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RESEARCH ARTICLE

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Exploring Diversity within *Chytridiales* and *Rhizophydiales* (*Chytridiomycota*) in Korea

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ABSTRACT

Chytridiomycota is the most species-rich phylum of basal lineage fungi with a worldwide distribution. Its species constitute essential components of freshwater ecosystems. However, the diversity of this group in Korea remains understudied. A survey of *Chytridiales* and *Rhizophydiales* fungi was conducted in soil and freshwater environments in Korea, and seven strains were isolated. Based on morphological and molecular data, a previously unidentified, novel *Rhizophydium* species was discovered, designated *Rhizophydium multiplex* sp. nov. In addition, *Chytriomyces hyalinus* and *Globomyces pollinis-pini* were isolated for the first time in Korea. Detailed descriptions and illustrations of the three species are provided. This study highlights the potential diversity of chytrid fungi in Korea.

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Chytrid; diversity; freshwater; morphology; soil; taxonomy

1. Introduction

Chytridiomycota (chytrids) is an early diverging lineage of fungi distinguished by a motile zoospore with a single, polar flagellum [1]. The thalli of these fungi are typically microscopic and have varied morphology. Members of this phylum are widely distributed worldwide and have been identified in freshwater, terrestrial, and marine environments [2–4]. Chytrid fungi play essential roles in nutrient cycling, decomposition of organic matter, and regulating microbial communities' dynamics [5–7]. The growing interest in aquatic fungi, driven by advancements in DNA sequencing, has yielded profound insights into their potential ecological functions within these ecosystems. Chytrids are also pathogens to amphibian species, and plants. For example, *Batrachochytrium dendrobatidis* that grows in the keratinized skin cells of amphibians and is pathogenic to many species, causing population declines and extinction of some species [2,8,9]. *Synchytrium endobioticum* is an obligate parasite that infects some other plants of the genus *Solanum* and causes potato wart disease [10].

Classification of the *Chytridiomycota* has changed significantly over the years. Analysis of large-scale multigene phylogenies and morphological data suggests that *Chytridiomycota* is not monophyletic, resulting in the description of the new phylum *Blastocladiomycota* [11,12]. The new categorization of *Chytridiomycota* was supported by the comprehensive classification of fungi conducted by Hibbett et al. [13], with *Chytridiomycota* retained in a restricted sense, while *Blastocladiomycota* and *Neocallimastigomycota* are segregate phyla of flagellated fungi. *Chytridiomycota* has been described as containing nine classes comprising 10 orders [14]. In the annotation of genera of basal clades of fungi, two classes, 13 orders, 57 families, and 151 genera were recognized within the phylum according to the data available on these basal clades [15]. Currently, there are 15 recognized orders within *Chytridiomycota*: *Chytridiales*, *Cladochytriales*, *Gromochytriales*, *Lobulomycetales*, *Mesochytriales*, *Nephridiophagales*, *Polychytriales*, *Polyphagales*, *Rhizophydiales*, *Rhizophlyctidales*, *Saccopodiales*, *Spizellomycetales*, *Synchytriales*, *Zygophlyctidales*, and *Zygorhizidiales* [3,16]. Among these, *Rhizophydiales* and *Chytridiales* are the two largest orders.

Rhizophydiales contains numerous species of simple, eucarpic, endogenously developing chytrid fungi [17]. Most species have been retrieved from pollen baits, but some species grow on various other substrates,

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including decaying plant material, serpent skin, and algae [18,19]. *Rhizophydiales* comprises 19 families, 26 genera, and 244 species [16]. Only two species, *Batrachochytrium dendrobatidis* and *Rhizophydium koreanum* have been described in Korea [20].

Chytridiales includes eight families, 24 genera, and 331 species [16]. Members of the order are found in aquatic and terrestrial habitats, as well as parasites of algae, plants, and animals [3,21–23]. They exhibit diverse thallus forms that include inoperculate or operculate sporangia [12,22]. In Korea, there are no documented occurrences of *Chytridiales* species.

Research on the biodiversity of *Chytridiomycota* in Korea is scarce. Only three species, *B. dendrobatidis* Longcore, Pessier & D.K. Nichols, *Synchytrium minutum* (Pat.) Gäum., and *R. koreanum* Hyang B. Lee, S.J. Jeon, T.T.T. Nguyen have been reported in Korea to date [20,24]. To help fill this knowledge gap, we surveyed chytrid fungi in soil and freshwater environments in Korea. As a result of these efforts, we report seven strains of *Chytridiomycota*, representing three species.

In this study, we described a new species of *Rhizophydium multiplex* as well as two new records, *Chytriomyces hyalinus*, and *Globomyces pollinis-pini*, identified in soil and freshwater ecosystems in Korea.

2. Materials and methods

2.1. Sample collection, fungal isolation, and morphological studies

Freshwater and soil samples were collected from various regions in Korea as shown in Table S1. Samples were placed in polyethylene bags or sterile falcon tubes and maintained at ambient temperature until transported to the laboratory. Then, samples were processed according to the methodology described by Barr [25] and Davis et al. [26], and baited with pollen grains. Cultures were incubated for 7–14 days at 20 °C, and pure cultures were established on PmTG culture medium [25] (1 g peptonized milk, 1 g tryptone, 5 g glucose, 10 g agar, and 1 L distilled water, supplemented with 200 mg/L streptomycin sulfate and penicillin G). Pure isolates were maintained on PmTG agar slants in screwcap test tubes and stored in DMSO at −80 °C. The holotype was deposited at Chonnam National University (CNUFC) Fungarium (Gwangju, South Korea), as inactive dried cultures. Ex-type living cultures were deposited at the Environmental Microbiology Laboratory Fungarium, Chonnam National University (Gwangju, South Korea). The morphological features of pure cultures were observed under a differential interference contrast (DIC) microscope (Olympus BX51, Olympus, Tokyo, Japan).

2.2. DNA extraction, polymerase chain reaction, amplicon purification, and sequencing

Genomic DNA was extracted from cultures growing on PmTG using the Solg™ Genomic DNA Preparation Kit (SolGent Co. Ltd., Daejeon, South Korea) following the manufacturer's protocol. The purified DNA was stored at −20 °C for later use. For the amplification of the ITS and the LSU regions of rDNA, the primer pairs ITS5/ITS4 and LR0R/LR5 [27,28] were used, respectively. The PCR amplification products were then purified using an AccuPrep PCR Purification Kit (Bioneer, Daejeon, South Korea) and sequenced on the ABI PRISM 3730XL Genetic Analyzer (Applied Biosystems, Foster City, CA) using the same primers utilized in PCR.

2.3. Sequence alignment and phylogenetic analyses

Sequences were aligned using MAFFT v.7 (https://mafft.cbrc.jp/alignment/server) for each of the molecular markers, and then trimmed at both ends. Sequence alignment datasets were subsequently concatenated using MEGA7 [29]. Maximum-likelihood (ML) analyses were performed using RAxML-HPC BlackBox v.8.2.12 [30] on the XSEDE of the CIPRES Science Gateway (http://www.phylo.org/) [31] with rapid bootstrap (bs) analysis, followed by 1000 bs replicates. The resulting trees were visualized with FigTree v1.4.2 [32]. Bootstrap values are labeled on nodes. Values less than 75% bs are not shown. Newly obtained sequences and related sequences were deposited in GenBank (Table 1).

3. Results

3.1. Phylogenetic analyses

The phylogenetic tree of *Chytriomyces*, *Globomyces*, and *Rhizophydium* species and related taxa was determined using a combined sequence dataset of two loci (ITS and LSU). The aligned dataset contained 1638 characters (756 characters for ITS and 882 characters for LSU). The best RAxML tree with a final likelihood value of −22605.510955 is presented (Figure 1). Phylogenetic analyses of the combined ITS and LSU sequence dataset grouped the seven newly isolated strains in three species groups. Three strains, CNUFC YBW31, CNUFC YBW32, and CNUFC CPW16, were identified as *G. pollinis-pini*.

Table 1. Taxa used in this study and their GenBank accession numbers.

Species	Strain	GenBank accession no.	
		ITS	LSU
Alphamyces chaetifer	ARG025 [ET]	EF585646	EF585606
Batrachochytrium dendrobatidis	JEL197 [T]	NR_119535	AY546693
Betamyces americaemeridionalis	ARG063	EF585664	EF585624
Brevicalcar kilaueaense	JEL0350	MT730703	MT730703
Chytriomyces hyalinus	ARG085	JX905538	JX905511
Chytriomyces hyalinus	ARG097	JX905540	JX905513
Chytriomyces hyalinus	**CNUFC CHW6**	**PQ624791**	**PQ624798**
Coralloidiomyces digitatus	PL163L [T]	NR_119652	EF634248
Delfinachytrium mesopotamicum	BAFC ARG 113 [T]	NR_111810	NG_042746
Delfinachytrium mesopotamicum	ARG16	JX905544	JX905517
Fimicolochytrium jonesii	JEL0569	MT730748	MT730748
Globomyces pollinis-pini	ARG068 [ET]	NR_119649	EF585625
Globomyces pollinis-pini	JEL300	DQ485622	DQ485556
Globomyces pollinis-pini	**CNUFC YBW31**	**PQ632292**	**PQ624795**
Globomyces pollinis-pini	**CNUFC YBW32**	**PQ632293**	**PQ624796**
Globomyces pollinis-pini	**CNUFC CPW16**	**PQ632294**	**PQ624797**
Gorgonomyces haynaldii	ARG024	EF585645	EF585605
Gorgonomyces haynaldii	ARG026 [ET]	EF585647	EF585607
Gorgonomyces limnicus	MFLUCC 23-0066 [T]	OR051770	OR051781
Mesochytrium penetrans	CALU-X-10	NA	FJ804153
Paranamyces uniporus	PL-157 [T]	DQ485685	DQ485594
Paranamyces uniporus	WJD193	KP723828	KP723821
Pateramyces corrientinensis	ARG046	NR_111261	EF585617
Pateramyces pingflumenensis	MFLUCC 23-0068 [T]	OR051766	OR051777
Powellomyces hirtus	CBS 663.73 [T]	JN943812	JN941005
Rhizoclosmatium globosum	JEL800	OL739367	MK543211
Rhizophydium brooksianum	JEL136 [T]	AY353256	NG_060069
Rhizophydium echinocystoides	B8	NA	MH933969
Rhizophydium jobii	OAS6 [T]	MN787067	MN759470
Rhizophydium globosum	JEL222	DQ485616	DQ485551
Rhizoclosmatium persicum	MP067 [T]	NA	NG_070922
Rhizoclosmatium pessaminum	JEL823 [T]	MT730833	NG_070937
Rhizophlyctis rosea	BR186	AY349106	AY349079
Rhizophlyctis rosea	CBS 576.84	EU379222	EU379179
Rhizophydium koreanum	CNUFC 17CPW1-1 [T]	NA	NG_081462
Rhizophydium koreanum	CNUFC 17CPW1-2	NA	MH298650
Rhizophydium multiplex	**CNUFC CHS56** [T]	PQ636463	**PQ624792**
Rhizophydium multiplex	**CNUFC CHS20**	PQ636464	**PQ624793**
Rhizophydium multiplex	**CNUFC CHS23**	PQ636465	**PQ624794**
Rodmanochytrium pyriforme	MP72	NA	MK543214
Rodmanochytrium sphaericum	CCIBt4546	MT410717	MT406235
Rodmanochytrium sphaericum	MP60	NA	MK543212
Rhopalophlyctis sarcoptoides	JEL794	NA	MK558057
Rhopalophlyctis sarcoptoides	B10	NA	MH933970
Uebelmesseromyces harderi	ATCC 24053	DQ485595	AY349087
Urceomyces sphaerocarpus	ARG038	EF585655	EF585615
Urceomyces sphaerocarpus	ARG048 [ET]	NR_119648	NG_042450

ATCC: American Type Culture Collection (Manassas, VA); CBS: Centraalbureau voor Schimmelcultures (Utrecht, The Netherlands); CCIBt: Culture Collection of Institute of Botany (São Paulo, Brazil); CNUFC: Chonnam National University Fungal Collection (Gwangju, South Korea); MFLU: Mae Fah Luang University Herbarium (Chiang Rai, Thailand); NA: no sequence available. "T" and "ET" represent ex-type and epitype, respectively. The sequences obtained in this study are in bold.

CNUFC CHW6 clustered with the known species *Chytriomyces hyalinus*. Other strains, CNUFC CHS56, CNUFC CHS20, and CNUFC CHS23, grouped in a single clade (Figure 1).

3.2. Taxonomy

Rhizophydium multiplex Hyang B. Lee **sp. nov.**

Index Fungorum number: IF 902434; Figure 2.

Etymology: Refers to a species producing multiple papillae.

Type: Republic of Korea, Gyeonggi Province, Suwon, Jangan-gu, Suwon stream, from a soil sample, February 25 2024, holotype CNUFC h2409, ex-type culture CNUFC CHS56.

Description: On PmTG agar, sporangia hyaline, spherical, up to 165 µm diam., and exhibiting multiple papillae. Discharge pores 5.5–13.5 µm diam. Rhizoids branched, 29.5–52.5 µm in length. Germlings possessed a rhizoidal axis. Zoospores released through a discharge pore and ranged (3.5–) 4–5.5(–6) µm diam. Upon discharge, zoospores were usually germinated in clusters. Resting spores not observed.

Additional material examined: Republic of Korea, Daejeon, Yuseong-gu, Sindong, Somunsanseong Fortress, from a soil sample, November 13 2021, culture CNUFC CHS20 and CNUFC CHS23.

Notes: A BLASTn search of the ITS and LSU region of CNUFC CHS56, CNUFC CHS20 and CNUFC

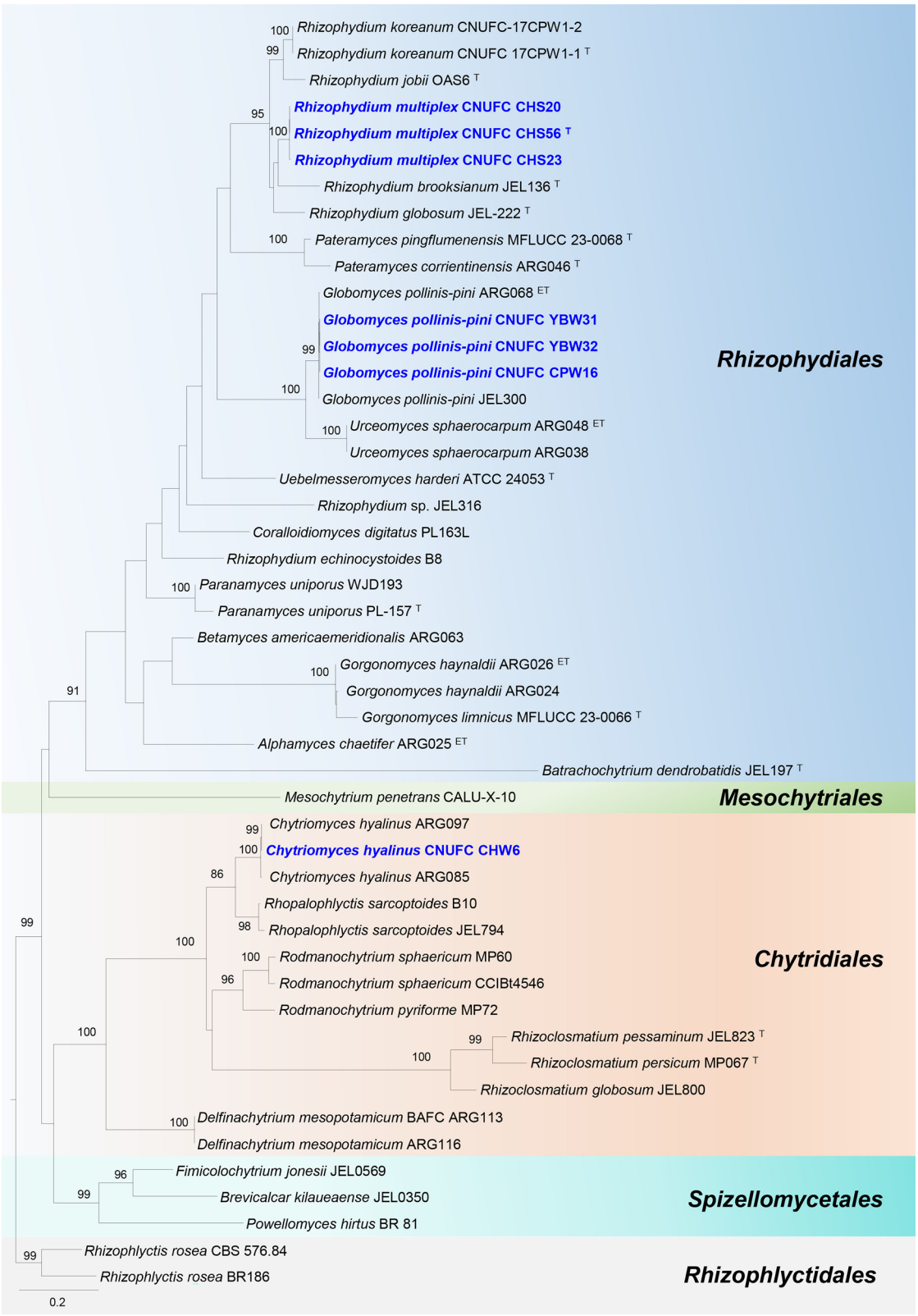

Figure 1. Phylogenetic relationships among *Chytriomyces, Globomyces and Rhizophydium* species, and related taxa as determined by combined ITS and LSU sequence analyses. The numbers above or below branches represent maximum-likelihood bootstrap percentages. Bootstrap values >75 are shown. *Rhizophlyctis rosea* CBS 576.84 and *Rh. rosea* BR186 were used as outgroups. Ex-type and epitype strains are marked with ^{T}, and ^{ET}, respectively. Newly generated sequences in this study are in bold blue.

CHS23 showed similarity of 93.85% (229/244 bp) and 96.83% (915/945) with ex-type species *Rhizophydium brooksianum* JEL136 (GenBank accession no. NG_060069).

Chytriomyces hyalinus Karling, American Journal of Botany 32 (7): 363 (1945) (Figure 3).

Description: On PmTG agar, colony light-brown, slowly growth. Thallus monocentric, epibiotic,

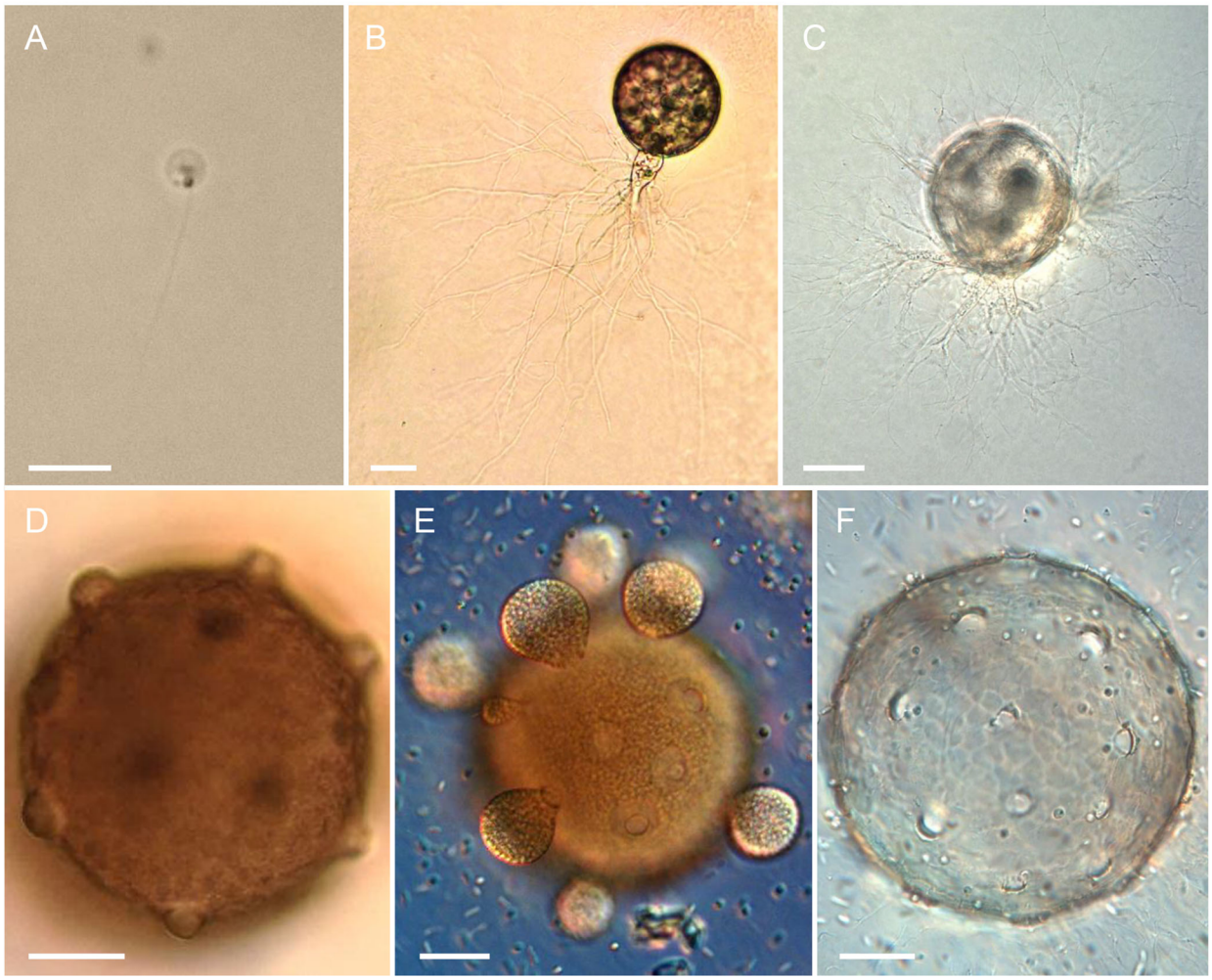

Figure 2. Morphology of *Rhizophydium multiplex* on PmTG agar medium. (A) Zoospore; (B, C) immature zoosporangium with rhizoid; (D) mature zoosporangium with multiple papillae; (E) mature zoosporangium released zoospores; (F) empty zoosporangium with discharged pores. Scale bars: A = 10 μm, B–F = 20 μm.

eucarpic. Sporangia hyaline, spherical, 27–49.5 μm diam. Operculum apical or subapical, shallow, or saucer-shaped, 8–15.5 μm. Zoospores oval to spherical, 4.5–6 μm diam. Flagellum 10–13 μm long. Rhizoids well-developed, branched.

Strain examined: Republic of Korea, Jeonbuk Province, Gochang-gun, Haeri-myeon, Bangchuk-ri, a freshwater sample, February 17 2023, culture CNUFC CHW6.

Notes: A BLASTn search of the ITS and LSU region of CNUFC CHW6 showed similarity of 100% (631/631 bp) and 100% (800/800 bp) with *Chytriomyces hyalinus* (GenBank accession nos. JX905538 and JX905513), respectively.

Globomyces pollinis-pini (A. Braun) Letcher, Mycological Research 112(7): 777 (2008) (Figure 4).

Description: On PmTG agar, colony white ivory, slowly growth. Thallus monocentric, eucarpic, epibiotic. Sporangia spherical, 19.5–31 μm diam. Zoospores spherical, some irregular, 4.5–6 μm diam., with a posterior flagellum. Flagellum 25–31.5 μm long. Rhizoids from a single axis, sparsely branched. Resting spores not observed.

Strain examined: Republic of Korea, Gwangju, fields of paddy rice at Chonnam National University (35°10′23.8″N 126°53′53.2″E), a freshwater sample, January 15 2024, culture CNUFC YBW31 and CNUFC YBW32; Gyeonggi Province, Suwon-si, Jangan-gu, Suwon stream, from a freshwater sample, February 25 2024, culture CNUFC CPW16.

Notes: A BLASTn search of the ITS and LSU region of CNUFC YBW31, CNUFC YBW32, and CNUFC CPW16 showed similarity of 100% (731/731 bp) and 100% (849/849 bp) with epitype strain of *G. pollinis-pini* ARG068 (GenBank accession nos. NR_119649 and NG_042451), respectively.

4. Discussion

In this study, we described a newly identified species *Rhizophydium multiplex*, as well as two species *C. hyalinus*, and *G. pollinis-pini*, not previously reported in Korea, classified through a polyphasic taxonomy approach based on morphological and phylogenic analysis of ITS and LSU rDNA.

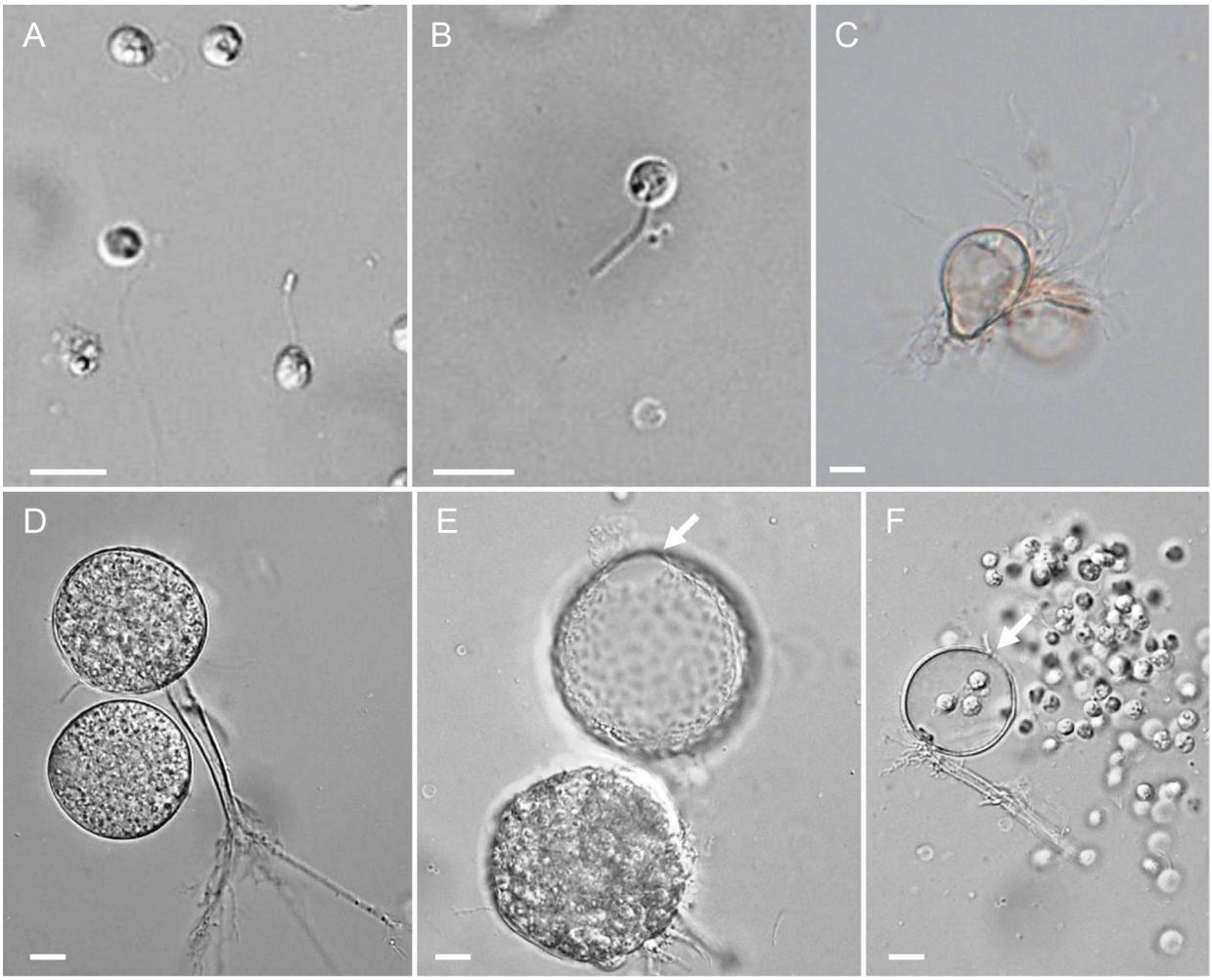

Figure 3. Morphology of *Chytriomyces hyalinus* on PmTG agar medium. (A) Zoospores; (B) zoospore germination; (C) rhizoids developed from thallus; (D) zoosporangium with a long rhizoid axis; (E, F) empty zoosporangium with attached operculum (white arrow). Scale bars = 10 µm.

In the constructed phylogenetic tree (Figure 1), *R. multiplex* is phylogenetically related to *R. brooksianum*, isolated from pollen bait in a water culture containing garden soil from Penobscot County, Maine [33]. *Rhizophydium multiplex* is distinguished from *R. brooksianum* by its larger mature zoosporangium and discharge pore and size. *Rhizophydium brooksianum* has fewer discharge pores compared to *R. multiplex*. The genus *Rhizophydium* is the oldest genus within the order *Rhizophydiales*, proposed by Schenk [34] and validated by Rabenhorst [35], with *Rhizophydium globosum* as the type species. The species of this genus are characterized by the formation of spherical zoosporangia with multiple discharging pores and branched rhizoids arising from the sporangium [36,37]. Members of the genus inhabit aquatic ecosystems, predominantly as algal parasites and as saprotrophs on pollen, keratin, and the soil [36–40]. Several species in chytrids play an important functional role in lake nutrient cycles and food webs [5,41]. McKindles et al. [42] list *Rhizophydium* sp. as an obligate parasite of *Planktothrix agardhii* from Laurentian Great Lakes Embayment. Kol [43] reported that a chytrid, morphologically identified as *Rhizophydium sphaerocarpum*, can infect the glacier alga *Ancylonema nordenskioldii* on a glacier in Alaska.

In recent years, ultrastructural and molecular analyses have been implemented to classify genus species, resulting in significant taxonomical changes [44,45]. Many *Rhizophydium* species have been reclassified into new genera [19,44–46]. Currently, there are 218 accepted species in this genus [16]. Only one species from a freshwater habitat has been reported in Korea [20].

The genus *Chytriomyces* belonging to the order *Chytridiales*, family *Chytridiaceae*, was described by Karling [47] with the concurrent descriptions of *C. hyalinus* and *C. aureus*, observed on chitin fragments or mayfly exuviae collected in Brazil and the eastern United States. However, Karling did not specify which species would serve as the genus type. Members of this genus are commonly found in soil, mud, and water [21,22,47–50]. Until now, 29 *Chytriomyces* species have been described according to the Index Fungorum database (*Source*: www.indexfungorum.org as of October 2024). Multigene

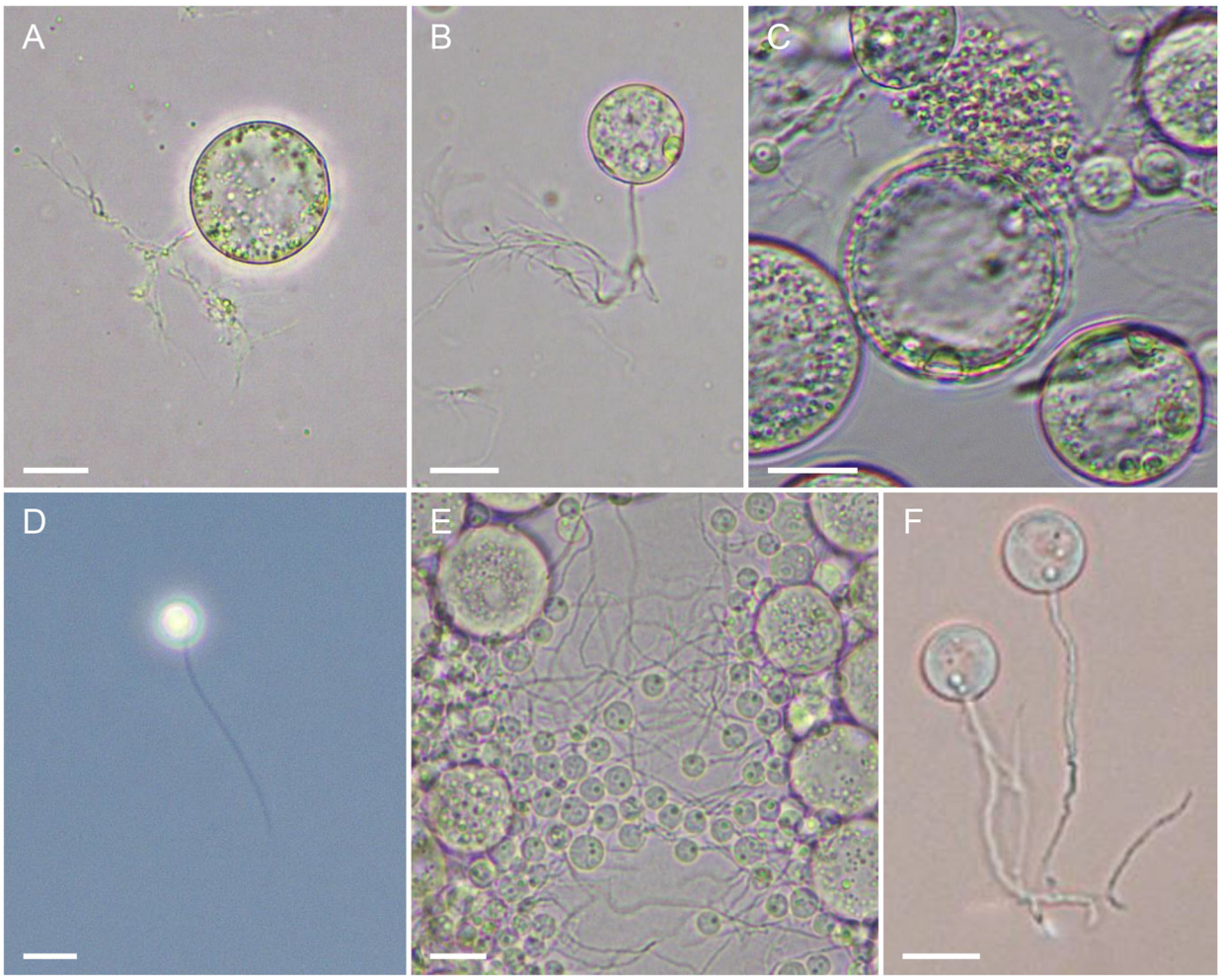

Figure 4. Morphology of *Globomyces pollinis-pini* on PmTG agar medium. (A, B) Mature zoosporangium with basal rhizoid; (C) mature zoosporangium with cleaved zoospores being discharged; (D) zoospore; (E, F) germling with a rhizoidal axis. Scale bars = 10 μm.

phylogenetic analysis of a combined ITS and LSU sequences dataset indicates that our strain CNUFC CHW6 and *C. hyalinus* ARG097 clustered together with 100% MLBS support (Figure 1). Moreover, the strain identified in this study is similar to *C. hyalinus*, as described by Karling [47], such as shape of the sporangium, zoospores, and operculum. Our strain CNUFC CHW6 has some differences in size of sporangia and zoospores in comparison to previously described by Karling [47] (sporangia: 10–60 μm; zoospores: 3–3.5 × 5–5.5 μm). The type and strains in the present study were isolated from freshwater habitats.

Genus *Globomyces* belonging to the order *Rhizophydiales*, family *Globomycetaceae*, was described by Letcher et al. [51], and typified by *G. pollinis-pini* (A. Braun) Letcher. The genus is characterized by sporangium spherical with a single discharge pore. Zoospore contains a single lipid globule partially covered with a prominent fenestrated cisterna [51]. Species of *Globomyces* are found in soil, freshwater, or algae [51]. Currently, it contains two species, *G. pollinis-pini* and *Urceomyces sphaerocarpus* (Zopf) Letcher [16,51]. Genus *Globomyces* has not previously been reported in Korea. The combined ITS and LSU phylogeny indicates that our strains clustered together with *G. pollinis-pini* strains (ARG 068 (epitype), and JEL300) with 100% MLBS support (Figure 1). The morphological characteristics of *G. pollinis-pini* CNUFC YBW31/YBW32/CPW16 were similar to *G. pollinis-pini* described by Letcher et al. [51]. We observed minor differences in the size of certain microstructures between the Korean and type strains. Sporangia size of Korean specimen (19.5–31 μm) is slightly larger than that of *G. pollinis-pini* ARG 068 (reaching up to 25 μm). *Globomyces pollinis-pini* was isolated from water and soil [51] and from water sample in the current study.

Until now, only three *Chytridiomycota* species have been documented in Korea. The diversity of chytrid fungi in Korea has still not been adequately researched. The information presented in this article contributes to our understanding of the diversity and distribution of chytrid fungi in Korea. In this study, one new species and two new records belonging to *Rhizophidiales*

and one species belonging to *Chytridiales* were isolated from soil and water habitats in Korea. This implies that there are diverse chytrid fungi in various habitats in Korea that should be identified and characterized. Further research will focus on the diversity of *Rhizophidiales* and *Chytridiales* from different habitats and sampling sites across Korea.

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Disclosure statement

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

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