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Spirodecosporaceae fam. nov. (*Xylariales*, *Sordariomycetes*) and two new species of *Spirodecospora*

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Abstract: The genus *Spirodecospora* has been placed in *Xylariaceae* based on morphological similarities. *Spirodecospora* spp., found on bamboo in Japan, were taxonomically and phylogenetically studied using molecular data for first time. Molecular phylogenetic analyses were based on the DNA sequence data of three regions: the nuclear ribosomal internal transcribed spacer (ITS) region, the large subunit (LSU) of rDNA, and the second largest RNA polymerase II subunit (*rpb2*) gene. Results showed that *Spirodecospora* formed an independent lineage from other known families in *Xylariales*. The new family *Spirodecosporaceae* is introduced in this study to accommodate this lineage based on the phylogenetic evidence and morphological differences from the other known families. *Spirodecospora* is characterised by having deeply immersed ascomata with a cylindrical ostiolar neck, unitunicate, cylindrical asci with I+, wedge-shaped apical ring, and broadly ellipsoidal to fusoid, aseptate, brown, verruculose ascospores with spirally or almost straight linear ornamentation. Based on morphological observations and molecular phylogenetic analyses, *S. melnikii* and two new species of *Spirodecospora*, *S. paramelnikii* and *S. paulospiralis*, are described and illustrated. A key to the four accepted species of *Spirodecospora* is provided.

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INTRODUCTION

The bambusicolous fungal genus, *Spirodecospora*, is characterised by obpyriform ascomata deeply immersed in the host, cylindrical, unitunicate asci with a I+, wedge-shaped, subapical ring, and broadly ellipsoidal to fusoid, olivaceous to brown, unicellular ascospores with conspicuous warts which are spirally arranged around the ascospores and surrounded by a mucilaginous sheath (Lu *et al.* 1998). This genus is similar to *Anthostomella*, but can be distinguished from the latter by the comparatively large-sized ascomata and ascospores with spiral ornamentations (Lu *et al*. 1998). *Spirodecospora* was established to accommodate *S. bambusicola* on *Bambusa* sp. (Lu *et al*. 1998), at the time without knowledge of the older name, *Anthostomella melnikii*, described from *Sasa* sp. (Vasilyeva 1990). These two species were considered conspecific, and only *S. melnikii* (= *A. melnikii*), which has priority, was accepted in *Spirodecospora* (Mel'nik & Hyde 2003).

Many fungi previously treated as members of *Xylariaceae* were proposed to be classified in separate families within *Xylariales* (*e.g. Barrmaeliaceae*, *Hypoxylaceae*, and *Vamsapriyaceae*; Voglmayr *et al.* 2018, Wendt *et al.* 2018, Sun *et al.* 2021). Furthermore, recent molecular phylogenetic studies showed that species of the xylariaceous genus *Anthostomella*, which were similar to *Spirodecospora*, were polyphyletic within *Xylariales* and phylogenetically distant from *Xylariaceae* (Daranagama *et al.* 2015, 2016). *Spirodecospora* has been considered to belong to the family *Xylariaceae* (Lu *et al.* 1998) based on similarities in the ultrastructure of ascus apices. However, these morphological similarities with xylariaceous taxa are not sufficient for a sound evaluation whether *Spirodecospora* belongs to *Xylariaceae sensu stricto*. Although several spirodecospora-like genera (*e.g. Albicollum*, *Helicogermslita*, *Leptomassaria*, and *Spiririma*), which have helicoid germ slits around the ascospore, were shown phylogenetically to be found throughout *Xylariaceae* (Voglmayr *et al.* 2022), no sequence data are available for any species of *Spirodecospora*.

In our ongoing taxonomic study of bambusicolous fungi in Japan (*e.g.* Tanaka *et al*. 2009, Hashimoto *et al*. 2015a, b, Sugita & Tanaka 2022), several specimens of *Spirodecospora* from bamboo were collected and obtained in axenic culture. The aim of this study is to reveal the phylogenetic placement of *Spirodecospora* at the family level and to clarify the interspecific relationships within the genus.

MATERIALS AND METHODS

Morphological observations

All specimens were collected on different species of bamboo in Japan. Morphological characteristics of sexual morphs were observed through preparations mounted in distilled water by differential interference microscopy (Olympus BX53) using images captured with an Olympus digital camera (DP21). Measurements of all structures except for ascomatal section were taken from material mounted in distilled water. Sections of ascomata were mounted in diluted lactophenol cotton blue. Lugol's solution was used to test the amyloidity of ascal apex, and Indian ink was used to observe the mucilaginous sheath of ascospores. Images stacking multiple focus points were produced using CombineZP (https://combinezp.software.informer.com/) to observe the fine structure of spore surface. Single spore isolates were obtained from all specimens, and fungal cultures were preserved and deposited at Hirosaki University and NARO Genebank, Japan (MAFF). Colony characteristics were recorded from growth on potato dextrose agar (PDA) from Becton, Dickinson and Company (MD, USA), after a week at 25 °C in the dark, and colony colours were recorded by referring to Rayner (1970). Several mycelial agar pieces were placed on water agar containing sterilised rice straws (rice straw agar: RSA) to observe sporulation *in vitro*. After the substrates were colonised at 25 °C for 2 wk, the plates were incubated at 25 °C under blacklight blue illumination for 2–4 mo to observe sporulation. All specimens were deposited at the herbarium of Hirosaki University (HHUF).

DNA extraction, PCR, and phylogenetic analyses

DNA was extracted from the cultures using the ISOPLANT II kit (Nippon Gene, Tokyo, Japan) following the manufacturer's instructions. The following loci were amplified and sequenced: the internal transcribed spacer (ITS) region with primers ITS1 and ITS4 (White *et al.* 1990); the large subunit nuclear ribosomal DNA (LSU) with primers LR0R (Rehner & Samuels 1994) and LR5 or LR7 (Vilgalys & Hester 1990); and the second largest RNA polymerase II subunit (*rpb2*) with primers fRPB2-5F and fRPB2-7cR (Liu *et al.* 1999). PCR products were purified using the FastGene Gel/PCR Extraction Kit (Nippon Gene, Tokyo, Japan) following the manufacturer's instructions and sequenced at SolGent (South Korea). Newly generated sequences were deposited in GenBank.

The multiple alignment program MUSCLE implemented in MEGA v. 7.0 (Kumar *et al.* 2016) was used to align the ITS, LSU, and *rpb2* sequences. The maximum-likelihood (ML) and Bayesian methods were used for phylogenetic analysis. The optimum substitution models for each dataset were estimated using Kakusan4 software (Tanabe 2011) based on the Akaike information criterion (AIC; Akaike 1974) and Bayesian information criterion (BIC; Schwarz, 1978) for ML analysis and Bayesian analysis, respectively. The TreeFinder Mar 2011 program (http://www.treefinder.de) for ML analysis was executed based on models selected using the AICc4 parameter. ML bootstrap support (MLBS) values were obtained using 1 000 bootstrap replicates. The Bayesian analysis program, MrBayes v. 3.2.6 (Ronquist *et al.* 2012), was executed with substitution models selected based on the BIC4 parameter. Two simultaneous and independent Metropolis-coupled Markov chain Monte Carlo (MCMCMC) runs were performed for 1 000 000 generations, with the tree sampled every 1 000 generations. The convergence of the MCMCMC procedure was assessed from the effective sample size scores (all > 100) using MrBayes and Tracer v. 1.6 (Rambaut *et al.* 2014). The first 25 % of the trees were discarded as burn-in. The remainder was used to calculate the 50 % majority-rule trees and to determine the posterior probabilities (PPs) for individual branches. Multiple sequence alignments and trees were deposited in TreeBASE (S29719).

To clarify the taxonomic placement of newly sequenced *Spirodecospora* species, a molecular phylogenetic analysis based on ITS-LSU-*rpb2* combined dataset consisting of 73 strains of *Xylariales* was performed (Table 1). *Bombardia bombarda* and *Sordaria fimicola* were used as outgroups.

RESULTS

The data matrix used for ML and Bayesian phylogenetic analyses comprised 559 bp from ITS, 1 465 bp from LSU and 1 065 bp from *rpb2*. Of the 3 089 characters included in the alignment, 1 360 were variable, 1 141 were parsimony informative, and 1 693 were conserved. ML analysis of the combined dataset was conducted based on the selected substitution model for each partition (J2+G for ITS, GTR+G for LSU, J2+G for the first of *rpb2*, TVM+G for the second codon positions of *rpb2*, and HKY85+G for the third codon positions of *rpb2*). The ML tree with the highest log likelihood (lnL = –38,040.76) is shown in Fig. 1. The tree topology recovered via Bayesian analysis was almost identical to that of the ML tree. Phylogenetic analysis based on three loci showed a monophyletic clade consisting of all *Spirodecospora* strains, along with 14 lineages of known families in *Xylariales* (Fig. 1). The *Spirodecospora* clade was shown as an independent and fully supported (100 % MLBS/1.0 Bayesian PP) clade. Families *Coniocessiaceae* and *Hansfordiaceae* were the most closely related lineages to *Spirodecospora*, but their relationships were not statistically supported. As a result of the phylogenetic analyses, the new family *Spirodecosporaceae* is established to accommodate the single genus *Spirodecospora*. Two new species, *S. paramelnikii* and *S. paulospiralis*, are described and illustrated below.

TAXONOMY

Spirodecosporaceae R. Sugita & Kaz. Tanaka, ***fam. nov.*** MycoBank MB 846055.

Type genus: *Spirodecospora* B.S. Lu *et al*.

Ascomata deeply immersed in host tissue, solitary, subglobose. *Ostiolar neck* cylindrical, periphysate. *Ascomatal wall* composed of several layers of polygonal, dark brown cells. *Paraphyses* numerous, septate, unbranched, filamentous, hyaline. *Asci* unitunicate, with (4–)8 ascospores, cylindrical, broadly rounded at the apex; apical ring I+, wedge-shaped. *Ascospores* broadly ellipsoidal to fusoid, aseptate, brown, verruculose, with spirally to almost straight linear ornamentations around the ascospores, surrounded by a mucilaginous sheath.

Notes: *Spirodecosporaceae* is distinguished from *Coniocessiaceae* and *Hansfordiaceae* by its morphological differences and/or phylogenetic relationships. The asci of *Coniocessiaceae* clearly

Table 1. Isolates and GenBank accessions of sequences used in the phylogenetic analysis. The newly obtained strains and sequences are shown in bold.

Species	Specimen/Strain	GenBank accession numbers			Reference
		ITS	LSU	*rpb2*	
Anthostoma decipiens	CBS 133221	KC774565	KC774565	–	Jaklitsch *et al.* (2014)
Arecophila clypeata	GZUCC0110	MT742129	MT742136	MT741732	Li *et al.* (2022)
Astrocystis bambusicola	MFLUCC 17-0127	MF467942	MF467944	MF467946	Hyde *et al.* (2017)
Barrmaelia macrospora	CBS 142768	KC774566	KC774566	MF488995	Jaklitsch *et al.* (2014), Voglmayr *et al.* (2018)
Barrmaelia rhamnicola	CBS 142772	MF488990	MF488990	MF488999	Voglmayr *et al.* (2018)
Biscogniauxia nummularia	MUCL 51395	KY610382	KY610427	KY624236	Wendt *et al.* (2018)
Bombardia bombarda	AFTOL-ID 967	–	DQ470970	DQ470923	Spatafora *et al.* (2006)
Cainia graminis	CBS 136.62	MH858123	AF431949	–	Lumbsch *et al.* (2002), Vu *et al.* (2019)
Circinotrichum maculiforme	CBS 122758	KR611875	KR611896	–	Crous *et al.* (2015)
Collodiscula bambusae	GZUH 0102	KP054279	KP054280	KP276675	Li *et al.* (2015)
Collodiscula japonica	CBS 124266	JF440974	JF440974	KY624273	Jaklitsch & Voglmayr (2012), Wendt *et al.* (2018)
Coniocessia anandra	CBS 125766	GU553338	GU553349	–	Asgari & Zare (2011)
Coniocessia cruciformis	CBS 125769	GU553336	GU553347	–	Asgari & Zare (2011)
Coniocessia maxima	CBS 593.74	GU553332	GU553344	–	Asgari & Zare (2011)
Coniocessia nodulisporioides	CBS 125779	GU553339	GU553350	–	Asgari & Zare (2011)
Creosphaeria sassafras	STMA 14087	KY610411	KY610468	KY624265	Wendt *et al.* (2018)
Cryptovalsa rabenhorstii	CBS 125574	KC774567	KC774567	–	Jaklitsch *et al.* (2014)
Daldinia concentrica	CBS 113277	AY616683	KY610434	KY624243	Triebel *et al.* (2005), Wendt *et al.* (2018)
Diatrype disciformis	MFLU 17-1549	MW240629	MW240559	MW658621	Samarakoon *et al.* (2022)
Diatrype virescens	CBS 128344	MH864890	MH876339	–	Vu *et al.* (2019)
Emarcea castanopsidicola	CBS 117105	MK762710	MK762717	MK791285	Samarakoon *et al.* (2020)
Emarcea eucalyptigena	CBS 139908	MK762711	MK762718	MK791286	Samarakoon *et al.* (2020)
Entosordaria perfidiosa	CBS 142773	MF488993	MF488993	MF489003	Voglmayr *et al.* (2018)
Fasciatispora arengae	MFLUCC 15-0326a	MK120275	MK120300	MK890794	Doilom *et al*. (2018)
Fasciatispora cocoes	MFLUCC 18-1445	MN482680	MN482675	MN481517	Hyde *et al.* (2020)
Graphostroma platystomum	CBS 270.87	JX658535	DQ836906	KY624296	Zhang *et al.* (2006), Stadler *et al.* (2014), Wendt *et al.* (2018)
Halorosellinia krabiensis	MFLUCC 17-2469	MN047119	MN017883	–	Dayarathne *et al.* (2020)
Hansfordia pruni	CBS 194.56	MK442585	MH869122	KU684307	Crous *et al.* (2019a), Vu *et al.* (2019)
Hansfordia pulvinata	CBS 144422	MK442587	MK442527	–	Crous *et al.* (2019a)
Hypomontagnella monticulosa	MUCL 54604	KY610404	KY610487	KY624305	Wendt *et al.* (2018)
Hypoxylon fragiforme	MUCL 51264	KC477229	KM186295	KM186296	Stadler *et al.* (2013), Daranagama *et al.* (2015)
Idriella lunata	CBS 204.56	KP859044	KP858981	–	Hernández-Restrepo *et al.* (2016)
Induratia fengyangensis	CGMCC 2862	HM034856	HM034859	HM034849	Zhang *et al.* (2010)
Induratia thailandica	MFLUCC 17-2669	MK762707	MK762714	MK791283	Samarakoon *et al.* (2020)
Induratia ziziphi	MFLUCC 17-2662	MK762705	MK762712	MK791281	Samarakoon *et al.* (2020)
Jackrogersella multiformis	CBS 119016	KC477234	KY610473	KY624290	Kuhnert *et al.* (2014), Wendt *et al.* (2018)
Kretzschmaria deusta	CBS 163.93	KC477237	KY610458	KY624227	Stadler *et al.* (2013), Wendt *et al.* (2018)
Lopadostoma dryophilum	CBS 133213	KC774570	KC774570	KC774526	Jaklitsch *et al.* (2014)
Lopadostoma fagi	CBS 133206	KC774575	KC774575	KC774531	Jaklitsch *et al.* (2014)

Table 1. (Continued).

Species	Specimen/Strain	GenBank accession numbers			Reference
		ITS	LSU	*rpb2*	
Lopadostoma gastrinum	CBS 134632	KC774584	KC774584	KC774537	Jaklitsch *et al.* (2014)
Lopadostoma turgidum	CBS 133207	KC774618	KC774618	KC774563	Jaklitsch *et al.* (2014)
Microdochium fisheri	CBS 242.90	KP859015	KP858951	KP859124	Hernández-Restrepo *et al.* (2016)
Microdochium lycopodinum	CBS 122885	JF440979	JF440979	KP859125	Jaklitsch & Voglmayr (2012), Hernández-Restrepo *et al.* (2016)
Microdochium phragmitis	CBS 285.71	KP859013	KP858949	KP859122	Hernández-Restrepo *et al.* (2016)
Microdochium seminicola	CBS 139951	KP859038	KP858974	KP859147	Hernández-Restrepo *et al.* (2016)
Nemania serpens	FR AT-114	DQ631942	DQ840075	DQ631948	Tang *et al.* (2007), Fournier *et al.* (2010)
Obolarina dryophila	MUCL 49882	GQ428316	GQ428316	KY624284	Pažoutová *et al.* (2010), Wendt *et al.* (2018)
Paraxylaria rosacearum	TASM 6132	MG828941	MG829050	–	Wanasinghe *et al.* (2018)
Paraxylaria xylostei	MFLU 17-1636	MW240640	MW240570	–	Samarakoon *et al.* (2022)
Poronia punctata	CBS 656.78	KT281904	KY610496	KY624278	Senanayake *et al.* (2015), Wendt *et al.* (2018)
Requienella fraxini	CBS 140475	KT949910	KT949910	–	Jaklitsch *et al.* (2016)
Requienella seminuda	CBS 140502	KT949912	KT949912	MK523300	Jaklitsch *et al.* (2016), Voglmayr *et al.* (2019)
Rosellinia aquila	MUCL 51703	KY610392	KY610460	KY624285	Wendt *et al.* (2018)
Sarcoxylon compunctum	CBS 359.61	KT281903	KY610462	KY624230	Wendt *et al.* (2018)
Sordaria fimicola	CBS 723.96	MH862606	AY780079	AY780194	Miller & Huhndorf (2005), Vu *et al.* (2019)
Spirodecospora melnikii	**MAFF 247741 = KH 89**	**LC731932**	**LC731941**	**LC731950**	This study
	MAFF 247742 = KT 1729	**LC731933**	**LC731942**	**LC731951**	This study
	MAFF 247743 = KT 3457	**LC731934**	**LC731943**	**LC731952**	This study
	MAFF 247744 = KT 3760	**LC731935**	**LC731944**	**LC731953**	This study
	MAFF 247745 = KT 3911	**LC731936**	**LC731945**	**LC731954**	This study
	MAFF 247746 = KT 4092	**LC731937**	**LC731946**	**LC731955**	This study
	MAFF 247747 = RSU 52	**LC731938**	**LC731947**	–	This study
Spirodecospora paramelnikii	**MAFF 247748 = KT 4131**	**LC731939**	**LC731948**	**LC731956**	This study
Spirodecospora paulospiralis	**MAFF 247749 = KT 4143**	**LC731940**	**LC731949**	**LC731957**	This study
Stromatoneurospora phoenix	BCC82040	MT703666	MT735133	MT742605	Becker *et al.* (2020)
Vamsapriya bambusicola	MFLUCC 11-0477	KM462835	KM462836	KM462834	Dai *et al.* (2014)
Vamsapriya indica	MFLUCC 12-0544	KM462839	KM462840	KM462841	Dai *et al.* (2014)
Vamsapriya khunkonensis	MFLU 13-0367	KM462830	KM462831	KM462829	Dai *et al.* (2014)
Vamsapriya yunnana	KUMCC 18-0008	MG833874	MG833873	MG833875	Jiang *et al.* (2018)
Xylaria hypoxylon	CBS 122620	KY610407	KY610495	KY624231	Wendt *et al.* (2018)
Zygosporium minus	HKAS99625	MF621586	MF621590	–	Li *et al.* (2018)
Zygosporium oscheoides	MFLUCC 14-0402	MF621585	MF621589	–	Li *et al.* (2018)
Zygosporium pseudomasonii	CBS 146059	MN562147	MN567654	MN556815	Crous *et al.* (2019b)

differ from those of *Spirodecosporaceae* in having a non-amyloid or amyloid, V-shaped to sinuous, apical ring (Asgari & Zare 2011, Wanasinghe *et al.* 2018). *Hansfordiaceae*, which contains hyphomycetous species without any known sexual morph (Crous *et al*. 2019a), cannot be morphologically compared to *Spirodecosporaceae*, which lacks asexual morphs.

The type species of the genus *Spirodecospora* was previously placed in *Xylariaceae* based on similarities in the apical ascus structure (Lu *et al.* 1998). However, members of *Xylariaceae sensu stricto* have a conspicuously larger, wedge- to inverted hat-shaped ascus apical apparatus (Tang *et al.* 2009, Jaklitsch & Voglmayr 2012, Wittstein *et al.* 2020, Pi *et al.* 2021, Samarakoon

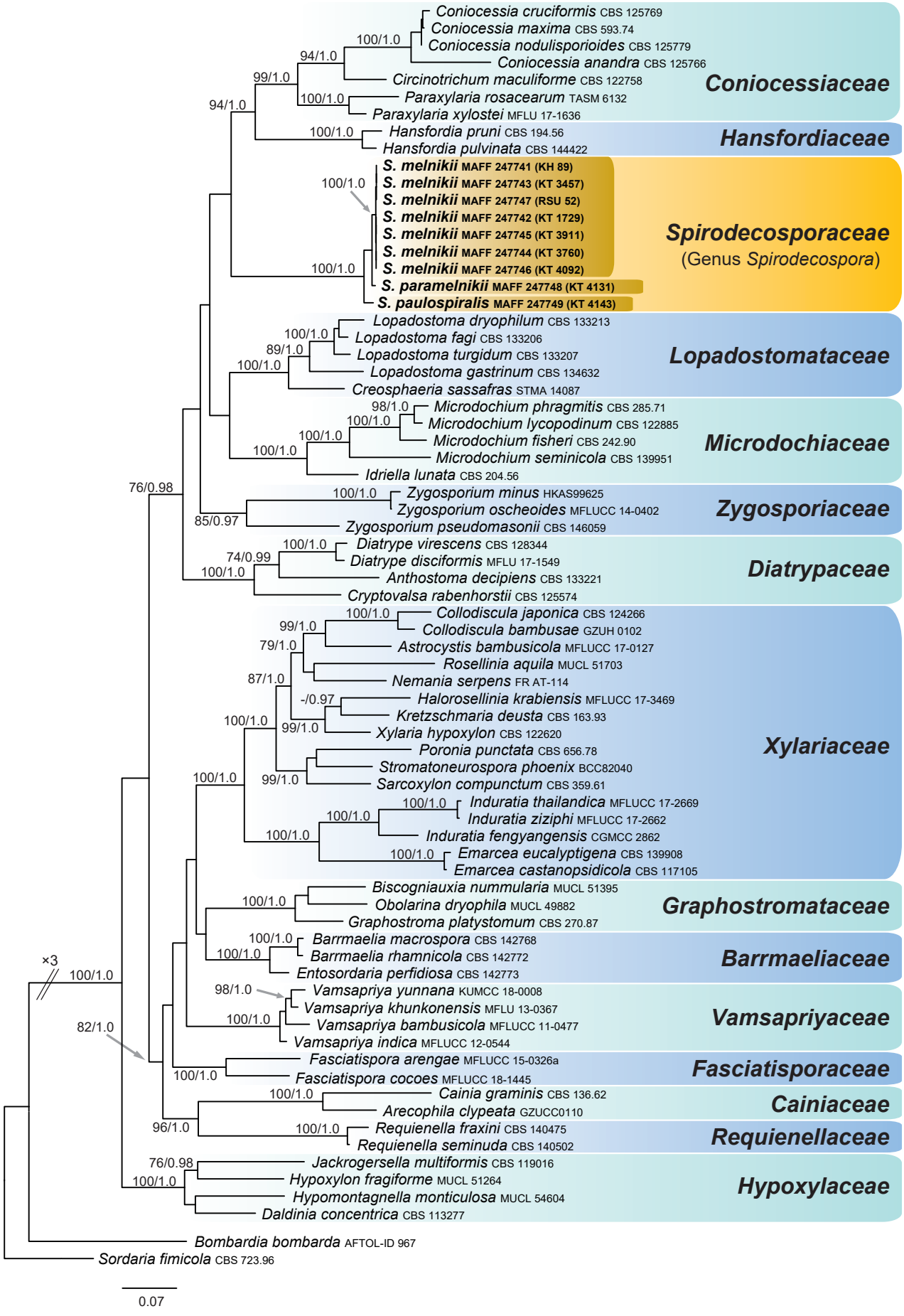

Fig. 1. Maximum-likelihood (ML) tree of *Xylariales* based on combined ITS, LSU and *rpb2* sequences. ML bootstrap support (MLBS) higher than 70 % and Bayesian posterior probabilities (PP) above 0.95 are presented at the nodes as MLBS PP. A hyphen ('-') indicates values lower than 70 % MLBS or 0.95 PP. The newly obtained sequences are shown in bold. The scale bar represents expected nucleotide substitutions per site.

et al. 2022). In contrast, that of *Spirodecosporaceae* is more compact, flattened, and wedge-shaped (Lu *et al.* 1998; Figs 2O, 3M, 4L in this study).

Spirodecospora B.S. Lu *et al.*, *Fungal Diversity Res. Ser*. **1**: 170. 1998.

Type species: *Spirodecospora bambusicola* B.S. Lu *et al*.

Notes: *Spirodecospora bambusicola* (Lu *et al*. 1998) was considered a synonym of *S. melnikii* (= *Anthostomella melnikii*; Vasilyeva 1990) by Mel'nik & Hyde (2003). However, they are now interpreted as distinct species; for details see notes under *S. melnikii*. Currently, no molecular data of *S. bambusicola*, the type species, are available. However, the morphological similarity between *S. bambusicola* and other three species observed in this study suggests that they are congeneric.

No asexual morph was observed in culture for any *Spirodecospora* species. In *S. melnikii* and *S. paulospiralis*, single ascospore isolates produced ascomata in culture, suggesting that they are homothallic.

Spirodecospora melnikii (Lar. N. Vassiljeva) K.D. Hyde & Melnik, *Fungal Diversity* **12**: 152. 2003. Figs 2, 5A–G.
Basionym: *Anthostomella melnikii* Lar. N. Vassiljeva, *Mikol. Fitopatol.* **24**: 209. 1990.

Ascomata deeply immersed in host tissue, solitary, subglobose, 420–750 µm high, 270–580 µm diam. *Ostiolar neck* cylindrical, 150–210 µm high, 110–170 µm diam, periphysate, visible as black dot on the substrate. *Ascomatal wall* 11–16.5 µm thick, composed of 5–8 layers of polygonal, 3.5–7.5 × 2.5–5 µm, dark brown cells. *Paraphyses* numerous, septate, unbranched, filamentous, hyaline, 1.5–3.5 µm wide. *Asci* unitunicate, cylindrical, 190–265 × 17.5–25 µm, 8-spored, broadly rounded at the apex; apical ring I+, wedge-shaped, 8–9 × 3.5–4.5 µm. *Ascospores* 30–36.5 × 12–17 µm (av. 33.9 × 13.7 µm, n = 70), l/w 2.0–2.9 (av. 2.5, n = 70), broadly ellipsoidal to fusoid, brown, conspicuously verruculose, with spirally linear ornamentations around the ascospores, surrounded by a mucilaginous sheath.

Culture characteristics: Colonies on PDA at 25 °C attaining 14–24 mm diam after 1 wk in the dark, whitish to pale mouse grey; reverse white to grey olivaceous. The sexual morph formed on RSA, with ascospores being similar to those on the host, measuring 34–40 × 13.5–16.5 µm; asexual morph not observed.

Specimens examined: **Japan**, Aomori, Nakatsugaru, Nishimeya, Shirakami Aqua village, on dead culms of *Sasa* sp., 28 Aug. 2007, *K. Hirayama*, KH 89 (HHUF 30651), living culture MAFF 247741; *ibid*. Shinjyou, Hiraoka, on dead culms of *Sasa* sp., 26 May 2019, *R. Sugita*, *S. Narita*, *M. Tanaka* & *R. Maekawa*, RSU 52 (HHUF 30657), living culture MAFF 247747; Yamagata, Mt. Chokai (elevation 1 150 m), on dead twigs of *Sasa* sp., 5 Jul. 2014, *K. Tanaka*, KT 3457 (HHUF 30653), living culture MAFF 247743; Nagano, Ueda, Tsukuba University, Sugadaira Research Station, on dead twigs of *Sasa cernua*, 28 Jun. 2004, *T. Shirouzu*, KT 1729 (HHUF 30652), living culture MAFF 247742; Kouchi, Takaoka, near Tengu plateau, on dead twigs of *Sasa* sp., 16 Mar. 2017, *K. Tanaka*, *A. Hashimoto, T. Takahashi & K. Arayama*, KT 3760 (HHUF 30654), living culture MAFF 247744; Hiroshima, Hatsukaichi, Yoshiwa, on dead twigs of *Sasa* sp., 18 Feb. 2020, *K. Tanaka*, *R. Sugita*, *S. Narita* & *M. Tanaka*, KT 4092 (HHUF 30656), living culture MAFF 247746; Yamaguchi, Atokaneshimo, near Mt. Tokusagamine, on dead twigs of *Sasa* sp., 27 Mar. 2018, *K. Tanaka*, *K. Arayama* & *R. Sugita*, KT 3911 (HHUF 30655), living culture MAFF 247745.

Notes: We recognise *S. melnikii* and *S. bambusicola* as different species based on morphological differences and host range. The asci of *S. melnikii* are consistently 8-spored, while those of *S. bambusicola* are 4–8-spored (Lu *et al*. 1998). Although the ascospore dimensions overlap, those of *S. melnikii* ((30–)33–36(–39.6) × 14–16.5 µm; Vasilyeva 1990) are consistently slightly smaller than those of *S. bambusicola* (28–45 × 11–15 µm; Lu *et al.* 1998). In addition, both species occur on different hosts: *S. melnikii* was originally found on *Sasa kurilensis* (Vasilyeva 1990), which belongs to the tribe *Arundinarieae*, while the host plant of *S. bambusicola* is *Bambusa* sp., which belongs to *Bambuseae*. We identified our specimens collected on *Sasa* spp. as *S. melnikii* based on the smaller ascospore size and the host plant.

Spirodecospora paramelnikii R. Sugita & Kaz. Tanaka, ***sp. nov.*** MycoBank MB 846056. Figs 3, 5H.

Etymology: Refers to morphological similarity to *Spirodecospora melnikii*.

Ascomata deeply immersed in host tissue, solitary, subglobose, 480–500 µm high, 510–520 µm diam. *Ostiolar neck* cylindrical, 32–38 µm high, 25–32.5 µm diam, periphysate, visible as black dot on the substrate. *Ascomatal wall* 12.5–20 µm thick, composed of 5–8 layers of polygonal, 5.5–7.5 × 3.5–4.5 µm, dark brown cells. *Paraphyses* numerous, septate, unbranched, filamentous, hyaline, 2–3 µm wide. *Asci* unitunicate, cylindrical, 275–290 × 22.5–30 µm, 8-spored, broadly rounded at the apex; apical ring I+, wedge-shaped, 8–10 × 4.5–6.5 µm. *Ascospores* 37–46.5 × 13.5–20 µm (av. 40.2 × 16.4 µm, n = 50), l/w 2.0–3.0 (av. 2.5, n = 50), broadly ellipsoidal to fusoid, brown, conspicuously verruculose, with spirally linear ornamentations around the ascospores, surrounded by a mucilaginous sheath.

Culture characteristics: Colonies on PDA at 25 °C attaining 18–23 mm diam after 1 wk in the dark, smoke grey; reverse honey. No sporulation observed on RSA.

Typus: **Japan**, Kagawa, Takamatsu, Mt. Otaki, on dead twigs of *Sasa* sp., 21 Feb. 2020, *K. Tanaka*, *R. Sugita*, *S. Narita* & *M. Tanaka*, KT 4131 (**holotype** HHUF 30658), living ex-type culture MAFF 247748.

Notes: *Spirodecospora paramelnikii* is phylogenetically close to *S. melnikii,* which also occurs on *Sasa* spp. However, the ascospores of *S. paramelnikii* are larger (37–46.5 × 13.5–20 µm) than those of *S. melnikii* (30–36.5 × 12–17 µm). Sequence differences between the two species were found at six positions without gaps in the ITS (98.9 % homology) and at 12–14 positions with a single amino acid substitution in *rpb2* (98.8 %).

Spirodecospora paulospiralis R. Sugita & Kaz. Tanaka, ***sp. nov.*** MycoBank MB 846057. Figs 4, 5I.

Etymology: From the Latin *paulo*, meaning a little (or somewhat), in reference to the almost straight to slightly curved, spiral ornamentations of ascospores.

Fig. 2. *Spirodecospora melnikii* (**A, D–F, AA, AB.** RSU 52 = HHUF 30657; **B, X, Y.** KT 3457 = HHUF 30653; **C, L, P, U, Z.** KT 4092 = HHUF 30656; **G–K, M–O, Q–T, V.** KT 3911 = HHUF 30655; **W.** Culture KT 3760 = MAFF 247744) **A–D.** Ascomata in face view (**D.** Transverse section). **E–H.** Longitudinal section of ascomata. **I.** Ostiolar neck of ascoma. **J.** Ascomatal wall in section (**G–J** in diluted lactophenol cotton blue). **K.** Paraphyses. **L, M.** Asci. **N, O.** Apex of asci (**O.** I+ apical ring in Lugol). **P–AB.** Ascospores (**P.** In Indian ink; **Q.** Focus stacking image; **X–AB.** Germinating ascospores). All in distilled water, except where noted. Scale bars: A, B, D–F = 500 µm; C, G–I = 100 µm; J, K, N–AB = 10 µm; L, M = 20 µm.

Fig. 3. *Spirodecospora paramelnikii* (KT 4131 = HUFF 30658, holotype) **A–D.** Ascomata in face view (**D.** Transverse section). **E–G.** Longitudinal section of acomata **H.** Acomatal wall in section (**G, H** in diluted lactophenol cotton blue). **I.** Paraphyses. **J, K.** Asci. **L, M.** Apex of asci (**M.** I+ apical ring in Lugol). **N–V.** Ascospores (**T.** Focus stacking image; **U.** In Indian ink; **V.** Germinating ascospore). All in distilled water, except where noted. Scale bars: A–F = 500 µm; G = 100 µm; H, I, L–V = 10 µm; J, K = 20 µm.

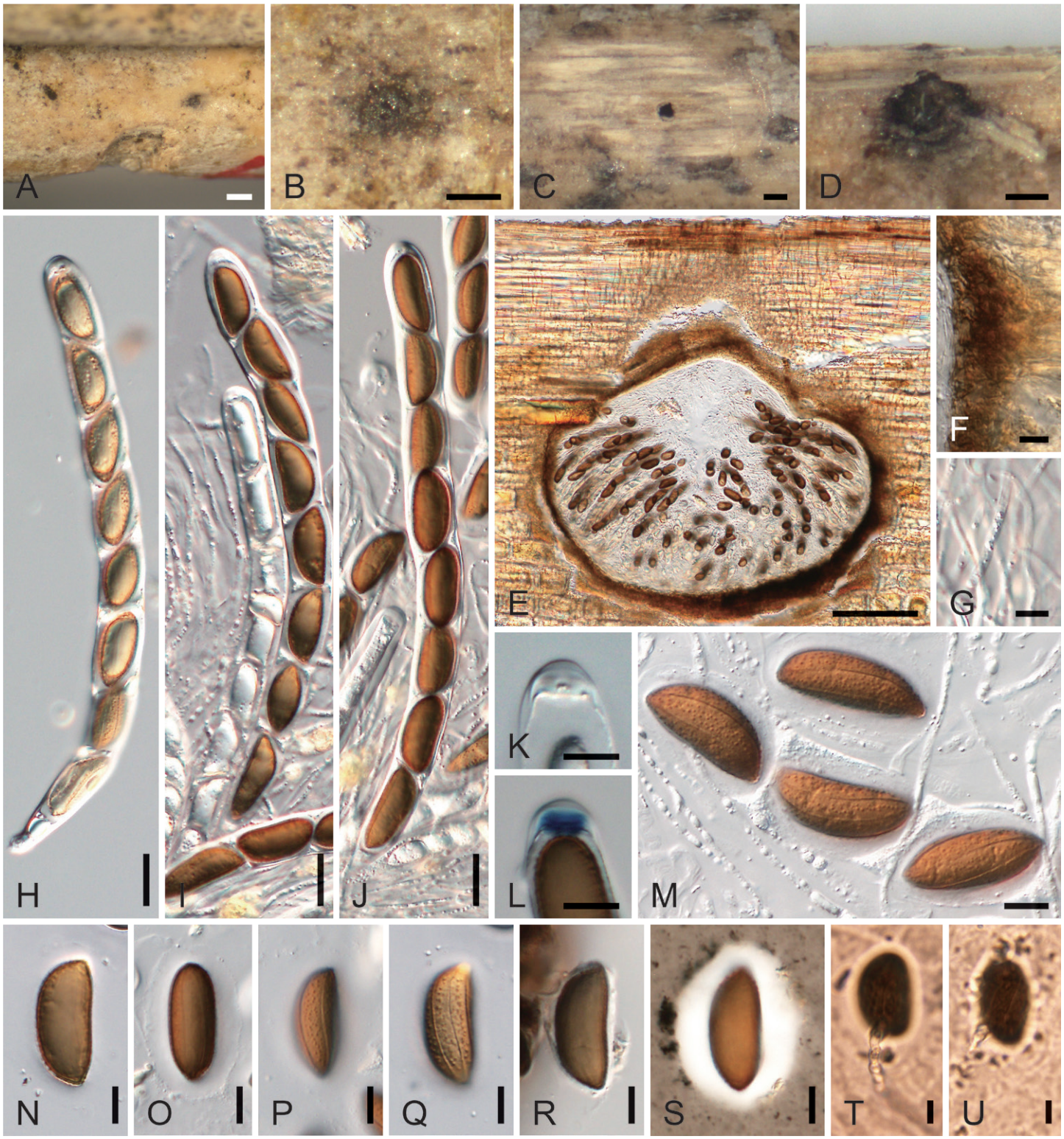

Fig. 4. *Spirodecospora paulospiralis* (**A–Q, S–U.** KT 4143 = HUFF 30659, holotype; **R.** Culture KT 4143 = MAFF 247749, ex-holotype) **A–C.** Ascomata in face view (**C.** Transverse section) **D, E.** Longitudinal section of ascomata. **F.** Ascomatal wall in section (**E, F** in diluted lactophenol cotton blue). **G.** Paraphyses. **H–J.** Asci. **K, L.** Apex of asci (**L.** I+ apical ring in Lugol). **M–U.** Ascospores (**M.** Focus stacking image; **S.** In Indian ink; **T, U.** Germinating ascospores). All in distilled water, except where noted. Scale bars: A = 500 µm; B–D = 200 µm; E = 100 µm; F, G, K–U = 10 µm; H–J = 20 µm.

Ascomata deeply immersed in host tissue, solitary, subglobose, 550–630 µm high, 380–530 µm diam. *Ostiolar neck* cylindrical, 50–55 µm high, 35–50 µm diam, periphysate, visible as black dot on the substrate. *Ascomatal wall* 10–15 µm thick, composed of 5–8 layers of polygonal, 3.5–5.5 × 2.5–4 µm, dark brown cells. *Paraphyses* numerous, septate, unbranched, filamentous, hyaline, 1.5–3.5 µm wide. *Asci* unitunicate, cylindrical, 245–280 × 17–20 µm, 8-spored, broadly rounded at the apex; apical ring I+, wedge-shaped, 5.5–9.5 × 3.5–6.5 µm. *Ascospores* 28–36.5 × 11–14 µm (av. 31.6 × 12.5 µm, n = 50), l/w 2.2–3.2 (av. 2.5, n = 50), broadly ellipsoidal to fusoid, brown, slightly verruculose, with some gently curved to almost straight linear ornamentations around the ascospores, surrounded by a mucilaginous sheath.

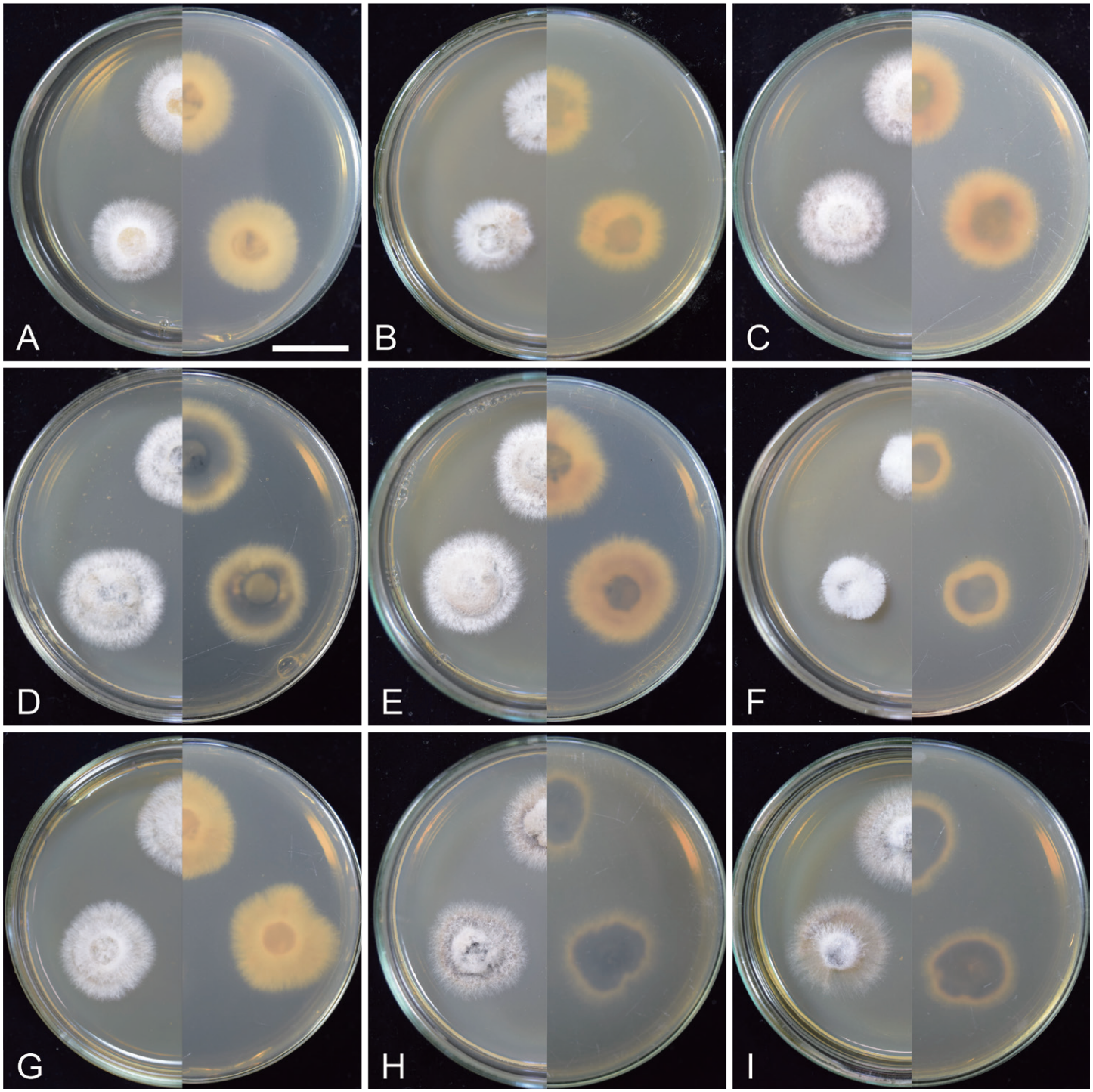

Fig. 5. Colony characters of *Spirodecospora* species on PDA at 25 °C in the dark after 1 wk. **A–G.** *S. melnikii* (**A.** KT 1729 = MAFF 247742; **B.** KT 3457 = MAFF 247743; **C.** KT 3760 = MAFF 247744 **D**; KT 3911 = MAFF 247745; **E.** KT 4092 = MAFF 247746; **F.** KH 89 = MAFF 247741; **G.** RSU 52 = MAFF 247747). **H.** *S. paramelnikii* (KT 4131 = MAFF 247748). **I.** *S. paulospiralis* (KT 4143 = MAFF 247749). Scale bar = 2 cm.

Culture characteristics: Colonies on PDA at 25 °C attaining 17–22 mm diam after 1 wk in the dark, smoke grey to honey; reverse grey olivaceous. The sexual morph formed on RSA, and ascospores were similar to those on the host, measuring 27.5–34 × 12.5–14 µm; asexual morph not observed.

Typus: **Japan**, Tokushima, Yoshinogawa, Kawashima, on dead twigs of *Pleioblastus chino*, 21 Feb. 2020, *K. Tanaka*, *R. Sugita*, *S. Narita* & *M. Tanaka*, KT 4143 (**holotype** HHUF 30659), living ex-type culture MAFF 247749.

Notes: *Spirodecospora paulospiralis* is morphologically similar to *S. melnikii*. However, it differs from *S. melnikii* in having ascospores with almost straight to slightly curved ornamentation. Furthermore, the ITS sequence of *S. paulospiralis* differed in 35 positions, with 19 gaps from that of *S. melnikii* (89.1 % homology) and in 34 positions, with 24 gaps from that of *S. paramelnikii* (89.6 %). The *rpb2* sequence of *S. paulospiralis* differed in 29 positions with 11 amino acid substitutions from that of *S. melnikii* (97.1 %) and in 24 positions, with 10 amino acid substitutions from that of *S. paramelnikii* (97.7 %).

Key to species of *Spirodecospora*

1. Ascospores with gently curved to almost straight linear ornamentations, slightly verruculose; on *Pleioblastus* sp. .... *S. paulospiralis*
1. Ascospores with spirally linear ornamentations, conspicuously verruculose 2

2. Asci (4–)8-spored; ascospores 28–45 × 11–15 µm; on *Bambusa* sp. ..... *S. bambusicola*
2. Asci 8-spored; on *Sasa* spp. 3

3. Ascospores, 30–36.5 × 12–17 µm ..... *S. melnikii*
3. Ascospores larger, 37–46.5 × 13.5–20 µm ..... *S. paramelnikii*

DISCUSSION

This study represents the first record of DNA sequence data of species in the genus *Spirodecospora*, which allowed us to assess their phylogenetic position using molecular phylogenetic analyses. Based on morphological observations and phylogenetic analysis, we propose the establishment of a novel family, *Spirodecosporaceae,* to accommodate the genus *Spirodecospora*. *Spirodecospora* was placed in *Xylariaceae* (Lu *et al.* 1998) because of the similarity of the apical structure of asci with that of similar genera of *Xylariaceae sensu lato*, such as *Anthostomella*, *Lopadostoma*, and *Pandanicola*. However, the apical structure of asci differs significantly between *Spirodecospora* and *Xylaria longipes* (*Xylariaceae sensu stricto*). According to detailed images obtained from transmission electron microscopy (TEM), it is short cuneiform in the former (Lu *et al*. 1998) but long cylindrical to doliiform in the latter (Beckett & Crawford 1973). Molecular data in our study also support the exclusion of *Spirodecospora* from *Xylariaceae* (Fig. 1). The ascomata of *Spirodecospora* are deeply immersed in the hard bamboo tissues. This characteristic is very similar to that of species in *Vamsapriyaceae*, which also occur on bamboo; however, *Vamsapriyaceae* is distantly related to *Spirodecospora* (Fig. 1).

The most conspicuous feature of *Spirodecospora* is the spirally linear ornamentations surrounding the ascospores. Recent phylogenetic analysis on xylariaceous taxa revealed the existence of several genera having brown, unicellular ascospores with spirally coiling germ slits (Voglmayr *et al.* 2022). The spiral structure found in *Spirodecospora* was also originally regarded as a germ slit (Vasilyeva 1990), but this interpretation was not accepted in later studies (Lu *et al.* 1998, Mel'nik & Hyde 2003). According to the images obtained from scanning electron microscopy (SEM; Lu *et al.* 1998), the structure of this longitudinal line is formed by the alignment of small-sized, tightly packed verruculose ornamentations (SVO; *ca.* 270 nm diam). There are also large-sized verruculose ornamentations (LVO; *ca*. 500 nm diam) interdisposed between the lines; Lu *et al.* (1998) clearly showed that ascospores of *Spirodecospora* lack germ slits or germ pores. We agree with this observation but speculate that the spiral ornamentation of ascospores may be correlated with spore germination. A single germ tube emerged from the lateral wall of each ascospore in the three *Spirodecospora* species observed in our study. During germination, a less-melanised longitudinal fissure was found along with spirally linear ornamentation of ascospores (see Figs 2X–AB, 4T). This fissure may have occurred due to the spore cell wall around SVO or LVO rupturing before germination. However, a detailed observation of germinating ascospores using SEM (*e.g.* Waugh *et al.* 2001) or comparisons using TEM between ascospores of *Spirodecospora* without a defined germ slit and some xylariaceous taxa with a typical germ slit (*e.g.* Beckett 1976, 1979) will be required to confirm this. Since the germination rates of ascospores were considerably low in all *Spirodecospora* species examined in this study, it is also necessary to determine the appropriate conditions for spore germination within this genus.

Bambusicolous fungi tended to form phylogenetically independent lineages. For example, *Vamsapriyaceae*, established for the saprobic bambusicolous genus *Vamsapriya,* was a distinct family remote from other xylariaceous families (Dai *et al.* 2014, Sun *et al.* 2021). The bambusicolous anthostomella-like genus *Nigropunctata* was shown to be phylogenetically distinct from any known family in *Xylariales* (Samarakoon *et al.* 2022). More than 1 000 species of ascomycetes, including asexual taxa, have been recorded on bamboo, but only less than 180 species have been sequenced thus far (Dai *et al.* 2018). Most lineages of bambusicolous fungi tend to deviate from existing families or genera found on other host plants, even though they have morphological similarities to other known fungal groups (Tanaka *et al.* 2009). Further phylogenetic studies on the described bambusicolous fungi, which lack sequence information, will undoubtedly aid the discovery of many novel lineages distantly related to known ascomycetous families and genera.

Most fungi on bamboo are considered non-host-specific because they are not plant pathogens (Hyde *et al.* 2002). Indeed, many fungi have been reported from various bamboo hosts as plurivorous species. For example, *Collodiscula japonica* has been recorded on *Phyllostachys*, *Pleioblastus*, and *Sasa* (Hino 1961), but the conspecificity of fungi on these different hosts should be re-evaluated at the molecular level. Species in the dinemasporioid genera found on bamboos, such as *Dinemasporium*, *Neopseudolachnella*, and *Pseudolachnella*, appear to have relatively distinct host specificity, at least at the genus level of bamboo (Hashimoto *et al.* 2015a, b). We believe that careful evaluation is necessary for indicating the monophyly of fungal species that are parasitic on different genera or higher ranks (*e.g.* tribe) of bamboo. All four species recognised within *Spirodecospora* were found on bamboo, and these host genera of *Spirodecospora* belong to the subfamily *Bambusoideae*. The host plant of *S. bambusicola*, *Bambusa*, is classified in the tribe *Bambuseae* (the tropical woody bamboos). However, hosts of the other three species of *Spirodecospora*, *Pleioblastus* and *Sasa*, are classified in the tribe *Arundinarieae* (the temperate woody bamboos) (Zhang *et al.* 2020). Therefore, we treated *S. bambusicola* on *Bambusa* sp. as a distinct species based on its different host plant and ascospore sizes, although no sequence data of this species are currently available. To clarify the importance of differences in hosts for species delimitation of bambusicolous fungi and to improve the nomenclatural stability of *Spirodecosporaceae* and *Spirodecospora*, it would

be necessary to obtain additional information about the generic type (*S. bambusicola*), which requires resampling of fresh collections from *Bambusa*, resolving its DNA phylogeny, and subsequent epitypification.

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