.2109
3. Dai LD, He SH (2016) New species and new records of *Aleurodiscus*. (Basidiomycota) in China. Mycological Progress 15:717–730. https://doi.org/10.1007/s11557-016-1202-z

4. 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

5. Dai LD, Wu SH, Nakasone KK, Burdsall HH, He SH (2017a) Two new species of *Aleurodiscus*. (Russulales, Basidiomycota) on bamboo from tropics. Mycoscience 58:213-220. https://doi.org/10.1016/j.myc.2017.02.001

6. Dai LD, Zhao Y, He SH (2017b) Three new species of *Aleurodiscus* l. (Russulales, Basidiomycota) on bamboos from East Asia. Cryptogamie, Mycologie 38:227-239. https://doi.org/10.7872/crym/v38.iss2.2017.227

7. Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. Molecular Ecology 2:113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

8. Ghobad-Nejhad M, Langer E (2018) A new species in *Aleurodiscus* l. (Stereaceae, Russulales) from Iran. Phytotaxa 351:264-272. https://doi.org/10.11646/phytotaxa.351.4.2

9. Gorjón SP, Greslebin AG, Rajchenberg M (2013) The genus *Aleurodiscus*. (Stereaceae, Russulales) in the Patagonian Andes. Mycological Progress 12:91–108. https://doi.org/10.1007/s11557-012-0820-3

10. Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41:95–98.

11. Larsson KH (2007) Re-thinking the classification of corticioid fungi. Mycological Research 111:1040–1063. https://doi.org/1016/j.mycres.2007.08.001

12. Larsson E, Larsson KH (2003) Phylogenetic relationships of russuloid basidiomycetes with emphasis on aphyllorophoralean taxa. Mycologia 95:1037–1065. https://doi.org/2307/3761912

13. Maekawa N, Yang ZL, Zang M (2002) Corticioid fungi (Basidiomycetes) collected in Sichuan Province, China. Mycotaxon 83:81-95.

14. Maninder K, Avneet PS, Dhingra GS, Ryvarden L (2014) *Aleurodiscus himalaicus* (Agaricomycetes) sp. nov. from India. Synopsis Fungorum 32:5–7.

15. 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). Molecular Phylogenetics and Evolution 43:430–451. https://doi.org/1016/j.ympev.2006.08.024

16. 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 Research 44:D51–D57. https://doi.org/1093/nar/gkv1105

17. Miller SL, Larsson E, Larsson K-H, Verbeken A, Nuytinck J (2006) Perspectives in the new Russulales. Mycologia 986:960–970. https://doi.org/10.1080/15572536.2006.11832625
Table

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  | TEF1  |
| *Acanthobasidium bambusicola*                   | He 2357                | KU559343 | KU574833 | –     |
| *Acanthofungus rimosus*#                        | Wu 9601-1              | MF043521 | AY039333 | –     |
| *Acanthophysellum cerussatum*                   | He 20120920-3          | KU559339 | KU574830 | KU992716 |
| *Aleurobotrys botryosus*#                       | He 2712                | KX306877 | KY450788 | –     |
| *Aleurocystidiellum disciforme*                 | He 3159                | KU559340 | KU574831 | KU992721 |
| *Aleurocystidiellum subcruentatum*#            | He 2886                | KU559341 | KU574847 | KU992720 |
| *Aleurodiscus alpinus*                         | Wu 1407-59             | MF043522 | MF043527 | –     |
| *Aleurodiscus alpinus*                         | Wu 1407-55*            | –     | MF043526 | LC269190 |
| *Aleurodiscus alpinus*                         | Wu 1407-61             | MF043523 | MF043528 | –     |
| *Aleurodiscus amorphus*#                       | Ghobad-Nejad-2464      | KU559342 | KU574832 | KU992717 |
| *Aleurodiscus amorphus*#                       | KHL 4240               | AF506397 | AF506397 | –     |
| *Aleurodiscus bambusinus*                      | He 4261                | KY706207 | KY706219 | LC430911 |
| *Aleurodiscus bicomis*                         | Wu 1308-101            | LC433893 | LC433900 | LC433907 |
| *Aleurodiscus bicomis*                         | Wu 1308-125*           | LC433899 | LC433906 | LC433912 |
| *Aleurodiscus canadensis*                      | Wu 1207-90             | KY706203 | KY706225 | –     |
| *Aleurodiscus dextrinoideocerussatus*          | EL25-97                | AF506401 | AF506401 | –     |
| *Aleurodiscus dextrinoideophyses*              | He 4105                | MH109050 | KY450784 | –     |
| *Aleurodiscus effusus*                         | He 2261                | KU559344 | KU574834 | KU992719 |
| *Aleurodiscus formosanus*                      | Chen 2736*             | LC433894 | LC433901 | LC433908 |
| *Aleurodiscus formosanus*                      | Chen 2748              | LC433895 | LC433902 | LC433909 |
| *Aleurodiscus formosanus*                      | Chen 2739              | LC433896 | LC433903 | –     |
| *Aleurodiscus formosanus*                      | WEI 19-274             | LC514405 | LC514406 | –     |
| *Aleurodiscus gigasporus*                      | Wu 0108-15             | KY706205 | KY706213 | –     |
| *Aleurodiscus grantii*                         | HHB-14417              | KU559363 | KU574821 | KU992708 |
| *Aleurodiscus grantii*                         | HHB-14418              | KU559364 | KU574822 | –     |
| *Aleurodiscus isabellinus*                     | He 5283                | MH109052 | MH109046 | LC430912 |
| *Aleurodiscus mesaverdense*                    | FP-120155              | KU559359 | KU574817 | –     |
| Species                                   | Accession Numbers |
|-------------------------------------------|--------------------|
| *Aleurodiscus mirabilis*                  | Dai 13281          |
|                                           | KU559350           |
|                                           | KU574839           |
|                                           | KU992711           |
| *Aleurodiscus oakesii*                    | He 2243            |
|                                           | KU559352           |
|                                           | KU574840           |
|                                           | –                  |
| *Aleurodiscus oakesii*                    | HHB11890-A-sp      |
|                                           | KU559365           |
|                                           | KU574823           |
|                                           | –                  |
| *Aleurodiscus parvisporus*                | Wu 1307-84         |
|                                           | LC433897           |
|                                           | LC433904           |
|                                           | LC433910           |
| *Aleurodiscus parvisporus*                | Wu 1307-88         |
|                                           | LC433898           |
|                                           | LC433905           |
|                                           | LC433911           |
| *Aleurodiscus pinicola*                   | Wu 1106-16         |
|                                           | MF043524           |
|                                           | MF043529           |
|                                           | –                  |
| *Aleurodiscus pinicola*                   | Wu 1308-54*        |
|                                           | MF043525           |
|                                           | MF043530           |
|                                           | LC269191           |
| *Aleurodiscus senticosus*                 | Wu 1209-7*         |
|                                           | MH596849           |
|                                           | MF043531           |
|                                           | LC271169           |
| *Aleurodiscus senticosus*                 | Wu 1209-9          |
|                                           | MH596850           |
|                                           | MF043533           |
|                                           | LC269192           |
| *Aleurodiscus senticosus*                 | Wu 9610-1          |
|                                           | MH596851           |
|                                           | MF043532           |
|                                           | LC269193           |
| *Aleurodiscus sichuanensis*               | Wu 0010-18*        |
|                                           | MH596852           |
|                                           | MF043534           |
|                                           | LC269194           |
| *Aleurodiscus senticosus*                 | He 4935            |
|                                           | LC430904           |
|                                           | LC430907           |
|                                           | –                  |
| *Aleurodiscus subroseus*                  | He 4807            |
|                                           | MH109054           |
|                                           | MH109048           |
|                                           | –                  |
| *Aleurodiscus subroseus*                  | He 4895            |
|                                           | LC430903           |
|                                           | LC430910           |
|                                           | LC430913           |
| *Aleurodiscus tenuissimus*                | He3575             |
|                                           | KX306880           |
|                                           | KX842529           |
|                                           | –                  |
| *Aleurodiscus thailandicus*               | He 4099            |
|                                           | KY450781           |
|                                           | KY450782           |
|                                           | –                  |
| *Aleurodiscus tropicus*                   | He 3830            |
|                                           | KX553875           |
|                                           | KX578720           |
|                                           | LC269195           |
| *Aleurodiscus verrucosporus*              | He 4491            |
|                                           | KY450786           |
|                                           | KY450790           |
|                                           | –                  |
| *Aleurodiscus wakefieldiae*               | He 2580            |
|                                           | KU559353           |
|                                           | KU574841           |
|                                           | KU992710           |
| *Boidinia macrospora*                     | Wu 9202-21         |
|                                           | AF506377           |
|                                           | AF506377           |
|                                           | –                  |
| *Conferticium heimii*                     | CBS321.66          |
|                                           | AF506381           |
|                                           | AF506381           |
|                                           | –                  |
| *Conferticium ravum*                      | NH13291            |
|                                           | AF506382           |
|                                           | AF506382           |
|                                           | –                  |
| *Gloeocystidiellum aspellum*              | LIN 625            |
|                                           | AF506432           |
|                                           | AF506432           |
|                                           | –                  |
| *Gloeocystidiellum porosum*               | Wu 1608-176        |
|                                           | LC430905           |
|                                           | LC430908           |
|                                           | –                  |
| *Gloeocystidiopsis cryptacanthus*         | KHL10334           |
|                                           | AF506442           |
|                                           | AF506442           |
|                                           | –                  |
| *Gloeocystidiopsis flammea*               | CBS324.66          |
|                                           | AF506437           |
|                                           | AF506437           |
|                                           | –                  |
| *Heterobasidion parviporum*               | 91605              |
|                                           | KJ651503           |
|                                           | KJ651561           |
|                                           | KU985089           |
| *Megalocystidium chelidonium*             | LodgeSJ110.1       |
|                                           | AF506441           |
|                                           | AF506441           |
|                                           | –                  |
| *Megalocystidium leucoxanthum*            | HK9808             |
|                                           | AF506420           |
|                                           | AF506420           |
|                                           | –                  |
| Species                  | Accession Numbers |
|-------------------------|-------------------|
| Megalocystidium wakullum| Oslo-930107       |
|                         | AF506443          |
|                         | AF506643          |
|                         | –                 |
| Neoaleurodiscus fujii#  | He 2921           |
|                         | KU559357          |
|                         | KU574845          |
|                         | KU992709          |
| Stereum complicatum     | He 2234           |
|                         | KU559368          |
|                         | KU574828          |
|                         | KU992706          |
| Stereum hirsutum#       | Wu 1109-127       |
|                         | LC430906          |
|                         | LC430909          |
|                         | –                 |
| Stereum ostrea          | He 2067           |
|                         | KU559366          |
|                         | KU574826          |
|                         | KU992703          |
| Stereum sanguinolentum  | He 2111           |
|                         | KU559367          |
|                         | KU574827          |
|                         | KU992705          |
| Xylobolus frustulatus   | He 2231           |
|                         | KU881905          |
|                         | KU574825          |
|                         | KU992704          |

* Holotype, # Generic type

**Figures**
Figure 1

ML tree of Aleurodiscus and related genera of Stereaceae inferred from the 28S-ITS-TEF1 markers. ML bootstrap values $\geq 50\%$ and PP $\geq 0.7$ from the Bayesian analysis are indicated at internodes. The target studied species are shown in boldface type.
Figure 2

Basidiocarps. A. Aleurodiscus bicornis (holotype, Wu 1308-125). B. A. formosanus (holotype, Chen 2736). C. A. parvisporus (holotype, Wu 1307-84).
Figure 3

Aleurodiscus bicorns (Wu 1308-125) A. Basidiocarp section. B. Generative hyphae. C. Skeletal hyphae. D. Subhymenial hyphae. E. Acanthophyses. F. Basidia. G. Dendrohyphidia. H. Hyphidia. I. Basidiospores. J. Gloeocystidia (scale bar = 10 μm).
Figure 4

Aleurodiscus formosanus (Chen 2736) A. Basidiocarp section. B. Binding hyphae. C. Generative hyphae. D. Acanthophyses. E. Gloeocystidia. F. Basidia. G. Hyphidia. H. Basidiospores (scale bar = 10 μm).
Figure 5

Aleurodiscus parvisporus (Wu 1307-84) A. Basidiocarp section. B. Skeletal hyphae. C. Generative hyphae. D. Subhymenial hyphae. E. Gloeocystidia. F. Basidia. G. Acanthophyses. H. Hyphidia. I. Basidiospores (scale bar = 10 μm).