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A phylogenetic and taxonomic re-evaluation of the *Bipolaris* - *Cochliobolus* - *Curvularia* Complex

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Abstract Three genera, *Cochliobolus*, *Bipolaris* and *Curvularia* form a complex that contains many plant pathogens, mostly on grasses (*Poaceae*) with a worldwide distribution. The taxonomy of this complex is confusing as frequent nomenclatural changes and refinements have occurred. There is no clear morphological boundary between the asexual genera *Bipolaris* and *Curvularia*, and some species show intermediate morphology. We investigated this complex based on a set of ex-type cultures and collections from northern Thailand. Combined gene analysis of rDNA ITS (internal transcribed spacer), GPDH (glyceraldehyde 3-phosphate dehydrogenase), LSU (large subunit) and EF1-α (translation elongation factor 1-α) shows that this generic complex divides into two groups. *Bipolaris* and *Cochliobolus* species clustered in Group 1 along with their type species, whereas *Curvularia* species (including species named as *Bipolaris*, *Cochliobolus* and *Curvularia*) clustered in Group 2, with its generic type. The nomenclatural conflict in this complex is resolved giving priority to the more commonly used established generic names *Bipolaris* and *Curvularia*. Modern descriptions of the genera *Bipolaris* and *Curvularia* are provided and species resolved in this study are transferred to one of these genera based on their phylogeny.

Keywords Anamorph · Generic complex · Neotype · Nomenclature · Pathogens · *Pseudocochliobolus*

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Introduction

Species of *Cochliobolus* Drechsler (1934), with asexual states in *Bipolaris* Shoemaker (1959) and *Curvularia* Boedijin (1933), are important plant pathogens associated with over 60 host genera (Sivanesan 1987; Manamgoda et al 2011; Agrios 2005). A few species in these genera are occasionally involved in opportunistic infections of vertebrates (Rinaldi et al. 1987; Dasgupta et al. 2005; Hoog et al. 2005). Accurate identification and precise naming of species are crucial since the name is the key to accessing all accumulated knowledge (Cai et al. 2009, 2011; Hyde et al. 2010; Hawksworth et al. 2011; Ko Ko et al. 2011; Udayanga et al. 2011). Frequent name changes as a result of refinements to the taxonomy in *Bipolaris*, *Curvularia* and *Cochliobolus* have caused confusion

for many plant pathologists and mycologists (Sivanesan 1987; Manamgoda et al. 2011). *Bipolaris* and *Curvularia* share many morphological similarities (Sivanesan 1987). There are some *Bipolaris* species with short, straight conidia showing intermediate conidial characters between these two genera. Those *Bipolaris* species with short, straight conidia differ from the generic type *Bipolaris maydis*, which has large, gently curving conidia. With the use of molecular taxonomy many uncertainties of conventional taxonomy can be resolved (Valente et al. 1999; Mendoza et al. 2001). Phylogenetic studies of *Bipolaris* and *Curvularia* have shown that the genus *Bipolaris* is not monophyletic and some *Bipolaris* species with short straight conidia cluster with *Curvularia* (Goh 1998; Berbee et al. 1999; Emami and Hack 2002; Manamgoda et al. 2011).

Pseudocochliobolus was primarily separated from *Cochliobolus* on the basis of sexual morphology (Tsuda et al. 1977), but has generally been treated as a synonym (Alcorn 1983). In *Pseudocochliobolus*, the degree of ascospore coiling is less than in *Cochliobolus*, and stromatic tissue is present below the ascomata. High intraspecific variation of the above characters was found by Alcorn (1983), who doubted their use in generic delineation. Both genera produce *Bipolaris* and *Curvularia* asexual states, which was the basis for Alcorn (1983) to synonymise *Pseudocochliobolus* with *Cochliobolus*. In his monograph, Sivanesan (1987) also treated *Pseudocochliobolus* as a synonym of *Cochliobolus*.

Berbee et al. (1999) presented a phylogenetic analysis of 32 *Bipolaris*, *Cochliobolus* and *Curvularia* species using combined ITS and GPDH gene regions. Their phylogenies showed two main groups. Group 1 included highly virulent pathogens such as *Cochliobolus heterostrophus* (Drechsler) Drechsler, the type of *Cochliobolus*. Group 2 included species transferred from *Cochliobolus* to *Pseudocochliobolus*. Berbee et al. (1999) did not reinstate *Pseudocochliobolus* as a separate genus, but showed that ITS and GPDH genes provide sufficient phylogenetic information for the separation of *Cochliobolus* species into two groups. Later a generic tree using Brn1 gene analysis also showed that *Bipolaris* separated into two major clades with respect to *Pseudocochliobolus* and *Cochliobolus* (Shimizu et al. 1998), whereas *Curvularia* strains clustered only in Group 2 (Berbee et al. 1999). Phylogenetic analysis of *Pleosporaceae* by Kodsueb et al. (2006) also revealed that *Cochliobolus* and its anamorphs broadly divided into two groups.

In the present study we used sequences from four gene regions (ITS, GPDH, LSU and EF1-α) from 19 ex-type strains of *Bipolaris, Cochliobolus* and *Curvularia* spp., and recently collected cultures from northern Thailand to reconstruct their phylogenetic relationships. The objectives of this study were to 1) establish whether the genera *Bipolaris* and *Curvularia* are monophyletic; 2) resolve their relationships with *Cochliobolus* and *Pseudocochliobolus*; and 3) conclude which generic names should be retained in order to redefine their circumscriptions based on phylogenetic groupings.

Materials and methods

Fungal isolates

Sixty one isolates belonging to more than 35 species of *Bipolaris, Cochliobolus* and *Curvularia* were used in this study and this included 19 ex-type or ex-epitype strains (Table 1). Fresh collections were also obtained from Chiang Rai and Chiang Mai provinces in northern Thailand. Fresh specimens were incubated for 1–2 days in a moist chamber and fungi were isolated by a modified single spore suspension method (Chomnunti et al. 2011). Conidia were taken from the sporulating samples and placed in 400 μl sterilized water on a sterilized glass slide. The spore suspension was then transferred to water agar media with a sterilized pipette tip. The plates were left overnight to germinate and germinated spores were individually transferred to PDA or MEA. Details of all ex-type strains and fresh strains used are listed in Table 1.

DNA extraction

Genomic DNA was extracted using a modified protocol of Guo et al. (2000). Fresh mycelium (0.5g) was scraped from the surface of a colonised agar plate and transferred to 1.5 ml micro centrifuge tubes. The mycelium was grounded for 3–5 min with a sterilised glass pestle after adding 600 μl of preheated (60 °C) 2× CTAB extraction buffer (2 %(w/v) CTAB, 100 mM Tris–HCl, 1.4 M NaCl, 20 mM EDTA, pH 8.0) and 0.2 g sterilised quartz sand. The solution was incubated at 60 °C with a gentle swirling. The mixture was subsequently centrifuged the 12,000 rpm for 15 min at 25 °C followed by chloroform isoamyl extraction repeatedly. DNA was precipitated with isopropanol and centrifuged at 12,000 rpm for 15 min at 25 °C. The precipitate was treated with 70 % ethanol centrifuged at 12,000 rpm for 5 min at 25 °C. DNA was dried under a regular air flow for 20 min, resuspended in 70 μl TE buffer and stored in −20 °C.

PCR amplification

The DNA fragments were amplified in an automated thermal cycler (DongShen EDC-810- Eastwin, LifeSciences). Amplification was performed in a 25 μl reaction volume which contained 2.5 μl 10× PCR buffer, 1 μl of each primer (10 μM), 1 μl template DNA, and 0.25 μl Taq DNA polymerase (Promega, Madison, WI, USA). Primers ITS1 and ITS4 (Glass and Donaldson 1995) were used to amplify the 5.8 S and flanking ITS regions. The thermal cycling program was: 3 min initial denaturation at 95 °C, followed by 30 cycles of 30 s denaturation at 94 °C, 30 s primers annealing at 52 °C, 1 min extension at 72 °C, and a 10 min extension at 72 °C. To amplify the GPDH gene the primers gpd1 and gpd2 (Berbee et

Table 1 Details of isolates subjected to multi-gene DNA sequence analysis

Species	Accession no.	Host	Location	GenBank No.				Reference
				ITS	GPDH	28s RNA	EF 1-α	
Alternaria alternata	**EGS 34.0160**			**AF 071346**	**AF081400**			Berbee et al. 1999
Bipolaris chloridis	**CBS 242.77**	*Chloris gayana*	Australia	**JN192372**	**JN600961**			Manamgoda et al. 2011
Bipolaris cynodontis	ICMP 6128	*Cynodon dactylon*	New Zealand	JX256412	JX276427	JX256380	JX266581	This study
Bipolaris maydis	C5 (141-1-2)			AF071325	AF081380			Berbee et al. 1999
Bipolaris melinidis	**BRIP 12898**	*Melinis munitiflora*	Australia	**JN601035**	**JN600972**	**JX256411**		Manamgoda et al. 2011
								This study
Bipolaris microlaenae	**CBS 280.91**	*Microlaenae stipoidis*	Australia	**JN601032**	**JN600974**	**JN600995**	**JN601017**	Manamgoda et al. 2011
Bipolaris oryzae	MFLUCC 10-0694	*Oryza sativa*	Thailand	JX256413	JX276428	JX256381	JX266582	This study
	MFLUCC 10-0714	*Oryza sativa*	Thailand	JX256414		JX256382	JX266583	This study
	MFLUCC 10-0716	*Oryza sativa*	Thailand	JX256415	JX276429	JX256383	JX266584	This study
	MFLUCC 10-0715	*Oryza sativa*	Thailand	JX256416	JX276430	JX256384	JX266585	This study
	MFLUCC 10-0733	*Oryza sativa*	Thailand	JX256417	JX276431	JX256385	JX266586	This study
Bipolaris peregianensis	**BRIP 12790**	*Cynodon dactylon*	Australia	**JN601034**	**JN600977**	**JN601000**	**JN601022**	Manamgoda et al. 2011
Bipolaris sorokiniana	ICMP 6233	*Lolium perenne*	Solomon Islands	JX256418		JX256386	JX266587	This study
	A20			AF071329	AF081385			Berbee et al. 1999
Bipolaris victoriae	CBS 174.57	*Avena sativa*	USA	JN601027	AF081407	JN600983	JN601005	Manamgoda et al. 2011
Bipolaris zeae	8641			AF081452				This study
Bipolaris zeiocola	CcA			AF158110				This study
Bipolaris sp.	MFLUCC 10-0720	*Oryza sativa*	Thailand	JX256419	JX276432		JX266588	This study
Curvularia alcornii	**MFLUCC 10-0703**	*Zea mays*	Thailand	**JX256420**	**JX276433**	**JX256387**	**JX266589**	This study
	MFLUCC 10-0705	*Panicum* sp.	Thailand	JX256421	JX276434	JX256388	JX266590	This study
Curvularia asianensis	MFLUCC 10-0687	*Oryza sativa*	Thailand	JX256422	JX276435	JX256389	JX266591	This study
	MFLUCC 10-0704	Bamboo	Thailand	JX256423		JX256390	JX266592	This study
	MFLUCC 10-0711	*Panicum* sp.	Thailand	**JX256424**	**JX276436**	**JX256391**	**JX266593**	This study
	MFLUCC 10-0685	*Saccharum officinarum*	Thailand	JX256425	JX276437	JX256392	JX266594	This study
Curvularia australien sis comb.nov**	CBS 172.57[a]	*Oryza sativa*	Vietnam	JN61026	JN61036	JN600981	JN601003	Manamgoda et al. 2011
*Curvularia coicis***	**CBS 192.29[a]**	*Coix lacryma*	Japan	**AF081447**	**AF081410**	**JN600984**	**JN601006**	Manamgoda et al. 2011; Berbee et al. 1999
Curvularia cymbopogonis	88109-1[a]			AF071351	AF081403			Berbee et al. 1999
Curvularia ellisii	**CBS 193.62[a]**	Air	Pakistan	**JN192375**	**JN600963**	**JN600985**	**JN601007**	Manamgoda et al. 2011
Curvularia gladioli	ICMP 6160	*Gladiolus* sp.	New Zealand	JX256426	JX276438	JX256393	JX266595	This study
	DAOM164725			AF071337	AF081392			Berbee et al. 1999
Curvularia gudauskasii	DAOM165085			AF071338	AF081393			Berbee et al. 1999
Curvularia graminicola	**BRIP 23186[a]**		Australia	**JN192376**	**JN600964**	**JN600986**	**JN601008**	Manamgoda et al. 2011

Table 1 (continued)

Species	Accession no.	Host	Location	GenBank No.				Reference
				ITS	GPDH	28s RNA	EF 1-α	
Curvularia hawaiiensis comb.nov**	MFLUCC 10-0730[a]	*Panicum* sp.	Thailand	JX256427	JX276439			This study
	BRIP 10971[a]	*Chloris gayana*	Australia	JN601030	JN600967	JN600989	JN601011	Manamgoda et al. 2011
	BRIP 10972[a]	*Chloris gayana*	Australia	JN192377	JN600968	JX256394	JN601012	Manamgoda et al. 2011
	BRIP 15933[a]	*Chloris gayana*	Australia	JN601028	JN600965	JN600987	JN601009	Manamgoda et al. 2011
	CBS 173.57[a]	*Oryza sativa*	Hawaii	**JN601029**	**JN600966**			Manamgoda et al. 2011
Curvularia heteropogonis	**CBS 284.91**	*Heteropogon contortus*	Australia	**JN192379**	**JN600969**	**JN600990**	**JN601013**	Manamgoda et al. 2011
Curvularia ischaemi	**ICMP 6172**	*Ischaemum indicum*	Solomon Islands	**JX256428**	**JX276440**	**JX256395**		This study
*Curvularia lunata***	**CBS 730.96 (Neo type)**	human lung biopsy	USA	**JX256429**	**JX276441**	**JX256396**	**JX266596**	This study
	CBS 157.34	Unknown	Indonesia	JX256430	JX276442	JX256397	JX266597	This study
	MFLUCC 10-0706	*Oryza sativa*	Thailand	JX256431	JX276443	JX256398	JX266598	This study
	MFLUCC 10-0695	*Panicum sp.*	Thailand	JX256432	JX276444	JX256399		This study
Curvularia ovariicola comb.nov	**CBS 470.90[a]**	*Eragrostis interrupta*	Australia	**JN192384**	**JN600976**	**JN600998**	**JN601020**	Manamgoda et al. 2011
	BRIP 15882[a]			**JN601031**	**JN600971**	**JN600992**	**JN601015**	Manamgoda et al. 2011
Curvularia perotidis comb.nov	**CBS 350.90[a]**	*Perotis rara*	Australia	**JN192385**		**JN600999**	**JN601021**	Manamgoda et al. 2011
Curvularia ravenelii comb.nov	**BRIP 13165[a]**	*Sporobolus fertilis*	Australia	**JN192386**	**JN600978**	**JN601001**	**JN601024**	Manamgoda et al. 2011
*Curvularia spicifera***	CBS 274.52[a]	Soil	Spain	JN192387	JN600979	JX256400	JN601023	Manamgoda et al. 2011
Curvularia tripogonis comb.nov	**BRIP 12375[a]**	Unknown	Australia	**JN192388**	**JN600980**	**JN601002**	**JN601025**	Manamgoda et al. 2011
Curvularia tuberculata	**CBS 146.63**	*Zea mays*	Rajasthan	**JX256433**	**JX276445**	**JX256401**	**JX266599**	This study
Curvularia trifolii	ICMP 6149	*Setaria glauca*	New Zealand	JX256434	JX276457	JX256402	JX266600	This study
Curvularia sp.	MFLUCC 10-0686	*Oryza sativa*	Thailand	JX256435	JX276446	JX256403	JX266601	This study
Curvularia sp.	MFLUCC 10-0688	*Echinocola* sp.	Thailand	JX256436	JX276447			This study
Curvularia sp.	MFLCCC 10-0690	*Oryza sativa*	Thailand	JX256437	JX276448	JX256405	JX266602	This study
Curvularia sp.	MFLUCC 10-0691	*Oryza sativa*	Thailand	JX256438	JX276449	JX256406	JX266604	This study
Curvularia sp.	MFLUCC 10-0692	*Oryza sativa*	Thailand	JX256439	JX276450	JX256407	JX266605	This study
Curvularia sp.	MFLUCC 10-0738	*Oryza sativa*	Thailand	JX256440	JX276451			This study
Curvularia sp.	MFLUCC 10-0717	*Oryza sativa*	Thailand	JX256441	JX276452	JX256408	JX266606	This study
Curvularia sp.	MFLUCC 10-0709	*Oryza sativa*	Thailand	JX256442	JX276453	JX256409		This study
Curvularia sp.	MFLCCC 10-0739	*Oryza sativa*	Thailand	JX256443	JX276454	JX256404	JX266603	This study
Curvularia sp.	ICMP 10344	lawn	Solomon Islands	JX256444	JX276455			This study
Curvularia sp.	ICMP 13910	*Actinidia deliciosa*	Solomon Islands	JX256445	JX276456	JX256410		This study

[a] Species transferred from *Bipolaris* to *Curvularia*

** Species previously named as *Pseudocochliobolus*

ex- Type cultures and sequences are bold

al. 1999) were used. The amplification program included an initial denaturation step at 96 °C for 2 min at 96 °C, followed by 35 PCR cycles with 1 min at 96 °C, 1 min at 52 °C and 45 s at 72 °C. With each cycle, time was extended at 72 °C by 4 s with a final 10 min extension at 72 °C. The EF-1α and LSU regions were amplified using EF 983/2218R and LR5/LROR primers respectively (Schoch et al. 2009). The LSU amplification program included an initial denaturation step at 95 °C for 3 min followed by 30 cycles of 40 s denaturation at 94 °C, 50 s primer annealing at 52 °C, 1 min extension at 72 °C. The same PCR reaction was used to amplify EF-1α with the changes of annealing temperature 54 °C.

Sequence alignment and phylogenetic analysis

The sequences were aligned with Clustal X (Thompson et al. 1997) and optimized by the online sequence alignment tool MAFFT (Katoh et al. 2009). Phylogenetic analyses were performed in PAUP v4.0b10 (Swofford 2002). Ambiguously aligned regions were excluded from all analyses. All gaps were treated as missing data and trees were viewed by Tree View (Page 1996).

Results

We sequenced 37 isolates of *Bipolaris, Cochliobolus* and *Curvularia*. PCR using primer pairs ITS1/ITS4, gpd1/gpd2, LR5/LROR and EF 983/2218R yielded specific PCR products of approximately 540 bp (ITS), 530 bp (GPDH), 900 bp (LSU) and 1,200 bp (EF-1α). The data were used to generate phylograms using individual and combined gene analyses (Figs. 1 and 2). Maximum parsimony analyses of the combined ITS and GPDH (Fig. 1) and of a combined dataset of the four loci (Fig. 2) showed 11 species clustering in Group 1 and 23 species clustering in Group 2. Group 1 comprised species of *Bipolaris* (Shoemaker 1959) and *Cochliobolus* (Drechsler 1934), while Group 2 comprised species of *Curvularia,* and others that were *Bipolaris*- and *Cochliobolus*-like in morphology. All species previously named in *Pseudocochliobolus* clustered in Group 2.

Utilization of different genes in resolving species of *Bipolaris, Cochliobolus* and *Curvularia*

The phylogenetic analyses showed that all species studied separated into two well-supported groups; Groups 1 and 2 (Figs. 1 and 2). The combined dataset resulted in a better resolution than any individual dataset (data not presented). Resolutions of the terminal clades in the multi-locus tree (Fig. 2) are better than in the combined ITS and GPDH tree (Fig. 1).

Species named as *Bipolaris, Cochliobolus* and *Curvularia* clustered in Group 2, with the generic type of *Curvularia*, in the multi-gene analysis using ITS, GPDH, EF1-α and LSU gene sequence data with 91 % bootstrap support (Fig. 2). *Bipolaris* and *Cochliobolus* species clustered in Group 1 with 80 % bootstrap support. In a combined analysis using ITS and GPDH gene regions (Fig. 1), 13 species named as *Bipolaris, Cochliobolus* and *Curvularia* separated into Group 2 with the generic type of *Curvularia* with 96 % bootstrap support, while 31 taxa clustered in Group 2 with 94 % bootstrap support.

The phylogenetic data presented in Figs. 1 and 2 resolve two monophyletic groups which indicate separate generic status. Group 1 is characterised by large canoe-shaped conidia, and lack stromata. Group 2 species have straight to curved conidia, and usually stromata below the ascomata. *Bipolaris maydis* and *Cochliobolus heterostrophus* are the asexual and sexual states of the same biological species and are the generic types of *Cochliobolus* and *Bipolaris.* This species nests in Group 1, which represents species of *Bipolaris* and *Cochliobolus* related to *Cochliobolus heterostrophus*. Group 2 represents species of "*Bipolaris*", "*Cochliobolus*", *Curvularia* (and *Pseudocochliobolus*) related to *Curvularia lunata*. *Bipolaris australiensis, B. coicis, B. ellisii*, *B. graminicola*, *B. hawaiiensis, B. ovariicola, B. ravenelii, B. spicifera, B. perotidis* and *B. tripogonis,* also cluster with group 2 (Figs. 1 and 2). Apart from the *Bipolaris* species cited above, those species that remain in Group 1 are monophyletic and show morphological characters typical to its type species *Bipolaris maydis.* We therefore transfer *B. australiensis, B. coicis, B. ellisii*, *B. graminicola*, *B. hawaiiensis, B. ovariicola, B. ravenelii, B. spicifera, B. perotidis* and *B. tripogonis* to *Curvularia* based on the phylogenetic data derived in this study.

Based on the phylogenetic data given here the generic name applied to Group 1 species should be either *Bipolaris* or *Cochliobolus,* and to Group 2 should be either *Pseudocochliobolus* or *Curvularia*. In Group 1, *Cochliobolus* is an older name than *Bipolaris* and should be selected (McNeill et al. 2006; Hawksworth 2012). As an economically important pathogen, *Bipolaris* is more commonly used than *Cochliobolus* among mycologists and plant pathologists. In *Index Fungorum* there are 56 *Cochliobolus* and 116 *Bipolaris* names, which show that sexual recombination is not established for many species of *Bipolaris*. If *Cochliobolus* is chosen as a name for Group 1, a larger number of name changes will result than if *Bipolaris* is chosen. We propose conserving *Bipolaris,* prioritizing it over *Cochliobolus*. In Group 2, *Curvularia* which is the oldest name has been used because this species name is and more commonly used compared to *Pseudocochliobolus* and besides this name has already been well recognised by plant pathologists.

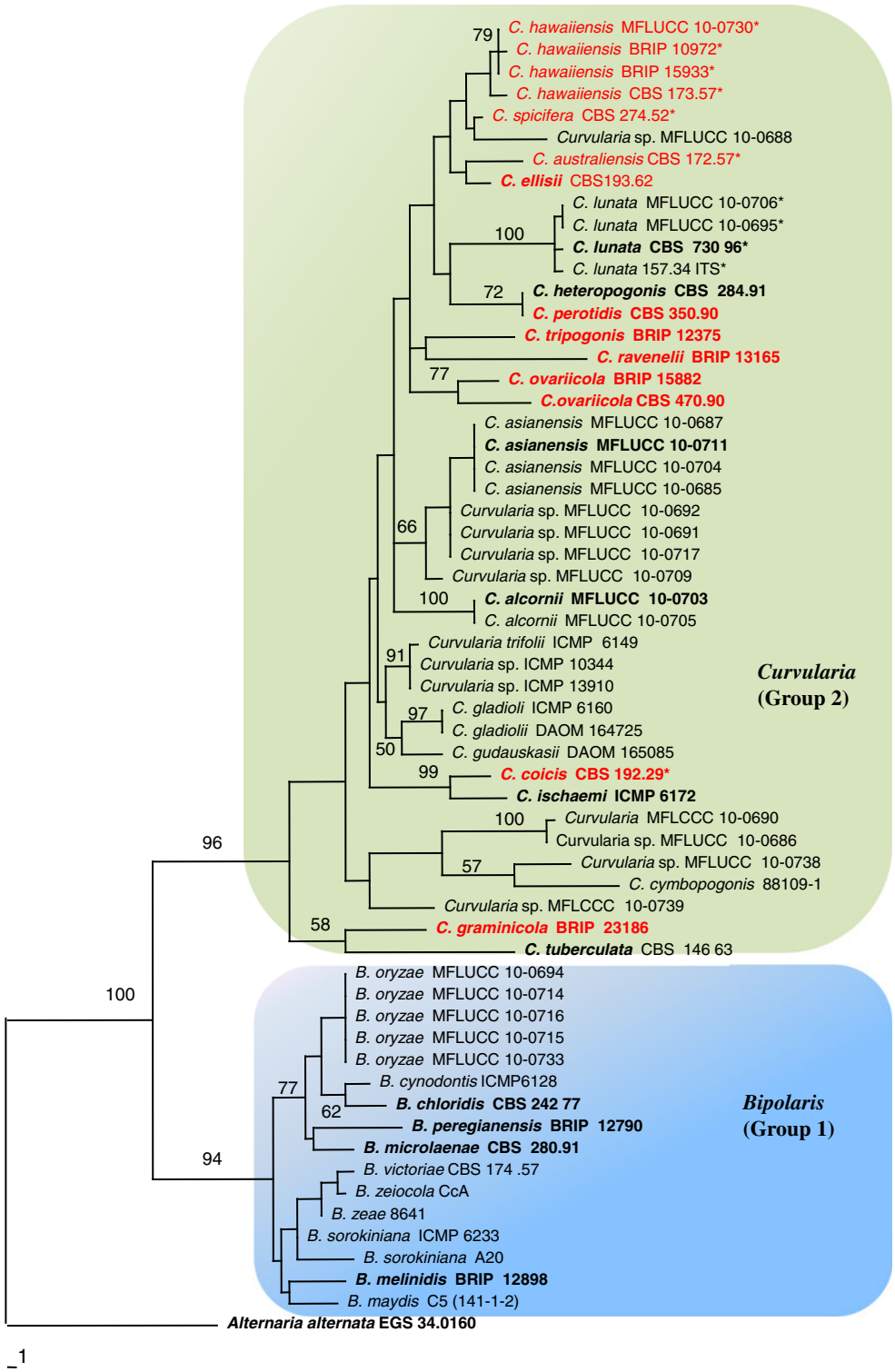

Fig. 1 Phylogram generated from the parsimony analysis based on combined genes of ITS and GPDH sequence data derived from ex-type, ex-epitype and isolates from northern Thailand. The tree is rooted with *Alternaria alternata*. Bootstrap values of more than 50 are shown in the tree. Species transferred from *Bipolaris* to *Curvularia* are shown in red. All ex-type cultures are in bold.*species previously named as *Pseudocochliobolus*

As a result we apply the name *Bipolaris* for all species in Group 1 and *Curvularia* for all species in Group 2. Conidial morphologies of the two genera are shown in Fig. 3. The circumscriptions of *Bipolaris* and *Curvularia* are amended and the species resolved in this study are transferred to the appropriate genus based on their phylogeny.

Taxonomy

Bipolaris Shoemaker

Generic type *Bipolaris maydis* (Y. Nisik. & C. Miyake) Shoemaker *Mycelium* hyaline, pale brown, grey or black.

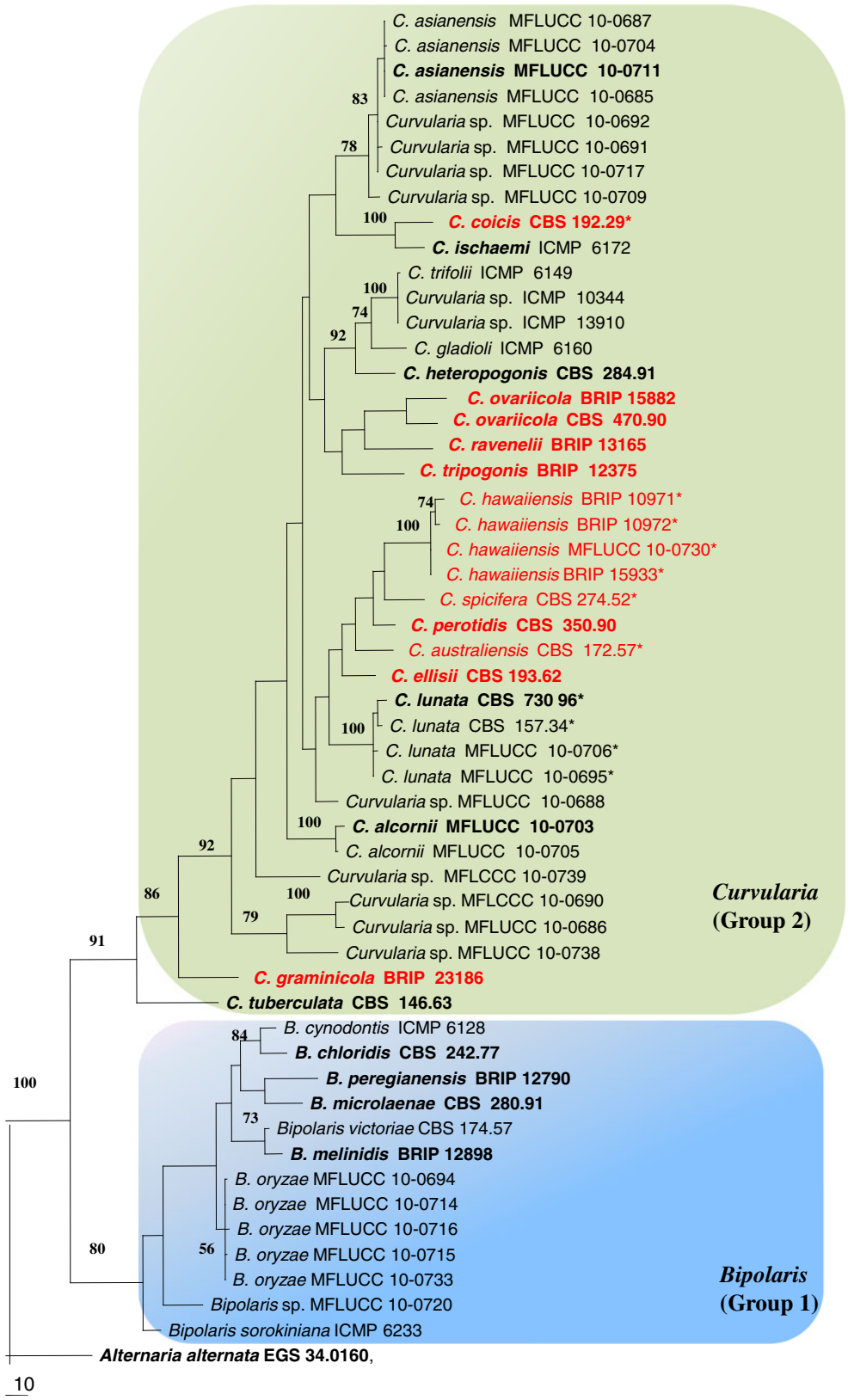

Fig. 2 Phylogram generated from the parsimony analysis based on combined genes of ITS, GPDH, LSU, EF1-α sequence data derived from ex-type, ex-epitype and isolates form northern Thailand. The tree is rooted with *Alternaria alternata*. Bootstrap values of more than 50 are shown in the tree. Species transferred from *Bipolaris* to *Curvularia* are shown in red. All ex-type cultures are in bold. *species previously named as *Pseudocochliobolus*

Colonies growing rapidly, grey to dark grey. Aerial mycelium fluffy or cottony. Colony raised or convex with papillate surface, lobate undulate or sometimes with edge entire

Bipolaris Ascomata up to 700 μm diam, brown or black, immersed, erumpent, partially embedded or superficial, free or on flat stroma, mostly globose to ellipsoidal, sometimes

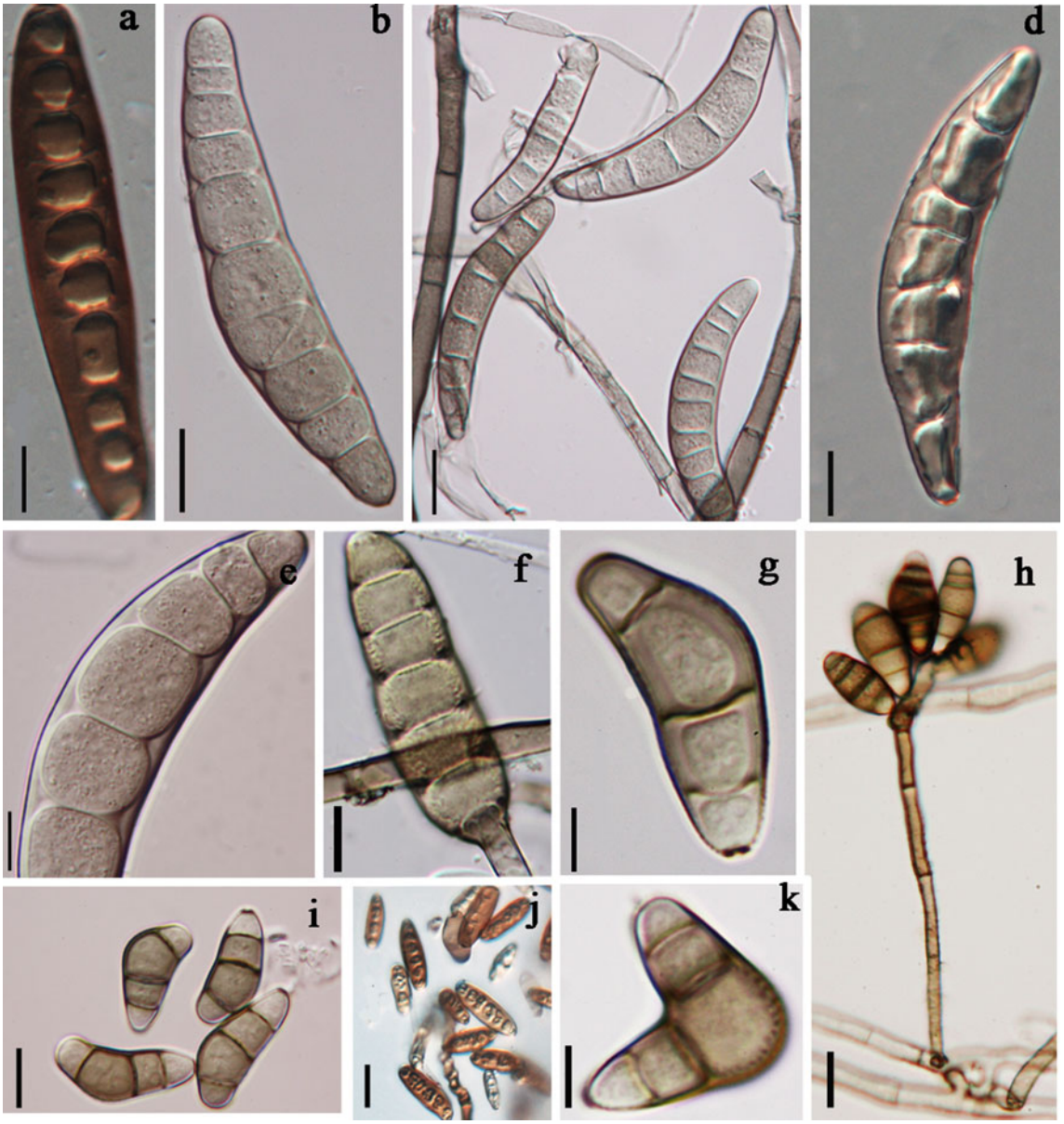

Fig. 3 Conidial morphology of the amended genera *Bipolaris* and *Curvularia* (**a**). Large, 9-distoseptate conidia of *Bipolaris eleusines* from holotype BRIP 16334 (**b, e, f**). Large gently curving canoe-shaped conidia with more than 5 distoseptate and conidiophores of *Bipolaris oryzae* on rice seed MFLUCC10-0964 **c.** Large gently curving canoe-shaped conidia of *Bipolaris oryzae* on rice seed MFLUCC 10-0714 (**d**). Large gently curving canoe-shaped conidia of *Bipolaris peregianensis* on holotype BRIP 12790 (**g**). Curved, 3-distoseptate conidia of *Curvularia alcornii* on PDA (**h**). Conidiophore of *Curvularia asianensis* (MFLUCC 10-0685) on PDA (×40) (**i**). Conidia of *Curvularia* spp. (MFLUCC 10-0688) (**j**). Straight conidia of *Curvularia hawaiiensis* on isotype BRIP 12105 (**k**). Curved, 4-distoseptate conidia of *Curvularia* spp. (MFU0048) (Scale bars: a, e=15 μm, b=15 μm, c=50 μm, f, h=20 μm, g=5 μm, d, k, i, j=10 μm

ampulliform or flattened, forming on hard host substratum, smooth or covered with vegetative filaments, ostiole central, often papillate or with a neck, neck can be sub-conical, conical, paraboloid or cylindrical. Peridium comprising pseudoparenchymatous cells of equal thickness or slightly thickened at the apex. Hamathecium comprising septate, filiform, and branched pseudoparaphyses. *Asci* 2–8 spored, clavate, cylindrical-clavate or broadly fusoid, straight or slightly curved, thin-walled, bitunicate, fissitunicate, often becoming more or less distended prior to dehiscence, short pedicellate, rounded at the apex. *Ascospores* fasciculate, filiform or flageliform, hyaline or sometimes pale yellow or pale brown at maturity, septate, helically coiled within the ascus, degree of ascospore coiling can be moderate to very strongly coiled, sometimes with free ends, often with a thin mucilaginous sheath. *Conidiophores* single, branched and sometimes arranged in small groups, straight to flexuous and sometimes geniculate. Conidiogenous node smooth or verrucose. *Conidia* mostly curved, canoe-shaped, fusoid

or obclavate, rarely straight, 2–14 pseudoseptate (usually more than 6), hyaline to deep olivaceous, germinating by the production of two polar germ tubes, one from the apex and other one immediate to the basal scar.

Notes: Eleven species used in our analysis are resolved in *Bipolaris* based on multigene analysis (Figs. 1 and 2). *Bipolaris* comprises species that are morphologically similar bearing long, slender, gently curving conidia and with ascospores coiled in a helix in the ascus. Ascomata do not develop on columnar stromata in the *Bipolaris* species resolved in this study.

Accepted species in Bipolaris

Bipolaris chloridis (Alcorn) Alcorn, Mycotaxon 16: 373 (1983)

≡ *Drechslera chloridis* Alcorn, Trans. Br. Mycol. Soc. 67: 148 (1976)
= *Cochliobolus chloridis* Alcorn, Trans. Br. Mycol. Soc. 70: 61 (1978)

Bipolaris cynodontis (Marignoni) Shoemaker, in Azbukina et al. (eds), Overs. K. danske Vidensk. Selsk. Forh. Medlemmers Arbeider 79: (1959)

≡ *Helminthosporium cynodontis* Marignoni, Micromicetidi Schio: 27 (1909)
≡ *Bipolaris cynodontis* (Marignoni) Shoemaker, Can. J. Bot. 37: 883 (1959)
≡ *Drechslera cynodontis* (Marignoni) Subram. & B.L. Jain, Curr. Sci. 35: 354 (1966)
= *Cochliobolus cynodontis* R.R. Nelson, Mycologia 56:67 (1964)

Bipolaris maydis (Y. Nisik. & C. Miyake) Shoemaker, Can. J. Bot. 33: 882 (1959)

≡ *Helminthosporium maydis* Y. Nisik. & C. Miyake Sci. Res. Alumni Assoc. Mirioka agric. Col. Japan 3:46 (1926)
≡ *Drechslera maydis* (Y. Nisik. & C. Miyake) Subram. & B.L. Jain, Curr. Sci. 35: 354 (1966)
= *Ophiobolus heterostrophus* Drechsler, J. Agric. Res. 31: 701 (1925)
= *Cochliobolus heterostrophus* (Drechsler) Drechsler, Phytopathology 24: 973 (1934)

Bipolaris melinidis Alcorn, Mycotaxon 15: 7 (1982)

= *Cochliobolus melinidis* Alcorn, Mycotaxon 15: 5 (1982)
= *Drechslera curvispora* El Shafie, Trans. Br. Mycol. Soc. 78: 545 (1982)≡*Bipolaris curvispora* (El Shafie) Sivan., Mycol. Pap.158: 47 (1987)
= *Drechslera pluriseptata* Khetarpal, Nath & Lal, Ind. Phytopath. 37: 320 (1984)

Bipolaris microlaenae Alcorn, Mycotaxon 39: 382 (1990)

= *Cochliobolus microlaenae* Alcorn, Mycotaxon 39: 381 (1990)

Bipolaris oryzae (Breda de Haan) Shoemaker, Can. J. Bot. 37: 883 (1959)

≡ *Helminthosporium oryzae* Breda de Haan, Bulletin Inst. Bot. Buitenzorg 6: 11 (1900)
≡ *Drechslera oryzae* (Breda de Haan) Subram. & B.L. Jain, Can. J. Bot. 37: 883 (1959)
≡ *Luttrellia oryzae* (Breda de Haan) Gornostaĭ [as 'Lutrellia'], in Azbukina et al. (eds), Vodorosli, Griby I Mkhi Dal'nego Vostoka (Vladivostok): 81 (1978)
= *Helminthosporium macrocarpum* Grev, Scott. crypt. fl., 2: 148 (1824) [1825]
= *Ophiobolus miyabeanus* S. Ito & Kurib, Proc. Imp. Acad. Hokkaido Imp. Univ 6 (1927)
≡ *Cochliobolus miyabeanus* (S. Ito & Kurib.) Drechsler ex Dastur, Indian. J. Agri. Res 12: 733 (1942)
= *Spondylocladium macrocarpum* (Grev.) G. Arnaud, Bull. trimest. Soc. mycol. Fr. 69: 288 (1954) [1953]

Bipolaris peregianensis Alcorn, Mycotaxon 15: 9 (1982)

= *Cochliobolus peregianensis* Alcorn, Mycotaxon 15: 9 (1982)

Bipolaris sorokiniana (Sacc.) Shoemaker, Can. J. Bot. 37: 884 (1959)

≡ *Helminthosporium sorokinianum* Sacc. in Sorok, Trans. Soc. Nat. Univ. Kazan 22: 15 (1890)
≡ *Drechslera sorokiniana* (Sacc.) Subram. & Jain, Curr. Sci. 35: 354 (1966)
= *Helminthosporium sativum* Pammel, C.M. King & Bakke, B. Iowa. State. Coll. 116: 180 (1910)
= *Ophiobolus sativus* S. Ito & Kurib, Trans. Sapporo nat. Hist. Soc. 10: 138 (1929)
≡ *Cochliobolus sativus* (S. Ito & Kurib.) Drechsler ex Dastur, Indian J Agr Res 12: 733 (1942)
= *Helminthosporium acrothecioides* Lindf, Sevensk bot. Tidskr. 12: 562 (1918)
= *Helminthosporium californicum* Mackie & G.E. Paxton, Phytopathology 13: 562 (1923)
≡ *Bipolaris californica* (Mackie & G.E. Paxton) Gornostaĭ [as 'californicum'], in Azbukina et al. (eds), Vodorosli, Gribyi Mkhi Dal'nego Vostoka (Vladivostok): 80 (1978).

Bipolaris victoriae (F. Meehan & H.C. Murphy) Shoemaker, Can. J. Bot. 37: 882 (1959)

≡ *Helminthosporium victoriae* F. Meehan & H.C. Murphy, Science, N.Y. 104: 413 (1946)
≡ *Helminthosporium sativum* var. *victoriae* (F. Meehan & H.C. Murphy) H.R. Rosen, Wiser & J.O. York, Beitr. Bau. Flecht. 533: 22 (1953)

≡ *Drechslera victoriae* (F. Meehan & H.C. Murphy) Subram. & B.L. Jain, Curr. Sci. 35: 355 (1966)
= *Cochliobolus victoriae* R.R. Nelson, Phytopathology 50: 775 (1960)

Bipolaris zeae Sivan., Trans. Br. mycol. Soc. 84: 418 (1985)

= *Cochliobolus zeae* H.S. Chang, Bot. Bull. Acad. sin., Taipei 33: 175 (1992)

Bipolaris zeicola (Stout) Shoemaker, Can. J. Bot. 37: 885 (1959)

≡ *Helminthosporium zeicola* Stout, Mycologia 22: 273 (1930)
≡ *Drechslera zeicola* (Stout) Subram. & B.L. Jain, Curr. Sci. 35: 355 (1966)
= *Helminthosporium carbonum* Ullstrup, Phytopathology 34: 219 (1944)
=*Drechslera carbonum* (Ullstrup) Sivan., Bitunicate Ascomycetes and their Anamorphs (Vaduz): 369 (1984)
=*Cochliobolus carbonum* R.R. Nelson, Phytopathology 49: 809 (1959)

Curvularia Boedijn

= *Curvusporium Corbetta* [as '*Curvosporium*'], Riso 12(3): 28, 30 (1963)
=*Malustela* Bat. & J.A. Lima, *Publções Inst. Micol. Recife* 263: 5 (1960)

Generic type: Curvularia lunata Boedjin

Mycelium brown, grey or black, cottony or velvety. *Ascomata* superficial, globose to ellipsoidal, dark brown to black, free or frequently developing from columnar stromata or flat stromata, with a well defined ostiolar beak. Peridium coriaceous, carbonaceous, pseudoparenchymatous. Hamathecium comprising pseudoparaphyses, filiform, septate and sometimes branched. *Asci* 1–8-spored, bitunicate, fissitunicate, cylindrical to cylindrical clavate, pedicel short. *Ascospores* fasciculate, usually parallel, loosely coiled or highly coiled at the extremities of the ascus, filamentous, filiform to flageliform and somewhat tapered at the extremities, 3–20 septate, hyaline or somewhat pigmented at maturity. *Conidiophores* branched or unbranched, straight to flexuous, septate, smooth to verruculose, often geniculate sometimes nodulose. Conidiogenous cells polytretic, integrated, sometime when mature becoming either intercalary, sympodial, cylindrical, cicatrized or sometimes swollen. Conidiogenous nodes smooth to verrucose. *Conidia* straight oblong, ellipsoidal, clavate, fusiform, subcylindrical or lunate, rounded at the ends or sometimes tapering slightly towards the base, pale brown, medium reddish brown to dark brown, 3–10 distoseptate (usually 3–5), conidial wall smooth to verrucose. Hilum protuberant in some species. Stromata formed in some species.

Notes: Twenty-five isolates named as *Curvularia* were used in this study and all are retained in *Curvularia*. These species are listed below alphabetically. Nine species named as *Bipolaris* cluster within the "*Curvularia*" clade (group 2) and thus are transferred to *Curvularia* based on the multigene analysis (Figs. 1 and 2). These species are listed below as novel combinations along with the *Curvularia* species retained in the genus. The transferred species have morphological characteristics typical of *Curvularia* such as developing stromata.

Accepted species in Curvularia

Curvularia asianensis Manamgoda, L. Cai, K.D. Hyde.
Mycobank number: MB 800646
This species is described in a separate publication (Manamgoda et al. 2012)

Curvularia alcornii Manamgoda, L. Cai, K.D. Hyde.
MycoBank number: MB 800665
This species is described in a separate publication (Manamgoda et al. 2012)

Curvularia australiensis (M.B. Ellis) Manamgoda, L. Cai. & K.D. Hyde, **comb. nov.** Mycobank: MB 564767

≡ *Drechslera australiensis* Bugnic. ex M.B. Ellis, Dematiaceous Hyphomycetes: 413 (1971)
≡ *Bipolaris australiensis* (M.B. Ellis) Tsuda & Ueyama, Mycologia 73: 90 (1981)
= *Pseudocochliobolus australiensis* Tsuda & Ueyama, Mycologia 73: 92 (1981)
≡ *Cochliobolus australiensis* (Tsuda & Ueyama) Alcorn, Mycotaxon 16: 373 (1983)

Curvularia coicis Castell., Nuovo G bot. Ital. 62: 554 (1959)

≡ *Helminthosporium coicis* Nisikado, Sp. Rep. Ohara Inst. Agric. Res. 4: 136 (1928)
≡ *Drechslera coicis* (Nisikado) Subram. & Jain, Curr. Sci. 35: 354 (1966)
≡ *Bipolaris coicis* (Nisikado) Shoemaker, Can. J. Bot. 37: 883 (1959)
= *Pseudocochliobolus nisikadoi* Tsuda, Ueyama & Nishihara, Mycologia 69: 1117 (1977)
≡*Cochliobolus nisikadoi* (Tsuda, Ueyama & Nishih.) Alcorn, Mycotaxon 16: 373 (1983)

Curvularia cymbopogonis (C.W. Dodge) J.W. Groves & Skolko [as 'cymbopogi'], Canadian Journal of Research, Section C 23: 96 (1945)

≡ *Helminthosporium cymbopogonis* C.W. Dodge [as 'cymbopogi'], Ann. Mo. bot. Gdn 29: 139 (1942)
= *Cochliobolus cymbopogonis* J.A. Hall & Sivan., Trans. Br. mycol. Soc. 59(2): 315 (1972)

Curvularia ellisii S.I. Ahmed & M. Qureshi [as 'ellisi'], Pakist. J. scient. ind. Res. 3(3): 177 (1960)

≡ *Drechslera ellisii* Danquah, Trans. Br. mycol. Soc. 64: 545 (1975)
≡ *Bipolaris ellisii* (Danquah) Alcorn, Trans. Br. mycol. Soc. 81: 174 (1983)
= *Cochliobolus ellisii* Alcorn, Trans. Br. mycol. Soc. 81: 172 (1983)

Curvularia gladioli Boerema & Hamers, Netherlands Journal of Plant Pathology, Supplement 95(3): 10 (1989)

Curvularia gudauskasii Morgan-Jones & Karr, Mycotaxon 3(3): 559 (1976)

Curvularia graminicola Alcorn, Proc. R. Soc. Qd. 107: 2 (1998)

= *Cochliobolus graminicola* Alcorn, Proc. R. Soc. Qd. 107: 1 (1998)

Curvularia hawaiiensis (Bugnic.) Manamgoda, L. Cai & K.D. Hyde, **comb. nov.** Mycobank: MB 800543

≡ *Helminthosporium hawaiiensis* Bugnic., Rev. gén. Bot. 62: 238 (1955)
≡ *Drechslera hawaiiensis* Bugnic. ex M.B. Ellis, Dematiaceous Hyphomycetes: 415 (1971)
≡ *Bipolaris hawaiiensis* (M.B. Ellis) J.Y. Uchida & Aragaki, Phytopathology 69: 1115 (1979)
= *Cochliobolus hawaiiensis* Alcorn, Trans. Br. mycol. Soc.70: 64 (1978)
≡ *Pseudocochliobolus hawaiiensis* (Alcorn) Tsuda & Ueyama, Mycologia 73: 92 (1981)

Curvularia heteropogonis Alcorn, Mycotaxon 39: 374 (1990)

= *Cochliobolus heteropogonis* Alcorn 1990

Curvularia ischaemi McKenzie, Trans. Br. mycol. Soc. 77(2): 446 (1981)

Curvularia lunata (Wakker) Boedijn, Bull. Jard. bot. Buitenz, 3 Sér. 13(1): 127 (1933)

≡ *Acrothecium lunatum* Wakker, De Ziektan van het Suikerriet op Java: 196 (1898)
= *Cochliobolus lunatus* R.R. Nelson & F.A. Haasis, Mycologia 56: 316 (1964)
= *Pseudocochliobolus lunatus* (R.R. Nelson & F.A.Haasis) Tsuda, Ueyama & Nishih, Mycologia 69: 1118(1978) [1977]
= *Helminthosporium caryopsidum* Sacc, Annls mycol.12: 313 (1914)
≡ *Curvularia caryopsidum* (Sacc.) S.C Teng., Fungi of China: 760 (1963)

Vegetative hyphae septate, branched, subhyaline to brown, smooth to asperulate, 1.5–5 μm wide, anastomosing. Conidiophores semimacronematous to macronematous, mononematous, septate, simple or branched, often with a bulbous base and geniculate or bent at the apex, light- to dark brown, smooth to asperulate with cell walls often thicker than those of the vegetative hyphae, 39–430 μm long, 4–9 μm wide at the base and 2.5–6 μm wide towards the center. Conidiogenous cells terminal and intercalary, polytretic, subcylindrical, clavate, and subglobose or irregularly shaped, 4–20×3–13 μm, proliferating sympodially. Percurrent proliferation also observed occasionally. Conidiogenous loci usually somewhat thickened and darkened, pores up to 1 μm wide. Conidia almost always four-celled, smooth to asperulate, often curved at the third cell from base, which is larger than the others, intermediate cells brown to dark brown, end cells subhyaline to light brown, 21–31×9–13 μm; hilum non-protruding, flat, darkened and thickened, 1.5–3 μm wide. Atypical, bifurcate conidia and microcyclic conidiation rarely observed. Colonies on CMA attaining 7.2 cm in 7 days at 27 °C, funiculose to cottony, olivaceous black, with a fimbriate margin; reverse black. Colonies on MEA attaining 70 mm at the same temperature and time of incubation, cottony and grey at the center, tan and velvety towards the periphery, with a fimbriate margin; reverse brown at the center, cream-coloured towards the periphery (Fig. 4)

NEOTYPE designated here: USA, Florida, from human lung biopsy specimen, 1975, collectors unknown, exneotype (CBS 730.96)

Notes: *C. lunata* was first described as *Acrothecium lunatum* from decaying leaves of sugarcane in Java (Wakker 1898). Boedijin (1933) transferred this species to his newly erected genus *Curvularia* and chose it as the type species, citing new isolations from air, mango fruit and other substrates. Unfortunately, none of Wakker and Went's or Boedijn's material could be located. Boedijn deposited in CBS an isolate (CBS 157.34) of *C. lunata* from Java from an unknown substrate in 1934. This culture is unable to sporulate and so we chose as a neotype CBS 730.96, which is genetically very similar (identities: ITS 100 %, gpd 99 %) to the Boedijn strain. A re-examination of this species complex is now possible to confirm the placement of cryptic species.

Curvularia ovariicola (Alcorn) Manamgoda, L. Cai & K.D Hyde**, comb. nov.** Mycobank: MB 800544

≡ *Bipolaris ovariicola* Alcorn, Mycotaxon 15: 45 1982

Fig. 4 Morphology of *Curvularia lunata* (from ex-neotype). a. Colony on CMA after 6 day at 27 °C, b–d. Conidiophores and conidia, e. Conidiophore with a bulbous base and a swollen terminal conidiogenous cell, f. Conidiophore apex with a geniculate, sympodial rachis, g. Percurrent proliferation of a conidiophore, h–k. Conidia, l. Atypical bifurcate conidium, m. Microcyclic conidiation. Scale bars a=10 mm, b–m=5 μm

= *Cochliobolus ovariicola* Alcorn, Mycotaxon 39: 388 (1990)

Curvularia perotidis (Alcorn) Manamgoda, L. Cai, K.D. Hyde**, comb. nov.** Mycobank number: MB 799999

≡ *Bipolaris perotidis* Alcorn, Mycotaxon 15: 13 (1982)
= *Cochliobolus perotidis* Alcorn, Mycotaxon 15: 11 (1982)

Curvularia ravenelii (M.A. Curtis) Manamgoda, L. Cai, K.D. Hyde**, comb. nov.** MycoBank: MB 800547

≡ *Helminthosporium ravenelii* M.A. Curtis ex Berk, J. Linn. Soc., Bot. 10: 360 (1868) [1869]
≡ *Napicladium ravenelii* (M.A. Curtis) Speg, Anal. Soc. cient. argent. 26: 71 (1888).
≡ *Bipolaris ravenelii* (M.A. Curtis) Shoemaker, Can. J. Bot. 33: 884 (1959)
≡ *Drechslera ravenelii* (M.A. Curtis) Subram. & B.L. Jain, Curr. Sci. 35: 354 (1966)
= *Cochliobolus ravenelii* Alcorn, Mycotaxon 13(2): 341 (1981)
= *Helminthosporium hoffmannii* Berk. [as 'hoffmanni'], Intr. crypt. bot. : 298 (1857)

= *Helminthosporium tonkinense* P. Karst. & Roum, Revue mycol., Toulouse 12: 78 (1890)
= *Heterosporium callospermum* Speg, Anal. Soc. cient. argent. 22: 213 (1857)

Curvularia spicifera (Bainier) Boedijn, Bull. Jard. bot. Buitenz, 3 Sér. 13(1): 127 (1933)

≡ *Helminthosporium spiciferum* (Bainier) Nicot, Öst. bot. Z. 100: 482 (1953)
≡ *Bipolaris spicifera* (Bainier) Subram., Hyphomycetes (New Delhi): 756 (1971)
≡ *Dendryphion spiciferum* (Bainier) Sacc. & Traverso, Syll. fung. (Abellini) 19: 560 (1910)
= *Pseudocochliobolus spicifer* (R.R. Nelson) Tsuda, Ueyama & Nishih., Mycologia 69(6): 1119 (1978) [1977]
= *Helminthosporium tetramera* McKinney, Bull. U.S. Department of Agriculture 1347: 33 (1925)
≡ *Curvularia tetramera* (McKinney) Boedijn ex J.C. Gilman, Manual of Soil Fungi: 303 (1945)
≡ *Bipolaris tetramera* (McKinney) Shoemaker, Can. J. Bot. 37(5): 884 (1959)
≡ *Drechslera tetramera* (McKinney) Subram. & B.L. Jain, Curr. Sci. 35: 355 (1966)

Curvularia tripogonis (A.S. Patil & V.G. Rao) Manamgoda, L. Cai and K.D. Hyde**, comb. nov.** Mycobank: MB 800545

≡ *Drechslera tripogonis* A.S. Patil & V.G. Rao, Trans. Br. mycol. Soc. 59:340 (1972)
≡ *Bipolaris tripogonis* (A.S. Patil & V.G. Rao) Alcorn, Mycotaxon 13: 344 (1981)
= *Cochliobolus tripogonis* Alcorn, Mycotaxon 13: 342 (1981)

Curvularia trifolii (Kauffman) Boedijn, Bull. Jard. bot. Buitenz, 3 Sér. 13(1): 128 (1933)

Curvularia tuberculata B.L. Jain, Trans. Br. mycol. Soc. 45(4): 539 (1962)

= *Cochliobolus tuberculatus* Sivan., Trans. Br. mycol. Soc. 84(3): 548 (1985)

Discussion

Single and combined phylogenetic analysis to resolve the *Bipolaris, Cochliobolus* and *Curvularia* generic complex

A comparison of single and combined gene analyses of this generic complex showed that the combined tree (ITS and GPDH) best resolved in Groups 1 (*Bipolaris*) and 2 (*Curvularia*) (Fig. 1). The four gene phylogeny provided a better resolution for taxa at the terminal clades, which has also been reported for other Dothideomycetes (Boonmee et al. 2011; Hunter et al. 2006; Liu et al. 2011; Schoch et al. 2009; Zhang et al. 2012).

Separation of *Bipolaris, Cochliobolus* and *Curvularia* species into two well-defined groups

The multilocus phylogenetic trees (Figs. 1 and 2) resolved two well-supported groups in this generic complex, and these findings are in agreement with previous studies (Shimizu et al. 1998; Berbee et al. 1999; Kodsueb et al. 2006). As reported in these studies, our analyses show that the traditionally circumscribed *Bipolaris* and *Curvularia* cannot be combined into a single monophyletic genus (Berbee et al. 1999; Goh 1998; Shimizu et al. 1998). The trees show that two groups can be resolved in the complex. All highly pathogenic, economically important fungi in the previous generic complex are found in genus *Bipolaris* (Group 1). The *Bipolaris* clade also includes some economically less important species. For example, the economically important pathogen *B. sorokiniana* clusters with *B. zeae*.

Curvularia species cluster separately as group 2 in the phylogenetic analyses. The conidia of *Curvularia* tend to be short (in most species less than 100 μm) and usually straight or curved. When curved, the conidia have intermediate cells inordinately enlarged and this contributes to their curvature. The conidia of *Bipolaris* species are usually larger and more septate than those of *Curvularia* (usually more than 100 μm) and can be straight or gently curved. In the sexual state, stroma can be found in *Curvularia.* The degree of ascospore coiling shows variation within *Bipolaris* and *Curvularia*. The heterogeneity of this character has been discussed previously (Alcorn 1983; Berbee et al. 1999). Although the asexual morphs cluster in two well defined groups based on molecular data and morphology, their sexual morphs are quite similar indicating that the asexual states have evolved and differentiated more rapidly than the sexual morphs.

In the combined ITS and GPDH gene analysis, *Cochliobolus homomorphus* Luttr. & Rogerson did not fit into either Group 1 or Group 2 (Berbee et al. 1999). In this study, we excluded the taxon from all the analyses. *Cochliobolus homomorphus* was isolated as airspora (ex-type culture CBS 156.60) and a few living cultures are available. We considered that *Cochliobolus homomorphus* had conidial morphology similar to *Curvularia* and future work is needed.

Future study

In this study, we looked at some species previously named in *Bipolaris* (19), *Cochliobolus* (25), and *Curvularia* (12). There are 95 *Bipolaris,* 30 *Cochliobolus* and 101 *Curvularia* species which have not been sequenced and thus not assigned to either of these newly circumscribed genera.

These orphaned taxa retain their current names and will require future studies to clarify their taxonomic position.

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Agrios GN (2005) Plant pathology, 5th edn. Academic, Amsterdam

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