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FUNGAL DISEASES

Various species of *Pyricularia* constitute a robust clade distinct from *Magnaporthe salvinii* and its relatives in Magnaporthaceae

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Abstract In a phylogenetic analysis of species of Magnaporthaceae based on nucleotide sequences of rDNA-ITS and the *RPB1* gene, isolates of the tested species were divided into two clusters with high bootstrap support. One group was composed of *Pyricularia* spp.; the other was composed of *Magnaporthe salvinii*, *M. rhizophila*, *M. poae*, *Gaeumannomyces graminis*, and *G. incrustans*. On the basis of this result, we concluded that *Pyricularia* spp. constitute a large but distinct phylogenetic species group that is not congeneric with *Magnaporthe salvinii*, the type species of *Magnaporthe*.

Keywords *Magnaporthe* · *Pyricularia* · *Gaeumannomyces*

The generic name, *Pyricularia*, has been assigned to the anamorphs of filamentous fungi that cause blast disease on monocot species. The best known species is *P. oryzae* Cavara, pathogenic on staple crops including rice, wheat, and millet (Kato et al. 2000). Among its close relatives are *P. grisea* Saccardo, pathogenic on crabgrass, *Pyricularia* sp. (LS) isolated from *Leersia*/*Setaria*, and *Pyricularia* sp. (CE) isolated from *Cenchrus*/*Echinochloa* (Hirata et al. 2007). These four species are members of the *P. oryzae*/*grisea* species complex and indistinguishable in conidial morphology. *Pyricularia* also includes several species defined by morphological features such as *P. zizaniaecola* Hashioka, pathogenic on *Zizania*, *P. zingiberi* Y. Nisikado on *Zingiber*, *P. higginsii* Luttr. on *Cyperus*, *Pyricularia* sp. (SsPb) on *Sasa*/*Phyllostachys* (Hirata et al. 2007).

In the 1970s, teleomorphs of *P. grisea* and *P. oryzae* were discovered in several laboratories (Hebert 1971; Kato et al. 1976; Ueyama and Tsuda 1975; Yaegashi and Nishihara 1976). These species produced nonstromatic black perithecia with long necks and four-celled, spindle-shaped ascospores. The teleomorphs of *P. grisea* and *P. oryzae* were, at first, collectively designated as *Magnaporthe grisea* (T.T. Hebert) M.E. Barr (Barr 1977; Yaegashi and Udagawa 1978), but they are now called *M. grisea* and *M. oryzae* B.C. Couch, respectively (Couch and Kohn 2002).

The blast fungi are primarily airborne and colonize leaves and panicles of host plants. However, the genus *Magnaporthe* also includes soilborne, root-infecting species such as *M. rhizophila* D.B. Scott & Deacon (Scott and Deacon 1983), and *M. poae* Landschoot & N. Jackson (Landschoot and Jackson 1989). In addition, the family Magnaporthaceae (Cannon 1994), typified by the genus *Magnaporthe*, includes *Gaeumannomyces* spp., widely distributed soilborne pathogens. These two groups (airborne and soilborne species) also differ in their anamorphs; the blast fungi produce pyriform conidia, whereas *M. rhizophila*, *M. poae*, and *Gaeumannomyces* spp. produce *Phialophora*-like conidia (Zhang et al. 2011). Furthermore,

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Table 1 Isolates used in this study

Species	Isolate[a]	Host	Locality	Isolation year	Allele	
					rDNA-ITS	*RPB1*
Pyricularia oryzae	Guy11	*Oryza sativa*	Guiana (Combi)	1978	IT1	RP1
	Ken54-20 (MAFF235005)	*O. sativa*	Japan (Yamaguchi)	1954	IT1 (AB274418)	RP1 (AB818003)
	Ina72 (MAFF235003)	*O. sativa*	Japan (Nagano)	1957	IT2 (AB274420)	RP1
	0903-4	*O. sativa*	Japan (Tochigi)	1976	IT3 (AB818014)	RP1
	CHNOS 59-6-1	*O. sativa*	China (Yunnan)	1989	IT1	RP1
	CHNOS 60-8-1	*O. sativa*	China (Yunnan)	1989	IT1	RP1
	Br10	*O. sativa*	Brazil (Parana)	1990	IT3	RP1
	PO-04-7501	*O. sativa*	Indonesia (Jawa Timur)	1975	IT1	RP1
	GFSI1-7-2	*Setaria italica*	Japan (Gifu)	1977	IT4 (AB274422)	RP1
	NRSI3-1-1	*S. italica*	Japan (Nara)	1977	IT4	RP1
	NNSI3-2-1	*S. italica*	Japan (Nagano)	1984	IT4	RP1
	IN77-20-1-1	*S. italica*	India (Mysore)	1977	IT4	RP1
	Z2-1 (MAFF244064)	*Eleusine coracana*	Japan (Kagawa)	1977	IT5	RP2
	Br58	*Avena sativa*	Brazil (Parana)	1990	IT5 (AB274424)	RP2 (AB818004)
	Br7	*Triticum aestivum*	Brazil (Parana)	1990	IT5	RP2
	Br48 (IMI368172)	*T. aestivum*	Brazil (Mato Grosso do Sul)	1990	IT5	RP2
	Br115.7	*T. aestivum*	Brazil (Parana)	1992	IT5	RP2
	Br118.2D	*T. aestivum*	Brazil (Parana)	1992	IT5	RP2
	WK3-1 (MAFF244065)	*Lolium perenne*	Japan (Yamaguchi)	1996	IT5	RP2
	Br35	*Brachiaria plantaginea*	Brazil (Parana)	1990	IT4	RP2
	NI986 (MAFF244066)	*Eragrostis lehmanniana*	Japan (Kumamoto)	1975	IT6 (AB818015)	RP2
Pyricularia sp. (CE)[b]	Br38	*Echinochloa colonum*	Brazil (Parana)	1990	IT7 (AB818016)	RP3 (AB818005)
P. grisea	Dig41	*Digitaria sanguinalis*	Japan (Hyogo)	1990	IT8 (AB274428)	RP4 (AB818006)
	NI907	*D. sanguinalis*	Japan (Tochigi)	1974	IT9 (AB274429)	RP4
	IBDS4-1-1 (MAFF244068)	*D. sanguinalis*	Japan (Ibaraki)	1985	IT8	RP4
	NI980	*Digitaria smutsii*	Japan (Kumamoto)	1975	IT9	RP4
	Br29 (IMI368175)	*Digitaria horizontalis*	Brazil (Sao Paulo)	1990	IT9	RP4
	Br33	*Digitaria horizontalis*	Brazil (Parana)	1990	IT10 (AB274430)	RP4
P. zizaniaecola	IBZL3-1-1	*Zizania latifolia*	Japan (Ibaraki)	1985	IT11	RP5
	KYZL201-1-1	*Z. latifolia*	Japan (Kyoto)	2003	IT11 (AB274432)	RP5 (AB818007)
P. zingiberi	HYZiM101-1-1-1	*Zingiber mioga*	Japan (Hyogo)	1990	IT12 (AB274433)	RP6 (AB818008)
	HYZiM201-0-1	*Z. mioga*	Japan (Hyogo)	2002	IT13 (AB274434)	RP7 (AB818009)
	HYZiM202-1-2	*Z. mioga*	Japan (Hyogo)	2003	IT12	RP6
	HYZiM201-1-1	*Z. mioga*	Japan (Hyogo)	2003	IT13	RP6

Table 1 continued

Species	Isolate[a]	Host	Locality	Isolation year	Allele	
					rDNA-ITS	*RPB1*
Pyricularia sp. (SsPb)[b]	INA-B-92-45	*Sasa* sp.	Japan (Aichi)	1992	IT14 (AB274435)	RP8 (AB818010)
	INA-B-93-19	*Phyllostachys bambusoides*	Japan (Aichi)	1993	IT15 (AB274436)	RP9 (AB818011)
Pyricularia sp. (Kb)[b]	FKKB201-1-5	*Kyllinga brevifolia*	Japan (Fukuoka)	2003	IT16 (AB818017)	RP10 (AB818012)
	FKKB201-3-2 (MAFF244067)	*K. brevifolia*	Japan (Fukuoka)	2003	IT16	RP10
P. higginsii	HYCI201-1-1	*Cyperus iria*	Japan (Hyogo)	2002	IT17 (AB274438)	RP11 (AB818013)

[a] Accession numbers in public culture collections are in parentheses. (MAFF, Microorganisms Section of the NIAS Genebank, National Institute of Agrobiological Sciences Tsukuba, Japan; IMI, CABI Bioscience, UK Centre, Egham, UK.)

[b] Refer to Hirata et al. (2007)

M. salvinii (Catt.) R.A. Krause & R.K. Webster, the type species of the genus (Krause and Webster 1972), is different from both of the two groups; its infection cycle is primarily dependent on sclerotia that colonize the leaf sheath although it forms bicolored conidia. This circumstantial evidence led Zhang et al. (2011) to question whether *Magnaporthe* and *Gaeumannomyces* were monophyletic taxa. On the basis of the results from multilocus phylogenetic analyses, they considered that both *Magnaporthe* and *Gaeumannomyces* were polyphyletic and suggested that anamorphic and ecological features were more informative than the teleomorphic characters in defining monophyletic natural groups. However, they used only four *M. oryzae*/*P. oryzae* isolates as representatives of *Pyricularia* for their analysis. As mentioned already, several phylogenetically distinct, morphological species (Hirata et al. 2007) have been described in *Pyricularia*. Their teleomorphs have not yet been discovered, and their phylogenetic positions in Magnaporthaceae have been still unclear.

At the nomenclatural sessions of the International Botanical Congress in Melbourne, 2011, it was decided that, after 1 January 2013, one fungus can only have one correct name (Hawksworth 2011) and that other names will be considered synonyms. Based on the new nomenclatural code for algae, fungi, and plants (McNeill et al. 2012), all legitimate fungal names are treated equally for the purposes of establishing priority (Wingfield et al. 2012). Therefore, *P. oryzae* and *P. grisea* as former anamorphic names may compete with former teleomorphic names *M. oryzae* and *M. grisea*, respectively, for priority. In the present study, we performed phylogenetic analyses using diverse blast fungi including various species. As a result of the obtained phylogenetic structure of Magnaporthaceae, we discuss which generic name should be adopted for the blast fungi, *Magnaporthe* or *Pyricularia*.

The *Pyricularia* isolates tested are listed in Table 1. Genomic DNA was extracted as described by Nakayashiki et al. (1999). According to the number of informative sites reported by Zhang et al. (2011), two loci were selected for analysis: a portion of the nu-rRNA gene repeat (rDNA-ITS: ITS1, 5.8S and ITS2) and a portion of the largest subunit of RNA polymerase II gene (*RPB1*). The rDNA-ITS region was amplified with primers ITS5 (5′-GGAAGTAAAAG TCGTAACAAGG-3′) and ITS4 (5′-TCCTCCGCTTATT GATATGC-3′) (White et al. 1990) as described by Hirata et al. (2007). The *RPB1* gene was amplified in a 20 μL reaction containing 1 U rTaq DNA polymerase (TOYOBO, Osaka, Japan), 1 × PCR buffer provided by the manufacturer, 200 μM each dNTP, 0.2 μM primers RPB1-Ac (5′-G ARTGYCCDGGDCAYTTYGG-3′) and RPB1-Cr (5′-CC NGCDATNTCRTTRTCCATRTA-3′) (Zhang et al. 2011), 1.5 mM $MgCl_2$, and 1 ng of template DNA using a

Table 2 GenBank accessions used in this study

Species	Isolate[a]	Host	Locality	GenBank accession		
				rDNA-ITS	*RPB1*	Reference
Cryphonectria parasitica	EP155	*Castanea dentata*		Cryphonectria parasitica EP155 v2.0 [b]		
Gaeumannomyces graminis var. *graminis*	M33	*Stenotaphrum secundatum*	USA (Florida)	JF710374	JF710442	Zhang et al. (2011)
	M53	unknown	USA (Florida)	JF414847	JF710443	Zhang et al. (2011)
	M54	unknown	USA (Florida)	JF414848	JF710444	Zhang et al. (2011)
	M57	*Stenotaphrum secundatum*	USA (Florida)	JF414849	JF710446	Zhang et al. (2011)
G. graminis var. *tritici*	M55	*Triticum* sp.	USA (Montana)	JF414850	JF710445	Zhang et al. (2011)
	R3-111a-1	*Triticum aestivum*		Magnaporthe comparative Database [c]		
G. incrustans	M51	*Zoysia matrella*	USA (Kansas)	JF414846	JF710440	Zhang et al. (2011)
	M26 (ATCC64417)	*Cynodon* sp.	USA (Kansas)	JF414842	JF710435	Zhang et al. (2011)
	M35	unknown	unknown	JF414843	JF710437	Zhang et al. (2011)
	M45	*Poa pratensis*	USA (New Jersey)	JF414844	JF710438	Zhang et al. (2011)
Magnaporthe oryzae	70-15	–	–	Magnaporthe grisea Database [d]		
	M25	*Oryza sativa*	unknown	JF414839	JF710449	Zhang et al. (2011)
	M60	*Festuca arundinacea*	USA (New Jersey)	JF414840	JF710447	Zhang et al. (2011)
	M61	*Festuca arundinacea*	USA (New Jersey)	JF414841	JF710448	Zhang et al. (2011)
M. poae	73-15 (ATCC64411)	*Triticum aestivum*		Magnaporthe comparative Database [c]		
	M1	unknown	USA (New Jersey)	JF414827	JF710425	Zhang et al. (2011)
	M12	*Poa annua*	USA (Pennsylvania)	JF414828	JF710426	Zhang et al. (2011)
	M14	unknown	unknown	JF414829	JF710427	Zhang et al. (2011)
	M15	*Poa annua*	USA (Pennsylvania)	JF414830	JF710428	Zhang et al. (2011)
	M16	unknown	USA (Pennsylvania)	JF414831	JF710429	Zhang et al. (2011)
	M17	*Poa annua*	USA (New Jersey)	JF414832	JF710430	Zhang et al. (2011)
	M47	*Poa pratensis*	USA (New Jersey)	JF414836	JF710433	Zhang et al. (2011)
	M48	*Poa pratensis*	USA (New Jersey)	JF414837	JF710434	Zhang et al. (2011)
M. rhizophila	M22	unknown	unknown	JF414833	JF710431	Zhang et al. (2011)
	M23	*Poa pratensis*	unknown	JF414834	JF710432	Zhang et al. (2011)
	M46	*Poa pratensis*	unknown	JF414845	JF710439	Zhang et al. (2011)
M. salvinii	M21 (ATCC44754)	*Oryza sativa*	Japan	JF414838	JF710441	Zhang et al. (2011)

[a] *ATCC* American type culture collection, Manassas, Virginia, USA

[b] http://genomeportal.jgi-psf.org/Crypa2/Crypa2.home.html

[c] http://www.broadinstitute.org/annotation/genome/magnaporthe_comparative/MultiHome.html

[d] http://www.broadinstitute.org/annotation/genome/magnaporthe_grisea/MultiHome.html

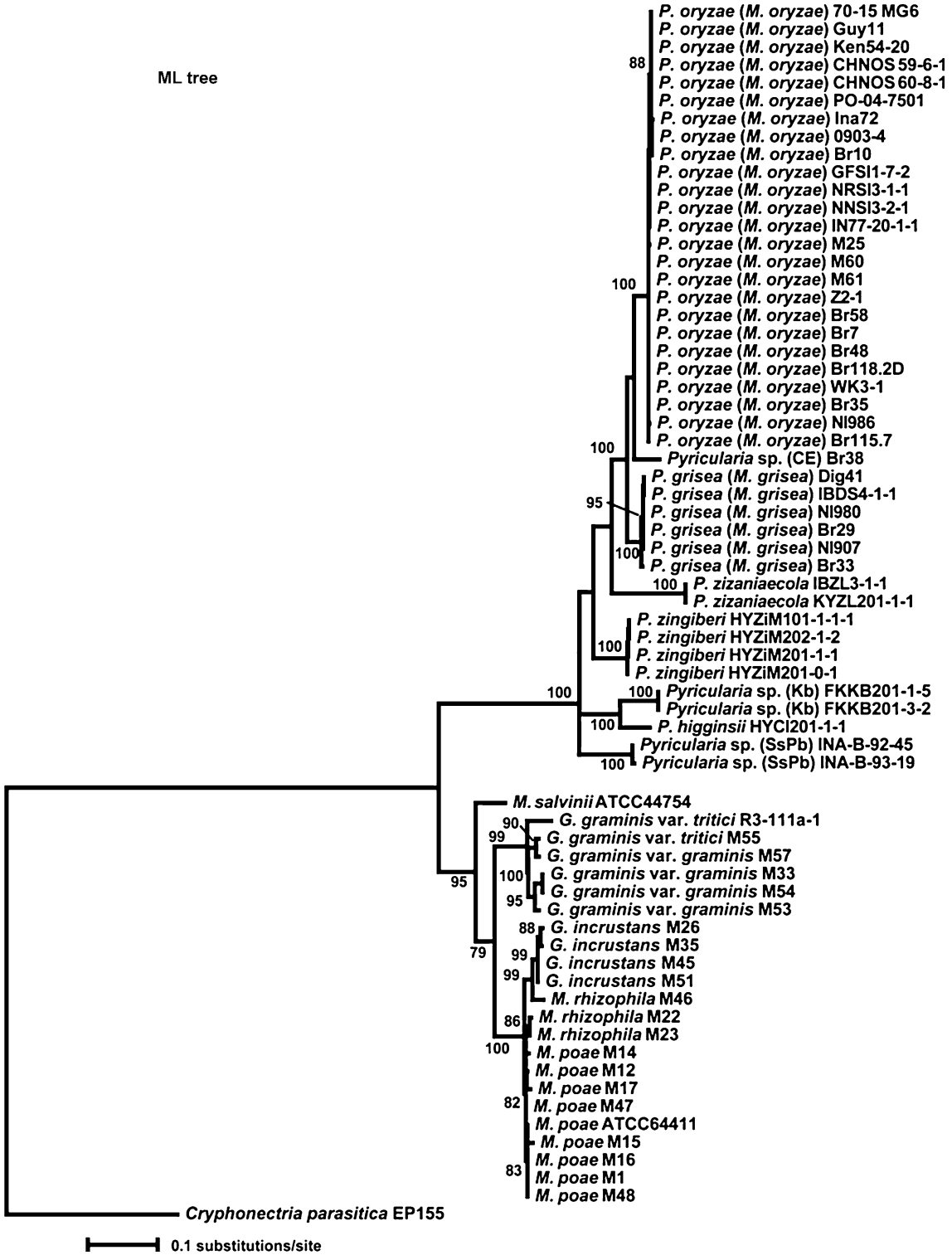

Fig. 1 Maximum likelihood (ML) phylogenetic tree based on rDNA-ITS (ITS1, 5.8S and ITS2) and *RPB1* nucleotide sequences of Magnaporthaceae isolates. The tree was rooted using *Cryphonectria parasitica* EP155 as an outgroup. Numbers at nodes represent bootstrap support >75 % from 500 replicates

Mastercycler (Eppendorf, Hamburg, Germany). PCR cycling conditions for *RPB1* were 1 min at 95 °C; 30 cycles of 1 min at 94 °C, 1 min at 60 °C, 1 min at 72 °C; and 5 min at 72 °C. PCR products were purified with USB ExoSAP-IT (Affymetrix, Santa Clara, CA, USA), and sequenced directly with the same primers as in the

amplification using BigDye Terminator v3.1 Cycle Sequencing Kit and ABI PRISM 3130*xl* Genetic Analyzer (Life Technologies, Carlsbad, CA, USA). The sequences were assembled with SeqMan II (DNASTAR, Madison, WI, USA) and deposited in GenBank (see Table 1). The nucleotide sequences of rDNA-ITS and *RPB1* reported by Zhang et al. (2011) and those of model organisms (*Cryphonectria parasitica* EP155, *Gaeumannomyces graminis* var. *tritici* R3-111a-1, *Magnaporthe oryzae* 70-15 and *M. poae* ATCC 64411) were downloaded from GenBank and genome databases (Table 2).

Nucleotide sequences of each locus were aligned with the program CLUSTAL W (Thompson et al. 1994), and manually optimized using the program MEGA 5.10 (Tamura et al. 2011). Combined alignments were analyzed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) methods. *Cryphonectria parasitica* EP155 was used as an outgroup. The MP analysis was performed with MEGA 5.10 using the Close-Neighbor-Interchange (CNI) algorithm at a search level of 1. The initial tree for the CNI search was created by random addition for 10 replications. Nodal supports were assessed using 500 bootstrap replicates. The best-fit model for the ML and BI analyses was selected using the corrected Akaike information criteria in the program jModelTest 2.1.1 (Darriba et al. 2012; Guindon and Gascuel 2003). The ML analysis with the GTR + G model was carried out using MEGA 5.10. Nodal supports were assessed using 500 bootstrap replicates. Bayesian analysis was conducted with the program MrBayes 3.2.1 (Ronquist et al. 2012) using the GTR + G model and consisted of two runs of four chains each. The two runs were performed for 500,000 generations, sampling every 100 generations. Average standard deviations of split frequency values lower than 0.01 were taken as an indication that convergence had been achieved. After the first 1,250 trees were discarded, a 50 % majority rule consensus tree was constructed based on the remaining samples. The tree was visualized using the program FigTree v1.4.0 (available at http://tree.bio.ed.ac.uk/software).

The ML tree is shown in Fig. 1. The isolates of Magnaporthaceae species tested were divided into two clusters with high bootstrap support. One cluster was composed of the blast fungi and harbored all of the morphologically distinct *Pyricularia* species (Fig. 2). The other was composed of soilborne pathogens, *M. rhizophila*, *M. poae*, *G. graminis*, and *G. incrustans*. *Magnaporthe salvinii* was included in the latter cluster. *Gaeumannomyces* was split into two subclusters; one was composed of all isolates of *G. graminis* var. *graminis* and *G. graminis* var. *tritici*, while the other was *G. incrustans*, grouped together with soilborne *Magnaporthe* species. Similar results were obtained from the MP and BI analyses (Online resources 1 and 2).

As mentioned already, the species analyzed in the present study is divided into three groups based on the ecological and anamorphic features; (1) *Pyricularia* spp. mainly colonizing leaves and panicles, (2) *Gaeumannomyces* spp. and soilborne *Magnaporthe* spp. colonizing roots, and (3) *M. salvinii* colonizing leaf sheath. The present study showed that *M. salvinii*, the type species of *Magnaporthe*, is clustered with group (2) and distinct from group (1) (the blast fungi). The high bootstrap support at the nodes of the two clusters suggests that each of them is a monophyletic clade derived from a common ancestor. Although species classified in the same genus *Magnaporthe* are found in both clades, their differences in anamorphs and infection behaviors are not so trivial as those found among species of the same genus. We suggest that the two clades should logically be separated as distinct genera and have different generic names.

Tsuda and Ueyama (1982), one of the three teams that discovered the teleomorph of *P. oryzae* (Ueyama and Tsuda 1975), found that the teleomorph of the blast fungus was different from typical *Magnaporthe* in morphology of ascospores, especially structure at their tips, and mode of their germination. Based on these observations, they concluded that the teleomorph of the blast fungus should not

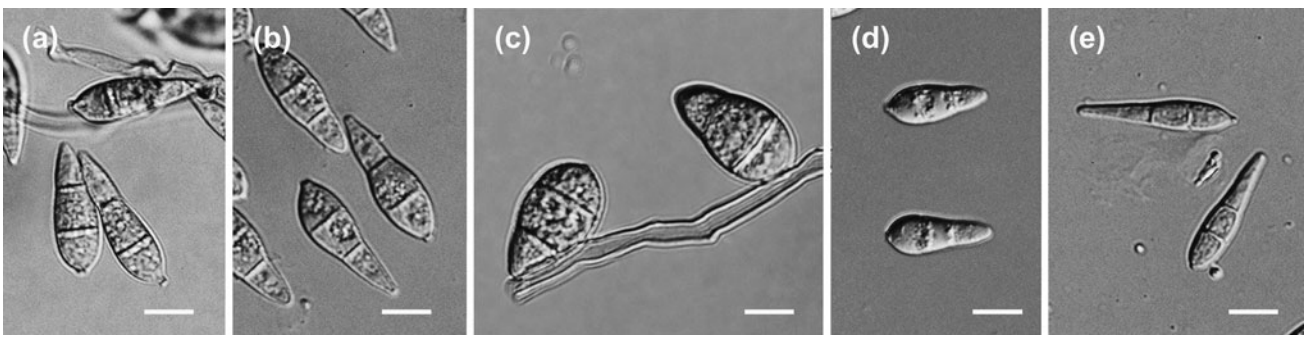

Fig. 2 Pyriform conidia produced by *Pyricularia* spp. **a** *P. oryzae* (*Triticum* isolate, Br48). **b** *P. grisea* (*Digitaria* isolate, Dig41). **c** *P. zizaniaecola* (*Zizania* isolate, KYZL201-1-1). **d** *P. zingiberi* (*Zingiber* isolate, TKZiM202-1). **e** *P. higginsii* (*Cyperus* isolate, HYCI201-1-1). *Bars* = 10 μm

be designated as *Magnaporthe* and argued that a new teleomorph genus should be established for it. Our phylogenetic analyses also suggest that *Magnaporthe*, typified by *M. salvinii*, should not be connected with the blast fungi, that have long been called *Pyricularia* species.

Luo and Zhang (2013) suggested synonymizing *M. salvinii* to *Nakataea oryzae* (Cattaneo) J. Luo & Zhang, recombined from *Sclerotium oryzae* Cattaneo, an anamorphic synonym of *M. salvinii*. According to this treatment, the generic name *Magnaporthe* will correspondently be synonymized to *Nakataea* Hara. It should be noted that *Nakataea* is apparently different from *Pyricularia*, especially in conidial shape and pigmentation (Luo and Zhang 2013). Based on their morphological and phylogenetic considerations, they suggested that the blast fungus should not be congeneric with the type species of *Magnaporthe*.

Taken together, we conclude that the blast fungi composed of various species constitute a large, but distinct phylogenetic group of fungi that is not congeneric with *M. salvinii*, the type species of *Magnaporthe*. If *Magnaporthe* is adopted as the generic name of the blast fungi, therefore, the type species of *Magnaporthe* must be replaced with some species in the clade of blast fungi. On the basis of these considerations, we propose that the clade of the blast fungi should be designated *Pyricularia* simply based on its priority, as suggested by Luo and Zhang (2013), and that the name *Magnaporthe* should be used for its type or closely related species in the *M. salvinii* clade.

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