学位論文

フンタマカビ綱菌類の分類学的研究

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1. 緒言

子のう菌門は菌界において最も大きなグループであり (Kirk et al. 2008)、有性世代に「子のう」と呼ばれる子のう胞子を生産する袋状の細胞を持つことによって特徴づけられる。一方で、子のう菌門のうち無性世代菌類は、子のうを有していない。従来子のう菌類の分類体系は主に有性世代の形態に基づいて構築されてきたが、系統の推定が困難な無性世代の形態はあまり重要視されてこなかった。近年、子のう菌類の分類に DNA 塩基配列に基づく分子系統解析が導入されている。分子系統解析は、分類群間の塩基配列の差異によって系統関係を推定するものであり、これまで形態的特徴に基づいて構築されてきた菌類の分類体系を再評価することが可能になってきている。その結果、過去に規定されてきた科や属のような分類学的所属や枠組みが、再検討される事例が多く示され (Daranagama et al. 2015, 2016, Hashimoto et al. 2017, Wendt et al. 2018)、さらに、今まで重要視されてこなかった無性世代形態についても、系統を把握するうえでの有用性が明らかになりつつある。

日本において、タケ類を宿主とする菌類が多く記載されてきた (Hino 1961)。タケ類はイネ科タケ亜科に所属する 1,500 種以上の植物の総称であり、世界的に広く分布している (Dai et al. 2017)。これまでに、タケ類を宿主とする菌類は 1,300 種以上が記録されており、その中では子のう菌類が最も多く、800 種である (Dai et al. 2017)。日本のタケ類は 12 属 662 種が報告されており、世界的に見ても多くの種多様性があることが知られている。日本産タケ類からは 258 種 (50 科 172 属) の菌類が記載されており、その多くが子のう菌類である (Hino 1961)。一方で、そのほとんどは DNA 塩基配列が得られておらず、それらの種の科や属の所属については調査が必要と考えられる。Tanaka et al. (2009) は、タケ類を宿主とする菌類は、他の植物を宿主とする菌類と形態が類似していたとしても、分子系統学的に科や属レベルで既知の菌類系統から外れる傾向があることを示した。さらに、日本産タケ類の内生菌の包括的な調査では、リボソーム DNA 小サブユニット (SSU) と核リボソーム内部転写スペーサー領域 (ITS) の配列に基づくと、既知の菌類と配列が一致しないことから、タケ類内生菌には新属または新種と推定される多くの新規系統群が存在していることが示唆された (Morakotkarn et al. 2009)。このことより、タケ類を宿主とする菌類を調査することによって、分子系統学的に未知の分類群をより多く発見することが可能であると考えられる。

フンタマカビ綱菌類は、子のう菌門においてクロイボタケ綱に次いで二番目に大きな分類群である。陸生から水生など様々な環境に生息し、植物に対して、病原性、寄生性、腐生性、内生、菌類に対して寄生性、ヒトを含む動物に対して病原性、寄生性を示すような、多くの種が報告されている (Maharachchikumbura et al. 2016, Perdomo et al. 2013, Luo et al. 2019)。本綱は、タケ類を宿主とする菌類の中では種多様性が最も

高く、菌界最大の分類群であるクロイボタケ（159 種が報告）を凌ぐ、295 種からなることが知られている（Dai et al. 2018）。さらに、これらのフンタマカビ綱に所属する科や属の数は、32 科・105 属と菌界最大であり、多様な分類群で構成されていることがうかがえる (Maharachchikumbura et al. 2016, Dai et al. 2017, 2018, Senanayake et al. 2017, Luo etal. 2019, Réblová et al. 2021, Samarakoon et al. 2022)。これらの科や属についても、その多くでは DNA 塩基配列が得られておらず、分子系統学的な系統把握は進んでいない。

本研究では、日本における野外調査によって、タケ類を含む幅広い植物からフンタマカビ綱に所属すると推定される有性世代の菌類を採集した。それらはフンタマカビ亜綱やクロサイワイタケ亜綱にそれぞれ所属する既知の属と形態的に類似していた。しかし、暫定的に取得された配列を比較した結果、これら菌類には既知の科、属、種などの分類群と一致しないものが含まれていた。本研究ではこれら菌類について、科および属の分類学的所属の把握を、有性世代と無性世代の両世代の形態および、DNA 塩基配列に基づく分子系統解析によって試みることを目的とした。また、これら菌類を用いて、タケ類を宿主とする菌類における、宿主特異性についての考察を行った。

2. *Thyridium* 属と *Phialemoniopsis* 属の分類学的再検討

ABSTRACT

様々な植物上に発生する、腐生的または半活物栄養的な子のう菌類として知られていた *Thyridium* 属を、分類学的および分子系統学的に改訂した。核リボソーム内部転写スペーサー領域 (ITS)、リボソーム DNA 大サブユニット (LSU)、RNA ポリメラーゼ大サブユニット II (RPB2)、転写伸長因子 1-alpha (TEF1)、アクチン (ACT)、β チューブリン (TUB2) の 6 領域の配列を、本属の種の分子系統解析に用いた。医学的に重要な種を内包する *Phialemoniopsis* 属を、分子的な証拠と無性世代の形態的類似性をもとに *Thyridium* 属の異名とした。*Thyridium* 属の属概念について、分生子果不完全菌類型および不完全糸状菌類型の両方を形成する複雑な無性世代を有する種を含むように拡大した。本研究では、*Thyridium* 属の基準種 *T. vestitum* に加え、形態比較および分子系統解析により本属内に 9 種を認めた。*Phialemoniopsis* 属の全 7 種を *Thyridium* 属のメンバーとして扱い、新組み合わせを提唱した。タケ類を宿主とする菌類の *Pleospora punctulata* を *Thyridium* 属に移し、エピタイプ指定した。新種 *T. flavostromatum* をモウソウチク (*Phyllostachys pubescens*) から記載した。*Phialemoniopsis* 属を基準属とする Phialemoniopsis 科を Thyridium 科の異名とした。Thyridium 科を収容するために新目 Thyridium 目を設立し、本目がフンタマカビ綱において十分に支持される単系統クレードであることを確認した。

INTRODUCTION

Thyridium was originally established to accommodate species with cylindrical, uniseriate, 8-spored asci and muriform, dark-coloured, ascospores (Nitschke 1867). Species of this genus occur on various plants as saprobic or hemibiotrophic fungi (Eriksson and Yue 1989, Taylor et al. 1997, Checa et al. 2013). Currently, *Thyridium* includes 33 species and is placed in Thyridiaceae (family incertae sedis, Sordariomycetes; Yue and Eriksson 1987; Index Fungorum, http://www.indexfungorum.org, 2021). The type species *T. vestitum* has been verified to produce both coelomycetous and hyphomycetous asexual morphs, which have phialidic conidiogenous cells with collarette and ellipsoidal to allantoid hyaline conidia (Leuchtmann and Müller 1986).

Molecular information on *Thyridium* species is available only for two non-type strains (CBS 113027, CBS 125582) of the type species *T. vestitum* (Lutzoni et al. 2004, Spatafora et al. 2006, Vu et al. 2019); however, the phylogenetic relationships among species of this genus are unclear. A recent study on the phylogeny of Sordariomycetes has shown that *T. vestitum* is closely related to two *Phialemoniopsis* spp. (*P. endophytica* and *P. ocularis*), but their phylogenetic and taxonomic relationships have not been clarified (Dong et al. 2021, Hyde et al. 2021).

The genus *Phialemoniopsis* was placed in Phialemoniopsidaceae (Diaporthomycetidae family incertae sedis, Sordariomycetes; Hyde et al. 2021). Species of this genus are widely distributed in various environments and substrates, including industrial water, plant materials, raw sewage, and soil (Gams and McGinnis 1983, Halleen et al. 2007, Su et al. 2016). Several species have been reported from parts of the human body, such as blood, eye, toenail, skin, and sinus (Perdomo et al. 2013, Tsang et al. 2014), and some of them have also been isolated from patients with keratomycosis and phaeohyphomycosis (Perdomo et al. 2013, Desoubeaux et al. 2014). All species in this genus are known to be asexual.

In our ongoing taxonomic study of sordariomycetous fungi in Japan, several new specimens of *Thyridium*-like sexual morphs were collected. Single ascospore isolates from these specimens formed typical *Phialemoniopsis*-like asexual morphs in culture, suggesting that both genera are closely related. This study aims to reveal the taxonomic and phylogenetic relationships between *Thyridium* and *Phialemoniopsis*, and to clarify their ordinal position in Sordariomycetes.

MATERIALS AND METHODS

Isolation and morphological observation

All materials were obtained from Japan. Morphological characteristics were observed in preparations mounted in distilled water by differential interference and phase contrast microscopy (Olympus BX53) using images captured with an Olympus digital camera (DP21). All specimens were deposited in the herbarium at Hirosaki University (HHUF), Hirosaki, Japan. Single spore isolations were performed from all specimens. Colony characteristics were recorded from growth on potato dextrose agar (PDA), malt extract agar (MEA), and oatmeal agar (OA) from Becton, Dickinson and Company (MD, USA), after a week at 25 °C in the dark. Colony colours were recorded according to Rayner (1970). To observe the asexual morphs in culture, 5 mm squares of mycelial agar were placed on water agar containing sterilised plant substrates such as rice straws and banana leaves. Then these plates were incubated at 25 °C for 2 weeks in the dark. When the substrates were colonised, the plates were incubated at 25 °C under black light blue illumination for 1–2 weeks to observe sporulation.

Phylogenetic analyses

DNA was extracted from four isolates 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 and Samuels 1994) and LR5 or LR7 (Vilgalys and Hester 1990), the second largest RNA polymerase II subunit (RPB2) gene with primers fRPB2-5F and fRPB2-7cR (Liu et al. 1999), the translation elongation factor 1-alpha (TEF1) gene with primers 983F and 2218R (Rehner and Buckley 2005), the actin (ACT) gene with primers Act-1 and Act-5ra (Voigt and Wöstemeyer 2000) and the beta-tubulin (TUB2) gene with primers TUB-F and TUB-R (Cruse et al. 2002). 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). Sequences were obtained completely in ITS and partially in others, respectively. Newly generated sequences were deposited in GenBank (Table 1).

Primary analysis of LSU-RPB2-TEF1 sequences from 88 strains of Sordariomycetes (Table 1) was conducted to clarify the ordinal/familial placement of *Thyridium* (or

Phialemoniopsis) species. *Barrmaelia rhamnicola* and *Entosordaria perfidiosa* (Xylariomycetidae) were used as outgroups. As a secondary analysis, single gene trees of ITS, ACT and TUB2, and a combined tree of these three loci were generated to assess the species boundaries of 17 strains within *Thyridium*/*Phialemoniopsis* (Table 2). All sequence alignments (LSU, ITS, RPB2, TEF1, ACT and TUB2) were produced using the server version of MAFFT (http://www.ebi.ac.uk/Tools/msa/mafft), checked and refined using MEGA v. 7.0 (Kumar et al. 2016).

Phylogenetic analyses were conducted using maximum-likelihood (ML) and Bayesian methods. The optimum substitution models for each dataset were estimated using Kakusan4 software (Tanabe 2011) based on the Akaike information criterion (AIC; Akaike 1974) for ML analysis and the Bayesian information criterion (BIC; Schwarz 1978) for Bayesian analysis. ML analyses were performed using the TreeFinder Mar 2011 program (http://www.treefinder.de) based on the models selected with the AICc4 parameter (used sequence length as sample size). ML bootstrap support (ML BS) values were obtained using 1,000 bootstrap replicates. Bayesian analyses were performed using MrBayes v. 3.2.6 (Ronquist et al. 2012), with substitution models selected based on the BIC4 parameter (used sequence length as sample size). Two simultaneous and independent Metropolis-coupled Markov chain Monte Carlo (MCMC) runs were performed for 9,000,000 generations for primary analysis and 1,000,000 generations for secondary analyses (except for the ITS dataset for 1,500,000 generations) with the tree sampled every 1,000 generations. Convergence of the MCMC procedure was assessed from the effective sample size scores (all > 100) using MrBayes and Tracer v. 1.6 (Rambaut et al. 2014). First 25% of the trees were discarded as burn-in, and the remainder were used to calculate the 50% majority-rule trees and to determine the posterior probabilities (PPs) for individual branches. These alignments were submitted to TreeBASE under study number S28934.

Table 1. Isolates and GenBank accessions of sequences used in the phylogenetic analyses of Sordariomycetes (Fig. 1).

Taxon	Isolate[a]	Status[b]	GenBank accession numbers[a]			Ref.[c]
			LSU	RPB2	TEF1	
Acrodictys aquatica	MFLUCC 18-0356	HT	MG835712	–	–	47
Acrodictys bambusicola	HSAUP myr9510		KX033564	–	–	44
Annulatascus velatisporus	A70 18		AY316354	–	–	3
Annulusmagnus triseptatus	CBS 128831		GQ996540	JQ429258	–	25, 29
Ascitendus austriascus	CBS 131685		GQ996539	JQ429257	–	25, 29
Atractospora reticulata	CBS 127884	HT	KT991660	KT991649	–	41
Atractospora thailandensis	KUMCC 16-0067	HT	MF374362	MF370951	MF370962	45
Barbatosphaeria arboricola	CBS 127689	HT	KM492862	KM492901	–	38
Barbatosphaeria barbirostris	CBS 121149		EF577059	KM492903	–	18, 38
Barbatosphaeria varioseptata	CBS 137797	HT	KM492869	KM492907	–	38
Barrmaelia rhamnicola	CBS 142772	ET	MF488990	MF488999	MF489009	52
Bombardia bombarda	AFTOL-ID 967		DQ470970	DQ470923	DQ471095	14
Calosphaeria pulchella	CBS 115999	IT	AY761075	GU180661	FJ238421	8, 27
Camarops microspora	CBS 649.92		AY083821	DQ470937	–	13, 14
Camarotella costaricensis	MM-149		KX430484	KX451954	KX451982	43
Cancellidium cinereum	MFLUCC 18-0424	HT	MT370363	MT370486	MT370488	57
Cancellidium griseonigrum	MFLUCC 17-2117	HT	MT370364	MT370487	–	57
Ceratolenta caudata	CBS 125234	HT	JX066704	JX066699	–	33
	PRM 899855		JX066705	–	–	33
Chaetosphaeria ciliata	ICMP 18253		GU180637	GU180659	–	27
Chaetosphaeria curvispora	ICMP 18255		GU180636	GU180655	–	27
Cryptadelphia groenendalensis	SH12		EU528007	–	–	20
	SMH3767		EU528001	–	–	20
Diaporthe phaseolorum	NRRL 13736		U47830	–	–	1
Distoseptispora obpyriformis	MFLUCC 17-1694	HT	MG979764	MG988415	MG988422	48
Distoseptispora rostrata	MFLUCC 16-096	HT	MG979766	MG988417	MG988424	48
Endoxyla operculata	UAMH 11085		JX460992	KY931927	–	34, 49
Entosordaria perfidiosa	CBS 142773	ET	MF488993	MF489003	MF489012	52
Fluminicola aquatica	MFLUCC 15-0962	HT	MF374366	–	MF370960	45
Fluminicola saprotrophitica	MFLUCC 15-0976	HT	MF374367	MF370954	MF370956	45
Gnomonia gnomon	CBS 199.53		AF408361	DQ470922	DQ471094	2, 14
Jobellisia fraterna	SMH2863		AY346285	–	–	4
Jobellisia luteola	SMH2753		AY346286	–	–	4
Lanspora coronata	AFTOL-ID 736		U46889	DQ470899	–	14
Lasiosphaeria ovina	SMH4605		AY436413	AY600284	DQ836908	6, 7. 16
Lentomitella cirrhosa	ICMP 15131	ET	AY761085	KM492911	–	11, 38
Lentomitella crinigera	CBS 138678		KY931811	–	–	49
Linocarpon livistonae	HKUM 6520		DQ810205	DQ810248	–	10
Magnaporthe salvinii	M 21		JF414887	–	JF710406	28
Magnaporthiopsis agrostidis	CBS 142740	HT	KT364754	–	KT364756	37
Melanconis stilbostoma	CBS 109778		AF408374	EU219299	EU221886	2
Myrmecridium montsegurinum	JF 13180	HT	KT991664	KT991654	–	41
Myrmecridium schulzeri	CBS 100.54		EU041826	–	–	17
Myrmecridium thailandicum	CBS 136551	HT	KF777222	–	–	30
Neolinocarpon enshiense	HKUCC 2983		DQ810221	DQ810244	–	10
Neolinocarpon globosicarpum	HKUCC 1959		DQ810224	DQ810245	–	10
Ophiostoma piliferum	CBS 158.74		DQ470955	DQ470905	DQ471074	14
Ophiostoma stenoceras	CBS 139.51		DQ836904	DQ836891	DQ836912	16

Table 1. Continued.

Taxon	Isolate[a]	Status[b]	GenBank accession numbers[a]			Ref.[c]
			LSU	RPB2	TEF1	
Papulosa amerospora	AFTOL-ID 748		DQ470950	DQ470901	DQ471069	14
Pararamichloridium caricicola	CBS 145069	HT	MK047488	–	–	46
Pararamichloridium livistonae	CBS 143166	HT	MG386084	–	–	54
Pararamichloridium verrucosum	CBS 128.86	HT	MH873621	–	–	56
Phaeoacremonium fraxinopennsylvanica	M.R. 3064		HQ878595	HQ878609	–	26
Phaeoacremonium novae-zealandiae	CBS 110156	HT	AY761081	–	–	8
Phomatospora bellaminuta	AFTOL-ID 766		FJ176857	FJ238345	–	23
Phomatospora biseriata	MFLUCC 14-0832A		KX549448	–	–	51
Phyllachora graminis	TH-544		KX430508	–	–	43
Pleurostoma ootheca	CBS 115329	IT	AY761079	HQ878606	FJ238420	8, 23, 26
Pseudostanjehughesia aquitropica	MFLUCC 16-0569	HT	MF077559	–	MF135655	53
Pseudostanjehughesia lignicola	MFLUCC 15-0352	HT	MK849787	MN124534	MN194047	55
Pyricularia borealis	CBS 461.65		DQ341511	–	–	24
Pyricularia bothriochloae	CBS 136427	HT	KF777238	–	–	30
Rhamphoria delicatula	CBS 132724		FJ617561	JX066702	–	22, 33
Rhamphoria pyriformis	CBS 139024		MG600397	MG600401	–	50
Rubellisphaeria abscondita	CBS 132078	HT	KT991666	KT991657	–	41
Sordaria fimicola	CBS 723.96		AY780079	DQ368647	–	9, 19
Spadicoides bina	CBS 137794		KY931824	KY931851	–	49
Sporidesmium minigelatinosa	NN 47497		DQ408567	DQ435090	–	12
Sporidesmium parvum	HKUCC 10836		DQ408558	–	–	12
Thyridium cornearis	CBS 131711	HT	KJ573450	–	LC382144	36
Thyridium curvatum	CBS 490.82	HT	AB189156	–	LC382142	15
Thyridium endophyticum	ACCC 38980	HT	KT799560	–	–	42
Thyridium flavostromatum	**KT 3891 = MAFF 247509**	HT	**LC655963**	**LC655967**	**LC655971**	This study
Thyridium hongkongense	HKU39	HT	KJ573447	–	–	36
Thyridium limonesiae	CBS 146752	HT	MW050976	–	–	58
Thyridium oculorum	CBS 110031	HT	KJ573449	–	LC382145	36
Thyridium pluriloculosum	CBS 131712	HT	HE599271	–	LC382141	32
	KT 3803 = MAFF 247508		**LC655964**	**LC655968**	**LC655972**	This study
Thyridium punctulatum	**KT 1015 = MAFF 239669**		**LC655965**	**LC655969**	**LC655973**	This study
	KT 3905 = MAFF 247510	ET	**LC655966**	**LC655970**	**LC655974**	This study
Thyridium vestitum	CBS 113027		AY544671	DQ470890	DQ471058[d]	5, 14
	CBS 125582		MH875182	–	–	56
Tirisporella beccariana	BCC 36737		JQ655450	–	–	39
Tirisporella bisetulosus	BCC 00018		EF622230	–	–	21
Wongia griffinii	BRIP 60377		KU850470	–	KU850466	40
Woswasia atropurpurea	CBS 133167	HT	JX233658	JX233659	–	31
Xylochrysis lucida	CBS 135996	HT	KF539911	KF539913	–	35
Xylolentia brunneola	PRA-13611	HT	MG600398	MG600402	–	50

[a] Strains and sequences generated in this study are shown in **bold**.

[b] ET = epitype; HT = holotype; IT = isotype

[c] 1: Viljoen et al. 1999; 2: Castlebury et al. 2002; 3: Raja et al. 2003; 4: Huhndorf et al. 2004; 5: Lutzoni et al. 2004; 6: Miller and Huhndorf 2004a; 7: Miller and Huhndorf 2004b; 8: Réblová et al. 2004; 9: Miller and Huhndorf 2005; 10: Bahl 2006; 11: Réblová 2006; 12: Shenoy et al. 2006; 13: Smith et al. 2006; 14: Spatafora et al. 2006; 15: Yaguchi et al. 2006; 16: Zhang et al. 2006; 17: Arzanlou et al. 2007; 18: Réblová 2007; 19: Tang et al. 2007; 20: Huhndorf et al. 2008; 21: Pinruan et al. 2008; 22: Réblová 2009; 23: Schoch et al. 2009; 24: Thongkantha et al. 2009; 25: Réblová et al. 2010; 26: Réblová 2011; 27: Réblová et al. 2011; 28: Zhang et al. 2011; 29: Réblová et al. 2012; 30: Crous et al. 2013; 31: Jaklitsch et al. 2013; 32: Perdomo et al. 2013; 33: Réblová 2013; 34: Untereiner et al. 2013; 35: Réblová et al. 2014; 36: Tsang et al. 2014; 37: Crous et al. 2015c; 38: Réblová et al. 2015; 39: Suetrong et al. 2015; 40: Khemmuk et al. 2016; 41: Réblová et al. 2016; 42: Su et al. 2016; 43: Mardones et al. 2017; 44: Xia et al. 2017; 45: Zhang et al. 2017; 46: Crous et al. 2018; 47: Hyde et al. 2018; 48: Luo et al. 2018; 49: Réblová et al. 2018; 50: Réblová and Štěpánek 2018; 51: Senanayake et al. 2018; 52: Voglmayr et al. 2018; 53: Yang et al. 2018; 54: Crous et al. 2019a; 55: Luo et al. 2019; 56: Vu et al. 2019; 57: Hyde et al. 2021; 58: Martinez et al. 2021.

[d] This TEF1 sequence (DQ471058) of *Thyridium vestitum* was excluded from this analysis. A Blast search using this sequence suggested that it is close to *Phialemonium obovatum* (Cephalothecales) rather than *Thyridium*/*Phialemoniopsis* (Thyridiales).

Table 2. Isolates and GenBank accessions of sequences used in the phylogenetic analyses of *Thyridium* species (Fig. 2).

Taxon	Isolate[a]	Substrate/Host	Status[b]	GenBank accession numbers[a]			Ref.[c]
				ITS	ACT	TUB2	
Thyridium cornearis	CBS 131711	human corneal fluid	HT	KJ573445	HE599252	HE599301	1, 2
	UTHSC 06-1465	shin aspirate		HE599285	HE599253	HE599302	2
Thyridium curvatum	CBS 490.82	skin lesion	HT	AB278180	HE599258	HE599307	2
	UTHSC R-3447	human eye		HE599291	HE599259	HE599308	2
Thyridium endophyticum	ACCC 38979	lower stem of *Luffa cylindrica* (endophyte)		KT799556	KT799553	KT799562	4
	ACCC 38980	lower stem of *Luffa cylindrica* (endophyte)	HT	KT799557	KT799554	KT799563	4
Thyridium flavostromatum	**KT 3891 = MAFF 247509**	dead twigs of *Phyllostachys pubescens*	HT	**LC655959**	**LC655979**	**LC655975**	This study
Thyridium hongkongense	HKU39	the right forearm nodule biopsy of a human	HT	KJ573442	KJ573452	KJ573457	3
Thyridium limonesiae	CBS 146752	Skin nodule	HT	MW050977	MW349126	MW048608	6
Thyridium oculorum	CBS 110031	human keratitis	HT	KJ573444	HE599247	HE599296	2, 3
	UTHSC 05-2527	peritoneal dialysis catheter		HE599281	HE599249	HE599298	2
Thyridium pluriloculosum	CBS 131712	human toe nail	HT	HE599286	HE599254	HE599303	2
	KT 3803 = MAFF 247508	dead wood of *Betula maximowicziana*	HT	**LC655960**	**LC655980**	**LC655976**	This study
	UTHSC 09-3589	synovial fluid		HE599287	HE599255	HE599304	2
Thyridium punctulatum	**KT 1015 = MAFF 239669**	dead culms of *Phyllostachys pubescens*		**LC655961**	**LC655981**	**LC655977**	This study
	KT 3905 = MAFF 247510	dead twigs of *Phyllostachys nigra* var. *nigra*	ET	**LC655962**	**LC655982**	**LC655978**	This study
Thyridium vestitum	CBS 125582			MH863721	–	–	5

[a] Strains and sequences generated in this study are shown in **bold**.

[b] ET = epitype; HT = holotype

[c] 1: Tang et al. 2007; 2: Perdomo et al. 2013; 3: Tsang et al. 2014; 4: Su et al. 2016; 5: Vu et al. 2019; 6: Martinez et al. 2021.

RESULT

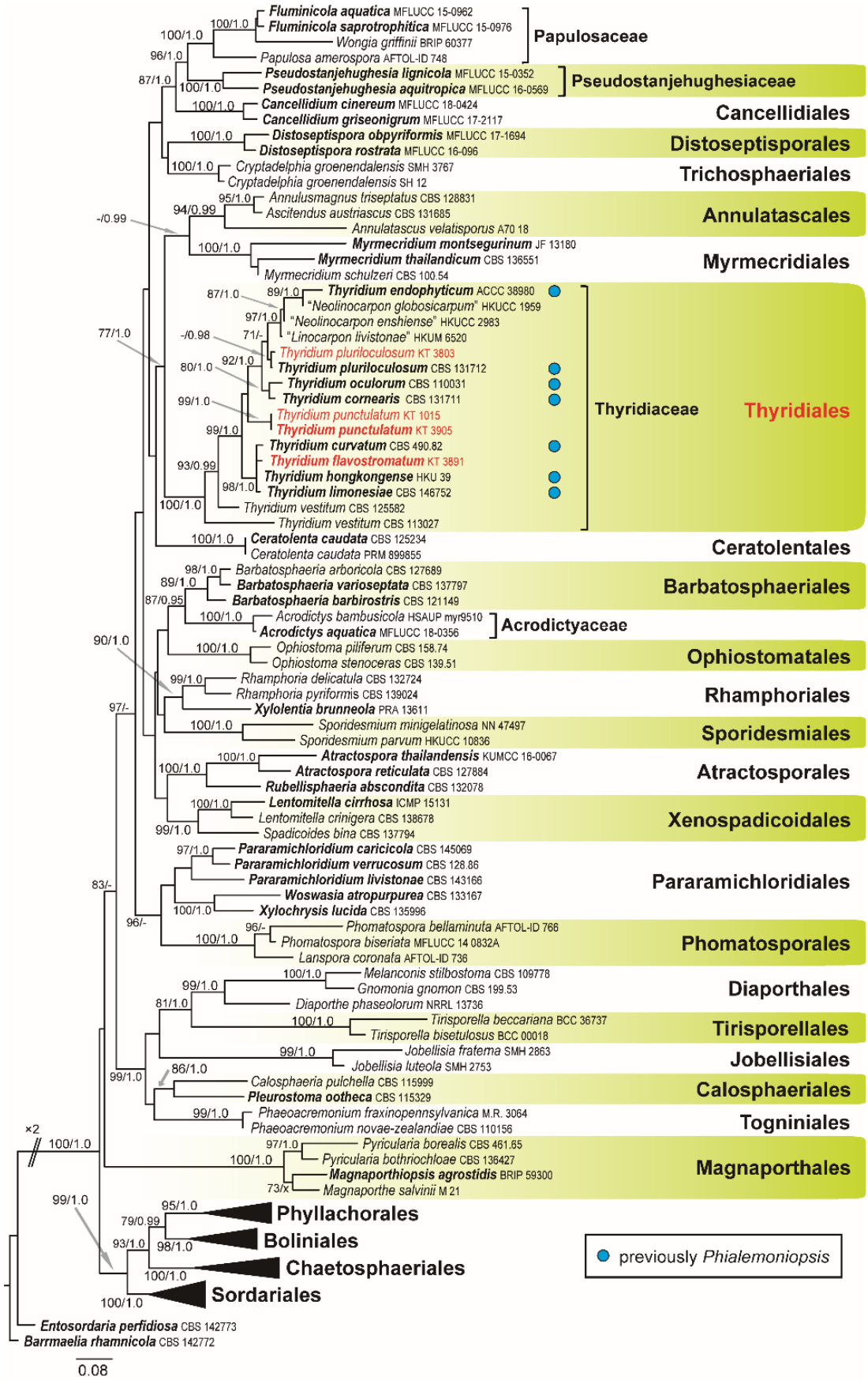
Phylogeny

For primary analysis, ML and Bayesian phylogenetic trees were generated using an aligned sequence dataset comprising of LSU (1,205 base pairs), RPB2 (1,059 bp) and TEF1 (954 bp). Of the 3,218 characters included in the alignment, 1,478 were variable and 1,686 were conserved. This combined dataset provided higher confidence values for ordinal and familial classification than those of individual gene trees, with 25 orders and three families (order unknown) being reconstructed in Sordariomycetes (Fig. 1). ML analysis of the combined dataset was conducted based on the selected substitution model for each partition (GTR+G for LSU, J2+G for the first and third codon positions of RPB2, J1+G for the second codon positions of RPB2, F81+G for the first codon positions of TEF1, JC69+G for the second codon positions of TEF1, and J2+G for the third codon position of TEF1). The ML tree with the highest log likelihood (–4,3687.562) is shown in Fig. 1. Topology recovered by Bayesian analysis was almost identical to that of the ML tree. All species previously described as *Phialemoniopsis* (marked with blue circle in Fig.

1), one species of "*Linocarpon*", two species of "*Neolinocarpon*" and four strains newly obtained in this study formed a monophyletic clade with the type species of *Thyridium* (*T. vestitum*). Their monophyly was completely supported (100% ML BS/1.0 Bayesian PP; Fig. 1). The family Thyridiaceae was found to be related to Annulatascales and Myrmecridiales but did not cluster with any existing order in Sordariomycetes.

For secondary analysis, ML and Bayesian phylogenetic trees were generated using sequences of ITS (483 bp), ACT (646 bp), TUB2 (375 bp), and a combined dataset of these three regions (1,504 bp). The selected substitution models for each region were as follows: J2ef+G for ITS, F81+H for the first and second codon positions of ACT, J2+G for the third codon position of ACT, K80+H for the first codon positions of TUB2, JC69+H for the second codon position of TUB2 and TN93+H for the third codon position of TUB2. The ML trees with the highest log likelihood (–1,172.0198 in ITS, –1,196.6012 in ACT, –859.37115 in TUB2 and –3,315.7254 in ITS-ACT-TUB2) are shown in Fig. 2. Our results confirmed close phylogenetic relationships between *Thyridium* and *Phialemoniopsis* (Fig. 2A–D). Except for ACT (Fig. 2B) and TUB2 (Fig. 2C), where sequence data of *T. vestitum* were unavailable, the existence of ten distinct species was suggested (Fig. 2A, D). The following three lineages were found in our four strains (Fig. 2A–D): 1) a bambusicolous lineage (KT 3891) close to *T. curvatum* and *T. limonesiae*, 2) a fungus on *Betula maximowicziana* (KT 3803) nested with *T. pluriloculosum*, which was previously reported from clinical sources (Perdomo et al. 2013), and 3) another bambusicolous lineage represented by two strains (KT 1015 and KT 3905).

Fig. 1 Maximum-likelihood tree of Sordariomycetes based on combined LSU, RPB2 and TEF1 sequence. ML bootstrap proportion (BP) greater than 70% and Bayesian posterior probabilities (PP) above 0.95 are presented at the nodes as ML BP/Bayesian PP and a node not present in the Bayesian analysis is shown with 'x'. A hyphen ('-') indicates values lower than 70% BP or 0.95 PP. Ex-holotype, isotype, paratype and epitype strains are shown in bold and the newly obtained sequences are shown in red. Strains previously described as *Phialemoniopsis* species are marked with a blue circle. The scale bar represents nucleotide substitutions per site.


Fluminicola aquatica MFLUCC 15-0962
Fluminicola saprotrophitica MFLUCC 15-0976
Wongia griffinii BRIP 60377
Papulosa amerospora AFTOL-ID 748
Papulosaceae
Pseudostanjehughesia lignicola MFLUCC 15-0352
Pseudostanjehughesia aquitropica MFLUCC 16-0569
Pseudostanjehughesiaceae
Cancellidium cinereum MFLUCC 18-0424
Cancellidium griseonigrum MFLUCC 17-2117
Cancellidiales
Distoseptispora obpyriformis MFLUCC 17-1694
Distoseptispora rostrata MFLUCC 16-096
Distoseptisporales
Cryptadelphia groenendalensis SMH 3767
Cryptadelphia groenendalensis SH 12
Trichosphaeriales
Annulusmagnus triseptatus CBS 128831
Ascitendus austriascus CBS 131685
Annulatascus velatisporus A70 18
Annulatascales
Myrmecridium montsegurinum JF 13180
Myrmecridium thailandicum CBS 136551
Myrmecridium schulzeri CBS 100.54
Myrmecridiales
Thyridium endophyticum ACCC 38980
"Neolinocarpon globosicarpum" HKUCC 1959
"Neolinocarpon enshiense" HKUCC 2983
"Linocarpon livistonae" HKUM 6520
Thyridium pluriloculosum KT 3803
Thyridium pluriloculosum CBS 131712
Thyridium oculorum CBS 110031
Thyridium cornearis CBS 131711
Thyridium punctulatum KT 1015
Thyridium punctulatum KT 3905
Thyridium curvatum CBS 490.82
Thyridium flavostromatum KT 3891
Thyridium hongkongense HKU 39
Thyridium limonesiae CBS 146752
Thyridium vestitum CBS 125582
Thyridium vestitum CBS 113027
Thyridiaceae
Thyridiales
Ceratolenta caudata CBS 125234
Ceratolenta caudata PRM 899855
Ceratolentales
Barbatosphaeria arboricola CBS 127689
Barbatosphaeria varioseptata CBS 137797
Barbatosphaeria barbirostris CBS 121149
Barbatosphaeriales
Acrodictys bambusicola HSAUP myr9510
Acrodictys aquatica MFLUCC 18-0356
Acrodictyaceae
Ophiostoma piliferum CBS 158.74
Ophiostoma stenoceras CBS 139.51
Ophiostomatales
Rhamphoria delicatula CBS 132724
Rhamphoria pyriformis CBS 139024
Xylolentia brunneola PRA 13611
Rhamphoriales
Sporidesmium minigelatinosa NN 47497
Sporidesmium parvum HKUCC 10836
Sporidesmiales
Atractospora thailandensis KUMCC 16-0067
Atractospora reticulata CBS 127884
Rubellisphaeria abscondita CBS 132078
Atractosporales
Lentomitella cirrhosa ICMP 15131
Lentomitella crinigera CBS 138678
Spadicoides bina CBS 137794
Xenospadicoidales
Pararamichloridium caricicola CBS 145069
Pararamichloridium verrucosum CBS 128.86
Pararamichloridium livistonae CBS 143166
Woswasia atropurpurea CBS 133167
Xylochrysis lucida CBS 135996
Pararamichloridiales
Phomatospora bellaminuta AFTOL-ID 766
Phomatospora biseriata MFLUCC 14 0832A
Lanspora coronata AFTOL-ID 736
Phomatosporales
Melanconis stilbostoma CBS 109778
Gnomonia gnomon CBS 199.53
Diaporthe phaseolorum NRRL 13736
Diaporthales
Tirisporella beccariana BCC 36737
Tirisporella bisetulosus BCC 00018
Tirisporellales
Jobellisia fraterna SMH 2863
Jobellisia luteola SMH 2753
Jobellisiales
Calosphaeria pulchella CBS 115999
Pleurostoma ootheca CBS 115329
Calosphaeriales
Phaeoacremonium fraxinopennsylvanica M.R. 3064
Phaeoacremonium novae-zealandiae CBS 110156
Togniniales
Pyricularia borealis CBS 461.65
Pyricularia bothriochloae CBS 136427
Magnaporthiopsis agrostidis BRIP 59300
Magnaporthe salvinii M 21
Magnaporthales
Phyllachorales
Boliniales
Chaetosphaeriales
Sordariales
Entosordaria perfidiosa CBS 142773
Barrmaelia rhamnicola CBS 142772
previously Phialemoniopsis
0.08

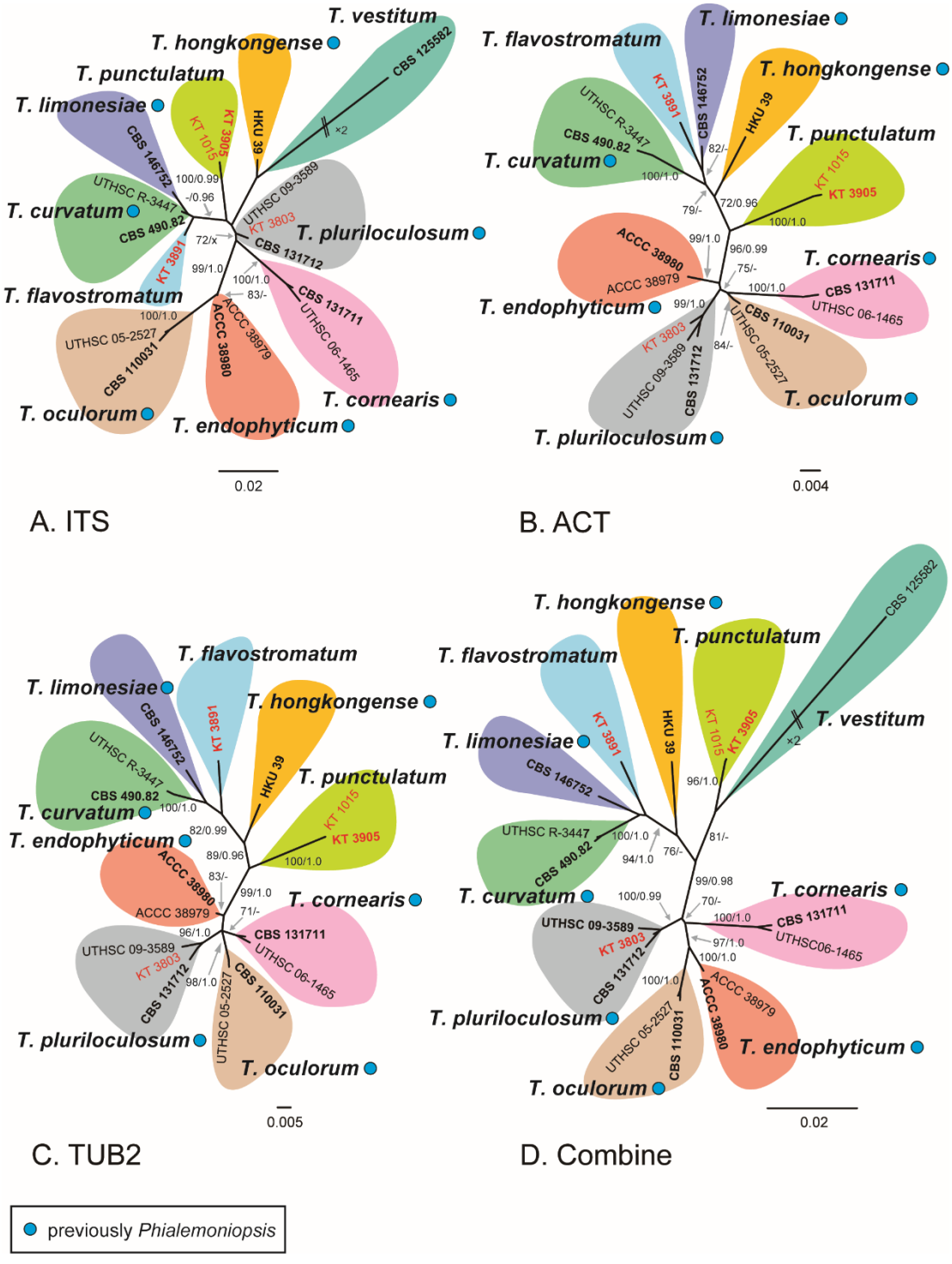


Fig. 2 Maximum-likelihood tree of *Thyridium* species based on each ITS (A), ACT (B), TUB2 (C) and combined sequences (ITS-ACT-TUB2; D). ML bootstrap proportion (BP) greater than 70% and Bayesian posterior probabilities (PP) above 0.95 are presented at the nodes as ML BP/Bayesian PP. A hyphen ('-') indicates values lower than 70% BP or 0.95 PP and a node not present in the Bayesian analysis is shown with 'x'. Ex-holotype and epitype strains are shown in bold and the newly obtained sequences are shown in red. Strains previously as *Phialemoniopsis* species are marked with a blue circle. The scale bars represent nucleotide substitutions per site.

TAXONOMY

A new order, Thyridiales, is introduced to accommodate Thyridiaceae because its lineage is phylogenetically and morphologically distinct from any known orders in Sordariomycetes. We concluded *Thyridium* and *Phialemoniopsis* to be congeneric based on their morphological similarities and phylogenetic relatedness. An expanded generic circumscription of *Thyridium* that integrates the generic concept of *Phialemoniopsis* is provided below. One new species and eight new combinations of *Thyridium* are proposed.

Thyridiales R. Sugita & Kaz. Tanaka, ord. nov. MycoBank MB841916

Type family. Thyridiaceae J.Z. Yue & O.E. Erikss., Syst. Ascom. 6(2): 233 (1987).

Sexual morph. Stromata scattered to grouped. Ascomata perithecial, subglobose to ampulliform. Ostiolar neck cylindrical, periphysate. Paraphyses numerous, unbranched, cylindrical, hyaline. Asci unitunicate, cylindrical, with an apical annulus, pedicellate. Ascospores obovoid to ellipsoid, muriform, hyaline to brown.

Asexual morph. Coelomycetous asexual morph: Conidiomata pycnidial, globose to subglobose. Conidiogenous cells phialidic. Conidia ellipsoidal to obovoid, aseptate, hyaline. Hyphomycetous synasexual morph: Colonies effuse or sporodochial. Conidiophores micronematous, mononematous, simple or branched, hyaline, thin-walled. Conidiogenous cells phialidic. Conidia ellipsoidal to allantoid, aseptate, hyaline.

Notes. Thyridiaceae has been treated as incertae sedis in Sordariomycetes (Yue and Eriksson 1987). Members of Thyridiaceae differ from Myrmecridiales by having pycnidial conidiomata, becoming cup-shaped in the coelomycetous state and micronematous conidiophores with monophialidic conidiogenous cells in the hyphomycetous state. Myrmecridiales have brown thick-walled conidiophores with polyblastic conidiogenous cells (Crous et al. 2015b). Annulatascales have relatively massive refractive, well-developed, conspicuous apical annulus in asci (Wong et al. 1999, Campbell and Shearer 2004, Dong et al. 2021). In contrast, those of members of Thyridiaceae are compact and inconspicuous. Therefore, a new order, Thyridiales, is introduced for this lineage.

Thyridiaceae J.Z. Yue & O.E. Erikss., Syst. Ascom. 6(2): 233 (1987).

Phialemoniopsidaceae K.D. Hyde & Hongsanan, [as Phialemoniopsaceae] Fungal Divers. 107: 95 (2021).

Type genus. *Thyridium* Nitschke, Pyrenomyc. Germ. 1: 110 (1867).

Notes. Phialemoniopsidaceae is considered a synonym of Thyridiaceae because *Phialemoniopsis*, the type genus of Phialemoniopsidaceae, was revealed congeneric with *Thyridium* and is placed in the synonymy of the latter genus in this study. The type genera of both families, that is, *Thyridium* and *Phialemoniopsis*, share many morphological features in their asexual states, as noted below.

***Thyridium* Nitschke, Pyrenomyc. Germ. 1: 110 (1867).**

Melanospora subgen. Bivonella Sacc., Syll. fung. (Abellini) 2: 464 (1883).
Bivonella (Sacc.) Sacc., Syll. fung. (Abellini) 9: 989 (1891).
Pleurocytospora Petr., Annls mycol. 21: 256 (1923).
Sinosphaeria J.Z. Yue & O.E. Erikss., Syst. Ascom. 6: 231 (1987).
Phialemoniopsis Perdomo, Dania García, Gené, Cano & Guarro, Mycologia 105: 408 (2013).

Type species. *Thyridium vestitum* (Fr.) Fuckel, Jb. nassau.Ver. Naturk. 23–24: 195 (1870) [1869–70].

Sexual morph. Stromata scattered to grouped, subepidermal to erumpent, yellowish to dark brown, red in KOH or not changing. Ascomata perithecial, subglobose to ampulliform, single to grouped, immersed in stromata to erumpent through host surface. Ascomatal wall composed of several layers of polygonal, dark brown cells. Ostiolar neck cylindrical, short or long, separated or convergent in upper stromata, periphysate. Paraphyses numerous, septate, unbranched, cylindrical, hyaline. Asci unitunicate, cylindrical, broadly rounded at the apex, with a pronounced non-amyloid apical annulus, pedicellate. Ascospores obovoid or ellipsoid, smooth, pale brown to brown, with several transverse and 0–3 longitudinal or oblique septa.

Asexual morph. Coelomycetous and/or hyphomycetous morphs formed. Coelomycetous asexual morph: Conidiomata pycnidial, single to grouped, superficial or immersed in stromata, globose to subglobose, composed of polygonal to prismatic cells, often becoming cup-shaped when mature, surrounded by setose hyphae. Conidiomatal

wall composed of several layers of polygonal, dark brown cells. Ostiolar neck cylindrical, central, periphysate. Setose hyphae erect, usually unbranched, septate, cylindrical, with slightly pointed or blunt tips, hyaline to pale brown, smooth-walled. Conidiophores hyaline, thin-walled, simple or irregularly branched, with branches bearing a small group of phialides terminally. Phialides swollen at the base, tapering at the tip, hyaline. Conidia obovoid to oblong, with a slightly apiculate base, hyaline, smoothwalled, in slimy masses. Hyphomycetous synasexual morph: Colonies effuse or sporodochial. Conidiophores micronematous, mononematous, hyaline, thin-walled, simple or irregularly branched, with branches bearing a small group of phialides terminally. Phialides swollen at the base, tapering at the tip, hyaline. Adelophialides absent or rarely present. Conidia ellipsoidal to allantoid, with a slightly apiculate base, hyaline, smooth-walled, in slimy head. Chlamydospores absent or rarely present, hyaline to pale brown, thick- and rough-walled.

Notes. The newly obtained *Thyridium* collections formed synasexual morphs, coelomycetous and hyphomycetous, in culture that were similar to those of Phialemoniopsis, having coelomycetous and/or hyphomycetous conidial states in culture (Perdomo et al. 2013). In this study, *Phialemoniopsis* is treated as a synonym of *Thyridium* because of their morphological similarities in asexual morphs and phylogenetic relatedness. The genus *Pleurocytospora* has been proposed as a synonym of *Thyridium* by culture studies (Leuchtmann and Müller 1986). We agree that the morphological features of *Pleurocytospora*, such as phialidic conidiogenous cells and hyaline, ellipsoidal conidia formed from both coelomycetous and hyphomycetous states (Leuchtmann and Müller 1986), are almost identical to those of the generic concept of *Thyridium* emended here.

We accept both *Bivonella* and *Sinosphaeria* as synonyms of *Thyridium*, as proposed in previous studies (Eriksson and Yue 1989, Checa et al. 2013). *Sinosphaeria* (typified by *S. bambusicola* = *Thyridium chrysomallum*; Yue and Eriksson 1987) was established as a new genus without knowing the existence of *Bivonella* (typified by *B. lycopersici*; Saccardo 1891). Both genera are characterised by yellowish stromata. The validity of these genera being synonymised under *Thyridium* is confirmed by the presence of *T. flavostromatum*, which has yellowish stromata, in the strongly supported *Thyridium* clade (Fig. 1).

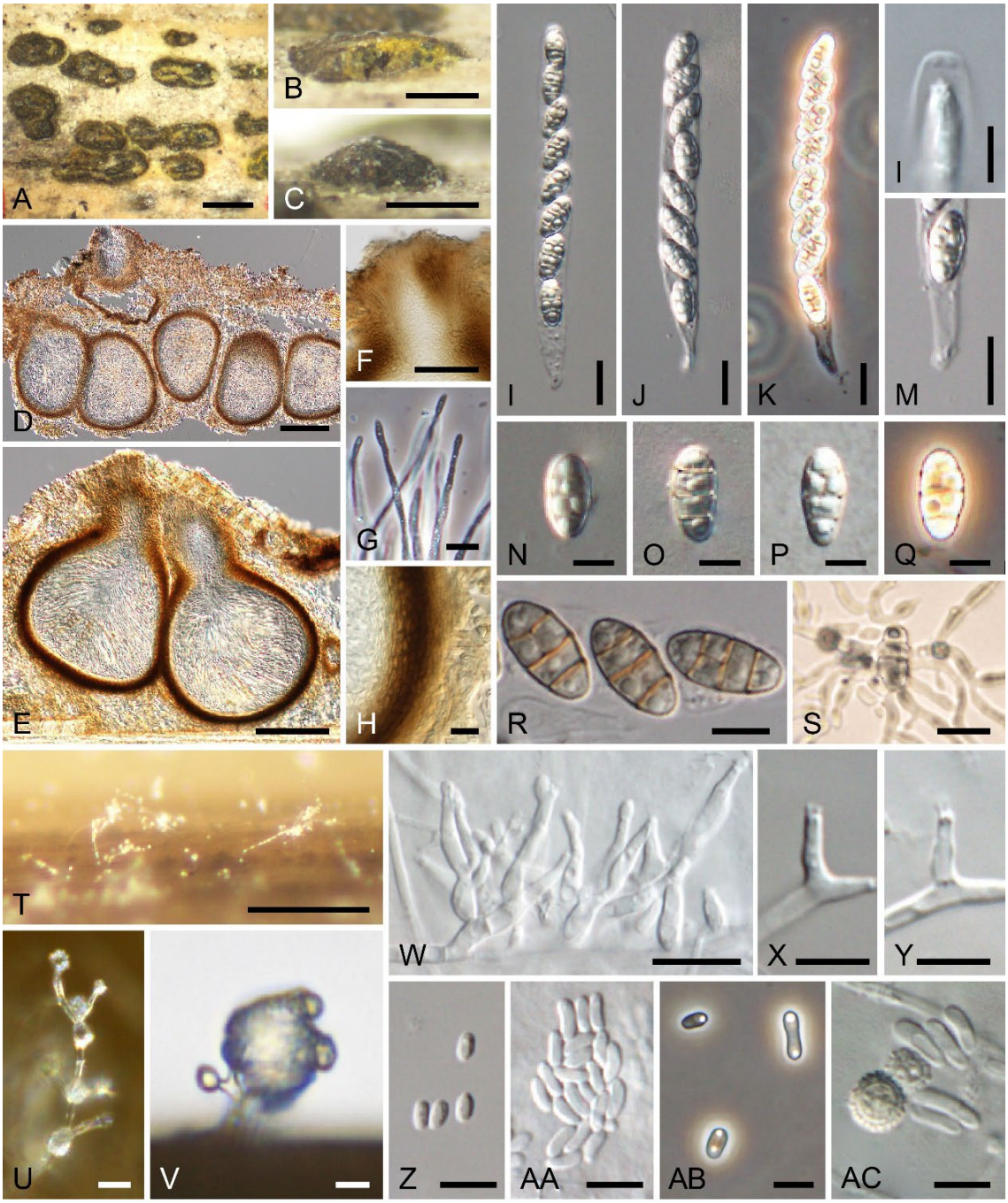


Fig. 3 ***Thyridium flavostromatum*** (**A–S.** KT 3891 = HHUF 30647; **T–AC.** culture KT 3891 = MAFF 247509) **A–S.** Sexual morph **A–C.** Appearance of stromata on substrate **D, E.** Ascomata in longitudinal section (**D.** in 2% KOH) **F.** Ostiolar neck of ascoma **G.** Paraphyses **H.** Ascomatal wall **I–K.** Asci **L.** Apex of the ascus **M.** Stipe of the ascus **N–R.** Ascospores **S.** Germinating ascospore **T–AC.** Hyphomycetous asexual morph **T.** Sporulation in culture **U.** Phialides **V.** Slimy conidial heads **W.** Conidiophores **X.** Phialide **Y.** Adelophialide **Z–AB.** Conidia **AC.** Chlamydospores and conidia. Scale bars: **A** = 1 mm, **B, C** = 500 µm, **D, E** = 100 µm, **F** = 50 µm, **G–K, M, S, U, V** = 10 µm, **L, N–R, W–AC** = 5 µm, **T** = 250 µm.

***Thyridium flavostromatum* R. Sugita & Kaz. Tanaka, sp. nov.**
MycoBank MB841917
Figs. 3, 6A

Holotype. Japan, Yamaguchi, Nagato, Misumikami, near Kusaritoge, on dead twigs of *Phyllostachys pubescens*, 26 March 2018, K. Tanaka, K. Arayama and R. Siguta, KT 3891 (HHUF 30647, holotype designated here), living culture MAFF 247509.

Etymology. The name refers to yellowish stromata.

Sexual morph. Stromata scattered to grouped, subepidermal, becoming erumpent to superficial, 0.7–1.4 mm long, 0.4–0.7 mm wide, yellowish to dark brown, red in 2% KOH. Ascomata perithecial, subglobose to ampulliform, mostly 2–6 grouped, 190–240 μm high, 200–220 μm diam., immersed in stromata to erumpent through host surface. Ascomatal wall 15–23 μm thick, composed of 5–8 layers of polygonal, 2.5–7 × 1.5–3.5 μm, dark brown cells. Ostiolar neck central, cylindrical, 80–140 μm long, 55–90 μm wide, periphysate. Paraphyses numerous, septate, unbranched, cylindrical, 50–105 μm long. Asci unitunicate, cylindrical, 62.5–90 × 6.5–10 μm (av. 78.7 × 7.8 μm, n = 30), broadly rounded at the apex, with a pronounced non-amyloid apical annulus, short-stalked (5–17.5 μm long), with 8 ascospores. Ascospores obovoid to ellipsoid, smooth, hyaline to pale brown, with 3 transverse and 0–2 vertical septa, 9.5–14 × 5–7.5 μm (av. 11.3 × 5.8 μm, n = 50), l/w 1.4–2.5 (av. 2.0, n = 50).

Asexual morph (nature). Not observed.

Asexual morph (culture). Hyphomycetous asexual morph formed. Conidiophores micronematous, mononematous, hyaline, thin-walled, simple or irregularly branched, with branches bearing a group of 2–3 phialides terminally. Phialides swollen at the base, tapering at the tip, hyaline, 3–6 × 1–1.5 μm. Adelophialides rarely present. Conidia ellipsoidal to allantoid, with a slightly apiculate base, hyaline, smooth-walled, 2–7 × 1–2.5 μm (av. 4.1 × 1.6 μm, n = 50). Chlamydospores rarely present, solitary, 3.5–6.5 μm diam., hyaline to pale brown, thick- and rough-walled.

Culture characteristics. Colonies on MEA at 25 °C attained 28–29 mm diam. after a week in the dark, whitish. On OA attained 35–37 mm diam., whitish. On PDA attained 28–31 mm diam., whitish to buff (45; Rayner 1970) (Fig. 6A).

Notes. Phylogenetic analyses based on ITS, ACT, and TUB2 sequences suggested that *T. flavostromatum* was closely related to *T. curvatum, T. hongokgense* and *T. limonesiae* (Fig. 2), of which only *T. hongokgense* has unknown conidial state. Although *T. curvatum* forms sporodochial conidiomata (Perdomo et al. 2013), those are not found in *T. flavostromatum*. Conidia of *T. limonesiae* (2.3–4.9 × 1.4–2 μm; Martinez et al. 2021)

are smaller than those of *T. flavostromatum* (2–7 × 1–2.5 µm). *Thyridium flavostromatum* is similar to *T. lasiacidis* on *Lasiacis ligulata* (Samuels and Rogerson 1989) in 1) having yellowish stromata becoming red in KOH, and 2) ellipsoidal ascospores with three transverse septa, with or without one longitudinal septum in 1–2 median cells. However, *T. lasiacidis* differs from *T. flavostromatum* by ascomata with a longer ostiolar neck (90–170 µm long) and dark brown ascospores with terminal pale brown cells (Samuels and Rogerson 1989).

***Thyridium pluriloculosum* (Perdomo, Dania García, Gené, Cano & Guarro) R. Sugita & Kaz. Tanaka, comb. nov.**

MycoBank MB841918

Figs. 4, 6B

Basionym. *Phialemoniopsis pluriloculosa* Perdomo, Dania García, Gené, Cano & Guarro, Mycologia 105: 412 (2013).

Holotype. USA, Nevada, human toe nail, D.A. Sutton, CBS H-20782, living culture CBS 131712 = UTHSC 04–7 = FMR 11070 (not seen).

Sexual morph. Stromata scattered to grouped, pulvinate, circular to elliptical in outline, elevated beyond bark surface forming pustules, 0.6–0.7 mm high, 0.9–1.0 mm diam., dark brown to black. Ascomata perithecial, subglobose to ampulliform, 4–8 grouped, 700–780 µm high, 220–280 µm diam., immersed in stromata. Ascomatal wall 17–25 µm thick, composed of 7–10 layers of polygonal, 4–6.5 × 2–4 µm, dark brown cells. Ostiolar neck central, cylindrical, 400–430 µm long, 100–110 µm wide, periphysate. Paraphyses septate, unbranched, cylindrical, 92.5–110 µm long, 3.5–5.5 µm wide. Asci unitunicate, cylindrical, 110–175 × 9–12.5 µm (av. 145.6 × 10.3 µm, n = 15), broadly rounded at the apex, with a pronounced non-amyloid apical annulus, pedicellate (12.5–27.5 µm long), with 8 ascospores. Ascospores fusiform to ellipsoid, smooth, brown, with 3 transverse and 0–2 oblique or vertical septa, 13.5–18 × 6–8 µm (av. 15.5 × 7.3 µm, n = 50), l/w 1.7–2.6 (av. 2.1, n = 50).

Asexual morph (nature). Conidiomata pycnidial, globose to subglobose, grouped, 220–300 µm high, 90–150 µm diam., immersed in stromata. Conidiomatal wall 8–18 µm thick, composed of 3–5 layers of polygonal, 3–4.5 × 2.5–4 µm, dark brown cells. Ostiolar neck central, cylindrical, 80–110 µm long, 90–110 µm wide, composed of polygonal cells, periphysate. Conidiophores hyaline, thin-walled, with branches bearing a group of 2–5 phialides terminally. Phialides tapering toward the tip, hyaline, 11–16 × 1–2 µm. Conidia

ellipsoidal, with a slightly apiculate base, hyaline, smooth-walled, 3–4.5 × 1–2 µm (av. 3.7 × 1.5 µm, n = 50). Chlamydospores not observed.

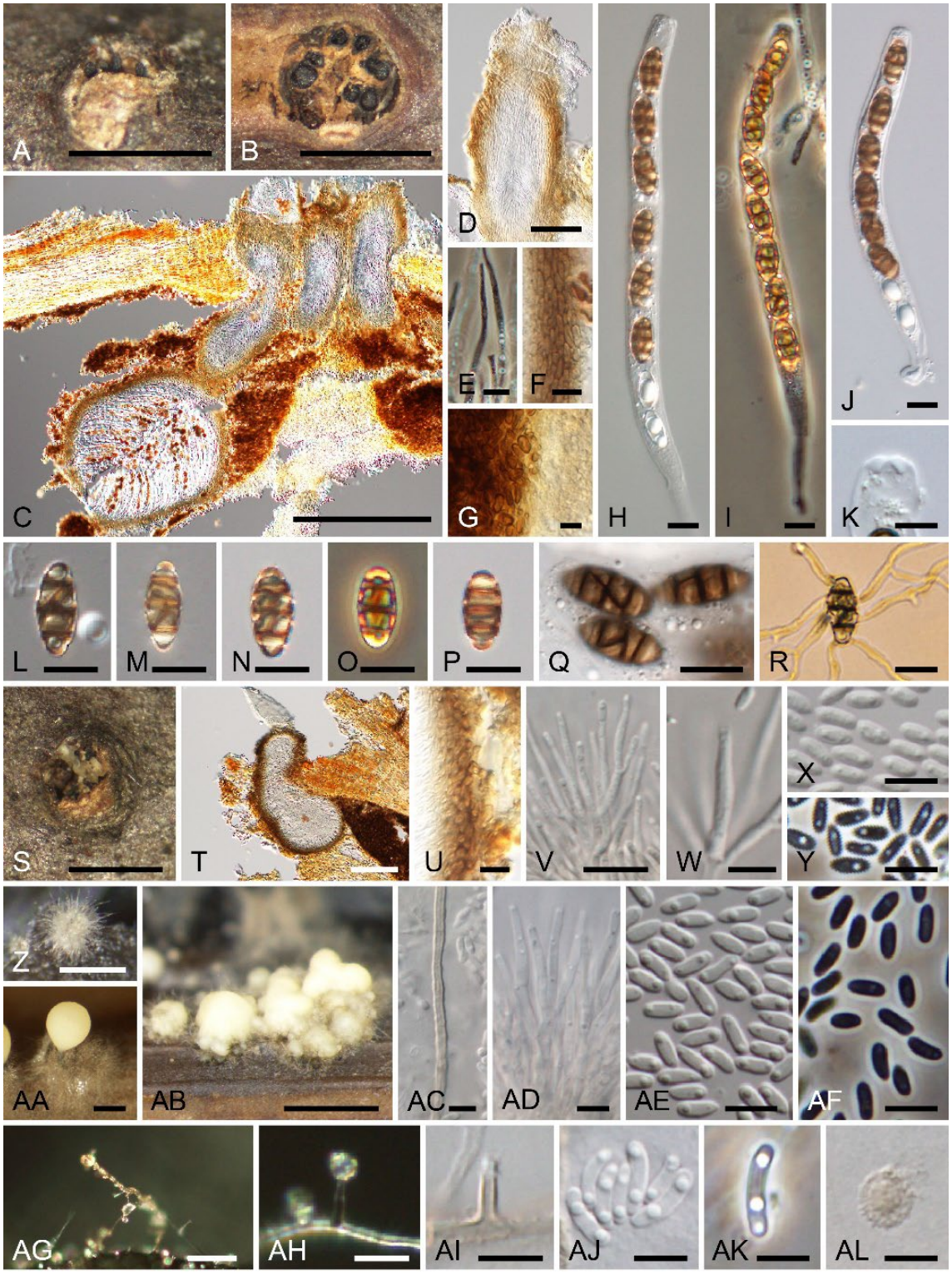


Fig. 4 ***Thyridium pluriloculosum*** (**A–Y.** KT 3803 = HHUF 30648; **Z–AL.** culture KT 3803 = MAFF 247508) **A–R.** Sexual morph **A, B.** Appearance of stromata on substrate (**B.** transverse sections) **C.** Ascomata in longitudinal section, **D.** Ostiolar neck of ascoma **E.** Paraphyses **F.** Ascomatal wall **G.** Pseudostromatic tissue **H–J.** Asci **K.** Apex of ascus **L–Q.** Ascospores **R.** Germinating ascospore **S–AF.** Coelomycetous asexual morph (**S–Y.** Nature, **Z–AF.** Culture) **S.** Appearance of conidiomata on substrate **T.** Conidiomata in longitudinal section **U.** Conidiomatal wall **V.** Conidiophores **W.** Phialide **X, Y.** Conidia **Z–AB.** Conidiomata in culture (**AB.** multiloculate conidiomata) **AC.** Setose hypha of conidiomata **AD.** Conidiophores with groups of phialides **AE, AF.** Conidia **AG–AL.** Hyphomycetous synasexual morph **AG, AH.** Sporulation in culture **AI.** Phialide **AJ, AK.** Conidia **AL.** Chlamydospores. Scale bars: **A, B, S, AB** = 1 mm, **C, Z, AA** = 500 μm, **D, T** = 100 μm, **AG, AH** = 20 μm, **E–J, L–R, U, V** = 10 μm, **K, W–Y, AC–AF, AI–AL** = 5 μm.

Asexual morph (culture). Coelomycetous asexual morph: Conidiomata pycnidial, scattered, single to grouped, superficial, globose to subglobose, 180–380 μm high, mostly 80–580 μm diam., up to 1170 μm diam. when grouped, often becoming cup-shaped when mature, surrounded by setose hyphae. Conidiomatal wall composed of polygonal to prismatic, 3–4.5 × 2.5–4 μm, dark brown cells. Setose hyphae erect, usually unbranched, septate, up to 360 μm long, 2–3 μm wide, pale brown. Conidiophores hyaline, thin-walled, simple or irregularly branched, with branches bearing a group of 2–5 phialides terminally. Phialides tapering toward the tip, hyaline, 10–25 × 1–2.5 μm. Conidia ellipsoidal, with a slightly apiculate base, hyaline, smooth-walled, in slimy masses, 3–4.5 × 1–2 μm (av. 3.8 × 1.4 μm, n = 50). Hyphomycetous synasexual morph: Conidiophores micronematous, mononematous, hyaline, simple or rarely branched. Phialides slightly tapering toward the tip, 4–11 × 1–2.5 μm, hyaline. Adelophialide absent. Conidia allantoid, hyaline, smooth-walled, in slimy heads, 3–9 × 1–2.5 μm (av. 6.2 × 1.7 μm, n = 50). Chlamydospores rarely present, solitary, 3.5–6.5 μm diam., hyaline to pale brown, thick- and rough-walled.

Culture characteristics. Colonies on MEA at 25 °C attained 31–33 mm diam. after a week in the dark, whitish. On OA attained 32–36 mm diam., whitish to grey olivaceous (107). On PDA attained 32–33 mm diam., whitish to buff (45) (Fig. 6B).

Specimen examined. Japan, Aomori, Hirakawa, Hirofune, Shigabo Forest Park, on dead twigs of *Betula maximowicziana*, 10 October 2017, K. Tanaka, KT 3803 (HHUF 30648), living culture MAFF 247508.

Notes. The conidia from aerial hyphae of strain KT 3803 were larger (3–9 × 1–2.5 μm) in culture than those of the original description of *Thyridium pluriloculosum* (3–5 × 1–2.5 μm; Perdomo et al. 2013). However, we identified this new collection on *Betula maximowicziana* as *T. pluriloculosum*, based on the high sequence homology of three loci with ex-type culture of this species (CBS 131712; 99.6% in ITS, 99.2% in ACT, and 99.5% in TUB2). The sexual-asexual relationship of *T. pluriloculosum* was verified in this study. Although this species has been reported from clinical sources as an asexual

morph (Perdomo et al. 2013), the recently collected material represents a sexual morph on plant material.

In *Thyridium*, *T. betulae* has also been recorded on *Betula* sp. in France (Roumeguère 1891). Although sequences of *T. betulae* are unavailable for molecular comparison, it is clearly different from *T. pluriloculosum* in having ascospores with 5–7 transverse and one longitudinal septum.

***Thyridium punctulatum* (I. Hino & Katum.) R. Sugita & Kaz. Tanaka, comb. nov.**
MycoBank MB841919
Figs. 5, 6C

Basionym. *Pleospora punctulata* I. Hino & Katum., Icones Fungorum Bamb. Jpn.: 181 (1961).

Holotype. Japan, Shizuoka, Fuji Bamboo Garden, on dead twigs of *Phyllostachys nigra* var. *henonis*, 1 April 1958, K. Katumoto, YAM 21851.

Epitype. Japan, Yamaguchi, Hagi, Akiragi, near Chikurindoro-park, on dead twigs of *Phyllostachys nigra* var. *nigra*, 26 March 2018, K. Tanaka, K. Arayama and R. Sugita, KT 3905 (HHUF 30649 epitype designated here; MBT10004137), ex-epitype culture MAFF 247510.

Sexual morph. Stromata scattered to grouped, subepidermal, becoming erumpent to superficial, 0.5–1.2 mm long, 0.2–0.4 mm wide, dark brown. Ascomata perithecial, subglobose to conical, single to 2–3 grouped, 130–190 μm high, 140–230 μm diam., immersed in stromata to erumpent through host surface. Ascomatal wall 7–15 μm thick, composed of 3–5 layers of polygonal, 3–6.5 × 1–4.5 μm, dark brown cells. Ostiolar neck central, cylindrical, 37–85 μm long, 37–63 μm wide, periphysate. Paraphyses numerous, septate, unbranched, cylindrical, hyaline, 77–103 μm long. Asci unitunicate, cylindrical, 67.5–105 × 7.5–11.5 μm (av. 82.9 × 9.4 μm, n = 60), broadly rounded at the apex, with a pronounced non-amyloid apical annulus, short-stalked (3.5–11.5 μm long), with 8 ascospores. Ascospores ellipsoid to oblong, smooth, pale brown, with 3 transverse and 1–2 vertical septa, 10–15 × 5–9 μm (av. 12.8 × 7.0 μm, n = 60), l/w 1.4–2.4 (av. 1.8, n = 60).

Asexual morph (nature). Not observed.

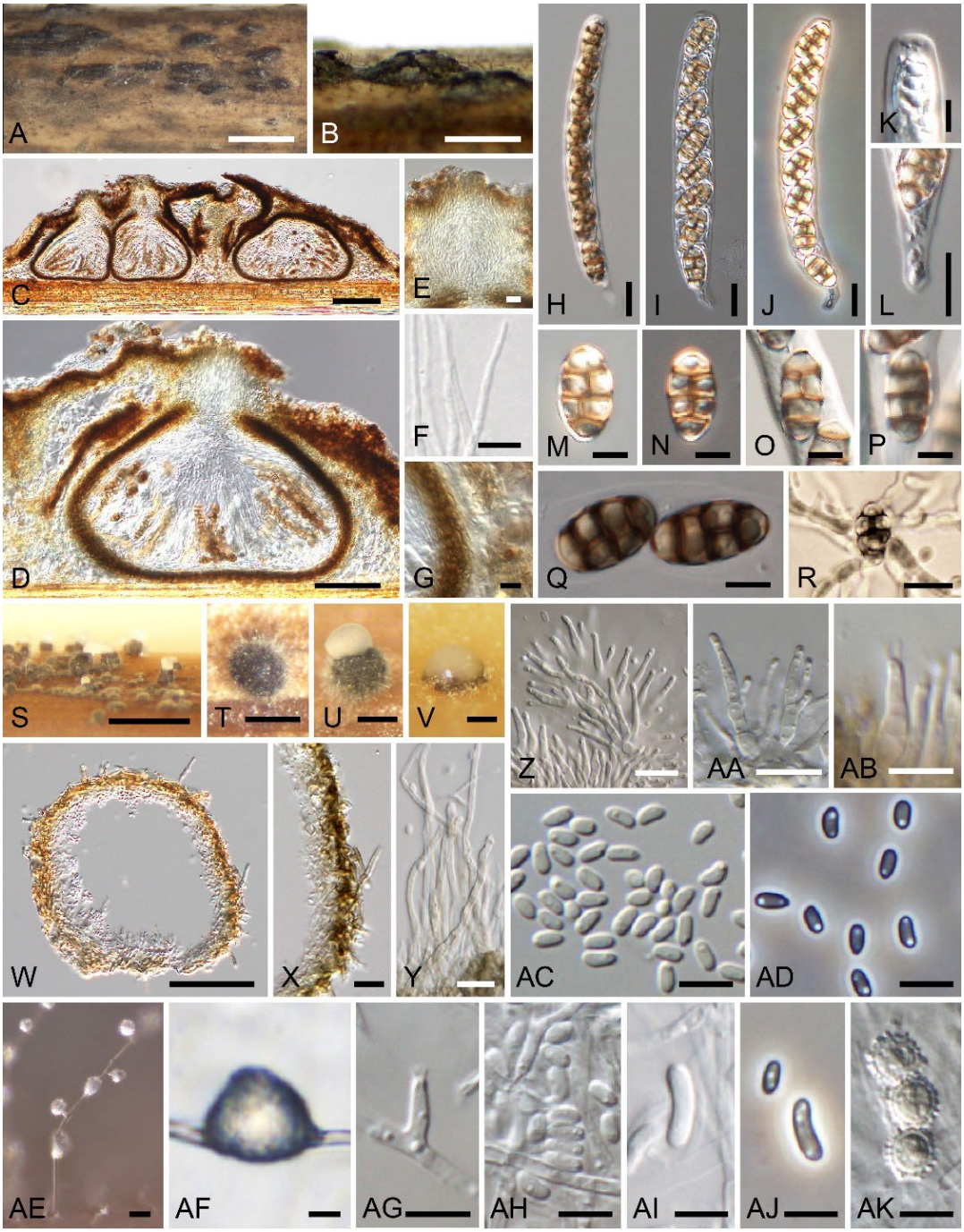


Fig. 5 ***Thyridium punctulatum*** (**A–N, Q, R.** KT 3905 = HHUF 30649; **O, P.** YAM 21851; **S, T, W–AB.** culture KT 1015 = JCM 13159 = MAFF 239669; **U, V, AC–AK.** culture KT 3905 = MAFF 247510) **A–R.** Sexual morph **A, B.** Appearance of stromata on substrate **C, D.** Ascomata in longitudinal section, **E.** Ostiolar neck of ascoma **F.** Paraphyses **G.** Ascomatal wall **H–J.** Asci **K.** Apex of ascus **L.** Stipe of ascus **M–Q.** Ascospores **R.** Germinating ascospore **S–AD.** Coelomycetous asexual morph **S–V.** Conidiomata in culture **W.** Conidioma in longitudinal section **X.** Conidiomatal wall **Y.** Setose hyphae of conidiomata **Z, AA.** Conidiophores **AB.** Phialides **AC, AD.** Conidia **AE–AK.** Hyphomycetous synasexual morph **AE.** Conidiophore **AF.** Slimy head **AG.** Phialide **AH–AJ.** Conidia **AK.** Chlamydospores. Scale bars: **A, S** = 1 mm, **B** = 500 µm, **C, W** = 100 µm, **D** = 50 µm, **E–J, L, R, X–AA, AE, AF** = 10 µm, **K, M–Q, AB–AD, AG–AK** = 5 µm, **T–V** = 200 µm.

Asexual morph (culture). Coelomycetous asexual morph: Conidiomata pycnidial, single to grouped, superficial, globose to subglobose, 100–250 μm high, 170–620 μm diam., composed of polygonal to prismatic, 3.5–7.5 × 2.5–4 μm cells, often becoming cup-shaped when mature, surrounded by setose hyphae. Setose hyphae erect, usually unbranched, septate, up to 225 μm long, 1.5–2.5 μm wide, pale brown. Conidiophores hyaline, thin-walled, simple or irregularly branched, with branches bearing a group of 2–5 phialides terminally. Phialides swollen at the base, tapering at the tip, 7–20 × 1–3 μm, hyaline. Conidia ellipsoidal to obovoid, with a slightly apiculate base, hyaline, smooth-walled, in slimy masses, 2–3.5 × 1–2 μm (av. 2.9 × 1.4 μm, n = 50). Hyphomycetous synasexual morph: Conidiophores micronematous, mononematous, hyaline, thin-walled, simple or irregularly branched, with branches bearing a group of 2–3 phialides terminally. Phialides swollen at the base, tapering at the tip, hyaline, 3–9 × 1–2 μm. Adelophialide absent. Conidia ellipsoidal to allantoid, hyaline, smoothwalled, in slimy heads, 2.5–8 × 1–3 μm (av. 4.3 × 1.6 μm, n = 87). Chlamydospores rarely present, solitary or chained, 4–5.5 μm diam., hyaline to pale brown.

Culture characteristics. Colonies on MEA at 25 °C attained 31–32 mm diam. after a week in the dark, granulose, whitish. On OA attained 38–39 mm diam., granulose, whitish. On PDA attained 35–36 mm diam., whitish to buff (45) (Fig. 6C).

Other specimen examined. Japan, Iwate, Morioka, Ueda, Campus of Iwate University, on dead culms of *Phyllostachys pubescens*, 17 February 2003, K. Tanaka and Y. Harada, KT 1015 (HHUF 29350), living culture JCM 13159 = MAFF 239669.

Notes. This species has been described from *Phyllostachys nigra* var. *henonis*, as a species of *Pleospora* (Dothideomycetes; Hino 1961). Our phylogenetic analysis (Fig. 1) shows that this species is a member of the genus *Thyridium* (Sordariomycetes). The morphological features of this species are consistent with those of the genus *Thyridium*, including immersed to erumpent, single to grouped, perithecial ascomata with a cylindrical ostiolar neck, unitunicate asci and muriform, pigmented ascospores (Eriksson and Yue 1989). Therefore, we propose a new combination, *T. punctulatum*, for *Pleospora punctulata*.

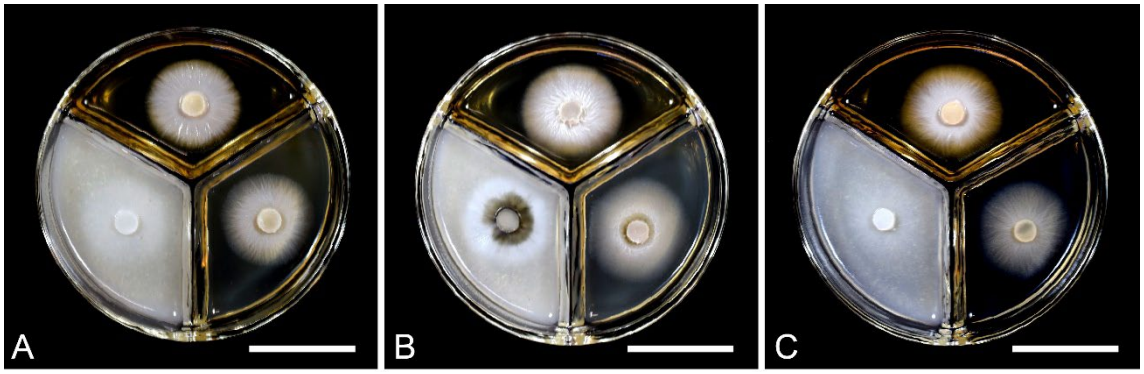


Fig. 6 Colony characters of *Thyridium* species used in this study on MEA (bottom right), OA (bottom left) and PDA (upper) within 1 week at 25 °C in the dark. **A.** *T. flavostromatum* (culture KT 3891 = MAFF 247509) **B.** *T. pluriloculosum* (culture KT 3803 = MAFF 247508) **C.** *T. punctulatum* (culture KT 3905 = MAFF 247510). Scale bars: A–C = 3 cm.

Thyridium cornearis **(Perdomo, Dania García, Gené, Cano & Guarro) R. Sugita** & Kaz. Tanaka, comb. nov.
MycoBank MB841920

Basionym. *Phialemoniopsis cornearis* Perdomo, Dania García, Gené, Cano & Guarro, Mycologia 105: 408 (2013).

Thyridium curvatum **(W. Gams & W.B. Cooke) R. Sugita & Kaz. Tanaka, comb. nov.**
MycoBank MB841921

Phialemoniopsis curvata (W. Gams & W.B. Cooke) Perdomo, Dania García, Gené, Cano & Guarro, Mycologia 105: 410 (2013).

Basionym. *Phialemonium curvatum* W. Gams & W.B. Cooke, Mycologia 75: 980 (1983).

Thyridium endophyticum **(Lei Su & Y.C. Niu) R. Sugita & Kaz. Tanaka, comb. nov.**
MycoBank MB841922

Basionym. *Phialemoniopsis endophytica* Lei Su & Y.C. Niu, Mycol. Progr. 15: 3 (2016).

Thyridium hongkongense **(Tsang, Chan, Ip, Ngan, Chen, Lau, Woo) R. Sugita & Kaz. Tanaka, comb. nov.**
MycoBank MB841923

Basionym. *Phialemoniopsis hongkongensis* Tsang, Chan, Ip, Ngan, Chen, Lau, Woo, J. Clin. Microbiol. 52: 3284 (2014).

Thyridium limonesiae **(A. Riat, L.W. Hou & Crous) R. Sugita & Kaz. Tanaka, comb. nov.**
MycoBank MB841927

Basionym. *Phialemoniopsis limonesiae* A. Riat, L.W. Hou & Crous, Emerging Microbes & Infections 10: 403 (2021).

Thyridium oculorum **(Gené & Guarro) R. Sugita & Kaz. Tanaka, comb. nov.**
MycoBank MB841924

Phialemoniopsis ocularis (Gené & Guarro) Perdomo, Dania García, Gené, Cano & Guarro, Mycologia 105: 411 (2013).

Basionym. Sarcopodium oculorum Gené & Guarro, J. Clin. Microbiol. 40: 3074 (2002).

DISCUSSION

We show that the asexual genus *Phialemoniopsis* (established by Perdomo et al. 2013) is a synonym of the sexual genus *Thyridium* (established by Nitschke 1867). We found a new species of *Thyridium* (*T. flavostromatum*), transferred *Pleospora punctulata* into *Thyridium*, and proposed seven new combinations in *Thyridium* for strains previously treated in *Phialemoniopsis*. We provided a revised generic circumscription of *Thyridium* based on both sexual and asexual characteristics and revealed the phylogenetic relationships of species within this genus.

The genus *Thyridium* has been defined mainly on the basis of sexual characters (Nitschke 1867, Eriksson and Yue 1989). Currently, 33 species are recorded in this genus (http://www.indexfungorum.org, 2021). Asexual morphs are unknown in most species of *Thyridium*, with the exceptions of *T. flavum* and *T. vestitum*, in which asexual morphs have been recorded based on sexual-asexual association on the same specimen (Petch 1917) and on the basis of culture study (Leuchtmann and Müller 1986, this study), respectively. In contrast, the genus *Phialemoniopsis* has been defined based only on asexual characters (Perdomo et al. 2013). Its ordinal affiliation within Sordariomycetes

has not been resolved, but recent phylogenetic analyses of this class suggest that *Phialemoniopsis* is close to *Thyridium* (Hyde et al. 2021). In our phylogenetic analysis, all species previously described as *Phialemoniopsis* (marked with blue circle; Fig. 1) were clustered in a single clade, including the type species of *Thyridium* (*T. vestitum*), as well as two new strains proposed here (*T. flavostromatum* and *T. punctulatum*). Both genera have similar asexual morphs, which have conidiophores bearing small groups of phialides, hyaline phialidic conidiogenous cells, and ellipsoidal or allantoid, hyaline conidia in both coelomycetous and hyphomycetous states (Petch 1917, Leuchtmann and Müller 1986, Perdomo et al. 2013). Morphological and molecular phylogenetic evidence clearly shows that *Phialemoniopsis* is congeneric with *Thyridium*.

Synonymising *Phialemoniopsis* under *Thyridium* expanded information about the asexual morphs of *Thyridium*. In this genus, only *T. vestitum* has been demonstrated to have asexual morphs by culture studies (Leuchtmann and Müller 1986). It has both coelomycetous and hyphomycetous complex asexual morphs, which have phialidic conidiogenous cells with collarette and ellipsoidal to allantoid hyaline conidia (Leuchtmann and Müller 1986). Members of *Phialemoniopsis* also have coelomycetous and/or hyphomycetous conidial states (Perdomo et al. 2013, Tsang et al. 2014, Su et al. 2016, Martinez et al. 2021). The close relationship of *Phialemoniopsis* and *Thyridium* suggests that such complex asexual morphs may be common within *Thyridium* species.

In *Thyridium*, *T. endophyticum* and *T. curvatum* have been isolated from both plants and animals (Gam and McGinnis 1983, Halleen et al. 2007, Perdomo et al. 2013, Su et al. 2016, Ito et al. 2017). There are several examples of fungal species, including human pathogens, detected from various substrates. For example, *Phaeoacremonium minimum* is a pathogen on grapevines, where it forms both sexual and asexual morphs (Crous et al. 1996, Pascoe et al. 2004), but it has also been reported as a causative agent of subcutaneous phaeohyphomycosis in humans as asexual morph (Choi et al. 2011). Other species of *Thyridium* may also have cryptic life cycles and can colonise each host substrate at different reproductive stages. An example of this prediction can be found in *T. pluriloculosum*. This species was originally found in human nails as an asexual fungus (Perdomo et al. 2013), and its sexual state was rediscovered on twigs of *Betula maximowicziana* in our study.

Epitypification of the type species of *Thyridium* (*T. vestitum*) will be a necessary issue in the future. We used sequences from two non-type strains (CBS 113027, CBS 125582) of this species for phylogenetic analyses but they did not form a monophyletic clade (Fig. 1). Sequence differences between these two strains were found at 34 positions with four gaps in the LSU. These results indicate that the strains obtained from *Acer*

pseudoplatanus (CBS 113027) and no host information (CBS 125582) in Austria are not conspecific. A fresh collection of *T. vestitum* on original host plant from the type locality (*Ribes rubrum*, Sweden; Fries 1823) and its phylogenetic analysis are required to fix generic circumscription of *Thyridium*.

Thyridiales established here may encompass other genera and families with morphologies distinct from the genus *Thyridium* (Thyridiaceae). Some species of "*Linocarpon*" and "*Neolinocarpon*" are nested within the Thyridiales (Fig. 1). *Linocarpon* and *Neolinocarpon* sensu stricto belong to Linocarpaceae (Chaetosphaeriales) and are morphologically distinct from *Thyridium* in having filiform, straight or curved, unicellular, hyaline, or pale-yellowish ascospores (Huhndorf and Miller 2011, Konta et al. 2017). The "*Linocarpon*" and "*Neolinocarpon*" species phylogenetically unrelated to *Linocarpon* and *Neolinocarpon* sensu stricto may be new lineages in Thyridiaceae or belong to its own new undescribed family. However, we cannot clarify the phylogenetic/taxonomic relatedness of these atypical *Linocarpon*-like species because none of them are ex-types and their morphological information are unavailable. Further molecular phylogenetic study of these fungi based on protein-coding sequences and finding additional specimens/isolates of "*Linocarpon*" and "*Neolinocarpon*" species related to *Thyridium* will be necessary to clarify their taxonomic affiliation and better understand the concept of Thyridiales.

3. *Spirodecospora* 属の分類学的所属の検討

ABSTRACT

Spirodecospora 属は形態的類似性をもとにクロサイワイタケ科に置かれていた。日本のタケ類から発見した *Spirodecospora* 属菌について、分子系統的な分類研究を初めて試みた。分子系統解析は、核リボソーム内部転写スペーサー領域 (ITS)、リボソーム DNA 大サブユニット (LSU)、RNA ポリメラーゼ大サブユニット II (RPB2) の DNA 塩基配列に基づいて行った。その本研究の結果、*Spirodecospora* 属はクロサイワイタケ目の他の既知の科から独立した系統群を形成することが明らかになった。既知の科との分子系統学的な根拠と形態学的な差異に基づき、本属菌の所属として新科 Spirodecospora 科を設立した。*Spirodecospora* 属は円筒形の孔口頸部のある深く埋没した子のう果、単列、円筒形、I+の楔形先端リングを持つ子のう、幅の広い楕円形から紡錘形、無隔壁、褐色、らせん状またはほとんど真直ぐな線状装飾物を持つ、小いぼ状突起のある子のう胞子によって特徴づけられる。形態観察と分子系統解析により、*S. melnikii* と本属の 2 新種 *S. paramelnikii* および *S. paulospiralis* を記載し、図示した。*Spirodecospora* 属の 4 種について検索表を示した。

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 and 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 and Samuels 1994) and LR5 or LR7 (Vilgalys and 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). Sequences were obtained completely in ITS and partially in others, respectively. 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 3). *Bombardia bombarda* and *Sordaria fimicola* were used as outgroups.

Table 3. 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. (2015a)
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)

Table 3. Continued.

Species	Specimen/Strain	GenBank accession numbers			Reference
		ITS	LSU	RPB2	
Lopadostoma dryophilum	CBS 133213	KC774570	KC774570	KC774526	Jaklitsch et al. (2014)
Lopadostoma fagi	CBS 133206	KC774575	KC774575	KC774531	Jaklitsch et al. (2014)
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
Spirodecospora melnikii	**MAFF 247742 = KT 1729**	**LC731933**	**LC731942**	**LC731951**	This study
Spirodecospora melnikii	**MAFF 247743 = KT 3457**	**LC731934**	**LC731943**	**LC731952**	This study
Spirodecospora melnikii	**MAFF 247744 = KT 3760**	**LC731935**	**LC731944**	**LC731953**	This study
Spirodecospora melnikii	**MAFF 247745 = KT 3911**	**LC731936**	**LC731945**	**LC731954**	This study
Spirodecospora melnikii	**MAFF 247746 = KT 4092**	**LC731937**	**LC731946**	**LC731955**	This study
Spirodecospora melnikii	**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)

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 (InL = –38,040.76) is shown in Fig. 7. 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. 7). The *Spirodecospora* clade was shown as an independent and strongly supported (100 % MLBS/1.0 Bayesian PP) clade. Families Coniocessiaceae and Hansfordiaceae were the most closely related lineage 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 MB846055.

Type genus. *Spirodecospora* B.S. Lu, K.D. Hyde & W.H. Ho.

Sexual morph. 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.

Asexual morph. Not observed.

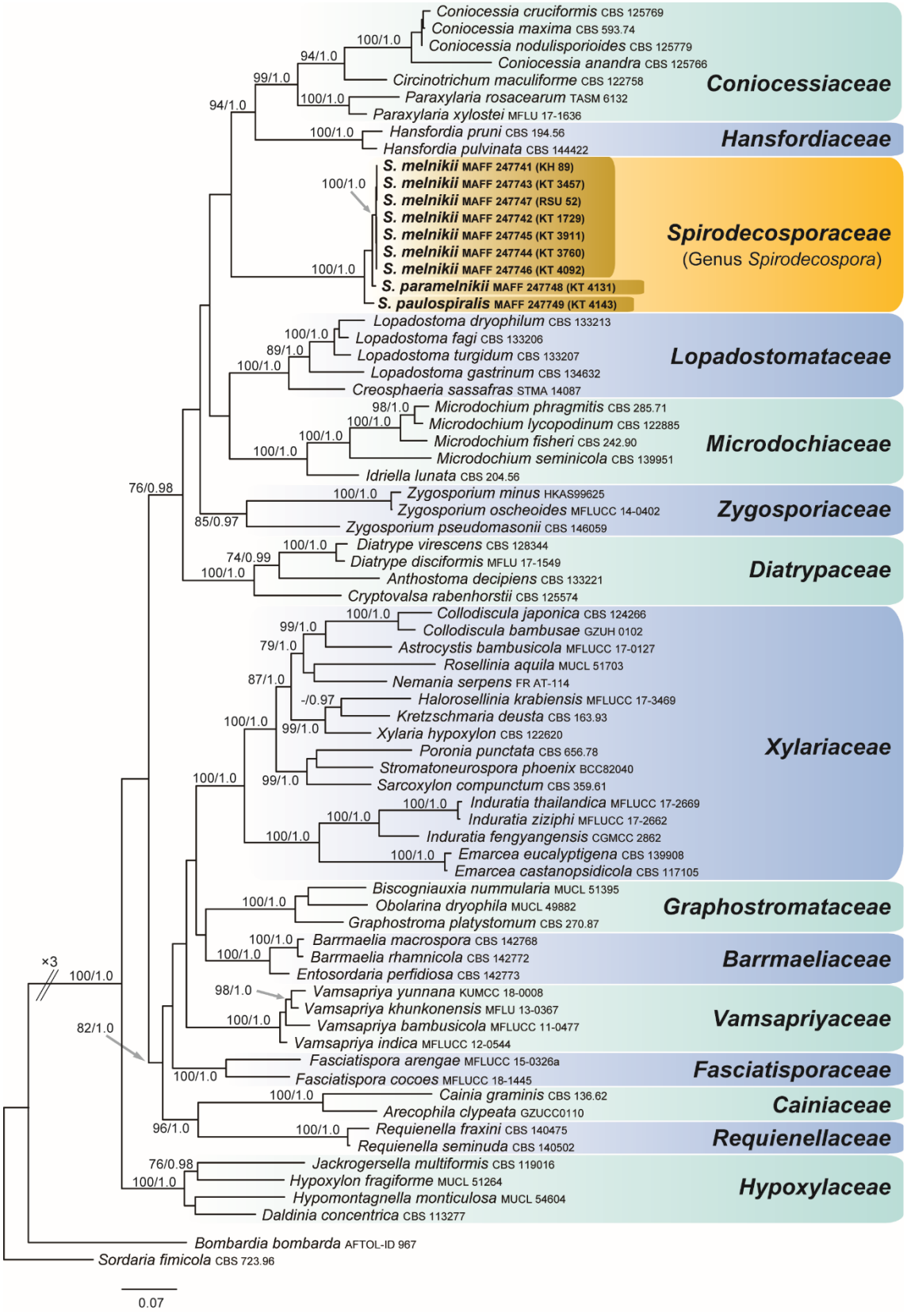

Coniocessia cruciformis CBS 125769
Coniocessia maxima CBS 593.74
Coniocessia nodulisporioides CBS 125779
Coniocessia anandra CBS 125766
Circinotrichum maculiforme CBS 122758
Paraxylaria rosacearum TASM 6132
Paraxylaria xylostei MFLU 17-1636
Coniocessiaceae
Hansfordia pruni CBS 194.56
Hansfordia pulvinata CBS 144422
Hansfordiaceae
S. melnikii MAFF 247741 (KH 89)
S. melnikii MAFF 247743 (KT 3457)
S. melnikii MAFF 247747 (RSU 52)
S. melnikii MAFF 247742 (KT 1729)
S. melnikii MAFF 247745 (KT 3911)
S. melnikii MAFF 247744 (KT 3760)
S. melnikii MAFF 247746 (KT 4092)
S. paramelnikii MAFF 247748 (KT 4131)
S. paulospiralis MAFF 247749 (KT 4143)
Spirodecosporaceae
(Genus Spirodecospora)
Lopadostoma dryophilum CBS 133213
Lopadostoma fagi CBS 133206
Lopadostoma turgidum CBS 133207
Lopadostoma gastrinum CBS 134632
Creosphaeria sassafras STMA 14087
Lopadostomataceae
Microdochium phragmitis CBS 285.71
Microdochium lycopodinum CBS 122885
Microdochium fisheri CBS 242.90
Microdochium seminicola CBS 139951
Idriella lunata CBS 204.56
Microdochiaceae
Zygosporium minus HKAS99625
Zygosporium oscheoides MFLUCC 14-0402
Zygosporium pseudomasonii CBS 146059
Zygosporiaceae
Diatrype virescens CBS 128344
Diatrype disciformis MFLU 17-1549
Anthostoma decipiens CBS 133221
Cryptovalsa rabenhorstii CBS 125574
Diatrypaceae
Collodiscula japonica CBS 124266
Collodiscula bambusae GZUH 0102
Astrocystis bambusicola MFLUCC 17-0127
Rosellinia aquila MUCL 51703
Nemania serpens FR AT-114
Halorosellinia krabiensis MFLUCC 17-3469
Kretzschmaria deusta CBS 163.93
Xylaria hypoxylon CBS 122620
Poronia punctata CBS 656.78
Stromatoneurospora phoenix BCC82040
Sarcoxylon compunctum CBS 359.61
Induratia thailandica MFLUCC 17-2669
Induratia ziziphi MFLUCC 17-2662
Induratia fengyangensis CGMCC 2862
Emarcea eucalyptigena CBS 139908
Emarcea castanopsidicola CBS 117105
Xylariaceae
Biscogniauxia nummularia MUCL 51395
Obolarina dryophila MUCL 49882
Graphostroma platystomum CBS 270.87
Graphostromataceae
Barrmaelia macrospora CBS 142768
Barrmaelia rhamnicola CBS 142772
Entosordaria perfidiosa CBS 142773
Barrmaeliaceae
Vamsapriya yunnana KUMCC 18-0008
Vamsapriya khunkonensis MFLU 13-0367
Vamsapriya bambusicola MFLUCC 11-0477
Vamsapriya indica MFLUCC 12-0544
Vamsapriyaceae
Fasciatispora arengae MFLUCC 15-0326a
Fasciatispora cocoes MFLUCC 18-1445
Fasciatisporaceae
Cainia graminis CBS 136.62
Arecophila clypeata GZUCC0110
Cainiaceae
Requienella fraxini CBS 140475
Requienella seminuda CBS 140502
Requienellaceae
Jackrogersella multiformis CBS 119016
Hypoxylon fragiforme MUCL 51264
Hypomontagnella monticulosa MUCL 54604
Daldinia concentrica CBS 113277
Hypoxylaceae
Bombardia bombarda AFTOL-ID 967
Sordaria fimicola CBS 723.96
0.07

Fig. 7 Maximum-likelihood tree of Xylariales based on combined ITS, LSU and RPB2 sequence. ML bootstrap support (MLBS) higher than 70 % and Bayesian posterior probabilities (PP) above 0.95 are presented at the nodes as MLBS/Bayesian 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 nucleotide substitutions per site.

Notes. Spirodecosporaceae is distinguished from Coniocessiaceae and Hansfordiaceae by its morphological differences and/or phylogenetic relationships. The asci of Coniocessiaceae clearly differ from those of Spirodecosporaceae in having a non-amyloid or amyloid, V-shaped to sinuous, apical ring (Asgari and 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 and Voglmayr 2012, Wittstein et al. 2020, Pi et al. 2021, Samarakoon et al. 2022). In contrast, that of Spirodecosporaceae is more compact, flattened, and wedge-shaped (Lu et al. 1998; Figs. 8O, 9M, 10L in this study).

***Spirodecospora* B.S. Lu, K.D. Hyde & W.H. Ho, Fungal Diversity Res. Ser. 1: 170. 1998.**

Type species. *Spirodecospora bambusicola* B.S. Lu, K.D. Hyde & W.H. Ho.

Notes. *Spirodecospora bambusicola* (Lu et al. 1998) was considered a synonym of *S. melnikii* (= *Anthostomella melnikii*; Vasilyeva 1990) by Mel'nik and 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 Divers. 12: 152. 2003.** Figs. 8, 11A–G.

Basionym. *Anthostomella melnikii* Lar. N. Vassiljeva, Mikol. Fitopatol. 24: 209. 1990.

Sexual morph. 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.

Asexual morph. Not observed.

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 August 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 1150 m), on dead twigs of *Sasa* sp., 5 July 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 June 2004, T. Shirouzu, KT 1729 (HHUF 30652), living culture MAFF 247742; Kouchi, Takaoka, near Tengu plateau, on dead twigs of *Sasa* sp., 16 March 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 February 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 March 2018, K. Tanaka, K. Arayama & R. Sugita, KT 3911 (HHUF 30655), living culture MAFF 247745.


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Fig. 8. ***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.

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 MB846056. Figs. 9, 11H.

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

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

Sexual morph. 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.

Asexual morph. Not observed.

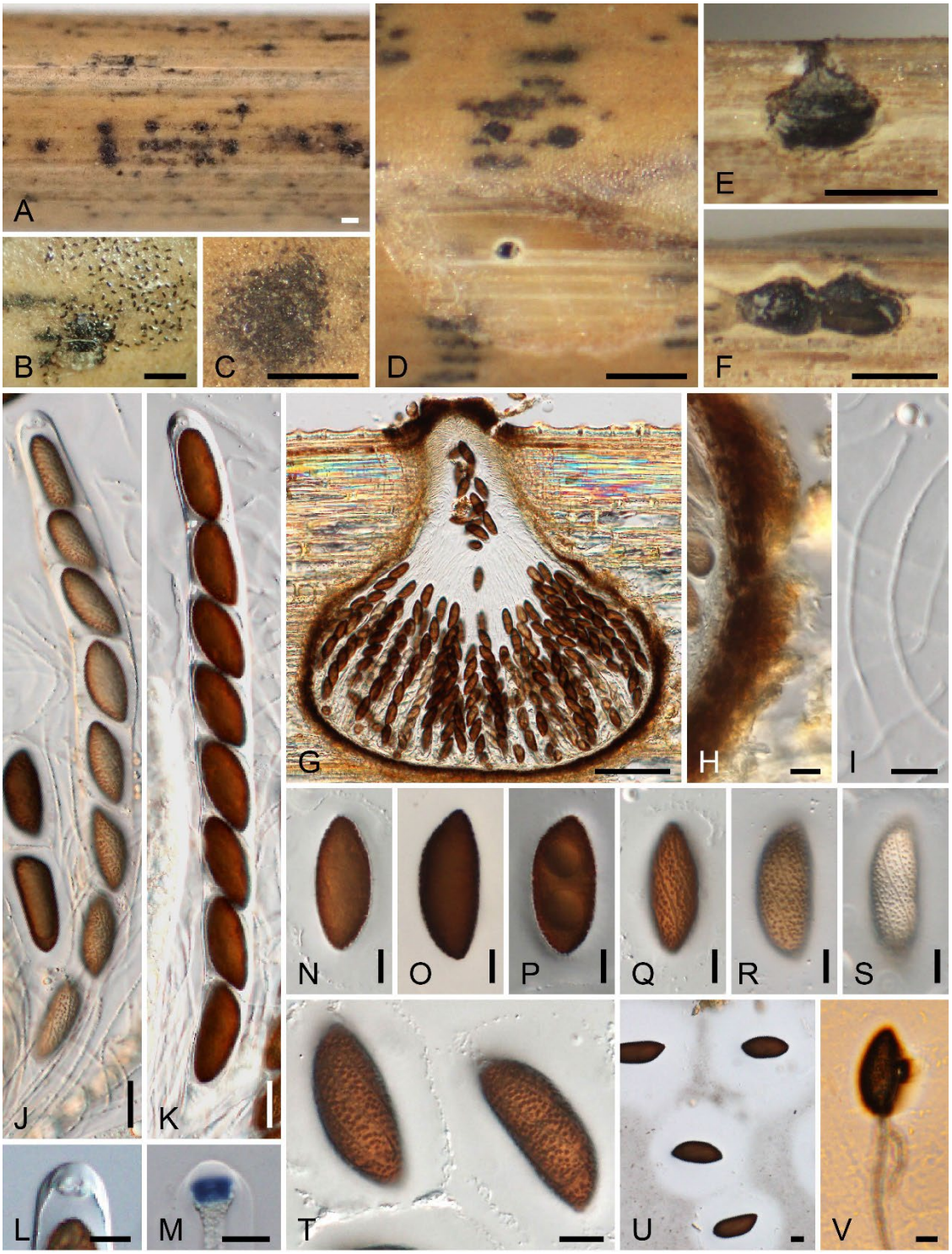

Fig. 8. ***Spirodecospora paramelnikii*** (KT 4131 = HUFF 30658, holotype) **A–D.** Ascomata in face view (D. Transverse section) **E–G.** Longitudinal section of acomata **H.** Acomatal wall in section (**G, H** in diluted lactophenol cotton blue) **I.** Paraphyses **J, K.** Asci **L, M.** Apex of asci (**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.

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.

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 MB846057. Figs. 10, 11I.

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

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

Sexual morph. 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.

Asexual morph. Not observed.

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.

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 %).

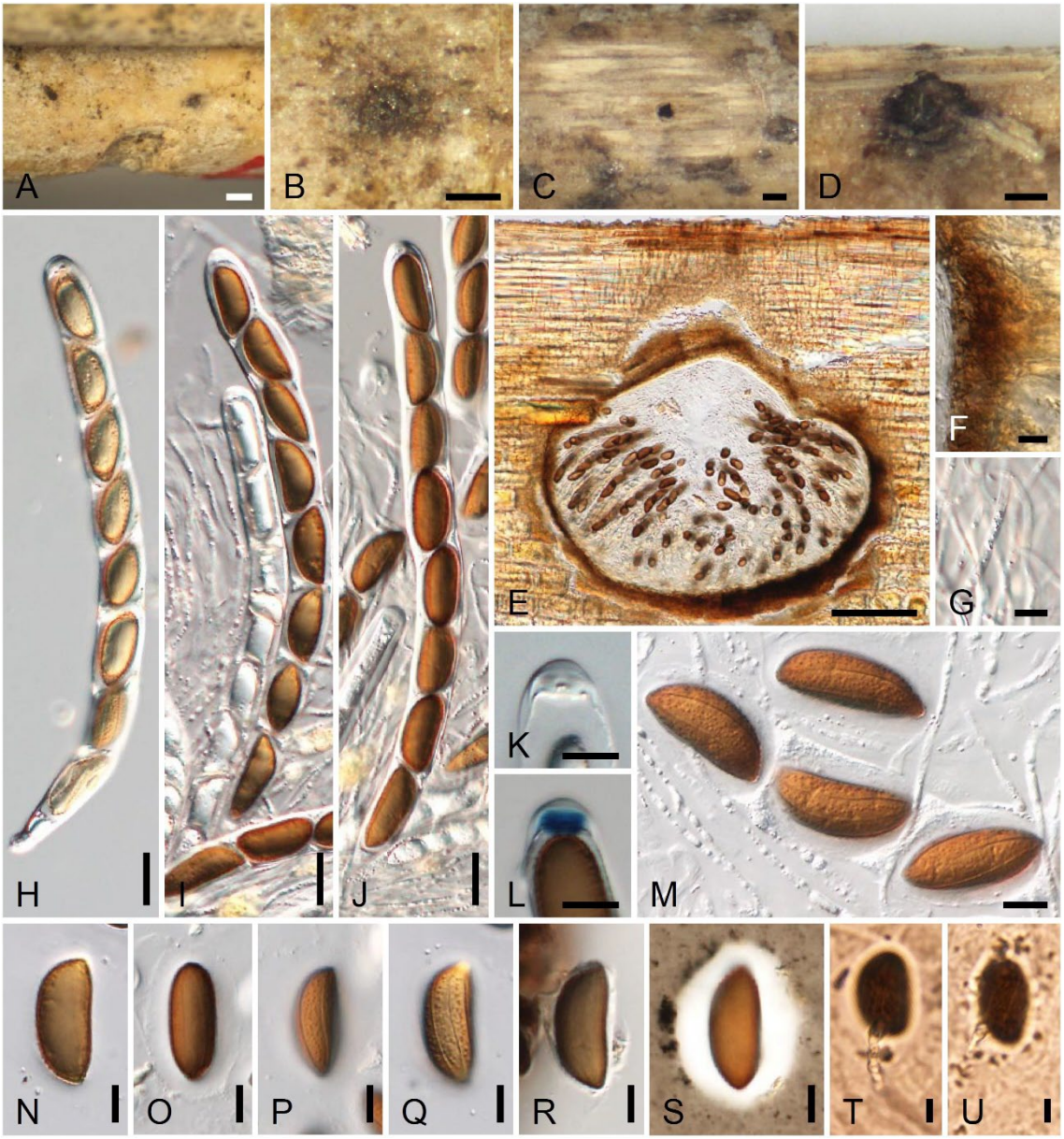

Fig. 10. ***Spirodecospora paulospiralis*** (**A–Q, S–U.** KT 4143 = HUFF 30659, holotype; **R.** culture KT 4143 = MAFF 247749, ex-holotype) **A–C.** Ascomata in face view (**C.** Transverse section) **D, E.** Longitudinal section of ascomata **F.** Ascomatal wall in section (**E, F** in diluted lactophenol 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.

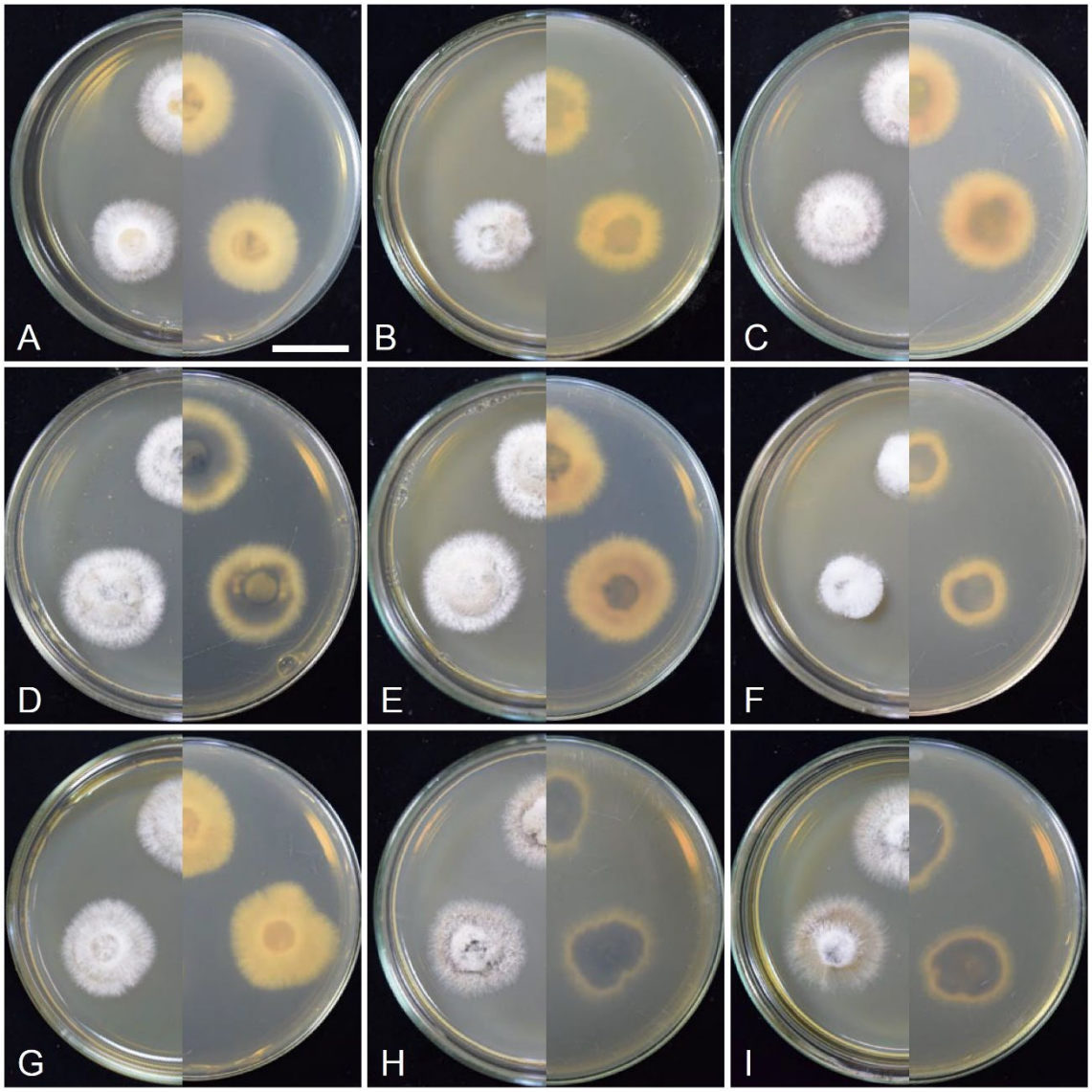

Fig. 11. Colony characters of *Spirodecospora* species on PDA at 25 °C in the dark after one week. **A–G.** *S. melnikii* (**A.** KT 1729 = MAFF 247742 **B.** KT 3457 = MAFF 247743 **C.** KT 3760 = MAFF 247744 **D.** KT 3911 = MAFF 247745 **E.** KT 4092 = MAFF 247746 **F.** KH 89 = MAFF 247741 **G.** RSU 52 = MAFF 247747) **H.** *S. paramelnikii* (KT 4131 = MAFF 247748) **I.** *S. paulospiralis* (KT 4143 = MAFF 247749). Scale bar = 2 cm.

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 and Crawford 1973). Molecular data in our study also support the exclusion of *Spirodecospora* from Xylariaceae (Fig. 7). 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. 7).

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 and 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. 8X–AB, 10T). 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.

4. 総合考察

有性世代と無性世代の形態的調査と分子系統解析

菌類の科および属を正確に規定するためには、「有性世代の形態情報」、「無性世代の形態情報」、および「DNA 塩基配列に基づく分子系統学的情報」の 3 つの要素を全て組み合わせることが重要である。多くの場合は、分子系統情報を含めたどちらか一方の世代の形態を用いても、科や属の推定は可能である。例えば、本論文の 3 節で扱った *Spirodecospora* 属は無性世代が観察されておらず、有性世代の大まかな形態的類似性を根拠にクロサイワイタケ科 (フンタマカビ綱、クロサイワイタケ目) に所属すると考えられていた。しかし、本研究で新しく DNA 塩基配列を取得することで、その正確な科の所属 (新科 Spirodecospora 科) を明らかにすることができた (Sugita et al. 2022)。*Fasciatispora* 属も同様に、有性世代の子のうの構造の類似性からクロサイワイタケ科に所属すると推定されたが (Hyde and Wong 1999)、分子系統解析に基づき、Fasciatispora 科に所属すると示された (Hyde et al. 2020)。一方で、無性世代のみが知られている *Spegazzinia* 属は、分生子形成様式の類似性をもとに Apiospora 科 (フンタマカビ綱、クロサイワイタケ目) に所属するとされていたが (Hyde et al. 1998)、DNA 塩基配列を取得したことで、Didymosphaeria 科 (クロイボタケ綱、Pleospora 目) に所属することが示された (Tanaka et al. 2015)。しかし、中には分子情報とどちらか一方の世代を把握していても、正確に科や属を規定できない場合がある。例えば、本論文の 2 節で扱った *Thyridium* 属と *Phialemoniopsis* 属である (Sugita and Tanaka 2022)。植物に腐生的または半活物栄養的に生じる *Thyridium* 属 (Thyridium 科) は、主に有性世代の形態をもとに規定されてきた属であり (Eriksson and Yue 1989, Taylor et al. 1997, Checa et al. 2013)、基準種 *T. vestitum* が配列決定されていた。一方で、ヒトの体の一部から報告されている *Phialemoniopsis* 属 (本研究以前は Phialemoniopsis 科) は無性世代のみが知られていた属であり (Perdomo et al. 2013)、所属する 7 種全てで配列情報が得られていた。これらは従前から個別の属として認識されていたが、本研究で、子のう胞子由来の *Thyridium* 属菌の培養下で形成した無性世代の形態が、*Phialemoniopsis* 属の無性世代形態と同一のものであるということから、同属であると結論付けた。このように、例え、分子情報とどちらか片方の世代の形態が明らかになっていても、科や属の把握が困難である場合がある。本研究では、DNA 塩基配列に基づく分子系統情報に加えて、有性世代と無性世代の両方に基づくことで、詳細な科や属の規定が可能となることを明らかにした。

タケ類を宿主とする菌類の系統的独立性と宿主特異性

タケ類由来菌類は、他の植物由来の既知の菌類群と形態的に類似していても、分子系統学的に科や属レベルで独立する傾向が知られていた (Tanaka et al. 2009)。本論文 3 節の研究においても、*Spirodecospora* 属のメンバーは、全てタケ類から採集されたものであり、形態的に類似すると考えられていたクロサイワイタケ科とは科レベルで大きく異なる系統であった (Sugita et al. 2022)。Pleospora 目において、Tetraplosphaeria 科 (Tanaka et al. 2009)、Bambusicola 科 (Dai et al. 2012, Hyde et al. 2013)、Roussoella 科 (Liu et al. 2014)、Occultibambusa 科 (Dai et al. 2017) は、タケ類を宿主とする属で構成される科である。このような菌類は、明らかにタケ類を好んで宿主としており、タケ類上で他の植物を宿主とする菌類から独立して進化してきたことと考えられる。

また、タケ類を宿主とする菌類の中には、特定の属に対して宿主特異的に生じる種が存在すると考えられる。以前までは、タケ類を宿主とする多くの菌類は腐生的であると考えられていた。Zhou and Hyde (2001) は、植物内生菌と植物腐生菌が宿主特異性を持つという根拠には、十分な説得力がないと述べた。Hyde et al. (2002) は、タケ類の稈に発生する菌類はほとんどが病原性ではなく、そのために宿主特異的ではないとした。しかしながら、タケ類に発生する菌類のいくつかは、宿主となるタケ類の属レベルやそれ以上の分類ランクレベルに対して、宿主特異的であると考えられる。*Dinemasporium* 属、*Neopseudolachnella* 属、*Pseudolachnella* 属などの *Dinemasporium* 型の属の種は、少なくとも宿主となるタケ類の属レベルにおいて、比較的異なる宿主特異性を持っているようであった (Hashimoto et al. 2015a, b)。本論文 3 節においても、*Spirodecospora* 属内において、ササ属由来の種とメダケ属由来の種は系統的に異なることから、タケ類の属が異なれば付随する菌類種も異なることを示唆した (Sugita et al. 2022)。このようなタケ類に生じる菌類のいくつかは、単純な腐生菌ではなく、宿主のタケ類が生きている状態のときに、内生的に組織内に侵入し、宿主が弱体化または死んだときに、宿主上で胞子形成を行っている可能性がある (半腐生的)。このような場合、一般的な腐生菌と異なり、内生的なステージの時に菌類は宿主のタケ類に対して特異的であると考えられる。Kuo et al. (2014) は、宿主となる植物に対する菌類の内生性、病原性、腐生性は動的であり、バランスの取れた相互関係を持っていることを示した。この研究によれば、菌類が植物組織に内生している時に、相互関係のバランスが崩れたり、宿主が死んだりすると、病原性または腐生性を発揮する。クロサイワイタケ科に所属する *Linosporopsis* 属は、宿主の生きた葉に内生菌として存在し (非寄生的)、落葉したのちに葉上に子実体を形成することが報告された (Voglmayr and Beenken 2020)。Morakotkarn et al. (2009) が示したように、タケ類には 3 綱 11 目にまたがる多くの内生

菌が存在している。これらの菌類のいくつかは、タケ類に対して特異的かつ半腐生的である可能性が考えられる。

今後、1) タケ類から発見された菌類の科や属を検討する場合、例え他の植物に見られる既知の菌類と形態的に類似していても大きく系統が異なる可能性があるため、既知の菌類系統と分子系統学的に詳細な比較をする必要がある。そして、2) タケ類を宿主とする菌類を同定する場合、単純な腐生菌と見なすのではなく、宿主特異性を持つ可能性を考慮し、注意深く種同定を行う必要がある。さらに、3) タケ類の様々な属に渡って報告されている既知種についても (例えば *Anthostomella rehmii* はマダケ属 (*Phyllostachys*) とササ属 (*Sasa*) から、*A. flagellariae* はメダケ属 (*Pleioblastus*)、ホウライチク属 (*Bambusa*)、*Dendrocalamus* 属、マダケ属 (*Phyllostachys*) から報告; Lu and Hyde 2000)、種内に複数の種が存在する可能性を、分子系統学的に再検討する必要があると考えられる。

5. 摘要

フンタマカビ綱において目の所属が不明であった *Thyridium* 科を収容するために、新目 *Thyridium* 目を設立した。ヒトの体の一部から報告されていた医学的に重要な *Phialemoniopsis* 属は、分子系統解析および無性世代の形態的類似性を根拠に、様々な植物に腐生的または半活物栄養的に発生する *Thyridium* 属の異名とした。これにより、*Thyiridum* 属の無性世代について属概念を拡大し、従前 *Phialemoniopsis* 属と記載されていた 7 種を *Thyridium* 属に転属した。日本のタケ類を宿主とする菌類 *Pleospora punctulata* についてエピタイプ指定を行い、形態的類似性および分子系統学的根拠をもとに *Thyridium* 属に移した。モウソウチク (*Phyllostachys pubescens*) から新種 *T. flavostromatum* を記載した。

今まで形態的特徴にのみ基づいて規定されてきた *Spirodecospora* 属について、DNA 塩基配列を初めて取得した。形態的差異および分子系統解析により、*Spirodecospora* 属を収容するクロサイワイタケ目の新科 Spirodecospora 科を設立した。同種とされていた *S. bambusicola* と *S. melnikii* を、子のうと子のう胞子の形態的差異および宿主の違いから別種と見なし、また、2 新種 *S. paramelnikii* と *S. paulospiralis* を記載したことで、*Spirodecospora* 属内に計 4 種を認識した。これら 4 種を同定するために重要な形態を示した、種の検索表を提供した。

本研究を通して、フンタマカビ綱における新規分類群として、1 新目 (Thyridium 目)、1 新科 (Spirodecospora 科) を設立することで、高次レベルでの分類体系の構築に寄与した。さらに、3 新種 (*S. paramelnikii*、*S. paulospiralis*、*T. flavostromatum*)、8 新組み合わせ (*T. pluriloculosum*、*T. punctulatum*、*T. cornearis*、*T. curvatum*、*T. endophyticum*、*T. hongkongense*、*T. limonesiae*、*T. oculorum*) を提唱し、日本産フンタマカビ綱菌類の多様性の一端を明らかにした。

6. 謝辞

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