Fungal Diversity (2012) 56:63–76
DOI 10.1007/s13225-012-0197-2

Trichomeriaceae, a new sooty mould family of Chaetothyriales

Putarak Chomnunti · D. J. Bhat · E. B. Gareth Jones · Ekachai Chukeatirote · Ali H. Bahkali · Kevin D. Hyde

Received: 17 July 2012 / Accepted: 1 August 2012 / Published online: 26 August 2012

Abstract *Trichomerium* is a genus of foliar epiphytes with the appearance of sooty moulds, mostly occurring on the surface of living leaves and apparently gaining their nutrients from insect exudates. Species have ascostromata with setae and develop on a loosely interwoven mycelial mass of dark brown hyphae, while asci have a bitunicate appearance with hyaline ascospores. In this study, we made 16 collections of *Trichomerium* from Thailand. All were isolated, and the LSU and ITS rDNA gene regions sequenced. Phylogenetic analysis indicated that the *Trichomerium* species form a monophyletic clade within *Chaetothyriales* and warrant the introduction of a new family *Trichomeriaceae*. Bootstrap support for the *Chaetothyriales* is 100 % and clearly separates *Trichomeriaceae* from *Capnodiales* which are morphologically very similar. A detailed account of *Trichomerium* is provided and we describe and illustrate three new species based on morphological and molecular data. We propose that *T. foliicola* is adopted as the generic type of *Trichomerium* because it has been impossible to obtain the holotype specimen of *T. coffeicola* and also no molecular data exists in worldwide databases for this species or genus.

Keyword Foliar epiphytes · Phylogeny · Sooty moulds · *Trichomerium*

P. Chomnunti · K. D. Hyde
International Fungal Research and Development Centre,
The Research Institute of Resource Insects,
Chinese Academy of Forestry,
Bailongsi,
Kunming, Yunnan, People's Republic of China 650224

P. Chomnunti · D. J. Bhat · E. Chukeatirote · K. D. Hyde
Institute of Excellence in Fungal Research, School of Science,
Mae Fah Luang University,
Chiang Rai 57100, Thailand

P. Chomnunti · E. Chukeatirote · K. D. Hyde (✉)
School of Science, Mae Fah Luang University,
Chiang Rai 57100, Thailand
e-mail: kdhyde3@gmail.com

E. B. G. Jones
Institute of Ocean and Earth Sciences (IOES), C308,
Institute of Postgraduate Studies Building, University of Malaya,
50603, Kuala Lumpur, Malaysia

A. H. Bahkali
College of Science, Botany and Microbiology Department,
King Saud University,
Riyadh 1145, Saudi Arabia

Introduction

The taxonomy of genera of foliar epiphytes is poorly known as they have not been well-studied. No molecular data is available for most genera and therefore an understanding of the higher level classification of these fungi is rather inadequate. We have, therefore, initiated a research program to collect and study these important taxa using morphology and phylogeny. Our initial study (Chomnunti et al. 2012) resulted in the transfer of the genus *Trichomerium,* previously placed in *Capnodiaceae* to *Chaetothyriaceae* in *Chaetothyriales*. We have also provided an account of *Microthyriaceae* (Wu et al. 2011) and are presently studying other genera of foliar epiphytes. Examples of foliar epiphyte genera with a sooty mold-like appearance are *Aithaloderma*, *Capnodaria*, *Phragmocapnias* and *Scorias*. Chomnunti et al. (2011) gave an account of the genera in *Capnodiaceae*, while Chomnunti et al. (2012) dealt with species of *Chaetothyriaceae.* The genus *Trichomerium* was placed in *Chaetothyriaceae* but no further data was provided (Chomnunti et al. 2011). Hughes and Seifert (2012) provided notes on the taxonomy and nomenclature of sooty mould names, but further work is required to resolve their interrelationship, especially at the molecular level.

Trichomerium was introduced by Spegazzini (1918) based on *Trichomerium coffeicola* (Puttemans) Speg. (1918) and it is estimated that the genus now includes 23 species (Kirk et al. 2008). Thirty-one names are listed in Index Fungorum. *Trichomerium* species are all foliar epiphytes, with superficial, setiferous, uniloculate ascostromata surrounded by loosely interwoven mycelium, with bitunicate asci and hyaline, septate ascospores (Spegazzini 1918). Batista and Ciferri (1963), Hughes (1976), Reynolds (1982), Reynolds and Gilbert (2005), Kwee (1988), Thaung (2006) and Chomnunti et al. (2011) have also commented on this genus.

Batista and Ciferri (1963) provided a key, descriptions and illustrations for several *Trichomerium* species and placed them in *Capnodiaceae*. They characterized the fruiting body (perithecium) as globose, long and sessile with scattered setae, aparaphysate and with 8-spored asci. Unfortunately, the key is hard to follow and the illustrations are sketchy and therefore it is very hard to understand Batista and Ciferri's concept for the genus and its species. Hughes (1976) later transferred *Trichomerium* to *Triposporiopsidaceae*, but subsequent workers did not follow this arrangement. *Triposporiopsidaceae* is based on the genus *Triposporiopsis* which is now considered to be a species of *Phragmocapnias* and thus a synonym of *Capnodiaceae*. Reynolds (1982) re-examined all available collections and literature on *Trichomerium* and placed all species names as synonym under *T. grandisporum* (Ellis & G. Martin) Bat. & Cif., thus treating the genus as monotypic. The generic type, *T. coffeicola* was included as a synonym although it is not clear if Reynolds (1982) had examined the type material which has smaller ascospores than *T. grandisporum*. Recently, Chomnunti et al. (2011) transferred *Trichomerium* from *Capnodiaceae* to *Chaetothyriaceae* based on the morphology of the ascostromata and possession of trans-septate hyaline ascospores.

In this study, we re-describe the genus *Trichomerium* based on six specimens collected and examined from northern Thailand, including combined LSU and ITS rDNA sequence analysis. We have also examined type material of *T. coffeicola* var. *macrosporum* and describe three new species.

Material and methods

Isolates and morphology Specimens of *Trichomerium* sp. on living leaves were collected from various localities and plants in northern Thailand, taken to the laboratory in zip-lock plastic bags and examined under the microscope for morphological characters. Single spore isolates were obtained following the method of Chomnunti et al. (2011) and colonies maintained on potato dextrose agar (PDA) at 28 °C. Cultures were used for a molecular study and deposited at Mae Fah Luang University Culture Collection (MFLUCC), BIOTEC Culture Collection (BCC) and International Fungal Research & Development Centre (IRFDC culture collection), the latter under material transfer agreement (MTA) No. 3/2010. The herbarium specimens are deposited at the Mae Fah Luang University (MFLU) Herbarium, Chiang Rai, Thailand.

DNA isolation, amplification and sequencing Genomic DNA was extracted from fungal mycelium using Biospin Fungus Genomic DNA Extraction Kit (BioFlux®) according to the manufacturer's protocol for maximum yield. Partial 28S rDNA and 5.8S rDNA regions were amplified using primers LROR and LR6 and ITS5 and ITS4, respectively (Vilgalys and Hester 1990, White et al. 1990). Amplification reaction mixtures contained 50 ng of template DNA, 1X PCR buffer, 0.5 μM of each primer in a 25 μL volume, 0.5 U of Taq DNA Polymerase, 400 μM of each dNTP, 3 mM of $MgCl_2$. The PCR conditions were an initial denaturation at 94 °C for 5 min, followed by 35 cycles each consisting of 1 min denaturation at 94 °C, annealing for 30 s at 55 °C and extension at 72 °C for 1 min and a final extension at 72 °C for 5 min. PCR products were checked on 1 % agarose electrophoresis gels stained with ethidium bromide. The purified PCR products were then sequenced using the ABI-PRISM3730 DNA Analyzer (Applied Biosystems).

Phylogenetic analysis DNA sequences were analyzed with available sequences of the *Capnodiaceae*, *Chaetothyriaceae* and *Herpotrichiellaceae* obtained from GenBank. Sequences were aligned using BioEdit (Hall 1999) and Clustal X v.1.83 (Thompson et al. 1997) and phylogenetic analysis were performed using PAUP* v. 4.0b10 (Swofford 2002). Ambiguous regions in the alignments were excluded from the phylogenetic analyses, gaps were treated as missing data. Maximum parsimony (MP) was performed with the heuristic search option on and addition of sequence using 1000 random with a stepwise starting tree, tree bisection and reconnection (TBR) as the branch-swapping algorithm. The parsimony scores including tree length (TL), consistency index (CI), retention index (RI) and homoplasy index (HI) were calculated. Clade stability was estimated in bootstrap (BT) analysis with 1000 replicates (Hillis and Bull 1993). Model of substitution used for Bayesian analyses was using MrModeltest 2.2 (Nylander 2004). The Bayesian analyses were performed in MrBayes 3.04b (Huelsenbeck and Ronquist 2001). Bayesian analyses were conducted with the Markov chains run from random starting tree for 1 000 000 generations and trees were sampled every 100 generations. The Markov Chain Monte Carlo (MCMC) algorithm was used to estimate posterior probabilities (PP) and obtained for each clade. Trees were visualized in TreeView (Page 1996). Details of sequences used are presented in Table 1. The LSU and ITS region were used in the phylogenetic analysis to determine generic or family

Table 1 LSU and ITS rDNA sequences included in this analysis, which were obtained from GenBank

Species	Strain no.	Host	Country	Collector(s)	GenBank Accession no.*	
					LSU	ITS
Antennariela placitae	CBS 124785	*Eucalyptus placita*	Australia	B.A. Summerell	GQ303299	GQ303268
*Capnodiales s*p.	CN-Cre-Bo3-1	*Cremotogaster* sp. ant carton	Cameroon	R. Blatrix	HQ634619	HQ634619
*Capnodiales s*p.	CN-Cre-Bo1-6	*Cremotogaster* sp. ant carton	Cameroon	R. Blatrix	HQ634616	HQ634616
Capnodiales sp.	CN-Cre-Bo1-5	*Cremotogaster* sp. ant carton	Cameroon	R. Blatrix	HQ634615	HQ634615
Capnodiales sp.	M-Camp6	*Cremotogaster* sp. - Camponotus sp. ant carton	Malaysia	U. Maschwitz	HQ634627	HQ634627
Capnodiales sp.	CN-Cre-Bo2-2	*Cremotogaster* sp. ant carton	Cameroon	R. Blatrix	HQ634618	HQ634618
Capnodium coffeae	CBS 147.52	*Coffea robusta*	Zaire	–	DQ247800	AJ244239
Capronia fungicola	ATCC42523	Ascoma, on angiosperm wood	Brazil	G.J. Samuels	FJ358224	
Capronia fungicola	CBS614.96	Ascoma, on angiosperm wood	Brazil	G.J. Samuels	FJ358224	
Capronia mansonii	CBS 101.67	*Populus tremula*	Sweden	F. Mangenot	AY004338	AF050247
Capronia munkii	AFTOL-ID 656	*Populus*	Canada	C. Myrholm	EF413604	–
Capronia semiimmersa	MUCL40572	Rotten wood	–	W. Untereiner	AF050283	FJ358226
Ceramothyrium carniolicum	CBS 175.95	*Pyrola rotundifolia*	Sweden	K.& L. Holm	FJ358232	–
Ceramothyrium thailandica	MFLU (CC) 10–79	*Lagerstroemia* sp.	Thailand	Chomnunti	HQ895835	HQ895838
Chaetothyriales sp.	CN-Cre-Bo1-4	*Cermatogaster* sp. ant carton	Cameroon, Bonaberi	R. Blatrix	HQ634614	HQ634614
Chaetothyriales sp.	CN-Phe1-1	*Pheidole sp.*ant carton	Costa Rica	R. Blatrix	HQ634622	HQ634622
Chaetothyriales sp.	CN-Cre-Bo3-2	*Cermatogaster* sp. ant carton	Cameroon, Bonaberi	R. Blatrix	HQ634620	HQ634620
Chaetothyriales sp.	M-Cre 2	*Cermatogaster* sp. ant carton	Thailand	U. Maschwitz	HQ634630	HQ634630
Chaetothyriales sp.	M-Camp4	*Cermatogaster* sp.- *Camponotus* sp. ant carton	Malaysia	V. Mayer	HQ634626	HQ634626
Chaetothyriales sp.	CR08/2-2	*Azteca brevis* (Formicidae) ant carton	Costa Rica	V. Mayer	FJ538959	FJ538959
Chaetothyriales sp.	CR08/2-1	*Azteca brevis* (Formicidae) ant carton	Costa Rica	V. Mayer	FJ538960	FJ538960
Chaetothyriales sp.	CR07/3-2	*Azteca brevis* (Formicidae) ant carton	Costa Rica	V. Mayer	FJ538958	FJ538958
Chaetothyriales sp.	M-Mo2	*Monomorium* sp.	Malaysia	U. Maschwitz	HQ634636	HQ634636
Chaetothyriales sp.	CR072 1	*Azteca brevis* (Formicidae) ant carton	Costa Rica	V. Mayer	FJ538955	FJ538955
Chaetothyriales sp.	CN-Cre-Bo1-2	*Cermatogaster* sp. ant carton	Cameroon	R. Blatrix	HQ634613	HQ634613
Chaetothyriales sp.	CR07/2-4	*Azteca brevis* (Formicidae) ant carton	Costa Rica	V. Mayer	FJ538957	FJ538957
Chaetothyriales sp.	CR07/3-1	*Azteca brevis* (Formicidae) ant carton	Costa Rica	V. Mayer	FJ538956	FJ538956
Cladophialophora australiensis	CBS112793	Sport drink	Australia	–	EU035402	EU035402
Cladophialophora minourae	CBS556.83	Decaying wood	Japan	T. Iwatsu	FJ358235	AY251087
Cladophialophora potulentorum	CBS112222	Sport drink	Australia	N.J. Charley	EU035409.	EU035409.
Conidioxyphium gardeniorum	CPC 14327	*Gardenia jasminoides*	USA	Dunn Milton	GU301807	–
Coniosporium perforans	CBS 885.95	Marble	Greece		FJ358237	AJ244230
Cyphellophora laciniata	ATCC 14166	*Homo sapiens*	Switzerland	K.M. Wissel	FJ358239	EU035416
Exopphiala castellanii	CBS 158.58	Human, skin	Sri Lanka	A. Castellani	FJ358241	JF747070
Exophiala castellanii	CBS 158.58	*Homo sapiens*	Sri Lanka	Castellani	FJ358241	GU225940
Exophiala jeanselmei	CBS 507.90	Human	Uruguay	–	AF050271	AF050271
Exophiala nigra	dH12296	Soil under ice	Russia	–	FJ358244	–
Fumagospora capnodioides	CBS 131.34	Sooty mold on *Bursaria spinosa*	Indonesia	–	EU019269	AJ244240
Fonsecaea pedrosoi	CBS 271.37	Human, chromoblastomycosis	Argentina	Negroni P.	AB114127	AB114127
Glyphium elatum	CBS 268.34	Salix	Colorado	–	AF346420	–
Leptoxyphium fumago	CBS 123.26	*Hibiscus tiliaceus*	Indonesia	–	GU214430	
Leptoxyphium madagascariense	CBS 124766	*Eucalyptus camaldulensis*	Madagascar	M.J. Wingfield	GQ303308	GQ303277
Microxyphium aciculiforme	CBS 892.73	*Polyscias guilfoylei*	Brazil	–	GU301847	–
Microxyphium citri	CBS 451.66	Fruit	Spain	H.A. van der Aa	GU301848	–

Table 1 (continued)

Species	Strain no.	Host	Country	Collector(s)	GenBank Accession no.*	
					LSU	ITS
Microxyphium theae	CBS 202.30	*Thea sinensis*	Indonesia	–	AU301849	–
Phaeococcomyces catenatus	CBS 650.76	Air	Switzerland	H. Clémençon	AF050277	AF050277
Phaeosaccardinula ficus	MFLU (CC) 10–80	*Ficus* sp.	Thailand	KD. Hyde.	HQ895837	HQ895840
Phaeococcomyces nigricans	CBS 625.76	Paint solution in store	USA	–	AF361048	AF050278
Polychaeton citri	CBS 116435	*Citrus aurantium*, leaf, with *Pseudococcus citri*	Iran	R. Zare & W.Gams	GU214469	GU214649
Rhinocladiella atrovirens	MUCL 9905	honey	France	A.Calandron	AF050289	AF050289
Rhinocladiella fasciculata	CBS132.86	Decayed wood	India	–	EU041864	EU041807
Trichomerium deniqulatum	**MFLUCC10-0884**	***Psidium guajava***	**Thailand**	**Putarak Chomnunti**	**JX313660**	**JX313654**
Trichomerium foliicola	**MFLUCC10-0078**	***Murraya paniculata***	**Thailand**	**Putarak Chomnunti**	**JX313661**	**JX313655**
Trichomerium foliicola	**MFLUCC10-0054**	***Mangifera indica***	**Thailand**	**Putarak Chomnunti**	**JX313657**	**JX313651**
Trichomerium foliicola	**MFLUCC10-0073**	***Psidium guajava***	**Thailand**	**Putarak Chomnunti**	**JX313658**	**JX313652**
Trichomerium foliicola	**MFLUCC10-0058**	***Phoenix dactylifera***	**Thailand**	**Samantha C. Karunarathna**	**JX313659**	**JX313653**
Trichomerium gloeosporum	**MFLUCC10-0087**	***Ficus* sp.**	**Thailand**	**KD. Hyde**	**JX313662**	**JX313656**
Veronaea botryosa	CBS 350.65	Goat dung	India	BC. Lodha	EU041874	EU041817
Venturia inaequalis	CBS 535.76	*Sorbus aria*	Switzerland	–	EU035460	EU035460

ITS the ITS regions including 5.8S rDNA; LSU: 28S rDNA. New sequences generated are in bold. *ATCC* American Type Culture Collection, Virginia, USA; CBS: Fungal Biodiversity Centre, Utrecht, The Netherlands; *CPC* Culture collection of P.W. Crous, housed at CBS. MFLU CC: Culture collection, Mae Fah Luang University, MUCL: Culture Collection, Catholic University of Louvain (UCL)

*Cheewangkoon et al. (2009),Voglmayr et al. (2010), Gueidan et al. (2008), Lumbsch et al. (2000), Crous et al. (2007a), Tsuneda et al. (2011), de Hoog et al. (2011), Crous et al. (2007b), Schoch et al. (2009), Untereiner & Naveau (1999), Crous et al. (2009), Arazanlou et al. (2007)

placements. *Venturia inaequalis* was selected as outgroup. Sequences data are deposited in GenBank.

Results

Molecular phylogeny

The phylogenetic analysis includes representative sequences of *Capnodiaceae* and *Chaetothyriaceae*; the alignment of combined partial LSU and ITS rDNA comprised 73 taxa and 199 base pairs were excluded, the remaining 1131 included characters used in analysis, 767 characters were constant, 56 were variable characters are parsimony-uninformative and 308 were parsimony informative. A heuristic search found 100 equally parsimonious tree with the length (TL) of 1191 steps (CI=0.472, RI=0.846, RC=0.399, HI=0.528). All trees were similar in topology and not significantly different. A best scoring Maximum Parsimony tree is shown in Fig. 1. The phylogenetic tree obtained from Bayesian and maximum likelihood analyses is in agreement with a previous study based on MP analysis (Voglmayr et al. 2010). The six new *Trichomerium* strains formed a monophyletic group and clustered with nine strains of *Chaetothyriales* sp. associated with ants with 98 % of bootstrap support, but received a 100 % posterior probability (PP) in the Bayesian analysis (Clade A). The *Trichomerium* strains included the new species *T. deniquelatum, T. foliicola* and *T. gloeosporum* which clustered with high bootstrap support (89 % bootstrap support and 100 % PP). Other sequences of *Chaetothyriales* spp. associated with ants (CR08/2-2, CR08/2-1, CR07/3-2, M-Mo2) also grouped within clade A with 97 % of bootstrap support, but received a 100 % PP.

GenBank sequences for *Coniosporium perforans, Glyphium elatum* and *Knufia cryptophialidica* clustered in Clade B with strong support (100 % bootstrap support and 100 % PP). Species in Clade C are mostly teleomorphic genera of *Chaetothyriales* and form a monophyletic cluster (78 % bootstrap support and 100 % PP). Taxa in Clade D are members of *Herpotrichiellaceae* (anamorphic *Chaetothyriales*), some being human pathogens or rock inhabiting fungi. Clade E comprised 15 taxa of *Capnodiaceae* with five strains of *Capnodiales* isolated from ants (Voglmayr et al. 2010) and cluster together with strong support (100 % bootstrap support and 100 % PP). Phylogenetic dataclearly shows that *Trichomerium* belongs in *Chaetothyriales* and incorporates a strongly supported new family, *Trichomeriaceae* which is introduced below.

Trichomeriaceae Chomnunti & K.D. Hyde, fam. nov. MycoBank 800935

Epiphytes on living trees or *saprobes* on honey dew insect excretions. The colonies are often mixed together with capnodiaceous taxa. *Thallus* comprised of mycelium on host surface with septate, brown hyphae. *Ascostromata* arise from mycelium mass, which is a subiculum, and are sessile, spherical, brown, uniloculate, ostiolate, surrounded

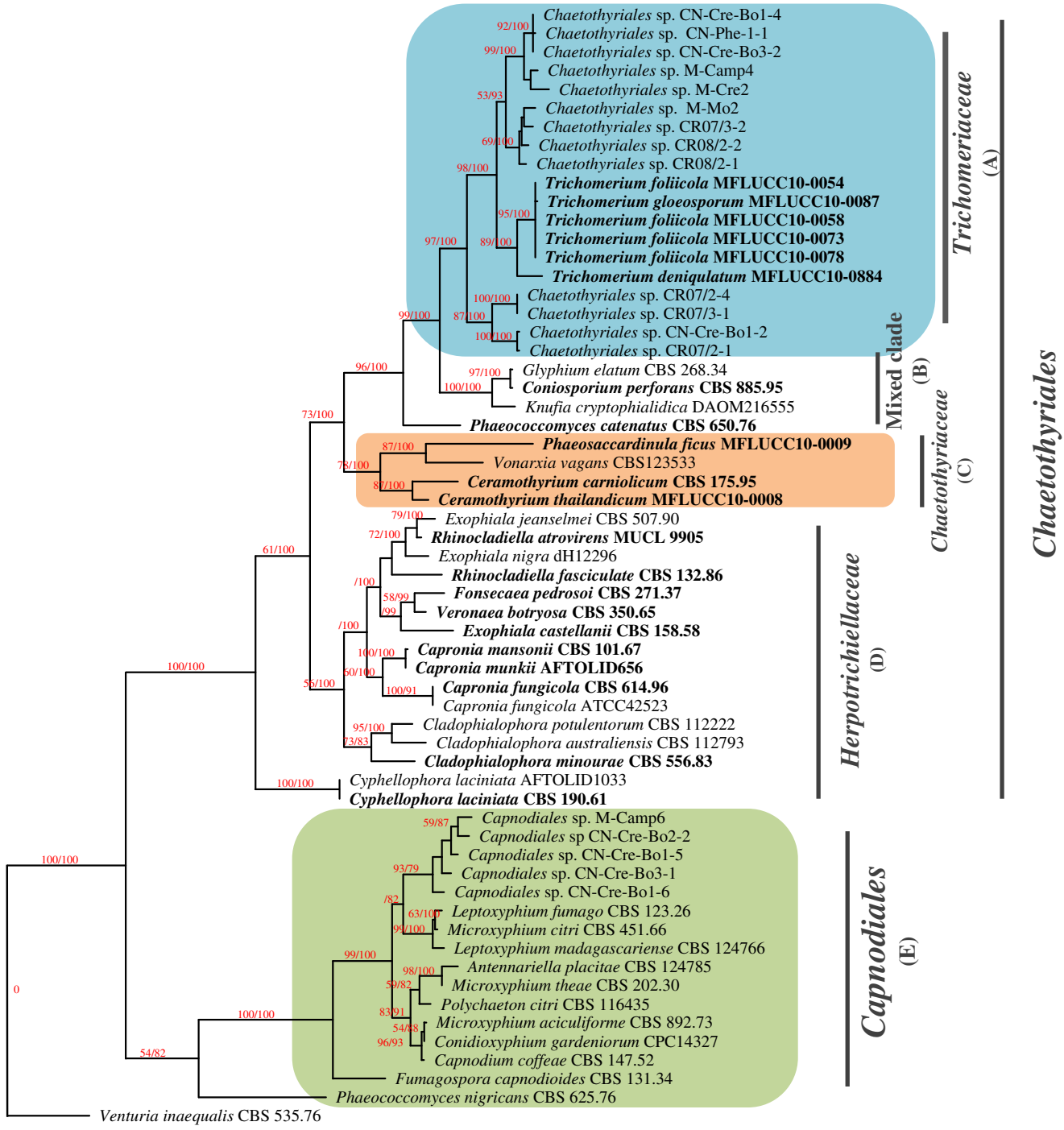

Fig. 1 A Maximum parsimony tree obtained from a data set of 73 taxa including representatives of *Chaetothyriales* and *Capnodiales*, comprising two genes (LSU, ITS). The first set of numbers above the nodes are bootstrap values over 50 % and the second represents Bayesian posterior probabilities of more than 90 % and expressed as percentages. New sequences and types are in bold

by setae. *Setae* brown to dark brown or olivaceous, erect, straight or curved, septate or continuous. *Peridium* pale brown to brown or olivaceous, comprising several layers of cells of *textura angularis*. *Asci* apparently bitunicate, with an apical ring, cylindrical to clavate, with overlapping ascospores and an apical ring. *Ascospores* hyaline, septate, fusiform, round at ends, with or without a mucilaginous sheath.

Family type: ***Trichomerium*** Speg.

Trichomerium Speg. Physis, B. Aires 4: 284 (1918).

MycoBank 5560

Foliar epiphytes on living leaves or *saprobes* on honey dew insect excretions. *Colonies* often mixed with capnodiaceous taxa. *Thallus* arising from the compacted mycelium on the host surface, composed of septate, cylindrical, pale brown to brown hyphae. *Ascostromata* arise from the mycelial mass, which is a subiculum, and are sessile, globose to subglobose, brown, uniloculate, with a central ostiole, with setae surrounding the upper part. *Setae* brown to dark brown or olivaceous, erect, straight or curved, septate or continuous. *Peridium* pale brown to brown or olivaceous, comprising 2–3 layers of cells of *textura angularis*. *Pseudoparaphyses* indistinct. *Asci* bitunicate, with an apical ring, cylindrical to clavate, with overlapping ascospores. *Ascospores* hyaline, septate, fusiform, narrowly rounded at both ends, widest in the centre, with or without a mucilaginous sheath.

Anamorph: possibly *Tripospermum* Speg. (1918) (Kirk et al. 2008).

Typification details:

Trichomerium coffeicolum (Puttemans) Speg., Physis, B. Aires 4: 284 (1918).

≡ ***Limacinia coffeicola*** Puttemans, Cryptog. Mycol. 20: 163 (1904).

Trichomerium coffeicolum (≡ *Limacinia coffeicola*) was described by Puttemans (1904) from living leaves of *Coffea arabica*. A translation of the species diagnosis reads "*Perithecium* black, ovoid, truncate at the neck, covered by dark-sooty, simple, continuous, long and tapered setae, aparaphysate. *Asci* diversified, often elongated, 50–70×15–20 μm, with hyaline, sub-fusoid, 2-septate, 3-guttulate, 15–18×5–6 μm, irregularly arranged ascospores" (Fig. 2).

Puttemans (1904) added, "…this species was common on the surface of the leaves. The mycelium is developed and surrounded with conidia and this seems identical to the mycelium and conidial forms of *Capnodium*. The genera lacked *Tripospermum* and *Limacinia* forms. I still cannot confirm the relationship with *Capnodium*".

We have tried to locate the type material of this species from URM and P but were not successful. Reynolds (1982) studied many specimens of *Trichomerium* Speg., including the type and concluded that the genus comprised a single species *T. grandisporum* and *T. coffeicola* was listed as a synonym. The description and drawings provided by Puttemans (1904) are informative and the generic concept for *Trichomerium* based on these illustrations of *T. coffeicola* is clear. In the protologue of Puttemans (1904) the ascospores are also smaller than those reported for *T. grandisporum* (15–18×5–6 versus 18–32×5–10 μm) and we doubt these taxa are the same species.

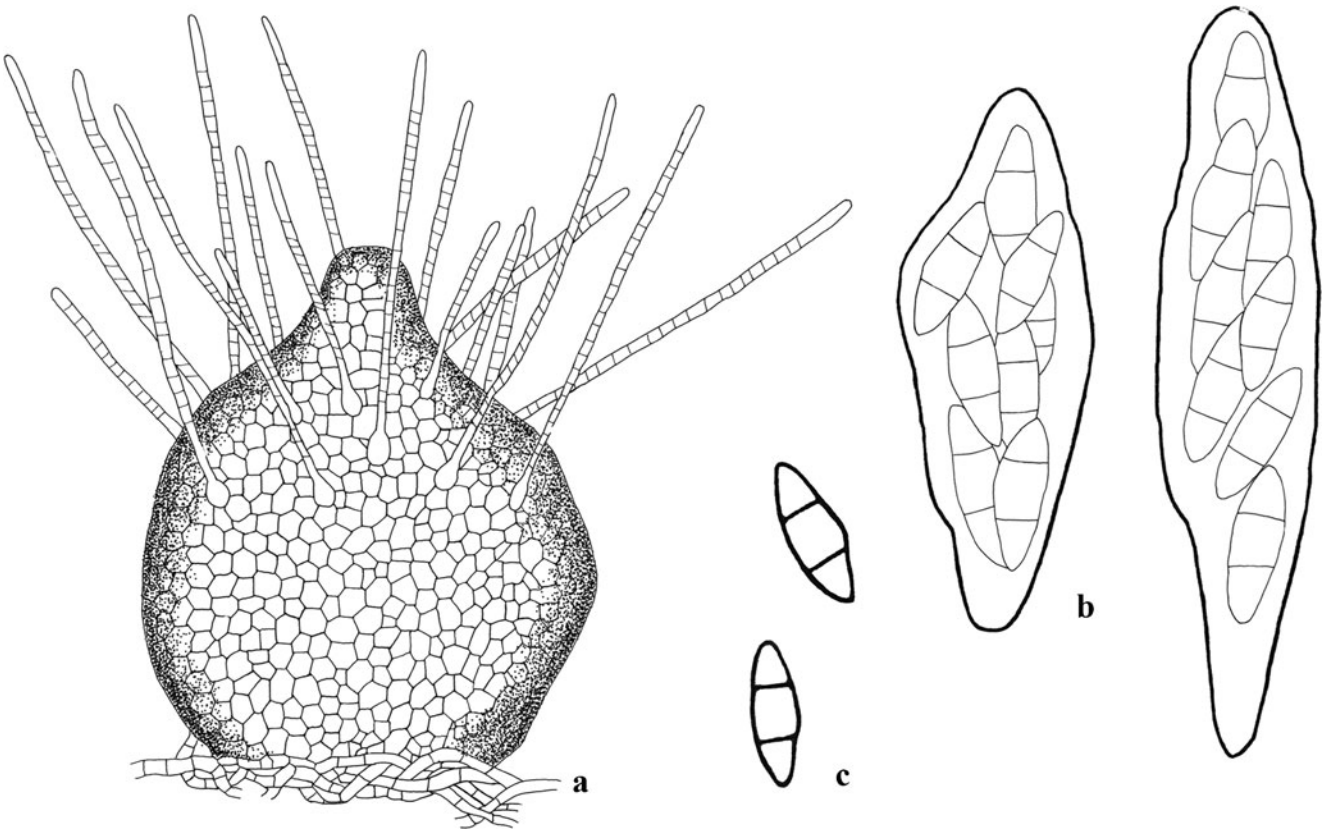

Fig. 2 **a–c** ***Trichomerium coffeicola*** Puttemans. **a** Ascostromata with apical setae. **b** Asci. **c** 2-septate ascospores. (Redrawn from M.A. Puttemans 1904)

Here we therefore treat *Trichomerium* in the sense of *T. coffeicolum* based only on the protologue description and drawing. In this treatment *T. deniquelatum, T. foliicola* and *T. gloeosporum* are typical of *Trichomerium* and we suggest that it would be pragmatic to list *T. foliicola* as type of the genus in the Lists of Accepted Names to be developed by the subcommittee dealing with Dothideomycete names to be approved by the General Committee on Nomenclature (GCN) (Hawksworth 2012). This will ensure stability in application of the generic name. *Trichomerium foliicola* is supported by both herbaria and living material and, in addition, molecular sequence data. Of course if fresh collections of *Trichomerium coffeicolum* were found and sequenced this would not be necessary.

Trichomerium foliicola Chomnunti & K.D. Hyde, **sp. nov.** (Figs. 3a–l)

MycoBank 801117

Etymology: from the Latin *foliicola* meaning on living leaf, referring to various living host.

Black sheets of mycelia cover the leaves of the host and support dark brown superficial, gregarious ascostromata. The hyphae are septate, cylindrical, pale brown to brown with constrictions at the septa, mostly narrow; 3.5–7 μm wide ($\bar{x}$ = 5.5 μm, *n*=20). *Ascostromata* initials arising from a small irregular group of cells formed by the repeated division of a few hyphal cells, usually at a hyphal branches and becoming dense. *Ascostromata* 133–179 μm diam, 140–181 μm high ($\bar{x}$ = 158 × 162 μm, *n*=20), subglobose to globose, brown, with abundant straight, aseptate to septate, dark brown to brown setae, up to 15 setae, mostly on the upper half of the ascostroma, (44–) 61–118×4–7 μm ($\bar{x}$ = 83 × 6 μm, *n*=20) present on a single ascostromata. Ostiole central, ostiolar canal 32 μm wide at the base, 39 μm high, with an apical ring, with periphyses. Ascostroma wall 17–24 μm wide ($\bar{x}$ = 20 μm, *n*=20), thick-walled, inwardly hyaline, pale brown and brown towards the outside, comprised of 2–3 layers of *textura angularis*. *Asci* (47–) 63–70×(14–) 20–26 μm ($\bar{x}$ = 65 × 22 μm, *n*=10), 8-spored, ellipsoid to clavate, some obovoid, apparently bitunicate, with apical ring, aparaphysate. *Ascospores* 19–22×6–7 μm ($\bar{x}$ = 21 × 7 μm, *n*=20) tri-seriate, hyaline with 2–3 septa, fusoid, with narrowly rounded ends.

Culture characteristics Ascospores germinating on PDA within 12 h and germ tubes produce from both end cells and from the middle cell. Colonies growing slowly on PDA, reaching a diam of 2.5 cm. after 14 days at 28 °C. Mycelium initially black with dark green margin visible from both sides of the dish, colony on PDA velvety, radial towards the edge.

Material examined THAILAND, Chiang Rai Province, Mae Ka Jan, on living leaf of *Murraya paniculata*, 11 October 2009, Putarak Chomnunti, DPC 042 (MFLU10−0007, **holotype**), ex-type living culture in MFLUCC10-0078= BCC40643; *Ibid*., 16 December 2009, Putarak Chomnunti (MFLU10-0683); *Ibid.,* 7 March 2010, Putarak Chomnunti (MFLU10-0987). *Ibid*., Baan Du, on living leaf of *Mangifera indica*. 8 July 2009, Putarak Chomnunti, DPC 015 (MFLU09-0651), living culture in MFLUCC10-0054= BCC38853; *Ibid.,* 2 September 2009, Putarak Chomnunti (MFLU09-0684); *Ibid.,* 24 May 2011, Putarak Chomnunti (MFLU11-1151); *Ibid*., on living leaf of *Psidium guajava*, 25 October 2009, Putarak Chomnunti, DPC 020 (MFLU10-0002); living culture in MFLUCC10-0073= BCC41091; *Ibid.,* 22 April 2010, Putarak Chomnunti (MFLU10-0988); *Ibid*., on living leaf of *Phoenix dactylifera*, 11 August 2009, Samantha Chandranath Karunarathna, DPC 023 (MFLU09-0656); living culture in MFLUCC10-0058= BCC39630; *Ibid*., 4 May 2010, Putarak Chomnunti (MFLU10-0989); *Ibid.,*20 August 2010, Putarak Chomnunti (MFLU10-0990); BRAZIL, Recife, Pernambuco, on leaves of *Didymopanax morotoni*, 4 February 1956, Severino José da Silva, URM 5302 (holoype); CUBA, Santiago de las Vesgas, in fragments of leaves of an unidentified host, 7 May 1913, F.L. Stevens (URM 13335); *Ibid*., on leaves of *Sanchezia nobilis* Hook., 19 January 1922, Charles and Ballon (URM 13483).

Notes: Trichomerium foliicola is similar to *T. didymopanacis* described from *Didymopanax morototoni* by Batista and Ciferri (1963) and referred to *Capnodiales*. *Trichomerium didymopanacis* was described as having epiphyllous colonies with superficial, black, septate mycelium, with non-setose, narrowed, globose, membranous ascostromata, and with a central ostiole. Ascostromata have numerous setae which are erect, straight or curved, brown, and with obtuse tips. Asci are ellipsoid, sessile, and aparaphysate. Ascospores are fusoid, with rounded ends, 1–3 septate and hyaline (Batista and Ciferri 1963). The drawing provided in the protologue however, is not detailed. We examined the type of *T. didymopanacis* (URM 5302), however the material was not in good condition and we could not find ascostromata. Although, the ascostroma, asci and ascospores in the description of *T. didymopanacis* provided in Batista and Ciferri (1963) overlap with those of *T. foliicola* (Table 2), it is not equivocal that these are the same species. We prefer to introduce a new species to avoid any confusion.

Trichomerium deniqulatum Chomnunti & K.D. Hyde, **sp. nov.** (Figs. 4a–j)

MycoBank 800933

Etymology: from the Latin '*denique*' meaning short, referring to short setae.

Black sheets of mycelia cover the leaves of the host which produce dark brown superficial, gregarious ascostromata. *Mycelium* superficial, septate, cylindrical, pale brown to brown hyphae, constricted at the septa; 5–7 μm wide ($\bar{x}$ = 6 μm, *n*=20). *Ascostromata* initials arise from a small irregular group of cells formed by the repeated division of a

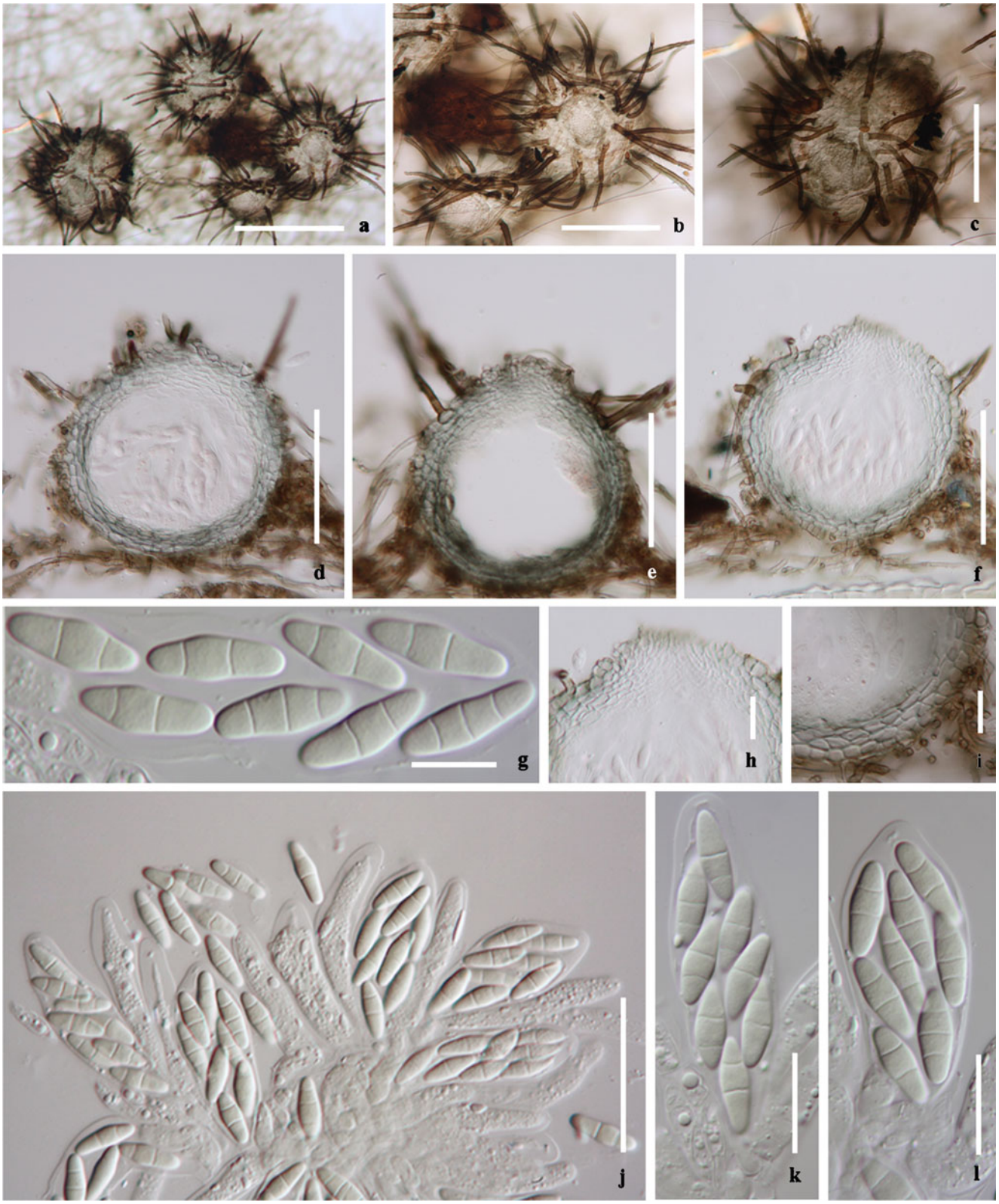

Fig 3 **a–l** ***Trichomerium foliicola*** (holotype). **a–c** Ascostromata with ostiole and setae. **d–f** Vertical section through ascostromata. **g** Ascospores. **h** Ostiolar canal. **i** Peridium. **j–l** Asci and ascospores. Bars: **a–f**=100 μm. **k, l**=50 μm, **h, i**=20 μm, **g**=10 μm

Table 2 Synopsis of characters of *Trichomerium* species mentioned in this study.

Taxa	Setae	Ascomata	Ascospores	Host in protologue	References
T. coffeicola Speg.	Dark-sooty setae, simple, continuous, long and tapered	Ascostromata, conoid, neck truncate	15–18×5–6 µm hyaline, subfusoid, 3-guttulate, 2-septate	*Coffea arabica*	Spegazzini (1918)
T. deniqulatum Chomnunti & K.D. Hyde	(28–)32–54×3.7–6 µm, setae sparse, indistinct, aseptate to septate, brown	154–175×163–180 µm	18–25×6–8 µm, fusoid, 3-septate, constricted at the septa, middle two cells wider and obliquely septate	*Psidium guajava*	This paper
T. didymopanacis Bat. & Cif.	50–130×5–8 µm, numerous erect, straight or curved, simple with obtuse apex, septate, brown	105–150 µm.	16–24.5×5–7.5 µm, fusoid, with rounded ends, 1–3 septate, hyaline	*Didymopanax morototoni*	Batista and Ciferri (1963)
T. foliicola Chomnunti & K.D. Hyde	(44–) 61–118×4–7 µm, abundant, clearly septate and continuous, brown	133–179×140–181 µm	19–22×6–7 µm, 2–3 septate, not constricted, fusiod	*Murraya paniculata*	This paper
T. gloeosporum Chomnunti & K.D. Hyde	71–127×4–7 µm, abundant, clearly septate, brown-black, olivaceous	116–140×113–150 µm	17–26×5–7 µm, fusiod, 2–3 septate, not constricted, covered by hyaline sheath	*Ficus* sp.	This paper
T. hirtellum Bat.	56–65×5–7.5 µm, setose, septate to continuous all around the ascostromata, black	90–150 diam. µm, globose or pyriform	14.5–19.5×6–8.5 µm, fusoid, 2-septate, hyaline	*Persea*	Batista (1951)
T. ornatum Bat. & Cif.	58–120×5–9 µm, setae erect, simple, straight or curved, light brown or olivaceous, septate, obtuse, dull brown apex	125–250 diam. µm, globose with central ostiole	22–27×6–10 µm, cylindric-fusoid at first 1-septate then 3-septate, not constricted, hyaline	*Ocotea* sp.	Batista and Ciferri (1963)
T. pelliculosum (Berk. & Ravenel) Cif. & Bat.	54–95×5–10 µm, erect setae, curved or not, setae apex rounded to narrowed, base slightly thickened, brownish	80–145 µm diam	15–22×4–7 µm, fusiod, 1–3 septate, hyaline, not constricted, polystichous	*Prunus, Magnolia*	Batista and Ciferri (1963)
T. portoricense Speg.	Numerous	250 µm diam	30×10 µm, fusiform, 3-septate, hyaline and olive when mature	*Psidium guajava*	Spegazzini (1924)

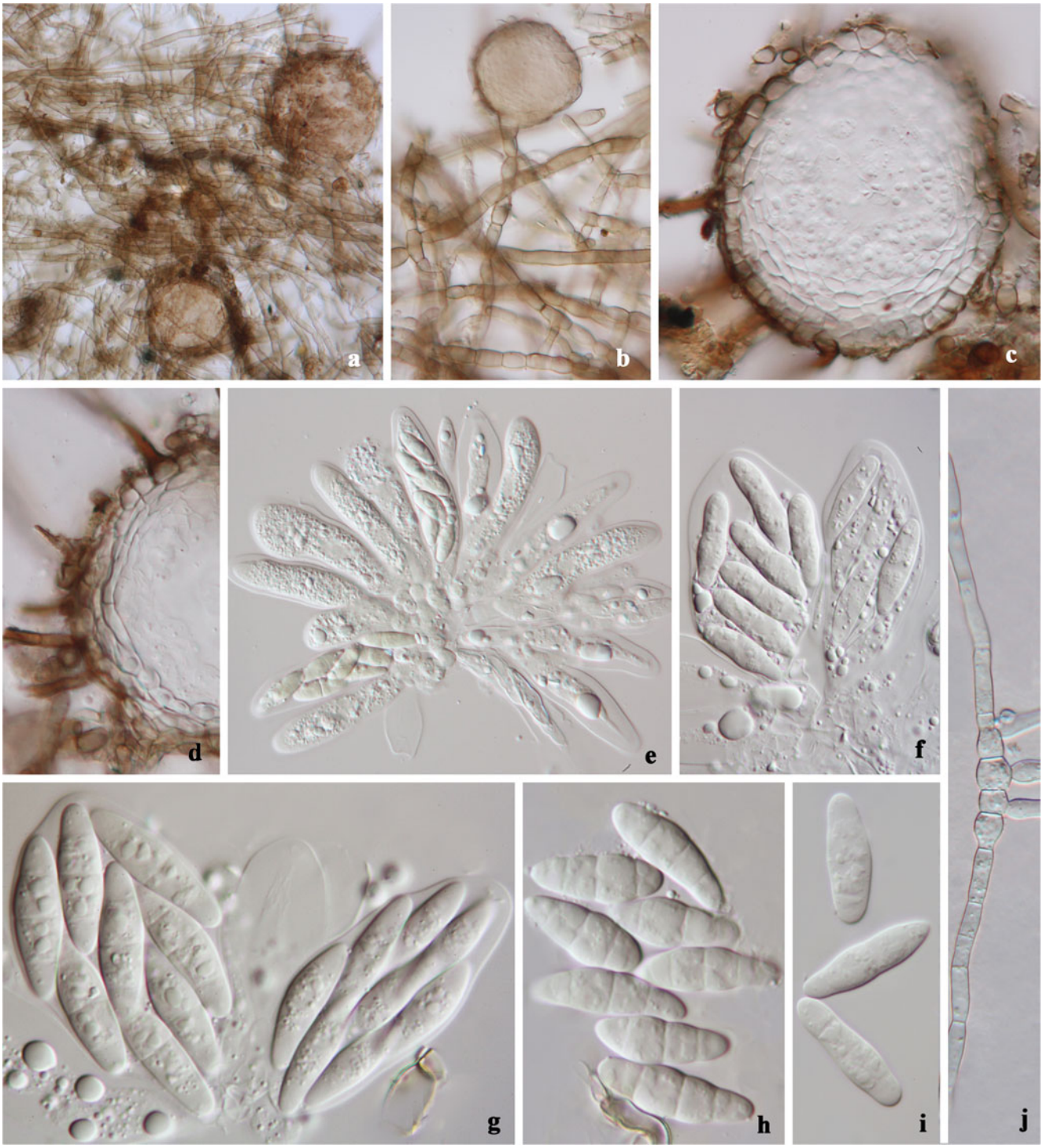

Fig. 4 **a–j** ***Trichomerium deniqulatum*** (holotype). **a–b** Mycelium with immature ascostromata. **c** Vertical section through ascostromata. **d** Peridium. **e–g** Asci with apical ring in **g** (*right* ascus). **h–i** Ascospores. **j** Germination of ascospore. Bars: **a**=100 μm. **b**, **c**, **e**= 50 μm, **d**, **f**, **g**, **h**=20 μm, **i**, **j**=10 μm

few hyphal cells young ascomata are brown and mixed with the hyphae. *Ascostromata* 154–175 μm diam, 163–180 μm high ($\bar{x}$ = 165 × 168 μm, *n*=10), subglobose to globose, sessile, brown, with up to 5 setae around the upper half of the perithecium; setae sparse, indistinct, aseptate to septate, brown, straight, with cylindrical cells, (28–)32–54×3.7–6 μm ($\bar{x}$ = 43 × 5 μm, *n*=20), aparaphysate. *Ascostroma wall* 12–15 μm wide ($\bar{x}$ = 13 μm, *n*=20) thick-walled, inwardly hyaline, brown towards the outside, comprised 2–3-layers of *textura angularis*. *Asci* 47–60×22–31 μm ($\bar{x}$ = 54 × 25 μm,

n=10), 8-spored, ellipsoid to clavate, some subglobose, apparently bitunicate with an apical ring, aparaphysate. *Ascospores* 18–25×6–8 μm ($\bar{x}$ = 22 × 7 μm, n=20), triseriate, hyaline, fusoid, 3-septate, some with longitudinal septa, constricted at the septa, middle two cells wider and obliquely septate.

Culture characteristics Ascospores germinating on PDA within 12 h and germ tubes arise from both end cells (Fig. 4j). Colonies growing slowly on PDA, reaching a diam of 4 cm after 14 days at 28 °C, velvety, radiating towards the edge. Mycelium initially black and dark green at the margin.

Material examined THAILAND, Chiang Rai Province, Mae Fah Luang University, on living leaf of *Psidium guajava*. 12 September 2009, Putarak Chomnunti, DPC 039 (MFLU11-1150, holotype), ex-type living culture in MFLUCC10-0084= BCC40712; *Ibid*., 28 June 2010, Putarak Chomnunti (MFLU11-1152); *Ibid.,* 11 October 2010, Putarak Chomnunti (MFLU11-1153)

Notes: Batista and Ciferri (1963) described several species of *Trichomerium* with sparse setae mostly on the upper part of ascomstromata including *T. coffeicola, T. crotonis* Bat., *T. plumieriae* Bat. & Cif., *T. stuhlmannianum* (Henn.) Bat. & Cif. and *T. stuhlmannianum* var. *biseptatum* Bat. & Cif. *Trichomerium deniqulatum* has few setae on the ascostromata and differs from others in size of setae and ascospores, the number of septa on the ascospores. *T. deniqulatum* differs from *T. coffeicola* in having shorter setae (43×5 versus 100×3–4 μm). In *T. crotonis* ascospores are 3–5 septate, while in *T. deniqulatum* ascospores are 2–3 septate. In *T. plumieriae* ascospores are slightly smaller (20 μm long versus 22 μm long) and in *T. stuhlmannianum* var. *biseptatum* ascospores are not more than 2-septate, while in *T. deniqulatum*, ascospores are 2–3-septate and with or without longitudinal septa. We considered short setae and ascospores with longitudinal septa as major characters to recognize the new species.

Trichomerium gloeosporum Chomnunti & K.D. Hyde, **sp. nov.** (Figs. 5a–m)

MycoBank 800934

Etymology: from the Latin *gloeoid* meaning slimy, referring to ascospore outer sheath.

Black sheets of superficial of mycelia cover the surface of leaves of the host. The hyphae are septate, cylindrical, pale brown to brown, constricted at the septa, 4–7 μm wide ($\bar{x}$ = 5 μm, n=20). *Ascostromata* initials arise from a small group of irregular cells formed by repeated division of a few hyphal cells, when young brown and mixed with hyphae. *Ascostromata* 116–140 μm diam, 113–150 μm high ($\bar{x}$ = 128 × 138 μm, n=10), subglobose to globose, sessile, brown, with abundant setae, up to 10 setae around the upper half of the ascostromata; setae septate, brownish to dark brown or olivaceous, straight, with cylindrical cells, 71–121×4–7 μm ($\bar{x}$ = 100 × 6 μm, n=20). *Ascostroma wall* 2–3 layered, 15–21 μm wide ($\bar{x}$ = 18 μm, n=20), thick walled, hyaline at the inner layers, brown at the outer layers, comprised of cells *textura angularis*. *Asci* 62–86×18–23 μm ($\bar{x}$ = 75 × 21 μm, n=20), 8-spored, ellipsoidal to cylindrical, with short pedicel, apparently bitunicate, with an apical ring, aparaphysate. *Ascospores* 17–26×5–7 μm ($\bar{x}$ = 22 × 6 μm, n=25), bi-seriate, hyaline, fusoid, 2–3-septate, not constricted at the septa, narrowly rounded at the ends, with a conspicuous mucilaginous sheath.

Culture characteristics Ascospores germinating on PDA within 12 h and germ tubes produced from both end cells. Colonies growing slowly on PDA, reaching a diam of 3 cm after 14 days at 28 °C. Mycelium initially black with dark green margins, colony on PDA velvety, radial toward to the edge.

Material examined THAILAND, Chiang Rai Province, Muang District, near Baan Du, Ban Kua Krae, *Ficus* sp. tree in rice field, on living leaf, 4 October 2010, K.D. Hyde, DPC 051 (MFLU10-0016, holotype), ex-type living culture in MFLUCC10-0087; *Ibid*., 30 January 2011, Putarak Chomnunti (MFLU11-1154).

Notes: *Trichomerium gloeosporum* is distinct from hitherto described species in the genus in having ascospores with a distinct mucilaginous sheath. Conidia of a *Trichomerium* sp**.** were associated with the sooty mould, but we could not establish that they were related to the sexual morph. We collected material of a *Trichomerium* sp. from *Phoenix dactylifera* but unfortunately the specimen had too few of ascostromata to derive any valid morphological description. However, we derived a pure culture of the fungus from the specimen and carried out phylogenetic analysis. The culture did not produce any reproductive structures and therefore, at this stage, only the culture and sequence data are available. The sequence data is 95 % similar to *T. gloeosporum* and also very close to *T. foliicola*, hence accommodated under this species but further collections are needed to establish its identity.

Discussion

In this study, we report on the morphology and sequence data for six freshly collected strains of *Trichomerium* isolated from Thailand. The strains are described as the new species *T. foliicola* (4 strains), *T. deniqulatum* (1 strain) and *T. gloeosporum* (1 strain), based on phylogenetic and morphological

Fig. 5 **a–m** ***Trichomerium gloeosporum*** (holotype). **a** Sooty mould on living leaf of *Ficus* sp. **b** Ostiole. **c** Vertical section through ascostromata. **d** Peridium. **e** Setae. **f** Conidia. **g–i** Asci. **j–m** Ascospores. Bars: **c, d, g**=50 μm, **b, e, f, h, i**=20 μm, **j–m**=10 μm

data. The phylogenetic data show that the three species belong to *Chaetothyriales* and cluster with *Chaetothyriales* spp. from ant nests chambers (Voglmayr et al. 2010). They are not closely related to *Chaetothyriaceae, Herpotrichiellaceae* or *Capnodiaceae.* Consequently, a new family, *Trichomeriaceae*, typified by sessile, setiferous ascostromata, with ostiolate, aparaphysate ascostromata, bitunicate asci with an apical ring and 2–3–septate to trans-septate, hyaline, ascospores with or without a sheath, is introduced. Ascostromata with a mycelial cover, asci with an apical ring and trans-septate and sheathed ascospores are not known in *Capnodiaceae*. We treat *Trichomerium* in the sense of *T. foliicola* as the holotype specimen of *T. coffeicola,* the generic type is unavailable and also no molecular data exists for this species.

Reynolds (1982) examined several species of *Trichomerium*, clumped them under *T. grandisporum* and considered the genus to be monotypic. We have not followed Reynolds (1982) approach, as we believe the concept for *Trichomerium* as based on the generic type of *Limacinia coffeicola* Puttemans (1904) is clear. Furthermore, we accept four species in the present study and we believe that further studies of types and fresh collections will show the genus to be more speciose. Reynolds and Gilbert (2005) assigned the genus *Trichomerium* based on his concept of *Trichomerium grandisporum* (Ellis & G. Martin) Bat. & Cif. to *Capnodiaceae* using molecular sequence data (unpublished), which otherwise clustered with a black yeast clade (Berbee 1996). Recently, Chomnunti et al. (2011) excluded *Trichomerium* from *Capnodiaceae* on the basis of ascostromata and trans-septate hyaline ascospores and transferred the genus to *Chaetothyriaceae*. In this study, we diagnose *Trichomerium* based on morphological characteristics and DNA sequence data and accommodate the genus in a new family *Trichomeriaceae* in *Chaetothyriales*.

Acknowledgments This work was supported by the Thailand Research Fund BRG528002. Roger Fagner Ribeiro Melo is kindly thanked for examining material from URM. We thank the International Fungal Research & Development Center, IFRD Research Institute of Resource Insects and Mycological Department of Chinese Academic of Science for supporting the molecular work. Eric McKenzie is thanked for improving the manuscript.

References

Arzanlou M, Groenewald JZ, Gams W, Braun U, Shin HD, Crous PW (2007) Phylogenetic and morphotaxonomic revision of *Ramichloridium* and allied genera. Stud Mycol 58:57–93

Batista AC (1951) Alguns fungos de fumagina de Pernambuco. Mycopathol Mycol Appl 5:147–172

Batista AC, Ciferri R (1963) Capnodiales. Capnodiales. Saccardoa 2:1–296

Berbee ML (1996) Loculoascomycete origins and evolution of filamentous ascomycete morphology based on 18 S rDNA gene sequence data. Mol Biol Evol 13:462–470

Cheewangkoon R, Groenewald JZ, Summerell BA, Hyde KD, To-anun C, Crous PW (2009) *Myrtaceae*, a cache of fungal biodiversity. Persoonia 23:55–85

Chomnunti P, Schoch CL, Aguirre-Hudson B, Ko Ko TW, Hongsanan S, Jones EBG, Kodsueb R, Phookamsak R, Chukeatirote E, Bahkali AH, Hyde KD (2011) Capnodiaceae. Fungal Divers 51:103–134. doi:10.1007/ss13225-011-0145-6

Chomnunti P, Ko Ko TW, Chukeatirote E, Cai L, Jones EBG, Kodsueb R, Chen H, Hassan BA, Hyde KD (2012) Phylogeny of Chaetothyriaceae in northern Thailand including three new species. Mycologia 104:382–395. doi:10.3852/11-066

Crous PW, Schoch CL, Hyde KD, Wood AR, Gueidan C, de Hoog GS, Groenewald JZ (2009) Phylogenetic lineages in the Capnodiales. Stud Mycol 64:17–47

Crous PW, Schubert K, Braun U, de Hoog GS, Hocking AD, Shin HD, Groenewald JZ (2007a) Opportunistic, human–pathogenic species in the Herpotrichiellaceae phenotypically similar to saprobic or phytopathogenic species in the Venturiaceae. Stud Mycol 58:185–217

Crous PW, Braun U, Groenewald JZ (2007b) *Mycosphaerella* is polyphyletic. Stud Mycol 58:1–32

de Hoog GS, Vicente AV, Najafzadeh MJ, Harrak MJ, Badali H, Seyedmousavi S (2011) Waterborne *Exophiala* species causing disease in cold-blooded animals. Persoonia 27:46–72

Gueidan C, Villasenor CR, de Hoog GS, Gorbushina AA, Untereiner WA, Lutzoni F (2008) A rock-inhabiting ancestor for mutualistic and pathogen-rich fungal lineages. Stud Mycol 61:111–119

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp Ser 41:95–98

Hawksworth DL (2012) Managing and coping with names of pleomorphic fungi in a period of transition. Mycosphere 3(2):143–155. doi:10.5943/mycosphere/3/2/4

Hillis DM, Bull JJ (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Syst Biol 42:182–192

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17(8):754–755

Hughes SJ (1976) Sooty moulds. Mycologia 68:693–820

Hughes SJ, Seifert KA (2012) Taxonomic and nomenclatural notes on sooty mould name based on species mixtures: *Hormiscium handelii* and *Torula lecheriana*. Mycoscience 53:17–24

Kirk PM, Cannon PF, David JC, Stalpers JA (2008) Ainsworth & Bisby's dictionary of the fungi. UK, CAB International

Kwee LM (1988) Studies on some sooty moulds on guava in Malaysia. Pertanika 11:349–355

Lumbsch HT, Lindemuth R, Schmitt I (2000) Evolution of filamentous Ascomycetes inferred from LSU rDNA sequence data. Plant Biol 2:525–529

Nylander JAA (2004) Mr Model test 2.0. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Page RDM (1996) TreeView: an application to display phylogenetic trees on personal computers. Comput Appl Biosci 12:357–358

Puttemans A (1904) Contribution à l'étude de la fumagine des Caféiers. Bull Soc Mycol Fr 20:152–154

Reynolds DR (1982) Foliicoloius Ascomycetes: 4. The capnodiaceous genus *Trichomerium* Spegazzini emend. Mycotaxon 14:189–220

Reynolds DR, Gilbert GS (2005) Epifoliar fungi from Queensland, Australia. Aust Syst Bot 18:265–289

Schoch CL, Crous PW, Groenewald JZ, Boehm EWA, Burgess TI, de Gruyter J, de Hoog G, Dixon LJ, Grube M, Gueidan C, Harada Y, Hatakeyama S, Hirayama K, Hosoya T, Huhndorf SM, Hyde KD, Jones EBG, Kohlmeyer J, Kruys A, Lucking R, Lumbsch HT, Marvanova L, Mbatchou JS, McVay AH, Miller AN, Mugambi GK, Muggia L, Nelsen MP, Nelson P, Owensby CA, Phillips AJL, Phongpaichit S, Pointing SB, Pujade-Renaud V, Raja HA, Rivas Plata E, Robbertse B, Ruibal C,

Sakayaroj J, Sano T, Selbmann L, Shearer CA, Shirouzu T, Slippers B, Suetrong S, Tanaka K, Volkmann-Kohlmeyer B, Wingfield MJ, Wood AR, Woudenberg JHC, Yonezawa H, Zhang Y, Spatafora JW (2009) A class-wide phylogenetic assessment of Dothideomycetes. Stud Mycol 64:1–5

Spegazzini CL (1918) Notas mycological. Physics 4:281–295

Spegazzini CL (1924) Algunos honguitos Portoriqueños. Bol Acad Nac Ci 26:335–368

Swofford DL (2002) PAUP: Phylogenetic analysis using parsimony, version 4.0b10. Sinauer Associates, Sunderland

Thaung MM (2006) Biodiversity of phylloplane ascomycetes in Burma. Aust Mycol 25(1):5–23

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality ananlysis tools. Nucleic Acids Res 25:4876

Tsuneda A, Hambleton S, Currah RS (2011) The anamorph genus *Knufia* and its phylogenetically allied species in *Coniosporium, Sarcinomyces* and *Phaeococcomyces*. Botany 89:523–536

Untereiner WA, Naveau FA (1999) Molecular systematics of the *Herpotrichiellaceae* with an assessment of the phylogenetic positions of *Exophiala dermatitidis* and *Phialophora Americana*. Mycologia 91:67–83

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. J Bacteriol 172:4238–4246

Voglmayr H, Mayer V, Maschwitz U, Moog J, Djieto-Lordon C, Blatrix R (2010) The diversity of ant-associated black yeasts: insights into a newly discovered world of symbiotic interactions. Fungal Biol 115:1077–1091

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications:315–322. Academic, San Diego

Wu HX, Schoch CL, Boonmee S, Bahkali AH, Chomnunti P, Hyde KD (2011) A reappraisal of Microthyriaceae. Fungal Divers 51:189–248. doi:10.1007/s13225-011-0143-8