

Resolving the polyphyletic nature of *Pyricularia* (*Pyriculariaceae*)

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Abstract: Species of *Pyricularia* (magnaporthe-like sexual morphs) are responsible for major diseases on grasses. *Pyricularia oryzae* (sexual morph *Magnaporthe oryzae*) is responsible for the major disease of rice called rice blast disease, and foliar diseases of wheat and millet, while *Pyricularia grisea* (sexual morph *Magnaporthe grisea*) is responsible for foliar diseases of *Digitaria*. *Magnaporthe salvinii*, *M. poae* and *M. rhizophila* produce asexual spores that differ from those of *Pyricularia sensu stricto* that has pyriform, 2-septate conidia produced on conidiophores with sympodial proliferation. *Magnaporthe salvinii* was recently allocated to *Nakataea*, while *M. poae* and *M. rhizophila* were placed in *Magnaporthiopsis*. To clarify the taxonomic relationships among species that are magnaporthe- or pyricularia-like in morphology, we analysed phylogenetic relationships among isolates representing a wide range of host plants by using partial DNA sequences of multiple genes such as LSU, ITS, RPB1, actin and calmodulin. Species of *Pyricularia* s. str. belong to a monophyletic clade that includes all *P. oryzae*/*P. grisea* isolates tested, defining the *Pyriculariaceae*, which is sister to the *Ophiocerales*, representing two novel families. These clades are clearly distinct from species belonging to the *Gaeumannomyces pro parte/Magnaporthiopsis/Nakataea* generic complex that are monophyletic and define the *Magnaporthaceae*. A few magnaporthe- and pyricularia-like species are unrelated to *Magnaporthaceae* and *Pyriculariaceae*. *Pyricularia oryzae*/*P. grisea* isolates cluster into two related clades. Host plants such as *Eleusine*, *Oryza*, *Setaria* or *Triticum* were exclusively infected by isolates from *P. oryzae*, while some host plant such as *Cenchrus*, *Echinochloa*, *Lolium*, *Pennisetum* or *Zingiber* were infected by different *Pyricularia* species. This demonstrates that host range cannot be used as taxonomic criterion without extensive pathotyping. Our results also show that the typical pyriform, 2-septate conidium morphology of *P. grisea*/*P. oryzae* is restricted to *Pyricularia* and *Neopyricularia*, while most other genera have obclavate to more ellipsoid 2-septate conidia. Some related genera (*Deightoniella*, *Macgarvieomyces*) have evolved 1-septate conidia. Therefore, conidium morphology cannot be used as taxonomic criterion at generic level without phylogenetic data. We also identified 10 novel genera, and seven novel species. A re-evaluation of generic and species concepts within *Pyriculariaceae* is presented, and novelties are proposed based on morphological and phylogenetic data.

Key words: *Magnaporthaceae*, *Magnaporthe*, *Pyricularia*, *Pyriculariaceae*, Phylogeny, Systematics.

Taxonomic novelties: New families: *Ophiocerales* Klaubauf, Lebrun & Crous, *Pyriculariaceae* Klaubauf, Lebrun & Crous; **New genera:** *Bambusicularia* Klaubauf, Lebrun & Crous, *Barretomyces* Klaubauf, Lebrun & Crous, *Bussabanomyces* Klaubauf, Lebrun & Crous, *Kohlmeyeriopsis* Klaubauf, Lebrun & Crous, *Macgarvieomyces* Klaubauf, Lebrun & Crous, *Neopyricularia* Klaubauf, Lebrun & Crous, *Proxipyricularia* Klaubauf, Lebrun & Crous, *Pseudopyricularia* Klaubauf, Lebrun & Crous, *Slopeiomyces* Klaubauf, Lebrun & Crous, *Xenopyricularia* Klaubauf, Lebrun & Crous; **New species:** *Bambusicularia brunnea* Klaubauf, Lebrun & Crous, *Pseudopyricularia cyperii* Klaubauf, Lebrun & Crous, *Pseudopyricularia kyllingae* Klaubauf, Lebrun & Crous, *Pyricularia ctenantheicola* Klaubauf, Lebrun & Crous, *Pyricularia penniseticola* Klaubauf, Lebrun & Crous, *Pyricularia pennisetigena* Klaubauf, Lebrun & Crous, *Pyricularia zingibericola* Klaubauf, Lebrun & Crous; **New combinations:** *Barretomyces calatheae* (D.J. Soares, F.B. Rocha & R.W. Barreto) Klaubauf, Lebrun & Crous, *Bussabanomyces longisporus* (Bussaban) Klaubauf, Lebrun & Crous, *Kohlmeyeriopsis medullaris* (Kohlm., Volk.-Kohlm. & O.E. Erikss.) Klaubauf, Lebrun & Crous, *Macgarvieomyces borealis* (de Hoog & Oorschot) Klaubauf, Lebrun & Crous, *Macgarvieomyces juncicola* (MacGarvie) Klaubauf, Lebrun & Crous, *Magnaporthiopsis maydis* (Samra, Sabet & Hing.) Klaubauf, Lebrun & Crous, *Neopyricularia commelinicola* (M.J. Park & H.D. Shin) Klaubauf, Lebrun & Crous, *Proxipyricularia zingiberis* (Y. Nisik.) Klaubauf, Lebrun & Crous, *Pseudopyricularia higginsii* (Luttr.) Klaubauf, Lebrun & Crous, *Xenopyricularia zizaniicola* (Hashioka) Klaubauf, Lebrun & Crous; **Neotypification (basonym):** *Pyricularia zizaniicola* Hashioka.

Published online 25 October 2014; <http://dx.doi.org/10.1016/j.simyco.2014.09.004>. Hard copy: September 2014.

INTRODUCTION

The *Magnaporthaceae* contains several genera that are important plant pathogens of *Poaceae*, most notably *Magnaporthe* (now *Nakataea sensu Luo & Zhang 2013*), *Pyricularia*, and *Gaeumannomyces*. The family was originally described with six genera and 20 species, and presently includes 13 genera and more than 100 species (Cannon 1994, Bussaban *et al.* 2005, Thongkantha *et al.* 2009, Zhang *et al.* 2011). The family also includes genera (*Ophioceras*, *Pseudohalonectria*, *Ceratospheeria*) that occur in aquatic habitats, or on dead plant materials such as wood (Shearer *et al.* 1999, Réblová 2006, Huhndorf *et al.* 2008, Thongkantha *et al.* 2009). The *Magnaporthaceae* is currently defined by having perithecial ascomata immersed in

host tissue, frequently with long necks, and cylindrical asci that stain positive in Meltzer's reagent. Ascospores are highly variable in their morphology. Genera with filiform ascospores (*Gaeumannomyces*) tend to have simple, pigmented conidiophores with flared collarettes, and curved, aseptate conidia (harpophora-like). Genera with fusiform ascospores tend to have pigmented median cells (*Nakataea* = *Magnaporthe*), simple, pigmented conidiophores, or septate, pyriform to obclavate, pigmented conidia (*Pyricularia* and related genera).

The present study does not aim to revise all genera in *Magnaporthales* (Hernandez-Restrepo *et al.* unpubl data), but focuses primarily on species that are pyricularia-like in morphology. The genus *Pyricularia* (in reference to the pyriform shape of its conidia; Bussaban *et al.* 2005, Murata *et al.* 2014)

includes species that are pathogenic on a wide range of monocot plants. Of these, *Pyricularia oryzae* (sexual morph *Magnaporthe oryzae*), the causal agent of the rice blast disease of rice, is one of the most widely distributed diseases of this crop, and is highly destructive leading to up to 30 % yield loss worldwide (Skamnioti & Gurr 2009). *Pyricularia oryzae* isolates from rice are mostly host-specific and only infect few host plants beside rice (barley and *Lolium*) (Ou 1985, Kato et al. 2000, Couch et al. 2005, Tosa & Chuma 2014). *Pyricularia oryzae* isolates from other host plants such as *Eleusine*, *Setaria* and *Triticum* are also host-specific, and unable to infect rice (Kato et al. 2000, Couch et al. 2005, Murata et al. 2014, Tosa & Chuma 2014). A close relative species of *P. oryzae* is *Pyricularia grisea*, which is indistinguishable in conidium, perithecium and ascopore morphology. *Pyricularia grisea* isolates from *Digitaria* were shown to form a distinct clade by phylogenetic analysis (Kato et al. 2000, Couch & Kohn 2002, Hirata et al. 2007, Faivre-Rampant et al. 2008, Choi et al. 2013) and infect crabgrass (*Digitaria*), but not other hosts (Mackill & Bonham 1986, Kato et al. 2000, Tsurushima et al. 2005, Chen et al. 2006, Faivre-Rampant et al. 2008, Choi et al. 2013). However, some *P. oryzae* isolates from rice and other grasses and some *P. grisea* isolates from crabgrass showing cross-infectivity on crabgrass and rice, respectively have been described (Choi et al. 2013). Sexual morphs were reported for *P. grisea* and *P. oryzae*. However, the genus *Pyricularia* comprises several other species for which the sexual morph has not yet been discovered. Such *Pyricularia* species include *P. higginsii* pathogenic on *Cyperus* (Luttrell 1954, Hashioka 1973), *P. zingiberi* pathogenic on *Zingiber* (Kotani & Kurata 1992), *P. zizaniaecola* pathogenic on *Zizania* (Hashioka 1973) and *P. commelinicola* on *Commelina* (Park & Shin 2009). Other notable pathogens from the *Magnaporthaceae* include *Nakataea oryzae*, *Gaeumannomyces graminis*, *Magnaportheopsis poae* and *M. rhizophila*.

The aims of the present study were to determine the phylogenetic relationships among species of *Pyricularia* compared to *P. oryzae*/*P. grisea*, as well as those taxa now accommodated in *Magnaportheopsis* and *Nakataea*, using multilocus sequence analysis. This study allowed defining two novel families, *Ophioceraeae* and *Pyriculariaceae*, as well as novel genera and species.

MATERIALS AND METHODS

Isolates

A global collection of 153 isolates was included in this study (Table 1). Cultures for morphological observation were inoculated in a three-point position onto the following agar media: Cornmeal agar (CMA), oatmeal agar (OA), 2 % potato dextrose agar (PDA) and 2 % malt extract agar (Oxoid) (MEA). All media were prepared as described previously (Crous et al. 2009, Samson et al. 2010). Representative isolates were deposited in the CBS-KNAW Fungal Biodiversity Centre (CBS), Utrecht, The Netherlands.

DNA extraction, amplification and sequencing

Fungal cultures were grown on a cellophane disc on MEA to easily scrape off mycelium. Genomic DNA was extracted using

the UltraClean Microbial DNA isolation kit (MoBio Laboratories, USA), according to the manufacturer's instructions. Parts of the following loci were amplified and sequenced: RPB1, partial RNA polymerase II largest subunit gene; ITS, internal transcribed spacer regions and intervening 5.8S nuclear ribosomal RNA (nrRNA) gene; LSU, partial nrRNA gene large subunit (28S); ACT, partial actin gene and CAL, partial calmodulin gene.

The reactions were performed in 20 μ L mixtures containing 1 μ L of genomic DNA, 2 mM MgCl₂ (Bioline, Germany), 4 μ L 5 \times Colourless GoTaq[®] Flexi Buffer (Promega, USA), 80 μ M dNTPs (Promega), 0.2 μ M of each primer and 0.10 μ L GoTaq[®] Flexi DNA Polymerase (Promega).

The primers V9G (de Hoog & Gerrits van den Ende 1998) and LR5 (Viigalys & Hester 1990) were used to amplify the ITS + LSU region by using the following PCR programme: initial denaturation at 94 °C for 5 min, followed by 35 cycles of 94 °C for 30 s, 52 °C for 30 s, 72 °C for 2 min, and finally an additional 7 min at 72 °C. The primers ACT-512F and ACT-783R were used for actin and CAL-228F and CAL-737R for calmodulin (Carbone & Kohn 1999). The following PCR programme was used for actin/calmodulin: initial denaturation at 94 °C for 5 min, followed by 35 cycles of 95 °C for 15 s, 61/55 °C for 20 s, 72 °C for 40 s, and final extension at 72 °C for 5 min. For amplification of RPB1 the primers RPB1F and RPB1R (see Table 2) were designed for the *Nakataea/Gaeumannomyces* group from unpublished sequence data of eight *P. oryzae* strains and one *P. grisea* strain, as well as public genomes of *P. oryzae* 70-15, *Magnaportheopsis poae* ATCC 64411 and *Gaeumannomyces graminis* var. *tritici* R3111a. The following PCR programme was used: initial denaturation at 94 °C for 5 min, followed by 12 cycles of 94 °C for 30 s, 57–51 °C (decreasing for 0.5° every cycle) for 20 s, 72 °C for 70 s; 25 cycles of 94 °C for 30 s, 51 °C for 20 s, 72 °C for 70 s; and finally an additional 5 min at 72 °C.

Both strands of the PCR fragments were sequenced with the BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, USA) using the primers indicated in Table 2. The products were analysed on an ABI Prism 3730 XL DNA Sequencer (Applied Biosystems). Contigs were assembled by using the forward and reverse sequences with the programme SeqMan from the LaserGene v. 9 package (DNASTAR, USA).

Genomic sequences of *Cryphonectria parasitica* strain EP155, *Gaeumannomyces graminis* var. *tritici* strain R3111a, *P. oryzae* strain 70-15 and *M. poae* strain ATCC 64411 were retrieved from Broad Institute (www.broadinstitute.org); *G. graminis* var. *tritici*, *P. oryzae* and *M. poae*) and JGI Genome Portal (<http://genomeportal.jgi.doe.gov/>; *C. parasitica*) databases (Dean et al. 2005).

Phylogenetic analyses

Megablast searches of the NCBI's GenBank nucleotide database were used to supplement the sequence data generated in this study, especially to populate the overview LSU phylogeny. Sequences were aligned using the online version of MAFFT (<http://mafft.cbrc.jp/alignment/software/>) and the alignments were manually adjusted using MEGA v. 5.2 (Tamura et al. 2011). Analyses were performed with the individual and combined datasets to test the robustness of each included locus. Phylogenetic trees were reconstructed by Bayesian Inference (BI)

Table 1. Collection details and GenBank accession numbers of isolates included in this study (“–” = unknown).

Species	Location	Substrate	Collector	Culture collection no ¹	GenBank Accession no ²				
					ITS	LSU	RPB1	ACT	CAL
<i>Bambusicularia brunnea</i>	Japan: Aichi	<i>Sasa</i> sp.	S. Koizumi	CBS 133599 = MAFF 240225 = INA-B-92-45(Ss-1J) (ex-type)	KM484830	KM484948	KM485043	AB274449	AB274482
	Japan: Aichi	<i>Phyllostachys bambusoides</i>	S. Koizumi	CBS 133600 = MAFF 240226 = INA-B-93-19(Ph-1J)	AB274436	KM484949	KM485044	AB274450	AB274483
<i>Barretomyces calathea</i>	Brazil: Minas Gerais	<i>Calathea longifolia</i>	D.J. Soares	CBMAI 1060 (ex-type)	GU294490	–	–	–	–
	Brazil: Minas Gerais	<i>Calathea longifolia</i>	P.W. Crous	CBS 129274 = CPC 18464	KM484831	KM484950	KM485045	KM485162	KM485231
<i>Buergenerula spartinae</i>	USA	<i>Spartina alterniflora</i> , leaves	R.V. Gessner	ATCC 22848	JX134666	DQ341492	JX134720	–	–
<i>Bussabanyomycus longisporus</i>	Thailand: Chiang Mai	<i>Amomum siamense</i> , leaf endophyte	B. Bussaban	CBS 125232 (ex-type)	KM484832	KM484951	KM485046	–	–
<i>Cryphonectria parasitica</i>	USA: Connecticut	<i>Castanea dentata</i>	N. DePalma	EP155 = ATCC 38755	Genome	Genome	Genome	Genome	Genome
<i>Deightonella roumegueri</i>	Netherlands: Utrecht	<i>Phragmites australis</i> , leaves	W. Quaedvlieg	CBS 128780 = CPC 18916 (ex-type)	JF951153	JF951176	KM485047	KM485163	KM485232
<i>Gaeumannomyces graminis</i> var. <i>avenae</i>	Netherlands: Flevoland	<i>Avena sativa</i> , root	–	CBS 187.65	JX134668	JX134680	JX134722	–	–
	Australia: Western Australia	<i>Avena sativa</i>	–	CBS 870.73 = DAR 20999	KM484833	DQ341495	KM485048	–	–
<i>Gaeumannomyces graminis</i> var. <i>graminis</i>	USA: Arkansas	<i>Oryza sativa</i>	–	CBS 235.32	JX134669	JX134681	KM485049	–	–
	Netherlands: near Barendrecht	<i>Ctenanthe</i> sp., stem base	–	CBS 352.93 = PD 93/290	KM484834	DQ341496	KM485050	–	–
<i>Gaeumannomyces graminis</i> var. <i>tritici</i>	UK: England	<i>Deschampsia caespitosa</i> , dead culm and sheath	M.B. & J.P. Ellis	CBS 387.81	KM484835	KM484952	KM485051	–	–
	Australia: New South Wales	<i>Stenotaphrum secundatum</i>	J. Kuiper	CBS 902.73 = DAR 17502	KM484836	KM484953	KM485052	–	–
	Australia: New South Wales	<i>Pennisetum clandestinum</i>	P. Wong	CBS 903.73 = DAR 23471	KM484837	KM484954	KM485053	–	–
	USA: Florida	<i>Stenotaphrum secundatum</i>	–	M33	JF710374	JF414896	JF710442	–	–
	Netherlands: Flevoland	<i>Hordeum vulgare</i>	–	CBS 186.65	KM484838	KM484955	KM485054	KM485164	–
	Netherlands	–	–	CBS 247.29	KM484839	KM484956	KM485055	–	–
<i>Gaeumannomyces</i> sp.	–	<i>Triticum aestivum</i>	–	CBS 249.29 = IMI 083849	KM484840	KM484957	KM485056	–	–
	Australia: Western Australia	<i>Triticum aestivum</i>	A. Parker	CBS 905.73 = DAR 23140	KM484841	KM484958	KM485057	–	–
	USA: Montana	<i>Triticum</i> sp.	–	M55	JF414850	JF414900	JF710445	–	–
	USA: Washington	<i>Triticum aestivum</i>	–	R3-111a-1	Genome	Genome	Genome	Genome	Genome
	Netherlands: Groningen	Soil in potato field	–	CBS 117.83	KM484842	KM484959	KM485058	–	–
	UK: Wales	<i>Carex rostrata</i>	M.B. Ellis	CBS 388.81	KM484843	KM484960	KM485059	–	–

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Table 1. (Continued)

Species	Location	Substrate	Collector	Culture collection no ¹	GenBank Accession no ²				
					ITS	LSU	RPB1	ACT	CAL
<i>Harpophora radiculicola</i>	South Africa	<i>Zea mays</i>	–	CBS 149.85 = PREM 45754 (isotype of <i>Phialophora zeicola</i>)	KM484844	KM484961	KM485060	KM485165	KM485233
	Canada: Ontario	<i>Zea mays</i> , root	R.F. Cain	CBS 296.53 = MUCL 28970 = TRTC 23660 (isotype of <i>Phialophora radiculicola</i>)	KM484845	KM484962	KM485061	–	KM485234
	South Africa	<i>Zea mays</i> , root	–	CPC 18682 = Z 383 Y	KM484846	KM484963	KM485062	KM485166	KM485235
	South Africa	<i>Zea mays</i> , root	–	CPC 18683 = Z 390 G	KM484847	KM484964	KM485063	KM485167	KM485236
	South Africa	<i>Zea mays</i> , root	–	CPC 18685 = Z 397 L	KM484848	KM484965	KM485064	KM485168	KM485237
	South Africa	<i>Zea mays</i> , root	–	CPC 18689 = Z 426 AJ	KM484849	KM484966	KM485065	KM485169	KM485238
<i>Harpophora</i> sp.	UK: England	<i>Zea mays</i> , root	–	CBS 350.77 = ATCC 28234 = IMI 187786	KM484850	KM484967	KM485066	–	–
	Germany	<i>Triticum aestivum</i> , seedling	–	CBS 541.86	KM484851	DQ341497	KM485067	–	–
<i>Kohlmeyeriopsis medullaris</i>	USA: North Carolina	<i>Juncus roemerianus</i>	–	CBS 117849 = JK5528S	KM484852	KM484968	KM485068	–	–
	USA: North Carolina	<i>Juncus roemerianus</i>	–	CBS 118210 = JK5522N = ATCC MYA-3560	KM484853	KM484969	KM485069	–	–
<i>Macgarvieomyces borealis</i>	UK: Scotland	<i>Juncus effusus</i> , leaf spots	G.D. MacGarvie	CBS 461.65 (ex-type)	KM484854	DQ341511	KM485070	KM485170	KM485239
<i>Macgarvieomyces juncicola</i>	Netherlands	<i>Juncus effusus</i> , stem base	G.S. de Hoog	CBS 610.82	KM484855	KM484970	KM485071	KM485171	KM485240
<i>Magnaportha griffinii</i>	Australia: Queensland	<i>Cynodon dactylon</i> × <i>Cynodon transvaalensis</i>	A.M. Stirling	TS99	JQ390311	–	–	–	–
	Australia: South Australia	<i>Cynodon dactylon</i> × <i>Cynodon transvaalensis</i>	P. Toy	TY2	JQ390312	–	–	–	–
<i>Magnaporthiopsis incrustans</i>	–	–	–	M35	JF414843	JF414892	JF710437	–	–
<i>Magnaporthiopsis maydis</i>	USA: Kansas	<i>Zoysia matrella</i>	–	M51	JF414846	JF414895	JF710440	–	–
	Egypt	<i>Zea mays</i>	H.A. Elshafey	CBS 662.82A	KM484856	KM484971	KM485072	–	–
	India: Rajasthan, Jaipur	<i>Zea mays</i>	B.S. Siradhana	CBS 663.82A	KM484857	KM484972	KM485073	–	–
	India: Rajasthan, Jaipur	<i>Zea mays</i>	B.S. Siradhana	CBS 663.82B	KM484858	KM484973	KM485074	–	–
	India: Bihar, Messina	<i>Zea mays</i> hybrid "Ganga Safed 2"	M.M. Payak	CBS 664.82	KM484859	KM484974	KM485075	–	–
<i>Magnaporthiopsis poae</i>	USA	<i>Triticum aestivum</i>	P.J. Landschoot	ATCC 64411	Genome	Genome	Genome	Genome	Genome
	USA: New Jersey	<i>Poa pratensis</i>	–	M47	JF414836	JF414885	JF710433	–	–
<i>Magnaporthiopsis rhizophila</i>	–	<i>Poa pratensis</i>	–	M23	JF414834	JF414846	JF710432	–	–

Table 1. (Continued)

Species	Location	Substrate	Collector	Culture collection no ¹	GenBank Accession no ²				
					ITS	LSU	RPB1	ACT	CAL
<i>Nakataea oryzae</i>	Japan	<i>Oryza sativa</i>	–	ATCC 44754 = M21 = Roku-2	JF414838	JF414887	JF710441	–	–
	Italy	–	–	CBS 202.47	KM484860	KM484975	KM485076	–	–
	Italy	<i>Oryza sativa</i>	–	CBS 243.76	KM484861	DQ341498	KM485077	–	–
	Burma	<i>Oryza sativa</i> , straw	–	CBS 252.34	KM484862	KM484976	KM485078	–	–
	–	–	–	CBS 253.34	KM484863	KM484977	KM485079	–	–
	Japan: Takada	<i>Oryza sativa</i> , stem	–	CBS 288.52	KM484864	KM484978	KM485080	–	–
	USA: California	<i>Oryza sativa</i>	R.K. Webster	CBS 726.74	KM484865	KM484979	KM485081	–	–
	USA: California	<i>Oryza sativa</i>	R.K. Webster	CBS 727.74	KM484866	KM484980	KM485082	–	–
	<i>Nakataea</i> sp.	USA: Arkansas	<i>Oryza sativa</i>	–	CBS 332.53	KM484867	KM484981	KM485083	–
<i>Neopyricularia commelinicola</i>	South Korea: Hongcheon	<i>Commelina communis</i> , leaves	H.D. Shin & M.J. Park	CBS 128303 = KACC 44637	KM484868	KM484982	KM485084	KM485172	KM485241
	South Korea: Pocheon	<i>Commelina communis</i>	M.J. Park	CBS 128306 = KACC 43869	FJ850123	KM484983	KM485085	KM485173	KM485242
	South Korea: Hongcheon	<i>Commelina communis</i>	H.D. Shin & M.J. Park	CBS 128307 = KACC 44083	FJ850125	KM484984	KM485086	KM485174	KM485243
	South Korea: Hongcheon	<i>Commelina communis</i> , leaves	H.D. Shin & M.J. Park	CBS 128308 = KACC 43081 (ex-type)	FJ850122	KM484985	KM485087	KM485175	–
<i>Omnidemptus affinis</i>	Australia: Queensland	<i>Panicum effusum</i> var. <i>effusum</i> , grass leaves	V.P. Cooper	ATCC 200212 (ex-type)	JX134674	JX134686	JX134728	–	–
<i>Ophioceras commune</i>	China: Yunnan	Rotten wood	–	M91	JX134675	JX134687	JX134729	–	–
	China: Yunnan	Rotten wood	–	M92	JX134676	JX134688	JX134730	–	–
<i>Ophioceras dolichostomum</i>	Hong Kong	Wood	–	CBS 114926 = HKUCC 3936 = KM 8	JX134677	JX134689	JX134731	–	–
<i>Ophioceras leptosporum</i>	UK: England	Dead stem of dicot plant (probably <i>Urtica dioica</i>)	–	CBS 894.70 = ATCC 24161 = HME 2955 (ex-type of <i>Gaeumannomyces leptosporus</i>)	JX134678	JX134690	JX134732	–	–
<i>Proxypyricularia zingiberis</i>	Japan: Hyogo	<i>Zingiber mioga</i>	I. Chuma	CBS 132195 = MAFF 240224 = HYZIM201-1-1-1 (Z-4J)	KM484869	KM484986	KM485088	AB274448	KM485244
	Japan: Hyogo	<i>Zingiber mioga</i>	I. Chuma	CBS 132196 = MAFF 240223 = HYZIM202-1-2 (Z-3J)	KM484870	–	KM485089	AB274447	KM485245

(continued on next page)

Table 1. (Continued)

Species	Location	Substrate	Collector	Culture collection no ¹	GenBank Accession no ²				
					ITS	LSU	RPB1	ACT	CAL
<i>Proxipyrularia zingiberis</i>	Japan: Hyogo	<i>Zingiber mioga</i>	M. Ogawa	CBS 132355 = MAFF 240221 = HYZIM101-1-1-1 (Z-1J)	AB274433	KM484987	KM485090	KM485176	AB274481
	Japan: Hyogo	<i>Zingiber mioga</i>	H. Kato	CBS 133594 = MAFF 240222 = HYZiM201-0-1 (Z-2J)	AB274434	KM484988	KM485091	AB274446	KM485246
<i>Pseudopyricularia cyperi</i>	Japan	<i>Zingiber officinale</i>	Y. Nisikado	CBS 303.39 = MUCL 9449	KM484871	KM484989	KM485092	KM485177	KM485247
	Japan: Hyogo	<i>Cyperus iria</i>	H. Kato	CBS 133595 = MAFF 240229 = HYCI201-1-1(Ci-1J) (ex-type)	KM484872	KM484990	AB818013	AB274453	AB274485
	Israel	<i>Cyperus rotundus</i>	R. Kenneth	CBS 665.79	KM484873	DQ341512	KM485093	KM485178	KM485248
	Philippines: Sto Tomas, Batangas	<i>Cyperus rotundus</i>	IRRI	PH0053 = Cr88383	KM484874	–	KM485094	KM485179	KM485249
<i>Pseudopyricularia higginsii</i>	New Zealand: Auckland, Mount Albert	<i>Typha orientalis</i> , dead leaves	C.F. Hill	CBS 121934 = 09/2007/1470	KM484875	KM484991	KM485095	KM485180	KM485250
<i>Pseudopyricularia kyllingae</i>	Japan: Hyogo	<i>Kyllinga brevifolia</i>	I. Chuma	CBS 133597 = MAFF 240227 = HYKB202-1-2(K-1J) (ex-type)	KM484876	KM484992	KM485096	AB274451	AB274484
	Philippines: Los Banos	<i>Cyperus brevifolius</i>	IRRI	PH0054 = Cb8959	KM484877	KM484993	KM485097	KM485181	KM485251
<i>Pyricularia ctenantheicola</i>	Greece: Almyros, imported from Brazil via Netherlands	<i>Ctenanthe oppenheimiana</i>	A.C. Pappas & E.J. Paplomatas	GR0001 = Ct-4 = ATCC 200218	KM484878	KM484994	KM485098	KM485182	KM485252
	Greece: Almyros, imported from Brazil via Netherlands	<i>Ctenanthe oppenheimiana</i>	A.C. Pappas & E.J. Paplomatas	GR0002 (ex-type)	KM484879	–	KM485099	KM485183	KM485253
<i>Pyricularia grisea</i>	Brazil: Goias, Goiana	<i>Digitaria sanguinalis</i>	J.-L. Nottéghem	BR0029	KM484880	KM484995	KM485100	DQ240874	DQ240890
	Brazil	<i>Digitaria horizontalis</i>	–	Br33	AB274430	KM484996	–	–	KM485254
	Korea: Woanju	<i>Echinochloa crus-galli</i> var. <i>frumentacea</i>	H.K. Sim	CBS 128304 = KACC 41641	KM484881	–	KM485101	KM485184	KM485255
	South Korea: Suwon	<i>Lolium perenne</i>	C.K. Kim	CR0024	KM484882	KM484997	KM485102	KM485185	KM485256
	Japan	<i>Digitaria smutsii</i>	–	JP0034 = NI980	KM484883	–	KM485103	KM485186	KM485257
	Philippines: Sto Tomas, Batangas	<i>Digitaria ciliaris</i>	IRRI	PH0055 = Dc88420	KM484884	–	KM485104	DQ240877	DQ240893
	USA: Delaware	<i>Digitaria</i> sp.	B. Valent	US0043 = G184	KM484885	–	KM485105	KM485187	KM485258
	<i>Pyricularia oryzae</i>	Burkina Faso	<i>Paspalum</i> sp.	J.-L. Nottéghem	BF0028	KM484886	KM484998	KM485106	KM485188
	Brazil	<i>Triticum</i> sp.	J.-L. Nottéghem	BR0032	KM484887	–	KM485107	DQ240884	DQ240900
	Brazil	<i>Triticum</i> sp.	J.-L. Nottéghem	BR0045	KM484888	–	KM485108	KM485189	KM485260
	Romania	–	–	CBS 255.38	KM484889	KM484999	KM485109	KM485190	KM485261

Table 1. (Continued)

Species	Location	Substrate	Collector	Culture collection no ¹	GenBank Accession no ²				
					ITS	LSU	RPB1	ACT	CAL
<i>Pyricularia oryzae</i>	Japan: Nagano	–	–	CBS 365.52 = MUCL 9451	KM484890	KM485000	KM485110	KM485191	KM485262
	–	–	–	CBS 375.54	KM484891	KM485001	KM485111	KM485192	KM485263
	–	<i>Oryza sativa</i> , seed	–	CBS 433.70	KM484892	KM485002	KM485112	KM485193	KM485264
	Egypt	<i>Oryza sativa</i>	–	CBS 657.66	KM484893	KM485003	KM485113	KM485194	KM485265
	Israel	<i>Echinochloa crus-galli</i>	–	CBS 658.66	KM484894	KM485004	KM485114	KM485195	KM485266
	Israel	<i>Stenotaphrum secundatum</i>	–	CBS 659.66	KM484895	KM485005	KM485115	KM485196	KM485267
	Côte d'Ivoire: Bouaké	<i>Leersia hexandra</i>	J.-L. Nottéghem	CD0067	KM484896	KM485006	KM485116	KM485197	KM485268
	Côte d'Ivoire: Ferkessédougou	<i>Eleusine indica</i>	J.-L. Nottéghem	CD0156	KM484897	KM485007	KM485117	KM485198	KM485269
	South Korea: Suwon	<i>Phleum pratense</i>	C.K. Kim	CR0020	KM484898	KM485008	KM485118	KM485199	KM485270
	South Korea: Yongin	<i>Panicum miliaceum</i>	C.K. Kim	CR0021	KM484899	–	KM485119	KM485200	KM485271
	South Korea: Suwon	<i>Lolium hybridum</i>	C.K. Kim	CR0026	KM484900	KM485009	KM485120	KM485201	KM485272
	South Korea: Suwon	<i>Festuca elalior</i>	C.K. Kim	CR0029	KM484901	KM485010	KM485121	KM485202	KM485273
	France: Camargue	<i>Oryza sativa</i>	J.-L. Nottéghem	FR0013	KM484902	KM485011	KM485122	DQ240885	DQ240901
	Gabon: Wey	<i>Zea mays</i>	J.-L. Nottéghem	GN0001	KM484903	KM485012	KM485123	DQ240882	DQ240898
	French Guiana	<i>Oryza sativa</i>	J.-L. Nottéghem	Guy11 = FGSC 9462	KM484904	KM485013	KM485124	KC167438	AF396024
	India: Uttar Pradesh	<i>Setaria</i> sp.	J. Kumar	IN0108 = VII-765-1	KM484905	KM485014	KM485125	KM485203	KM485274
	Japan	<i>Eleusine indica</i>	H. Yaegashi	JP0017 = C10	AF074404	KM485015	–	AF395970	AF396018
	Japan	<i>Eragrostis curvula</i>	H. Yaegashi	JP0028 = K76-79	KM484906	KM485016	KM485126	AF395961	KM485275
	Japan	<i>Eriochloa villosa</i>	–	JP0033 = NI859	KM484907	KM485017	KM485127	KM485204	KM485276
	Japan	<i>Eragrostis curvula</i>	H. Kato	JP0038 = IN909	KM484908	–	KM485128	AF395964	KM485277
	Japan	<i>Anthoxanthum odoratum</i>	–	JP0039 = NI904	KM484909	KM485018	KM485129	KM485205	KM485278
	Japan	<i>Phalaris arundinacea</i>	–	JP0040 = NI901	KM484910	KM485019	KM485130	KM485206	KM485279
	Philippines	<i>Oryza sativa</i>	IRRI	PH0014 = PO6-6	KM484911	–	KM485131	DQ240888	DQ240904
	Philippines: Los Banos	<i>Brachiaria mutica</i>	IRRI	PH0035 = Bm8309 = PH0075	KM484912	–	KM485132	KM485207	KM485280
	Philippines: Cabanatuan	<i>Cynodon dactylon</i>	IRRI	PH0051 = Cd88215	KM484913	KM485020	KM485133	KM485208	KM485281
	Philippines: Los Banos	<i>Leptochloa chimensis</i>	IRRI	PH0060 = LcA8401	KM484914	–	–	KM485209	KM485282
	Philippines: Cabanatuan	<i>Paspalum distichum</i>	IRRI	PH0062 = Pd8824	KM484915	KM485021	KM485134	KM485210	KM485283
Philippines: Los Banos	<i>Rottboellia exalta</i>	IRRI	PH0063 = ReA8401 = ATCC 62619	KM484916	KM485022	KM485135	KM485211	KM485284	
Philippines	<i>Echinochloa colona</i>	IRRI	PH0077 = Ec8202	KM484918	KM485024	KM485137	KM485213	KM485286	
Philippines	<i>Panicum repens</i>	J. M. Bonman	PH0079 = GPr8212	KM484919	KM485025	KM485138	KM485214	KM485287	

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Table 1. (Continued)

Species	Location	Substrate	Collector	Culture collection no ¹	GenBank Accession no ²					
					ITS	LSU	RPB1	ACT	CAL	
<i>Pyricularia oryzae</i>	Portugal	<i>Stenotaphrum secundatum</i>	A. Lima	PR0067	KM484920	KM485026	KM485139	KM485215	KM485288	
	Portugal	<i>Stenotaphrum secundatum</i>	A. Lima	PR0104	KM484921	KM485027	KM485140	KM485216	KM485289	
	Rwanda: Kununya	<i>Eleusine coracana</i>	J.-L. Nottéghem	RW0012	KM484922	–	KM485141	AF395959	AF396014	
	USA: Kentucky	<i>Setaria viridis</i>	M. Farman	US0071	KM484923	KM485028	KM485142	KM485217	–	
	Vietnam: O Mon	<i>Leersia hexandra</i>	B. Couch	VT0032	KM484924	KM485029	KM485143	KM485218	KM485290	
	–	Laboratory strain	–	70-15 = ATCC MYA-4617 = FGSC 8958	Genome	Genome	Genome	Genome	Genome	
" <i>Pyricularia parasitica</i> "	USA: Iowa	<i>Phyllachora graminis</i>	–	CBS 376.54 = ICMP 14696 = MUCL 9450 = QM 1092	AY265340	KM485030	–	–	–	
<i>Pyricularia penniseticola</i>	Burkina Faso: Kamboinse	<i>Pennisetum typhoides</i>	J.-L. Nottéghem	BF0017	KM484925	KM485031	KM485144	DQ240878	DQ240894	
	Côte d'Ivoire: Bouake	<i>Pennisetum typhoides</i>	J.-L. Nottéghem	CD0086	KM484926	–	KM485145	DQ240879	DQ240895	
	Côte d'Ivoire: Odienne	<i>Digitaria exilis</i>	J.-L. Nottéghem	CD0143	KM484927	–	KM485146	KM485219	–	
	Côte d'Ivoire: Madiani	<i>Pennisetum</i> sp.	J.-L. Nottéghem	CD0180	KM484928	–	KM485147	DQ240880	DQ240896	
	Mali: Longorola Sikasso	<i>Pennisetum typhoides</i>	J.-L. Nottéghem	ML0031 (ex-type)	KM484929	–	KM485148	KM485220	–	
	Mali	<i>Digitaria exilis</i>	J.-L. Nottéghem	ML0048	KM484930	–	KM485149	KM485221	–	
<i>Pyricularia pennisetigena</i>	Brazil: Imperatriz	<i>Cenchrus echinatus</i>	–	BR0067	KM484931	KM485032	KM485150	KM485222	KM485291	
	Brazil: Primeiro de Maio	<i>Echinochloa colona</i>	H. Kato	BR0093	KM484932	–	KM485151	KM485223	KM485292	
	Brazil	<i>Cenchrus echinatus</i>	S. Igarashi	Br36	KM484933	KM485033	–	–	KM485293	
	Japan: Kumamoto	<i>Cenchrus ciliaris</i>	N. Nishihara	CBS 133596 = MAFF 305501 = NI981(Cc-1J)	KM484934	KM485034	KM485152	KM485224	AB274475	
	Mali: Cinzana	<i>Pennisetum</i> sp.	J.-L. Nottéghem	ML0036 (ex-type)	KM484935	–	KM485153	KM485225	KM485294	
	Philippines: Plaridel	<i>Cenchrus echinatus</i>	IRRI	PH0047 = Ce88454	KM484936	–	KM485154	KM485226	KM485295	
	USA: Tifton	<i>Pennisetum glaucum</i>	H. Wells	US0044 = 83P-25	KM484937	–	–	KM485227	KM485296	
	USA: Tifton	<i>Pennisetum glaucum</i>	H. Wells	US0045 = 84P-19	KM484938	–	KM485155	KM485228	–	
	<i>Pyricularia</i> sp.	Brazil	<i>Setaria geniculata</i>	S. Igarashi	Br37	KM484939	KM485035	–	–	AB274474
	<i>Pyricularia</i> sp.	Japan: Chiba	<i>Leersia oryzoides</i>	N. Nishihara	CBS 133598 = MAFF 305509 = NI919 (Leo-1J) = JP0036	KM484940	KM485036	KM485156	AB274440	AB274473
<i>Pyricularia variabilis</i>	Thailand	<i>Amomum siamense</i> , healthy leaves	–	CMUZE0229 = ICMP 14487	AY265333	–	–	–	–	
<i>Pyricularia zingibericola</i>	Réunion	<i>Zingiber officinale</i>	J.-C. Girard	RN0001	KM484941	KM485037	KM485157	KM485229	KM485297	
<i>Pyriculariopsis parasitica</i>	Hong Kong: Discovery Bay	<i>Musa</i> sp., leaves	K.D. Hyde	CBS 114973 = HKUCC 5562 = Maew HK 1	–	DQ341514	–	–	–	

Table 1. (Continued)

Species	Location	Substrate	Collector	Culture collection no ¹	GenBank Accession no ²				
					ITS	LSU	RPB1	ACT	CAL
<i>Rhexodenticula cylindrospora</i>	Cuba: Pinar del Rio	<i>Nectandra antillana</i> , leaf litter	R.F. Castañeda & M. Saikawa	CBS 244.95 = INIFAT C94/182	KM484942	KM485038	–	–	–
	Cuba: Pinar del Rio	<i>Nectandra antillana</i> , leaf litter	R.F. Castañeda	CBS 318.95 = INIFAT C94/182 (ex-type)	KM484943	KM485039	–	–	–
<i>Slopeiomyces cylindrosporus</i>	UK: England	Grass roots; associated with <i>Phialophora graminicola</i>	D. Hornby	CBS 609.75 (ex-type)	KM484944	KM485040	KM485158	–	–
	UK: England	Grass roots; associated with <i>Phialophora graminicola</i>	D. Hornby	CBS 610.75 (ex-type)	JX134667	DQ341494	JX134721	–	–
	UK: England	Grass roots; associated with <i>Phialophora graminicola</i>	D. Hornby	CBS 611.75 (ex-type)	KM484945	KM485041	KM485159	–	–
<i>Xenopyricularia zizaniicola</i>	Japan: Kyoto	<i>Zizania latifolia</i>	K. Yoshida & K. Hirata	CBS 132356 = MAFF 240220 = KYZL201-1-1 (Zz-2J)	KM484946	KM485042	KM485160	AB274444	AB274480
	Japan: Ibaraki	<i>Zizania latifolia</i>	N. Hayashi	CBS 133593 = MAFF 240219 = IBZL3-1-1(Zz-1J) (ex-neotype)	KM484947	–	KM485161	KM485230	AB274479

¹ ATCC: American Type Culture Collection, Virginia, U.S.A.; BCC: BIOTEC Culture Collection, National Center for Genetic Engineering and Biotechnology (BIOTEC), Bangkok, Thailand; CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CPC: Culture collection of Pedro Crous, housed at CBS; DAR: Plant Pathology Herbarium, Orange Agricultural Institute, Forest Road, Orange. NSW 2800, Australia; FGSC: Fungal Genetics Stock Center, University of Kansas Medical Center, KS, U.S.A.; HKUCC: The University of Hong Kong Culture Collection, Hong Kong, China; ICMP: International Collection of Microorganisms from Plants, Landcare Research, Auckland, New Zealand; IMI: International Mycological Institute, CBI-Bioscience, Egham, Basingstoke, United Kingdom; INIFAT: Alexander Humboldt Institute for Basic Research in Tropical Agriculture, Ciudad de La Habana, Cuba; KACC: Korean Agricultural Culture Collection, National Institute of Agricultural Biotechnology, Rural Development Administration, Suwon, Republic of Korea; MAFF: Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Ibaraki, Japan; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium; PD: Plant Protection Service, nVWA, Division Plant, Wageningen, The Netherlands; PREM: South African National Collection of Fungi (NCF), Mycology Unit, Biosystematics Division, Plant Protection Institute, Agricultural Research Council, Roodeplaat, Pretoria, South Africa; QM: Quartermaster Research and Development Center, U.S. Army, Massachusetts, U.S.A.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial large subunit (28S) of the nrRNA gene operon; RPB1: partial RNA polymerase II largest subunit gene; ACT: partial actin gene; CAL: partial CAL gene. Genome sequences of *C. parasitica* strain EP155: JGI Genome Portal; Genome sequences of *G. graminis* var. *tritici* strain R3111a, *P. oryzae* strain 70-15 and *M. poae* strain ATCC 64411: Broad Institute.

Table 2. Details of primers used and/or developed for this study.

Locus ¹ and primer name	Sequence (5' – 3')	Orientation	Reference
Actin			
ACT-512F	ATG TGC AAG GCC GGT TTC GC	Forward	Carbone & Kohn (1999)
ACT-783R	TAC GAG TCC TTC TGG CCC AT	Reverse	Carbone & Kohn (1999)
Calmodulin			
CAL-228F	GAG TTC AAG GAG GCC TTC TCC C	Forward	Carbone & Kohn (1999)
CAL-737R	CAT CTT TCT GGC CAT CAT GG	Reverse	Carbone & Kohn (1999)
ITS			
ITS4	TCC TCC GCT TAT TGA TAT GC	Reverse	White <i>et al.</i> (1990)
ITS5	GGA AGT AAA AGT CGT AAC AAG G	Forward	White <i>et al.</i> (1990)
V9G	TTA CGT CCC TGC CCT TTG TA	Forward	de Hoog & Gerrits van den Ende (1998)
LSU			
LR5	TCC TGA GGG AAA CTT CG	Reverse	Vilgalys & Hester (1990)
NL1	GCA TAT CAA TAA GCG GAG GAA AAG	Forward	O'Donnell (1993)
RPB1			
RPB1F	AGA CGA TYG AGG AGA TCC AGT T	Forward	This study
RPB1R	ART CCA CAC GCT TAC CCA TC	Reverse	This study

¹ ACT: partial actin gene; CAL: partial CAL gene; ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial large subunit (28S) of the nrRNA gene operon; RPB1: partial RNA polymerase II largest subunit gene.

using MrBayes v. 3.2.2 ((Ronquist *et al.* 2012); LSU only) and maximum parsimony (MP) using PAUP v. 4.0b10 (Swofford 2003) for all datasets as described by Crous *et al.* (2006). To check the congruency of the individual datasets, a 70 % neighbour-joining (NJ) reciprocal bootstrap was performed (Mason-Gamer & Kellogg 1996, Lombard *et al.* 2010). Novel sequences derived in this study were lodged at GenBank, and the alignments and phylogenetic trees in TreeBASE (www.treebase.org/treebase/index.html).

Morphology

For morphological characterisation, cultures were grown on synthetic nutrient-poor agar (SNA; Nirenberg 1976), supplemented with autoclaved barley seeds, water agar supplemented with autoclaved barley seeds and leaves, as well as OA. Plates were inoculated with agar plugs from cultures growing on MEA, PDA or OA. Plates were incubated at 23–25 °C under a regime of 12 h dark/12 h near-ultraviolet light, and examined after 1–3 wk for sporulation. Observations were made with a Zeiss V20 Discovery stereo-microscope, and with a Zeiss Axio Imager 2 light microscope using differential interference contrast (DIC) illumination and an AxioCam MRc5 camera and software. Measurements and photographs were made from structures mounted in clear lactic acid. The 95 % confidence intervals were derived from 30 observations ($\times 1\,000$ magnification), with the extremes given in parentheses. Ranges of the dimensions of other characters are given. Colony diameter and other macroscopic features were recorded after 1 wk of incubation at 25 °C in the dark. Colony colours were determined using the colour charts of Rayner (1970). Specimens were deposited in the fungarium at CBS (CBS H) in Utrecht, and taxonomic novelties in MycoBank (Crous *et al.* 2004).

RESULTS

DNA phylogeny

We combined the LSU sequences obtained from our *Pyricularia/Magnaporthe* species (Table 1) with sequences from NCBI corresponding to other *Pyricularia/Magnaporthe* species. The LSU dataset consists of 99 aligned sequences, including the outgroup *Peziza vesiculosa*. It contains 772 characters, of which 336 constitute unique site patterns (BI analysis with the GTR model, dirichlet (1,1,1,1) state frequency distribution and inverse gamma-shaped rate variation across sites). 405 characters were constant, 62 were variable and parsimony-uninformative while 305 were parsimony informative (MP analysis). A maximum of 1 000 equally most parsimonious trees were retained from this analysis (Tree length = 1362, CI = 0.438, RI = 0.785 and RC = 0.343, Fig. 1). The majority of strains clustered in the *Magnaporthales* (Thongkantha *et al.* 2009). However, “*Pyricularia*” *parasitica*, based on CBS 376.54, clusters in the *Chaetothyriales* (*Eurotiomycetes*) and *Rhexodenticulata cylindrospora* (= *Pyricularia lauri*, *Nakataea cylindrospora*) is placed *incertae sedis* in the *Sordariomycetes*, but in both the parsimony (69 % bootstrap support) and Bayesian analyses (posterior probability of 1.0), this clade is related to *Boliniales* and *Sordariales*.

Within *Magnaporthales*, the different clades were not well-resolved using LSU sequences (Fig. 1). Therefore, LSU was supplemented with RPB1 sequences to generate a novel phylogenetic tree restricted to species from *Magnaporthales*. The combined LSU/RPB1 dataset consists of 101 aligned sequences including *Cryphonectria parasitica* as outgroup. This dataset contains 1 391 characters, of which the LSU dataset contributed 748 characters and the RPB1 dataset contributed 643 characters; 772 characters were constant, while 131 were variable and

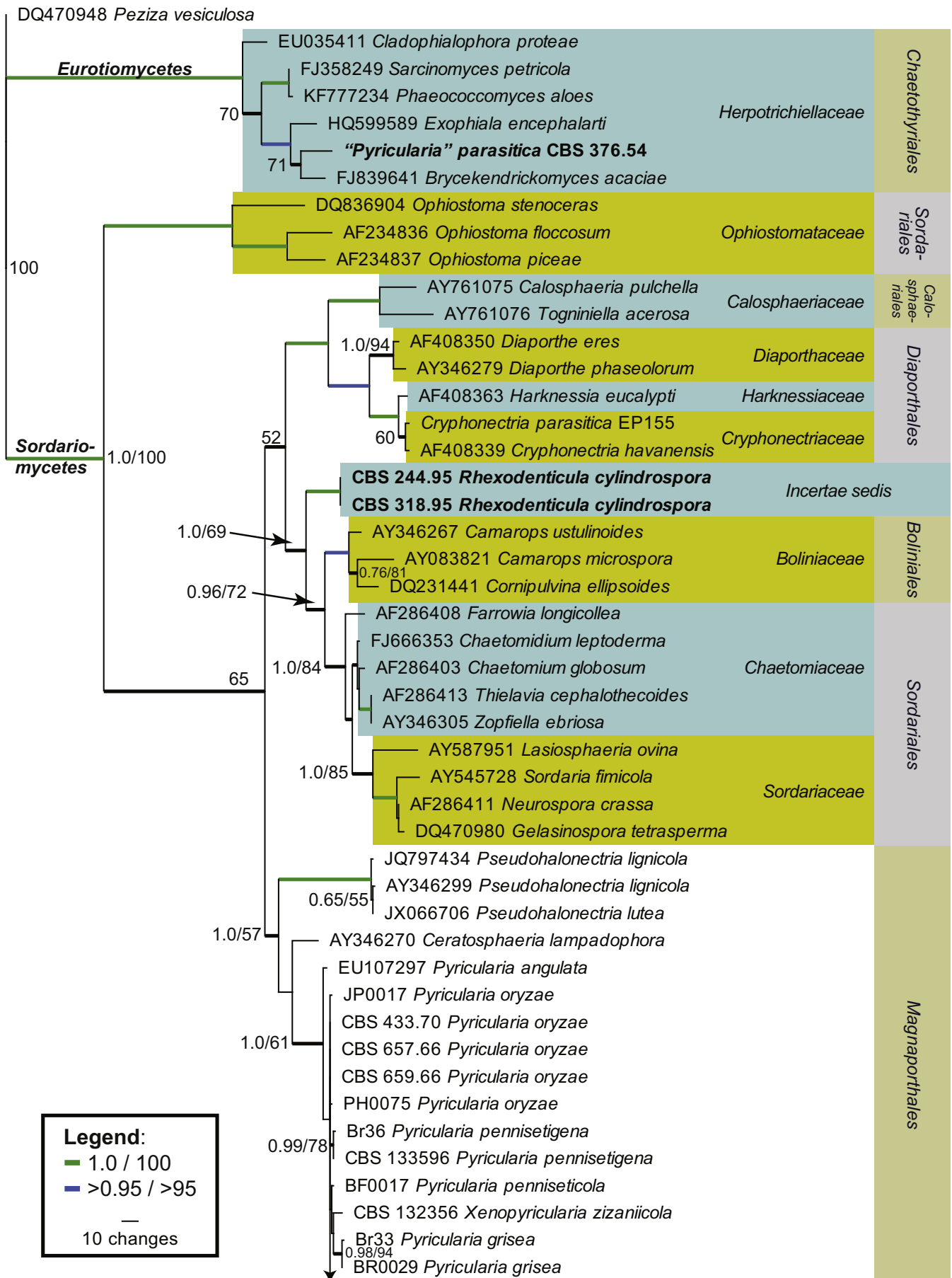


Fig. 1. The first of 1000 equally most parsimonious trees (Tree length = 1362, CI = 0.438, RI = 0.785 and RC = 0.343) obtained from a maximum parsimony analysis of the LSU alignment. The bootstrap support values (integers) from 1000 replicates and the posterior probability values (values ≤ 1.0) are indicated as numbers at the nodes or as coloured branches (see legend) and the scale bar represents 10 changes. Thickened branches reflect those branches present in the strict consensus parsimony tree. Families are highlighted in the horizontal coloured boxes, orders in the vertical coloured boxes and classes are shown to the left of the tree. *"Pyricularia" parasitica* and *Rhexodenticula cylindrospora* are shown in bold text. The tree was rooted to *Peziza vesiculosa* (GenBank DQ470948).

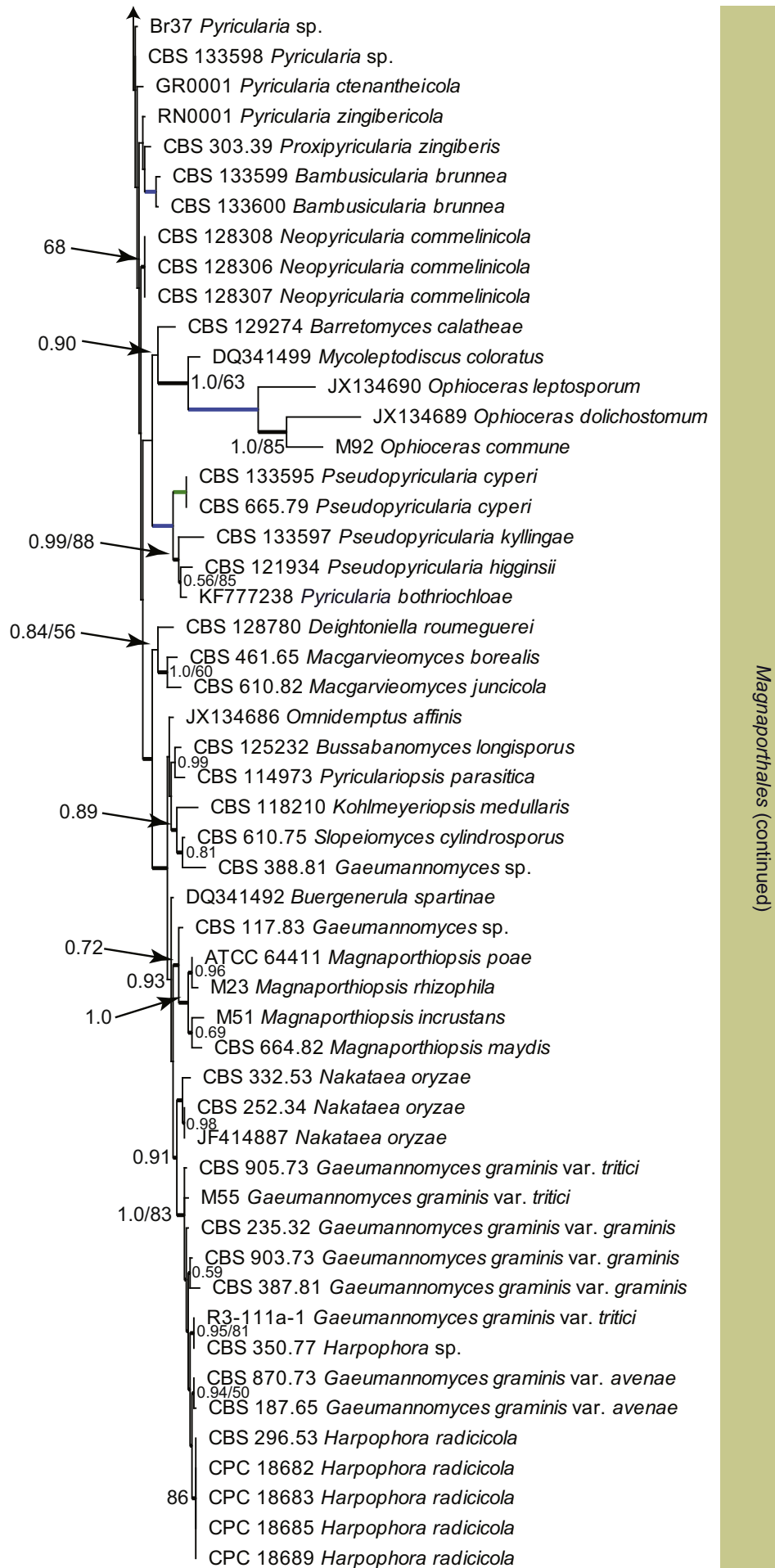


Fig. 1. (Continued).

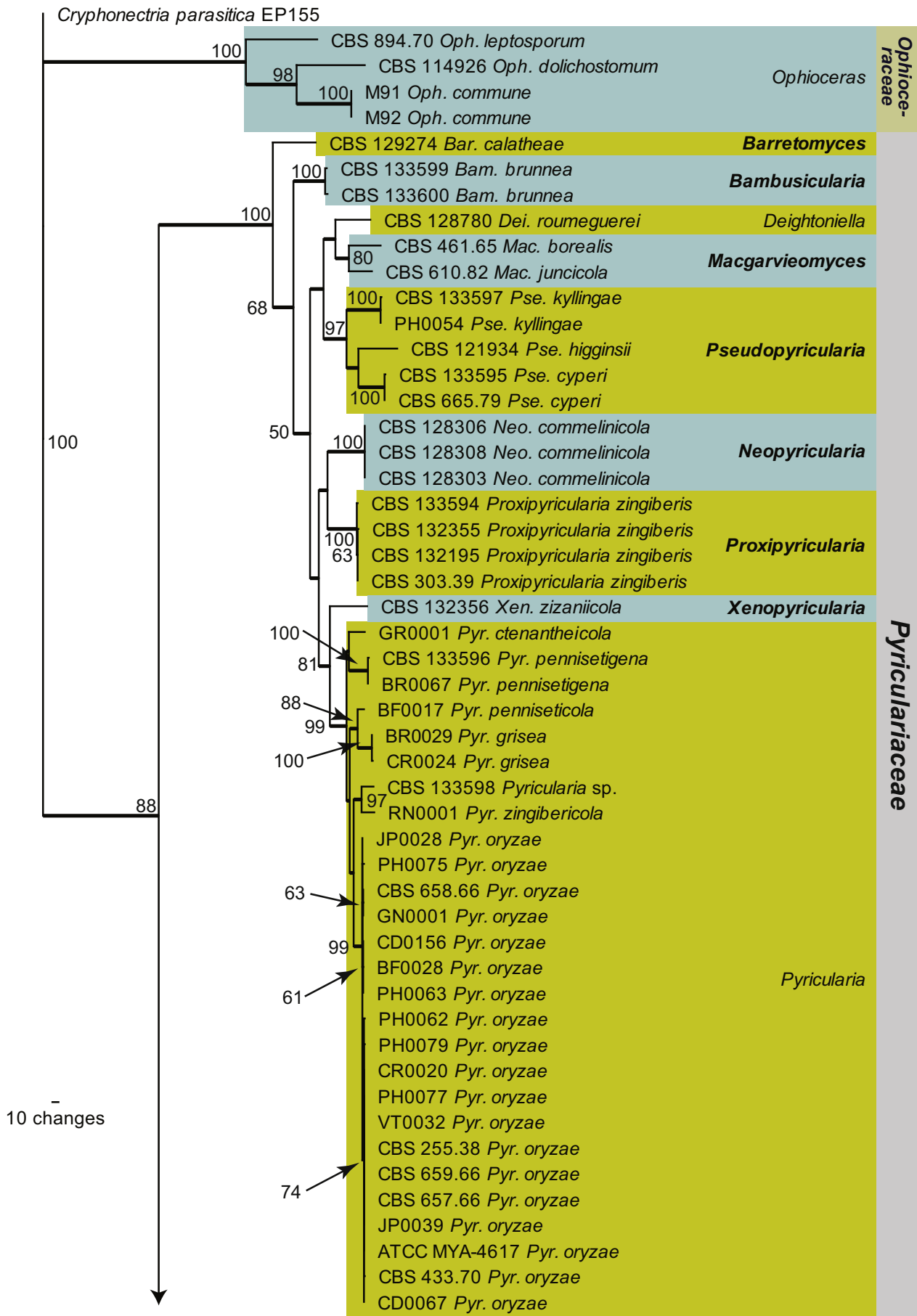


Fig. 2. The first of two equally most parsimonious trees (Tree length = 2483, CI = 0.416, RI = 0.879 and RC = 0.365) obtained from a maximum parsimony analysis of the combined LSU/RPB1 alignment. The bootstrap support values from 1000 replicates are indicated at the nodes and the scale bar represents the number of changes. Thickened branches reflect those branches present in the strict consensus tree. Genera are highlighted in the horizontal coloured boxes, families in the vertical coloured boxes and novel species and families are shown in **bold** text. The tree was rooted to *Cryphonectria parasitica* strain EP155.

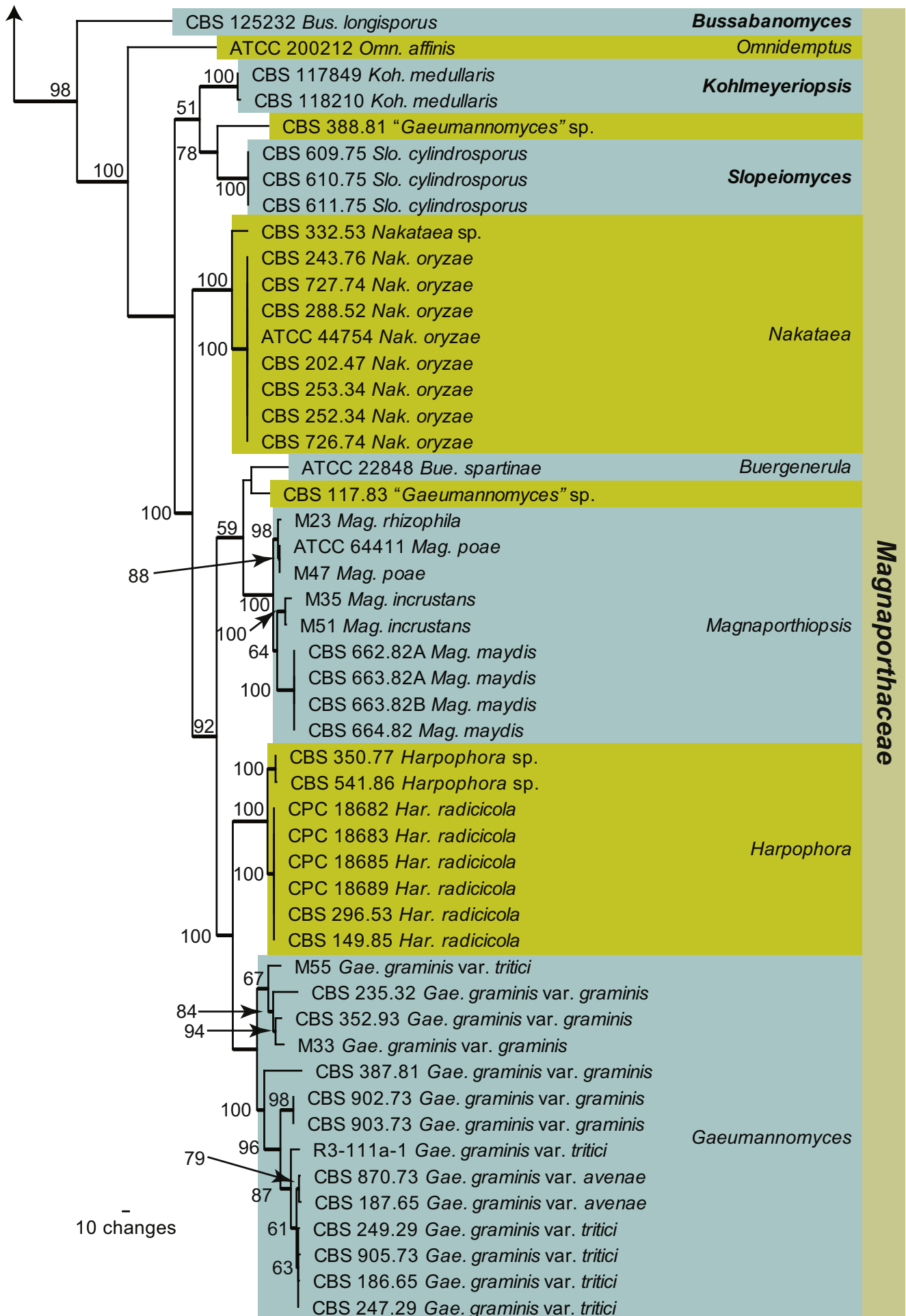


Fig. 2. (Continued).

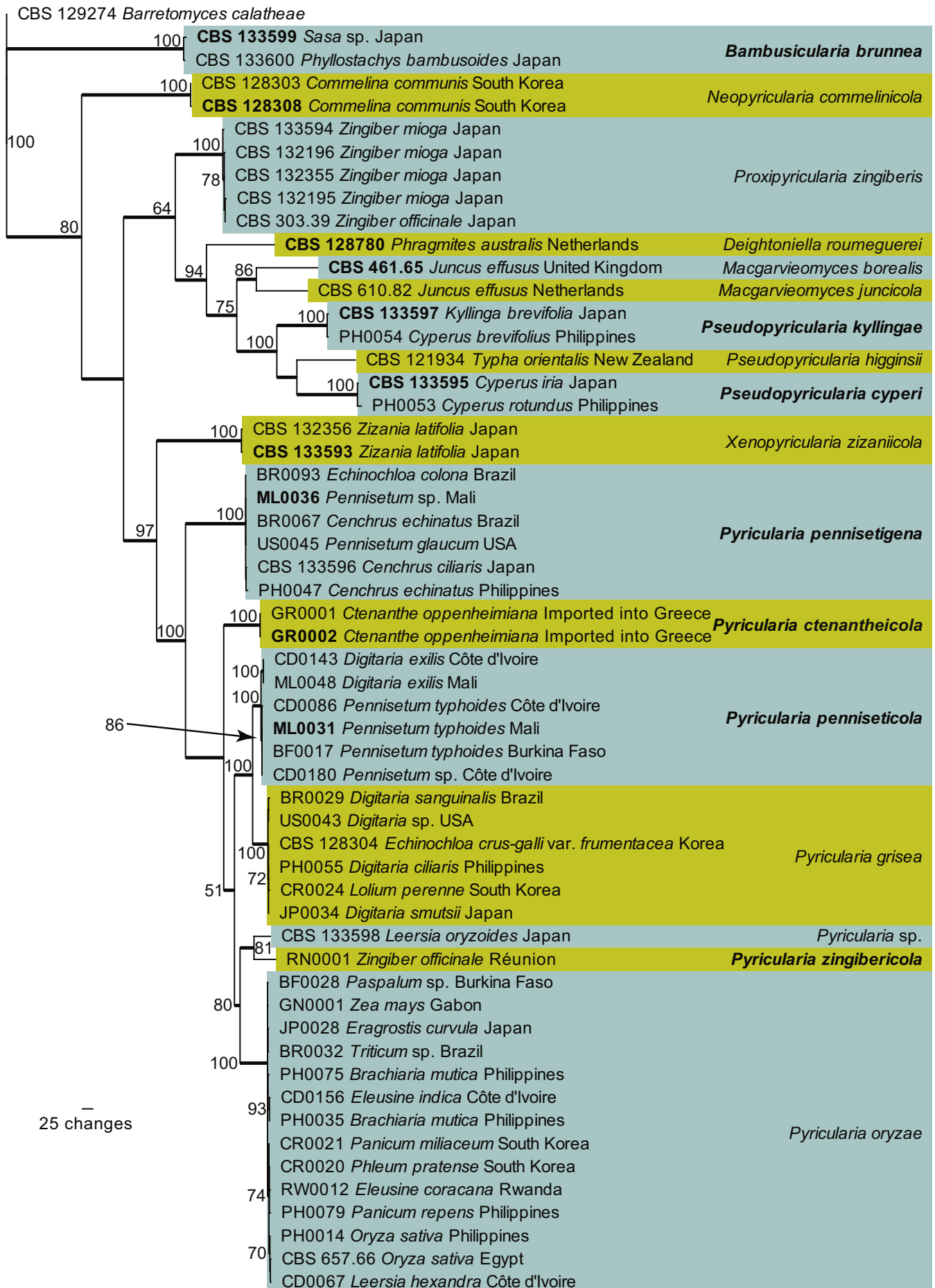


Fig. 3. The first of 192 equally most parsimonious trees (Tree length = 2587, CI = 0.563, RI = 0.821 and RC = 0.462) obtained from a maximum parsimony analysis of the combined ACT/ITS/RPB1 alignment. The bootstrap support values from 1000 replicates are indicated at the nodes and the scale bar represents the number of changes. Thickened branches reflect those present in the strict consensus tree. Species are highlighted in the coloured boxes and ex-type strain numbers and novel species are shown in bold text. The tree was rooted to *Barretomyces calatheae* strain CBS 129274.

parsimony-uninformative and 488 were parsimony informative (LSU: 539, 74, 135 characters respectively and RPB1: 233, 57, 353 characters respectively). Two equally most parsimonious trees were retained from this analysis (Tree length = 2483, CI = 0.416, RI = 0.879 and RC = 0.365), the first of which is shown in Fig. 2. This phylogenetic tree delimited three families, of which two are described as new (*Ophioceraaceae*, *Pyriculariaceae*), and 19 genus clades, ten of which represent novel genera, described in the Taxonomy Section. A further two lineages represent “*Gaeumannomyces*” spp., but these species defined clades distinct from other known species of the genus and are not treated further here.

To improve the resolution of the clades within *Pyriculariaceae*, we combined ACT/ITS/RPB1 sequences. The combined dataset consists of 56 sequences including *Barretomyces calathea* as outgroup, since it defines a clade basal to other species from this family (Fig. 2). This dataset contains 1866 characters, of which the ACT dataset contributed 364 characters, the ITS dataset contributed 507 characters and the RPB1 dataset contributed 995 characters: 1018 characters were constant, 118 were variable and parsimony-uninformative and 730 were parsimony informative (ACT: 94, 34, 236 characters respectively, ITS: 324, 27, 156 characters respectively, and RPB1: 600, 57, 338 characters respectively). A total of 192 equally most parsimonious trees were retained from this analysis (Tree length = 2587, CI = 0.563, RI = 0.821 and RC = 0.462), the first of which is shown in Fig. 3. The phylogenetic tree delimited 17 species clades, seven of which represent novel species described in in the Taxonomy section.

Taxonomy

Magnaporthales Thongk., Vijaykr. & K.D. Hyde, Fungal Diversity 34: 166. 2009.

Magnaporthaceae P.F. Cannon, Systema Ascomycetum 13: 26. 1994.

Ascomata perithecial, immersed, scattered to separate, globose to subglobose, black, with long unilateral, cylindrical, black, periphysate neck; wall of several layers of *textura epidermoidea*. *Paraphyses* hyaline, thin-walled, septate, intermingled among asci. *Asci* 8-spored, subcylindrical, unitunicate, short-stipitate or not, with a large apical ring staining in Meltzer's iodine reagent. *Ascospores* curved to sigmoid, septate, filiform or fusoid, hyaline to olivaceous, with bluntly rounded ends, lacking sheath. *Mycelium* with simple to lobed brown appressoria. *Asexual morphs* hyphomycetous, at times formed from sclerotia, with simple, unbranched or branched conidiophores. *Conidiogenous cells* integrated, pigmented, phialidic with collarettes, or denticulate. *Conidia* hyaline to pale brown, septate to aseptate, variable in shape, straight or curved.

Type genus: *Nakataea* Hara (= *Magnaportha* R.A. Krause & R.K. Webster)

Type species: *Nakataea oryzae* (Catt.) J. Luo & N. Zhang

Genera included: *Buergenerula*, *Bussabanomyces*, *Endopyricularia*, *Gaeumannomyces*, *Harpophora*, *Kohlmeyeriopsis*, *Magnaporthiopsis*, *Nakataea*, *Omnidemptus*, *Pyriculariopsis* and *Slopeiomyces*.

Notes: Other than being phylogenetically distinct, the *Magnaporthaceae* is distinguished from the *Pyriculariaceae* by their asexual morphs, which are either phialophora-like, or with falcate versicoloured conidia on brown, erect conidiophores.

Bussabanomyces Klaubauf, Lebrun & Crous, gen. nov. MycoBank MB810195.

Etymology: Named after Dr. B. Bussaban, who collected this fungus from Chiang Mai, Thailand.

Mycelium consisting of verruculose, pale brown, branched, septate hyphae. *Conidiophores* macronematous, rarely branched, straight, septate, pale brown near the base, subhyaline at the apex. *Conidiogenous cells* cylindrical, terminal, denticulate; denticles cylindrical, thin-walled, mostly cut off by a septum to form a separating cell. *Conidia* solitary, dry, obclavate, hyaline to pale brown, smooth, 4(–5)-septate.

Type species: *Bussabanomyces longisporus* (Bussaban) Klaubauf, Lebrun & Crous

Notes: Morphologically similar to *Pyricularia*, but distinct in that conidiophores are usually unbranched, with terminal conidiogenous cells that give rise to 4(–5)-septate, pale brown conidia.

Bussabanomyces longisporus (Bussaban) Klaubauf, Lebrun & Crous, comb. nov. MycoBank MB810196.

Basionym: *Pyricularia longispora* Bussaban, Mycologia 95: 520. 2003.

Illustrations: See Bussaban et al. (2003).

Mycelium consisting of verruculose, pale brown, branched, septate hyphae, 3–5 µm diam. *Conidiophores* macronematous, up to 400 µm long, 3–4.6 µm diam, rarely branched, straight, septate, pale brown near the base, subhyaline at the apex. *Conidiogenous cells* cylindrical, denticulate; each denticle cylindrical, thin-walled, mostly cut off by a septum to form a separating cell. *Conidia* 47–72 × 5.6–7.6 µm, solitary, dry, obclavate, hyaline to pale brown, smooth, 4(–5)-septate. (Description from Bussaban et al. 2003).

Culture characteristics: Colonies on MEA pale olivaceous-grey, irregularly raised with a hairy edge, velutinous, reaching 2.3–2.4 cm after 1 wk; reverse umber to chestnut. Similar appearance on CMA and OA with slightly bigger colony diameters, 2.6–3.1 cm. On PDA colonies were olivaceous, with central tufts. No sporulation was observed.

Material examined: Thailand, Chiang Mai, Doi Suthep-Pui National Park, isolated as an endophyte from leaves of *Amomum siamense*, Feb. 2000, B. Bussaban (holotype BCC11377, culture ex-type CBS 125232).

Harpophora W. Gams, Stud. Mycol. 45: 192. 2000.

Mycelium consisting of olivaceous-brown hyphae, with typical “runner hyphae” and narrower lateral hyphae. *Conidiogenous cells* phialidic, resembling those of *Phialophora*, solitary on hyphae or aggregated in clusters, faintly pigmented, with a conspicuous, divergent collarette. *Conidia* borne in slimy heads,

cylindrical, but prominently curved, hyaline. (Description from Gams 2000).

Type species: Harpophora radiculola (Cain) W. Gams

Harpophora radiculola (Cain) W. Gams, Stud. Mycol. 45: 192. 2000.

Basionym: Phialophora radiculola Cain, Canad. J. Bot. 30: 340. 1952.

= *Phialophora zeicola* Deacon & D.B. Scott, Trans. Brit. mycol. Soc. 81: 256. 1983.

≡ *Harpophora zeicola* (Deacon & D.B. Scott) W. Gams, Stud. Mycol. 45: 192. 2000.

Materials examined: Canada, Ontario, Chatham, on *Zea mays*, 1950, R.F. Cain, **isotypes** of *P. radiculola*, specimens CBS H-7592, 7593, cultures **ex-isotype** CBS 296.53 = MUCL 28970 = TRTC 23660. **South Africa**, on *Zea mays*, **isotype** of *P. zeicola*, specimens PREM 45754, CBS H-7597, culture **ex-isotype** CBS 149.85.

Notes: When Gams (2000) introduced the genus *Harpophora*, it was assumed to be the asexual morph of *Gaeumannomyces*. The latter genus however, clusters apart in the *Magnaporthaceae*, and has harpophora-like asexual morphs. Furthermore, based on phylogenetic analyses of several isolates of *H. zeicola* from South Africa (Fig. 1), as well as the ex-type isolate of *H. radiculola* and *H. zeicola*, the latter must be reduced to synonymy under the older name *H. radiculola*.

Kohlmeyeriopsis Klaubauf, Lebrun & Crous, **gen. nov.** MycoBank MB810197.

Etymology: Named after Jan Kohlmeyer and Brigitte Volkman-Kohlmeyer, who dedicated their careers to studying marine fungi, and collected this genus in the process.

Ascomata ellipsoid, immersed, ostiolate, dark brown, solitary, with long cylindrical periphysate necks, lateral or central; wall consisting of 3–4 layers of *textura angularis*. *Paraphyses* hyaline, septate, unbranched. *Asci* 8-spored, fusoid to cylindrical, short stipitate, unitunicate, with a large apical ring staining in Meltzer's iodine reagent. *Ascospores* filamentous, tapering towards the base, indistinctly septate, hyaline, coiled in the ascus, producing appressoria at germination. Asexual morph trichocladium-like. *Mycelium* consisting of pale brown, septate, branched hyphae. *Conidiophores* reduced to conidiogenous cells, short, with lateral branches, giving rise to conidia. *Conidia* 2-celled, with a brown, large ellipsoidal, rarely with kidney-shaped apical cell, and 1–2 small, cylindrical or doliform, pale brown basal cells.

Type species: Kohlmeyeriopsis medullaris (Kohlm., Volkman-Kohlm. & O.E. Erikss.) Klaubauf, Lebrun & Crous

Notes: *Gaeumannomyces medullaris* was originally described from dead culms of *Juncus roemerianus* in North Carolina (Kohlmeyer et al. 1995). They described it as an aggressive cellulose decomposer, specific to the marine environment, commonly forming the trichocladium-like asexual morph in culture (Kohlmeyer & Volkman-Kohlmeyer 1995). The genus *Gaeumannomyces* has harpophora-like asexual morphs, and the genus *Trichocladium* is heterogeneous (Seifert et al. 2011), and genetically unrelated to this fungus, for which a new genus is introduced.

Kohlmeyeriopsis medullaris (Kohlm., Volkman-Kohlm. & O.E. Erikss.) Klaubauf, Lebrun & Crous, **comb. nov.** MycoBank MB810198.

Basionym: Gaeumannomyces medullaris Kohlm., Volkman-Kohlm. & O.E. Erikss., Mycologia 87: 540. 1995.

= *Trichocladium medullare* Kohlm. & Volkman-Kohlm., Mycotaxon 53: 349. 1995.

Illustrations: See Kohlmeyer et al. (1995).

Materials examined: USA, North Carolina, Broad Creek, Carteret County, on *Juncus roemerianus*, isol. Kohlmeyer JK5528S, deposited by C. Schoch, CBS 117849; North Carolina, Broad Creek, Carteret County, on *Juncus roemerianus*, isol. Kohlmeyer JK 5522N, deposited by C. Schoch, CBS 118210.

Magnaporthiopsis J. Luo & N. Zhang, Mycologia 105: 1021. 2013.

Plant pathogenic. *Ascomata* perithecial, solitary or gregarious, superficial or immersed, globose, with a cylindrical neck, black, smooth; wall consisting of two layers. *Asci* unitunicate, clavate, with a refractive ring. *Ascospores* fusoid, septate, hyaline or yellow-brown, smooth, biseriolate. *Paraphyses* hyaline, septate, branched. *Hyphopodia* simple. *Conidiophores* solitary, branched or not. *Conidiogenous cells* phialidic, hyaline. *Conidia* subglobose to ovoid, aseptate, hyaline, smooth. (Description from Luo & Zhang 2013).

Type species: Magnaporthiopsis poae (Landsch. & N. Jacks.) J. Luo & N. Zhang

Notes: Luo & Zhang (2013) introduced *Magnaporthiopsis* to accommodate species with black, globose perithecia with long cylindrical necks, clavate asci with an apical ring, septate, fusoid ascospores, and a harpophora-like asexual morph.

Magnaporthiopsis maydis (Samra, Sabet & Hing.) Klaubauf, Lebrun & Crous, **comb. nov.** MycoBank MB810225.

Basionym: Cephalosporium maydis Samra, Sabet & Hing., Phytopathology 53: 404. 1963.

≡ *Harpophora maydis* (Samra, Sabet & Hing.) W. Gams, Stud. Mycol. 45: 192. 2000.

Materials examined: Bihar, Messina, on *Zea mays* hybrid "Ganga Safed 2", Mar 1976, M.M. Payak, CBS 664.82. **Egypt**, on *Zea mays*, Dec. 1982, H.A. Elshafey, CBS 662.82A. **India**, Rajasthan, Jaipur, on *Zea mays*, Dec. 1982, B.S. Siradhana, CBS 663.82A, CBS 663.82B.

Notes: Gams (2000) introduced the genus *Harpophora*, based on *H. radiculola* for a group of species that are phialophora-like in morphology, with cylindrical, curved conidia. *Harpophora* is however heterogeneous (e.g. *Gaeumannomyces* has harpophora-like asexual morphs), and *H. maydis* clusters with species of *Magnaporthiopsis* (see Fig. 2), hence a new combination is introduced to accommodate it.

Nakataea Hara, The diseases of the rice-plant, 2nd ed.: 185. 1939.

= *Nakataea* Hara, Nippon-gaikingaku: 318. 1936. nom. nud.

Plant pathogenic. *Sclerotia* spherical to subspherical, black, formed on the host and in culture. *Ascomata* perithecial, globose,

dark brown, immersed in leaf sheaths; wall consisting of 5–12 layers of thick-walled dark cells; neck frequently protruding from the leaf tissue. *Asci* 8-spored, subcylindrical, thin-walled, short-stipitate, deliquescent at maturity, spirally twisted, 3-septate, slightly constricted at septa, fusiform, curved, granular, with median cells turning yellowish brown. *Conidiophores* solitary, erect, brown, smooth, branched or not, septate, with integrated terminal *conidiogenous cells* forming a rachis with several denticles, each separated from the conidiogenous cell by a septum. *Conidia* solitary, falcate to sigmoid, smooth, 3-septate, widest in the middle, end cells hyaline, median cells medium brown.

Type species: Nakataea sigmoidea (Cavara) Hara

Nakataea oryzae (Catt.) J. Luo & N. Zhang, *Mycologia* 105: 1025. 2013.

Basionym: Sclerotium oryzae Catt., Arch. Triennale Lab. Bot. Crittog. 1: 10. 1877.

= *Helminthosporium sigmoideum* Cavara, Mat. Lomb.: 15. 1889.

≡ *Nakataea sigmoidea* (Cavara) Hara, as "*sigmoideum*", Nippon-gaikyōgaku: 318. 1936. nom. nud.

≡ *Nakataea sigmoidea* (Cavara) Hara, as "*sigmoideum*", The diseases of the rice-plant 2nd ed.: 185. 1939.

= *Leptosphaeria salvinii* Catt., Arch. Labor. Bot. Critt. Univ. Pavia 2, 3: 126. 1879.

≡ *Magnaporthe salvinii* (Catt.) R.A. Krause & R.K. Webster, *Mycologia* 64: 110. 1972.

Additional synonyms listed in MycoBank.

Materials examined: Burma, on straw of *Oryza sativa*, date and collector unknown, CBS 252.34. *Italy*, no collection details, CBS 202.47; on *Oryza sativa*, sent to CBS for identification by Centro di Ricerche sul Riso, Mortara, Italy, Nov 1975, collector unknown, specimen CBS H-14204, culture CBS 243.76. *Japan*, on *Oryza sativa*, date and collector unknown, ATCC 44754 = M21 = Roku-2; Takada, on stem of *Oryza sativa*, date and collector unknown, CBS 288.52. *USA*, California, Davis, on *Oryza sativa*, Dec. 1974, R.K. Webster, specimens CBS H-14203; CBS H-14205, cultures CBS 726.74, CBS 727.74. *Unknown*, CBS 253.34.

Notes: The genus *Nakataea* (based on *N. sigmoidea*, described from rice in Italy) has some similarity to *Pyricularia* in general morphology, but differs in having falcate conidia with darker median cells (Luo & Zhang 2013). *Magnaporthe oryzae* (= *M. salvinii*), the type of *Magnaporthe*, forms a *Nakataea* asexual morph, and hence Luo & Zhang (2013) introduced the combination *N. oryzae* for this fungus, as the name *Nakataea* (1939) is older than *Magnaporthe* (1972). This decision effectively reduced *Magnaporthe* to synonymy under *Nakataea*. The majority of species formerly treated as *Magnaporthe*, fall in the *Pyricularia* complex (Murata et al. 2014).

Pyriculariopsis M.B. Ellis, In: Ellis, Dematiaceous Hyphomycetes (Kew): 206. 1971.

Plant pathogenic. *Mycelium* consisting of smooth, hyaline to brown, branched, septate hyphae; hyphae developing chains of globose, swollen chlamydospores that give rise to black microsclerotia. *Conidiophores* forming from hyphae or microsclerotia, solitary, erect, straight or curved, unbranched, medium brown, thick-walled, smooth, subcylindrical, septate; base bulbous, lacking rhizoids. *Conidiogenous cells* integrated, terminal, medium brown, smooth, forming a rachis with several protruding denticles, and minute marginal frill due to rhexolytic secession. *Conidia* solitary, obclavate, smooth, guttulate, 3-septate, two median cells brown, apical and basal cell olivaceous to

subhyaline; hilum truncate, slightly protruding, with marginal frill, unthickened, not darkened; apex tapering, subacutely rounded, with persistent mucoid cap.

Type species: Pyriculariopsis parasitica (Sacc. & Berl.) M.B. Ellis

Pyriculariopsis parasitica (Sacc. & Berl.) M.B. Ellis, Dematiaceous Hyphomycetes (Kew): 207. 1971. Fig. 4.

Basionym: Helminthosporium parasiticum Sacc. & Berl., Revue mycol., Toulouse 11: 204. 1889.

On SNA on sterile barley seed. *Mycelium* consisting of smooth, hyaline to brown, branched, septate hyphae, 3–4 µm diam; hyphae developing chains of globose, swollen chlamydospores that give rise to black microsclerotia. *Conidiophores* forming from hyphae or microsclerotia, solitary, erect, straight or curved, unbranched, medium brown, thick-walled, smooth, subcylindrical, 60–180 × 6–8 µm, 3–10-septate; base bulbous, 10–16 µm diam, lacking rhizoids. *Conidiogenous cells* 10–50 × 7–8 µm, integrated, terminal, medium brown, smooth, forming a rachis with several protruding denticles, 2–4 µm long, 3–5 µm diam, and minute marginal frill due to rhexolytic secession. *Conidia* solitary, obclavate, smooth, guttulate, 3-septate, two median cells brown, apical and basal cell olivaceous to subhyaline, (30–)40–55(–60) × (7–)8–9(–12) µm; apical cell 18–22 µm long, basal cell 8–11 µm long; hilum truncate, slightly protruding, 2–3 µm diam with marginal frill, unthickened, not darkened; apex tapering, subacutely rounded, with persistent mucoid cap, 2–3 µm diam.

Culture characteristics: Colonies on MEA with white aerial mycelium, mouse-grey in centre, raised, cottony, round, reaching up to 5 cm diam after 1 wk; reverse with dark mouse-grey in centre. Colonies on CMA and OA transparent, with very thin, spreading mycelium with scattered dark spots of sporulation, covering full plate after 1 wk. Colonies on PDA transparent with dark mouse-grey areas, flat, covering plate after 1 wk; reverse with some dark spots.

Material examined: Hong Kong, Discovery Bay, Lantau Island, on leaves of *Musa* sp., 5 Oct. 1999, K.D. Hyde, CBS 114973 = HKUCC 5562 = Maew HK 1.

Notes: The denticles of *Pyriculariopsis* are similar to those of *Pyricularia*. The main difference lies in the conidium pigmentation, septation, and the persistent apical mucoid cap. In *Pyricularia* conidia are 2-septate, uniformly olivaceous to medium brown, and the apical mucoid cap is not persistent, leaving the apex with what appears to be a marginal frill surrounding the apex (mucoid remnant?), from where the globoid mucoid cap extended.

Slopeiomyces Klaubauf, Lebrun & Crous, *gen. nov.* MycoBank MB810199.

Etymology: Named after D.B. Slope, who collected this fungus from cereal roots in Rothamsted Experimental Station, UK.

Perithecia superficial, globose, black, solitary, sometimes 2–3 aggregated, with cylindrical, black, periphysate neck bearing hyphae; wall consisting of several layers of *textura prismatica* to *angularis*. *Paraphyses* hyaline, septate, unbranched. *Asci* 8-spored, clavate, straight to curved, with a non-amyloid apical ring staining in Congo red. *Ascospores* hyaline, cylindrical to

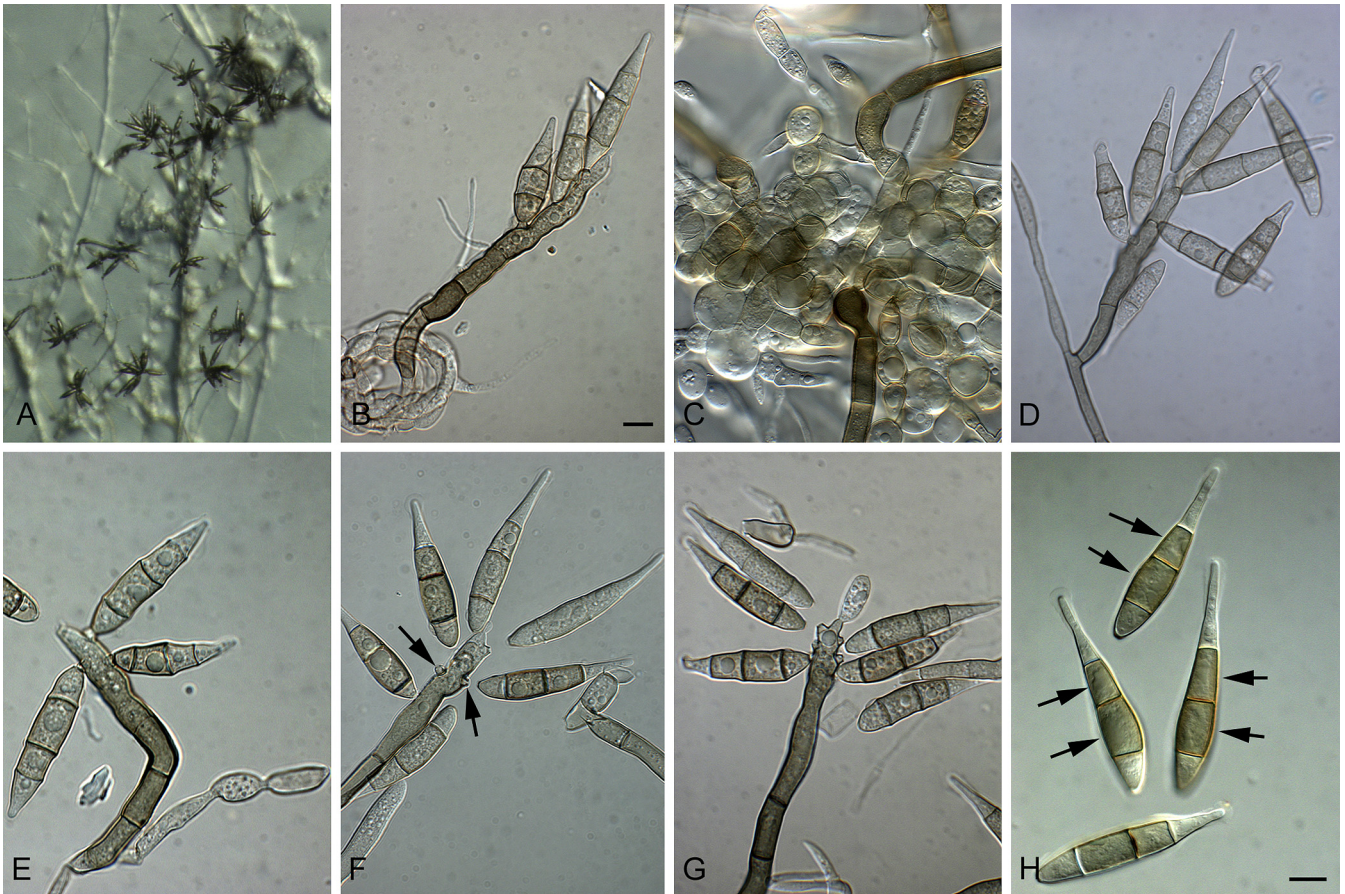


Fig. 4. *Pyriculariopsis parasitica* (CBS 114973). A–G. Conidiophores sporulating on SNA, having a rachis with conidia. H. Arrows indicate conidial median cells with darker pigmentation. Scale bars = 10 μ m.

fusoid, septate, slightly curved, tapering somewhat to base, forming appressoria at germination. *Asexual morph* phialophora-like. *Conidiogenous cells* developing on hyphae, phialidic, sub-cylindrical to ampulliform with flared collarette, hyaline. *Conidia* hyaline, aseptate, apex rounded, pointed towards base, straight to curved or sigmoid.

Type species: *Slopeiomyces cylindrosporus* (D. Hornby, Slope, Gutter. & Sivan.) Klaubauf, Lebrun & Crous

Notes: *Slopeiomyces* is morphologically similar to *Gaeumannomyces* in the general morphology of its sexual and asexual morphs, the production of appressoria, and its ecology, being a root pathogen of *Poaceae* (Hornby *et al.* 1975). The only obvious morphological difference lies in its ascospores, which are much shorter and wider than observed in species of *Gaeumannomyces*. The link between *S. cylindrosporus* and the asexual morph originally used in inoculation experiments, *Phialophora radiciola* var. *graminis*, could not be confirmed. Phylogenetically, however, *Slopeiomyces* is clearly distinct from *Gaeumannomyces* (see Fig. 2).

Slopeiomyces cylindrosporus (D. Hornby, Slope, Gutter. & Sivan.) Klaubauf, Lebrun & Crous, **comb. nov.** MycoBank MB810200.

Basionym: *Gaeumannomyces cylindrosporus* D. Hornby, Slope, Gutter. & Sivan., *Trans. Br. mycol. Soc.* 69: 21 (1977).

Materials examined: UK, on grass roots, associated with *Phialophora graminicola*, Dec. 1975, D. Hornby, cultures **ex-type** CBS 609.75, CBS 610.75, CBS 611.75.

Ophioceraeae Klaubauf, Lebrun & Crous, **fam. nov.** MycoBank MB810201.

Ascomata perithecial, immersed to superficial, scattered to separate, globose to subglobose, black, with long cylindrical, black, periphysate neck, pale brown at apex; wall consisting of several layers of *textura angularis*. *Paraphyses* hyaline, thin-walled, septate, intermingled among asci. *Asci* 8-spored, sub-cylindrical to narrowly fusoid, unitunicate, short-stipitate or not, with a large apical ring staining in Meltzer's iodine reagent. *Ascospores* curved to sigmoidal, septate, filiform, hyaline to olivaceous, with bluntly rounded ends, lacking sheath.

Type genus: *Ophioceras* Sacc., *Syll. fung.* (Abellini) 2: 358. 1883.

Type species: *Ophioceras dolichostomum* (Berk. & M.A. Curtis) Sacc., *Syll. fung.* (Abellini) 2: 358 (1883)

Genus included: *Ophioceras*.

Notes: Although *Ophioceras* is morphologically similar to *Gaeumannomyces*, the two genera can be distinguished by the aquatic habit of *Ophioceras*, occurring on wood and herbaceous material, versus the plant pathogenic nature of *Gaeumannomyces*, which has harpophora-like asexual morphs, mycelial appressoria, and a perithecial peridium of *textura epidermoidea* (Walker 1980, Chen *et al.* 1999). Although the family placement of *Ophioceras* was not resolved, the genus was temporarily added to the *Magnaporthaceae* (established for necrotrophic and hemibiotrophic plant pathogens infecting root and shoots of

Poaceae and *Cyperaceae*; Cannon 1994) awaiting further study (Shearer 1989, Shearer *et al.* 1999, Chen *et al.* 1999). As shown in the present analyses (Fig. 2) *Ophioceras* clearly clusters separate from the *Magnaporthaceae* in the *Magnaporthales*, and hence a separate family, the *Ophiocerales*, is introduced to accommodate it.

Pyriculariaceae Klaubauf, Lebrun & Crous, **fam. nov.** MycoBank MB810202.

Ascomata perithecial, immersed, black, with long cylindrical necks covered in setae. *Asci* subcylindrical, unitunicate, short-stipitate, with a large apical ring staining in Meltzer's iodine reagent. *Paraphyses* hyaline, thin-walled, septate, intermingled among asci. *Ascospores* septate, fusiform, often with median cells pigmented, lacking sheath. *Asexual morphs* hyphomycetous, with simple, branched conidiophores. *Conidiogenous cells* integrated, pigmented, denticulate. *Conidia* hyaline to brown, transversely septate, apical mucoid appendage rarely present.

Type genus: *Pyricularia* Sacc.

Type species: *Pyricularia grisea* Sacc.

Genera included: *Bambusicularia*, *Barretomyces*, *Deightonella*, *Macgarvieomyces*, *Neopyricularia*, *Proxipyricularia*, *Pseudopyricularia*, *Pyricularia*, *Xenopyricularia*.

Bambusicularia Klaubauf, Lebrun & Crous, **gen. nov.** MycoBank MB810203.

Etymology: Named after its occurrence on bamboo.

Plant pathogenic. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae. *Conidiophores* solitary, erect, straight or curved, unbranched, flexuous to geniculate, dark brown, finely roughened, up to 500 µm long, multi-septate; base bulbous, lacking rhizoids. *Conidiogenous cells* integrated, terminal and intercalary, pale brown at apex, intercalary cells medium brown, finely roughened, with several protruding denticles. *Conidia* solitary, ellipsoid to obclavate, medium brown, finely roughened, granular to guttulate, 2-septate, hilum truncate, somewhat protruding.

Type species: *Bambusicularia brunnea* Klaubauf, Lebrun & Crous

Notes: The main distinguishing character between *Bambusicularia* and *Pyricularia* is in their conidiophore morphology. Conidiophores in *Bambusicularia* are flexuous, longer, wider and darker brown than seen in species of *Pyricularia*. Conidia are pale brown, but appear to have darker brown septa. The two genera are also phylogenetically distinct (Figs 2, 3).

Bambusicularia brunnea Klaubauf, Lebrun & Crous, **sp. nov.** MycoBank MB810204. Fig. 5.

Etymology: Named after its dark brown conidiophores.

On SNA on sterile barley seed. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae, 2–3 µm diam. *Conidiophores*

solitary, erect, straight or curved, unbranched, flexuous to geniculate, dark brown, finely roughened, 280–500 × 5–7 µm, 5–11-septate; base bulbous, lacking rhizoids, 7–10 µm diam. *Conidiogenous cells* 20–120 × 4–6 µm, integrated, terminal and intercalary, pale brown at apex, intercalary cells medium brown, finely roughened, with several protruding denticles, 1–2 µm long, 1.5–2 µm diam. *Conidia* solitary, ellipsoid to obclavate, medium brown, finely roughened, granular to guttulate, 2-septate, (20–) 21–25(–27) × 10–11(–11.5) µm; apical cell 4–7 µm long, basal cell 6–9 µm long; hilum truncate, protruding, 0.5–1 µm long, 1.5–2 µm diam.

Culture characteristics: Colonies on MEA white, round, cottony, slightly raised, reaching 3.8 cm diam after 1 wk; reverse ochreous. Colonies on PDA transparent with white centre, flat, round, slightly cottony, reaching up to 3.7 cm after 1 wk, with diffuse, hairy margin. Colonies on CMA and OA transparent, smooth, flat, round, reaching up to 3.3 cm diam after 1 wk; colonies fertile.

Materials examined: **Japan**, Aichi, on *Sasa* sp. (*Poaceae*), 1992, S. Koizumi [**holotype** CBS H-21839, culture **ex-type** CBS 133599 = MAFF 240225 = INA-B-92-45(Ss-1J)]; Aichi, on *Phyllostachys bambusoides* (*Poaceae*), 1993, S. Koizumi, CBS 133600 = MAFF 240226 = INA-B-93-19(Ph-1J).

Note: Isolate CBS 133600 sporulated poorly, and had slightly larger conidia than CBS 133599, measuring (23–) 25–30(–34) × (7–)8–9 µm; apical cell 7–11 µm long, basal cell 7–10 µm long.

Barretomyces Klaubauf, Lebrun & Crous, **gen. nov.** MycoBank MB810205.

Etymology: Named after Prof. dr. Robert W. Barreto, in acknowledgement of his contribution to mycology and plant pathology in Brazil.

Plant pathogenic. *Mycelium* consisting of verruculose, pale brown, branched, septate hyphae. *Conidiophores* macro-nematous, rarely branched, straight, septate, pale brown near the base, subhyaline at the apex. *Conidiogenous cells* cylindrical, terminal, denticulate; each denticle cylindrical, thin-walled, mostly cut off by a septum to form a separating cell. *Conidia* solitary, dry, obclavate, basal and terminal cell hyaline to pale brown, median cell darker brown, smooth, 4(–5)-septate.

Type species: *Barretomyces calathea* (D.J. Soares, F.B. Rocha & R.W. Barreto) Klaubauf, Lebrun & Crous

Notes: *Barretomyces calathea*, which is a foliar pathogen of *Calathea longifolia* in Brazil (Soares *et al.* 2011), was originally described in *Pyriculariopsis* based on its versicoloured conidia (with paler basal cell). Furthermore, they noted this species to have schizolytic secession, and Ellis (1971) defined *Pyriculariopsis* as having schizolytic secession, in contrast to the rhexolytic secession observed in *Pyricularia*. We have however found conidiogenesis to be variable, and not a good taxonomic criterion in distinguishing these genera.

Barretomyces calathea (D.J. Soares, F.B. Rocha & R.W. Barreto) Klaubauf, Lebrun & Crous, **comb. nov.** MycoBank MB810206. Fig. 6.



Fig. 5. *Bambusicularia brunnea* (CBS 133599). A. Sporulation on sterile barley seed on SNA. B, C. Sporulation on sterile barley leaves. D–H. Conidiophores bearing conidia. I. Conidia. Scale bars = 10 μ m.

Basionym: *Pyriculariopsis calathea* D.J. Soares, F.B. Rocha & R.W. Barreto, Mycol. Prog. 10: 317. 2011.

Leaf spots amphigenous, 0.5–11 cm diam, progressing from small yellow spots to large, circular to elliptic, grey-brown lesions, sometimes with a darker centre and with concentric circles, the outer region being dark-brown, surrounded by a large chlorotic border; sometimes coalescing, leading to leaf necrosis; disease symptoms also occurring on leaf petioles, as brown spots. On SNA medium. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae, 2–3.5 μ m diam. *Conidiophores* forming from hyphae, solitary, erect, straight or curved, unbranched, medium brown, smooth, 70–160 \times 4–6 μ m, 2–9-septate. *Conidiogenous cells* 20–70 \times 5–6 μ m, integrated, terminal and intercalary, pale to medium brown, smooth, forming a rachis with several protruding flat-tipped denticles, 1–3 μ m long, 1–2 μ m diam. *Conidia* solitary, obclavate, smooth, basal and terminal cell hyaline to pale brown, median cell darker brown, granular to guttulate, 2-septate, (19–)28–32(–35) \times (5.5–)6–7(–8) μ m; apical cell

tapered, 9–12 μ m long, basal cell 7–9 μ m long; base tapering prominently to a truncate, protruding hilum, 1–1.5 μ m diam.

Culture characteristics: Colonies on MEA white, round, raised, with a thick, furry texture, reaching 3 cm diam after 1 wk; reverse cinnamon. Colonies on OA white with a mouse grey centre, reaching 3.2 cm after 1 wk. Colonies on CMA white to pale mouse grey, round with entire edge, flat, felty, exuding droplets, reaching 3.3 cm after 1 wk, sporulating in centre. Colonies on PDA whitish, transparent with vinaceous-buff centre, irregular in shape, felty, reaching 2.8 cm after 1 wk.

Materials examined: **Brazil**, Minas Gerais, Viçosa, 'Mata do Seu Nico' on *Calathea longifolia* (Marantaceae), Dec. 2003, D.J. Soares (*holotype* VIC 30699, culture *ex-type* culture CBMAI 1060); Minas Gerais, Viçosa, on *C. longifolia*, Aug. 2010, P.W. Crous, CBS 129274 = CPC 18464.

Notes: A microconidial state was observed being similar in morphology to that reported for *P. oryzae* (Chuma *et al.* 2009, Zhang *et al.* 2014), and also observed in this study for



Fig. 6. *Barretomyces calatheae* (CBS 129274). A. Leaf spot on *Calathea longifolia* in Brazil. B–G. Conidiophores bearing conidia. H. Conidia. Scale bars = 10 µm.

P. grisea. The denticles of *Barretomyces* are different to those of *Pyricularia*, in that they are flat-tipped, but with a central pore.

Deightoniella S. Hughes, Mycol. Pap. 48: 27. 1952.
= *Utrechtiana* Crous & Quaedvl., Persoonia 26: 153. 2011.

Plant pathogenic. *Conidiophores* solitary, erect, aggregated, brown, smooth, becoming pale brown towards apex, base swollen, partly immersed in epidermis, but lacking rhizoids, with circular scar where base of conidiophore is attached to immersed hyphal network; conidiophore with swellings (twisted growth) along its axis, swellings coinciding with internal conidiophore proliferation (percurrently) through conidial scars; lacking transverse septa and reduced to conidiogenous cells (though some species have a basal septum). *Conidiogenous cells* integrated terminal, with truncate and flattened scar; sometimes thickened, not darkened, nor refractive. *Conidia* pale brown, ellipsoid to pyriform, guttulate to granular, finely verruculose, 1-septate slightly above the conidial median, thin-walled, apex bluntly to acutely rounded, base obtusely rounded with a flattened, darkened and thickened hilum that has a central pore, and minute marginal frill.

Type species: Deightoniella africana S. Hughes

Deightoniella roumegueri (Cavara) Constant., Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 86(2): 137. 1983. Fig. 7.

Basionym: Scolicotrichum roumegueri Cavara (as “roumegueri”), in Briosi & Cavara, Funghi Parass. Piante Colt. od Utili, Fasc. 5: no. 112. 1890.

= *Utrechtiana cibiessia* Crous & Quaedvl., Persoonia 26: 153. 2011.

Description and illustration: Constantinescu (1983), Crous et al. (2011).

Material examined: Netherlands, Utrecht, De Uithof University Campus, intersection of Harvardlaan with Uppsalalaan, on leaves of *Phragmites australis* growing along water canals, 14 Dec. 2010, W. Quaedvlieg (*holotype* of *U. cibiessia* CBS H-20594, cultures *ex-type* CPC 18917, 18916 = CBS 128780).

Notes: Deightoniella as presently defined is heterogeneous. The genus *Deightoniella* (based on *D. africana*, occurring on leaves of *Imperata cylindrica* var. *africana*; *Poaceae*) has solitary conidiophores, with conidiogenous cells that rejuvenate percurrently. *Deightoniella* is distinct from *Neodeightoniella*, as the latter does not undergo percurrent rejuvenation, has conidiophores arranged in fascicles, well-developed apical and intercalary conidiogenous loci, and conidia with mucoid caps (Crous et al. 2013).

Macgarvieomyces Klaubauf, Lebrun & Crous, *gen. nov.*
Mycobank MB810207.

Etymology: Named after Quentin D. MacGarvie, the Scottish plant pathologist that first named these species.

Plant pathogenic. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae. *Chlamydospores* brown, ellipsoid, arranged in chains. *Conidiophores* solitary, erect, straight or curved, mostly unbranched, medium brown, smooth, septate. *Conidiogenous cells* integrated, terminal, rarely intercalary, medium brown, smooth, forming a rachis with several protruding denticles, appearing flat-tipped. *Conidia* solitary, narrowly

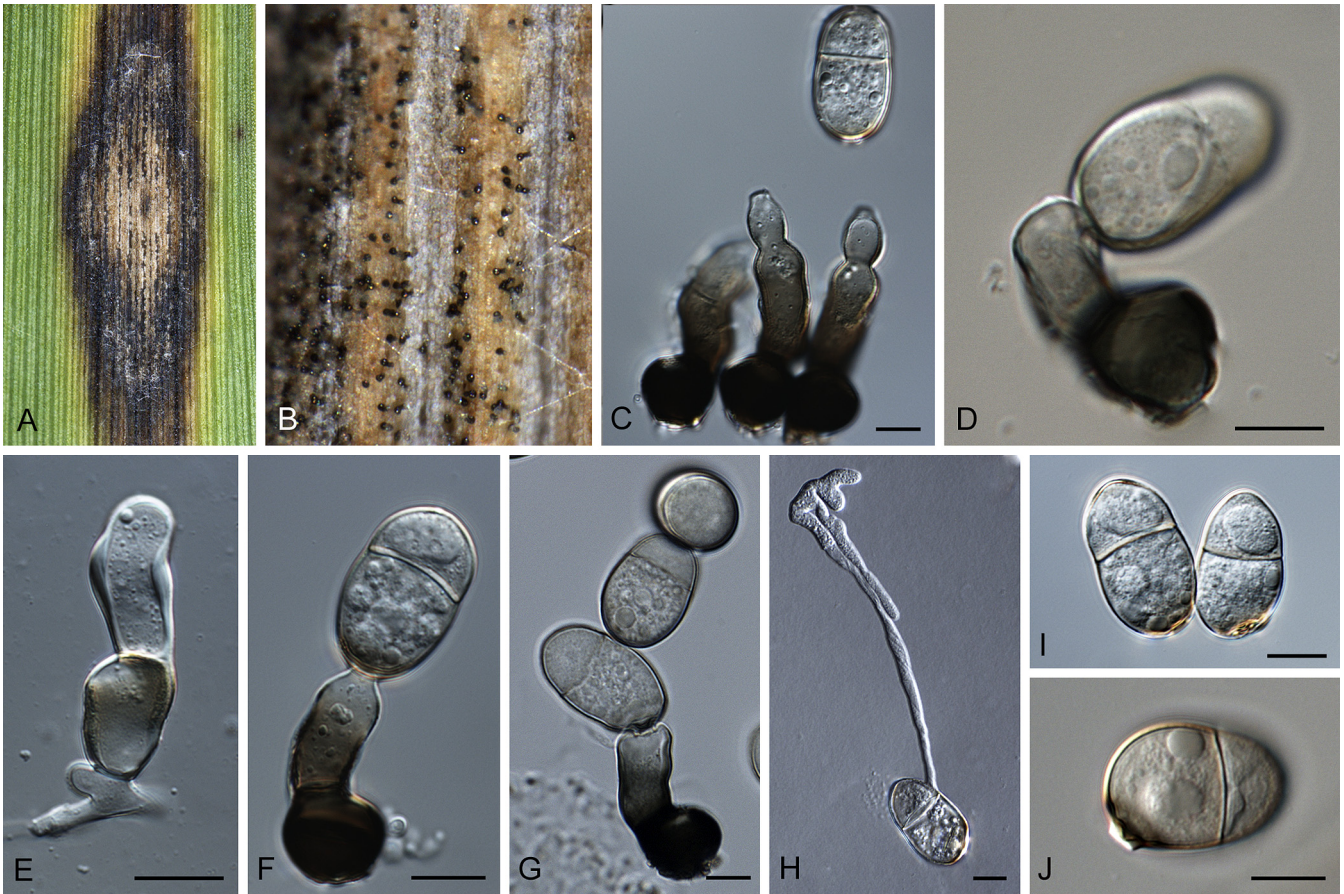


Fig. 7. *Deightonella roumeguerei* (CBS 128780). A. Leaf spot on *Phragmites australis*. B. Close-up of conidiophores on leaf surface. C–G. Conidiophores bearing conidia. H. Germinating conidium. I, J. Conidia. Scale bars = 10 µm.

obclavate, hyaline, smooth, granular and guttulate, medianly 1-septate; hilum somewhat thickened, not refractive, nor darkened.

Type species: Macgarvieomyces borealis (de Hoog & Oorschot) Klaubauf, Lebrun & Crous

Notes: MacGarvie described two species occurring on *Juncus* in the genus *Diplorhynchium*. de Hoog (1985) treated this genus as synonym of *Dactylaria*, but preferred to retain the plant pathogenic species in *Pyricularia*. As these taxa are clearly not congeneric with *Pyricularia* (Figs 2, 3), a new genus, *Macgarvieomyces*, is herewith introduced to accommodate them.

Macgarvieomyces borealis (de Hoog & Oorschot) Klaubauf, Lebrun & Crous, **comb. nov.** MycoBank MB810208. *Basionym:* *Pyricularia borealis* de Hoog & Oorschot (as “*boreale*”), Stud. Mycol. 26: 114. 1985. (a nom. nov. for *D. juncicola* MacGarvie 1965).

≡ *Diplorhynchium juncicola* MacGarvie, Trans. Br. mycol. Soc. 48(2): 269. 1965.

≡ *Dactylaria juncicola* (MacGarvie) G.C. Bhatt & W.B. Kendr., Canad. J. Bot. 46: 1257. 1968.

Illustration: de Hoog (1985).

On OA. *Conidiophores* scattered, pale olivaceous-brown, thick-walled near the base, 7–9 µm diam, tapering towards the apex, 30–70 µm long, 1–3-septate. *Conidiogenous cells* apical, with flat-tipped denticles, 2 µm diam, unthickened, not pigmented. *Conidia* solitary, 1–4 per conidiogenous cell, subhyaline,

ellipsoid with obtuse apex, tapering in basal cell towards obconically truncate base, slightly constricted at median septum, 16–17(–40) × 6–9 µm. (Description from de Hoog 1985).

Culture characteristics: Colonies on MEA buff to rosy buff with entire edge, umbonate to conical colony with somewhat velvety texture, reaching up to 3.3 cm diam after 2 wk; reverse ochreous and buff towards the edge. Colonies on CMA and OA transparent with smooth surface, reaching up to 3.5 cm diam after 2 wk. On PDA whitish to buff colony with honey centre, irregular outline, slightly furrowed in centre, reaching up to 3 cm diam after 2 wk; colony reverse whitish to buff with honey centre. No sporulation was observed.

Material examined: UK, Scotland, Moorland near Carnwat in Lanarkshire, 275 m alt. and near East Graigs, Edinburgh, 33 m alt., associated with leaf spots on *Juncus effusus*, Apr 1964, G.D. MacGarvie, culture **ex-type** CBS 461.65.

Macgarvieomyces juncicola (MacGarvie) Klaubauf, Lebrun & Crous, **comb. nov.** MycoBank MB810209. *Fig. 8.* *Basionym:* *Pyricularia juncicola* MacGarvie, Scientific Proc. R. Dublin Soc., Ser. B 2(no. 16): 155. 1968.

On SNA on sterile barley seed. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae, 1.5–2 µm diam. *Chlamydospores* arranged in intercalary chains, ellipsoid, hyaline to pale brown, smooth, 5–7 µm diam, frequently giving rise to conidiophores. *Conidiophores* solitary, erect, straight or curved, mostly unbranched, medium brown, smooth, 50–200 × 3–5 µm, with basal septum, developing additional septum if branched.

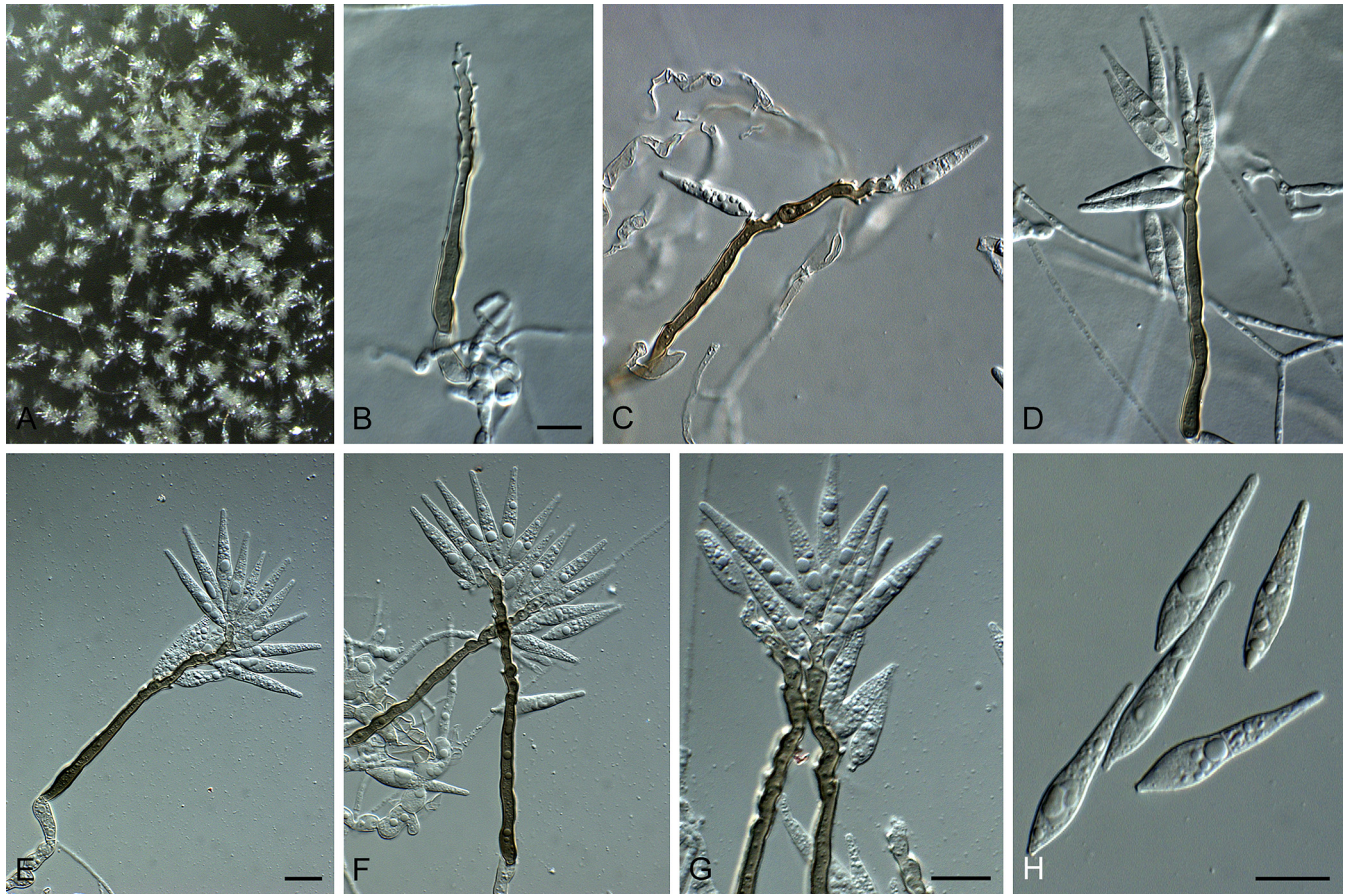


Fig. 8. *Macgarvieomyces juncicola* (CBS 610.82). A. Colony sporulating on OA. B–G. Conidiophores and conidia forming on SNA. H. Conidia. Scale bars = 10 µm.

Conidiogenous cells 50–180 × 3–5 µm, integrated, terminal, rarely intercalary, medium brown, smooth, forming a rachis with several protruding denticles, 1.5–2 µm long, 1–1.5 µm diam. *Conidia* solitary, narrowly obclavate, hyaline, smooth, granular and guttulate, medianly 1-septate, (17–)25–30(–32) × (4–)5 µm; hilum somewhat thickened, 1–1.5 µm diam.

Culture characteristics: Colonies on MEA isabelline with pale olivaceous grey central mycelium, slightly raised wool-like texture, round and hairy edge, reaching up to 2.6 cm after 1 wk; reverse iron grey. On CMA and OA olivaceous to grey olivaceous, flat, smooth and velutinous surface, undulate edge. Colonies fertile on MEA, CMA and OA. Colonies on PDA white with buff centre, round, flat, fringed edge, reverse white with buff centre.

Material examined: **Netherlands**, on stem base of *Juncus effusus*, 3 Nov. 1982, G.S. de Hoog, specimens CBS H-11668; CBS H-1764; CBS H-17648, culture CBS 610.82.

Note: *Macgarvieomyces borealis* and *M. juncicola* can be distinguished based on conidial dimensions, because conidia of *M. juncicola* are on average longer and narrower.

Neopyricularia Klaubauf, Lebrun & Crous, **gen. nov.** MycoBank MB810210.

Etymology: Named after its morphological similarity to *Pyricularia*.

Plant pathogenic. *Conidiophores* solitary or in fascicles, sub-cylindrical, erect, olivaceous, smooth, rarely branched, septate,

with sympodial growth. *Conidiogenous cells* terminal and intercalary, olivaceous, with denticulate conidiogenous loci, slightly darkened, and rhexolitic secession. *Conidia* solitary, formed sympodially, pyriform to obclavate, narrowed toward tip, rounded at the base, 2-septate, subhyaline to pale brown, with a distinct protruding basal hilum, and minute marginal frill.

Type species: *Neopyricularia commelinicola* (M.J. Park & H.D. Shin) Klaubauf, Lebrun & Crous

Neopyricularia commelinicola (M.J. Park & H.D. Shin) Klaubauf, Lebrun & Crous, **comb. nov.** MycoBank MB810507. Fig. 9.

Basionym: *Pyricularia commelinicola* M.J. Park & H.D. Shin, Mycotaxon 108: 452. 2009.

Description: Park & Shin (2009).

Materials examined: **South Korea**, Hongcheon, Bukbang-ri, 37°48'1" N, 127°51'9" E, on leaves of *Commelina communis*, 9 Sep. 2007, H.D. Shin & M.J. Park (**holotype** KUS (F) 22838, culture **ex-type** CBS 128308 = KACC 43081); Hongcheon, on *C. communis*, 30 June 2009, H.D. Shin & M.J. Park, CBS 128303 = KACC 44637; Pocheon, on *C. communis*, 29 July 2008, M.J. Park, CBS 128306 = KACC 43869; Hongcheon, on *C. communis*, 27 Oct. 2008, H.D. Shin & M.J. Park, CBS 128307 = KACC 44083.

Notes: Characteristic for this species is its long, flexuous, branched, pale brown, smooth conidiophores, with a terminal rachis, with terminal and intercalary conidiogenous cells with denticle-like loci that are 2–3 µm long and wide, not thickened, but trapping air (also in conidial hila), so appearing thickened.

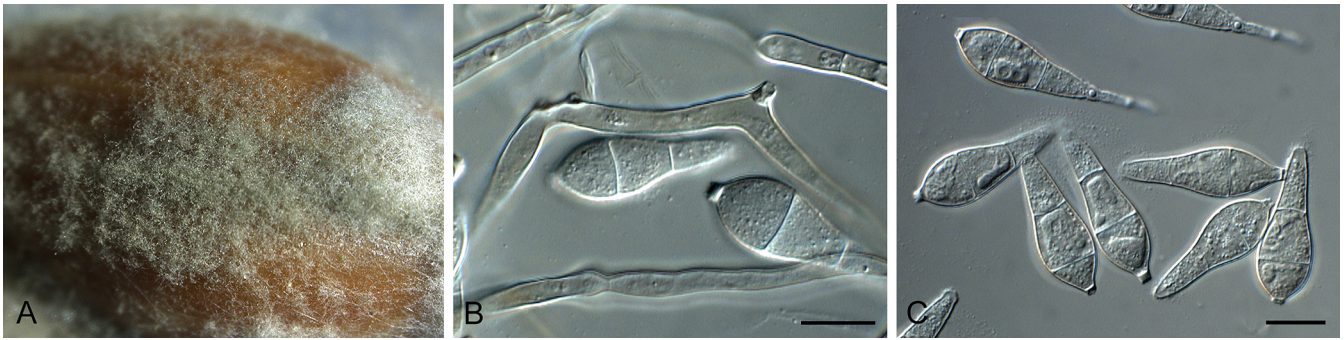


Fig. 9. *Neopyricularia commelinicola* (CBS 128308). A. Sporulation on sterile barley seed on SNA. B. Conidiophores and conidia. C. Conidia. Scale bars = 10 μ m.

Conidia are pyriform to obclavate, subhyaline to pale brown, 2-septate, (27–)30–38(–40) \times (9–)10–11(–13) μ m (on SNA). Phylogenetically *P. commelinicola* does not cluster within clades corresponding to species of *Pyricularia* s. str. (Figs 2, 3), and hence a new genus is introduced to accommodate it.

Proxipyricularia Klaubauf, Lebrun & Crous, **gen. nov.** MycoBank MB810211.

Etymology: Named after the fact that it is morphologically similar to the genus *Pyricularia*.

Plant pathogenic. *Conidiophores* solitary or in fascicles, subcylindrical, erect, olivaceous to medium brown, smooth, septate. *Conidiogenous cells* terminal and intercalary, pale brown, with denticulate conidiogenous loci and rhexitic secession. *Conidia* solitary, formed sympodially, pyriform to obclavate, narrowed toward tip, rounded at the base, 2-septate, subhyaline to pale brown, with a distinct protruding basal hilum, frequently with minute marginal frill.

Type species: *Proxipyricularia zingiberis* (Y. Nisik.) Klaubauf, Lebrun & Crous

Note: *Proxipyricularia* is morphologically similar to *Pyricularia*, but phylogenetically distinct (Figs 2, 3).

Proxipyricularia zingiberis (Y. Nisik.) Klaubauf, Lebrun & Crous, **comb. nov.** MycoBank MB810212. Fig. 10.

Basionym: *Pyricularia zingiberis* Y. Nisik. (as “*Piricularia zingiberi*”), Ber. Ohara Inst. Landwirt. Forsch. 1(2): 216. 1917.



Fig. 10. *Proxipyricularia zingiberis* (CBS 133594). A. Conidiophore forming on SNA. B. Conidia. Scale bars = 10 μ m.

On SNA on sterile barley seed. *Conidiophores* solitary or in fascicles, subcylindrical, erect, olivaceous to medium brown, smooth, 2–4-septate, 50–180 \times 1.5–4 μ m. *Conidiogenous cells* terminal and intercalary, pale brown, with denticulate conidiogenous loci and rhexitic secession. *Conidia* 14–20(–24) \times (5–)6–8(–9.5) μ m, apical cell 5–8 μ m long, basal cell 5–7 μ m long, solitary, pyriform to obclavate, narrowed toward tip, rounded at the base, 2-septate, subhyaline to pale brown, with a distinct protruding basal hilum and marginal frill.

Materials examined: Japan, Hyogo, on *Zingiber mioga*, 2002, H. Kato, CBS 133594 = MAFF 240222 = HYZiM201-0-1(Z-2J); location unknown, on *Zingiber officinale*, Jan 1939, Y. Nisikado, CBS 303.39 = MUCL 9449; Hyogo, on *Zingiber mioga*, 2003, I. Chuma, CBS 132195 = MAFF 240224 = HYZiM201-1-1-1(Z-4J); Hyogo, on *Zingiber mioga*, 2003, I. Chuma, CBS 132196 = MAFF 240223 = HYZiM202-1-2(Z-3J); Hyogo, on *Zingiber mioga*, 1990, M. Ogawa, CBS 132355 = MAFF 240221 = HYZiM 101-1-1-1(Z-1J).

Notes: *Proxipyricularia zingiberis* is phylogenetically distant (Figs 2, 3) from *Pyricularia* s. str., although morphologically, it appears similar, with medium brown conidiophores and a terminal and intercalary denticulate rachis, and subhyaline, 2-septate, obclavate conidia. Isolates of *P. zingiberis* from *Zingiber mioga* and *Z. officinale* are able to infect both plants, but not *Oryza*, *Setaria* or *Panicum* spp. (Nishikado 1917, Kato et al. 2000). Nishikado (1917) regarded the fungus from *Zingiber* as genetically distant from *Pyricularia* species isolated from rice or other *Poaceae*, as well as (Kato et al. 2000) using RFLP patterns and (Hirata et al. 2007) using multilocus sequence analysis.

Pseudopyricularia Klaubauf, Lebrun & Crous, **gen. nov.** MycoBank MB810213.

Etymology: Named after its morphological similarity to *Pyricularia*.

Plant pathogenic. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae. *Conidiophores* solitary, erect, straight or curved, branched or not, medium brown, finely roughened, septate. *Conidiogenous cells* integrated, terminal, rarely intercalary, medium brown, finely roughened, forming a rachis with several protruding, flat-tipped denticles. *Conidia* solitary, obclavate, pale to medium brown, finely roughened, guttulate, 2-septate; hilum truncate, slightly protruding, unthickened, not darkened.

Type species: *Pseudopyricularia kyllingae* Klaubauf, Lebrun & Crous

Notes: Several isolates previously identified as representative of *P. higginsii* were found to belong to a complex of three related

species (Fig. 3) classified into *Pseudopyricularia* (*P. cyperi*, *P. kyllingae* and *P. higginsii*). Taxa in this complex are primarily distinguished from *Pyricularia* s. str. by having short, determinate, brown conidiophores with an apical rachis with flat-tipped denticles. It was also based on this character, that Ellis (1976) originally suspected *P. higginsii* to represent a species of *Dactylaria*.

Pseudopyricularia cyperi Klaubauf, Lebrun & Crous, sp. nov. MycoBank MB810214. Fig. 11.

Etymology: Named after the host genus from which it was collected, *Cyperus*.

On SNA on sterile barley seed. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae, 1–2 µm diam. *Conidiophores* solitary, erect, straight or curved to geniculate, branched, medium brown, smooth, 40–100 × 3–4 µm, 1–5-septate. *Conidiogenous cells* 35–70 × 3–4 µm, integrated, terminal and intercalary, pale brown, smooth, forming a rachis with several protruding, flat-tipped denticles, 2–3 µm long, 1.5–2 µm diam. *Conidia* solitary, obclavate, medium brown, smooth to finely roughened, granular and guttulate, 2-septate, (22–) 25–28(–35) × (4–)5(–6) µm; apical cell 12–17 µm long, basal cell 7–9 µm long; hilum truncate, slightly protruding, 1.5–2 µm diam, unthickened, not darkened.

Culture characteristics: Colonies on MEA buff, round, raised, cottony, reaching up to 1.8 cm diam after 1 wk; reverse ochreous. On CMA and OA transparent, round to undulate colonies with smooth surface. Colonies on PDA white, round, diffuse edge, cottony, reaching up to 2.2 cm diam after 1 wk; reverse buff.

Materials examined: **Israel**, on *Cyperus rotundus*, date unknown, R. Kenneth, specimen CBS H-17647, culture CBS 665.79. **Japan**, Hyogo, on *Cyperus iria*, 2002, H. Kato (**holotype** CBS H-21840, culture **ex-type** CBS 133595). **Philippines**, Sto Tomas, Batangas, on *Cyperus rotundus*, 1983, IRRI collector unknown, CR88383 (Borromeo et al. 1993) = PH0053.

Notes: The distinguishing character of this species is its conidiophores that are commonly branched, forming a rachis with flat-tipped denticles. Morphologically it is similar to *P. higginsii*, except that conidia are longer and narrower in culture (26.1–28.6 × 6–6.1 µm; av. 26.1 × 6.1 µm) (Luttrell 1954).

Pseudopyricularia higginsii (Luttr.) Klaubauf, Lebrun & Crous, **comb. nov.** MycoBank MB810215.

Basionym: *Pyricularia higginsii* Luttr., Mycologia 46: 810. 1954.
= *Dactylaria higginsii* (Luttr.) M.B. Ellis, Dematiaceous Hyphomycetes (Kew): 173. 1976.

Material examined: **New Zealand**, Auckland, Mount Albert, Carrington Road, UNITEC Technical Institute, on dead leaves of *Typha orientalis*, 30 Apr. 2007, C.F. Hill, specimen in PDD, culture CBS 121934.

Notes: *Pyricularia higginsii* was originally described from *Cyperus* sp. in Georgia (Luttrell 1954). Conidiophores were described as being 3-septate, up to 76 µm long, while conidia were 2-septate, 17.5–36.5 × 5.3–6.5 µm (av. 28 × 6 µm), in culture 26.1–28.6 × 6–6.1 µm (av. 26.1 × 6.1 µm) (Luttrell 1954). Species in the *Pseudopyricularia higginsii* complex are all very similar based on their conidial dimensions, and fresh collections from Georgia would be required to resolve the phylogeny of *P. higginsii*.

Pseudopyricularia kyllingae Klaubauf, Lebrun & Crous, sp. nov. MycoBank MB810218. Fig. 12.

Etymology: Named after the host genus from which it was collected, *Kyllinga*.

On SNA on sterile barley seed. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae, 1.5–2 µm diam. *Conidiophores* solitary or in fascicles of 2–3, erect, straight or curved, branched or not, medium brown, finely roughened, 50–80 × 4–6 µm, 1–3-septate. *Conidiogenous cells* 15–60 × 3–4 µm, integrated, terminal, rarely intercalary, medium

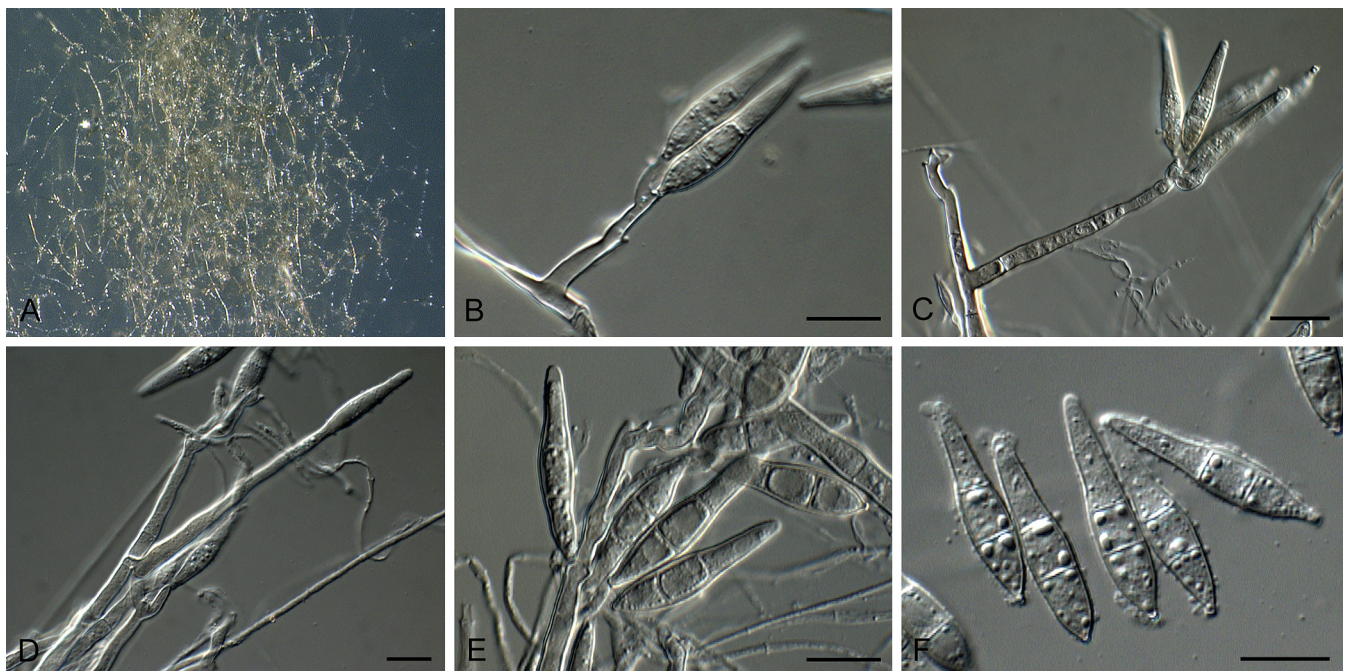


Fig. 11. *Pseudopyricularia cyperi* (CBS 133595). A. Sporulation on SNA. B–E. Conidiophores. F. Conidia. Scale bars = 10 µm.

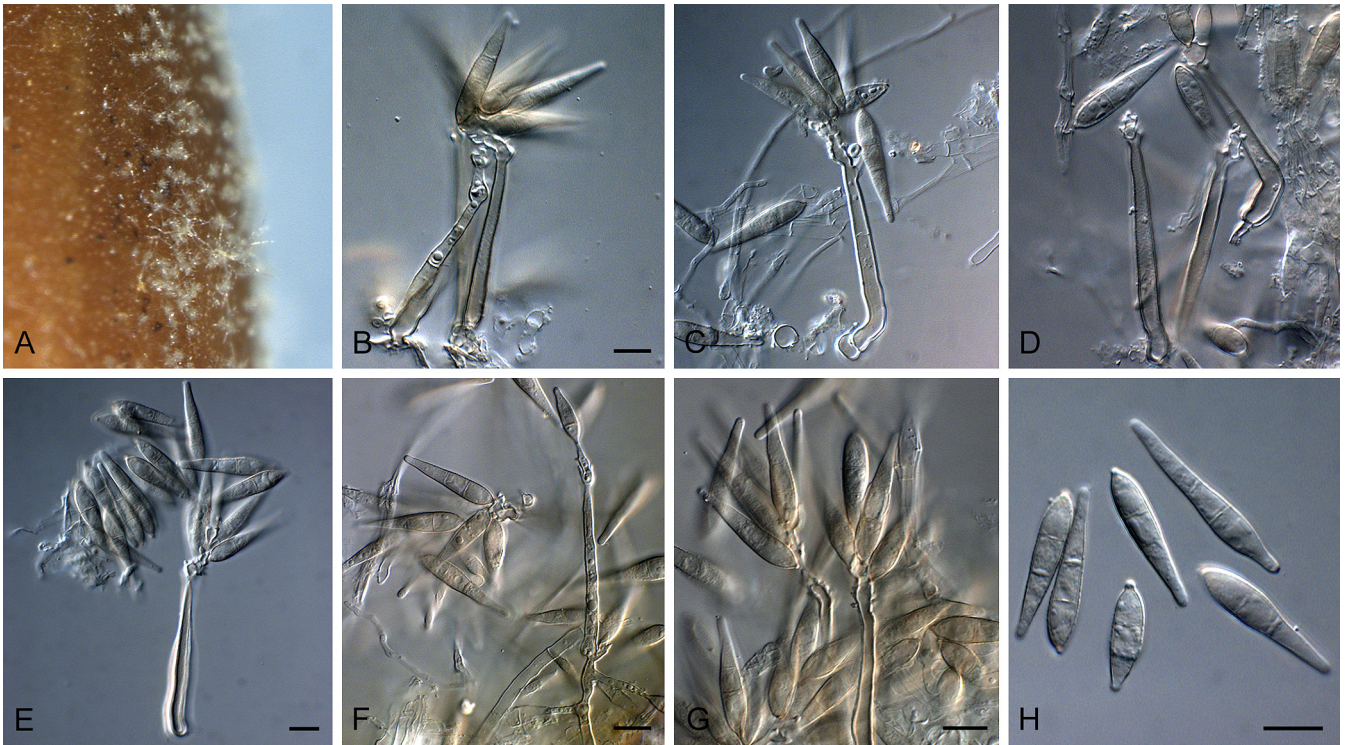


Fig. 12. *Pseudopyricularia kyllingae* (CBS 133597). A. Sporulation on sterile barley seed on SNA. B–G. Conidiophores and conidia. H. Conidia. Scale bars = 10 μ m.

brown, finely roughened, forming a rachis with several protruding, flat-tipped denticles, 1–2 μ m long, 1–1.5 μ m diam. *Conidia* solitary, obclavate, pale to medium brown, finely roughened, guttulate, 2-septate, (23–)27–30(–35) \times (5–)6(–7) μ m; apical cell 12–20 μ m long, basal cell 9–10 μ m long; hilum truncate, slightly protruding, 1–1.5 μ m diam, unthickened, not darkened.

Culture characteristics: Colonies on MEA transparent, funiculate, reaching up to 6.5 cm diam after 1 wk; reverse ochreous. On CMA transparent smooth colony, reaching up to 5 cm diam after 1 wk. On PDA transparent colony, plate covering after 1 wk; transparent reverse.

Materials examined: **Japan**, Hyogo, on *Kyllinga brevifolia*, 2003, I. Chuma (**holotype** CBS H-21841, culture **ex-type** CBS 133597). **Philippines**, Los Banos, Laguna, on *Cyperus brevifolius*, 1989, IIRRI collector unknown, CB8959 (Borromeo *et al.* 1993) = PH0054.

Note: Morphologically similar to *P. higginsii* (26.1–28.6 \times 6–6.1 μ m; av. 26.1 \times 6.1 μ m *sensu* Luttrell 1954), except that conidia of *P. kyllingae* (23–35 \times 5–7 μ m; av. 29 \times 6 μ m) are longer in culture.

Pyricularia Sacc., *Michelia* 2(no. 6): 20. 1880.

Plant pathogenic. *Conidiophores* solitary or in fascicles, subcylindrical, erect, brown, smooth, rarely branched, with sympodial proliferation. *Conidiogenous cells* terminal and intercalary, pale brown, with denticulate conidiogenous loci and rhexolytic secession. *Conidia* solitary, pyriform to obclavate, narrowed toward tip, rounded at the base, 2-septate, hyaline to pale brown, with a distinct basal hilum, sometimes with marginal frill. *Ascomata* perithecial, solitary to gregarious, subspherical, brown to black, base immersed in host tissue, with long neck protruding above plant tissue; wall consisting of several layers of brown *textura angularis*. *Asci* 8-spored, hyaline, subcylindrical to

clavate, unitunicate, short-stipitate, with prominent apical ring. *Paraphyses* intermingled among asci, unbranched, septate. *Ascospores* bi- to multiseriate in asci, hyaline, guttulate, smooth-walled, fusiform, curved with rounded ends, transversely 3-septate, slightly constricted at septa.

Type species: *Pyricularia grisea* Sacc., *Michelia* 2(no. 6): 20. 1880.

Pyricularia ctenantheicola Klaubauf, Lebrun & Crous, **sp. nov.** MycoBank MB810219. Fig. 13.

Etymology: Named after the host genus from which it was collected, *Ctenanthe*.

On SNA on sterile barley seed. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae, 1.5–2 μ m diam. *Conidiophores* solitary, erect, straight or curved, branched or not, medium brown, smooth, 70–200 \times 3–5 μ m, 1–6-septate; base bulbous, lacking rhizoids, 7–10 μ m diam. *Conidiogenous cells* 40–110 \times 3–5 μ m, integrated, terminal and intercalary, pale brown, smooth, with several protruding denticles, 1–2 μ m long, 1–1.5 μ m diam. *Conidia* solitary, pyriform to obclavate, pale brown, finely roughened, granular to guttulate, 2-septate, (19–)20–24(–33) \times (6–)7(–8) μ m; apical cell 7–10 μ m long, basal cell 5–7 μ m long; hilum truncate, 0.5–1.5 μ m long, 1.5–2 μ m diam, unthickened, not darkened.

Culture characteristics: Colonies on MEA white to vinaceous buff, cottony, with undulating margin, reaching up to 2.7 cm diam after 1 wk; reverse ochreous to umber. Colonies on CMA pale luteous, with hazel centre, reaching up to 2.5 cm diam after 1 wk. Colonies on PDA hazel, with smoke grey tufts, reaching up to 3.5 cm diam after 1 wk; reverse hazel. Colonies on OA reaching up to 3.5 cm after 1 wk, sporulating abundantly after 1 wk in the dark.

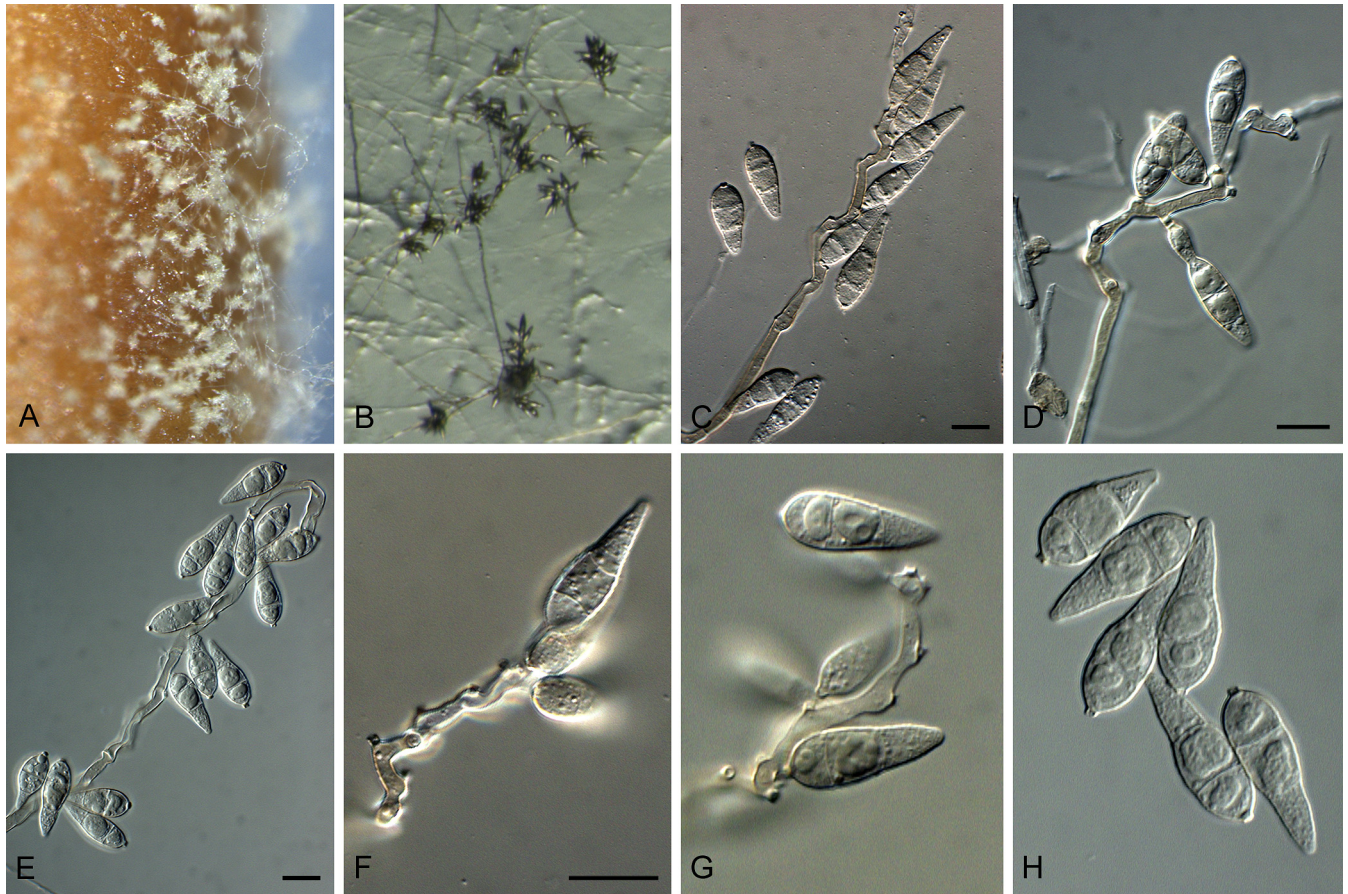


Fig. 13. *Pyricularia ctenantheicola* (GR0002). A. Sporulation on sterile barley seed on SNA. B. Sporulation on SNA. C–G. Conidiophores and conidia. H. Conidia. Scale bars = 10 µm.

Materials examined: Greece, Almyros, on *Ctenanthe oppenheimiana* imported from Brazil via Netherlands, 1998, A.C. Pappas & E.J. Paplomatas (**holotype** CBS H-21842, culture **ex-type** CBS 138601 = GR0002); *ibid.*, GR0001 = Ct-4 = ATCC 200218.

Note: Although the leaf spot disease of *Ctenanthe* has previously been reported (Pappas & Paplomatas 1998), the fungus was never officially named.

***Pyricularia grisea* Sacc.,** *Michelia* 2(no. 6): 20. 1880. **Fig. 14.**

Basionym: *Ceratospheeria grisea* T.T. Hebert, *Phytopathology* 61(1): 86. 1971.

= *Magnaporthe grisea* (T.T. Hebert) M.E. Barr, *Mycologia* 69(5): 954. 1977.

Materials examined: Brazil, on *Digitaria horizontalis*, date and collector unknown, Br33; Goias, Goiana, on *Digitaria sanguinalis*, 1989, J.-L. Nottéghem, BR0029. Japan, on *Digitaria smutsii*, date and collector unknown, JP0034 = NI980. Korea, Woanju, on *Echinochloa crus-galli* var. *frumentacea*, date unknown, H.K. Sim, CBS 128304 = KACC 41641. Philippines, Sto Tomas, Batangas, on *Digitaria ciliaris*, 1988, IIRI collector unknown, Dc88420 (Borromeo *et al.* 1993) = PH0055. South Korea, Suwon, on *Lolium perenne*, 1991, C.K. Kim, CR0024. USA, Delaware, on *Digitaria* sp., 1991, B. Valent, US0043 = G-184.

Note: Isolates of *P. grisea* were observed to form apical mucilaginous droplets on their macroconidia in culture, as well as produce microconidia on SNA, as observed previously in *P. oryzae* (Chuma *et al.* 2009, Zhang *et al.* 2014).

***Pyricularia oryzae* Cavara,** *Fung. Long. Exsicc.* 1: no. 49. 1892. **Fig. 15.**

= *Magnaporthe oryzae* B.C. Couch, *Mycologia* 94(4): 692. 2002.

Materials examined: Brazil, on *Triticum aestivum*, 1989, J.-L. Nottéghem, BR0032, BR0045. Burkina Faso, on *Paspalum* sp., 1990, collector unknown, BF0028 = CBS 138602. Côte d'Ivoire, Bouaké, on *Leersia hexandra*, 1983, J.-L. Nottéghem, CD0067; Ferkessedougou, on *Eleusine indica*, 1989, J.-L. Nottéghem, CD0156. Egypt, on *Oryza sativa*, date and collector unknown, CBS 657.66. France, Camargue, on *Oryza sativa*, 1988, J.-L. Nottéghem, FR0013. French Guyana, on *Oryza sativa*, 1978, J.-L. Nottéghem, Guy11 = FGSC 9462. Gabon, Wey, on *Zea mays*, 1985, J.-L. Nottéghem, GN0001. India, Uttar Pradesh, on *Setaria* sp., date unknown, J. Kumar, IN0108. Israel, Masmiah, on *Echinochloa crus-galli*, date and collector unknown, CBS 658.66; Rishon-le-Zion, on *Stenotaphrum secundatum*, date and collector unknown, CBS 659.66. Japan, on *Eragrostis curvula*, 1983, H. Kato, JP0038; on *Eriochloa villosa*, date and collector unknown, JP0033; on *Phalaris arundinacea*, date and collector unknown, JP0040; on *Anthoxanthum odoratum*, date and collector unknown, JP0039; on *Eleusine indica*, 1974, H. Yaegashi, JP0017; on *Eragrostis curvula*, 1976, H. Yaegashi, JP0028; Nagano, host, date and collector unknown, CBS 365.52 = MUCL 9451. Philippines, Los Banos, Laguna, on *Brachiaria mutica*, 1983 IIRI collector unknown, BmA8309 (Borromeo *et al.* 1993) = PH0035 = PH0075; Cabanatuan, Nueva Ecija, on *Cynodon dactylon*, 1988, IIRI collector unknown, Cd88215 (Borromeo *et al.* 1993) = PH0051; on *Echinochloa colona*, 1982, IIRI collector unknown, PH0077 = Ec8202; Los Banos, Laguna, on *Leptochloa chimensis*, 1984, IIRI collector unknown, Lc8401 (Borromeo *et al.* 1993) = PH0060; on *Oryza sativa*, 1980, IIRI collector unknown, PO6-6 (Wang *et al.* 1994) = PH0014; on *Panicum repens*, 1982, J. M. Bonmam, Pr8212 = PH0079; Cabanatuan, Nueva Ecija, on *Paspalum distichum*, 1988, IIRI collector unknown, Pd8824 (Borromeo *et al.* 1993) = PH0062; Los Banos, Laguna, on *Rottboellia exalta*, 1984, IIRI collector unknown, ReA8401 (Borromeo *et al.* 1993) = PH0063 = ATCC 62619. Portugal, on *Stenotaphrum secundatum*, 1992, A. Lima, PR0067, PR0104. Romania, no further details, CBS 255.38. Rwanda, Kunyanya, on *Eleusine coracana*, 1990, J.-L. Nottéghem, RW0012. South Korea, Suwon, on *Festuca elalior*, date unknown, C.K. Kim, CR0029; Suwon, on *Lolium hybridum*, 1991, C.K. Kim, CR0026; Suwon, on *Pheum pratense*, 1991, C.K. Kim, CR0020; Yongin, on *Panicum miliaceum*, date unknown, C.K. Kim, CR0021. USA, Kentucky, on *Setaria viridis*, 1998, M. Farman, US0071. Vietnam, Ô Môn, on *Leersia hexandra*, 2002, B. Couch, VT0032. Unknown, no collection details,

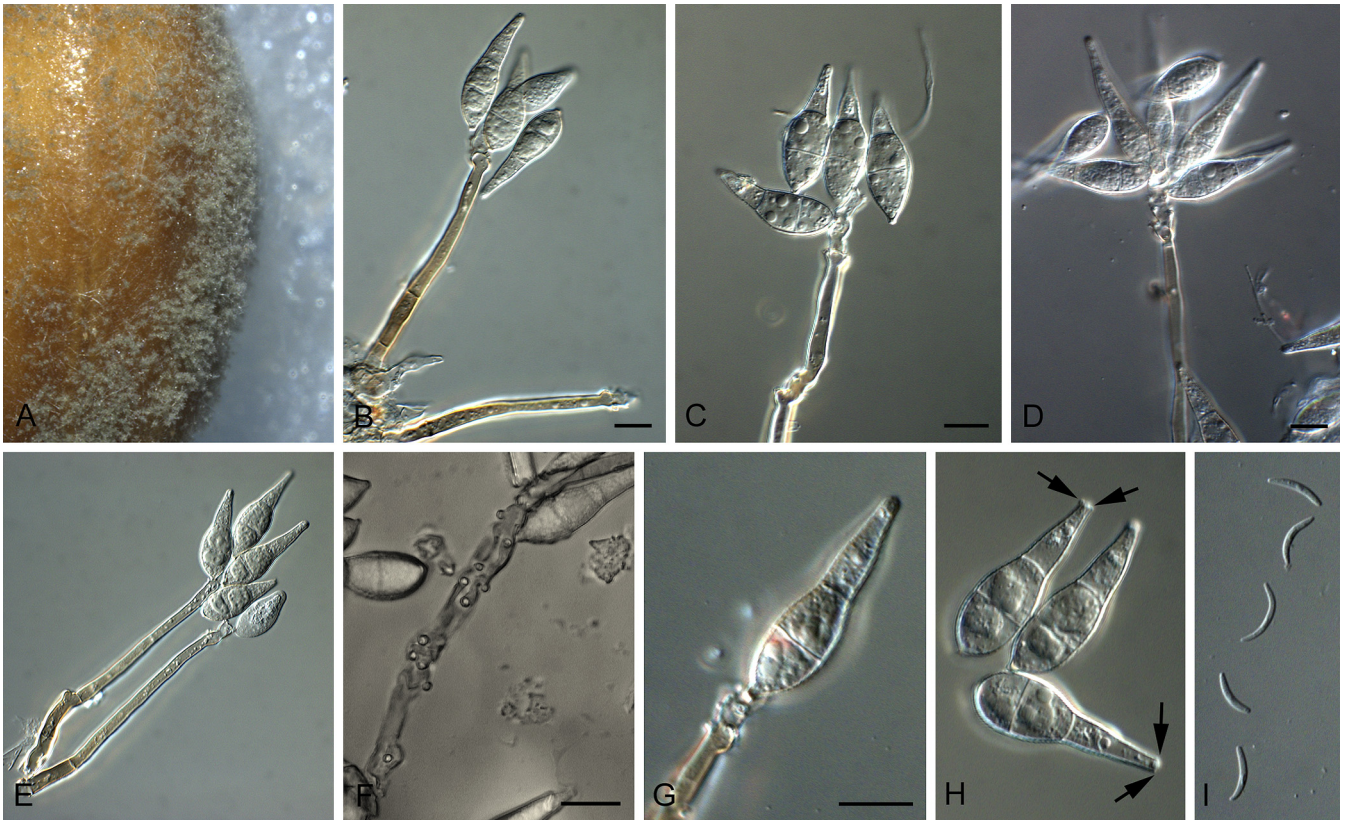


Fig. 14. *Pyricularia grisea* (BR0029). A. Sporulation on sterile barley seed on SNA. B–G. Conidiophores and conidia. H. Macroconidia (arrows indicate apical marginal frill, which is a remnant of the apical mucoid cap). I. Microconidia. Scale bars = 10 μ m.

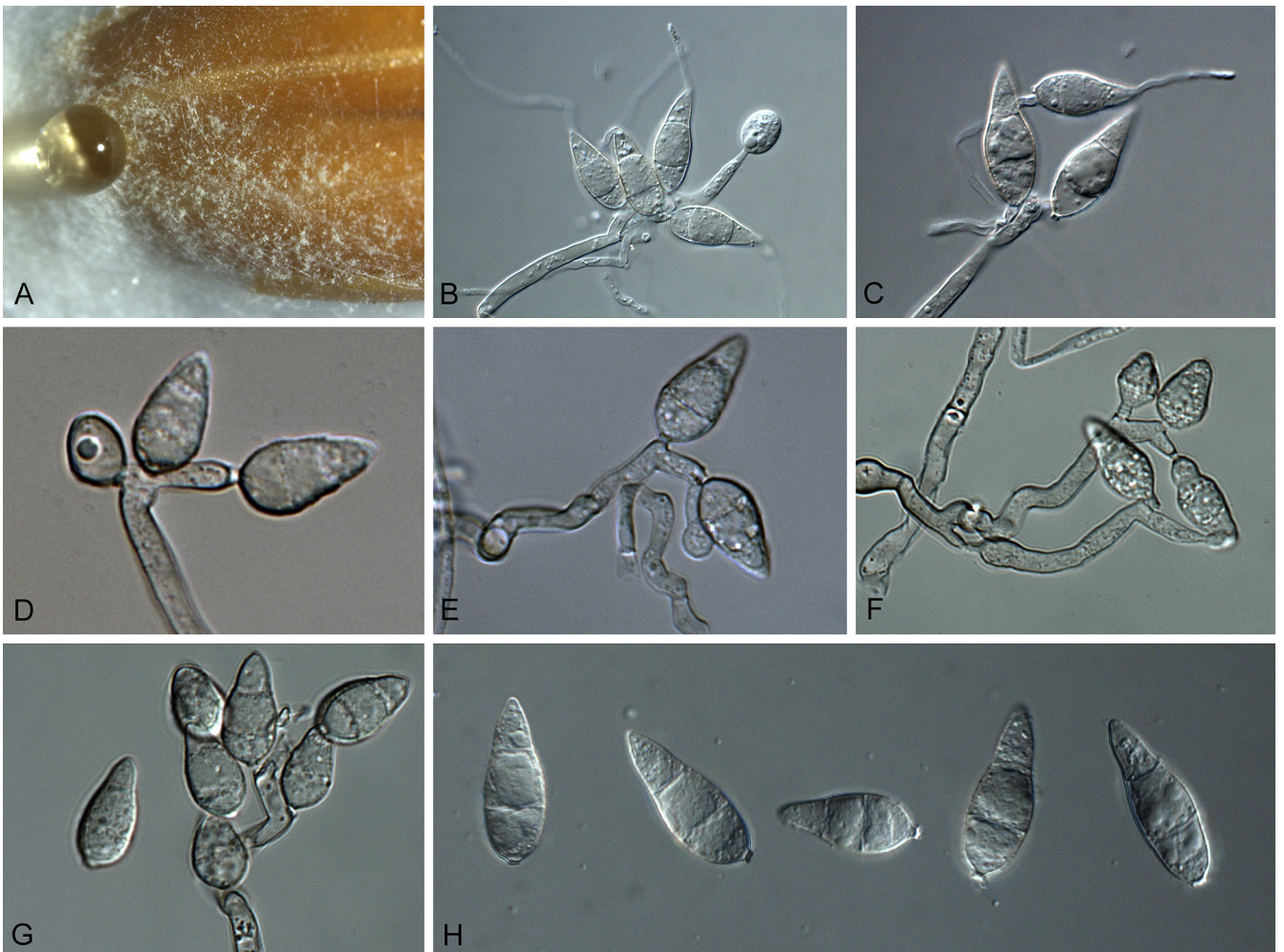


Fig. 15. *Pyricularia oryzae* (BF0028). A. Sporulation on sterile barley seed on SNA. B–G. Conidiophores and conidia. H. Conidia. Scale bars = 10 μ m.

CBS 375.54; on *Oryza sativa*, date and collector unknown, 70-15 = ATCC MYA-4617 = FGSC 8958; laboratory strain, progeny from a cross between strains with different host specificity, CBS 433.70.

***Pyricularia penniseticola* Klaubauf, Lebrun & Crous, sp. nov.** MycoBank MB810220. Fig. 16.

Etymology: Named after the host genus from which it was collected, *Pennisetum*.

On SNA on sterile barley seed. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae, 1.5–2 µm diam. *Conidiophores* solitary, erect, straight or curved, frequently branched, medium brown, smooth, 100–350 × 4–6 µm, multi-septate; base bulbous, lacking rhizoids. *Conidiogenous cells* 40–130 × 3–4 µm, integrated, terminal and intercalary, pale brown, smooth, forming a rachis with several protruding denticles, 1–2 µm long, 1–1.5 µm diam, with rhexolytic secession. *Conidia* solitary, pyriform to obclavate, pale brown, finely roughened, granular to guttulate, 2-septate, (23–)25–30(–35) × (8–)9(–10) µm; apical cell 9–13 µm long, basal cell 7–10 µm long; attenuated towards a truncate hilum, 0.5–1 µm long, 1.5–2 µm diam, with minute marginal frill.

Culture characteristics: Colonies on MEA pale olivaceous grey, cottony, reaching up to 3 cm diam after 1 wk; reverse olivaceous-black. Colonies on CMA reaching up to 3 cm diam after 1 wk. Colonies on PDA iron-grey, reaching up to 4.5 cm diam after 1 wk, reverse olivaceous-black. Colonies on OA up to 3.6 cm diam after 1 wk, surface sectoring.

Materials examined: **Burkina Faso**, Kamboise (Guaga), *Pennisetum typhoides*, 27 Sept. 1990, J.-L. Nottéghem, BF0017. **Côte d'Ivoire**, Bouake, *P. typhoides*, 1 Dec. 1983, J.-L. Nottéghem, CD0086; Odiene, *Digitaria exilis*, 1 Oct. 1989, J.-L. Nottéghem, CD0143; Madiani, *Pennisetum* sp., 17 Oct. 1991, J.-L. Nottéghem, CD0180. **Mali**, Segou field 2, *D. exilis*, 17 Oct. 1993, J.-L. Nottéghem, ML048; Longorola Sikasso, on *P. typhoides*, 14 Sept. 1990, J.-L. Nottéghem (**holotype** CBS H-21843, **culture ex-type** ML0031 = CBS 138603).

***Pyricularia pennisetigena* Klaubauf, Lebrun & Crous, sp. nov.** MycoBank MB810221. Fig. 17.

Etymology: Named after the host genus from which it was collected, *Pennisetum*.

On SNA on sterile barley seeds. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae, 1.5–2 µm diam. *Conidiophores* solitary, erect, straight or curved, unbranched, medium brown, smooth, 60–150 × 4–6 µm, 2–3-septate; base arising from hyphae, not swollen, lacking rhizoids. *Conidiogenous cells* 40–95 × 3–5 µm, integrated, terminal and intercalary, pale brown, smooth, forming a rachis with several protruding denticles, 0.5–1 µm long, 1.5–2 µm diam. *Conidia* solitary, pyriform to obclavate, pale brown, smooth, granular to guttulate, 2-septate, (25–)27–29(–32) × (8–)9(–10) µm; apical cell 10–13 µm long, basal cell 6–9 µm long; hilum truncate, protruding, 1–1.5 µm long, 1.5–2 µm diam, unthickened, not darkened.

Culture characteristics: Colonies on MEA cottony to velvety, buff, smoke grey, with broad white rim, reaching up to 4.8 cm diam after 1 wk; reverse iron grey with pale margin. Colonies on CMA buff with grey dots, reaching up to 5.0 cm diam after 1 wk.

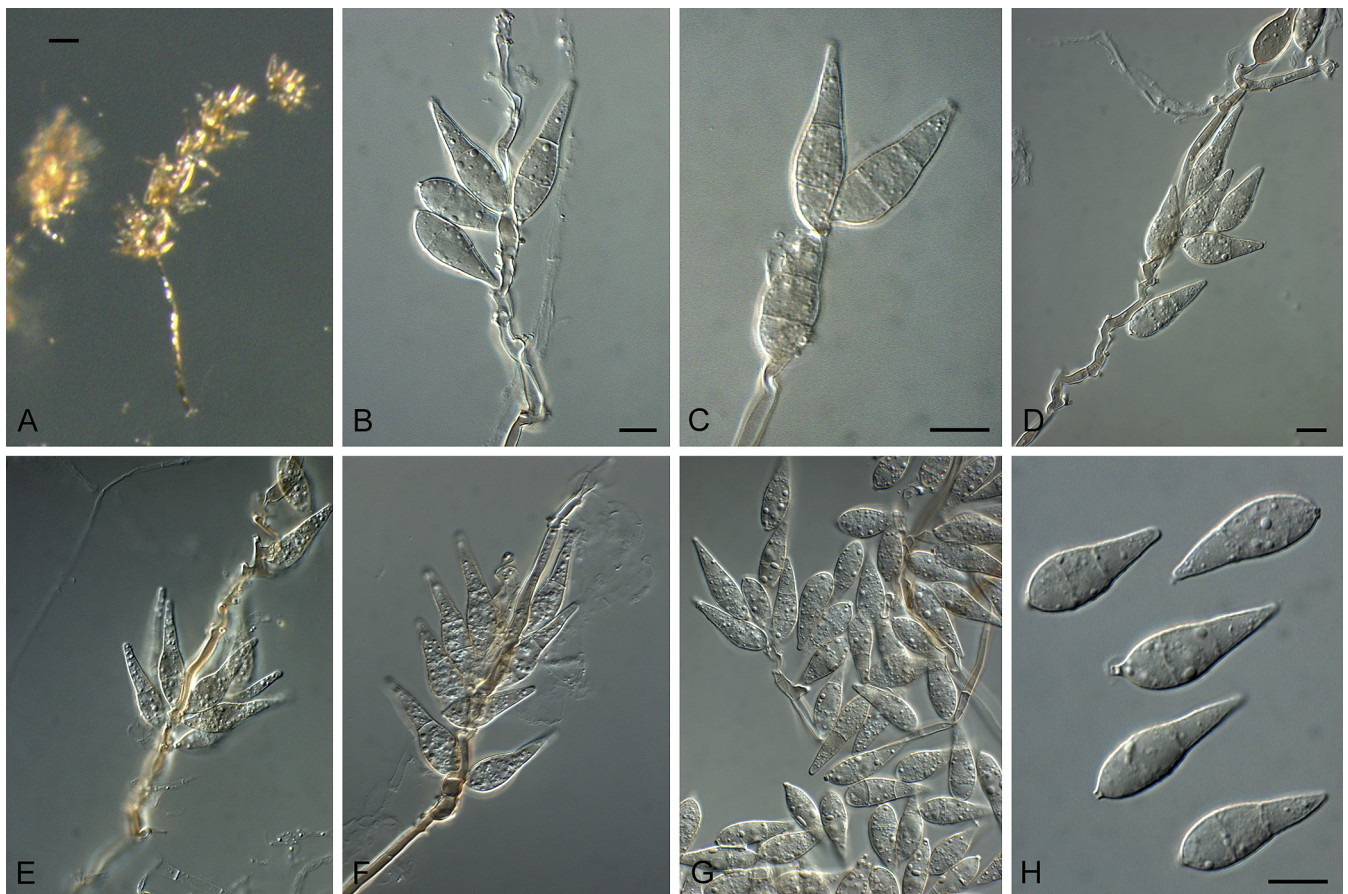


Fig. 16. *Pyricularia penniseticola* (ML0031). A. Sporulation on SNA. B–G. Conidiophores and conidia. H. Conidia. Scale bars = 10 µm.

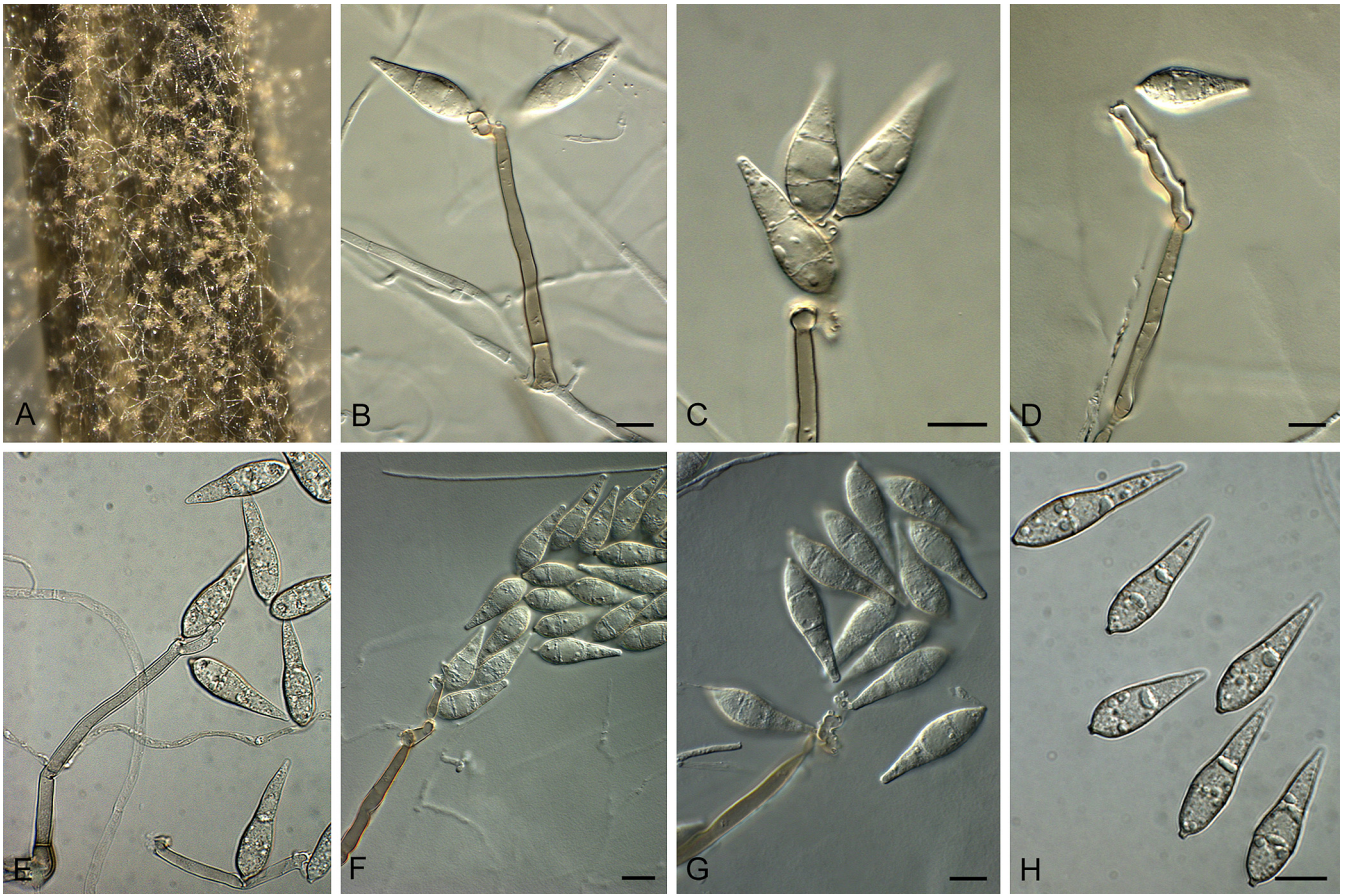


Fig. 17. *Pyricularia pennisetigena* (ML0036). A. Sporulation on sterile barley leaf on SNA. B–G. Conidiophores and conidia. H. Conidia. Scale bars = 10 μ m.

Colonies on OA buff, reaching up to 5.0 cm diam after 1 wk, sporulating after 4 d in the dark. Colonies on PDA fuscous black with grey centre, and broad white rim, flat, erose, reaching up to 5.0 cm diam after 1 wk; reverse brown.

Materials examined: **Brazil**, on *Cenchrus echinatus*, date unknown, S. Igarashi, Br36; Imperatriz, on *C. echinatus*, 28 Feb. 1990, collector n.a., BR0067; Primeiro de Maio, on *Echinochloa colona*, 1 Apr. 1990, H. Kato, BR0093. **Japan**, Kumamoto, on *Cenchrus ciliaris*, 1975, N. Nishihara, CBS 133596 = MAFF 305501 = NI981(Cc-1J). **Mali**, Cinzana, on *Pennisetum* sp., 19 Sept. 1990, J.-L. Nottéghem (**holotype** CBS H-21844, culture **ex-type** ML0036 = CBS 138604). **Philippines**, Plaridel, Bucalan, on *Cenchrus echinatus*, 1988, IIRRI collector unknown, Ce88454 (Borromeo *et al.* 1993) = PH0047. **USA**, Tifton, *Pennisetum glaucum*, 1983, H. Wells, US0044 = 83P-25, Tifton, *Pennisetum glaucum*, 1984, H Wells, US0045 = 84P-19 (Kang *et al.* 1995).

Notes: Another forgotten species on this host is *P. penniseti* (Prasada & Goyal 1970). *Pyricularia penniseti* was described as having conidia that are pyriform and 2-septate, 18.4–36.7 \times 7.4–11 μ m. In spite of differences in conidial dimensions to *P. penniseticola* and *P. pennisetigena*, no cultures are presently available to determine if it would also be distinct on a phylogenetic basis.

Pyricularia zingibericola Klaubauf, Lebrun & Crous, **sp. nov.** MycoBank MB810222. Fig. 18.

Etymology: Named after the host genus from which it was collected, *Zingiber*.

On SNA on sterile barley seed. *Mycelium* consisting of smooth, hyaline, branched, septate hyphae, 1.5–2 μ m diam.

Conidiophores solitary, erect, straight or curved, branched or not, medium brown, smooth, 100–200 \times 4–6 μ m, 3–8-septate; base bulbous, lacking rhizoids, 5–7 μ m diam. *Conidiogenous cells* 45–70 \times 3–4 μ m, integrated, terminal and integrated, pale brown, smooth, with several protruding apical denticles, 1–1.5 μ m long, 1–2 μ m diam. *Conidia* solitary, pyriform to obclavate, pale brown, smooth to finely roughened, guttulate, 2-septate, (18–)20–23(–25) \times (7–)8(–10) μ m; apical cell 8–10 μ m long, basal cell 5–7 μ m long; hilum truncate, protruding, 0.5–1 μ m long, 1.5–2 μ m diam, unthickened, not darkened.

Culture characteristics: Colonies on MEA transparent to white with leaden grey centre, sulcate colony with entire edge, some irregular tufts, sporulating in centre, reaching up to 4 cm diam after 1 wk; reverse pale with olivaceous grey centre. Colonies on OA white with some dark spots, greenish olivaceous in centre, flat, smooth, cotton-like surface, reaching up to 4.5 cm diam after 1 wk. Colonies on CMA grey olivaceous to olivaceous black with olivaceous grey centre, entire edge, flat colony, slightly wool-like surface, reaching up to 4 cm diam after 1 wk. Colonies on PDA transparent with some greenish olivaceous parts, white centre, umbonate, powdery surface in centre, reaching up to 4.5 cm diam after 1 wk; reverse greenish olivaceous.

Material examined: Réunion, on *Zingiber officinale*, J.-C. Girard (**holotype** CBS H-21845, culture **ex-type** RN0001 = CBS 138605).

Notes: *Pyricularia zingibericola*, which appears to be unique on *Zingiber*, has smaller conidia than *P. leersiae* (20–)

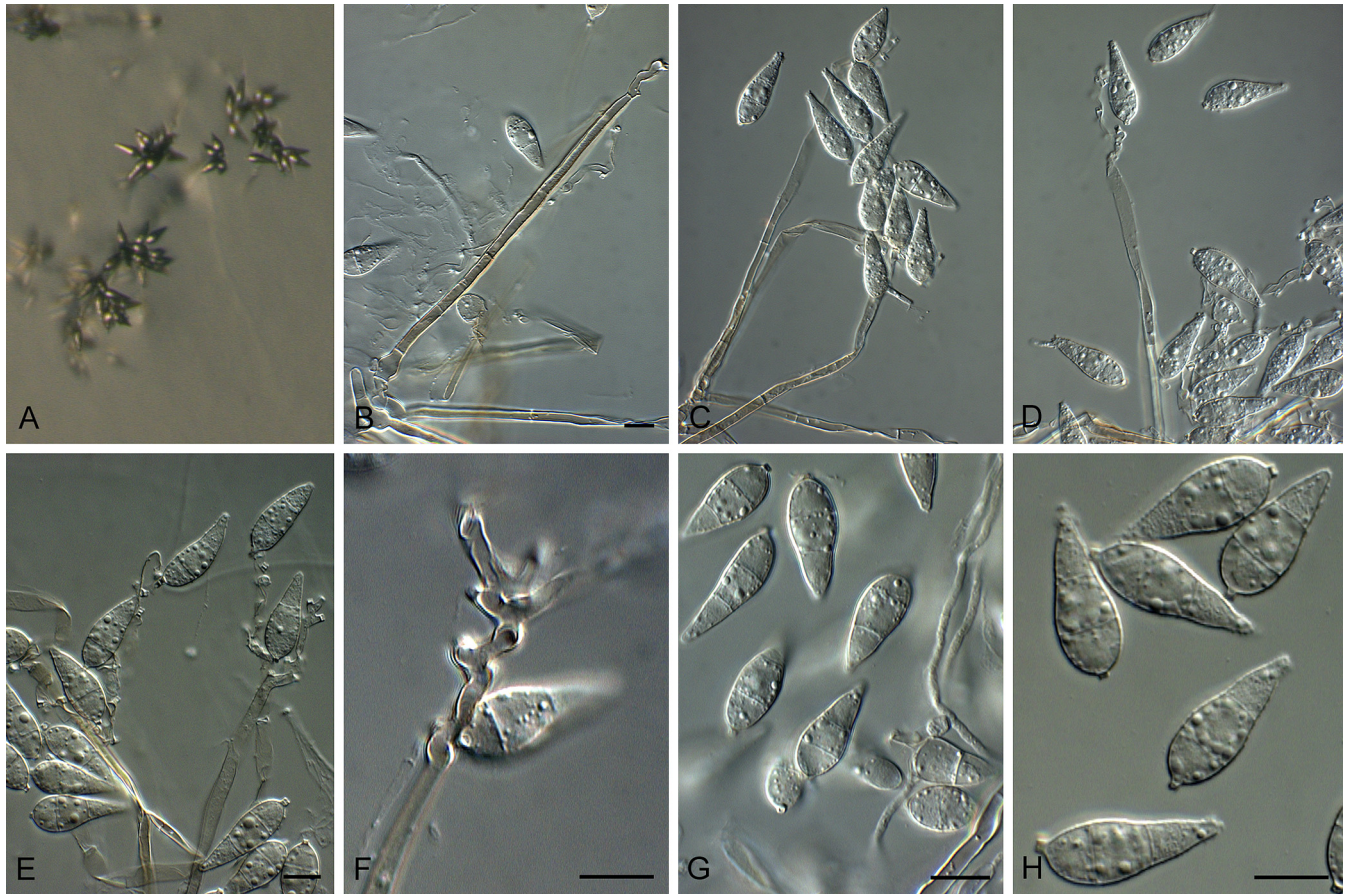


Fig. 18. *Pyricularia zingibericola* (RN0001). A. Sporulation on SNA. B–F. Conidiophores and conidia. G, H. Conidia. Scale bars = 10 μ m.

27(–35) \times (7–)8.6(–10) μ m, which is also known to occur on *Leersia* (Hashioka 1973). Presently no cultures of *P. leersiae* are available to facilitate a molecular comparison.

Xenopyricularia Klaubauf, Lebrun & Crous, **gen. nov.**
Mycobank MB810223.

Etymology: Named after its morphological similarity to *Pyricularia*.

Plant pathogenic. *Conidiophores* solitary or in fascicles, sub-cylindrical, erect, medium brown, smooth, flexuous, branched, with sympodial growth. *Conidiogenous cells* terminal and intercalary, pale brown, denticulate conidiogenous loci. *Conidia* solitary, formed sympodially, obovoid, narrowed toward tip, rounded at the base, 2-septate, pale brown, with central cell appearing slightly darker brown, with a distinct protruding basal hilum.

Type species: *Xenopyricularia zizaniicola* (Hashioka) Klaubauf, Lebrun & Crous

Xenopyricularia zizaniicola (Hashioka) Klaubauf, Lebrun & Crous, **comb. nov.** MycoBank MB810224. Fig. 19.

Basionym: *Pyricularia zizaniicola* Hashioka (as “*zizaniaecola*”), *Trans. Mycol. Soc. Japan* 14(3): 264. 1973.

\equiv *Pyricularia zizaniicola* Hashioka (as “*zizaniaecola*”), *Res. Bull. Agr. Gifu Univ.* 29: 21. 1970. (nom. nud.)

Description and illustration: Hashioka (1973).

Materials examined: Japan, Gifu, on *Zizania latifolia*, 15 Sep. 1967, Y. Hashioka (**holotype** presumably lost); Ibaraki, on *Zizania latifolia*, 1985, N. Hayashi, (**neotype** designated here CBS H-21846, culture **ex-neotype** CBS 133593 = MAFF 240219 = IBZL3-1-1(Zz-1J)); Kyoto, on *Zizania latifolia*, 2003, K. Yoshida & K. Hirata, CBS 132356 = MAFF 240220 = KYZL201-1-1(Zz-2J).

Notes: *Xenopyricularia zizaniicola* has long, flexuous, pale brown, branched conidiophores. Conidia are brown, 2-septate, obovoid, (22–)25–28(–35) \times (12–)13(–14) μ m (on SNA), with a small protruding hilum, 0.5–1 μ m long, 1 μ m diam. Morphologically *Xenopyricularia* resembles *Pyricularia*, except that its conidia are very wide and more obovoid than are typical *Pyricularia* conidia, and some appear to be irregularly pigmented. The present culture corresponds very well with the original description and illustrations provided by Hashioka (1973), who cited conidia as being (24–)27.7(–33) \times (10.5–)13.5(–15.5) μ m, and is therefore designated as neotype.

Another forgotten species on this host is *Pyricularia zizaniae* Hara, (as “*Piricularia*”) *Trans. Shizuoka Agric. Soc.* 336: 29. 1925. Translated from Japanese: “*Leaf spots* small, circular, later elongate, brown, ellipsoid to fusiform, finally greyish brown with brown border, 2–8 \times 2–6 mm. *Caespituli* mainly hypophyllous, sooty-coloured. *Conidiophores* linear, 60–130 \times 2.5–4 μ m, rarely branched, solitary or densely fasciculate, dark brown and swollen at the base, paler and attenuate toward the apex,



Fig. 19. *Xenopyricularia zizaniicola* (CBS 133593). A. Sporulation on sterile barley seed on SNA. B–D. Conidiophores and conidia (arrows indicate conidiogenous loci in D). E, F. Conidia. Scale bars = 10 μ m.

geniculate at the apex. *Conidia* pyriform to clavate, rounded at base, attenuate at apex, 1–2-septate, not constricted at septa, protruding at base, hyaline to pale smoky in colour. *Notes:* When it was inoculated onto rice, it was not pathogenic. This disease was observed in shaded area". *Pyricularia zizaniae* has conidia that are described as being 1–2-septate, (18–) 22(–28) \times 7(–10) μ m. No cultures are available, however, to determine if it could represent a second species of *Xenopyricularia*.

Sordariales, incertae sedis

Rhexodenticula W.A. Baker & Morgan-Jones, Mycotaxon 79: 363. 2001.

Mycelium immersed and superficial, consisting of branched, septate, pale brown to brown, smooth hyphae that become verruculose. *Conidiophores* solitary, erect, subcylindrical, straight or curved, unbranched, medium brown, finely verruculose, septate. *Conidiogenous cells* integrated, terminal, subclavate, pale brown, finely verruculose, forming a rachis with several protruding denticles, and rhexolytic secession. *Conidia* solitary, fusoid-ellipsoidal, finely verruculose, medium brown, guttulate, 3-septate; base rounded, hilum truncate, slightly protruding, with minute marginal frill.

Type species: *Rhexodenticula cylindrospora* (R.F. Castañeda, Saikawa & Hennebert) W.A. Baker & Morgan-Jones

Notes: An isolate deposited at CBS as *Pyricularia lauri* (CBS 244.95, on leaf litter of *Nectandra antillana*, Cuba) was morphologically identical to the ex-type isolate of *Rhexodenticula cylindrospora* (CBS 318.95, also isolated from leaf litter of *Nectandra antillana*, Cuba). Although the phylogenetic position of the genus is still unclear, it does not belong to the

Magnaporthaceae, but appears to be sister to *Boliniales* and *Sordariales* (Fig. 1).

Rhexodenticula cylindrospora (R.F. Castañeda, Saikawa & Hennebert) W.A. Baker & Morgan-Jones, Mycotaxon 79: 363. 2001. Fig. 20.

Basionym: *Nakataea cylindrospora* R.F. Castañeda, Saikawa & Hennebert, Mycotaxon 59: 457. 1996.

On SNA on sterile barley seed. *Mycelium* consisting of finely verruculose, hyaline, branched, septate hyphae, becoming brown and verruculose, 2.5–3 μ m diam. *Conidiophores* solitary, erect, subcylindrical, straight or curved, unbranched, medium brown, finely verruculose, 40–90 \times 4–5 μ m, 1–6-septate. *Conidiogenous cells* 10–20 \times 3–5 μ m, integrated, terminal, subclavate, pale brown, finely verruculose, forming a rachis with several protruding denticles, 1 μ m long and in diam, with rhexolytic secession. *Conidia* solitary, fusoid-ellipsoidal, finely verruculose, medium brown, guttulate, 3-septate, (15–) 17–19(–20) \times (4–)5(–6) μ m; base rounded, hilum truncate, slightly protruding, 1 μ m long and diam, with minute marginal frill.

Culture characteristics: Colonies on MEA mouse-grey, vinaceous buff at the margin, sulcate, velutinous, reaching up to 1.7 cm diam after 15 d; reverse isabelline with sepia centre. Colonies on OA dark mouse-grey with greenish black rim, undulate, funiculate, reaching up to 2.1 cm diam after 15 d. Colonies on PDA buff to honey, isabelline in centre, undulate, sulcate, reaching up to 1.5 cm diam after 15 d; reverse buff to honey, isabelline in centre.

Materials examined: Cuba, Pinar del Rio, leaf litter of *Nectandra antillana*, 9 Aug. 1994, R.F. Castañeda, culture **ex-type** CBS 318.95 = INIFAT C94/182; on leaf litter of *N. antillana*, 9 Aug. 1994, R.F. Castañeda & M. Saikawa, CBS 244.95 = INIFAT C94/182.

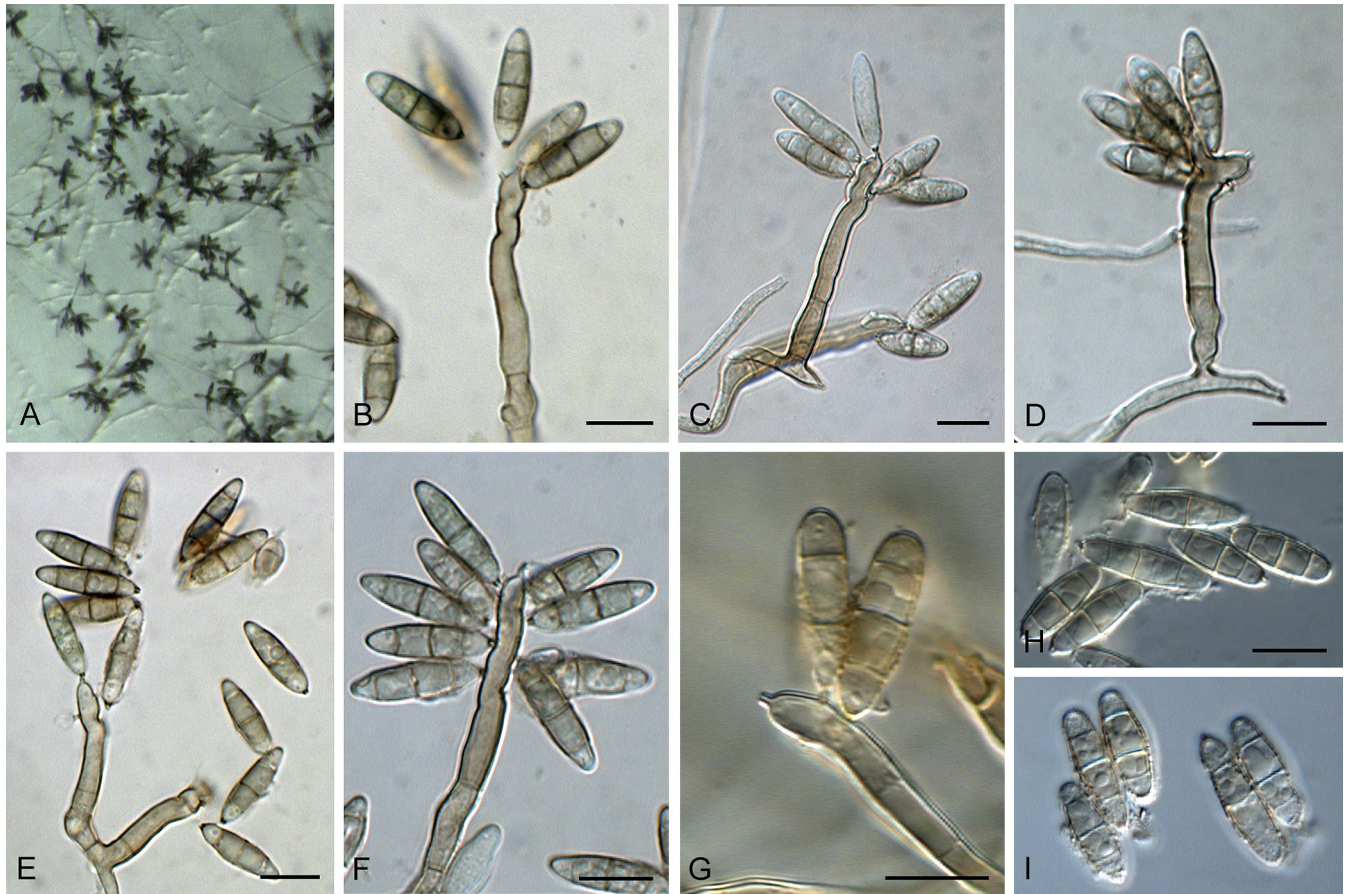


Fig. 20. *Rhexodenticula cylindrospora* (CBS 318.95). A. Sporulation on SNA. B–G. Conidiophores and conidia. H, I. Conidia. Scale bars = 10 µm.

DISCUSSION

Prior to this study, the *Magnaporthales* contained a single family, the *Magnaporthaceae* (Thongkantha et al. 2009). However, the elucidation of *Nakataea* as older name for *Magnaporthe* (Luo & Zhang 2013) justified a reevaluation of the genera included in this order, as many are quite extreme in their morphology and ecology. Based on the results of our phylogenetic analyses (Fig. 2), three clear clades could be distinguished, one corresponding to *Magnaporthaceae* (based on *Nakataea*), and two other clades corresponding to new families, *Pyriculariaceae* (based on *Pyricularia*), and *Ophioceraceae* (based on *Ophioceras*). The genus *Pseudohalonectria*, which clusters basal to these three families (Fig. 1) is polyphyletic (Thongkantha et al. 2009) and is closely related to species of *Ceratospheeria* (Réblová 2006, Huhndorf et al. 2008, Thongkantha et al. 2009), but could not be treated due to a lack of cultures. These families have different ecological characteristics. *Magnaporthaceae* and *Pyriculariaceae* are mainly composed of plant pathogenic species, some of which are of major importance in plant pathology (*Gaeumannomyces*, *Nakataea* and *Pyricularia*). *Ophioceraceae* and *Pseudohalonectria* (*incertae sedis*) are mainly composed of aquatic or wood-associated saprobic species. *Magnaporthaceae* is distinguished from the *Pyriculariaceae* by their asexual morphs, which are phialophora- or harpophora-like, or with falcate versicoloured conidia on brown, erect conidiophores in the case of *Magnaporthaceae*, and *Pyricularia* or pyricularia-like, characterised by pyriform 2-septate conidia and rhexolytic secession, in the case of *Pyriculariaceae*. Although *Ophioceras* is morphologically similar to *Gaeumannomyces*, the two genera

can be distinguished by the aquatic habit of *Ophioceras*, occurring on wood and herbaceous material, versus the plant pathogenic nature of *Gaeumannomyces*, which has harpophora-like asexual morphs, mycelial appressoria, and a perithecial peridium of *textura epidermoidea* (Walker 1980, Chen et al. 1999). The allocation of *Ophioceras* to the *Magnaporthaceae* has always been seen as a temporary measure, awaiting further study (Shearer 1989, Shearer et al. 1999). As shown in the present analyses (Fig. 2), *Ophioceras* clusters separate from the *Magnaporthaceae* and *Pyriculariaceae* in the *Magnaporthales*, and hence a separate family, the *Ophioceraceae*, had to be defined for these taxa. Several genera were distinguished in the *Magnaporthaceae* in the present study, namely *Buergenerula*, *Bussabanomyces*, *Gaeumannomyces*, *Harpophora*, *Kohlmeyeriopsis*, *Magnaporthiopsis*, *Nakataea*, *Omnidemtus*, *Pyriculariopsis* and *Slopeiomyces*. The *Pyriculariaceae* includes eight additional genera, namely *Bambusicularia*, *Barretomyces*, *Deightoniella*, *Macgarvieomyces*, *Neopyricularia*, *Proxipyricularia*, *Pseudopyricularia* and *Xenopyricularia* and four novel *Pyricularia* species.

Some previously published and rather broadly defined species of *Pyricularia* and *Magnaporthe* clustered outside these families. These include isolate CBS 244.95, which was originally identified as *Pyricularia lauri*, and is shown here to represent *Rhexodenticula cylindrospora* (*incertae sedis*) (Fig. 1). In addition, an isolate deposited at CBS as *Pyricularia parasitica* (CBS 376.54, sterile on SNA) clustered in the *Chaetothyriales* (Fig. 1), and sequences of *Magnaporthe griffinii* (ITS GenBank JQ390311, JQ390312) proved to be distant to the *Sordariomycetes* (not included).

The *Magnaporthaceae* phylogeny (Fig. 2) provided good support (BS = 100 %) for several genera that were included in the analysis, namely *Magnaporthiopsis*, *Nakataea*, and two new genera, *Kohlmeyeriopsis* (for *Gaeumannomyces medullaris*), and *Slopeiomyces* (for *Gaeumannomyces cylindrosporus*) except *Gaeumannomyces pro parte*. The genus *Pyriculariopsis* was omitted from the final analysis however, due to the lack of a RPB1 sequence.

The *Pyriculariaceae* phylogenies (Figs 2, 3) delineated *Pyricularia* from *Deightoniella*, as well as novel genera such as *Bambusicularia* (based on *Bambusicularia brunnea*), *Barretomyces* (based on *Barretomyces calathea* = *Pyriculariopsis calathea*), *Macgarvieomyces* (based on *Macgarvieomyces borealis* = *Pyricularia borealis*), *Neopyricularia* (based on *Neopyricularia commelinicola* = *Pyricularia commelinicola*), *Proxypyricularia* (based on *Proxypyricularia zingiberis* = *Pyricularia zingiberis*), *Pseudopyricularia* (based on *Pseudopyricularia kyllingae*), and *Xenopyricularia* (based on *Xenopyricularia zizaniicola* = *Pyricularia zizaniicola*).

Several new species were introduced in *Pyricularia*, namely *P. ctenantheicola* (occurring on *Ctenanthe openheimiana* in Greece), *P. penniseticola* (occurring on *Digitaria exilis* and *Pennisetum typhoides* in West African countries such as Burkina Faso, Ivory Coast, and Mali), *P. pennisetigena* (occurring on *Cenchrus ciliaris*, *Cenchrus echinatus*, *Echinochloa colona* and *Pennisetum glaucum* in Brazil, Japan, Mali, Philippines and the USA), and *P. zingibericola* (occurring on *Zingiber officinale* in Réunion Island). The surprising high number of undescribed *Pyricularia* species encountered in this study suggests that *Pyricularia* is actually a species-rich genus, and that sampling leaf spot diseases of different members of *Poaceae* could reveal many more novel taxa.

What started out as an investigation into the systematics of *Pyricularia*, not only delineated four novel species, but also several novel pyricularia-like genera. The genus *Pyricularia* is defined by having pale brown conidiophores and a terminal and intercalary denticulate rachis, and subhyaline, 2-septate, pyriform conidia (Yaegashi & Nihihara 1978, Murata *et al.* 2014). Surprisingly, the pyriform 2-septate conidial shape was also found for isolates from *Neopyricularia* (Fig. 3), whereas other *Pyriculariaceae* genera had conidia that varied in shape from obclavate to more ellipsoid. Other than conidial shape, it appears that conidial septation also varies among *Pyriculariaceae* species. Indeed, three species from two related genera (*Deightoniella*, *Macgarvieomyces*, Fig. 3) have 1-septate conidia. Since other related genera (*Neopyricularia*, *Proxypyricularia*, *Pseudopyricularia*) that are basal to *Deightoniella* and *Macgarvieomyces* (Fig. 3), have 2-septate conidia, it is likely that a common ancestor of these related genera had 2-septate conidia.

Our phylogenetic study showed that the host plant from which *Pyricularia* isolates were sampled could not be used as a taxonomic criterion, since the host range varied depending on the fungal species. For example, *Pyricularia* isolates sampled from infected leaves of *Eleusine*, *Oryza*, *Setaria* and *Triticum* were exclusively clustering in the *P. oryzae* clade (Table 1, Fig. 3). These isolates are known to be strictly host-specific, and to have a shared evolutionary origin (Tosa & Chuma 2014). The genetic groups (sub-species) underlying these host-specific forms could not be differentiated by the multilocus sequences used in this study, but were clearly delineated using additional genetic markers (Borromeo *et al.* 1993, Kato *et al.* 2000, Couch *et al.* 2005, Hirata *et al.* 2007, Choi *et al.* 2013, Saleh *et al.* 2014).

On the contrary, isolates from host plants such as *Cenchrus*, *Echinochloa*, *Lolium*, *Pennisetum* and *Zingiber* belong to different *Pyricularia* clades corresponding to unrelated species. For example, isolates sampled from infected *Pennisetum* leaves in West Africa belong to two unrelated fungal species, *P. pennisetigena* and *P. penniseticola* (Fig. 3). Similarly, isolates sampled from infected *Echinochloa* leaves belong to three fungal species, *P. oryzae*, *P. grisea* and *P. pennisetigena* (Fig. 3). This could reflect that *Echinochloa* is infected by different *Pyricularia* species, as some *P. oryzae* isolates from rice are pathogenic to *Echinochloa* (Mackill & Bonham 1986, Serghat *et al.* 2005). It is therefore clear from this study that some host plants can be infected by more than one species of *Pyricularia*.

It would not be fitting to round off a paper on *Pyricularia* and *Magnaporthe* without commenting on the ongoing debate about generic names. The decision to allocate the rice pathogen *M. salvinii* to *Nakataea*, has reduced *Magnaporthe* to synonymy under *Nakataea*, rendering the family *Magnaporthaceae* without the genus *Magnaporthe*. Although the genus *Magnaporthe* has proven to be polyphyletic, we would have advocated a different approach in view of stability for the application of this name in literature. Likewise, the same can be said for *Pyricularia*, which also turned out to be polyphyletic, forming a generic complex. Although we introduce several genera to address this heterogeneity, *Pyricularia* can fortunately be retained as a well-defined genus in the *Pyriculariaceae*.

ACKNOWLEDGEMENTS

We thank Prof. Yukio Tosa and Prof. Yong-Hwan Lee for providing cultures or DNA for phylogenetic analysis. We thank the technical staff, Arien van Iperen (cultures), Marjan Vermaas (photographic plates), and Mieke Starink-Willems (DNA isolation, amplification and sequencing), as well as Federico Santoro and Alessandro Trotta (cultures, DNA isolation, amplification and sequencing) for their invaluable assistance.

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