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Lentimurisporaceae, a new pleosporalean family with divergence times estimates

Ning-Guo LIU[a,b,c], Chuan-Gen LIN[c], Jian-Kui LIU[a], Milan C. SAMARAKOON[c,d], Sinang HONGSANAN[c], D. Jayarama BHAT[e], Kevin D. HYDE[c], Eric H. C. MCKENZIE[f] & Juangjun JUMPATHONG[b,g]*

[a]*Guizhou Key Laboratory of Agricultural Biotechnology, Guizhou Academy of Agricultral Sciences, Guiyang 550006, China*

[b]*Faculty of Agriculture, Natural Resources and Envinonment, Naresuan University, Phitsanulok 65000, Thailand*

[c]*Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand*

[d]*Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand*

[e]*Azad Housing Society, No. 128/1-J, Curca, P.O. Goa Velha 403108, India*

[f]*Landcare Research, Private Bag 92170, Auckland, New Zealand*

[g]*Center for Agricultural Biotechnology, Naresuan University, Phitsanulok, 65000, Thailand*

Abstract – The new hyphomycetous genus *Lentimurispora,* based on *L. urniformis* sp. *nov.* collected from decaying wood in Phayao, Thailand, is introduced. It is characterized by micronematous conidiophores, monoblastic conidiogenous cells, and muriform, lenticular conidia with dark brown central cells and paler peripheral cells. Phylogenetic analysis based on the combined LSU, SSU and *TEF1*α sequences data of 110 taxa was carried out to infrer their phylogenetic relationships. The new genus formed a well-supported monophyletic clade with *Bahusandhika indica, Berkleasmium micronesicum* and *Be. nigroapicale* within Pleosporales. A new family, Lentimurisporaceae is established to accommodate this clade. Divergence times establishment was performed and the results showed that the new family was diverged approximately 78 (49–118) MYA.

Asexual morphs / Evolution / Hyphomycetes / Phylogeny / Taxonomy

* Corresponding author, email: ljiankui@gmail.com

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INTRODUCTION

Hyphomycetes are the asexually reproducing part of the fungal life cycle of ascomycetes and basidiomycetes (Seifert *et al.*, 2011). They are geographically widespread and widely disseminated in the environment. More than 1500 genera have been recognized as hyphomycetous (Ellis, 1971, 1976; Kirk *et al.*, 2008; Seifert *et al.*, 2011; Wijayawardene *et al.*, 2017a, b, 2018). The taxonomy of hyphomycetes is unsettled and remains problematic, especially in their systematic placements, since few species are linked with their sexual morphs or are phylogenetically well-investigated (Seifert *et al.*, 2011; Wijayawardene *et al.*, 2017b).

Pleosporales is the largest order of Dothideomycetes, currently including 64 families (Zhang *et al.*, 2009, 2012; Hyde *et al.*, 2013; Liu *et al.*, 2017; Wijayawardene *et al.*, 2018), and it also contains numerous coelomycetous and hyphomycetous species (Wijayawardene *et al.*, 2016, 2017a). Many Pleosporales species are fungal pathogens associated with a wide variety of hosts, parasitising living plants, lichens, other fungi, insects or mammals (Phookamsak *et al.*, 2014; Ariyawansa *et al.*, 2015; Liu *et al.*, 2017). They also occur commonly as saprobes in dead aquatic and terrestial plant tissues (Shearer *et al.*, 2009; Zhang *et al.*, 2012; Hyde *et al.*, 2013). Coelomycetous fungi are the asexual morphs of many pleosporalean taxa, especially phoma-like asexual morphs and their relatives (Aveskamp *et al.*, 2008, 2010; de Gruyter *et al.*, 2009, 2010; Wijayawardene *et al.*, 2012, 2016). However, the order also contains many hyphomycetous species. The ubiquitous genus *Alternaria* Nees, characterized by brown phaeodictyospores in chains and with tapering beaked apical cells, resides in Pleosporaceae (Ariyawansa *et al.*, 2015). The type species of *Bipolaris* Shoemaker, *B. maydis* (Y. Nisik. & C. Miyake) Shoemaker, which belongs in the family Pleosporaceae, is linked with the sexual morph *Cochliobolus heterostrophus* (Drechsler) Drechsler (Manamgoda *et al.*, 2011). *Alternaria* and *Bipolaris* have world-wide distribution and include significant plant pathogens which are commonly associated with leaf spots, leaf blights, root rots and other diseases in over 100 host plant species (Manamgoda *et al.*, 2011; Ariyawansa *et al.*, 2015). *Pithomyces* Berk. & Broome, which has brown, subspherical and muriform conidia, is placed in Astrosphaeriellaceae (Wanasinghe *et al.*, 2018) and *Thyrostroma* Höhn., characterized by cylindrical or clavate, brown, sometimes muriform conidia, resides in Dothidotthiaceae (Senwanna *et al.*, 2018), two pleosporalean families.

Some early usage of molecular clocks in the fungi were those of Li *et al.* (2005) who revealed the direction of evolution of trapping devices in nematode trapping fungi, and Vijaykrishna *et al.* (2006) who showed that freshwater and marine fungi evolved from terrestrial ancestors. Evolutionary estimates using molecular clocks have been increasingly common in fungal taxonomy in recent years (Prieto & Wedin, 2013; Hongsanan *et al.*, 2016, 2017; Samarakoon *et al.*, 2016; Hyde *et al.*, 2017; Liu *et al.*, 2017), and several works refer to Pleosporales (Phukhamsakda *et al.*, 2016; Liu *et al.*, 2017). Hyde *et al.* (2017) proposed a series of evolutionary periods as a guide to determine the higher ranks of fungi, of which family rank would correspond to 50–150 MYA.

During a survey on brown-spored hyphomycetes in Thailand, a rare taxon was encountered. Its conidial morphology is similar to species of *Hermatomyces* Speg. However, phylogenetic analyses indicated that it is closely related to the genera *Bahusandhika* Subram. and *Berkleasmium* Zobel., with which it formed a distinct phylogenetic clade. Therefore, a new genus, *Lentimurispora*, is introduced

to accommodate this new taxon. A new family, Lentimurisporaceae is introduced to accommodate the new genus, along with the genus *Bahusandhika* and two *Berkleasmium* species. The divergence times of Lentimurisporaceae was estimated and discussed using a molecular clock analysis.

MATERIALS & METHODS

Collections and examination of specimens

Fresh samples of decaying wood were collected from Phayao Province, Thailand in September 2016. The sample was processed and examined following the method described by Taylor & Hyde (2003). The sample was incubated in plastic boxes with sterile and moist tissue at 25–30 ℃ for 3 days, and then examined using a Motic SMZ 168 Series dissecting microscope. Fruiting bodies of an interesting hyphomycete were mounted in a drop of water for microscopic studies and photomicrography. The species was examined with a Nikon ECLIPSE 80i compound microscope fitted with a Cannon 600D digital camera. Measurements were performed using the Tarosoft (R) Image Frame Work software and a photo-plate was prepared using Adobe Photoshop CS3 software (Adobe Systems, USA).

Single conidium isolation was carried out following the method described in Chomnunti *et al.* (2014). Germinated spores were individually transferred to potato dextrose agar (PDA) media plates and incubated at 25 ℃. Dried specimens were deposited in the herbarium of Mae Fah Luang University (MFLU), Chiang Rai, Thailand, and the herbarium of Cryptogams Kunming Institute of Botany Academia Sinica (HKAS). Pure cultures were deposited in the Mae Fah Luang University Culture Collection (MFLUCC). Facesoffungi (FOF) numbers were acquired as in Jayasiri *et al.* (2015) and MycoBank numbers as in MycoBank Database (Crous *et al.*, 2004).

DNA extraction, PCR amplification and sequencing

Fresh mycelia were scraped using a sterile scalpel from pure cultures growing on PDA medium for one month at 25 ℃. Genomic DNA was extracted using DNA Extraction Kit (Sangon Biotech, Shanghai, P.R. China) following the manufacture's protocol. Two partial gene portions and one protein coding gene were used in this study: the large subunits of the nuclear ribosomal RNA genes (28S, LSU), the small subunits of the nuclear ribosomal RNA genes (18S, SSU) and the translation elongation factor 1-alpha gene (TEF1α). Part of LSU locus was amplified with the primers LROR and LR5 (Vilgalys & Hester, 1990), part of SSU with primers NS1 and NS4 (White *et al.*, 1990), and part of TEF1α with primers 983F and 2218R (Rehner & Buckley, 2005). Polymerase chain reaction (PCR) was carried out in 25 µl reaction volume containing 12.5 µl 2 × PCR Master Mix (TIANGEN Co., P.R. China), 9.5 µl ddH_2O, 1 µl of each primer and 1 µl DNA template. PCR conditions for both LSU and SSU were as follows: 3 min at 94 ℃ (initial denaturation), followed by 40 cycles 45 s at 94 ℃ (denaturation), 50 s at 56 ℃ (annealing), 1 min at 72 ℃ (extension), with a final extension 10 min at 72 ℃. The PCR products were examined using 1% agarose electrophoresis gel stained with ethidium bromide. Purified PCR products were sequenced by the commercial company Sangon Biotech (Shanghai, P.R. China).

Phylogenetic analysis

Sequences generated from different primers were analyzed with other sequences obtained from GenBank. The related sequences were determined by using a BLAST search to reveal the close matches with taxa in Pleosporales (Dothideomycetes). Consequently, sequences for the taxa sampling representative of this order were sampled as well as some representatives of other orders of Dothideomycetes (Table 1) regarding previously published studies (Pinnoi *et al.*, 2007; Zhang *et al.*, 2012; Beimforde *et al.*, 2014; Pratibha *et al.*, 2014; Thambugala *et al.*, 2015; Liu *et al.*, 2017). Arthoniomycetes were used as outgroups. Sequences newly generated in this study were deposited in GenBank (Table 1). Datasets for each gene (LSU, SSU and *TEF1*α) were aligned separately using BioEdit (Hall, 1999). This program was also used to build the combined dataset. Alignments were checked visually and optimized manually using AliView (Larsson, 2014). The software package jModelTest2.1.1 was used to select the best-fitting models of nucleotide substitution for each gene. The Bayesian information criterion supported the GTR + I + G model as the best fit for LSU, SSU and *TEF1*α. Topological congruence of the three datasets was checked by visual comparison of phylogenetic trees obtained from maximum likelihood-based analysis with RAxML (Stamatakis, 2006). A maximum likelihood analysis was performed at the CIPRES webportal (Miller *et al.*, 2010) using RAxML v.7.2.8 as part of the "RAxML-HPC2 on TG" tool (Stamatakis, 2006). A general time reversible model (GTR) was applied with a discrete gamma distribution and four rate classes. Fifty thorough maximum likelihood (ML) tree searches were done in RAxML v. 7.2.7 under the same model. One thousand non-parametric bootstrap iterations were run with the GTR model and a discrete gamma distribution. The resulting replicates were plotted on to the best scoring tree obtained previously.

The model of evolution was estimated by using MrModeltest 2.2 (Nylander 2004). Posterior probabilities (PP) (Rannala & Yang 1996, Zhaxybayeva & Gogarten 2002) were determined by Markov Chain Monte Carlo sampling (BMCMC) in MrBayes 3.2.6 (Ronquist *et al.*, 2012). Four simultaneous Markov chains were run for 10 million generations and trees were sampled every 1000th generation, thus 10,000 trees were obtained. The suitable burn-in phases were determined by inspecting likelihoods and parameters in Tracer version 1.6 (Rambaut *et al.*, 2014). Based on the tracer analysis, the first 1,000 trees representing 10% were discarded as the burn-in phase in the analysis. The remaining trees were used to calculate posterior probabilities in the majority rule consensus tree (critical value for the topological convergence diagnostic set to 0.01).

Trees were visualized with FigTree v1.4.0 (Rambaut, 2006) and the layout was edited using Adobe Illustrator CS6 software (Adobe Systems, USA).

Fossil calibration, divergence time and evolutionary rate estimations

The fossil calibrations used in the analyses followed the methodology described in Phukhamsakda *et al.* (2016). Reliable fossils (1, 2) and one secondary (3) calibration were selected for the divergence times estimations based on the phylogenetic analyses. The fossil 1, *Metacapnodium succinum* (Metacapnodiaceae) was used to calibrate the minimum age of Capnodiales (normal distribution, mean = 100, SD = 150, providing 95% credibility interval of 346 MYA) (Rikkinen *et al.*, 2003; Hongsanan *et al.*, 2016; Pérez-Ortega *et al.*, 2016; Phukhamsakda *et al.*, 2016). The fossil 2, *Margaretbarromyces dictyosporus* was used to calibrate the crown age of *Aigialus* (Aigialaceae) (gamma distribution, offset = 35, shape = 1.0,

scale = 25, providing 95% credibility interval of 110 MYA) (Mindell *et al.*, 2007; Phukhamsakda *et al.*, 2016). The split between Arthoniomycetes and Dothideomycetes was calibrated using the results from Phukhamsakda *et al.* (2016) as the secondary calibration (normal distribution, mean = 300, SD = 50, providing 95% credibility interval of 382 MYA).

Evolutionary estimate was performed by BEAST 1.8.0 (Drummond *et al.*, 2012) Aligned sequence data were partitioned separately for each LSU, SSU, *TEF1*α data set, and were loaded to prepare an XML file constructed with BEAUti v1.8.0. Clock and substitution models were set to be unlinked (independently estimated for each gene partition), while the tree prior parameters were set to be linked across partitions (concatenation). We applied a lognormal relaxed clock (uncorrelated). The tree prior was shared by all tree models; this consisted of a birth/death incomplete sampling tree prior and was used to model the speciation of nodes in the topology with uniform prior on probability of splits and extinctions. The analysis was performed for 50 million generations in BEAST v1.8.0, and sampling parameters every 1000 generations. Tracer v1.6 (Rambaut *et al.*, 2014) was used to check the effective sample sizes (ESS) (ESS>200). The first of 10% trees were discarded as a burn-in phase. The remaining trees were combined in LogCombiner v.1.8.0. A maximum clade creditability tree was generated by TreeAnnotator v1.8.0. The tree was visualized with FigTree v1.4.0 (Rambaut, 2006).

RESULTS

Phylogenetic analyses

Partial nucleotide sequences of the LSU, SSU and *TEF1*α ribosomal RNA were used to determine the phylogenetic position of the new species. One hundred and ten strains were retrieved from GenBank and fresh specimen, representing Arthoniomycetes and Dothideomycetes. Single gene analyses were carried out in order to compare the topology and clade stability. The manually adjusted LSU, SSU and *TEF1*α alignment contained 2873 characters (903 for LSU, 1038 for SSU, 932 for *TEF1*α), including coded alignment gaps.

Maximum likelihood and Bayesian analyses of the combined dataset inferred highly similar tree topologies. In the most likely tree (-ln = 30910.164742), the new taxon clustered with maximal support (ML-bs = 100%, PP = 1.00) with *Bahusandhika indica* (GUFCC 18001), *Berkleasmium micronesicum* (BCC8141) and *Be. nigroapicale* (BCC 8220) (Figure 1), but is, however, clearly separated from the other taxa nesting in that clade which clustered together with significant support (ML-bs = 87%, PP = 1.00). This clade is suggested to have a monophyletic and sister relationship with Floricolaceae (ML-bs = 100%, PP = 1.00). However, the monophyly of these two clades is only supported by Bayesian inference (PP = 0.95). Consequently, a new family is introduced to accommodate these taxa. *Berkleasmium* is shown to be polyphyletic, which agrees with a previous study (Pinnoi *et al.*, 2007).

As the new family is not phylogenetically closely related to the two suborders, i.e. Massarineae and Pleosporineae, three families (Latoruaceae, Massarinaceae and Periconiaceae) were selected to represent Massarineae, and three families (Didymellaceae, Neophaeosphaeriaceae and Pleosporaceae) were selected

Table 1. DNA sequences and GenBank numbers used for the phylogenic analyses

Species	*Strain number*	*GenBank accession number*		
		LSU	*SSU*	*TEF1α*
Aigialus grandis	BCC 18419	GU479774	GU479738	GU479838
Aigialus mangrovei	BCC 33563	GU479776	GU479741	GU479840
Aigialus parvus	BCC 18403	GU479778	GU479743	GU479842
Aigialus rhizophorae	BCC 33572	GU479780	GU479745	GU479844
Aliquandostipite khaoyaiensis	CBS 118232	GU301796		GU349048
Amniculicola immersa	CBS 123083	FJ795498	GU456295	GU456273
Amorosia littoralis	NN 6654	AM292055	AM292056	
Angustimassarina populi	MFLUCC 13-0034	KP888642	KP899128	KR075164
Anteaglonium abbreviatum	GKM 1029	GQ221878		GQ221915
Anteaglonium parvulum	GKM219N	GQ221881		GQ221916
Arthonia dispersa	UPSC2583	AY571381	AY571379	
Ascocratera manglicola	BCC 09270	GU479782	GU479747	GU479846
Astrosphaeriella fusispora	MFLUCC 10-0555	KT955462	KT955443	KT955425
Asymmetrispora tennesseensis	ANM 911	GU385207		GU327769
Aurantiascoma minimum	GKM 169 N	GU385165		GU327768
Bahusandhika indica	GUFCC 18001	KF460274		
Berkleasmium ariense	NFCCI 4026	KY039165		
Berkleasmium crunisia	BCC 17023	DQ280271		
Berkleasmium micronesicum	BCC 8141	DQ280272	DQ280268	

Berkleasmium nigroapicale	BCC 8220	DQ280273	DQ280269	
Berkleasmium sp.	BCC 17003	DQ280274	DQ280270	
Berkleasmium typhae	BCC 12536	DQ280275		
Botryosphaeria dothidea	CBS 115476	NG_027577	DQ677998	DQ767637
Capnodium salicinum	CBS 131.34	DQ678050	DQ677997	
Caryospora minima		EU196550	EU196551	
Cladosporium cladosporioides	CBS 170.54	AY213694	DQ678004	
Coelodictyosporium pseudodictyosporium	MFLUCC 13-0451	KR025862		
Cyclothyriella rubronotata	CBS 141486	KX650544	KX650507	KX650519
Delitschia chaetomioides	SMH 3253.2	GU390656		GU327753
Delitschia winteri	CBS 225.62	DQ678077	DQ678026	DQ677922
Dendrographa leucophaea f. *minor*		AF279382	AF279381	
Dissoconium aciculare	CBS 204.89	GU214419	GU214523	
Exosporium stylobatum	CBS 160.30	JQ044447		
Floricola striata	JK5678I	GU301813	GU296149	GU479852
Gloniopsis calami	MFLUCC 15-0739	KX646363	KX669034	KX671965
Gloniopsis praelonga	CBS 112415	FJ161173	FJ161134	FJ161090
Guttulispora crataegi	MFLUCC 13-0442	KP888639	KP899125	KR075161
Halotthia posidoniae	BBH 22481	GU479786	GU479752	
Herpotrichia diffusa	CBS 250.62	DQ678071	DQ678019	DQ677915
Hypsostroma caimitalense	GKM 1165	GU385180		
Hypsostroma saxicola	SMH 5005	GU385181		

Table 1. DNA sequences and GenBank numbers used for the phylogenic analyses (continued)

Species	*Strain number*	*GenBank accession number*		
		LSU	*SSU*	*TEF1α*
Hysterium angustatum	CBS 236.34	FJ161180	GU397359	FJ161096
Jahnula seychellensis	SS2113	EF175665	EF175644	
Latorua caligans	CBS 576.65	KR873266		
Latorua grootfonteinensis	CBS 369.72	KR873267		
Lentimurispora urniformis	**MFLUCC 18-0497**	**MH179144**	**MH179160**	**MH188055**
Leptoxyphium cacuminum	MFLUCC 10-0049	JN832602	JN832587	
Ligninsphaeria jonesii	MFLUCC 15-0641	KU221037		
Ligninsphaeria jonesii	GZCC 15-0080	KU221038		
Lindgomyces ingoldianus	ATCC 200398	AB521736	AB521719	
Lindgomyces rotundatus	KT 1096	AB521740	AB521723	
Lophiostoma macrostomum	JCM 13544	AB619010	AB618691	LC001751
Lophiotrema lignicola	CBS 122364	GU301836	GU296166	GU349072
Lophiotrema nucula	CBS 627.86	GU301837	GU296167	GU349073
Massaria anomia	CBS 591.78	GU301839	GU296169	
Massaria inquinans	M19	HQ599402	HQ599444	HQ599342
Massarina corticola	CBS 154.93	FJ795448	FJ795491	
Massarina eburnean	CBS 473.64	GU301840	GU296170	GU349040
Massariosphaeria phaeospora	CBS 611.86	GU301843	GU296173	
Mauritiana rhizophorae	BCC 28866	GU371824	GU371832	GU371817

Melanomma pulvis-pyrius	CBS 124080	GU456323	GU456302	GU456265
Murispora rubicunda	IFRD 2017	FJ795507	GU456308	GU456289
Neoastrosphaeriella krabiensis	MFLUCC11-0025	JN846729	JN846739	
Neophaeosphaeria filamentosa	CBS 102202	GQ387577	GQ387516	GU349084
Neoroussoella bambusae	MFLUCC 11-0124	KJ474839		KJ474848
Neotrematosphaeria biappendiculata	KTC 1124	GU205227	GU205256	
Nigrograna fuscidula	CBS 141476	KX650547	KX650509	KX650522
Nigrograna mackinnonii	CBS 110022	GQ387614	GQ387553	KF407985
Occultibambusa bambusae	MFLUCC 13-0855	KU863112	KU872116	KU940193
Occultibambusa chiangraiensis	MFLUCC 16-0380	KX655546	KX655551	KX655561
Ohleria modesta	MGC	KX650562		KX650533
Ohleria modesta	OM	KX650563	KX650513	KX650534
Paradictyoarthrinium diffractum	MFLUCC 13-0466	KP744498	KP753960	
Paradictyoarthrinium hydei	MFLUCC 17-2512	MG747497		
Periconia byssoides	H 4600	AB807570	AB797280	AB808546
Phoma herbarum	CBS 276.37	DQ678066	DQ678014	DQ677909
Phyllosticta capitalensis	CBS 226.77	KF206289	KF766300	
Piedraia hortae	CBS 480.64	GU214466	AY016349	
Pleomassaria siparia	CBS 279.74	DQ678078	DQ678027	DQ677923
Pleospora herbarum	CBS 191.86	DQ247804	DQ247812	DQ471090
Polyschema congolensis	CBS 542.73	EF204502		
Polyschema terricola	CBS 301.65	EF204504	EF204519	

Table 1. DNA sequences and GenBank numbers used for the phylogenic analyses (continued)

Species	*Strain number*	*GenBank accession number*		
		LSU	*SSU*	*TEF1α*
Preussia funiculata	CBS 659.74	GU301864	GU296187	GU349032
Prosthemium orientale	MAFF 239509	AB553748	AB553641	
Pseudoastrosphaeriella bambusae	MFLUCC 11-0205	KT955475		KT955437
Pseudoastrosphaeriella thailandensis	MFLUCC 10-0553	KT955477	KT955456	KT955439
Psiloglonium araucanum	CBS 112412	FJ161172	FJ161133	FJ161089
Pteridiospora javanica	MFLUCC 11-0159	KJ742940	KJ739607	KJ739605
Racodium rupestre	L346	EU048583	EU048575	
Racodium rupestre	L424	EU048582	EU048577	
Rimora mangrovei	JK 5246A	GU301868	GU296193	
Roccella fuciformis	Tehler 8171	FJ638979		
Roussoella nitidula	MFLUCC 11-0634	KJ474842		KJ474851
Salsuginea ramicola	KT 2597.1	GU479800	GU479767	GU479861
Salsuginea ramicola	KT 2597.2	GU479801	GU479768	GU479862
Schismatomma decolorans	Ertz 5003 (BR)	NG_027622	NG_013155	
Scorias spongiosa	CBS 325.33	KF901821		
Sigarispora ravennica	MFLUCC 14-0005	KP698414	KP698415	
Sporormia fimetaria	UPS:Dissing Gr.81.194	GQ203729		
Tetraplosphaeria sasicola	MAFF 239677	AB524631	AB524490	
Thyridaria acaciae	CBS 138873	KP004497		

Thyridaria broussonetiae	CBS 141481	KX650568	KX650515	KX650539
Torula herbarum	CBS 111855	KF443386	KF443391	KF443403
Torula hollandica	CBS 220.69	KF443384	KF443389	KF443401
Triplosphaeria maxima	MAFF 239682	AB524637	AB524496	
Tubeufia chiangmaiensis	MFLUCC 11-0514	KF301538	KF301543	KF301557
Tubeufia javanica	MFLUCC 12-0545	KJ880036	KJ880035	KJ880037
Westerdykella ornata	CBS 379.55	GU301880	GU296208	GU349021
Wicklowia aquatica	F76-2	GU045445	GU266232	
Zopfia rhizophila	CBS 207.26	DQ384104		

1. The new taxon is indicated in bold.
2. ATCC: American Type Culture Collection, USA; BBH: National Science and Technology Development Agency, Thailand; BCC: BIOTEC Culture Collection, Thailand; CBS: CBS-KNAW Fungal Biodiversity Centre, The Netherlands; IFRD: International Fungal Research & Development Centre, China; KTC: Botany Department, Pedagogical University, Poland; JCM: Japan Collection of Microorganisms, Japan; MAFF: MAFF Genebank, Ministry of Agriculture Forestry and Fisheries, Japan; MFLUCC: Mae Fah Luang University Culture Collection, Thailand; NFCCI: National Fungal Culture Collection of India, India; NN: NovoNordisk culture collection (now Novozymes, Bagsvaerd, Denmark); SMH: Saint Meinrad College of Liberal Arts, Biology Deparment, USA; UPS: Botany Section, Museum of Evolution, Sweden

to represent Pleosporineae. The phylogenetic positions of these two suborders did not match previous studies as sister clades (Zhang *et al.*, 2012, Hyde *et al.*, 2013; Liu *et al.*, 2017). This might result from the reduced taxa sampling used here compared to previously mentioned studies.

Divergence time estimations

The comparable results (95% CI) are listed in Table 2. According to the divergence times estimates, the crown age of Dothideomycetes (A) and stem age of the clade consists with the taxa in Botryosphaeriales, Capnodiales, Jahnulales and Tubeufiales are around 255 (166–344) MYA in Late Permian. The orders Hysteriales and Pleosporales diverged approximately 213 (139–297) MYA in Late Triassic. The crown age of Pleosporales is around 195 (124–271) MYA in Early Jurassic. Among the Pleosporales families, Floricolaceae and Lentimurisporaceae fam. *nov*. diverged approximately 78 (49–118) MYA in Late Cretaceous. According to this analysis, the crown age of Floricolaceae is around 46 (24–76) MYA, while the crown age of the Lentimurisporaceae is around 34 (16–60) MYA in Eocene. Divergence times of other orders and families in the analysis are shown in Figure 2.

TAXONOMY

Lentimurisporaceae N.G. Liu, J.K. Liu & K.D. Hyde, ***fam. nov.***

MycoBank number: MB 824920; *Facesoffungi number*: FoF 04590

Etymology: Referring to the name of the type genus.

Colonies on natural substrate superfical, punctiform or powdery, scattered, brown to black. *Mycelium* mostly immersed. *Conidiomata* sporodochial. *Conidiophores* micronematous to macronematous, simple, septate or aseptate. *Conidiogenous cells* blastic, terminal, hyaline or brown. *Conidia* muriform or fusiform, cylindrical or rhomboidal, solitary or catenate in simple or branched chains.

Type genus: *Lentimurispora* N.G. Liu, Bhat & K.D. Hyde

Note: The new family Lentimurisporaceae is established for *Bahusandhika*, two *Berkleasmium* species (*Be. micronesicum* and *Be. nigroapicale*), and the new genus *Lentimurispora.*

Lentimurispora N.G. Liu, Bhat & K.D. Hyde, ***gen. nov.***

MycoBank number: MB 824921; *Facesoffungi number*: FoF 04591

Etymology: Referring to the lenticular, muriform conidia

Type species: *Lentimurispora urniformis* N.G. Liu, McKenzie & K.D. Hyde

Saprobic on dead wood. **Sexual morph:** Undetermined. **Asexual morph:** *Colonies* on natural substrate superfical, black, scattered, gregarious, velvety, punctiform. *Mycelium* immersed. *Conidiomata* sporodochial. *Conidiophores* micronematous, forming sporodochia. *Conidiogenous cells* monoblastic, holoblastic, integrated, hyaline, wedge-shaped. *Conidia* smooth, multiseptate, constricted at the septa, muriform, lenticular with dark brown central cells and pale coloured peripheral cells.

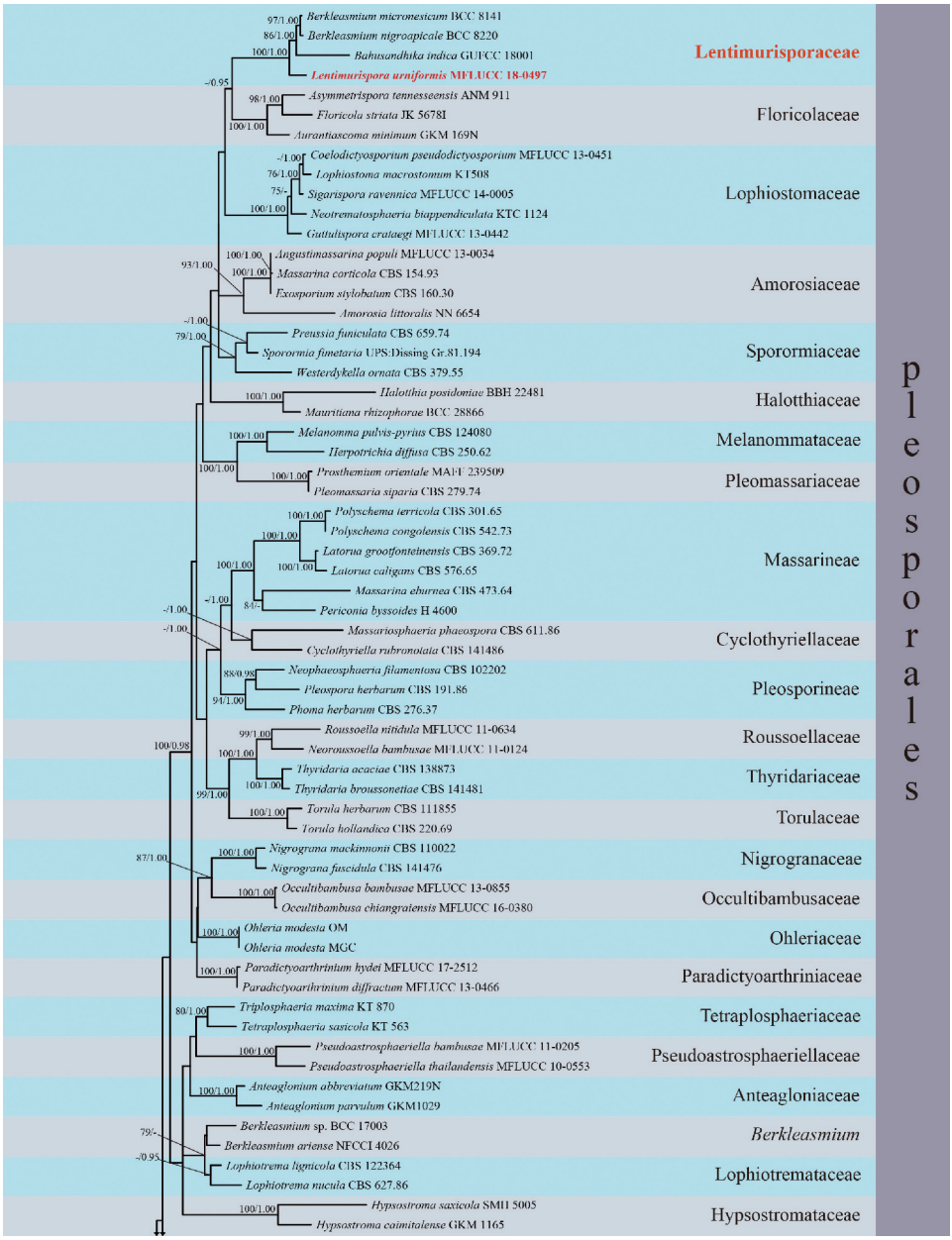

Fig 1. Maximum likelihood (RAxML) tree based on analysis of a combined dataset of LSU, SSU and *TEF1α* **sequence data. Bootstrap support values for ML greater than** 75% and Bayesian posterior probabilities greater than 0.95 are given near nodes. The tree is rooted with four species of Arthoniomycetes. The new genus and new family are indicated in bold and red.

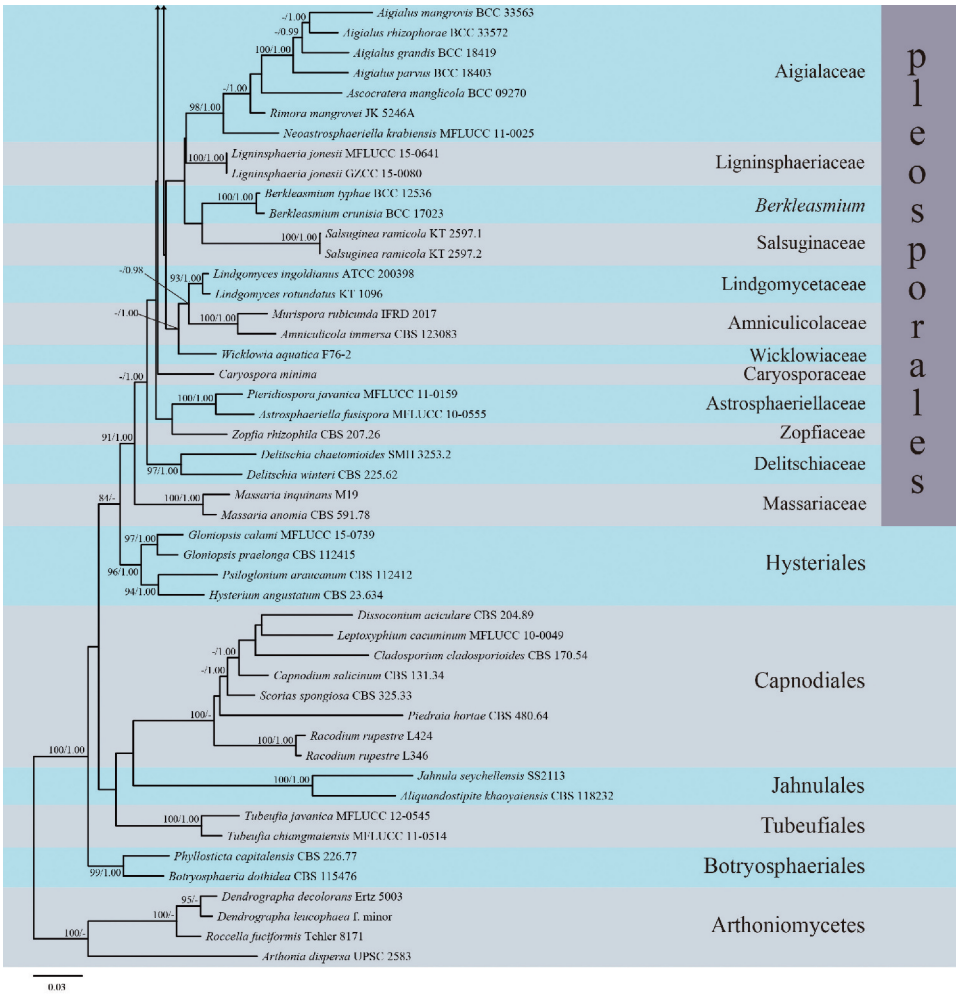

Fig. 1 (*continued*)

Table 2 Divergence times (MYA) with 95% credibility intervals (CI)

Node	*Node name*	*Node age*	*Geological time scales*
A	Dothideomycetes crown group	255 (166–344)	Late Permian
B	Hysteriales–Pleosporales	213 (139–297)	Late Triassic
C	Pleosporales crown group	195 (124–271)	Early Jurassic
D	Floricolaceae–Lentimurisporaceae	78 (49–118)	Late Cretaceous
E	Lentimurisporaceae crown group	34 (16–60)	Late Eocene
F	Floricolaceae crown group	46 (24–76)	Eocene

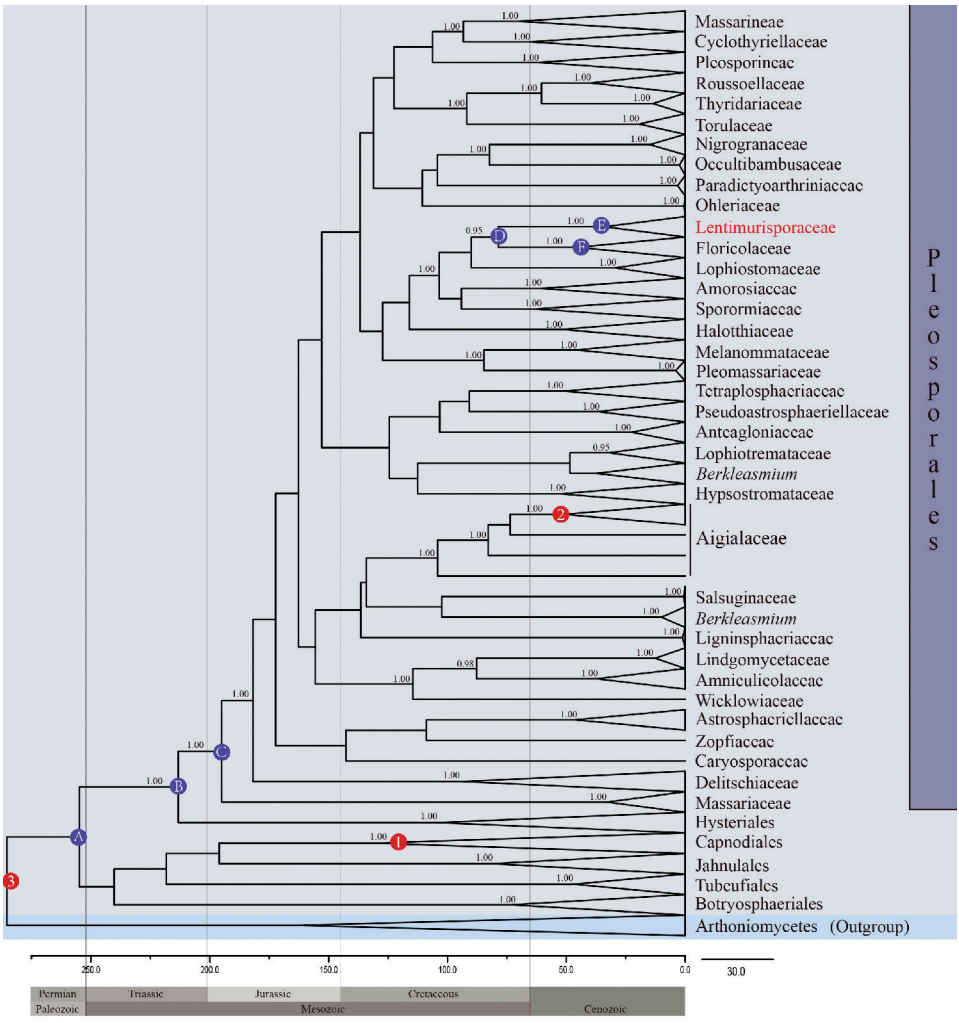

Fig. 2. Maximum clade credibility (MCC) tree with divergence times estimates obtained from BEAST. Numbers in the red circles indicate the fossil (1, 2) and secondary (3) points. Letters in the blue circles indicate the median age and 95% highest posterior density (HPD), see Table 2. Posterior probabilities greater than 0.95 are given near nodes.

Lentimurispora urniformis N.G. Liu, McKenzie & K.D. Hyde, ***sp. nov.*** Figure 3

MycoBank number: MB 824958; *Facesoffungi number*: FoF 04592

Etymology: "urna" meaning vase in Latin, referring to the vase-shaped conidiogenous cells.

Holotype: MFLU 18-0717

Saprobic on dead wood. **Sexual morph:** Undetermined. **Asexual morph:** *Colonies* on natural substratum dry, superfical, black, scattered, gregarious, velvety, punctiform. *Mycelium* immersed in the substratum, composed of branched, septate,

hyaline hyphae. *Conidiophores* micronematous, forming sporodochia, simple, indistinct, hyaline. *Conidiogenous cells* 17−38 × 7−12 μm (= 22.3 × 9.6 μm, n = 20), monoblastic, holoblastic, integrated, terminal, hyaline, smooth, wedge-shaped, inverted vase-like, clavate, narrowed towards the base, truncate at apex after conidial secession, with dense cytoplasm. *Conidia* 11−15 × 17−21 μm (= 13.2 × 19.2 μm, n = 30), acrogenous, thick-walled, smooth, multiseptate, slightly constricted at the septa; young conidia always with conidiogenous cell attached, median brown, usually with an obvious, dark, longitudinal septum, and a paler tansverse septum, without subhyaline or pale brown peripheral cells; mature conidia cushion-like, muriform, lenticular with dark brown central cells and subhyaline to pale brown peripheral cells.

Culture characters: Conidia germinated on water agar within 24 hours. Germ tubes produced from basal cell. Colonies reaching about 4 cm diameter after 10 days on PDA at 25 ℃. Mycelia superficial, with entire edge, dark brown at the center, paler towards the edge from both above and below.

Material examined: THAILAND, Phayao Province, Mae Chai District, on decaying wood, 27 September 2016, C.G. Lin, Lin16-5 (MFLU 18-0717, **holotype**; HKAS 97463, **isotype**), ex-type living culture MFLUCC 18-0497

Notes: In the blast search on LSU in NCBI, the newly generated sequence is related to strains of *Berkleasmium micronesicum* BCC 8141 and *Be. nigroapicale* BCC 8220, with similarity of 821/845 (97%) and 819/847(97%), respectively. *Lentimurispora urniformis* formed a distinct and strongly supported lineage (ML-bs = 100% and PP = 1.00), as a sister clade of *Bahusandhika* and *Berkleasmium*. Thus, its distinctiveness was confirmed by both morphology and phylogeny.

Bahusandhika Subram., Journal of the Indian Botanical Society 35(4): 469 (1956)

Colonies on natural substrate effuse, brown to black. *Conidiophores* present or absent, when present borne terminally or laterally on the hyphae, straight or flexuous, brown, septate, with or without constrictions at the septa, sometimes reduced to a stalk cell. *Conidiogenous cells* blastic, spherical, ovoid or ampulliform, smooth or verrucose. *Conidia* catenate in simple or branched chains, fusiform, cylindrical or rhomboidal, brown, smooth or verrucose.

Type species: *Bahusandhika indica* (Subram.) Subram.

Note: *Bahusandhika* was introduced by Subramanian (1956) with *B. indica* as type species to accommodate *Polydesmus indicus* (Subramanian, 1954). Crane & Miller (2016) synonymized *Latorua* Crous (Crous *et al.*, 2015) under *Bahusandhika* on the basis of morphological similarity of the conidiogenous cells and conidia, as well as the similar conidial development. However, in our phylogenetic analysis, *Bahusandhika indica* fell within the new family Lentimurisporaceae, while *Latorua caligans* CBS 576.65 and *L. grootfonteinensis* CBS 369.72 formed a monophyletic clade within Latoruaceae, which resides in the suborder Massarineae. Therefore, we accept *Bahusandhika* and *Latorua* as distinct genera.

Berkleasmium Zobel, *Icones fungorum hucusque cognitorum* 6: 4 (1854)

Colonies on natural substrate punctiform, scattered, brown to black. *Conidiophores* macronematous, mononematous, simple, smooth, septate or aseptate, hyaline to pale brown. *Conidiogenous cells* blastic, terminal, hyaline. *Conidia* acrogenous, solitary, muriform with several transverse and longitudinal septa, constricted at septa, oval to ellipsoidal, broadly obclavate or obpyriform, brown, smooth, some with a hyaline, truncate basal cell.

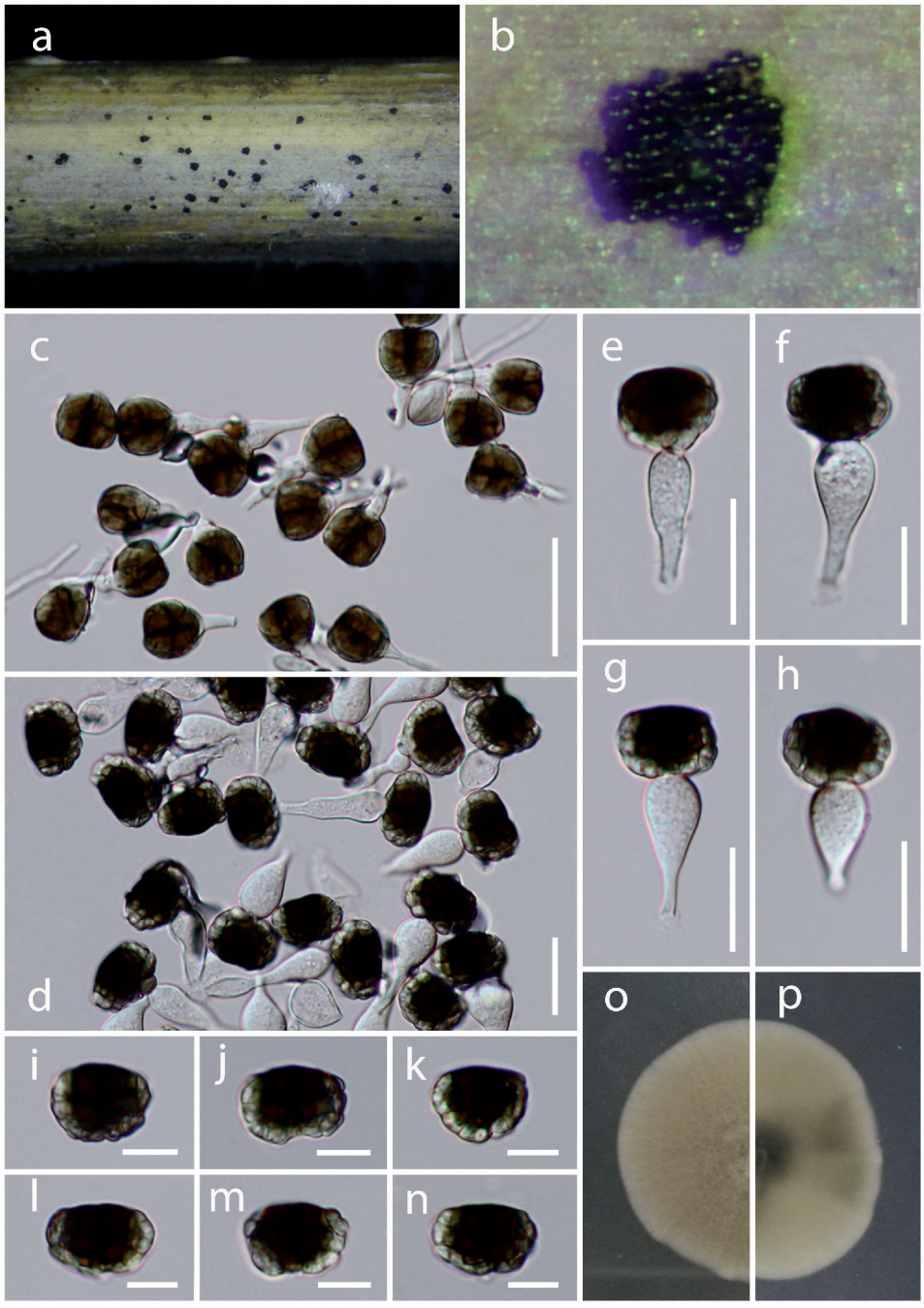

Fig. 3. *Lentimurispora urniformis* (MFLU 18-0717, holotype) **a, b.** Colonies on substrate. **c.** Mainly young conidia without pale periphaeral cells. **d-h.** Mature conidia with peripheral cells and conidiogenous cells attached. **i-n.** Mature conidia without conidiogenous cells attached. **o, p.** Colony on PDA. Scale bars:c-h = 20 μm, i-n = 10 μm.

Type species: *Berkleasmium concinnum* (Berk.) S. Hughes

Species included in Lentimurisporaceae:

Berkleasmium micronesicum Matsush., Matsushima Mycological Memoirs No. 2: 4 (1982)

Description and illustrations: see Matsushima (1982)

Berkleasmium nigroapicale Bussaban, Lumyong, P. Lumyong, McKenzie & K.D. Hyde, *Fungal Diversity* 8: 80 (2001)

Description and illustrations: see Bussaban *et al.* (2001)

Notes: *Berkleasmium* was established by Corda & Zobel (1854) with *Be. cordeanum* Zobel as the type species. Previously, this genus comprised only dematiaceous hyphomycetes. Pinnoi *et al.* (2007) studied the phylogenetic affinities of *Berkleasmium* to the Pleosporales, based on 18S and 28S rDNA sequences, and found that *Berkleasmium* is not monophyletic. Tanney & Miller (2017) reported the first sexual morph of *Berkleasmium*. Their independent collections of the type species, *Be. cordeanum*, was linked to its sexual morph *Neoacanthostigma septoconstrictum* (Tubeufiaceae, Tubeufiales, Boonmee *et al.*, 2014), based on ITS and LSU sequence data. This connection was also supported by re-examination of the *N. septoconstrictum* type specimen, and *Be. cordeanum* reference specimens (Tanney & Miller, 2017). Therefore, *N. septoconstrictum* was synonymized under *Be. cordeanum* due to nomenclatural priority. However, their study did not deal with other *Berkleasmium* species, and due to the lack of fresh specimens, the present study maintains the genus as polyphyletic. Insufficient sequence data are available at present and a comprehensive revision on the genus is necessary to reveal its phylogenetic affinities.

DISCUSSION

A new family Lentimurisporaceae is introduced to encompass the new genus *Lentimurispora*, as well as *Bahusandhika* and two *Berkleasmium* species. These three genera formed a well-supported monophyletic clade (ML-bs = 100% and PP = 1.00), which is sister to the family Floricolaceae. Currently, only coelomycetous asexual morphs have been reported in Floricolaceae (Thambugala *et al.*, 2015). Species in Lentimurisporaceae are all dematiaceous hyphomycetes without known sexual morphs. However, phylogenetic analysis indicated that these taxa have phylogenetic affinities with members of Pleosporales and are therefore expected to have pleosporaceous sexual morphs. Lentimurisporaceae species have been described mostly as saprobes on decomposing woody substrates from terrestrial habitats. Two species of *Bahusandhika*, *B. caligans* and *B. terrestris*, were isolated from soil (Batista & Upadhyay, 1965; Crane & Miller, 2016). Aquatic species are not known in Lentimurisporaceae.

The genus *Bahusandhika* Subram. is torula-like. Pratibha *et al.* (2014) studied the phylogenetic placement of *Bahusandhika* and found that *B. indica* has a close affinity with *Be. micronesicum* and *Be. nigroapicale*. There are nine epithets of *Bahusandhika* listed in Index Fungorum (June, 2018), but we accept eight species in this genus since *B. grootfonteinensis* should be excluded and remain as *Latorua grootfonteinensis*. Unfortunately, sequence data is available for only *B. indica* (ITS and LSU) and thus, the phylogenetic placement of other *Bahusandhika* species is unclear. More sequence data are needed to reveal if this genus is monophyletic.

The divergence times have been used as an additional evidence for the establishment of new taxa, especially in ranking higher taxa (Phukhamsakda *et al.*, 2016; Hongsanan *et al.*, 2016, 2017; Hyde *et al.*, 2017; Liu *et al.*, 2017; Zhao *et al.*, 2017). The stem age of the Pleosporales and Hysteriales overlap with those proposed age (150-250 MYA), and the result is similar with previous studies by Phukhamsakda *et al.* (2016) and Liu *et al.* (2017). The recommendation for the family divergence times is 50–150 MYA (Hyde *et al.*, 2017). In this study, Lentimurisporaceae and its sister family Floricolaceae share the stem age of 78 MYA, which justifies the establishment of the new family. The split Nigrogranaceae–Occultibambusaceae 82 (38–133) MYA, Melanommataceae–Pleomassariaceae 84 (47–130) MYA occurred at a similar age to Floricolaceae–Lentimurisporaceae 78 (49–118) MYA in Cretaceous. Asexual morphs in Nigrogranaceae are coelomycetous in terrestrial habitats, and often saprobic in bark of decayed twigs or in old fructifications of pyrenomycetes, and are sometimes human pathogens (Jaklitsch & Voglmayr, 2016). Occultibambusaceae species often occur as saprobes in dead bamboo culms or teak branches (Dai *et al.*, 2017), sometimes in dead culms of Poaceae (Jayasiri *et al.*, 2016). Asexual morphs in Occultibambusaceae are also coelomycetous on natural substrates (Hatakeyama *et al.*, 2008; Dai *et al.*, 2017). However, Jayasiri *et al.* (2016) and Doilom *et al.* (2017) found *Neooccultibambusa* species produce chlamydospores from mycelia on media. Interestingly, those celomycetous asexual morphs prominent clades, so called families, such as Didymellaceae (Aveskamp *et al.*, 2008, 2010; de Gruyter *et al.*, 2009, 2010) and Phaeosphaeriaceae (Phookamsak *et al.*, 2014), have been diverged targeting similar habitats with different nutrition and substrates. Mainly, the prevailed environment factors might play a crucial role for the development of those changes to develop a successfully survived group.

Many species in Melanommataceae occur on twigs or bark of woody plants in terrestrial, marine or freshwater habitats, and they are wide spread saprobes or hyperparasites in temperate and subtropical regions (Tian *et al.*, 2015; Li *et al.*, 2017). Hyphomycetous genera in this family, such as *Exosporiella* P. Karst., *Fusiconidium* J.F. Li, Phookamsak & K.D. Hyde, *Monotosporella* S. Hughes, *Nigrolentilocus* R.F. Castañeda & Heredia, and *Phragmocephala* E.W. Mason & S. Hughes, form fusiform, ellipsoidal to obovoid conidia with only transverse septa, which are broadly truncate base (Yanna & Hyde, 2002; Tian *et al.*, 2015; Su *et al.*, 2015; Li *et al.*, 2017). The asexual morphs in Pleomassariaceae are mostly coelomycetous and rarely hyphomycetous. The only hyphomycetous genus *Beverwykella* Tubaki is morphologically distinguishable from Lentimurisporaceae by its conidia and conidial successions.

Species in *Hermatomyces*, which was introduced by Spegazzini (1910) with *H. tucumanensis* Speg. as the type species, produce dimorphic conidia. One type has lenticular to cylindrical, muriform conidia, with subhyaline to pale brown peripheral cells and dark brown central cells (Tibpromma *et al.*, 2016, 2017), similar to *Lentimurispora urniformis*, but unlike *Hermatomyces*, *L. urniformis* has micronematous conidiophores. Despite the distinguishable morphology, *Hermatomyces* is accommodated in Lophiotremataceae (Tibpromma *et al.*, 2016, 2017; Doilom *et al.*, 2017), while *Lentimurispora* resides in the new family Lentimurisporaceae. Another genus *Vanakripa* Bhat, W.B. Kendr. & Nag Raj, described by Bhat & Kendrick (1993), also shares similar characters to *Lentimurispora*, in having micronematous conidiophores and blastic, hyaline, obpyriform, vermiform "separating cells". However, Seifert *et al.* (2011) are inconclusive whether the inflated cells beneath the conidia are part of the conidium or the conidiophore.

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