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RESEARCH ARTICLE

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Eight Fungal Species Associated with Ambrosia Beetles in Korea

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ABSTRACT
Ambrosia fungi are well-known for their symbiotic interactions with ambrosia beetles, acting as a sole food source of larvae and adult beetles. As a first step to reveal these interactions, extensive survey on the fungal symbionts of ambrosia beetles dwelling in Korea. Eight fungal species isolated from 15 ambrosia beetle species were not known for their presence in Korea. Seven of these belonged to two orders of Ascomycota; Microascales (*Ambrosiella beaveri, A. catenulate, and A. roeperi*) and Ophiostomatales (*Leptographium verrucosum*, *Raffaelea cyclorhipidii, R. subfusca,* and *Sporothrix eucastaneae*) and one to Polyporales of Basidiomycota (*Irpex subulatus*). This is the first report of these species in Korea with taxonomic descriptions.

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1. Introduction

Ambrosia fungi are collective group of fungi which have symbiotic relationship with ambrosia beetles which excavate tunnels and cultivate fungal gardens for sole nutrient sources in the tree sapwood [1,2]. Most of these fungi are known to be dispersed only by their insect partners on mycangia, a specialized spore carrying organ of female beetles, when female ambrosia beetles explore new host trees [2,3]. Several lineages of fungi in the orders of Mircroascales (*Ambrosiella*, *Toshionella*, and *Phialophoropsis*) [4–7] and Ophiostomatales (*Afroraffaelea*, *Raffaelea*, and *Dryadomyces*) [8–11] were historically known as ambrosia fungi. Recent studies have expanded the fungal diversity to Hypocreales with a group of *Fusarium* species comprising the Ambrosia Fusarium clade (AFC) [12–14] and to Basidiomycota with *Irpex subulatus* (former *Flavodon subulatus* and *F. ambrosius*) [15,16] as new members.

Dying or freshly dead trees were known as the home of majority of ambrosia beetles resulting in little or no economic impact on agricultural or natural ecosystem. But a few ambrosia beetles attack stressed trees or even healthy trees causing devastating consequences with their fungal symbionts. Korean oak wilt disease which destroyed landscape of National Park in the central part of South Korea during last 20 years since its first occurrence in 2004 is one of example among others. Causal agent is attributed to *Dryadomyces quercus-mongolicae* (*Raffaelea quercus-mongolicae*) carried by one of ambrosia beetle *Platypus koryoensis* [17]. More than 50 ambrosia beetles in subfamilies Scolytinae and Platypodinae (Coleoptera, Curculionidae) were known to reside in South Korea [18]. However, little is known for their fungal partners even including the list of interacting fungal species except two species. Only one species, *D. quercus-mongolicae*, was reported as the symbiont of ambrosia beetle, *P. koryoensis* [17]. Although *Ambrosiella grosmaniae*, one of representative ambrosia fungal species, was known to reside in Korea, a strain of this species was isolated from soil samples without mentioning on the possible interactions with ambrosia beetles [19].

As a first step to reveal these special interactions, we explored fungal species interacting with ambrosia beetles in forests of Korea. During this survey, eight fungal species of which presence has not been recorded in Korea were identified with pure cultures isolated from 15 ambrosia beetles. We first report these eight fungal species with taxonomic descriptions.

2. Materials and methods

2.1. Beetle collection and fungal isolation

Ambrosia beetles were collected from nine sites using multiple funnel traps over three years (Supplementary Tables 1 and 2). Several *Platypus koryoensis* samples

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were collected directly from the tunnels of infected trees using forceps. All the beetle samples were kept alive on moistened tissue paper and identified under a dissecting microscope (Olympus LG-PS2; Olympus, Tokyo, Japan).

Surface of female ambrosia beetles were washed with sterile saline and ground using a disposable homogenizer (Ultra Grinder B and Tissue Grinder Motor, Taeshin Bioscience, Namyangju, South Korea) with 200 ul sterile saline. The ground samples were serial diluted up to 100 folds with sterile saline and 10 ul of each dilute was dropped on potato dextrose agar (PDA, BD Difco, Franklin Lakes, NJ) amended with 50 ppm Rose Bengal (Samchun chemicals, Seoul, South Korea), 100 ppm streptomycin sulfate (Sigma-Aldrich; Merck, Darmstadt, Germany), and 100 ppm kanamycin (Sigma-Aldrich; Merck, Darmstadt, Germany). While incubating up to one week at 23 °C, representative each morphotype of fungal colonies was subcultured on a new PDA without Rose Bengal and antibiotics. Pure culture of each strain was obtained by single spore isolation, and was deposited in the National Institute of Biological Resources (NIBR) Culture Collection in Korea in Korea after molecular and morphological identification.

2.2. DNA extraction, sequencing, and phylogenetic analysis

Genomic DNA was extracted from the fungal isolates grown on PDA for 7–10 d using a DNeasy® Plant Mini Kit (Qiagen, Hilden, Germany). For initial species identification, the internal transcribed spacer (ITS) region of the ribosomal DNA was amplified and sequenced using the universal primers ITS1F [20] and ITS4 [21]. The primers, LR0R and LR5 [22], are used for the amplification of nuclear large subunit (28S) ribosomal DNA (LSU). The translation elongation factor 1-alpha (tef1) was amplified using the primer pairs EFCF1.5 and EFCF6 for *Ambrosiella* [5], EF1-983F and EF1-2218R for *Geosmithia* [23], and EF2F and EF2R for *Leptographium* [24,25], respectively. The tef1 gene was sequenced using the internal primers EFCF2, EFCF3, and EFCer3 for *Ambrosiella* [5,7,26]. The beta-tubulin (TUB) gene was amplified using the primer pair Bt2a and Bt2b [27]. The second largest subunit of RNA polymerase II (RPB2) was amplified using the primer pair OphRPB2F1 or OphRPB2F2 and OphRPB2R1 for Ophiostomatales [28], and fRPB2-5F and fRPB2-7cR for *Geosmithia* [29], respectively. The PCR conditions included an initial denaturation at 94 °C for 5 min, 35 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for ITS and LSU, 58 °C for tef1, TUB, and RPB2 for 30 s extension at 72 °C for 1 min (1.5 min for tef1), and final extension at 72 °C for 10 min. All contigs were trimmed and assembled using the Sequencher version 5.0 DNA sequence analysis software (Gene Codes Corporation, Ann Arbor, MI), and aligned using MAFFT (multiple alignments using fast Fourier transform) version 7 [30]. A phylogenetic analysis was conducted based on maximum likelihood (ML) RAxML HPC BlackBox version 8.1.11 [31], using the default option with the GTR substitution model and bootstrap test (1000 replicates) in the CIPRES cluster server (https://www.phylo.org/) at the San Diego Supercomputing Center.

2.3. Morphology

For growth rate studies and observation of the fungal micromorphs, each strain was cultured on 9-cm petri dishes at 25 °C on malt extract agar (MEA; Difco) in the dark. The *Ambrosiella* strains were cultured on MYEA (2% Difco malt extract, 0.2% Difco yeast extract, and 1.5% agar). Microscopic observation of hyphae, conidia, and conidiophores were conducted using a ZEISS Axio Imager M2 (Carl ZEISS Microscopy GmbH) equipped with an Axiocam 506 mono digital camera.

3. Results and discussion

Survey on symbiotic fungi from 216 ambrosia beetle samples belonging to 25 weevil species that reside in South Korea were conducted during 2020–2022. A total of 140 potential ambrosia fungal isolates were obtained, which were grouped into 12 genera. After phylogenetic analysis and morphological observation, we found that eight species, with 67 isolates from 56 samples of 15 weevil species, were not recorded in Korea (Table 1 and Table 2). We report three species of *Ambrosiella*, one *Leptographium*, two *Raffaelea*, and one *Sporothrix* of Ascomycota, as well as one *Irpex* in Basidiomycota with taxonomic description for the first time in Korea.

Genus *Ambrosiella* (Ceratocystidaceae, Microascales, Ascomycota) is one of the representative ambrosia fungi currently accomodating ten member species [2,4–6,32–35]. Only one species, *A. grosmanniae*, was known to reside in Korea [19]. Here we report additional three species, *A. beaveri*, *A. roeperi*, and *A. catenulata*, from *Cnestus mutilatus*, *Anisandrus apicalis*, and *Xylosanndrus crassiusculus*, respectively (Figures 1 and 2). Strains of genus *Ambrosiella* were grouped with the type strain of each species in phylogenetic tree with concatenated sequences of ITS and TEF1 regions (Figure 1). Thirteen strains of

Table 1. Number of Ambrosia fungal strains isolated in this study.

Phylum	Order	Species	Host	Host sample	Fungal strains
Ascomycota	Microascales	*Ambrosiella beaveri*	*Cnestus mutilatus*	13	13
		A. catenulata	*Anisandrus apicalis*	1	5
		A. roeperi	*Xylosandrus crassiusculus*	7	7
	Ophiostomatales	*Leptographium verrucosum*	*Debus defensus*	1	1
		Raffaelea cyclorhipidii	*Euwallacea interjectus*	1	1
		R. subfusca	*E. interjectus*	1	1
			E. validus	4	4
		Sporothrix eucastaneae	*Ambrosiophilus atratus*	2	2
			Cyclorhipidion bodoanum	2	2
			Cy. pelliculosum	2	2
			E. validus	4	4
			Xyleborinus saxesenii	3	3
			Xylosandrus germanus	1	1
			Xylo. crassiusculus	5	5
			Scolytoplatypus sinensis	1	1
			Platypus koryoensis	1	1
Basidiomycota	Polysporales	*Irpex subulatus*	*Ambrosiodmus rubricollis*	5	5
			Ambrosiophilus atratus	3	3
Total				57	61

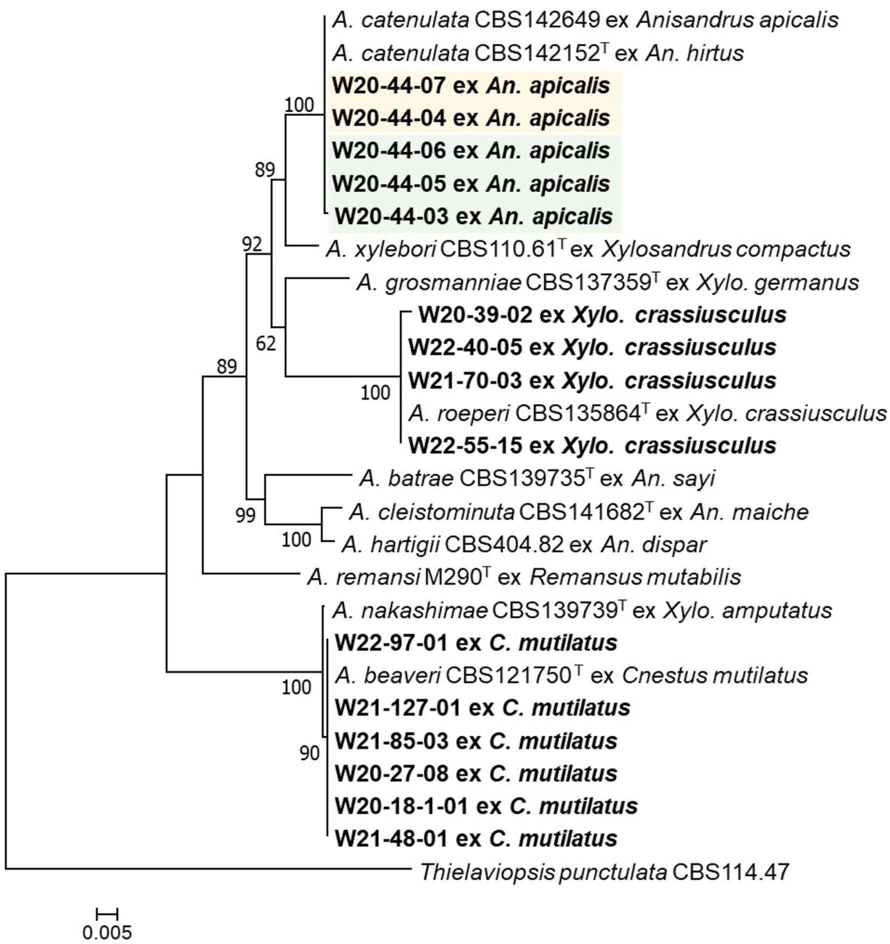

Figure 1. Phylogenetic tree of *Ambrosiella* species. A phylogenetic tree was drawn by maximum-likelihood analysis based on the ITS and TEF sequences. Bold indicates strains obtained from this study.

A. beaveri and seven strains of *A. roeperi* exhibited similar morphological characters with those of type strain. However, two types of colonies were observed among five strains of *A. catenulata*. Two strains (W20-44-04 and W20-44-07) showed typical cultural morphs, i.e., gray to olivaceous colony with abundant aerial mycelia like those described for type strain CBS142152^T on MYEA as well as on PDA (Figure 2(C); [32]). A new cultural morphology, i.e., flat brownish cream mycelia with flourish sporodochia and secreting dark brown pigments, was observed for the three isolates both on MYEA and PDA (Figure 2(D)). These two morphotypes were isolated from the same sample of *Anisandrus apicalis* collected from Inje, Gangwon province, and shared identical sequences each other and with the type strain in ITS and TEF1

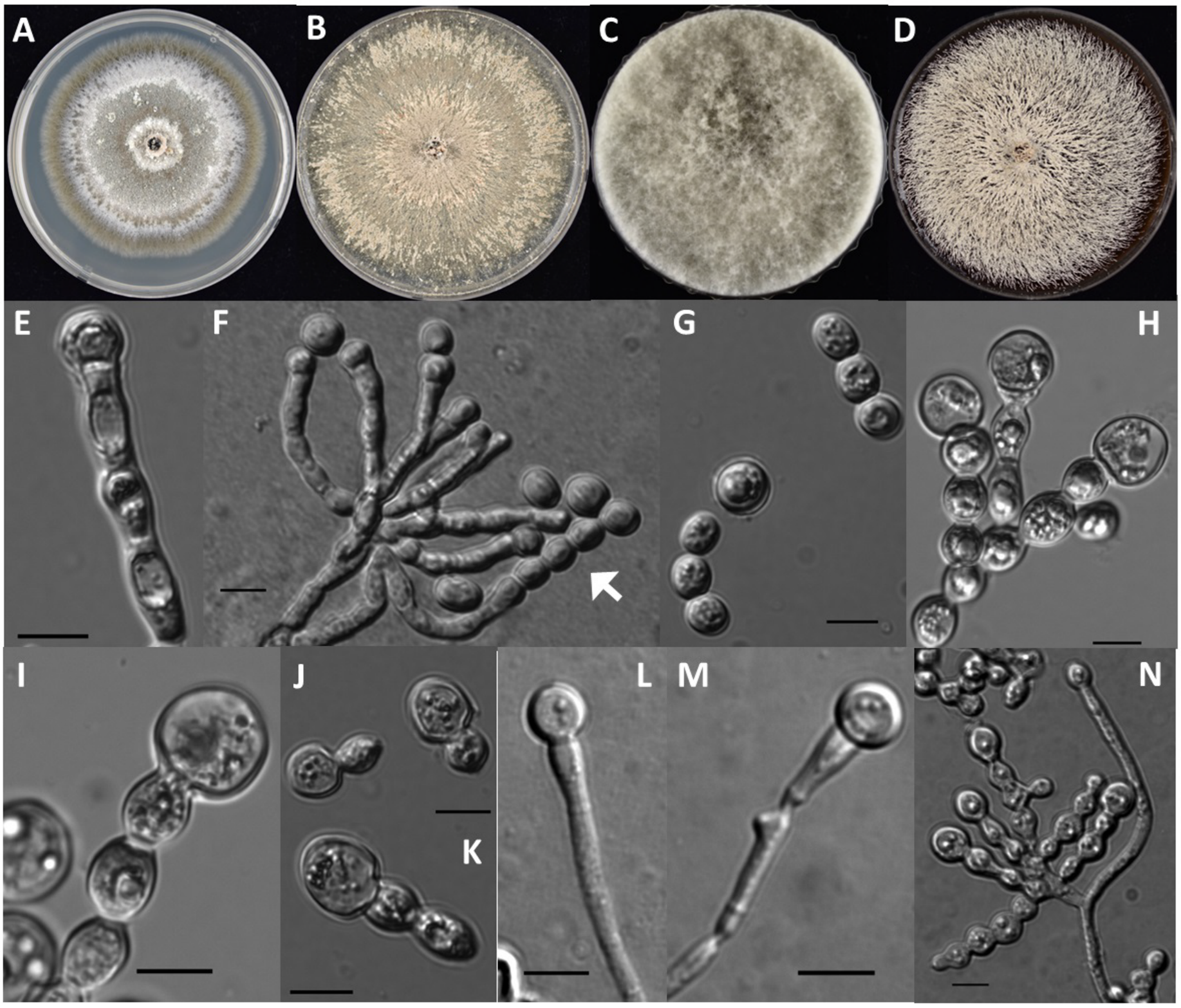

Figure 2. Morphological characters of *Ambrosiella* species. (A,E–G) *Ambrosiella beaveri* (W20-18-1-01). (B,H–K) *Ambrosiella roeperi* (W20-39-02). (C and D,L–N). *Ambrosiella catenulata* (C,L,M W20-44-04, D,N. W20-44-05). Growth on MYEA (A,B) and PDA (C,D) 9 d at 25 °C. € phialoconidiophore. (F) aleurioconidiophore with chains of conidia. (G) Condia. (H and I) Aleuriconidiophore. (J) Conidia. (K0 aleuriconidia. (L) Aleuriconidiophore. (M and N) Conidiophore. Scale bars: 10 μm (E–N).

regions. Genetic bases underlying these two morphotypes remained to be uncovered. *Ambrosiella* species are known to have specific association with ambrosia beetles having mesonotal pouch mycangia at species level and exhibited monophyletic group [5,32,36,37]. Strains of each species identified in this study were also isolated from different beetle species of tribe Xyleborini, as such, also support the hypothesis of specific association of *Ambrosiella* species and weevil species.

Raffaelea is commonly associated with ambrosia beetles, including those belonging to the tribes Xyleborini and Platypodini, and currently houses 27 species within the order Ophiostomatales of Ascomycota [11,28,37]. In South Korea, *Dryadomcyes quercus-mongolicae* (previously *Raffaelea quercus-mongolicae*) was reported as a new species in 2009 [17], but no further records of *Raffaelea* have been reported since then. In this study, we identified *R. cyclorhipidii* and *R. subfusca* after phylogenetic analyses with β-tubulin and RPB2 sequences and morphological observations (Figure 3 and Supplementary Figure 1). *R. cyclorhipidii* was reported to be associated with *Cyclorhipidion* [11]. In this study, strains of this species were only isolated from *Euwallacea interjectus*. *R. subfusca* was first reported as a symbiont of *Xyleborus glabratus* [9]. It was also isolated from *Euwallacea validus* [11]. In this study, four strains were isolated from *E. validus*, and one from *E. interjectus*. Each species of *Raffaelea* is known to interacts with several species of host ambrosia beetles [2,9,11,35,38–40]. Our data also showed asymmetric association of *Raffaelea* species and the relevant insect host.

Two genera, *Leptographium* and *Sporothrix* are generally regarded as bark beetle associates with a few species in association with ambrosia beetles. The genus *Leptographium* of Ophiostomatales is currently accommodating more than 100 species. A few species including *L. tardum*, *L. trypodendri*, and *L. verrucosum* were recognized in association with ambrosia beetles [41–44]. Three bark beetle associated species,

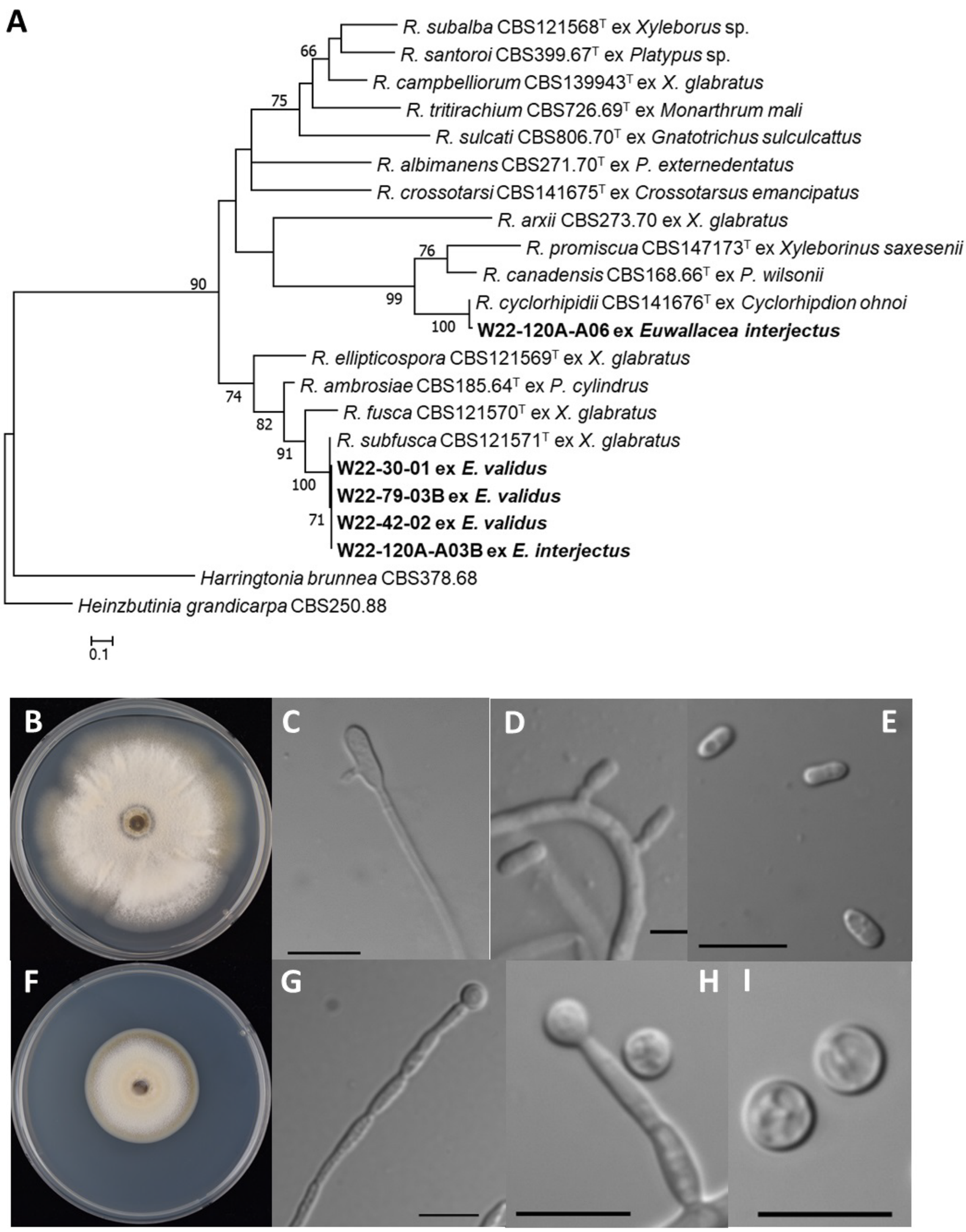

Figure 3. Phylogenetic tree and morphological characters of *Raffaelea* species. (A) Phylogenetic tree drawn by maximum-likelihood analysis based on the tubulin sequences. Bold indicates strains obtained from this study. (B–E) *Raffaelea cyclorhipidii* (W22-120A-A06). (C and D) conidiophore. (E) conidia. (F–I) *Raffaelea subfusca* (W22-120A-A03B). (G) Conidiophore. (H) Conidiophore and conidia. (I) Conidia. (B and F) growth on MEA 14 d at 25 °C. Scale bars: 10 µm (C–E, G–I).

i.e., *L. koreanum*, *L. pini-densiflorae*, and *L. procerum*, were reported from imported timber or from a bark beetle residing pine trees in Korea [45–47]. We identified a strain from an ambrosia beetle, *Debus defensus,* as *L. verrucosum* based on phylogeny and morphology (Figure 4), representing the first observation of this species in South Korea.

The genus *Sporothrix* (Ophiostomatales) currently accommodates 97 accepted species (Mycobank), which has been found from diverse environments, such as soil, plant materials, mites, and beetles [28,48]. To date, four species, i.e., *S. eucastaneae*, *S. cracoviensis*, *Sporothrix* sp. 4, and *Sporothrix* sp. 9, have been documented to be potentially associated with ambrosia beetles [49,50]. In this study, we obtained 22 strains which were identified as *S. eucastaneae* based on phylogeny with ITS and tubulin sequences and morphology (Figure 5). These were

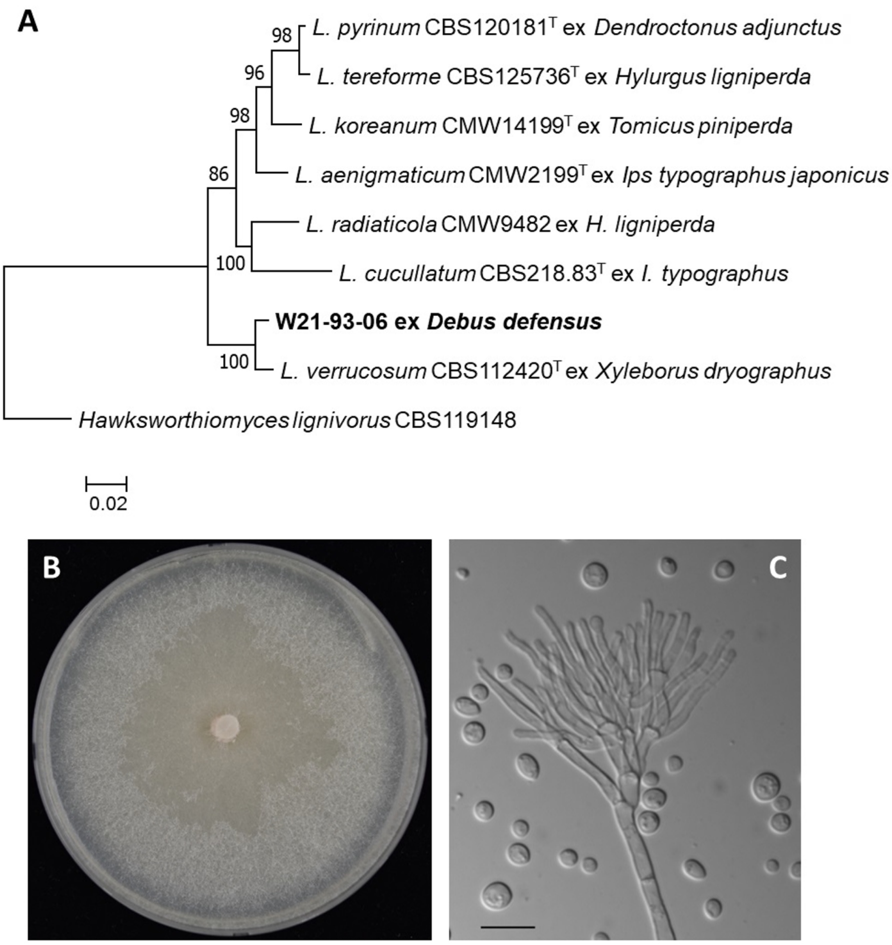

Figure 4. Phylogenetic tree and morphology of *Leptographium verrucosum*. (A) Phylogenetic tree drawn by maximum-likelihood analysis based on the LSU, TEF, and RPB2 sequences. Bold indicates strain obtained from this study. (B) Growth on MEA 9 d 25 °C. (C) Conidiophore and conidia. Scale bar 10 μm.

isolated from nine ambrosia beetle species that are different from previous reports (Table 1).

One basidiomycetous fungus, *Irpex subulatus* (previous *Flavodon ambrosius* and *F. subulatus*) is known as symbiont of two genera of ambrosia beetles, *Ambrosiodmus* and *Ambrosiophilus* [15,51]. Li et al. isolated this species from *Ambrosiophilus atratus* inhabiting South Korea [52], but they did not provide any detailed morphological description. In this study, we obtained 8 strains of this species from 8 samples of two ambrosia beetles, *Ambrosiodmus rubricollis* and *Ambrosiophilus atratus*. These isolates had the same sequences with the type strain in ITS and LSU regions and exhibited similar morphology (Figure 6). Therefore, we provided a taxonomy description of isolates from ambrosia beetles living in South Korea.

3.1. Taxonomic description

Genus *Ambrosiella*

Ambrosiella species, known as general ambrosia fungi, are associated with genera *Cnestus, Xylosandrus,* and *Anisandrus* in tribe Xyleborini. The genus *Ambrosiella*, with *A. xylebori* as the type species was first discovered and described by Brader, Arx, and Hennebert [35,52], currently accommodating ten species. These species have single- or short-chain aleurioconidia at the terminus of the aleuriodonidiophore of phialides [5,9]. They are known to exhibit a specific association with Ambrosia beetles. Three species of *Ambrosiella* were described in this report: *A. beaveri* from *Cnestus mutilatus*, *A. catenulata* from *Anisandrus apicalis,* and *A. roeperi* from *Xylosandrus crassiusculus.*

Ambrosiella beaveri Six, Z.W. de Beer & W.D. Stone, in Six et al. Antonie van Leeuwenhoek 96:23, 2009. Mycobank MB504757 (Figure 2).

Description: Colonies on MYEA 4.6–5.2 cm in diameter after 7 d at 25 °C, surface growth flat, olivaceous to gray, Sporodochia white, becoming gray with age, reverse dark olive to dark gray, odor sour. Mycelia hyaline to light brown, melanized, septate, branched hyphae. Aleurioconidiophores and phialoconidiophores hyaline smooth, simple to branched, 56.48–125.47 μm long for aleurioconidiophores, 45.17–123.49 μm long for phialoconidiophores, producing single or chain aleurioconidia on the terminal conidiophore. Aleurioconidia hyaline, globose to

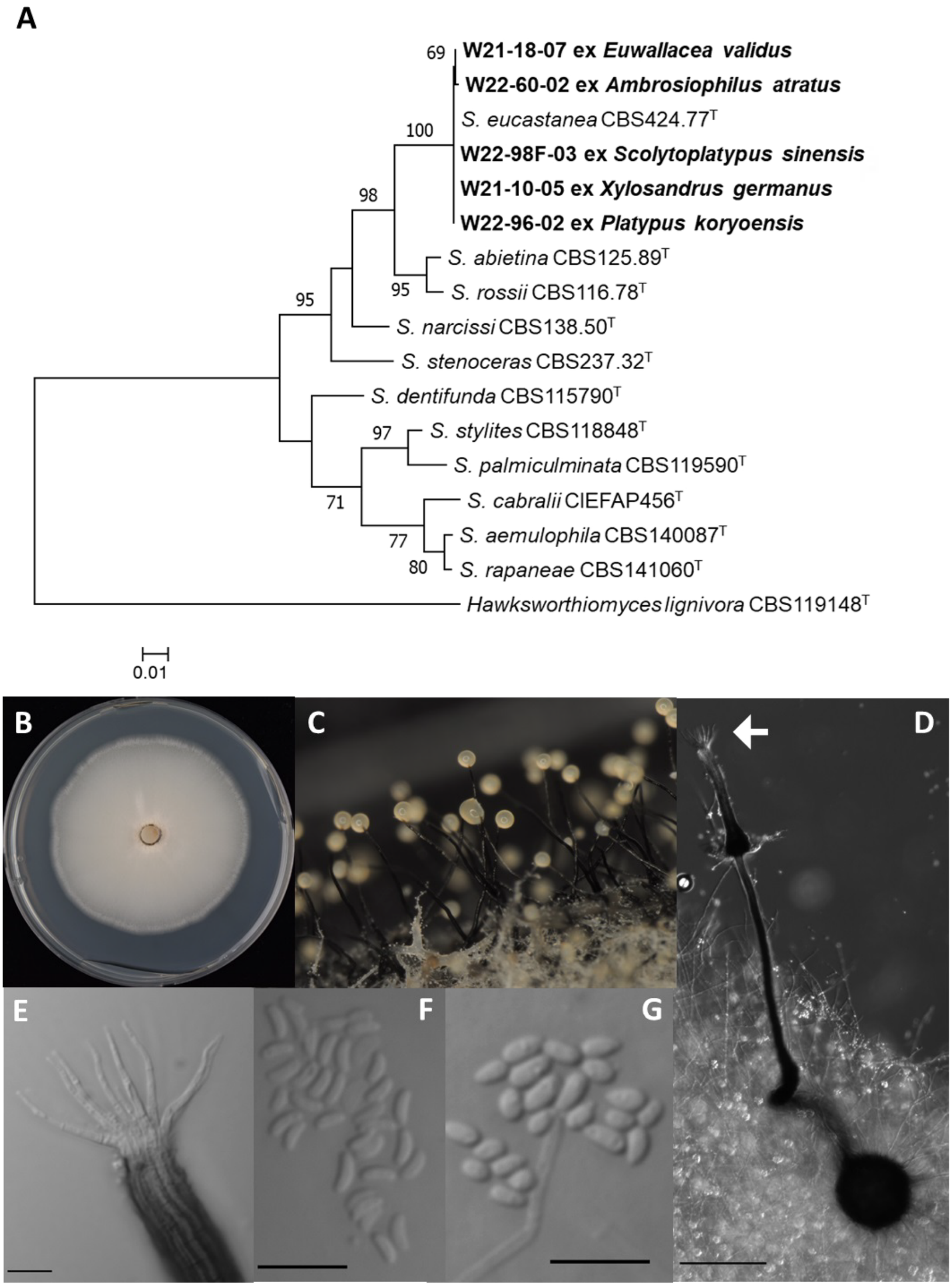

Figure 5. Phylogenetic tree and morphological characteristics of *Sporothrix eucastanea*. (A) Phylogenetic tree drawn by maximum-likelihood analysis based on the ITS, LSU, and tubulin sequences. Bold indicates strains obtained from this study. (B and C) strain W22-96-02 growth on MEA 14 d 25 °C. (D) Ascoma. (E) Ostiolar hyphae. (F) Ascospores. (G) Conidiophore and conidia. Scale bars: 100 µm (D), 10 µm (E–G).

subglobose, aseptate, 7.46–10.84 × 8.47–13.57 µm (Figure 2(A,E–G)).

Strains examined: Thirteen isolates of *Ambrosiella beaveri* were obtained from *Cnestus mutilatus* in this study, Bukhansan National Park, Seoul (W21-127-01, W21-128-01, W21-129-01); Goseong, GW (W20-27-08, W20-28-06); Pocheon, GG (W20-18-1-01, W21-49-01); Namyangju, GG (W21-48-01); Gyeryongsan National Park, Gongju, CN (W22-97-01); Iksan, JB (W21-85-03, W21-103-02, W21-105-01, W22-118-02) of Republic of Korea.

Notes: *Ambrosiella beaveri* is known as a symbiont of *Cnestus mutilatus* and has been reported in the United States, Taiwan [5,32,34]. Our data also support the specific association between *Ambrosiella* and weevil species in tribe Xyloborini (Table 1, Figure 1). *A. beaveri* has two types of conidiophores: Aleurioconidiophores and Phialoconidiophores. The

Table 2. Fungal strains used in this study.

Scientific name	Strains	NIBR	Host	ITS	LSU	TEF1	TUB	RPB2	Locality**	Collection date	References
Microascales, Ceratocystidaceae, *Ambrosiella*											
A. batrae	CBS139735^T		*Anisandrus sayi*	KR611322	–	KT290320	–	–	Michigan, USA	–	[5]
A. beaveri	CBS121750^T		*Cnestus mutilatus*	KF669875	–	KT318380	–	–	Mississippi, USA	–	[4,5]
	W20-18-1-01	NIBRFGC000510442	*Cnestus mutilatus*	OR646610	–	OR902774	–	–	Pocheon, GG	June 9, 2020	This study
	W20-27-08	NIBRFGC000510441	*Cnestus mutilatus*	OR646611	–	OR902775	–	–	Goseong, GW	June 11, 2020	This study
	W20-28-06	NIBRFGC000510440	*Cnestus mutilatus*	=OR646610	–	=OR902774	–	–	Goseong, GW	June 11, 2020	This study
	W21-48-01	NIBRFGC000509220	*Cnestus mutilatus*	OR646612	–	OR902776	–	–	Namyangju, GG	May 27, 2021	This study
	W21-49-01	NIBRFGC000509221	*Cnestus mutilatus*	=OR646612	–	=OR902774	–	–	Pocheon, GG	May 27, 2021	This study
	W21-85-03	NIBRFGC000509222	*Cnestus mutilatus*	OR646613	–	OR902777	–	–	Iksan, JB	June 9, 2021	This study
	W21-103-02	NIBRFGC000509223	*Cnestus mutilatus*	=OR646615	–	=OR902777	–	–	Iksan, JB	June 18, 2021	This study
	W21-105-01	NIBRFGC000509224	*Cnestus mutilatus*	=OR646611	–	=OR902777	–	–	Iksan, JB	June 18, 2021	This study
	W21-127-01	NIBRFGC000510439	*Cnestus mutilatus*	OR646614	–	OR902778	–	–	Seoul	June 28, 2021	This study
	W21-128-01	NIBRFGC000509226	*Cnestus mutilatus*	=OR646612	–	=OR902774	–	–	Seoul	June 28, 2021	This study
	W21-129-01	NIBRFGC000509227	*Cnestus mutilatus*	=OR646610	–	=OR902777	–	–	Seoul	June 28, 2021	This study
	W22-97-01	NIBRFGC000510438	*Cnestus mutilatus*	OR646615	–	OR902779	–	–	Gongju, CN	May 25, 2022	This study
	W22-118-02	NIBRFGC000510437	*Cnestus mutilatus*	=OR646615	–	=OR902777	–	–	Iksan, JB	June 17, 2022	This study
A. catenulata	CBS142152^T		*Anisandrus hirtus*	LC175301	–	LC175269	–	–	Taiwan	–	[32]
	CBS142649		*Anisandrus apicalis*	MG950184	–	MG944394	–	–	Japan	–	[6]
	W20-44-04	NIBRFGC000510436	*Anisandrus apicalis*	OR646616	–	OR902781	–	–	Inje, GW	June 22, 2020	This study
	W20-44-05	NIBRFGC000510435	*Anisandrus apicalis*	OR646617	–	OR902782	–	–	Inje, GW	June 22, 2020	This study
	W20-44-07	NIBRFGC000510434	*Anisandrus apicalis*	OR646618	–	OR902784	–	–	Inje, GW	June 22, 2020	This study
	W20-44-03	NIBRFGC000510433	*Anisandrus apicalis*	OR646619	–	OR902780	–	–	Inje, GW	June 22, 2020	This study
	W20-44-06	NIBRFGC000510432	*Anisandrus apicalis*	OR646620	–	OR902783	–	–	Inje, GW	June 22, 2020	This study
A. cleistominuta	CBS141682^T		*Anisandrus maiche*	KX909940	–	KX925309	–	–	Ohio, USA	–	[33]
A. grosmanniae	CBS137359^T		*Xylosandrus germanus*	KR611324	–	KT318382	–	–	Iowa, USA	–	[5]
A. hartigii	CBS404.82		*Anisandrus dispar*	KF669873	–	KT318383	–	–	Germany	–	[4,5]
A. nakashimae	CBS139739^T		*Xylosandrus amputatus*	KR611323	–	KT318381	–	–	Georgia, USA	–	[5]
A. remamsi	M290^T		*Remansus mutabilis*	KX342068	–	KX354426	–	–	Madagascar	–	[7]
A. roeperi	CBS135864^T		*Xylosandrus crassiusculus*	KF669871	–	KT318384	–	–	Georgia, USA	–	[4,5]
	W20-39-02	NIBRFGC000510431	*Xylosandrus crassiusculus*	OR646621	–	OR902785	–	–	Pocheon, GG	June 22, 2020	This study
	W21-70-03	NIBRFGC000509212	*Xylosandrus crassiusculus*	OR646622	–	OR902786	–	–	Jeju	June 9, 2021	This study
	W22-32-04	NIBRFGC000510430	*Xylosandrus crassiusculus*	=OR646622	–	=OR902786	–	–	Pocheon, GG	April 29, 2022	This study
	W22-40-05	NIBRFGC000510429	*Xylosandrus crassiusculus*	OR646623	–	OR902787	–	–	Iksan, JB	April 29, 2022	This study
	W22-55-15	NIBRFGC000510428	*Xylosandrus crassiusculus*	OR646624	–	OR902788	–	–	Gongju, CN	May 4, 2022	This study
	W22-71-04	NIBRFGC000510427	*Xylosandrus crassiusculus*	=OR646621	–	=OR902785	–	–	Gongju, CN	May 17, 2022	This study
	W22-85-05	NIBRFGC000510426	*Xylosandrus crassiusculus*	=OR646622	–	=OR902786	–	–	Pocheon, GG	May 25, 2022	This study
A. xylebori	CBS110.61^T		*Xylosandrus compactus*	KF669874	–	KT318385	–	–	Ivory Coast	–	[4,5]
Ophiostomatales, Ophiostomataceae, *Leptographium*											
L. aenigmaticum	CMW2199^T		*Ips typographus japonicus*	–	OM514716	OM631791	–	OM631619	Japan	–	[28]
L. cucullatum	CBS218.83^T		*Ips typographus*	–	OM514724	OM631801	–	OM631626	Norway	–	[28]
L. koreanum	CMW14199^T		*Tomicus piniperda*	–	OM514733	OM631808	–	OM631633	South Korea	–	[28]
L. pyrinum	CBS120181^T		*Dendroctonus adjunctus*	–	OM514781	OM631819	–	OM631642	USA	–	[28]
L. radiaticola	CMW9482		*Hylurgus ligniperda*	–	OM514742	OM631820	–	OM631643	Chile	–	[28]
L. tereforme	CBS125736^T		*Hylurgus ligniperda*	–	OM514786	OM631828	–	OM631649	California, USA	–	[28]
L. verrucosum	CBS112420^T		*Xyleborus dryographus*	–	OM514787	OM631830	–	OM631650	Germany	–	[28]
	W21-93-06	NIBRFGC000510219	*Debus defensus*	–	OR687372	OQ726118	–	OQ622128	Pocheon, GG	June 14, 2021	This study

(*Continued*)

Table 2. Continued.

Scientific name	Strains	NIBR	Host	ITS	LSU	TEF1	TUB	RPB2	Locality**	Collection date	References
Ophiostomatales, Ophiostomataceae, *Raffaelea*											
R. albimanens	CBS271.70[T]		*Platypus externedentatus*	–	–	–	EU977471	OM631705	South Africa	–	[28,54] [28]
R. ambrosiae	CBS185.64[T]		*Platypus cylindrus*	–	–	–	EU977472	OM631706	England, UK	–	[54] [28]
R. arxii	CBS273.70		*Xyleborus torquatus*	–	–	–	MW066753	OM631708	South Africa	–	[28,39]
R. campbelliorum	CBS139943[T]		*Xyleborus glabratus*	–	–	–	KR018442	–	Florida, USA	–	[55]
R. canadensis	CBS168.66[T]		*Platypus wilsonii*	–	–	–	EU977473	–	Canada	–	[54]
R. crossotarsi	CBS141675[T]		*Crossotarsus emancipatus*	–	–	–	KX267114	OM631709	Taiwan	–	[11,28]
R. cyclorhipidii	CBS141676[T]		*Cyclorhipidion ohnoi*	–	–	–	KX267115	OM631710	Taiwan	–	[11,28]
	W22-120-A-A06	NIBRFGC000510421	*Euwallacea interjectus*	–	–	–	OR902793	OR902797	Jeju	August 9, 2022	This study
R. ellipticospora	CBS121569[T]		*Xyleborus glabratus*	–	–	–	KJ909298	–	South Carolina, USA	–	[10]
R. fusca	CBS121570[T]		*Xyleborus glabratus*	–	–	–	KJ909301	–	South Carolina, USA	–	[10]
R. promiscua	CBS147173[T]		*Xyleborinus saxesenii*	–	–	–	MW066750	–	South Africa	–	[39]
R. santoroi	CBS399.67[T]		*Platypus* sp.	–	–	–	EU977476	–	Argentina	–	[54]
R. subalba	CBS121568[T]		*Xyleborus* sp.	–	–	–	KJ909305	OM631712	South Carolina, USA	–	[10,28]
R. subfusca	CBS121571[T]		*Xyleborus glabratus*	–	–	–	KJ909307	–	South Carolina, USA	–	[10]
	W22-42-02	NIBRFGC000510422	*Euwallacea validus*	–	–	–	OR902790	–	Iksan, JB	April 29, 2022	This study
	W22-30-01	NIBRFGC000510420	*Euwallacea validus*	–	–	–	OR902789	OR902794	Pocheon, GG	April 29, 2022	This study
	W22-79-03B	NIBRFGC000510419	*Euwallacea validus*	–	–	–	OR902791	OR902795	Gongju, CN	May 20, 2022	This study
	W22-120-A-A03B	NIBRFGC000510418	*Euwallacea interjectus*	–	–	–	OR902792	OR902796	Jeju	August 9, 2022	This study
R. sulcati	CBS806.70[T]		*Gnatotrichus sulculcattus*	–	–	–	EU977477	–	Canada	–	[54]
R. tritirachium	CBS726.69[T]		*Monarthrum mali*	–	–	–	EU977478	–	Pennsylvania, USA	–	[54]
Ophiostomatales, Ophiostomataceae, *Sporothrix*											
S. abietina	CBS125.89[T]		*Pseudohylesinus* sp.	OM501526	OM514853	–	KX590755	–	Mexico	–	[28,48]
S. aemulophila	CBS140087[T]		*Rapanea melanophloeos*	OM501527	OM514854	–	KT192607	–	South Africa	–	[28,38]
S. cabralii	CMW38098[T]		*Nothofagus pumilio*	OM501533	OM514861	–	KT381295	–	Argentina	–	[56]
S. dentifunda	CBS115790[T]		(*Quercus* sp.)*	OM501535	OM514865	–	AY495445	–	Hungary	–	[57] [28]

(*Continued*)

Table 2. Continued.

Scientific name	Strains	NIBR	Host	ITS	LSU	TEF1	TUB	RPB2	Locality**	Collection date	References
S. eucastaneae	CBS424.77^{T}		Canker on *Castanea dentata*	KX590814	KX590843	–	KX590753	–	North Carolina, USA	–	[48]
	W21-18-07	NIBRFGC000510417	*Euwallacea validus*	OR646625	OR687373	–	OR860320	–	Inje, GW	May 13, 2021	This study
	W22-53-03-1	NIBRFGC000510416	*Euwallacea validus*	=OR646626	=OR687377	–	=OR860319	–	Gongju, CN	May 4, 2022	This study
	W22-79-04	NIBRFGC000510415	*Euwallacea validus*	=OR646625	=OR687375	–	=OR860319	–	Gongju, CN	May 20, 2022	This study
	W22-105-06	NIBRFGC000510414	*Euwallacea validus*	=OR646628	=OR687376	–	=OQ622159	–	Gongju, CN	June 8, 2022	This study
	W22-96-02	NIBRFGC000510240	*Platypus koryoensis*	OR646626	OR687374	–	OQ622163	–	Gongju, CN	May 25, 2022	This study
	W22-34-05B	NIBRFGC000510225	*Cyclorhipidion bodoanum*	=OR646628	=OR687374	–	OQ622157	–	Pocheon, GG	April 29, 2022	This study
	W22-75-02	NIBRFGC000510239	*Cyclorhipidion bodoanum*	=OR646626	=OR687375	–	OQ622162	–	Gongju, CN	May 17, 2022	This study
	W22-60-02	NIBRFGC000510232	*Ambrosiophilus atratus*	OR646627	OR687375	–	OQ622159	–	Gongju, CN	May 4, 2022	This study
	W22-74-02	NIBRFGC000510243	*Ambrosiophilus atratus*	=OR646628	=OR687375	–	OQ622161	–	Gongju, CN	May 17, 2022	This study
	W22-57-06	NIBRFGC000510413	*Xyleborinus saxesenii*	=OR646627	=OR687373	–	=OQ622159	–	Gongju, CN	May 4, 2022	This study
	W22-80-05	NIBRFGC000510412	*Xyleborinus saxesenii*	=OR646626	=OR687373	–	=OQ622159	–	Gongju, CN	May 20, 2022	This study
	W22-92-02	NIBRFGC000510411	*Xyleborinus saxesenii*	=OR646626	=OR687375	–	=OQ622159	–	Gongju, CN	May 25, 2022	This study
	W22-98F-03	NIBRFGC000510241	*Scolytoplatypus sinensis*	OR646628	OR687376	–	OQ622164	–	Gongju, CN	May 25, 2022	This study
	W21-10-05	NIBRFGC000510443	*Xylosandrus germanus*	OR646629	OR687377	–	OR860319	–	Iksan, JB	April 19, 2021	This study
	W22-36-05	NIBRFGC000510226	*Cyclorhipidion pelliculosum*	=OR646626	=OR687375	–	OQ622158	–	Iksan, JB	April 29, 2022	This study
	W22-72-03	NIBRFGC000510238	*Cyclorhipidion pelliculosum*	=OR646628	=OR687375	–	OQ622160	–	Gongju, CN	May 17, 2022	This study
	W21-51-05	NIBRFGC000510410	*Xylosandrus crassiusculus*	=OR646629	=OR687374	–	=OR860320	–	Pocheon, GG	May 4, 2022	This study
	W22-63-03	NIBRFGC000510409	*Xylosandrus crassiusculus*	=OR646625	=OR687374	–	=OR860319	–	Pocheon, GG	May 4, 2022	This study
	W22-71-03	NIBRFGC000510408	*Xylosandrus crassiusculus*	=OR646625	=OR687377	–	=OR860319	–	Gongju, CN	May 17, 2022	This study
	W22-95-03	NIBRFGC000510407	*Xylosandrus crassiusculus*	=OR646626	=OR687373	–	=OQ622159	–	Gongju, CN	May 25, 2022	This study
	W22-89-06	NIBRFGC000510406	*Xylosandrus crassiusculus*	=OR646628	=OR687376	–	=OR860320	–	Iksan, JB	May 25, 2022	This study
S. narcissi	CBS138.50^{T}		(*Narcissus* sp.)*	OM501548	OM514876	–	KX590765	–	Netherlands	–	[28,48]
S. palmiculminata	CBS119590^{T}		(*Protea repens*)*	OM501551	OM514879	–	DQ316153	–	South Africa	–	[28,58]
S. rapaneae	CBS141060^{T}		(*Rapanea melanophloeos*)*	OM501558	OM514885	–	KU639624	–	South Africa	–	[28,38]
S. rossii	CBS116.78^{T}		*Dendroctonus adjunctus*	OM501559	OM514886	–	KX590754	–	New Mexico, USA	–	[28,48]
S. stenoceras	CBS237.32^{T}		(Pine pulp)*	AF484462	DQ294350	–	DQ296074	–	Norway	–	[59,60]
S. stylites	CBS118848^{T}		(Pine utility poles)*	OM501563	OM514890	–	EF139096	–	South Africa	–	[28,61]
Basidiocomycota, Polyporales, Irpicaceae, *Irpex*											
I. flavus	Wu 0705-1			MZ636988	MZ637149	–	–	–	Taiwan	–	[62]
I. hydnoides	KUC20121109-01		(*Acer* and other deciduouds wood)*	KJ668510	KJ668362	–	–	–	South Korea	–	[63]
I. jinshaensis	Dai 22042^{T}		(fallen angiosperm branches)*	MZ787973	MZ787965	–	–	–	China	–	[64]
I. latemarginatus	FP-55521-T			KP135024	KP135202	–	–	–	USA, Louisiana	–	[65]
I. lenis	Wu 1608-22^{T}			JN710525	JN710525	–	–	–	China	–	[66]
I. rosettiformis	Meijer3729			JN649346	JN649346	–	–	–	Brazil	–	[67]

(*Continued*)

Table 2. Continued.

Scientific name	Strains	NIBR	Host	ITS	LSU	TEF1	TUB	RPB2	Locality**	Collection date	References
I. subulatus	Hulcr 6853^T		*Ambrosiodmus minor*	KR119072	KR119075	–	–	–	Florida, USA	–	[15]
	Dai 5929		(dead, decious wood)*	KY131837	KY131896	–	–	–	China	–	[68]
	W21-92-01	NIBRFGC000509225	*Ambrosiodmus rubricollis*	OR646636	OR687378	–	–	–	Pocheon, GG	June 14, 2021	This study
	W22-37-01	NIBRFGC000510405	*Ambrosiodmus rubricollis*	OR646637	OR687379	–	–	–	Iksan, JB	April 29, 2022	This study
	W22-66-01	NIBRFGC000510404	*Ambrosiodmus rubricollis*	=OR646638	=OR687378	–	–	–	Pocheon, GG	May 4, 2022	This study
	W22-91-01-1	NIBRFGC000510403	*Ambrosiodmus rubricollis*	=OR646638	=OR687378	–	–	–	Iksan, JB	May 25, 2022	This study
	W22-117-02	NIBRFGC000510402	*Ambrosiodmus rubricollis*	=OR646638	=OR687378	–	–	–	Iksan, JB	June 17, 2022	This study
	W21-03-07	NIBRFGC000510218	*Ambrosiophilus atratus*	OR646638	OR687380	–	–	–	Iksan, JB	April 19, 2021	This study
	W22-29-01	NIBRFGC000510228	*Ambrosiophilus atratus*	OR646639	OR687381	–	–	–	Pocheon, GG	April 29, 2022	This study
	W22-39-03	NIBRFGC000510229	*Ambrosiophilus atratus*	=OR646638	=OR687378	–	–	–	Iksan, JB	April 29, 2022	This study
Out group											
Thielaviopsis punctulata	CBS114.47			AF275495	–	KX925310	–	–	California, USA	–	[33]
Heinzbutinia grandicarpa	CBS250.88		(*Quercus robor*)*	–	–	–	KX590762	OM631616	Poland	–	[28,48]
Harringtonia brunnea	CBS378.68		*Monarthrum* sp.	–	–	–	EU977460	–	USA	–	[54]
Hawksworthiomyces lignivorus	CBS119148		(Eucalyptus pole)*	OM501410	OM514756	OM631782	EF139104	OM631611	South Africa	–	[28,61]
Phanerochaetella angustocystidiata	Wu 9606-39		(angiosperm)*	MZ637020	GQ470638	–	–	–	Taiwan	–	[62,70]

*Fungal strains were obtained from plants or other origins rather than beetles.
**Locality abbreviations: GG: Gyenggi-do; GW: Gangwon-do; CN: Chungcheongnam-do; JB: Jeollabuk-do; JN: Jeollanam-do

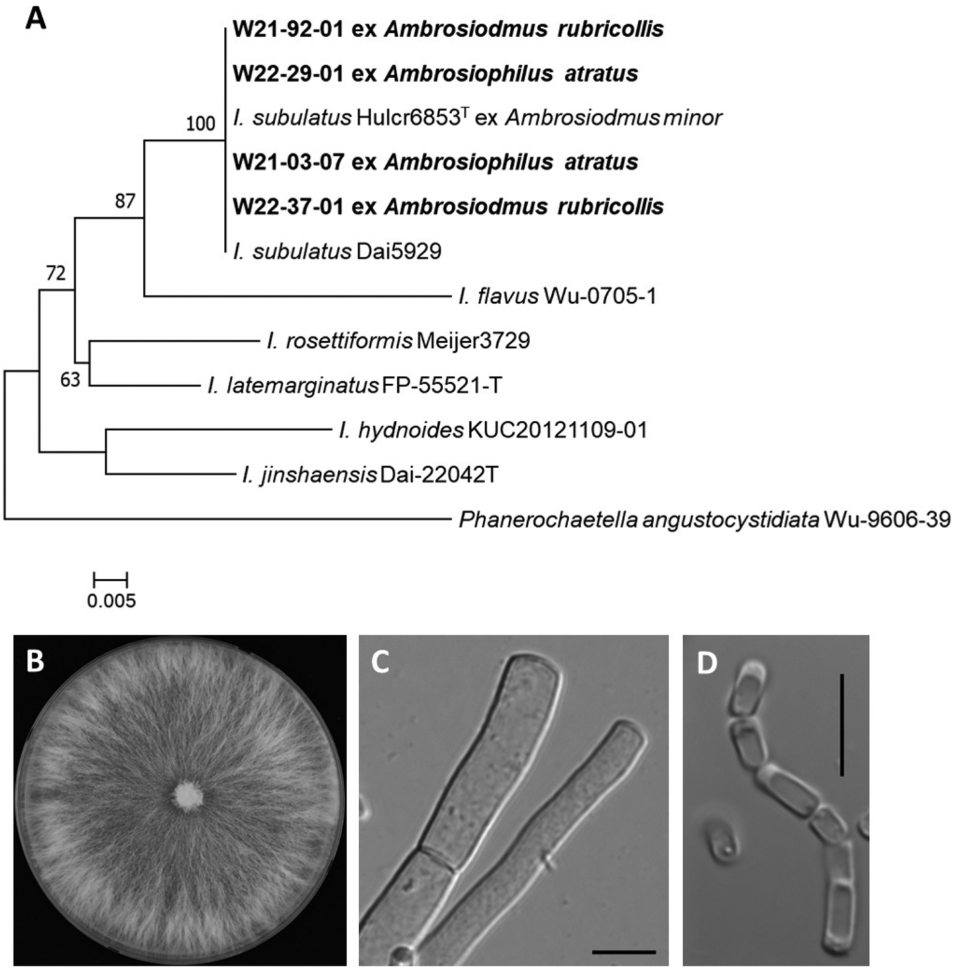

Figure 6. Phylogenetic tree and morphological characteristics of *Irpex subulatus*. (A) Phylogenetic tree drawn by maximum-likelihood analysis based on the ITS and LSU sequences. Bold indicates strains obtained from this study. (B) Strain W22-29-01 growth on MEA 7 d 25 °C. (C) Hyphae. (D) arthroconidia, produced from fragmentation of small hyphae. Scale bars: 10 μm (C and D).

isolates showed a morphology similar to that of the type strain CBS 121750. This is the first report of *A. beaveri* isolated in South Korea.

Ambrosiella roeperi T. C. Harrington & McNew, Harrington et al. Mycologia 106:841, 2014. Mycobank MB805798 (Figure 2).

Description: Colonies on MYEA 6.2–7.2 cm in diameter after 5 d at 25 °C, surface growth flat, light brown to olivaceous and gray, droplets of clear, red-brown liquid scattered across the surface, sporodochia white to light brown, reverse dark brown to black, odor sour. Mycelia hyaline to light brown, melanized, septate, branched hyphae. Aleurioconidiophores hyaline simple to branched, 20.92–70.41 μm long, producing single or chain of aleurioconidia on the terminal conidiophore. Aleurioconidia hyaline, thick-walled, globose to subglobose, aseptate, 6.66–13.26 × 9.16–14.89 μm, aleurioconidia carrying one or two conidiophore cells detached from the aleurioconidiophores (Figure 2(B,H–K)).

Strains examined: All strains of *Ambrosiella roeperi* were isolated from *Xylosandrus crassiusculus*, collected at Pocheon, GG (W20-39-02, W22-32-04, and W22-85-05); Gyeryongsan National Park, Gongju, CN (W22-55-15, W22-71-04); Iksan, JB (W22-40-05); and Seoguipo, Jeju (W21-70-03), Republic of Korea.

Note: *Ambrosiella roeperi* is known as symbiont of *Xylosandrus crassiusculus* and has been reported in the United States, Taiwan, and Japan [4,5,7,32]. This species is usually known to bear aleurioconidia from a single conidiophore. In this study, all the isolates of *A. roeperi* were obtained from *Xylosandrus crassiusculus* and grouped together with type strain by phylogenetic analysis (Figure 1). In addition, these isolates exhibited the same morphological characteristics including aleurioconidia to those of the type strain (CBS 135864). This is the first report of *A. roeperi* isolated in Korea.

Ambrosiella catenulata Y. T. Lin and H. H. Shih, Lin et al. Mycoscience 2017. Mycobank MB818077 (Figure 2).

Description: Colonies on MYEA 5.9–6.2 cm in diameter after 5 d at 25 °C, surface growth flat, odor sour, two types of cultural morphology were observed; (1)

typical colony as type strain, i.e., white to olive, gray, covered with abundant aerial mycelia, conidiophores rarely observed, (2) colony flat and white to brown, sporodochia spherical, white to light gray composed of abundant conidiophores, reverse brown to black. Aleurioconidiophores are hyaline, smooth, simple to branched, 47.59–79.53 µm long, producing a terminal or branched chain of aleurioconidia. Conidiophores are hyaline, smooth, simple, 93.13–145.95 µm long, producing conidia at a single end. Aleurioconidia and conidia hyaline: globose to subglobose, aseptate, 7.63–11.12 × 8.94–12.53 µm (Figure 2(C,D,L–N)).

Strains examined: All strains of *Ambrosiella catenulata* were isolated from *Anisandrus apicalis* collected from Inje, GW, Republic of Korea (W20-44-03, W20-44-04, W20-44-05, W20-44-06, and W20-44-07).

Notes: *Ambrosiella catenulata* was first reported by Lin with the type strain CBS142152 isolated from the gallery of *Anisandrus hirtus* in Taiwan [32]. This species has also been reported in Japan [7]. Colonies on PDA of the type strain exhibited olivaceous to gray with abundant aerial mycelia. This species has also been isolated from *Eccoptopterus spinosus* [32]. Mayers et al. [7] isolated *A. catenulata* from Japanese *Anisandrus apicalis* but provided no taxonomic description. In this study, we observed two types of cultural morphology on MYEA: the presence or absence of abundant aerial mycelia. The flat mycelium type (W20-44-03, W20-44-05, and W20-44-06) beared abundant aleuriconidiophores, whereas the typical aerial mycelium type (W20-44-04 and W20-44-07) was covered with fluffy aerial hyphae with rare terminal conidiophore. These strains were isolated from the same sample of *Anisandrus apicalis* collected at Inje, Gangwon Province, and had the same sequences in ITS and were grouped with *A. catenulata* in the multigene phylogenetic analysis (Figure 1). We report *A. catenulata* in South Korea for the first time.

Genus *Raffaelea*

Raffaelea is one of fungal genus associated with ambrosia beetles with *R. ambrosia* as the type species [35]. *Raffaelea* has been described as an asexual genus in the Ophiostomatales, but sexual structures were found in several species, including *R. seticollis, R. deltoideospora,* and *R. vaginata* [38] improving the generic description. A group of species in *Raffaelea*, i.e., *R. quercivora, R. sulphurea, R. montetyi, R. quercivora,* and *R. quercus-mongolicae* were recently re-assigned to a new genus *Dryadomyces* with *D. amasae* as the type species after molecular phylogenetic analysis [28,69]. Recently, a new genus, *Harringtonia*, was introduced to accomodate the *Raffaelea lauricola* complex [28].

Raffaelea cyclorhipidii D. R. Simmons and Y. T. Huang, in Simmons et al. IMA Fungus. 7(2):265-273, 2016. MB817173 (Figure 3).

Description: Colonies on MEA 22.9–23.9 mm in diameter after 7 d at 25 °C surface wrinkled, moderate aerial mycelium, surface mycelium cream becoming olive and brown with age, reverse subhyaline, moderate sporulation. The conidiophores are hyaline, and simple, producing usually a single conidiogenous cell on the terminal end of the conidiophore, 22.92–78.36(115.29) µm long. Conidia hyaline, flask-shaped, elliptical to elongate, aseptate, 2.49–5.07 × 5.47–9.07 µm. The conidia then produce budding cells. The sexual morphs are unknown (Figure 3(B–E)).

Strais examined: W22-120-A-A06 was isolated from *Euwallacea interjectus*, Jeju, Republic of Korea.

Note: The type strain of *R. cyclorhipidii* (CBS 141676) was isolated from *Cyclorhipidion ohnoi* and only reported in Taiwan [11]. Conidia are usually formed on terminal conidiophores and are elliptically elongated. Occasionally, conidia have yeast-like budding cells. Isolate W22-120-A-A06 was cultured from *Euwallacea interjectus*. The sequences of the β-tubulin and RPB2 genes were 99% identical to those of the type strain, and a similar morphology was observed.

Raffaelea subfusca T.C. Harrington, Aghayeva & Fraedrich, Harrington et al. Mycotaxon. 111:337-361, 2010. MB515294 (Figure 3).

Description: Colonies on MEA 14.1–14.5 mm in diameter after 7 d at 25 °C, light beige becoming dark brown in the center and light brown at the edges with age, reverse cream to brownish, wrinkled, moderate sporulation. Conidiophores hyaline simple to branched, producing single conidia at the terminal ends, 17.54-89.65 µm long. Conidia hyaline globose to subglobose, 3.53–5.74 × 3.88–6.09 µm. The sexual morphs are unknown (Figure 3(F–1)).

Strains examined: Three strains (W22-30-01, W22-42-02, and W22-79-03B) were isolated from *Euwallacea validus*, Pocheon, GG, Iksan, JB, Gyeryongsan National Park, Gongju, CN, respectively, and one strain (W22-120-A-A03B) was isolated from *Euwallacea interjectus*, Jeju, Republic of Korea.

Notes: *R. subfusca* was first isolated from *Xyleborus glabratus* and has been reported across the USA [9, 11]. This species produces a single conidium at the terminal end of the conidiophores. In this study, four isolates were obtained from other ambrosia beetles, *E. validus* and *E. interjectus,* and grouped with the type strain of *R. subfusca* (CBS 121571) (Figure 3(A)).

Leptographium verrucosum (Gebhardt, R. Kirschner & Oberw.) Z.W. de Beer & M.J. Wingf. In de Beer et al. Biodiversity Series 12:245-322, 2013. MB801083 (Figure 4).

Basionym: *Ophiostoma verrucosum* Gebhardt, R. Kirschner & Oberw, Mycol. Progress 1: 378. 2002

Description: Colonies on MEA 5.1–5.5 cm in diameter after 5 d at 25 °C, surface mycelium flat, hyaline, cream with agar, not pigmented, abundant sporulation. Conidiophores hyaline, penicillate-morphology, 54.99–137.82 µm long, consists of 2–4 branched, smooth, metula 8.45–15.04 × 2.51–3.37 µm, phialides 8.88–23.15 × 1.56–1.93 µm, septate. Conidia hyaline aseptate, globose to subglobose, ellipsoid, 2.54–5.64 × 2.74–6.21 µm (Figure 4). We did not observe any sexual morphs such as ostiole, perithecia, and neck.

Strains examined: W21-93-06 was isolated from *Debus defensus*, Pocheon, GG, Republic of Korea.

Notes: *Leptographium verrucosum* was first reported as *Ophiostoma verrucosum* based on morphology by Gebhardt in Germany [41], and later was transferred to the genus *Leptographium* based on LSU sequences by De Beer et al. [70]. Recently, this group was retained in the *Leptographium* incertae sediment (Lineage VI) [28]. The type strain of *L. verrucosum* (CBS 112420) was isolated from *Xyleborus dryographus*. Our strain, W21-93-06, was grouped with type in a multigene phylogeny based on LSU, tef, and RPB2 sequences (Figure 4). Sexual structures were not found in this study, while the anarmorphs were similar.

Sporothrix eucastaneae (R. W. Davidson) Z. W. de Beer, T. A. Duong, and M. J. Wingf. In de Beer et al. Studies in Mycology 83:165-191. 2016. MB81751 (Figure 5).

Basionym: *Ceratocystis eucastaneae* R.W. Davidson, Mycologia 70: 856. 1978.

Description: Colonies on MEA 26.6–34.6 mm in diameter after 9 d at 25 °C, mycelium dense white, exhibited black perithecia and long black necks on the surface with age, reverse cream. Perithecia black, globose, partly embedded in the agar, 88.78–155.57 µm in diameter, with long black straight or curved necks, 395.37–574.18 µm long. Ostiolar filaments hyaline, about 7–9 in number, 21.64–38.43 µm long, 1.32–1.77 µm at the apex and 2.07–3.49 µm at the base, tapering to the apex. Ascospores hyaline, slightly curved, 1.45–1.96 × 3.21–4.68 µm. Conidiophores hyaline, Conidia hyaline, elongate ovoid, 1.95–3.24 × 3.15–6.58 µm, produced at the base or terminal conidiophore (Figure 5).

Strains examined: A total of 21 strains were obtained from nine ambrosia beetles. Four strains were isolated from *Euwallacea validus*, Inje, GW (W21-18-07), Gyeryongsan National Park, Gongju, CN (W22-53-03-1, W22-79-04, and W22-105-06); One strain was isolated from *Platypus koryoensis*, Gyeryongsan National Park, Gongju, CN (W22-96-02); and two from *Cyclorhipidion bodoanum*, Pocheon, GG (W22-34-05B), Gyeryongsan National Park, Gongju, CN (W22-75-02); two from *Ambrosiophilus atratus*, Gyeryongsan National Park, Gongju, CN (W22-60-02, W22-74-02); three from *Xyleborinus saxesenii*, Gyeryongsan National Park, Gongju, CN (W22-57-06, W22-80-05, W22-92-02); one from *Scolytoplatypus sinensis*, Gyeryongsan National Park, Gongju, CN (W22-98F-03); one from *Xylosandrus germanus*, Iksan, JB (W21-10-05); two from *Cyclorhipidion pelliculosum*, Gyeryongsan National Park, Gongju, CN (W22-72-03), Iksan, JB (W22-36-05); five from *Xylosandrus crassiusculus*, Pocheon, GG (W21-51-05, W22-63-03), Gyeryongsan National Park, Gongju, CN (W22-71-03, W22-95-03), Iksan, JB (W22-89-06), Republic of Korea.

Note: *Sporothrix eucastaneae* was grouped with the *S. gossypina* complex and isolated from various species of bark beetles and ambrosia beetles [50]. This species has been reported in USA and Poland. *S. eucastaneae* was first described as *Ceratocysits eucastaneae* [71], and was transferred to the genus *Sporothrix* based on multigene phylogeny [48]. In this study, we identified 21 isolates of *S. eucastaneae* from nine species of ambrosia beetles, which were grouped with the type strain (CBS 424.77) in the multigene phylogeny with ITS, LSU, and tubulin sequences (Figure 5). In addition, all the isolates produced sexual and asexual structures similar to those of the type strain.

Irpex subulatus (Ryvarden) B. Liu, Y. C. Dai, Tian et al. Phytotaxa. 533:73–82. 2022. MB841368 (Figure 6).

Basionym: *Oxyporus subulatus* Ryvarden. Nordic Journal of Botany 2(3) 280 (1982).

Flavodon subulatus (Ryvarden) F. Wu, Jia J. Chen & Y. C. Dai, Mycologia 109(5): 761 (2017).

Flavodon ambrosius D.R. Simmons, You Li, C.C. Bateman & J. Hulcr, Mycotaxon 131(2): 279 (2016).

Description: Colonies on MEA 7.4–8.0 cm in diameter after 5 d at 25 °C, white becoming yellow with age, aerial mycelium, cottony. Mycelial hyaline and smooth septa. Arthroconidia hyaline, cylindrical, aseptate, 2.53–4.80 × 3.70–10.65 µm (Figure 6). Sexual morphs were not observed.

Strains examined: Five strains were isolated from *Ambriosiodmus rubricollis*, Pocheon, GG (W21-92-01, W22-66-01), Iksan, JB (W22-37-01, W22-91-01-1, and W22-117-02); three from *Ambrosiophilus atratus*, Pocheon, GG (W22-29-01), Iksan, JB (W21-03-07, W22-39-03), Republic of Korea.

Notes: *Irpex subulatus* was first described as *Oxyporus subulatus* [72], and transferred to the genus *Flavodon* by phylogenetic analysis in 2017 [68]. Simultaneously, a new symbiotic relationship between *Flavodon ambrosius* and *Ambrosiodomus* was reported [51]. Jusino suggested that *F. subulatus* was an earlier synonym of *F. ambrosius* based on similar morphology and ribosomal DNA sequences [73]. Recently, this species was transferred from *F. subulatus* and *F. ambrosius* to *Irpex subulatus* based on the multigene phylogeny [64]. This species has been reported in USA, China, Vietnam, and South Korea [15,16,51,52]. *I. subulatus*, up to date, is the only Basidiomycetous ambrosia fungus isolated from two genera of ambrosia beetles, *Ambrosiophilus* and *Ambrosiodmus* [15,51]. We obtained eight strains from two ambrosia beetles, *Ambriosiodmus rubricollis* and *Ambrosiophilus atratus*. These strains were closely located to the type strain of *I. subulatus* in the phylogeny based on the ITS region and LSU sequence and also produced arthroconidia (Figure 7).

Disclosure statement

No potential conflict of interest was reported by the author.

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References

[1] Batra LR. Ambrosia beetles and their associated fungi: research trends and techniques. Proc Indian Acad Sci (Plant Sci). 1985;94(2–3):137–148. doi: 10.1007/BF03053133.

[2] Batra LR. Ambrosia Fungi – a taxonomic revision, and nutritional studies of some species. Mycologia. 1967;59(6):976–1017. doi: 10.1080/00275514.1967.12018485.

[3] Beaver RA. Insect–fungus relationships in the bark and ambrosia beetles. In Wilding N, Collins NM, Hammond PM, Webber JF, editors. Insect-fungus interactions. Cambridge (MA): Academic Press; 1989. p. 121–143.

[4] Harrington TC, McNew D, Mayers C, et al. *Ambrosiella roeperi* sp. nov. is the mycangial symbiont of the granulate ambrosia beetle, *Xylosandrus crassiusculus*. Mycologia. 2014;106(4):835–845. doi: 10.3852/13-354.

[5] Mayers CG, McNew DL, Harrington TC, et al. Three genera in the Ceratocystidaceae are the respective symbionts of three independent lineages of ambrosia beetles with large, complex mycangia. Fungal Biol. 2015;119(11):1075–1092. doi: 10.1016/j.funbio.2015.08.002.

[6] Mayers CG, Harrington TC, Masuya H, et al. Patterns of coevolution between ambrosia beetle mycangia and the Ceratocystidaceae, with five new fungal genera and seven new species. Persoonia. 2020;44(1):41–66. doi: 10.3767/persoonia.2020.44.02.

[7] Mayers CG, Harrington TC, McNew DL, et al. Four mycangium types and four genera of ambrosia fungi suggest a complex history of fungus farming in the ambrosia beetle tribe Xyloterini. Mycologia. 2020;112(6):1104–1137. doi: 10.1080/00275514.2020.1755209.

[8] Harrington TC, Fraedrich SW, Aghayeva DN. Raffaelea lauricola, a new ambrosia beetle symbiont and pathogen on the Lauraceae. Mycotaxon. 2008;104:399–404.

[9] Harrington TC, Aghayeva DN, Fraedrich SW. New combinations in Raffaelea, Ambrosiella, and Hyalorhinocladiella, and four new species from the redbay ambrosia beetle, Xyleborus glabratus. Mycotaxon. 2010;111(1):337–361. doi: 10.5248/111.337.

[10] Dreaden TJ, Davis JM, de Beer ZW, et al. Phylogeny of ambrosia beetle symbionts in the genus Raffaelea. Fungal Biol. 2014;118(12):970–978. doi: 10.1016/j.funbio.2014.09.001.

[11] Simmons DR, de Beer ZW, Huang YT, et al. New Raffaelea species (Ophiostomatales) from the USA and Taiwan associated with ambrosia beetles and plant hosts. IMA Fungus. 2016;7(2):265–273. doi: 10.5598/imafungus.2016.07.02.06.

[12] Kasson MT, O'Donnell K, Rooney AP, et al. An inordinate fondness for Fusarium: phylogenetic diversity of fusaria cultivated by ambrosia beetles in the genus Euwallacea on avocado and other plant hosts. Fungal Genet Biol. 2013;56:147–157. doi: 10.1016/j.fgb.2013.04.004.

[13] O'Donnell K, Sink S, Libeskind-Hadas R, et al. Discordant phylogenies suggest repeated host shifts in the Fusarium-Euwallacea ambrosia beetle mutualism. Fungal Genet Biol. 2015;82:277–290. doi: 10.1016/j.fgb.2014.10.014.

[14] Aoki T, Kasson MT, Berger MC, et al. *Fusarium oligoseptatum* sp. nov., a mycosymbiont of the ambrosia beetle *Euwallacea validus* in the Eastern US and typification of *F. ambrosium*. Fungal Syst Evol. 2018;1(1):23–39. doi: 10.3114/fuse.2018.01.03.

[15] Li Y, Simmons DR, Bateman CC, et al. New fungus-insect symbiosis: culturing, molecular, and histological methods determine saprophytic polyporales mutualists of Ambrosiodmus ambrosia beetles. PLoS One. 2015;10(9):e0137689. doi: 10.1371/journal.pone.0137689.

[16] Kasson MT, Wickert KL, Stauder CM, et al. Mutualism with aggressive wood-degrading *Flavodon ambrosius* (Polyporales) facilitates niche expansion and communal social structure in Ambrosiophilus ambrosia beetles. Fungal Ecol. 2016;23:86–96. doi: 10.1016/j.funeco.2016.07.002.

[17] Kim KH, Choi YJ, Seo ST, et al. *Raffaelea quercus-mongolicae* sp. nov. associated with *Platypus koryoensis* on oak in Korea. Mycotaxon. 2009;110(1):189–197. doi: 10.5248/110.189.

[18] Park S, Smith SM, Cognato AI, et al. Catalogue of Korean Xyleborine ambrosia beetles (Coleoptera: curculionidae: scolytinae) with seven new species. J Asia-Pac Biodivers. 2020;13(2):210–228. doi: 10.1016/j.japb.2020.01.002.

[19] Park S, Ten L, Lee SY, et al. New Recorded Species in Three Genera of the Sordariomycetes in Korea. Mycobiology. 2017;45(2):64–72. doi: 10.5941/MYCO.2017.45.2.64.
[20] Gardes M, Bruns TD. ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. Mol Ecol. 1993;2(2):113–118. doi: 10.1111/j.1365-294x.1993.tb00005.x.
[21] White TJ, Bruns T, Lee S, et al. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In Innis MA, Gelfand DH, Sninsky JJ, White TJ, editors. PCR protocols: a sequencing guide to methods and applications. San Diego (CA): Academic Press; 1990. p. 315–322.
[22] Vilgalys R, Hester M. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several cryptococcus species. J Bacteriol. 1990;172(8):4238–4246. doi: 10.1128/jb.172.8.4238-4246.1990.
[23] Rehner SA, Buckley E. A Beauveria phylogeny inferred from nuclear ITS and EF1-α sequences: evidence for cryptic diversification and links to Cordyceps teleomorphs. Mycologia. 2005;97(1):84–98. doi: 10.3852/mycologia.97.1.84.
[24] Marincowitz S, Duong TA, Wilhelm de Beer Z, et al. Cornuvesica: a little known mycophilic genus with a unique biology and unexpected new species. Fungal Biol. 2015;119(7):615–630. doi: 10.1016/j.funbio.2015.03.007.
[25] Jacobs K, Bergdahl DR, Wingfield MJ, et al. *Leptographium wingfieldii* introduced into North America and found associated with exotic *Tomicus piniperda* and native bark beetles. Mycol Res. 2004;108(Pt 4):411–418. doi: 10.1017/s0953756204009748.
[26] Oliveira LS, Harrington TC, Ferreira MA, et al. Species or genotypes? Reassessment of four recently described species of the Ceratocystis Wilt pathogen, *Ceratocystis fimbriata*, on Mangifera indica. Phytopathology. 2015;105(9):1229–1244. doi: 10.1094/PHYTO-03-15-0065-R.
[27] Glass NL, Donaldson GC. Development of primer sets designed for sse with the PCR to amplify conserved genes from filamentous ascomycetes. Appl Environ Microbiol. 1995;61(4):1323–1330. doi: 10.1128/aem.61.4.1323-1330.1995.
[28] de Beer ZW, Procter M, Wingfield MJ, et al. Generic boundaries in the Ophiostomatales reconsidered and revised. Stud Mycol. 2022;101(1):57–120. doi: 10.3114/sim.2022.101.02.
[29] Liu YJ, Whelen S, Hall BD. Phylogenetic relationships among ascomycetes: evidence from an RNA polymerse II subunit. Mol Biol Evol. 1999;16(12):1799–1808. doi: 10.1093/oxfordjournals.molbev.a026092.
[30] Katoh K, Rozewicki J, Yamada KD. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Brief Bioinform. 2019;20(4):1160–1166. doi: 10.1093/bib/bbx108.
[31] Stamatakis A. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics. 2014;30(9):1312–1313. doi: 10.1093/bioinformatics/btu033.
[32] Lin Y-T, Shih H-H, Hulcr J, et al. Ambrosiella in Taiwan including one new species. Mycoscience. 2017;58(4):242–252. doi: 10.1016/j.myc.2017.02.004.
[33] Mayers CG, Harrington TC, Ranger CM. First report of a sexual state in an ambrosia fungus: *ambrosiella cleistominuta* sp. nov. associated with the ambrosia beetle *Anisandrus maiche*. Botany. 2017;95(5):503–512. doi: 10.1139/cjb-2016-0297.
[34] Six DL, Stone WD, de Beer ZW, et al. *Ambrosiella beaveri*, sp. nov., associated with an exotic ambrosia beetle, *Xylosandrus mutilatus* (Coleoptera: curculionidae, Scolytinae), in Mississippi, USA. Antonie Van Leeuwenhoek. 2009;96(1):17–29. doi: 10.1007/s10482-009-9331-x.
[35] V, Arx, JA, Hennebert GL. Deux Champignons Ambrosia. Mycopathol Mycol Appl. 1965;25(3-4):309–315. doi: 10.1007/BF02049918.
[36] Kostovcik M, Bateman CC, Kolarik M, et al. The ambrosia symbiosis is specific in some species and promiscuous in others: evidence from community pyrosequencing. Isme J. 2015;9(1):126–138. doi: 10.1038/ismej.2014.115.
[37] Mayers CG, Harrington TC, Bph W. Mycangia define the diverse ambrosia beetle-fungus symbioses. In: The convergent evolution of agriculture in humans and insects. Cambridge (MA): The MIT Press, 2022. p. 105–142. doi: 10.7551/mitpress/13600.003.0013.
[38] Musvuugwa T, de Beer ZW, Duong TA, et al. New species of Ophiostomatales from Scolytinae and Platypodinae beetles in the Cape Floristic Region, including the discovery of the sexual state of Raffaelea. Antonie Van Leeuwenhoek. 2015;108(4):933–950. doi: 10.1007/s10482-015-0547-7.
[39] Nel WJ, Wingfield MJ, de Beer ZW, et al. Ophiostomatalean fungi associated with wood boring beetles in South Africa including two new species. Antonie Van Leeuwenhoek. 2021;114(6):667–686. doi: 10.1007/s10482-021-01548-0.
[40] Procter M, Nel WJ, Marincowitz S, et al. A new species of Raffaelea from beetle-infested *Leucaena leucocephala*. Fungal Syst Evol. 2020;6(1):305–314. doi: 10.3114/fuse.2020.06.16.
[41] Gebhardt H, Kirschner R, Oberwinkler F. A new Ophiostoma species isolated from the ambrosia beetle *Xyleborus dryographus* (Coleoptera: Scolytidae). Mycol Progress. 2002;1(4):377–382. doi: 10.1007/s11557-006-0034-7.
[42] Jankowiak R, Strzałka B, Bilański P, et al. Two new *Leptographium* spp. reveal an emerging complex of hardwood-infecting species in the Ophiostomatales. Antonie Van Leeuwenhoek. 2017;110(12):1537–1553. doi: 10.1007/s10482-017-0905-8.
[43] Jankowiak R, Strzałka B, Bilański P, et al. Diversity of Ophiostomatales species associated with conifer-infesting beetles in the Western Carpathians. Eur J Forest Res. 2017;136(5-6):939–956. doi: 10.1007/s10342-017-1081-0.
[44] Jankowiak R, Ostafińska A, Aas T, et al. Three new *Leptographium* spp. (Ophiostomatales) infecting hardwood trees in Norway and Poland. Antonie Van Leeuwenhoek. 2018;111(12):2323–2347. doi: 10.1007/s10482-018-1123-8.
[45] Hong J-H, Jang Y, Jang S, et al. First report of *Leptographium pini-densiflorae* causing sapstain on *Pinus densiflora* in Korea. Mycotaxon. 2015;130(3):867–874. doi: 10.5248/130.867.
[46] Kim JJ, Lim YW, Breuil C, et al. A new Leptographium species associated with *Tomicus piniperda* infesting

pine logs in Korea. Mycol Res. 2005;109(Pt 3):275–284. doi: 10.1017/s0953756204002060.
[47] Kim G-H, Kim J-J, Lim YW, et al. Ophiostomatoid fungi isolated from *Pinus radiatalogs* imported from New Zealand to Korea. Can J Bot. 2005;83(3):272–278. doi: 10.1139/b04-170.
[48] de Beer ZW, Duong TA, Wingfield MJ. The divorce of Sporothrix and Ophiostoma: solution to a problematic relationship. Stud Mycol. 2016;83(1):165–191. doi: 10.1016/j.simyco.2016.07.001.
[49] Ostafińska A, Jankowiak R, Bilański P, et al. Six new species of Sporothrix from hardwood trees in Poland. MycoKeys. 2021;82:1–32. doi: 10.3897/mycokeys.82.66603.
[50] Jankowiak R, Strzałka B, Bilański P, et al. Ophiostomatoid fungi associated with hardwood-infesting bark and ambrosia beetles in Poland: taxonomic diversity and vector specificity. Fungal Ecol. 2019;39:152–167. doi: 10.1016/j.funeco.2019.02.001.
[51] Simmons DR, Li Y, Bateman CC, et al. *Flavodon ambrosius* sp. nov., a basidiomycetous mycosymbiont of Ambrosiodmus ambrosia beetles. mycotaxon. 2016;131(2):277–285. doi: 10.5248/131.277.
[52] Li Y, Bateman CC, Skelton J, et al. Wood decay fungus *Flavodon ambrosius* (Basidiomycota: Polyporales) is widely farmed by two genera of ambrosia beetles. Fungal Biol. 2017;121(11):984–989. doi: 10.1016/j.funbio.2017.08.004.
[53] Brader L. Etude de la Relation Entre le Scolyte Des Rameaux du Cafeier, Xyleborus Compactus Eichh. (X. morstatti Hag.), et sa Plante-Hote. 1964;64:1–109.
[54] Massoumi Alamouti S, Tsui CK, Breuil C. Multigene phylogeny of filamentous ambrosia fungi associated with ambrosia and bark beetles. Mycol Res. 2009;113(Pt 8):822–835. doi: 10.1016/j.mycres.2009.03.003.
[55] Campbell AS, Ploetz RC, Dreaden TJ, et al. Geographic variation in mycangial communities of *Xyleborus glabratus*. Mycologia. 2016;108(4):657–667. doi: 10.3852/15-133.
[56] de Errasti A, de Beer ZW, Coetzee MPA, et al. Three new species of Ophiostomatales from *Nothofagus* in Patagonia. Mycol Progress. 2016;15(2):1–15. doi: 10.1007/s11557-016-1158-z.
[57] Aghayeva DN, Wingfield MJ, Kirisits T, et al. *Ophiostoma dentifundum* sp. nov. from oak in Europe, characterized using molecular phylogenetic data and morphology. Mycol Res. 2005;109(10):1127–1136. doi: 10.1017/S0953756205003710.
[58] Roets F, de Beer ZW, Dreyer LL, et al. Multi-gene phylogeny for Ophiostoma spp. reveals two new species from *Protea infructescences*. Stud Mycol. 2006;55(1):199–212. doi: 10.3114/sim.55.1.199.
[59] de Beer ZW, Harrington TC, Vismer HF, et al. Phylogeny of the *Ophiostoma stenoceras-Sporothrix schenckii* complex. Mycologia. 2003;95(3):434–441. doi: 10.1080/15572536.2004.11833088.
[60] Zipfel RD, de Beer ZW, Jacobs K, et al. Multi-gene phylogenies define Ceratocystiopsis and Grosmannia distinct from Ophiostoma. Stud Mycol. 2006;55:75–97. doi: 10.3114/sim.55.1.75.
[61] de Meyer EM, de Beer ZW, Summerbell RC, et al. Taxonomy and phylogeny of new wood- and soil-inhabiting Sporothrix species in the *Ophiostoma stenoceras-Sporothrix schenckii* complex. Mycologia. 2008;100(4):647–661. doi: 10.3852/07-157R.
[62] Chen CC, Chen CY, Wu SH. Species diversity, taxonomy and multi-gene phylogeny of phlebioid clade (Phanerochaetaceae, Irpicaceae, Meruliaceae) of Polyporales. Fungal Diversity. 2021;111(1):337–442. doi: 10.1007/s13225-021-00490-w.
[63] Jang Y, Jang S, Lee J, et al. Diversity of wood-inhabiting polyporoid and corticioid fungi in Odaesan National Park, Korea. Mycobiology. 2016;44(4):217–236. doi: 10.5941/MYCO.2016.44.4.217.
[64] Tian X-M, Man X-W, Liu Z-B. *Irpex jinshaensis* sp. nov. and *I. subulatus* comb. nov. (Irpicaceae, Polyporales), evidenced by morphological characters and phylogenetic analysis. Phytotaxa. 2022;533(1):73–82. doi: 10.11646/phytotaxa.533.1.4.
[65] Floudas D, Hibbett DS. Revisiting the taxonomy of Phanerochaete (Polyporales, Basidiomycota) using a four gene dataset and extensive ITS sampling. Fungal Biol. 2015;119(8):679–719. doi: 10.1016/j.funbio.2015.04.003.
[66] Miettinen O, Larsson E, Sjökvist E, et al. Comprehensive taxon sampling reveals unaccounted diversity and morphological plasticity in a group of dimitic polypores (Polyporales, Basidiomycota). Cladistics. 2012;28(3):251–270. doi: 10.1111/j.1096-0031.2011.00380.x.
[67] Sjökvist E, Larsson E, Eberhardt U, et al. Stipitate stereoid basidiocarps have evolved multiple times. Mycologia. 2012;104(5):1046–1055. doi: 10.3852/11-174.
[68] Wu F, Chen JJ, Ji XH, et al. Phylogeny and diversity of the morphologically similar polypore genera *Rigidoporus*, Physisporinus, *Oxyporus*, and *Leucophellinus*. Mycologia. 2017;109(5):749–765. doi: 10.1080/00275514.2017.1405215.
[69] Wu SH, Nilsson HR, Chen CT, et al. The white-rotting genus Phanerochaete is polyphyletic and distributed throughout the phleboid clade of the Polyporales (Basidiomycota). Fungal Diversity. 2010;42(1):107–118. doi: 10.1007/s13225-010-0031-7.
[70] De Beer ZW, Seifert KA, Wingfield MJ. A nomenclator for ophiostomatoid genera and species in the Ophiostomatales and Microascales. BiodiverSity SerieS. 2013;12:245–322.
[71] Davidson RW. A New Species of Ceratocystis on Endothia Parasitica Canker of American Chestnut. Mycologia. 1978;70(4):856–858. doi: 10.1080/00275514.1978.12020293.
[72] Hjortstam K, Ryvarden L. Aphyllophorales from Northern Thailand. Nord J Bot. 1982;2(3):273–281. doi: 10.1111/j.1756-1051.1982.tb01189.x.
[73] Jusino MA, Skelton J, Chen C-C, et al. Sexual reproduction and saprotrophic dominance by the ambrosial fungus Flavodon subulatus (= *Flavodon ambrosius*). Fungal Ecol. 2020;47:100979. doi: 10.1016/j.funeco.2020.100979.