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ORIGINAL ARTICLE

A novel marine genus, *Halobyssothecium* (Lentitheciaceae) and epitypification of *Halobyssothecium obiones* comb. nov.

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Abstract
A novel marine genus, *Halobyssothecium* (Lentitheciaceae), is introduced to accommodate *Byssothecium obiones* (= *Halobyssothecium obiones*) with evidence from phylogenetic analyses of concatenated LSU, SSU, ITS rDNA, and TEF1 sequence data. We could not locate any type material for this species and there is no molecular data available for the type of this species. Therefore, an epitype is designated for the precise delineation of this taxon. A detailed morphological description and DNA characterization based on LSU, SSU, ITS rDNA, and TEF1 sequence data are provided for the epitype, obtained from *Spartina* culms in Eastney, Langstone Harbour, Hampshire, UK.

Keywords New genus · Marine fungi · *Passeriniella* · *Leptosphaeria* · Phylogeny · *Spartina* · Taxonomy

Introduction

Byssothecium obiones (P. Crouan & H. Crouan) M.E. Barr was introduced by Crouan and Crouan (1867) as *Pleospora obiones* P. Crouan & H. Crouan from *Halimione portulacoides* (L.) Moq. However, the protologue lacks collection details and includes few morphological characters. The protologue of *Pleospora obiones* (Crouan and Crouan 1867) was as follows "*P. obionei* Crn. Mscr. Perithecium de 1 millim., naissant sous 1'écorce, noir, conique, à ostiole très-court, thèques étroites subcylindriques à 8 spores jaunâtre, oblongues, subtoruleuses à 3 cloisons. Sur les tiges mortes d'Obione. Pr. r.". There are few other records of *Byssothecium obiones* from the original host *Halimione portulacoides* (Crouan and Crouan 1867; Grove 1933), while this species has been reported mostly from *Spartina* and/or *Phragmites* (Jones 1963; Hyde and Mouzouras 1988; Barr 2002). *Byssothecium obiones* occurring on decaying *Spartina* culm, has been assigned to various other genera viz. Didymosphaeria, *Heptameria*, *Pleospora*, *Leptosphaeria*, and *Passeriniella* (Jones 1962; Kohlmeyer and Kohlmeyer 1979; Hyde and Mouzouras 1988; Khashnobish and Shearer 1996a, 1996b; Barr 2002). Saccardo (1944) synonymized *Pleospora obiones* as *Leptosphaeria obiones* (Crouan & Crouan) Sacc. Subsequently, Apinis and Chester (Apinis and Chesters 1964) transferred it to the genus *Passeriniella*, named as *P. discors* (Sacc. & Ellis) Apinis & Chesters. Hyde and Mouzouras (1988) described ascospore morphologies of *L. obiones* as not typical of *Leptosphaeria* and hence referred it as *Passeriniella obiones*. Based on molecular analysis, Khashnobish and Shearer (1996a, 1996b) showed that *Byssothecium obiones* belonged to neither *Leptosphaeria* nor *Phaeosphaeria*. Barr (2002) assigned the species to *Byssothecium* in *Teichosporaceae* based on its versicolorous ascospores, two dark brown central cells and hyaline terminal

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cells. Suetrong et al. (2009) stated that byssothecium-like taxa grouped with *Mycosphaerella (*Capnodiales*)* in their preliminary analyses. However, the origin of the sequence (JK 4748) that Suetrong et al. (2009) used in their analyses is not related to any type material and morphologically it resembles *B. obiones*. They therefore, did not assign it to any family because the culture could not be verified. Jones et al. (2015) assigned the species to Dacampiaceae (Pleosporales). However, Wijayawardene et al. (2018) included *Passeriniella* under Dothideomycetes genera *incertae sedis*. Jones (1962) documented two distinct ascospore measurements, 24–32 × 8–10 μm and 38–56 × 16–22 μm for this species obtained from drift wood and *Spartina townsendii* culm. Ascospore dimensions of *B. obiones* are different in various studies (Table 1). However, it was recommended that further samplings should be made and sequenced to elucidate collections with significantly larger ascospore measurements to further confirm the exact phylogenetic placement of this taxon (Suetrong et al. 2009).

In this study, a novel genus *Halobyssothecium* (Lentitheciaceae) is introduced to accommodate *B. obiones*. An epitype (sensu Ariyawansa et al. 2014) is designated, for *H. obiones* collected from *Spartina* culms in Eastney, Langstone Harbour, Hampshire, UK. This is identical to the original material and later records by Saccardo (1944), Hyde and Mouzouras (1988), and Khashnobish and Shearer (Khashnobish and Shearer 1996a, 1996b). However, asci and ascospore measurements were lacking in the original description by Crouan and Crouan (1867) therefore, we have not been able to compare this with our species. Descriptions, detailed color images, and combined LSU, SSU, ITS, rDNA and TEF1 phylogenetic analysis are also provided.

Material and methods

Fungal sampling and morphology

Fresh material was collected on *Spartina* culms from Eastney, Langstone Harbour, Hampshire, UK. Specimens were placed in Zip-lock plastic bags and incubated at room temperature in the laboratory. They were examined with a Motic SMZ 168 stereomicroscope. Rehydrated fruiting bodies were used to observe morphological characteristics of ascomata, asci, ascospores and other tissues and characters were photographed with a Canon 550D digital camera fitted to the Nikon ECLIPSE 80i compound microscope. Photomicrographs were arranged with Adobe Photoshop v. CS6 and all measurements were made with Tarosoft v. 0.9.0.7. Specimens were preserved and deposited at the Mae Fah Luang University Herbarium (MFLU).

Fruiting bodies were removed from the substrate using a sterilized needle and placed in a few drops of sterilized distilled water on a sterilized cavity slide and spore suspensions were prepared as described in Chomnunti et al. (2014). Germinating ascospores were aseptically transferred to Petri-dishes containing potato dextrose agar (PDA) prepared in 50% concentrations of sterilized natural seawater (Atlas 2006). Colony characters were recorded after 3 weeks. Living cultures are deposited at Mae Fah Luang University Culture Collection (MFLUCC) and the International Collection of Microorganisms from Plants (ICMP), New Zealand. Faces of fungi and Index Fungorum numbers were registered according to Jayasiri et al. (2015) and Index Fungorum (2018).

DNA extraction, PCR amplification, and sequencing

The fungal isolate MFLUCC 15-0381 was grown on seawater PDA plate for 1 month at 25 °C. Mycelium from the colony was scraped by a sterilized scalpel and transferred to a 1.5-ml Eppendorf tube, and genomic DNA was extracted using Biospin Fungus Genomic DNA Extraction Kit (BioFlux®, China) (Hangzhou, P. R. China). All amplification reactions for PCR were performed in 25 μl reaction volume composing of the following: 1× PCR buffer, 0.2 mM dNTP, 0.5 mM of each primer, 2 mM $MgCl_2$, 1.5 units Taq polymerase, and 5~10 ng genomic DNA. PCR thermal cycle parameters for all DNA fragments amplification was as follows: an initial step of 3 mins at 94 °C, followed by 35 cycles of 30 s at 94 °C, 58 s at 30 °C, and 1 min at 72 °C, with a final extension of 10 min at 72 °C. The ITS rDNA regions were amplified using the universal primer pair ITS4 and ITS5 and the 18S and 28S rDNA genes were amplified using the universal primer pair NS1 and NS4 and primer pair LR0R and LR5 respectively (Vilgalys and Hester 1990; White et al. 1990; Rehner and Samuels 1994). One protein coding gene was also amplified, sequenced and analyzed in this study. The primer pair 983F and 2218R was used to amplify the translation elongation factor-1α [TEF1] (Rehner and Buckley 2005). PCR products were purified and sequenced with both primers at the Sunbiotech Company, Beijing, China.

Phylogenetic analysis

Other sequences used in the analyses (Fig. 1) were obtained from GenBank based on NCBI BLAST search in GenBank and recently published data in Ariyawansa et al. (2014). The multiple alignments of all consensus sequences, as well as the reference sequences were automatically generated with MAFFT v. 7 (http://mafft.cbrc.jp/alignment/server/index.html; Katoh and Standley 2013) and were improved manually when necessary using BioEdit v. 7.0.5.2 (Hall 1999). Alignment gaps were treated as missing characters in the analysis of the combined dataset and ambiguous regions

Table 1 Different ascospore measurements reported for *Byssoethecium obiones*

Ascospore measurements (μm)	Observed by
28–33 × 9.5–13	Johnson (1956)
28–35 × 10–11	Holm (1957)
24–32 × 8–10	Jones (1962)
38–56 × 16–22	
Same as Jones (1962) (they did not present actual data)	Apinis and Chesters (1964)
28–33 × 11–13	Lucas and Webster (1967)
27.2–40.8 × 13.6–20.4	Cavaliere (1968)
36–38 × 9–14	Kohlmeyer and Kohlmeyer (1979)
25–38 × 9–14	Hyde and Mouzouras (1988)
28–34 × 10–14	Khashnobish and Shearer (1996a, 1996b)
24–32 × 8–10	Barr (2002)

were excluded manually, where they occurred in relatively conserved regions.

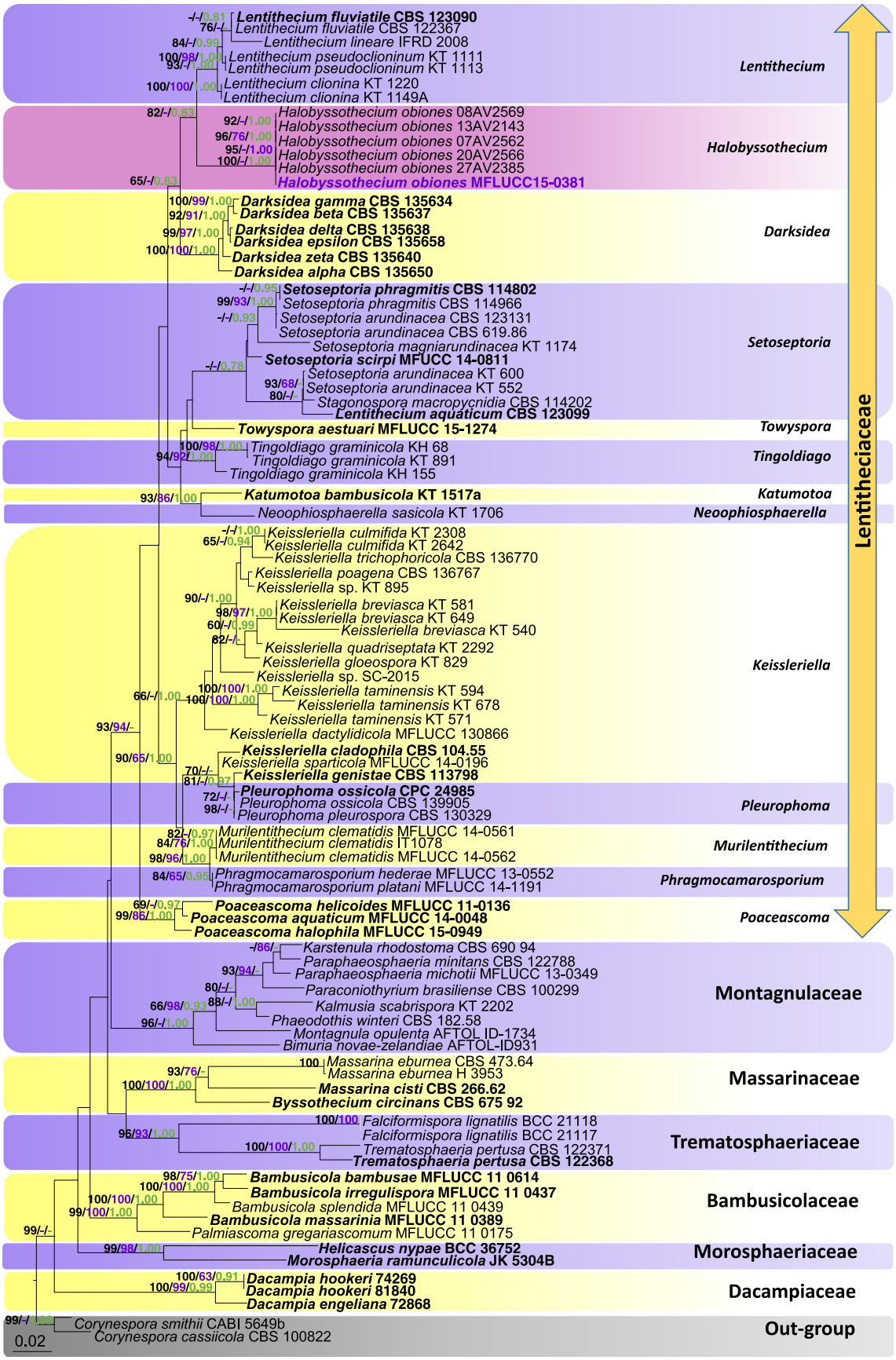
Phylogenetic analyses of combined SSU, LSU, ITS rDNA, and TEF1 dataset which comprises 92 selected strains (Table 2) belonging to the families Bambusicolaceae, Dictyosporiaceae, Lentitheciaceae, Leptosphaeriaceae, Lophiostomataceae, Macrodiplodiopsidaceae, Massarinaceae, Morosphaeriaceae, Montagnulaceae, Parabambusicolaceae, Periconiaceae, Pleosporaceae, Sulcatisporaceae, and Trematosphaeriaceae were performed. For the maximum likelihood (RAxML) analysis, sequence alignments were converted to PHYLIP file (.phy) using ALTER (alignment transformation environment; http://sing.ei.uvigo.es/ALTER/; 2018). Maximum likelihood trees were generated using the RAxML-HPC2 on XSEDE (8.2.8) (Stamatakis et al. 2008; Stamatakis 2014) in the CIPRES Science Gateway platform (Miller and Maner 2010) using GTR+I+G model of evolution. The two different gene datasets from the respective gene regions were also used for maximum-parsimony [MP] analysis, in which searches for most parsimonious trees were conducted with the heuristic search algorithm with tree-bisection-reconnection [TBR] branch swapping in PAUP* 4.0b4b (Swofford and Documentation 2002). 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 and Hasegawa 1989) were performed in order to determine whether trees were significantly different. The Bayesian tree for the combined SSU, LSU, ITS rDNA, and TEF1 sequence data was generated by using MCMC sampling in MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001; Zhaxybayeva and Gogarten 2002) for 1000,000 MCMC generations using four chains and partition analysis with 100 sample frequencies which produced 10,000 trees. The first 1000 (10% from total) trees were the burn-in phase, which were discarded, and the remaining 9000 trees were used to calculate the posterior probability. The MP was performed with PAUP v. 4.0b10 (Swofford and Documentation 2002). Phylograms were visualized with FigTree v1.4.0 program (Rambaut 2012) and reorganized in Microsoft PowerPoint (2016). The final alignment was deposited in TreeBASE (Reviewer access URL: http://purl.org/phylo/treebase/phylows/study/TB2:S23019?x-access-code=b9e0efaf9f326cc63b7956980be55796&format=html).

Results

Phylogenetic analysis

Two hundred sixty-one strains were included in the preliminary analysis with combined SSU, LSU, ITS rDNA, and TEF1 with *Hysterium pulicare* (CBS 12337) and *Hysterobrevium mori* (CBS 12356) as the out-group taxa (data not shown). The second analysis comprised 92 selected taxa with combined SSU, LSU, ITS rDNA, and TEF1 with *Corynespora cassiicola* (CBS 100822) and *Corynespora smithii* (CABI 5649b) as the out-group taxa. Parsimony analysis indicated that the alignment comprised 3409 characters (including gaps) and 2337 characters were constant; 211 variable characters were parsimony-uninformative; and 861 characters were parsimony informative. The best parsimonious tree out of 28 trees showed TL = 3841, CI = 0.407, RI = 0.696, RC = 0.283, and HI = 0.593 values. Tree topologies of maximum parsimony and Bayesian inference (not shown) was almost compatible with the best scoring RAxML tree, with a final likelihood value of − 24,033.675238 (Fig. 1).

Our preliminary dataset comprised representatives of the suborder Pleosporineae (data not shown). Strains of *Byssothecium obiones* (= *Halobyssothecium obiones*) (08AV2569, 13AV2143, 20AV2566, 27AV2385, and MFLUCC 15-0381) nested together with species of the family


Lentithecium fluviatile CBS 123090
Lentithecium fluviatile CBS 122367
Lentithecium lineare IFRD 2008
Lentithecium pseudoclioninum KT 1111
Lentithecium pseudoclioninum KT 1113
Lentithecium clionina KT 1220
Lentithecium clionina KT 1149A
Lentithecium
Halobyssothecium obiones 08AV2569
Halobyssothecium obiones 13AV2143
Halobyssothecium obiones 07AV2562
Halobyssothecium obiones 20AV2566
Halobyssothecium obiones 27AV2385
Halobyssothecium obiones MFLUCC15-0381
Halobyssothecium
Darksidea gamma CBS 135634
Darksidea beta CBS 135637
Darksidea delta CBS 135638
Darksidea epsilon CBS 135658
Darksidea zeta CBS 135640
Darksidea alpha CBS 135650
Darksidea
Setoseptoria phragmitis CBS 114802
Setoseptoria phragmitis CBS 114966
Setoseptoria arundinacea CBS 123131
Setoseptoria arundinacea CBS 619.86
Setoseptoria magniarundinacea KT 1174
Setoseptoria scirpi MFUCC 14-0811
Setoseptoria arundinacea KT 600
Setoseptoria arundinacea KT 552
Stagonospora macropycnidia CBS 114202
Lentithecium aquaticum CBS 123099
Setoseptoria
Towyspora aestuari MFLUCC 15-1274
Towyspora
Tingoldiago graminicola KH 68
Tingoldiago graminicola KT 891
Tingoldiago graminicola KH 155
Tingoldiago
Katumotoa bambusicola KT 1517a
Katumotoa
Neoophiosphaerella sasicola KT 1706
Neoophiosphaerella
Keissleriella culmifida KT 2308
Keissleriella culmifida KT 2642
Keissleriella trichophoricola CBS 136770
Keissleriella poagena CBS 136767
Keissleriella sp. KT 895
Keissleriella breviasca KT 581
Keissleriella breviasca KT 649
Keissleriella breviasca KT 540
Keissleriella quadriseptata KT 2292
Keissleriella gloeospora KT 829
Keissleriella sp. SC-2015
Keissleriella taminensis KT 594
Keissleriella taminensis KT 678
Keissleriella taminensis KT 571
Keissleriella dactylidicola MFLUCC 130866
Keissleriella cladophila CBS 104.55
Keissleriella sparticola MFLUCC 14-0196
Keissleriella genistae CBS 113798
Keissleriella
Pleurophoma ossicola CPC 24985
Pleurophoma ossicola CBS 139905
Pleurophoma pleurospora CBS 130329
Pleurophoma
Murilentithecium clematidis MFLUCC 14-0561
Murilentithecium clematidis IT1078
Murilentithecium clematidis MFLUCC 14-0562
Murilentithecium
Phragmocamarosporium hederae MFLUCC 13-0552
Phragmocamarosporium platani MFLUCC 14-1191
Phragmocamarosporium
Poaceascoma helicoides MFLUCC 11-0136
Poaceascoma aquaticum MFLUCC 14-0048
Poaceascoma halophila MFLUCC 15-0949
Poaceascoma
Lentitheciaceae
Karstenula rhodostoma CBS 690 94
Paraphaeosphaeria minitans CBS 122788
Paraphaeosphaeria michotii MFLUCC 13-0349
Paraconiothyrium brasiliense CBS 100299
Kalmusia scabrispora KT 2202
Phaeodothis winteri CBS 182.58
Montagnula opulenta AFTOL ID-1734
Bimuria novae-zelandiae AFTOL-ID931
Montagnulaceae
Massarina eburnea CBS 473.64
Massarina eburnea H 3953
Massarina cisti CBS 266.62
Byssothecium circinans CBS 675 92
Massarinaceae
Falciformispora lignatilis BCC 21118
Falciformispora lignatilis BCC 21117
Trematosphaeria pertusa CBS 122371
Trematosphaeria pertusa CBS 122368
Trematosphaeriaceae
Bambusicola bambusae MFLUCC 11 0614
Bambusicola irregulispora MFLUCC 11 0437
Bambusicola splendida MFLUCC 11 0439
Bambusicola massarinia MFLUCC 11 0389
Palmiascoma gregariascomum MFLUCC 11 0175
Bambusicolaceae
Helicascus nypae BCC 36752
Morosphaeria ramunculicola JK 5304B
Morosphaeriaceae
Dacampia hookeri 74269
Dacampia hookeri 81840
Dacampia engeliana 72868
Dacampiaceae
Corynespora smithii CABI 5649b
Corynespora cassiicola CBS 100822
Out-group
0.02

◀ **Fig. 1** Phylogram generated from maximum likelihood analysis of combined LSU, SSU, ITS rDNA, and TEF1 sequence data. Maximum likelihood bootstrap (ML, black) values ≥ 65%, maximum parsimony bootstrap (MP, purple) values ≥ 65%, and Bayesian posterior probabilities (PP, green) ≥ 0.80% are given above the nodes. The tree is rooted to *Corynespora cassiicola* (CBS 100822) and *Corynespora smithii* (CABI 5649b). Bar = 0.02 expected number of nucleotide substitutions per site per branch

Lentitheciaceae according to our preliminary phylogenetic analyses with concatenated LSU + SSU + ITS + TEF1 data. Strains of *B. circinans* (type species) (CBS 675.92) grouped distantly from *Byssothecium obiones*, but within Massarinaceae (data not shown). The second analysis, with concatenated SSU, LSU, ITS, and TEF1 data of selected taxa mostly in Lentitheciaceae, yielded a monophyletic clade comprising *B. obiones* (Fig. 1) with high statistical support (100% ML, 100% MP, 1.00 PP). Hence, it is referred to a new genus *Halobyssothecium*. *Byssothecium circinans* grouped within Massarinaceae and family Dacampiaceae formed a basal well-separated (100% ML, 100% MP, 1.00 PP) clade (Fig. 1). Neither *Byssothecium obiones* nor *B. circinans* (type) grouped within family Dacampiaceae in any of the above analyses.

Taxonomy

Halobyssothecium Dayarathne, E.B.G. Jones & K.D. Hyde, ***gen. nov.***

Index Fungorum number: IF554756; *Facesoffungi number:* FoF 03928

Etymology: Name reflects the saline environment where it is found and similarity to the genus *Byssothecium*.

Saprobic on salt marsh halophytes in marine habitats. **Sexual morph**: *Ascomata* subglobose or ellipsoidal, immersed to semi-immersed, scattered, ostiolate, carbonaceous, dark brown to black, gregarious. *Peridium* 30–45 μm, comprising two layers: outer layer of brown pseudoparenchyma; inner layer of elongated, hyaline cells. *Pseudoparaphyses* septate, branched. *Asci* 8-spored, clavate to subcylindrical, short pedicellate, thick-walled, without an apical apparatus. *Ascospores* versicolored, end cells hyaline, central cells brown, septate, and constricted at the septa, slightly curved. **Asexual morph:** Undetermined.

Type species: *Halobyssothecium obiones* (M.E. Barr) Dayarathne, E.B.G. Jones & K.D. Hyde, ***comb. nov.***

Notes: This novel genus is proposed to accommodate *Halobyssothecium obiones* from salt marsh halophytes, which is thus far reported only from marine habitats. *Halobyssothecium* shares similar morphological features with the family Lentitheciaceae viz. scattered, immersed to semi-immersed ascomata, pedicellate asci, bi-seriate, septate ascospores which are constricted at the septum (Zhang et al. 2009). Presently, there are 13 genera included in Lentitheciaceae, i.e., *Darksidea* (Knapp et al. 2015), *Katumotoa*, *Keissleriella*, *Lentithecium*, *Murilentithecium* (Wanasinghe et al. 2014, 2018), *Neoophiosphaerella* (Tanaka et al. 2015), *Phragmocamarosporium* (Wijayawardene et al. 2015), *Pleurophoma*, *Poaceascoma* (Phookamsak et al. 2015), *Setoseptoria* (Tanaka et al. 2015), *Tingoldiago* (Hyde et al. 2013; Knapp et al. 2015; Phookamsak et al. 2015; Tanaka et al. 2015), *Towyspora* (Li et al. 2016), and the novel genus. However, this genus is significantly different in morphology from all the other members of this family by having versicolored ascospores with brown central cells and hyaline end cells, which resemble *Byssothecium*.

Halobyssothecium obiones (M.E. Barr) Dayarathne, E.B.G. Jones & K.D. Hyde ***comb. nov.***

Index Fungorum number: IF554757; *Facesoffungi number:* FoF 03929; Fig. 2

Basionym: *Pleospora obiones* P. Crouan & H. Crouan, Florule Finistère (Paris): 22 (1867)

Synonymy: *Byssothecium obiones* (P. Crouan & H. Crouan) M.E. Barr, Mycotaxon 82: 378 (2002)

Passeriniella obiones (P. Crouan & H. Crouan) K.D. Hyde and Mouzouras, Trans. Br. mycol. Soc. 91(1): 183 (1988)

Didymosphaeria spartinae Grove, J. Bot., Lond. 71: 259 (1933)

Heptameria obiones (P. Crouan & H. Crouan) Cooke, Grevillea 18 (no. 86): 30 (1889)

Leptosphaeria discors Sacc. & Ellis, Michelia 2 (no. 8): 567 (1882)

Leptosphaeria obiones (P. Crouan & H. Crouan) Sacc., Syll. fung. (Abellini) 2: 24 (1883)

Leptosphaeria obiones f. evolutior Grove, J. Bot., Lond. 71: 281 (1933)

Leptosphaeria obiones (P. Crouan & H. Crouan) Sacc., Syll. fung. (Abellini) 2: 24 (1883) f. obiones

Metasphaeria discors (Sacc. & Ellis) Sacc., Syll. fung. (Abellini) 2: 173 (1883)

Passeriniella discors (Sacc. & Ellis) Apinis & Chesters, Trans. Br. mycol. Soc. 47(3): 432 (1964)

Saprobic on *Spartina* sp. *and other salt marsh halophytes* in marine habitats. **Sexual morph**: *Ascomata* 360–400 μm high, 340–380 μm diameter, subglobose or ellipsoidal, immersed to semi-immersed, scattered, ostiolate, carbonaceous, dark brown to black, gregarious. *Papilla* conical, 25–35 μm high, 130–145 μm wide at the apex, composed of several layers of pseudoparenchymatous cells. *Peridium* 30–45 μm wide, comprising two layers: outer layer of brown pseudoparenchyma; inner layer of elongated, hyaline cells. *Pseudoparaphyses* 4–6 μm wide, septate, branched. *Asci* 180–214 × 12–16 μm ($\bar{x}$ = 185.5 × 14 μm, *n* = 20), 8-spored, clavate to subcylindrical, short pedicellate with an ocular chamber. *Ascospores* 28–47 × 10–18 μm ($\bar{x}$ = 38.5 × 14 μm,

Table 2 Isolates used in this study for the analysis of combined LSU, SSU, ITS rDNA, and TEF1 sequence data and their GenBank accession numbers. Bold accession numbers from ex-type strains and italic bold accession numbers were generated in this study

Taxon	Strain no.	GenBank accession			
		LSU	SSU	ITS	TEF1
Bambusicola bambusae	MFLUCC 11-0614	**JX442035**	**JX442039**	**NR121546**	**KP761722**
Bambusicola irregulispora	MFLUCC 11-0437	**JX442036**	**JX442040**	**NR121547**	**KP761723**
Bambusicola massarinia	MFLUCC 11-0389	**JX442037**	**JX442041**	**NR121548**	–
Bambusicola splendida	MFLUCC 11-0439	JX442038	JX442042	NR121549	–
Bimuria novaezelandiae	AFTOL-ID931	–	–	–	DQ471087
Byssothecium circinans	CBS67592	GU205217	GU205235	–	GU349061
Corynespora cassiicola	CBS100822	GU301808	GU296144	–	GU349052
Corynespora smithii	CABI5649b	GU323201	–	–	GU349018
Dacampia engeliana	72868	KT383791	–	–	–
Dacampia hookeri	74269	KT383793	–	–	–
Dacampia hookeri	81840	KT383795	–	–	–
Darksidea alpha	CBS 135650	**KP184019**	**KP184049**	**NR137619**	**KP184166**
Darksidea beta	CBS 135637	**KP184023**	**KP184074**	**NR137957**	**KP184189**
Darksidea delta	CBS 135638	–	–	**NR137075**	–
Darksidea epsilon	CBS 135658	**KP184029**	**KP184070**	**NR137959**	**KP184186**
Darksidea gamma	CBS 135634	**KP184031**	**KP184073**	**NR137587**	**KP184188**
Darksidea zeta	CBS 135640	**KP184013**	**KP184071**	**NR137958**	**KP184191**
Falciformispora lignatilis	BCC 21117	GU371835	GU371835	KF432942	GU371820
Falciformispora lignatilis	BCC 21118	GU371826	GU371835	GU371835	GU371820
Halobyssothecium obiones	08AV2569	–	–	KX263859	–
Halobyssothecium obiones	13AV2143	–	–	KX263860	–
Halobyssothecium obiones	20AV2566	–	–	KX263862	–
Halobyssothecium obiones	27AV2385	–	–	KX263864	–
Halobyssothecium obiones	MFLUCC 15-0381	***MH376744***	***MH376745***	***MH377060***	***MH376746***
Halobyssothecium obiones	07AV2562	–	–	KX263858	–
Helicascus nypae	BCC36752	**GU479789**	**GU479755**	–	**GU479855**
Kalmusia scabrispora	KT2202	AB524594	AB524453	–	AB539107
Karstenula rhodostoma	CBS69094	GU301821	GU296154	–	GU349067
Katumotoa bambusicola	KT1517a	**AB524595**	**AB524454**	**LC014560**	**AB539108**
Keissleriella breviasca	KT540	AB807586	AB797296	–	AB808565
Keissleriella breviasca	KT581	AB807587	AB797297	–	AB808566
Keissleriella breviasca	KT649	AB807588	AB797298	–	AB808567
Keissleriella cladophila	CBS104.55	**GU301822**	**GU296155**	–	**GU349043**
Keissleriella culmifida	KT2308	AB807591	AB797301	LC014561	–
Keissleriella culmifida	KT2642	AB807592	AB797302	LC014562	–
Keissleriella dactylidicola	MFLUCC 13-0866	KT315506	KT315505	–	KT315507
Keissleriella dactylidis	MFLUCC 13-0751	KP197668	KP197666	KP197667	KP197669
Keissleriella genistae	CBS 113798	**GU205222**	**GU205242**	–	–
Keissleriella gloeospora	KT829	AB807589	AB797299	LC014563	–
Keissleriella poagena	CBS136767	KJ869170	–	KJ869112	–
Keissleriella quadriseptata	KT2292	AB807593	AB797303	AB811456	AB808572
Keissleriella sp.	KT895	AB807590	AB797300	–	AB808569
Keissleriella sparticola	MFLUCC 14-0196	KP639571	–	–	–
Keissleriella taminensis	KT571	AB807595	AB797305	LC014564	AB808574
Keissleriella taminensis	KT594	AB807596	AB797306	–	–
Keissleriella taminensis	KT678	AB807597	AB797307	LC014565	AB808575

Table 2 (continued)

Taxon	Strain no.	GenBank accession			
		LSU	SSU	ITS	TEF1
Keissleriella trichophoricola	CBS 136770	KJ869171	–	KJ869113	–
Lentithecium aquaticum	CBS 123099	**GU301823**	**GU296156**	–	**GU349068**
Lentithecium clionina	KT1149A	AB807540	AB797250	LC014566	AB808515
Lentithecium clionina	KT1220	AB807541	AB797251	–	AB808516
Lentithecium fluviatile	CBS 122367	**FJ795451**	**FJ795493**	–	**GU456290**
Lentithecium fluviatile	CBS 123090	FJ795450	FJ795492	–	–
Lentithecium lineare	IFRD2008	FJ795435	FJ795478	–	–
Lentithecium pseudoclioninum	KT1111	AB807544	AB797254	AB809632	AB808520
Lentithecium pseudoclioninum	KT1113	AB797255	AB807545	AB809633	AB808521
Massarina cisti	CBS 266.62	**FJ795447**	**FJ795490**	**LC014568**	**AB808514**
Massarina eburnea	CBS 473.64	GU301840	GU296170	–	GU349040
Massarina eburnea	H3953	AB521735	AB521718	–	AB808517
Montagnula opulenta	AFTOLID1734	DQ678086	AF164370	–	–
Morosphaeria ramunculicola	JK5304B	**GU479794**	**GU479760**	–	–
Murilentithecium clematidis	IT1078	KM408758	KM408760	KM408756	–
Murilentithecium clematidis	MFLUCC 14-0561	KM408758	KM408759	KM408756	KM454444
Murilentithecium clematidis	MFLUCC 14-0562	KM408760	KM408761	KM408757	KM454445
Neoophiosphaerella sasicola	KT1706	AB524599	AB524458	LC014577	AB539111
Palmiascoma gregariascomum	MFLUCC 11-0175	KP744495	KP753958	KP744452	–
Paraconiothyrium brasiliense	CBS100299	JX496124	AY642523	JX496011	AY642531
Paraphaeosphaeria michotii	MFLUCC 13-0349	KJ939282	KJ939285	KJ939279	–
Paraphaeosphaeria minitans	CBS122788	EU754173	EU754074	–	GU349083
Phaeodothis winteri	CBS18258	GU301857	GU296183	–	–
Phragmocamarosporium hederae	MFLUCC 13-0552	KP842915	KP842918	–	–
Phragmocamarosporium platani	MFLUCC 14-1191	KP842915.	KP842918	–	–
Pleurophoma ossicola	CBS139905	**KR476769**	–	**KR476736**	–
Pleurophoma ossicola	CPC24985	KR476770	–	NR137992	–
Pleurophoma pleurospora	CBS130329	JF740327	–	–	–
Poaceascoma aquaticum	MFLUCC 14-0048	**KT324690**	**KT324691**	–	–
Poaceascoma halophila	MFLUCC 15-0949	**MF615399**	**MF615400**	–	–
Poaceascoma helicoides	MFLUCC 11-0136	**KP998462**	**KP998463**	**KP998459**	**KP998461**
Setoseptoria arundinacea	CBS 123131	GU456320	GU456298	–	GU456281
Setoseptoria arundinacea	CBS 619.86	GU301824	GU296157	–	–
Setoseptoria arundinacea	KT552	AB807574	AB797284	–	AB808550
Setoseptoria arundinacea	KT600	AB807575	AB797285	LC014595	AB808551
Setoseptoria magniarundinacea	KT1174	AB807576	AB797286	LC014596	AB808552
Setoseptoria phragmitis	CBS 114802	**KF251752**	–	**KF251249**	**KF253199**
Setoseptoria phragmitis	CBS 114966	KF251753	–	KF251250	KF253200
Setoseptoria scirpi	MFUCC 14-0811	**KY770982**	**KY770980**	**MF939637**	**KY770981**
Stagonospora macropycnidia	CBS 114202	GU301873	GU296198	–	GU349026
Tingoldiago graminicola	KH155	AB521745	AB521728	LC014599	AB808562
Tingoldiago graminicola	KH68	AB521743	AB521726	LC014598	AB808561
Tingoldiago graminicola	KT891	AB521744	AB521727	–	AB808563
Towyspora aestuari	MFLUCC 15-1274	**KU248852**	**KU248853**	**NR148095**	–
Trematosphaeria pertusa	CBS 122368	**FJ201990**	**FJ201991**	**NR132040**	**KF015701**
Trematosphaeria pertusa	CBS 122371	GU301876	GU348999	KF015669	KF015702

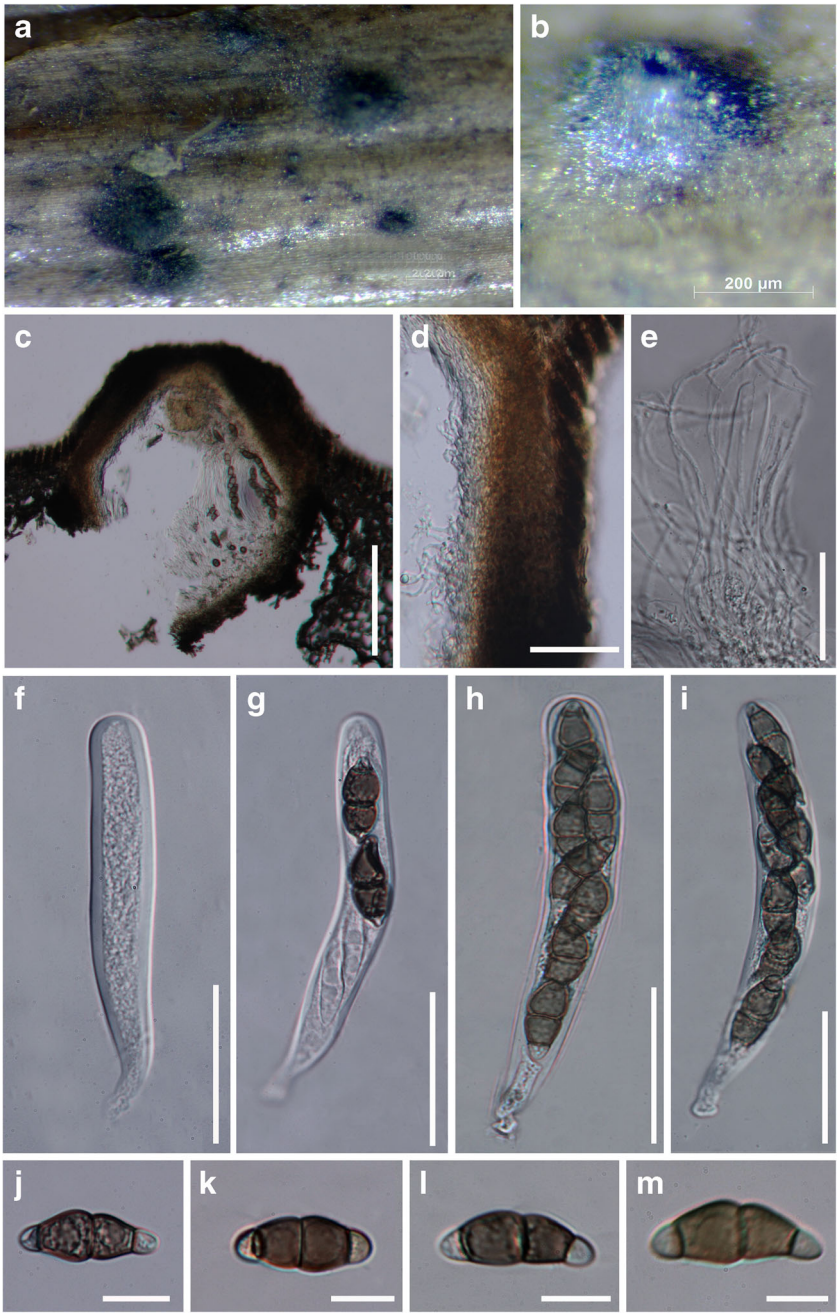


Fig. 2 ***Halobyssothecium obiones*** (MFLU 18–1075 **epitype**). **a**, **b** Appearance of ascomata on *Spartina* culms. **c** Sections of ascomata. **d** Section through peridium. **e** Pseudoparaphyses. **f**–**i** Asci. **j**–**m** Ascospores. Scale bars: **b**, 200 µm; **c**, 100 µm, **f**–**i**, 50 µm; **d**, **e**, **j**–**m**, 20 µm

$n = 20$), versicolored, end cells hyaline, central cells brown, 3-septate, and constricted at the septa, slightly curved. **Asexual morph***:* Not observed.

*Material examined***:** UK, Hampshire, Eastney, Langstone Harbour, on *Spartina* culms, January 2015, EBG Jones. GJ087 (MFLU 18–1075, **epitype**), ex-type living culture MFUCC 15–0381, ICMP.

Notes: Our new strain of *Halobyssothecium obiones* (MFLUCC) collected from *Spartina* sp. shares similar morphological features with previously described strains (Khashnobish and Shearer 1996a, 1996b; Barr 2002). However, the dark pigmented substance encrusting the ascospores after release from the ascus, as reported by Boise (1983) for *B. circinans* (type), was not seen in our observations and by Khashnobish and Shearer (1996a). We could not find the holotype of this species. We designate our new strain as the epitype for this taxon. During our BLAST analyses, ITS rDNA hits for this species mostly comprised Massarinaceae species and for LSU, SSU rDNA, and TEF1 data comprised Lentitheciaceae species. We made a preliminary analysis with representatives of different families that belong to the suborder Pleosporineae with several gene combinations (data not shown). Results showed that *B. obiones* did not group in

the same clade as *B. circinans* (type) or within families Massarinaceae or Dacampiaceae but, grouped in Lentitheciaceae. Hence, we constructed a final analysis with Lentitheciaceae representatives and strains of *B. obiones* (08AV2569, 13AV2143, 20AV2566, 27AV2385 and MFLUCC) formed a well-separated (100% ML, 100% MP, 1.00 PP) lineage within Lentitheciaceae (Fig. 1).

Discussion

Halobyssothecium obiones is a widely occurring species in temperate climates (see Kohlmeyer and Kohlmeyer (1979) for geographical distribution) and growing on a wide range of salt marsh halophytes (*Agropyron junceiforme*, *Halimione portulacoides*, *Spartina* spp.) and on intertidal wood and test panels. Its occurrence on wood and bamboo requires further investigation. It is particularly common on *Spartina* species, both in the Atlantic and Pacific Oceans.

Halobyssothecium obiones is characterized by scattered, immersed to semi-immersed ascomata, pedicellate asci, and bi-seriate, pale brown to brown, septate ascospores, which are constricted at the septum (Crouan and Crouan 1867; Jones 1963; Apinis and Chesters 1964; Wagner 1965; Kohlmeyer and Kohlmeyer 1979; Hyde and Mouzouras 1988; Barr 2002; Barata 2002). It has been transferred to a number of different genera, as shown by the synonymies of this species since introduced in 1883 (Suetrong et al. 2009). Only ITS rDNA sequence data were available in GenBank prior to this study. Both the morphological and phylogenetic data available for this species were insufficient to classify the taxon in a stable position (Suetrong et al. 2009). Hence, we recollected this species from *Spartina* culms, on which this species has been abundantly reported and conducted a morphological and molecular study on this marine fungus. Although morphological features have referred it to many genera, such as *Didymosphaeria*, *Heptameria*, *Pleospora*, *Leptosphaeria*, and *Passeriniella*, a detailed phylogenetic study placed it in the Lentitheciaceae with strong statistical support. Within the Lentitheciaceae, *H. obiones* formed a new lineage in a sister group to *Lentithecium* species.

Lack of authentic specimens and molecular data for *Halobyssothecium obiones* has resulted in taxonomic confusion over the past 135 years (Hyde and Mouzouras 1988; Barr 2002; Suetrong et al. 2009). Even though there are several records of this species from different locations, few records of it from the original host *Halimione portulacoides* have been reported (Crouan and Crouan 1883; Grove 1933), while the majority of the collections have been made from different *Spartina* species: *S. alterniflora* (Jones 1963; Gessner and Goos 1973), *S. densiflora* (Peña and Arambarri 1998), and *S. maritima* (Barata 1997, 2002). A Halobyssothecium obiones-like species has been reported with much larger ascospore measurements than that of the type material, namely 38–56 × 16–22 μm (Jones 1963; Cavaliere 1968; Webber 1970), suggesting this may be another species. Likewise, reports of its occurrence from mangrove habitats with smaller ascospores may be due to misidentification (Cribb and Cribb 1960). Therefore, to avoid future taxonomic confusion, we designate our new collection as an epitype for the taxon with DNA characterization with four genes, i.e., LSU, SSU, ITS rDNA, and TEF1. However, Ariyawansa et al. (2014) mentioned that the epitype specimens' designation should probably be in accordance with the same host and origin to the initial material. We believe that it is reasonable to designate a type for this taxon from *Spartina* culms as several isolates of *Byssothecium obiones* from *Spartina* spp. conforms to the morphology originally described and it has been reported in many studies (Jones 1963; Apinis and Chesters 1964; Kohlmeyer and Kohlmeyer 1979; Hyde and Mouzouras 1988; Barr 2002) in accordance with suggestions by Dayarthne et al. (Dayarathne et al. 2016).

Spartina species are abundant grasses of the tidal salt marshes in coastal environments and contribute significantly to estuarine primary productivity (Gessner 1972, Gessner and Goos 1973). Energy stored by the plant is released through decomposition as detritus or decomposer biomass and *Halobyssothecium obiones* has been reported on pieces of wood, driftwood and dead plant stems (5.6% studied substrates) found in the intertidal zone of two sandy beaches on the Portuguese west coast (Gessner 1972; Gessner and Goos 1973; Figueira and Barata 2007).

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