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RESEARCH ARTICLE

Unveiling the holomorph and novel host records of *Shearia formosa* (*Longiostiolaceae, Pleosporales*) in China

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ABSTRACT

Shearia belongs to the *Longiostiolaceae* (*Pleosporales*, *Dothideomycetes*) and is typified by *S. formosa*. Previously, *Shearia* species were reported by their asexual morph, and here we introduce the first sexual morph for *Shearia*. We also provide the sexual-asexual linkage of *S. formosa* with two new host records from *Magnolia sprengeri* and *Michelia alba* from China based on morpho-molecular analyses. The sexual morph of *S. formosa* is characterised by having perithecial ascomata with an erumpent ostiole, cellular pseudoparaphyses and asci embedded in a gelatinous matrix, short pedicellate asci with an ocular chamber, and transversely and vertically septate spores surrounded by a thick mucilaginous sheath. Our *S. formosa* isolates clustered with other authentic strains of *S. formosa* based on maximum parsimony, maximum likelihood, and Bayesian inference analyses of the combined sequence data of 28S ribosomal RNA (LSU), 18S small subunit rDNA (SSU), RNA polymerase II second largest subunit (*rpb2*), and the translation elongation factor 1-alpha gene (*tef*).

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Asexual morph; multi-loci phylogeny; *Pleosporales*; sexual morph; *Shearia formosa*; two new records

Introduction

Pleosporales (*Pleosporomycetidae*) is the largest order in *Dothideomycetes*, accounting for one-quarter of all described dothideomycetous species (Hyde et al. 2020; Hongsanan et al. 2020a, 2020b). Pleosporalean taxa occur in various habitats with different lifestyles, such as epiphytes, endophytes, or pathogens of living leaves or stems; saprobes on dead plant stems, leaves, or bark; hyperparasites on fungi or insects; and may be lichenized (Kruys et al. 2006; Bhunjun et al. 2021; Phukhamsakda et al. 2022; Su et al. 2022; Xu et al. 2022).

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The *Longiostiolaceae* was introduced by Phukhamsakda et al. (2020) to accommodate *Longiostiolum* and *Crassiperidium*. These genera were introduced by Li et al. (2016) and Matsumura et al. (2018), respectively, as *Pleosporales* genera *incertae sedis*. Wanasinghe et al. (2020) updated the taxonomic placement for *Shearia* in *Longiostiolaceae* by designating a neotype for *S. formosa*. Currently, *Crassiperidium*, *Longiostiolum*, and *Shearia* are accepted as members of the *Longiostiolaceae* (Hongsanan et al. 2020b; Wijayawardene et al. 2022a). Members of this family are characterised by their immersed to semi-immersed and subglobose to globose ascomata with a long ostiole, 4–8-spored, cylindrical to clavate asci, hyaline to brownish, and multi-septate ascospores (Phukhamsakda et al. 2020). Additionally, members of *Longiostiolaceae* produce pycnidial conidiomata or hyphomycetous-like structures under culture conditions (Phukhamsakda et al. 2020). Members of this family are commonly found on economically valuable dicotyledonous plants (Hongsanan et al. 2020b). In Japan, *Crassiperidium* species have been identified as pathogens of *Fagus* species, while *Longiostiolum* has been associated with *Tectona grandis* as saprobes in northern Thailand (Li et al. 2016).

Shearia was initially introduced by Petrak (1924), with *S. magnoliae* as the type species. However, based on morphology, Petrak (1962) considered *Stegonsporium formosa* to be the oldest name for *S. magnoliae* and proposed the new name, *Shearia formosa*. Sutton (1980) accepted *S. formosa* as the type species, considering *Pleomassaria magnoliae* as the sexual morph of *S. formosa* (also known as *Camarosporium magnoliae*). However, in Index Fungorum (2023), *S. magnoliae* is listed as the type species of *Shearia*. Wanasinghe et al. (2020) re-described the asexual morph of *S. formosa*, providing both morphology and sequence data for fungal isolates obtained from living branches of *Magnolia denudata* in China. Wijayawardene et al. (2022b) revealed a new host record of the asexual morph of *S. formosa* from *M. grandiflora* in China. However, no illustrations were provided for the sexual morph of *S. formosa*, and an accurate sexual-asexual linkage based on morphology and phylogeny has not been described.

In this study, we link the sexual and asexual morphs of *Shearia formosa*. We provide the first sexual morph for *Shearia* and the generic notes for this genus. In addition, we provide new host records from *Magnolia sprengeri* and *Michelia alba* from different locations in China. Morphological illustrations and phylogenetic analyses based on combined LSU, SSU, *rpb2*, and *tef* sequence data are also provided.

Materials & methods

Specimen collections, morphological studies, and isolations

Dead branches of *Magnolia sprengeri* and *Michelia alba* (*Magnoliaceae*) hanging on the tree were collected during 2018–2019 from Guiyang Province (average temperature 25 °C,) and Sichuan Province (average temperature 22–25 °C), China. The collection site in Guiyang Province was the forest area inside the Guizhou Academy of Agricultural Sciences premises that has limited human disturbances. In Sichuan Province, the collection site is the path in the university garden close to a stream that interacts with human activities and is subjected to continuous management practices. The samples were examined using a stereo microscope (SteREO Discovery v8, Zeiss, Germany) with an attached Axio Cam ERc5s camera (Zeiss, Germany). Photos were also captured using a Nikon

ECLIPSE Ni-U compound microscope (Nikon, Tokyo, Japan) with an attached Canon EOS 600D camera (Canon Inc., Tokyo, Japan). Peridium and ascus tips were mounted in water and Congo Red, while ascospores were mounted in water and Indian ink. Tarosoft (R) Image Frame Work was used for measurements (Tarosoft, Thailand), and Adobe Photoshop CS5 was used to process the images for the figures (Adobe Systems Inc., United States).

Pure fungal colonies were obtained through single spore isolation, as described by Senanayake et al. (2020). Germinating spores were transferred aseptically to potato dextrose agar (PDA) (potato infusion 6 g/l, dextrose 20 g/l, agar 20 g/l) (Qingdao Hope Bio-Technology Co., Ltd., China). The cultures were incubated in the dark at 25–30 °C for 4–6 weeks with frequent observations. The specimens were deposited in the herbarium of the Cryptogams Kunming Institute of Botany Academia Sinica (KUN-HKAS), Chinese Academy of Sciences, Kunming, China, and Mae Fah Luang University Herbarium (MFLU), Chiang Rai, Thailand, and cultures were deposited in the Mae Fah Luang University culture collection (MFLUCC).

DNA extraction, PCR amplification, and sequencing

For DNA extraction, fruiting bodies and fresh mycelium were scraped from the margins of colonies on PDA plates, which had been incubated at 28 °C for four weeks. Total DNA extraction kits (Sangon Biotech (Shanghai) Co., Ltd., P.R. China) were used according to the manufacturer's instructions. The amplification reactions were performed using a total volume of 25 µl containing 12.5 µl of 2X PCR Master Mix with dye (0.1 U Taq Polymerase/µl, 500 µM dNTP each), 20 mM Tris-HCl (pH 8.3), 100 mM KCl, and 3 mM $MgCl_2$), 1 µl of each primer (10 µM), 9.5 µl of double-distilled water, and 1 µl (50–100 ng) of DNA template.

The PCR thermal cycle programmes for each locus are tabulated in Table 1. PCR products were visualised on a 1% agarose gel stained with ethidium bromide (EtBr) with a D2000 DNA ladder (Sangon Biotech (Shanghai) Co., Ltd., P.R. China) under 100 mA voltage. All the PCR products were immediately stored at 4 °C until sequencing. The PCR products were purified, and DNA sequencing was performed using the same primers in an Applied Biosystems 3730 DNA analyzer at Sangon Biotech (Shanghai) Co., Ltd., P.R. China.

Phylogenetic analyses

The quality of the sequences was assessed by checking the quality of the chromatograms using BioEdit v. 7.2 (Hall 1999). The consensus sequences were assembled using

Table 1. Gene regions, primers, and PCR thermal cycle programmes used in this study, with corresponding references.

Genes/ loci	PCR primers (forward/reverse)	PCR conditions	References
LSU	LR0R/LR5	94 °C/30 s; 55 °C/50 s; 72 °C/90 s	Vilgalys and Hester (1990)
SSU	NS1/NS4	95 °C/ 30 s, 55 °C/ 50 s, 72 °C/30 s	White et al. (1990)
tef	EF1-983F/ EF1-2218R	95 °C/ 30 s, 58 °C/ 50 s, 72 °C/1 min	Rehner (2001)
*rpb*2	fRPB2-5F/fRPB2-7cR	95 °C/30 s, 58 °C/ 50 s, 72 °C/2 min	Liu et al. (1999)

Initial denaturation at 95 °C; 5 min, and final extension at 72 °C; 10 min; the number of thermal cycles for each 35.

Lasergene SeqMan Pro v.7 (DNASTAR, Inc., USA). Newly generated sequences were subjected to BLASTn searches at NCBI (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Sequences with high similarity indices were downloaded from GenBank, and reference sequence data were downloaded from Wanasinghe et al. (2020) (Table 2). The sequences of each locus (LSU, SSU, *rpb2*, and *tef*) were aligned using online MAFFT version 7 (Katoh et al. 2019) and manually edited using BioEdit version 7.2. The aligned sequence was trimmed using the gappyout option in TrimAl version 1.2 (Capella-Gutiérrez et al. 2009).

Phylogenetic analyses were performed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). The best-fit model was estimated using MrModeltest v. 2.2 for each locus (Nylander 2004), and the GTR + I + G model was selected for BI analysis. The MP analysis was carried out with PAUP v.4.0b 10 (Swofford 2002) using the heuristic search option with 1,000 replicates. The following parameters were calculated: tree length (TL), consistency indices (CI), retention indices (RI), rescaled consistency indices (RC), and homoplasy index (HI). The Kishino-Hasegawa test (KHT) (Kishino and Hasegawa 1989) was used to determine whether the trees were significantly different. The ML analysis was performed in the W-IQ-TREE web server using default settings (Trifinopoulos et al. 2016) with 1,000 replicates. The TIM2e + I + G4 as the evolutionary model, was selected using ModelFinder under Bayesian Information Criterion (BIC) for the combined alignment. The BI analysis was performed using MrBayes v. 3.2 on the XSEDE tool on the CIPRES Science Gateway (Miller et al. 2010). Six simultaneous Markov Chain Monte Carlo analyses were run for 1,000,000 generations, and trees were sampled at every 100th generation, yielding 10,000 trees. FigTree v. 1.4.0 was used to visualise the phylograms (Rambaut 2012), and Microsoft PowerPoint (2010) was used to edit the phylograms. All the accession numbers of the sequences used in this study are listed in Table 2.

Newly generated sequences in this study are indicated with a *, and ex-type strains are indicated in bold. Sequences unavailable in GenBank are indicated with "N/A". Abbreviations: CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; CPC: Collection of Pedro Crous housed at CBS; HHUF: Herbarium of Hirosaki University Fungi, Aomori, Japan; HKAS: Herbarium of Cryptogams Kunming Institute of Botany Academia Sinica; KT: Kazuaki Tanaka, Japan; KUMCC: Kunming Institute of Botany Culture Collection, Yunnan, China; MAFF: National Institute of Agrobiological Sciences, Japan; MFLU: Herbarium of Mae Fah Luang University Chiang Rai, Thailand; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; NTUCC: National Taiwan University Culture Collection; WU: Herbarium of the Institute of Botany, University of Vienna.

The accession numbers of the ITS region are MFLU 19–2114 – OR053805, MFLU 19–2115 – OR053806, HKAS 107010 – OR053807, HKAS 107011 – OR053808, HKAS 107033 – OR053809, and HKAS 107034 – OR053810.

Results

Phylogenetic analyses

Phylogenetic trees obtained from combined LSU, SSU, *rpb2*, and *tef* sequence data consisted of 54 taxa, with *Magnibotryascoma rubriostiolatum* (WU:33594), and *Teichospora*

Table 2. Names, strain numbers and corresponding GenBank accession numbers of the taxa used in the phylogenetic analyses.

Species	Strain	GenBank accession numbers			
		LSU	SSU	*tef*	*rpb2*
Ascochyta coronillae-emeri	MFLUCC 13–0820	MH069667	MH069673	N/A	MH069679
Bambusicola bambusae	**MFLUCC 11–0614**	**JX442035**	**JX442039**	**KP761722**	**KP761718**
Bambusicola massarinia	**MFLUCC 11–0389**	**JX442037**	**JX442041**	**N/A**	**KP761716**
Brevicollum hyalosporum	**MAFF 243400**	**NG_058715**	**NG_065123**	**LC271245**	**LC271249**
Brevicollum versicolor	**HHUF 30591**	**NG_058716**	**LC271237**	**LC271246**	**LC271250**
Camarosporidiella caraganicola	MFLUCC 14–0887	MF434209	MF434297	MF434385	N/A
Camarosporidiella eufemiana	**MFLUCC 17–0207**	**NG_069513**	**NG_063648**	**MF434408**	**N/A**
Crassiparies quadrisporus	**HHUF 30409**	**NG_059028**	**NG_061267**	**LC271248**	**LC271252**
Crassiperidium octosporum	KT 3008	LC373110	LC373086	LC373122	LC373134
Crassiperidium octosporum	**KT 2144**	**LC373108**	**LC373084**	**LC373120**	**LC373132**
Crassiperidium octosporum	KT 2894	LC373109	LC373085	LC373121	LC373133
Crassiperidium quadrisporum	KT 2798–1	LC373118	LC373094	LC373130	LC373142
Crassiperidium quadrisporum	**KT 2798–2**	**LC373119**	**LC373095**	**LC373131**	**LC373143**
Cucurbitaria berberidis	CBS 363.93	GQ387606	GQ387545	N/A	N/A
Cyclothyriella rubronotata	**CBS 141486**	**KX650544**	**NG_061252**	**KX650519**	**KX650574**
Cyclothyriella rubronotata	WU:36863	KX650542	N/A	KX650517	KX650572
Cyclothyriella rubronotata	CBS 121892	KX650541	N/A	KX650516	KX650571
Dothidotthia negundinicola	MFLUCC 16–1157	MK751815	MK751760	MK908015	MK920235
Dothidotthia symphoricarpi	CPC 12929	EU673273	EU673224	N/A	N/A
Flavomyces fulophazii	**CBS 135761**	**KP184040**	**KP184082**	**N/A**	**N/A**
Helminthosporiella stilbacea	**MFLUCC 15–0813**	**NG_081484**	**NG_081401**	**MT928151**	**N/A**
Herpotrichia diffusa	CBS 250.62	DQ678071	DQ678019	DQ677915	DQ677968
Herpotrichia pinetorum	CBS 200.31	DQ678080	DQ678029	DQ677925	DQ677978
Katumotoa bambusicola	**KT 1517a**	**AB524595**	**AB524454**	**AB539108**	**AB539095**
Lentithecium fluviatile	CBS 122367	GU301825	GU296158	GU349074	N/A
Leptosphaerulina australis	CBS 317.83	GU301830	GU296160	GU349070	GU371790
Longiostiolum tectonae	MFLUCC 12–0562	KU764700	NG_061231	N/A	N/A
Magnibotryascoma rubriostiolatum	**WU:33594**	**KU601590**	**N/A**	**KU601609**	**KU601599**
Massarina eburnea	CBS 473.64	GU301840	GU296170	GU349040	GU371732
Massariosphaeria clematidis	**MFLU 16–0174**	**NG_073843**	**NG_070645**	**N/A**	**N/A**
Melanomma pulvis-pyrius	CBS 124080	GU456323	GU456302	GU456265	GU456350
Multilocularia bambusae	**MFLUCC 11–0180**	**NG_059654**	**NG_061229**	**KU705656**	**N/A**
Murilentithecium clematidis	MFLUCC 14–0561	KM408758	KM408760	KM454444	KM454446
Neoaquastroma guttulatum	MFLUCC 14–0917	KX949740	KX949741	KX949742	N/A
Neocucurbitaria rhamni	**CBS 142391**	**MF795775**	**MF795838**	**MF795863**	**MF795817**
Parabambusicola thysanolaenae	**KUMCC 18–0147**	**NG_066435**	**NG_067681**	**MK098209**	**N/A**
Periconia didymospora	MFLUCC 13–0862	KP761731	KP761738	KP761728	KP761721
Pleomassaria siparia	CBS 279.74	DQ678078	DQ678027	DQ677923	DQ677976
Prosthemium canba	KT2083-1	AB553760	AB553646	N/A	N/A
Prosthemium orientale	KT1669	AB553748	AB553641	N/A	N/A
**Shearia formosa* (asexual morph)	HKAS107010	OQ703052	OQ703046	OQ708651	OQ766961
**S. formosa* (asexual morph)	HKAS107033	OQ703055	OQ703049	OQ708654	OQ766962
**S. formosa* (asexual morph)	MFLU 19–2114	OQ703054	OQ703048	OQ708652	OQ708657
**S. formosa* (sexual morph)	HKAS107011	OQ703053	OQ703047	OQ708656	OQ766960
**S. formosa* (sexual morph)	MFLU 19–2115	OQ703057	OQ703051	OQ708653	OQ766959
**S. formosa* (sexual morph)	HKAS107034	OQ703056	OQ703050	OQ708655	OQ766963
S. formosa	MFLUCC 20–0018	MT159621	MT159633	MT159604	MT159610
S. formosa	MFLUCC 20–0019	MT159620	MT159632	MT159603	MT159609
S. formosa	GMBCC1172	OM855601	OM855615	N/A	OM857557
S. formosa	MFLUCC 20–0017	MT159619	MT159631	MT159602	MT159608
Splanchnonema platani	CBS 222.37	KR909316	KR909318	KR909319	KR909322
Stemphylium vesicarium	**CBS 191.86**	**MH873624**	**GU238232**	**N/A**	**KC584471**
Stemphylium vesicarium	MFLUCC 14–0920	KY659563	KY659567	N/A	N/A
Teichospora trabicola	**WU:33582**	**KU601591**	**N/A**	**KU601601**	**KU601600**
Thyrostroma lycii	**MFLUCC 16–1170**	**MK751824**	**MK751769**	**MK908024**	**MK920241**
Tzeanania taiwanensis	NTUCC 17–005	MH461120	MH461126	MH461130	MH461128

trabicola (WU:33582) as the outgroup taxa (Figure 1). The final alignment comprised 3,434 characters, including gaps (LSU = 807, SSU = 959, *rpb2* = 1028, *tef* = 640). In the dataset used for parsimony analysis, 2286 characters were constant; 200 characters were parsimony-uninformative, and 957 characters were parsimony informative. The most parsimonious tree resulted with the following parameters: TL = 4871, CI = 0.378, RI = 0.668, RC = 0.252, HI = 0.622. The best ML tree (InL = −25930.505, α = 0.591, invar = 0.556) resulted in estimated base frequencies as follows: A = 0.250, C = 0.250, G = 0.250, and T = 0.250 substitution rates; AC = 1.24397, AG = 3.93954, AT = 1.24397, CG = 1.00000, CT = 7.16182, GT = 1.00000; The average standard deviation of split frequencies was 0.005 after 1,000,000 generations of runs.

Taxonomy

Shearia Petr., Annls mycol. 22(1/2): 180 (1924) ***amend***.

Saprobic on dead branches. **Sexual morph**: *Ascomata* perithecial, solitary or aggregated, globose to subglobose, immersed. *Ostiole* papillate, paraphysate. *Peridium* consists of two layers; outer layer sub-carbonaceous, thick-walled cells of *textura angularis*; inner layer thin-walled cells of *textura angularis*. *Hamathecium* consists of pseudoparaphyses embedded in a gelatinous matrix. *Asci* 8-spored, bitunicate, fissitunicate, cylindrical or oblong, short pedicellate, with an ocular chamber. *Ascospores* overlapping biseriate, fusoid to ellipsoid, muriform, transversely septate, vertical septa, constricted at the septa. **Asexual morph**: See Wanasinghe et al. (2020).

Type species: *Shearia formosa* (Ellis and Everh.) Petr., Sydowia 15 (1–6): 216 (1962)

Shearia formosa (Ellis and Everh.) Petr., Sydowia 15(1–6): 216 (1962) Figures 2 and 3.

≡ *Stegonsporium formosa* Ellis and Everh., Bull. Torrey bot. Club 10(7): 76 (1883)

= *Shearia magnoliae* (Shear) Petr., Annls mycol. 22(1/2): 180 (1924)

≡ *Camarosporium magnoliae* Shear, Bull. Torrey bot. Club 29: 455 (1902)

Index Fungorum number: IF339263, Facesoffungi number: FoF 07747.

Saprobic on dead *Magnolia sprengeri* Pamp. and *Michelia alba* DC. branches. **Sexual morph**: *Ascomata* 660–820 × 540–720 µm ($\bar{x}$ = 740 × 630 µm, n = 10), perithecial, solitary or aggregated, immersed with erumpent ostiole, visible as black dots on the host surface, unilocular, globose to subglobose, dark brown to black, ostiolate. *Ostiole* central, cylindrical, papillate, hyaline to light brown periphyses. *Peridium* two layers; outer peridium 56–113 µm wide ($\bar{x}$ = 82.5 µm, n = 10), sub-carbonaceous, comprising of dark brown to black, thick-walled cells of *textura angularis*, easily detached from the inner layers, weak contact with the host; inner peridium 15–20 µm wide ($\overline{x}$ = 17.5 µm, n = 10), comprising 4–5 layers of hyaline, relatively thin-walled cells of *textura angularis*. *Hamathecium* 1.5–3.8 µm wide ($\overline{x}$ = 2.3 µm, n = 20), hyaline, septate, branched, cellular pseudoparaphyses surrounding the asci, embedded in a gelatinous matrix. *Asci* 162–211 × 42–64 µm ($\overline{x}$ = 185 × 50 µm, n = 20), 8-spored, bitunicate, fissitunicate, cylindrical or oblong, short-pedicellate, apically rounded, with an ocular chamber. *Ascospores* 42–57 × 13–18 µm ($\overline{x}$ = 49 × 15 µm, n = 30), L/W 3.3, overlapping biseriate, fusoid to ellipsoid, muriform, upper part wider than lower part, 7–11-transversely septate, 2–3 vertical

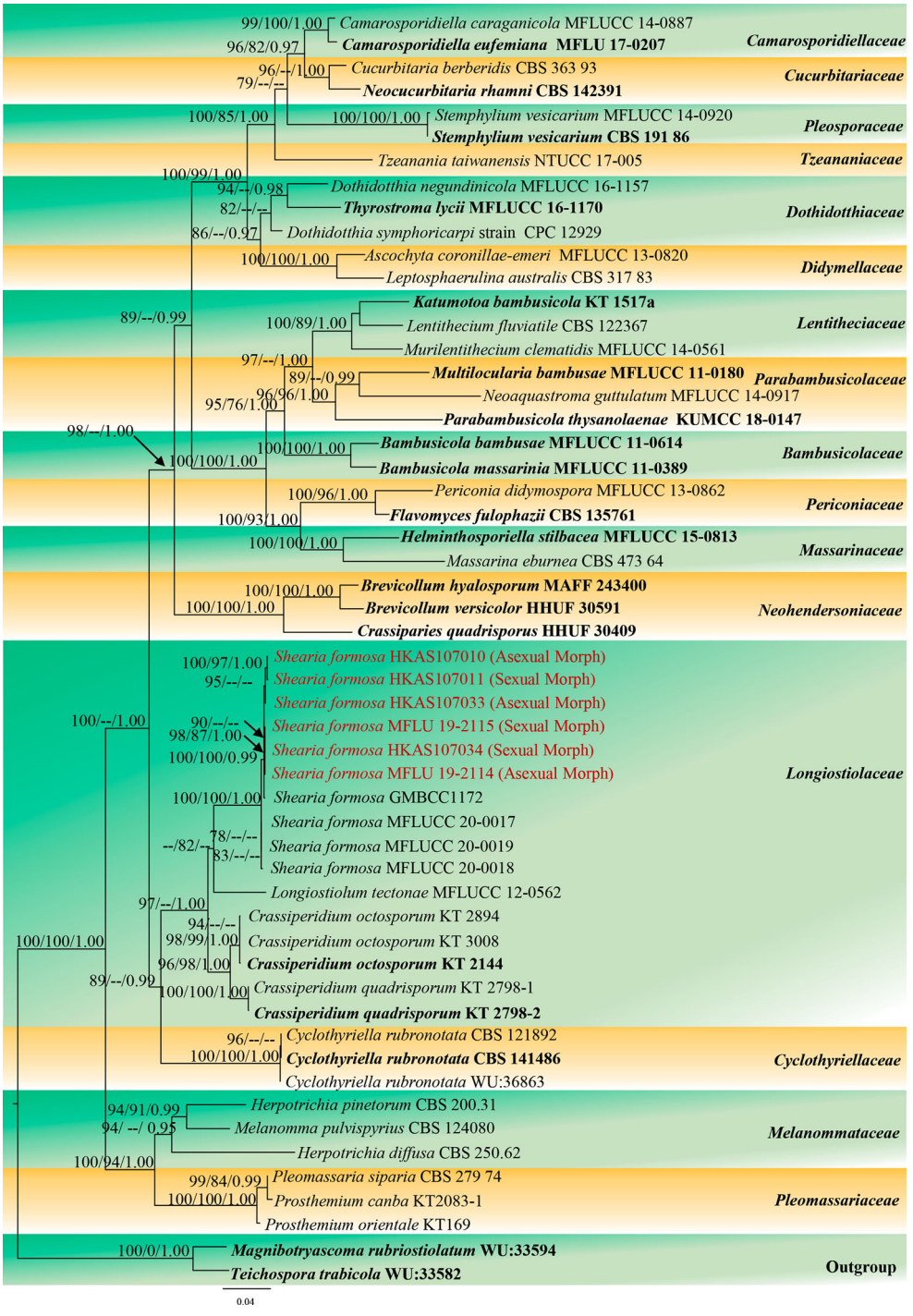

Figure 1. Phylogram generated from maximum likelihood based on the SSU–LSU– *rpb2*– *tef* matrix. The tree was rooted with *Magnibotryascoma rubriostiolatum* (WU:33594), and *Teichospora trabicola* (WU:33582). Bootstrap support values for MP and ML ≥ 75% and Bayesian posterior probabilities (PP) ≥ 0.95 are provided at the nodes as ML/MP/PP. Strains isolated in this study are in red, and ex-type strains are in bold.

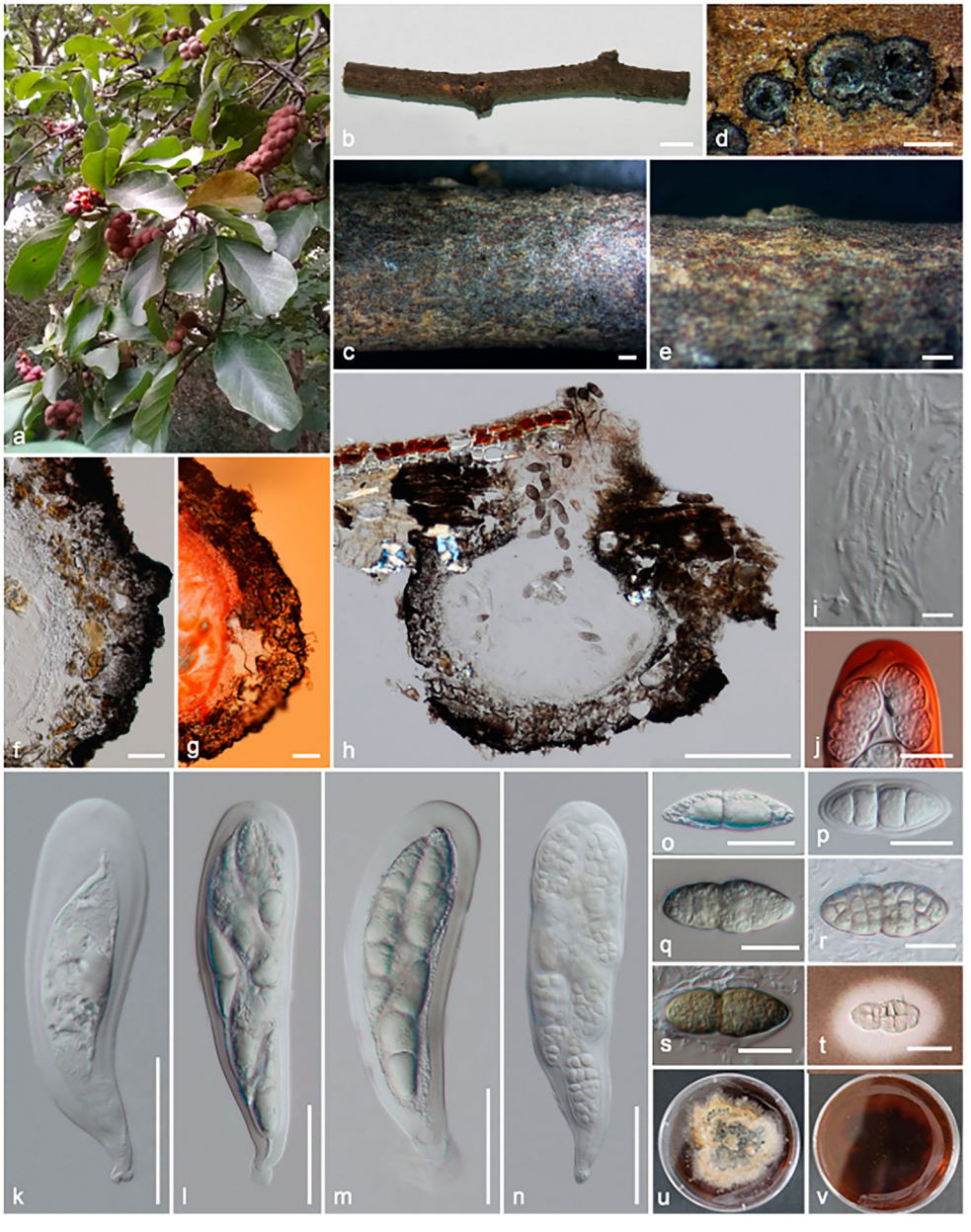

Figure 2. ***Shearia formosa*** (sexual morph) (MFLU 19-2115) a, b *Magnolia sprengeri* host. c, e Ascomata on the substrate. d Transverse section through ascomata. f, g Peridium (g in Congo Red). h Vertical section of an ascoma. i Pseudoparaphyses j Ascus tip in Congo Red. k-n Asci. o-t Ascospores (t in Indian ink). u,v Culture characteristics. Scale bars: b = 1 cm, c–e = 500 µm, h = 20 µm, f, g, k–n = 50 µm, j, o–v = 20 µm, i = 10 µm.

septa, constricted at the septa, initially hyaline, becoming yellowish brown at maturity, smooth-walled, surrounded by a thick mucilaginous sheath. **Asexual morph**: *Conidiomata* 820–840 × 620–790 µm ($\bar{x}$ = 825 × 690 µm, n = 10), solitary, sometimes gregarious, subglobose to globose, immersed with erumpent ostiole, visible as black dots on the host

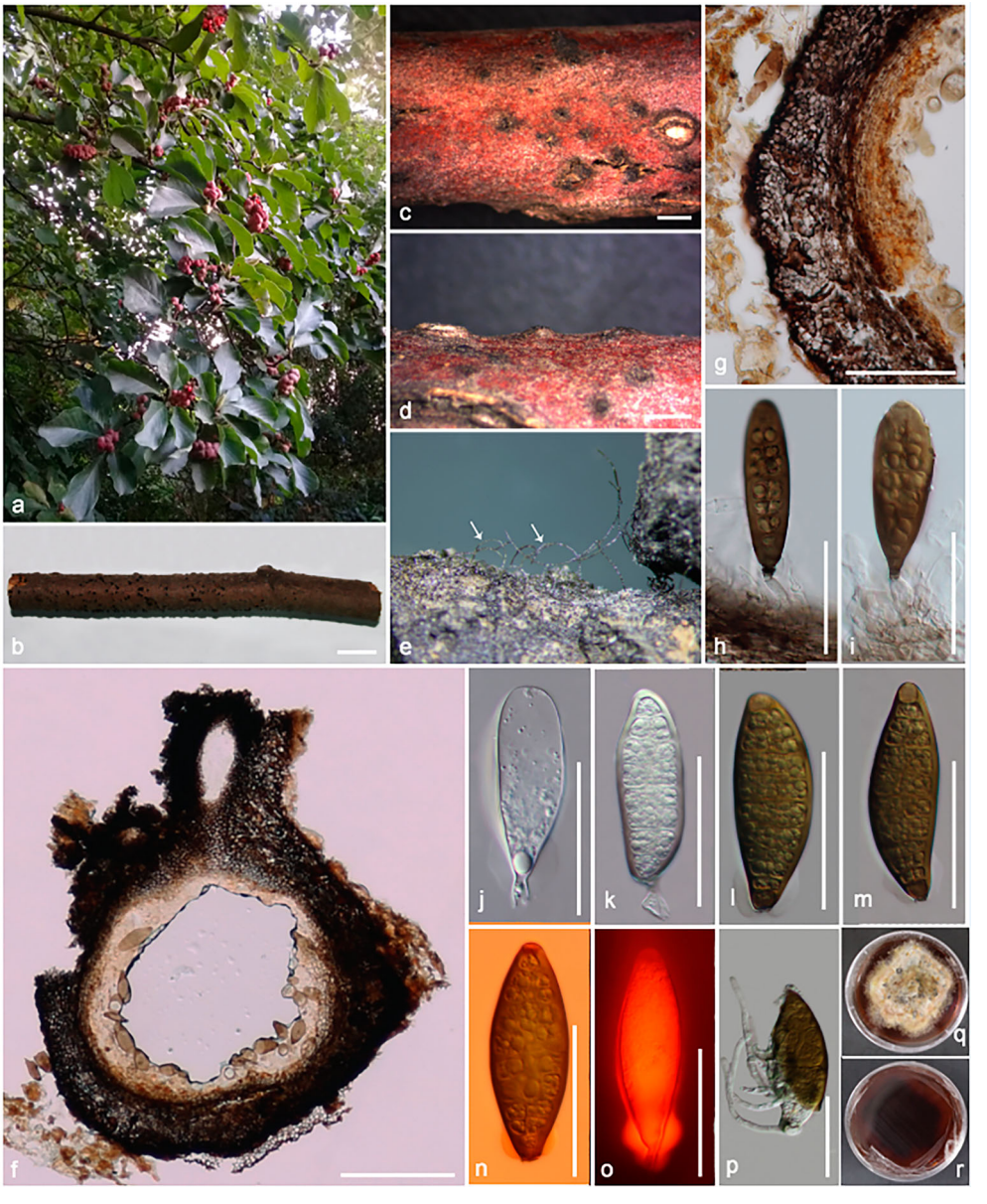

Figure 3. ***Shearia formosa*** (asexual morph) (MFLU 19-2114) **a, b** *Magnolia sprengeri* host. **c-e** Conidiomata on the substrate (**e** Ejected conidial chains, white arrows). f. Vertical sections through an ascoma. **g** Peridium. **h, i** Conidiogenous cells and developing conidia. **j-o** Conidia (n in Congo Red, o in Indian ink, with a basal sheath). **p** Germinated conidium. q, r Culture characteristics **Scale bars:** b = 1 cm, c–d = 1 mm, f = 200 µm, g = 100 µm, h–q = 100 µm.

surface, unilocular, dark brown, with centrally opening ostiole. *Ostiole* central papillate, hyaline periphyses. *Peridium* two zones; outer peridium 72–105 µm wide ($\bar{x}$ = 90.5 µm, n = 10), comprising of black to dark brown, thick-walled cells of *textura angularis*, easily detached from the inner layers, weak contact with the host; inner peridium 16–22 µm wide ($\bar{x}$ = 19 µm, n = 10), comprising 4–5 layers of light brown, relatively thin-walled,

small cells of *textura angularis*. *Conidiogenous cells* 7.5–17.8 × 5.5–14 µm ($\bar{x}$ = 11 × 10 µm, n = 10), hyaline to light brown, smooth surface, cylindrical to doliform, holoblastic, annellidic. *Conidia* 71.5–85.5 × 18–23.4 µm ($\bar{x}$ = 76.8 × 20.8 µm, n = 30), L/W 3.7, fusiform, guttulate, initially hyaline, becoming yellowish brown at maturity, 11–17-septate, truncate at base 3.2–5.4 µm wide ($\bar{x}$ = 4.4 µm, n = 10), with a basal sheath.

Culture characters: Colonies on PDA reaching 16.5 mm diam. after 14 days at 25 °C, irregular with smooth margin, slightly woolly flattened mycelia, upper surface initially white becoming greyish black with sporulation, lower surface yellowish brown to dark brown.

Material examined: CHINA, Guiyang Province, Guizhou Academy of Agricultural Sciences, on recently dead *Magnolia sprengeri* (*Magnoliaceae*) branches, M.C. Samarakoon, 1 Sept. 2018 (MFLU 19-2114, MFLU 19-2115); living cultures MFLUCC 23-0062, MFLUCC 23-0063; *ibid*, M.C. Samarakoon, 7 Oct. 2019 (HKAS107033, HKAS107034); living cultures MFLUCC 23-0064, MFLUCC 23-0065; *ibid*, China, Sichuan Province, Chengdu, UESTC premises, on recently dead *Michelia alba* (*Magnoliaceae*) branches, M.C. Samarakoon, 30 Sept. 2019 (HKAS107010, HKAS107011).

Note: In this study, microfungi were isolated from specimens collected from dead branches of *Magnolia sprengeri* and *Michelia alba* in China. According to phylogenetic analyses, our isolates (HKAS107010, HKAS107011, HKAS107033, HKAS107034, MFLU 19-2114, and MFLU 19-2115) grouped with the ex-neotype strain (MFLUCC 20-0019), living cultures (MFLUCC 20–0017 and MFLUCC 20-0018), and another authentic strain (GMBCC1172) of *S. formosa* by forming a monophyletic group (Figure 1) with 100% ML, 100% MP, 1.00 PP bootstrap support. The asexual morph of *S. formosa* in this study is similar to the descriptions and illustrations provided by Wanasinghe et al. (2020) and Wijayawardene et al. (2022b), with immersed, unilocular, dark brown conidiomata with a central papillate ostiole, holoblastic, annellidic, and cylindrical to doliiform conidiogenous cells, and fusiform conidia with a basal sheath. We identify our isolates as *S. formosa* based on morphological and phylogenetic results.

Discussion

Pleomassaria magnoliae was previously considered as the sexual morph of *Shearia formosa* (Sutton 1980), while the putative culture of *Pleomassaria maxima* (current name: *Splanchnonema maximum*; Index Fungorum 2023) was considered as *Shearia fusa* (current name: *Piricauda fusus*; Index Fungorum 2023) (Tanaka et al. 2005). Later, Hyde et al. (2011) considered *Shearia* as an anamorph of *Pleomassaria*. In this study, we compared different genera with *Shearia formosa* from our collection (Petrak 1924; Petrak 1962; Barr 1982; Tubaki et al. 1983; Tanaka et al. 2005). The comparison of *Pleomassaria magnoliae*, *P. maxima*, and *Shearia formosa* (our collection) is listed in Table 3.

Furthermore, we found similar morphological characteristics to *Shearia fusa* described in Wijayawardene et al. (2016) in terms of the shape and colour of conidiomata and conidia, as well as the basal sheath in conidia. However, we could not compare measurements of the morphological characteristics of *Shearia fusa* with our collection due to the lack of information in Wijayawardene et al. (2016).

Table 3. Synopsis of morphological characteristics and collection data of *Pleomassaria magnoliae*, *P. maxima*, and *Shearia formosa*.

Fungal Structure	*Pleomassaria magnoliae*	*Pleomassaria maxima*	*Shearia formosa*
Ascomata	Perithecial, gregarious, depressed, spherical or sublenticular	Perithecial, irregularly scattered or subcircinate, depressed-globose	Solitary or aggregatet, immersed, globose to subglobose
Ascomatal wall	coriaceo-carbonaceous, 600–800 µm	Not mentioned	Outer layer sub-carbonaceous, dark brown to black, thick-walled cells of *textura angularis* and inner layer composed of 4–5 layers of hyaline, relatively thin-walled cells of *textura angularis*, 71–133 µm
Asci (µm)	Clavate, very short stipitate, 8 spored, 195–230 × 55–60	Clavate to clindrical short stipitate, 8 spored, 200–260 × 45–60	Cylindrical or oblong, short pedicellate, apically rounded, with an ocular chamber, 8–spored, 162–211 × 42–64
Paraphyses/ pseudoparaphyses	Filiform paraphyses	Abundant paraphyses	Septate, branched, pseudoparaphyses, 1.5–3.8 µm wide
Ascospores	Oblong to ovate, constricted below the middle, at first hyaline and 3–6 septate, then olivaceous and muriform-septate finally deep brown, enclosed in a hyaline envelope, 66–78 µm exclusive of envelope	Subbiseriate, fusoid to oblong subacute, 6–15 septate, clathrate-muriform, generally constricted at the middle septum and sometimes at one or more septa, hyaline at first with a broad hyaline envelope, becoming dark brown, 60–90 × 20–22 µm	Fusoid to ellipsoid, muriform, upper part wider than the lower part, 7–11 transversely septate, 2–3 vertical septa, constricted at the septa, initially hyaline, becoming yellowish brown at maturity, overlapping biseriate, smooth-walled, surrounded by a thick mucilaginous sheath, 42–57 × 13–18 µm
Host	Dead *Magnolia obovata*	Dead *Magnolia* sp.	Dead *Magnolia denudata, M. grandiflora, M. sprengeri, Michelia alba*
Country	China and Japan	United States	China
Reference	Shear (1902)	Ellis and Everhart (1898)	Wanasinghe et al. (2020), Wijayawardene et al. (2022b), This study

Longiostiolaceae is currently composed of three genera *viz. Crassiperidium*, *Longiostiolum*, and *Shearia* (Hongsanan et al. 2020b; Wijayawardene et al. 2022a). Among these three genera, *Crassiperidium* was reported with both sexual and asexual morphs (Matsumura et al. 2018). *Longiostiolum* was described by Li et al. (2016) with only the sexual morphs. Tanaka et al. (2005) considered *Pleomassaria maxima* as the first sexual morph report of *Shearia formosa*, however, *Pleomassaria sensu stricto* grouped with *Prosthemium* (*Pleomassariaceae*) in Tanaka et al. (2010), and therefore, Wijayawardene et al. (2014) transferred *Pleomassaria* to *Prosthemium*. *Splanchnonema sensu stricto* also formed a well-established genus in *Pleomassariaceae* (Wijayawardene et al. 2017). Taxa linked to *Shearia*, such as *Camarosporium magnoliae*, were not related to *Prosthemium* (= *Pleomassaria*) sensu stricto or *Splanchnonema sensu stricto*, and are classified in *Pleomassariaceae* (Wanasinghe et al. 2020). Based on Wijayawardene et al. (2022b) and our phylogenetic analyses, *Shearia* strains belong to *Pleomassariaceae*. We omitted *Piricauda fusus* (= *Shearia fusa*) from our analysis due to the unavailability of sequence data in GenBank (Sayers et al. 2023).

In our phylogenetic analyses, we included sequences of *S. formosa* from the ex-neotype culture (MFLUCC 20-0019), which were introduced by Wanasinghe et al. (2020). We also included sequences from one host record (GMBCC1172) provided by Wijayawardene

Table 4. Synopsis of morphological characteristics of genera in *Longiostiolaceae*.

Fungal Structure	*Crassiperidium*	*Longiostiolum*	*Shearia*
Ascomata (µm)	scattered, immersed, depressed, globose to globose, 300–500 high, 750–1200 diam.	Solitary, to gregarious, scattered, immersed to semi-immersed, uniloculate, globose to subglobose, 255–500 high, 230–385 diam.	solitary or aggregated, immersed, globose to sub globose, 660–820 high, 720–540 diam.
Ascomata wall (µm)	rectangular to polygonal, pale brown to brown cells, 7.5–12.5 µm thick at the base, 130–160, thick at the sides	outer layer black to brown, thick-walled cells of *textura angularis*, inner layer hyaline and thin-walled cells of *textura angularis* 58–85 thick	outer layer sub-carbonaceous, dark brown to black, thick-walled cells of *textura angularis* and inner layer composed 4–5 layers of hyaline, relatively thin-walled cells of *textura angularis*, 71–133
Pseudoparaphyses (µm)	septate, 157.5–202.5 × 26–35	septate, branched, 1.8–2.9 wide	septate, branched, 1.5–3.8 wide
Asci (µm)	cylindrical to clavate, pedicellate, 4–8–spored, 157.5–202.5 × 26–35	clavate, apically rounded with ocular chamber, 8–spored, 135–150 × 22–33	cylindrical or oblong, short pedicellate, apically rounded, with an ocular chamber, 8-spored, 162–211 × 42–64
Ascospores (µm)	broadly fusiform, straight, thick-walled, with a submedian septate, 1–3-septate, hyaline, smooth-walled, 31–44 × 12–17	fusoid to narrowly fusoid, narrowly rounded ends, constricted at the centre septa, 7–10 transverse septa, hyaline and becoming pale brown at maturity, mostly overlapping biseriate to 3-seriate, smooth-walled, 57–59 × 8–12	fusoid to ellipsoid, muriform, upper part wider than lower part, 7–11 transversely septate, 2–3 vertical septa, constricted at the septa, initially hyaline, becoming yellowish brown at maturity, overlapping biseriate, smooth walled, surrounded by a thick mucilaginous sheath, 42–57 × 13–18
References	Matsumura et al. (2018)	Li et al. (2016)	This study

Table 5. Known hosts and distribution of *S. formosa*.

Host	Location	References
Magnolia denudata	Yunnan Province, Heilongtan, Kunming Institute of Botany	Wanasinghe et al. (2020)
M. grandiflora	China, Yunnan Province, Qujing Normal University	Wijayawardene et al. (2022b)
M. sprengeri	China, Guiyang, Guizhou Academy of Agricultural Sciences	This study
Michelia alba	UESTC premises, Chengdu, Sichuan, China	This study

et al. (2022b). However, we did not include *Pleomassaria magnoliae* and *P. maxima* in our phylogenetic analyses due to the lack of sequence data in GenBank.

In this study, we provide the sequence data and complete morphological description of the sexual morph of *S. formosa*. Additionally, we provide illustrations for the asexual morph of *S. formosa* and the sexual-asexual linkage for *S. formosa*. Previously, the sexual morphs of some members were reported but taxa were not listed under *Shearia* (*Pleomassaria magnoliae*, *Pleomassaria maxima, Shearia fusa*). Therefore, this is the first report of the sexual morph of *Shearia*.

Longiostiolaceae also consists of two other genera besides *Shearia*, *Crassiperidium* and *Longiostiolum*. A detailed morphological comparison of these three genera is provided in Table 4.

In previous studies, *S. formosa* has been reported from different *Magnolia* species in China (Table 5). Our isolates were also collected from a *Magnolia* species and *Michelia*

alba in China. We suggest further studies on *Magnoliaceae* species since different hosts are likely to provide a better understanding of the host preference of *Shearia* species.

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Disclosure statement

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

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References

Barr ME. 1982. On the *Pleomassariaceae (Pleosporales*) in North America. Mycotaxon. 15:349–383.

Bhunjun CS, Phukhamsakda C, Jeewon R, Promputtha I, Hyde KD. 2021. Integrating different lines of evidence to establish a novel ascomycete genus and family (*Anastomitrabeculia*, *Anastomitrabeculiaceae*) in *Pleosporales*. Journal of Fungi. 7(2):94. doi:10.3390/jof7020094.

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T. 2009. trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics. 25(15):1972–1973. doi:10.1093/bioinformatics/btp348.

Ellis JB, Everhart BM. 1898. New species of fungi from various localities. Bulletin of the Torrey Botanical Club. 25(9):501–514. doi:10.2307/2477837.

Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. In Nucleic acids symposium series. 41(41):95–98.

Hongsanan S, Hyde KD, Phookamsak R, Wanasinghe DN, McKenzie EHC, Sarma VV, Boonmee S, Lücking R, Bhat DJ, Liu NG, Tennakoon DS. 2020b. Refined families of *Dothideomycetes: Dothideomycetidae* and *Pleosporomycetidae*. Mycosphere. 11(1):1553–2107. doi:10.5943/mycosphere/11/1/13.

Hongsanan S, Hyde KD, Phookamsak R, Wanasinghe DN, McKenzie EHC, Sarma VV, Lücking R, Boonmee S, Bhat JD, Liu NG, Tennakoon DS. 2020a. Refined families of *Dothideomycetes*: orders and families *incertae sedis* in *Dothideomycetes*. Fungal Diversity. 105:17–318. doi:10.1007/s13225-020-00462-6.

Hyde KD, Jeewon R, Chen YJ, Bhunjun CS, Calabon MS, Jiang HB, Lin CG, Norphanphoun C, Sysouphanthong P, Pem D, Tibpromma S. 2020. The numbers of fungi: is the descriptive curve flattening? Fungal Diversity. 103:219–271. doi:10.1007/s13225-020-00458-2.

Hyde KD, McKenzie EHC, KoKo TW. 2011. Towards incorporating anamorphic fungi in a natural classification–checklist and notes for 2010. Mycosphere. 2(1):1–88.

Katoh K, Rozewicki J, Yamada KD. 2019. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics. 20(4):1160–1166. doi:10.1093/bib/bbx108.

Kishino H, Hasegawa M. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. 1989. Journal of Molecular Evolution. 29:170–179. doi:10.1007/BF02100115.

Kruys Å, Eriksson OE, Wedin M. 2006. Phylogenetic relationships of coprophilous *Pleosporales (Dothideomycetes, Ascomycota*), and the classification of some bitunicate taxa of unknown position. Mycological Research. 110(5):527–536. doi:10.1016/j.mycres.2006.03.002.

Li GJ, Hyde KD, Zhao RL, Hongsanan S, Abdel-Aziz FA, Abdel-Wahab MA, Alvarado P, Alves-Silva G, Ammirati JF, Ariyawansa HA, Baghela A. 2016. Fungal diversity notes 253–366: taxonomic and phylogenetic contributions to fungal taxa. Fungal Diversity. 78:1–237. doi:10.1007/s13225-016-0366-9.

Liu YJ, Whelen S, Hall BD. 1999. Phylogenetic relationships among ascomycetes: evidence from an RNA polymerse II subunit. Molecular Biology and Evolution. 16(12):1799–1808. doi:10.1093/oxfordjournals.molbev.a026092.

Matsumura M, Kato W, Hashimoto A, Takahashi YS, Shirouzu T, Tanaka K. 2018. *Crassiperidium (Pleosporales, Dothideomycetes)*, a new ascomycetous genus parasitic on *Fagus crenata* in Japan. Mycosphere. 9(6):1256–1267. doi:10.5943/mycosphere/9/6/13.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In 2010 Gateway Computing Environments Workshop (GCE). 1–8. doi:10.1109/GCE.2010.5676129.

Nylander JA. 2004. MrAIC. pl. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Petrak F. 1924. Mykologische Notizen. VII. Annales Mycologici. 22(1):1–182.

Petrak F. 1962. Ergebnisse einer revision der grundtypen verschiedener gattungen der askomyzeten und fungi imperfecti. Sydowia. 16:353–361.

Phukhamsakda C, McKenzie EHC, Phillips AJ, Gareth Jones EB, Bhat JD, Stadler M, Bhunjun CS, Wanasinghe DN, Thongbai B, Camporesi E, Ertz D. 2020. Microfungi associated with *Clematis (Ranunculaceae*) with an integrated approach to delimiting species boundaries. Fungal Diversity. 102:1–203. doi:10.1007/s13225-020-00448-4.

Phukhamsakda C, Nilsson RH, Bhunjun CS, de Farias AR, Sun YR, Wijesinghe SN, Raza M, Bao DF, Lu L, Tibpromma S, Dong W. 2022. The numbers of fungi: contributions from traditional taxonomic studies and challenges of metabarcoding. Fungal Diversity. 114(1):327–386. doi:10.1007/s13225-022-00502-3.

Rambaut A. 2012. FigTree, version 1.4.0. http://tree.bio.ed.ac.uk/software/figtree/.

Rehner S. 2001. Primers for Elongation Factor 1-α (EF1-α) Insect Biocontrol Laboratory USDA. ARS, PSI. p. 4.

Sayers EW, Cavanaugh M, Clark K, Pruitt KD, Sherry ST, Yankie L, Karsch-Mizrachi I. 2023. GenBank 2023 update. Nucleic Acids Research. 51(D1):D141–D144. doi:10.1093/nar/gkac1012.

Senanayake IC, Rathnayaka AR, Marasinghe DS, Calabon MS, Gentekaki E, Lee HB, Hurdeal VG, Pem D, Dissanayake LS, Wijesinghe SN, Bundhun D. 2020. Morphological approaches in studying fungi: collection, examination, isolation, sporulation and preservation. Mycosphere. 11(1):2678–2754. doi:10.5943/mycosphere/11/1/20.

Shear CL. 1902. Mycological notes and new species. Bulletin of the Torrey Botanical Club. 29(7):449–457. doi:10.2307/2478544.

Su W, Xu R, Bhunjun CS, Tian S, Dai Y, Li Y, Phukhamsakda C. 2022. Diversity of Ascomycota in Jilin: introducing novel woody litter taxa in *Cucurbitariaceae*. Journal of Fungi. 8(9):905. doi:10.3390/jof8090905.

Sutton BC. 1980. The Coelomycetes. Fungi imperfecti with pycnidia, acervuli and stromata. Kew, UK: Commonwealth Mycological Institute.

Swofford DL. 2002. PAUP Version 4.0 b10. Phylogenetic analysis using Parsimony. Sunderland: Sinauer.

Tanaka K, Mel'nik VA, Kamiyama M, Hirayama K, Shirouzu T. 2010. Molecular phylogeny of two coelomycetous fungal genera with stellate conidia, *Prosthemium* and *Asterosporium*, on Fagales trees. Botany. 88(12):1057–1071. doi:10.1139/B10-078.

Tanaka K, Ooki Y, Hatakeyama S, Harada Y, Barr ME. 2005. *Pleosporales* in Japan (5): *Pleomassaria, Asteromassaria*, and *Splanchnonema*. Mycoscience. 46(4):248–260. doi:10.1007/S10267-005-0245-9.

Trifinopoulos J, Nguyen LT, von Haeseler A, Minh BQ. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research. 44:W232–W235. doi:10.1093/nar/gkw256.

Tubaki K, Murata S, Nakagiri A. 1983. Materials for the fungus flora of Japan (33). Transactions of the Mycological Society of Japan. 24:121–125.

Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology. 172(8):4238–4246. doi:10.1128/jb.172.8.4238-4246.1990.

Wanasinghe DN, Wijayawardene NN, Xu J, Cheewangkoon R, Mortimer PE. 2020. Taxonomic novelties in *magnolia*-associated pleosporalean fungi in the Kunming botanical gardens (Yunnan, China). Plos ONE. 15(7):e0235855. doi:10.1371/journal.pone.0235855.

White TJ, Bruns T, Lee SJ, Taylor J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. PCR protocols: a guide to methods and applications. 18(1):315–322.

Wijayawardene NN, Crous PW, Kirk PM, Hawksworth DL, Boonmee S, Braun U, Dai DQ, D'souza MJ, Diederich P, Dissanayake A, Doilom M. 2014. Naming and outline of *Dothideomycetes*–2014 including proposals for the protection or suppression of generic names. Fungal Diversity. 69:1–55. doi:10.1007/s13225-014-0309-2.

Wijayawardene NN, Dai DQ, Zhu ML, Wanasinghe DN, Kumla J, Zhang GQ, Zhang TT, Han LS, Tibpromma S, Chen HH. 2022b. Fungi associated with dead branches of *Magnolia grandiflora*: a case study from Qujing, China. Frontiers in Microbiology. 13:954680. doi:10.3389/fmicb.2022.954680.

Wijayawardene NN, Hyde KD, Dai DQ, Sánchez-García M, Goto BT, Magurno F. 2022a. Outline of Fungi and fungus-like taxa – 2021. Mycosphere. 13:53–453. doi:10.5943/mycosphere/13/1/2.

Wijayawardene NN, Hyde KD, Lumbsch HT, Liu JK, Maharachchikumbura SS, Ekanayaka AH, Tian Q, Phookamsak R. 2017. Outline of *Ascomycota*. Fungal Diversity. 88:167–263. doi:10.1007/s13225-018-0394-8.

Wijayawardene NN, Hyde KD, Wanasinghe DN, Papizadeh M, Goonasekara ID, Camporesi E, Bhat DJ, McKenzie EHC, Phillips AJ, Diederich P, Tanaka K. 2016. Taxonomy and phylogeny of dematiaceous coelomycetes. Fungal Diversity. 77:1–316. doi:10.1007/s13225-016-0360-2.

Xu R, Su W, Tian S, Bhunjun CS, Tibpromma S, Hyde KD, Li Y, Phukhamsakda C. 2022. Synopsis of *Leptosphaeriaceae* and introduction of three new taxa and one new record from China. Journal of Fungi. 19:8(5):416. doi:10.3390/jof8050416.