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Phylogenetic placement of *Iodosphaeriaceae* (Xylariales, Ascomycota), designation of an epitype for the type species of *Iodosphaeria*, *I. phyllophila*, and description of *I. foliicola* sp. nov.

A.N. Miller^{1*}, M. Réblová²

¹Illinois Natural History Survey, University of Illinois Urbana-Champaign, Champaign, IL, USA

²Czech Academy of Sciences, Institute of Botany, 252 43 Průhonice, Czech Republic

*Corresponding author: amiller7@illinois.edu

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Abstract: The *Iodosphaeriaceae* is represented by the single genus, *Iodosphaeria*, which is composed of nine species with superficial, black, globose ascomata covered with long, flexuous, brown hairs projecting from the ascomata in a stellate fashion, unitunicate asci with an amyloid apical ring or ring lacking and ellipsoidal, ellipsoidal-fusiform or allantoid, hyaline, aseptate ascospores. Members of *Iodosphaeria* are infrequently found worldwide as saprobes on various hosts and a wide range of substrates. Only three species have been sequenced and included in phylogenetic analyses, but the type species, *I. phyllophila*, lacks sequence data. In order to stabilize the placement of the genus and family, an epitype for the type species was designated after obtaining ITS sequence data and conducting maximum likelihood and Bayesian phylogenetic analyses. *Iodosphaeria foliicola* occurring on overwintered *Alnus* sp. leaves is described as new. Five species in the genus form a well-supported monophyletic group, sister to the *Pseudosporidesmiaceae* in the Xylariales. Selenosporella-like and/or ceratosporium-like synasexual morphs were experimentally verified or found associated with ascomata of seven of the nine accepted species in the genus. Taxa included and excluded from *Iodosphaeria* are discussed.

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INTRODUCTION

Iodosphaeria was introduced by Samuels *et al.* (1987) to accommodate the type species, *I. phyllophila* based on *Lasiosphaeria phyllophila* (Mouton 1900), and a second species, *I. ripogoni*. Seven additional species have been added to the genus: *I. aquatica*, *I. arundinariae*, *I. honghensis*, *I. hongkongensis*, *I. podocarp*i, *I. polygoni*, and *I. tongrenensis* (Mycobank, www.mycobank.org, accessed on 7 Apr. 2021). Morphological and molecular analyses of *I. aquatica* have led to uncertainty in its taxonomic placement (Hsieh *et al.* 1997, Kang *et al.* 1999, Taylor & Hyde 1999). Jeewon *et al.* (2003) showed the genus to be paraphyletic when they included *I. aquatica* and another *Iodosphaeria* sp. in their molecular analyses. A key to all known species of *Iodosphaeria* was presented in Marasinghe *et al.* (2019).

Sexual morphs are comprised of superficial, black, globose to subglobose, non-stromatic ascomata with flat apices and covered with long, brown, flexuous hairs, a two-layered ascomal wall, cylindrical, 8-spored asci sometimes with an amyloid apical ring or ring is lacking, and ellipsoidal, allantoid or fusiform, hyaline, aseptate ascospores with or without a gelatinous sheath. Selenosporella- and ceratosporium-like synasexual morphs have been reported on the surface of ascomata in *I. tongrenensis* (Li *et al.* 2015), on field-collected material of *I. phyllophila* (Bell

& Mahoney 2016) and *I. ripogoni* (Samuels *et al.* 1987, Bell & Mahoney 2016) and in cultures of *I. phyllophila* (Samuels *et al.* 1987). Ceratosporium-like conidia were observed on the host surface in *I. honghensis* (Marasinghe *et al.* 2019). Members of *Iodosphaeria* are infrequently found worldwide as saprobes on a variety of hosts and a wide range of substrates including dead branches, stems, vines, leaves and petioles.

Iodosphaeria was initially placed in the *Amphisphaeriaceae* (Samuels *et al.* 1987) based on its synasexual morphs and amyloid ascal ring, but Barr (1990) later transferred it to the *Lasiosphaeriaceae* based on ascomal wall anatomy and centrum similarities. It was placed in the *Trichosphaeriaceae* by Réblová (1999). Hilber & Hilber (2002) created a new family, *Iodosphaeriaceae*, for the genus. The family, represented by *I. honghensis* and *I. tongrenensis*, is placed in the Xylariales based on morphology and phylogeny (Marasinghe *et al.* 2019).

Only three species, *I. aquatica*, *I. honghensis* and *I. tongrenensis*, have been sequenced and included in phylogenetic analyses. Because the type species has never been sequenced, ambiguity surrounds the placement of the genus and family. The type material of *I. phyllophila*, described from decaying leaves of *Betula alba* and *Corylus* from Belgium, is sparse and over 120 years old, so attempts to obtain molecular data from this material would be futile. The goals of this study were to designate an epitype of *I. phyllophila* from the

country of origin, obtain sequence data from the epitype and provide a stable phylogenetic placement for *Iodosphaeria* and *Iodosphaeriaceae*. During our investigation, two specimens of unknown *Iodosphaeria* from Canada were discovered and compared with the known species.

MATERIALS AND METHODS

Taxon sampling and morphological examination

Fresh specimens were collected in the field, dried and stored in paper packets. No attempts were made to obtain these specimens in culture. All specimens are deposited in Meise Botanic Garden (BR, Meise, Belgium), the Fungarium of the Illinois Natural History Survey (ILLS, Champaign, Illinois, USA) and the New Zealand Fungarium (PDD, Auckland, New Zealand). Other specimens were obtained from the Plant Pathology Herbarium, Cornell University (CUP, Ithaca, New York, USA), New Brunswick Museum (NBM, Saint John, Canada), and Staatliche Naturwissenschaftliche Sammlungen Bayerns (M, Munich, Germany).

Ascomata were squash-mounted in distilled water and micromorphological structures were examined on an Olympus BX51 compound microscope using differential interference or phase contrast microscopy. Images were processed using Adobe Photoshop 2021 (Adobe Systems Inc., Mountain View, California). A minimum of 30 measurements was taken for all morphological structures using Olympus cellSens Standard v. 1.14 image analysis software after digital capture with an Olympus DP70 or a XC50 5.0 megapixel digital camera using Olympus Imaging Software Cell[^]D. Sections of the ascomal wall were prepared at 25 µm thickness using a Physitemp BSF-3 freezing stage mounted on a Leica SM2000 sliding microtome.

Molecular data

DNA was extracted directly from ascomata using an E.Z.N.A.[®] Microelute Genomic DNA kit (Omega Bio-tek, Norcross, Georgia, USA) following the manufacturer's instructions. The entire internal transcribed spacer (ITS) region and the first 600 bp of the 5' end of 28S nuclear large subunit (LSU) were PCR amplified using known primers (Vilgalys & Hester 1990, White *et al.* 1990, Rehner & Samuels 1995). PCR reactions contained 12.5 µL GoTaq[®] Green Master Mix (Promega, Madison, Wisconsin, USA), 2.5 µL of BSA (bovine serum albumin, New England Biolabs, Ipswich, MA), 2.5 µL of DMSO (dimethyl sulfoxide, Fisher Scientific, Pittsburgh, PA), 1.5 µL of each 10 mM primer, and 3–5 µL genomic DNA. PCR amplification of ITS and LSU was performed on a Bio-Rad C1000 thermal cycler under the following conditions: initial denaturation at 94 °C for 2 min, followed by 40 cycles of 94 °C for 30 s, 41 °C for 45 s, and 72 °C for 1 min with a final extension step of 72 °C for 10 min. After verification on an ethidium bromide-stained 1 % TBE agarose gel, PCR products were purified with a Wizard[®] SV Gel and PCR Clean-Up System (Promega, Madison, Wisconsin, USA). Purified PCR products were used in 11 µL sequencing reactions to sequence both strands with BigDye Terminators v. 3.1 (Applied Biosystems, Foster City, CA) in combination with the following ITS primers: ITS1F, ITS2, ITS3, ITS4, and LSU primers: LROR, LR3. Sequences were generated on an Applied Biosystems 3730XL high throughput capillary sequencer at the Roy J. Carver

Biotechnology Center at the University of Illinois Urbana-Champaign (Champaign, Illinois, USA). Consensus sequences for each gene were assembled with Sequencher v. 5.4 (Gene Codes Corp., Ann Arbor, Michigan, USA) and each sequence was subjected to an individual BLASTn analysis to verify its identity. PCR amplifications of *rpb2* and *tef1-α* were unsuccessful.

Phylogenetic analyses

The ITS-LSU for newly sequenced taxa was added to the combined ITS-LSU-*rpb2-tef1-α* alignment from Réblová *et al.* (2021). The two protein-coding genes were kept in the analyses to provide backbone support for higher level taxa. Portions of the 5' and 3' ends of each gene were excluded from all analyses due to missing data in most taxa and aligned using MUSCLE (Edgar 2004). PartitionFinder2 (Lanfear *et al.* 2016) was used to determine the best-fit model for each dataset, which was the SYM+I+G model for ITS, and the GTR+I+G model for LSU, *rpb2* and *tef1-α*. A maximum likelihood (ML) analysis with 1 000 bootstrap replicates was performed using RAXML-HPC2 v. 8.2.12 (Stamatakis 2014) with a GTRCAT approximation using the CIPRES Science Gateway v. 3.3 portal (Miller *et al.* 2010). Bootstrap replicates were performed 1 000 times under the GTR model employing a GAMMA model of rate heterogeneity and the rapid bootstrapping option (Stamatakis *et al.* 2008). Clades with bootstrap support (BS) values ≥ 70 % were considered significant and strongly supported (Hillis & Bull 1993). Bayesian Inference (BI) analysis was performed using MrBayes v. 3.2.7 (Huelsenbeck & Ronquist 2001, 2005) under the GTR model on the CIPRES v. 3.3 portal. Constant characters were included and 10 M generations with trees sampled every 1 000th generation were run, resulting in 10 000 total trees. The first 2 500 trees were discarded as burn-in, and Bayesian posterior probabilities (PP) were determined from a consensus tree generated from the remaining 7 500 trees using PAUP v. 4.0b10 (Swofford 2002). Clades with PP ≥ 95 % were considered significant and strongly supported (Larget & Simon 1999, Alfaro *et al.* 2003).

RESULTS

Phylogenetic analysis

The ITS-LSU region was sequenced for *I. phyllophila*, *I. ripogoni* and the new species (Table 1) and ML and BI analyses were performed on ITS-LSU and ITS-LSU-*rpb2-tef1-α* datasets of 90 representatives of the *Xylariales* modified from Réblová *et al.* (2021). Outgroup taxa were *Bactrodesmium abruptum* and *B. diversum* (*Savoryellaceae*) and *Helicoascotaiwania lacustris* and *Pleurotheciella erumpens* (*Pleurotheciaceae*). Initially, we performed an ITS-LSU analysis (results not shown) to assess the placement of *Iodosphaeria* and the new species in the *Xylariales*. The backbone of the ML tree was largely unresolved and familial relationships were not supported. *Iodosphaeria*, consisting of six strains representing four species, *i.e.* *I. honghensis*, *I. phyllophila*, *I. ripogoni* and *I. tongrenensis*, formed a well-supported monophyletic group. However, the new species was placed outside this clade. The next analysis was based on the combined ITS-LSU-*rpb2-tef1-α* sequences in order to study phylogenetic relationships of *Iodosphaeria* with other members of the *Xylariales*. The alignment had 4 002 characters including gaps (ITS = 871 characters, LSU = 766,

Table 1. Specimens used in this study including specimen/strain, type status, GenBank accession numbers and source of sequences; T, E, I, N and P denote ex-type, ex-epitype, ex-neotype and ex-paratype strains.

Taxon	Specimen/Strain	Type Status	GenBank accession numbers				Reference
			ITS	LSU	<i>tef1-α</i>	<i>rpb2</i>	
<i>Acrocordiella occulta</i>	CBS 140500	E	KT949893	KT949893	—	—	Jaklitsch <i>et al.</i> (2016)
<i>Amphibambusa bambusicola</i>	MFLUCC 11-0617	T	KP744433	KP744474	—	—	Liu <i>et al.</i> (2015)
<i>Amphisphaeria flava</i>	MFLUCC 18-0361	T	MH971224	MH971234	—	—	Samarakoon <i>et al.</i> (2019)
<i>Amphisphaeria fuckelii</i>	CBS 140409	T	KT949902	KT949902	MH554435	MH554918	Jaklitsch <i>et al.</i> (2016), Liu <i>et al.</i> (2019)
<i>Amphisphaeria thailandica</i>	MFLU 18-0794	T	MH971225	MH971235	—	MK033640	Samarakoon <i>et al.</i> (2019)
<i>Annulohypoxyton michelianum</i>	CBS 119993		KX376320	KY610423	—	KY624234	Kuhnert <i>et al.</i> (2016), Wendt <i>et al.</i> (2018)
<i>Anthostoma decipiens</i>	CBS 133221		KC774565	KC774565	—	—	Jaklitsch <i>et al.</i> (2014)
<i>Anungitiomyces stellenboschiensis</i>	CPC 34726	T	MK876376	MK876415	—	—	Crous <i>et al.</i> (2019a)
<i>Arthrinium hysterinum</i>	ICMP 6889		MK014874	MK014841	MK017951	DQ368649	Pintos <i>et al.</i> (2019), Tang <i>et al.</i> (2007)
<i>Arthrinium pseudoparenchymaticum</i>	SICAUCC 18-0008		MK346319	MK346321	MK359205	MK359207	Wang <i>et al.</i> (2018)
<i>Astrosphaeriella erumpens</i>	S.M.H. 1291		—	AF279410	—	AY641073	Bhattacharya <i>et al.</i> (2000)
<i>Bactrodesmium abruptum</i>	CBS 145967		—	MN699410	MN704315	MN704290	Réblová <i>et al.</i> (2020)
<i>Bactrodesmium diversum</i>	CBS 142448		—	MN699412	MN704317	MN704292	Réblová <i>et al.</i> (2020)
<i>Barrmaelia macrospora</i>	CBS 142768	T	KC774566	KC774566	MF489005	MF488995	Jaklitsch <i>et al.</i> (2014), Voglmayr <i>et al.</i> (2017)
<i>Barrmaelia moravica</i>	CBS 142769	E	MF488987	MF488987	MF489006	MF488996	Voglmayr <i>et al.</i> (2017)
<i>Beltrania pseudorhombica</i>	CBS 138003	T	MH554124	KJ869215	MH554558	MH555032	Liu <i>et al.</i> (2019)
<i>Beltraniopsis neolitsea</i>	CBS 137974	T	KJ869126	KJ869183	—	—	Crous <i>et al.</i> (2014a)
<i>Biscogniauxia nummularia</i>	MUCL 51395	E	KY610382	KY610427	—	KY624236	Wendt <i>et al.</i> (2018)
<i>Brachiampulla verticillata</i>	ICMP 15065	P	MW144418	MW144402	MW147322	MW147336	Réblová <i>et al.</i> (2021)
<i>Brachiampulla verticillata</i>	ICMP 15993		MW144419	MW144403	MW147323	MW147337	Réblová <i>et al.</i> (2021)
<i>Cainia anthoxanthis</i>	MFLUCC 15-0539	T	KR092787	KR092777	—	—	Senanayake <i>et al.</i> (2015)
<i>Camillea obularia</i>	ATCC 28093		AF201714	KY610429	—	—	Wendt <i>et al.</i> (2018)
<i>Castanediella acaciae</i>	CBS 139896	T	KR476728	MH878661	—	—	Crous <i>et al.</i> (2015), Hernández-Restrepo <i>et al.</i> (2017)
<i>Castanediella cagnizarii</i>	MUCL 41095		KC775732	KC775707	KJ476985	—	Becerra-Hernández <i>et al.</i> (2016)

Table 1. (Ctd).

Taxon	Specimen/Strain	Type Status	GenBank accession numbers				Reference
			ITS	LSU	<i>tef1-α</i>	<i>rpb2</i>	
<i>Castanediella ramosa</i>	MUCL 39857		KC775736	KC775711	KJ476989	—	Becerra-Hernández <i>et al.</i> (2016)
<i>Clypeophysalospora latitans</i>	CBS 141463	T	KX820250	KX820261	—	—	Giraldo <i>et al.</i> (2017)
<i>Collodiscula japonica</i>	CBS 124266		JF440974	JF440974	—	—	Jaklitsch & Voglmayr (2012)
<i>Coniocessia cruciformis</i>	CBS 125769	T	MH863750	MH875218	—	—	Vu <i>et al.</i> (2019)
<i>Coniocessia minima</i>	CBS 125765	T	MH863746	MH875214	—	—	Vu <i>et al.</i> (2019)
<i>Cryptosphaeria eunomia</i> var. <i>fraxini</i>	CBS 223.87		KT425231	KT425295	—	KT425361	Trouillas <i>et al.</i> (2015)
<i>Cryptovalsa rabenhorstii</i>	CBS 125574		KC774567	KC774567	—	—	Jaklitsch <i>et al.</i> (2014)
<i>Cylindrium elongatum</i>	CBS 115974		KM231853	KM231733	KM231989	KM232429	Lombard <i>et al.</i> (2015)
<i>Cylindrium grande</i>	CBS 145578		MK876385	MK876426	MK876496	MK876482	Crous <i>et al.</i> (2019a)
<i>Daldinia concentrica</i>	CBS 113277		AY616683	KY610434	—	KY624243	Triebel <i>et al.</i> (2005), Wend <i>et al.</i> (2018)
<i>Delonicicola siamense</i>	MFLUCC 15-0670	T	MF167586	MF158345	—	MF158346	Perera <i>et al.</i> (2017)
<i>Diatrype disciformis</i>	CBS 197.49		—	DQ470964	DQ471085	DQ470915	Spatafora <i>et al.</i> (2007)
<i>Diatrypella vulgaris</i>	CBS 128329		MH864880	MH876328	—	—	Vu <i>et al.</i> (2019)
<i>Entosordaria perfidiosa</i>	CBS 142773	E	MF488993	MF488993	MF489012	MF489003	Voglmayr <i>et al.</i> (2017)
<i>Fasciatispora arengae</i>	MFLUCC 15-0326a		MK120275	MK120300	MK890790	MK890794	Doilom <i>et al.</i> (2018)
<i>Fasciatispora cocoes</i>	MFLUCC 18-1445		MN482680	MN482675	MN481516	MN481517	Hyde <i>et al.</i> (2020)
<i>Furfurella luteostiolata</i>	CBS 143620	T	MK527842	MK527842	MK523302	MK523273	Voglmayr <i>et al.</i> (2019)
<i>Graphostroma platystoma</i>	CBS 270.87		JX658535	DQ836906	DQ836915	KY624296	Zhang <i>et al.</i> (2006), Stadler <i>et al.</i> (2014), Wendt <i>et al.</i> (2018)
<i>Helicoascotaiwania lacustris</i>	CBS 145963	T	—	MN699430	MN704329	MN704304	Réblová <i>et al.</i> (2020)
<i>Hypocopra rostrata</i>	NRRRL 66178		KM067909	KM067909	—	—	Jayanetti <i>et al.</i> (2014)
<i>Hyponectria buxi</i>	UME 31430		—	AY083834	—	—	Unpublished
<i>Hypoxylon fragiforme</i>	MUCL 51264	E	KC477229	KM186295	—	KM186296	Stadler <i>et al.</i> (2013)
<i>Idriella lunata</i>	CBS 204.56	T	KP859044	KP858981	—	—	Hernández-Restrepo <i>et al.</i> (2016)
<i>Induratia thailandica</i>	MFLUCC 17-2669	T	MK762707	MK762714	—	MK791283	Samarakoon <i>et al.</i> (2020)
<i>Iodosphaeria foliicola</i>	NBM-F-07096	T	MZ509148	MZ509160	—	—	This study
<i>Iodosphaeria honghensis</i>	MFLU 19-0719	T	MK737501	MK722172	—	MK791287	Marasinghe <i>et al.</i> (2019)
<i>Iodosphaeria phyllophila</i>	PDD 56626		MZ509149	MZ509149	—	—	This study
<i>Iodosphaeria phyllophila</i>	FC 5099-2d		MZ509150	—	—	—	This study

Table 1. (Ctd).

Taxon	Specimen/Strain	Type Status	GenBank accession numbers				Reference
			ITS	LSU	<i>tef1-α</i>	<i>rpb2</i>	
<i>Iodosphaeria phyllophila</i>	ILLS00121493	E	MZ509151	—	—	—	This study
<i>Iodosphaeria ripogoni</i>	PDD 103350		MZ509152	MZ509152	—	—	This study
<i>Iodosphaeria tongrenensis</i>	MFLU 15-0393	T	KR095282	KR095283	—	—	Li <i>et al.</i> (2015)
<i>Kretzschmaria deusta</i>	CBS 163.93		KC477237	KY610458	—	KY624227	Stadler <i>et al.</i> (2013), Wendt <i>et al.</i> (2018)
<i>Leiosphaerella praeclara</i>	CBS 125586		JF440976	JF440976	—	—	Jaklitsch & Voglmayr (2012)
<i>Leptosillia acerina</i>	CBS 143939	E	MK527849	MK527849	MK523310	MK523282	Voglmayr <i>et al.</i> (2019)
<i>Leptosillia macrospora</i>	CBS 143627	E	MK527853	MK527853	MK523314	MK523286	Voglmayr <i>et al.</i> (2019)
<i>Lopadostoma gastrinum</i>	CBS 134632	N	KC774584	KC774584	—	—	Jaklitsch <i>et al.</i> (2014)
<i>Lopadostoma turgidum</i>	CBS 133207	E	KC774618	KC774618	—	KC774563	Jaklitsch <i>et al.</i> (2014)
<i>Melogramma campylosporium</i>	CBS 141086		JF440978	JF440978	—	—	Jaklitsch & Voglmayr (2012)
<i>Microdochium lycopodium</i>	CBS 125585	T	JF440979	JF440979	—	KP859125	Jaklitsch & Voglmayr (2012), Hernández-Restrepo <i>et al.</i> (2016)
<i>Muscodor yunnanensis</i>	WS38		MG866046	MG866038	—	MG866059	Chen <i>et al.</i> (2019)
<i>Neophysalospora eucalypti</i>	CBS 138864	T	KP004462	KP004490	—	—	Crous <i>et al.</i> (2014b)
<i>Nothodactylaria nephrolepidis</i>	CBS 146078	T	MN562132	MN567639	—	MN556809	Crous <i>et al.</i> (2019b)
<i>Oxydothis metroxylophilicola</i>	MFLUCC 15-0281	T	KY206774	KY206763	KY206778	KY206781	Konta <i>et al.</i> (2016)
<i>Oxydothis palmicola</i>	MFLUCC 15-0806	T	KY206776	KY206765	KY206780	KY206782	Konta <i>et al.</i> (2016)
<i>Phlogicylindrium eucalypti</i>	CBS 120080	T	DQ923534	DQ923534	—	MH554893	Summerell <i>et al.</i> (2006), Liu <i>et al.</i> (2019)
<i>Phlogicylindrium uniforme</i>	CBS 131312	T	JQ044426	JQ044445	—	—	Crous <i>et al.</i> (2011)
<i>Pleurotheciella erumpens</i>	CBS 142447	T	—	MN699435	MN704334	MN704311	Réblová <i>et al.</i> (2020)
<i>Pseudapiospora corni</i>	CBS 140736	N	KT949907	KT949907	—	—	Jaklitsch <i>et al.</i> (2016)
<i>Pseudomassaria chondrospora</i>	CBS 125600		JF440981	JF440981	—	—	Jaklitsch & Voglmayr (2012)
<i>Pseudosporidesmium lambertiae</i>	CBS 143169	T	MG386034	MG386087	—	—	Crous <i>et al.</i> (2017)
<i>Pseudotruncatella arezzoensis</i>	MFLUCC 14-0988	T	MG192320	MG192317	—	—	Perera <i>et al.</i> (2018)
<i>Pseudotruncatella bolusanthi</i>	CBS 145532	T	MK876407	MK876448	—	—	Crous <i>et al.</i> (2019a)
<i>Requienella seminuda</i>	CBS 140502		KT949912	KT949912	MK523328	MK523300	Jaklitsch <i>et al.</i> (2016), Voglmayr <i>et al.</i> (2019)
<i>Robillarda sessilis</i>	CBS 114312	E	KR873256	KR873284	—	—	Crous <i>et al.</i> (2015)
<i>Seiridium marginatum</i>	CBS 140403	E	KT949914	KT949914	MK523329	MK523301	Jaklitsch <i>et al.</i> (2016), Voglmayr <i>et al.</i> (2019)

Table 1. (Ctd).

Taxon	Specimen/Strain	Type Status	GenBank accession numbers				Reference
			ITS	LSU	<i>tef1-α</i>	<i>rpb2</i>	
<i>Selenodriella cubensis</i>	CBS 683.96	T	KP859053	KP858990	—	—	Hernández-Restrepo <i>et al.</i> (2016)
<i>Selenodriella fertilis</i>	CBS 772.83		KP859055	KP858992	—	—	Hernández-Restrepo <i>et al.</i> (2016)
<i>Sporidesmium knawiae</i>	CBS 123529	T	FJ349609	FJ349610	—	—	Crous <i>et al.</i> (2008)
<i>Strelitzomyces knysnanus</i>	CBS 146056	T	MN562135	MN567642	—	MN556810	Crous <i>et al.</i> (2019b)
<i>Subsessila turbinata</i>	MFLUCC 15-0831	T	KX762288	KX762289	KX762291	—	Lin <i>et al.</i> (2017)
<i>Vialaea insculpta</i>	DAOM 240257		JX139726	JX139726	—	—	Shoemaker <i>et al.</i> (2013)
<i>Vialaea minutella</i>	BRIP 56959		KC181926	KC181924	—	—	McTaggart <i>et al.</i> (2013)
<i>Xyladictyochaeta lusitanica</i>	CBS 142290	T	KY853479	KY853543	—	—	Hernández-Restrepo <i>et al.</i> (2017)
<i>Xylaria hypoxylon</i>	CBS 122620		KY610407	KY610495	—	KY624231	Wendt <i>et al.</i> (2018)
<i>Zygosporium mycophilum</i>	CBS 894.69		MH859474	MH871255	—	—	Vu <i>et al.</i> (2019)
<i>Zygosporium pseudomasonii</i>	CBS 146059	T	MN562147	MN567654	—	MN556815	Crous <i>et al.</i> (2019b)

rpb2 = 1107, *tef1- α* = 1258) and 2 366 unique character sites (RAxML). This combined four-loci alignment generated a tree with backbone support for familial relationships and correctly placed the new species in the *Iodosphaeria* clade. Therefore, this ML tree is shown in Fig. 1 and includes 34 well-supported families of the *Xylariales*. Five *Iodosphaeria* species form a moderately-supported monophyletic group (78 % BS, 1.0 PP), which is well-supported (100 % BS, 1.0 PP) as a sister clade to the *Pseudosporidesmiaceae*. *Iodosphaeriaceae* are not closely related to the *Amphisphaeriaceae* as previously suggested by Samuels *et al.* (1987), but rather occupies its own position as a distinct family in the *Xylariales*. The three representatives of *I. phyllophila* cluster with moderate support (83 % BS, 1.0 PP) and their ITS sequences, which are 611 bp in length, are 98.2–99.3 % similar with only a single gap. As expected, the specimens from Belgium (ILLS00121493) and France (FC5099-2d) are more closely-related to each other than they are to the specimen from New Zealand (PDD 56626). The new species occupies a basal position in the *Iodosphaeria* clade.

Taxonomy

Iodosphaeria Samuels *et al.*, *Mycotaxon* **28**: 486. 1987.

Sexual morph: *Ascomata* perithecial, solitary to gregarious, non-stromatic, superficial and easily removed from the substrate, subglobose to globose, black, covered with long, brown, flexuous hairs that project from the ascomata in a stellate fashion, coarse, brown, repent hyphae extending from the base of the ascomata, apex flattened or obtusely rounded, ostiolate, periphysate. *Ascomal wall* two-layered, outer layer of brown, angular cells, inner layer of hyaline, flattened cells.

Paraphyses hyaline, septate, inflated at the base, tapering towards the tip. *Asci* unitunicate, cylindrical to clavate, with an amyloid ring or ring lacking, 8-spored. *Ascospores* uniseriate to biseriate, ellipsoidal, ellipsoidal-fusiform or allantoid, aseptate, hyaline, smooth-walled, with or without a mucilaginous sheath. **Synasexual morphs:** selenosporella-like conidiophores and conidia and/or ceratosporium-like conidia have been observed in culture, on the surface of ascomata and on the repent hyphae. Selenosporella-like. *Conidiophores* macronematous, mononematous, pigmented, branched, septate. *Conidiogenous cells* integrated, terminal and discrete, lateral, polyblastic, single or in verticilli, with minute denticles along a short apical rachis; conidiogenesis holoblastic-denticulate. *Conidia* subcylindrical, slightly curved or straight, hyaline, aseptate. Ceratosporium-like. *Conidia* arising from aerial hyphae, pigmented, septate, staurosporous with two or more arms.

Taxa included in *Iodosphaeria*

Iodosphaeria foliicola A.N. Mill. & Réblová, *sp. nov.*, MycoBank MB 840507. Fig. 2A–G.

Etymology: Epithet derived from *folium* (L) leaf, and *incola* (L) dweller, referring to the substrate on which this species was found.

Typus: **Canada**, Prince Edward Island, Queens County, Port-la-Joye-Fort, Amherst National Historic Site, 46.1958N, -63.1342W, on overwintered leaves of *Alnus* sp., 5 Jun. 2011, A. Carter 1555 (**holotype** NBM-F-07096, isotype ILLS00121496), associated with a selenosporella-like asexual morph; GenBank ITS MZ509148, GenBank LSU MZ509160.

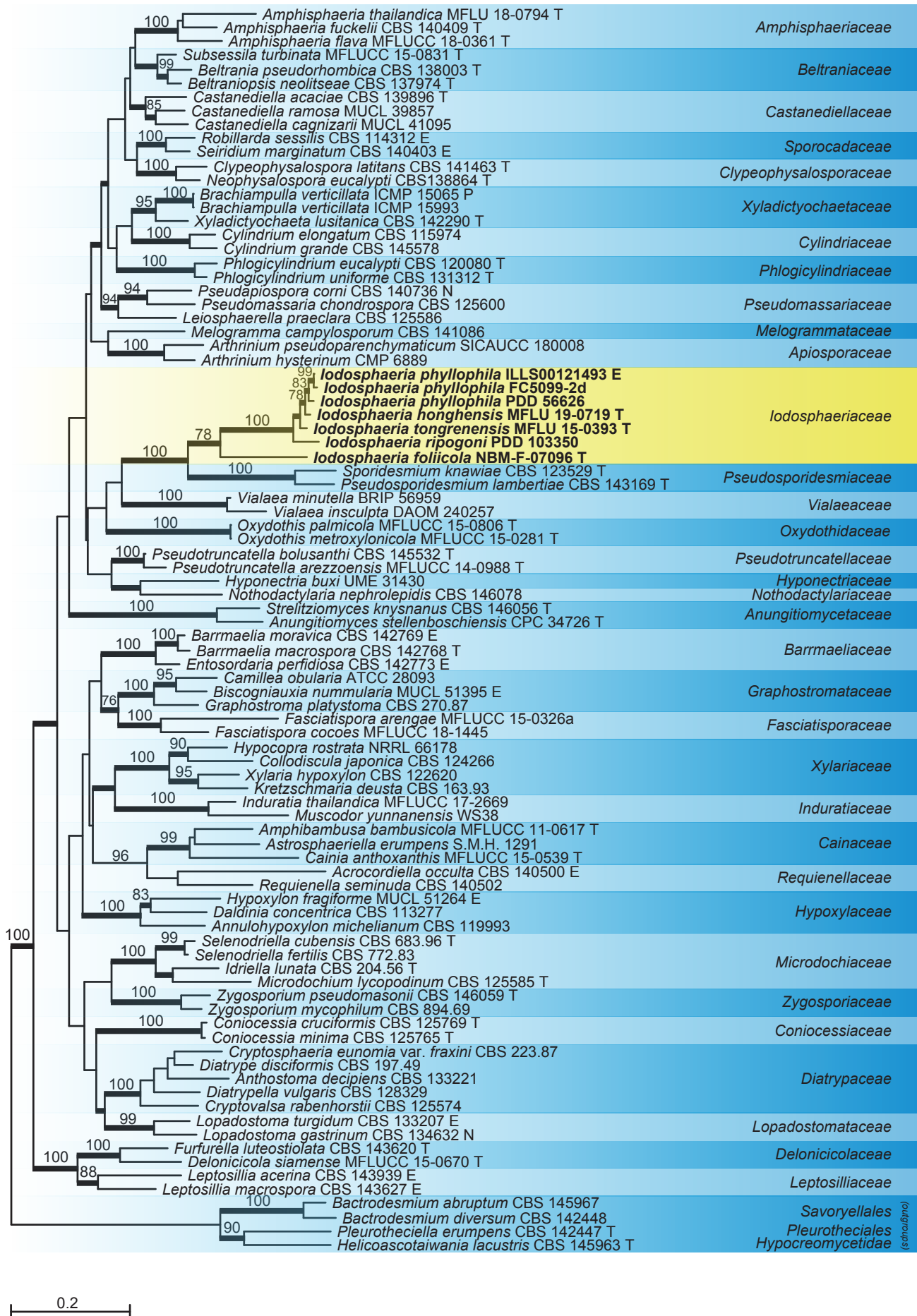


Fig. 1. Maximum likelihood tree generated from a RAxML analysis of combined ITS, LSU, *rpb2* and *tef1- α* sequences of selected members of the Xylariales. Members of *Iodosphaeria* are given in bold; T, E, N and P indicate ex-type, ex-epitype, ex-neotype and ex-paratype strains. Maximum likelihood bootstrap branch supports $\geq 75\%$ are shown above or below nodes and thickened branches indicate Bayesian posterior probabilities $\geq 95\%$.

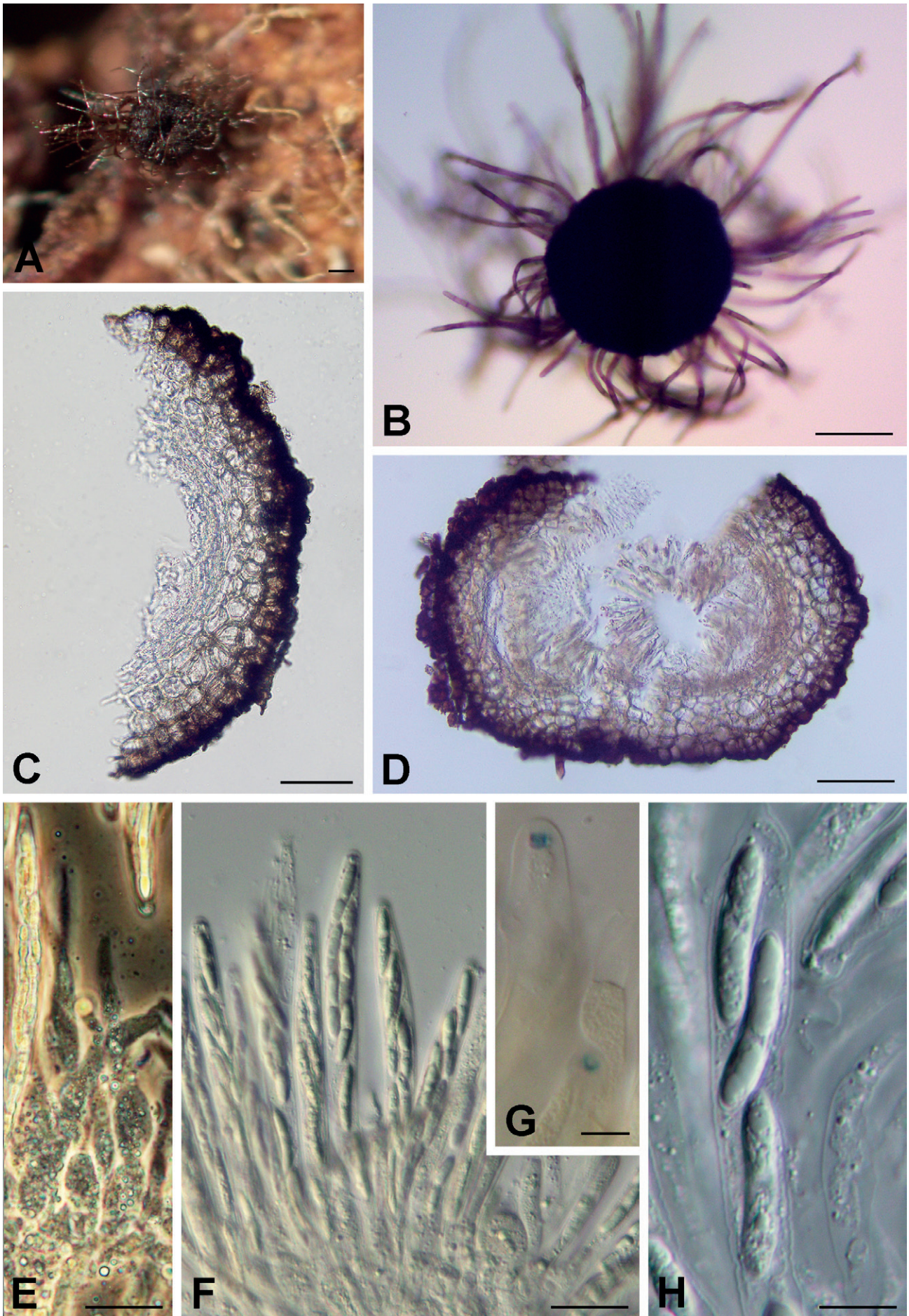


Fig. 2. *Iodosphaeria foliicola* NBM-F-07096. **A.** Ascoma on natural substrate. **B.** Ascoma mounted in water. **C, D.** Vertical sections of the ascomal wall. **E.** Paraphyses. **F.** Asci. **G.** Ascus apical apices with amyloid rings. **H.** Ascospores. Scale bars: A, B = 100 μ m; C, D = 50 μ m; E, F = 20 μ m; H = 10 μ m; G = 5 μ m.

Description: *Ascomata* globose to subglobose, 220–400 µm diam., superficial, solitary, black, covered with numerous, brown, septate, flexuous, rarely branched hairs, 145–320 × 6–9 µm, thick-walled (walls 1.5–2.5 µm thick), with rounded ends, singly or in fascicles; apex flattened, ostiolate, periphysate. Ascomal wall 50–70 µm wide, two-layered, outer layer composed of pseudoparenchymatous cells forming a *textura angularis*, composed of 5–8 layers of thin-walled cells, inner cell layers hyaline, outer cell layers becoming smaller and darker brown, outermost layer of thick-walled, melanized, dark brown cells, inner layer composed of 2–3 layers of thin-walled, hyaline, flattened, pseudoparenchymatous cells. *Paraphyses* sparse, hyaline, septate, of similar length as asci, basal cells inflated, tapering to 3–6 µm wide at apex, disintegrating at maturity. *Asci* cylindrical, 94–136 × 7.5–10 µm (120 ± 11.0 × 8.5 ± 0.5), 8-spored, apex rounded, short-stipitate, with a wedge-shaped, amyloid apical ring, 1.5–2.3 × 1–1.2 µm. *Ascospores* oblong to slightly allantoid, ends obtuse, aseptate, eguttulate, hyaline, smooth, 16.5–19.5 × 2.9–4 µm (18 ± 0.8 × 3.5 ± 0.4), without a mucilaginous sheath, uniseriate to biseriata in the ascus.

Habitat and distribution: Found in Canada on mostly the abaxial side of overwintered leaves of *Alnus* sp.

Additional specimens examined: **Canada**, Prince Edward Island, Queens County, Port-la-Joye-Fort, Amherst National Historic Site, 46.1958N, -63.1342W, on overwintered leaves of *Alnus* sp., 21 Jul. 2011, A. Carter 1554 (NBM-F-07095), associated with a selenosporella-like asexual morph.

Notes: *Iodosphaeria foliicola* is only known from two specimens growing on overwintered *Alnus* sp. leaves from Prince Edward Island, Canada. It is distinguished from other members of *Iodosphaeria* by its shorter asci (Fig. 2F) with an amyloid ascal ring (Fig. 2G) and oblong to allantoid, shorter ascospores (Fig. 2H) that lack guttules and a mucilaginous sheath. It closely resembles *I. honghensis*, but differs in its shorter, eguttulate ascospores (Table 2). *Iodosphaeria foliicola*, *I. phyllophila* and *I. tarda* can occur on dead fallen leaves, but *I. foliicola* can be separated by its longer asci and shorter, allantoid ascospores. The collector noted a selenosporella-like asexual morph was associated with both collections of *I. foliicola*, but was not found during our examinations.

Iodosphaeria honghensis Marasinghe *et al.* [as ‘*honghense*’], *Phytotaxa* **420**: 276. 2019.

This species is only known from the type specimen (MFLU 19-0719), which was found growing on dead twigs of an unidentified host from Yunnan Province in China (Marasinghe *et al.* 2019). It is distinguished from other species in the genus by its cylindrical to allantoid, guttulate ascospores that lack a mucilaginous sheath. A ceratosporium-like asexual morph was found growing on the host surface.

The unpublished *tef1-α* sequence (GenBank accession MK776957) from MFLU 19-0719, labeled as *Iodosphaeria* sp., was submitted to GenBank by D.S. Marasinghe & K.D. Hyde. Since the BLASTn search suggests closest relatives in the *Hypocreomycetidae* it is likely a contaminate; it should be removed from GenBank. However, four other sequences (SSU, ITS, LSU and *rpb2*) from this same voucher specimen under the original name, *I. honghense*, published by Marasinghe *et*

al. (2019) appear correct, but the taxonomic name should be updated to ‘*honghensis*’.

Iodosphaeria hongkongensis J.E. Taylor & K.D. Hyde, *Sydowia* **51**: 128. 1999.

This species is only known from four collections, all described as growing on either a dead petiole (holotype) or a dead rachis of a palm, *Archontophoenix alexandrae*, from Hong Kong (Taylor & Hyde 1999). It is separated from other species of *Iodosphaeria* by its smaller asci lacking an ascal ring and smaller, ellipsoidal to fusiform ascospores lacking a mucilaginous sheath. The only other species that lacks an apical ring is *I. ripogoni*, which possesses a mucilaginous sheath surrounding the ascospores. No asexual morph was observed on the host material.

Iodosphaeria phyllophila (Mouton) Samuels *et al.*, *Mycotaxon* **28**: 486. 1987.

Basionym: *Lasiosphaeria phyllophila* Mouton, *Bull. Soc. R. Bot. Belg.* **39**: 48, 1900.

This species is the most commonly collected in the genus, known from at least 20 collections (Dennis 1974, Samuels *et al.* 1987, MyCoPortal 2021). It was originally described as *Lasiosphaeria phyllophila* growing on rotten leaves of *Betula alba* and *Corylus* from Belgium (Mouton 1900). It has a wide distribution and is also known from Brazil, French Guiana, Great Britain, and New Zealand. It has been found growing on a variety of substrates on numerous hosts including leaves of *B. alba*, (Mouton 1900), *Alnus* (Kirchstein 1911) and *Corylus avellana* (Declercq 2008), dead twigs and fallen debris of *Alnus*, *Populus* and *Salix* (Ellis & Ellis 1985), dead stems of *Chamaenerion angustifolium* (Dennis 1974) and *Rubus idaeus* (Declercq 2008), cone scales (Dennis 1974), and on the rachis of *Cyathea dealbata*, *Gahnia* sp., and *Ripogonum scandens* (Samuels *et al.* 1987). *Iodosphaeria phyllophila* is distinguished by its amyloid ascal ring and longer, allantoid, non-guttulate ascospores. Selenosporella- and ceratosporium-like synasexual morphs were reported on field collected material (Bell & Mahoney 2016) and in cultures of *I. phyllophila* (Samuels *et al.* 1987). *Iodosphaeria phyllophila* and its synasexual morphs have previously been illustrated (Ellis & Ellis 1985, Samuels *et al.* 1987, Declercq 2008, Senanayake *et al.* 2015, Bell & Mahoney 2016).

Senanayake *et al.* (2015) revised a collection of *I. phyllophila* originating from New Zealand (PDD 32622, Samuels *et al.* 1987) and incorrectly referred to it as a holotype. The type material is preserved at BR, but since it is over 120 years old, attempts were not made to obtain molecular data directly from this specimen. Instead, a more recent specimen with numerous, fertile ascomata from Belgium was sequenced and chosen as epitype. The ascomata and ascospores of this newly designated epitype specimen have been previously illustrated (Declercq 2008; figs 3C, 4C). Both selenosporella- and ceratosporium-like synasexual morphs were found on and around ascomata of the epitype of *I. phyllophila*.

Typification: **Belgium**, Wachtebeke, Reepkes, IFBL C3.35, on stem of *Rubus idaeus*, 28 Jul. 2007, B. Declercq 07/068 (epitype designated here ILLS00121493; MBT 10002029; GenBank ITS MZ509151, **isoepitype** GENT), with selenosporella- and ceratosporium-like synasexual morphs, epitype designated for the **holotype:** *Lasiosphaeria phyllophila* Mouton, *Bull. Soc. Rot. Bot. Belg.* **39**: 48. 1900. (BR).

Table 2. Morphological characteristics, hosts, geographical distribution and references for species of *Iodosphaeria*.

Species	Length of asci (µm)	Ascal ring	Ascal ring amyloid	Shape of ascospores	Length of ascospores (µm)	Guttules in ascospores	Asexual morph(s)	Host(s)	Geographical distribution	Reference
<i>I. foliicola</i>	94–136	Present	Yes	Allantoid	16.5–19.5	Absent	Selenosporella-like	<i>Alnus</i> sp.	Canada	This study
<i>I. honghensis</i>	90–130	Present	Yes	Allantoid	18.5–22.5	Present	Ceratosporium-like	Unidentified	China	Marasinghe <i>et al.</i> (2019)
<i>I. hongkongensis</i>	80–102	Absent	n/a	Ellipsoidal	14–22	Absent	Unknown	<i>Archontophoenix alexandrae</i>	Hong Kong	Taylor & Hyde (1999)
<i>I. phyllophila</i>	105–138	Present	Yes	Allantoid	21–26.7	Absent	Selenosporella-like and ceratosporium-like	<i>Alnus</i> sp., <i>Betula alba</i> , <i>Chamaenerion angustifolium</i> , <i>Corylus avellana</i> , <i>Cyathea dealbata</i> , <i>Gahnia</i> sp., <i>Populus</i> sp. <i>Ripogonum scandens</i> , <i>Rubus idaeus</i> , <i>Salix</i> sp.	Belgium, Brazil, French Guiana, Great Britain, New Zealand	Samuels <i>et al.</i> (1987)
<i>I. podocarpi</i>	97–120	Present	Yes	Ellipsoidal	19–20	Absent	Selenosporella-like	<i>Podocarpus parlatorei</i>	Argentina	Catania & Romero (2012)
<i>I. polygoni</i>	150–180	Present	Yes	Ellipsoidal	18–23	Present	Ceratosporium-like	<i>Polygonum chinese</i>	Taiwan	Hsieh <i>et al.</i> (1997)
<i>I. ripogoni</i>	140–185	Absent	n/a	Ellipsoidal	21.5–26	Absent	Selenosporella-like and ceratosporium-like	<i>Ripogonum scandens</i>	New Zealand	Samuels <i>et al.</i> (1987)
<i>I. tarda</i>	70–85	Present	Yes	Ellipsoidal-fusiform	14–20	Absent	Unknown	<i>Corylus</i> sp., <i>Phyllostachys</i> sp.	France, Germany	Candoussau <i>et al.</i> (1996)
<i>I. tongrenensis</i>	150–210	Present	Yes	Ellipsoidal	18.5–22.5	Absent	Ceratosporium-like	Unidentified	China	Li <i>et al.</i> (2015)

Additional specimens examined: **France**, Las Muros, on scales of *Picea* cone, 24 Sep. 1997, *J. Fournier* FC 5099-2a (CUP); *Ibid.*, Sainte-Ogeu, on branch of *Vaccinium myrtillus?*, 1 Mar. 1992, *F. Candoussau* FC 5099-2c (CUP), *Ibid.*, Pyrénées Atlantiques, Oloron, Bugangue, 10 Jul. 1994, *F. Candoussau* FC 5099-2d (CUP). **New Zealand**, North Island, Auckland, Hūnua Ranges Regional Park, vic. Mangatangi Dam, -37.1158S, 175.2119E, on *Cyathea dealbata*, 1 Feb. 1989, *P.R. Johnson* (PDD 56626); *Ibid.*, Swanson, on rachis of *Cyathea dealbata*, 6 May 1981, *G.J. Samuels* 81-80 (PDD 45501); *Ibid.*, Waitemata City, Waitakere Range, Marguerite Track, on rachis of *Cyathea dealbata*, 15 May 1975, *G.J. Samuels* 75-289 (PDD 36844); Erua Forest, near National Park, on dead wood, 6 Apr. 2005, *A. Bell* 919 (PDD 83080), with selenosporella-like asexual morph. **Spain**, Basque region, Gipuzkoa Province, Tolosa, on twig of unidentified shrub, 14 Jan. 1995, *F. Candoussau* FC 5099-2b (CUP), with ceratosporium-like asexual morph.

Iodosphaeria podocarpi Catania & A.I. Romero, *Mycosphere* **3**[2]: 40. 2012.

This species is only known from the type specimen, which was found growing on a branch of *Podocarpus parlatorei* in Argentina (Catania & Romero 2012). It is unique in having shorter asci with an amyloid apical ring and ellipsoid to navicular or slightly allantoid, shorter ascospores. A selenosporella-like asexual morph was found growing near or among the ascomata.

Iodosphaeria polygoni W.H. Hsieh *et al.*, *Mycol. Res.* **101**: 841. 1997.

This species is only known from the type specimen found on stems of *Polygonum chinese* in Taiwan (Hsieh *et al.* 1997). It is unique in having longer asci and ellipsoidal, guttulate ascospores. A ceratosporium-like asexual morph was found associated with the repent network of brown hyphae occurring at the base of the ascomata.

Iodosphaeria ripogoni Samuels *et al.*, *Mycotaxon* **28**: 490. 1987.

This species is known from eight collections, all growing on the woody, vine-like stems of *Ripogonum scandens* from New Zealand (Samuels *et al.* 1987, Bell & Mahoney 2016, MyCoPortal 2021). It is distinguished by its lack of an ascal apical ring and its ellipsoidal ascospores that possess a mucilaginous sheath while still in the ascus. The only other species that lacks an apical ring is *I. hongkongensis*, which also lacks a mucilaginous sheath surrounding the ascospores. Although *I. tongrenensis* also has ascospores with a sheath, its asci possess an amyloid ascus ring. Selenosporella- and ceratosporium-like synasexual morphs were reported on the coarse, brown, repent hyphae that radiate from the ascomata and cover the surface of the substrate in field collected material of *I. ripogoni* (Samuels *et al.* 1987).

Additional specimen examined: **New Zealand**, North Island, Mt. Egmont National Park, Stratford, Dawson Falls Road, on dead stems of *Ripogonum scandens*, 18 Jan. 2013, *A. Bell* 1205 (PDD 103350), associated with selenosporella-like asexual morph.

Iodosphaeria tarda (Fuckel) A.N. Mill. & Réblová, *comb. nov.*, MycoBank MB 840508. Fig. 3A–J.

Basionym: *Sphaeria tarda* Fuckel, *Fungi Rhen. Exs., Suppl. Fasc.* **6**: no. 2021, 1867 [*Bot. Zeitung* **27**(6): 97. 1869].

Synonyms: *Trichosphaeria tarda* (Fuckel) Fuckel, *Jahrb.*

Nassauischen Vereins Naturk. **23–24**: 145 (1869–1870) 1870.

Pyrenochaeta tarda (Fuckel) Sacc., *Syll. fung.* **3**: 221. 1884.

Iodosphaeria tarda (Fuckel) M.E. Barr, *Mycol. Helv.* **8**: 14. 1996, *Nom. inval.* (Art. 41.4., Melbourne).

This species was published in the *exsiccatae* series *Fungi Rhen. Exs.* no. 2021 (Fuckel 1870) and is only known from two collections. The isotype has been found on *Corylus* in Germany, whereas the second specimen (FC 319, Candoussau *et al.* 1996) was collected on *Phyllostachys* from France. The isotype at FH was unavailable for study, but another specimen (M-0312560) of the *Fungi Rhen. Exs.* No 2021 at M was available. The latter specimen contains a decaying leaf of *Corylus* sp. with several ascomata arranged mainly along the leaf veins (Fig. 3A). The setae appears at first slightly rigid and erect, covering ascomata (Fig. 3C). Later, setae become decumbent, flexuous and project from the ascomal wall in a stellate fashion (Fig. 3B) leaving the top glabrous. The ascomata are subglobose, without a papilla but do not have the flattened apex that is typical of other species. Instead, the top is obtusely rounded. *Iodosphaeria tarda* is distinguished by its smaller asci and ascospores that are ellipsoidal-fusiform with a smooth wall. Ascospores in the French collection (FC 319) were reported oblong to nearly allantoid; for description and additional illustrations, see Candoussau *et al.* (1996). Candoussau *et al.* (1996) examined the specimen *Fungi Rhen. Exs.* No 2021 (FH), which originated from the Caroline Barbey-Boissier herbarium, labelled Barbey-Boissier 672. Although Candoussau *et al.* (1996) reported that *I. tarda* had a non-amyloid ascal ring, the specimen at M clearly shows an amyloid ring (Fig. 3I, J). The authors also reported no asexual morph or synasexual morph were found associated with either specimen, which agrees with our observations. Candoussau's collections were sent to CUP in 2019, but FC 319 was not found there. The illustrations in Candoussau *et al.* (1996) appear to be drawn by Margaret Barr, who proposed the (invalid) transfer to *Iodosphaeria*. It is possible that she sent FC 319 to MASS, which has been transferred to NY. However, this specimen does not exist at NY (B. Thiers, pers. comm.).

The transfer of the name to *Iodosphaeria* was invalidly published since Candoussau *et al.* (1996) did not reference the date of the basionym (Art. 41.4, Melbourne; McNeill *et al.* 2012). This is now corrected herein and we choose to maintain the same specific epithet.

Additional specimen examined: **Germany**, Johannisberg, on decaying leaf of *Corylus* sp., spring, Fuckel, *Fungi Rhen. Exs.* no. 2021 (isotype, M-0312560).

Iodosphaeria tongrenensis Q.R. Li *et al.*, *Phytotaxa* **234**: 125. 2015.

This species is only known from the type specimen, which was collected on dead twigs in the Guizhou Province in China (Li *et al.* 2015). It is separated from all other species in the genus by its amyloid apical ascal ring and ellipsoidal ascospores that are surrounded by a mucilaginous sheath. *Iodosphaeria ripogonii* is the only other species known to have ascospores with a sheath, but it lacks an apical ascus ring. A ceratosporium-like asexual morph was observed on the surface of ascomata in *I. tongrenensis*.



Fig. 3. *Iodosphaeria tarda* Fungi Rhen. Exs., Suppl., 2021. **A.** Ascomata on decaying leaf. **B, C.** Ascomata on natural substrate. **D.** Ascoma mounted in water. **E.** Vertical section of the ascomal wall. **F, G.** Setae **H.** Paraphyses. **I, J.** Ascus apical apices with amyloid rings. **K.** Ascospores. Scale bars: A = 1 cm; B, C = 500 μ m; D = 100 μ m; E, F, H = 20 μ m; G = 50 μ m; I–K = 5 μ m.

Excluded and doubtful species

Iodosphaeria aquatica K.D. Hyde, *Nova Hedwigia* **61**: 129. 1995.

This species is only known from the type specimen, which was collected on submerged wood in Queensland, Australia. The placement of *I. aquatica* in the genus was questioned by Hyde (1995) when he described it, others have suggested its taxonomic placement is unclear (Kang *et al.* 1999, Taylor & Hyde 1999), and Hsieh *et al.* (1997) excluded it based on the glabrous, pyriform, erumpent ascomata often with lateral necks and its aquatic habitat. The LSU sequence of *I. aquatica* from Jeewon *et al.* (2003), but listed as dothideomycete sp. in GenBank clearly does not belong in the genus. Its LSU sequence is ~98 % similar to *Lentistoma* spp. in the *Dothideomycetes*, but the erumpent, pyriform ascomata and aseptate ascospores of *I. aquatica* are significantly different from the immersed, subglobose ascomata and 1-septate ascospores with a narrow, bipolar sheath found in *Lentistoma* (Hashimoto *et al.* 2018). Additional material of *I. aquatica* should be collected and sequenced to properly place this species in the *Lophiostomataceae*. Likewise, the LSU sequence of *Iodosphaeria* sp. (AF452045) from voucher specimen HKUCC 3154 (Jeewon *et al.* 2003), but listed as dothideomycete sp. in GenBank is 94 % similar to *I. aquatica* and most likely a member of the *Pleosporales*.

Iodosphaeria arundinariae (Ellis & Everh.) M.E. Barr, *Mycotaxon* **46**: 47. 1993.

Basionym: *Trichosphaeria arundinariae* Ellis & Everh., *N. Amer. Pyrenomyc.* **153**. 1892.

This species is only known from the type specimen, which was originally described as *Trichosphaeria arundinariae* growing on an old culm of *Arundinaria* in Louisiana, USA (Ellis & Everhart 1892). It was transferred to *Iodosphaeria* by Barr (1993). It can be separated from other species in the genus based on its papillate ascomata, non-amyloid ascus ring, and ellipsoidal to fusiform, verruculose ascospores. Barr (1993) did not observe an asexual morph on the holotype. *Iodosphaeria arundinariae* deviates from the generic concept based on *I. phyllophila* in the diagnostic characteristics of ascomata, apical ring and ascospores suggesting certain heterogeneity. Therefore, it is argued that it should be treated as a doubtful species until it is recollected and its relationships are assessed with DNA sequence data.

DISCUSSION

Members of *Iodosphaeria* possess ascomata that are macroscopically nearly identical in shape, size and overall appearance being subglobose to globose, superficial, and black with long, flexuous brown setae. Species are delimited by a combination of limited microscopic characters including: 1) the length of the asci, particularly whether they are longer or shorter than 150 μm , 2) whether or not the asci possess an apical ring, which is always amyloid if present, 3) the shape (ellipsoidal, ellipsoidal-fusiform or allantoid) and length of the ascospores, and 4) whether or not the ascospores have guttules. Although lengths of asci and ascospores and the presence or absence of an apical ascus ring are definitive, objective characters, the shape of the ascospores and the presence or absence of guttules are more ambiguous, subjective characters. Six of the nine accepted

members of *Iodosphaeria*, exceptions being *I. hongkongensis*, *I. phyllophila* and *I. ripogoni*, are known from only one or two collections. Additional material of these six species needs to be recollected so that intraspecific variation, both molecular and morphological, can be examined to determine the significance of these characters in delimiting species.

Either selenosporella- and/or ceratosporium-like synasexual morphs were found in seven of the nine accepted species of *Iodosphaeria*. Both appear to be produced directly from the repent hyphae that radiate from ascomata over the surface of the substrate. Although the selenosporella-like synasexual morph produces conidiophores, the ceratosporium-like synasexual morph does not and conidia arise directly from the repent hyphae. Samuels *et al.* (1987) discovered both synasexual morphs in the only species of *Iodosphaeria* to be obtained in culture, *I. phyllophila*. These synasexual morphs are dematiaceous hyphomycetes with holoblastic conidiogenesis. Molecular data of *Ceratosporium* are unavailable and its systematic placement is unknown. Interestingly, species of *Ceratosporium* form selenosporella-like conidiophores directly on conidia (*e.g.* Hughes 1964), thus the occurrence of both synasexual morphs in the life cycle of *Iodosphaeria* is not surprising. A similar phenomenon, when selenosporella-like conidiophores are formed either on conidia or conidiophores of the respective asexual morph, was described for example in *Teratosperma* (Hughes 1951, Matsushima 1975), *Diplococcium* (Wang & Sutton 1998, Hernández-Restrepo *et al.* 2012) and *Endophragmiella* (*e.g.* Hughes 1979). The selenosporella-like morphotype appears polyphyletic in the *Ascomycota*. The genus *Selenosporella* (Arnaud 1953, MacGarvie 1968), typified with *S. curvispora*, was confirmed with molecular data to belong to the *Helminthosphaeriaceae* (Réblová *et al.* 2021). The family is rich in selenosporella-like asexual morphs and synasexual morphs, which have been linked with *Endophragmiella*, *Echinospaeria*, *Hilberina* and *Ruzenia* (Awao & Udagawa 1974, Matsushima 1975, Hughes 1979, Sivanesan 1983, Gams 1973, Miller & Huhndorf 2004). The selenosporella-like synasexual morph was described as part of the life cycle of several hyphomycetes such as *Acrodictys bambusicola* (*Diaporthales*) (Matsushima 1975), *Spadicoides* (*Xenosphadicoideales*) (Kuthubutheen & Nawawi 1991, Castañeda-Ruiz *et al.* 1997, Réblová *et al.* 2018), and also *Arachnophora excentrica* (Hughes 1979), *Polytretophora calcarata* (= *Spadicoides calcarata*, Kuthubutheen & Nawawi 1991) and *Quadracaea mediterranea* (Lunghini *et al.* 1996), whose systematic placements are unknown. In the *Xylariales*, selenosporella-like fungi have been linked with *Oxydothis* (Samuels & Rossman 1987) and were also classified in *Selenodriella* (Castañeda-Ruiz & Kendrick 1990, Hernández-Restrepo *et al.* 2016). However, these genera are unrelated to *Iodosphaeria* (Fig. 1).

Species of *Iodosphaeria* have been reported from Argentina, Belgium, Brazil, China, French Guiana, Great Britain, Hong Kong, New Zealand, Taiwan and the USA (Samuels *et al.* 1987, Barr 1993, Hyde 1995, Candoussau *et al.* 1996, Hsieh *et al.* 1997, Taylor & Hyde 1999, Catania & Romero 2012, Li *et al.* 2015, Table 2). Only 27 collections of *Iodosphaeria* occur in the MyCoPortal (MyCoPortal 2021), 19 of which are either *I. phyllophila* or *I. ripogoni* from New Zealand. One collection of *Iodosphaeria cf. ripogoni* (NY03380508), which Samuels *et al.* (1987) reported as immature and may be a new species, is reported from Hawaii on mistletoe; two previously unidentified specimens from Canada are

now described as *I. foliicola*, and the remaining five specimens are unidentified *Iodosphaeria* species from Costa Rica and Venezuela. *Iodosphaeria* occurs on many different hosts including *Alnus* sp., *Archontophoenix alexandrae*, *Betula alba*, *Chamaenerion angustifolium*, *Corylus avellana*, *Cyathea dealbata*, *Phyllostachys* sp., *Podocarpus parlatorei*, *Polygonum chinense*, *Populus* sp., *Ripogonum scandens*, *Rubus idaeus*, and *Salix* sp.

Several species of *Iodosphaeria* lack DNA data; only five of the nine species have been sequenced. Molecular data should be obtained from either voucher specimens or freshly-collected material for the remaining four species: *I. hongkongensis*, *I. podocarpi*, *I. polygoni*, and *I. tarda*, and for the doubtful species, *I. arundinariae*. This will enable a better understanding of the relationships, distributions, host associations and ecology of members of *Iodosphaeria*.

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