Studies in Fungi

ARTICLE

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https://doi.org/10.48130/SIF-2023-0006

Studies in Fungi **2023**, 8:6

A novel coniothyrium-like genus in *Coniothyriaceae* (*Pleosporales*) from salt marsh ecosystems in Thailand

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Abstract

In this study, a novel coniothyrium-like genus *Coniothyrioides* is introduced to *Coniothyriaceae* based on a fresh fungal collection from salt marsh habitats in Thailand. Coniothyrium-like taxa are taxonomically controversial and have been classified into different families in *Pleosporales* such as *Didymosphaeriaceae* (*Alloconiothyrium* and *Paraconiothyrium*), *Coniothyriaceae* (*Coniothyrium*) and *Didymellaceae* (*Microsphaeropsis*). However, our novel genus shares similar morphology to some key characters in *Coniothyriaceae* in having dark, globose pycnidia, uni-locular conidiomata, a central ostiole, a peridium of *textura angularis* cells, and doliiform conidiogenous cells with a periclinal thickening at the apex, while conidial morphologies are diverse. The presence of setae arising from the outer peridial wall is the main difference between *Coniothyrioides* and other closely related *Coniothyriaceae* genera. Phylogenetically, LSU-SSU-ITS sequence analyses confirm the placement of this novel genus as a distinct lineage within *Coniothyriaceae*. Species boundaries were defined, based on morphology and multi-gene phylogenetic analyses using maximum likelihood and Bayesian inference analyses. The comprehensive descriptions and micrographs are provided. Our findings expand the taxonomic knowledge of *Ascomycota* in salt marsh ecosystems.

Citation: Wijesinghe SN, Calabon MS, Xiao Y, Jones EBG, Hyde KD. 2023. A novel coniothyrium-like genus in *Coniothyriaceae* (*Pleosporales*) from salt marsh ecosystems in Thailand. *Studies in Fungi* 9:6 https://doi.org/10.48130/SIF-2023-0006

INTRODUCTION

In coastal ecosystems, salt marsh habitats are common and consist of diverse halophytes, grasses, herbs, and shrubs, as well as microorganisms[1,2]. These species-rich ecosystems are highly productive, and investigating fungal diversity in these habitats is important while many areas are still being explored[2,3]. Researchers are currently studying the taxonomy of fungi in marine and semi-marine environments and increasing the number of known taxa recorded[4–6]. *Ascomycota* was identified as the dominant group in world salt marsh ecosystems, including the highest diversity in *Pleosporales*, *Dothideomycetes*[2]. *Coniothyriaceae* is a pleosporalean family with a large number of terrestrial taxa, while taxa associated with salt marsh vegetation have rarely been reported[2].

Coniothyriaceae was established by Cooke[7] to accommodate *Coniothyrium* species. The type genus and species of *Coniothyriaceae* are *Coniothyrium* Corda and *C. palmarum* Corda, respectively[8–10]. This family was previously linked to *Leptosphaeriaceae*[11] and this was followed by several authors[12–16]. Subsequently, molecular data analyses for phoma-like asexual morphs were performed by de Gruyter et al.[17] based on LSU and ITS sequence data and revealed that *C. palmarum* is phylogenetically distant from *Leptosphaeriaceae* and closely related to *Coniothyriaceae*. de Gruyter et al.[17] reinstated *Coniothyriaceae* as a distinct family in *Pleosporales* and transferred several *Phoma* and *Pyrenochaeta* species into this family. Thus, the morphological variations of *Coniothyrium* species were expanded by the addition of more characters, such as setose pycnidia and conidiogenesis with elongated conidiophores[17]. Several authors later updated the placements of many *Coniothyrium* species with generic level changes and novel genera placed in different families[18,19].

Verkley et al.[19] studied morphology and phylogenetic relationships of coniothyrium-like and closely related taxa. These species are coelomycetous and characterized in having pycnidial or stromatic conidiomata and small, subhyaline to pigmented, 1- or 2-celled conidia[19]. The phenotypic plasticity of these coelomycetous species has made their taxonomic placements uncertain and, thus the majority of them have been placed in *Coniothyrium*[19–21]. Both *Coniothyrium* and coniothyrium-like species were identified as polyphyletic within *Pleosporales* and recent taxonomic treatments were mainly treated with combined morphology and molecular data analyses[12,16,17,19,21–32]. *Coniothyrium sensu stricto* is characterized by 1-septate conidia and grouping in *Coniothyriaceae*[17,19–21,33]. Currently, *Coniothyriaceae* consists of five genera, such as *Coniothyrium*, *Foliophoma* Crous, *Neoconiothyrium* Crous, *Ochrocladosporium* Crous & U. Braun

and *Staurosphaeria* Rabenh. (≡*Hazslinszkyomyces* Crous & R.K. Schumach.)[10,34].

Coniothyriaceae members have been identified as pathogens that cause necrotrophic and leaf spots on leaves, and saprobes on dead branches[10,17]. The sexual morph is characterized in having cucurbitaria-like, black, globose ascomata, short central ostiole, *textura angularis* peridium cells, branched, septate, cellular pseudoparaphyses, 8-spored, cylindrical, bitunicate asci and muriform, ellipsoidal ascospores that are initially hyaline and brown at maturity[10]. Asexual morphs are coelomycetous and sometimes differentiated with phoma-like, camarosporium-like, coniothyrium-like, or cladosporium-like asexual characters. They are characterized in having dark, globose, pycnidial conidiomata, with central, sometimes papillate ostiole, cells of *textura angularis* or *textura globulosa* in the conidiomatal wall, hyaline macroconidiogenous and microconidial cells and conidia. Conidial morphology is varied as macroconidia and microconidia. Macroconidia are ellipsoid, red-brown, and septation is from the central transverse septum to muriformly septate, while microconidia are hyaline, globose to ellipsoid and aseptate[9,10,24,27,35,36].

The aim of the study

In this study, we aim to expand the taxonomy of fungi associated with dead plant hosts in salt marsh ecosystems. We investigate salt marsh habitats in Thailand to collect fungal specimens and isolate them to find out the taxonomic novelties. Morphological illustrations, comprehensive descriptions, and multi-gene phylogenetic analyses are provided to confirm the placement of new findings.

MATERIALS AND METHODS

Sample collection, morphological studies, and isolation

Fungal specimens were collected from salt marsh habitats in Pranburi Province, Thailand, 2021. Samples were preserved in sterile Ziploc bags in the laboratory and incubated at room temperature 25 °C. Rehydrated specimens were observed to identify fungal fruiting bodies and macro-morphology was observed by using a Motic SMZ 168 compound stereomicroscope. Micro-morphologies (e.g., conidiomata, conidiogenous cells, conidia) were examined from hand-sectioned structures using a Nikon ECLIPSE 80i compound stereomicroscope, equipped with a Canon 600D digital camera. The measurements of photomicrographs were obtained using Tarosoft (R) Image Frame Work version 0.9.7. Images were edited with Adobe Photoshop CS6 Extended version 13.0.1 software (Adobe Systems, San Jose, California, USA).

Single-spore isolation was carried out as described by Senanayake et al.[37]. Germinated spores were aseptically transferred into fresh malt extract agar medium (MEA) prepared in 50% or 100% concentrations of sterilized natural seawater[38]. Culture plates were incubated at 25 °C for six weeks and inspected every week. Herbarium specimens are preserved at Mae Fah Luang University Herbarium (MFLU) in Chiang Rai, Thailand. All living cultures are deposited at Mae Fah Luang Culture Collection (MFLUCC). Facesoffungi and Index Fungorum numbers for new taxa were obtained[39,40].

DNA extraction, PCR amplification, sequencing

The methodologies for DNA extraction, PCR, gel electrophoresis, and sequencing were followed, as detailed in Dissanayake et al.[41]. The genomic DNA was extracted from fresh mycelium using the E.Z.N.A Fungal DNA Mini Kit- D3390-02 (Omega Bio-Tek, USA) following the guidelines of the manufacturer. DNA sequences were obtained for the internal transcribed spacer region (ITS1, 5.8S, ITS2), the small subunit (SSU), and the large subunit (LSU) of the nuclear ribosomal RNA gene. PCR thermal cycle programs for each locus region are presented in Table 1. Purification and sequencing were outsourced to the Bio Genomed Co. LTD laboratory (Biogenomed Co., Thailand). Newly generated sequences were submitted to NCBI GenBank (www.ncbi.nlm.nih.gov/genbank).

BioEdit v 7.0.9.0 program[45] was used to check the quality of the newly generated sequence chromatograms. For primary identification, contig sequences were checked with BLAST searches in NCBI. Sequences for phylogenetic analyses were downloaded from GenBank (Table 2) following Hyde et al.[25]. Each gene matrix was aligned with MAFFT version 7[46] with default parameters and manually adjusted for improvement where necessary using BioEdit v. 7.2[45]. The trimAl v1.4 software was used for the automated removal of spurious sequences or poorly aligned regions in each single gene alignment, and gappyout was selected as the automated trimming method[47]. Two separate phylogenetic analyses were conducted: Maximum Likelihood (ML) and Bayesian Inference (BI). LSU, SSU, and ITS concatenated dataset was analyzed for *Coniothyriaceae* and selected families in *Pleosporales*.

Taxon treatments

Phylogenetic analyses

In the phylogenetic analyses, maximum likelihood (ML) was executed using IQ-Tree web server (http://iqtree.cibiv.univie.ac.at/) with bootstrap support obtained from 1,000 pseudoreplicates[48, 49]. Bayesian Inference (BI) analysis was performed on the CIPRES Science Gateway portal under MrBayes on XSEDE (3.2.7a)[50]. Six simultaneous Markov chains were run for 1,000,000 generations, and trees were sampled every 1,000th generation, ending the run automatically when the standard deviation of split frequencies dropped below 0.01. The best nucleotide substitution models for each genetic marker were evaluated using jModelTest2 on XSEDE in the online CIPRES Portal (www.phylo.org/portal2)[51, 52]. The best-fit models under the AIC criterion were revealed to be GTR+I+G for ITS and LSU regions while GTR+I for SSU region. Phylogenetic trees were visualized with FigTree version 1.4.0[53] and edited in Microsoft PowerPoint (2019).

RESULTS

Phylogenetic analysis

The combined LSU, SSU, and ITS alignment was used to construct the final phylogenetic analysis (Fig. 1) of maximum likelihood (ML) and Bayesian inference (BI).

Table 1. Gene regions, primers, and PCR thermal cycle programs used in this study, with corresponding reference(s).

Genes/loci	PCR primers (forward/reverse)	PCR conditions	Reference (s)
ITS and LSU	ITS5/ITS4 and LR0R/LR5	94 °C; 2 min (95 °C; 30 s, 55 °C; 50 s, 72 °C; 90 s) × 35 thermal cycles, 72 °C; 10 min	[42–44]
SSU	NS1/NS4	95 °C; 3 min (95 °C; 30 s, 55 °C; 50 s, 72 °C; 30 s) × 35 thermal cycles, 72 °C; 10 min	[42]

Table 2. Taxa used in the phylogenetic analyses and their GenBank accession numbers. Sequences of new taxon generated in this study are in blue-bold and type strains are in black-bold.

Species	Strain/voucher number	GenBank accession numbers		
		ITS	LSU	SSU
Amarenographium ammophilae	MFLUCC 16–0296	KU848196	KU848197	KU848198
Ascochyta pisi	CBS 126.54	GU237772	EU754137	EU754038
Bipolaris microstegii	**CBS 132550**	NR_120160	NG_042690	NA
Bipolaris victoriae	**CBS 327.64**	NR_147489	NG_069233	NA
Comoclathris arrhenatheri	**MFLUCC 15–0465**	**NR_165855**	**NG_068240**	**NG_068374**
Coniothyrioides thailandica	**MFLUCC 22-0193**	**OQ023276**	**OQ023277**	**OQ025050**
Coniothyrium carteri	LG1401 MS6E	KX359604	KX359604	NA
Coniothyrium cereale	CBS 157.78	MH861123	JX681080	NA
Coniothyrium chiangmaiense	**MFLUCC 16–0891**	**KY568987**	**KY550384**	**KY550385**
Coniothyrium dolichi	CBS 124140	JF740183	GQ387611	GQ387550
Coniothyrium glycines	CBS 124455	JF740184	GQ387597	GQ387536
Coniothyrium palmarum	CBS 400.71	AY720708	EU754153	AY720712
Coniothyrium palmarum	CBS 758.73	NA	JX681085	EU754055
Coniothyrium sp.	B9-10-9	MW764153	NA	NA
Coniothyrium sp.	P16-10-4	MW764259	NA	NA
Coniothyrium telephii	CBS 188.71	JF740188	GQ387599	GQ387538
Coniothyrium telephii	CBS 856.97	JF740189	GQ387600	GQ387539
Coniothyrium telephii	UTHSC:DI16–189	LT796830	LN907332	NA
Coniothyrium triseptatum	**MFLU 19–0758**	**NR_171948**	**NG_073674**	**NA**
Curvularia heteropogonis	CBS 284.91	JN192379	JN600990	NA
Didymella azollae	A1	MT514913	MT514910	NA
Foliophoma camporesii	MFLUCC 18–1129	KY929151	KY929181	NA
Foliophoma fallens	CBS 161.78	KY929147	GU238074	GU238215
Foliophoma fallens	CBS 284.70	KY929148	GU238078	GU238218
Libertasomyces myopori	**CPC 27354**	**NR_145200**	**NG_058241**	**NA**
Libertasomyces platani	**CPC 29609**	**NR_155336**	**NG_059744**	**NA**
Libertasomyces quercus	**CBS 134.97**	**NR_155337**	**DQ377883**	**NA**
Melnikia anthoxanthii	MFLUCC 14–1010	NA	KU848204	KU848205
Neoconiothyrium hakeae	CPC 27616	KY173397	KY173490	NA
Neoconiothyrium hakeae	CPC 27620	KY173398	KY173491	NA
Neoconiothyrium multiporum	**CBS 353.65**	**NR_111617**	**JF740268**	**NA**
Neoconiothyrium multiporum	CBS 501.91	JF740186	GU238109	GU238225
Neoconiothyrium persooniae	**CBS 143175**	**NR_156386**	**NG_058509**	**NA**
Neoconiothyrium viticola	**CPC 36397**	**NR_165929**	**NG_068326**	**NA**
Neoplatysporoides aloeicola	**CPC 24435**	**NR_154230**	**NG_058160**	**NA**
Ochrocladosporium elatum	CBS 146.33	EU040233	EU040233	NA
Ochrocladosporium frigidarii	**CBS 103.81**	**NR_156512**	**NG_064123**	**NA**
Phaeosphaeria chiangraina	**MFLUCC 13–0231**	**KM434270**	**KM434280**	**KM434289**
Phaeosphaeria musae	MFLUCC 11–0133	KM434267	KM434277	KM434287
Phaeosphaeria thysanolaenicola	**MFLUCC 10–0563**	**NR_155642**	**NG_069236**	**NG_063559**
Phaeosphaeria oryzae	**CBS 110110**	NR_156557	NG_069025	NG_061080
Phaeosphaeriopsis dracaenicola	**MFLUCC 11–0157**	**NR_155644**	**NG_059532**	**KM434292**
Pleospora herbarum	MFLUCC 14-0920	KY659560	KY659563	KY659567
Querciphoma carteri	CBS 101633	JF740180	GQ387593	GQ387532
Querciphoma carteri	CBS 105.91	JF740181	GQ387594	GQ387533
Querciphoma carteri	Gv5	MT819903	NA	NA
Querciphoma carteri	UASWS2031	MN833930	NA	NA
Shiraia bambusicola	NBRC 30753	AB354987	AB354968	NA
Shiraia bambusicola	NRBC 30771	AB354990	AB354971	NA
Shiraia bambusicola	NRBC 30772	AB354991	AB354972	NA
Staurosphaeria aloes	CBS 136437	KF777142	KF777198	NA
Staurosphaeria aloes	**CPC 21572**	**NR_137821**	**NG_067283**	**NA**
Staurosphaeria aptrootii	**CBS 483.95**	**NR_155186**	**NA**	**NA**
Staurosphaeria lycii	**CPC 30998**	**KY929150**	**KY929180**	**NA**
Staurosphaeria lycii	CPC 31014	KY929151	KY929181	NA
Staurosphaeria rhamnicola	MFLUCC 17–0813	MF434200	MF434288	MF434376
Staurosphaeria rhamnicola	**MFLUCC 17–0814**	**NR_154461**	**MF434289**	**NG_063659**
Stemphylium vesicarium	CBS 191.86	MH861935	MH873624	GU238232

NA: Sequences not available in GenBank.

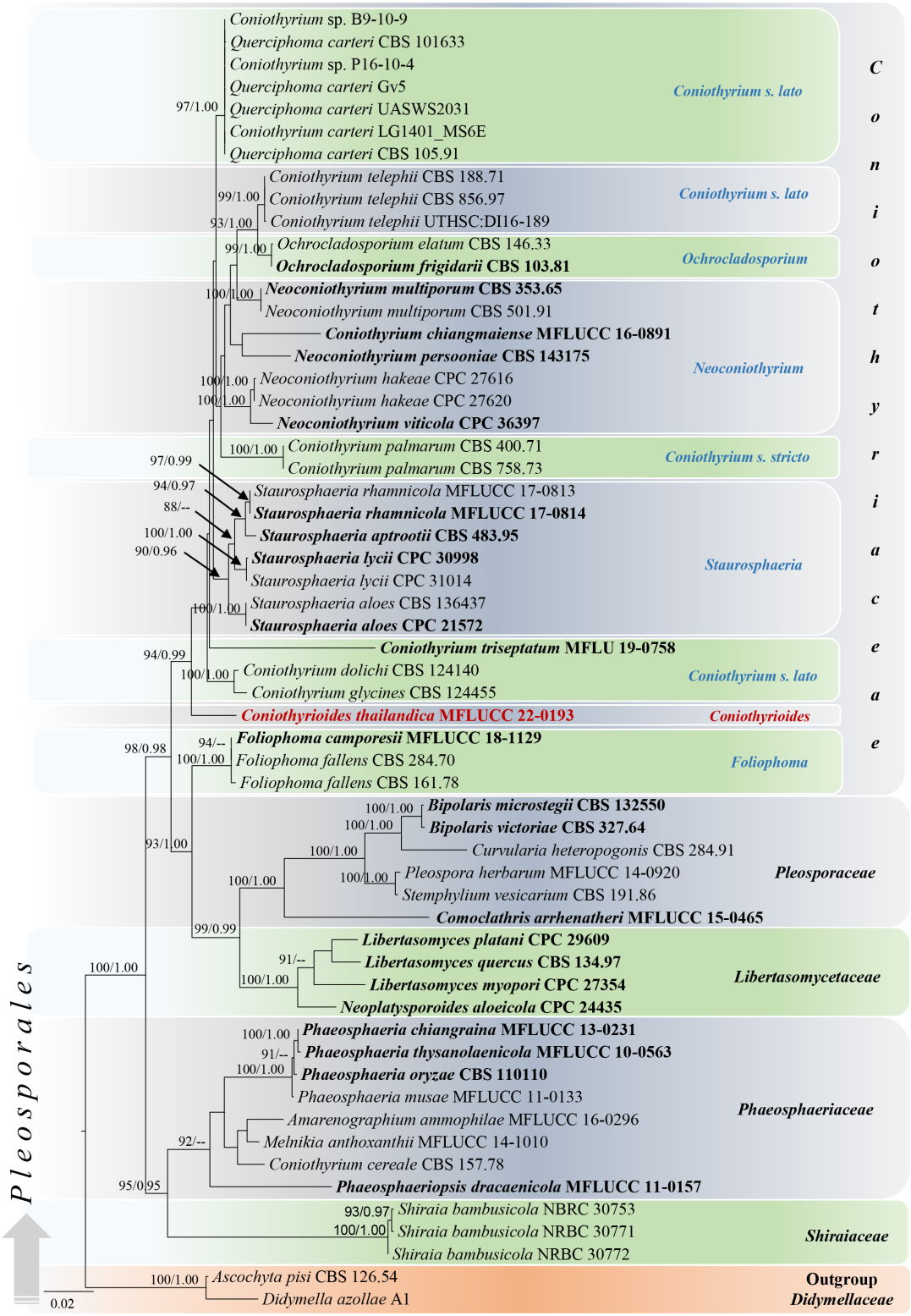

Fig. 1 Phylogram generated from maximum likelihood analysis based on combined LSU, SSU, and ITS sequenced data. Fifty-eight strains were included in the combined sequence analyses, which comprised 2251 characters with gaps (LSU = 800, SSU = 948, ITS = 503). Single gene analyses were also performed, and topology and clade stability were compared from the combined gene analyses. *Ascochyta pisi* Lib. (CBS 126.54) and *Didymella azollae* E. Shams, F. Dehghanizadeh, A. Pordel & M. Javan-Nikkhah (A1) were used as the outgroup taxa. The final ML optimization likelihood is -10163.644. The matrix included 494 distinct alignment patterns including undetermined characters. Estimated base frequencies were obtained as follows: A = 0.245, C = 0.219, G = 0.274, T= 0.262; substitution rates AC = 2.73290, AG = 3.93954, AT = 2.73290, CG = 1.0, CT = 7.93321, GT = 1.0 and the gamma distribution shape parameter α = 0.439534. Bootstrap support values for ML (first set) equal to or greater than 75% and BYPP equal to or greater than 0.95 are given above or below the nodes. The strains from the current study are in red bold and the type strains are in black bold. The scale bar represents the expected number of nucleotide substitutions per site.

Morphological analyses

Coniothyrioides Wijes., M.S. Calabon, E.B.G. Jones & K.D. Hyde, gen. nov.

Index Fungorum number: 555045; Facesoffungi number: 13901 Fig. 2

Etymology – Resembling *Coniothyrium* taxa

Saprobic on a submerged decaying wood in salt marsh ecosystems. Sexual morph: Undermined. Asexual morph: Coelomycetous. Forming conspicuous, round to irregular, black pycnidia. *Conidiomata* semi-immersed, erumpent through the host substrate, globose to subglobose, solitary, scattered to aggregated, uni-loculate, ostiolate, covered in setae, rigid when dehydrated, black. *Setae* originated from the outermost layers of conidiomatal wall, divergent, brown, with hyaline apex, septate, smooth-walled, uniformly wide from base to apex. *Conidiomatal wall* composed of several layers, from outer to inner layers black, dark brown, pale brown to hyaline cells of *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity, doliiform to subcylindrical, smooth-walled, hyaline, enteroblastic, phialidic conidiogenesis with periclinal thickening at the apex. *Conidia* solitary, ellipsoidal to obovoid, rounded at the apex, aseptate, initially hyaline, becoming pale to dark brown at maturity, smooth-walled, sometimes finely verruculose, with smaller guttules at young and indistinct at maturity.

Type species – *Coniothyrioides thailandica*

Note – *Coniothyrioides* gen. nov. is a monotypic genus associated with decaying woody substrates in salt marsh habitats in central Thailand. This genus is characterized in having pycnidial conidiomata with the cells of *textura angularis* wall surrounded by distinct setae, doliiform to subcylindrical, hyaline conidiogenous cells, and ellipsoidal to obovoid, aseptate and hyaline to brown conidia. Based on some conidial characteristics such as aseptate, hyaline to brown conidia the genus shares similar morphologies to coniothyrium-like taxa[19], by ellipsoidal to subcylindrical conidia sharing similar

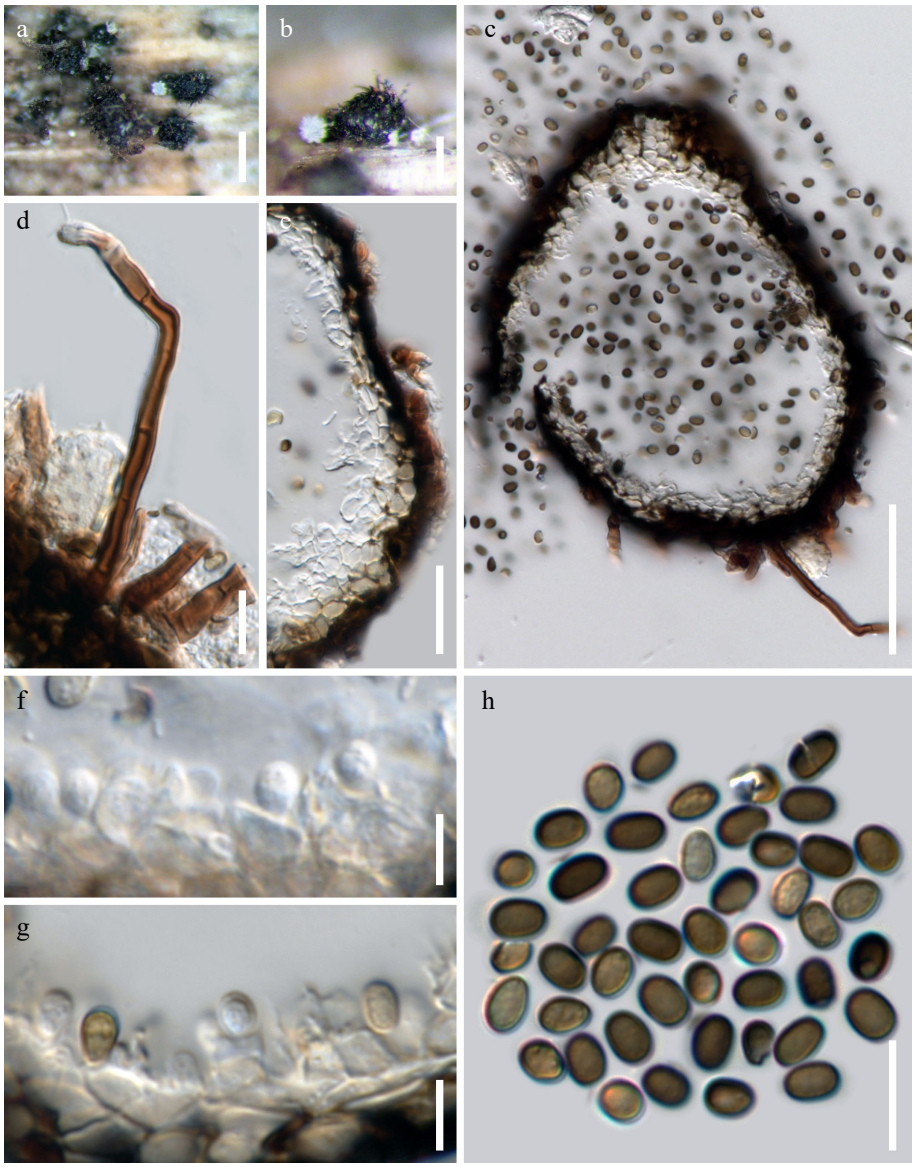

Fig. 2 *Coniothyrioides thailandica* sp. nov. (MFLU 22-0276, holotype). (a) & (b) Appearance of conidiomata on a submerged decaying woody substrate. (c) Longitudinal section of conidioma. (d) Conidiomatal wall. (e) The appearance of setae. (f) & (g) Conidiogenous cells with developing conidia. (h) Conidia. Scale bars: a = 200 μm, b = 100 μm, c = 50 μm, d = 20 μm, e, h = 10 μm, f, g = 5 μm.

characters to *Coniothyrium* and *Neoconiothyrium*[9,16,20,24]. However, other accepted genera in *Coniothyriaceae* differ from this genus in conidial morphologies: *Foliophoma* has only hyaline conidia except for *F. camporesii* D. Pem & K.D. Hyde; *Hazslinszkyomyces* has muriformly septate conidia[27]; *Ochrocladosporium* has cladosporium-like conidia[35]. Moreover, phylogenetically *Coniothyrioides* forms a distinct lineage within *Coniothyriaceae* (Fig. 1). *Coniothyrium carteri* (Gruyter & Boerema) Verkley & Gruyter (LG1401_MS6E) was the closest species based on BLAST result of ITS (94.33% similarity) and *C. telephii* (Allesch.) Verkley & Gruyter (UTHSC:DI16-189) was the closest species LSU sequence data (99.31% similarity) and sequences are lacking for SSU in the GenBank. The genus is known from its asexual morph and the sexual morphology was not observed.

In our phylogenetic analyses, *Foliophoma* species were grouped outside of *Coniothyriaceae* with closer to *Libertasomycetaceae* and *Pleosporaceae* species. *Foliophoma* was introduced by Crous & Groenewald[27] to accommodate *F. fallens* (Sacc.) Crous, in *Coniothyriaceae* based on the parsimony analyses of single LSU and ITS sequence data. *Foliophoma camporesii* was later introduced based on morphology and maximum likelihood analyses of LSU-SSU- ITS sequence data by Hyde et al.[25]. Based on morphology, *Foliophoma* species share similar characteristics to the species of *Coniothyriaceae* in having dark brown conidiomata, conidial wall with *textura angularis* cells, phialidic conidiogenesis sometimes with periclinal thickening or percurrent proliferation, and mainly ellipsoidal shaped conidia. However, the type species of the genus, *F. fallens* differs other *Coniothyriaceae* taxa in having eustromatic conidiomata. Based on this taxonomic uncertainty, more fresh collections with additional coding genes are required to clarify the accurate placement of *Foliophoma*.

Coniothyrioides thailandica Wijes., M.S. Calabon, E.B.G Jones & K.D. Hyde, sp. nov.

Index Fungorum number: 555050; Facesoffungi number: 13902

Etymology – The name reflects the county Thailand, from where the species was isolated.

Saprobic on a submerged and decaying woody substrate. Sexual morph: Undermined. Asexual morph: Coelomycetous. *Conidiomata* 150–200 μm high, 100–150 μm diam. ($\bar{x}$ = 160 × 130 μm), pycnidial, semi-immersed, erumpent through the host substrate, globose to subglobose, solitary, scattered to aggregated, uni-loculate, ostiolate, covered by setae, rigid when dehydrated, black. *Setae* 3–5 μm wide, originating from the outermost layers of conidiomatal wall, divergent, brown, with hyaline apex, septate, smooth-walled, uniformly wide from base to apex. *Conidiomatal wall* 15–20 μm wide, equally thickened, composed of several layers, outermost layers dark brown to black, towards inside pale brown to hyaline cells of *textura angularis*, surrounded by setae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* 4–5 μm long × 2.5–3.5 μm wide, lining the inner cavity, doliiform to subcylindrical, smooth-walled, hyaline, enteroblastic, phialidic conidiogenesis with periclinal thickening at the apex. *Conidia* 3–5 × 2.5–3 μm ($\bar{x}$ = 4.5 × 2.7 μm, n = 20), solitary, ellipsoidal to obovoid, rounded at the apex, aseptate, initially hyaline, becoming pale to dark brown at maturity, smooth-walled, sometimes finely verruculose, with smaller guttules at young and indistinct at maturity.

Culture characteristics – On MEA, colony circular with a filamentous margin, reaching 40–45 mm diam. in 25 d at 25 °C, light gray from above, brown from center becoming light gray in the margin below, surface rough, dry, flat, with dense mycelia, edge filiform.

Material examined – Thailand, Pranburi Province, on a submerged decaying wood, 23 March 2021, Mark S. Calabon, SPAR26 (MFLU 22-0276, holotype), ex-type living cultures, MFLUCC 22-0193.

GenBank numbers – ITS = OQ023276, LSU = OQ023277, SSU = OQ025050.

Notes – *Coniothyrioides thailandica* sp. nov. shares morphological characters with other representatives in *Coniothyriaceae* in having pycnidial, globose, uni-locular conidioma with a central ostiole, peridial wall with the cells of *textura angularis*, and doliiform to subcylindrical conidiogenous cells, phialidic conidiogenesis with a periclinal thickening at the apex. The synopsis of asexual morphological characters for the generic types of the family including their hosts and localities is presented in Table 3. Based on the presence of conidiomatal setae, our species (MFLU 22-0276) resembles *Neoconiothyrium*[24]. In addition, our species resembles *Foliophoma camporesii* (MFLU 17-1006) in having hyaline to brown and aseptate conidia but differs in having larger conidiomata (150–200 × 100–150 vs 40–47 × 40–69 μm) and the presence of setae on the wall (Table 3). Phylogenetically, our strain (MFLUCC 22-0193) formed an independent lineage within *Coniothyriaceae* with 94% ML and 0.99 BI statistical support (Fig. 1). The base pair differences between our stain and the strains represent type species of other genera in *Coniothyriaceae* are listed (Table 4). Thus, the evidence based on both morphology and phylogeny, we establish *Coniothyrioides* as a new genus in *Coniothyriaceae* with *C. thailandica* as the type species.

Members of *Coniothyriaceae* have high morphological plasticity and it is not adequate to use only morphology for identification at the genus level. *Coniothyrium dolichi* (Mohanty) Verkley & Gruyter (≡*Pyrenochaeta dolichi* Mohanty, CBS 124140) and *C. glycines* (R.B. Stewart) Verkley & Gruyter (≡*P. glycines* R.B. Stewart, CBS 124455) form a separate clade within *Coniothyriaceae* (Fig. 1). Based on the morphology observed from corn meal agar medium (CMA) by Grondona et al.[54], *C. dolichi* differs to our species by having two types of conidiogenous cells including discrete, ampulliform conidiogenous cells and integrated, cylindrical conidiogenous cells on filiform, septate conidiophores in the same conidioma, while our species has doliiform to subcylindrical conidiogenous cells and conidiophores are reduced to conidiogenous cells[54]. The pycnidial conidiomata and the ostiole of *C. dolichi* covered by dark brown, septate setae resembles our species and conidia are aseptate, ellipsoid, and hyaline with more or fewer guttules while our species has brown conidia at maturity[54]. The original description of *C. dolichi*, mentioned that conidia were greenish-yellow in mass similar to coniothyrium-like conidia, as well as to our species[55]. Also, a monodictys-like synanamorph was reported in *C. dolichi* based on its dark brown to black, dictyosporous conidia by differs from our species[17,54,56]. *Coniothyrium glycines* produces monophialidic, ampulliform, conidiogenous cells and aseptate, ellipsoidal conidia (4–8 × 1–3 μm), while our species has doliiform to subcylindrical conidiogenous cells[57,58]. The unique character of *C. glycines* is

Table 3. Synopsis of asexual morphological characters of related genera of *Coniothyriaceae*.

Species	Conidiomata (μm)	Conidiomata wall (μm)	Conidiogenous cells (μm)	Conidia (μm)	Habitat(s) and host(s)	Locality	Reference
Coniothyrioides thailandica (holotype: MFLU 22-0276)	150–200 high, × 100–150 diam., pycnidial, semi-immersed, erumpent, dark brown to black, globose to subglobose, uni-locular, ostiolate	15–20 wide, black, dark brown to hyaline cells of *textura angularis*,Brown, septate setae (3–5 μm wide,) with hyaline apex	4–5 long × 2.5–3.5 wide, hyaline, doliiform to subcylindrical, enteroblastic, phialidic conidiogenesis with periclinal thickening	3–5 × 2.5–3, ellipsoidal to obovoid, aseptate, rounded at apex, initially hyaline, becoming pale to dark brown at maturity	On decaying wood in salt marsh habitat	Thailand	This study
Coniothyriumpalmarum (CBS 400-71)	Immersed, dark brown, globose, pale to uni-locular	brown, thick-walled cells of *textura angularis*	hyaline, phialidic conidiogenesis, doliiform to cylindrical	Subcylindrical, spherical, ellipsoid or broadly clavate, 0(–1)-septate, apex obtuse, brown, base truncate, sometimes minute marginal frill	On *Chamaerops humilis* (*Arecaceae*)	Italy	[16]PP, [20]GN
Foliophoma fallens (holotype: CBS 284.70)	120–250 wide, eustromatic, globose, uni-multi locular, 1–3 ostiolate	3–6 layers,brown *textura angularis*	5–7 × 4–5, hyaline, phialidic conidiogenesis with thickening or proliferation at apex, dolliform to subcylindrical, periclinal	(5–)5.5–6(–7) × (3–)4(–5), broadly ellipsoidal, aseptate, hyaline, guttulate or granular, apex obtuse, base truncate to bluntly rounded	Leaf spot on *Nerium oleander* (*Apocynaceae*)	Italy	[27]
**Foliophoma camporesii* (holotype: MFLU 17-1006)	40–47 × 40–69, pycnidial, immersed to semi-immersed, globose to subglobose, ellipsoidal or irregular, carbonaceous	15–40, 1–2-layered of cells of *textura angularis*	2–4 × 2–3, hyaline, globose to short cylindrical, phialidic conidiogenesis with periclinal thickening or percurrent proliferation at apex	2–6 × 3–5, ovoid to ellipsoidal, aseptate, hyaline when immature, brown at maturity	On dead stems of *Maclura pomifera* (*Moraceae*)	Italy	[25]
Hazslinszkyomyces aloes (≡*Camarosporium aloes*: ex-type - CPS 21572)	250 diam, pycnidial, erumpent, brown, globose, central ostiolate	3–6 layers of brown *textura angularis*	5–10 × 4–5, hyaline, ampulliform to doliiform, apex with several inconspicuous percurrent proliferation,	(9–)11–13(–14) × (4–)6–7(–8), ellipsoid, initially hyaline, aseptate, becoming pale brown, subcylindricalto clavate or obovoid with 3 transverse eusepta, constricted at median septum or not, apex obtuse, base bluntly rounded to truncate	Dead bark of *Aloe dichotoma* (*Xanthorrhoeaceae*)	South Africa	[27]
Neoconiothyrium persooniae (ex-type CPC 32021 = CBS 143175)	100–200 diam, superficial, ellipsoid to obpyriform, 1–2 papillate ostioles, 10–15 diam, with or without setae	3–6 layers, hyaline *textura angularis*	5–8 × 4–5, hyaline, doliiform to ampulliform, phialidic, with periclinal thickening or percurrent proliferation	(5–)6–7(–8) × 3(–4), ellipsoid to subclavate, aseptate, initially hyaline medium brown, becoming cylindrical and at times 1-septate, apex subobtuse, base bluntly rounded	On leaves of *Persoonia laurina* subsp. *laurina* (*Proteaceae*)	Australia	[24]
Ochrocladosporium elatum (CBS 146.33)	–	–	Integrated as lateral peg-like loci on hyphalcells, or erect, subcylindrical, up to 25 μm long, 2.5–4 μm wide,with 1–3 terminal loci, occasionally lateral, 1–1.5 μm wide	Ramoconidia, 10–40 × 3–5, subcylindrical to ellipsoid, hyaline to pale brown, 0(–1)-septate, giving rise to branchedchains of conidia that are subcylindrical to ellipsoid, aseptate, (7–)8–10(–14) × (3–)4(–4.5), olivaceous brown	Wood pulp	Sweden	[35]

'–' observed morphologies on cultures, therefore conidiomata and wall characters are not recorded. '*' species which is not represent a generic type. [GN] - based on the generic description. [PP] - based on the photographic plate provided.

Table 4. The base pair comparisons of our strain (MFLUCC 22-0193) with the strains representing type species of other genera in *Coniothyriaceae*.

Species	Strain	LSU	SSU	ITS
Coniothyrium palmarum	CBS 400-71	14/800 (1.75%)	3/948 (0.3%)	69/487 (14.10%)
Foliophoma fallens	CBS 284.70	8/800 (1%)	2/948 (0.2%)	66/497 (13.27%)
Hazslinszkyomyces aloes	CPC:21572	6/800 (0.75%)	–	52/497 (10.46%)
Neoconiothyrium persooniae	CBS:143175	20/800 (2.5%)	–	49/497 (9.85%)
Ochrocladosporium elatum	CBS 146.33	13/800 (1.62%)	–	53/497 (10.66%)

well-defined, dark brown to black, melanized sclerotia covered with setae which differs from our species and other *Coniothyrium* taxa. Based on the multi-gene phylogeny provided by de Gruyter et al.[17] and the results of our study, the placements of these two species were confirmed in *Coniothyriaceae*. Also, *Coniothyrium triseptatum* Dayar., Thyagaraja & K.D. Hyde (MFLU 19-0758) creates a separate lineage in *Coniothyriaceae* (Fig. 1) and only sexual morph was reported for this fungus. Therefore, we could not compare the morphology of *C. triseptatum* with our species[31].

DISCUSSION

In this study, we introduced the novel genus *Coniothyrioides* in *Coniothyriaceae*, with *C. thailandica* as the type species, following the guidelines and major criteria for defining generic and species boundaries in *Dothideomycetes* by Chethana et al.[59] and Pem et al.[60]. The coelomycetous asexual morph of *Coniothyrioides* was associated with the decaying and submerged wood in the salt marsh habitats. Traditionally, morphology is used to delimit coelomycetes by considering the characteristics of conidiomata, conidiophores, conidiogenesis, and conidia including host associations[20,32,61]. However, accurate taxonomy of most coniothyrium-like species is challenging because of their simplicity, plasticity, and morphological variations[19]. In our study, genera in *Coniothyriaceae* differ in some conidial morphologies. For instance, *Coniothyrium* is characterized by aseptate to 1-septate, ellipsoidal to clavate or cylindrical, brown conidia[9,17,62], *Foliophoma* with aseptate, ovoid ellipsoidal, only hyaline or hyaline-brown conidia, and *Hazslinszkyomyces* ellipsoidal to obovoid, transversely and muriformly septate, uniformly brown conidia[27]. *Neoconiothyrium* species have aseptate or 1-septate, ellipsoid to subclavate or subcylindrical, hyaline to medium brown conidia[24] while *Ochrocladosporium* species have cladosporium-like pale brown, aseptate or 1-septate conidia that occurring in branched chains[35]. *Coniothyrioides thailandica* is characterized by aseptate, ellipsoidal to obovoid, hyaline to pale or dark brown conidia. However, the phylogenetic analyses in this study reveal these morphological differences are not strong enough for generic delimitation of the family. Some characteristics of *Coniothyrioides* overlap with those of other accepted genera in the family, such as the conidiogenous cell morphology of *Coniothyrium* and *Foliophoma* which have doliiform to cylindrical or subcylindrical, hyaline, phialidic conidiogenesis with periclinal thickening and conidia show aseptate, ellipsoid-associated shapes, and hyaline to brown pigmentation (Table 3).

The number of fungi was estimated at between 2.2 to 3.8 million[63], with about 100,000-150,000 known species and fungus-like taxa[64–66]. There are 151,834 species listed in SpeciesFungorum[67].Anup-to-dateonlinedatabase(https://coelomycetes.org/) for coelomycetes is being implemented[21,32]. As coniothyrium-like taxa are frequently collected and morphologically similar, it is likely that they will remain unidentified. Therefore, it is to be expected that if molecular data are incorporated in morpho-taxonomic studies of these groups, will help identify many more novel taxa. This has occurred in other genera, which are plant pathogens and ecologically more important. According to Bhunjun et al.[65] *Coniothyrium* is one of the most speciose genera listed in Species Fungorum in 2021 and studies of coniothyrium-like taxa may yield more novel species. A few records of *Coniothyriaceae* taxa have been identified in salt marsh ecosystems, such as *Coniothyrium obiones* Jaap (India and Portugal) and as unidentified *Coniothyrium* species (USA)[2]. However, Wanasinghe et al.[29] referred the placement of *C. obiones* in *Neocamarosporiaceae* based on multi-gene phylogeny. In marine habitats, *C. cerealis* E. Müll. was isolated as an alga-derived fungus in the Baltic Sea by Elsebai et al.[68, 69].

In this study, we discussed the morphology and multi-gene phylogenetic analyses results of our new collection to verify its identity and phylogenetic placement in *Coniothyriaceae*. Based on ecological and geographical data on salt marsh fungi, we noted lack records of *Coniothyriaceae* worldwide (see Calabon et al.[2]). Thus, we propose that additional collections be conducted in order to identify other *Coniothyriaceae* taxa and improve our understanding of fungal diversity in salt marsh ecosystems, a topic that is currently understudied.

ACKNOWLEDGMENTS

S.N. Wijesinghe would like to thank Mae Fah Luang University on behalf of the Graduate Studies Support Grant (Grant No. Oh 7702(6)/125) for financial support and Mushroom Research Foundation (MRF), Thailand. Further, S.N. Wijesinghe would like to thank Dr. Udeni Jayalal, Dr. Samantha C. Karunarathna, and Dr. Gothamie Weerakoon for their precious advice during this study. M.S. Calabon is grateful to the Department of Science and Technology – Science Education Institute (DOST-SEI). K.D. Hyde would like to thank the National Research Council of Thailand (NRCT) grant 'Total fungal diversity in a given forest area with implications towards species numbers, chemical diversity and biotechnology' (Grant No. N42A650547).

Conflict of interest

Kevin David Hyde is the Editorial Board member of Journal *Studies in Fungi*. He is blinded from reviewing or making decisions on the manuscript. The article was subject to the journal's standard procedures, with peer-review handled independently of Kevin David Hyde and his research groups.

Dates

Received 14 December 2022; Accepted 15 January 2023; Published online 27 February 2023

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