# *Tubeufiales*, ord. nov., integrating sexual and asexual generic names

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Abstract *Tubeufiaceae* is based on the generic type *Tubeufia*, which is characterized by superficial, oval and bright ascomata, bitunicate asci, mostly long fusiform to filiform, transeptate ascospores and hyphomycetous asexual states with helicosporous conidia. Most species in this family are saprobic on terrestrial woody substrates and some are aquatic. Their distinct morphology as well as combined LSU, SSU and TEF1 sequence analysis show that Tubeufiaceae should be accommodated in a new order Tubeufiales, which is introduced in this paper. Phylogenetic analyses of combined LSU and ITS sequences were used to resolve genera and species within the family Tubeufiaceae. In this study, we examine and incorporate sexual and asexual states of genera in Tubeufiales to provide a modern treatment, based on single names. An epitype for Tubeufia javanica, the type species of Tubeufia, is designated and represents Tubeufia sensu stricto. The genera Acanthophiobolus, Acanthostigma, Boerlagiomyces,

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S. Boonmee · J.-K. Liu · W.-J. Li · D.-Q. Dai · K. D. Hyde School of Science, Mae Fah Luang University, Muang, Chiang Rai 57100, Thailand Chlamydotubeufia, Kamalomyces, Podonectria, Thaxteriella and Thaxteriellopsis are accepted, Acanthostigmina is reinstated, and the asexual genera Aquaphila, Helicoma, Helicomyces, Helicosporium and Tamhinispora are accepted in Tubeufiaceae. Three new genera Acanthohelicospora, Helicangiospora and Neoacanthostigma are introduced. The genus Bifrontia is added to the family based on morphological similarity. The incongruous morphological genera Acanthostigmella, Amphinectria, Chaetocrea, Chaetosphaerulina, Glaxoa, Malacaria, Melioliphila, Paranectriella, Puttemansia, Rebentischia and Uredinophila are excluded from Tubeufiaceae despite having characteristic ascomata with setae and multiseptate long spores. A key to genera accepted in Tubeufiaceae is provided.

**Keywords** *Dothideomycetes* · Helicospores · New genus · Phylogeny · Taxonomy · *Tubeufiaceae* 

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## Introduction

The family *Tubeufiaceae* was established in *Pleosporales* by Barr (1979) based on the generic type *Tubeufia* and included five genera i.e. *Letendraeopsis, Melioliphila, Podonectria, Rebentischia* and *Thaxteriella*, while a recent treatment by Boonmee et al. (2011) included 20 genera (Table 1). *Allonecte, Byssocallis, Letendraeopsis* and *Taphrophila* were considered atypical and excluded from the family. Most genera of *Tubeufiaceae* have uniloculate, superficial, pigmented ascomata e.g. pale brown, brown, and dark brown to black, multi-celled, hyaline ascospores, and produce helicosporous asexual states (Tsui et al. 2006; Boonmee et al. 2011). For a comprehensive review of *Tubeufiaceae*, see Boonmee et al. (2011).

Molecular techniques are being used to establish taxonomic relationships among genera in *Dothideomycetes* (Lutzoni et al. 2004; Hibbett et al. 2007; Hyde and Zhang 2008; Lücking 2008; Brock et al. 2009; Eberhardt 2010; Figueiredo et al. 2010; Liu et al. 2011, 2012; Zhang et al. 2012) and establish their higher level placement in a natural classification system (Hyde et al. 2013; Ariyawansa et al. 2014a, b; Hongsanan et al. 2014; Phookamsak et al. 2014;

Thambugala et al. 2014: Wijavawardene et al. 2014). Some studies on Tubeufiaceae have also incorporated molecular analyses and these results were reviewed in Boonmee et al. (2011). Basically, in recent phylogenetic analyses of Tubeufiaceae, species in different sexual and asexual genera of Tubeufiaceae were scattered throughout the trees (Tsui and Berbee 2006; Tsui et al. 2006). Therefore generic concepts were difficult to resolve and it proved impossible to establish which asexual genera were linked to sexual morphs. Morphological characterization and phylogenetic reconstruction have shown that members of *Tubeufiaceae* form a monophyletic clade in Dothideomycetes, and are a sister lineage to Pleosporales (Tsui and Berbee 2006; Schoch et al. 2006, 2009; Boonmee et al. 2011; Zhang et al. 2011, 2012; Hyde et al. 2013). The objective of the present paper is to introduce a new order Tubeufiales to accommodate the monophyletic family Tubeufiaceae, which has previously been classified in Pleosporales. Integration of sexual and asexual names in Tubeufiaceae is now possible and each genus should have a single name (Taylor 2011; Gams et al. 2012; McNeill et al. 2012; Hawksworth et al. 2013). In this paper we epitypify or designate authentic sequenced specimens for type species of genera in order to stabilize the understanding of each genus. In this way we are able to connect asexual and sexual genera

Table 1 Various treatments of Tubeufiaceae, Tubeufiales. A question mark (?) indicates that the position of the taxon is uncertain

Barr 1979	Barr 1980	Rossman 1987	Kirk et al. 2001	Lumbsch and Huhndorf 2010	Boonmee et al. 2011	In this study
Letendraea	Allonectria	Allonectria	Acanthophiobolus	Acanthostigma	Acanthostigma	Acanthohelicospora
Melioliphila	Boerlagiomyces	Boerlagiomyces	Acanthostigmella	Acanthophiobolus	Acanthophiobolus	Acanthophiobolus
Podonectria	Byssocallis	Byssocallis	Allonecte	Acanthostigmella	?Acanthostigmella	Acanthostigma
Rebentischia	Letendraea	Letendraea	Amphinectria	Allonecte	?Amphinectria	Acanthostigmina
Thaxteriella	Melioliphila	Malacaria	Boerlagiomyces	?Amphinectria	Aquaphila	Aquaphila
Tubeufia	Paranectriella	Melioliphila	Borinquenia	Boerlagiomyces	?Boerlagiomyces	Bifrontia
	Podonectria	Paranectriella	Byssocallis	Byssocallis	?Chaetocrea	?Boerlagiomyces
	Puttemansia	Podonectria	Chaetocrea	Chaetocrea	Chaetosphaerulina	Chlamydotubeufia
	Rebentischia	Puttemansia	Glaxoa	Chaetosphaerulina	?Glaxoa	Helicangiospora
	Tubeufia	Rebentischia	Letendraea	Glaxoa	Kamalomyces	Helicoma
		Tubeufia	Letendraeopsis	Letendraeopsis	?Malacaria	Helicomyces
		Uredinophila	Malacaria	Malacaria	?Melioliphila	Helicosporium
			Melioliphila	Melioliphila	?Paranectriella	Kamalomyces
			Paranectriella	Paranectriella	Podonectria	Neoacanthostigma
			Podonectria	Podonectria	?Puttemansia	Podonectria
			Puttemansia	Puttemansia	Rebentischia	Tamhinispora
			Rebentischia	Rebentischia	Thaxteriella	Thaxteriella
			Taphrophila	Taphrophila	Thaxteriellopsis	Thaxteriellopsis
			Thaxterina	Thaxteriella	Tubeufia	Tubeufia
			Tubeufia	?Thaxteriellopsis	?Uredinophila	
			Uredinophila	Thaxterina		
				Tubeufia		
				Uredinophila		

through molecular analysis and determine priorities for the linked genera.

## Materials and methods

## Examination of herbarium specimens

The generic types or authentic specimens of tubeufiaceous genera, namely *Acanthostigmella*, *Acanthostigmina*, *Bifrontia*, *Chaetocrea*, *Helicoma*, *Helicomyces*, *Helicosporium*, *Malacaria*, *Paranectriella*, *Puttemansia*, *Rebentischia*, *Thaxteriella*, *Tubeufia* and *Uredinophila* were obtained from the repositories of U. S. National Fungus Collections (BPI), Farlow Reference Library and Herbarium of Cryptogamic Botany in Harvard University (FH), Kew Royal Botanic Gardens (K), Natural History Museum, University of Oslo, Botanical Museum (O) and Naturhistorisches Museum Wien (W). Morphological features were examined and photomicrographs made using Carl Zeiss Microscopes, measurement confirmed using software of Micro Imaging GmbH. AxioVs40 V 4.8.2.0 (2006–2010).

## Fresh collections

Decaying wood samples were randomly collected from sampling sites in the forests of Chiang Mai and Chiang Rai provinces, northern Thailand. Samples were taken to the laboratory in Zip-lock plastic bags. The material was examined under a Motic SMZ 168 series microscope. Micromorphological structures were photographed using a Nikon ECLIPSE 80i compound microscope fitted with a Canon 450D digital camera and measurements made using Tarosoft (R) Image Frame Work program. Figures were processed with an Adobe Photoshop CS3 Extended version 10.0 (Adobe Systems Inc., USA). Type materials are deposited in the herbarium of Mae Fah Luang University (Herb. MFLU), Chiang Rai, Thailand, with isotypes in the New Zealand Fungal and Plant Disease Collection (PDD) and cultures in Mae Fah Luang University Culture Collection (MFLUCC), BIOTEC Culture Collection (BCC), Thailand and International Collection of Microorganisms from Plants (ICMP), New Zealand; some isolates are maintained in IFRD culture collection, International Fungal Research & Development Centre, Kunming, China, under the Material Transfer Agreement No. 4/2010 (MTA).

## Isolation of fungi

Single spore isolates were made on water agar (WA) or malt extract agar (MEA, Difco Laboratories, Detroit, Michigan, USA) and germinating spores were aseptically transferred to fresh MEA plates and incubated at 28 C for 7 days following the methods of Boonmee et al. (2011) and Chomnunti et al. (2011, 2014). Cultures were grown for 1–2 months and morphological characters such as colour, colony shape, and texture recorded. The cultures were checked for asexual states after 30–60 days of growth.

## DNA sequences

Genomic DNA was extracted from fungal mycelium grown on MEA at 28 C for 30 days. Four genes were amplified with universal primers, namely the internal transcribed spacer (ITS: ITS5/ITS4) region of ribosomal DNA, large subunit nuclear ribosomal DNA (LSU: LROR/LR5), small subunit nuclear ribosomal DNA (SSU: NS1/NS4) and the translation elongation factor-1 alpha (TEF1a: TEF1 983/2218R) (White et al. 1990; Vilgalys and Hester 1990; Schoch et al. 2009). The PCR products were purified and sequenced with the same primers.

#### Molecular data analyses

## Phylogenetic trees

BLAST search of new sequences were performed to verify the identities of species with sexual and asexual states, Tubeufiaceae in the GenBank database (Kodsueb et al. 2004; Tsui and Berbee 2006; Tsui et al. 2006; Promputha and Miller 2010; Boonmee et al. 2011; Sánchez et al. 2012). Details of sequences are provided in Supplementary Table 1. Two datasets were carried out for phylogenetic analyses of tubeufiaceous fungi. The first dataset aims to deal with the classification of Tubeufiales wihin Dothideomycetes (Chomnunti et al. 2012; Liu et al. 2012; Ariyawansa et al. 2013; Hyde et al. 2013; Pérez-Ortega et al. 2014), which used multi-gene LSU, SSU and TEF, comprising 141 taxa including the outgroup (Schismatomma decolorans (Turner & Borrer ex Sm.) Clauzade & Vězda DUKE 0047570, Arthoniomycetes). The second dataset focus on phylogenetic relationships within taxa of the Tubeufiaceae (Tsui et al. 2006; Promputtha and Miller 2010; Boonmee et al. 2011; Sánchez et al. 2012), focued by using the combination of LSU and ITS sequences, consisting of 68 taxa including the outgroup (Botryosphaeria dothidea (Moug.) Ces. & De Not. CBS115476, Botryosphaeriales). Sequences and alignments were prepared using BioEdit (Hall 1999). Alignment data were parsed with Gblocks (Castersana 2000) following the default setup. Phylogeny website tools "ALTER" (Glez-Peña et al. 2010) was used to transfer the alignment file for RAxML analysis. The reconstruction of the maximum likelihood (ML) analysis usingRAxML v. 7.2.8 (Stamatakis et al. 2008) as part of the "RAxML-HPC BlackBox on TG tool" performed at the

CIPRES Science Gateway v. 3.3 (http://www.phylo.org/ portal2/; Miller et al. 2010). All free model parameters will be estimated by RAxML and ML estimate of 25 per site rate categories. Final ML search were conducted under the GTRG AMMA model.

The Bayesian command was generated using FaBox 1.41 (Villesen 2007). To determine Bayesian posterior probability was performed using Old MrBayes 3.1.2 on XSEDE, parameters setting of 2 parallel runs, 4 chains, carried out for 4 000 000 generations, sample frequency every 1,000 generations, and all other parameters were left as default (Huelsenbeck and Ronquist 2001). The 50 % majority rule consensus tree was constructed from the remaining trees in Treeview (Page 1996).

## **Results and discussion**

#### Phylogenetic study

The phylogenetic tree was built from a multigene analyses of 140 taxa in of Dothideomycetes with Schismatomma decolorans (Arthoniomycetes) as the outgroup (Fig. 1). The dataset comprises 141 taxa, with 3,415 characters, 1,682 constant characters, 1,368 parsimony informative characters and 365 variable characters which are parsimony uninformative (TL=8531, CI=0.317, RI=0.646, RC=205, HI=683). Twenty orders are recognized in Dothideomycetes, and a distinct calde was formed, namely Tubeufiales, and has a close relationship with the order Patellariales and Botryosphaeriales, which shows the same phylogenetic relationships with the previous studies of Schoch et al. (2009) and Hyde et al. (2013). However, it is far removed from *Pleosporales* where the family *Tubeufiaceae* was previously assigned (Barr 1979). The recently introduced order Abrothallales (Perez-Ortega et al. 2014) was included in our analysis. Perez-Ortega et al. (2014) stated that Abrothallales formed a sister group of Jahnulales and close with Patellariales. In our phylogenetic analysis, Abrothallales formed a sister group with Lichenoconiales and is close to Jahnulales. However, it is not related to Patellariales which is always close with Tubeufiaceae.

The phylogenetic tree in Fig. 2 resulted from the molecular analysis of LSU and ITS combined data. The data setup consists of 67 taxa, with 1,096 characters, 777 characters are constant, 244 were parsimony informative and 75 variable characters were parsimony uninformative (TL=1091, CI= 0.420, RI=0.731, RC=0.307, HI=0.580). The taxa in the tree can be divided into 13 clades (namely A-M), each receiving moderate to strong statistical support and having representative sharing distinguished morphology (Fig. 2). Phylogenetic trees were drawed in Treeview (Page 1996) and MEGA 5 (Tamura et al. 2011).

Clade A is represented by taxa of Helicoma sensu stricto (86 % BS and 1.00 PP), which includes an authentic strain of the type species of Helicoma (H. muelleri Corda). Putatively named strains of Helicosporium linderi R.T. Moore (NBRC 9207), T. paludosa (P. Crouan & H. Crouan) Rossman (HKUCC 9118, ANM 196, ANM 1169) and Thaxteriella helicoma (W. Phillips & Plowr.) J.L. Crane, Shearer & M.E. Barr (JCM 2739, UBCF 13877) clustered in this clade and we recognize them in *Helicoma* in the phylogenetic tree (Fig. 2), but do not formally synonymize them as we have not seen voucher material. Helicoma rugosa asexual morphs formed in cultures of Thaxteriella helicoma (JCM 2739 and UBCF 13877). Tubeufia khunkornensis Boonmee & K.D. Hyde (MFLUCC 10-0119, ex-type strain), T. inthanonensis Boonmee & K.D. Hyde (MFLUCC 11-0003, ex-type strain) and T. miscanthi W.H. Hsieh, Chi Y. Chen & Sivan., epitypified here are synonymized under Helicoma. Helicoma chiangraiense, H. fagacearum and H. siamense formed distinct groups at the base of Clade A, and we therefore introduce them as new species of Helicoma.

Clade B is the genus *Thaxteriellopsis sensu stricto* represented by four stains of the type species *T. lignicola* Sivan., Panwar & S.J. Kaur, of which MFLUCC 10–0124 is the exeptiype.

Clade C represents the monotypic genus *Helicangiospora*, which is introduced in this study. Its morphology is similar with *Acanthostigma*, but it is phylogenetically distinct (Clade E). In addition, its asexual morph is unique in producing conidial helicospores borne in a capsule, which distinguishes this genus from all known genera of *Tubeufiaceae*.

Clade D is Helicosporium sensu stricto (84 % BS and 1.00 PP) represented by helicosporium-like taxa. The type species Helicosporium vegetum Nees is represented by four strains (NBRC 30345, CBS 941. 72, BCC 3332 and BCC 8125), however, these four strains did not cluster together. Strain CBS 941. 72 has been considered to be the authentic strain of H. vegetum, and at least two strains (BCC 3332 and BCC 8125) are probably not H. vegetum sensu stricto. Two strains of Tubeufia cerea (Berk. & M.A. Curtis) Höhn. (CBS 254.75 and NBRC 9014) also cluster with H. vegetum sensu stricto (99 % BS and 1.00 PP) and are thus synonymised. Helicosporium guianense Linder (CBS 269.52) also clusters with H. vegetum sensu stricto and is probably wrongly named. An ex-type strain of Acanthostigma patagonicum R.M. Sánchez, A.N. Mill. & Bianchin. (MVB 573 BBB) and Helicoma vaccinii Carris (CBS 216.90) clustered in this clade

Fig. 1 RAXML phylogenetic placement of the new order *Tubeufiales* and allied orders within the *Dothideomycetes*. RAXML bootstrap support values  $\geq$  50 % (BS) and Bayesian posterior probabilities  $\geq$  0.95 (PP) are shown at the nodes (values below these thresholds not shown). The tree was rooted with *Schismatomma decolorans* DUKE 0047570 (*Arthoniomycetes*). Ex-type strains are in *bold* 

а	Proma betae CBS 109410	
	1.00 Pleospora herbarum CBS 191.86	
	59 Cochliobolus heterostrophus CBS 134.39	
	1.00 Ophiosphaerella herpotricha CBS 620.86	
	1.00 Phaeosphaeria oryzae CBS 110110	
	<b>85</b> Entodesmium rude CBS 650.86	
	Dothidotthia aspera CPC 12933	
	1.00 Dothidotthia symphoricarpi CPC 12929	
	Leptosphaeria doliolum CBS 505.75	
	<i>Leptosphaeria dryadis</i> CBS 643.86	
	95 Phoma exigua CBS 431.74	
	76 <b>1.00</b> <i>Leptosphaerulina australis</i> CBS 317.83	
	Montagnula opulenta CBS 168.34	
	66 Bimuria novae-zelandiae CBS 107.79	Pleosporales
	66 Massarina eburnea CBS 473.64	·····
	69 Bambusicola bambusae MFLUCC 11-0614	
	Trematosphaeria pertusa CBS 122371	
	<sup>98</sup> <i>Lentithecium aquaticum</i> CBS 123099	
	Morosphaeria ramunculicola JK 5304B	
	87 Lophiostoma scabridisporum BCC 22835	
	63 1.00 Lophiostoma quadrinucleatum GKM 1233	
	Melanomma pulvis-pyrius CBS 124080	
	91 Amniculicola parva CBS 123092	
	<b>85</b> 1.00 Amniculicola immersa CBS 123083	
	<b>0.99</b> Lindgomyces ingoldianus ATCC 200398	
	93 Neoastrosphaeriella krabiensis MFLUCC 11-0025	
	1.00 Aigialus grandis BCC 18419	
	64 97 Psiloglonium araucanum CBS 112412	
	89 Hysterium angustatum CBS 236.34	
	61 0.97 Psiloalonium simulans CBS 206.34	Hysteriales
	100 Hysterobrevium smilacis CBS 114601	
	B5 Gloniopsis subrugosa CBS 123346	
	Glonium stellatum CBS 207.34	
	$^{81}$	
	1.00 tor Mytilinidion mytilinellum CBS 303.34	Mytilinialaies
	1.00 Mytilinidion acicola FB 0349	
	100 Uwehraunia commune CBS 132091	
	$\frac{100}{100}$ Bamichloridium aniculatum CBS 156.59	
	0.99 100 Dissoconium aciculare CBS 204.89	
	0 99	
	86 1.00 Mycocnhaerella graminicola CBS 202 38	
	0.99 Catanulostroma abiatic CBS 459 93	Cannodiales
		capitoulaies
	75 Cooring anonging CBC 225 22	
	0.99 Scorias sportylosa CBS 323.33	
	100 Laptour Concere CBS 147.52	
	Leploxypinium furnayo CBS 123.20	
	55 1.00 Cladosportum nerbarum cls 399.80	
	100 Minimative biopeniaum CBC 247 22	
		Myriangiales
	0.99 <u>12</u> <u>96</u> Elsinoe phaseoli CBS 165.31	
	Elsinoe centrolobi CBS 222.50	
	100 Los Dothidos himonhago CPS 100 50	
	1.00 1.00 Dethides inexplots CBS 188.58	Dathidaalaa
<u>97</u>		Dotniaeales
1.00	100 Dotniora ellyptica CBS 736./1	
	Dotniora cannabinae CBS 737.71	
	<b>93</b> Lichenothelia cf. calcarea L1323	
	82 Lichenothelia cf. calcarea L1324	Lichanothalialac
	Lichenothelia convexa L1609	LICHENOLITEIIAIES
	Lichenothelia convexa L1608	
	Anisomeridium ubianum 94	Monohlastiales
	Megalotremis verrucosa 104	, ionobiastares
	84 Botryobambusa fusicoccum MFLUCC 11-0143	
	Lasiodiplodia theobromae CBS 164.96	
	Cophinforma eucalypti MFLUCC 11-0425	
97	99 Botryosphaeria dothidea CBS 115476	
1.00	Botryosphaeria agaves MFLUCC 11-0125	
93	Kellermania macrospora CBS 131716	Botryosphaeriales
1.00	Kellermania yuccigena CBS 131727	
	60 Guignardia bidwellii CBS 237.48	
	Guignardia gaultheriae CBS 447.70	
	93 Guignardia citricarpa CBS 102374	
	68 Melanops tulasnei CBS 116805	
	Aplosporella prunicola STE-U 6326	
	✓ Saccharata proteae CBS 115206	



and we therefore rename them as *Helicosporium* in the phylogenetic tree (Fig. 2). We do not formally synonymize them as the basal grouping of these two species in this Clade is variable and the morphology differs.

Clade E represents *Acanthostigma sensu stricto* with three taxa, including the type species *A. perpusillum* De Not. This clade always clustered together with *Helicosporium sensu stricto*, and the position is stable in indivual gene analysis (data not shown).

Clade F with seven taxa represents *Tubeufia sensu stricto* which is the type genus of *Tubeufiaceae*. The type species, *T. javanica* Penz. & Sacc. is epitypified and a new species *T. chiangmaiensis* is introduced in this study. With the exception of *T. cylindrothecia* (Seaver) Höhn. (BCC 3559), the other four taxa from the study of Tsui et al. (2006) were identified as species of *Helicomyces* and *Helicoma*. In our phylogenetic analysis, these strains clustered together and formed a distinct clade, therefore, we rename them as *Tubeufia* species in the phylogenetic tree (Fig. 2), but do not formally synonymize them as we have not seen voucher material. The morphology of *Tubeufia sensu stricto* are detailed based on *T. javanica* and *T. chiangmaiensis*.

Clade G (*Helicomyces sensu stricto*) is phylogenetically close to the *Tubeufia sensu stricto* clade and is represented by an authentic strain of the type species, *H. roseus* Link (CBS 283.51), plus two cultures of *Tubeufia paludosa* (CBS 120503, epitypified herein). *Tubeufia paludosa* is also synonymised under *Helicomyces*. The putatively named strains of *Helicosporium indicum* P.Rag. Rao & D. Rao (CBS 374.93) and *H. talbotii* Goos (MUCL 33010) also cluster with *Helicomyces sensu stricto*. These are renamed as *Helicomyces* species in the phylogenetic tree (Fig. 2), but they are not formally synonymized as we have not seen voucher material.

Clade H represents the monotypic genus *Tamhinispora*, which was introduced by Rajeshkumar and Sharma (2013). Its morphology is similar with *Chlamydotubeufia*, but differs by its ovoid, dictyoseptate conidia with apical appendages. This genus is the second group of *Tubeufiales* known only from freshwater, and the other one is *Aquaphila*. They differ as *Aquaphila* produces sickle-shaped conidia, while *Tamhinispora* has ovoid, dictyoseptate conidia with apical appendages. The sexual morph of *Tamhinispora* is unknown.

Clade I represents the genus *Chlamydotubeufia* incuding three species, which form a well-supported clade (85 % BS and 1.00 PP). Both asexual and sexual morphs occur in this genus, and it is a well-defined genus. *Chlamydotubeufia chlamydosporum* (Shearer) Boonmee & K.D. Hyde and *C. huaikangplaensis* Boonmee & K.D. Hyde cluster with 100 % BS and 1.00 PP but we do not synonymise them here as the tree is not well-populated and it is not clear that are morphologically identical (Shearer 1987; Boonmee et al. 2011). Clade J represents the freshwater genus *Aquaphila sensu stricto*. The type species *A. albicans* Goh, K.D. Hyde & W.H. Ho and its tubeufia-like sexual state (*Tubeufia asiana* Sivichai & K.M. Tsui) formed a well-supported clade and has a close relationship with *Chlamydotubeufia*. Based on our phylogenetic analysis, we synonymize *Tubeufia asiana* under *Aquaphila albicans*.

Clade K represents the new genus *Acanthohelicospora* with *A. pinicola* as the type species. Three species with two strains from *Acanthostigma* and two species from *Helicosporium* are renamed *Acanthohelicospora* in Fig. 2 based on both morphological and phylogenetic studies. However, as these are not ex-type strains they are not formally transferred. This genus produces a unique helicosporous asexual state that distinguishes it from other genera in *Tubeufiaceae*.

Clade L represents *Acanthostigmina sensu stricto* with three strains of the type species *A. minuta* (Fuckel) Clem. & Shear and two strains of *Acanthostigma multiseptatum* Promp. & A.N. Mill. There are no ex-type strains *A. minuta*. We synonymize *Acanthostigma multiseptatum* (one ex-type strain) under *Acanthostigmina* based on the phylogenetic result.

Clade M is basal in *Tubeufiaceae* and represents the new genus *Neoacanthostigma* with *N. fusiforme* as the type species. All the three species are represented by ex-type strains. The species *N. septoconstrictum* and *N. filiforme* were previously named *Acanthostigma*, however, their morphological characters, such as the asci and ascospores, differ from these genera. Thus they are synonymized under *Neoacanthostigma* here.

## Taxonomy

# *Tubeufiales* S. Boonmee & K.D. Hyde, ord. nov., *Index Fungorum number*: IF 550704, *Facesoffunginumber*: FoF 00203

Saprobic, common on decorticated or decaying woody and herbaceous substrates, often associated with decaying fungi, less common on leaves, terrestrial and aquatic habitats, widespread in temperate to tropical regions. Sexual state: Ascomata completely superficial, seated on a subiculum, unilocular, globose-subglobose or clavate to obovate, soft-textured, solitary to gregarious, partially grouped, translucent or not, pale brown, brown to black, minutely papillate and with ostiolar, collapsing cupulate, laterally or not when dry, with radiating mycelium or appendages at base, with or without setose or hairy appendages. Peridium somewhat thickened, mostly composed of cells of textura angularis, thick-walled cells, pale yellow, brown, dark brown to black externally, with thin layers of textura prismatica inwardly, cells narrow, slightly elongate, hyaline, pale brown to brown. Hamathecium comprising numerous filiform, septate, branched, sometimes



Fig. 2 Phylogenetic representation of *Tubeufiaceae* and its members. The tree is rooted with Botryosphaeria dothidea CBS115476 (Botryosphaeriales). RAxML bootstrap support values≥70 % (BS) and Bayesian posterior probabilities  $\geq 0.95$  (PP) are shown at the nodes and bold (values below these thresholds not shown). Ex-type strains are in bold. The type species of each genus is in blue. Thick lines on branches determine clades that are resolved in the RAxML consensus

anastomosing, hyaline pseudoparaphyses, embedded in a gelatinous matrix. Asci 8-spored, bitunicate, fissitunicate, saccate or cylindrical-clavate, sometimes broadly oblongsubclavate, with or without an apically rounded, distinct ocular chamber, with or without a distinct pedicel. Ascospores 2-3-seriate to fasciculate in ascus, elongate, cylindricsubfusiform to narrowly oblong, tapering towards narrow, subacute ends, distinctly multiseptate, hyaline to pale brown, smooth or minutely verrucose. Asexual states: hyphomycetous; helicosporous, chlamydosporous and phragmosporous. Conidiophores mononematous, macro- to micronematous, erect, flexuous, septate, pale brown, brown to dark brown. Conidiogenous cells holoblastic, mono- or polyblastic, integrated or discrete, terminal or intercalary. Conidia usually elongate, filiform to fusiform, curved, helicoid with varying number of coils, septate, sometimes dictyosporous, phragmosporous, hyaline to variously coloured, smooth-walled to verrucose.

Ordinal type: Tubeufiaceae M.E. Barr, Mycologia 71: 948 (1979), Facesoffunginumber: FoF 00204

Monotypic, characters same as for Tubeufiales.

Family type: Tubeufia Penz. & Sacc.

*Notes*: Below we list the genera accepted in the Tubeufiaceae. Acceptance is based on morphological characteristics and/ or molecular data. Generic names based on sexual or asexual types are treated equally.

#### Key to genera of Tubeufiaceae

1
1. Ascomata lacking 0.15
2. Ascomata with setose appendages or flexuous hyphae,
seated directly on substrate 0.3
2. Ascomata without appendages, seated on a basal
subiculum
3. Asexual state known in culture 0.4
3. Asexual state not known 0.7
4. Conidia dictyochlamydosporous, black Chlamydotubeufia
4. Conidia helicosporous, hyaline to pale brown $\ldots \ldots 0.5$
5. Conidia born in sheath, helicoma-like Helicangiospora
, 8 I
5. Conidia born on hyphae, helicosporium-like 0.6
<ul><li>5. Conidia born on hyphae, helicosporium-like 0.6</li><li>6. Conidiophores mononematous Acanthohelicospora</li></ul>
<ul> <li>5. Conidia born on hyphae, helicosporium-like 0.6</li> <li>6. Conidiophores mononematous Acanthohelicospora</li> <li>6. Conidiophores micronematous Neoacanthostigma</li> </ul>
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<ul> <li>5. Conidia born on hyphae, helicosporium-like 0.6</li> <li>6. Conidiophores mononematous Acanthohelicospora</li> <li>6. Conidiophores micronematous Neoacanthostigma</li> <li>7. Ascospores filiform, spiral in asci Acanthophiobolus</li> <li>7. Ascospores fusiform, clavate-fusiform, cylindric-fusoid, 2–</li> </ul>

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8. Ascospores muritorin, dictyoseptate <i>boeriugiomyces</i>
8. Ascospores phragmosporous, trans-septate 0.9
9. Ascospores greater than 30-septate Kamalomyces
9. Ascospores less than 30-septate 0.10
10. Ascospores equally 5-septate <i>Thaxteriellopsis</i>
10. Ascospores greater than 5-septate0.11
11. Ascomata greater than $200 \mu m$ diam; ascospores hyaline
to pale brown Acanthostigmina
11. Ascomata less than $200\mu m$ diam; ascospores hya-
line
12. Ascomata on scale insects Podonectria
12. Ascomata on decaying or rotting wood0.1312
13. Ascospores allantoid or vermiform, equally 7-
septate
13. Ascospores elongated cylindrical-subfusiform, greater
than 7-septate
14. Ascomata pale vellow to pale brown; with numerous
pseudoparaphyses Iubeufia
14. Ascomata dark brown to black: lacking
14. Ascomata dark brown to black; lacking pseudoparaphyses
<ul> <li>14. Ascomata dark brown to black; lacking pseudoparaphyses</li></ul>
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pseudoparaphyses <i>Iubeujia</i> 14. Ascomata dark brown to black; lacking pseudoparaphyses <i>Bifrontia</i> 15. Conidia dictyosporous, apically appendaged, heavily pigmented <i>Bifrontia</i> 15. Conidia phragmosporous, helicosporous, light pigmented <i>Conidia</i> 16. Conidia fusoid to sickle-shaped, slightly curved, always aquatic       0.16         16. Conidia coiled, aquatic or terrestrial       0.17         17. Conidiophores absent; conidia borne directly on hyphae       0.18         18. Conidia coiled 1–1½ times; conidial filament greater than 6µm wide       0.18
<ul> <li>14. As comata dark brown to black; lacking pseudoparaphyses</li></ul>

## Accepted genera

Tubeufia Penz. & Sacc., Malpighia 11(11-12): 517 (1898), Facesoffunginumber: FoF 00063

Saprobic on decorticated or decaying woody and herbaceous substrates, often associated with other fungi, in terrestrial habitats, widespread in temperate to tropical regions. Sexual state: Ascomata superficial, seated on a subiculum, spherical to clavate-obovate, oval to ellipsoid, bright to yellowish-brown when young, brown to dark brown when mature or dry, apex rounded, narrow at base, darkly pigmented, occasionally collapsing when dry. Peridium comprising pale brown cells of textura angularis, and small textura prismatica subhyaline cells at innermost layers. Hamathecium comprising numerous filiform, septate, branched, hyaline pseudoparaphyses. Asci 8-spored, bitunicate, fissitunicate, saccate or cylindric-clavate, with or without an ocular chamber. Ascospores fasciculate in ascus, elongate cylindric-subfusiform or narrowly oblong, greater than 5-septate, not constricted at septa, hyaline to pale brown, smooth-walled. Asexual state: hyphomycetous, helicosporous.

## Type species: Tubeufia javanica Penz. & Sacc.

Notes: Tubeufia sensu stricto (Clade F, Fig. 2) comprises species related to T. javanica having light-coloured, superficial, smooth-walled ascomata and hyaline to pale brown, elongate cylindric-subfusiform or narrowly oblong ascospores. In this paper, we describe, illustrate and designate an epitype specimen for T. javanica (MFLUCC 12-0545), and introduce T. chiangmaiensis as a new species. By designating an epitype with sequence data we aim to stabilize the genus so that related species and asexual states can be placed in this genus. The asexual morphs of Tubeufia sensu stricto are helicosporous as four species with helicomyces-like and helicoma-like conidia cluster in Clade G, i.e. Tubeufia cylindrothecia, T. intermedium, T. lilliputeus, T. roseus and T. talbotii. However, we could not examine the characters of these strains deposited in GenBank and thus do not formally synonymize them. With the introduction of one new species below, Tubeufia sensu stricto presently comprises only two species and several putatively named strains in GenBank.

*Tubeufia javanica* Penz. & Sacc., Malpighia 11(11–12): 517 (1898), *Facesoffunginumber:* FoF 00063 Fig. 3

*Holotype*: INDONESIA, Java, Tjibodas, on withered culm of *Bambusa emarcidis*, 2 Mar 1987 (PAD)

Epitype designated here: MFLU 13-0371

Saprobic on culms or sheaths of bamboo. Sexual state: Ascomata 376–505(-550) µm high×(200-)224–260(-280)  $\mu m$  diam., superficial, seated on a subiculum, solitary, sometimes gregarious, oblong, subclavate to obclavate, creamwhite to yellowish when young, pale brown to brown when mature, apex rounded, base narrow, brown to dark brown, collapsing when dry, compressed subiculum hyphae, 2.5- $5\,\mu m$  wide, partially branched, septate, dark brown, and irregular. Peridium  $15-25 \,\mu m$  wide, comprising light brown cells of textura angularis, and small textura prismatica subhyaline cells inwardly. Hamathecium comprising numerous,  $1-2 \mu m$ wide, filiform, septate, branched, hyaline pseudoparaphyses. Asci  $(140-)164-221(-230) \times 14-18(-22) \ \mu m$  $(\bar{x}=194 \times 16 \mu m, n=20)$ , 8-spored, bitunicate, fissitunicate, cylindrical, short pedicellate, apically rounded, with an ocular chamber. Ascospores (95-)100.5-117(-120)×4-5 µm  $(\bar{x}=109 \times 4.5 \mu m, n=20)$ , fasciculate, broad filiform, cylindrical to long subfusiform, elongate, ends rounded, 14-17septate, not constricted at septa, hyaline to pale yellow or brown, smooth-walled. Asexual state: Unknown.

*Cultural characteristics*: Ascospores germinating on PDA within 24 h and germ tubes produced from both ends. Colonies growing slowly on PDA, reaching 4.5 mm in 2 weeks at 28 C, effuse, velvety to hairy, edge fimbriate, olive to olive brown, dark brown in PDA media. *Mycelium* superficial and partially

**Fig. 3** *Tubeufia javanica* (MFLU 13–0371, **epitype**). **a**, **b** Ascomata formed on natural substrate. **c** Close up of pale reddish-brown ostiole. **d** Side view of ascoma located on a subiculum. **e** L.S. of ascoma. **f** Peridium. **g** Pseudoparaphyses. **h**–**j** Asci. **k** Ruptered ascus. **I–o** Ascospores. **p** Germinating ascospore. **q** Dark brown colonies on PDA. **r**, **s** Growth on plant substrates and aerial hyphae in culture. *Scale bars*: **a** =  $500 \mu m$ , **b**–**c** =  $200 \mu m$ , **d**–**e**, **h**–**k** =  $100 \mu m$ , **f** =  $40 \mu m$ , **e** =  $5 \mu m$ , **I–p** = 50, **q**–**r** = 10 mm, **s** =  $20 \mu m$ 

immersed, branched, septate, pale brown to olivaceous brown, smooth, asexual spores not formed within 60 days.

*Material examined*: THAILAND, Chiang Rai, Muang, Khun Korn Waterfall, on dead culm of bamboo Kunth ex Dumort (*Poaceae*), 31 July 2012, Dong-Qin Dai, DDQ00239 (MFLU 13–0371, **epitype of** *Tubeufia javanica* **designated here**; PDD 104450, **iso-epitype**), ex-type living culture = MFLUCC 12–0545 = ICMP 20067; Chiang Rai, Muang, Khun Korn Waterfall, on dead culm-sheath of bamboo, 21 July 2013, S. Boonmee KK-11 (MFLU 14–0222), living culture = MFLUCC 14–0438.

*Notes*: We requested the type speciman from PAD and BO but this is not present in either herbarium and therefore must be presumed lost. We therefore designate our fresh collection as epitype to stabilize applications of the genus and species. The epitype is representative of the iconotype and description provided in the protologue, and the location in Asia and bamboo host are also appropriate for epitypification (Penzig and Saccardo 1904; Boonmee et al. 2011).

*Tubeufia chiangmaiensis* S. Boonmee & K.D. Hyde, sp. nov. *Index Fungorum number*: IF 550705, *Facesoffunginumber*: FoF 00172 Fig. 4

*Etymology*: named after Chiang Mai, the location where it was collected.

Holotype: MFLU 11-1149

Saprobic on dead wood. Sexual state: Ascomata  $(200-)238-324 \,\mu m$  high×(180-) 227-269  $\mu m$  diam.  $(\bar{x}=266\times 228\mu m)$ , superficial, solitary, scattered, globosesubglobose to ovate, dark brown, with hyphae developing from ascomatal base onto substrate, slightly flat at the apex, brown to dark brown, ostiolate, collapsing when dry. Peridium 25–29 $\mu$ m wide, comprising 4–5 layers of brown to reddish-brown cells of textura angularis, and small, subhyaline to light brown cells of textura prismatica inwardly. Hamathecium comprising numerous, ca.  $1-1.5 \mu m$  wide, filiform, septate, branched, hyaline pseudoparaphyses. Asci (114.5) (114.5)  $(1120-137\times11-14(-16) \mu m (\bar{x}=127\times13\mu m, n=20),$ 8-spored, bitunicate, fissitunicate, elongate cylindrical to slightly clavate, apedicellate, thick-walled, rounded at apex, with an ocular chamber, tapering towards narrow base, sessile. Ascospores  $46-53(-55.5)\times(3.5-)4-4.5\,\mu m$  $(\bar{x}=50\times4\mu m, n=20)$ , overlapping 2–3-seriate, cylindricfusiform, tapering toward ends, with pad-like mucilage at both ends, straight to slightly curved, 7-septate, not constricted at





**Fig. 4** *Tubeufia chiangmaiensis* (MFLU 11–1149, holotype). a Ascomata on substrate. b L.S. of ascoma. c Peridium. d Hamathecium and pseudoparaphyses. e–g Asci. h–j Ascospores with mucilaginous pad-like appendage at both ends, marked by *arrows*. k Germinating

septum, hyaline, pale brown when mature, smooth-walled. Asexual state: Unknown.

*Cultural characteristics*: Ascospores germinating on MEA within 12 h and germ tubes produced from both ends. *Colonies* growing on MEA, reaching 5 mm in 7 days at 28 C, mycelium partly superficial, partly immersed, slightly effuse, radially striate, with fimbriate edge, dark-coloured; asexual spores not formed within 60 days.

ascospore. **l**, **m** Colonies on MEA from surface and reverse. Note dark brown colonies. *Scale bars*:  $\mathbf{a}-\mathbf{b} = 100 \,\mu m$ ,  $\mathbf{c}$ ,  $\mathbf{h}-\mathbf{k} = 30 \,\text{mm}$ ,  $\mathbf{d} = 5 \,\mu m$ ,  $\mathbf{e}-\mathbf{g} = 50 \,\mu m$ ,  $\mathbf{l}-\mathbf{m} = 10 \,\text{mm}$ 

*Material examined*: THAILAND, Chiang Mai, Mae Taeng, Mushroom Research Center, N19°17.123' E 98°44.009', elev. *ca.* 900 msl., on dead wood of an unidentified tree, 23 June 2011, Saranyaphat Boonmee MRC-06 (MFLU 11–1149, **holotype**); ex-type living cultures = MFLUCC 11–0514 = BCC 52386 = ICMP 20074.

Notes: Tubeufia chiangmaiensis has morphological characters typical of the genus, such as brown, globosesubglobose ascomata with basal mycelium, which darken when dry, fissitunicate, elongated, cylindrical-clavate asci, and cylindrical-fusiform, 7-transeptate, hyaline to pale brown ascospores, with pad-like mucilage at both ends. *Tubeufia cylindrothecia* has oblong translucent peridial ascomata, ascospores lack mucilaginous pad-like appendages and are smaller when compared to *Tubeufia chiangmaiensis* (Seaver 1909). *Tubeufia chiangmaiensis* differs from *T. javanica* in ascomatal and ascospore features (Penzig and Saccardo 1904; Rossman 1977; Sivanesan 1984, Fig. 3). Combined molecular analysis of LSU and ITS genes places *T. chiangmaiensis* and *T. cylindrothecia* (BCC 3559) within *Tubeufia sensu stricto* (Clade F) with strong support (100 % BS and 1.00 PP, Fig. 2). **Other accepted genera** 

*Acanthohelicospora* Boonmee & K.D. Hyde gen. nov., *Index Fungorum number*: IF 550572, *Facesoffunginumber*: FoF 00206

*Etymology*: From 'acantho' referring to the sexual morph having setae and 'helicospora' referring to the helicosporous conidia of the asexual morph.

Saprobic on dead wood. Sexual state: Ascomata superficial, solitary, scattered, globose to subglobose, black, ostiolate, surrounded with black setae that taper to an acute apex. Peridium composed of several layers, with outer layer of cells compressed and black, with inner layer comprising brown cells of textura angularis. Hamathecium comprising numerous, filiform, septate, branched, hyaline pseudoparaphyses. Asci 8-spored, bitunicate, cylindrical, pedicellate, with thick, rounded apex, lacking an ocular chamber. Ascospores overlapping fasciculate, long fusiform-cylindrical, straight to slightly curved, greater than 7-septate, not constricted at any septum, hyaline, smooth-walled. Asexual state: hyphomycetous, helicosporous, helicomyces-like. Conidiophores mononematous, erect, pale brown to brown, smooth-walled. Conidiogenous cells holoblastic, terminal or intercalary, dentate, smooth, with a thickened and truncate conidiogenous loci. Conidia helicosporous, with wide filaments, coiled, curved, elongated, tapering to narrowly rounded ends, multiseptate, not constricted at septum, hyaline, guttulate, smooth-walled.

*Type species: Acanthohelicospora pinicola* Boonmee & K.D. Hyde

*Notes*: The genus *Acanthohelicosporium* has welldeveloped spectacular setae on the ascomata, cylindrical asci and oblong ascospores. The asexual state of *Acanthohelicospora pinicola* developed in culture and appears similar to *Helicosporium*, except that the conidiophores are micronematous and not setiferous as in the former (Ellis 1971; Seifert et al. 2011). Thus, the monotypic genus *Acanthohelicospora* is typified by *A. pinicola* which differs from all hitherto described species of *Acanthostigma* and *Acanthostigmina* (Réblová and Barr 2000; Kodsueb et al. 2004; Promputtha and Miller 2010; Sánchez and Bianchinotti 2010; Sánchez et al. 2012). Acanthostigma scopulum Peck and Acanthohelicospora pinicola share some morphological features (Réblová and Barr 2000; Kodsueb et al. 2004; Promputtha and Miller 2010), however, they differ in the dimensions of the ascomata, asci and ascospores including the number of septa. Acanthohelicospora pinicola groups with an asexual species named Helicosporium guianense Linder with high support (96 % BS and 0.99 PP), in a sister group to Acanthostigma scopulum and Helicosporium aureum (Corda) Linder with 83 % BS support (Clade K, Fig. 2). Putatively named strains of Acanthostigma scopulum, A. aureum and A. guianense in GenBank are here renamed as Acanthohelicospora in the phylogenetic tree (Fig. 2), but are not formally synomymised as these are not ex-type strains and their characters are unknown.

*Acanthohelicospora pinicola* Boonmee & K.D. Hyde, sp. nov., *Index Fungorum number*: IF 550573, *Facesoffunginumber*: FoF 00173 Figs. 5–6

Etymology: Epithet named for the host, Pinus.

Holotype: MFLU 10–0049

Saprobic on dead wood of Pinus. Sexual state: Ascomata  $116-148 \,\mu m \text{ high} \times 108-138 \,\mu m \text{ diam.}$  ( $\overline{x}= 129.5 \times 122 \,\mu m$ ), superficial, solitary, scattered, globose to subglobose, black, ostiolate, surrounded by  $39-72 \times 5-7.5 \,\mu m$ , black setae which taper to an acute apex. Peridium 12-18.5 µm wide, composed of several layers, outer layer of compressed and black-walled cells, inner layer comprising brown-walled cells of textura angularis. Hamathecium comprising numerous, ca. 2 µm wide, filiform, septate, branched, hyaline pseudoparaphyses. Asci  $131.5 - 183 \times 14 - 18 \,\mu m$  ( $\overline{x} = 150 \times 16 \,\mu m$ ), 8-spored, bitunicate, cylindrical, pedicellate, with thick and rounded apex, lacking an ocular chamber. Ascospores 41.5-57×3- $4\mu m$  ( $\bar{x}=50.5\times 3\mu m$ ), overlapping fasciculate, long fusiform-cylindrical, straight to slightly curved, 7-8(-9)-septate, not constricted at any septum, hyaline, smooth-walled. Asexual state: hyphomycetous, helicosporous. Conidiophores mononematous, erect,  $3-5 \mu m \log \times 2-4 \mu m$  wide, pale brown to brown, smooth-walled. Conidiogenous cells holoblastic, terminal or intercalary, dentate, smooth, with a thickened and truncate conidiogenous loci. Conidia helicosporous,  $(53-)65-92(-99) \ \mu m \ \log \times 16-20(-25)$  $\mu m$  diam., filaments  $2\mu m$  wide, when coiled, curved and coiled in 1-2 dimension, elongate, tapering to narrowly rounded ends, multiseptate, not constricted at the septum, hyaline, guttulate, smooth-walled.

*Cultural characteristics*: Ascospores germinating on MEA within 12 h and germ tubes produced at both ends. *Colonies* slow growing on MEA, reaching less than 5 mm in 7 days at 28 C, slightly convex, undulating to raised, dentate, with slightly radial striations and lobate edges, brown. Asexual state produced in culture. *Mycelium* superficial, composed of branched, septate, smooth, hyaline, pale brown to brown hyphae.



Fig. 5 Acanthohelicospora pinicola (MFLU 10–0049, holotype). a Superficial ascomata on substrate. Note ascomata surrounded by *black setae*. b L.S. of ascoma. c Peridium with *dark setae*. d Single seta. e

Pseudoparaphyses. f, g Asci. h–m Ascospores. Scale bars:  $\mathbf{a}$ – $\mathbf{b}$  = 100  $\mu m$ , c–d, h–m = 20  $\mu m$ , e = 5  $\mu m$ , f–g = 50  $\mu m$ 



Fig. 6 *Acanthohelicospora pinicola* (MFLU 10–0049, holotype). Colonies and asexual state on MEA culture. **a** Germinating ascospore. **b**, **c** Colonies on MEA from surface and reverse. Note dark brown colonies. **d** 

Arial mycelium on culture. e-g Conidiophores developing on hyphae. h Conidiogenous cells. i-l Conidia. *Scale bars*:  $\mathbf{a}-\mathbf{c} = 10 \text{ mm}, \mathbf{d}-\mathbf{i} = 5 \mu m$ ,  $\mathbf{e}-\mathbf{l} = 10 \mu m$ 

*Material examined*: THAILAND, Chiang Rai, Muang, Doi Tung, elev. *ca.* 1,509 mls., on dead wood of *Pinus* L. (*Pinaceae*), 6 November 2009, Saranyaphat Boonmee DT-06 (MFLU 10–0049, **holotype** = PDD 104451, **isotype**), extype cultures = MFLUCC 10–0116 = BCC 52036 = IFRD 2196.

Acanthophiobolus Berl., Atti Congl. Bot. Intern. Di Genova, 1892: 571 (1893) [1892]

Saprobic on cloth. Sexual state: Ascomata superficial, globose to subglobose, reddish-brown to dark brown, ostiole central, with red brown to dark brown setae, setae septate, tapering towards apex. Peridium comprising several-layers; inner layer composed of textura prismatica-porrecta and hyaline to pale, outer layer composed of 2–3 layers of dark brown cells of textura angularis. Hamathecium comprising filiform pseudoparaphyses. Asci 8-spored, bitunicate, elongate, cylindro-clavate, short pedicellate. Ascospores spirally

arranged in ascus, filiform, septate, hyaline (from Boonmee et al. 2011). Asexual state: Unknown.

*Notes*: This monotypic genus for which no molecular data are available was illustrated in Boonmee et al. (2011). The genus differs from *Acanthostigma* morphologically. The ascomata of *Acanthophiobolus* are bright coloured with much longer setae, and the asci are elongate-cylindrical with long filiform, trans-septate ascospores. We therefore maintain *Acanthophiobolus* as a distinct genus in *Tubeufiaceae*.

*Type species: Acanthophiobolus helminthosporus* (Rehm) Berl., Die Pilze des Weinstockes, Vienna: 571 (1893) [1892]

Acanthostigma De Not., Sfer. Ital., 85 (1863)

*Saprobic* on dead wood. **Sexual state**: *Ascomata* superficial, scattered, globose to subglobose, mostly dark brown to black, occasionally collapsing when dry, with distinct dark setae, ostiolate. *Peridium* consisting of several-layers of

*textura angularis. Hamathecium* with numerous, cellular, branching and anastomosing pseudoparaphyses. *Asci* 8-spored, bitunicate, fissitunicate, clavate, short pedicellate, broadly rounded and thickened at apex. *Ascospores* overlapping 2–3-seriate, fusiform, narrowly rounded at both ends, with one of middle cells often broader than others, tapering towards the ends, trans-septate, straight or slightly curved, not-constricted or slightly constricted at septa, mostly hyaline, guttulate when immature, smooth-walled. **Asexual state**: Chlamydospores only known from culture (from Boonmee et al. 2011).

*Notes*: Acanthostigma sensu stricto is based on Acanthostigma perpusillum and the description given by de Notaris (1863). Réblová and Barr (2000) monographed and accepted six species in Acanthostigma. Morphologically all species are characterised by dark brown to black ascomata covered by dark setae; ascospores are usually broadly fusiform to clavate, asymmetrical, trans-septate and hyaline. The multigene phylogenetic analysis indicates that several Acanthostigma epithets are polyphyletic and belong within the Tubeufiaceae (Promputtha and Miller 2010; Boonmee et al. 2011; Sánchez et al. 2012).

The type species A. perpusillum was described and illustrated in Boonmee et al. (2011), while a new species, A. chiangmaiensis Boonmee & K.D. Hyde, was also introduced. Other species previously regarded as Acanthostigma (e.g. Acanthostigma filiforme Promp. & A.N. Mill., A. minutum (Fuckel) Sacc.) are scattered in the phylogenetic tree, indicating that ascomata with setae have evolved on more than one occasion and is not a reliable character for determining genera in this family. We searched for herbarium specimens of Acanthostigma perpusillum from several herbaria (e.g. GE, PAD, RO and TO), but none are available for study. Réblová and Barr (2000) reexamined, described and illustrated this species and Boonmee et al. (2011) made drawings of the taxon based on Réblová and Barr (2000). The species has brown opaque, short setae on reddish-brown to dark brown ascomata. In this paper we treat Acanthostigma perpusillum strain UAMH 7237 as an authentic specimen to represent Acanthostigma sensu stricto. Molecular analysis indicat that A. perpusillum and A. chiangmaiensis has moderate support (72 % BS) in Clade E (Fig. 2). A putative strain of A. minutum (MVB 781 (BBB), Argentina, Sánchez et al. 2012) forms a long subbranch with A. perpusillum and A. chiangmaiensis but with weak support. Therefore, two species A. chiangmaiensis and A. minutum are accepted in the genus based on phylogeny (Fig. 2). Helicosporium sensu stricto forms a sister clade (Clade D). No asexual state has been reported for Acanthostigma perpusillum, however, A. chiangmaiensis formed chlamydospores in culture. Additionally A. filiforme Promp. & A.N. Mill. and A. septoconstrictum Promp. & A.N. Mill. and A. multiseptatum described in Promputtha and Miller (2010)

are transferred to *Neoacanthostigma* and *Acanthostigmiana* respectively based on morphology and molecular data.

*Type species: Acanthostigma perpusillum* de Not., Sfer. Ital.: 207 (1863)

Acanthostigmina Höhn., Sber. Akad. Wiss. Wien, Math.naturw. Kl., Abt. 1 118: 1499 [39 repr.] (1909), Facesoffunginumber: FoF 00207

Saprobic on rotten wood, widespread in tropical regions. Sexual state: Ascomata superficial, solitary, scattered, some clustered, globose to subglobose, dark brown, ostiolate, surrounded by sparse, dark brown to black setae; setae relatively long, tapering to an acute apex. Peridium thick, comprising several layers of textura angularis to subglobosa, inwardly comprising brown to reddish-brown, small brown cells of textura subprismatica. Hamathecium comprising numerous, filiform, septate, branched, hyaline and pale brown pseudoparaphyses, embedded in a gelatinous matrix. Asci 8spored, bitunicate, broadly cylindric-subclavate, pedicellate, thickened at apex, without an ocular chamber. Ascospores 2-3-seriate, elongate, cylindric-fusiform, curved, tapering towards sub-rounded ends, less than 10-septate, slightly constricted at septum, hyaline when young and pale brown at maturity, some surrounded by a mucilaginous sheath, smoothwalled. Asexual state: Unknown.

*Type species: Acanthostigmina minuta* (Fuckel) Clem. & Shear

Notes: The genus Acanthostigmina was introduced by von Höhnel (1909a) with A. minuta (Fuckel) Höhn. as the type species. Saccardo (1883) had earlier included this species in Acanthostigma. Subsequently Acanthostigmina minuta has been placed in other genera (Barr 1980; Crane et al. 1998; Réblová and Barr 2000). In this study, we re-examined a specimen of Acanthostigmina minutum from Germany which Réblová and Barr (2000) considered to be representative of the species (Rehm exsiccatae, Ascomycete No. 1568, PAD) (Fig. 7). Rehm's exsiccatae specimen (BPI 624355) is characterized by dark brown to black ascomata, moderately stiff setae, broadly cylindric-subclavate, apically thickened asci and 5-9-septate, hyaline to pale brown ascospores with a thin mucilaginous sheath. This differs from the description of Acanthostigma minutum from the PAD neotype provided by Réblová and Barr (2000) in which the ascospores were more than 10-septate, hyaline and without a mucilaginous sheath, whereas in other characters they are rather similar. Unlike Acanthostigmina minuta, Acanthostigma perpusillum has ascomata covered by numerous setae; in addition these species differ in the size and shape of asci and ascospores.

Molecular data indicate that three non-type isolates of *Acanthostigmina minutum* from North America (ANM283, ANM818 and ANM880) formed a single clade distant from the *Acanthostigma perpusillum* clade (Promputtha and Miller 2010). Sánchez and Bianchinotti



Fig. 7 *Acanthostigmina minuta* (BPI 624355). a Ascomata. b LS of ascoma. c Setae. d Peridium. e Pseudoparaphyses. f, g Asci. h, i Ascospores. *Scale bars*:  $\mathbf{a}-\mathbf{b} = 200 \,\mu m$ ,  $\mathbf{c}-\mathbf{d}$ ,  $\mathbf{f}-\mathbf{i} = 50 \,\mu m$ ,  $\mathbf{e} = 5 \,\mu m$ 

(2010) found a collection in Argentina identified as *Acanthostigma minutum* MVB 781 (BBB), which Sánchez et al. (2012) showed to cluster with *Acanthostigma perpusillum*. In our multigene phylogenetic analysis, the North American strains of *Acanthostigmina minuta* (ANM810, ANM818 and

ANM238) formed a monophyletic clade that clustered with two strains of *Acanthostigmina multiseptatum* (ANM475 and ANM665), although with weak support (Clade L, Fig. 2). We therefore treat Clade L as *Acanthostigmina sensu stricto* comprising *A. minuta* and *A. multiseptatum*.

*Type species: Acanthostigmina minuta* (Fuckel) Clem. & Shear, Gen. Fung. (Minneapolis): 270 (1931), *Facesoffunginumber*: FoF 00174 Fig. 7

 $\equiv$  Lasiosphaeria minuta Fuckel, Jb. nassau. Ver. Naturk. 23–24: 148 (1870) [1869–70]

Saprobic on decaying wood of a rotten branch of Fagus svlvatica. Sexual state: Ascomata (211-)234-299 µm high  $\times$  (216-)226–270  $\mu m$  diam., superficial, solitary, scattered, occasionally clustered, globose-subglobose, dark brown, ostiolate, surrounded by sparse, erect, dark brown to black setae, (30-)56-84(-105)  $\mu m$  long, tapering towards an acute end at apex. Peridium  $29-34 \mu m$  wide, with several layers of brown to reddish-brown cells, comprising textura angularis to subglobosa, inwardly with small brown cells of textura subprismatica. Hamathecium comprising ca.  $(1-)1.5-2 \mu m$ wide, numerous filiform, septate, branched, hyaline to pale brown pseudoparaphyses, embedded in a gelatinous matrix. Asci (73-)84–118×20–29.5  $\mu m$  ( $\bar{x}=98\times24\mu m$ , n=20), 8spored, bitunicate, broadly cylindric-subclavate, pedicellate, thickened at apex, without an ocular chamber. Ascospores  $(42-)47-60 \times 6-9 \,\mu m \ (\bar{x}=52 \times 7 \,\mu m \ , n=20), 2-3$ -seriate, elongate-fusiform, curved, tapering towards rounded ends, (6-)7-9-septate, broader at fourth and fifth cells from apex, slightly constricted at septum, hyaline to pale brown when mature, occasionally surrounded by a mucilaginous sheath, smooth-walled. Asexual state: Unknown.

*Material examined*: GERMANY, Bavarian Alps Mts., Kampenwand, elev. *ca* 1200 msl., on decaying wood branch of *Fagus sylvatica* L. (*Fagaceae*), June 1904, Rehm H., Ascomyceten no. 1568 (BPI 624355).

## New combination:

*Acanthostigmina multiseptatum* (Promp. & A.N. Mill.) Boonmee & K.D Hyde **com. nov.**, *Index Fungorum number*: IF 550681

 $\equiv$  Acanthostigma multiseptatum Promp. & A.N. Mill., Mycologia 102(3): 577 (2010)

*Aquaphila* Goh, K.D. Hyde & W.H. Ho, Mycol. Res. 102(5): 588 (1998)

Saprobic on submerged woody substrates, widespread in tropical regions. *Mycelial colonies* partly developed inside wood and partly on wood surface. **Sexual state**: *Ascomata* superficial, gregarious, globose to subglobose, dark brown to black, with brown setae, straight, thick-walled, tapering to an acute apex. *Peridium* outer layer of *textura angularis* comprising black-walled cells, cell of inner layer, elongate, pale brown to subhyaline. *Pseudoparaphyses* filiform, *ca*. 2 mm wide, hyphae-like, branched, hyaline. *Asci* 8-spored, bitunicate, cylindroclavate, with long pedicels, apically rounded. *Ascospores* 2–3-seriate, cylindrical fusiform, 7-transverse septa, hyaline to pale brown, smooth (from Tsui et al. 2007). **Asexual state**: *Conidiophores* semi-macronematous, mononematous, borne as lateral branches from superficial hyphae, hyaline, delicate, septate, simple or branched, flexuous to geniculate. *Conidiogenous cells* integrated, terminal or intercalary, denticulate, monoblastic or polyblastic, proliferation sympodial, indeterminate. Conidial secession schizolytic. *Conidia* borne singly, acrogenous and becoming lateral as a result of conidiophore proliferation, hyaline, fusoid to falcate or sigmoid, broad, multi-euseptate, apedicellate (from Goh et al. 1998).

Notes: Clade J represents Aquaphila and comprises species with darkly pigmented ascomata covered by dark setae, cylindrical-clavate and apically thickened asci, and fusiform 6-7-septate ascospores. The asexual form occurs in an aquatic habitat and produces curved conidia that are distinct from the type species in the sister genus Chlamydotubeufia, C. huaikangplaensis that produces dictyochlamydospores (Tsui et al. 2007; Boonmee et al. 2011) and other Tubeufia species. The ex-type strain of Tubeufia asiana (BCC 3463) clusters in Clade J with Aquaphila albicans Goh, K.D. Hyde & W.H. Ho, with robust support (100 % BS and 1.00 PP). Tubeufia asiana was introduced as the asexual state of Aquaphila albicans by Tsui et al. (2007). Our phylogenetic analysis shows it to clusters far from Tubeufia sensu stricto; Aquaphila albicans is the older name and thus Tubeufia asiana is a synonym.

*Type species: Aquaphila albicans* Goh, K.D. Hyde & W.H. Ho, Mycol. Res. 102(5): 588 (1998)

*≡ Tubeufia asiana* Sivichai & K.M. Tsui, Mycologia 99(6): 885 (2008) [2007]

*Bifrontia* Norman, Bot. Notiser: 18 (1872), *Facesoffunginumber*: FoF 00208

Saprobic on dead wood. Sexual state: Ascomata superficial, seated on a subiculum, solitary or gregarious, globose to subglobose, black, cupulate, turbinate, collapsing when mature or dried, central ostiole. Peridium thick-walled, outer layer composed of 3–4-layers of brown cells of textura subangularis, innermost layers of 2–3-layers of hyaline cells of textura subprismatica. Hamathecium with sparse pseudoparaphyses. Asci 8-spored, bitunicate, fissitunicate, fusiform, broadly rounded above, thick-walled, narrowing towards the base, short-pedicellate, arranged in rows on basal cells of ascomata. Ascospores overlapping fasciculate, longfusiform, straight to slightly curved, 7–9-septate, constricted at septa, pale brown, smooth-walled. Asexual state: Unknown.

Lectotype species designated here: Bifrontia compactior Norman, Bot. Notiser: 19 (1872), Facesoffunginumber: FoF 00175 Fig. 8

**Fig. 8** *Bifrontia compactior* (O-F72543, **holotype**). **a**, **b** Herbarium material and labels. **c**, **d** Black ascomata on host surface. **e** Vertical section of ascoma. **f**, **g** Close up of peridium and sparse pseudoparaphyses. **h-j**, **l**, **m** Asci with ascospores - note **l**, **m**, stained in cotton *blue reagent*; **k**, **n-p** Ascospores; note n stained in cotton *blue reagent*. *Scale bars*: **c** = 200  $\mu$ m, **d** = 100  $\mu$ m, **e** = 50  $\mu$ m, **f** = 20  $\mu$ m, **g** = 10  $\mu$ m, **h-j**, **l-m** = 10  $\mu$ m, **k**, **n-p** = 5  $\mu$ m



Saprobic on dead wood of Salix glauca. Sexual state: Ascomata 100–150 µm high×190–250 µm diam., superficial, seated on a subiculum, solitary or gregarious, globose to subglobose, black, cupulate, turbinate, collapsing when mature or dried, central ostiole ambiguous. Peridium thickwalled,  $35-50 \mu m$  wide, composed of 3-4-layers of brown cells of textura angularis, innermost layers of 2-3-layers of hyaline cells of textura subprismatica. Hamathecium comprising sparse pseudoparaphyses. Asci 55-100×14.5-25 µm  $(\bar{x}=75\times 17\mu m, n=20)$ , 8-spored, bitunicate, fissitunicate, fusiform, broadly rounded above, thick-walled, narrow towards at base, short-pedicellate, arranged in rows on basal cells of ascomata. Ascospores 40–60×4–6  $\mu m$  ( $\overline{x}$ = 48 × 5 $\mu m$ , n=10), overlapping fasciculate, long-fusiform, straight to slightly curved, 7–9-septate, constricted at septa, pale brown, smooth-walled. Asexual state: Unknown.

*Material examined*: NORWAY, Finnmark, Hammerfest: Prope Hammerfest Finmarki, on wood of *Salix glauca* L. (*Salicaceae*), J.M. Norman, date of collection unknown (O-F72543, **holotype**).

*Notes: Bifrontia* was introduced by Norman (1872) with two species but neither was designated as the type for the genus. *Bifrontia compactior* Norman was listed first in the diagnosis for the genus and is typical of the protologue. Therefore we designate herein *B. compactior* as the lectotype of the genus. This species has typical characteristics of *Tubufiaceae* except that the hamathecium rarely includes pseudoparaphyses. We refer this genus to *Tubeufiaceae*.

*Boerlagiomyces* Butzin., Willdenowia 8(1): 39 (1977), *Facesoffunginumber*: FoF 00209

Boerlagella Penz. & Sacc., Malpighia 11(9–10): 404 (1897)

Saprobic on decaying wood. Sexual state: Ascomata superficial, seated on a subiculum, globose, scattered, with flexuous, hairy, black, velvety, septate setae, surrounded by black mycelium. Peridium composed of carbonaceous, multilayered walls. Hamathecium composed of filiform, hyaline pseudoparaphyses. Asci 8-spored, bitunicate, cylindric-clavate, narrowing towards base, short-pedicellate or apedicellate, apically rounded. Ascospores 2–3-seriate, cylindric-fusoid, gently curved, obtuse at both ends, muriform, multiseptate, not constricted at septa, hyaline, smooth-walled (adapted from Penzig and Saccardo 1904). Asexual state: Unknown.

*Notes*: The genus *Boerlagiomyces* was introduced by Butzin (1977) with *B. velutinus* (Penz. & Sacc.) Butzin as the type species. The genus is distinctive in producing superficial, whitish to pale brown, soft ascomata with large hyaline, muriform ascospores that often develop on submerged wood in freshwater. Crane et al. (1998) monographed and accepted six species in *Boerlagiomyces* in *Tubeufiaceae*. This genus presently comprises nine species according to Index Fungorum (2014). A putative strain of *Boerlagiomyces*  websteri Shearer & J.L. Crane was placed with *Rhytisma* acerinum (Pers.) Fr. in *Rhytismataceae* by Kodsueb et al. (2006); this seems unlikely. *Garethjonesia* has been considered a synonym of *Boerlagiomyces* (Stanley and Hyde 1997; Crane et al. 1998), however they are morphologically distinct. The habitats (aquatic versus terrestrial) also differ. We treat *Garethjonesia* here as a good genus in Ascomycetes *incertae* sedis.

*Type species:* **Boerlagiomyces velutinus** (Penz. & Sacc.) Butzin, Willdenowia 8(1): 39 (1977), *Facesoffunginumber*: FoF 00176 Fig. 9

*≡ Boerlagella velutina* Penz. & Sacc., Malpighia 11(9–10): 404 (1897)

Saprobic on decaying wood or culms in petioles of *Plectocomia* sp. **Sexual state**: *Ascomata* 500–600  $\mu$ m diam., superficial, seated on black subiculum, globose to pyriform, dark brown, scattered, ostiolate, with sparse, flexuous, black, septate, velvety, hyphal appendages,  $210-250 \times 3-6 \mu$ m, black, septate, surrounded black mycelium. *Peridium* composed of carbonaceous, multilayered walls. *Hamathecium* composed of filiform, hyaline pseudoparaphyses. *Asci* 200– $250 \times 30-35 \mu$ m, 8-spored, bitunicate, elongate, cylindric-clavate, apically rounded, narrowing towards base, shortpedicellate or apedicellate. *Ascospores* 90–120×12–14 $\mu$ m, 2–3-seriate, cylindric-fusoid, gently curved, obtuse at both ends, muriform, 25–30-septate, not constricted at septa, hyaline, smooth-walled (adapted from Penzig and Saccardo 1904). **Asexual state**: Unknown.

*Chlamydotubeufia* Boonmee & K.D. Hyde, Fungal Diversity 51(1): 78 (2011)

Saprobic on decaying wood in terrestrial habitats, widespread in temperate to tropical regions. Sexual state: Ascomata superficial, solitary, globose-subglobose, ostiolate, surrounded by dark setae. Peridium thick-walled, dark brown to black, composed of cells of *textura angularis*. Hamathecium composed of cellular hyaline pseudoparaphyses, embedded in a mucilaginous matrix. Asci 8-spored, bitunicate, fissitunicate, cylindric-clavate to broadly clavate, short-pedicellate, rounded at apex. Ascospores 2-3seriate, hyaline, narrowly fusiform, broad at supra-median, slightly curved, multiseptate, slightly constricted at septum, with asymmetrical ends. Asexual state: hyphomycetous, helicosporous, also producing a dictyochlamydosporous state in culture and often on wood. Dictyochlamydospores broadly oblong, elongate, multiseptate, at first reddish-brown, becoming black (from Boonmee et al. 2011).

*Type species:* **Chlamydotubeufia huaikangplaensis** Boonmee & K.D. Hyde, Fungal Diversity 51(1): 78 (2011) Figs. 10–11

*Chlamydotubeufia* (Clade I) includes terrestrial taxa and produces dictyochlamydospores. This genus is distinct from the aquatic genus *Aquaphila* (Clade J) which produces sickle-shaped conidia (Tsui et al. 2007; Boonmee et al. 2011). In

**Fig. 9** *Boerlagiomyces velutinus* (Redrawn from Penzig and Saccardo 1904), as *Boerlagella velutina.* **a**, **b** Substrate and ascoma, 500–600 μm diam. **c** Ascus, mycelium and pseudoparaphyses, ascus size: 200–250×30–35 μm **d** 

Ascospores,  $90-120 \times 12-14 \mu m$ 



addition to the type species, *C. huaikangplaensis*, two other species are included in this genus, specifically *C. chlamydosporum* and *C. khunkornensis*. A new collection of *Chlamydotubeufia huaikangplaensis* is illustrated below (THAILAND, Chiang Mai, Mae Taeng, Mushroom Research Centre, N19°17.123' E 98°44. 009', elev. *ca.* 900 msl., on dead wood of an unidentified tree, 23 June 2011, Saranyaphat Boonmee, MRC-02 (MFLU 11–1145) = living culture = MFLUCC 11–0509).

*Helicangiospora* Boonmee, Bhat & K.D. Hyde, gen. nov., *Index Fungorum number*: IF 550574, *Facesoffunginumber*: FoF 00210

*Etymology: Helicangiospora*, referring to conidial spores produced endogenously within a vessel-like conidiogenous cell.

Saprobic on dead wood. Sexual state: Ascomata superficial, solitary to clustered, scattered, globose to subglobose, dark brown to black, with abundant setae, ostiolate. Setae stiff, tapering to an acute tip at apex. Peridium composed of several outer layer cells of textura angularis, darkened, innermost layer comprising pale brown to hyaline cells of textura subprismatica. Hamathecium comprising ca.  $2\mu m$  wide, numerous, filiform, septate, branched, hyaline pseudoparaphyses. Asci 8-spored, bitunicate, fissitunicate, cylindrical-clavate or saccate, with rounded apex, pedicellate, ocular chamber not apparent. Ascospores overlapping 1–3-seriate, fusiform, hyaline, tapering toward the ends, supramedianly wider, trans-septate, smooth-walled. Asexual state: hyphomycetous, helicosporous. Conidiogenous cells terminal, integrated, holoblastic, globose, occasionally



Fig. 10 *Chlamydotubeufia huaikangplaensis* (MFLU 11–1145). **a** Ascomata on substrate. **b** L.S. of ascoma. **c** Single seta. **d** L.S. of peridium. **e** Pseudoparaphyses. **f**–**h** Asci. **i**–**k** Ascospores. *Scale bars*: **a**, **b** = 100  $\mu$ m, **c**, **f**–**h** = 50  $\mu$ m, **d** = 40  $\mu$ m, **e** = 5  $\mu$ m, **i**–**k** = 20  $\mu$ m

subglobose to oval, golden-brown to olive-brown. *Conidia* helicosporous, developing endogenously within conidiogenous cells, released by breaking wall of conidiogenous cell, trans-septate, tapering towards rounded

ends, not constricted at septum, coiled once, hyaline, pale brown at maturity.

*Type species: Helicangiospora lignicola* Boonmee, Bhat & K.D. Hyde



Fig. 11 *Chlamydotubeufia huaikangplaensis* (MFLU 11–1145). Colonies on MEA. a Germinating ascospore. b, c Colonies on MEA from surface and reverse. Note dark brown colonies. d Chlamydospores

*Notes*: Phylogenetically *Helicangiospora lignicola* does not group with any other taxa and is basal to Clades A-B, although lacks support. The genus is also morphologically distinct as it produces a unique helicoma-like asexual state in culture (Fig. 13). The holoblastic conidia are initiated at the tip of a conidiogenous cell by formation of a globose, moderately dark brown cell within which the characteristic helicosporous conidia differentiate endogenously. The helicoid conidia are released by schizolytic break down of the outer thick-walled sphaerical capsule. Endogenous differentiation of the conidium is seen in most phialidic type

growing on substrate. Note chlamydospores produced on media, with and without substrate. **e** Chlamydospores on plant tissues.  $\mathbf{f}$ - $\mathbf{j}$  Chlamydospores. *Scale bars*:  $\mathbf{a} = 20 \mu m$ ,  $\mathbf{b}$ - $\mathbf{d} = 10 \text{ mm}$ ,  $\mathbf{e}$ - $\mathbf{j} = 40 \mu m$ 

conidiogenesis wherein the conidial primordium is differentiated enteroblastically within the phialide, but in most genera maturation of conidia is exogenous. In asexual genera, such as, *Chalara*, *Fusichalara*, *Sporoschisma*, and *Sporoschismopsis*, not only differentiation but also maturation of the conidia takes place within the venter of the phialide (Bhat 2010). However, these structures are not similar to what is seen in the asexual state of the present specimen. Therefore, the genus *Helicangiospora* is established to accommodate this unique species that produces helicosporous conidia within a conidiogenous capsule. *Type species: Helicangiospora lignicola* Boonmee, Bhat & K.D. Hyde, **sp. nov.**, *Index Fungorum number*: IF 550575, *Facesoffunginumber*: FoF 00177 Figs. 12–13

*Etymology*: From *lignin* referring to wood and -icola meaning associated with in reference to growing on wood.

Holotype: MFLU 11-0137

Saprobic on dead wood. Sexual state: Ascomata (216-)296-351  $\mu m$  high × 266-340  $\mu m$  diam. ( $\bar{x}= 286 \times 308 \mu m$ ), superficial, solitary to clustered, scattered, globose to subglobose, dark brown to black, with abundant setae, ostiolate. *Setae* stiff, tapering to an acute tip at apex, 56–77  $\mu m$  long. *Peridium* 36–56  $\mu m$  wide, composed of several outer cells of *textura angularis*, darkened; innermost comprising thin layers of pale brown to hyaline cells of *textura subprismatica*. *Hamathecium* comprising *ca*.  $2\mu m$  wide, numerous, filiform, septate, branched, hyaline pseudoparaphyses. *Asci* (77-)80–106×15–19  $\mu m$  ( $\bar{x}=93 \times 17\mu m$ , n=20), 8-spored, bitunicate, fissitunicate,



Fig. 12 *Helicangiospora lignicola* (MFLU 11–0137, holotype). a Ascomata on substrate. b L.S. of ascoma. c L.S. of peridium. d Single seta. e Pseudoparaphyses. f–i Asci. j–l Ascospores. *Scale bars*:  $\mathbf{a}$ – $\mathbf{b}$  = 100 µm, c, j–l = 20 µm, d = 40 µm, e = 5 µm, f–i = 50 µm



**Fig. 13** *Helicangiospora lignicola* (MFLU 11–0137, **holotype**). a Germinating ascospore. **b**, **c** Colonies on MEA from surface and reverse. **d**, **e** Mycelium and development of conidia in culture. **f** Conidiogenous cells.

cylindrical-clavate or saccate, with rounded apex, pedicel *ca*.  $11 \mu m$  long, ocular chamber not apparent. *Ascospores* 

Note the formation of conidium at this stage. **g**–**j** Endogenous development of conidium. **j** Release of conidium. **k**–**n** Conidia. *Scale bars*: **a** =  $20 \mu m$ , **b**, **c** = 10 mm, **d**–**n** =  $5 \mu m$ 

(40-)45–53×5–8 $\mu m$  ( $\overline{x}$ = 47 × 7 $\mu m$ , n=20), overlapping 1–3-seriate, fusiform, hyaline, slightly curved, tapering toward

ends, supramedianly wider, 6–7-septate, not constricted at septum, smooth-walled. **Asexual state**: hyphomycetous, helicosporous. *Conidiogenous cells* terminal, integrated, holoblastic, globose, sometimes subglobose to oval, goldenbrown to olive-brown,  $12-17.5 \,\mu m$  diam. *Conidia* helicosporous, differentiating endogenously within idiogenous cells, released by break down of wall of conidiogenous cell,  $12-17 \,\mu m$  diam when coiled, filaments  $4-7 \,\mu m$  wide, 5-septate, tapering towards rounded ends, not constricted at septum, coiled once, hyaline, pale brown at maturity, mostly smooth-walled, sometimes vertucose, slightly bulging at the septa.

*Cultural characteristics*: Ascospores germinating on MEA within 12 h. *Colonies* slow growing on MEA, less than 5 mm diam in 7 days at 28 C, slightly convex, with an undulate edge, white or pale brown and dark brown, white at margin. *Mycelium* superficial, septate, branched, smooth, pale brown, with hyphae producing erect, septate conidiophores.

*Material examined*: THAILAND, Chiang Rai, Muang, Doi Pui, elev. *ca.* 403–936 msl., on dead wood of an unidentified tree, 10 May 2011, Saranyaphat Boonmee, DP-03 (MFLU 11–0137 **holotype**; PDD 104452 **isotype**); ex-type living culture = MFLUCC 11–0378 = BCC 52029 = ICMP 20069.

Helicoma Corda, Icon. fung. (Prague) 1: 15 (1837), Facesoffunginumber: FoF 00211

Possible synonyms (Index Fungorum 2014, not seen)

Lituaria Riess, Bot. Ztg. 11: 136 (1853)

Helicocoryne Corda 1854, Icon. fung. (Prague) 6: 9 (1854)

*Drepanospora* Berk. & M.A. Curtis [as 'Drepanispora'], in Berkeley, Grevillea 3(no. 27): 105 (1875)

*Helicopsis* P. Karst., Revue mycol., Toulouse 11(no. 42): 96 (1889)

Troposporella P. Karst., Hedwigia 31: 299 (1892)

Helicosporella G. Arnaud, Bull. trimest. Soc. mycol. Fr. 69: 292 (1954) [1953]

*Helicosporina* G. Arnaud ex Rambelli, Mycopath. Mycol. appl. 13: 110 (1960)

Helicominopsis Deighton, Mycol. Pap. 78: 20 (1960)

Moorella P.Rag. Rao & D. Rao, Mycopath. Mycol. appl. 22: 51 (1964)

Saprobic on woody substrata. Mycelium partly immersed, pale brown, septate, branched hyphae. Sexual state: Ascomata superficial, solitary, sometimes clustered, gregarious, superficial, subglobose, oval to obovoid, with soft texture, dark brown, pale brown above, with a central papillate ostiole, rarely with setae. Setae up to  $80 \mu m$  long, dark brown, tapering towards subacute apex, widest at base, septate. Peridium thickwalled, composed of brown to reddish-brown cells of textura angularis. Hamathecium comprising numerous, filiform, septate, branched, hyaline pseudoparaphyses. Asci 8-spored, bitunicate, elongate to cylindric-clavate, thickened at apex, pedicellate. Ascospores 2–3-seriate, elongate-fusiform, subcylindrical, tapering towards subacute ends, up to 10septate, not constricted at septum, hyaline, smooth-walled. **Asexual state**: *Conidiophores* superficial, macronematous, crowded, erect, dark brown, septate, rarely branched, darkened and slightly constricted at septum. *Conidiogenous cells* monoblastic to polyblastic, sometimes branched at apex, brown to dark brown, smooth. *Conidia* tightly coiled  $1-1\frac{1}{2}$ times, conidial filament  $6-9\mu m$  wide, hyaline to pale brown, tapering towards the flattened end with a basal scar, septate, slightly constricted at septum, smooth-walled.

Type species: Helicoma muelleri Corda

Notes: The genus Helicoma was introduced by Corda (1837), with the type species *H. muelleri* Corda. The genus is distinguished by its relatively short, erect, thick, dark brown, smooth conidiophores, holoblastic conidiogenous cells and helicoid, hvaline, thick-walled, brown to dark brown conidia forming from terminal, denticulate conidiophores (Goos 1986; Seifert et al. 2011). Illustrations presented here are based on BPI 447569 considered authentic material of H. muelleri on natural substrate and determined by D. Linder. Various Helicoma species have been connected with sexual taxa in Tubeufiaceae and the links are confused (Tsui et al. 2006, 2007; Zhao et al. 2007; Boonmee et al. 2011). The sexual state is described from Helicoma rugosa (BPI 1104599, dried culture: BER 12 80-4). Putatively named strains of Helicosporium linderi R.T. Moore (NBRC 9207), T. paludosa (P. Crouan & H. Crouan) Rossman (HKUCC 9118, ANM 196, ANM 1169) and Thaxteriella helicoma (W. Phillips & Plowr.) J.L. Crane, Shearer & M.E. Barr (JCM 2739, UBCF 13877) clustered in this clade and we rename them as *Helicoma* in the phylogenetic tree (Fig. 2), but do not formally synonymize them as we have not seen voucher material. Asexual morphs regarded as Helicoma rugosa formed in cultures of Thaxteriella helicoma (JCM 2739 and UBCF 13877). Tubeufia khunkornensis Boonmee & K.D. Hyde (MFLUCC 10-0119, ex-type strain), T. inthanonensis Boonmee & K.D. Hyde (MFLUCC 11-0003, ex-type strain) and T. miscanthi W.H. Hsieh, Chi Y. Chen & Sivan., epitypified here are synonymized under Helicoma. Helicoma chiangraiense, H. fagacearum and H. siamense formed distinct groups at the base of Clade A, and we therefore introduce them as new species of Helicoma.

*Type species: Helicoma muelleri* Corda, Icon. fung. (Prague) 1: 15 (1837), *Facesoffunginumber*: FoF 00178 Fig. 14

Saprobic on woody substrates. Mycelium composed of partly immersed and partly superficial, pale brown, septate, branched hyphae. Sexual state: Unknown. Asexual state: Conidiophores (43-)80–153.5  $\mu$ m long × 7–10  $\mu$ m wide ( $\bar{x}$ = 106 × 8 $\mu$ m , n=20), superficial, macronematous, crowded, erect, dark brown, septate, rarely branched, darkened at septum. Conidiogenous cells monoblastic to polyblastic, sometimes branched at apex, brown to dark brown, smooth-walled. Conidia (15-)16–19(–21)  $\mu$ m diam., and conidial filament 6–9 $\mu$ m wide ( $\bar{x}$ = 17 × 7 $\mu$ m , n=20),

Fig. 14 Helicoma muelleri (BPI 447569). a Conidiophores with attached apical conidium on natural substrate. b, c Squash mount of conidiophores with conidial development at the apex (*arrows*). d Conidiophores with detached conidia and minute denticles (*arrows*). e-g Conidia. *Scale bars*: a, d-g =  $20 \mu m$ , b-c =  $50 \mu m$ 



tightly coiled  $1-1\frac{1}{2}$  times, hyaline to pale brown, tapering toward flat end and with a basal scar 4-7(-8)  $\mu m$  wide, septate, slightly constricted at septum, smooth-walled.

*Material examined*: USA, New Hampshire, Bartlett, on dead wood (undermined substrate), R. Thaxter, April 1901; Detr. D. Linder, BPI 447569.

*Notes*: The sequence (*Helicoma muelleri* CBS 964.69) of this species was used in the molecular analysis of Tsui et al. (2006). We treat this as an authentic specimen but the species needs epitypfiying with a fresh collection.

#### New combinations:

*Helicoma khunkornense* (Boonmee & K.D. Hyde) S. Boonmee & K.D. Hyde, **comb. nov.**, MycoBank: MB 804554

 $\equiv$  *Tubeufia khunkornensis* Boonmee & K.D. Hyde, Fungal Diversity 51(1): 86 (2011).

*Notes:* This species produced a helicoma-like asexual state in culture, with brown helicoid conidia on thick robust conidiophores (Fig. 4, in Boonmee et al. 2011). It grouped in *Helicoma sensu stricto* (Clade A) with high support (95 % BS and 1.00 PP) in the phylogenetic analysis (Fig. 2) and therefore is synonymised under *Helicoma*. *Material examined*: THAILAND, Chiang Rai, Muang, Khun Korn Waterfall, elev. as 671 msl., N19°51–54' E 99°35.39', on dead wood of an unidentified tree, 13 November 2009, S. Boonmee KK-08 (MFLU 10–0052, **holotype**), extype culture MFLUCC 10–0119 = IFRD 2180 = BCC 52297.

*Helicoma inthanonense* (Boonmee & K.D. Hyde) S. Boonmee & K.D. Hyde, **comb. nov.**, MycoBank: MB 804555

 $\equiv$  *Thaxteriella inthanonensis* Boonmee & K.D. Hyde, Fungal Diversity 51(1): 86 (2011).

*Notes*: This species produces a helicoma-like asexual state in culture, with brown helicoid conidia formed on slender, hyaline conidiophores (Boonmee et al. 2011). It may also be similar to *Drepanospora pannosa* Berk. & M.A. Curtis as it forms secondary microconidia (Seifert et al. 2011). This was considered to be the asexual state of *Tubeufia helicoma*. In the phylogenetic tree in Clade A (Fig. 2), this appears to be a different species from *Helicoma rugosa* (=*Tubeufia helicoma*), but all three taxa are congeneric.

*Material examined*: THAILAND, Chinag Mai, Doi Inthanon, Jom Thong, elev. 800–1,000 msl., N18°31.576' E 98°29.790', on dead bark of an unidentified tree, 16 November 2010, Rungtiwa Phookamsak (MFLU 11–0003, holotype), ex-type culture MFLUCC 11–0003 = BCC 52153.

- *Helicoma rugosa* (C. Booth) S. Boonmee & K.D. Hyde, comb. nov., *Facesoffunginumber*: FoF 00179 Fig. 15
  - *≡ Tubeufia rugosa* C. Booth, *Mycol. Pap.* 94: 13 (1964)

 $\equiv$  Thaxteriella helicoma (W. Phillips & Plowr.) J.L. Crane, Shearer & M.E. Barr, Can. J. Bot. 76(4): 610 (1998)

*= Sphaeria helicoma* W. Phillips & Plowr., Grevillea, 6:26 (1877)



Fig. 15 *Helicoma rugosa* (BPI 1104599, dried culture: BER 12 80–4). **a** Ascomata. **b** L.S. ascoma. **c** Single seta. **d** Peridial wall. **e** Pseudoparaphyses. **f–h** Asci. **i–k** Ascospores. **l** Colony on dried culture.

**m** Mycelium. **n** Conidiophore (*arrows*). **o**-**q** Conidiophores with attached conidia. Scale bars:  $\mathbf{a}-\mathbf{c} = 100\,\mu m$ ,  $\mathbf{c}-\mathbf{d}$ ,  $\mathbf{i}-\mathbf{k}$ ,  $\mathbf{n}-\mathbf{q} = 20\,\mu m$ ,  $\mathbf{f}-\mathbf{h} = 50\,\mu m$ ,  $\mathbf{e}$ ,  $\mathbf{m} = 5\,\mu m$ ,  $\mathbf{l} = 1$  cm

Saprobic on leafy substrata. Sexual state: Ascomata (242-)303-340 μm high×(218-) 238-263(-331) μm diam., superficial, solitary, sometimes clustered, gregarious, subglobose, oval to obovoid, with soft texture, dark brown, pale brown above, with a central papillate ostiole, with rare setae. Setae  $61-80 \mu m$  long, dark brown, tapering towards subacute apex, widest at base, septate. Peridium 39-44 µm wide, composed of brown to reddish-brown cells of textura angularis. Hamathecium comprising numerous,  $1-2 \mu m$  wide, filiform, septate, branched, hyaline pseudoparaphyses. Asci  $(90-)96-135 \times 15-20 \,\mu m \ (\bar{x}= 112 \times 19 \,\mu m \ , n=20), 8$ -spored, bitunicate, elongate to cylindric-clavate, thickened at apex, with  $(7-)20-31.5 \mu m$  long pedicels, ocular chamber not observed. Ascospores 42–61×5–8.5  $\mu m$  ( $\overline{x}$ = 53 × 6 $\mu m$ , n=20), 2-3-seriate, elongate-fusiform, subcylindrical, tapering towards subacute ends, (8-)9-10-septate, not constricted at septum, hyaline, smooth-walled. Asexual state: hyphomycetous, helicosporous. Conidiophores macronematous, thick-walled, septate, branched, brown to moderately brown. Conidiogenous cells monoblastic to polyblastic, terminal or intercalary, dentate, brown to dark brown, darkened at basal septum. Conidia  $(17-)22-28\,\mu m$  diam., conidial filaments  $4-5\,\mu m$  wide  $(\bar{x}=24\times5\mu m, n=20)$ , helicoid, tightly coiled 2-3<sup>1</sup>/<sub>2</sub> times, hyaline to pale brown, tapering toward flattened end and scar, multiseptate, not constricted at septum, smooth-walled.

*Cultural characteristics* (based on dried culture): *Colonies* dark brown, superficial and partly immersed in mycelium, with dark brown, septate, branched hyphae.

*Material examined*: BERMUDA, Devonshire Marsh, Devonshire Parish, on leaves of *Sabal bermudiana* L.H. Bailey (*Arecaceae*), coll. R.P. Korf and A.Y. Rossman (AR-BER 12), on 18 January 1980; det. A.Y. Rossman (BPI 1104599, dried culture: BER 12 80–4).

Notes: Helicoma rugosa based on Tubeufia rugosa C. Booth was originally described as Sphaeria helicoma W. Phillips & Plowr. (1877). Pirozynski (1972) redescribed and transferred the fungus to Tubeufia based on that helicosporium asexual morph. Subsequently, Crane et al. (1998) transferred it to Thaxteriella because of the pigmented ascomata and peridial wall structure. In addition, Thaxteriella helicoma also produced a helicoid asexual state in culture (Fig. 15). According to molecular analysis (Clade A, Fig. 2), the putative isolates of Thaxteriella helicoma (JCM 2739 and UBC F13877) cluster in Helicoma sensu stricto, while the strain from UBC F13877 clustered with the generic type species Helicoma muelleri CBS 964.69 with strong support (100 % BS and 1.00 PP). The placement of Helicoma rugosa in Helicoma is well-supported by morphology and molecular phylogeny. Although Sphaeria helicoma is an older name it cannot be used to represent this species as it would result in a tautonym; the name of a genus and species that are the same are not allowed in botanical nomenclature. Therefore we used the next available synonym which is Helicoma rugosa.

*Helicoma miscanthi* (W.H. Hsieh, Chi Y. Chen & Sivan.), Boonmee & K.D. Hyde, **comb. nov.**, *Index Fungorum numbeter*: IF 550637, *Facesoffunginumber*: FoF 00180 Fig. 16

 $\equiv$  *Tubeufia miscanthi* W.H. Hsieh, C.Y. Chen & Sivan., Mycol. Res. 102: 234 (1978)

Saprobic on dead wood. Sexual state: Ascomata 285- $358(-373) \ \mu m \ high \times 299 - 339(-386) \ \mu m \ diam.$  $(\bar{x}=330\times 334\mu m)$ , superficial, solitary, scattered, globosesubglobose to ovate, flat to slightly shrunken on apex, lacking obvious setae, hyphae developing from ascomatal base on substrate, brown to dark brown when fresh, with a waxy covering on ascomal wall, pale brown when dry, darkened at centre, ostiolate. Peridium 51-58 µm wide, comprising several layers of brown to red brown cells of textura angularis. Hamathecium comprising numerous, ca.  $3-4\mu m$  wide, long filiform, septate, unbranched, hyaline pseudoparaphyses. Asci (142-)154-188(-194)×  $19-26(-30) \ \mu m \ (\bar{x}= 172 \times 24 \ \mu m \ , n=20), 8$ -spored, bitunicate, cylindric-clavate, rounded at apex, mostly apedicellate, ocular chamber not observed. Ascospores (122-)131-165(-187.5)×  $7-10\,\mu m$  ( $\overline{x}= 147 \times 9\mu m$ , n=20), fasciculate, cylindric-clavate, elongate, tapering towards rounded ends, slightly curved, 19-23(-25)-septate, slightly constricted, hyaline, with minutely globose cells, smooth-walled. Asexual state: Unknown.

*Cultural characteristics*: Ascospores germinating on MEA within 12 h and germ tubes produced from both ends. *Colonies* growing on MEA slowly, less than 5 mm in 7 days at 28 C, slightly effuse, undulate to fimbriate at margin, dark, with white or pale brown aerial mycelium, asexual spores not formed within 60 days.

*Material examined*: THAILAND, Chiang Mai, Muang, Huai Kok Ma, Doi Su Thep, N18°48.365' E98°54.522', elev. 1015 msl., on dead wood of an unidentified tree, 21 April 2011, Saranyaphat Boonmee, DST-03 (MFLU 11–0134, **epitype** designated here; PDD 104453, **iso-epitype**), ex-type living culture = MFLUCC 11–0375 = BCC 52033 = ICMP 20072.

Notes: One fresh tubeufia-like specimen with globose, light-coloured ascomata, numerous pseudoparaphyses, cylindrical, elongated asci and cylindrical, many septate, hyaline ascospores is identical with Tubeufia miscanthi (Hsieh et al. 1998). Tubeufia miscanthi was transferred to Taphrophila (T. miscanthi) by Réblová and Barr (2000) as it has elongate fusiform and fasciculate ascospores arranged in the ascus. However, Tubeufia miscanthi is morphologically different from the type species Taphrophila cornu-capreoli (Scheuer 1988; Hsieh et al. 1998). Our data indicates that Taphrophila miscanthi should be referred to Helicoma as it lies in Clade A, supported with 95 % BS and 1.00 PP (Fig. 2). Samuels et al. (1979), and Barr (1980) considered T. miscanthi to be identical to T. paludosa but this is not supported here. We epitypify this name here with the new collection from Thailand.



Fig. 16 *Helicoma miscanthi* (MFLU 11–0134, epitype). a Herbarium specimen. b Ascomata on substrate. c L.S. of ascoma. d Peridium. e Pseudoparaphyses. f, g Asci. h, i Ascospores. j Germinating ascospore. k,

*Helicoma siamense* Boonmee & K.D. Hyde, **sp. nov.**, MycoBank: MB 804557, *Facesoffunginumber*: FoF 00181 Figs. 17–18

*Etymology*: in reference to its occurrence in Thailand (Siam). *Holotype*: MFLU 10–0053

*Saprobic* on dead wood. **Sexual state**: *Ascomata* 221–306 $\mu$ *m* high×180–268 $\mu$ *m* diam. ( $\bar{x}$ = 270 × 233 $\mu$ *m*), superficial, solitary, scattered, with basal subiculum, globose to subglobose, reddish-brown to dark brown, with a central ostiole,

**l** Colonies on MEA from surface and reverse. *Scale bars*:  $\mathbf{b}-\mathbf{c} = 100 \,\mu m$ ,  $\mathbf{d} = 40 \,\mu m$ ,  $\mathbf{e} = 5 \,\mu m$ ,  $\mathbf{f}-\mathbf{j} = 50 \,\mu m$ ,  $\mathbf{k}-\mathbf{l} = 10 \,\text{mm}$ 

covered by brown mycelium, collapsing when dry. *Peridium* 30–48  $\mu$ m wide, composed of several-layers of cells of *textura* angularis, with outer layer cells darkened and inner layer cells pale brown to hyaline. *Hamathecium* comprising numerous, wide, filiform, septate, branched, hyaline pseudoparaphyses. As ci (123-)127.5–139(-144)×(14-)17–20  $\mu$ m ( $\bar{x}$ = 133.5 × 18 $\mu$ m , n=20), 8-spored, bitunicate, cylindrical to clavate, short-pedicellate,with a rounded apex. Ascospores (49.5-)59–64.5(-68)×5–7.5  $\mu$ m ( $\bar{x}$ = 62 × 6.5  $\mu$ m , n=20),



**Fig. 17** *Helicoma siamense* (MFLU 10–0053, **holotype**). **a** Ascomata (*arrows*). **b** L.S. of ascoma. **c** Peridium. **d** Pseudoparaphyses embedded in a gelatinous matrix. **e**–**g** Asci. **h**–**n** Ascospores with multiple cells. *Scale bars*: **a**–**b** =  $100 \mu m$ , **c**, **h**–**n** =  $20 \mu m$ , **d** =  $5 \mu m$ , **e**–**g** =  $50 \mu m$ 



Fig. 18 *Helicoma siamense* (MFLU 10–0053, holotype). a Germinating ascospore. b, c Colonies on MEA, surface and reverse. Note black colonies. d Mycelium development in culture. e–I Conidiophores and conidia. *Scale bars*: a, g–I = 20 $\mu$ m, b–c = 10 mm, d–f = 5 $\mu$ m

overlapping 2–3-seriate, cylindric-fusiform, tapering towards rounded ends, widest at supramedian part, slightly curved, 11– 12-septate, not constricted at septa, hyaline, smooth-walled. **Asexual state**: hyphomycetous, helicosporous. *Conidiophores* macronematous, 2–3  $\mu$ m wide, erect, smooth, pale brown to brown, smooth. *Conidiogenous cells* holoblastic. *Conidia* helicosporous, 24–36  $\mu$ m diam. when coiled, filaments 7– 10  $\mu$ m wide, coiled 2–3 times, multiseptate, slightly constricted, darkened at septa, partly heavily pigmented, vertucose, roughwalled, brown to reddish-brown, narrow at base and wide at upper half on uncoiling.

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*Cultural characteristics*: Ascospores germinating on MEA within 24–36 h and germ tubes produced from many cells. *Colonies* growing on MEA slowly, 6 mm in 7 days at 28 C, flat, sparsely hairy, fimbriate, dark brown. *Mycelium* partly superficial, partly immersed, composed of branched, septate, smooth, pale brown to reddish-brown, red pigmented hyphal filaments.

*Material examined*: THAILAND, Chiang Rai, Muang, Khun Korn Waterfall, elev. 671 msl., N19°51–54' E 99°35.39', on decaying wood of an unidentified tree, 13 November 2009, Saranyaphat Boonmee, KK-09 (MFLU 10–0053, **holotype**; PDD 104454, **isotype**); ex-type living culture = MFLUCC 10–0120 = BCC 52298 = IFRD 2184.

*Notes*: This taxon is morphologically similar to *Tubeufia* and was initially identified as a species of *Tubeufia sensu stricto* (Samuels et al. 1979; Sivanesan 1984; Rossman 1987). *Helicoma siamense* is different from *T. javanica* in size, shape and dimensions of the ascomata and ascospores and produces helicoma-like conidia that are multiseptate, helicoid with coloured, verrucose, conidial filaments. Phylogenetic analysis shows that *H. siamense* clusters with *Helicoma sensu stricto* (Clade A, Fig. 2) with high support (97 % BS and 1.00 PP). It differs morphologically and phylogenetically from other taxa in this Clade and thus is introduced as a new species.

Helicoma chiangraiense Boonmee & K.D. Hyde, sp. nov., MycoBank: MB 804558, *Facesoffunginumber*: FoF 00182 Fig. 19

*Etymology*: In reference to its occurrence in Chiangrai, Thailand.

Holotype: MFLU 10–0048

Saprobic on dead wood. Sexual state: Ascomata  $(183-)240-285 \,\mu m$  high ×  $(189-)241-296 \,\mu m$  diam.  $(\bar{x}=242.5\times254\mu m)$ , superficial, solitary, scattered, subglobose, ellipsoidal-ovate, with few hyphae developing from ascomatal base on substrate, dark brown to black, velvety, ostiolate. Peridium 28-34 µm wide, comprising 3-4 layers, composed of cells of textura angularis, with inner cells brown and outer cells dark brown. Hamathecium comprising ca.  $0.5-1 \mu m$  wide, numerous, filiform, hyaline pseudoparaphyses. Asci (146-)153-179.5×18-23(-26) µm  $(\bar{x}=163.5\times21\mu m, n=20)$ , 8-spored, bitunicate, cylindrical, apically thickened and rounded, with a  $14.5-24 \mu m \log ped$ icel. Ascospores (63-)72–93.5×5–7.5  $\mu m$  ( $\bar{x}$ = 81 × 6 $\mu m$ , n= 20), overlapping fasciculate, cylindric-fusiform, with tapering and rounded ends, straight to slightly curved, 11-13-septate, not constricted at septa, hyaline, smooth-walled. Asexual state: Unknown.

*Cultural characteristics*: Ascospores germinating on MEA within 12 h and germ tubes produced at both ends. *Colonies* growing slowly on MEA, reaching less than 5 mm in 7 days at 28 C, effuse, velvety, with a convex surface, with dark continuous margin, asexual spores not formed within 60 days.

*Material examined*: THAILAND, Chiang Rai, Muang, Doi Pui, elev. *ca.* 403–936 msl., on dead wood of *Fagaceae*, 15 August 2009, Saranyaphat Boonmee, DP-01 (MFLU 10– 0048 **holotype**; PDD 104455 **isotype**); ex-type living culture = MFLUCC 10–0115 = BCC 39624, 39625 = IFRD 2195 = ICMP 20068.

*Notes*: *Helicoma chiangraiense* differs from other species of *Helicoma* in having a sexual morph of dark brown to black, shiny, non setose ascomata with distinct ostioles (Fig. 19a). *Helicoma chiangraiense* groups with the *Helicoma sensu stricto* (Clade A, Fig. 2) with high support (92 % BS and 0.98 PP).

*Helicoma fagacearum* Boonmee & K.D. Hyde, sp. nov., MycoBank: MB 804557, *Facesoffunginumber*: FoF 00183 Fig. 20

*Etymology*: in reference to its occurrence on *Fagus*.

Holotype: MFLU 11-0138

Saprobic on dead wood. Sexual state: Ascomata 256- $300(-324) \ \mu m \ high \times 235 - 258(-265) \ \mu m \ diam.$  $(\bar{x}=282\times 251\mu m)$ , superficial, solitary, scattered, with a subiculum composed of dark brown hyphae, with black stalk, globose to subglobose, broadly ellipsoid-ovate, yellowish or brownish, pale brown, ostiolate, collapsing, brown when dry. Peridium 43–51 µm wide, comprising several layers of angular and prismatic cells, with inner cells pale brown, with outer cells reddish-brown to brown. Hamathecium with numerous, ca.  $1.5 \,\mu m$  wide, filiform, septate, branched, hyaline pseudoparaphyses. Asci (121-)134–160(–179)×10–14  $\mu m$  $(\bar{x}=144 \times 12 \mu m, n=20)$ , 8-spored, bitunicate, elongate-cylindrical, apically thickened when young, pedicellate, rounded at apex. Ascospores (63-)71-86.5 × 4-6.5  $\mu m$  ( $\bar{x}$ = 78 × 5 $\mu m$  , n=20), overlapping 2–3-seriate, cylindric-fusiform, tapering towards rounded ends, straight to slightly curved, 9-12(-13)septate, not constricted at septum, hyaline, pale brown at maturity, guttulate when young, smooth-walled. Asexual state: Unknown.

*Cultural characteristics*: Ascospores germinating on MEA within 12 h and germ tubes produced at both ends. *Colonies* growing on MEA slowly, reaching less than 5 mm in 7 days at 28 C, slightly convex on surface, with undulating margin, white or pale brown to dark brown, turning dark with age, asexual spores not formed within 60 days.

*Material examined*: THAILAND, Chiang Rai, Muang, Doi Pui, elev. *ca.* 403–936 msl., on dead wood of *Fagaceae*, 10 May 2011, Saranyaphat Boonmee, DP-04 (MFLU 11–0138 **holotype**; PDD 104456 **isotype**); ex-type living culture = MFLUCC 11–0379 = BCC 52030 = ICMP 20071.

*Notes*: *Helicoma fagacearum* was found on wood of *Fagaceae* in northern Thailand. Morphologically, this species is similar to *Helicoma miscanthi* in its coloured ascomata with yellowish white surface, brown peridium and pale brown ascospores. An asexual morph did not develop in culture. Our phylogenetic study shows that *Helicoma fagacearum* groups with *Helicoma sensu stricto* (Clade A, Fig. 2) with a good support (89 % BS and 0.99 PP).

*Helicomyces* Link, Mag. Gesell. naturf. Freunde, Berlin 3(1–2): 21 (1809), *Facesoffunginumber*: FoF 00212

Saprobic on woody substrata. Mycelium composed of partly immersed and partly superficial, pale brown, septate, sparsely branched hyphae, with masses of crowded conidia. **Sexual state**: Ascomata superficial, seated on a thin subiculum, uniloculate, subglobose, clavate to obovate, coriaceous, solitary to gregarious, pale brown to reddish-brown, centrally ostiolate, perhaps collapsing when dry, with radiating mycelium or appendages at base. Peridium composed of



Fig. 19 *Helicoma chiangraiense* (MFLU10–0048, holotype). a Superficial ascomata on substrate. White oozing mass of ascospores at apex of ascomata. b L.S. of ascoma. c. C.S. of peridium. d Pseudoparaphyses embedded in a mucilaginous matrix. e, f Asci. g–i Ascospores. j

Germinating ascospore. **k**, **l** Colonies on MEA from surface and reverse, colonies dark brown. *Scale bars*: **a–b**, **e–f** =  $100 \mu m$ , **c** =  $20 \mu m$ , **d** =  $5 \mu m$ , **g–j** =  $50 \mu m$ , **k–l** = 10 mm

cells of *textura angularis*, with external pale yellow, or brownish to brown layer, with inner hyaline layer. *Hamathecium* comprising numerous  $1-2 \mu m$  wide, filiform septate, branched, anastomosing, hyaline pseudoparaphyses. *Asci* 8spored, bitunicate, fissitunicate, saccate or cylindric-clavate, apically rounded, with or without an ocular chamber, long pedicellate. *Ascospores* overlapping fasciculate, elongate,



cylindric-subfusiform or narrowly oblong, tapering towards narrow, subacute ends, 10–11-septate, not constricted at septum, hyaline, occasionally pale brown, guttulate when immature, smooth-walled. **Asexual state**: *Conidiophores* macronematous, erect, short, septate, thick-walled, pale to moderately dark brown. *Conidiogenous cells* monoblastic or polyblastic, terminal or intercalary, integrated, subhyaline, denticulate. *Conidia* loosely coiled  $2\frac{1}{2}$ –4 times, becoming loosely uncoiled in water, conidial filament 4.5–6  $\mu m$  wide, rounded at apical end, hyaline to pale yellow, multiseptate, with up to 56-septate, slightly constricted at septum, smoothwalled.

## Type species: Helicomyces roseus Link

Notes: The genus Helicomyces Link (1809) typified by H. roseus Link is characterized by slender, loosely coiled, multiseptate, hyaline, helicoid conidia that are filamentous and white to pinkish in mass. Helicomyces roseus is frequently associated with an asexual state referred to as Tubeufia cylindrothecia as first determined by Seaver and Waterston (1940) and later by Barr (1980). Tsui and Berbee (2006) and Tsui et al. (2006, 2007) have shown that species referred to as Helicomyces are polyphyletic with sexual states in Acanthostigma and Tubeufia. According to our phylogenetic study (Fig. 2), we therefore treat Clade G as Helicomyces sensu stricto based on authentic sequences of Helicomyces roseus CBS 283.51 with 76 % BS and 0.99 PP support. Two isolates of Tubeufia paludosa (CBS 120503 as epitype and AR 4206) and two species of Helicosporium (H. indicum and H. talbotii) cluster with an isolate of H. roseus CBS 283.51 in Helicomyces sensu stricto.

*Type species*: *Helicomyces roseus* Link, Mag. Gesell. naturf. Freunde, Berlin 3(1-2): 21 (1809), *Facesoffunginumber*: FoF 00184 Fig. 21

Saprobic on woody substrata. Mycelium partly immersed, partly superficial, pale brown, septate, sparsely branched hyphae, with masses of crowded conidia. Sexual state: Unknown. Asexual state: Conidiophores erect,  $3-4 \times 2-3 \mu m$  ( $\overline{x}=4 \times 3 \mu m$ , n=5), septate, thick-walled, pale to moderately dark brown, macronematous, short. Conidiogenous cells monoblastic or polyblastic, terminal or intercalary, integrated, subhyaline, denticulate. Conidia (40-)47–65(–75)  $\mu m$  diam., and conidial filament 4.5–6 $\mu m$  wide ( $\overline{x}=54 \times 6 \mu m$ , n=20), with (298.5-)360–398 $\mu m$  long, loosely coiled 2½–4 times, becoming loosely uncoiled in water, rounded at apical end, bright, hyaline to pale yellow, multiseptate, up to 56-septate, slightly constricted at septum, smooth-walled.

*Material examined*: USA, North Carolina, Bearwallow Cove, on rotten wood, W.W. Diehl, 4 January 1927, Detr: J.A. Stevenson (BPI 421361).

*Helicomyces paludosa* (P. Crouan & H. Crouan), Boonmee & K.D. Hyde, **comb. nov**., *Index Fungorum number*: IF 550689, *Facesoffunginumber*: FoF 00185 Fig. 22  $\equiv$  *Nectria paludosa* P. Crouan & H. Crouan, Florule du Finistere p. 38. 1867

 $\equiv$  *Tubeufia paludosa* (P. Crouan & Crouan) Rossman, Mycologia 69(2): 383 (1977)

Saprobic on decorticated or decaying woody and herbaceous substrates, in terrestrial habitats, widespread in temperate to tropical regions. Sexual state: Ascomata (267-)278-297(-312)  $\mu m$  high×180-203  $\mu m$  diam., superficial, seated on a thin subiculum, uniloculate, subglobose, clavate to obovate, coriaceous, solitary to gregarious, pale brown to reddish-brown, centrally ostiolate, collapsing when dry, with radiating mycelium or appendages at base. Peridium composed of cells of textura angularis, with outer pale yellow, or brownish to brown layer, with inner hyaline layer connected with membranous tissues. Hamathecium comprising numerous,  $1-2\mu m$  wide, filiform, septate, branched, anastomosing, hyaline pseudoparaphyses. Asci 112-152(-158)×12- $16 \mu m$  ( $\bar{x}= 128 \times 14 \mu m$ , n=20), 8-spored, bitunicate, fissitunicate, saccate or cylindric-clavate, sessile or with a pedicel, sometimes as long as ca. 21–24(-33)  $\mu m$ , apically rounded, with or without an ocular chamber. Ascospores  $(53-)59-73(-78)\times 4-6\,\mu m$  ( $\bar{x}=65\times 5\mu m$ , n=20), overlapping fasciculate, elongate, cylindric-subfusiform or narrowly oblong, tapering towards narrow, subacute ends, (9-)10-11(-13)-septate, not constricted at median septum, hyaline, occasionally pale brown, guttulate when immature, smoothwalled. Asexual state: Unknown.

*Material examined*: USA, Tennessee, Blount Co., Great Smoky Mountains National Park, 25 mi W Gatlinburg, Cades Cove, Gregory Ridge Trail, alt. 1950 ft. 35°33'45"N 83°50' 45"W, on rotten wood of unindentified angisoperm, A.Y. Rossman, 6 September 2005 (BPI 871087), living culture = CBS 120503 = AR 4206.

Notes: Nectria paludosa P Crouan & H Crouan was placed in Tubeufia as T. paludosa (P. Crouan & H. Crouan) Rossman based on its bitunicate asci (Rossman 1977). Tubeufia paludosa was also considered an earlier name for T. javanica, by Rossman (1977). Barr (1980) considered T. paludosa dissimilar from T. javanica, but accepted the synonymy in view of the similar coloured ascomata and cylindrical ascospores. The original descriptions of T. paludosa and T. javanica are similar in having ovoid, translucent, light-colored ascomata, filiform, cylindrical asci and filiform, hyaline and guttulate ascospores (Saccardo 1883; Saccardo and Sydow 1899). However, the illustrations of Tubeufia javanica in Penzig and Saccardo (1904) and T. paludosa in Samuels et al. (1979) and Sivanesan (1984) indicate there are differences in structure of the ascomata. Samuels et al. (1979) examined and described T. paludosa, and considered the asexual state found near the ascomata to be helicomyces-like. Tsui et al. (2006, 2007), Tsui and Berbee (2006), Schoch et al. (2009) and Promputtha and Miller (2010) investigated the molecular phylogeny of Tubeufia paludosa. Their phylogenetic analyses Fig. 21 *Helicomyces roseus* (BPI 421361). **a** Conidia arise directly from hyphal cells on natural substrata. **b**, **c** Conidiophores with attached conidia. **d**-**g** Conidia. *Scale bars*: **a**, **g** =  $100 \mu m$ , **b**-**f** =  $50 \mu m$ 



suggest that *T. paludosa* is related with the helicosporous asexual morphs. We therefore consider the collection BPI 871087 to be *Tubeufia paludosa* (CBS 120503 as epitype). On the basis of phylogenetic placement (Clade G, Fig. 2), two cultures of *Tubeufia paludosa* (from CBS 120503 and AR 4206) are related with an asexual species *Helicosporium indicum* Rao & D. Rao with 73 % BS and 0.96 PP supports. An authentic strain of *Helicomyces roseus* (CBS 283.51) and *Helicosporium talbotii* (MUCL 33010) cluster with 92 % BS support and also form a subclade with *Tubeufia paludosa* with 76 % BS and 0.99 PP support within *Helicomyces sensu stricto* (Clade G).

*Helicosporium* Nees, Syst. Pilze (Würzburg): 68 (1816) [1816–17], *Facesoffunginumber*: FoF00213

*Helicotrichum* Nees & T. Nees, Nova Acta Acad. Caes. Leop.-Carol. 9: 246 (1818) *?Drepanospora* Berk. & M.A. Curtis [as 'Drepanispora'], in Berkeley, Grevillea 3(no. 27): 105 (1875)

Saprobic on leaves, bark, and twigs, or on stromata of Diatrype stigma, Diatrypaceae (Xylariales), on decorticated or decaying wood, in terrestrial habitats or submerged in freshwater, widespread in temperate to tropical regions. Sexual state: Ascomata superficial, solitary, scattered, globose-subglobose, bright yellow brown to yellow orange, collapsing when dry, darkened near ostiole. Peridium of several layers, composed of bright yellow cells of textura prismatica to angularis. Hamathecium comprising numerous, filiform, septate, branched, hyaline pseudoparaphyses. Asci 8-spored, bitunicate, cylindric-clavate, apedicellate, thickened at apex, with an acute ocular chamber. Ascospores biseriate, elongate-fusiform, tapering towards narrowly subacute ends, trans-septate, hyaline. Asexual state: hyphomycetous, helicosporous.

Fig. 22 Helicomyces paludosa (BPI 871087, CBS 120503; reillustrated from Hyde et al. 2013). **a** Ascomata seated on sparse hyphae. **b** Squash mount of ascoma showing peridium. **c** Pseudoparaphyses. **d** Asci with thickened apex. **e**–**g** Ascospores. Note asci and ascospores in cotton blue reagent. *Scale bars*: **a** =  $100 \,\mu m$ , **b**, **e**–**g** =  $20 \,\mu m$ , **c** =  $5 \,\mu m$ , **d** =  $50 \,\mu m$ 



*Conidiophores* macronematous, mononematous, setiferous, erect, septate, unbranched, dark brown, fertile in middle, sterile, tapering towards narrow subacute at apex, smooth-walled, arising directly on substrate, from thick-walled, close-ly septate, recumbent hyphae, crowded or in fascicles, glistening, light coloured. *Conidiogenous cells* polyblastic, intercalary, rarely terminal, with lateral minute denticles each with single conidium. *Conidia* coiled  $3\frac{1}{2}-4\frac{1}{2}$  times, tightly to loosely coiled, rounded at apical end, truncate at base, hyaline, 7–13-septate, slightly constricted at septa, smooth-walled.

## Type species: Helicosporium vegetum Nees

Notes: Helicosporium was introduced by Nees (1817) based on H. vegetum. At present Helicosporium species are polyphyletic within the family Tubeufiaceae and are related with sexual states in the genera Acanthostigma, Acanthostigmina and Tubeufia (Tsui and Berbee 2006; Tsui et al. 2006, Fig. 2). In our analysis, the type species of Helicosporium, H. vegetum is linked with Tubeufia cerea (Berk. & M.A. Curtis) Höhn. (Clade D, Fig. 2) with high support (99 % BS and 1.00 PP) and thus synonymized. In Helicosporium ascomata are bright yellow brown to yellow orange and formed on stromata of other fungi, and ascospores are elongate-fusiform, tapering towards narrowly subacute ends, trans-septate, hyaline, with hyaline, helicoid conidia and borne directly on small denticles on setiferous conidiophores which are terminally sterile. The ex-type cultures of Helicoma vaccinii (CBS 216.90) and Acanthostigma

*patagonica* (MVB 573 BBB) cluster in Clade D (Fig. 2) with strains of *Helicosporium sensu stricto*. *Helicoma vaccinii* produces terminal conidia (Carris 1989) while no asexual state is known for *Acanthostigma patagonica* (Sánchez et al. 2012).

*Type species: Helicosporium vegetum* Nees, Syst. Pilze (Würzburg): 68 (1816) [1816–17], *Facesoffunginumber*: FoF 00186 Figs. 23–24

*≡ Tubeufia cerea* (Berk. & M.A. Curtis) Höhn., *Sber. Akad. Wiss. Wien*, Math.-naturw. Kl., Abt. 1 128: 562 (1919)

= Sphaeria cerea Berk. & M.A. Curtis, Grevillea 4(no. 31): 108 (1876)

Saprobic on leaves, bark, and twigs, or on stromata of Diatrype stigma, Diatrypaceae (Xylariales), on decorticated or decaying wood, in terrestrial habitats, or submerged in freshwater, widespread in temperate to tropical regions. Sexual state: Ascomata 180–211  $\mu$ m high×186–226  $\mu$ m diam., superficial, solitary, scattered, globose-subglobose, bright yellow brown to yellow orange, collapsing when dry, darkened near ostiole. Peridium 23-26 µm wide, comprising several layers, composed of bright yellow cells of textura prismatica to angularis. Hamathecium comprising numerous,  $1-1.5 \mu m$ wide, filiform, septate, branched, hyaline pseudoparaphyses. Asci 68-82(-92)×(7-)8-12 $\mu m$  ( $\bar{x}$ = 75 × 10 $\mu m$  , n=20), 8spored, bitunicate, cylindric-clavate, apedicellate, thickened at apex, with an acute ocular chamber. Ascospores  $35-46 \times$  $3-5\,\mu m$  ( $\overline{x}=39\times4\mu m$ , n=10), biseriate, elongate-fusiform, tapering towards narrowly subacute ends, 8-9-septate, slightly

Fig. 23 Helicosporium cereum (BPI 1107327 as Tubeufia cerea). a Ascomata on fungal stromata. b Section of ascoma. c Peridium. d Pseudoparaphyses. e, f Asci. g–i Ascospores. Scale bars: a =  $200 \mu m$ , b =  $100 \mu m$ , c =  $50 \mu m$ , d =  $5 \mu m$ , e–i =  $20 \mu m$ 



curved, hyaline, smooth-walled. Asexual state: hyphomycetous, helicosporous. *Conidiophores* (98-)107–220  $\mu m$ long×3–5 $\mu m$  ( $\bar{x}$ = 148 × 4 $\mu m$ , n=20), macronematous, mononematous, setiferous, erect, septate, unbranched, dark brown, fertile in middle, sterile, tapering toward narrow subacute at apex, smooth-walled, arising directly on substrate, from thick-walled, closely septate, repentent hyphae, crowded or in fascicles, glistening, light coloured. *Conidiogenous cells* polyblastic, intercalary, rarely terminal, with lateral minute denticles each with single conidium. *Conidia* 10–15 $\mu m$  diam. and conidial filament 1–2 $\mu m$  wide ( $\bar{x}$ = 13 × 1.5 $\mu m$ , n=20), coiled 3½–4½ times, tightly to loosely coiled, rounded at apical end, truncate at base, 7–13-septate, slightly constricted at septa, hyaline, smooth-walled.

*Notes*: Von Höhnel (1919) transferred *Sphaeria cerea* Berk. & M.A. Curtis to *Tubeufia* as *T. cerea*, based on bitunicate asci, and narrow elongate, multi-septate ascospores. *Tubeufia cerea* is often found on stromata of species belonging in *Diatrypaceae (Xylariales)*. Morphologically, *Tubeufia cerea* was distinguished from all other species in the genus by its yellow brown to yellow orange ascomata (Bigelow and Barr 1963; Booth 1964; Samuels et al. 1979; Barr 1980). Booth (1964) provided a description and illustration of *Tubeufia cerea* based on the type specimen and provided a list of synonyms. The asexual state found near the ascomata were identified as *Helicosporium vegetum* Nees by Booth (1964), Samuels et al. (1979) and Barr (1980). Phylogenetic analysis links *Tubeufia cerea* with *Helicosporium vegetum* with high support (Tsui and Berbee 2006; Tsui et al. 2006) and this is supported in our study (Clade D, Fig. 2). *Tubeufia cerea* (Berk. & M.A. Curtis) Höhn. is therefore treated as a synonym of *Helicosporium vegetum*.

*Material examined*: USA, Virginia, Falls Church, on rotten wood, C.L. Shear, May 1936; Detr: J.A. Stevenson (BPI 447464, material of asexual state); Virginia, Shenandoah National Park, Beams Gap, on stromata of *Diatrype stigma (Diatrypaceae, Xylariales)*, on dead wood, A.Y. Rossman (1925), 19 June 1983; Detr: A.Y. Rossman (BPI 1107327, sexual state of *Tubeufia cerea*).

*Kamalomyces* R.K. Verma, N. Sharma & Soni, Forest Fungi of Central India: 196 (2008)

Fig. 24 Helicosporium vegetum (BPI 447464) a Conidiophores with conidia on natural substrate. **b**, **c** Conidiophores with minute denticles (*arrows*). **d**–**f** Conidia stained in cotton blue in **f**. Scale bars:  $\mathbf{a} = 100 \,\mu m$ ,  $\mathbf{b} = 50 \,\mu m$ ,  $\mathbf{c} = 5 \,\mu m$ ,  $\mathbf{d}$ –**f** =  $10 \,\mu m$ 



Saprobic on dead bamboo. Sexual state: Ascomata forming on a subiculum of crowded black mycelium, superficial, clustered to solitary, globose to subglobose, stalked, ostiolate. Peridium comprising 3–4 layers of darkened cells of textura angularis, dull at margin. Hamathecium comprising filiform, branched pseudoparaphyses, embedded in a gelatinous matrix. Asci 8-spored, bitunicate, thick-walled, saccate-clavate, pedicellate, with an ocular chamber. Ascospores fusiform to clavate, slightly tapering toward rounded ends, trans-septate with crowded septa, straight or slightly curved, upper part broad, hyaline (from Boonmee et al. 2011). Asexual state: Unknown.

*Notes*: This genus has ascomata that form on a subiculum of crowded, black mycelium and fusiform to clavate, transseptate, hyaline ascospores with crowded septa (Boonmee et al. 2011). There are presently two species (Dubey and Neelima 2013), both from bamboo.

ofEtymology: neo – a new genus similar to Acanthostigma.in.Saprobic on dead wood. Sexual state: Ascomata superficedcial, solitary, scattered, globose to subglobose, reddish-brown

Facesoffunginumber: FoF00214

cial, solitary, scattered, globose to subglobose, reddish-brown to dark brown, to black, surrounded by black shining setae, tapering towards an acute tip, ostiolate. *Peridium* composed of several layers of brown cells of *textura angularis*. *Hamathecium* comprising numerous, filiform, septate, branched, hyaline pseudoparaphyses. *Asci* 8-spored, bitunicate, cylindric-clavate, with a short rounded pedicel, with thick and rounded apex, ocular chamber not observed. *Ascospores* fasciculate, cylindrical, narrowly fusiform, tapering towards narrow, subacute ends, trans-septate, hyaline, smooth-walled. **Asexual state**: hyphomycetous, helicosporous. *Conidiophores* micronematous, holoblastic, polyblastic, dentate on creeping hyphae, up to  $5 \mu m \log n$ 

Neoacanthostigma Boonmee, Bhat & K.D. Hyde, gen.

nov., Index Fungorum number: IF 550576,

hyaline. *Conidia* helicosporous, coiled in  $1-2\frac{1}{2}$  dimensional times, tapering towards rounded ends, multiseptate, hyaline, with mucilaginous pads at ends.

*Type species: Neocanthostigma fusiforme* Boonmee, Bhat & K.D. Hyde

Notes: The type species of Neoacanthostigma, N. fusiforme, clusters with the type strain of Acanthostigma septoconstrictum Promp. & A.N. Mill. in an individual clade in the multigene analysis (Clade M, Fig. 2) with high support (99 % BS and 1.00 PP). These taxa appear to be related, therefore, we synonymize Acanthostigma septoconstrictum under Neoacanthostigma based on phylogenetic suggestion. Two strains of Acanthostigma filiforme (ANM101, ex-type and ANM514) also cluster in Clade M, although with weak support (Fig. 2) and is synonymised under *Neoacanthostigma*. Neoacanthostigma is similar to Acanthostigma in that ascomata are covered with setae, asci are bitunicate, ascospores are cylindrical to narrowly fusiform and the asexual state is helicosporous (Réblová and Barr 2000). Species in this genus would previously have been referred to Acanthostigma, while their asexual states are helicoma-like or helicomyceslike. These genera are morphologically distinct. In Neoacanthostigma the ascomata have long setae and the ascospores are narrowly fusiform to symmetrical, while in Acanthostigma the ascomatal setae are short and the ascospores are asymmetrical, fusiform to clavate (Réblová and Barr 2000; Boonmee et al. 2011). The hyaline conidiophores are moniliaceous and micronematous formed directly from mycelium, not typical of Helicoma, Helicomyces or Helicosporium. Phylogenetically species of Neocanthostigma in Clade M are basal to Clades A-L (Fig. 2).

*Neoacanthostigma fusiforme* Boonmee, Bhat & K.D. Hyde, **sp. nov.**, *Index Fungorium number*: IF 550577, *Facesoffunginumber*: FoF 00187 Figs. 25–26

*Etymology*: in reference to the symmetrical fusiform ascospores.

Holotype: MFLU 11-1146

Saprobic on dead wood. Sexual state: Ascomata  $(111-)126-138 \,\mu m$  high  $\times 98-100(-125) \,\mu m$  diam.  $(\bar{x}=125\times107\mu m)$ , superficial, solitary, scattered, globose to subglobose, reddish-brown to dark brown to black, surrounded by shining black setae (27-)48-73 µm long, tapering towards an acute tip, ostiolate. Peridium 13-14 µm wide, composed of several layers of brown cells of textura angularis. Hamathecium comprising ca.  $1.5-2 \mu m$  wide, numerous, filiform, septate, branched, hyaline pseudoparaphyses. Asci 71-84×10-11(-12)  $\mu m$  $(\bar{x}=79 \times 11 \mu m, n=20)$ , 8-spored, bitunicate, cylindric-clavate, with a short rounded pedicel, with thick and rounded apex, ocular chamber not observed. Ascospores (32-)40-48×  $3-4.5\,\mu m$  ( $\bar{x}=43\times4\mu m$ , n=20), fasciculate, cylindrical, narrowly fusiform, tapering towards narrow, subacute ends, straight to slightly curved, 5-7-septate, not constricted at septum, with mucilaginous pads at ends, hyaline, smoothwalled. **Asexual state**: hyphomycetous, helicosporous. *Conidiophores* up to  $5\mu m$  long, micronematous, holoblastic, polyblastic, dentate on creeping hyphae, hyaline, smoothwalled. *Conidia* helicosporous, (17-)23–30 $\mu m$  diam. when coiled, conidial filaments  $2\mu m$  wide, coiled in 1–2½ dimensional times, tapering toward rounded ends, multiseptate, not constricted at septa, hyaline, smooth-walled.

*Cultural characteristics*: Ascospores germinating on MEA within 8 h and germ tubes produced at both ends. *Colonies* growing on MEA slowly, less than 5 mm diam in 7 days at 28 C, slightly raised-radially with lobate to entire edge, grayish to pale brown, laterally becoming dark brown. *Mycelium* developing on substrate, superficial, with hyaline to pale brown hyphae.

*Material examined*: THAILAND, Chiang Mai, Mae Taeng, Mushroom Research Centre, N19°17.123' E 98°44. 009', elev. *ca.* 900 msl., on dead wood of an unidentified tree, 23 June 2011, Saranyaphat Boonmee, MRC-03(T) (MFLU 11–1146 **holotype**; PDD 104457 **isotype**); ex-type living culture = MFLUCC 11–0510 = BCC 52383 = ICMP 20073.

New combinations:

*Neoacanthostigma septoconstrictum* (Promp. & A.N. Mill.) S. Boonmee & K.D. Hyde, **comb. nov.**, *Index Fungorum number*: IF 550683

 $\equiv$  Acanthostigma septoconstrictum Promp. & A.N. Mill., Mycologia 102(3): 579 (2010)

*Neoacanthostigma filiforme* (Promp. & A.N. Mill.) S. Boonmee & K.D. Hyde, **comb. nov.**, *Index Fungorum number* IF 550684

 $\equiv$  Acanthostigma filiforme Promp. & A.N. Mill., Mycologia 102(3): 575 (2010)

Podonectria Petch, Trans. Br. mycol. Soc. 7: 146 (1921)

Associated with scale insects. Sexual state: Ascomata superficial, scattered, solitary, subglobose-globose, light yellowreddish, covered with light brown mycelium. Peridium composed of several-layers of pale yellowish brown cells of *textura angularis. Hamathecium* comprising filiform, septate, branched, hyaline pseudoparaphyses, embedded in a gelatinous matrix. Asci 8-spored, bitunicate, cylindro-clavate, short pedicellate. Ascospores 2–3-seriate, clavate to fusiform, hyaline to pale brown, trans-septate, wall minutely verruculose (from Boonmee et al. 2011). Asexual state: parasitic on scale insectis, hyphomycetous, phragmosporous, Tetracrium, by forming holoblastic conidia and borne on sympodially proliferating conidiogenous cells (from Pirozynski 1977).

*Notes*: The genus is tentatively included in *Tubeufiaceae* pending fresh collections and phylogenetic analysis. Its sexual state is compatible with *Tubeufiaceae*, however, the asexual states are atypical in producing conidia on sympodial conidiophores (Pirozynski 1977; Sivanesan 1984; Rossman 1987).

*Type species*: *Podonectria coccicola* (Ellis & Everh.) Petch, Trans. Br. mycol. Soc. 7: 146 (1921)



Fig. 25 *Neocanthostigma fusiforme* (MFLU 11–1146, holotype). a Ascomata on substrate (*arrows*). b L.S. of ascoma. c Setae. d Peridium. e Pseudoparaphyses. f–h Asci. i–k Ascospores. Note spores becoming

*Tamhinispora* K.C. Rajeshk. & Rahul Sharma, Mycosphere 4(2): 166 (2013), *Facesoffunginumber*: FoF00215

yellow when stained in Melzer's reagent in Fig. k. Note the mucilaginous pads at the ends. *Scale bars*:  $\mathbf{a}-\mathbf{b} = 100\,\mu m$ ,  $\mathbf{c}$ ,  $\mathbf{f}-\mathbf{h} = 50\,\mu m$ ,  $\mathbf{d}$ ,  $\mathbf{i}-\mathbf{k} = 20\,\mu m$ ,  $\mathbf{e} = 5\,\mu m$ 

Saprobic on submerged wood. Mycelium mostly semiimmersed or immersed, single or interwoven. Stroma none. Setae and hyphopodia absent. Sexual state: Unknown. Fig. 26 Neocanthostigma fusiforme (MFLU 11–1146, holotype). a Germinating ascospore. b Colonies on MEA. Note colonies are grayish to pale brown. c, d Growth of asexual state on plant tissues produced on the media with and without substrate. e Aerial mycelium in culture. f Conidiophores formed on hyphae (*arrows*). g–j Conidia. *Scale bars*: a = 20  $\mu$ m, b–d = 10 mm, e–f = 5  $\mu$ m, g–j = 10  $\mu$ m



Asexual state: *Conidiophores* absent. *Conidiogenous* cells, semi-macronematous, unbranched, intercalary in hyphae, al-most sessile. *Conidia* solitary, dry, simple, mostly ovoid or irregular, dictyoseptate, smooth-walled, mature conidia dark brown to blackish with apical appendages. *Apical appendages* rudimentary or well-developed, arising from apex of conidia, diverging or radiating, pale to dark brown, septate, apex rounded (from Rajeshkumar and Sharma 2013).

*Type species*: *Tamhinispora indica* K.C. Rajeshk. & Rahul Sharma

*Notes*: This unique genus with only an asexual state was described from submerged wood in India (Rajeshkumar and Sharma 2013). The dark brown conidia are adorned with brown to blackish apical appendages, albeit small, are reminiscent of ascomata of *Tubeufiaceae*. In the phylogenetic analyses it groups basal to Clade F and Clade G of *Tubeufia* and *Helicomyces*, with 0.99 PP support clade (Fig. 2).

*Type species:* **Tamhinispora indica** K.C. Rajeshk. & Rahul Sharma, Mycosphere 4(2): 167 (2013), *Facesoffunginumber*: FoF 00188 Fig. 27

*Thaxteriella* Petr., Annls mycol. 22(1/2): 63 (1924), *Facesoffunginumber*: FoF00216

*Saprobic* on dead bark. *Mycelium* forming a dense velvety subiculum on surface of bark, comprising black hyphae. **Sexual state**: *Ascomata* superficial or slightly embedded on a basal subiculum, solitary or densely gregarious, globose to

turbinate, black, shiny, often with small apical papillae at central ostiolate apex, often collapses when dry. Peridium comprising two strata, outer layer of thick-walled, dark brown cells of textura angularis and inner layer of brown cells of textura globosa. The apical region is composed of less thickwalled cells that disintegrate to form an ostiole. Hamathecium composed of filamentous, septate, branched, anastomosing, hyaline pseudoparaphyses. Asci 8-spored, bitunicate, cylindrical to broadly clavate or subclavate, usually with a short pedicel, thickened at apex with an ocular chamber. Ascospores cylindrical to long fusiform, tapering towards rounded to subacute ends, trans-septate, hyaline. Asexual state: hyphomycetous, helicosporous. Conidiophores erect, up to  $180 \mu m$ long, brown to dark brown, light-coloured at apex. Conidia  $17-21\,\mu m$  diam., pleurogenous, developing on cylindrical pegs arising form cells of conidiophores, 11/2-13/4 times coiled, 5-12-septate, hyaline to pale olivaceous brown (from Sivanesan 1984).

*Notes*: No sequences exist in GenBank for the type species of *Thaxteriella*, *T. corticola* and other species in the genus. *Thaxteriella pezizula* was included in this genus by Petrak (1953) based on morphological consistency with the genus, as recognized by globose or oblate globose, darkly pigmented, shiny, ascomata, collapsing in the middle when dry and filiform ascospores (Berkeley 1876; Linder 1929; Barr 1980; Sivanesan 1984). In addition, Linder (1929) determined



Fig. 27 *Tamhinispora indica* (AMH 9555: holotype; re-illustrated from Rajeshkumar and Sharma 2013). **a–c** Conidial spores formed on natural substrate. **d–h** Immature and mature conidia with developing apical appendages. *Scale bars*:  $\mathbf{e}-\mathbf{i} = 20 \mu m$ ,  $\mathbf{j} = 10 \text{ mm}$ 

that *Thaxteriella pezizula* produced a helicoma-like hyphomycetous asexual state. *Thaxteriella* may therefore be a synonym of *Helicoma*. Boonmee et al. (2011) introduced *Thaxteriella inthanonensis* as a new species in *Thaxteriella*, and this species clusters with *Helicoma sensu stricto* as reported

*Type species:* **Thaxteriella corticola** Petr., Annls mycol. 22(1/2): 63 (1924)

*Thaxteriella pezizula* (Berk. & M.A. Curtis) Petr., Sydowia 7(1–4): 110 (1953), *Facesoffunginumber*: FoF 00189 Fig. 28

 $\equiv$  Sphaeria pezizula Berk. & M.A. Curtis, Grevillea 4(no. 31): 106 (1876)

Saprobic on woody substrates. Mycelium forming a dense velvety subiculum on the surface of the bark, comprising black hyphae. Sexual state: Ascomata 236–374×365–422µm diam., superficial, seated on mycelium, solitary to clustered, scattered on substrate, globose to subglobose, turbinate, dark brown to black, shiny, ostiolate, collapsing on drying. Peridium 44.5–55µm, several layers, somewhat thickened, composed of dark brown cells of textura angularis. Hamathecium of 2–3.5µm wide, filiform, septate, branched, hyaline pseudoparaphyses. Asci (102-)113–146(–151)×25–34µm ( $\bar{x}$ = 128 × 30µm, n=20), 8-spored, bitunicate, broadly cylindric-subclavate, shorted pedicellate, thickened at apex, lacking a distinct ocular chamber. Ascospores 47–61×9.5–

 $13 \mu m$  ( $\overline{x}=53 \times 11 \mu m$ , n=20), overlapping 2–3-seriate, cylindrical to long fusiform, tapering towards rounded ends, 7septate, straight or slightly curved, not constricted at septa, hyaline to pale-yellowish. **Asexual state**: hyphomycetous, helicosporous. *Conidiophores* erect, up to  $180 \mu m$  long, brown to dark brown, light-coloured at apex. *Conidia*  $17-21 \mu m$ diam., pleurogenous, develop on cylindrical pegs arising from cells of conidiophores,  $1\frac{1}{2}-1\frac{3}{4}$  times colied, 5–12-septate, hyaline to pale olivaceous brown (from Sivanesan 1984).

*Material examined*: Unknown location, on dead wood of undetermined timber, collector and date collected are unknown (BPI 800530).

*Thaxteriellopsis* Sivan., Panwar & S.J. Kaur, Kavaka 4: 39 (1977) [1976]

Saprobic on dead wood. Sexual state: Ascomata superficial, borne on a thin, dark brown subiculum, solitary or scattered, globose to subglobose, reddish-brown to dark brown, with brown to dark brown, septate, setae, mostly at the apex. Peridium comprising 3–4 layers of red brown to dark brown cells of textura angularis. Hamathecium comprising filiform, hyaline pseudoparaphyses, embedded in a gelatinous matrix. Asci 8-spored, bitunicate, cylindrical to clavate, apically rounded, short pedicellate, with long apical region with amorphous contents. Ascospores 2–3-seriate, fusiform to clavate, broader above, straight to slightly curved, 5-septate, constricted Fig. 28 Thaxteriella pezizula (BPI 800530). a, b Ascomata collapsing when dry (in a). c L.S. of ascoma. d Peridium. e Pseudoparaphyses. f, g Asci. h–j Ascospores. Scale bars: a–c =  $200 \mu m$ , d =  $50 \mu m$ , e =  $5 \mu m$ , f–g =  $50 \mu m$ , h–j =  $20 \mu m$ 



at septum, hyaline, smooth-walled. **Asexual state**: hyphomycetous, helicosporous. Micronematous conidialike structures, develop directly from hyphae in culture (from Boonmee et al. 2011).

*Notes: Thaxteriellopsis* is a strongly-supported genus in the phylogenetic analysis with 100 % BS and 1.00 PP (Clade B, Fig. 2). The type species, *T. lignicola*, is associated with a moorella-like asexual morph (Subramanian and Sekar 1982). Boonmee et al. (2011) found that *Thaxteriellopsis lignicola* produced micronematous, brown, helicosporous, septate, conidia-like structures directly on the hyphae in culture. For an account of this genus, see Boonmee et al. (2011).

*Type species: Thaxteriellopsis lignicola* Sivan., Panwar & S.J. Kaur, Kavaka 4: 39 (1977) [1976]

Genera excluded from *Tubeufiaceae* (*Tubeufiales*) *Paranectriellaceae* S. Boonmee & K.D. Hyde This new family was introduced by Hyde et al. (2013) to accommodate two genera, namely *Paranectriella* and *Puttemansia*.

Paranectriella (Henn. ex Sacc & D. Sacc) Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 119: 899 (1910)

Notes: The genus Paranectriella based on P. juruana was first recognized as a subgenus of Paranectria by Hennings (1904), which was validated by Saccardo and Saccardo (1905). Von Höhnel (1910) later raised Paranectriella to generic rank. Pirozynski (1977) recognized Paranectriella and redescribed the type species, distinguishing Paranectriella having bitunicate asci from Paranectria with untunicate asci. Barr (1980) suggested that Paranectriella be included in Tubeufiaceae due to its habit as a tropical hyperparasite. Rossman (1987) accepted the genus Paranectriella in Tubeufiaceae, describing P. juruana as a parasitic species with bright white to yellow ascostromata containing many locules in a peripheral layer, bitunicate asci, pseudoparaphyses and ascospores with polar spine-like appendages. The ascostromata occur on hyaline, relatively loose mycelium appearing intermediate between an ascostromata and a subiculum. The associated asexual states of Paranectriella are hyphomycetous, staurosporous, referred to as Araneomyces and Titaea (Saccardo 1876; von Höhnel 1909b; Kirschner and Piepenbring 2006; Hyde et al. 2011). The description and illustration here are based on an authentic specimen of Paranectriella juruana (BPI 632134). Morphologically, P. juruana is characterized by bright ascostromata and ascospores with appendaged ends. These characters are atypical of genera in Tubeufiaceae, which have cylindrical ascospores and hyphomycetous, helicosporous asexual states. Paranectriella was placed in a new family Paranectriellaceae in Hyde et al. (2013).

*Type species: Paranectriella juruana* (Henn.) Henn. ex Piroz., Kew Bull 31: 598 (1977)

 $\equiv$  *Paranectria juruana* Henn., Hedwigia 43(4): 245 (1904) *Notes:* A detailed description of *Paranectriellaceae* based on *P. juruana*, was given in Hyde et al. (2013).

**Puttemansia** Henn., Hedwigia 41: 112 (1902), Facesoffunginumber: FoF00217

Parasitic on lower surface of leaves of Nectandra sp. Sexual state: Ascostromata up to 1 mm diam., superficial, solitary, sometimes in groups, pale yellow to vinaceous buff, stipitate, covered by hairy setae, white to hyaline, septate, multi-loculate. Locules globose-subglobose, slightly flattened at apex, non-ostiolate. Peridium composed of cells of textura prismatica to oblonga, hyaline to pale brown. Hamathecium comprising numerous filiform, branched, anastomosing, hyaline pseudoparaphyses, embedded in a gelatinous matrix. Asci 8-spored, bitunicate, oblong, elongate to cylindrical-clavate, rounded at apex, obtuse at base. Ascospores 1-2-seriate, fusiform, widest near central septum, tapering towards narrow ends, 3-septate, slightly constricted at septum, with continuous basal appendage, hyaline, smooth-walled. Asexual state: hyphomycetous, staurosporous, Guelichia, Tetranacrium (Hyde et al. 2011).

## Type species: Puttemansia lanosa Henn.

Notes: Hennings (1902) introduced the genus Puttemansia as a member of Pezizaceae. Clements and Shear (1931), and Rogerson (1970) placed Puttemansia in Hypocreaceae, (Hypocreales) based on charactistics of hairy appendages and bright ascomata. Pirozynski (1977) and Rossman (1978) provided detailed descriptions of several species of Puttemansia and found that all species had bitunicate asci. Rossman (1978) suggested that Puttemansia was similar to Podonectria and Tubeufia in Tubeufiaceae having bright, fleshy ascomata, bitunicate asci and multi-septate ascospores (Barr 1980). Rossman (1987) provided detailed descriptions of six species and accepted them in Tubeufiaceae, with Puttemansia lanosa Henn. was treated as a synonym of Puttemansia albolanata (Speg.) Höhn. The asexual states of Puttemansia are considered to be the hyphomycetous genera Guelichia Speg., Tetranacrium H.J. Huds. & B. Sutton and Titaea Sacc., as they were commonly associated with Puttemansia lanosa (Hennings 1902; Petrak and Sydow 1936; Barr 1980; Rossman 1987; Hyde et al. 2011). The description and illustration herein, is from an authentic specimen of Puttemansia lanosa (BPI 632856). Morphological features of the fungus are cup-shaped ascostromata, white hairy mycelium, and broadly fusiform appendaged ascospores, characters that are atypical of Tubeufiaceae.

*Puttemansia lanosa* is similar to *Paranectriella juruana* in that ascostromata are light coloured and ascospores three septate with appendages. However, they differ as ascostromata of *Puttemansia lanosa* contain fewer locules (2–10) and ascospores have a basal spine-like appendage. In *Paranectriella juruana* the ascostromata contain many locules (*ca.* 30), while ascospores have spine-like appendages at both ends. The genus *Puttemansia* therefore, is referred to the *Paranectriellaceae*, based on morphological similarities (Fig. 90 in Hyde et al. 2013).

*Type species:* **Puttemansia lanosa** Henn., Hedwigia 41: 112 (1902), *Facesoffunginumber*: FoF 00190 Fig. 29

= *Guelichia paradoxa* Speg., Anal. Soc. cient. argent. 22(2): 174 (1886)

Parasitic on lower surface of leaves of Nectandra sp. Sexual state: Ascostromata up to 1 mm diam., superficial, solitary, sometimes grouped, pale yellow to vinaceous buff, stipitate, covered by flexuous setae,  $200-386 \times 6-9 \mu m$ , white to hyaline, septate, multi-loculate. Locules (244-)259- $306(-567) \ \mu m \ \text{high} \times (314-)371-421 \ \mu m \ \text{diam}.$  $(\bar{x}=334\times 370\mu m)$ , globose-subglobose, slightly flattened at apex, non-ostiolate. Peridium 64-73 µm wide, composed of cells of *textura prismatica* to *oblonga*, hyaline to pale brown. Hamathecium comprising numerous filiform,  $1-2 \mu m$ wide, branched, anastomosing, hyaline pseudoparaphyses, embedded in a gelatinous matrix. Asci (104-)112- $133(-140) \times 16.5 - 22 \,\mu m \ (\bar{x} = 120 \times 19 \,\mu m)$ , 8-spored, bitunicate, oblong, elongate to cylindrical-clavate, rounded at apex, obtuse at base. Ascospores  $(30-)38-50(-56)\times 9 11 \mu m$  ( $\overline{x} = 42 \times 10 \mu m$ ), 1–2-seriate, fusiform, widest near central septum, tapering towards narrow ends, 3-septate, slightly constricted at septum, with continuous basal appendage, hyaline, smooth-walled. Asexual state: hyphomycetous, staurosporous, Guelichia, Tetranacrium (Hyde et al. 2011).

*Material examined*: COSTA RICA, San Pedro de San Ramon, on leaves of *Nectandra* sp. Rol. ex Rottb. (*Lauraceae*), 8 October 1926, Alberto M. Brenes, *Fungi costaricensis* 157 (BPI 632856).

## Pleosporales incertae sedis

Based on Hyde et al. (2013) the *Pleosporales* comprises 31 families whose members are saprobic on dead plant material

Fig. 29 Puttemansia albolanata (BPI 632856) a, b Ascostromata on leaf. c Section of ascoma. d Loose mycelium of ascostromata. e Peridium. f Pseudoparaphyses. g–i Immature and mature asci. j– m Ascospores with basal spinelike appendage. Scale bars: a = 5 mm, b =  $500 \mu m$ , c =  $200 \mu m$ , d– e =  $100 \mu m$ , g–i =  $50 \mu m$ , f =  $5 \mu m$ , j–m =  $20 \mu m$ 



in freshwater, marine, or terrestrial environments, and a large number, especially as asexual states, are pathogens on living plants (Zhang et al. 2009; Boonmee et al. 2012; Liu et al. 2012). Characteristics include perithecial ascomata usually with distinct ostioles, abundant pseudoparaphyses, pedicellate, cylindro-clavate asci usually with distinct ocular chambers and various ascospore types. *Glaxoa* and *Rebentischia*  are not typical of any family in *Pleosporales* and are therefore placed in *Pleosporales incertae sedis*.

Glaxoa Cannon, Syst. Ascom. 15(1-2): 122 (1997)

*Notes: Glaxoa* is a monotypic genus, typified by *Glaxoa pellucida* (Cannon 1997). Herein, we provide a drawing from Cannon (1997), because the type material of *G. pellucida*, which we have examined (IMI 362099), is in poor condition.

*Glaxoa pellucida* can clearly be distinguished from all genera in *Tubeufiaceae* by its 1-septate ascospores. Cannon (1997) placed *Glaxoa* in *Tubeufiaceae* because it was similar to *Letendraea*, which is presently treated as a member of *Pleosporales* (Boonmee et al. 2011). *Glaxoa* is therefore placed in *Pleosporales incertae cedis*.

*Type species:* **Glaxoa pellucida** P.F. Cannon, Syst. Ascom. 15(1–2): 122 (1997), *Facesoffunginumber*: FoF 00191 Fig. 30

*Rebentischia* P. Karst., Fungi Fenniae Exsiccati, Fasc. 9: no. 881 (1869), *Facesoffunginumber*: FoF00218

Saprobic on decaying wood. Sexual state: Ascomata superficial, solitary or scattered, globose-subglobose, black, coriaceous, ostiolate, sometimes collapsed when dry. Peridium thick, composed of cells of textura angularis, with dark brown to black cells. Pseudoparaphyses numerous,  $1-2\mu m$  wide, flexuous, hyaline, septate, branched. Asci 8-spored, bitunicate, fissitunicate, cylindric-clavate, short pedicellate, apically thickened. Ascospores biseriate, elongate-obovoid, trans-septate, brownish to dark brown, light at apex, base tapering to hyaline appendage. Asexual state: Unknown.

#### Type species: Rebentischia pomiformis P. Karst.

Notes: Karsten (1869) introduced the genus *Rebentischia* based on *R. pomiformis. Rebentischia* has been placed in different families (Saccardo 1877, 1883; Müller 1950; Von Arx and Müller 1975). Barr (1980) included *Rebentischia* in *Tubeufiaceae* based on its temperate saprobic habit, darkly pigmented ascomata, bitunicate asci, and elongated, multiseptate ascospores. In addition, Barr (1980) placed *Rebentischia pomiformis* in synonymy with *R. massalongi* as first suggested by Von Arx and Müller (1975). Only two

accepted species, *R. massalongi* (Mont.) Sacc. (=*R. pomiformis* P. Karst.) and *R. unicaudata* (Berk. & Broome) Sacc. were discussed by Barr (1980). Barr (1980) also suggested that coelomycetous taxa, such as asteromella-like fungi found near the ascomata might be the asexual state of *Rebentischia massalongi. Rebentischia pomiformis* has darkened ascospores with a setiform basal appendage appears typical of *Pleosporales.* The genus is therefore included in *Pleosporales incertae sedis.* 

*Type species:* **Rebentischia pomiformis** P. Karst., Fungi Fenniae Exsiccati, Fasc. 9: no. 881 (1869), *Facesoffunginumber:* FoF 00192 Fig. 31

Saprobic on decaying wood of Acer platanoides. Sexual state: Ascomata 249–287 μm high×270–296(-323) μm diam., superficial, solitary or scattered, globose-subglobose, bluish-black, velvety, coriaceous, ostiolate, sometimes collapsed when dry. Peridium thick,  $25-28 \mu m$  wide, composed of dark brown to black-cells cells of textura angularis. *Hamathecium* comprising numerous,  $1-2 \mu m$  wide, flexuous, hyaline, septate, branched pseudoparaphyses. Asci (99-)106- $126 \times 15 - 20 \,\mu m$  ( $\bar{x}= 112.5 \times 17 \,\mu m$ , n=10), 8-spored, bitunicate, fissitunicate, cylindric-clavate, short pedicellate, apically thickened, with an ocular chamber. Ascospores 24- $29(-35) \times 6 - 10 \, \mu m$  ( $\overline{x} = 27 \times 8 \, \mu m$ , n = 20), biseriate, elongateobovoid, 4-septate, slightly constricted at septum, brownish to dark brown, lighter at apex, base tapering to 4–8.5(–14)  $\mu m$ long, narrow, hyaline appendage, smooth-walled. Asexual state: Unknown.

Material examined: FINLAND, Abo, on wood of Acer platanoides L. (Sapindaceae), 7 April 1861, P.A. Karsten,

Fig. 30 Glaxoa pullucida (a,b IMI362099, holotype, c–e redrawn from Cannon 1997). a Herbarium packet. b Surface view. c Ascoma. d Asci and interascal tissue. e Ascospores. Scale bars:  $\mathbf{a}$ - $\mathbf{b}$  = detailed of Glaxoa pullucida specimen, c =  $50 \mu m$ , d–e =  $10 \mu m$ 





Fig. 31 *Rebentischia pomiformis* (FH, holotype). a Scattered ascomata on host. b Ascoma in section. c Peridium. d Wide flexuous pseudoparaphyses. e-g Immature and mature asci. h–l Ascospores with basal appendage. *Scale bars*:  $\mathbf{a} = 200 \,\mu m$ ,  $\mathbf{b} = 100 \,\mu m$ , c, e–g =  $50 \,\mu m$ ,  $\mathbf{d} = 5 \,\mu m$ ,  $\mathbf{h}$ –l =  $10 \,\mu m$ 

Finland Fungi 881, Farlow Herbarium, Harvard University, Herbarium of F. Theissen (FH, **holotype**).

Dothideomycetes genera incertae sedis

One-hundred and sixteen genera are listed as *incertae sedis* in the class *Dothideomycetes* in Lumbsch and Huhndorf (2010). Below we add a further four genera previously placed in *Tubeufiaceae* that cannot be placed in any family or order with certainty.

Acanthostigmella Höhn., Annls mycol. 3(4): 327 (1905), Facesoffunginumber: FoF00219

Saprobic on dead stems of grasses. Sexual state: Ascomata superficial, solitary, scattered, globose-subglobose, dark brown, with 23–74  $\mu$ m long dark brown, apically acute, septate setae, darkened papilla and ostiole. Peridium thin-walled, composed of brown to red brown, 3–  $6.5 \mu$ m diam. cells of textura angularis. Hamathecium lacking pseudoparaphyses. Asci 8-spored, bitunicate, oblong, subclavate to broadly obovoid, with a blunt, wide, rounded pedicel, almost apedicellate. Ascospores 2–3seriate in ascus, ellipsoid, fusoid, ends rounded, 2–3septate, constricted at septum, yellow brown, smoothwalled. Asexual state: see notes.

## Type species: Acanthostigmella genuflexa Höhn.

Notes: Acanthostigmella was proposed by Von Höhnel (1905) based on the type species A. genuflexa. Material from FH was not in good condition and devoid of any fungi. M.E. Barr had annotated the specimen as containing broken fragments bearing a few perithecia and small spored species of Gaeumannomyces. Two slides were present in the exsiccata and Barr (1977) obtained her description from these. A more recent collection (IMI 252801) similar to the species drawn from the FH type slides by Barr (1977) is illustrated below. Morphologically, this specimen is different from all genera in Tubeufiaceae with small ascomata containing a distinct papilla surrounded by setae, lack of pseudoparaphyses, broadly obovoid to fusoid asci, and 2-3-septate, yellow brown ascospores (von Höhnel 1905; Barr 1977). Barr (1977, 1980) and Rossman (1987) suggested that A. genuflexa would be better accommodated in *Herpotrichiellaceae* (*Chaetothryriales*) rather than Tubeufiaceae. Based on molecular data of Acanthostigmella brevispina M.E. Barr & Rogerson, Untereiner et al. (1995) placed the taxon in Dothideomycetes (Figs. 22 and 23 in Untereiner et al. 1995). Whether this species is related to A. genuflexa is debatable because of the presence of pseudoparaphyses, a hyphomycetous asexual state and fungicolous habitat. The placement of this genus therefore has to be Dothideomycetes genera incertae sedis.

The asexual states of *Acanthostigmella* are listed as hyphomycetous, helicosporous, dictyosporous and xenosporiumlike (Hyde et al. 2011). However, no asexual state is linked to the generic type.

*Type species: Acanthostigmella genuflexa* Höhn., Annls mycol. 3(4): 327 (1905), *Facesoffunginumber*: FoF 00193 Fig. 32

 $\equiv$  Acanthostigma genuflexum (Höhn.) Sacc. & Trotter, in Saccardo, Syll. fung. (Abellini) 22: 209 (1913)

 $\equiv$  *Tubeufia genuflexa* (Höhn.) Arx & E. Müll., Stud. Mycol. 9: 83 (1975)

Saprobic on dead stems of grasses. Sexual state: Ascomata 20–79  $\mu$ m high×36–77  $\mu$ m diam., superficial, solitary, scattered, globose-subglobose, dark brown; with surface setae, papillate and with darkened, 13–20  $\mu$ m diam. ostiola, with setae 23–74  $\mu$ m long, dark brown, apical acute, septate. Peridium thin-walled, ca. 4.5–5  $\mu$ m wide, composed of brown to reddish-brown cells 3–6.5  $\mu$ m diam. of textura angularis. Hamathecium lacking pseudoparaphyses. Asci 19–23×8–11  $\mu$ m ( $\bar{x}$ = 21 × 9  $\mu$ m , n=10), 8-spored, bitunicate, oblong, subclavate to broadly obovoid, with a blunt, wide, rounded pedicel, almost apedicellate. Ascospores 7–11×2–3  $\mu$ m ( $\bar{x}$ = 9 × 3  $\mu$ m , n=10), 2–3-seriate in ascus, ellipsoid, fusoid, rounded at both ends, 2–3-septate, constricted at septum, yellow brown, smooth-walled. Asexual state: Unknown.

**Fig. 32** Acanthostigmella genuflexa (**a**, **b** holotype FH, **c**–I Material of herb. K, as IMI 252801). **a**, **b** Herbarium package and specimen. **c** Ascomata on substrate. **d** Close up of ascomata with long setae. **e** Peridial wall. **f**, **g** Immature and mature asci. **h**–**j** Ascospores. *Scale bars*: **a** =  $500 \mu m$ , **b** =  $100 \mu m$ , **c**–**d** =  $50 \mu m$ , **e**–**j** =  $10 \mu m$ 

*Material examined*: AUSTRIA, Langenschönbichl, Tulln, 3 June 1905, v Höhnel (FH, **holotype**, poor specimen); UK, Suffolk, Halesworth (Canal side), on dead stem of *Phalaris arundinacea* L. (*Poaceae*), M.B. and J.P. Ellis, 21 June 1979 (IMI 252801).

*Chaetocrea* Syd., Annls mycol. 25(1/2): 18 (1927), *Facesoffunginumber*: FoF00220

*Fungicolous* associated with black areas of fungi on leaves. **Sexual state**: *Ascomata* superficial, solitary or gregarious, globose-subglobose, membranous, white to pale yellow, covered by apically branched setae. *Peridium* comprising whitish yellow cells of *textura angularis*. *Hamathecium* comprising filiform, septate, branched, hyaline pseudoparaphyses, developing over asci. *Asci* 8-spored, bitunicate, elongate-clavate, cylindrical, short pedicellate, apically thickened, without an obvious ocular chamber. *Ascospores* fasciculate, filiform, tapering narrowly towards lower end, with several septa, hyaline. **Asexual state**: Unknown.

## Type species: Chaetocrea parasitica Syd.

Notes: Chaetocrea was introduced by Sydow (1927) for a single species Chaetocrea parasitica and placed in the Hypocreaceae as it had bright-coloured ascomata. Chaetocrea parasitica was described as fungicolous, growing on blackened areas of Cyclostomella disciformis which parasitized leaves of Nectandra sanguine. Rossman et al. (1999) studied genera in the Hypocreaceae (Hypocreales) and transferred Chaetocrea to Tubeufiaceae based on its bitunicate asci, pseudoparaphyses and long ascospores. Chaetocrea parasitica has predominantly branching, pale yellow setae atypical of Tubeufiaceae. Therefore Chaetocrea is treated as a member of Dothideomycetes genera incertae sedis.

*Type species:* Chaetocrea parasitica Syd., Annls mycol. 25(1/2): 19 (1927), Facesoffunginumber: FoF 00194 Fig. 33

*Fungicolous* associated with black areas of *Cyclostomella disciformis* on leaves of *Nectandra sanguine*. **Sexual state**: *Ascomata* 161–187 µm high×169–189 µm diam., superficial, solitary or gregarious, globose-subglobose, membranous, white to pale yellow, translucent or crystal-like, covered by 35–44(–48) µm long×7–10µm wide, apically branched, septate, pale yellow setae. *Peridium* 23–26µm wide, 3–4 layers of white-yellow cells of *textura angularis*. *Hamathecium* comprising 2–2.5µm wide, filiform, septate, branched, hyaline pseudoparaphyses, developing above asci. *Asci* 95–  $108(-121)\times17-21µm$  ( $\bar{x}=102\times19µm$ , n=10), 8-spored, bitunicate, elongate-clavate, cylindrical, short-pedicellate, apically thickened, without an obvious ocular chamber. *Ascospores* (63-)71–83×5–6.5µm ( $\bar{x}=76\times6µm$ , n=10), fasciculate, filiform, tapering narrowly towards lower end,



Fig. 33 Chaetocrea parasitica (W, holotype). a Cyclostomella disciformis on leaf and ascomata of Chaetocrea parasitica (right figure) on blackened fungus. b Apically branching setae. c Section of ascoma. d Peridium. e Pseudoparaphyses. f-h Asci. i-k Ascospores. Scale bars: a =  $200 \mu m$ , b, i-k =  $20 \mu m$ , c =  $100 \mu m$ , d, f-h =  $50 \mu m$ , e =  $5 \mu m$ 



(6-)7–9-euseptate, not constricted at septum, hyaline, smoothwalled. **Asexual state**: Unknown.

*Material examined*: COSTA RICA, La Caja, near San Jose, parasitic on *Cyclostomella disciformis* Pat., growing on leaves of *Nectandra sanguinea* Rol. ex Rottb (*Lauraceae*), 4 January 1925 (No. 166), Acqu. 1978, No. 11007: F. Petrak Pilzherbarium (W, **holotype**).

*Malacaria* Syd., Annls mycol. 28(1/2): 69 (1930), *Facesoffunginumber*: FoF00221

*Fungicolous* associated with *Irenina glabra (Meliolaceae)*; comprising branched and coloured, superficial mycelium, on leaves of *Coffea robusta*, pantropical. **Sexual state**: *Ascomata* superficial, solitary, globose-subglobose, pale brown to orange brown, soft-textured, with a membranous wall, centrally ostiolate, darkened and collapsing when dry. *Peridium* composed of 3–5-layers of pale orange cells of *textura angularis*. *Hamathecium* with numerous filiform, septate, unbranched, hyaline pseudoparaphyses. *Asci* 8-spored, bitunicate, oblong-subclavate, rounded at apex, obtuse at base. *Ascospores* fasciculate, elongate-fusiform, slightly curved, 3–(–4)-septate,

slightly constricted at septa, pale brown, smooth-walled, apically subacute, continuous with basal filiform or thread-like, hyaline appendage. **Asexual state**: Unknown.

Type species: Malacaria meliolicola Syd.

Notes: Sydow (1930) introduced the genus Malacaria, typified by M. meliolicola for species commonly associated with species of Meliolaceae growing on leaves. Rossman (1983) treated M. flagellata as a synonym of M. meliolicola, based on its similar morphology. She assigned a lectotype for Paranectria flagellata (=Malacaria flagellata) and, since the type of M. meliolicola was lost, she also assigned it as the neotype of this species (Rossman 1987). Malacaria meliolicola was included in Tubeufiaceae based on its soft ascomata, bitunicate asci and pseudoparaphyses. In this study, we reexamined the lectotype specimen. Malacaria meliolicola has pale smoke-grey ascospores and unbranched septate pseudoparaphyses and is atypical of genera in Tubeufiaceae. The placement of Malacaria is therefore uncertain and the genus is treated as Dothideomycetes genera incertae cedis.

*Type species: Malacaria meliolicola* Syd., Annls mycol. 28(1/2): 69 (1930), *Facesoffunginumber*: FoF 00195 Fig. 34

*= Paranectria flagellata* Hansf., Proc. Linn. Soc. London 153(1): 28 (1941)

 $\equiv$  *Malacaria flagellata* (Hansf.) Hansf., Mycol. Pap. 15: 128 (1946)

*Fungicolous* associated with *Irenina glabra* (*Meliolaceae*); comprising branched and coloured, superficial mycelium, on leaves of *Coffea robusta*, pantropical. **Sexual state**: *Ascomata* 144–170  $\mu$ m high×125–176  $\mu$ m diam., superficial, solitary, globose-subglobose, pale brown to orange brown, soft in texture, membranous, centrally ostiolate, darkened and collapsing when dry. *Peridium* 12–14  $\mu$ m wide, composed of 3–5 layers, of pale orange cells of *textura angularis*. *Hamathecium* of *ca.* 1–1.5  $\mu$ m wide, numerous, filiform, septate, unbranched, hyaline pseudoparaphyses. *Asci* 53–72.5(–80)× 11–21  $\mu$ m ( $\bar{x}$ = 65 × 17 $\mu$ m , *n*=15), 8-spored, bitunicate, oblong-subclavate, rounded at apex, obtuse at base. *Ascospores* 42–51×4–5 $\mu$ m ( $\bar{x}$ = 46 × 4 $\mu$ m , *n*=10), fasciculate, elongate-fusiform, slightly curved, 3–(–4)-septate, slightly constricted at septum, pale brown, smooth, apically subacute, continuous

with basal *ca*. 43–65 $\mu$ m long, filiform or thread-like, hyaline appendage. Asexual state: Unknown.

*Material examined*: UGANDA, Kampala, elev. 4000 ft., on leaves of *Coffea robusta* and associated with *Irenina glabra* (Berk. & M.A. Curtis) F. Stevens (*Meliolaceae*), collected by Hansford G.C., 1871 (K (M): 177970, **neotype** of *Malacaria meliolicola*).

Uredinophila Rossman, Mycol. Pap. 157: 43 (1987), Facesoffunginumber: FoF00222

*Parasitic* on *Pucciniales* on leaves of *Dryopteris tetragona*. **Sexual state**: *Ascomata* superficial on substrate and surrounded by rust fungi, developing on a subiculum, globose to subglobose, solitary, scattered, translucent, yellow to orange, soft, apex with hyaline hairs. *Peridium* composed of hyaline or pale yellow cells of *textura angularis*. *Hamathecium* comprising numerous,  $1-2\mu m$  wide, cylindrical, branched, hyaline *pseudoparaphyses*, exending above asci, embedded in a gelatinous matrix. *Asci* 8-spored, bitunicate, cylindrical-clavate, with short knob-like pedicel, apex rounded. *Ascospores* fasciculate, helically coiled, filiform or fusiform, narrowly elongate, tapering to a narrow

# Fig. 34 Malacaria meliolicola

(K (M): 177970, **neotype**). **a** Fungus on black colonies of *Meliolaceae*. Orange coloured mycelium are those of the fungal parasite. **b** Section of ascoma. **c** Peridium. **d** Pseudoparaphyses. **e**-**g** Asci. **h**-**k** Ascospores with long, basal appendage. *Scale bars*: **a** = 500  $\mu$ m, **b** = 50  $\mu$ m, **c**-**k** = 20  $\mu$ m



rounded base, trans-septate, hyaline. Asexual state: Unknown.

## Type species: Uredinophila tropicalis (Speg.) Rossman

*Notes*: Rossman (1987) introduced the genus *Uredinophila* for two mycoparasitic fungi associated with rusts, i.e. *U. erinacea* (Rehm) Rossman and *U. tropicalis* (Speg.) Rossman. *Uredinophila* was excluded from *Ophionectria* based on its bitunicate asci and spirally elongated ascospores (Rossman 1977); and referred to *Tubeufiaceae* by Rossman (1987) who provided a key, descriptions and illustrations of the two species. We reexamined an authentic specimen of *U. tropicalis* (BPI 632877) listed by Rossman (1987) which has characters that are atypical of *Tubeufiaceae*. Therefore, *Uredinophila* is placed in *Dothideomycetes* genera *incertae sedis*.

*Type species:* Uredinophila tropicalis (Speg.) Rossman, Mycol. Pap. 157: 45 (1987), *Index Fungorum number:* IF 130896, *Facesoffunginumber:* FoF 00196 Fig. 35

 $\equiv$  Ophionectria tropicalis Speg., Anal. Soc. cient. argent. 16(5): 242 (1883)

Parasitic associated with Desmella superficialis (Pucciniales) on leaves of Dryopteris tetragona. Sexual state: Ascomata (122-)134–176(–196)  $\mu m$  high×(111-)141– 167(–196)  $\mu m$  diam. ( $\bar{x}$ = 156 × 156 $\mu m$ ), superficial on substrate and surrounded by rust fungi, developing on a subiculum, globose to subglobose, solitary, scattered, translucent, yellow to orange, soft, apex with (16-)21.5–35(–39)  $\mu m$ long, hyaline hairs, rounded at ends, lacking septa. Peridium 9.5–13 $\mu m$  wide, composed of hyaline or pale yellow, 6–9 $\mu m$ 



Fig. 35 Uredinophila tropicalis (BPI 632877). a Ascomata associated with a rust. b, c Squash mount of ascomata. d Close up of setae and peridial wall. e Pseudoparaphyses. f, g Asci. h, i Ascospores. Scale bars: a =  $100 \mu m$ , c, f-i =  $50 \mu m$ , d =  $20 \mu m$ , e =  $5 \mu m$  wide, cells of *textura angularis*. *Pseudoparaphyses* numerous,  $1-2\mu m$  wide, cylindrical, cellular, branched, hyaline, extending above asci, embedded in a gelatinous matrix. *Asci* (85-)92.5–115×12–15 $\mu m$  ( $\overline{x}=99\times13\mu m$ ), bitunicate, 8-spored, cylindrical-clavate, with short knob-like pedicel, with rounded apex. *Ascospores* (96-)107.5–113×3.5–5 $\mu m$  ( $\overline{x}=103\times4\mu m$ ), fasciculate, helically coiled, filiform or fusiform, narrowly elongate, with rounded apex, tapering to a narrow rounded base, with 7 or more septa, not constricted at septa, hyaline, smooth-walled. **Asexual state**: Unknown.

*Material examined*: VENEZUELA, Caguita, near Pueto La Cruz, fungicolous, associated with uredosoris of the fern rust *Desmella superficialis*, on leaves of *Dryopteris tetragona* (Sw.) Urb. (*Dryopteridaceae*), H. Sydow, 27 December 1927, Sydow 840 (BPI 632877, issued as *Ophionectria tropicalis*).

#### Ascomycetes genera incertae sedis

Garethjonesia K.D. Hyde, Aust. Syst. Bot. 5(4): 408 (1992)

*Notes*: This genus was introduced from freshwater by Hyde (1992), but was later synonymized with *Boerlagiomyces* by Stanley and Hyde (1997). The genus is rather distinct and differs from *Boerlagiomyces* in having much lighter ascomata, bicelled asci and large lacunose ascospores. The asci were described as unitunicate, but this was questioned by Stanley and Hyde (1997). We re-examined the figures in Hyde (1992) and the asci appear to be unitunicate (although this cannot be clearly determined); this is however supported by the fact that the paraphyses are larg, oval and taper at the ends. We therefore treat *Garethjonesia* as a distinct genus which should be placed in the Ascomycetes, genera incertae sedis. *Boerlagiomyces grandisporus* Stanley & K.D. Hyde is also similar and should probably also be placed in *Garethjonesia*.

*Type species:* Garethjonesia lacunosispora K.D. Hyde, Aust. Syst. Bot. 5(4): 411 (1992)

Doubtful Dothideomycete genera

Amphinectria Speg., Boln Acad. nac. Cienc. Córdoba 26(2-4): 346 (1924)

*Notes*: We provide above a brief description of *Amphinectria portoricensis* based on the protologue of (1924), the original drawing in the herbarium packet and the rather depauperate type material. Petrak (1951) examined the type specimen of *A. portoricensis*, which has immature asci, and concluded that the species is a lichen. Pirozynski (1977) later questionably synonymised *Amphinectria* with *Melioliphila*, while Rossman (1987) examined the type specimen of *A. portoricensis* and could not find any ascomata that resembled those described by Spegazzini suggesting that the identity of this species is obscure. Rossman et al. (1999) placed *A. portoricensis* in *Tubeufiaceae* with uncertainty and remarked that, until another specimen is located and studied, *Amphinectria* will remain an ambiguous member. A second species in the genus, *Amphinectria erubescens*, was

transferred to the genus *Hydropisphaera* (*Bionectriaceae*), based on its orange ascomata and unitunicate asci (Vizioli 1923; Rossman et al. 1999). According to the original annotations of Spegazzini (LPS 13394, holotype), this genus and species is ambiguous and is unlike any other members of *Tubeufiaceae*. Therefore we treat *Amphinectria* as a doubtful genus.

*Type species:* Amphinectria portoricensis Speg., Boln Acad. nac. Cienc. Córdoba 26(2–4): 346 (1924), Facesoffunginumber: FoF 00197 Fig. 36

*Parasitic* on leaf surface of *Comocladia glabra* (Schult.) Spreng. *Subiculum* 5–10 mm diam., orbicular, slightly transparent, inconspicuous, loosely attached to epidermis, with 2–  $3\mu m$  diam., branching, radial hyphae. **Sexual state**: *Ascomata* 200–250 $\mu m$  diam., superficial, globose, solitary, yellow brown to brown, membranous, developing at centre of subiculum, minutely papilla, ostiolate, collapsing when dry, lacking pseudoparaphyses. *Asci* (70-)75–100×(15-)25–  $30\mu m$ , 8-spored, bitunicate, cylindrical-ellipsoid, bluntly rounded at apex, with a short, bifurcate pedicel. *Ascospores* (32-)40–45×(6-)8–10 $\mu m$ , 2-seriate in ascus, cylindricalfusoid, tapering towards sub-rounded ends, slightly inequilateral or curved, 7–9-septate, slightly constricted at septum, hyaline, smooth-walled, lacking a gelatinous sheath (from Spegazzini 1924). **Asexual state**: Unknown.

*Chaetosphaerulina* I. Hino, Bulletin Miyazaki Coll. Agric. Forest. 10: 62 (1938)

This genus was redescribed and redrawn from the protologue by Boonmee et al. (2011). It is similar to several genera of *Tubeufiaceae* (e.g. *Thaxteriella*). The holotype at YAM appear to have been lost. The genus is therefore treated as doubtful until it can be rediscovered.

*Type species:* **Chaetosphaerulina yasudai** I. Hino, Canad. J. Plant Sci. 10: 62 (1938)

Melioliphila Speg., Boln Acad. nac. Cienc. Córdoba 26(2-4): 344 (1924)

Notes: Melioliphila was introduced by Spegazzini (1924) for mycoparasitic species associated with Meliola (Meliolaceae). Initially, Melioliphila was placed in the Hypocreales (Saccardo 1972), but later transferred into "hypocreoid Dothideales" by Pirozynski (1977). Barr (1980) transferred Melioliphila to Tubeufiaceae based on its mycoparasitic habit and having bitunicate asci and elongate ascospores. Rossman (1979, 1987) reported that M. graminicola (F. Stev) Speg. (≡Calonectria graminicola F. Stev.) is a synonym of *M. volutella* (Berk. & Broome) Rossman (≡*Calonectria volutella*). Melioliphila graminicola was also placed in Tubeufiaceae by Rossman (1987, 1999). We could not loan the type of *M. graminicola* due to LPS policy. Paratype specimens of M. graminicola (BPI632019) examined were in poor condition. Therefore, we used the drawings of Spegazzini (1924) and original herbarium packet (www. cybertruffle.org.uk/spegazzini/ 001626a) to illustrate Fig. 36 *Amphinectria portoricensis* (Redrawn from LPS 13394, **holotype**). **a**, **b** Material in LPS packet (**holotype**). **c**, **d** Substrate and ascoma. **e** Asci. **f** Ascospores



*M. graminicola*. According to Spegazzini (1924), *M. graminicola*, has hyaline setae, elliptical-fusoid asci, fusoid ascospores and lacks pseudoparaphyses, is atypical of genera in *Tubeufiaceae*. Therefore, *Melioliphila* is treated as a doubtful genus in *Dothideomycetes*.

*Type species: Melioliphila graminicola* Speg., Boln Acad. nac. Cienc. Córdoba 26(2–4): 344 (1924), *Facesoffunginumber*: FoF 00198 Fig. 37

Parasitic on Meliola panici (Meliolaceae) growing on leaves of Lasiacis divaricata in Puerto Rico. Sexual state: Ascomata 150–200 $\mu$ m diam., globose, developing on a poorly developed, yellowish to fleshy-pink, subiculum, covered by powder-like, white colonies, with sparsely radiating setae. Setae 50–100×8–10 $\mu$ m, erect, narrowly tapering towards apex, hyaline, septate. Hamathecium lacking pseudoparaphyses. Asci 70–90×10–14 $\mu$ m, 8-spored, bitunicate, elliptical-fusoid, short pedicellate, somewhat flattened at apex. Ascospores 30–40×4–5 $\mu$ m, 2-seriate, narrowly-fusoid, initially with minute appendages at both ends and appendages disappearing and both ends becoming blunt when mature, 7–9-guttulate present when immature, becoming 7–9-septate when mature, hyaline to pale smoky (from Spegazzini 1924). **Asexual state**: Unknown.

*Notes*: The brief description and drawing of *Melioliphila graminicola* is provided based on the protologue of Spegazzini (1924) and the drawing on the herbarium packet (www. cybertruffle.org.uk/spegazzini/eng/001626a).

## Conclusion

Based on molecular phylogenetic studies, family *Tubeufiaceae* is placed in order *Tubeufiales*. This recognition is strongly supported by morphological characteristics of asexual and sexual states. The sexual morph of *Tubeufiales* 

Fig. 37 Melioliphila

Ascospores





is circumscribed by uniloculate, pseudothecial, superficial ascomata, which bear setae in some genera, a pseudoparaphysate hamathecium, bitunicate asci, multi-septate, hyaline to pale brown cylindrical ascospores and often connected with hyphomycetous, helicosporous asexual states (Tsui and Berbee 2006; Tsui et al. 2006, 2007; Boonmee et al. 2011).

Furthermore, all genera and new species are provided with detailed descriptions and illustrations. Phylogenetic placement of Tubeufiales was determined using combined data set of LSU and ITS gene regions. Our morpho-molecular analyses confirm that Tubeufiales, Tubeufiaceae, comprises 19 genera viz. Acanthohelicospora, Acanthophiobolus, Acanthostigma, Acanthostigmina, Aquaphila, Boerlagiomyces, Bifrontia, Chlamydotubeufia, Helicangiospora, Helicoma, Helicomyces, Helicosporium, Kamalomyces, Neoacanthostigma, Podonectria, Tamhinispora, Thaxteriella, Thaxteriellopsis and Tubeufia. Presently, GenBank has over 100 sequences of Tubeufiales including different gene regions such as LSU, SSU and ITS. In this study

we have used the combined data sets of LSU and ITS gene regions to resolve genera of Tubeufiaceae. In addition, a fresh collection of *Tubeufia javanica* is introduced as the epitype for Tubeufia sensu stricto. We exclude Acanthostigmella, Amphinectria, Chaetocrea, Chaetosphaerulina, Glaxoa, Malacaria, Melioliphila, Paranectriella, Puttemansia, Rebentischia and Uredinophila from Tubeufiaceae, based on morphological studies of type species.

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