RESEARCH ARTICLE

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Taxonomic Re-Evaluation of the Genus Fuscoporia in the Republic of Korea Including Three Unrecorded Species

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ABSTRACT

The genus Fuscoporia (Hymenochaetaceae, Basidiomycota) comprises poroid white-rot fungi characterized by dark brown hymenial setae, a dimitic hyphal system, and encrusted generative hyphae. Despite the ecological and commercial significance of Fuscoporia species, their identification has been challenging owing to their morphological overlap with other genera of Hymenochaetaceae and to the limited resolution of nuclear ribosomal DNA markers. With the advances in molecular research, Fuscoporia has been revised to include species from Inonotus sensu lato and Phellinus sensu lato, and 71 new species have been reported over the past decade. In Korea, a comprehensive taxonomic study elucidating the true diversity of Fuscoporia is yet to be conducted. Among the 11 Fuscoporia species reported in Korea, two were identified solely based on morphological characteristics, and four were identified based on nuclear ribosomal DNA regions, which have limited resolution for species identification in Fuscoporia. To investigate the current status of Fuscoporia species native to Korea, we conducted a phylogenetic study using four genetic markers (ITS + nrLSU + RPB2 + TEF1), along with morphological characteristics, and re-analyzed the GenBank records deposited from Korea. Ten Fuscoporia species were identified, including three previously unrecorded species. A detailed description of the unrecorded species and a list of proposed Korean names for all Fuscoporia species in Korea are provided. This study will guide further taxonomic and applied research of Fuscoporia by providing a species identification key and a verified multigenetic database, in addition to confirming the sequences in public database.

ARTICLE HISTORY

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KEYWORDS

Basidiomycota; Hymenochaetaceae: Phellinus; taxonomy; wood decaying fungi

1. Introduction

The genus Fuscoporia Murrill in the family Hymenochaetaceae (Hymenochaetales, Basidiomycota) comprises yellowish-to-rusty poroid fungal species that cause white rot. They play essential roles in the forest ecosystem, acting as wood decomposers or parasites on diverse angiosperm and gymnosperm species [1,2]. Some Fuscoporia species, such as F. gilva (Schwein.) T. Wagner & M. Fisch and rhabarbarina (Berk.) Groposo, Log.-Leite & *F*. Góes-Neto, have commercial value for their known antibacterial, antiviral, and antioxidant properties [3-6].

Fuscoporia, typified by Fuscoporia ferruginosa (Schrader) Murrill, was first proposed by Murrill in 1907 and later defined by morphological characteristics such as resupinate to pileate basidiomes, smooth, thin-basidiospores, dimitic hyphal system with stellate crystals at the end of the generative hyphae, and presence of brownish setae [7]. However, owing to its morphological similarity to the other genera of Hymenochaetaceae, it was not widely accepted as an

independent genus and was instead considered synonymous with Phellinus. Fuscoporia became widely accepted only when Wagner and Fischer [8] reported the molecular phylogeny of Hymenochaetales based on nuclear large subunit (nrLSU) sequences, revising several genera and transferring many species to Fuscoporia. Subsequently, new Fuscoporia species have been reported worldwide based on multigenetic phylogeny [9-15].

In the Republic of Korea, Fuscoporia species had been classified as Phellinus until two species, namely F. ferrea (Pers.) G. Cunn. and F. senex (Nees & Mont.) Ghob.-Nejh., were reported as Fuscoporia based on internal transcribed spacer (ITS) + nrLSU sequences, and four species, namely F. contigua (Pers.) G. Cunn., F. ferruginosa, F. gilva, and F. viticola (Schwein.) Murrill, were transferred from Phellinus [16,17]. Subsequently, the following five new species were reported based on multigenetic phylogeny and detailed morphological observations: F. dolichoseta Y. Cho, D. Kim & Y. W. Lim,

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F. gilvoides Y. Cho, D. Kim & Y. W. Lim, *F. koreana* Y. Cho, D. Kim & Y. W. Lim, *F. reticulata* Y. Cho, D. Kim & Y. W. Lim, and *F. semicephala* Y. Cho, D. Kim & Y. W. Lim [18]. In summary, 11 *Fuscoporia* species have been reported in Korea. However, two *Fuscoporia* species, namely *F. contigua* and *F. viticola*, were identified based solely on the morphological descriptions of European or North American species without supporting molecular evidence. Furthermore, re-identification is necessary for the four *Fuscoporia* species previously identified through ITS + nrLSU: *F. ferrea*, *F. ferruginosa*, *F. gilva*, and *F. senex* [16,17], as recent studies have consistently reported the limited resolution of ribosomal DNA sequences within the genus *Fuscoporia* [9,18].

The main objective of the present study was to investigate the true diversity of Fuscoporia in Korea by applying the current taxonomic revisions. To achieve this, we conducted a phylogenetic analysis on unstudied Fuscoporia specimens and all GenBank sequences of Fuscoporia deposited from Korea using four genetic markers: ITS + nrLSU + RNA polymerase II subunit 2 gene (RPB2) + translation elongation factor 1 gene (TEF1). Our research shows that four of the 11 reported species are not phylogenetically verified to be present in Korea, while three unrecorded species are present, totaling 10 Fuscoporia species. We provide detailed morphological descriptions, sequences, a taxonomic key, and Korean names for all Fuscoporia species in Korea. This study contributes to the accurate identification of Fuscoporia species in Korea based on morphological and molecular analyses.

2. Materials and methods

2.1. Specimens studied

In total, 47 specimens were obtained from two fungaria in Korea: the Korea University Fungus Collection (KUC) and Seoul National University Fungus Collection (SFC) (Table S1). The specimens were collected from Korea between 2012 and 2023. Images and notes on the characteristics of fresh basidiomes were recorded in the collection field.

2.2. Molecular analysis

2.2.1. DNA extraction, PCR, and sequencing

Genomic DNA extraction was performed using $1 \times 1 \text{ cm}$ tissue samples from dried specimens with cetyltrimethylammonium bromide (CTAB) and the AccuPrep Genomic DNA Extraction Kit (Bioneer, Daejeon, South Korea) according to the manufacturer's instructions.

Polymerase chain reaction (PCR) was conducted on a C1000 thermal cycler (Bio-Rad, Hercules, CA) using a PCR Premix (Bioneer, Daejeon, South Korea). The ITS region was amplified using the primer sets ITS1F/ITS4B [19] with the following conditions: initial denaturation at 95°C for 5 min; 35 cycles of 95°C for 40s, 55°C for 40s, and 72°C for 60s; and a final extension at 72°C for 10min. The nrLSU region was amplified using the primer sets LR0R/LR7 [20] with the following conditions: initial denaturation at 95°C for 5 min; 35 cycles of 95°C for 40s, 55°C for 40s, and 72°C for 90s; and a final extension at 72°C for 10 min. For the protein-coding genes RPB2 and TEF1, the primer sets bRPB2-6F/ bRPB2-7.1R [21] and EF595F/EF1160R [22] were used for PCR, respectively. The PCR conditions for RPB2 were as follows: initial denaturation at 94°C for 2 min; 36 cycles of 94°C for 45s, 58°C for 45s, and 72°C for 60s; and a final extension at 72°C for 10 min. The PCR conditions for TEF1 were as follows: initial denaturation at 95 °C for 4 min; 35 cycles of 95°C for 30s, 55°C for 45s, and 72°C for 60s; and a final extension at 72°C for 10 min.

The PCR products were purified using the Expin[™] PCR Purification Kit (GeneAll Biotechnology, Seoul, South Korea) and sequenced using an ABI 3730XL machine (Applied Biosystems, Waltham, MA) at Bioneer (Daejeon, South Korea) using PCR primer sets. The forward and backward sequences of each specimen were assembled using Geneious Prime 2023.0.4 (https:// www.geneious.com). The final sequences have been deposited in GenBank (Table 1).

2.2.2. Phylogenetic analysis

In addition to the 59 newly acquired sequences, 76 Fuscoporia sequences deposited from Korea were obtained from GenBank. For the phylogenetic analysis, a dataset of four genetic markers (ITS+nrLSU+ RPB2+TEF1) was constructed, including 201 published or type-derived sequences of Fuscoporia [15,18,26]. Alignment, trimming, concatenation, model selection, and maximum-likelihood (ML) tree construction were performed using FunVIP ver. 0.3.23.1 (https://github. com/Changwanseo/FunVIP) with the "accurate" preset: alignment was performed by MAFFT ver. 7.453 [33] and tree construction was performed by RAxML 8.2.12 [34] with 1000 bootstrap replications. Three outgroup samples were used: Coniferiporia sulphurascens (FP-134848-SP), Coniferiporia weirii (FP-134801-SP), and Phellinidium asiaticum (Wei 5610) [31,32].

Subsequently, the newly acquired sequences and the GenBank sequences deposited from Korea were analyzed by a BLASTn search at the NCBI website against the nr/nt database (date accessed: August 10

Table 1. List of	Fuscoporia s	specimens	and	GenBank	accessions	used	in	the	stud	y
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			Acce					
Species	Specimens	ITS	nrLSU	RPB2	TEF1	Locality	Reference	Remarks
Fuscoporia	Dai_16892	MH050752	MH050766	MH079393	MN848822	China	[9]	ТҮРЕ
acutimarginata								
Fuscoporia ambigua	JV_0509/151	MN816707	MN809996	MN848792	MUCCCOR	USA	[23]	TYPE
Fuscoporia	JV_1309/13-J	KJ940023	MG008463		MH636385	USA	[24]	TYPE
Fuscoporia atlantica	SP 445618	KP058515	KP058517			Brazil	[25]	TYPE
, Fuscoporia	 Dai_15636	MG008397	MG008450	MH079402	MH636408	China	[9]	TYPE
australasica								
Fuscoporia	Dai_18879	MN816705	MN810015	MN848767	MN848850	Australia	[26]	ТҮРЕ
australiana Fuscoporia	Dai 16599	MN816711	MN809999		MN848808	Thailand	[26]	TYPF
bambusae	bul_10000					manana	[20]	
Fuscoporia	Cui_8692	MN816739	MT032486		MN848813	China	[26]	TYPE
bambusicola	0400400	011074045					[10]	T) (D.F.
Fuscoporia	OAB0132	ON8/6015				Benin	[13]	TYPE
Fuscoporia	Dai 17388	MN121765	MN121824			Brazil	[9]	
callimorpha	Dai_17389	MN121766	MN121825			Brazil	[9]	
Fuscoporia	JV_1908/74	MT676832	MT676833			French	[27]	TYPE
caymanensis						Guiana		
Fuscoporia	JV_1607/93	MG008444	MG008460		MH636389	Costa Rica	[24]	TYPE
centroamericana Fuscoporia chinensis	Dai 15713	MN816721	MN810008	MN848771	MN848846	China	[26]	TVPF
Fuscoporia chrvsea	JV 1607/106-J	MN816736	MN810027	MN848773	MN848818	Costa Rica	[20]	
Fuscoporia contigua	Dai_16025	MG008401	MG008454	MH079406	MH636386	USA	[24]	
Fuscoporia	JV_1407/92	MG008446	MG008461		MH636400	Costa Rica	[24]	TYPE
costaricana	Wa: 4047		110220524			China	[20]	
Fuscoporia aiscipes Fuscoporia	SFC20140723-58	ON427788*	HQ328524 ON427816*	ON479797*	ON479820*	Korea	[20] [18]	
dolichoseta	SFC20161006-16	ON427789*	ON427817*	ON479798*	ON479821*	Korea	[18]	
	SFC20190731-26	ON427790*	ON427818*	ON479799*		Korea	[18]	
	SFC20191015-23	ON427765*	ON427795*	ON464731*	0000000	Korea	[18]	TYPE
	SFC20230516-01 KUC20121123-07	OR/24641* K 1668545*	OR976466* OR976469*	OR727960*	OR/2/969*	Korea Korea	This study	
Fuscoporia eucalypti	Dai_18792	MN816731	MN810022	MN848778	MN848831	Australia	[26]	TYPE
Fuscoporia ferrea	Cui_11801	KX961101	KY189101	MN159387	MN848823	China	[26]	
	FP-133592-Sp	KU139189	KU139259	KU139319	KU139379	USA	[28]	-
	MUCL_45984	KX961112	KY189112		MH636403	France	[26]	lype
	SEC20150211-02	ON427768*	ON427797*	ON479779*	ON479805*	Korea	This study	locality
	SFC20150522-09	ON427769*	ON427798*	ON479780*		Korea	This study	
	SFC20190322-16	ON427770*	ON427799*	ON479781*	ON479806*	Korea	This study	
	SFC20190731-43	ON427771*	ON427800*	ON479782*	ON479807*	Korea	This study	
Fuscoporia	Dai 13200	MN816702	MN809993	MN848793	MN848802	France	[17]	
ferruginosa	JV_1309/4	KX961102	KY189102	MH079405	MH636398	Slovakia	[26]	
Fuscoporia gilva	CMW47749	MH599106	MH599129		MT108963	South Africa	[29]	
	CMW48145	MH599105	MH599130		MT108962	South Africa	[29]	T
	JV_0/09/75	MIN816720	MIN810007		MIN848852	USA	[26]	Type locality
	JV 1209/65	MN816719	MN810006	MN848768	MN848851	USA	[26]	
								locality
	ASIS24343	KF692068*				Uncertain	Unpublished,	
	65620450302.22	01407700*		01470702*	01470045*	K	Seok et al.	
Fuscoporia gilvoides	SFC20150702-23	ON427784*	ON/107810*	ON4/9/93*	ON479815*	Korea	[18]	
	SFC20160629-33	ON427785*	ON427813*	ON479795*	ON479817*	Korea	[18]	
	SFC20180426-12	ON427763*	ON427793*	ON464729*	ON479802*	Korea	[18]	TYPE
	SFC20180905-15	ON427786*	ON427814*	ON479796*	ON479818*	Korea	[18]	
	SFC20230613-05	OR724642*	OR976467*	OR727962*	OR727967*	Korea	This study	
	KMCC04881	MN823149*	01970408	OR/2/903	OR/2/908	Uncertain	Unpublished,	
							Han	
	OK552	MN080324*				Uncertain	Unpublished,	
- ·	D 1 4 4 4 0 5		0.1150.0000		0.1444540		An et al.	-
ruscoporia bainanonsis	Dal_16105		UN520809		UN616518	China	[10]	IYPE
Fuscoporia insolita	Spirin 5208	MN816724	MN810016		MN848800	Russia	[26]	TYPE
	Spirin_5251	KJ677113				Russia	[30]	
	KUC20121102-22	OR724636*	OR976461*			Korea	This study	
Fuscoporia	Dai_11403	MN816717	MN810003	MN848795	MN848807	China	[26]	TYPE
karsteniana	Udi_13/1/	VIIV010/18	10111010004		1111048805	China	[20]	

Table 1. Continued.

			Acce	ession				
Species	Specimens	ITS	nrLSU	RPB2	TEF1	Locality	Reference	Remarks
Fuscoporia koreana	SFC20150625-05	ON427776*	ON427805*	ON479787*	ON479810*	Korea	[18]	
	SFC20150625-07	ON427777*	ON427806*	ON479788*	ON479811*	Korea	[18]	
	SFC20160726-93	ON427762*	ON427792*	ON464728*	ON479801*	Korea	[18]	TYPE
	SFC20171019-11	ON427778*	ON427807*	ON479789*	ON479812*	Korea	[18]	
	SFC20180725-17	ON427779*	ON427808*	ON479790*	ON479813*	Korea	[18]	
	SFC20220913-11	OR724640*	OR976465*	OR995755*	OR727966*	Korea	This study	
	KUC20121123-27	KJ668544*	KJ668397*			Korea	[17]	
	PG	PP065751*				Uncertain	Unpublished,	
							Kim et al.	
Fuscoporia latispora	JV_0610/VIIK1	MG008436	MG008469		MH636396	Mexico	[24]	TYPE
Fuscoporia	Dai_11860	MG008406	MG008457		MH636390	China	[24]	TYPE
monticola								
Fuscoporia palomari	JV_1004/5-J	MN816737				USA	[26]	TYPE
Fuscoporia	Dai_18858	MN816712	MN810010	MN848769	MN848843	Australia	[26]	TYPE
plumeriae	CL 111/ 100 10					6 J 46	[0.0]	
Fuscoporia	CMW48060	MH599103	MH599126		MT108961	South Africa	[29]	TUDE
pulviniformis	CMW48600	MH599102	MH599127		MT108960	South Africa	[29]	TYPE
Fuscoporia	Dai_17443	MH050755	MH050764			Brazil	[9]	
punctatiformis	Da: 15722	MU050740		MU070200	MN040024	China	[26]	TVDE
Fuscoporia	Dai_15/23			MH079398	MIN848824	China	[20]	TTPE
ταπιμιζοία	Dal_10155			MHU/9399		China	[20] This study	
	SFC20100510-07	ON427772*	ON427801*	ON479783"	ON479808"	Korea	This study	
Europaria	SEC20170324-13	ON427766*	01427802	UN4/9/04"	01479009	Korea	[10]	
raticulata	SEC20121010-19	ON427761*	ON/27701*	ON464727*	ON/70800*	Korea	[10]	TVDE
Fuscoporia	Dai 16226	MN816743	MN810035	MN848784	MN848838	China	[76]	11rL
rhaharharina	Dai_10220	MN816744	MN810035	MN848785	MN848836	China	[20]	
Fuscoporia	IV 1407/84	MN816740	MN810030	MN848774	MN848819	Costa Rica	[26]	Type
roseocinerea	<u>JU_1107/01</u>		1111010050				[20]	locality
Fuscoporia rufitincta	IV 0904/142	K 1940030	KX058574			USA	[24]	Type
		107 10000	101000071			0011	[= -]	locality
Fuscoporia sarcites	JV 0402/20-K	MZ264225	MZ264218			Venezuela	[15]	
Fuscoporia	SFC20170524-08	ON427764*	ON427794*	ON464730*	ON479803*	Korea	[18]	TYPE
semicephala	SFC20170712-20	ON427787*	ON427815*		ON479819*	Korea	[18]	
Fuscoporia senex	Dai 15775	MN816746	MN810038	MN848787	MN848834	China	[26]	
,	 Dai17043	MN816747	MN810039	MN848786	MN848835	China	[26]	
		ON427774*	ON427803*	ON479785*	OR995756*	Korea	This study	
	SFC20150908-49	ON427775*	ON427804*	ON479786*	OR995757*	Korea	This study	
	KUC20110922-13	JX463658*	JX463652*			Korea	[17]	
Fuscoporia septiseta	Dai_12820	MG008405	MN810033		MH636394	USA	[26]	TYPE
Fuscoporia setifera	Dai_15706	MH050759	MH050769	MN159391	MN848842	China	[26]	
	Dai_15710	MH050758	MH050767	MN159390	MN848841	China	[26]	
	KUC20140509-06	OR724637*	OR976462*		OR727964*	Korea	This study	
	KUC20140613-42	OR724638*	OR976463*			Korea	This study	
	KUC20191011-06B	OR724639*	OR976464*		OR727965*	Korea	This study	
Fuscoporia shoreae	Dai_17818	MN816735	MN810026		MN848816	Singapore	[26]	TYPE
Fuscoporia sinica	Dai_15468	MG008412	MG008459		MH636392	China	[24]	TYPE
Fuscoporia sinuosa	Dai_20499	MZ264227	MZ264220			China	[15]	TYPE
Fuscoporia	Dai_16201	MN816708	MN809997	MN848796	MN848811	China	[26]	TYPE
subchrysea	D 1 4 4 9 9 4	10/0 / 1 0 07	10/0 50 / 70				10.01	
Fuscoporia	Dai_16326	KX961097	KY0534/2	MH0/9400	MN848826	China	[26]	T) (0.5
subferrea	Dai_16327	KX961098	KY0534/3	MH0/9401		China	[9]	TYPE
Fuscoporia	Dai_19655	MZ264228	MZ264221			Sri Lanka	[15]	TYPE
submurina	Dai_19656	MZ264230	MZ264223	11040700	MUCOCAOC	Sri Lanka	[15]	
Fuscoporia toruiosa	JV_1312/19-KOUT	KX961107	KY 189107	MIN848780	MH636406	Spain	[26]	
	JV_1405/2	KX961106	KY 189106	MIN848779	MH636405	Czech	[26]	
Fuscanaria viticala	Ha 2122	MN1016775	MN010017			Republic	[26]	
Fuscoporia vilicola	THE_2125	MNI916727	MC009462			USA	[20]	
ruscoporia	JV_1312/20-ROUL	1010727	MG006462			Spain	[20]	
wanibergii	Cui: 0100	MUDEDZEC	MN010020	MNI040700		China	[0]	Turne
ruscoporid	Cul_0102	סכ/טכטחואו	1111010029	1111046/89		Clilla	[2]	locality
Phellinidium	Wei 5610	KB350571	KC850177			China	[31]	Outgroup
asiaticum	Wei_3010	Ινεοεαν	10039422			Child	[31]	ourgroup
Coniferinoria	FP-134848-SP	MT420687	MT416462		MT470375		[32]	Outaroup
sulnhurascens	JF UTU JF	11172000/			105/5	0.511	[32]	ourgioup
Coniferinoria weirii	FP-134801-SP	MT420698	MT416467	MT386029	MT470382	USA	[32]	Outaroup
conneripona wenn							[J=]	Sargioup

Sequences obtained in this study are indicated with bold. Sequences submitted from Korea are indicated with asterisks (*), while some of their localities are uncertain. 2023), and ML trees were constructed based on two additional combinations (ITS and ITS + nrLSU) to confirm their identity and assess the accuracy of each method.

2.3. Morphological observation

Macroscopic characteristics such as color, length, width, and thickness of the pileus, context, and hymenophore were observed with the naked eye. The size of the pores and the margin of the hymenophore were observed using a Nikon SMZ1500 stereomicroscope (Nikon, Tokyo, Japan).

For the microscopic analysis, dried tissue from each specimen was sectioned and mounted in a drop of 5% KOH. The features of the hyphae, basidia, cystidia, basidiospores, and setae were observed under a Nikon 80i compound light microscope (Nikon, Tokyo, Japan) at ×400 magnification. A minimum of 20 elements were measured for each feature. For basidiospores, 5% of the extreme length and width values are provided in parentheses. "L", "W", and "Q" refer to the length, width, and length/width ratio of the basidiospores, respectively; "x/y" refers to the number of elements measured (x) and the number of specimens (y); "CB-" refers to acyanophilous in cotton blue; and "IKI-" refers to neither amyloid nor dextrinoid in Melzer's reagent. All colors were described according to the "Methuen Handbook of Colour" [35].

3. Results

Sequences of the four genetic markers were obtained from 17 Fuscoporia specimens (Table 1). The ITS + nrLSU + RPB2 + TEF1 dataset was constructed, comprising 345 sequences from 53 Fuscoporia species and three outgroup species. The concatenated sequence alignment contained 3218 bp, with ITS = 1–665, nrLSU = 666–2014, *RPB2* = 2015– 2689, and TEF1 = 2690-3218, including gaps. Fuscoporia species in Korea were re-identified by a BLASTn search and phylogenetic analysis based on three combinations of sequences (ITS, ITS + nrLSU, and ITS + nrLSU + RPB2 + TEF1) (Table S2). Two public Fuscoporia sequences (accession number: KA17-0255, accession number: KMCC04909) were excluded because they showed the highest similarity to Tapinella panuoides and Sanghuangporus vaninii based on a BLASTn search.

A total of 10 Korean *Fuscoporia* species were identified based on four genetic markers (Figure 1). Eight out of the 10 clades were well-supported with high bootstrap values (>98). However, *F. gilvoides*

had a moderate bootstrap value (75), and F. dolichoseta was not well-supported, having a low bootstrap value (<60). Seventeen newly analyzed specimens were divided into eight distinct taxa. Five of them corresponded to previously reported species, and three corresponded to unrecorded species in Korea. Seventy-six GenBank sequences submitted from Korea were identified as eight previously reported species in multigene phylogeny. However, in the BLASTn search, three species (F. dolichoseta, F. gilvoides, and F. senex) could not be identified because of conflicting top-hit results. These species also formed species complexes with other global Fuscoporia species in the ITS phylogeny. In the case of F. gilvoides, the ITS region was highly similar to that of F. karsteniana, whereas sequences of nrLSU, RPB2, and TEF1 regions were significantly different (Figure S1). In the ML tree based on the ITS + nrLSU region, F. senex formed a species complex with F. rhabarbarina.

Detailed descriptions of unrecorded species and species with limited morphological records are provided in the Taxonomy section. A list of *Fuscoporia* species in Korea with the newly proposed Korean names is also provided (Table S3).

4. Taxonomy

4.1. Unrecorded species in Korea

Fuscoporia insolita Spirin, Vlasák & Niemelä, Annales Botanici Fennici 51 (6): 404 (2014) (Figures 2(A) and 3(A))

Description: Basidiomes perennial, resupinate, up to 2–6 mm thick. Pore surface nodulose, partly cracked, dark grayish brown (7F5); margin sterile, distinct, tomentose, light brown (6D8), fading to amber yellow (4B6), up to 2.5 mm wide. Pores circular to angular, grayish brown (8E3), 5–6 pores per mm; dissepiments entire. Tubes stratified, corky, grayish brown (7D3), up to 5 mm thick, each annual layer up to 2 mm thick. Subiculum corky, darker than tube layer, 1 mm thick.

Hyphal system dimitic; generative hyphae thin-walled, branched, simple septate, hyaline, $2.0-2.7 \,\mu\text{m}$ wide in tubes, rare in subiculum, encrusted with crystals at dissepiment edge; skeletal hyphae dominant in both tubes and subiculum, thick-walled, unbranched, dark brown, $3.2-4.3 \,\mu\text{m}$ wide.

Basidia barrel-shaped or utriform with four sterigmata, simple septum at the base, $8.0-10.9(-11.6) \times 4.1-$ 5.1(-5.3) µm; basidioles smaller in size. *Basidiospores* cylindrical, thin-walled, smooth, some guttulate, hyaline, IKI-, CB-, (5.2-)5.4-7.6(-7.9) × 2.0-2.8µm,



Figure 1. Maximum-likelihood tree of *Fuscoporia* species based on four genetic markers (ITS + nrLSU + RPB2 + TEF1). Bootstrap values >60 are indicated at the nodes. A total of 10 species were identified, including three unrecorded species indicated by green color. Seven species indicated by gray color have been previously reported in Korea. Strains whose sequences were newly obtained in this study are indicated in bold, and sequences submitted from Korea are highlighted in blue.

 $L = 5.9 \,\mu\text{m}$, $W = 2.1 \,\mu\text{m}$, Q = 2.7. *Cystidioles* conspicuous, narrowly lageniform, thin-walled, hyaline, 15.7–24.6 × 3.4–4.2 μ m. *Hymenial setae* rare, obclavate or lanceolate, straight, acute at the apex, thick-walled, aseptate, dark brown, 14.2–26.1 × 3.8–6.0 μ m. *Mycelial setae* absent.

Specimens examined: Korea, Gangwon-do, Pyeongchanggun, Jinbu-myeon; 37°42′13″N 128°33′59″E, 872 m, Mt. Odae; November 2 2012 (KUC20121102-22).

Notes: Specimens from Korea have larger basidiospores than that of the holotype with $(4.3-)4.7-7.2-(-8.3) \times (1.8-)1.9-2.4(-2.5) \ \mu m \ [30].$



Figure 2. Macroscopic morphology of unrecorded *Fuscoporia* species. (A) *F. insolita* (KUC20121102-22); (B) *F. ramulicola* (SFC20160316-07); (C) *F. setifera* (KUC20140509-06) (ba: basidiome; po: pore surface). Scale bar = 1 mm.



Figure 3. Microscopic morphology of unrecorded *Fuscoporia* species. (A) *F. insolita*; (B) *F. ramulicola*; (C) *F. setifera* (s: basid-iospores; b1: basidia; b2: basidioles; c: cystidioles; se: setae; h1: generative hyphae; h2: skeletal hyphae; e: encrusted generative hyphae).

Fuscoporia ramulicola (Pers.) Y.C. Dai & Q. Chen, MycoKeys 61: 82 (2019) (Figures 2(B) and 3(B))

Description: Basidiomes annual, resupinate, inseparable, up to 1.5 mm thick. Pore surface cracked, grayish brown (6D3); margin sterile, paler than tubes, 1 mm wide. Pores circular to angular, 7–9 pores per mm; dissepiments entire. Tubes corky, orange grey (6B2), up to 1 mm deep. Subiculum corky, darker than tube layer, oak brown (5D6), up to 0.4 mm thick.

Hyphal system dimitic; generative hyphae thin-walled, branched, simple septate, hyaline, 1.8– $3.0 \,\mu\text{m}$ wide in tubes, $1.7-2.6 \,\mu\text{m}$ wide in subiculum, encrusted with crystals at dissepiment edge; skeletal hyphae dominant in both tubes and subiculum, thick-walled, unbranched, rusty brown, $2.5-3.6 \,\mu\text{m}$ wide in tubes, $2.3-3.0 \,\mu\text{m}$ wide in subiculum.

Basidia clavate with four sterigmata, simple septum at the base, some with small guttules, 11.6– 16.4 × 4.0–6.4 µm; basidioles smaller in size. *Basidiospores* cylindrical, thin-walled, smooth, mostly guttulate, hyaline, IKI–, CB–, (6.1–)6.3–7.7(– 8.4) × (2.2–)2.4–3.0(–3.1) µm, L = 7.02 µm, W = 2.73 µm, Q = 2.59. *Cystidioles* fusoid, lageniform or cylindric-flexuous, thin-walled, hyaline, 10.9–39.7 × 2.5–4.3 µm. *Hymenial setae* subulate, acute at the apex, some are slightly bent at base, thick-walled, aseptate, dark brown, 14.2–44.4 × 3.7– 8.7 µm. *Mycelial setae* absent.

Specimens examined: Korea, Gangwon-do, Yangyanggun, Seo-myeon, Songeo-ri, 38°4'3.56"N 128°31'51.52"E, 240 m, on dead trunk of *Alnus*; March 16 2016 (SFC20160316-07). Korea, Jeollanam-do, Goheunggun, Yeongnam-myeon, Paryeong-ro, Mt. Paryeong, on dead trunk of angiosperm; May 24 2017 (SFC20170524-13).

Notes: Specimens from Korea have larger basidia and basidiospores, and smaller hymenial setae than those of the holotype with basidia of $9-11 \times 4.5 5.5 \,\mu\text{m}$, basidiospores of $(5.2-)5.8-7(-7.2) \times (1.8-)2 2.5(-2.8) \,\mu\text{m}$ ($L = 6.37 \,\mu\text{m}$ and $W = 2.28 \,\mu\text{m}$), and setae of $35-60 \times 4.5-7 \,\mu\text{m}$ [9]. Some larger cystidioles are found in the specimens from Korea, while the longest cystidiole recorded for the holotype from China is $22 \,\mu\text{m}$ [9].

Fuscoporia setifera (T. Hatt.) Y.C. Dai, Fungal Diversity 45: 217 (2010) (Figures 2(C) and 3(C))

 \equiv *Phellinus setifer* T. Hatt., Mycoscience 40(6): 483 (1999).

Description: Basidiomes annual, effused-reflexed, soft corky; pileus conchate, laterally fused, projecting up to 3 cm wide and up to 0.5 cm thick; pileal surface hairy, strigose, reddish brown (10F7), light reddish brown (6B6) near the margin. *Pore surface* paler than pileal surface, yellowish brown (5E6); margin distinct, hispid, 1–1.5 mm wide. *Pores* angular, 2–4 pores per mm; dissepiments entire at first, later dentate and protruding. *Tubes* corky, reddish brown (8D7), up to 2.5 mm deep. *Context* caramel (5C7), corky, thin.

Hyphal system dimitic; generative hyphae thin- to slightly thick-walled, branched, simple septate, hyaline, $2-3\,\mu\text{m}$ wide in tubes and context, encrusted with crystals at dissepiment edge; skeletal hyphae dominant in both tubes and context, thick-walled, rarely branched, light brown, $2-4\,\mu\text{m}$ wide in tubes and context.

Basidia clavate with four sterigmata, simple septum at the base, $10.0-17.1 \times 3.9-6.9 \mu m$; basidioles smaller in size. *Basidiospores* cylindrical, thin-walled, smooth, hyaline, IKI-, CB-, $(5.7-)6.2-8.6(-8.9) \times (1.9-)2.0-2.8(-3.0) \mu m$, $L = 7.45 \mu m$, $W = 2.37 \mu m$, Q = 3.16. *Cystidioles* rare, cylindrical to narrowly lageniform, hyaline, thin-walled, $13.5-36.3 \times 2.5-6.9 \mu m$. *Hymenial setae* subulate, straight, acute at the apex, some with elongated base, thick-walled, aseptate, dark brown, $30.0-50.0 \times 4.8-7.8 \mu m$. *Mycelial setae* absent.

Specimens examined: Korea, Chungcheongbuk-do, Jecheon-si, Hansu-myeon, Songgye-ri 693-1; 36°49'13"N 128°6'0"E, 455 m, Mt. Worak; May 9 2014 (KUC20140509-06). Korea, Gyeongsangbuk-do, Cheongsong-gun, Juwangsan-myeon, Sangui-ri, Geumeungwang-i; 36°25'8"N 129°9'45"E, 789 m, Mt. Juwang; 11 Oct 2019 (KUC20191011-06B). *Notes:* Specimens from Korea have longer basidiospores and larger cystidioles than those of the holotype specimen examined from Japan with basidiospores of $5.5-7.5 \times 1.5-2.5 \,\mu m$ [36].

4.2. Phylogenetically validated species in Korea

Fuscoporia ferrea (Pers.) G. Cunn., Bull. N.Z. Dept. Sci. Industr. Res. 73: 7 (1948) (Figures 4(A) and 5(A))

≡ Phellinus ferreus (Pers.) Bourdot & Galzin, Hyménomyc. de France (Sceaux): 627 (1928).

Description: Basidiomes perennial, resupinate, inseparable, up to 9 mm thick. Pore surface yellowish brown (5D8); margin sterile, paler than pore surface, 1–2 mm wide. Pores more or less circular, 5–6 pores per mm. Tubes corky, orange grey (6B2), up to 5 mm deep, dissepiments entire. Subiculum oak brown (5D6), corky, up to 4 mm thick.

Hyphal system dimitic; generative hyphae thin- to slightly thick-walled, branched, simple septate, hyaline to pale yellow, $2.1-2.9\,\mu$ m wide in tubes, $1.8-2.7\,\mu$ m wide in subiculum, encrusted with crystals at dissepiment edge; skeletal hyphae dominant in both tubes and subiculum, thick-walled, unbranched, rusty brown, $2.1-3.3\,\mu$ m wide in tubes, $2.4-4.2\,\mu$ m wide in subiculum.

Basidia clavate with four sterigmata, simple septum at the base, some with small guttules, $10.7-13.7 \times 3.8 5.7 \mu$ m; basidioles smaller in size. Basidiospores cylindric, hyaline, thin-walled, smooth, mostly guttulate, IKI-, CB-, $(5.4-)6.2-7.8(-8.2) \times (2.3-)2.5-3.2(-3.3)$ μ m, $L = 7.03 \mu$ m, $W = 2.80 \mu$ m, Q = 2.53. Cystidioles fusoid, lageniform or cylindric-flexuous, hyaline, thin-walled, $13.5-39.4 \times 1.9-4.3 \mu$ m. Hymenial setae subulate, straight, acute at the apex, some with elongated base, dark brown, thick-walled, aseptate, 21.7- $43.4 \times 5.5-8.4 \mu$ m. Mycelial setae absent.

Specimens *examined*: Korea, Gangwon-do, Inje-gun, Girin-myeon, 37°55'5.12"N 128°24'15.83"E, 357 m, Mt. Bangtae Natural Recreational Forest; February 23 2015 (SFC20150211-02). Korea, Gangwon-do, Inje-gun, Girin-myeon, Jindong-ri, 38°9'11.77"N 128°23'23.61"E, Mt. Seorak; May 9 2015 (SFC20150522-09). Korea, Gyeongsangbukdo, Bonghwa-gun, 37°4'23.25"N 128°57'39.77"E, Mt. Taebaek, Baekchoen valley, on dead trunk of angiosperm; March 22 2019 (SFC20190322-16) Gangwon-do, Taebaek-si; 37°6'34.30"N Korea, 128°56'43.17"E, Mt. Taebaek, fallen branch on July 2019 (SFC20 of angiosperm; 31 190731-43).



Figure 4. Macroscopic morphology of *Fuscoporia* species. (A) *F. ferrea* (SFC20150211-02); (B) *F. senex* (SFC20150812-50). Scale bar = 1 mm.



Figure 5. Microscopic morphology of *Fuscoporia* species. (A) *F. ferrea*; (B) *F. senex* (s: basidiospores; b1: basidia; b2: basidioles; c: cystidioles; se: setae; h1: generative hyphae; h2: skeletal hyphae; e: encrusted generative hyphae).

Notes: Korean specimens of Fuscoporia ferrea have slightly bigger basidiospores than holotype specimens $(5-9 \times 2-3 \mu m)$, but are identical in having perennial basidiomes and pore size of up to 6 per mm [37]. This species has similar morphological characteristics with those of *F. insolita* and *F. ramulicola* in having cylindric basidiospores and no mycelial setae. Fuscoporia ferrea possessed abundant hymenial setae, whereas *F. insolita* has extremely rare hymenial setae [30]. Also, *F. ramulicola* is different from *F. ferrea* in having smaller pore size (7–9 pores per mm) than those of *F. ferrea*.

Fuscoporia senex (Nees & Mont.) Ghob.-Nejh., in Ghobad-Nejhad & Dai, Mycotaxon 101: 208 (2007) (Figures 4(B) and 5(B))

 \equiv *Phellinus senex* (Nees & Mont.) Imazeki, Bull. Govt Forest Exp. Stn Meguro 57: 115 (1952).

Description: Basidiomes perennial, pileate, solitary to imbricate, 2–10 cm wide, 0.3–2.1 cm thick. Pore surface chestnut brown (6F7); margin sterile, paler than pore surface, 1–2 mm wide. Pores circular, 7–10 pores per mm, dissepiments entire. Tubes corky, orange grey (6B2), up to 5 mm deep. Context tan (6E7), corky, up to 1.4 cm thick.

Hyphal system dimitic; generative hyphae thin- to thick-walled, branched, simple septate, hyaline, $1.8-2.5 \,\mu$ m wide in tubes, encrusted with crystals at dissepiment edge; skeletal hyphae dominant in both tubes and context, thick-walled, unbranched, rusty brown, $2.8-3.7 \,\mu$ m wide in tubes.

Basidia short clavate to barrel-shaped with four sterigmata, simple septum at the base, mostly guttulate, 7.1–10.7 × 4.0–5.6 µm; basidioles smaller in size. Basidiospores broadly ellipsoid to subglobose, thin-walled, smooth, mostly guttulate, hyaline, IKI–, CB–, (3.6–)3.8–4.5(–4.7) × (2.8–)3.0–3.7(–3.8) µm, L = 4.14 µm, W = 3.26 µm, Q = 1.28. Cystidioles rare, fusoid to lageniform, thin-walled, hyaline, 16.8– 33.8 × 2.4–4.4 µm. Hymenial setae subulate, straight, acute at the apex, some with elongated base, thick-walled, aseptate, dark brown, 17.3–35.2 × 5.5– 7.4 µm. Mycelial setae absent.

Specimens examined: Korea, Seoul, Jongno-gu, Jong-ro, Jongmyo; August 12 2014 (SFC20150812-50). Korea, Incheon, Ganghwa-gun, Hwado-myeon, Heungwang-ri; September 8 2016 (SFC20150908-49).

Notes: Korean specimens of *F. senex* have slightly smaller basidiospores compared to the specimens from Iran $(3.6-4.5 \times 2.5-3.2 \mu m)$ [38]. *Fuscoporia senex* is different from other pileate *Fuscoporia* species in Korea in having smaller pore size (7–10 pores per mm).

4.3. Taxonomic key to Fuscoporia species in Korea (Figure 6)

5. Discussion

In this study, 10 *Fuscoporia* species were verified through multigenetic marker phylogeny (Figure 1), and their identification was further supported by morphological observations. Three of these (*F. insolita*, *F. ramulicola*, and *F. setifera*) were identified as species previously unrecorded in Korea. Descriptions are provided for three unrecorded species and two species that have not been previously described in detail. Additionally, errors in those previously identified only by ITS or ITS + nrLSU were confirmed by analyzing the GenBank sequences submitted from Korea. The sequences were derived from 24 *Fuscoporia* specimens: 21 from Korea and three from an uncertain locality.

The three previously unrecorded species reported in this study were originally described from Japan, China, and Far East Russia [9,30,36], which are located relatively close to Korea. The specimens examined in this study showed minor variations in their morphological characteristics from the holotype description (see Notes for details). In particular, all three species had slightly larger basidiospores than those of the corresponding holotypes, which may be derived from the differences in measurement methods as well as regional variations. However, key characteristics other than basidiospores were consistent with the holotype. For example, specimens of F. insolita in Korea have seemingly absent, rare hymenial setae, which were regarded as the primary anatomic characteristics of F. insolita [30]. Similarly, specimens of F. ramulicola exhibit annual, resupinate basidiomes with



Figure 6. Taxonomic key for 10 Korean *Fuscoporia* species. The branch length does not indicate the genetic distance between species. Four recorded species not supported with sequence evidence (*F. contigua*, *F. ferruginosa*, *F. gilva*, and *F. viticola*) were excluded.

small pores and cylindrical basidiospores [9], whereas *F. setifera* has a strigose pileus with larger pores and cylindrical basidiospores [36]. These key characteristics are unique within the *Fuscoporia* species in Korea, making it relatively simple to identify the three unrecorded species.

The other seven *Fuscoporia* species verified in Korea are difficult to identify based solely on

morphology, especially by macroscopic characteristics. For example, *F. gilvoides*, *F. semicephala*, and *F. koreana* exhibit a wide range of macromorphological features that overlap each other. However, their microscopic characteristics differed slightly; only *F. koreana* has septate skeletal hyphae, and *F. gilvoides* has smaller basidiospores [18]. For correct identification in taxonomic and other applied studies, the verified specimens were carefully examined and a taxonomic key for *Fuscoporia* species in Korea was proposed (Figure 6). Macroscopic characteristics were primarily used as criteria for the convenience of fieldwork, and microscopic characteristics were then used to identify species that were difficult to identify with macroscopic characteristics. Nevertheless, carrying out a phylogenetic analysis is recommended to distinguish all *Fuscoporia* species because their morphological differences are challenging to recognize.

The specimen previously reported as F. ferruginosa (KUC20121123-07) was re-identified as F. dolichoseta, and all specimens previously reported as F. gilva (KMCC04881, OK552, and KUC20121123-27) were re-identified as either F. gilvoides or F. koreana. F. ferruginosa is phylogenetically close to F. dolichoseta, forming a species complex in the ITS tree because of limited resolution. It also has a resupinate basidiome and mycelial setae, which can be easily confused with F. dolichoseta [18,39]. Likewise, F. gilva is a well-known species with typical brownish effused-reflexed to pileate basidiomes, which are extremely similar to those of numerous Fuscoporia species, including F. gilvoides and F. koreana. Therefore, many misidentified sequences of F. gilva have been submitted to GenBank without any type-derived sequences for correct identification [18]. This makes identification challenging, especially using a BLASTn search. Fuscoporia gilva has been frequently analyzed in applied research owing to its anti-inflammatory and antioxidative properties [3-5,40]. Therefore, accurate identification is especially crucial for F. gilva to avoid the accumulation of erroneous data.

Additionally, four previously reported Fuscoporia species (F. contigua, F. ferruginosa, F. gilva, and F. viticola) were not verified to be present in Korea. The only F. gilva sequence uploaded from Korea (ASIS24343) was unpublished and had an uncertain locality. Considering that these species were initially reported from North America and New Zealand [41,42], are mainly found in North America, Europe, and Southwest China [24,26], and are morphologically similar to the Asian species reported in Korea, there is a high possibility that previous reports on these four species from Korea may have misidentified them. However, the limited sample size in this study cannot be overlooked, particularly given that Fuscoporia species are relatively frequent across the country. Therefore, collecting more specimens and verifying them through phylogenetic analysis is necessary to validate their presence in Korea.

In this study, eight out of 10 Fuscoporia species in Korea formed a distinct clade that was well supported in the ML tree constructed using a concatenated sequence dataset of ITS + nrLSU + RPB2 + TEF1. However, two species (F. dolichoseta and F. gilvoides) were not supported with high bootstrap values. As we included all records of Fuscoporia deposited from Korea, strains with only the ITS sequence were contained in the dataset. Also, we collected mainly the type-derived or type locality sequences for each species to exclude a few sequences that were suspected to contain errors, such as paraphyletic clade and swapping of sequences among species. This missing data and the use of fewer reference sequences may have lowered the bootstrap values compared to the previous multigene phylogenetic tree of Fuscoporia [18]. Nevertheless, including additional genes for the phylogenetic tree can enhance the accuracy of analysis even when the gene is missing for some taxa [43].

Our results of the ML tree inferred based only on the ITS region also addressed the importance of the multigene phylogenetic tree. Three clades formed species complexes in the ML tree inferred based only on the ITS region: (i) F. dolichoseta complex with four other species, (ii) F. gilvoides complex with F. gilva and F. karsteniana, and (iii) F. senex complex with F. rhabarbarina. Our result supports that assessing multigenetic markers in phylogenetic analyses increases reliability and resolution [44]. This further indicates that the ITS region, as the genetic region commonly used for fungal identification, does not provide sufficient resolution within Fuscoporia. Therefore, analysis of multigenetic markers, including protein-coding genes, is necessary to accurately identify Fuscoporia species at the species level.

In conclusion, similarities in morphology and ITS sequences combined with misleading sequences in the public database might have resulted in previous misidentification of *Fuscoporia* in Korea. To address this problem, the present study provides a taxonomic key for morphological identification as well as a verified multigenetic database for phylogenetic analysis. This research will serve as the basis to accurately identify native *Fuscoporia* species and investigate their pharmaceutical properties.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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