RESEARCH ARTICLE

# Three Unreported Fungi Isolated From Reservoirs in Korea: *Mortierella biramosa*, *Paraphoma radicina*, and *Sordaria macrospora*

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# **ABSTRACT**

Freshwater ecosystems have a large reserve of latent biological resources that play an essential ecological role, and have significant economic and social value. Fungi in freshwater are prospective materials that can be used in the food, medicine, and biomass energy fields. In this study, three promising fungal species were isolated from freshwater ecosystems in Korea. These isolates were identified as *Mortierella biramosa*, *Paraphoma radicina*, and *Sordaria macrospora*, based on their cultural and morphological characteristics, as well as molecular phylogenetic analyses. These species were previously unknown in Korea. The finding allows us to explore its physiological and biochemical characteristics in more detail and use them as biological resources.

Keywords: Cultivation, Freshwater, Fungi, Morphology, Phylogeny





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#### INTRODUCTION

Freshwater ecosystems have many biological resources and play an important ecological role in the material cycle, energy flow, and environmental maintenance [1]. Biological resources are vital for the development of healthy freshwater ecosystems and have significant economic and social value [1,2]. Among these diverse biological resources, microorganisms are promising materials with great potential for use in the food, medicine, and biomass energy fields [3,4]. In particular, fungal resources are prospective materials for the development of biocontrol agents, medicines, cosmetics, and food [5,6].

Many recent studies have indicated that fungi are abundant in freshwater ecosystems. With advances in DNA sequencing technology, diverse fungal taxa have been discovered in a range of freshwater habitats [7-9]. Culture-independent detection provides information on the taxonomic diversity of aquatic fungi [10-12]. However, studies on freshwater fungi to determine their ecological functions and physiological features are still lacking. To understand the physiological ecology of fungi, cultivation followed by isolation from their natural habitats is necessary. Cultivation-based techniques facilitate the identification of morphological,

physiological, and biochemical characteristics of fungi for subsequent use as biological resources.

According to previous studies, the predominant fungal genera in freshwater habitats are *Aspergillus*, *Penicillium*, and *Cladosporium* [13-16], which have been frequently isolated from freshwater using culture-based methods. However, in the present study, three fungal species that are not linked to the predominant genera were isolated from reservoirs in Korea, namely *Paraphoma radicina*, *Sordaria macrospora*, and *Mortierella biramosa*. These have not been previously reported in Korea. We investigated morphological and molecular phylogenetic characteristics of these fungal species.

## MATERIALS AND METHODS

## **Fungal isolation**

Soil sediment, clams, and freshwater samples were collected from the reservoirs (Table 1). To isolate fungal strains from the soil sediment, a dilution plate method was used with a 1:10 dilution. The soil suspension was spread onto potato dextrose agar (PDA; Difco, Detroit, MI, USA). For the water samples, a simple plating technique was used for spreading the samples onto the PDA. The clamshells were washed with distilled water and cut into 2 mm<sup>2</sup> pieces, before being placed on the PDA. Rifampicin (15 ppm) was added to the medium to limit bacterial growth. After incubation for 2-3 days at 25°C in the dark, new hyphal tips were isolated from the outgrowing mycelia and then transferred onto fresh PDA. The new isolates were incubated for approximately 10 days at 25°C. The resultant cultures were deposited at the Nakdonggang National Institute of Biological Resources (NNIBR).

Table 1. Information on Mortierella, Paraphoma, and Sordaria isolates from reservoirs in Korea.

Sequence ID	Species	Culture No.	Source	Sampling date	Sampling location	GenBank Acc. No. 28S/ITS/β-tubulin
W251	Paraphoma radicina	NNIBRFG31692	Water	29 June 2016	Donggok-dong Gwangsan-gu, Gwangju (35°04'59.4"N, 126°46'35.3"E)	OM758251/ OM758271/-
W471	Sordaria macrospora	NNIBRFG31693	Shellfish	04 Jan. 2017	Mangyeong-eup, Gimje-si, Jeollabuk-do (35°51'10.0"N, 126°49'22.2"E)	OM758252/ OM758272/ OM970804
W913	Mortierella biramosa	NNIBRFG24241	Soil sediment	15 May 2019	Ungchi-myeon, Boseong-gun, Jeollanam-do (34°41'51.3"N, 126°59'21.9"E)	OM758253/ OM758273/-

ITS: the internal transcribed spaer of rDNA.

# **Cultural and morphological analyses**

The characteristics of the cultures were investigated 3-7 days after inoculation of the isolates on PDA at 25°C in the dark. After a week, the microscopic structures of the isolates were observed under a Zeiss Axio Imager A2 microscope (Carl Zeiss, Oberkochen, Germany), and then photographed using an Axiocam 512 color camera (Carl Zeiss).

## DNA extraction, amplification, and sequencing

The genomic DNA of the strains was isolated using the MagListo 5 M plant Genomic DNA Extraction Kit (Bioneer, Daejeon, Korea), based on magnetic bead technology. The 28S large subunit (LSU) and internal transcribed spacer (ITS) of ribosomal DNA regions were amplified with PCR using primer sets LROR/LR5 [17] and ITS1/ITS4 [18], respectively. The partial nuclear β-tubulin gene of the *Sordaria* isolate was amplified using Bt2a/Bt2b [19]. The DNA amplicons were purified using an AccuPrep PCR Purification Kit (Bioneer), and sequenced by Macrogen, Inc. (Seoul, Korea). The sequences were registered in the National Center for Biotechnology Information (NCBI) GenBank database (Table 1).

# Phylogenetic analysis

The DNAStar software package version 5.05 (DNAStar, Inc., Madison, WI, USA) was used for sequence editing. The edited sequences were blasted to search for the closest reference sequences from the NCBI. The sequence data for Korean strains and reference sequences from previously published type or authentic isolates were aligned using MAFFT 7 [20], with the Q-INS-i algorithm [21]. Minimum evolution (ME) and maximum likelihood (ML) analyses were used to construct phylogenetic trees with MEGA X [22] using the Tamura-Nei model. Bootstrapping analysis was performed with 1,000 replicates. Multilocus phylogenetic analysis was performed after the sequences of the individual markers had been concatenated in SequenceMatrix v1.7.8 [23].

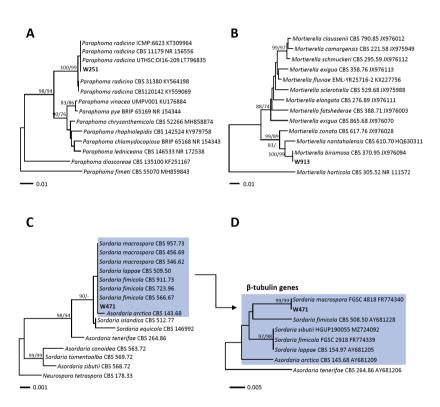
## **RESULTS**

The three fungal strains W251, W471, and W913, were isolated from water, shellfish, and soil sediment, respectively, from three different reservoirs, and were investigated phylogenetically and morphologically.

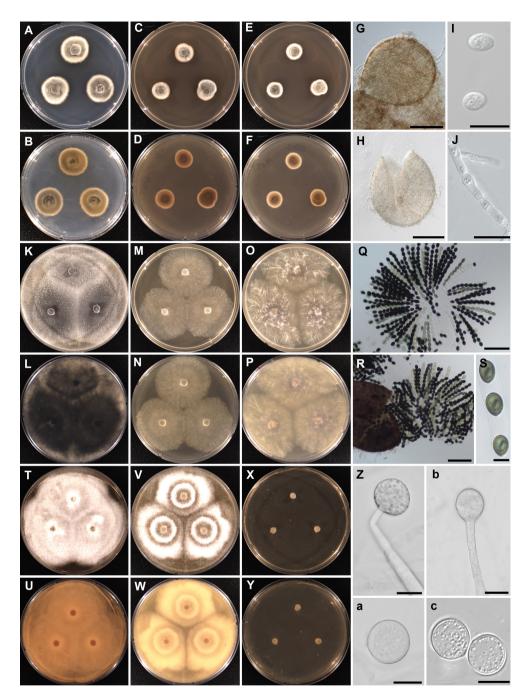
The isolate W251 belonging to the species *Paraphoma radicina* matched the epitype strain of CBS 11179 (NR\_156556 in ITS, NG\_070446 in 28S rDNA) with sequence similarities of 100% (486/486 bp) in ITS and 99.8% (843/845 bp) in 28S rDNA in the BLASTn search. The ITS and 28S rDNA sequences of isolate W471 belonging to the *Sordaria macrospora* were identical to those of strain CBS 346.62 (MH858175 in ITS, MH869769 in 28S rDNA). The sequence of β-tubulin of W471 was identical to that of strain FGSC 4818 (FR774340) belonging to species *S. macrospora*. With β-tubulin sequences, *S. macrospora* can be distinguished from the other known *Sordaria* species, whereas its ITS and 28S rDNA sequences were identical to those of *S. lappae* and *S. fimicola*. The isolate W913 of the species *Mortierella biramosa* matched the CBS 370.95 strain (JX976094 in ITS, HQ667389 in 28S) with sequence similarities of 100% (555/555 bp) for ITS and 99.9% (872/873 bp) for 28S rDNA sequences.

Phylogenetic relationships between the Korean and other previously published authentic isolates were analyzed using ME and ML analyses of the ITS rDNA sequences for *Paraphoma* (Fig. 1A) and *Mortierella* (Fig. 1B), and the concatenated alignment of ITS and 28S rDNA sequences for *Sordaria* (Fig. 1C). In

Fig. 1, only the ME tree is shown because the topologies constructed from both analyses are congruent. The Korean isolate W251 was grouped with previously published isolates of species *Paraphoma radicina*, including the epitype strain of CBS 11179, with high bootstrap values of 100% for ME and 99% for ML. In the BLASTn search results, the ITS sequence of the Korean isolate W251 was identical to that of strain CBS 111.79 (NR\_156556). The ITS sequence of isolate W913 was identical to that of the authentic strain CBS 370.95 (JX976094) of species *Mortierella biramosa*, and the two strains were grouped together in the phylogenetic tree. This grouping was supported by high bootstrap values of 100% for ME and 99% for ML. The Korean isolate W471 was grouped with three *Sordaria* species, namely *S. macrospora*, *S. lappae*, and *S. fimicola* in the tree inferred from a concatenated alignment of ITS and 28S rDNA sequences. In the β-tubulin tree (Fig. 1D) for the indistinguishable taxa in the ITS and 28S tree (in the blue box in Fig. 1C), the isolate W471 was grouped with *S. macrospora* with a high bootstrap value of 99% in ME and ML, and was distinguishable from *S. lappae* and *S. fimicola*.



**Fig. 1.** Minimum evolution phylogenetic trees of (A) *Paraphoma*, (B) *Mortierella* species based on ITS rDNA sequences, (C) *Sordaria* species based on a combined dataset of internal transcribed spacer (ITS) and 28S rDNA sequences, and (D)  $\beta$ -tubulin sequences of *Sordaria* species in a blue box of (C). Bootstrapping values of minimum evolution and maximum likelihood, higher than 70%, are presented above the branches (1,000 replicates). The scale bar represents the number of nucleotide substitutions per site. The strains that were collected in Korea are shown in bold.



**Fig. 2.** Cultural and morphological characteristics of *Paraphoma radicina* NNIBRFG31692 (W251; A-J), *Sordaria macrospora* NNIBRFG31693 (W471; K-S), and *Mortierella biramosa* NNIBRFG24241 (W913; T-c). Colonies on potato dextrose agar (first column), V8 juice agar (second column), corn meal agar (third column) after incubation for 72 h at 25°C; upper at obverse view and lower at reverse view. *Paraphoma radicina*: pycnidia (G, H), conidia (I), and conidiogenous cells (J) (scale bars: G, H=100 μm, I, J=10 μm). *Sordaria macrospora*: rosettes of asci (Q), opening of perithecium (R) and ascospores (S) (scale bars: Q, R=100 μm, S=20 μm). *Mortierella biramosa*: sporangium on the sporangiophores (Z, b, a) and chlamydospores (c). Scale bars: 20 μm.

### **Taxonomy**

#### Paraphoma radicina (McAlpine) Morgan-Jones & J.F. White (1983) [MB#109141] (Fig. 2A-J)

**Description:** Colonies formed a radiate pattern with short and dense aerial mycelia on PDA, V8A, and CMA at 25°C. Aerial mycelium white to pale grey. Pycnidia setose; globose to subglobose; brown to blackish-brown; non-papillate or papillate ostioles; 180-450  $\mu$ m in diameter. Conidiogenous cells bottle-shaped; 5-7×3-7  $\mu$ m. Conidia aseptate; ellipsoidal to subglobose; 3-6×1-3  $\mu$ m.

**Isolate examined:** Korea, Gwangju; Gwangsan-gu; Donggok-dong (35°04'59.4"N 126°46'35.3"E), ex freshwater, June 29, 2016, Y.-J. Choi (NNIBRFG31692, W251).

#### Sordaria macrospora Auersw. (1866) [MB#237763] (Fig. 2K-S)

**Description:** Sparse aerial mycelia of pale white color formed on the PDA, V8A, and CMA. After two weeks, dark pycnidia and perithecia formed on the PDA. Vegetative hyphae hyaline; up to 5  $\mu$ m wide. Perithecia pyriform; setose; 370-400 $\times$ 250-300  $\mu$ m. Setae were scarce; smooth-walled. Asci with truncate apex and apical rings unitunicate; aseptate, cylindrical; 8 spored, 160-175 $\times$  ca. 20  $\mu$ m in size; formed rosettes. Ascospores uniseriate; linearly arranged; green to pale brown, later brown; 22-35 $\times$ 15-20  $\mu$ m.

**Isolate examined:** Korea, Jeollabuk-do; Gimje-si; Mangyeong-eup (35°51'10.0"N 126°49'22.2"E), ex clamshell, Jan. 4, 2017, Y.-J. Choi (NNIBRFG31693, W471).

#### Mortierella biramosa Tiegh. (1875) [MB#240881] (Fig. 2T-c)

Description: Colonies formed a radiate pattern with cottony aerial mycelia on PDA and V8A. On CMA showed submerged growth. Colony diameter on PDA, V8A, and CMA >70 mm at 25°C, after 72 h. Sporangiophores 300-1,500 μm long. Sporangia globose; 30-40 μm in diameter. Sporangiospores globose; smooth-walled with granular contents 5-8 μm in diameter. Chlamydospores globose; 15-35 μm in diameter. Isolate examined: Korea, Jeollanam-do, Boseong-gun, Ungchi-myeon (34°41'51.3"N 126°59'21.9"E), ex soil sediment, May 15, 2019, B. Nam and Y.-J. Choi (NNIBRFG24241, W913).

#### DISCUSSION

Cultural, morphological, and phylogenetic characteristics of the isolate W251 was identical to *Paraphoma radicina* (McAlpine) Morgan-Jones & J.F. White [24], which is the type species for the genus *Paraphoma*. This genus was initially introduced as a section of *Phoma* but later resurrected as a distinct genus. It is differentiated by its setose pycnidia and dictyochlamydospores [24,25]. *Paraphoma* have been predominantly isolated from the rhizosphere and the phyllosphere of crops and trees, with several species being identified as plant pathogens [25-27], but also reported in freshwater [28-30] and brackish [31] habitats. *P. radicina* has been isolated from wood and herbaceous debris submerged in aquatic ecosystems [29-31]. The Korean isolate W251 was isolated from reservoir water. *P. radicina* produces chemical compounds for antimicrobial activity against bacteria and fungi [28,29]. El-Elimat et al. [29] identified nine compounds belonging to isochromenones, isobenzofuranones, and tetrahydronaphthalenes from *P.* 

radicina isolated from wood in a lake, and then evaluated their antimicrobial activity. Of these compounds, clearanol C and isobenzofuranone showed promising antimicrobial activity against *Staphylococcus aureus* and *Candida albicans*, respectively. *P. radicina* could be useful as a bioresource in bioindustry. The presence of *P. radicina* in freshwater habitat is also remarkable. This species may play an ecologically important role in biogeochemical cycles in freshwater ecosystems, as they are distributed across a diverse range of sources, such as plant debris and water.

Isolate W471 obtained from shellfish on the reservoir shore was consistent with the cultural, morphological, and phylogenetic descriptions of Sordaria macrospora Auersw. [32,33]. This species serves as a model organism for studying fungal sexual fruiting body formation [34]. The genus Sordaria has been reported in freshwater environments [35,36] as well as in wood [37-39] and grass [40], and other terrestrial plants. S. macrospora is a well-known coprophilous fungus that is commonly isolated from herbivore dung [41]. However, the Korean isolate W471 was found in clam shells in the reservoir riparian zone. To our knowledge, S. macrospora inhabiting freshwater mollusks has not been previously recorded. Previous studies have reported shellfish-derived fungi focusing on pathogenic fungi, such as Aspergillus, Fusarium, and Penicillium, isolated from marine bivalve mollusks [42-44], whereas saprophytic fungi associated with freshwater bivalves have been poorly studied. There is a lack of research on the role of fungi in the metabolism of bivalves, although the presence of fungi in mollusks has long been known [45]. Future studies are warranted to investigate the ecological role of fungi inhabiting bivalve mollusks. The class Sordariomycetes, including the genus Sordaria, is a key freshwater fungal group, which accounts for half of the total known fungi in freshwater ecosystems [35,46]. This study demonstrated the presence of Sordaria in clam shells. Their ecological functions should be studied further to understand the relationship between Sordaria and shellfish.

Isolate W913 was identified as *Mortierella biramosa* Tiegh. based on their cultural, morphological, and molecular phylogenetic analyses [47-49]. This strain was found from the soil sediment in the reservoir in the present study. The genus *Mortierella* is commonly found in terrestrial ecosystems and is known for being beneficial in promoting plant growth [50-52]. Some members of *Mortierella* produce an important polyunsaturated fatty acid and arachidonic acid (ω-6,5,8,11,14-cis-eicosatetraenoic acid; ARA). They have diverse functions in the human body and broad applications in industrial fields [53]. This group is also distributed in freshwater ecosystems, including water, plants, and soil [54,55], with a remarkable capacity to decompose organic matter [56]. *Mortierella elongata*, *M. horticola*, *M. humilis* [55], and a new species, *M. fluviae* [57], were reported in a freshwater sample in Korea. *M. biramosa* W913 obtained in the present study was also isolated from the littoral zones of the reservoir. The presence of *Mortierella* in freshwater has often been documented, but their ecological roles are still unknown. The *Mortierella* species in freshwater ecosystems may be highly valuable. Therefore, further research is required to analyze their biological activities.

Given the biochemical and biophysical distinctions highlighted in previous studies, these isolates could be used as bioresources. Therefore, this study provides essential information for future studies on the potential use of these isolates as biological materials.

## **CONFLICT OF INTERESTS**

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

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## REFERENCES

- Bailey RC, Norris RH, Reynoldson TB. Bioassessment of freshwater ecosystems. Bioassessment of freshwater ecosystems: Using the reference condition approach. Boston: Springer; 2004. p. 1-15.
- 2. Carpenter SR, Stanley EH, Vander Zanden MJ. State of the World's freshwater ecosystems: Physical, chemical, and biological changes. Annu Rev Environ Resour 2011;36:75-99.
- 3. Sharma P, Slathia PS, Raina N, Bhagat D. Chapter 9 Microbial diversity in freshwater ecosystems and its industrial potential. In: Bandh SA, Shafi S, Shameem N, editors. Freshwater Microbiology. Cambridge: Academic Press; 2019. p. 341-92.
- 4. Okafor N. Ecology of microorganisms in freshwater. In: Okafor N, editor. Environmental microbiology of aquatic and waste systems. Dordrecht: Springer Netherlands; 2011. p. 111-22.
- 5. Kalra R, Conlan XA, Goel M. Fungi as a potential source of pigments: Harnessing filamentous fungi. Fungal Divers 2020;8:369.
- Kaur K, Verma RK. Chapter 2 fungal resources: Current utilization, future prospects, and challenges. In: Singh J, Gehlot P, editors. New and Future Developments in Microbial Biotechnology and Bioengineering. Amsterdom: Elsevier; 2020. p. 15-38.
- 7. Grossart H-P, van den Wyngaert S, Kagami M, Wurzbacher C, Cunliffe M, Rojas-Jimenez K. Fungi in aquatic ecosystems. Nat Rev Microbiol 2019;17:339-54.
- 8. Krauss G-J, Solé M, Krauss G, Schlosser D, Wesenberg D, Bärlocher F. Fungi in freshwaters: Ecology, physiology and biochemical potential. FEMS Microbiol Rev 2011;35:620-51.
- Grossart H-P, Wurzbacher C, James TY, Kagami M. Discovery of dark matter fungi in aquatic ecosystems demands a reappraisal of the phylogeny and ecology of zoosporic fungi. Fungal Ecol 2016;19:28-38.
- Wurzbacher C, Warthmann N, Bourne EC, Attermeyer K, Allgaier M, Powell JR, Detering H, Mbedi S, Grossart H-P, Monaghan MT. High habitat-specificity in fungal communities in oligo-mesotrophic, temperate Lake Stechlin (North-East Germany). MycoKeys 2016;16:17-44.
- 11. Ishida S, Nozaki D, Grossart H-P, Kagami M. Novel basal, fungal lineages from freshwater phytoplankton and lake samples. Environ Microbiol Rep 2015;7:435-41.
- Jobard M, Rasconi S, Solinhac L, Cauchie HM, Sime-Ngando T. Molecular and morphological diversity of fungi and the associated functions in three European nearby lakes. Environ Microbiol 2012;14:2480-94.
- 13. Čomić L, Ranković B, Novevska V, Ostojić A. Diversity and dynamics of the fungal community in Lake Ohrid. Aquat Biol 2010;9:169-76.
- Gonçalves VN, Vaz AB, Rosa CA, Rosa LH. Diversity and distribution of fungal communities in lakes of Antarctica. FEMS Microbiol Ecol 2012;82:459-71.

- Shearer CA, Descals E, Kohlmeyer B, Kohlmeyer J, Marvanová L, Padgett D, Porter D, Raja HA, Schmit JP, Thorton HA, et al. Fungal biodiversity in aquatic habitats. Biodivers Conserv 2007;16:49-67.
- 16. Jones EBG, Pang K-L. Tropical aquatic fungi. Biodivers Conserv 2012;21:2403-23.
- 17. Vilgalys R, Hester M. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J Bacteriol 1990;172:4238-46.
- 18. White T, Bruns TD, Lee SB, Taylor JW. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA GD SJ, White TJ, editor. PCR Protocols: A Guide to Methods and Applications. New York: Academic Press, Inc; 1990. p. 315-22.
- 19. Glass NL, Donaldson GC. Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous ascomycetes. Appl Environ Microbiol 1995;61:1323-30.
- 20. Katoh K, Standley DM. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Mol Biol Evol 2013;30:772-80.
- 21. Katoh K, Toh H. Improved accuracy of multiple ncRNA alignment by incorporating structural information into a MAFFT-based framework. BMC Bioinformatics 2008;9:212.
- 22. Kumar S, Stecher G, Li M, Knyaz C, Tamura K. MEGA X: Molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol 2018;35:1547-9.
- 23. Vaidya G, Lohman DJ, Meier R. SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. Cladistics 2011;27:171-80.
- 24. Morgan-Jones G, White JF. Studies in the genus *Phoma*. III. *Paraphoma*, a new genus to accommodate *Phoma radicina*. Mycotaxon 1983;18:57-65.
- 25. de Gruyter J, Woudenberg JHC, Aveskamp MM, Verkley GJM, Groenewald JZ, Crous PW. Systematic reappraisal of species in *Phoma* section *Paraphoma*, *Pyrenochaeta* and *Pleurophoma*. Mycologia 2010;102:1066-81.
- 26. Moslemi A, Ades PK, Crous PW, Groom T, Scott JB, Nicolas ME, Taylor PWJ. *Paraphoma chlamydocopiosa* sp. nov. and *Paraphoma pye* sp. nov., two new species associated with leaf and crown infection of pyrethrum. Plant Pathol. 2018;67:124-35.
- 27. Aveskamp MM, de Gruyter J, Woudenberg JHC, Verkley GJM, Crous PW. Highlights of the Didymellaceae: A polyphasic approach to characterise *Phoma* and related pleosporalean genera. Stud Mycol 2010;65:1-60.
- 28. El-Elimat T, Raja HA, Figueroa M, Al Sharie AH, Bunch RL, Oberlies NH. Freshwater fungi as a source of chemical diversity: A review. J Nat Prod 2021;84:898-916.
- 29. El-Elimat T, Raja HA, Figueroa M, Falkinham JO, Oberlies NH. Isochromenones, isobenzofuranone, and tetrahydronaphthalenes produced by *Paraphoma radicina*, a fungus isolated from a freshwater habitat. Phytochemistry 2014;104:114-20.
- 30. Magaña-Dueñas V, Cano-Lira JF, Stchigel AM. New Dothideomycetes from freshwater habitats in Spain. J Fungi 2021;7:1102.
- 31. Jeon YJ, Goh J, Mun HY. Diversity of fungi in brackish water in Korea. Kor J Mycol 2020;48:457-73.
- 32. Auerswald B. Sordaria macrospora. Hedwigia 1866;5:192.
- 33. Crous PW, Verkley GJM, Groenewald JZ, Samson RA. Fungal biodiversity. Utrecht: CBS-KNAW, Fungal Biodiversity Centre.; 2009.

- 34. Teichert I, Pöggeler S, Nowrousian M. *Sordaria macrospora*: 25 years as a model organism for studying the molecular mechanisms of fruiting body development. Appl Microbiol Biotechnol 2020;104:3691-704.
- 35. Luo Z-L, Hyde KD, Liu J-K, Maharachchikumbura SSN, Jeewon R, Bao DF, Bhat DJ, Lin CG, Li WL, Yang J, et al. Freshwater Sordariomycetes. Fungal Divers 2019;99:451-660.
- 36. Froyd CA, Coffey EED, van der Knaap WO, van Leeuwen JFN, Tye A, Willis KJ. The ecological consequences of megafaunal loss: Giant tortoises and wetland biodiversity. Ecol Lett 2014;17:144-54.
- 37. Ivanová H. *Sordaria fimicola* (Ascomycota, Sordariales) on *Acer palmatum*. Folia Oeco 2015;42:67-71.
- 38. Kirker GT, Wagner TL, Diehl SV. Relationship between wood-inhabiting fungi and *Reticulitermes* spp. in four forest habitats of northeastern Mississippi. Int Biodeterior Biodegrad 2012;72:18-25.
- 39. Abdel-Azeem A, Salem F. Biodiversity of laccase producing fungi in Egypt. Mycosphere 2012;3:900-920.
- 40. Souza A, da Costa M, Estrela L, Paz L. Cultural, morphological and morphometric ascpects of the *Sordaria fimicola* in leaves of massambara grass (*Sorghum arundinaceum*). Rev Agric Neotrop 2019;6:34-44.
- 41. Kück U, Pöggeler S, Nowrousian M, Nolting N, Engh I. *Sordaria macrospora*, a model system for fungal development. In: Anke T, Weber D, editors. Physiology and Genetics: Selected Basic and Applied Aspects. Berlin, Heidelberg: Springer Berlin Heidelberg; 2009. p. 17-39.
- 42. Geiger M, Guitton Y, Vansteelandt M, Kerzaon I, Blanchet E, Robiou du Pont T, Frisvad JC, Hess P, Pouchus YF, Grovel O. Cytotoxicity and mycotoxin production of shellfish-derived *Penicillium* spp., a risk for shellfish consumers. Lett Appl Microbiol 2013;57:385-92.
- 43. Borzykh OG, Zvereva LV. Mycobiota of the bivalve mollusk *Anadara broughtoni* (Schrenck, 1867) from various parts of peter the great Bay, Sea of Japan. Russ J Mar Biol 2015;41:321-3.
- 44. Santos A, Hauser-Davis RA, Santos MJS, De Simone SG. Potentially toxic filamentous fungi associated to the economically important *Nodipecten nodosus* (Linnaeus, 1758) scallop farmed in southeastern Rio de Janeiro, Brazil. Mar Pollut Bull 2017;115:75-9.
- 45. Bornet ME, Flahault C. Sur quelques plantes vivant dans le test calcaire des mollusques. Bulletin de la SBF 1889;36:148-77.
- 46. Cai L, Hu D-M, Liu F, Hyde K, Jones EBG. 3. The molecular phylogeny of freshwater Sordariomycetes and discomycetes. In: Jones EBG, Hyde KD, Pang K-L, editors. Freshwater Fungi: and Fungal-like Organisms. Berlin, Boston: de Gruyter; 2014. p. 47-72.
- 47. Gams W. Two little-known species of Mortierella. Sydowia 1985;38:97-105.
- 48. Tieghem Pv. Nouvelles recherches sur les Mucorinées. Annales des Sciences Naturelles Botanique 1875;6:5-175.
- 49. Petkovits T, Nagy LG, Hoffmann K, Wagner L, Nyilasi I, Griebel T, Schnabelrauch D, Vogel H, Voigt K, Vágvölgyi C, et al. Data partitions, Bayesian analysis and phylogeny of the Zygomycetous fungal family Mortierellaceae, inferred from nuclear ribosomal DNA sequences. PLoS One 2011;6:e27507.
- 50. Ozimek E, Hanaka A. *Mortierella* species as the plant growth-promoting fungi present in the agricultural soils. Agriculture 2021;11:7.
- 51. Wu D, Zhang M, Peng M, Sui X, Li W, Sun G. Variations in soil functional fungal community structure associated with pure and mixed plantations in typical temperate forests of China. Front Microbiol 2019;10:1636.

- 52. Li F, Chen L, Redmile-Gordon M, Zhang J, Zhang C, Ning Q, Li W. *Mortierella elongata*'s roles in organic agriculture and crop growth promotion in a mineral soil. Land Degrad Dev 2018:29:1642-51.
- 53. Archer DB, Connerton IF, MacKenzie DA. Filamentous fungi for production of food additives and processing aids. Adv Biochem Engin/Biotechnol 2008;111:99-147.
- 54. Nguyen TTT, Lee HB. Characterization of a Zygomycete fungus, *Mortierella minutissima* from freshwater of Yeongsan river in Korea. Kor J Mycol 2016;44:346-9.
- 55. Nguyen TTT, Park SW, Pangging M, Lee HB. Molecular and morphological confirmation of three undescribed species of *Mortierella* from Korea. Mycobiology 2019;47:31-9.
- 56. Ellegaard-Jensen L, Aamand J, Kragelund BB, Johnson AH, Rosendahl S. Strains of the soil fungus *Mortierella* show different degradation potentials for the phenylurea herbicide diuron. Biodegradation 2013;24:765-74.
- 57. Hyde KD, Hongsanan S, Jeewon R, McKenzie EHC, Jones EBG, Phookamsak R, Ariyawansa HA, Boonmee S, Zhao Q, Abdel-Aziz FA, et al. Fungal diversity notes 367-490: Taxonomic and phylogenetic contributions to fungal taxa. Fungal Divers 2016;80:1-270.