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Anthostomella-like fungi on bamboo: four new genera belonging to a new family *Pallidoperidiaceae* (*Xylariales*)

Ryosuke Sugita[a, b], Ryuichi Yoshioka[a], Kazuaki Tanaka[a*]

[a] *Faculty of Agriculture and Life Science, Hirosaki University, 3 Bunkyo-cho, Hirosaki, Aomori, 036-8561, Japan*

[b] *The United Graduate School of Agricultural Sciences, Iwate University, 18-8 Ueda 3 chome, Morioka, Iwate, 020-8550, Japan*

ABSTRACT

This study investigates the phylogeny and taxonomy of *Anthostomella*-like fungi (*Xylariales*, *Sordariomycetes*) found in association with bamboo in Japan. Four new genera, *Amphigermslita* (including three new species, i.e., *A. deformis*, *A. fusiformis*, and *A. pseudofusiformis*), monotypic *Crassipseudostroma* (*C. phyllostachydis*) and *Minuticlypeus* (*M. discosporus*), and *Pallidoperidium* (two new species, *P. exasperatum* and *P. paraexasperatum*), and one known genus, *Nigropunctata* (one new species, *N. complanata*) are recognized and described. These five genera were found to constitute a distinct monophyletic lineage based on molecular phylogenetic analyses utilizing sequences of ITS and LSU nrDNA, *rpb2*, and *tef1-α* sequences. A new family, *Pallidoperidiaceae*, is proposed to accommodate these bambusicolous *Anthostomella*-like fungi. The identification of this lineage contributes to our understanding of the evolutionary relationships and classification of these bambusicolous fungi. It suggests that these five genera share a unique evolutionary history and possess shared morphological and ecological characteristics.

Keywords: 13 new taxa, *Ascomycota*, *Sordariomycetes*, *Xylariaceae*, *Xylariomycetidae*

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1. Introduction

Based on molecular evidence, numerous fungi that were previously classified in the family *Xylariaceae* (*Xylariales*, *Sordariomycetes*) due to morphological similarities have been reclassified and excluded from this family. *Biscogniauxia* Kuntze, *Daldinia* Ces. & De Not., and *Hypoxylon* Bull. have been considered to be morphologically typical of the family *Xylariaceae*, but recent phylogenetic analyses have shown that these genera should be classified into separate families *Graphostromataceae* and *Hypoxylaceae* within *Xylariales* (Hsieh et al., 2005; Wendt et al., 2018). *Spirodecospora* B.S. Lu et al. has been considered a member of the family *Xylariaceae* based on similarities in the ultrastructure of the ascus apices (Lu et al., 1998). However, a taxonomic and molecular phylogenetic study revealed that this genus is a distinct lineage from *Xylariaceae* and was proposed to be classified as a novel family, *Spirodecosporaceae* (Sugita et al., 2022).

The genus *Anthostomella* Sacc. (Lu & Hyde, 2000; Saccardo, 1875a), which includes over 400 described species, has traditionally been affiliated with the *Xylariaceae* based on morphological characteristics (Index Fungorum; http://www.indexfungorum.org/names/names.asp, accessed on 5 May 2023). This genus exhibits heterogeneity and it is characterized by immersed to semi-immersed ascomata with or without clypeus; (4–)8-spored, uniseriate to biseriate, cylindrical to broadly cylindrical, or occasionally clavate asci with an amyloid or inamyloid subapical apparatus, or lacking any visible apical structures; and mostly ellipsoid to inequilaterally ellipsoid, unicellular ascospores or composed of a larger brown cell and a hyaline basal dwarf cell, or rarely with bipolar dwarf cells (Lu & Hyde, 2000). Associated asexual morphs are known as *Geniculosporium*-, *Nodulisporium*-, and *Virgariella*-like (Francis et al., 1980; Hyde & Goh, 1998). Recent molecular phylogenetic studies have shown that *Anthostomella*-like fungi are polyphyletic within *Xylariales*, and some are distantly related to *Xylariaceae* (Daranagama et al., 2015, 2016). Several newly discovered lineages have been established as new genera (*Alloanthostomella* Daranag. et al., *Anthostomelloides* Tibpromma & K.D. Hyde, *Haploanthostomella* Konta & K.D. Hyde, *Neoanthostomella* D.Q. Dai & K.D. Hyde, *Nigropunctata* Samarak. & K.D. Hyde, *Pseudoanthostomella* Daranag. et al., and *Xenoanthostomella* Mapook & K.D. Hyde; Dai et al., 2017; Daranagama et al., 2015; Hyde et al., 2020; Konta et al., 2021; Samarakoon et al., 2022; Tibpromma et al., 2017). However, our current understanding of the phylogenetic relationships among *Anthostomella*-like fungi is still incomplete and requires further investigation.

Anthostomella-like fungi have been frequently reported in association with bamboo worldwide (Eriksson & Yue, 1998). During

* Corresponding author.
Kazuaki Tanaka
Faculty of Agriculture and Life Science, Hirosaki University, 3 Bunkyo-cho, Hirosaki, Aomori, 036-8561, Japan
E-mail: k-tanaka@hirosaki-u.ac.jp (K. Tanaka)

the survey of sordariomycetous fungi on bamboo in Japan (e.g., Sugita & Tanaka, 2022; Sugita et al., 2022), many *Anthostomella*-like specimens were collected. These collections share several morphological features but seem to be different from what is considered today a typical *Anthostomella* (Eriksson, 1966; Francis, 1975; see also Discussion). Despite their ecological importance, their phylogeny and taxonomy remain poorly understood, particularly in the context of the Japanese bamboo ecosystem. This study aims to fill this knowledge gap by employing advanced molecular techniques to elucidate the evolutionary relationships and taxonomic classification of these fungi in Japan and clarify their familial position in *Xylariales*.

2. Materials and methods

2.1. Isolation and morphological observation

All specimens were collected from various bamboo species in Japan and deposited in the herbarium of Hirosaki University (HHUF). Morphological characteristics were observed in preparations mounted in distilled water or 2% KOH by differential interference microscopy (BX53, Olympus, Tokyo) using images captured with an Olympus digital camera (DP21). Sections of ascomata were mounted in diluted lactophenol cotton blue. Lugol's solution was used to test the amyloidity of ascal apex, and Indian ink was used to observe the mucilaginous sheath of ascospores. The structures of ascospores and ascal apex were drafted on graph paper and digitized using a CLIP STUDIO PAINT (https://www.clipstudio.net/). Single-spore isolates were obtained from all specimens according to the methods of Tubaki (1978) or Shearer et al. (2004) with some modification. Fungal cultures were preserved and deposited at Hirosaki University and the NARO Genebank, Japan (MAFF). Several mycelial agar pieces were placed on water agar containing sterilized rice straw (rice straw agar: RSA) to observe sporulation in vitro. After the rice straws were colonized at 25 °C for 2 wk, the plates were incubated at 25 °C under blacklight blue illumination for 1–2 mo to observe sporulation.

2.2. DNA extraction, PCR, and phylogenetic analyses

DNA was extracted from the cultures using an ISOPLANT II kit (Nippon Gene, Tokyo, Japan) following the manufacturer's instructions. The following loci were amplified and sequenced: the internal transcribed spacer (ITS barcode) regions (ITS1-5.8S-ITS2) with primers ITS1 and ITS4 (White et al., 1990); the large subunit nuclear ribosomal DNA (LSU) with primers LR0R (Rehner & Samuels, 1994) and LR5 or LR7 (Vilgalys & Hester, 1990); the second largest RNA polymerase II subunit (*rpb2*) with primers fRPB2-5F and fRPB2-7cR (Liu et al., 1999); and the translation elongation factor 1-alpha (*tef1*) gene with primers 983F and 2218R (Rehner & Buckley, 2005). PCR products were purified using the FastGene Gel/PCR Extraction Kit (Nippon Gene, Tokyo, Japan) following the manufacturer's instructions and commercially sequenced at SolGent Co., Ltd. (Daejeon, South Korea). Newly generated sequences were deposited in GenBank (Table 1).

Primary analysis of partial ITS (5.8S-ITS2), LSU, *rpb2*, and *tef1* sequences from 136 strains of *Xylariales* was conducted to clarify the familial placement of *Anthostomella*-like fungi. ITS1 was excluded from the primary analysis due to alignment difficulties. The isolates and GenBank accession numbers for the sequences generated in this study are listed in Table 1. Other sequences of *Xylariales* (e.g., Crous et al., 2019; Dai et al., 2017; Daranagama et al., 2015, 2016; Samarakoon et al., 2022; Voglmayr et al., 2022) were retrieved from GenBank (see Supplementary Table S1 for details on the sources of the sequences). Species in the *Diaporthales*, *Sordariales* (Samarakoon et al., 2022), and *Thyridiales* (Sugita & Tanaka, 2022) were selected as outgroups. As a secondary analysis, single-gene trees of complete ITS (including ITS1), LSU, *rpb2*, and *tef1*, and a combined tree of these four loci were generated to assess the species/genera boundaries of the 27 strains within *Pallidoperidiaceae*. All sequence alignments were performed using the server version of MAFFT (http://www.ebi.ac.uk/Tools/msa/mafft) and checked and refined using MEGA v. 7.0 (Kumar et al., 2016).

Maximum-likelihood (ML) and Bayesian methods were used for phylogenetic analyses. The optimum substitution models for each dataset were estimated using Kakusan4 software (Tanabe, 2011) based on the Akaike information criterion (AIC; Akaike, 1974) and Bayesian information criterion (BIC; Schwarz, 1978) for the ML and Bayesian analyses, respectively. The TreeFinder program (http://www.treefinder.de) for ML analysis was executed based on models selected using the AICc4 parameter. ML bootstrap support (MLBS) values were obtained using 1,000 bootstrap replicates. The

Table 1. Isolates and GenBank accessions of sequences newly obtained in this study

Fungal name	Host name[a, b]	Original no.	Specimen	Type[c]	Strain	GenBank accession numbers			
						ITS	LSU	*rpb2*	*tef1*
Amphigermslita deformis	*S. kurilensis* (A)	KT 2300	HHUF 30660	H	MAFF 247791	LC760553	LC760572	LC760592	LC760605
Amphigermslita deformis	*S. senanensis* (A)	KT 3827	HHUF 30661	P	MAFF 247792	LC760554	LC760573	LC760593	LC760606
Amphigermslita fusiformis	*Sasa* sp. (A)	KT 4096	HHUF 30663	H	MAFF 247793	LC760555	LC760574	LC760594	LC760607
Amphigermslita fusiformis	*S. kurilensis* (A)	RSU 115	HHUF 30664	P	MAFF 247794	–	LC760575	LC760595	LC760608
Amphigermslita pseudofusiformis	*Sasa* sp. (A)	RSU 50	HHUF 30662	H	MAFF 247795	LC760556	LC760576	LC760596	LC760609
Crassipseudostroma phyllostachydis	*Ph. bambusoides* (A)	KT 4115	HHUF 30678	H	MAFF 247796	LC760557	LC760577	LC760597	LC760610
Minuticlypeus discosporus	*Pl. simonii* (A)	KT 3877	HHUF 30672	P	MAFF 247797	LC760558	LC760578	LC760598	LC760611
Minuticlypeus discosporus	*Ph. bambusoides* (A)	KT 4150	HHUF 30673	H	MAFF 247798	LC760559	LC760579	–	LC760612
Nigropunctata complanata	*C. quadrangularis* (A)	KT 3837	HHUF 30674	P	MAFF 247799	LC760560	LC760580	LC760599	LC760613
Nigropunctata complanata	*B. multiplex* var. *elegans* (B)	KT 3846	HHUF 30675	H	MAFF 247800	LC760561	LC760581	LC760600	LC760614
Nigropunctata complanata	*B. multiplex* (B)	KT 3851	HHUF 30676	P	MAFF 247801	LC760562	LC760582	LC760601	LC760615
Nigropunctata complanata	*Ps. japonica* var. *tsutsumiana* (A)	KT 3857	HHUF 30677	P	MAFF 247802	LC760563	LC760583	LC760602	LC760616
Pallidoperidium exasperatum	*Pl. simonii* (A)	KT 3101	HHUF 30174	H	MAFF 247803	LC760564	LC760584	LC760603	LC760617
Pallidoperidium exasperatum	*C. quadrangularis* (A)	KT 3830	HHUF 30665	P	MAFF 247804	LC760565	LC760585	–	LC760618
Pallidoperidium exasperatum	*Se. okuboi* (A)	KT 4066	HHUF 30666	P	MAFF 247805	LC760566	LC760586	–	LC760619
Pallidoperidium exasperatum	*Pl. hindsii* (A)	KT 4071	HHUF 30667	P	MAFF 247806	LC760567	LC760587	–	LC760620
Pallidoperidium paraexasperatum	*Sasae. sasakiana* (A)	KT 3817	HHUF 30668	H	MAFF 247807	LC760568	LC760588	–	LC760621
Pallidoperidium paraexasperatum	*Ph. pubescens* (A)	KT 3890	HHUF 30669	P	MAFF 247808	LC760569	LC760589	–	LC760622
Pallidoperidium paraexasperatum	*B. multiplex* (B)	KT 4063	HHUF 30670	P	MAFF 247809	LC760570	LC760590	–	LC760623
Pallidoperidium paraexasperatum	*Ph. aurea* (A)	KT 4090	HHUF 30671	P	MAFF 247810	LC760571	LC760591	LC760604	LC760624

[a] Abbreviation of host names: *B.* = *Bambusa*, *C.* = *Chimonobambusa*, *Ph.* = *Phyllostachys*, *Pl.* = *Pleioblastus*, *Ps.* = *Pseudosasa*, *S.* = *Sasa*, *Sasae.* = *Sasaella*, *Se.* = *Semiarundinaria*

[b] Parentheses after the host name indicate the tribe within the subfamily, *Bambusoideae*: (A) = tribe *Arundinarieae*, (B) = tribe *Bambuseae*

[c] H = holotype, P = paratype

Bayesian analysis program, MrBayes v. 3.2.6 (Ronquist et al., 2012), was executed with substitution models selected based on the BIC4 parameter. Two simultaneous and independent Metropolis-coupled Markov chain Monte Carlo (MCMCMC) runs were performed for 5,000,000 generations, with the tree sampled every 1,000 generations. The convergence of the MCMCMC procedure was assessed from the effective sample size scores (all > 100) using MrBayes and Tracer version 1.6 (Rambaut et al., 2014). The first 25% of the trees were discarded as burn-ins. The remainder was used to calculate the 50% majority-rule trees and to determine the posterior probabilities (PPs) for individual branches. Multiple sequence alignments and trees were deposited in TreeBASE (S30263).

3. Results

3.1. Phylogeny

For the primary analysis, ML and Bayesian phylogenetic trees were generated using an aligned sequence dataset comprising partial ITS (excluding ITS1), LSU, *rpb2*, and *tef1*. The datasets used and statistics resulting from the phylogenetic analyses in this study (e.g., number of characters and selected substitution models) are provided in Supplementary Table S2. The ML tree with the highest log-likelihood (lnL = −77,338.511) is shown in Fig. 1. This combined dataset provided higher confidence values for familial classification than the individual gene trees, with 39 families reconstructed in *Xylariales*. The topology recovered by the Bayesian analysis was almost identical to that of the ML tree. *Anthostomella*-like fungi newly obtained in this study were separated into five genera, including the known genus *Nigropunctata*. The lineage encompassing these five genera with strong support values (100% MLBS/1.0 Bayesian PP) is proposed as the new family *Pallidoperidiaceae*. This new family was closely related to *Melanographium* Sacc., a hyphomycete genus with synnematous conidiomata. The clade composed of *Anthostomella* sensu stricto, *Pseudoanthostomella*, and *Alloanthostomella* strains was revealed as the closest relative to the above lineages (83% MLBS /0.99 BPP).

For secondary analysis, ML and Bayesian phylogenetic trees were generated using an aligned sequence dataset of members of the *Pallidoperidiaceae* comprising complete ITS (including ITS1), LSU, *rpb2*, and *tef1*. The statistics and models used for these datasets are listed in Supplementary Table S2. The ML trees with the highest log-likelihood (–2,470.2237 in ITS, –3,375.7424 in LSU, –3,650.8568 in *rpb2*, –2,879.8167 in *tef1*, and –12,254.421 in ITS-LSU-*rpb2*-*tef1*) are shown in Supplementary Fig. S1 and Fig. 2. The topology recovered by the Bayesian analysis was almost identical to that of the ML tree. In the combined tree of *Pallidoperidiaceae*, five distrinct lineages were constructed, representing the phylogenetic relationships among the five genera, such as *Amphigermslita* R. Sugita & Kaz. Tanaka, *Crassipseudostroma* R. Sugita & Kaz. Tanaka, *Minuticlypeus* R. Sugita & Kaz. Tanaka, *Nigropunctata*, and *Pallidoperidium* R. Sugita & Kaz. Tanaka. Genera *Amphigermslita*, *Minuticlypeus*, and *Pallidoperidium* formed a fully supported monophyletic clade (100% MLBS/1.0 BPP), respectively, while *Nigropunctata* had moderate support (75% MLBS/0.98 BPP). Although the clades of most genera in the single-gene trees (Supplementary Fig. S1) were identical to those of the combined tree (Fig. 2), *Nigropunctata* did not cluster as a monophyletic clade in ITS and formed a monophyly with high support value in only *rpb2* tree (100% MLBS/1.0 BPP).

3.2. Taxonomy

Pallidoperidiaceae R. Sugita & Kaz. Tanaka, fam. nov.
MycoBank no.: MB 848590.

Type genus: *Pallidoperidium* R. Sugita & Kaz. Tanaka

Sexual morph: Ascomata deeply immersed in host, solitary to aggregated, subglobose, with or without clypeus. Ostiolar neck conical to cylindrical, periphysate, with or without internal setose hyphae, visible as black dots on the substrate. Ascomatal wall composed of several layers of polygonal, hyaline to dark brown cells, often with pseudostromatic tissue at the periphery. Paraphyses numerous, septate, filamentous, hyaline. Asci unitunicate, (6–)8-spored, cylindrical, broadly rounded at the apex; apical apparatus amyloid or inamyloid, discoid to inverted, hat-shaped. Ascospores brown, fusiform to ellipsoid, unicellular, smooth or rough, surrounded by mucilaginous appendages, with one or two germ slits.

Asexual morph: Conidiomata sporodochial, scattered, solitary, superficial. Conidiophores micronematous, septate, branched. Conidiogenous cells blastic, integrated, terminal and intercalary, with sympodial proliferation. Conidia falcate, one-celled, hyaline.

Notes: We established a new family, *Pallidoperidiaceae*, to accommodate four novel *Anthostomella*-like genera (*Amphigermslita*, *Crassipseudostroma*, *Minuticlypeus*, and *Pallidoperidium*) and a known genus (*Nigropunctata*). Although monophyly between *Pallidoperidiaceae* and *Melanographium* was strongly supported (Fig. 1), we did not consider *Melanographium* as a member of *Pallidoperidiaceae* because of their remarkable morphological differences (Fig. 2).

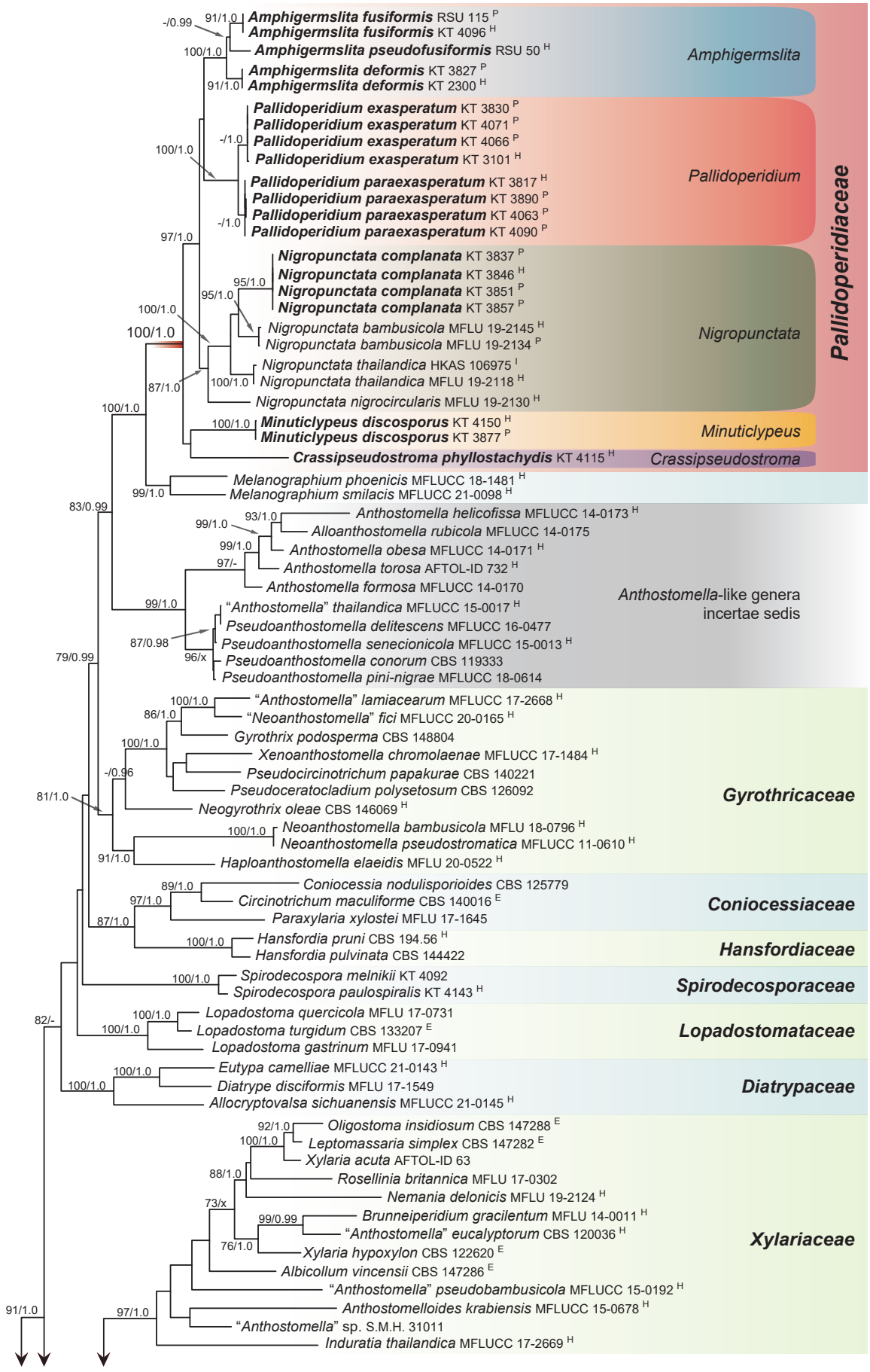
As shown in Fig. 2, among the five genera, significant differences were observed in the characteristics of ascospores (shape, germ slits, and mucilaginous appendages) and ascus apical apparatus (shape and amyloidity). *Crassipseudostroma* (I) and *Pallidoperidium* (III) share ellipsoid ascospores with a germ slit extending over the full-length, but *Crassipseudostroma* differs from *Pallidoperidium* in having asci with an inamyloid apical apparatus and ascospores with mucilaginous pads at the ends. *Amphigermslita* (IV) has asci with an amyloid, wedge-shaped apical apparatus and ascospores with a short germ slit at the both ends, which are unique characteristics within *Pallidoperidiaceae*. Ascospores of *Minuticlypeus* (II) and *Nigropunctata* (V) are ellipsoid to oblong, flattened fusiform in side view, surrounded by a mucilaginous sheath, and asci with an amyloid, inverted, hat-shaped apical apparatus. However, ascospores of *Nigropunctata* spp. are surrounded by a fibrous sheath near the spore wall. Setose hyphae of ascomatal ostiolar neck are found in *Amphigermslita*, *Crassipseudostroma*, and *Minuticlypeus*, but have not been observed in *Nigropunctata* and *Pallidoperidium*.

Amphigermslita R. Sugita & Kaz. Tanaka, gen. nov.
MycoBank no.: MB 848591.

Etymology: From the Greek *amphi-*, meaning on both sides, in reference to the ascospores with a short germ slit at the both ends.

Type species: *Amphigermslita fusiformis* R. Sugita & Kaz. Tanaka.

Sexual morph: Ascomata perithecial, immersed, solitary, subglobose. Ostiolar neck cylindrical, periphysate, with internal setose hyphae, without clypeus. Ascomatal wall composed of polygonal, dark brown cells. Paraphyses septate, unbranched, cylindrical, hyaline. Asci unitunicate, cylindrical, (6–)8-spored; apical apparatus


Amphigermslita fusiformis RSU 115 P
Amphigermslita fusiformis KT 4096 H
Amphigermslita pseudofusiformis RSU 50 H
Amphigermslita deformis KT 3827 P
Amphigermslita deformis KT 2300 H
Amphigermslita
Pallidoperidium exasperatum KT 3830 P
Pallidoperidium exasperatum KT 4071 P
Pallidoperidium exasperatum KT 4066 P
Pallidoperidium exasperatum KT 3101 H
Pallidoperidium paraexasperatum KT 3817 H
Pallidoperidium paraexasperatum KT 3890 P
Pallidoperidium paraexasperatum KT 4063 P
Pallidoperidium paraexasperatum KT 4090 P
Pallidoperidium
Nigropunctata complanata KT 3837 P
Nigropunctata complanata KT 3846 H
Nigropunctata complanata KT 3851 P
Nigropunctata complanata KT 3857 P
Nigropunctata bambusicola MFLU 19-2145 H
Nigropunctata bambusicola MFLU 19-2134 P
Nigropunctata thailandica HKAS 106975 I
Nigropunctata thailandica MFLU 19-2118 H
Nigropunctata nigrocircularis MFLU 19-2130 H
Nigropunctata
Minuticlypeus discosporus KT 4150 H
Minuticlypeus discosporus KT 3877 P
Minuticlypeus
Crassipseudostroma phyllostachydis KT 4115 H
Crassipseudostroma
Pallidoperidiaceae
Melanographium phoenicis MFLUCC 18-1481 H
Melanographium smilacis MFLUCC 21-0098 H
Anthostomella helicofissa MFLUCC 14-0173 H
Alloanthostomella rubicola MFLUCC 14-0175
Anthostomella obesa MFLUCC 14-0171 H
Anthostomella torosa AFTOL-ID 732 H
Anthostomella formosa MFLUCC 14-0170
"Anthostomella" thailandica MFLUCC 15-0017 H
Pseudoanthostomella delitescens MFLUCC 16-0477
Pseudoanthostomella senecionicola MFLUCC 15-0013 H
Pseudoanthostomella conorum CBS 119333
Pseudoanthostomella pini-nigrae MFLUCC 18-0614
Anthostomella-like genera incertae sedis
"Anthostomella" lamiacearum MFLUCC 17-2668 H
"Neoanthostomella" fici MFLUCC 20-0165 H
Gyrothrix podosperma CBS 148804
Xenoanthostomella chromolaenae MFLUCC 17-1484 H
Pseudocircinotrichum papakurae CBS 140221
Pseudoceratocladium polysetosum CBS 126092
Neogyrothrix oleae CBS 146069 H
Neoanthostomella bambusicola MFLU 18-0796 H
Neoanthostomella pseudostromatica MFLUCC 11-0610 H
Haploanthostomella elaeidis MFLU 20-0522 H
Gyrothricaceae
Coniocessia nodulisporioides CBS 125779
Circinotrichum maculiforme CBS 140016 E
Paraxylaria xylostei MFLU 17-1645
Coniocessiaceae
Hansfordia pruni CBS 194.56 H
Hansfordia pulvinata CBS 144422
Hansfordiaceae
Spirodecospora melnikii KT 4092
Spirodecospora paulospiralis KT 4143 H
Spirodecosporaceae
Lopadostoma quercicola MFLU 17-0731
Lopadostoma turgidum CBS 133207 E
Lopadostoma gastrinum MFLU 17-0941
Lopadostomataceae
Eutypa camelliae MFLUCC 21-0143 H
Diatrype disciformis MFLU 17-1549
Allocryptovalsa sichuanensis MFLUCC 21-0145 H
Diatrypaceae
Oligostoma insidiosum CBS 147288 E
Leptomassaria simplex CBS 147282 E
Xylaria acuta AFTOL-ID 63
Rosellinia britannica MFLU 17-0302
Nemania delonicis MFLU 19-2124 H
Brunneiperidium gracilentum MFLU 14-0011 H
"Anthostomella" eucalyptorum CBS 120036 H
Xylaria hypoxylon CBS 122620 E
Albicollum vincensii CBS 147286 E
"Anthostomella" pseudobambusicola MFLUCC 15-0192 H
Anthostomelloides krabiensis MFLUCC 15-0678 H
"Anthostomella" sp. S.M.H. 31011
Induratia thailandica MFLUCC 17-2669 H
Xylariaceae

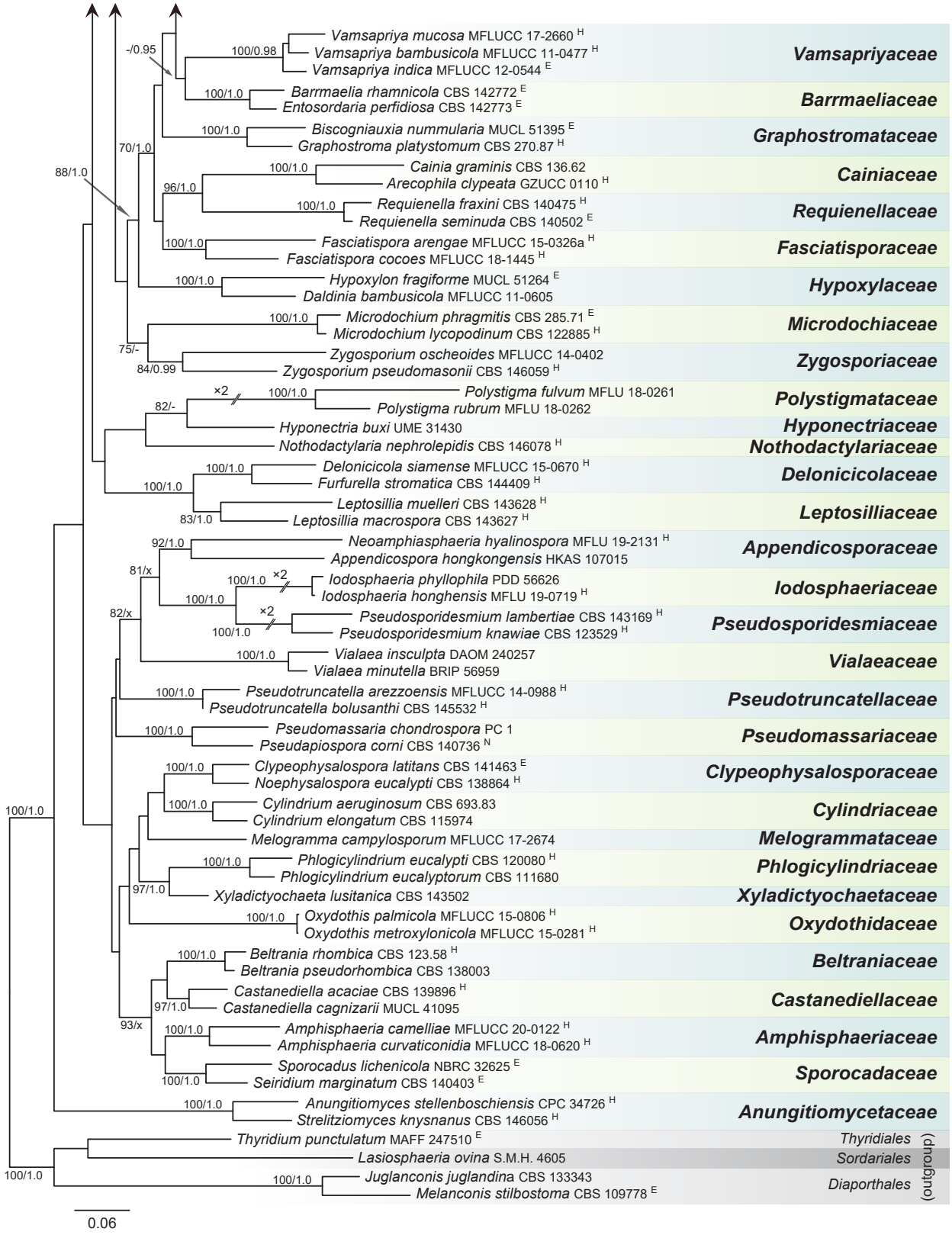


Fig. 1 Maximum-likelihood (ML) tree of *Xylariales* based on combined ITS (5.8S-ITS2), LSU, *rpb2*, and *tef1* sequences. ML bootstrap support (MLBS) higher than 70% and Bayesian posterior probabilities (BPP) above 0.95 are presented at the nodes as MLBS/BPP and a node not present in the Bayesian analysis is shown with 'x'. A hyphen ('-') indicates values lower than 70% MLBS or 0.95 BPP. The newly obtained sequences are shown in bold. The scale bar represents expected nucleotide substitutions per site. E, H, I, N and P after strain numbers indicate ex-epitype, ex-holotype, ex-isotype, ex-neotype, and ex-paratype strains, respectively.

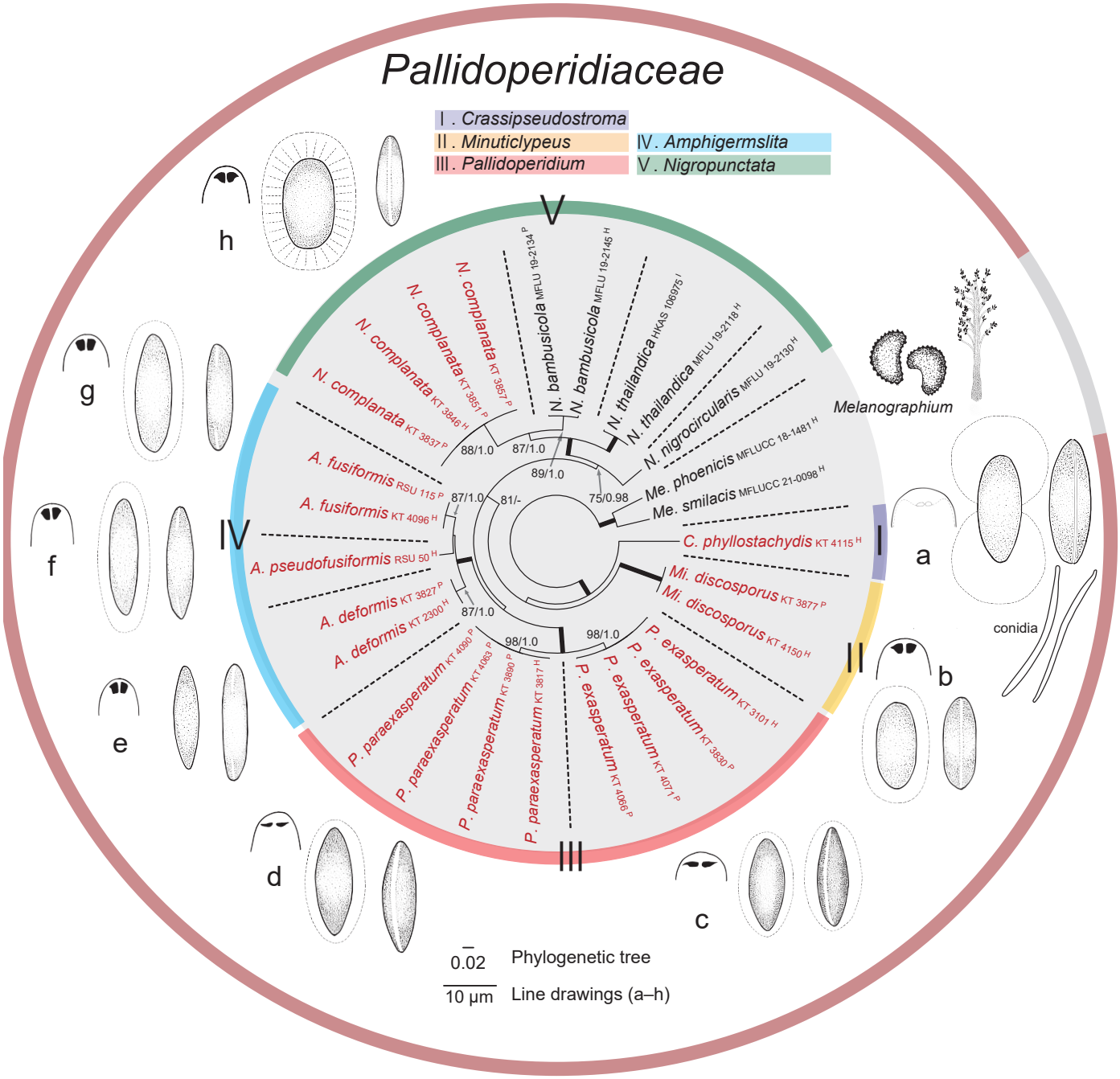


Fig. 2 Maximum-likelihood (ML) tree of *Pallidoperidiaceae* based on combined ITS (ITS-5.8S-ITS2), LSU, *rpb2*, and *tef1* sequences. ML bootstrap support (MLBS) higher than 70% and Bayesian posterior probabilities (BPP) above 0.95 are presented at the nodes as MLBS/BPP. A hyphen ('-') indicates values lower than 70% MLBS or 0.95 BPP. The newly obtained sequences are shown in red. Line drawings indicate ascus apical apparatus and ascospores of species within the family (a: *Crassipseudostroma phyllostachydis*. b: *Minuticlypeus discosporus*. c: *Pallidoperidium exasperatum*. d: *P. paraexasperatum*. e: *Amphigermslita deformis*. f: *A. pseudofusiformis*. g: *A. fusiformis*. h: *Nigropunctata complanata*). Thickened branches indicate branch support with 100% MLBS/1.00 BPP. The scale bars represent nucleotide substitutions per site and size of fungal structures (10 µm). H, I, and P after strain numbers indicate ex-holotype, ex-isotype, and ex-paratype strains, respectively.

amyloid, wedge-shaped. Ascospores ellipsoid to fusoid, unicellular, brown, oblong in side view, with a short germ slit at the both ends, surrounded by a sheath.

Asexual morph: Not observed.

Notes: *Amphigermslita* formed a monophyletic lineage as a sister clade to the genus *Pallidoperidium*, although this relationship was not supported (Figs. 1, 2). *Pallidoperidium* differs from *Amphigermslita* in having asci with a thin discoid apical apparatus and ascospores with a germ slit extending over the full-length. *Amphigermslita* is similar to *Entosordaria* (Sacc.) Höhn. (*Barrmaeliaceae*, *Xylariales*) in having ascospores with short apical germ slits, but the latter has two-celled ascospores with an apical germ apparatus consisting of radial slits (Voglmayr et al., 2018).

Amphigermslita deformis R. Sugita & Kaz. Tanaka, sp. nov. Fig. 3. MycoBank no.: MB 848592.

Etymology: From the Latin *deformis*, meaning abnormal, in reference to the deformed ascospores often observed.

Typus: JAPAN, Hokkaido, Rishiri island, Kutsugata-trail, on

dead culms of *Sasa kurilensis*, 28 Jul 2007, K. Tanaka & G. Sato, KT 2300 (HHUF 30660, holotype), ex-type culture MAFF 247791.

Sexual morph: Ascomata perithecial, deeply immersed in host tissue, solitary to aggregated, subglobose, 300–360 μm high, 420–490 μm diam. Ostiolar neck cylindrical, periphysate, 125–160 μm high, 85–100 μm wide, with setose hyphae of up to 50 μm long, 2–3 μm wide, without clypeus. Ascomatal wall 7.5–20 μm thick, composed of 3–5 layers of polygonal, 4.5–5.5 × 1.8–2.2 μm, dark brown cells. Paraphyses numerous, septate, unbranched, cylindrical, hyaline, 1–2.5 μm wide. Asci unitunicate, cylindrical, 120–165 × 8.5–10 μm (av. 141.8 × 9.6 μm, n = 9), (6–)8-spored; apical apparatus amyloid, wedge-shaped, 2–3 μm high, 4.5–5.5 μm diam. Ascospores fusoid with tapered ends, unicellular, brown, 17.5–25(–27.5) × 5–7.5 μm (av. 20.9 × 5.8 μm, n = 90), l/w 2.9–4.5 (av. 3.6, n = 44),

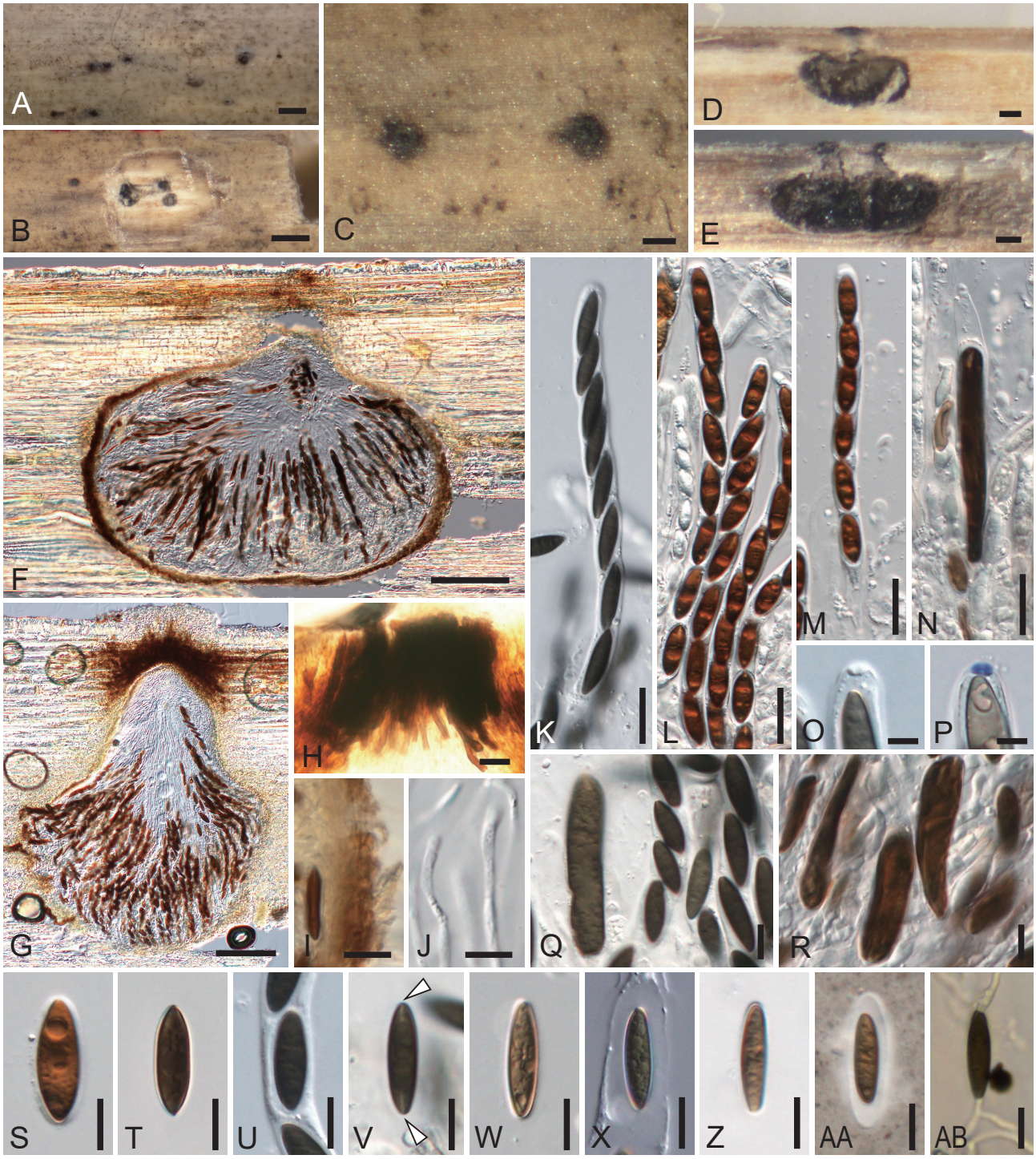


Fig. 3 *Amphigermslita deformis* (A–F, H, N, R, V–AB from KT 3827. G, I–M, O–Q, S–U from KT 2300). A–C: Ascomata in face view (B: Transverse section). D–G: Longitudinal section of ascomata. H: Setose hyphae of ascomatal ostiolar neck. I: Ascomatal wall in section (F–I in diluted lactophenol cotton blue). J: Paraphyses. K–N: Asci (K, L: 8-spored. M: 6-spored. N: With an irregular ascospore). O, P: Apex of asci (P: Amyloid apical apparatus in Lugol). Q–AB: Ascospores (Q, R: Normal and irregular ascospores. V: Arrowheads indicate germ slits. AA: In Indian ink. AB: Germinating ascospore). K, O, T–V in 2% KOH. All in distilled water, except where noted. *Bars*: A, B 500 μm; C–G 100 μm; H–J, Q–AB 10 μm; K–N 20 μm; O, P 5 μm.

narrow fusoid to oblong in side view, 3.5–6.5(–7) μm thick (av. 5.0 μm, n = 46), often forming deformed spores irregular in size and shape (up to 70 μm long; Fig. 3N, Q, R), with a short germ slit at the both ends, surrounded by a mucilaginous sheath.

In culture, no sporulation observed on RSA.

Additional specimen examined: JAPAN, Shizuoka, Sunto, Nagaizumi, Fuji Bamboo Garden, on dead culms of *Sasa senanensis*, 24 Nov 2017, K. Tanaka & K. Arayama, KT 3827 (HHUF 30661, paratype), ex-paratype culture MAFF 247792.

Note: *Amphigermslita deformis* is similar to *Anthostomella uniseriata* J. Fröhl. & K.D. Hyde on palm, but the latter have ascospores with a full-length germ slit (Fröhlich & Hyde, 2000).

Amphigermslita fusiformis R. Sugita & Kaz. Tanaka, sp. nov. Fig. 4. MycoBank no.: MB 848593.

Etymology: From the Latin *fusiformis*, meaning fusiform, in reference to the ascospore shape.

Typus: JAPAN, Hiroshima, Otake, near Oze river, on dead twigs of *Sasa* sp., 18 Feb 2020, K. Tanaka, R. Sugita, S. Narita & M. Tanaka, KT 4096 (HHUF 30663, holotype), ex-type culture MAFF 247793.

Sexual morph: Ascomata perithecial, deeply immersed in host tissue, solitary, subglobose, 320–400 μm high, 350–520 μm diam. Ostiolar neck cylindrical, 100–170 μm high, 190–230 μm wide, with setose hyphae of up to 50 μm long, 2.5–3.5 μm wide, without clypeus. Ascomatal wall 5–7.5 μm thick, composed of 3–5 layers of polygonal, 3–7.5 × 2.5–4 μm, dark brown cells. Paraphyses numerous, septate, unbranched, cylindrical, hyaline, 2–2.5 μm wide. Asci unitunicate, cylindrical, 115–140 × 10.5–12.5 μm, 8-spored; apical apparatus amyloid, wedge-shaped, 1.5–3.5 μm high, 3.5–4.5 μm diam. Ascospores fusoid with tapered ends, unicellular, brown,

Fig. 4 *Amphigermslita fusiformis* (A–D, F, H, J, L, M, O–S, Z–AB from KT 4096. E, G, I, K, N, T–Y from RSU 115). A–E: Ascomata in face view (C: Transverse section). F, G: Longitudinal section of ascomata. H: Setose hyphae of ascomatal ostiolar neck. I: Ascomatal wall in section (G–I in diluted lactophenol cotton blue). J, K: Asci. L, M: Apex of asci (M: Amyloid apical apparatus in Lugol). N: Paraphyses. O–AB: Ascospores (Y: Arrowheads indicate germ slits. Z: In Indian ink. AA, AB: Germinating ascospores). All in distilled water, except where noted. *Bars*: A–C 500 μm; D–G 100 μm; H, I, N–AB 10 μm; J, K 20 μm; L, M 5 μm.

16–25 × 5.5–7.5 μm (av. 20.4 × 6.6 μm, n = 100), l/w 2.3–4.1 (av. 3.2, n = 53), narrow fusoid to oblong in side view, 4.5–6 μm thick (av. 5.1 μm, n = 47), with a short germ slit at the both ends, surrounded by a mucilaginous sheath.

In culture, the sexual morph formed on RSA. The ascospores were similar to those on the host, measuring 16.5–23 × 5.5–8 μm (av. 20.1 × 6.5 μm, n = 100), l/w 2.4–3.8 (av. 3.1, n = 100).

Additional specimen examined: JAPAN, Hiroshima, Otake, near Oze river, on dead twigs of *Sasa kurilensis*, 18 Feb 2020, R. Sugita, K. Tanaka, S. Narita & M. Tanaka, RSU 115 (HHUF 30664, paratype), ex-paratype culture MAFF 247794.

Notes: The ascospores of *A. fusiformis* are similar to those of *A. deformis*. However, *A. fusiformis* does not have deformed ascospores. Sequence differences between the two species were found at 23 positions with 21 gaps in the ITS (91.2% homology), at 41 positions with five amino acid substitutions in the *rpb2* (95.9%), and at 17 positions with two amino acid substitutions in the *tef1* (98.2%).

Amphigermslita pseudofusiformis R. Sugita & Kaz. Tanaka, sp. nov. Fig. 5.
MycoBank no.: MB 848594.

Etymology: From the Greek *pseudo*, meaning spurious, in reference to morphological similarity to *Amphigermslita fusiformis*.

Typus: JAPAN, Aomori, Shinjo, Hiraoka, on dead culms of *Sasa* sp., 26 May 2019, R. Sugita, S. Narita, M. Tanaka & R. Maekawa, RSU 50 (HHUF 30662, holotype), ex-type culture MAFF 247795.

Sexual morph: Ascomata perithecial, deeply immersed in host tissue, solitary, subglobose, 430–440 μm high, 410–420 μm diam. Ostiolar neck cylindrical, 165–180 μm high, 85–115 μm wide, with setose hyphae of up to 40 μm long, 2–3 μm wide. Ascomatal wall 10–15 μm thick, composed of 3–5 layers of polygonal, 4–5 × 2.5–3.5 μm, dark brown cells. Paraphyses numerous, septate, unbranched,

Fig. 5 *Amphigermslita pseudofusiformis* (RSU 50). A–C: Ascomata in face view (B: Transverse section). D–F: Longitudinal section of ascomata. G: Setose hyphae of ascomatal ostiolar neck. H: Ascomatal wall in section (F–H in diluted lactophenol cotton blue). I: Paraphyses. J, K: Asci. L, M: Apex of asci (M: Amyloid apical apparatus in Lugol). N–X: Ascospores (U: Arrowheads indicate germ slits. V: In Indian ink. W, X: Germinating ascospores). All in distilled water, except where noted. *Bars*: A, B 500 μm; C–F 100 μm; G–I, N–X 10 μm; J, K 20 μm; L, M 5 μm.

cylindrical, hyaline, 1–2.5 μm wide. Asci unitunicate, cylindrical, 130–170 × 8.5–14 μm (av. 147.3 × 11.5 μm, n = 10), 8-spored; apical apparatus amyloid, wedge-shaped, 2–3 μm high, 3–4 μm diam. Ascospores ellipsoid to fusoid, with slightly rounded ends, unicellular, brown, 16–24 × 5.5–7 μm (av. 20.2 × 6.5 μm, n = 50), l/w 2.8–3.7 (av. 3.2, n = 27), fusoid to oblong in side view, 4.5–6.5 μm thick (av. 5.6 μm, n = 23), with a short germ slit at the both ends, surrounded by a mucilaginous sheath.

In culture, no sporulation observed on RSA.

Notes: *Amphigermslita pseudofusiformis* shares numerous morphological characteristics with *A. fusiformis* but has larger asci (130–170 × 8.5–14 μm vs. 115–140 × 10.5–12.5 μm). The ascospores of *A. pseudofusiformis* have slightly rounded ends, whereas those of *A. fusiformis* have tapered ends.

Crassipseudostroma R. Sugita & Kaz. Tanaka, gen. nov.
MycoBank no.: MB 848595.

Etymology: From the Latin *Crassi-*, meaning thick, in reference to the thick pseudostromatic tissue.

Type species: *Crassipseudostroma phyllostachydis* R. Sugita & Kaz. Tanaka.

Sexual morph: Ascomata perithecial, immersed, solitary, subglobose. Ostiolar neck cylindrical, with internal setose hyphae, with a less-developed clypeus. Ascomatal wall composed of polygonal, brown cells, surrounded by pseudostromatic tissue mixed with host cells. Paraphyses numerous, septate, unbranched, cylindrical, hyaline. Asci unitunicate, cylindrical, 8-spored, with an inamyloid apical apparatus. Ascospores fusiform to ellipsoid, unicellular, brown, fusiform in side view, smooth, with mucilaginous pads, with a germ slit.

Asexual morph: *Libertella*-like. Conidiomata sporodochial, scattered, punctiform, superficial. Conidiophores micronematous, mononematous, hyaline to pale brown, straight to flexuous, septate, often branched. Conidiogenous cells holoblastic, with sympodial proliferation. Conidia falcate to narrow cylindrical, unicellular, hyaline, straight to flexuous, aseptate, rounded at the apex, smooth.

Notes: The ascospores of *Crassipseudostroma* recall those of the genus *Gigantospora* B.S. Lu & K.D. Hyde, which are ellipsoid, unicellular, smooth-walled, with polar hyaline rounded pad-like mucilaginous appendages and a full-length germ slit. However, *Gigantospora* is characterized by clavate asci with an amyloid, discoid, apical apparatus and very large ascospores (80–94 μm long; Lu & Hyde, 2003). *Crassipseudostroma* and *Minuticlypeus* were clustered in the single-gene trees of ITS and *rpb2* (Supplementary Fig. S1b, c) and the combined tree (Fig. 1) of the four regions (ITS-LSU-*rpb2*-*tef1*), whereas this sister relationship was highly supported only in *rpb2* (97% MLBS/1.0 BPP; Supplementary Fig. S1c). *Crassipseudostroma* has ascomata with a well-developed cylindrical ostiolar neck, asci with an inamyloid apical apparatus, and fusiform to ellipsoid ascospores with mucilaginous pads at both ends. On the other hand, *Minuticlypeus* differs from this genus in having ascomata with a short ostiolar neck, asci with an amyloid apical apparatus, and ellipsoid to oblong ascospores surrounded by a mucilaginous sheath.

Crassipseudostroma phyllostachydis R. Sugita & Kaz. Tanaka, sp. nov. Fig. 6.
MycoBank no.: MB 848596.

Etymology: The epithet reflects the generic name of host plant, *Phyllostachys*.

Typus: JAPAN, Kochi, Tosa, Doi, on dead culms of *Phyllostachys bambusoides*, 20 Feb 2020, K. Tanaka, R. Sugita, S. Narita & M. Tanaka, KT 4115 (HHUF 30678, holotype), ex-type culture MAFF 247796.

Sexual morph: Ascomata perithecial, deeply immersed in host tissue, solitary, subglobose, 350–540 μm high, 300–580 μm diam. Ostiolar neck cylindrical, 52–58 μm high, 20–30 μm wide, with setose hyphae of up to 50 μm long, 3–5 μm wide, with a less-developed clypeus, often forming brown, circle area around the ostioles on the substrate. Ascomatal wall 7.5–10 μm thick, composed of 3–5 layers of polygonal, brown cells, 4.5–5.5 × 3–3.5 μm, surrounded by pseudostromatic tissue mixed with host cells, 50–120 μm thick. Paraphyses numerous, septate, unbranched, cylindrical, hyaline, 2.5–5 μm wide. Asci unitunicate, cylindrical, 185–215 × 10.5–12.5 μm, 8-spored, with an inamyloid apical apparatus. Ascospores fusiform to ellipsoid, unicellular, brown, 19–25(–32.5) × 7.5–10 μm (av. 22.2 × 8.5 μm, n = 50), l/w 2.0–3.1 (av. 2.5, n = 50), fusiform in side view, 6–8 μm (av. 7.3 μm, n = 16), smooth, with mucilaginous pads at both ends, with a straight germ slit extending over the full-length.

In culture, *Libertella*-like asexual morph formed on RSA. Conidiomata sporodochial, scattered, punctiform, superficial, grayish white, 77.5–115 μm. Conidiophores micronematous, mononematous, hyaline to pale brown, straight to flexuous, septate, often branched, 77.5–115 × 2.5–3 μm. Conidiogenous cells integrated, terminal and intercalary, cylindrical, holoblastic, with sympodial proliferation, 2–3 μm wide. Conidia falcate to narrow cylindrical, hyaline, straight to flexuous, aseptate, rounded at the apex, smooth, 20.5–32.5 × 1–2 μm (av. 25.9 × 1.6 μm, n = 20).

Notes: *Crassipseudostroma phyllostachydis* is similar to *Anthostomella bipileatus* J. Fröhl. & K.D. Hyde, which also has ascospores with mucilaginous pads at both ends, but the latter has smaller asci (av. 93.7 × 8.4 μm; Fröhlich & Hyde, 2000). The ascospores of *C. phyllostachydis* superficially resemble those of *Anthostomella chionostoma* (Durieu & Mont.) Sacc., but *A. chionostoma* has carbonaceous ascomata and asci with an amyloid, massive, subapical apparatus similar to those of *Rosellinia* De Not. (Lu & Hyde, 2000).

Minuticlypeus R. Sugita & Kaz. Tanaka, gen. nov.
MycoBank no.: MB 848597.

Etymology: From the Latin *minutus*, meaning minute, in reference to tiny clypeus of ascomata.

Type species: *Minuticlypeus discosporus* R. Sugita & Kaz. Tanaka.

Sexual morph: Ascomata perithecial, immersed, solitary, subglobose. Ostiolar neck conical, periphysate, with sparse setose hyphae, surrounded by pseudostromatic tissue, with a minute clypeus. Ascomatal wall composed of polygonal, dark brown cells. Paraphyses numerous, septate, unbranched, cylindrical, hyaline. Asci unitunicate, cylindrical, 8-spored; apical apparatus amyloid, inverted, hat-shaped. Ascospores ellipsoid to oblong, unicellular, brown, flattened fusiform in side view, surrounded by a mucilaginous sheath, with a germ.

Asexual morph: Not observed.

Notes: *Minuticlypeus* resembles *Nigropunctata* in having deeply immersed ascomata, cylindrical asci with an amyloid apical apparatus, and ellipsoid to oblong ascospores with a germ slit extending over the full-length. However, these two genera were not closely related (Figs. 1, 2). The ascomatal ostiolar neck of *Minuticlypeus* is short, conical, and with sparse setose hyphae, whereas that of *Nigropunctata* is well-developed, cylindrical, and glabrous.

Minuticlypeus discosporus R. Sugita & Kaz. Tanaka, sp. nov. Fig. 7.

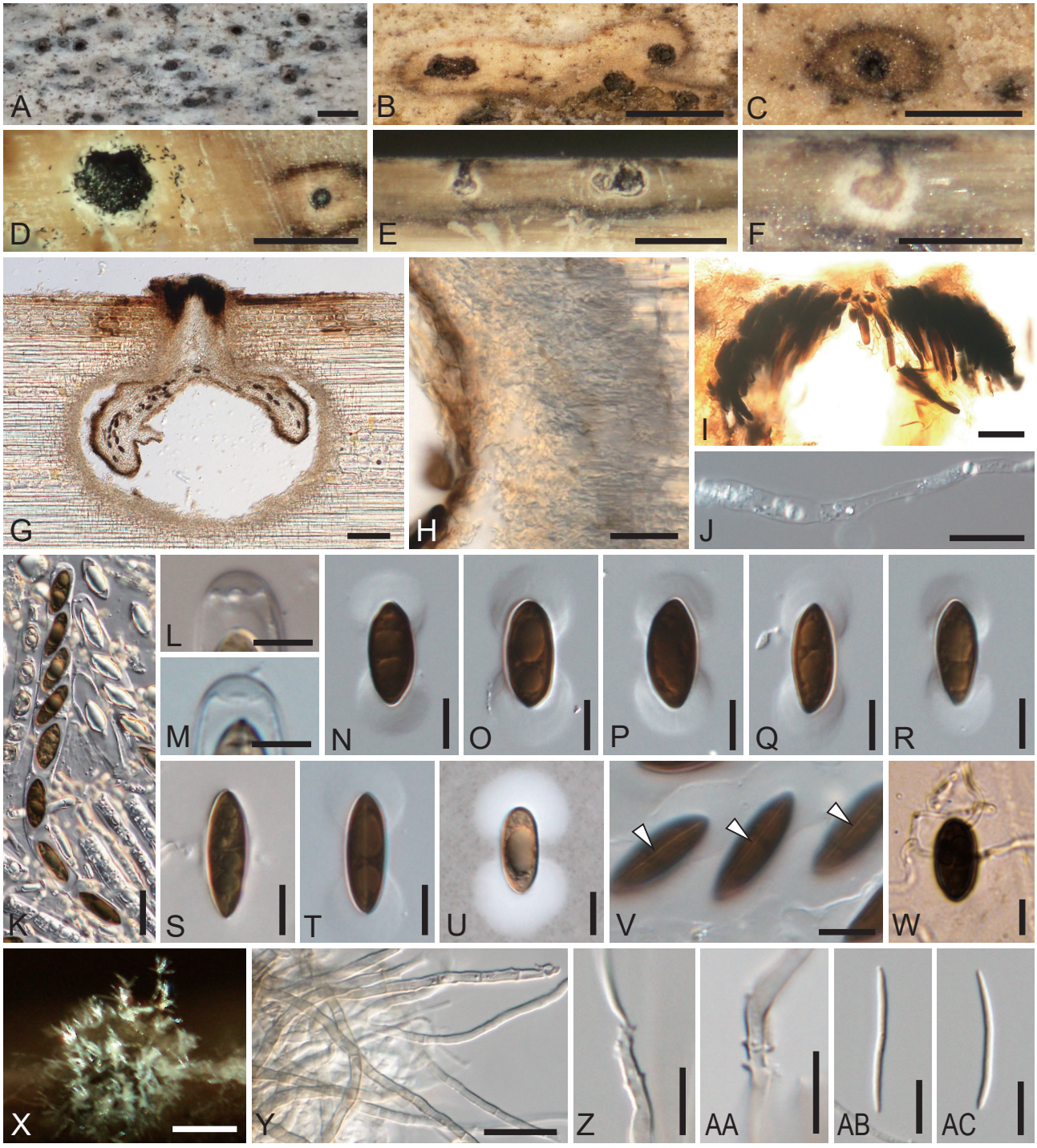


Fig. 6 *Crassipseudostroma phyllostachydis* (A–W from KT 4115. X–AC from Culture KT 4115). A–D: Ascomata in face view (D: Transverse section). E–G: Longitudinal section of ascomata. H: Ascomatal wall and pseudostromatic tissue in section. I: Setose hyphae of ascomatal ostiolar neck (G–I in diluted lactophenol cotton blue). J: Paraphysis. K: Ascus. L, M: Apex of asci. N–W: Ascospores (U: In Indian ink. V: Arrowheads indicate a germ slit. W: Germinating ascospore). X: Sporodochium in culture. Y: Conidiophores. Z, AA: Conidiogenous cells on conidiophore. AB, AC: Conidia. All in distilled water, except where noted. *Bars*: A, B, X 1 mm; C–F 500 μm; G 100 μm; H–K, Y 20 μm; L–W, Z–AC 10 μm.

MycoBank no.: MB 848598.

Etymology: From the Latin *discus*, meaning disk, in reference to the flattened ascospores.

Typus: JAPAN, Tokushima, Awa, Donari, on dead twigs of *Phyllostachys bambusoides*, 21 Feb 2020, K. Tanaka, R. Sugita, S. Narita & M. Tanaka, KT 4150 (HHUF 30673, holotype), ex-type culture MAFF 247798.

Sexual morph: Ascomata perithecial, deeply immersed in host tissue, solitary, subglobose, 290–410 μm high, 310–430 μm diam. Ostiolar neck short conical, periphysate, 65–80 μm high, 80–120 μm wide, with sparse setose hyphae of up to 10 μm long, 2–3 μm wide, with thin clypeus surrounded by pale to dark brown pseudostromatic tissue, often forming dark brown, circle area around the ostioles on the substrate. Clypeus minute, thin, dark brown, 50–70 μm high, 100–160 μm wide. Ascomatal wall 5–10 μm thick, com-

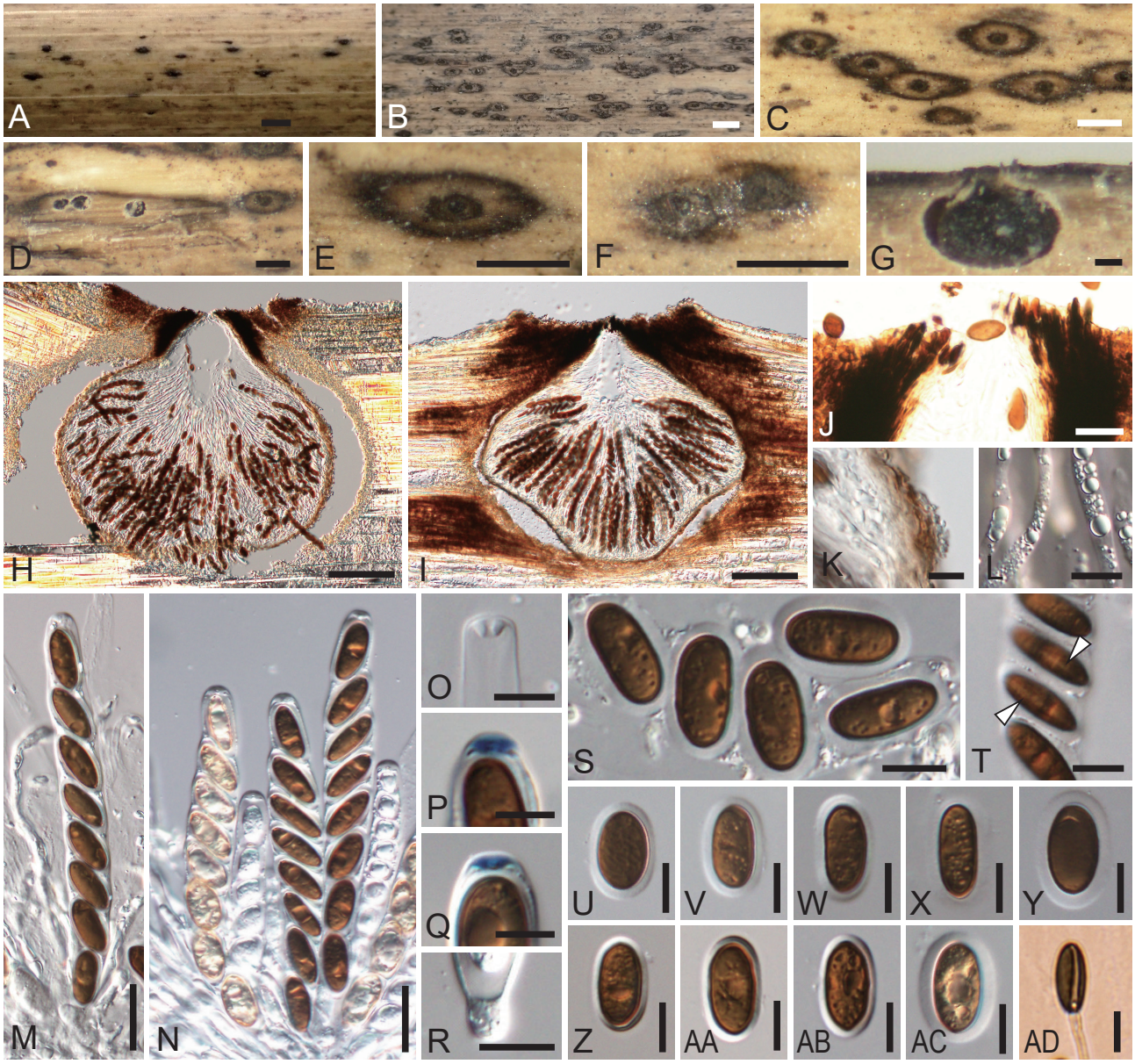


Fig. 7 *Minuticlypeus discosporus* (A, F, I, L, N, P–R, T, Z–AD from KT 3877. B–E, G, H, J, K, M, O, S, U–Y from KT 4150). A–F: Ascomata in face view (D: Transverse section). G–I: Longitudinal section of ascomata. J: Setose hyphae of ascomatal ostiolar neck. K: Ascomatal wall in section (H–K in diluted lactophenol cotton blue). L: Paraphyses. M, N: Asci. O–Q: Apex of asci (P, Q: Amyloid apical apparata in Lugol). R: Stipe of ascus. S–AD: Ascospores (T: Arrowheads indicate a germ slit. AD: Germinating ascospore). All in distilled water, except where noted. *Bars*: A, B 1 mm; C–F 500 μm; G–I 100 μm; J, M, N 20 μm; K, L, O–AD 10 μm.

posed of polygonal, 3.5–5 × 3–4 μm, dark brown cells. Paraphyses numerous, septate, unbranched, cylindrical, hyaline, 2–2.5 μm wide. Asci unitunicate, cylindrical, 105–130 × 12.5–16.5 μm, short-stipitate, 8-spored; apical apparatus amyloid, inverted, hat-shaped, 1–2.5 μm high, 3.5–6 μm diam. Ascospores ellipsoid to oblong, with rounded ends, unicellular, brown, 15–20.5 × 7.5–10.5 μm (av. 17.1 × 8.7 μm, n = 50), l/w 1.5–2.5 (av. 2.0, n = 50), flattened fusiform in side view, 5–7.5 μm thick (av. 6.4 μm, n = 50), surrounded by a mucilaginous sheath, with a germ slit extending over the full-length.

In culture, the sexual morph formed on RSA, and ascospores were slightly smaller than those on the host, measuring 14–19 × 6.5–8.5 μm (av. 16.8 × 7.5 μm, n = 100), l/w 1.8–2.9 (av. 2.3, n = 100).

Additional specimen examined: JAPAN, Yamaguchi, Shimonoseki, Ozuki, on dead twigs of *Pleioblastus simonii*, 26 Mar 2018, K. Tanaka, K. Arayama & R. Sugita, KT 3877 (HHUF 30672, paratype), ex-paratype culture MAFF 247797.

Notes: *Minuticlypeus discosporus* shares similar ascomatal morphology with *Anthostomella rhaphidophylli* B.S. Lu & K.D. Hyde, but the latter has longer asci (137.5–155 × 12.5–15 μm) and slightly larger ascospores (16.5–25 × 9–12.5 μm, av. 21.2 × 10.6 μm). The ascospores of *M. discosporus* are similar to those of *Anthostomella flagellariae* (Rehm) B.S. Lu & K.D. Hyde, but the latter has ascomata with a well-developed, cylindrical ostiolar neck (Lu & Hyde, 2000).

Nigropunctata Samarak. & K.D. Hyde, Fungal Diversity 112: 68, 2022.

Notes: The genus *Nigropunctata* was previously treated as *Xylariales* genus *incertae sedis* (Samarakoon et al., 2022), but in this

study, we accepted it within the *Pallidoperidiaceae*. This genus shares many characteristics with the other four genera of this family (*Amphigermslita*, *Crassipseudostroma*, *Minuticlypeus*, and *Pallidoperidium*), for example, they all have globose, deeply immersed ascomata in host tissue, cylindrical to conical ostiolar neck, unitunicate, cylindrical asci, and unicellular, brown ascospores with a germ slit.

Monophyly of *Nigropunctata* received moderate to high support values (Fig. 1: 87% MLBS/1.0 BPP; Fig. 2: 75% MLBS/0.98 BPP) in phylogenetic trees based on four loci. However, the clade of this genus was poorly supported in the *tef1* tree (less than 70% MLBS or 0.95 BPP), and the genus was shown to be polyphyletic in the ITS tree (Supplementary Fig. S1). These discrepancies may be due to *N. nigrocircularis* Samarak. & K.D. Hyde, is a marginal species of *Nigropunctata*. This species differs morphologically from the core of *Nigropunctata* (e.g., *N. bambusicola* Samarak. & K.D. Hyde). The ascomatal ostiolar neck of *N. nigrocircularis* is cylindrically constricted near the top (Samarakoon et al., 2022, 2023), but this characteristic is not shared with other *Nigropunctata* species. To fully comprehend the morphological circumscription of the genus *Nigropunctata*, it is imperative to evaluate additional members of the genus.

Nigropunctata complanata R. Sugita & Kaz. Tanaka, sp. nov. Fig. 8. MycoBank no.: MB 848599.

Etymology: From the Latin *complanatus*, meaning flattened, in reference to the ascospore shape.

Typus: JAPAN, Shizuoka, Sunto, Nagaizumi, Fuji Bamboo Garden, on dead twigs of *Bambusa multiplex* var. *elegans*, 24 Nov 2017,

Fig. 8 *Nigropunctata complanata* (A, C, E, P, W, X, Z from KT 3851. B, U, V from KT 3837. D, F–J, L, N, O, Q–T, Y, AA, AB from KT 3846. K, M, AC from KT 3857). A–F: Ascomata in face view (D: Transverse section). G, H: Longitudinal section of ascomata. I: Ostiolar neck of ascoma. J: Ascomatal wall in section (H–J in diluted lactophenol cotton blue). K: Paraphyses. L, M: Asci. N–P: Apex of asci (O, P: Amyloid apical apparata in Lugol). Q–AC: Ascospores (Y: Arrowhead indicates a germ slit. AA: In Indian ink. AB, AC: Germinating ascospores). All in distilled water, except where noted. *Bars*: A–D 500 μm; E–H 100 μm; I 50 μm; J, K, N–AC 10 μm; L, M 20 μm.

K. Tanaka & K. Arayama, KT 3846 (HHUF 30675, holotype), ex-type culture MAFF 247800.

Sexual morph: Ascomata perithecial, deeply immersed in host tissue, solitary, subglobose, 340–400 μm high, 390–450 μm diam. Ostiolar neck conical to cylindrical, periphysate. Clypeus thick, dark brown, 75–90 μm high, 270–410 μm diam. Ascomatal wall 5–17.5 μm, composed of 3–5 layers of polygonal, 3.5–7.5 × 2.5–4.5 μm, dark brown cells. Paraphyses numerous, septate, unbranched, cylindrical, hyaline, 2.5–4.5 μm wide. Asci unitunicate, cylindrical, 130–175 × 13–20 μm (av. 154.8 × 17.8 μm, n = 23), 8-spored; apical apparatus amyloid, inverted, hat-shaped, 2.5–3 μm high, 4.5–5 μm diam. Ascospores ellipsoid to oblong, with rounded ends, unicellular, brown, 14.5–19.5 × 7.5–10 μm (av. 17.1 × 8.6 μm, n = 120), l/w 1.6–2.5 (av. 2.0, n = 84), flattened fusiform in side view, 4.5–7 μm (av. 6.0 μm, n = 73), surrounded by a mucilaginous sheath which fibrous near spore wall, with a germ slit extending over the full-length.

In culture, no sporulation observed on RSA.

Additional specimens examined: JAPAN, Shizuoka, Sunto, Nagaizumi, Fuji Bamboo Garden, on dead culms of *Chimonobambusa quadrangularis*, 24 Nov 2017, K. Tanaka & K. Arayama, KT 3837 (HHUF 30674, paratype), ex-paratype culture MAFF 247799; ibid., on dead twigs of *Bambusa multiplex*, 24 Nov 2017, K. Tanaka & K. Arayama, KT 3851 (HHUF 30676, paratype), ex-paratype culture MAFF 247801; ibid., on dead twigs of *Pseudosasa japonica* var. *tsutsumiana*, 24 Nov 2017, K. Tanaka & K. Arayama, KT 3857 (HHUF 30677, paratype), ex-paratype culture MAFF 247802.

Notes: *Nigropunctata complanata* is similar to *Anthostomella flagellariae* and *A. oblongata* B.S. Lu & K.D. Hyde in having ellipsoid unicellular ascospores with a straight germ slit. However, *A. flagellariae* has shorter asci (100–115 × 11.5–12.5 μm), and *A. oblongata* has asci with an inamyloid apical apparatus and concaved ascospores (Lu & Hyde, 2000). Phylogenetically, *N. complanata* is close to the generic type (*N. bambusicola*, MFLU 19-2145) but is different at 31 positions with 32 gaps in the ITS (identity 472/535 = 88.2%). Ascospores of *N. complanata* (14.5–19.5 × 7.5–10 μm, l/w 2.0) are slightly wider than those of the latter species (12.5–19 × 5–8 μm, l/w 2.4; Samarakoon et al., 2022). Recently, two new species of *Nigropunctata*, *N. hydei* Samarak. and *N. saccata* Samarak. have been described from bamboo in Thailand (Samarakoon et al., 2023). Comparisons of *rpb2* sequences between these two species and *N. complanata* indicate that they are not conspecific (vs. *N. hydei*, 833/938 = 88.8%; vs. *N. saccata*, 870/938 = 92.8%). In the ITS region, there was 87% (433/499) sequence identity between *N. complanata* and *N. hydei*, whereas the identity between *N. complanata* and *N. saccata* was exceptionally low (371/588 = 63.1%), implying that errors might be present in the sequences of *N. saccata* (MW240658 and MW240663).

Pallidoperidium R. Sugita & Kaz. Tanaka, gen. nov.
MycoBank no.: MB 848600.

Etymology: From the Latin *pallidus*, meaning pale, in reference to the pale ascomatal walls.

Type species: *Pallidoperidium exasperatum* R. Sugita & Kaz. Tanaka.

Sexual morph: Ascomata perithecial, immersed, solitary, subglobose. Ostiolar neck conical to cylindrical, periphysate. Ascomatal wall thick, inconspicuous, composed of hyaline to pale brown cells, surrounded by pseudostromatic tissue. Paraphyses numerous, septate, unbranched, cylindrical, hyaline. Asci unitunicate, cylindrical, 8-spored; apical apparatus amyloid, thin discoid. Ascospores ellipsoid to fusiform, unicellular, brown, rough, surrounded by a mucilaginous sheath, with a germ slit.

Asexual morph: Not observed.

Notes: *Pallidoperidium* is characterized by an ascomatal wall composed of hyaline to pale brown cells. This feature was not observed in other genera (*Amphigermslita*, *Crassipseudostroma*, *Minuticlypeus*, and *Nigropunctata*) of this family.

Pallidoperidium exasperatum R. Sugita & Kaz. Tanaka, sp. nov. Fig. 9.
MycoBank no.: MB 848601.

Etymology: From the Latin *exasperatus*, meaning roughened, in reference to the rough-walled ascospores.

Typus: JAPAN, Tokyo, Ogasawara, Hahajima, near Tsukigaoka Shrine, on dead stems of *Pleioblastus simonii*, 14 Sep 2012, K. Tanaka, A. Hashimoto & T. Sato, KT 3101 (HHUF 30174, holotype), ex-type culture MAFF 247803.

Sexual morph: Ascomata perithecial, deeply immersed in host tissue, solitary, subglobose, 300–440 μm high, 320–390 μm diam. Ostiolar neck conical to cylindrical, periphysate, 150–170 μm high, 90–140 μm wide. Ascomatal wall 7.5–15 μm thick, inconspicuous, composed of 3–5 layers of elongate 3–7 × 1.5–2.5 μm cells, hyaline at the inside, pale brown towards the outside, surrounded by pseudostromatic tissue. Pseudostromatic tissue thick, pale brown, 37.5–55 μm thick. Paraphyses numerous, septate, unbranched, cylindrical, hyaline, 2.5–4 μm wide. Asci unitunicate, cylindrical, 110–150 × 9.5–12.5 μm (av. 141.5 × 11.4 μm, n = 10), 8-spored; apical apparatus amyloid, thin discoid, 1–1.5 μm high, 4.5–5 μm diam. Ascospores ellipsoid to fusiform, unicellular, brown, (15.5–)17–22.5 × 6–7.5 μm (av. 19.3 × 6.7 μm, n = 60), l/w 2.5–3.4 (av. 2.9, n = 60), rough, surrounded by a mucilaginous sheath, with a germ slit extending over the full-length.

In culture, no sporulation observed on RSA.

Additional specimens examined: JAPAN, Shizuoka, Sunto, Nagaizumi, Fuji Bamboo Garden, on dead culms of *Chimonobambusa quadrangularis*, 24 Nov 2017, K. Tanaka & K. Arayama, KT 3830 (HHUF 30665, paratype), ex-paratype culture MAFF 247804; Yamaguchi, Mine, Omine, Higashibun, Raihukudai, Hikoyamachi-kurin-park, on dead culms of *Semiarundinaria okuboi*, 17 Feb 2020, K. Tanaka, R. Sugita, S. Narita & M. Tanaka, KT 4066 (HHUF 30666, paratype), ex-paratype culture MAFF 247805; ibid., on dead culms of *Pleioblastus hindsii*, 17 Feb 2020, K. Tanaka, R. Sugita, S. Narita & M. Tanaka, KT 4071 (HHUF 30667, paratype), ex-paratype culture MAFF 247806.

Notes: *Anthostomella puiggarii* Speg. on *Bambusa* sp. shares morphological features with *P. exasperatum*: deeply immersed, subglobose ascomata, asci with an amyloid, discoid apical apparatus, and unicellular, ellipsoid ascospores with a full-length germ slit. However, *A. puiggarii* has smaller ascospores than *P. exasperatum* (10.5–13 × 4–5 μm; Lu & Hyde, 2000). The ascospores of *Anthostomella hinoana* Katum. on *Dianella ensifolia* are somewhat similar to those of *P. exasperatum* but are smaller (8–9.5 × 3–3.5 μm), smooth, and without a mucilaginous sheath (Katumoto, 1984).

Pallidoperidium paraexasperatum R. Sugita & Kaz. Tanaka, sp. nov. Fig. 10.
MycoBank no.: MB 848602.

Etymology: From the Greek *para-*, meaning near, in reference to morphological similarity to *Pallidoperidium exasperatum*.

Typus: JAPAN, Shizuoka, Sunto, Nagaizumi, Fuji Bamboo Garden, on dead culms of *Sasaella sasakiana*, 24 Nov 2017, K. Tanaka

Fig. 9 *Pallidoperidium exasperatum* (A, E, G, M–P, Z from KT 3101. B, Q, R, W, X from KT 4071. C, F, H–J, S, T from KT 3830. D, K, L, U, V, Y from KT 4066). A–E: Ascomata in face view (E: Transverse section). F–H: Longitudinal section of ascomata. I: Ostiolar neck of ascoma. J: Ascomatal wall and pseudostromatic tissue in section (G–J in diluted lactophenol cotton blue). K: Paraphyses. L, M: Asci. N, O: Apex of asci (O: Amyloid apical apparatus in Lugol). P–Z: Ascospores (S–U, X: Arrowheads indicate a germ slit. V: In Indian ink. W: Rough surface structure of ascospores. X–Z: Germinating ascospores). N, U, W in 2% KOH. All in distilled water, except where noted. *Bars*: A, E 500 μm; B–D, F–H 100 μm; I 50 μm; J, L, M 20 μm; K, P–Z 10 μm; N, O 5 μm.

& K. Arayama, KT 3817 (HHUF 30668, holotype), ex-type culture MAFF 247807.

Sexual morph: Ascomata perithecial, deeply immersed in host tissue, solitary, subglobose, 290–350 μm high, 320–340 μm diam. Ostiolar neck conical to cylindrical, periphysate, 90–100 μm high, 75–100 μm wide. Ascomatal wall 10–20 μm thick, inconspicuous, composed of 3–5 layers of elongate 5–10 × 2.5–3 μm cells, hyaline at the inside, pale brown towards the outside, surrounded by pseudostromatic tissue. Pseudostromatic tissue thick, pale brown, 90–125 μm thick. Paraphyses numerous, septate, unbranched, cylindrical, hyaline, 2.5–4 μm wide. Asci unitunicate, cylindrical, 140–165 × 10–12.5 μm (av. 151.3 × 11.5 μm, n = 13), 8-spored; apical apparatus amyloid, thin discoid, 1–1.5 μm high, 4.5–5 μm diam. Ascospores ellipsoid to fusiform, unicellular, brown, 15–19 × 5.5–7.5 μm (av. 16.8 × 6.4 μm, n = 60), l/w 2.2–3.3 (av. 2.6, n = 60), rough, surrounded by a mucilaginous sheath, with a germ slit extending over the full-length.

In culture, the sexual morph formed on RSA, with ascospores being similar to those on the host, measuring 13–20.5 × 5–8 μm (av. 17.0 × 6.4 μm, n = 95), 1/w 2.1–3.1 (av. 2.7, n = 95).

Additional specimens examined: JAPAN, Yamaguchi, Nagato, Misumikami, near Kusaritoge, on dead twigs of *Phyllostachys pu-*

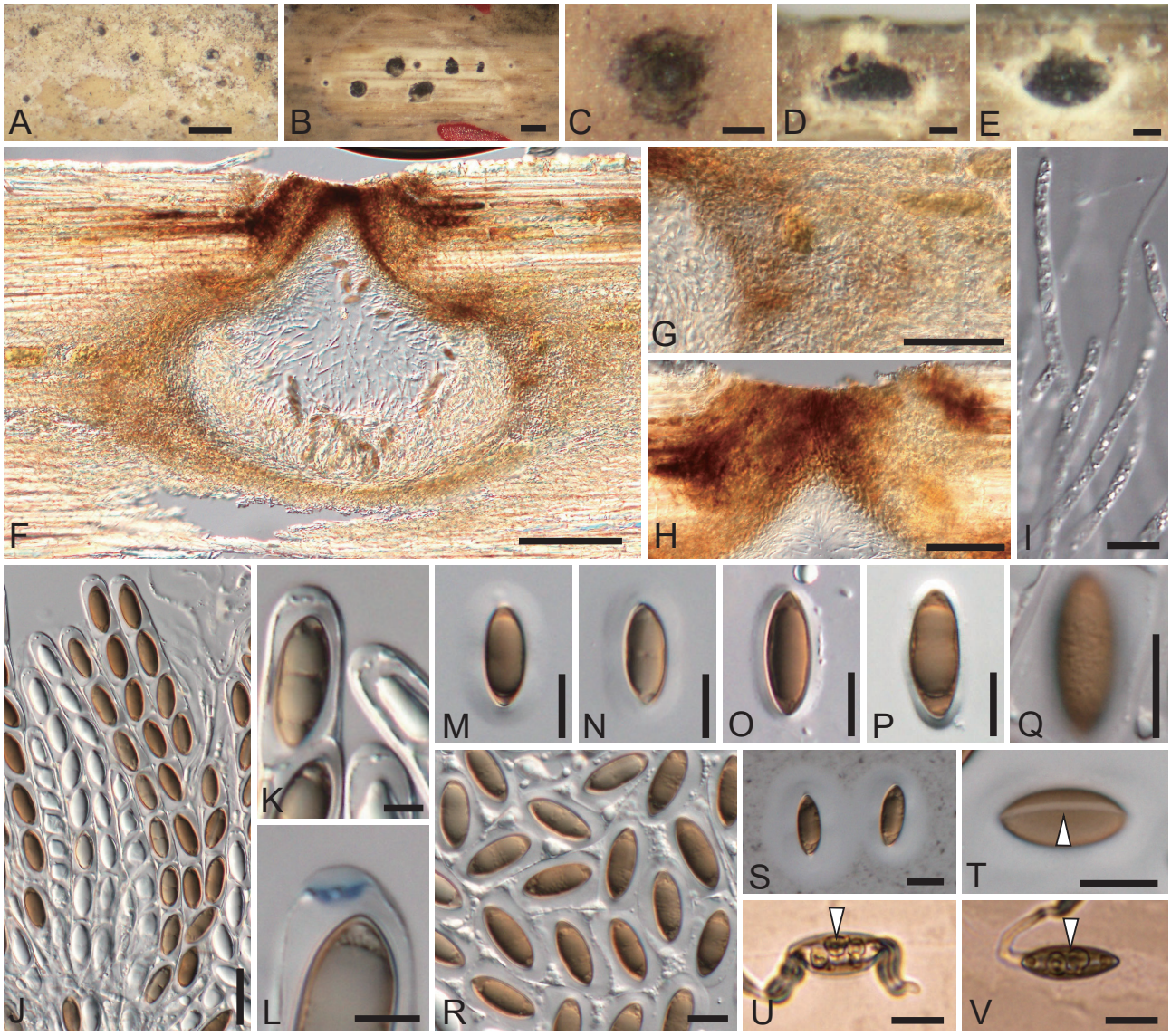


Fig. 10 *Pallidoperidium paraexasperatum* (A, I, T from KT 3890. B, C, F–H, J–N, Q–S, U from KT 3817. D, E, O from KT 4063. P, V from KT 4090). A–C: Ascomata in face view (B: Transverse section). D–F: Longitudinal section of ascomata. G: Ascomatal wall and pseudostromatic tissue in section. H: Ostiolar neck of ascoma (F–H in diluted lactophenol cotton blue). I: Paraphyses. J: Asci. K, L: Apex of asci (L: Amyloid apical apparatus in Lugol). M–V: Ascospores (Q: Rough surface structure of ascospore. S: In Indian ink. T–V: Arrowheads indicate a germ slit. U, V: Germinating ascospores). All in distilled water, except where noted. *Bars*: A, B 500 μm; C–F 100 μm; G, H 50 μm; I, M–V 10 μm; J 20 μm; K, L 5 μm.

bescens, 26 Mar 2018, K. Tanaka, K. Arayama & R. Sugita, KT 3890 (HHUF 30669, paratype), ex-paratype culture MAFF 247808; Yamaguchi, Mine, Omine, Higashibun, Raihukudai, near Hikoya-machikurin-park, on dead culms of *Bambusa multiplex*, 17 Feb 2020, K. Tanaka, R. Sugita, S. Narita & M. Tanaka, KT 4063 (HHUF 30670, paratype), ex-paratype culture MAFF 247809; Yamaguchi, Hagi, Akiragi, near Chikurindoro-park, on dead twigs of *Phyllostachys aurea*, 18 Feb 2020, K. Tanaka, R. Sugita, S. Narita & M. Tanaka, KT 4090 (HHUF 30671, paratype), ex-paratype culture MAFF 247810.

Notes: *Pallidoperidium paraexasperatum* morphologically resembles *P. exasperatum* but has slightly smaller ascospores [15–19 × 5.5–7.5 μm vs. (15.5–)17–22.5 × 6–7.5 μm]. There were sequence differences between these two species, which were at 16 positions with 15 gaps in the ITS (94% homology), at 26 positions with two amino acid substitutions in *rpb2* (97.4%), and at 19 positions with a single amino acid substitution in *tef1* (98%).

4. Discussion

In this study, our examination of *Anthostomella*-like fungi on bamboo led to the discovery and introduction of one new family, four new genera, and eight new species. To establish the taxonomic conclusion, it was essential to determine the phylogenetic position of *Anthostomella* sensu stricto. The placement of the genus *Anthostomella* remains problematic and unresolved. However, in this study, we provisionally determined the phylogenetic position of *Anthostomella* by considering the lineage that includes several *Anthostomella* spp. as the closest relatives ("*Anthostomella*-like genera *incertae sedis*" in Fig. 1). It is important to note that no sequence data is currently available for the type species of *Anthostomella*, and there are other lineages that include species referred to as "*Anthostomella*" (e.g., *Gyrothricaceae* and *Xylariaceae* in Fig. 1; Samarakoon et al., 2022).

Anthostomella was established based on three species [*A. limitata* Sacc., *A. tomicoides* Sacc., and *A. perfidiosa* (De Not.) Sacc.)] by

Saccardo (1875a), but he did not designate the type species of this genus. Subsequently, Eriksson (1966) selected *A. limitata* as the generic type from the three original species. On the other hand, Francis (1975) argued that *A. limitata* is not a typical species for this genus because it has ascomata without a clypeus and proposed *A. tomicoides* as the generic type. This opinion of Francis (1975) has been accepted in subsequent studies (e.g., Daranagama et al., 2015; Lu & Hyde, 2000; Rappaz, 1995). However, the former lectotypification of *Anthostomella* (Eriksson, 1966) is valid and has to be followed as pointed out by Voglmayr et al. (2018). No type specimens were officially designated for *A. limitata* (Saccardo, 1875a, b), and the original specimens are currently unknown (Francis, 1975). In the protologue of this species, several plants collected in Italy were listed as hosts, including *Cornus sanguinea* (*Cornaceae*), *Rubus fruticosus* (*Rosaceae*), *Kerria japoniaca* (*Rosaceae*), *Viburnum lantana* (*Adoxaceae*), *Ruscus aculeata* (*Asparagaceae*), *Angelica sylvestris* (*Apiaceae*), *Vinca major* (*Apocynaceae*), and *Salix babylonica* (*Salicaceae*). To fully resolve the phylogenetic position of *Anthostomella*, it is necessary to collect a fresh specimen on any of these plants in the type locality that matches the original description (Saccardo, 1875b) or authentic illustration (no. 129 in Saccardo, 1877) of *A. limitata*, neotypify the specimen, and obtain sequencing data from the ex-neotype culture.

We established a new family, *Pallidoperidiaceae*, to accommodate five genera of *Anthostomella*-like fungi. All species of these *Anthostomella*-like genera were collected from bamboo. Most lineages of bambusicolous fungi tend to deviate from existing families found on other host plants, even though they have morphological similarities to other known fungal families (Tanaka et al., 2009). Another example of an *Anthostomella*-like fungal group on bamboo is *Spirodecosporaceae*, which has been determined to represent a phylogenetically distinct lineage within *Xylariales*, *Sordariomycetes* (Sugita et al., 2022). Similar examples are known for *Dothideomycetes*, namely, *Tetraplosphaeriaceae* (Tanaka et al., 2009), *Bambusicolaceae* (Hyde et al., 2013), and *Occultibambusaceae* (Dai et al., 2017). Sugita et al. (2022) suggested that many novel lineages distantly related to known ascomycetous families and genera will be discovered from bambusicolous fungi.

Melanographium is a dematiaceous hyphomycete genus with no known sexual morphs. No sequence data of type species *M. spleniosporum* Sacc. were available, but two other species of this genus were placed at the base of *Pallidoperidiaceae* in our phylogenetic analysis (Fig. 1). However, we did not accept *Melanographium* as a member of *Pallidoperidiaceae*. Morphological features of *Melanographium*, such as synnematous conidiomata and reniform pigmented conidia are quite different from known asexual morphs of species in *Pallidoperidiaceae* (Fig. 6). The clade composed of *Anthostomella*, *Pseudoanthostomella*, and *Alloanthostomella* was a sister group to *Pallidoperidiaceae* and *Melanographium* (83% MLBP/0.99 BPP; Fig. 1). Species in "*Anthostomella*-like genera *incertae sedis*" have small-sized (140–350 μm diam), globose ascomata with a glabrous ostiolar neck and occur on non-monocot host plants (Daranagama et al., 2015, 2016; Samarakoon et al., 2022) with the exception of *Anthostomella torosa* Kohlm. & Volkm.-Kohlm. on *Juncus roemerianus* (Kohlmeyer & Volkmann-Kohlmeyer, 2002). These features are clearly different from those of species in the *Pallidoperidiaceae*, which are characterized by middle-sized (300–580 μm diam), subglobose ascomata with an ostiolar neck with or without setose hyphal structure and bamboo host plants.

We recognized five genera in the *Pallidoperidiaceae*. The five sexually reproducing genera were morphologically similar in having subglobose ascomata deeply immersed in the host tissue, cylindrical asci, and one-celled brown ascospores. However, they are differentiated by shape and stainability of ascus apical structure and features of ascospore germ slit and mucilaginous sheath (Fig. 2), as well as shape of ascomatal ostiolar neck, presence or absence of setose hyphae and clypeus, and structure of peridial wall or pseudostromatic tissue. In the absence of molecular evidence, these observed differences can be interpreted as minor variations at the species-level within the same genus. Highly diverse and novel lineages will undoubtedly be included among *Anthostomella* species described based solely on morphological data. A more robust and clearer definition should be provided for a newly proposed genus to taxonomically revise a previously described species that lacks sequence data. Therefore, additional samples are required for *Crassipseudostroma* and *Minuticlypeus* represented by a single strain or species.

We described eight new species in the *Pallidoperidiaceae*. Among them, only one species (*Crassipseudostroma phyllostachydis*) formed an asexual morph in culture. The morphological features were clearly different from those of *Geniculosporium*-, *Nodulisporium*-, and *Virgariella*-like, which were previously known as asexual morphs of *Anthostomella*-like fungi (Francis et al., 1980; Hyde & Goh, 1998). The falcate conidia of *C. phyllostachydis* resemble those of *Libertella*-like, which are known in several species of xylariaceous genera, such as *Barrmaelia* Rappaz (Rappaz, 1995) in *Barrmaeliaceae* and *Creosphaeria* Theiss. (Ju et al., 1993), *Lopadostoma* (Nitschke) Traverso (Jaklitsch et al., 2014), and *Whalleya* J.D. Rogers et al. (Glawe & Rogers, 1986) in *Lopadostomataceae*. However, *Pallidoperidiaceae* was distantly related to these two families in the phylogenetic tree of *Xylariales* (Fig. 1). Within the "*Anthostomella*-like genera *incertae sedis*", phylogenetically close to *Pallidoperidiaceae*, asexual morphs are known for two species, *Anthostomella helicofissa* (Daranagama et al., 2015) and *Pseudoanthostomella pini-nigrae* (Daranagama et al., 2016). These species produce ellipsoid to fusiform conidia of relatively small dimensions (less than 5–8.5 × 2–3.5 μm), which are different from those of *Pallidoperidiaceae*. Lu and Hyde (2000) noted that it is difficult to use the characteristics of asexual morphs to distinguish species of *Anthostomella*. This is because obtaining pure cultures of *Anthostomella* (or xylariaceous species) can be difficult (Francis, 1975), and even if their isolates are available, only a few species may form asexual morphs under culture conditions. Nevertheless, repeated attempts to isolate fungi into axenic cultures (Jaklitsch & Voglmayr, 2012; Sugita et al., 2022) are important for obtaining asexual traits and accurate DNA sequence information. Although we defined *Pallidoperidiaceae* almost exclusively based on sexual morphs, an opposite approach, mainly based on asexual morphs, would be effective for understanding the phylogenetic relationships of xylariaceous fungi. Using several strains of setose hyphomycetes for phylogenetic analysis, Hernández-Restrepo et al. (2022) revealed phylogenetic connections among several *Anthostomella*-like fungi and *Circinotrichum*-like and *Gyrothrix* asexual morphs. They showed close relationship between *Circinotrichum*-like asexual morphs and *Xenoanthostomella chromolaenae* Mapook & K.D. Hyde with a sexual morph. They also showed that *Neoanthostomella viticola* Daranag. et al. clustered into a distinct clade, including many species of *Gyrothrix* (Corda) Corda (asexual morphs), and treated *N. viticola* as a synonym of the type species of *Gyrothrix*, *G. podosperma* (Corda) Rabenh.

Sugita et al. (2022) suggested that bambusicolous fungi may be more host-specific to some extent (at least at the level of the host tribe) than previously thought, based on the results of a taxonomic study on *Spirodecospora*. However, this does not seem to be restrictive to species within *Pallidoperidiaceae*. For example, *Nigropunctata complanata* and *Pallidoperidium paraexasperatum* were col-

lected from various genera of Bamboo belonging to the tribes *Arundinarieae* and *Bambuseae* in the same subfamily, *Bambusoideae* (Table 1). In contrast, the following species appeared to be generally host-specific. *Minuticlypeus discosporus* (two specimens) was collected from *Pleioblastus* and *Phyllostachys* (tribe *Arundinarieae*). The host plants of *Pallidoperidium exasperatum* (four specimens) were restricted to the tribe *Arundinarieae*, including *Chimonobambusa*, *Pleioblastus*, and *Semiarundinaria*. All three species of *Amphigermslita* (five specimens) were collected exclusively from *Sasa* spp. (tribe *Arundinarieae*). Our findings shed some light on the diversity and evolutionary relationships of *Anthostomella*-like fungi in the context of their bamboo host plants. However, the host specificities observed in this study are based on a limited number of samples and should be validated through future collections. While the host plants of bambusicolous fungi have been generally categorized as "Bamboo," obtaining more detailed host identification will be crucial for a comprehensive understanding of their ecology and taxonomy.

Disclosure

The authors declare no conflicts of interest. This study was conducted in accordance with the current laws in Japan.

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