



## *Homortomyces tamaricis* sp. nov. and convergent evolution of *Homortomyces* and *Stilbospora*

NALIN N. WIJAYAWARDENE<sup>1,2,3</sup>, KEVIN D. HYDE<sup>2,3</sup>, ERIO CAMPORESI<sup>4</sup>, D. JAYARAMA BHAT<sup>2,5</sup>, YU SONG<sup>7</sup>, EKACHAI CHUKEATIROTE<sup>2,3</sup>, YONG WANG<sup>7</sup> & JIN-HUA ZHANG<sup>1,6\*</sup>

<sup>1</sup> Guizhou Animal Husbandry and Veterinary Institute, Guiyang, P.R. China, 550005

<sup>2</sup> Institute of Excellence in Fungal Research and <sup>3</sup>School of Science, Mae Fah Luang University, Chiang Rai, 57100, Thailand

<sup>4</sup> A.M.B. Gruppo Micologico Forlivese “Antonio Cicognani”, Via Roma 18, Forlì, Italy; A.M.B. Circolo Micologico “Giovanni Carini”, C.P. 314, Brescia, Italy; Società per gli Studi Naturalistici della Romagna, C.P. 144, Bagnacavallo (RA), Italy

<sup>5</sup> Formerly, Department of Botany, Goa University, Goa 403 206, India

<sup>6</sup> Guizhou Nomal University, Guiyang, P.R. China, 550001

<sup>7</sup> Department of Plant Pathology, Agriculture College, Guizhou University, 550025, P.R. China

\* email: zhangjinhua990@msn.com

### Abstract

A new species *Homortomyces tamaricis* is introduced from Cervia, Italy. It is distinct from *H. combreti*, the type species of this monotypic genus, in having smaller conidia, smaller paraphyses and shorter supporting cells. Morphologically *Homortomyces* is similar to *Stilbospora*, which groups in *Diaporthales incertae sedis* in maximum-likelihood analysis of LSU rDNA sequences. Maximum-likelihood analysis of the combined data set of LSU and ITS rDNA sequences indicates that *Homortomyces* species cluster with *Tubeufiaceae* with 77% bootstrap support, but group as a distinct clade with high bootstrap value (100%). These two genera show convergent evolution since both share very similar morphological characters, but have distinct phylogenetic lineages. Further phylogenetic analyses are needed, when more strains of *Homortomyces* and related genera are available, to resolve the genus familial placement. We maintain the genus in *Dothideomycetes incertae sedis*. No sexual state has yet been reported for this genus.

**Key words:** coelomycetous fungi, molecular taxonomy, morphology, phylogenetics

### Introduction

Traditionally, identification of coelomycetous fungi was based solely on morphological characters (Sutton 1980, Nag Raj 1993, Wijayawardene *et al.* 2012a). However, the introduction of molecular based taxonomic methods has revolutionized taxonomic studies of coelomycetes (Wijayawardene *et al.* 2012b, Zhang *et al.* 2012, Hyde *et al.* 2013). It has been over 20 years since the introduction of PCR (White *et al.* 1990), and more and more taxonomic and phylogenetic studies have incorporated molecular based methods (de Gruyter *et al.* 2010, 2013, Crous *et al.* 2013). Recent studies on orphaned conidial fungi and their relationships with sexual states (Boonmee *et al.* 2011, Chomnunti *et al.* 2011, Dai *et al.* 2012, Zhang *et al.* 2012, Wijayawardene *et al.* 2013) have relied totally on DNA sequence analyses.

*Homortomyces* Crous & M.J. Wingf. in Crous *et al.* (2013: 111) is morphologically similar (with a few exceptions) to *Stilbospora* Persoon (1794: 93) However, in their phylogenetic analysis, Crous *et al.* (2013) showed *Homortomyces* (*Dothideomycetes incertae sedis*) to have a distinct phylogenetic lineage to that of *Stilbospora* (*Diaporthales incertae sedis*).

We collected a coelomycetous fungus that has very similar morphological characteristics to those found in *Homortomyces* and *Stilbospora*. BLAST search results of LSU and ITS rDNA sequences in GenBank showed the closest relative of our strain to be *Homortomyces combreti* Crous & M.J. Wingf. in Crous *et al.* (2013: 113), the type species of this monotypic genus. In this paper we introduce a new species of *Homortomyces*, discuss its phylogenetic placement and also compare it with the genus *Stilbospora*.

## Materials and methods

### Collection

Decaying plant materials (aerial litter) were collected near the sea in Cervia, Italy. Most of the material was from dead plants well adapted for high salinity conditions. Collected dead plant materials were placed in paper bags, brought to the laboratory and observed under a stereoscope to reveal fungal taxa.

### Morphological studies and isolation

Sections of conidiomata were made by free-hand under a stereoscope. Conidial characters were observed by removing conidiomata and placing them in a drop of distilled water on a clean slide. Squashed conidiomata were examined under a compound microscope (Nikon Eclipse E600 DIC microscope and a Nikon DS-U2 camera or a Nikon Eclipse 80i compound microscope fitted with a Canon 450D digital camera) and conidial characters determined.

Single conidial isolation was carried out using the method of Chomnunti *et al.* (2011) and germinating conidia were transferred aseptically to potato dextrose agar (PDA) plates and grown at 18°C. Colony colour and other characters were assessed after 1 week and 2 weeks. The specimens are deposited in the Mae Fah Luang University Herbarium (MFLU), Chiang Rai, Thailand. Living cultures are also deposited in the Culture Collection at Mae Fah Luang University (MFLUCC) and Department of Plant Pathology, Agriculture College, Guizhou University, China (HGUP).

### DNA extraction, PCR amplification and sequencing

Genomic DNA was extracted from fresh fungal mycelia by using a BIOMIGA Fungus Genomic DNA Extraction Kit (GD2416) (Wijayawardene *et al.* 2013). The amplification of rDNA regions of internal transcribed spacers (ITS) and large subunit (LSU) was carried out by using ITS5 and ITS4 (White *et al.* 1990) and LROR and LR5 (Vilgalys & Hester 1990) primers. The amplification conditions for ITS and LSU were carried out according to Liu *et al.* (2012). Amplified PCR fragments were then sent to SinoGenoMax, Beijing, China for DNA sequencing. The nucleotide sequence data obtained were deposited in GenBank (Table 1).

TABLE 1. Strains used in this study.

Taxon	Culture collection number <sup>1</sup>	GenBank accession number	
		LSU	ITS
<i>Acanthostigma minutum</i>	ANM 818	GQ850488	
<i>Acanthostigma multiseptatum</i>	ANM 475	GQ850492	GQ856145
<i>Acanthostigma perpusillum</i>	UAMH 7237	AY856892	
<i>Amphisphaeria umbrina</i>	AFTOL-ID 1229	FJ176863	
<i>Auerswaldia dothiorella</i>	MFLUCC 11-0438	JX646813	JX646796
<i>Botryobambusa fusicocum</i>	MFLUCC 11-0143	JX646809	JX646792
<i>Botryosphaeria corticola</i>	CBS 112549	AY928051	
<i>Botryosphaeria dothidea</i>	CMW 8000	AY928047	AY236949
<i>Botryosphaeria dothidea</i>	CBS 110302	EU673243	AY259092
<i>Botryosphaeria fusispora</i>	MFLUCC 10-0098	JX646806	
<i>Botryosphaeria lutea</i>	CBS 110299	AY928043	
<i>Botryosphaeria rhodina</i>	CBS 164.96	EU673253	AY640255
<i>Botryosphaeria sarmentorum</i>	IMI 63581b	AY928052	
<i>Chlamydotubeufia huaikangplaensis</i>	MFLUCC10-0926	JN865198	JN865210
<i>Chlamydotubeufia khunkornensis</i>	MFLUCC10-0118	JN865190	JN865202
<i>Cytospora diatrypelloidea</i>	CBS 120062	DQ923537	
<i>Diaporthe eres</i>	AR3538	AF408350	

..... continued on the next page

TABLE 1 (continued)

Taxon	Culture collection number <sup>1</sup>	GenBank accession number	
		LSU	ITS
<i>Diaporthe padi</i>	AR3419	AF408354	
<i>Diplodia cupressi</i>	CBS 168.87	EU673263	
<i>Diplodia mutila</i>	CBS 431.82		DQ377863
<i>Dothidea insculpta</i>	CBS 189.58	NG_027643	AF027764
<i>Dothiora elliptica</i>	CBS 736.71	GU301811	
<i>Dothiorella iberica</i>	CBS 115041	DQ377853	AY573202
<i>Fusicoccum mangiferum</i>	CBS 118532	DQ377921	
<i>Gnomonia dispersa</i>	CBS205.37	EU199128	
<i>Gnomoniella fraxini</i>	AR2789	AF362552	
<i>Guignardia citricarpa</i>	CBS 102374	GU301815	FJ538313
<i>Guignardia philoprina</i>	CBS 447.68	DQ377878	AF312014
<i>Harknessia karwarrae</i>	CPC 10928	AY720841	
<i>Harknessia pseudohawaiiensis</i>	CPC 17379	JQ706234	
<i>Helicomyces roseus</i>	CBS 283.51	AY856881	AY916464
<i>Homortomyces combreti</i>	CPC 19800		JX517280
<i>Homortomyces combreti</i>	CPC 19808	JX517291	JX517281
<i>Homortomyces tamaricis</i>	MFLUCC 13-0441	KF537345	KF537346
<i>Kellermania macrospora Kellermania yuccigena</i>	BPI 882817	JX444874	JX444858
	BPI 882828	JX444883	JX444868
<i>Lasiodiplodia parva</i>	CBS 494.78	EU673258	
<i>Lasiodiplodia theobromae</i>	CBS 164.96	EU673253	AY640255
<i>Neodeightonia subglobosa Neoscytalidium novaehollandiae</i>	CBS 448.91	DQ377866	EU673337
	WAC 12691		EF585543
<i>Phyllosticta brazilianiae</i>	LGMF330		JF343572
<i>Pilidiella castaneicola</i>	CBS143.97	AF408378	
<i>Schizoparme straminea</i>	CBS 149.22	AY339296	
<i>Spencermartinsia viticola</i>	CBS 117009	DQ377873	AY905554
<i>Stilbospora macrosperma</i>	CBS 121882	JX517298	
<i>Stilbospora macrosperma</i>	CBS 121883	JX517299	
<i>Thaxteriella inthanonensis</i>	MFLUCC11-0003	JN865199	JN865211
<i>Tubeufia aurantiella</i>	ANM 718	GQ850485	
<i>Tubeufia khunkornensis</i>	MFLUCC10-0119	JN865191	JN865203
<i>Tubeufia paludosa</i>	ANM 953	GQ850483	
<i>Valsa ceratosperma</i>	AR3416	AF408386	

<sup>1</sup>AFTOL: Assembling the Fungal Tree of Life. ANM: A.N. Miller; AR: Systematic Mycology and Microbiology Laboratory, USDA-ARS, Beltsville, Maryland, USA. CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands. CMW: Tree Pathology Co-operative Program, Forestry and Agricultural Biotechnology Institute, University of Pretoria, South Africa. CPC: Collection of Pedro Crous housed at CBS. DAOM: Plant Research Institute, Department of Agriculture (Mycology), Ottawa, Canada. IMI: International Mycological Institute, CABI-Bioscience, Egham, Basingstoke, Hampshire, U.K. LGMF: Culture Collection of Laboratory of Genetics of Microorganisms, Federal University of Parana, Curitiba, Brazil. MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand. WAC: Department of Agriculture Western Australia Plant Pathogen Collection, South Perth, Western Australia. UAMH: University of Alberta Micro fungus Collection and Herbarium, Edmonton, Alberta, Canada.

### Phylogenetic analyses

A BLAST search of LSU rDNA sequence was carried out and revealed the closest taxa to our strain. LSU sequences of closest relatives in *Botryosphaeriaceae*, *Pleosporaceae*, *Tubeufiaceae* (*Dothideomycetes*) and several strains in *Diaporthales* (to represent *Stilbospora* and closest taxa) were used to confirm the phylogenetic

placement. Maximum-likelihood analysis of combined data set of LSU rDNA and ITS rDNA was also carried out to confirm the placement of our strains in *Dothideomycetes*.

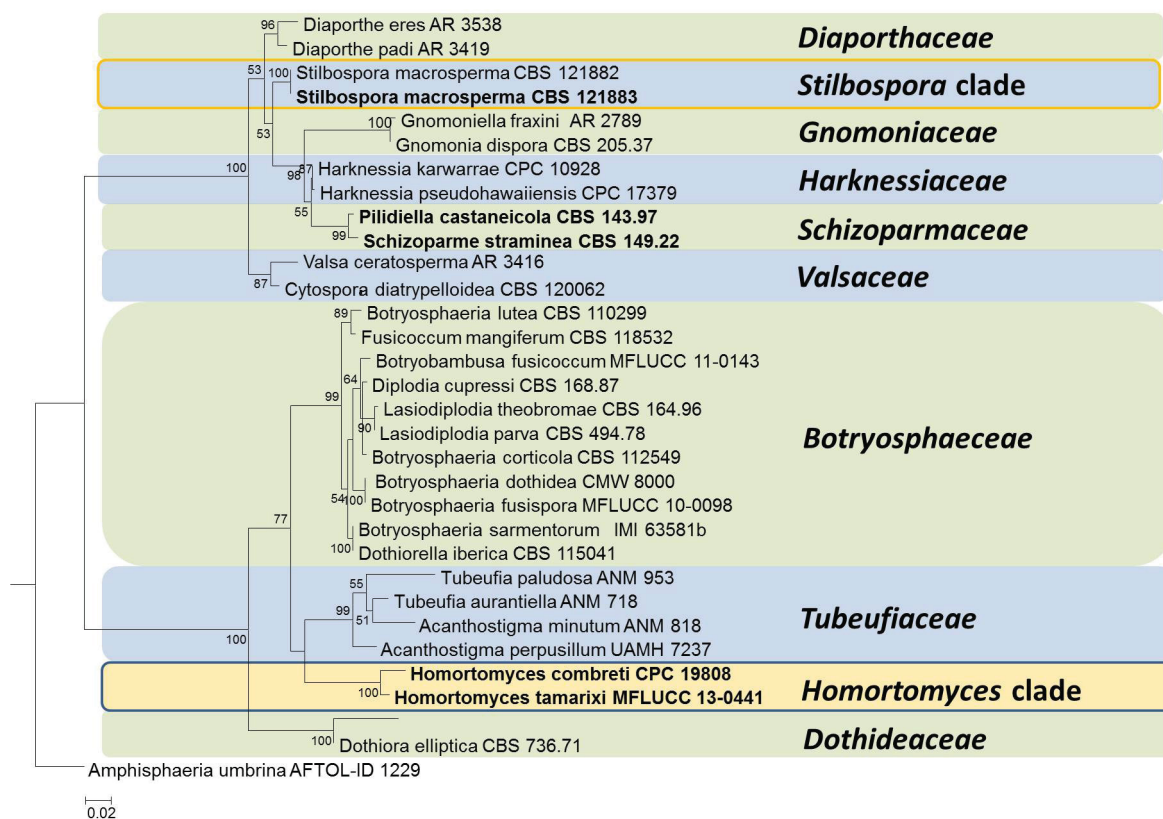
These sequences were downloaded from GenBank and aligned using Bioedit (Hall 2004) and ClustalX (Kohli & Bachhawat 2003). Alignments were checked and manual adjustments made where suitable and individual datasets concatenated into a combined dataset. Maximum-likelihood (ML) analyses was performed in RAxML (Stamatakis 2006) implemented in raxmlGUI v.0.9b2 (Silvestro & Michalak 2012). Maximum trees were visualized with Tree View (Page 1996).

## Results

### Phylogenetic analyses

#### LSU rDNA analysis

The LSU data set comprised 32 sequences from 31 taxa with *Amphisphaeria umbrina* (AFTOL-ID 1229) as the outgroup taxon. The dataset consists of 1,402 characters after alignment, of which 1,010 are conserved, 366 are variable and 244 are parsimony informative. A best scoring RAxML tree is shown (Fig. 1) and bootstrap support (BS) values of ML (equal to or above 50% based on 1,000 replicates) are shown on the upper branches.

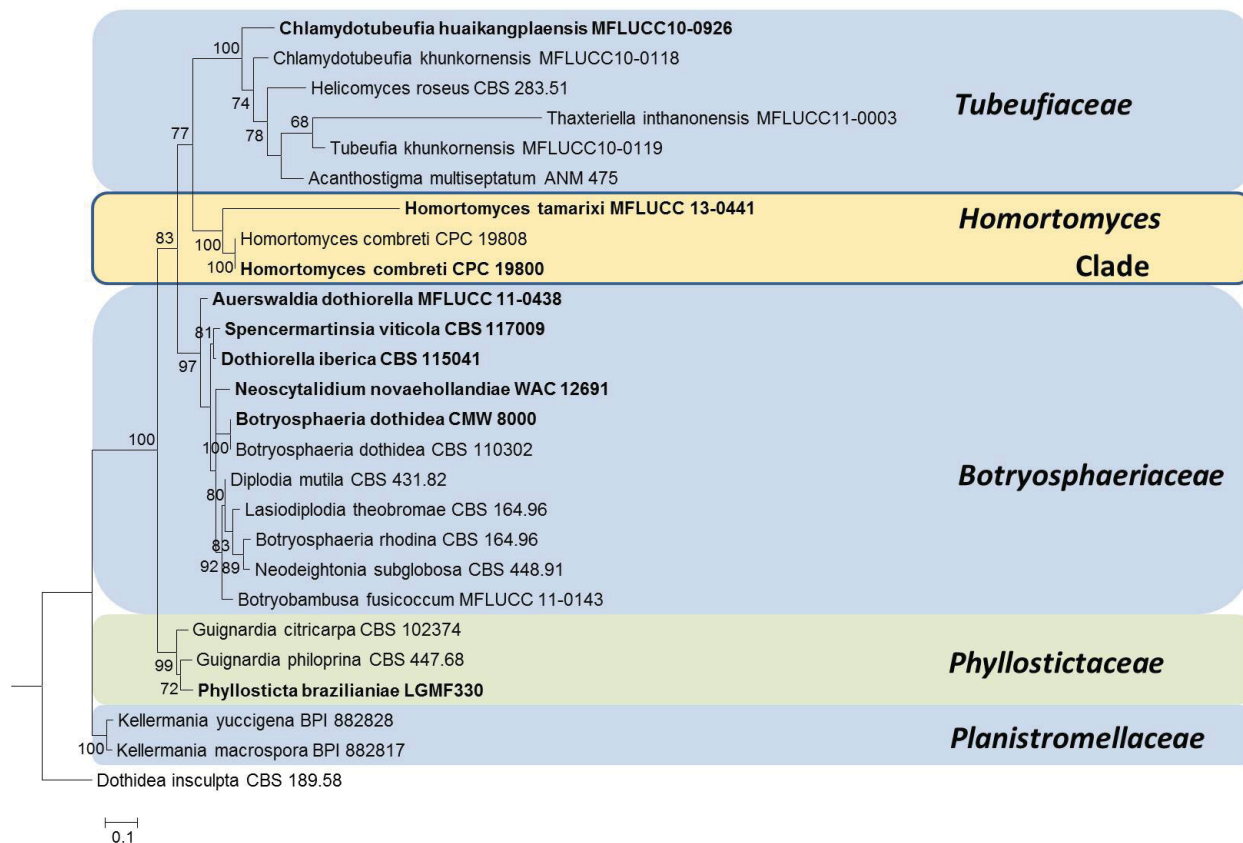


**FIGURE 1.** RAxML tree based on dataset of LSU sequences. Bootstrap support values for maximum-likelihood (ML) greater than 50% are given above the nodes. The GenBank numbers are given after the species names. The tree is rooted to *Amphisphaeria umbrina* (AFTOL-ID 1229). All sequences from type strains are in bold.

Our strain grouped with *Homortomyces combreti* (CPC 19808) with high bootstrap support (100%) in a sister clade to *Tubeufiaceae* (with low bootstrap support). Probably this *Homortomyces* clade belongs to *Tubeufiales* (Boonmee *et al.*, pers. comm). However, it is essential to include more sequences and carry out further molecular analyses. ITS sequences were also used in a separate analysis and in combined analysis with LSU sequences. However, neither analysis was successful and hence are not included.

The combined data set of LSU and ITS rDNA comprises 3,048 characters, of which 1,310 are conserved, 1,471 are variable and 666 are parsimony informative. The best tree generated by RAxML analysis is shown in Fig. 2 and bootstrap values of ML (equal or above 50% based on 1,000 replicates) are shown on the upper branches.

*Homortomyces tamaricis* (MFLUCC 13-0441) groups with *H. combreti* (CPC 19800 and CPC 19808) with high bootstrap value (100%) and this clade is the sister clade of *Tubeufiaceae* (with 77% bootstrap value).



**FIGURE 2.** RAxML tree based on combined dataset of LSU and ITS rDNA sequences. Bootstrap support values for maximum likelihood (ML) greater than 50% are given above the nodes. The GenBank numbers are given after the species names. The tree is rooted to *Dothidea insculpta* (CBS 189.58). All sequences from type strains are in bold.

## Taxonomy

*Homortomyces tamaricis* N.N. Wijayawardene, E. Camporesi & K.D. Hyde, *sp. nov.* Index Fungorum: IF 550192 (Fig. 3)

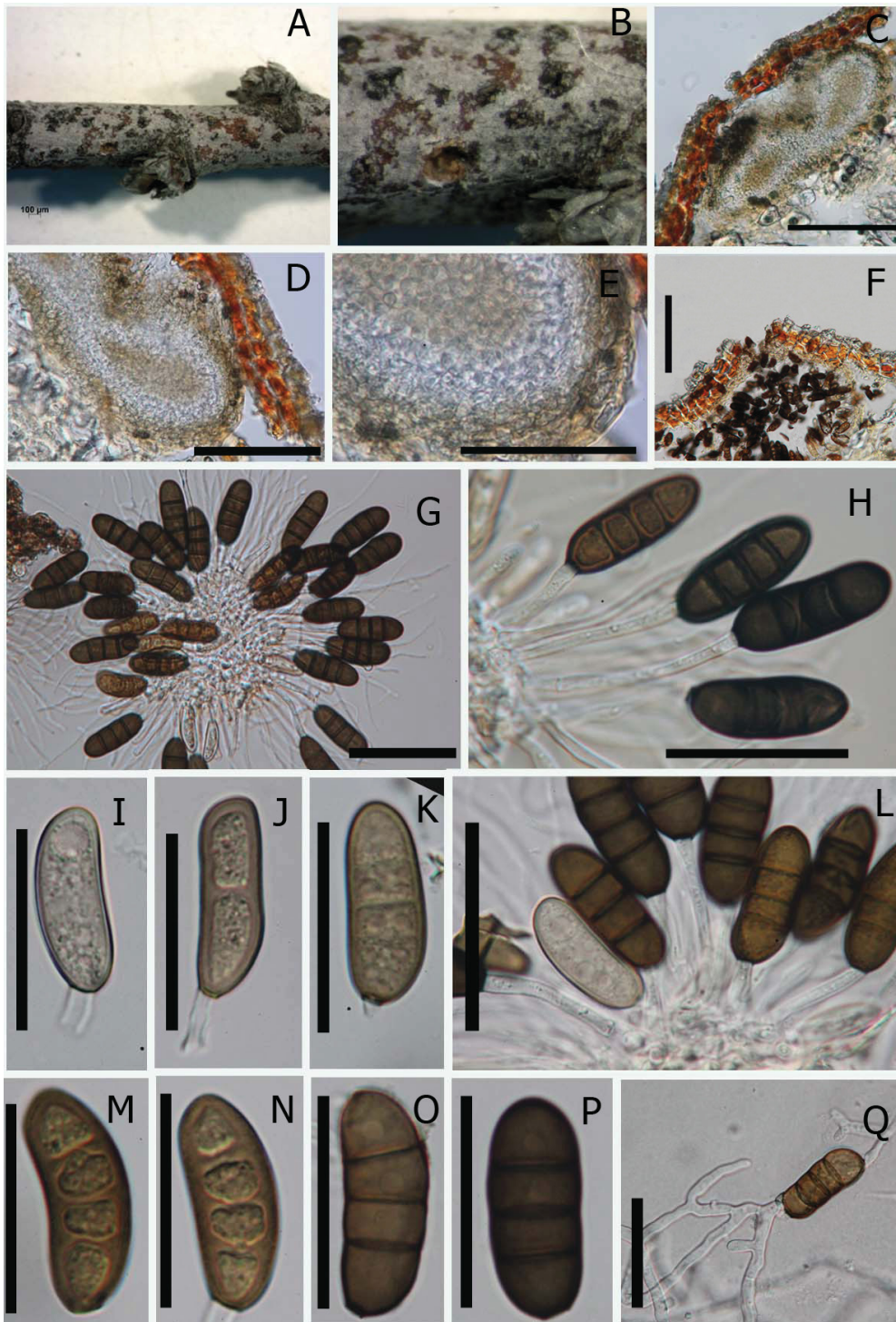
Differs from *Homortomyces combreti* by possessing smaller conidia ( $22\text{--}29 \times 9\text{--}11 \mu\text{m}$  vs.  $32\text{--}38 \times 13\text{--}16 \mu\text{m}$ ).

**Type:**—ITALY. Ravenna Province: Cervia, on dead branch of *Tamarix gallica*, 25 November 2012, *Erio Camporesi* (NNW IT927, holotype!), ex-type living cultures MFLUCC 13-0441 = HGUP Na9.

**Etymology:**—After the genus *Tamarix* on which the fungus was found.

*Saprobic* on dead branch of *Tamarix gallica*. Sexual state: Unknown. Asexual state: *Conidiomata*  $50\text{--}200 \mu\text{m}$  diam.,  $200\text{--}300 \mu\text{m}$  high, solitary or gregarious, immersed, pycnidial to irregular, uniloculate, subglobose. *Ostiole* central. *Pycnidium wall* with  $25\text{--}40 \mu\text{m}$  wide, outer layer, comprising about 5 cell layers, of brown-walled cells of *textura angularis*, with  $30\text{--}40 \mu\text{m}$  wide hyaline inner cell layer. *Paraphyses* numerous, aseptate, cylindrical, hyaline,  $23\text{--}70 \times 1\text{--}2 \mu\text{m}$ . *Conidiophores* reduced to conidiogenous cell with supporting cell, hyaline, percurrent

proliferation at the tip of the supporting cells,  $9\text{--}27 \times 2\text{--}3 \mu\text{m}$ . *Conidia*  $22\text{--}29 \times 9\text{--}11 \mu\text{m}$  ( $\bar{x} = 26.3 \times 10.2 \mu\text{m}$ ,  $n = 20$ ), ellipsoid to subcylindrical, straight to slightly curved, initially hyaline, after maturity golden brown to dark brown, smooth-walled, 3-euseptate, apex obtuse, base with scar.



**FIGURE 3.** *Homortomyces tamarixi* (holotype) A, B. Conidiomata on host *Tamarix gallica*. C. Cross section of conidioma. D–E. Conidioma wall. F. Ostiole. G, H, L. Conidia attach to conidiogenous cells. I–K, M–P. Conidia. Q. Germinating conidium. Scale bars: C, D = 120  $\mu\text{m}$ , E = 60  $\mu\text{m}$ , F–H, L = 30  $\mu\text{m}$ , I–K = 25  $\mu\text{m}$ , M–Q = 25  $\mu\text{m}$ .

**Cultural characteristics:**—Conidium germinates from apical and basal cells. Colonies on PDA at 20°C spreading, with irregular margins, not zonate, with thin mycelium, reaching 40 mm diam. after 2 weeks. Surface white, reverse yellowish brown.

## Discussion

The previously monotypic genus *Homortomyces* is typified by *H. combreti* (Crous *et al.* 2013). This genus is morphologically very similar to *Stilbospora*. The latter is characterised by cylindrical, fusiform to clavate, 3–4-euseptate, dark brown conidia that are truncate at the base (Sutton 1980). Both genera are coelomycetous and both share cylindrical, fusiform to clavate, 3–4-euseptate conidia but differ in the shape of conidiomata. *Homortomyces* species have pycnidial to intermediate conidiomata, while *Stilbospora* species have acervuli. Also, there is a scar at base of the conidia in *Homortomyces*. Crous *et al.* (2013) clearly showed that *Stilbospora macrosperma* Persoon (1801: 96) (CBS 121692–5, CBS 121882–3) grouped in *Diaporthales* in their phylogenetic analysis of LSU rDNA sequences. In our maximum-likelihood analysis (Fig. 1) of LSU rDNA sequences, *S. macrosperma* (CBS 121882 and CBS 121883) formed a distinct clade, having close affinity with *Gnomoniaceae*, *Harknessiaceae* and *Schizoparmaceae* in *Diaporthales*, while *Homortomyces* clustered closer with *Tubeufiaceae*. It is remarkable that species of *Homortomyces* and *Stilbospora* are morphologically similar yet are unrelated as molecular analyses show them to belong in different classes i.e. *Dothideomycetes* and *Sordariomycetes*, respectively. This is yet another example of convergent evolution or ‘the independent origination of similar organismic forms, as tantamount to experimental replication in the history of life and indicative of the robust counterfactual resilience of macroevolutionary pattern in the fungi’ (Powell 2008), which seems to have occurred often (Malagnac *et al.* 2008).

In our maximum likelihood analysis of the combined data set of LSU and ITS rDNA sequences (Fig. 2), the *Homortomyces* clade groups with *Tubeufiaceae* with high bootstrap value (77%). The *Homortomyces* clade and *Tubeufiaceae* clade are units with 100% bootstrap support. This indicates that *Homortomyces* might be a basal genus or family of *Tubeufiales* (Boonmee *et al.*, pers. comm), or a distinct order. This cannot be determined until sequence data is available for more species in these groups of fungi. Therefore, we keep *Homortomyces* in *Dothideomycetes* genera *incertae sedis* pending further studies.

*Homortomyces tamaricis* differs from *H. combreti* in several aspects, i.e. nature of conidia, supporting cells and paraphyses. Conidia of *Homortomyces tamaricis* (22–29 × 9–11 µm) are smaller than those of *H. combreti* (32–38 × 13–16 µm). The paraphyses of *H. combreti* are up to 100 µm long while in *H. tamaricis* they are up to only 70 µm long. Conidiogenous cells of both species are different in size, i.e. 20–60 × 3–5 µm and 9–27 × 2–3 µm in *H. combreti* and *H. tamaricis*, respectively.

We have not found any sexual state on host material and there were no hits of a sexual state in BLAST searches in GenBank. In our analysis and that of Crous *et al.* (2013) no sexual state groups with *Homortomyces*.

## Acknowledgments

Nalin N. Wijayawardene acknowledges the Mushroom Research Foundation (MRF), Chiang Rai Province, Thailand for providing Postgraduate Scholarship support. Erio Camporesi thanks Giancarlo Lombardi for his invaluable help in the collecting programme and identifying host plants. Gratitude is extended to the Guizhou Province Research Fund No. 20113045 for funding all molecular studies and Mae Fah Luang University grant for studying *Dothideomycetes* (no. 56101020032). This work was also supported by The Key Project of the National Science & Technology Program in the 12th Five-Year Plan of China: Rehabilitation technology and demonstration of rocky desertification in the karst plateau-gorge (Grant No.2011BAC09B01).

## References

- Boonmee, S., Zhang, Y., Chomnunti P., Chuksatirote, E., Tsui., C.K.M., Bahkali, A.H. & Hyde, K.D. (2011) Revision of lignicolous *Tubeufiaceae* based on morphological reexamination and phylogenetic analysis. *Fungal Diversity* 51: 63–102. <http://dx.doi.org/10.1007/s13225-011-0147-4>
- Chomnunti, P., Schoch, C.L., Aguirre-Hudson, B., Ko Ko, T.W., Hongsanan, S., Jones, E.B.G., Kodsueb, R., Phookamsak, R., Chuksatirote, E., Bahkali, A.H. & Hyde, K.D. (2011) *Capnodiaceae*. *Fungal Diversity* 51: 103–134. <http://dx.doi.org/10.1007/s13225-011-0145-6>
- Crous, P.W., Groenewald, J.Z., Lombard, L. & Wingfield, M.J. (2013) *Homortomyces* gen. nov., a new dothidealean pycnidial fungus from the Cradle of Humankind. *IMA Fungus* 3(2): 109–115. <http://dx.doi.org/10.5598/imafungus.2012.03.02.02>

- Dai, D.Q., Jayarama, B.D., Liu, J.K., Chukeatirote, E., Zhao, R.L. & Hyde, K.D. (2012) *Bambusicola*, a new genus from bamboo with asexual and sexual morphs. *Cryptogamie Mycologie* 33(3): 363–379.  
<http://dx.doi.org/10.7872/crym.v33.iss3.2012.363>
- Gruyter, J. de, Woudenberg, J.H.C., Aveskamp, M.M., Verkley, G.J.M., Groenewald, J.Z. & Crous, P.W. (2010) Systematic reappraisal of species in *Phoma* section *Paraphoma*, *Pyrenochaeta* and *Pleurophoma*. *Mycologia* 102: 1066–1081.  
<http://dx.org/10.3852/09-240>
- Gruyter, J. de, Woudenberg, J.H.C., Aveskamp, M.M., Verkley, G.J.M., Groenewald, J.Z. & Crous, P.W. (2013) Redisposition of *Phoma*-like anamorphs in *Pleosporales*. *Studies in Mycology* 75: 1–36.  
<http://dx.org/10.3114/sim0004>
- Hyde, K.D., Udayanga, D., Manamgoda, D.S., Tedersoo, L., Larsson, E., Abarenkov, K., Bertrand, Y.J.K., Oxelman, B., Hartmann, M., Kauserud, H., Ryberg, M., Kristiansson, E. & Nilsson, R.H. (2013) Incorporating molecular data in fungal systematics: a guide for aspiring researchers. *Current Research in Environmental & Applied Mycology* 3(1): 1–32.  
<http://dx.org/10.5943/cream/3/1/1>
- Kohli, D.K. & Bachhawat, A.K. (2003) CLOURE: Clustal Output Reformatter, a program for reformatting CLUSTALX/CLUSTALW outputs for use in SNP analysis and molecular systematics. *Nucleic Acids Research* 31: 3501–3502.  
<http://dx.org/10.1093/nar/gkg502>
- Liu, J.K., Phookamsak, R., Doilom, M., Wikee, S., Li, Y., Ariyawansa, H., Bhoonmee, S., Chomnunti, P., Dai, D.Q., Bhat, J.D., Romero, A.I., Zhuang, W.I., Monkai, J., Jones, E.B.G., Chukeatirote, E., Ko Ko, T.W., Zhao, Y.C., Wang, Y. & Hyde, K.D. (2012) Towards a natural classification of *Botryosphaeriales*. *Fungal Diversity* 57: 149–210.  
<http://dx.org/10.1007/s13225-012-0207-4>
- Malagnac, F., Bidard, F., Lalucque, H., Brun, S., Lambou, K., Lebrun, M.H. & Silar, P. (2008) Convergent evolution of morphogenetic processes in fungi: role of tetraspanins and NADPH oxidases 2 in plant pathogens and saprobes. *Communicative Integrative Biology* 1(2): 180–181.  
<http://dx.org/10.4161/cib.1.2.7198>
- Nag Raj, T.R. (1993) *Coelomycetous anamorphs with appendage-bearing conidia*. Mycologue Publications, Waterloo, Canada.
- Page, R.D.M. (1996) Tree View: an application to display phylogenetic trees on personal computers. *Computer Applications in the Biosciences* 12: 357–358.
- Persoon, C.H. (1794) *Dispositio methodica fungorum* 1: 81–128.
- Persoon, C.H. (1801) *Synopsis methodica fungorum* 1: 96.
- Powell, R. (2008) Convergent evolution and the limits of natural selection. *European Journal of Philosophy of Science* 2(3): 355–373.  
<http://dx.org/10.1007/s13194-012-0047-9>
- Silvestro, D. & Michalak, I. (2012) raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity and Evolution* 12(4): 335–337.  
<http://dx.org/10.1007/s13127-011-0056-0>
- Stamatakis, A. (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.  
<http://dx.org/10.1093/bioinformatics/btl446>
- Sutton, B.C. (1980) *The coelomycetes – fungi imperfecti with pycnidia, acervuli and stromata*. Commonwealth Mycological Institute, Kew, UK.
- White, T.J., Bruns, T., Lee, S. & Taylor J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (Eds.) *PCR protocols: a guide to methods and applications*. Academic Press, San Diego, California, U.S.A., pp. 315–322.  
<http://dx.org/10.1002/mrd.1080280418>
- Wijayawardene, D.N.N., McKenzie, E.H.C., Chukeatirote, E., Wang, Y. & Hyde K.D. (2012a) Coelomycetes. *Cryptogamie Mycologie* 33(3): 215–244.  
<http://dx.doi.org/10.7872/crym.v33.iss3.2012.215>
- Wijayawardene, D.N.N., Udayanga, D., McKenzie, E.H.C., Wang, Y. & Hyde, K.D. (2012b) The future of coelomycete studies. *Cryptogamie Mycologie* 33(3): 381–391.  
<http://dx.doi.org/10.7872/crym.v33.iss3.2012.381>
- Wijayawardene, D.N.N., Song, Y., Bhat, D.J., McKenzie, E.H.C., Chukeatirote, E., Wang, Y. & Hyde, K.D. (2013) *Wojnowicia viburni* sp. nov. from China and its phylogenetic placement. *Sydowia* 65(1): 181–190.
- Vilgalys, R. & Hester, M. (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172: 4238–4246.
- Zhang, H., Hyde, K.D., McKenzie, E.H.C., Bahkali, A.H. & Zhou, D. (2012) Sequence data reveals phylogenetic affinities of *Acrocalymma aquatica* sp. nov., *Aquasubmersa mircensis* gen. et sp. nov. and *Clohesyomyces aquaticus* (freshwater coelomycetes). *Cryptogamie Mycologie* 33(3): 333–346.  
<http://dx.doi.org/10.7872/crym.v33.iss3.2012.333>