Phytotaxa 176 (1): 156–163
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.176.1.15

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

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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 linage 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.*

 Accepted by Eric McKenzie: 25 Mar. 2014; published: 20 Aug. 2014

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

..... *continued on the next page*

TABLE 1 (continued)

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

[1]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, Bakeham Lane, 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.

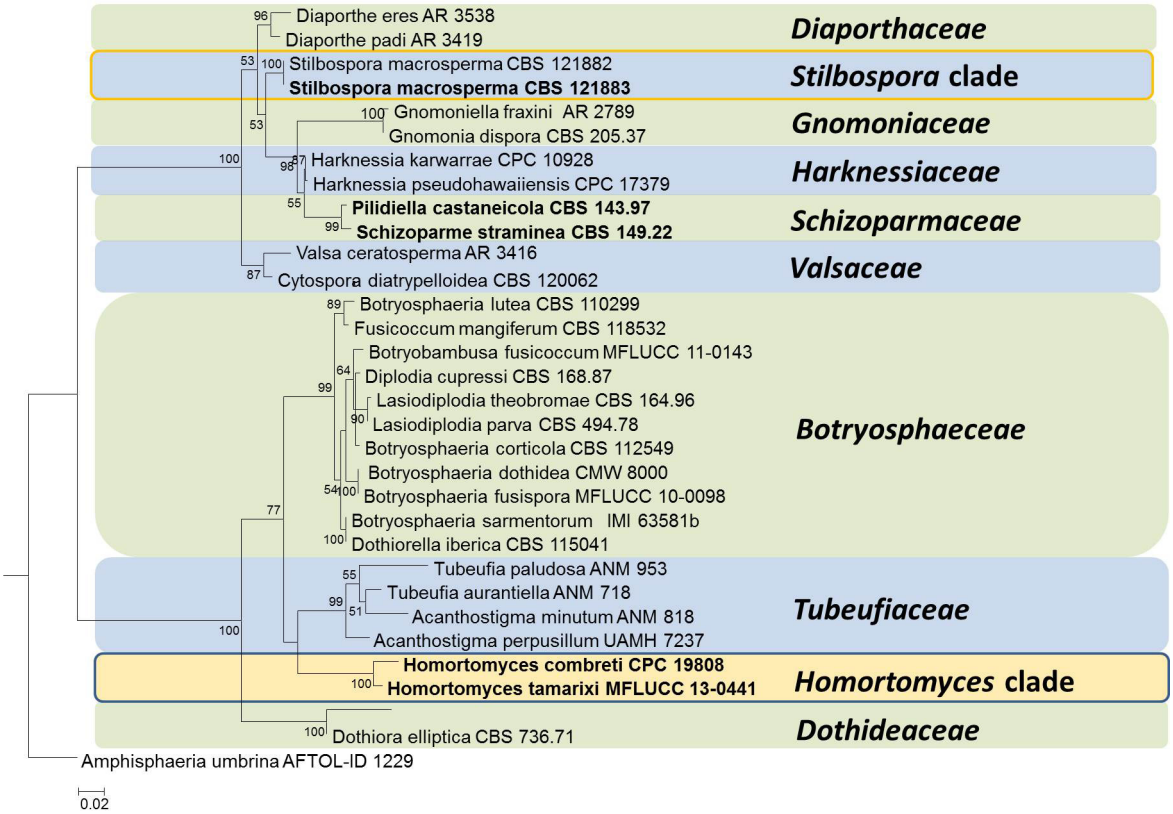

FIGURE 1. RAxML tree based on dataset of LSU sequences. Bootstrap support values for maximum-likelihood (ML) greater than 50% are given above the nodes. The GenBank numbers are given after the species names. The tree is rooted to *Amphisphaeria umbrina* (AFTOL-ID 1229). All sequences from type strains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

Combined analysis of LSU and ITS rDNA

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).

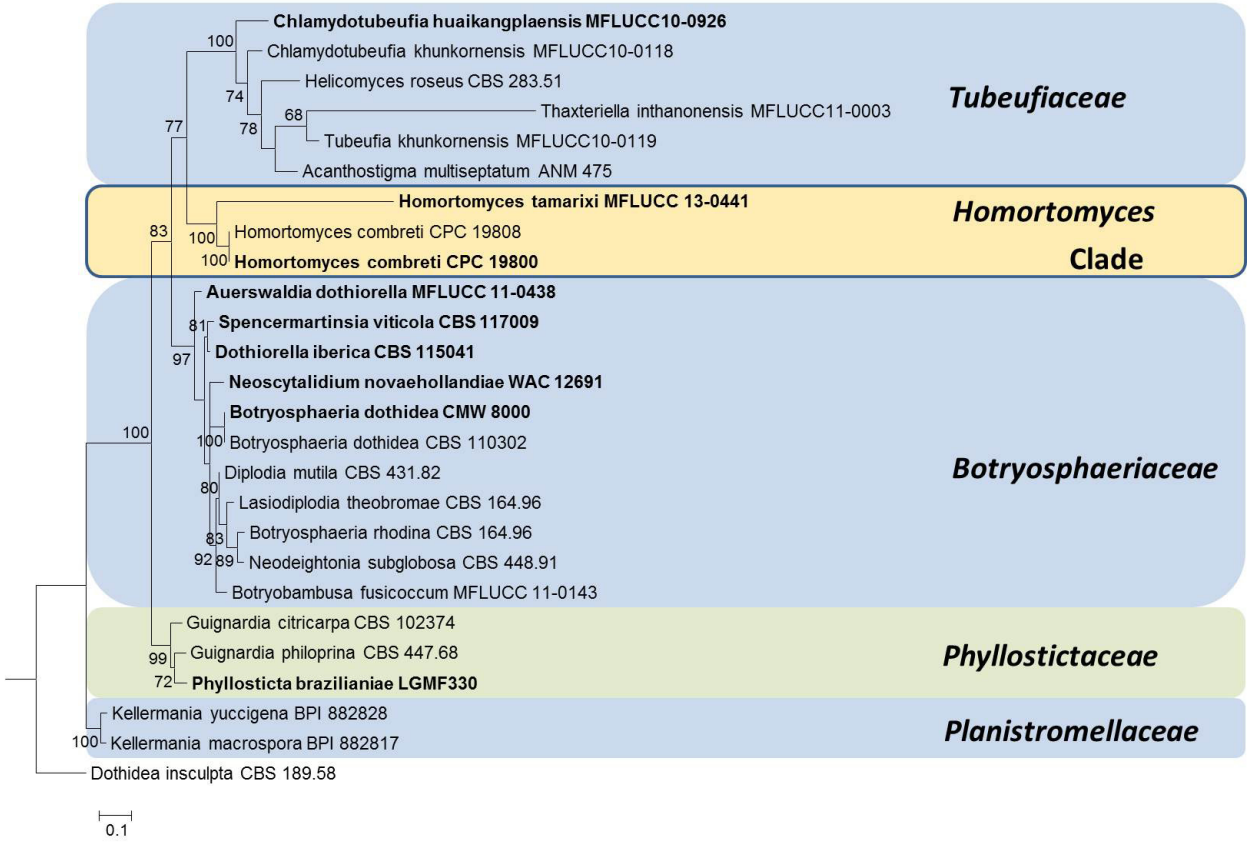

FIGURE 2. RAxML tree based on combined dataset of LSU and ITS rDNA sequences. Bootstrap support values for maximum likelihood (ML) greater than 50% are given above the nodes. The GenBank numbers are given after the species names. The tree is rooted to *Dothidea insculpta* (CBS 189.58). All sequences 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 (22–29 × 9–11 µm vs. 32–38 × 13–16 µm).

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* 50–200 µm diam., 200–300 µm high, solitary or gregarious, immersed, pycnidial to irregular, uniloculate, subglobose. *Ostiole* central. *Pycnidium wall* with 25–40 µm wide, outer layer, comprising about 5 cell layers, of brown-walled cells of *textura angularis*, with 30–40 µm wide hyaline inner cell layer. *Paraphyses* numerous, aseptate, cylindrical, hyaline, 23–70 × 1–2 µm. *Conidiophores* reduced to conidiogenous cell with supporting cell, hyaline, percurrent

proliferation at the tip of the supporting cells, 9−27 × 2−3 µm. *Conidia* 22−29 × 9−11 µm ($\bar{x}$ = 26.3 × 10.2 µm, 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.

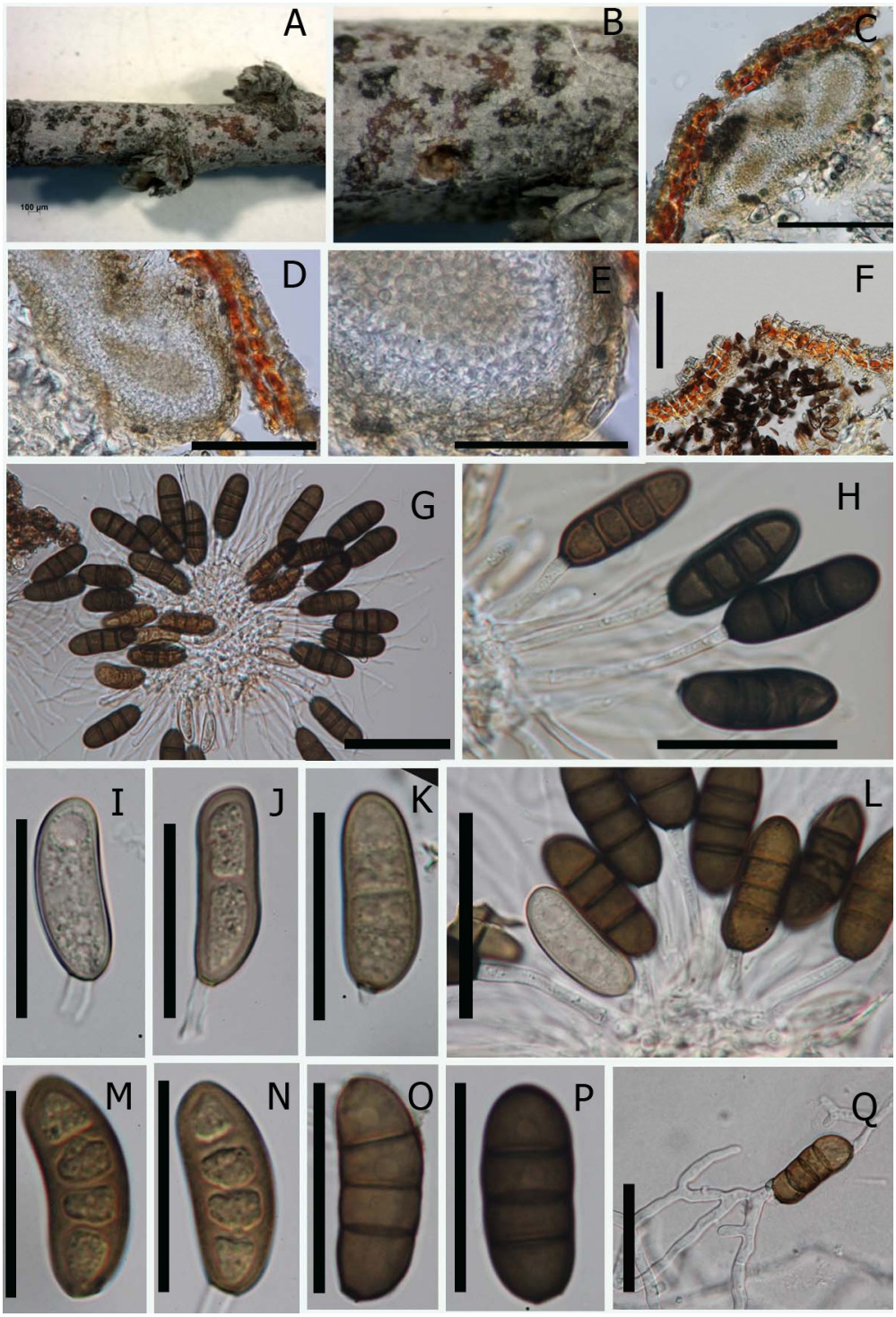

FIGURE 3. *Homortomyces tamarixi* (holotype) A, B. Conidiomata on host *Tamarix gallica.* C. Cross section of conidioma. D−E. Conidioma wall. F. Ostiole. G, H, L. Conidia attach to conidiogenous cells. I−K, M−P. Conidia. Q. Germinating conidium. Scale bars: C, D = 120 µm, E = 60 µm, F−H, L = 30 µm, I−K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

Cultural characteristics:—Conidium germinates from apical and basal cells. Colonies on PDA at 20ºC 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).

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