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Pseudodidymellaceae fam. nov.: Phylogenetic affiliations of mycopappus-like genera in *Dothideomycetes*

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Abstract: The familial placement of four genera, *Mycodidymella*, *Petrakia*, *Pseudodidymella*, and *Xenostigmina*, was taxonomically revised based on morphological observations and phylogenetic analyses of nuclear rDNA SSU, LSU, *tef1*, and *rpb2* sequences. ITS sequences were also provided as barcode markers. A total of 130 sequences were newly obtained from 28 isolates which are phylogenetically related to *Melanommataceae* (*Pleosporales*, *Dothideomycetes*) and its relatives. Phylogenetic analyses and morphological observation of sexual and asexual morphs led to the conclusion that *Melanommataceae* should be restricted to its type genus *Melanomma*, which is characterised by ascomata composed of a well-developed, carbonaceous peridium, and an aposphaeria-like coelomycetous asexual morph. Although *Mycodidymella*, *Petrakia*, *Pseudodidymella*, and *Xenostigmina* are phylogenetically related to *Melanommataceae*, these genera are characterised by epiphyllous, lenticular ascomata with well-developed basal stroma in their sexual morphs, and mycopappus-like propagules in their asexual morphs, which are clearly different from those of *Melanomma*. *Pseudodidymellaceae* is proposed to accommodate these four genera. Although *Mycodidymella* and *Xenostigmina* have been considered synonyms of *Petrakia* based on sexual morphology, we show that they are distinct genera. Based on morphological observations, these genera in *Pseudodidymellaceae* are easily distinguished by their synasexual morphs: sigmoid, multi-septate, thin-walled, hyaline conidia (*Mycodidymella*); globose to ovoid, dictyosporus, thick-walled, brown conidia with cellular appendages (*Petrakia*); and clavate with a short rostrum, dictyosporus, thick-walled, brown conidia (*Xenostigmina*). A synasexual morph of *Pseudodidymella* was not observed. Although *Alpinaria* was treated as member of *Melanommataceae* in a previous study, it has hyaline cells at the base of ascomata and pseudopycnidial, confluent conidiomata which is atypical features in *Melanommataceae*, and is treated as *incertae sedis*.

Key words: Foliar pathogen, Synasexual morph, Systematics.
Taxonomic novelties: New family: *Pseudodidymellaceae* A. Hashim. & Kaz. Tanaka; **New species:** *Melanomma japonicum* A. Hashim. & Kaz. Tanaka, *Pseudodidymella minima* A. Hashim. & Kaz. Tanaka; **New combination:** *Xenostigmina aceris* (Dearn. & Barthol.) A. Hashim. & Kaz. Tanaka.

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INTRODUCTION

The family *Melanommataceae* (*Pleosporales*) was proposed for its type genus, *Melanomma* (Winter 1887). Currently, more than 20 genera with diverse ecological and morphological features are recognised in this family (Tian *et al.* 2015). *Petrakia* and *Xenostigmina* have epiphyllous, lenticular ascomata with well-developed basal stroma, mycopappus-like propagules, and petrakia- or stigmina-like synasexual morphs, and were also accepted in *Melanommataceae* (Funk 1986, Funk & Dorworth 1988, Crous 1998, Crous *et al.* 2009, Butin *et al.* 2013, Tian *et al.* 2015). Subsequently, two additional genera, *Mycodidymella* and *Pseudodidymella*, were reported to be phylogenetically related to this family (Gross *et al.* 2017), although their morphological features were clearly different from those of *Melanomma*, which is characterised by carbonaceous ascomata, trabecular pseudoparaphyses, and aposphaeria-like coelomycetous asexual morphs (Barr 1987, 1990, Lumbsch & Huhndorf 2007, Kirk *et al.* 2008, Tian *et al.* 2015, Jaklitsch & Voglmayr 2017).

The genus *Petrakia* was originally characterised by sporodochial conidiomata and muriform, brown conidia with cellular, hyaline appendages (Sydow & Sydow 1913, Butin *et al.* 2013). Recently, the complete life cycle of *Pe. echinata*, which is the type species and a known causal agent of leaf blotch disease of *Acer* spp., was revealed (Butin *et al.* 2013). Subsequently, phylogenetic analysis using large subunit nrDNA sequences indicated that this genus is related to *Melanommataceae* or *Pleomassariaceae* (*Dothideomycetes*; Butin *et al.* 2013).

Xenostigmina zilleri, the type species of the genus, is a known pathogen that causes brown spot disease in *Acer macrophyllum* in Canada (Funk 1986). This species was originally described as *Cercosporella aceris* (Dearness 1917). Redhead & White (1985) introduced *Mycopappus*, and transferred two species to this genus, i.e. *C. aceris* and *C. alni*. The type species of *Mycopappus*, *Mycop. alni*, was suggested to be a member of *Sclerotiniaceae* (*Helotiales*, *Leotiomycetes*) based on its sclerotial morph and phylogenetic analyses using ITS sequences (Takahashi *et al.* 2006). *Mycopappus aceris* was excluded from the genus, because the synasexual morph of this species is the dothideomycetous taxon *X. zilleri* (Funk & Dorworth 1988, Crous 1998, Wei *et al.* 1998, Crous *et al.* 2009). According to phylogenetic analysis, this genus was accepted as *Melanommataceae* (Phookamsak *et al.* 2014, Tian *et al.* 2015).

The genera *Mycodidymella* and *Pseudodidymella* are also members of *Melanommataceae* that produce mycopappus-like propagules in their asexual morphs (Wei *et al.* 1997, 1998, Gross *et al.* 2017). The genus *Mycodidymella*, which is based on the type species *Mycod. aesculi*, is known as a pathogen of

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concentric ring spot disease in *Aesculus turbinata* (Wei *et al.* 1998). The life cycle of *Mycod. aesculi* is similar to those of *Petrakia* and *Xenostigmina*, except it has sigmoid and hyaline conidia in its synasexual morph. Although the synasexual morph of *Petrakia* seems to be clearly different from that of *Mycodidymella* and *Xenostigmina*, the latter two genera were synonymised with an older name, *Petrakia* (Jaklitsch & Voglmayr 2017).

The monotypic genus *Pseudodidymella* was established for *Pseudod. fagi* (Wei *et al.* 1997). The species was found to be associated with brown leaf spots of *Fagus crenata* in Japan, and was originally characterised by lenticular ascomata with a well-developed basal stroma and a pycnopleiospora-like asexual morph, which is characterised by sporodochial conidiomata and conidia with appendages (Wei *et al.* 1997). *Mycodidymella* is morphologically similar to this genus, but can be distinguished by its pycnopleiospora-like asexual morph (Wei *et al.* 1998). Gross *et al.* (2017) discovered *Pseudod. fagi* on *F. sylvatica* in Switzerland and suggested that the pycnopleiospora-like asexual morph has mycopappus-like propagules rather than individual conidia. Thus, morphological delimitation of these two genera is problematic and requires further research. According to a phylogenetic study using ITS sequences (Gross *et al.* 2017), four genera with mycopappus-like propagules (*Mycodidymella*, *Petrakia*, *Pseudodidymella*, and *Xenostigmina*) formed a strongly supported clade within *Melanommataceae sensu lato*; however, familial placement and generic validity of each genus remain unresolved.

During our ongoing studies of ascomycetous fungi in Japan (Tanaka *et al.* 2010, 2011, 2015, Hashimoto *et al.* 2015a, b, 2016, 2017), we collected strains which are morphologically similar or phylogenetically related to *Melanommataceae sensu lato*. The main objectives of the present study were to clarify familial placement of genera in this family, and establish a taxonomic framework of *Melanommataceae sensu lato* based on morphological observations and molecular phylogenetic analyses of small subunit nrDNA (18S; SSU), large subunit nrDNA (28S; LSU), translation elongation factor 1-α (*tef1*), and DNA-directed RNA polymerase II second largest subunit (*rpb2*) sequences. ITS sequences were also obtained as DNA barcode markers.

MATERIALS AND METHODS

Isolates

All fungal structures were studied in preparations mounted in distilled water. Morphological characters were observed by differential interference and phase contrast microscopy (Olympus BX53, Japan), and images captured with an Olympus digital camera (DP21, Japan). A total of 28 single-spore isolates were used for morphological observation and phylogenetic analyses (Table 1).

DNA isolation, amplification and phylogenetic analysis

DNA extraction was carried out with an ISOPLANT II kit (Nippon Gene, Japan) based on the manufacturer's protocol. Sequences of SSU, ITS, LSU, and *tef1* and *rpb2* were amplified by PCR with the primer pairs NS1/NS4, ITS1/ITS4 (White *et al.* 1990), LR0R/LR7 (Rehner & Samuels 1994, Vilgalys & Hester 1990), EF1-983F/EF1-2218R (Rehner & Buckley 2005), and fRPB2-5F/fRPB2-7cR (Liu *et al.* 1999), respectively. Amplifications were performed in 25 µL volumes that consisted of 2 µL DNA extract, 2.5 µL of 10 × TEMPase Buffer I, 10 mM dNTP mix, 1 µL of each 20-pM primer, 25 mL $MgCl_2$, 14.5 µL MilliQ water, and 0.5 µL TEMPase Hot Start DNA polymerase (Ampliqon, Denmark). PCRs were carried out on a PC 320 thermo-cycler (ASTEC, Japan) as follows: 95 °C for 15 min; followed by 35 cycles of 1 min at 94 °C, 1 min at the designated annealing temperature (42.2 °C for SSU, 61.5 °C for ITS, 46 °C for LSU, 60 °C for *tef1*, and 58 °C for *rpb2*), and 1 min at 72 °C; and a final denaturation of 7 min at 72 °C. The PCR products were directly sequenced at SolGent (South Korea).

Newly generated sequences were deposited in GenBank (Table 1). Sequences of 73 taxa of *Pleosporales* and *Hysteriales* were also phylogenetically analysed (Table 1). *Hysterium pulicare* and *Hysterobrevium mori* (*Hysteriaceae*, *Hysteriales*) were used as outgroups. All sequences were aligned using the MUSCLE algorithm as implemented in the program MEGA v. 5 (Tamura *et al.* 2011). Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian methods. The optimal substitution models for each dataset were estimated by Kakusan4 (Tanabe 2011) based on the Akaike information Criterion (AIC; Akaike 1974) for ML analysis and Bayesian information Criterion (BIC; Schwarz 1978) for the Bayesian analysis.

The ML analysis was performed using TreeFinder Mar 2011 (Jobb 2011) based on the models selected with the AICc4 parameter (a proportional model among genes and codons): J2+G for SSU; GTR+G for LSU; F81+G for the *tef1* first codon position, J1ef+G for the *tef1* second codon position, and J2+G for the *tef1* third codon position; and J2+G for the *rpb2* first codon position, J1+G for the *rpb2* second codon position, and J2+G for the *rpb2* third codon position. Bootstrap percentages (BPs) were obtained by 1 000 bootstrap replications.

Bayesian analysis was performed with MrBayes v. 3.2.2 (Ronquist *et al.* 2012) with substitution models for different regions selected with the BIC4 parameter (proportional model among loci and codons): K80+G for SSU; SYM+G for LSU; GTR+G for the *tef1* first codon position, JC69+G for the *tef1* second codon position, and GTR+G for the *tef1* third codon position; and GTR+G for the *rpb2* first codon position, GTR+G for the *rpb2* second codon position, and GTR+G for the *rpb2* third codon position. Two simultaneous, independent runs of Metropolis-coupled Markov chain Monte Carlo (MCMC) were performed for 2 M generations with trees sampled every 1 000 generations. Convergence of the MCMC runs assessed from the average standard deviation of split frequencies (<0.01) and effective sample size scores (all >100) using MrBayes v. 3.2.2 and Tracer v. 1.6 (Rambaut *et al.* 2014), respectively. The first 25 % of trees were discarded as burn-in, and the remaining trees were used to calculate 50 % majority rule trees and determine posterior probabilities (PPs) for individual branches. The alignment was submitted to TreeBase under study number S20165.

Morphology

Colony characteristics of cultures grown on 2 % potato dextrose agar (PDA; Difco, France) were observed after 3 wk incubation at 20 °C in the dark. Colours were noted based on those described by Rayner (1970).

To induce sexual or asexual fructification in culture, 5 mm square mycelial agar discs were placed on water agar that included sterilised natural substrate, such as *Aesculus turbinata*

Table 1. Specimens, isolates and new sequences used in this study.

Species	Original no.	Specimen no.[1]	Strain no.	Host/substrate	GenBank accession no.[2]				
					SSU	LSU	*tef1*	*rpb2*	ITS
Alpinaria rhododendri	KT 2520	HHUF 30554	CBS 142901	*Rhododendron brachycarpum*	**LC203314**	**LC203360**	**LC203388**	**LC203416**	**LC203335**
Melanomma japonicum	KT 2076	HHUF 30539^{P}	CBS 142902	dead wood	**LC203290**	**LC203336**	**LC203364**	**LC203392**	**LC203318**
	KT 3028	HHUF 30540^{P}	CBS 142903	*Fagus crenata*	**LC203291**	**LC203337**	**LC203365**	**LC203393**	**LC203319**
	KT 3425	HHUF 30541^{P}	CBS 142904	*F. crenata*	**LC203292**	**LC203338**	**LC203366**	**LC203394**	**LC203320**
	–	HHUF 26520^{H}	CBS 142905 = JCM 13124 = MAFF 239634	Dead wood	**LC203293**	**LC203339**	**LC203367**	**LC203395**	**LC203321**
Me. pulvis-pyrius	KT 2110	HHUF 30542	CBS 142906	*Acer* sp.	**LC203294**	**LC203340**	**LC203368**	**LC203396**	**LC203322**
	KT 2113	HHUF 30543	CBS 142907	Dead wood	**LC203295**	**LC203341**	**LC203369**	**LC203397**	**LC203323**
	AH 375	HHUF 30544	CBS 142908	*F. crenata*	**LC203296**	**LC203342**	**LC203370**	**LC203398**	**LC203324**
	KH 27	HHUF 30545	CBS 142909	Dead wood	**LC203297**	**LC203343**	**LC203371**	**LC203399**	**LC203325**
	KH 77	HHUF 30546	CBS 142910	Dead wood	**LC203298**	**LC203344**	**LC203372**	**LC203400**	**LC203326**
	KH 86	HHUF 30547	CBS 142911	Dead wood	**LC203299**	**LC203345**	**LC203373**	**LC203401**	**LC203327**
	KH 197	HHUF 30548	CBS 142912	Dead wood	**LC203300**	**LC203346**	**LC203374**	**LC203402**	**LC203328**
Mycodidymella aesculi	KT 3060	HHUF 30549	CBS 142913	*Aesculus turbinata*	**LC203301**	**LC203347**	**LC203375**	**LC203403**	**LC203329**
	H 2610	HHUF 22892^{H}	CBS 142914	*A. turbinata*	**LC203302**	**LC203348**	**LC203376**	**LC203404**	LC194192
	H 2620	–	CBS 142915	*A. turbinata*	**LC203303**	**LC203349**	**LC203377**	**LC203405**	**LC203330**
	AH 560	HHUF 30550	CBS 142916	*A. turbinata*	**LC203304**	**LC203350**	**LC203378**	**LC203406**	**LC203331**
Petrakia echinata	–	–	CBS 133072	*Acer pseudoplatanus*	**LC203305**	**LC203351**	**LC203379**	**LC203407**	–
	–	–	CBS 133070	*A. pseudoplatanus*	**LC203306**	**LC203352**	**LC203380**	**LC203408**	–
Pseudodidymella fagi	KT 3058	HHUF 30515	CBS 142917 = MAFF 245738	*F. crenata*	**LC203307**	**LC203353**	**LC203381**	**LC203409**	LC150785
	KT 3074-3	HHUF 30516	CBS 142918 = MAFF 245739	*F. crenata*	**LC203308**	**LC203354**	**LC203382**	**LC203410**	LC150786
	RF 5	HHUF 30517	CBS 142919 = MAFF 245741	*F. crenata*	**LC203309**	**LC203355**	**LC203383**	**LC203411**	LC150788
	H 2579	HHUF 22903^{H}	MAFF 245740	*F. crenata*	**LC203310**	**LC203356**	**LC203384**	**LC203412**	LC150787
	AH 561	HHUF 30553	CBS 142920	*F. crenata*	**LC203311**	**LC203357**	**LC203385**	**LC203413**	**LC203332**
Pseudod. minima	KT 2918	HHUF 30551^{H}	CBS 142921 = MAFF 246249	*Fagus japonica*	**LC203312**	**LC203358**	**LC203386**	**LC203414**	**LC203333**
	AH 556	HHUF 30552^{P}	CBS 142922	*F. japonica*	**LC203313**	**LC203359**	**LC203387**	**LC203415**	**LC203334**
Xenostigmina aceris	–	–	CBS 124109	*Acer macrophyllum*	**LC203315**	**LC203361**	**LC203389**	**LC203417**	–
	–	–	CBS 115685	*Acer* sp.	**LC203316**	**LC203362**	**LC203390**	**LC203418**	–
	–	–	CBS 115686	*Acer* sp.	**LC203317**	**LC203363**	**LC203391**	**LC203419**	–

[1] "H": holotype, "P": paratype.
[2] Sequences generated in this study are shown in bold.

and *Fagus crenata* leaves and rice straw, and the plates were incubated at 20 °C for 2 wk in the dark. When the substrate was colonised, the plates were incubated at 20 °C under blacklight blue illumination for 2 mo to observe sporulation. Cultures were deposited in the Westerdijk Fungal Biodiversity Institute (CBS), the Japan Collection of Microorganisms (JCM), and the Genebank Project of NARO, Japan (MAFF). Specimens were deposited in the Herbarium of Hirosaki University, Fungi (HHUF).

RESULTS

Phylogeny

The ML and Bayesian phylogenetic analyses were conducted using an aligned sequence dataset composed of 941 nucleotides from SSU, 1 276 from LSU, 886 from *tef1*, and 1 021 from *rpb2*. The alignment contained a total of 73 taxa, which consisted of 59 taxa (80.8 %) in SSU, 73 (100 %) in LSU, 63 (86.3 %) in *tef1*, 51 (69.9 %) in *rpb2* (Table 1 and 2). No significant conflict was observed among individual gene phylogenies, but the familial and generic nodes mostly lacked significant support in SSU and LSU phylogenetic trees generated (data not shown). However, this combined dataset provided higher confidence values for the familial level than did those of the individual gene trees (data not shown). Of the 3 824 characters included in the alignment, 1 205 were variable and 2 844 were conserved. The ML tree with the highest log likelihood (−26580.8637) is shown in Fig. 1. The Bayesian likelihood score was −26638.727. The topology recovered by the Bayesian analysis was almost identical to that of the ML tree, except for the position of *Aposphaeria corallinolutea*, *Bertiella macrospora*, *Herpotrichia macrotricha*,

Table 2. GenBank accession numbers of species used in the phylogenetic study.

Species name	Family	Strain no.[1]	GenBank accession no.			
			SSU	LSU	*tef1*	*rpb2*
Alpinaria rhododendri	*incertae sedis*	ANM 73	–	GU385198	–	–
A. rhododendri	*incertae sedis*	CBS 141994[E]	KY190004	KY189973	KY190009	KY189989
Alternaria alternata	*Pleosporaceae*	CBS 916.96[E]	DQ678031	DQ678082	DQ677927	DQ677980
Aposphaeria corallinolutea	*incertae sedis*	CBS 131287[H]	–	JF740330	–	–
Bertiella macrospora	*incertae sedis*	IL 5005	–	GU385150	–	–
Beverwykella pulmonaria	*incertae sedis*	CBS 283.53[H]	KY190005	GU301804	–	GU371768
Byssosphaeria jamaicana	*incertae sedis*	SMH 1403	–	GU385152	GU327746	–
B. rhodomphala	*incertae sedis*	GKM L153N	–	GU385157	GU327747	–
B. salebrosa	*incertae sedis*	SMH 2387	–	GU385162	GU327748	–
B. schiedermayeriana	*incertae sedis*	SMH 3157	–	GU385163	GU327745	–
B. siamensis	*incertae sedis*	MFLUCC 10-0099[H]	KT289897	KT289895	KT962059	KT962061
B. villosa	*incertae sedis*	GKM 204N	–	GU385151	GU327751	–
Corynespora cassiicola	*Corynesporascaceae*	CBS 100822	GU296144	GU301808	GU349052	GU371742
Cyclothyriella rubronotata	*Cyclothyriellaceae*	CBS 141486[E]	KX650507	KX650544	KX650519	KX650574
Gemmamyces piceae	*incertae sedis*	CBS 141555	KY190006	KY189976	KY190011	KY189992
Herpotrichia diffusa	*incertae sedis*	CBS 250.62	DQ678019	DQ678071	DQ677915	DQ677968
H. juniperi	*incertae sedis*	CBS 200.31	DQ678029	DQ678080	DQ677925	DQ677978
H. macrotricha	*incertae sedis*	GKM 196N	–	GU385176	GU327755	–
H. vaginatispora	*incertae sedis*	MFLUCC 13-0865[H]	KT934256	KT934252	KT934260	–
Hysterium pulicare	*Hysteriaceae*	CBS 123377	FJ161161	FJ161201	FJ161109	FJ161127
Hysterobrevium mori	*Hysteriaceae*	CBS 123563	FJ161155	FJ161196	FJ161104	–
Leptosphaeria doliolum	*Leptosphaeriaceae*	CBS 505.75	GU296159	GU301827	GU349069	KT389640
Lophiostoma arundinis	*Lophiostomataceae*	CBS 621.86	DQ782383	DQ782384	DQ782387	DQ782386
Massaria inquinans	*Massariaceae*	CBS 125591[E]	HQ599442	HQ599400	HQ599340	–
Massarina eburnea	*Massarinaceae*	CBS 473.64	GU296170	GU301840	GU349040	GU371732
Melanomma populina	*Melanommataceae*	CBS 543.70[E]	EU754031	EU754130	–	–
M. populina	*Melanommataceae*	CBS 350.82	–	JF740265	–	–
M. pulvis-pyrius	*Melanommataceae*	CBS 124080[E]	GU456302	GU456323	GU456265	GU456350
M. pulvis-pyrius	*Melanommataceae*	CBS 109.77	FJ201987	FJ201986	GU456274	GU456359
M. pulvis-pyrius	*Melanommataceae*	CBS 371.75	FJ201989	FJ201988	GU349019	GU371798
Muriformistrickeria rubi	*incertae sedis*	MFLUCC 15-0681[H]	KT934257	KT934253	KT934261	–
Neoophiosphaerella sasicola	*Lentitheciaceae*	MAFF 239644[E]	AB524458	AB524599	AB539111	AB539098
Nigrograna obliqua	*Nigrograneaceae*	CBS 141475[P]	KX650512	KX650558	KX650530	KX650579
Phragmocephala atra	*incertae sedis*	MFLUCC 15-0021	KP698729	KP698725	–	–
Praetumpfia obducens	*incertae sedis*	CBS 141474[E]	KY190008	KY189984	KY190019	KY190000
Prosthemium betulinum	*Pleomassariaceae*	CBS 279.74	DQ678027	DQ678078	DQ677923	KT216532
Prosthemium canba	*Pleomassariaceae*	KT 2083-1	AB553646	AB553760	–	–
Pseudostrickeria muriformis	*incertae sedis*	MFLUCC 13-0764[H]	KT934258	KT934254	KT934262	–
Pseudotrichia mutabilis	*incertae sedis*	PM 1	–	KY189988	KY190022	KY190003
Roussoella verrucispora	*Thyridariaceae*	CBS 125434[H]	AB524481	AB524622	AB539115	AB539102
Sarimanas shirakamiense	*incertae sedis*	KT 3000[H]	LC001712	LC001715	–	–
Seifertia azaleae	*incertae sedis*	DAOM 239136	–	EU030276	–	–
S. shangrilaensis	*incertae sedis*	MFLUCC 16-0238[H]	KU954102	KU954100	KU954101	–
Teichospora trabicola	*Teichosporaceae*	CBS 140730[E]	–	KU601591	KU601601	KU601600
Tumularia tuberculata	*incertae sedis*	CBS 256.84	–	GU301851	GU349006	–

[1] "H": ex-holotype, "P": ex-paratype, "E": ex-epitype.

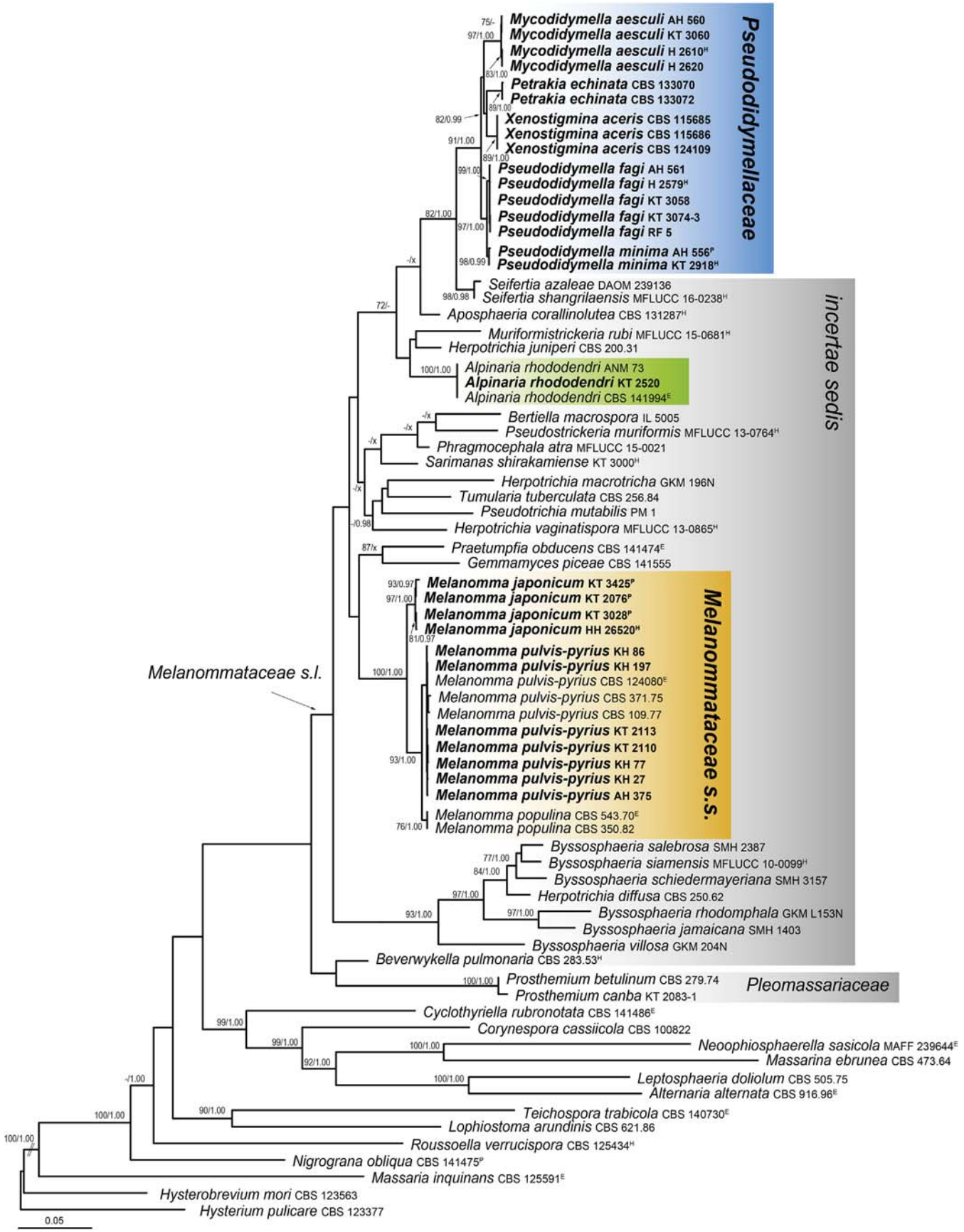


Fig. 1. Maximum-likelihood (ML) tree of *Melanommataceae sensu stricto* and *Pseudodidymellaceae* with its relatives. ML bootstrap percentages (BP) greater than 60 % and Bayesian posterior probabilities (PP) above 0.95 are presented at the nodes as ML BP/ Bayesian PP. A hyphen ("-") indicates values lower than 60 % BP or 0.95 PP, and a node not present in the Bayesian analysis is shown with "x". Ex-holotype, paratype, epitype, strains are indicated in with a superscript ^{H}, ^{P} and ^{E}, respectively. The newly obtained sequences are shown in bold. The scale bar represents nucleotide substitution per site.

Phragmocephala atra, *Pseudostrickeria murigormis* and *Sarimanas shirakamiense*.

Monophyly of the genera with mycopappus-like propagules (*Mycodidymella*, *Petrakia*, *Pseudodidymella*, and *Xenostigmina*) was well-supported (91 % ML BP/ 1.00 Bayesian PP). Although these four genera are phylogenetically related to *Melanommataceae sensu lato*, their morphological and ecological features are clearly distinct from those of the type genus *Melanomma*. Therefore, we establish a new family, *Pseudodidymellaceae*, to accommodate these genera with mycopappus-like propagules. Results from phylogenetic analyses of this study indicate that *Alpinaria*, formerly classified in *Melanommataceae sensu lato* (Jaklitsch & Voglmayr 2017), is phylogenetically distant from *Melanommataceae sensu stricto* (Fig. 1), but its familial placement is unresolved.

Taxonomy

Two families, including a new family (*Pseudodidymellaceae*), four genera, and seven species, including two new species and one new combination (*Melanomma japonicum*, *Pseudodidymella minima*, and *Xenostimgmina aceris*) are described below.

Melanommataceae G. Winter [as 'Melanommeae'], Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1.2: 220. 1887.

Saprobic on dead twigs of woody plants. Sexual morph: *Ascomata* globose to ovoid, immersed to superficial, gregarious, ostiolate. *Peridium* composed of thick-walled, pseudoparenchymatous, hyaline to brown cells. *Pseudoparaphyses* trabeculate, septate, branched and anastomosed. *Asci* bitunicate, fissitunicate, cylindrical, 8-spored. *Ascospores* olive brown, multiseptate, smooth. Asexual morph: *Conidiomata* pycnidial, globose to subglobose, superficial, black, ostiolate. *Peridium* composed of elongate, brown cells. *Conidiophores* absent. *Conidiogenous cells* holoblastic, ampliform to cylindrical, hyaline. *Conidia* ellipsoidal, hyaline, smooth, aseptate.

Type genus: *Melanomma* Nitschke ex Fuckel.

Notes: *Melanommataceae* was established by Winter (1887). *Byssosphaeria*, *Keissleriella*, *Melanomma*, *Ostropella*, and *Strickeria* have been referred to as members of *Melanommataceae*, and this family was characterised by gregarious ascomata composed of well-developed, carbonaceous or coriaceous peridium, trabecular pseudoparaphyses, and aposphaeria-like coelomycetous asexual morphs (Barr 1987). This familial concept was supported in "Outline of Ascomycota – 2007" for 18 genera (Lumbsch & Huhndorf 2007).

A study by Mugambi & Huhndorf (2009) on LSU and *tef1* sequences showed that *Melanommataceae* is composed of *Byssosphaeria*, *Herpotrichia*, *Melanomma*, and *Pseudotrichia*, and previous familial concepts did not reflect natural relationships. Several genera, such as *Keissleriella* and *Ostropella*, were phylogenetically scattered in other *Pleosporales* (Mugambi & Huhndorf 2009, Zhang *et al.* 2012, Tanaka *et al.* 2015), and *Strickeria* was placed in *Sporocadaceae* (*Xylariales*, *Sordariomycetes*) (Jaklitsch *et al.* 2016a). It was clear that the traditional concept of *Melanommataceae* is polyphyletic and needed revision (Kirk *et al.* 2008, Mugambi & Huhndorf 2009, Hyde *et al.* 2013). Later, two genera, *Tumularia* (as *Monotosporella*) and *Phragmocephala*, which have mononematous or synnematous conidiophores in their asexual morphs, were reported in *Melanommataceae* (Schoch *et al.* 2009, Su *et al.* 2015). Wijayawardene *et al.* (2012, 2014) also listed additional dematiaceous genera, *Exosporiella* and *Nigrolentilocus*, as members of this family without molecular evidence. A broad concept of *Melanommataceae* was proposed by Tian *et al.* (2015) and Jaklitsch & Voglmayr (2017), and *Mycodidymella*, *Petrakia* and *Xenostigmina* were treated as members of this family. However, the results of our phylogenetic analyses and morphological observations indicate that *Melanommataceae* should be restricted to its type genus, *Melanomma*.

Melanomma Nitschke ex Fuckel, Jb. nassau. Ver. Naturk. 23–24: 159. 1870 (1869–1870).

Synonym: *Moriolopis* Norman ex Keissl., Nytt Mag. Natur. 66: 88. 1927.

Saprobic on dead twigs of woody plants. Sexual morph: *Ascomata* globose to ovoid, immersed or erumpent to superficial, gregarious, with a short ostiolar neck. *Peridium* composed of thick-walled, pseudoparenchymatous, hyaline to brown cells. *Pseudoparaphyses* trabecular, septate, branched and anastomosed. *Asci* bitunicate, fissitunicate, cylindrical, 8-spored. *Ascospores* olive brown, sometimes with paler ends, strongly or slightly curved, multi-septate, smooth. Asexual morph: *Conidiomata* pycnidial, globose to subglobose, superficial, black, with a papillate ostiole. *Peridium* composed of elongate, brown cells. *Conidiophores* absent. *Conidiogenous cells* holoblastic, ampliform to cylindrical, hyaline, smooth. *Conidia* ellipsoidal, hyaline, smooth, aseptate.

Type species: *Melanomma pulvis-pyrius* (Pers.) Fuckel.

Notes: The genus *Melanomma* was established by Fuckel (1870). Species in this genus are known to be saprobes on decaying plant material or weak plant pathogens (Chesters 1938, Holm 1957, Zhang *et al.* 2008). *Melanomma pulvis-pyrius* is a well-studied, widespread species in this genus. However, other species have rarely been reported or have not been recorded since their initial description. Only a few species have received modern taxonomic treatment (Holm 1957, Mathiassen 1989, 1993, Barr 1990), although approximately 300 epithets are listed in Index Fungorum (http://indexfungorum.org). Asexual morphs of this genus were reported to be aposphaeria-like coelomycetes or *Nigrolentilocus* (Ichinoe 1970, Sivanesan 1984, Castañeda-Ruiz *et al.* 2001, Sánchez & Bianchinotti 2015, Tian *et al.* 2015).

Melanomma japonicum A. Hashim. & Kaz. Tanaka, **sp. nov.** MycoBank MB819613; Fig. 2.

Etymology: Referring to its country of origin, Japan.

Saprobic on dead twigs of woody plants. Sexual morph: *Ascomata* globose to ovoid, superficial, gregarious, 190–320 µm diam, 200–340 µm high. *Ostiolar neck* short papillate, composed of carbonaceous, thick-walled, black cells. *Peridium* 40–60 µm thick of two layers at side; outer layer 25–40 µm thick of elongate, thin-walled, 12–20 × 3–4 µm, brown cells; inner layer

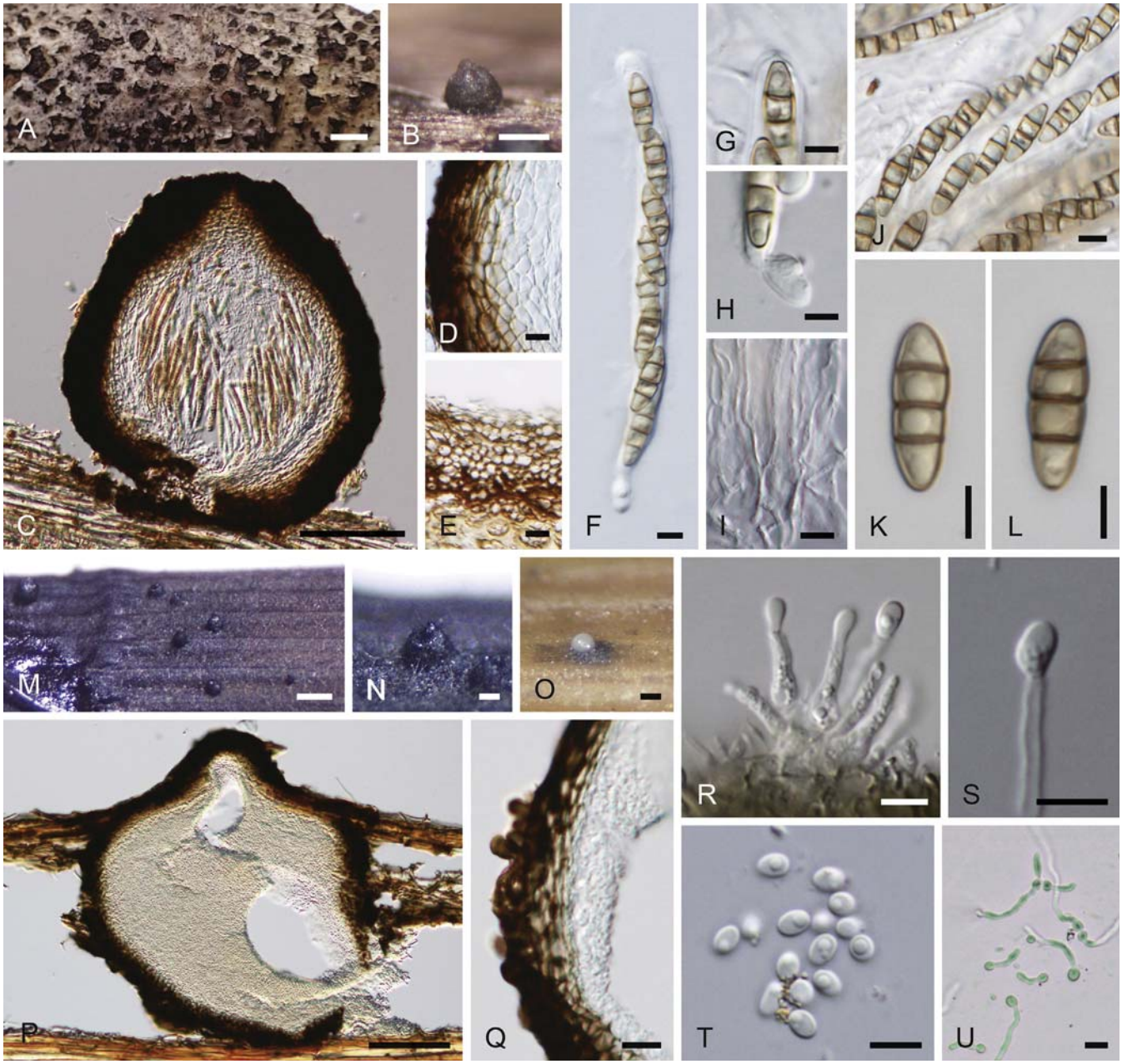


Fig. 2. *Melanomma japonicum.* **A, B.** Ascomata on substrate. **C.** Ascoma in longitudinal section. **D.** Lateral peridium of ascoma. **E.** Basal peridium of ascoma. **F.** Ascus. **G.** Apex of ascus. **H.** Stipe of ascus. **I.** Pseudoparaphyses. **J–L.** Ascospores. **M–O.** Conidiomata in culture. **P.** Conidioma in longitudinal section. **Q.** Peridium of conidioma. **R, S.** Conidiogenous cells. **T.** Conidia. **U.** Germinating conidia. **A, C–J** from HHUF 26520; **B, K, L** from HHUF 30540; **M–O** from culture CBS 142903; **P–U** from culture CBS 142905 = JCM 13124 = MAFF 239634. Scale bars: A, M = 500 µm; B = 200 µm; C, N–P = 100 µm; D, E, G–L, R–U = 5 µm; F, Q = 10 µm.

12.5–30 µm thick of globose to rectangular, 10–17.5 × 5–7 µm, hyaline cells; base of ascomata 40–53 µm thick, of two layers; outer layer 15–30 µm thick of elongate, thin-walled, 3.5–7.5 × 3.5–5 µm, brown cells; inner layer 10–30 µm thick of globose to rectangular, 7–10.5 × 6–9 µm, brown cells. *Pseudoparaphyses* trabeculate, 0.5 µm wide, septate, branched and anastomosed. *Asci* bitunicate, fissitunicate, cylindrical, 73–105 × 5.5–9 µm ($\overline{x}$ = 89.9 × 7 µm, n = 26), with a short stipe (7–16 µm long, $\overline{x}$ = 10.3 µm, n = 20), apically rounded with an ocular chamber, 8-spored. *Ascospores* fusiform, with broad rounded ends, straight to slightly curved, 12–19 × 3–7 µm ($\overline{x}$ = 15.1 × 4.6 µm, n = 151), l/w 2.5–4.9 ($\overline{x}$ = 3.4, n = 151), 3-septate, with a primary septum nearly median (0.44–0.57, $\overline{x}$ = 0.51, n = 75), olive brown, sometimes with paler ends, constricted at the septa, smooth. Asexual morph: *Conidiomata* pycnidial, globose to subglobose, up to 230 µm high in section, 150–250 µm diam, semi-immersed, solitary. *Ostiolar neck* short papillate, composed of thick-walled, black cells. *Peridium* 12–33.5 µm wide, composed of 8.5–16.5 × 3.5–7.5 µm, rectangular, brown cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, 8–13.5 × 2–3 µm, cylindrical, hyaline, smooth. *Conidia* cylindrical with rounded ends, 3–4 × 2–2.5 µm ($\overline{x}$ = 3.3 × 2.2 µm, n = 50), l/w 1.1–2.1 ($\overline{x}$ = 1.5, n = 50), hyaline, smooth, aseptate, guttulate when young.

Culture characteristics: Colonies on PDA attaining 25–27 mm diam within 21 d in the dark, floccose, centrally raised, smoke grey (Rayner 1970), grey olivaceous at centre; reverse smoke grey, grey olivaceous at margin (Fig. 8A); asexual morph formed.

Specimens examined: **Japan**, Aomori, Hakkoda, Okiagetai, on dead twigs of woody plant, 15 Apr. 2006, K. Tanaka, KT 2076 (HHUF 30539 paratype, ex-

paratype living culture CBS 142902); Akita, Kazuno, Hachimantai, Yakeyama, Mousen pass, on dead twigs of *Fagus crenata*, 24 Jun. 2012, K. Tanaka, KT 3028 (HHUF 30540 paratype, ex-paratype living culture CBS 142903); Kagoshima, Tarumizu, Mt. Oonogara, on dead twigs of *Fagus crenata*, 25 Oct. 2013, K. Tanaka, KT 3425 (HHUF 30541 paratype, ex-paratype living culture CBS 142904); Aomori, Hakkoda, near Yunotai, on dead twigs of woody plant, 21 Jul. 2001, Y. Harada (HHUF 26520 **holotype** designated here, ex-holotype living culture CBS 142905 = JCM 13124 = MAFF 239634).

Notes: This species is morphologically closest to *Me. pulvis-pyrius* in ascospore size, but the size of conidia of this species is slightly longer and slenderer (3–4 µm vs. (2–)2.5–3.5 µm long; 1.1–2.1 vs. 1.0–1.7 length/width). ITS sequences of these two species differed by 13 positions with one gap.

Melanomma pulvis-pyrius (Pers.) Fuckel, Jb. nassau. Ver. Naturk. 23–24: 160. 1870 (1869–1870). Fig. 3.

Saprobic on dead twigs of woody plants. Sexual morph: *Ascomata* globose to ovoid, 210–310(–410) µm diam. *Ostiolar neck* short papillate, composed of carbonaceous cells. *Peridium* 75–88 µm thick of two layers at side; outer layer 35–45 µm thick; inner layer 30–40 µm thick, 65–75 µm thick at base. *Pseudoparaphyses* trabeculate, 1–1.5 µm wide. *Asci* 71–92 × 5–8.5 µm ($\overline{x}$ = 82.1 × 6.3 µm, n = 14), with a short stipe (5–8 µm long, $\overline{x}$ = 5.7 µm, n = 12). *Ascospores* 11.5–15.5 × 4–5 µm ($\overline{x}$ = 13 × 4.2 µm, n = 75), l/w 2.5–3.6 ($\overline{x}$ = 3.1, n = 75), 3-septate, with a primary septum nearly median (0.45–0.58, $\overline{x}$ = 0.50, n = 75). Asexual morph: *Conidiomata* pycnidial, globose to subglobose, 160–300 µm diam, with a papillate ostiolar neck. *Peridium* 18.5–22 µm wide, composed of 4–16.5 × 2.5–5 µm, rectangular, brown cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, 8–17.5 × 1.5–4 µm, cylindrical, hyaline, smooth. *Conidia* cylindrical with rounded ends, (2–)2.5–3.5 × 2–2.5(–3) µm ($\overline{x}$ = 2.9 × 2.3 µm, n = 50), l/w 1.0–1.7 ($\overline{x}$ = 1.3, n = 50), hyaline, smooth, aseptate, guttulate when young.

Culture characteristics: Colonies on PDA attaining 22–24 mm diam within 21 d, floccose, fasciculate, centrally raised, pale olivaceous grey; reverse greyish sepia, olivaceous buff at margin (Fig. 8B); asexual morph formed.

Specimens examined: **Japan**, Aomori, Minamitsugaru, Owani, on dead twigs of *Acer mono* var. *mayrii*, 1 Jul. 2006, K. Tanaka, KT 2110 (HHUF 30542, culture CBS 142906); Hirosaki, Zatoishi, on dead twigs of woody plant, 8 Jul. 2006, H. Yonezawa, KT 2113 (HHUF 30543, culture CBS 142907); Noheji, near Mt. Eboshi, on dead twigs of *Fagus crenata*, 2 Sep. 2015, A. Hashimoto *et al.*, AH 375 (HHUF 30544, culture CBS 142908); Nishimeya, Ooshirosawa stream, on dead twigs of woody plant, 25 Jun. 2007, K. Hirayama *et al.*, KH 27 (HHUF 30545, culture CBS 142909); on dead twigs of woody plant, 21 Jul. 2007, K. Hirayama *et al.*, KH 77 (HHUF 30546, culture CBS 142910); Kawaratai, Ookawazoe, on dead twigs of woody plant, 28 Aug. 2007, K. Hirayama *et al.*, KH 86 (HHUF 30547, culture CBS 142911); on dead twigs of woody plant, 30 Aug. 2008, K. Hirayama *et al.*, KH 197 (HHUF 30548, culture CBS 142912).

Notes: The above specimens were identified as *Me. pulvis-pyrius*, the type species of *Melanomma*. The size of ascospores in our materials was almost identical to that of *Me. pulvis-pyrius* reported by Holm (1957), who observed the neotype of this species. The *rpb2* sequences of our isolates were identical or had one or two differences compared with those of *Me. pulvis-pyrius* (GU456350) obtained from the ex-epitype culture (CBS 124080).
Melanomma pulvis-pyrius is a well-studied species in *Melanomma*; its taxonomy and ontogeny of sexual morphs have been described (Chesters 1938), and it has been reported worldwide (Holm 1957, Sivanesan 1984, Vassilieva 1987, Vasyagina *et al.* 1987, Romero 1998, Mathiassen 1989, 1993, Zhang *et al.* 2008, Mugambi & Huhndorf 2009, Jaklitsch & Voglmayr 2017). However, this is the first report of *Me. pulvis-pyrius* from Japan. This species was epitypified by Zhang *et al.* (2008) based on a specimen collected from *Salix caprea* in France.

In the phylogenetic tree, *Me. pulvis-pyrius* clustered with *Me. populina* (CBS 543.70 and CBS 350.82) with moderate to strong support (93 % ML BP/ 1.00 Bayesian PP). Because we could not compare the characters of these two species, further study is needed in the future to confirm whether these two species are conspecific.

Pseudodidymellaceae A. Hashim. & Kaz. Tanaka, **fam. nov.** MycoBank MB819614.

Parasitic on living leaves of woody plants. Sexual morph: *Ascomata* subglobose to lenticular, immersed, ostiolate. *Peridium* pale brown to brown, distinctly thickened at base. *Pseudoparaphyses* septate, branched and anastomosed. *Asci* bitunicate, fissitunicate, cylindrical, 8-spored. *Ascospores* fusiform with rounded ends, straight, 1-septate, hyaline, smooth. *Spermatia* cylindrical, hyaline. Asexual morph: *Propagules* epiphyllous, white to yellowish, globose to subglobose, multicellular, with numerous, flexuous, cylindrical, multi-septate hyphal appendages, detached at stroma-like base composed of subglobose to oblong, hyaline to yellow cells. Synasexual morph: *Conidiomata* sporodochial, superficial. *Stromata* composed of globose to subglobose cells. *Conidiophores* reduced. *Conidiogenous cells* annellidic or holoblastic. *Conidia* clavate, sigmoid or rounded to oval or broadly ellipsoidal, phragmosporous to muriform, hyaline to brown, falcate to sigmoid.

Type genus: *Pseudodidymella* C.Z. Wei *et al.*

Notes: *Mycodidymella*, *Petrakia*, *Pseudodidymella*, and *Xenostigmina* have mycopappus-like propagules in their life cycles. Although sexual morphs of these genera were reported, and several molecular studies were performed, the phylogenetic placement of these genera remains unresolved (Crous *et al.* 2009, Butin *et al.* 2013, Li *et al.* 2016, Gross *et al.* 2017). According to the multi-locus phylogenies, these genera are closely related to each other (Li *et al.* 2016, Gross *et al.* 2017, Jaklitsch & Voglmayr 2017). Based on phylogenetic study, Phookamsak *et al.* (2014) proposed to include *Petrakia* and *Xenostigmina* in *Melanommataceae*. Tian *et al.* (2015) accepted these two genera in *Melanommataceae* in a subsequent study. In our study, the monophyly of these four genera with mycopappus-like propagules was strongly supported (91 % ML BP/ 1.00 Bayesian PP; Fig. 1). Therefore, we introduce a new family, *Pseudodidymellaceae*, to accommodate the above four genera. Species in this family bear several common features, including sexual morphs with lenticular and subcuticular ascomata erumpent from host tissue, asexual morphs with mycopappus-like propagules, and with or without a synasexual morph that has sporodochial conidiomata. *Pseudodidymellaceae* can be distinguished from *Melanommataceae sensu stricto* based on the presence of mycopappus-like propagules.

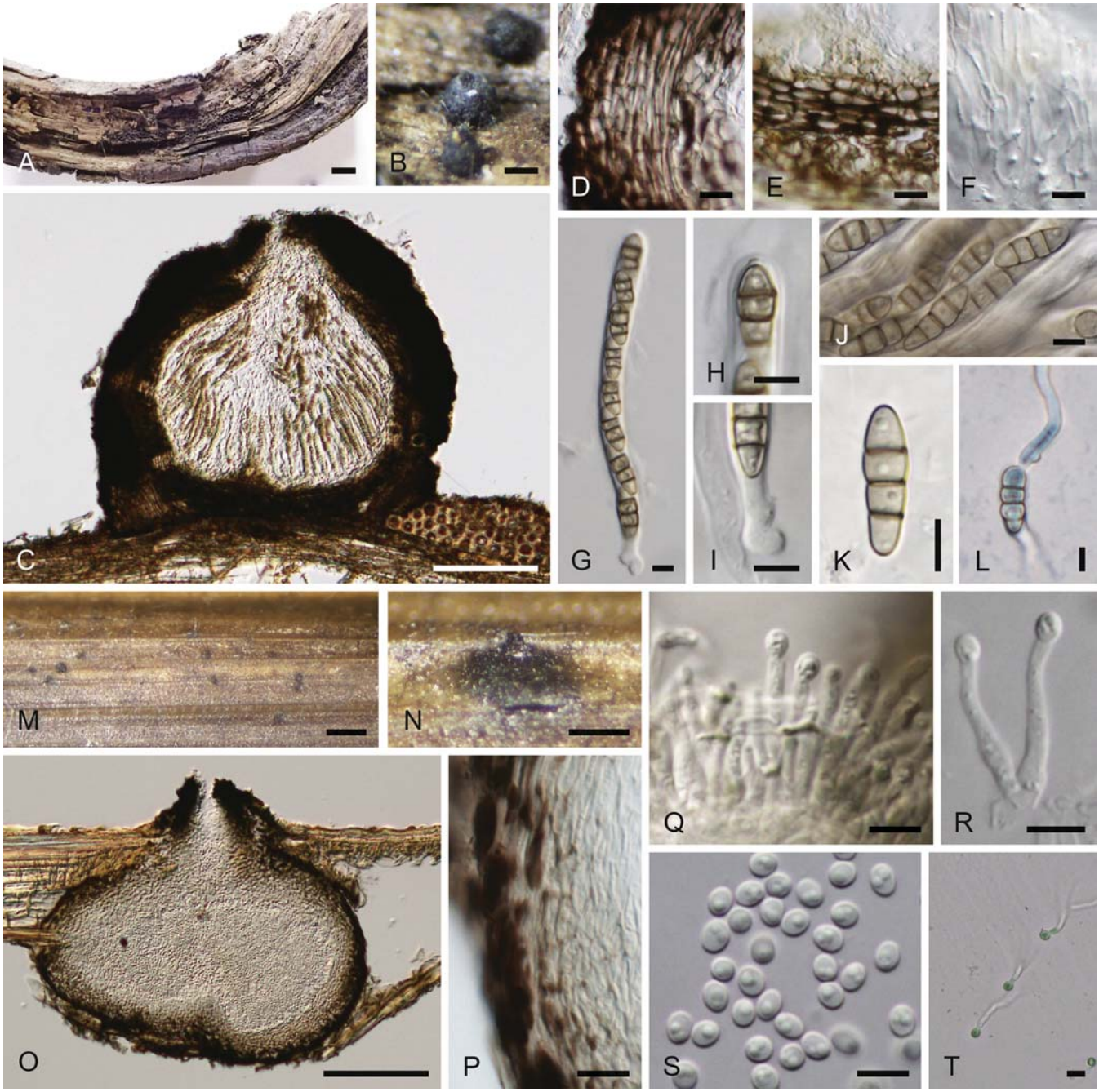


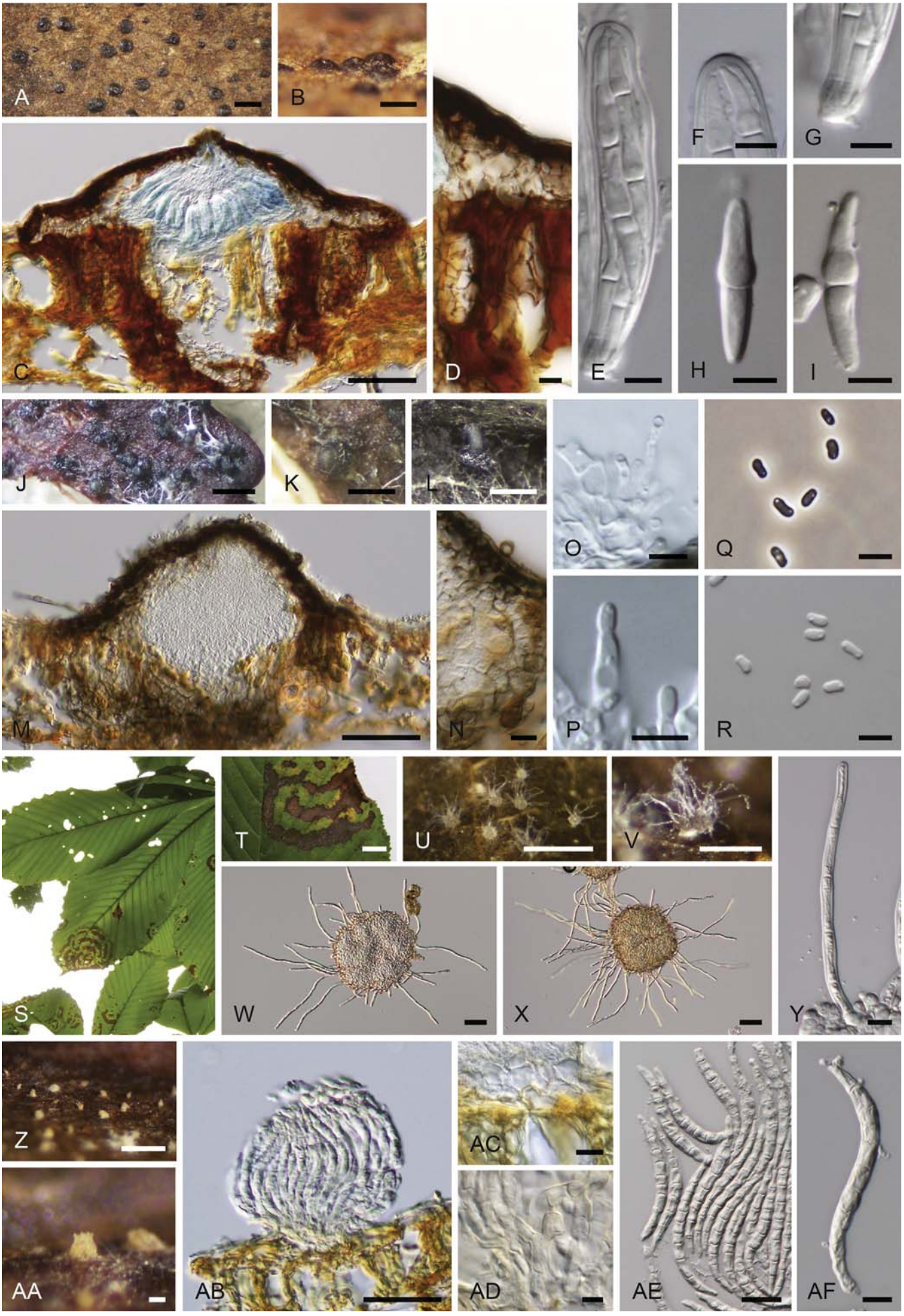
Fig. 3. *Melanomma pulvis-pyrius.* **A, B.** Ascomata on substrate. **C.** Ascoma in longitudinal section. **D.** Lateral peridium of ascoma. **E.** Basal peridium of ascoma. **F.** Pseudoparaphyses. **G.** Ascus. **H.** Apex of ascus. **I.** Stipe of ascus. **J, K.** Ascospores. **L.** Germinating ascospore. **M, N.** Conidiomata in culture. **O.** Conidioma in longitudinal section. **P.** Peridium of conidioma. **Q, R.** Conidiogenous cells. **S.** Conidia. **T.** Germinating conidia. **A–F, J–L** from HHUF 30544; **G–I** from HHUF 30543; **M–Q, T** from culture CBS 142912; **R, S** from culture CBS 142908. Scale bars: A, M = 500 µm; B, N = 200 µm; C, O = 100 µm; D, E, P = 10 µm; F–L, Q–T = 5 µm.

Mycodidymella C.Z. Wei *et al.*, Mycologia 90: 336. 1998.
Synonym: *Blastostroma* C.Z. Wei *et al.*, Mycologia 90: 337. 1998.

Parasitic on living leaves of woody plant. Sexual morph: *Ascomata* subglobose to lenticular, immersed, ostiolate. *Peridium* with rim-like side wall, composed of rectangular, thin-walled, pale brown cells, well-developed at base. *Pseudoparaphyses* septate, branched and anastomosed. *Asci* bitunicate, fissitunicate, cylindrical, 8-spored. *Ascospores* fusiform, 1-septate, hyaline, smooth. *Spermatia* cylindrical, hyaline. Asexual morph: *Propagules* epiphyllous, white to yellowish, globose to subglobose, multicellular; main bodies subglobose to oblong, bearing numerous, unbranched, flexuous, cylindrical, multi-septate hyphal appendages. Synasexual morph: *Conidiomata* sporodochial, white to yellowish. *Stromata* composed of globose to subglobose cells. *Conidiophores* absent. *Conidiogenous cells* holoblastic, hyaline. *Conidia* falcate to sigmoid, hyaline, multiseptate, obtuse at the apex, truncate at the base.

Type species: *Mycodidymella aesculi* C.Z. Wei *et al.*

Mycodidymella aesculi C.Z. Wei *et al.*, Mycologia 90: 336. 1998. Fig. 4.
Synonyms: *Blastostroma aesculi* C.Z. Wei *et al.*, Mycologia 90: 338. 1998.
Mycopappus aesculi C.Z. Wei *et al.*, Mycologia 90: 336. 1998.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Petrakia aesculi (C.Z. Wei *et al.*) Jaklitsch & Voglmayr, Sydowia 69: 91. 2017.

Parasitic on living leaves of *Aesculus turbinata*. Sexual morph: *Ascomata* subglobose to lenticular, solitary to 3–5 grouped, immersed, up to 210 µm high, 260–380 µm diam. *Ostiolar neck* short papillate, composed of thick-walled, black cells. *Peridium* 17.5–27.5 µm thick at side, with rim-like side wall, composed of rectangular, thin-walled, 10–13.5 × 6–9 µm, pale brown cells, at base 105–140 µm thick, composed of 8.5–11.5 × 6.5–8.5 µm, hyaline to pale brown cells. *Pseudoparaphyses* numerous, trabeculate, 0.8–1.3 µm wide, septate, branched and anastomosed. *Asci* bitunicate, fissitunicate, cylindrical, 45.5–60 × 7–12.5 µm ($\overline{x}$ = 53.3 × 10 µm, n = 20), with or without a short stipe, apically rounded with an ocular chamber, 8-spored. *Ascospores* fusiform with rounded ends, straight, 16–21.5 × 3–4.5 µm ($\overline{x}$ = 18.6 × 3.9 µm, n = 21), l/w 4.3–5.3 ($\overline{x}$ = 4.7, n = 21), with a septum nearly median (0.44–0.55, $\overline{x}$ = 0.51, n = 21), constricted at the septum, hyaline, smooth, guttulate when young. *Spermatia* 3–5 × 1–2 µm ($\overline{x}$ = 3.6 × 1.5 µm, n = 50), l/w 1.7–3.7 ($\overline{x}$ = 2.5, n = 50), cylindrical, hyaline. Asexual morph: *Propagules* epiphyllous, white to yellowish, globose to subglobose, 200–565 µm diam ($\overline{x}$ = 331.9 µm, n = 30); main bodies subglobose to oblong, 85–193 × 116–228 µm ($\overline{x}$ = 127.6 × 152.4, n = 30), composed of 7.5–10 µm diam cells; hyphal appendages 19 to 37, unbranched flexuous, cylindrical, 3–7-septate, 72–150 × 3.5–5.5 µm ($\overline{x}$ = 111.5 × 4.6, n = 30). Synasexual morph: *Conidiomata* sporodochial, white to yellowish. *Stromata* 15–20 µm thick, composed of hyaline, globose to subglobose cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, hyaline, smooth, 9–12 × 4–5.5 µm. *Conidia* falcate to sigmoid, 57–94 × 5.5–8.5 µm ($\overline{x}$ = 75.8 × 6.8, n = 50), hyaline, 8–13-septate, obtuse at the apex, truncate at the base.

Culture characteristics: Colonies on PDA attaining 31–40 mm diam within 21 d, velvety, floccose, centrally raised, buff, grey olivaceous at centre; reverse buff; grey olivaceous at centre (Fig. 8C); spermatial, asexual and synasexual morphs formed.

Specimens examined: **Japan**, Aomori, Minamitsugaru, Owani, on living leaves of *Aesculus turbinata*, 12 Aug. 2012, K. Tanaka *et al.*, KT 3060 (HHUF 30549, culture CBS 142913); Nishimeya, Kawaratai, Ookawazoe, near Annmon waterfall trail, on living leaves of *Aesculus turbinata*, 4 Oct. 1995, C. Z. Wei & Y. Harada (HHUF 23078 **holotype** of *Blastostroma aesculi*); 10 Sep. 2016, A. Hashimoto, AH 560 (HHUF 30550, culture CBS 142916); Hirakawa, Ikarigaseki, on living leaves of *Aesculus turbinata*, 18 Apr. 1995, C. Z. Wei & Y. Harada, H 2610 (HHUF 22892 **holotype** of *Mycodidymella aesculi*, ex-holotype living culture CBS 142914); on living leaves of *Aesculus turbinata*, 18 Apr. 1995, C. Z. Wei & Y. Harada, H 2620 (culture CBS 142915).

Notes: The genus *Mycodidymella* was established to accommodate a single species, *Mycod. aesculi*, and this species causes large concentric leaf spots on *Aesculus turbinata* in Japan (Wei *et al.* 1998). This species is morphologically characterised by lenticular ascomata and 1-septate, hyaline ascospores in the sexual morph, mycopappus-like propagules in the asexual morph, and blastostroma-like sigmoid conidia in the synasexual morph. The sexual morph of this species morphologically resembles those of *Didymella* or *Pseudodidymella*. Wei *et al.* (1998) assigned this genus to *Phaeosphaeriaceae* based on morphology. Later, familial placement of this genus was treated as *incertae sedis* in *Dothideomycetes* (Lumbsch & Huhndorf 2007). Recently, Butin *et al.* (2013) described the sexual morph of *Pe. echinata*, which is the type species of *Petrakia*; they found that the sexual morphology of *Petrakia* matches that of *Mycodidymella* and thus synonymised *Mycodidymella* with *Petrakia* (Butin *et al.* 2013). This proposal was accepted by subsequent studies (Tian *et al.* 2015, Li *et al.* 2016, Jaklitsch & Voglmayr 2017). However, *Mycod. aesculi* was not included in their analyses. Our phylogenetic study revealed that their monophyletic status was not supported in any analyses (below 60 % ML BP/ 0.95 Bayesian PP, Fig. 1). We retained *Mycodidymella* as a natural genus in *Pseudodidymellaceae* (discussed below).

Pseudodidymella C.Z. Wei *et al.*, Mycologia 89: 496. 1997.
Synonym: *Pycnopleiospora* C.Z. Wei *et al.*, Mycologia 89: 496. 1997.

Parasitic on living leaves of *Fagus* spp. Sexual morph: *Ascomata* subglobose to lenticular, solitary to grouped, immersed, ostiolate. *Peridium* composed of rectangular, thin-walled, pale brown cells, well-developed at base. *Pseudoparaphyses* septate, branched and anastomosed. *Asci* bitunicate, fissitunicate, cylindrical, 8-spored. *Ascospores* fusiform with rounded ends, 1-septate, hyaline, smooth. *Spermatia* cylindrical, hyaline. Asexual morph: *Propagules* epiphyllous, white to yellowish, globose, multicellular; main bodies globose, subglobose, hyaline to yellow, bearing numerous, unbranched, flexuous, multi-septate hyphal appendages.

Type species: *Pseudodidymella fagi* C.Z. Wei *et al.*

Notes: The genus *Pseudodidymella*, based on the type species *Pseudod. fagi*, has lenticular ascomata and a pycnopleiospora-like asexual morph which is characterised by sporodochial conidiomata and appendage-bearing conidia (Wei *et al.* 1997). Because its sexual morph morphologically resembles that of *Didymella*, this genus was considered a member of *Phaeosphaeriaceae* (Wei *et al.* 1997). The sexual morph of this genus superficially resembles that of *Mycodidymella*, but it can be distinguished based on its pycnopleiospora-like asexual morph (Wei *et al.* 1998). Since then, this genus has been treated as *incertae sedis* in *Dothideomycetes* (Lumbsch & Huhndorf 2007). Gross *et al.* (2017) discovered *Pseudod. fagi* on *Fagus sylvatica* in Switzerland; they noted that the asexual morph of this species was previously recorded as *Pycnopleiospora*, but actually has mycopappus-like propagules rather than individual conidia, and

Fig. 4. *Mycodidymella aesculi*. **A, B.** Ascomata on substrate. **C.** Ascoma in longitudinal section. **D.** Peridium of ascoma. **E.** Ascus. **F.** Apex of ascus. **G.** Stipe of ascus. **H, I.** Ascospores. **J–L.** Spermatogonia in culture. **M.** Spermatogonium in longitudinal section. **N.** Perdium of spermatogonium. **O, P.** Spermatogenous cells. **Q, R.** Spermatia. **S, T.** Leaves of *Aesculus turninata* with necrotic brown spots. **U, V.** Propagules on the leaf surface. **W, X.** Propagules. **Y.** Appendage of propagule. **Z, AA.** Sporodochia on the leaf surface. **AB.** Sporodochium in longitudinal section. **AC.** Stroma of sporodochium. **AD.** Conidiogenous cells. **AE, AF.** Conidia. **A–I** from HHUF 22892. **J–R** from culture CBS 142913. **S, T** from HHUF 30550. **U–Y** from HHUF 30549. **Z–AF** from HHUF 23078. Scale bars: A, J, T, Z = 500 µm; B, K, L, U, V = 250 µm; C, M, W, X, AA, AB = 50 µm; D, E, N, Y, AC, AE, AF = 10 µm; F–I, O–R, AD = 5 µm.

the original description (Wei *et al.* 1997) seemed to misinterpret over-mature propagules. They also confirmed that *Pseudodidymella* is phylogenetically related to other mycopappus-forming genera, such as *Mycodidymella*, *Petrakia*, and *Xenostigmina*, based on the ITS phylogeny. Thus, morphological delimitation of *Pseudodidymella* and *Mycodidymella* is problematic and requires further research. In the present study, we recollected *Pseudod. fagi* from its type locality, and compared the fresh materials to the holotype of *Py. fagi*. Based on morphological and phylogenetic comparisons of these specimens, we also conclude that Wei *et al.* (1997) misinterpreted the pieces of broken overmatured mycopappus-like propagules (Fig. 5AA and AB) as conidia of *Pseudodidymella*, but *Pseudodidymella* actually has mycopappus-like propagules in its asexual morph.

Species in this genus bear common features, with more than 60 hyphal appendages in mycopappus-like propagules. Although other related genera have sporodochial synasexual morphs, no synasexual morph is known from *Pseudodidymella* (Wei *et al.* 1997, Gross *et al.* 2017, present study). Morphologically, *Pseudodidymella* resembles *Mycodidymella*, but can be distinguished based on the rim-like walls of the ascomata, and numerous hyphal appendages in the asexual morph.

Pseudodidymella fagi C.Z. Wei *et al.*, Mycologia 89: 496. 1997. Fig. 5.
Synonym: *Pycnopleiospora fagi* C.Z. Wei *et al.*, Mycologia 89: 496. 1997.

Parasitic on living leaves of *Fagus crenata*. Sexual morph: *Ascomata* subglobose to lenticular, solitary to 3–5 grouped, immersed, up to 175 µm high, 200–300 µm diam. Ostiolar neck short papillate, composed of thick-walled, black cells. *Peridium* 20–22 µm thick at side, composed of rectangular, thin-walled, 7.5–10.5 × 6.5–8.5 µm, pale brown cells, at base 58–67 µm thick, composed of 10–13.5 × 5–11.5 µm, hyaline to pale brown cells. *Pseudoparaphyses* numerous, 1–2 µm wide, septate, branched and anastomosed. *Asci* bitunicate, fissitunicate, cylindrical, 49–76.5 × 10–14 µm ($\overline{x}$ = 60.3 × 11.5 µm, n = 20), with a short stipe (3.5–8 µm long, $\overline{x}$ = 6.1 µm, n = 20), apically rounded with an ocular chamber, 8-spored. *Ascospores* fusiform with rounded ends, straight, 18.5–24 × 4–5 µm ($\overline{x}$ = 20.5 × 4.3 µm, n = 20), l/w 4.3–5.6 ($\overline{x}$ = 4.8, n = 20), with a septum nearly median (0.47–0.58, $\overline{x}$ = 0.52, n = 20), constricted at the septum, hyaline, smooth, guttulate when young. *Spermatia* 3–5 × 1–1.5 µm ($\overline{x}$ = 3.9 × 1.2 µm, n = 50), l/w 2.1–4.8 ($\overline{x}$ = 3.3, n = 50), cylindrical, hyaline. Asexual morph: *Propagules* epiphyllous, white to yellowish, globose, 290–500 µm diam ($\overline{x}$ = 387.2 µm, n = 30); main bodies globose, 160–315 µm diam ($\overline{x}$ = 227.4 µm, n = 30), composed of subglobose, hyaline to yellow, 11.5–15 × 7.5–11.5 µm cells; hyphal appendages 63 to 138, unbranched, flexuous, cylindrical, 1–4-septate, 67–133 × 3–5 µm ($\overline{x}$ = 97.1 × 3.7 µm, n = 52).

Culture characteristics: Colonies on PDA attaining 27–37 mm diam within 21 d, velvety, plane, buff to olivaceous black at centre; reverse buff to olivaceous black at centre (Fig. 8D); spermatial and asexual morphs formed.

Specimens examined: **Japan**, Aomori, Nakatsugaru, Onikawabe, on living leaves of *Fagus crenata*, 12 Aug. 2012, K. Tanaka *et al.*, KT 3058 (HHUF 30515, culture CBS 142917 = MAFF 245738); Nishimeya, Ookawazoe, near Annmon waterfall trail, on living leaves of *Fagus crenata*, 2 Sep. 2012, K. Tanaka *et al.*, KT 3074-3 (HHUF 30516, culture CBS 142918 = MAFF 245739); 2 Sep. 2012, R. Fujimoto *et al.*, RF 5 (HHUF 30517, culture CBS 142919 = MAFF 245741); 10 Sep. 2016, A. Hashimoto, AH 561 (HHUF 30553, culture CBS 142920); Hirakawa, Ikarigaseki, on living leaves of *Fagus crenata*, 28 Apr. 1995, C. Z. Wei & Y. Harada, H 2579 (HHUF 22903, **holotype** of *Pseudodidymella fagi*, ex-holotype living culture MAFF 245740); artificial inoculation on leaves of *Fagus crenata*, 30 Sep. 1996, C. Z. Wei (HHUF 23672, **holotype** of *Pycnopleiospora fagi*).

Notes: This species was originally reported to cause brown leaf spots on *Fagus crenata* in Japan. More recently, it was reported from a new host, *F. sylvatica* (Gross *et al.* 2017). To elucidate its host spectrum, further surveys for this fungus and other species on *Fagus* is needed.

Pseudodidymella minima A. Hashim. & Kaz. Tanaka, **sp. nov.** MycoBank MB819615. Fig. 6.

Etymology: Referring to the smaller-sized propagules observed in this species.

Parasitic on living leaves of *Fagus japonica*. Sexual morph: Unknown. Asexual morph: *Propagules* epiphyllous, white to yellowish, globose, 110–220(–240) µm diam ($\overline{x}$ = 164.4 µm, n = 60); main bodies globose, multicellular, 78–168 µm diam ($\overline{x}$ = 115 µm, n = 60), composed of subglobose, 7.5–10 µm diam, hyaline to yellow cells; hyphal appendages 65 to 135, unbranched, flexuous, cylindrical, 1–2-septate or rarely aseptate, 27–44 × 3–6 µm ($\overline{x}$ = 35.5 × 4.4 µm, n = 59).

Culture characteristics: Colonies on PDA attaining 32–38 mm diam within 21 d, floccose, plane, smoke grey; reverse honey to isabelline (Fig. 8E); asexual morph formed.

Specimens examined: **Japan**, Iwate, Hanamaki, near Dai spa, on living leaves of *Fagus japonica*, 9 Oct. 2011, K. Tanaka, KT 2918 (HHUF 30551 **holotype** designated here; ex-holotype living culture CBS 142921 = MAFF 246249); 3 Sept. 2016, A. Hashimoto, AH 556 (HHUF 30552 paratype, ex-paratype living culture CBS 142922).

Notes: This species on *Fagus japonica* is easily distinguished from *Pseudod. fagi* on *F. crenata* by its much smaller propagules. Sequence differences between these two species were found at six nucleotide positions with one gap in the ITS sequences.

We did not observe the sexual or synasexual morph of *Pseudod. minima*. Further surveys are therefore needed to reveal the ecological features of this species.

Xenostigmina aceris (Dearn. & Barthol.) A. Hashim. & Kaz. Tanaka, **comb. nov.** MycoBank MB821403.
Basionym: *Cercosporella aceris* Dearn. & Barthol., Mycologia 9: 362. 1917.
Synonyms: *Mycopappus aceris* (Dearn. & Barthol.) Redhead & G.P. White, Canad. J. Bot. 63: 1430. 1985.
Petrakia aceris (Dearn. & Barthol.) Jaklitsch & Voglmayr, Sydowia 69: 90. 2017.
Stigmina zilleri A. Funk, Canad. J. Bot. 65: 482. 1987.
Xenostigmina zilleri (A. Funk) Crous, Mycol. Mem. 21: 155. 1998.
Mycosphaerella mycopappi A. Funk & Dorworth, Canad. J. Bot. 66: 295. 1988.

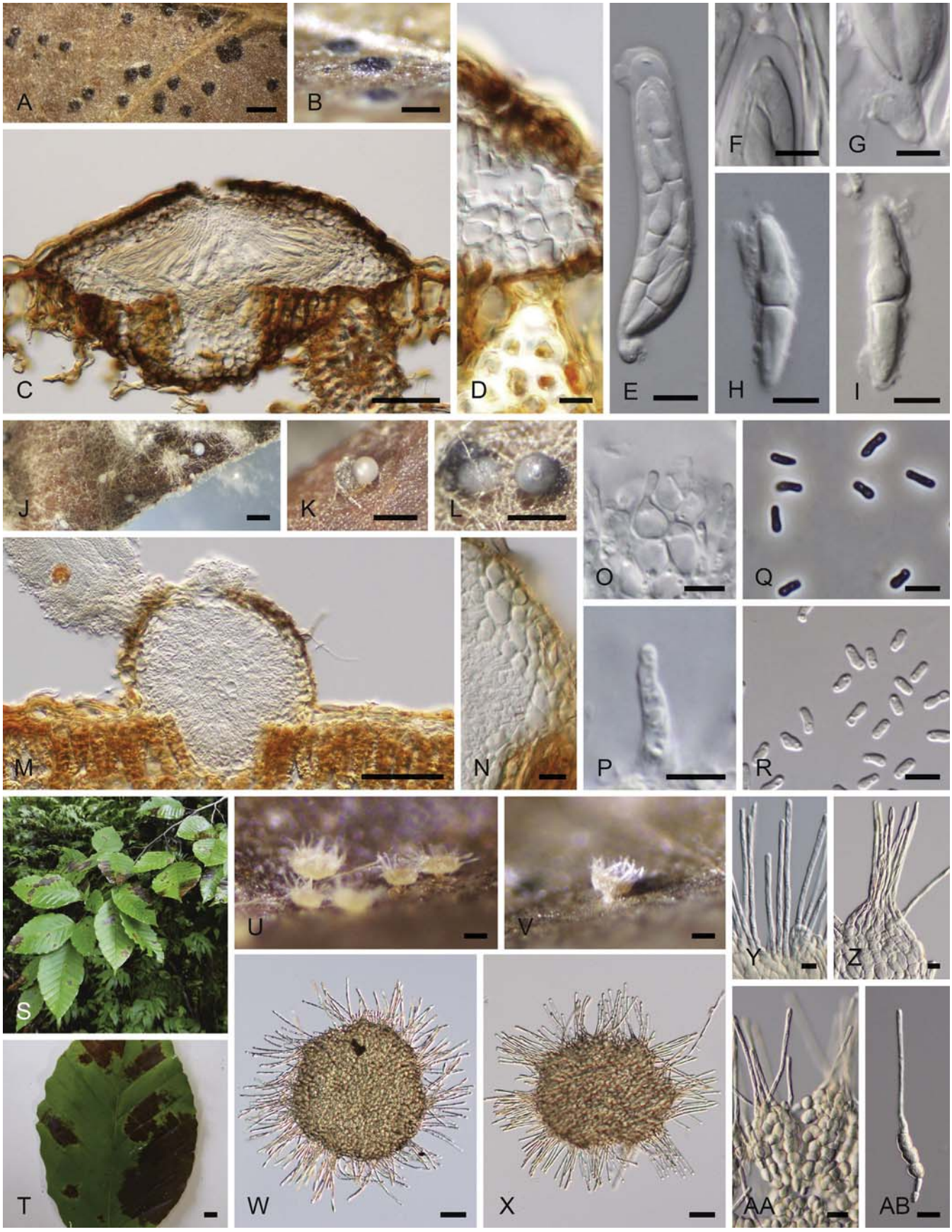

Fig. 5. *Pseudodidymella fagi.* **A, B.** Ascomata on substrate. **C.** Ascoma in longitudinal section. **D.** Peridium of ascoma. **E.** Ascus. **F.** Apex of ascus. **G.** Stipe of ascus. **H, I.** Ascospores. **J–L.** Spermatogonia in culture. **M.** Spermatogonium in longitudinal section. **N.** Perdium of spermatogonium. **O, P.** Spermatogenous cells. **Q, R.** Spermatia. **S, T.** Leaves of *Fagus crenata* with necrotic brown spots. **U, V.** Propagules on the leaf surface. **W, X.** Propagules. **Y–AB.** Appendages of propagule. **A–I** from HHUF 22903. **J–R** from culture CBS 142917 = MAFF 245738. **S, T** from HHUF 30553. **U, X, AA, AB** from HHUF 30516. **V, W, Z** from HHUF 23672. **Y** from HHUF 30517. Scale bars: A, J, T = 500 µm; B, K, L, U, V = 250 µm; C, M, W, X = 50 µm; D, E, N, Y–AB = 10 µm; F–I, O–R = 5 µm.

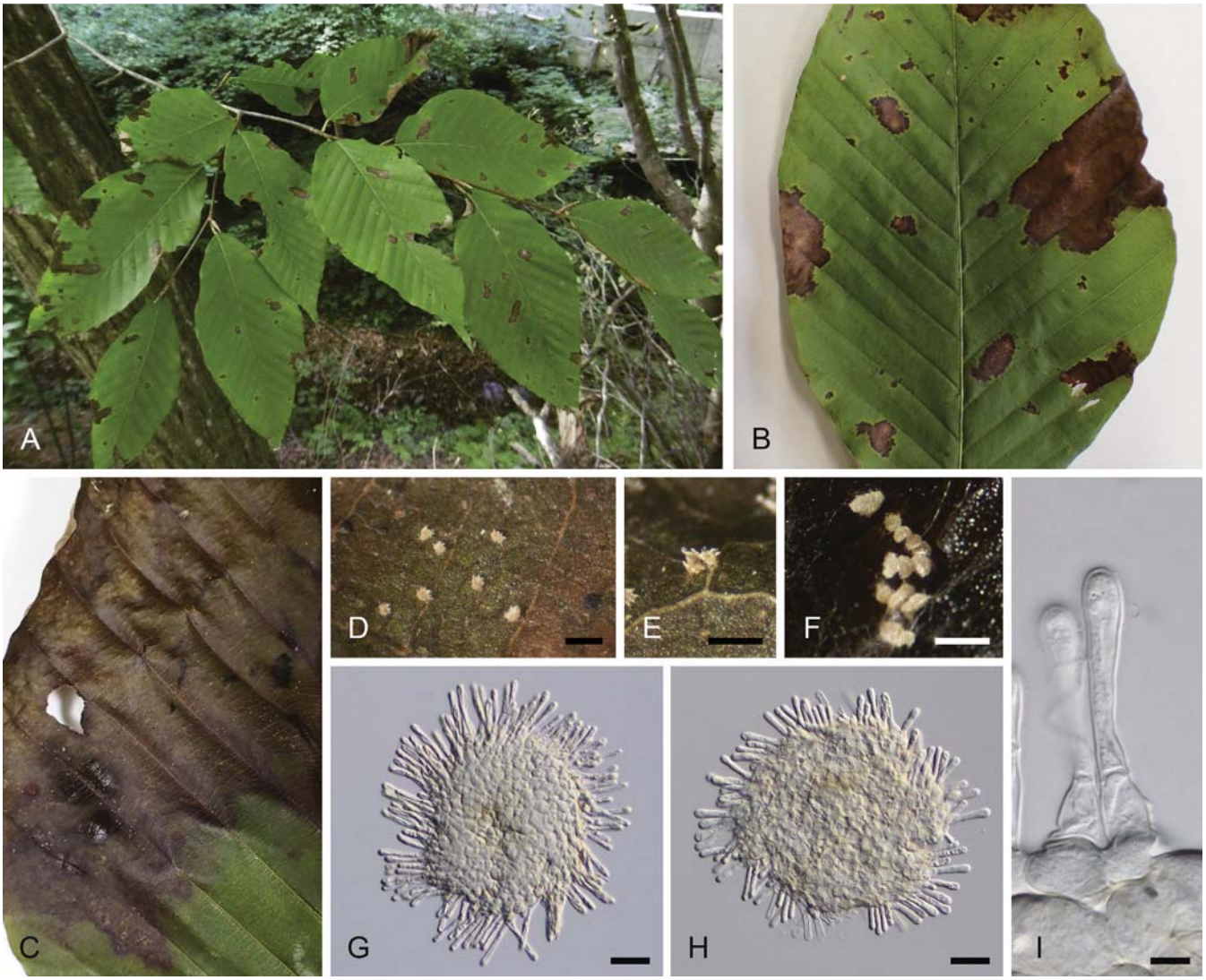

Fig. 6. *Pseudodidymella minima*. **A–C.** Leaves of *Fagus japonica* with necrotic brown spots. **D–F.** Propagules on the leaf surface. **G, H.** Propagules. **I.** Appendages of propagule. **A–C, H** from HHUF 30552. **D, E, G, I** from HHUF 30551. **F** from culture CBS 142921 = MAFF 246249. Scale bars: D–F = 250 µm; G, H = 50 µm; I = 5 µm.

Didymella mycopappi (A. Funk & Dorworth) Crous, Mycol. Mem. 21: 152. 1998.

Notes: *Xenostigmina zilleri* is the name that has been commonly used for this pathogen, although the epithet of *Cercosporella aceris* is older than that of *Stigmina zilleri* (Crous 1998, Crous *et al.* 2009, Phookamsak *et al.* 2014, Tian *et al.* 2015, Gross *et al.* 2017). Therefore, we proposed a new combination, *Xenostigmina aceris*.

Incertae sedis

Alpinaria Jaklitsch & Voglmayr, Sydowia 69: 84. 2017.

Saprobic on dead twigs of woody plants. Sexual morph: *Ascomata* globose to ovoid, immersed to superficial, gregarious, sometimes confluent, ostiolate. *Peridium* composed of elongate, thin-walled, brown cells, at base composed of elongate, hyaline cells. *Pseudoparaphyses* septate, branched and anastomosed. *Asci* bitunicate, cylindrical, 8-spored. *Ascospores* fusiform, multiseptate, smooth. Asexual morph: *Conidiomata* pseudopycnidial, globose to cylindrical, sometimes deformed, septate, confluent, multiloculate, scattered, semi-immersed, black, with one to two non-papillate ostiole. *Peridium* rectangular, brown cells. *Conidiophores* absent. *Conidiogenous cells* holoblastic, cylindrical, hyaline, smooth. *Conidia* cylindrical with rounded ends, hyaline, smooth, aseptate.

Type species: *Alpinaria rhododendri* (Niessl) Jaklitsch & Voglmayr.

Alpinaria rhododendri (Niessl) Jaklitsch & Voglmayr, Sydowia 69: 84. 2017. Fig. 7.
Basionym: *Cucurbitaria rhododendri* Niessl, Verh. Nat. Ver. Brünn 10: 200. 1872.
Synonyms: *Gibberidea rhododendri* (Niessl) Petr., Ann. Mycol. 32: 330. 1934; nom. illegit.
Melanomma rhododendri Rehm, Ber. Naturhist. Ver. Augsburg 26: 48. 1881.

Fig. 7. *Alpinaria rhododendri.* **A, B.** Ascomata on substrate. **C.** Ascoma in longitudinal section. **D.** Lateral peridium of ascoma. **E.** Ascus. **F.** Apex of ascus. **G.** Stipe of ascus. **H.** Pseudoparaphyses. **I–K.** Ascospores. **L, M.** Conidiomata in culture. **N.** Conidiomata in longitudinal section. **O.** Peridium of conidioma. **P, Q.** Conidiogenous cells. **R.** Conidia. **S.** Germinating conidia. **A–K** from HHUF 30554. **L–S** from culture CBS 142901. Scale bars: A, L = 500 µm; B, C, M, N = 100 µm; D, E, O = 10 µm; F–K, P–S = 5 µm.

Gibberidea rhododendri (Rehm) Petr., Krypt. Forsch. (München) 2: 160. 1931.
Gibberidea rhododendri (Rehm) Kirschst., Hedwigia 81: 206, 1944; nom. illegit.

Saprobic on dead twigs of ericaceous plants. Sexual morph: *Ascomata* globose to ovoid, immersed, becoming largely erumpent to superficial, gregarious, sometimes confluent, 140–190 µm high, 110–250 µm diam. Ostiolar neck short papillate, composed of carbonaceous, thick-walled, black cells. *Peridium* 55–75 µm thick at side composed of elongate, thin-walled, 12–13 × 5–6.5 µm, brown cells, 87–102 µm thick at base composed of elongate, thin-walled, 4–6 µm diam, hyaline cells. *Pseudoparaphyses* trabeculate, 1–1.5 µm wide, septate, branched and anastomosed. *Asci* bitunicate, cylindrical, 100–118 × 7–9 µm ($\overline{x}$ = 109.5 × 7.8 µm, n = 11), with a short stipe (3.5–10 µm long, $\overline{x}$ = 7 µm, n = 11). *Ascospores* fusiform, 13–21 × 5–6 µm ($\overline{x}$ = 16.5 × 5.6 µm, n = 50), l/w 2.2–4.2 ($\overline{x}$ = 3.0, n = 50), 3-septate, with a primary septum nearly median (0.42–0.57, $\overline{x}$ = 0.50, n = 50) and constricted, smooth, without sheath. Asexual morph: *Conidiomata* pseudopycnidial, globose to cylindrical, sometimes deformed, septate, confluent, multiloculate, scattered, semi-immersed, black, up to 190 µm high, 110–250 µm diam. *Ostiolar neck* mainly single, occasionally two, non-papillate. *Peridium* 20–25 µm wide, composed of 7.5–11.5 × 5–7 µm, rectangular, brown cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, 6–10.5 × 3–4.5 µm, cylindrical, hyaline, smooth. *Conidia* cylindrical with rounded ends, 2–4 × 1–2 µm ($\overline{x}$ = 3 × 1.6 µm, n = 50), l/w 1.1–2.6 ($\overline{x}$ = 1.9, n = 50), hyaline, smooth, aseptate, guttulate when young.

Culture characteristics: Colonies on PDA attaining 26–31 mm diam within 21 d, velvety, wet, olivaceous black, smoke grey at margin; reverse olivaceous black at centre (Fig. 8F); asexual morph formed.

Specimen examined: **Japan**, Iwate, Hachimantai, Yakeyama, near Goshogake spa, on leaf bud of *Rhododendron brachycarpum*, 9 Jul. 2008, Y. Harada, KT 2520 (HHUF 30554; culture CBS 142901).

Notes: The ascospore size in the material mentioned above is identical to that of *A. rhododendri* reported by Jaklitsch &

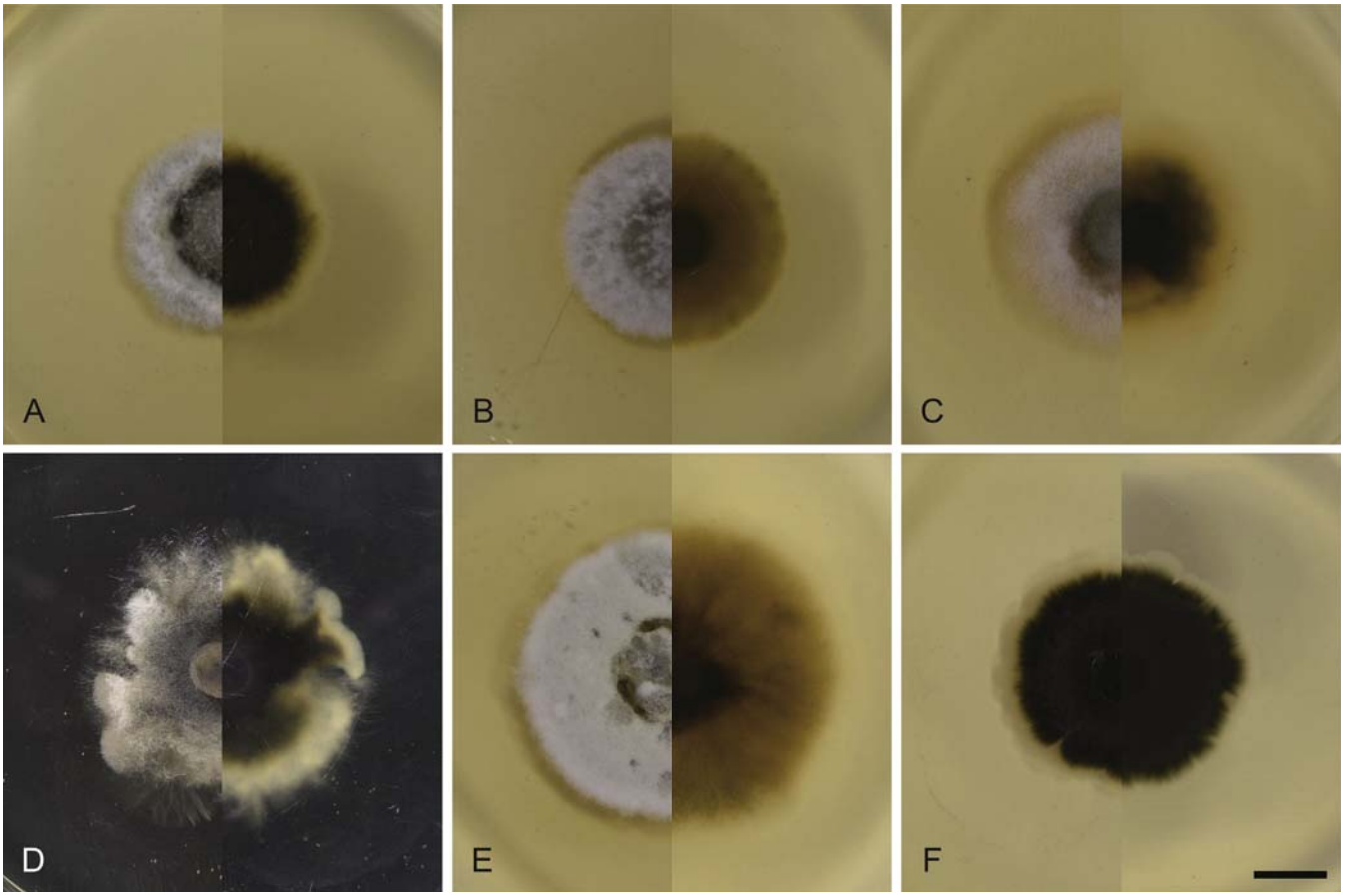

Fig. 8. Colony characters of *Melanomma* spp. and *Pseudodidymellaceae* spp. used in this study on PDA within 3 wk at 20 °C in the dark (left: upper, right: reverse). **A.** *Melanomma japonicum* (CBS 142905 = JCM 13124 = MAFF 239634, ex-holotype culture). **B.** *Me. pulvis-pyrius* (CBS 142908). **C.** *Mycodidymella aesculi* (CBS 142914, ex-holotype culture). **D.** *Pseudodidymella fagi* (MAFF 245740, ex-holotype culture of *Pycnopleiospora fagi*). **E.** *Pseudod. minima* (CBS 142921 = MAFF 246249, ex-holotype culture). **F.** *Alpinaria rhododendri* (CBS 142901). Scale bar: A–F = 1 cm

Voglmayr (2017), who designated the epitype of this species. The ITS, *tef1* and *rpb2* sequences from our material are completely identical to those from the ex-epitype strain of this species (CBS 141994). This species has been reported from twigs or buds of *Rhododendron* spp. in the Asia (*R. chrysanthum*; Müller 1959), Europe (*R. ferrugineum* and *R. hirsutum*; Jaklitsch & Voglmayr 2017), and North America (*Rhododendron* sp.; Mugambi & Huhndorf 2009). In addition, we collected this species on *R. brachycarpum* from the subalpine zone in Japan. *Alpinaria rhododendri* appears to be a relatively common species in the subalpine to alpine zone worldwide.

Alpinaria was recently established to accommodate a single species *A. rhododendri*, which was transferred from *Melanomma* because this species is phylogenetically distinct from the type species of *Melanomma*, and possesses ascomata with a roughened surface view of *textura prismatica* and *textura angularis* (Jaklitsch & Voglmayr 2017). Furthermore, they treated the genus as a member of *Melanommataceae* (Jaklitsch & Voglmayr 2017). Although no asexual morph was reported for this species (Müller 1959, Mugambi & Huhndorf 2009, Jaklitsch & Voglmayr 2017), we newly observed its asexual morph in culture (Fig. 7L–S). As a result of our observation of the asexual morph, as well as the sexual morph, we clarified that this species has atypical features for *Melanommataceae*; its ascomata are composed of hyaline cells at the base, and are pseudopycnidial. Confluent conidiomata are not found in sexual/asexual morphs of *Melanommataceae*. In our phylogenetic tree, the genus placement is confirmed outside *Melanommataceae sensu stricto* (Fig. 1). Therefore, we treat *Alpinaria* as *incertae sedis* in *Pleosporales* in this study; additional taxa related to this genus will be needed to resolve its familial placement.

DISCUSSION

Re-circumscription of *Melanommataceae sensu stricto*

Melanommataceae has been extensively studied in recent years based on phylogenetic evidence (Mugambi & Huhndorf 2009, Schoch *et al.* 2009, Wijayawardene *et al.* 2012, 2014, Butin *et al.* 2013, de Gruyter *et al.* 2013, Su *et al.* 2015, Tian *et al.* 2015, Li *et al.* 2016, Gross *et al.* 2017, Jaklitsch & Voglmayr 2017). The characters emphasised for members of this family include a carbonaceous peridium of ascomata and trabecular pseudoparaphyses. These species are known saprobes on decaying plant material, or, rarely, as plant pathogens. The familial concept of *Melanommataceae* was revised and expanded after in a study by Mugambi & Huhndorf (2009), who applied a molecular approach. A recent monograph of *Melanommataceae* was based on morphological and multi-gene phylogenetic data (Tian *et al.* 2015). Although monophyly of *Melanommataceae* was confirmed in previous studies, statistical support for *Melanommataceae sensu lato* was lacking (Mugambi & Huhndorf

2009, Schoch *et al.* 2009, Tian *et al.* 2015). Additionally, previous authors did not examine the asexual morphs, although various asexual morphs, such as those with mononematous, synnematous, and pycnidial conidiomata, are known to occur in this family. Two of the most striking genera are *Petrakia* and *Xenostigmina*, which have mycopappus-like propagules as asexual morphs, and were reported to be foliicolous necrotrophs (Funk 1986, Funk & Dorworth 1988, Crous 1998, Crous *et al.* 2009, Butin *et al.* 2013), whereas species of *Melanomma*, the type genus of this family, have aposphaeria-like pycnidial asexual morphs and are known to be saprobes on twigs of various plant hosts (Chesters 1938, Romero 1998, Zhang *et al.* 2008). Our multi-gene phylogenetic analyses of this family clearly showed the poly- and paraphyletic nature of *Melanommataceae sensu lato* (Fig. 1), and morphological observations of sexual and asexual morphs led to the conclusion that *Melanommataceae* should be restricted to the type genus *Melanomma*. In addition, four genera with mycopappus-like propagules in their asexual morphs (*Mycodidymella*, *Petrakia*, *Pseudodidymella*, and *Xenostigmina*) are separated from *Melanommataceae sensu stricto*, and we thus establish a new family, *Pseudodidymellaceae*, to accommodate these genera.

Relationships among genera in *Pseudodidymellaceae*

Mycodidymella and *Xenostigmina* are retained as natural genera in the present study. Butin *et al.* (2013) found that the sexual morph of *Mycodidymella* is similar to that of *Petrakia*, and thus recognised *Petrakia* in a broad sense and included *Mycodidymella* as a synonym. This treatment was supported by a later study (Li *et al.* 2016). Gross *et al.* (2017) showed these three genera are closely related based on an ITS phylogeny, but no taxonomic conclusions about their generic validities were made. Recently, Jaklitsch & Voglmayr (2017) proposed that *Mycodidymella* and *Xenostigmina* are synonyms of *Petrakia*. They considered that phylogenetic relatedness of *Xenostigmina* and *Petrakia*, and morphological similarity of the sexual morph and mycopappus-like propagules among these genera are strong arguments for synonymising them (Jaklitsch & Voglmayr 2017). Our phylogenetic analysis including *Mycodidymella* as well as *Xenostigmina* and *Petrakia* clarified that their monophyletic status was not well supported in any analyses (below 60 % ML BP/ 0.95 Bayesian PP, Fig. 1). Their sexual morphs are superficially similar as indicated by Jaklitsch & Voglmayr (2017), but *Mycodidymella* has deeper and more well-developed ascomata (up to 210 µm high) than those of *Petrakia* (up to 150 µm high) and *Xenostigmina* (up to 100 µm high). Additionally, their morphological characters of their synasexual morphs are also different; hyaline, up to 20 µm thick sporodochia, holoblastic conidiogenous cells, and sigmoid, multiseptate, thin-walled, hyaline conidia (*Mycodidymella*; this study); brown, up to 30 µm thick sporodochia, annellidic conidiogenous cells, and globose to ovoid, dictyosporus, thick-walled, brown conidia with cellular appendages (*Petrakia*; Butin *et al.* 2013, Li *et al.* 2016); and brown to black, up to 45 µm high sporodochia, holoblastic conidiogenous cells, and clavate with a short rostrum, dictyosporus, thick-walled, brown conidia (*Xenostigmina*; Funk 1986, Crous 1998). Therefore, we treat these genera as distinct based on morphological differences of sexual and synasexual morphs.

Synasexual morphs of these three genera are produced after leaves fall in late autumn (Funk & Dorworth 1988, Wei *et al.* 1997, Butin *et al.* 2013, Gross *et al.* 2017). Conidia of synasexual morphs were not observed on overwintered leaves for *Petrakia* and *Mycodidymella*, and their function in the disease cycle during the winter season has not been clarified (Wei *et al.* 1997, Butin *et al.* 2013). No synasexual morph is known from *Pseudodidymella*, despite their close relationship to the other three genera. Further studies on the *Pseudodidymella* synasexual morph are needed to elucidate the whole life cycle of this genus and produce robust taxonomic classifications for *Pseudodidymellaceae*.

Form and function of mycopappus-like propagules

The genus *Mycopappus* was established based on its type species *Mycop. alni* (on *Alnus*, *Betula*, *Crataegus*, and *Pyrus*; Redhead & White 1985, Braun *et al.* 2000, Takahashi *et al.* 2006), which produces epiphyllous, multicellular propagules in its asexual morph (Redhead & White 1985). Later, three species were assigned to in this genus: *Mycop. aceris* (on *Acer macrophyllum*; Redhead & White 1985), *Mycop. aesculi* (on *Aesculus turbinata*; Wei *et al.* 1998), and *Mycop. quercus* (on *Quercus acutissima*; Suto & Kawai 2000). Two species, *Mycop. alni* and *Mycop. quercus*, produce microconidia and sclerotia in culture (Redhead & White 1985, Suto & Kawai 2000), and the sexual morph of the latter species is characterised by stipitate apothecia and inoperculate asci (Suto & Suyama 2005). *Mycopappus alni* was suggested to be a member of *Sclerotiniaceae* (*Helotiales*, *Leotiomycetes*) based on its sclerotial morph and phylogenetic analyses using ITS sequences (Takahashi *et al.* 2006). The two other species, *Mycop. aceris* and *Mycop. aesculi*, were excluded from *Mycopappus sensu stricto*, because their sexual morphs belong to the dothideomycetous taxa, namely *Xenostigmina aceris* (Funk & Dorworth 1988, Crous 1998, Crous *et al.* 2009) and *Mycodidymella aesculi* (Wei *et al.* 1998), respectively. Morphological differences in mycopappus-like propagules among these lineages were indicated in a previous study (Suto & Kawai 2000). The main bodies of sclerotiniaceous species (*Mycop. alni* and *Mycop. quercus*) are composed of multi-septate claviform cells (Suto & Kawai 2000, Suto & Suyama 2005, Takahashi *et al.* 2006), whereas those of dothideomycetous species (*Mycod. aesculi* and *X. aceris*) are composed of aseptate globose cells (Redhead & White 1985, Wei *et al.* 1998). The morphological resemblance of mycopappus-like propagules between leotiomycetous and dothideomycetous lineages appears to be the result of convergent evolution due to similar ecological function, such as rain-splash dispersal across the leaf surface. A similar situation was reported in two phylogenetically distinct genera, *Spiroplana* (*Dothideomycetes*) and *Spirosphaera* (*Leotiomycetes*), which have spirally coiled, buoyant conidia that resulted in adaptation to water dispersal in terrestrial or aero-aquatic environments (Voglmayr *et al.* 2011).

The mycopappus-like propagules of *Pseudodidymellaceae* may contribute to secondary infection of host leaves with high inoculum potential. Wei *et al.* (1998) suggested that this morph plays an important role in disease development. Morphological variation of the propagules at the generic level was observed, but the taxonomic significance was not been examined in several studies (Redhead & White 1985, Wei *et al.* 1998, Butin *et al.*

2013, Gross *et al.* 2017, Jaklitsch & Voglmayr 2017). Our observations revealed that morphological features of propagules differed between *Mycodidymella*, *Petrakia*, and *Xenostigmina* (with few appendages), and *Pseudodidymella* (with numerous appendages). The hyphal appendages of *Pseudodidymella* could enhance fungal encounters with *Fagus* leaves that have conspicuous wax ornamentation (Denk 2003), as is the case of asexual fungi with conidial appendages (Nag Raj 1993, Hashimoto *et al.* 2015a). The morphological variation of propagules is also observed at the species level: *Pseudod. fagi* on *F. crenata* has a larger main body with longer appendages (Fig. 5W and X), and *Pseudod. minima* on *F. japonica* has a smaller main body with shorter appendages (Fig. 6G and H). These morphological variations of their propagules may be correlated with presence (in *F. japonica*) or absence (in *F. crenata*) of leaf papillae (Denk 2003) as a result of adaptation to the host surface.

A phoma-like morph is known in the life cycle in *Petrakia* (Butin *et al.* 2013). This morph is also observed in *Mycodidymella* and *Pseudodidymella* after fructification of mycopappus-like propagules (Fig. 4J–R and 5J–R). The conidial-like structures of this morph appear to be spermatia, because they do not germinate in water agar or glucose agar.

Speciation through host switching and host jumping

Plant pathogens frequently infect phylogenetically related hosts (Jackson 2004, Giraud *et al.* 2008, Walker *et al.* 2010, 2012, Mejía *et al.* 2011). The genus *Pseudodidymella* was originally established as a monotypic genus composed of the type species *Pseudod. fagi*, which was reported to be a pathogen of *F. crenata* (*Fagaceae*, *Fagales*) in Japan (Wei *et al.* 1997). Most recently, this species was re-discovered and reported to be a disease agent of *F. sylvatica* in Germany and Switzerland (Gross *et al.* 2017). A new species of this genus, *Pseudod. minima*, occurs on *F. japonica*. Members of *Pseudodidymella* appear to be host-specific on *Fagus*. Close host/fungus associations and coevolution were reported in members of *Gnomoniaceae*, *Phaeosphaeriaceae*, and *Sclerotiniaceae* (Jackson 2004, Walker *et al.* 2012, Ertz *et al.* 2015). Although ITS sequences of *Pseudod. fagi* were 100 % identical among isolates from *F. crenata* and *F. sylvatica* (Gross *et al.* 2017), those of *Pseudod. minima* differed from *Pseudod. fagi* based on six nucleotide positions and one gap in ITS sequences (this study). This result was compatible with host phylogeny: *F. crenata* and *F. sylvatica* are closely related to each other, but *F. japonica* is phylogenetically distantly related to the other species (Denk *et al.* 2005).

Alternatively, three genera, *Mycodidymella*, *Petrakia*, and *Xenostigmina*, are host-specific for *Acer* spp. or *Aesculus* (*Sapindaceae*, *Sapindales*), which are distantly related to *Fagales* (APG IV 2016). It has been recognised that several plant pathogens switch to unrelated host plants (Reddy *et al.* 1998, Takamatsu *et al.* 2000, Jackson 2004). Gross *et al.* (2017) also found that host switching occurred in members of *Pseudodidymellaceae*, and members of this family evolutionally diversified by host switching. Similar evolutionary processes that led to speciation through host jumping are known from *Clavicipitaceae*, which includes plant pathogens, insect pathogens, and mycoparasites (Kepler *et al.* 2012).

Future studies

The asexual genus *Seifertia* on *Rhododendron* spp. is characterised by synnematous conidiomata with cladosporium-like conidia (Li *et al.* 2016). Phylogenetic relatedness of this genus to members of *Pseudodidymellaceae* was suggested (Li *et al.* 2016, Gross *et al.* 2017). However, we prefer to not include this species in *Pseudodidymellaceae* and place it *incertae sedis*, because of the lack of mycopappus-like propagules in the life cycle. This genus might represent a new family; however, analysis of its sexual morph and further taxa related to this genus are needed to determine its familial placement. Another genus, *Alpinaria*, was originally established to accommodate the type species, *A. rhododendri*, which was segregated from *Melanomma* (Jaklitsch & Voglmayr 2017). They regarded the genus as a member of *Melanommataceae*, based on phylogenetic analyses (Jaklitsch & Voglmayr 2017). In the present study, we newly observed the asexual morph of *Alpinaria*, which had not been reported in previous studies (Müller 1959, Holm 1968, Mugambi & Huhndorf 2009, Jaklitsch & Voglmayr 2017). According to our phylogenetic analyses and morphological observations, this species is distantly related to *Melanommataceae sensu stricto* (Fig. 1) and has atypical features for *Melanommataceae*, such as hyaline cells at the base of ascomata and pseudopycnidial conidiomata. Several melanomma-like fungi that possess well-developed carbonaceous ascomata may have evolved several times within *Pleosporales*, such as in *Cyclothyriellaceae*, *Ohleriaceae*, *Nigrogranaceae*, *Teichosporaceae*, *Thyridariaceae* (Jaklitsch & Voglmayr 2016, Jaklitsch *et al.* 2016b). It seems that familial circumscriptions based merely on sexual morph characters is insufficient to distinguish the members of *Melanommataceae sensu lato*.

The present study revealed unexpected diversity of *Melanommataceae sensu* Tian *et al.* (2015). Our approaches, which combined morphological features of both sexual and asexual morphs with molecular phylogenetic analyses, enabled a re-circumscription of *Melanommataceae sensu stricto* and the establishment of *Pseudodidymellaceae*. To build a comprehensive taxonomic framework, further discovery of more specimens along with additional morphological and molecular data would help elucidate other unresolved lineages of *Melanommataceae sensu lato*.

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