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Multi-gene phylogeny of *Jattaea bruguierae*, a novel asexual morph from *Bruguiera cylindrica*

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Abstract

During our survey on marine-based ascomycetes of southern Thailand, fallen mangrove twigs were collected from the intertidal zones. Those specimens yielded a novel asexual morph of *Jattaea* (*Calosphaeriaceae*, Calosphaeriales), *Jattaea bruguierae*, which is confirmed as a new species by morphological characteristics such as nature and measurements of conidia and conidiophores, as well as a multigene analysis based on combined LSU, SSU, ITS and β-tubulin sequence data. *Jattaea* species are abundantly found from wood in terrestrial environments, while the asexual morphs are mostly reported from axenic cultures. *Jattaea bruguierae* is the first documentation of an asexual morph species from marine- habitats.

Key words – marine fungi – morphology – phylogeny – taxonomy

Introduction

Berlese (1900) introduced *Jattaea* Berl. and *Wegelina* Berl. as morphologically similar genera with hyaline, allantoid, one-celled ascospores and clavate asci. They can be distinguished primarily by characters of perithecia and length of the ostiolar neck; papillate to short-beaked in *Jattaea* vs. cylindrical elongate necks in *Wegelina*. *Jattaea algeriensis* Berl. was designated as a respective lectotype by Clements & Shear (1931). Later, the generic name *Jattaea* was accepted, with *Wegelina* as its synonym, to include species with hyaline, allantoid to suballantoid ascospores in clavate, stipitate asci without an apical annulus borne on individual cells on ascogenous hyphae and phialophora-like asexual morphs produced in axenic culture (Réblová 2011). *Jattaea* species occur usually solitarily, scattered or in small irregular to valsoid groups on wood beneath the periderm, around old fungal stromata or margins of the peeled bark or are rarely immersed in decaying wood. Some species, however, have ascomata arranged in 1–2 vertical levels and in larger groups similar to *Calosphaeria* Tul. & C. Tul. The asci in *Jattaea* are oblong-clavate to clavate and short- to long-stipitate. Multigene analyses by Réblová (2011) also confirmed that septation of ascospores, a diagnostic feature used to separate calosphaeria-like fungi into the genus

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Phragmocalosphaeria Petr., does not appear to be relevant in distinguishing genera in the Calosphaeriales M.E. Barr. Therefore, *Phragmocalosphaeria* Petr. is also synonymized under *Jattaea* and hence, it comprises both one-celled and septate ascospores. The genus *Jattaea* was recently revised using five genes and 17 species are accepted (Réblová et al. 2015).

Asexual morphs of *Jattaea* are morphologically seen as dematiaceous phialidic hyphomycetes and are referred to as phialophora-like (Damm et al. 2008). They are characterized by semi-macronematous, hyaline, subhyaline to pale yellow-brown conidiophores often reduced to conidiogenous cells such as phialides or adelo-phialides, i.e. single conidiogenous cells without a basal septum. Phialides are hyaline, subhyaline or pale brown, sometimes pigmented in the apical region just below the collarette; they are short-ampulliform to elongate-ampulliform to cylindrical, tapering, with a more or less conspicuous funnel-shaped collarette (Réblová et al. 2015).

The objective of this study is to introduce a novel, marine-based, asexual morph, *Jattaea bruguierae* from *Bruguiera cylindrica* (L.) from southern Thailand. Micro-morphology and maximum parsimony, maximum likelihood and Bayesian analyses of combined LSU, SSU, ITS and β–tubulin sequence data confirmed the phylogenetic placement of this novel species within the family *Calosphaeriaceae*.

Materials and methods

Sample collection, specimen examination and isolation

Fallen, decaying twigs of *Bruguiera cylindrica* were collected in a mangrove area at Ranong Mangrove Research Center, Mu 4 Tombol Ngao, Amphoe Maung, Ranong Province, Thailand (GPS: 9°43' to 9°57'N; 98°29' to 98°39'E). Twigs were placed in Zip-lock plastic bags and incubated at room temperature in the laboratory. Axenic strains were established from single conidia as described in Chomnunti et al. (2014) with half-strength sea water potato dextrose agar (PDA) (Atlas 2006). Germinating conidia were transferred, under a Motic SMZ 168 Stereo Zoom microscope, to half strength sea water malt extract agar (MEA, 2 % malt extract, Oxoid Ltd., England; 1.5 % agar, Difco, USA) and potato dextrose agar (PDA; 39 g/L distilled water and distilled sea water, Difco potato dextrose) for extraction of DNA, determination of growth rates and observation of cultural characteristics. Vegetative hyphae, conidiophores and conidia produced in half strength sea water MEA were observed after six weeks of incubation at 25 °C. Digital images of fruiting structures were captured with a Canon 450D digital camera fitted to a Nikon ECLIPSE 80i compound microscope. Squash mount preparations were prepared to determine micro-morphology. Measurements of morphological structures were taken using the Tarosoft (R) Image Frame Work program and images used for figures processed with Adobe Photoshop CS3 Extended v. 10.0 (Adobe®, San Jose, CA). Living cultures are deposited at the Culture Collection of Mae Fah Luang University (MFLUCC) and Thailand Bio Resource Research Center (TBRC). Measurements were taken with the Tarosoft (R) Image Frame Work and Adobe Photoshop CS3 Extended version 10.0 software was used to prepare the photo plates. The herbarium specimen of the new species along with a dry culture comprising conidial structures is deposited in the Mae Fah Luang University Herbarium (MFLU). Faces of fungi and Index Fungorum numbers were registered according to Jayasiri et al. (2015) and Index Fungorum (2017).

DNA extraction, PCR amplification and sequencing

The Biospin Fungus Genomic DNA Extraction Kit (BioFlux®, China), (Hangzhou, P. R. China) was used to extract DNA from fungal cultures grown on MEA for 14 days at 25 °C following manufacturer's instructions. Extracted genomic DNA was amplified by using PCR technique with the following ingredients: each amplification reaction contained 0.125 μL of 5 units/μL Ex-Taq DNA polymerase (TaKaRa), 2.5 μL of 10 × PCR buffer, 2 μL of 2 mM MgCl2, 2.5 μL of 2 mMdNTPs, 1 μL of 0.2–1.0 μM primer, <500 ng DNA template and was adjusted with double-distilled water to a total volume of 25 mL. Temperature profiles and primers used to amplify LSU, SSU, ITS and β–tubulin gene regions are listed in table 1. The PCR products were

observed on 1% agarose electrophoresis gels stained with Ethidium bromide. Purification and sequencing of PCR products were carried using the above-mentioned PCR primers at Sun biotech company (Beijing, China), for purification and direct sequencing with the same primers. Returned sequences were checked for ambiguity, assembled and deposited in GenBank.

Table 1 Genes/loci used in the study with respective PCR primers and protocols

Gene/loci	Primer		PCR protocol					Reference
	Fd	Rd	Initial denatu.	Denatu.	Anneal.	Extens.	Final ex.	
ITS LSU SSU	ITS4 LR0R NS1	ITS5 LR5 NS4	94°C, 4 min 1 cycle	94°C, 45 sec 35 cycles	56°C, 45 sec	72°C, 1 min	72°C, 10 min 1 cycle	White et al. (1990), Rehner & Samuels (1994), Vilgalys & Hester (1990).
β–tubulin	Bt2a	Bt2b	94°C, 3 min	94°C, 30 sec	56°C, sec 50	72°C, 1 min	72°C, 10 min	Glass & Donaldson (1995).

Phylogenetic analysis

ITS, LSU, SSU and β-tubulin sequence data was compared by BLAST searches in the GenBank database at the National Centre for Biotechnology Information (NCBI) and sequences were analyzed with other sequences of the family *Calosphaeriaceae* following Réblová et al. (2015). Sequence data were aligned by MAFFT v. 6.864b (http://mafft.cbrc.jp/alignment/server/index.html), and combined using Bioedit 7 (Hall 1999) and MEGA7 (Tamura et al. 2011) and refined visually. Phylogenetic analysis consisted of three methods: Maximum likelihood analysis (ML) was performed by RAxMl GUI v. 1.3 (Silvestro & Michalak 2012, Stamatakis 2014). The search strategy was set to rapid bootstrapping and the analysis was carried out with 1000 replicates using the GTRGAMMAI model of nucleotide substitution, which was the best model predicted for the combined ITS, LSU, SSU and β-tubulin data set by MrModeltest v. 2.3.

Bayesian analysis was performed using MrBayes v. 3.0b4 (Ronquist & Huelsenbeck 2003). Nucleotide substitution models were determined with MrModeltest v. 2.2 (Nylander 2004). A dirichlet state frequency was predicted for all four data partitions and GTR+I+G was the best model. The heating parameter was set to 0.2 and trees were saved every 1 000 generations (Ronquist et al. 2012). Posterior probabilities (PP) (Rannala et al. 1998, Zhaxybayeva & Gogarten 2002) were defined by Bayesian Markov Chain Monte Carlo (BMCMC) sampling method in MrBayes v. 3.0b4 (Huelsenbeck & Ronquist 2001). Six simultaneous Markovchains were run for 500000 generations and trees were sampled every 100th generation resulting in 10000 total trees. 8000 trees were used for calculating posterior probabilities (PP) in the majority rule consensus tree, after discarding the first 1000 trees representing the burn-in phase (20 %) of the analysis.

Parsimony analysis was performed to obtain the most parsimonious tree. Trees were inferred using the heuristic search option with 1000 random sequence additions. Maxtrees were setup to 1000 and branches of zero length were collapsed and all multiple parsimonious trees were saved. Descriptive tree statistics for parsimony (Tree Length [TL], Consistency Index [CI], Retention Index [RI], Relative Consistency Index [RC] and Homoplasy Index [HI]) were calculated for trees generated under different optimality criteria. Kishino-Hasegawa tests (KHT) (Kishino & Hasegawa 1989) were performed in order to determine whether trees were significantly different. Maximum likelihood analysis was performed using RAxML GUI v. 1.3 (Silvestro & Michalak 2012). General time reversible model (GTR) using proportion of invariable sites was applied with a discrete gamma distribution and four rate classes. The best scoring tree was selected with a final

Table 2 GenBank and culture collection accession numbers of isolates included in this study. Sequences generated in this study are in blue.

Taxon	Source	Gene Bank Accession			
		ITS	LSU	SSU	β–tubulin
Calosphaeria africana	**CBS 120870**	**EU367444**	**EU367454**	**EU367460**	**EU367464**
Calosphaeria africana	STE-U 6181	EU367445	EU367445	EU367461	EU367465
Calosphaeria pulchella	**CBS 115999**	**EU367451**	**AY761075**	**AY761071**	**KT716476**
Calosphaeria pulchella	CCTU 316	JX876610	JX876611	–	–
Calosphaeria pulchella	LM 06	HM237298	–	–	–
Calosphaeria pulchella	SS 07	HM237297	–	–	–
Calosphaeria pulchella	DC 04	HM237299	–	–	–
Calosphaeria pulchella	SM 05	HM237300	–	–	–
Flabellascus tenuirostris	**CBS 138680**	**KT716466**	**KT716457**	**–**	**KT716488**
Flabellascus tenuirostris	CBS 138690	KT716467	KT716458	–	KT716489
Flabellascus tenuirostris	CBS 138692	KT716468	KT716459	–	KT716483
Flabellascus tenuirostris	CBS 139026	KT716469	KT716460	–	KT716484
Jattaea algeriensis	**CBS 120871**	**EU367446**	**EU367456**	**EU367462**	**EU367466**
Jattaea algeriensis	STE-U 6400	EU367448	–	–	–
Jattaea algeriensis	STE-U 6399	EU367447	EU367457	–	–
Jattaea aphanospora	**PRM 934328**	**HQ878588**	**HQ878594**	**–**	**KT716477**
Jattaea aurea	CBS 140209	KT716462	KT716453	KT716447	KT716478
Jattaea bruguierae	**MFLUCC 15–1277**	**MG593190**	**MG593189**	**MG593191**	**MG593192**
Jattaea discreta	CBS 127681	HQ878587	HQ878593	HQ878597	KT716479
Jattaea leucospermi	**CBS 119343**	**EU552127**	**EU552127**	**–**	**–**
Jattaea mookgoponga	**CBS 120867**	**HQ878589**	**EU367458**	**EU367463**	**EU367467**
Jattaea mookgoponga	STE-U 6401	EU367450	EU367459	–	–
Jattaea mucronata	**MFLU 16-0534**	**KY034452**	**KY034451**	**MG593193**	**–**
Jattaea ribicola	**CBS 139779**	**KT716463**	**KT716454**	**KT716448**	**KT716480**

Table 2 Continued.

Taxon	Source	Gene Bank Accession			
		ITS	**LSU**	**SSU**	**β–tubulin**
Jattaea sp. 1	HNDC 06	GU361954	–	–	–
Jattaea sp. 2	YNDC 23	GU361945	–	–	–
Jattaea sp. 2	YNDC 19	GU361941	–	–	–
Jattaea sp. 3	CBS 122684	EU552160	EU552160	–	EU552167
Jattaea sp. 3	CMW 22119	EU552159	EU552159	–	–
Jattaea sp. 4	CBS 122685	EU552161	EU552161	–	EU552168
Jattaea taediosa	**PRM 934412**	**KT716464**	**KT716455**	**KT716449**	**KT716481**
Jattaea tumidula	**CBS 140208**	**KT716465**	**KT716456**	**KT716450**	**KT716482**
Phaeoacremonium minimum	**CBS 246.91**	**NR077126**	–	–	**AF246811**
Phaeoacremonium novae-zealandiae	**CBS 110156**	**NR136064**	–	–	**DQ173110**
Pleurostoma ochraceum	**CBS 131321**	**JX073270**	**JX073274**	**JX073269**	**JX073271**
Pleurostoma ootheca	**CBS 115329**	**HQ878590**	**AY761079**	**AY761074**	**JX073272**
Pleurostoma repens	**CBS 294.39**	–	**AY729813**	–	**JX073273**
Pleurostoma richardsiae	**CBS 270.33**	**NR135933**	–	**AY729812**	**AY579334**
Togniniella acerosa	**CBS113726**	**NR135947**	–	–	–
Togniniella acerosa	CBS113648	EU367453	–	–	KT716486
Togniniella acerosa	CBS125298	KT716470	KT716461	KT716451	KT716485

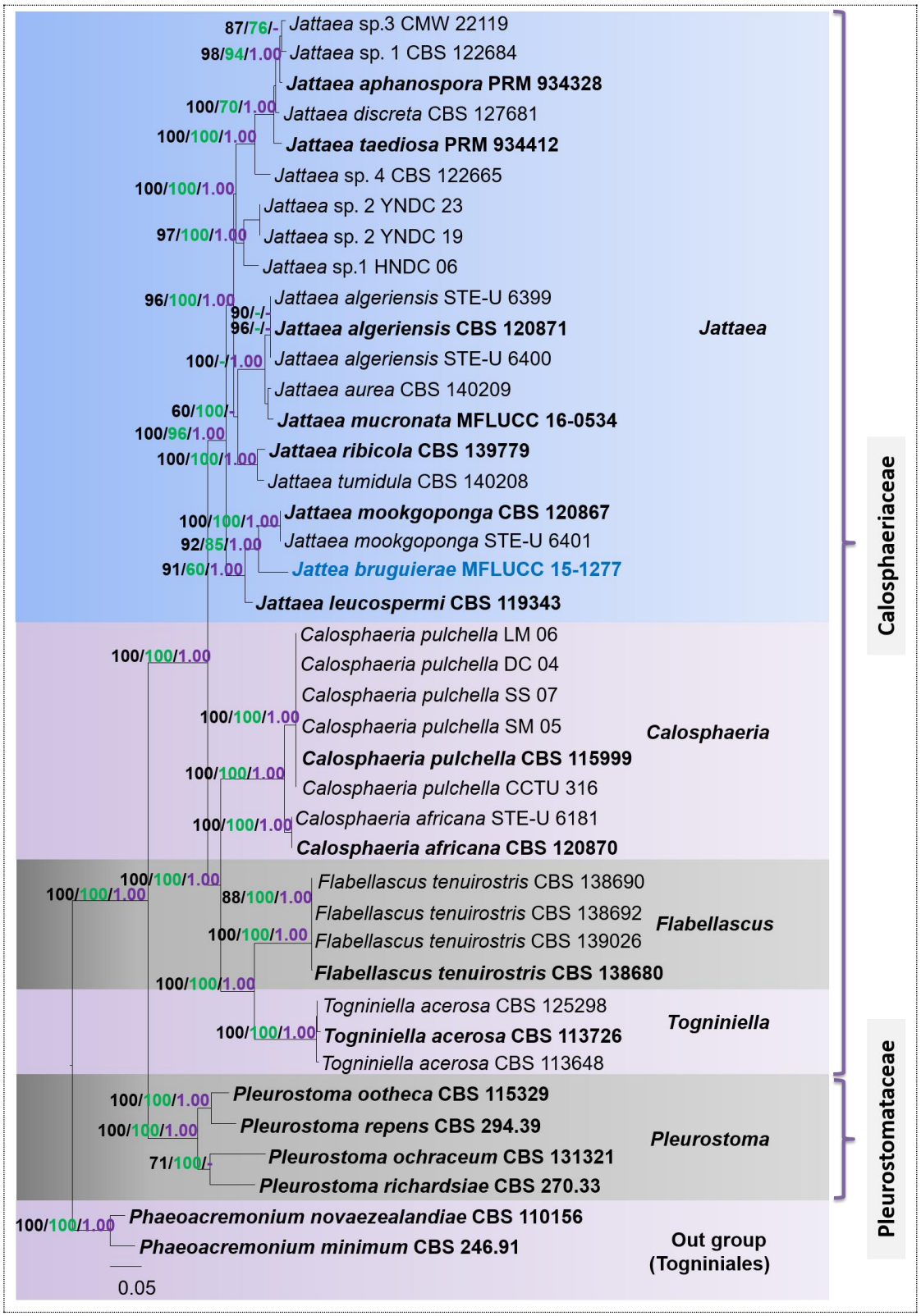

Fig. 1 – RAxML tree based on analysis of a combined dataset of ITS, LSU, SSU and β-tubulin sequence data. The scale bar indicates 0.05 changes. ML, MP bootstrap support values > 60 % from 1 000 replicates and BYPP > 0.95 from 5 million generations in Markov chains are shown at the nodes. Taxonomic novelty in blue and ex-type strains are in **bold** text. GenBank accession numbers are indicated at the end of the species name. The tree was rooted to *Phaeoacremonium novaezealandiae* and *Ph. minimum* (Togniniaceae).

likelihood value of -14937.759370. Resulting trees were visualized with TreeView v. 1.6.6 (Page 1996).Maximum likelihood bootstrap values (ML) ≥ 60 %, Bayesian posterior probabilities (PP) ≥ 0.90%) and Maximum parsimony bootstrap values (MP) ≥ 60% are given above the nodes (Fig. 1). Sequences generated in this study were deposited in GenBank and the final alignments and the trees obtained were deposited in TreeBASE (Reviewer access URL: http://purl.org/phylo/treebase/phylows/study/TB2:S21945?x-accesscode=df2103af4d865cd800e7a942930166e6&format=html) and are available under study accession no. S21945.

Results

Thirty-two taxa were included in the combined ITS, LSU, SSU and β-tubulin data set with *Phaeoacremonium novaezealandiae* and *Ph. minimum* as the out-group taxa. Parsimony analysis indicated that alignment comprised 3116 characters (including gaps) and 2354 characters were constant; 94 variable characters were parsimony-uninformative; and 668characters were parsimony informative. The most parsimonious tree out of 8 trees showed TL = 2219, CI = 0.574, RI = 0.798, RC = 0.458, HI = 0.426values. Tree topology of the maximum parsimony, Bayesian analysis (not shown) was almost compatible with the ML tree and the best scoring RAxML tree, with a final likelihood value of -14937.759370 is presented in Fig 1. The novel taxon *Jattaea bruguierae*, grouped as a separate lineage with high bootstrap support and high posterior probability (92% ML/ 85% MP, 1.00 PP) within *Calosphaeriaceae* in a clade comprising *Jattaea leucospermi* and *Jattaea mookgoponga*. However, *Jattaea leucospermi* and *J. mookgoponga* group in a monophyletic subclade with the strain of *J. bruguierae* (100% ML/ 96% MP/ 1.00 PP) among other *Jattaea* species.

Taxonomy

Jattaea bruguierae Dayarathne, Jones E.B.G. & K.D. Hyde, sp. nov. Fig. 2

Index Fungorum number: IF554045; Facesoffungi number: FoF03892

Etymology – Name reflects the host genus *Bruguiera*

Holotype – MFLU 17-2648

Saprobic on fallen decaying twigs of *Bruguiera cylindrica*. Sexual morph: Undetermined. Asexual morph: *Mycelium* composed of vegetative hyphae, on half-strength seawater MEA, hyaline, 2.5–3.5 µm wide, septate, branched, smooth, partly compacted to form hyphal strands. Conidiophores hyaline, simple or branched, elongated, erect or flexuous, up to 45 µm long, sometimes ending with sterile cells. Conidiogenous cells enteroblastic, phialidic with periclinical wall thickening, discrete or adelophialides, with discrete phialides subcylindrical to elongate-ampulliform and constricted base, single or in conidiophores,10–40 × 1–3 µm; adelophialides cylindrical, 2.5–8 × 1.5–3 µm; collarettes distinct,1–2.5 µm long, 1.5–2 µm wide, with 1.5 µm wide opening. Conidia 3.5–4.5 × 2.0–3.0 µm ($\bar{x}$ = 4 × 2.5 µm, n = 20), hyaline, aseptate, cylindrical with a tapered and truncate base, smooth-walled, sometimes held together in droplets.

Cultural characteristics – Colonies on half-strength seawater MEA flat, fimbriate edge,with floccose aerial mycelium; surface white, buff, cinnamon to orange, turning sepia with age, reverse pale luteous, orange, turning amber with age, 30 mm within 2 weeks (25 °C). Conditions for growth: min 15 °C, max 30 °C, opt 25 °C. Colonies on half-strength seawater PDA flat, fimbriate edge, with floccose aerial mycelium; surface white, buff, cinnamon, turning dark sepia with age, reverse pale luteous, orange, turning umber with age. 20 mm within 2 weeks (25 °C)

Material examined – THAILAND, Ranong Province, Amphoe Maung, Mu 4 Tombol Ngao, Ranong Mangrove Research Center (GPS: 9°43' to 9°57'N; 98°29' to 98°39'E), on fallen decaying twig of *Bruguiera cylindrica*, 6 December 2016, Monika C. Datarathne, MCD 038 (MFLU 17-2648 **holotype**), ex-type living culture, MFLUCC 15–1277, TBRC.

Notes – *Jattaea bruguierae* which is currently known only from its asexual morph, is distinct from *J. mookgoponga* by its hyaline, elongated conidiophores and cylindrical conidia with a tapered base, while *J. mookgoponga* comprises yellow brown conidiophores and cylindrical to

ellipsoidal conidia with obtuse ends on MEA (Damm et al. 2008). Based on phylogenetic analysis, *J. leucospermi* is also closely related to *Jattaea bruguierae* which is so far known only as a phialophora-like asexual morph.

Fig. 2 – *Jattaea bruguierae* (MFLU 17-2648, holotype). a Host. b, c Culture on half strength sea water MEA (b from upper, c from lower). d Appearance of type in culture. e Conidiophores. f–i Phialides. j–m Conidia. Scale bars: e, f = 20 µm, g–i = 10 µm, j–m= 5 µm.

Discussion

The present study introduces a new species in the genus *Jattaea* (*Jattaea bruguierae)*, provided with a morphological description, illustrations and combined analyses of LSU, SSU, ITS and β-tubulin sequence data. Recently, Réblová et al. (2015) has used combined LSU, SSU, ITS, RPB2 and β-tubulin genes in their phylogenetic reconstruction of Calosphaeriales. Unfortunately, we did not obtain RPB2 sequence data even after several attempts with different PCR temperature profiles by using the primers fRPB2-5F and fRPB2-7cR. However, the concatenated dataset of LSU, SSU, ITS and β-tubulin sequences reveals a phylogeny which is topologically congruent to Réblová et al. (2015). Hence, we are confident with our taxonomic arrangement of the novel taxon which is phylogenetically close to *Jattaea leucospermi* and *J. mookgoponga* with strong bootstrap support (100% ML/ 96% MP/ 1.00 PP, Fig. 1). Our species is morphologically different from all the other previously described species in having hyaline, elongated conidiophores and cylindrical conidia with a tapered base, while others have yellow brown conidiophores and cylindrical to ellipsoidal conidia with obtuse ends. Therefore, both morphological and phylogenetic support ensures that our species definition and justification for establishing a new species is scientifically valid within Calosphaeriaceae. *Jattaea* was recently revisited with 17 accepted species and asexual morphs linked to the genus comprise reduced, morphologically similar dematiaceous hyphomycetes with phialidic conidiogenous cells similar to *Phialophora* (Réblová et al. 2015). The asexual morphs of *Jattaea* have been experimentally established for nine of the 17 accepted species, i.e. *J. algeriensis* Berl., *J. aphanospora* Réblová & J. Fourn., *J. aurea* Réblová & J. Fourn., *J. discrete* (Berl.) Réblová, *J. leucospermi* Marinc., M.J. Wingf. & Crous, *J. mookgoponga* Damm & Crous, *J. ribicola* Réblová & Jaklitsch, *J. taediosa* (Sacc.) Réblová & Jaklitsch and *J. tumidula* (Sacc.) Réblová, by the previous studies of Damm et al. (2008), Réblová (2011) and Réblová et al. (2015). *Jattaea mookgoponga* and our novel species, *J. bruguierae* are known only as asexual morphs, while all the other asexual morphs have been linked with their sexual morphs (Réblová et al. 2015). Although the differences between asexual morphs of *Jattaea* based on their morphology they are distinctly different at the molecular phylogenetic level (Réblová 2011, Réblová et al. 2015) and as demonstrated in our study. Different authors have described colony characteristics of asexual morphs of *Jattaea* species in different culture media, such as normal PDA, MEA, potato-carrot agar (PCA, Gams et al. 1998), synthetic nutrient-poor agar medium (SNA, Nirenberg 1976). In our study, we described cultural characteristics of *J. bruguierae* on half-strength seawater PDA and half-strength seawater MEA media and it grew fast and sporulated well. However, we did not observe conidial structures on the host surface. Therefore, we designated a dry culture along with the herbarium material as the holotype. Our species also morphologically resembles asexual morphs of *Phaeoacremonium* spp. However, according to phylogenetic analysis it is confirmed that our novel species does not belong to *Phaeoacremonium*. *Jattaea mucronata,* introduced by Abdel-Wahab et al. (2017), is the first documentation of a sexual morph of *Jattaea* associated with a marine habitat while *J bruguierae* is the first record of an asexual morph from mangroves.

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