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ORIGINAL ARTICLE

Phaeonawawia, a novel chaetosphaeriaceous anamorph from submerged wood in Malaysia

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Abstract

The anamorphic taxon *Phaeonawawia diplocladielloidea* gen. et sp. nov. is described and illustrated from wood submerged in a freshwater stream in Malaysia. The fungus is generically distinct in the brown, short-stalked, bulbose or urceolate conidiogenous cells with a terminal pore rimmed with a flared collarette, producing large, dematiaceous, versicoloured, multi-euseptate, tetrahedral, or obpyramidal stauroconidia which bear hyaline filiform appendages at the end of the arms and enclosed by a thick, hyaline sheath. The new fungus is compared with some similar anamorphic fungi. Phylogenetic analyses by maximum likelihood and Bayesian inference approaches using the nuc rDNA ITS1-5.8S-ITS2 (ITS barcode) support the placement of this new fungus in the Chaetosphaeriaceae. The various anamorphic forms of chaetosphaeriaceous fungi are briefly discussed.

Keywords Dematiaceous hyphomycetes · Freshwater fungi · Phialoconidia · Phylogenetics · Staurospores

Introduction

Malaysia, with its warm and moist tropical climate, has been a country with a high diversity of fungi. Many new fungal taxa had been discovered and described during the past decades (Nawawi 1985a, b, 1987; Kuthubutheen and Nawawi 1991, 1994; Lee et al. 2012; Goh et al. 2013, 2014a, 2014b, 2015). During a survey of microfungi occurring on plant litter submerged in a stream in Malaysia, we found a unique hyphomycete producing large, dematiaceous, multi-euseptate, tetrahedral stauroconidia with hyaline filiform appendages at the end of the arms, and enclosed by a thick, hyaline sheath. Superficially the conidia resemble those of *Diplocladiella* G. Arnaud (Nawawi 1987; Cazau et al. 1993; Lee et al. 1998), but they are produced from brown, short-stalked, bulbose, doliiform to urceolate conidiogenous cells with a terminal pore rimmed with a flared collarette. A literature search has revealed that this fungus on submerged wood has not been previously described (Bhat and Sutton 1985; Goh and Hyde 1996; Goh and Tsui 2003; Seifert et al. 2011; Liu et al. 2016; Lin et al. 2019). As it cannot be suitably placed in any of the known genera of asexual fungi (Seifert et al. 2011), it is described and illustrated in this paper as a new genus. Morphological observation of this unique fungus was supplemented with scanning electron microscopy. The genus is compared with morphologically similar fungi: *Adautomilanezia*, *Anacacumisporium*, *Bahusutrabeeja*, *Conioscyphopsis*, *Craspedodidymum*, *Cyphellophora*, *Diplocladiella*, *Jerainum*, *Nawawia*, *Neonawawia*, *Obeliospora*, *Phialosporostilbe*, *Polybulbophiale*, *Polystratorictus*, *Pyrigemmula*, and *Triposporium*. We have successfully grown this new fungus in pure culture by single-spore isolation technique. DNA extraction was from these pure cultures and used for molecular studies. Phylogenetic relationship of this new genus was inferred by comparing the nuc rDNA ITS1-5.8S-ITS2 (ITS barcode).

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Materials and methods

Sample collection, mycological procedures, and molecular procedures

Plant materials including wood were collected in plastic bags and returned to the laboratory where they were incubated at

room temperature under a humid condition in sterile plastic boxes. Materials were examined periodically for the presence of fungal fruiting structures and species were identified primarily based on morphology. Single-spore isolations were made according to the method described in Goh (1999), and the fungi were grown on potato dextrose agar (PDA) slants and plates at 20 °C. Pure cultures from single spores were used for molecular studies. DNA extraction, PCR, and sequencing procedures were similar to the methodology described in Goh et al. (2015). The original specimen of the present fungus previously conserved at the herbarium of the Centre for Biodiversity Research, Faculty of Science, Universiti Tunku Abdul Rahman (UTAR, Perak campus), Kampar, Malaysia, has been recently transferred to Taiwan. Currently, the holotype of this taxon is deposited in the Herbarium (Herbarium Code: TNM) at the National Museum of Natural Science (NMNS), Taichung, Taiwan, whereas an isotype is deposited at the National Chiayi University (NCYU), Taiwan. The ultrastructural features of the present fungus were studied and photographed under the scanning electron microscope (FESEM, Model: JSM-6701F, JEOL, Japan) at UTAR. Air-dried fungal material was directly mounted and sputtered with gold for 60 s for scanning electron microscopy.

Phylogenetic analysis

Sequence data from the ITS region were used to infer phylogenetic placement of the new taxon. DNA sequences were first verified and subjected to BLAST searches to ease phylogenetic taxon sampling. DNA sequences for representative taxa within the Chaetosphaeriaceae retrieved from GenBank were included in our dataset with reference to recent publications (Crous et al. 2012; Liu et al. 2016; Lin et al. 2019). The analysis involved 83 ITS sequences of fungi (Table 1), with *Gelasinospora tetrasperma* CBS 178.33 (Sordariaceae) being the outgroup taxon. MAFFT was used for DNA alignment (Katoh and Standley 2013). Poorly aligned positions of DNA alignment were manually modified where necessary. There were in total 610 bp in the final dataset including gaps.

The sequences were analysed using MEGA 7 (Kumar et al. 2016). The evolutionary history was inferred using the maximum likelihood and Bayesian inference in RAxML v8.2.4 and MrBayes v3.2.6 under UBUNTU 19.10 (64 bit) operating system (Ronquist and Huelsenbeck 2003; Stamatakis 2014). For the RAxML, substitution model was GTR + G. Random seed for rapid bootstrapping and tree inferences were 5566. Analyses were repeated based on 1000 bootstrapped data sets. MrBayes was run for 1,000,000 generations under GTR + G substitution model, with trees sampled every 100 generations. The first 25% of sampled trees were discarded (relburnin).

Results

Taxonomy

Phaeonawawia Goh, gen. nov.

MycoBank: MB 836839

Type species: *Phaeonawawia diplocladielloidea* Goh, J.H. Ou & C.H. Kuo

Etymology: From Greek, *phaeo-* (dark grey or dark-coloured), and the generic name *Nawawia* Marvanová, denotes that this fungus is similar to *Nawawia* but producing dematiaceous conidia.

Conidial fungi, hyphomycetous. Colonies on natural substratum effuse, brown. Mycelium partly superficial, partly immersed in the substratum, consisting of smooth, brown branched, septate hyphae. Conidiomata none. Setae and hyphopodia absent. Conidiophores absent or rudimentary in the form of a basal stalk under the single conidiogenous cell. Conidiogenous cells phialidic, discrete or integrated, sessile or incorporated terminally in the basal stalk, bulbose, doliiform or ampulliform, with a distinct, rimmed opening at the apex. Conidia enteroblastic, exogenous, solitary, dry, enclosed by a thick hyaline sheath, tetrahedral, staurosporous, arms multieuseptate, dematiaceous, setulate. Conidial secession schizolytic. Phylogenetic position: Chaetosphaeriaceae.

Note: There are several hyphomycete genera which are similar to *Phaeonawawia*, morphological characters of which are compared in Table 2. These include genera that have a similar type of conidiogenesis, producing enteroblastic conidia from discrete bulbose or swollen phialides, such as *Adautomilanezia*, *Obeliospora*, *Conioscyphopsis*, *Cyphellophora*, *Polybulbophiale*, *Polystratorictus*, and *Pyrigemmula*. Examples of genera producing conidia from mononematous conidiophores with integrated phialidic conidiogenous cells include *Anacacumisporium*, *Bahusutrabeeja*, and *Craspedodidymum.* Genera that have setulate conidia include *Nawawia*, *Neonawawia*, *Obeliospora*, and *Phialosporostilbe*, whereas those producing dematiaceous staurospores are *Diplocladiella*, *Jerainum*, and *Triposporium*. To date, *Phaeonawawia* is the only known genus in the Chaetosphaeriaceae producing dry, multiseptate, dematiaceous, versicoloured stauroconidia from discrete bulbose phialides.

Phaeonawawia diplocladielloidea Goh, J.H. Ou & C.H. Kuo, sp. nov. (Figs. 1, 2, 3, 4, and 5)

MycoBank: MB 837328

Etymology: From Greek, *−oides* (resembling), and the generic name *Diplocladiella* G. Arnaud, the epithet "*diplocladielloidea*" denotes that this fungus is similar to *Diplocladiella* in producing dematiaceous stauroconidia.

Colonies on natural substratum effuse, brown, somewhat glistening. Mycelium partly superficial, partly immersed in the substratum, consisting of smooth, brown branched, septate

Table 1 Sources of sequences and spore groups of taxa used in present phylogenetic analysis

Fungal taxon	Culture code	GenBank ITS	Known anamorph (anamorphic group)	Saccardoan spore type	References
Adautomilanezia caesalpiniae	CC-LAMIC 102/12	KX821777	*Adautomilanezia caesalpiniae*	Phaeo-phragmo	Crous et al. 2016
Anacacumisporium appendiculatum	HMAS 245593	KT001555	*Anacacumisporium appendiculatum*	Phaeo-phragmo	Ma et al. 2016
Brunneodinemasporium brasiliense	CBS 112007	JQ889272	(Acervular coelomycetes)	Hyalo-setulo-amero	Crous et al. 2012, Lu et al. 2016
Brunneodinemasporium jonesii	GZCC 16-0050	KY026058	(Acervular coelomycetes)	Hyalo-setulo-amero	Lu et al. 2016
Chaetosphaeria abietis	CBS 427.83	AF178541	*Cylindrotrichum zignoellae* (Kylindria group)	Hyalo-didymo	Réblová and Winka 2000
Chaetosphaeria acutata	CBS 101312	AF178553	*Cylindrotrichum* sp. (Kylindria group)	Hyalo-didymo	Réblová and Winka 2000
Chaetosphaeria albida	PDD 92537	NR119666	(Anamorph unknown)	-	Atkinson et al. 2007
Chaetosphaeria bombycina	PDD 92538	NR119667	(Anamorph unknown)	-	Atkinson et al. 2007
Chaetosphaeria callimorpha	CBS 525.88	AF178555	*Dictyochaeta sp*. (Gongromeriza group)	Hyalo-setulo-amero	Réblová and Winka 2000
Chaetosphaeria catenulata	MFLU 18-1620	MK828637	*Catenularia* sp.	Phaeo-amero	Luo et al. 2019
Chaetosphaeria chloroconia	FMR 11940	KY853435	*Gonytrichum chlamydosporium* (Chloridium group)	Subhyalo-amero	Hernández-Restrepo et al. 2017
Chaetosphaeria ciliata	CBS 122132	EU488737	*Menispora ciliata* (Menispora group)	Hyalo-setulo-amero	Réblová and Seifert 2008
Chaetosphaeria cubensis	MFLU 18-1621	MK828638	*Catenularia* sp.	Phaeo-amero	Luo et al. 2019
Chaetosphaeria decastyla	FMR 11339	HF677176	(Kylindria group)	Phaeo-phragmo	Fernández et al. 2006
Chaetosphaeria dilabens	CBS 712.88	AF178557	*Chloridium* sp. (Gongromeriza group)	Hyalo-(or phaeo-)-amero	Réblová and Winka 2000
Chaetosphaeria ellisii	SMH2758	AY906940	*Craspedodidymum* sp.	Phaeo-amero	Huhndorf and Fernández 2005
Chaetosphaeria fennica	CBS 101641	AF178562	*Chloridium* sp. (Kylindria group)	Subhyalo-amero	Réblová and Winka 2000
Chaetosphaeria fusiformis	CBS 101429	AF178554	*Chloridium cylindrosporum* (Kylindria group)	Hyalo-phragmo	Réblová and Winka 2000
Chaetosphaeria hebetiseta	SMH2729	AY906955	*Chloridium* sp. (Gongromeriza group)	Hyalo-amero	Huhndorf and Fernández 2005
Chaetosphaeria inaequalis	CBS 102338	AF178564	*Gonytrichum caesium* (Chloridium group)	Subhyalo-amero	Réblová and Winka 2000
Chaetosphaeria innumera	MR 1175	AF178551	*Chloridium botryoideum* (Gongromeriza group)	Hyalo-amero	Réblová and Winka 2000
Chaetosphaeria lapaziana	SMH3043	AY906947	*Craspedodidymum* sp.	Phaeo-amero	Huhndorf and Fernández 2005
Chaetosphaeria lateriphiala	ANM 1070	JN673039	*Zanclospora* sp.	Hyalo-amero-scoleco	Raja et al. 2011
Chaetosphaeria lentomita	MR 1265	AF178548	*Chloridium pachytrachelum* (Gongromeriza group)	Hyalo-amero	Réblová and Winka 2000
Chaetosphaeria myriocarpa	M35	JF340253	*Chloridium clavaeforme* (Gongromeriza group)	Hyalo-amero	Arhipova et al. 2012
Chaetosphaeria myriocarpa	CBS 264.76	AF178552	*Chloridium clavaeforme* (Gongromeriza group)	Hyalo-amero	Réblová and Winka 2000
Chaetosphaeria ovoidea	FMR 12089	HF678528	*Menispora glauca* (Menispora group)	Hyalo-setulo-phragmo	Lin et al. 2019
Chaetosphaeria panamensis	SMH3596	AY906948	*Craspedodidymum* sp.	Phaeo-amero	Huhndorf and Fernández 2005
Chaetosphaeria pulviscula	MR 1120	AF178543	*Menispora caesia* (Menispora group)	Hyalo-setulo-phragmo	Réblová and Winka 2000
Chaetosphaeria pygmaea	MR 1365	AF178545	*Phialophora phaeophora* (Gongromeriza group)	Phaeo-amero	Réblová and Winka 2000
Chaetosphaeria raciborskii	PDD 92561	EU037895	(anamorph unknown)	-	Atkinson et al. 2007
Chaetosphaeria raciborskii	SMH2017	AY906949	*Craspedodidymum* sp.	Phaeo-amero	Huhndorf and Fernández 2005
Chaetosphaeria raciborskii	SMH2036	AY906950	*Craspedodidymum* sp.	Phaeo-amero	Huhndorf and Fernández 2005

Table 1 (continued)

Fungal taxon	Culture code	GenBank ITS	Known anamorph (anamorphic group)	Saccardoan spore type	References
Chaetosphaeria raciborskii	SMH2132	AY906951	*Craspedodidymum* sp.	Phaeo-amero	Huhndorf and Fernández 2005
Chaetosphaeria raciborskii	SMH3014	AY906952	*Craspedodidymum* sp.	Phaeo-amero	Huhndorf and Fernández 2005
Chaetosphaeria raciborskii	SMH3119	AY906953	*Craspedodidymum* sp.	Phaeo-amero	Huhndorf and Fernández 2005
Chaetosphaeria rubricunda	SMH2881	AY906954	*Craspedodidymum* sp.	Phaeo-amero	Huhndorf and Fernández 2005
Chaetosphaeria tortuosa	CBS 214.56	AF178558	*Menispora tortuosa* (Menispora group)	Hyalo-setulo-amero	Réblová and Winka 2000
Chaetosphaeria vermicularioides	NRRL 66001	KM056319	*Chloridium virescens* (Chloridium group)	Hyalo-amero	Gams and Holubová-Jechová 1976
Chloridium sp.	SR4	KP689244	*Chloridium* sp. (Chloridium group)	Hyalo-amero	Gams and Holubová-Jechová 1976
Chloridium virescens var. *chlamydosporum*	ICMP 15193	EF029220	(Chloridium group)	Hyalo-amero	Gams and Holubová-Jechová 1976
Codinaeopsis gonytrichoides	CBS 593.93	AF178556	*Dictyochaeta*-like (Menispora group)	Hyalo-setulo-amero	Réblová and Winka 2000
Cryptophiale udagawae	MFLU 18-1497	MH758198	*Cryptophiale udagawae*	Hyalo-scoleco-amero	Yang et al. 2018
Cryptophialoidea fasciculata	MFLU 18-1499	MH758195	*Cryptophialoidea fasciculata*	Hyalo-scoleco-didymo	Yang et al. 2018
Dictyochaeta fertilis	CBS 624.77	AF178540	*Dictyochaeta fertilis* (Menispora group)	Hyalo-setulo-amero	Réblová and Winka 2000
Dictyochaeta mimusopis	CBS 143435	MH107888	*Dictyochaeta mimusopis* (Menispora group)	Hyalo-setulo-amero	Crous et al. 2018
Dictyochaeta siamensis	MFLUCC 15-0614	KX609955	*Dictyochaeta siamensis* (Menispora group)	Hyalo-setulo-amero	Luo et al. 2016, Yang et al. 2016
Dictyochaeta simplex	CBS 966.69	AF178559	*Dictyochaeta simplex* (Menispora group)	Hyalo-setulo-amero	Réblová and Winka 2000
Dinemasporium decipiens	CBS 592.73	JQ889275	(Acervular coelomycetes)	Hyalo-setulo-amero	Crous et al. 2012
Dinemasporium morbidum	CBS 129.66	JQ889280	(Acervular coelomycetes)	Hyalo-setulo-amero	Crous et al. 2012
Dinemasporium nelloi	MFLU 14 C0811	KP711358	(Acervular coelomycetes)	Hyalo-setulo-amero	Liu et al. 2015
Gelasinospora tetrasperma (outgroup)	CBS 178.33	AY681178	*Chrysonilia tetrasperma* (outgroup)	N.A. (outgroup)	Cai et al. 2006
Infundibulomyces cupulata	BCC 11929	EF113976	(Cupulate coelomycetes)	Hyalo-setulo-amero	Somrithipol et al. 2008
Infundibulomyces oblongisporus	BCC 13400	EF113977	(Cupulate coelomycetes)	Hyalo-setulo-amero	Somrithipol et al. 2008
Kionochaeta castaneae	MFLU 19-0204	MN104610	*Kionochaeta castaneae*	Hyalo-amero	Lin et al. 2019
Kionochaeta microspora	MFLU 19-0206	MN104607	*Kionochaeta microspora*	Hyalo-amero	Lin et al. 2019
Menispora manitobaensis	KAS 1603	EU488738	*Menispora manitobaensis* (Menispora group)	Hyalo-setulo-amero	Réblová and Seifert 2008
Menisporopsis anisospora	CBS 109475	MH862827	*Menisporopsis anisospora*	Hyalo-setulo-amero	Lin et al. 2019
Menisporopsis breviseta	MFLU 19-0212	MN104612	*Menisporopsis breviseta*	Hyalo-setulo-amero	Lin et al. 2019
Menisporopsis theobromae	MFLUCC 15-0055	KX609957	*Menisporopsis theobromae*	Hyalo-setulo-amero	Liu et al. 2016
Nawawia filiformis	MFLU 18-1500	MH758196	*Nawawia filiformis*	Hyalo-setulo-amero	Yang et al. 2018
Neonawawia malaysiana	CBS 125544	GU229886	*Neonawawia malaysiana*	Hyalo-setulo-amero	Crous et al. 2009, Yang et al. 2018
Neopseudolachnella magnispora	HHUF 29977	AB934066	(Acervular coelomycetes)	Hyalo-setulo-phragmo	Hashimoto et al. 2015
Neopseudolachnella uniseptata	HHUF 29728	AB934067	(Acervular coelomycetes)	Hyalo-setulo-phragmo	Hashimoto et al. 2015
Phaeonawawia diplocladielloidea$^{\Phi}$	**UTAR-G1-1**	**MT946684**	***Phaeonawawia diplocladielloidea***	**Phaeo-setulo-stauro**	**This paper**

Table 1 (continued)

Fungal taxon	Culture code	GenBank ITS	Known anamorph (anamorphic group)	Saccardoan spore type	References
Phialosporostilbe scutiformis	MFLU 18-1502	MH758194	*Phialosporostilbe scutiformis*	Hyalo-setulo-amero	Yang et al. 2018
Pseudodinemasporium fabiforme	HHUF 29716	AB934068	(Acervular coelomycetes)	Hyalo-setulo-amero	Hashimoto et al. 2015
Pseudolachnella asymmetrica	HHUF 28777	AB934073	(Acervular coelomycetes)	Hyalo-setulo-phragmo	Hashimoto et al. 2015
Pseudolachnella botulispora	HHUF 29969	AB934074	(Acervular coelomycetes)	Hyalo-setulo-phragmo	Hashimoto et al. 2015
Pyrigemmula aurantiaca	CPC 18063	HM241692	*Pyrigemmula aurantiaca*	Phaeo-phragmo	Magyar et al. 2011
Pyrigemmula aurantiaca	CPC 18064	HM241693	*Pyrigemmula aurantiaca*	Phaeo-phragmo	Magyar et al. 2011
Rattania setulifera	GUFCC 15501	GU191794	*Rattania setulifera*	Hyalo-setulo-amero	Lin et al. 2019
Sporoschisma hemipsilum	MFLUCC 15-0615	KX505869	*Sporoschisma hemipsilum*	Phaeo-phragmo	Luo et al. 2016, Yang et al. 2016
Sporoschisma palauense	MFLUCC 15-0616	KX505870	*Sporoschisma palauense*	Phaeo-phragmo	Luo et al. 2016, Yang et al. 2016
Sporoschisma taitense	KUMCC 15-0241	KX455865	*Sporoschisma taitense*	Phaeo-phragmo	Luo et al. 2016
Striatosphaeria codinaeophora	MR 1230	AF178546	*Dictyochaeta* sp. (Menispora group)	Hyalo-setulo-amero	Réblová and Winka 2000
Striatosphaeria codinaeophora	monte6.2	KC928368	*Dictyochaeta* sp. (Menispora group)	Hyalo-setulo-amero	Réblová and Winka 2000
Tainosphaeria jonesii	GZCC 16-0065	KY026060	*Dictyochaeta*-like (Menispora group)	Hyalo-setulo-amero	Lu et al. 2016
Tainosphaeria siamensis	MFLUCC 15-0607	KX609956	*Dictyochaeta*-like (Menispora group)	Hyalo-setulo-amero	Lin et al. 2019
Thozetella fabacearum	MFLU 16-1021	KY212754	*Thozetella fabacearum*	Hyalo-setulo-amero	Perera et al. 2016
Thozetella havanensis	ICMP 14173	EF029184	*Thozetella havanensis*	Hyalo-setulo-amero	Paulus et al. 2004, Crous et al. 2012
Thozetella pinicola	RJ-2008	EU825197	*Thozetella pinicola*	Hyalo-setulo-amero	Jeewon et al. 2009
Zanclospora iberica	CBS 130426	KY853480	*Zanclospora iberica*	Hyalo-amero	Hernández-Restrepo et al. 2017

[Φ] The new fungus is highlighted in bold

Table 2 Comparison of hyphomycete genera similar to *Phaeonawawia*

Genus	Phylogenetic position	Setae	Conidiophores	Conidiogenous cells			
				Position	Shape/type	Collarette	Conidiogenesis
Adautomilanezia Gusmão, S.S. Silva, Fiuza, L.A. Costa & T.A.B. Santos	Chaetosphaeriaceae	Present	Absent or reduced	Discrete	Globose to subglobose with a distinct terminal pore	Absent or non-flaring	Enteroblastic
Anacacumisporium Y.R. Ma & X.G. Zhang	Chaetosphaeriaceae	Absent	Mononematous	Integrated	Cylindrical, mono- or polyphialidic	Absent or non-flaring	Enteroblastic
Bahusutrabeeja Subram. & Bhat	Chaetosphaeriaceae	Absent	Mononematous	Integrated	Cylindrical, monophialidic	Absent	Enteroblastic
Conioscyphopsis Goh & K.D. Hyde	(Unknown)	Absent	Absent	Discrete	Ampulliform with a distinct terminal pore	Flaring	Enteroblastic
Craspedodidymum Hol.-Jech.	Chaetosphaeriaceae	Absent	Mononematous	Integrated	Ampulliform with a cupulate collarette	Distinctly flaring	Enteroblastic
Cyphellophora G.A. de Vries	Chaetothyriales	Absent	Absent	Discrete	Ampulliform with a distinct terminal pore	Non-flaring	Enteroblastic
Diplocladiella G. Arnaud ex M.B. Ellis	(Unknown)	Absent	Mononematous	Integrated	Geniculate and cicatriced	Absent	Polyblastic
Jerainum Nawawi & Kuthub	(Unknown)	Absent	Mononematous	Integrated	Doliiform	Absent	Monoblastic
Nawawia Marvanová	Chaetosphaeriaceae	Absent	Mononematous	Integrated	Cylindrical, monophialidic	Non-flaring	Enteroblastic
Neonawawia J. Yang, J.K. Liu & K.D. Hyde	Chaetosphaeriaceae	Absent	Sporodochial	Integrated	Subclindrical to ampulliform	Absent or non-flaring	Enteroblastic
Obeliospora Nawawi & Kuthub	Leotiomycetes (or perhaps polyphyletic)	Present or absent	Absent or reduced	Integrated	Globose with a cupulate collarette	Distinctly flaring	Enteroblastic
***Phaeonawawia* Goh$^{\Phi}$**	**Chaetosphaeriaceae**	**Absent**	**Absent or reduced**	**Discrete**	**Doliiform or urceolate with a distinct terminal pore**	**Non-flaring or flaring**	**Enteroblastic**
Phialosporostilbe Mercado-Sierra and Mena-Portales 1985	Chaetosphaeriaceae	Present	Synnematous	Integrated	Cylindrical monophialide	Non-flaring	Enteroblastic
Polybulbophiale Goh & K.D. Hyde	(Unknown)	Absent	Reduced or mononematous	Integrated or discrete	Swollen ampulliform with a distinct terminal pore	Non-flaring	Enteroblastic
Polystratorictus Matsush. 1993	(Unknown)	Absent	Absent or reduced (monoverticillate)	Integrated or discrete	Urceolate with a distinct terminal pore	Non-flaring	Enteroblastic
Pyrigemmula D. Magyar & Shoemaker	Chaetosphaeriaceae	Absent	Absent	Discrete	Ampulliform or fusiform with a distinct terminal pore	Absent	Enteroblastic
Triposporium Corda	Helotiales (or perhaps polyphyletic)	Absent	Mononematous	Integrated	Cylindrical	Absent	Monoblastic

Table 2 (continued)

Genus	Regeneration	Conidia					References
		Shape	Pigmentation	Septation	Setulae	Texture	
Adautomilanezia Gusmão, S.S. Silva, Fiuza, L.A. Costa & T.A.B. Santos	Absent	Clavate	Dark	3-septate	Absent	Dry	Crous et al. 2016
Anacacumisporium Y.R. Ma & X.G. Zhang	Absent	Fusiform	Versicolored	3-septate	Present	Dry	Ma et al. 2016
Bahusutrabeeja Subram. & Bhat	Percurrent	Globose	Hyaline	Non-septate	Present	Slimy	Subramanian and Bhat 1977, Li et al. 2013
Conioscyphopsis Goh & K.D. Hyde	Percurrent	Ellipsoidal to ovate	Dark	Non-septate	Absent	Dry	Goh and Hyde 1998a
Craspedodidymum Hol.-Jech.	Percurrent	Ellipsoidal to subglobose	Dark	0–4-septate	Absent	Dry	Yanna et al. 2000, Pinruan et al. 2004, Ma et al. 2011
Cyphellophora G.A. de Vries	Absent	Falcate to sigmoid	Hyaline or brown	Multiseptate (phragmosporous)	Absent	Slimy	Decock et al. 2003
Diplocladiella G. Arnaud ex M.B. Ellis	Sympodial	Triangular or Y-shaped	Dark	Multiseptate (Staurosporous)	Present	Dry	Ellis 1976, Barbosa et al. 2007
Jerainum Nawawi & Kuthub	Percurrent	Triangular	Dark	Multiseptate (dictyosporous)	Present	Dry	Nawawi and Kuthubutheen 1992
Nawawia Marvanová	Percurrent	Tetrahedral	Hyaline	Non-septate	Present	Slimy	Goh et al. 2014b
Neonawawia J. Yang, J.K. Liu & K.D. Hyde	Absent or percurrent	5-lobed	Hyaline	Non-septate	Present	Slimy	Crous et al. 2009, Yang et al. 2018
Obeliospora Nawawi & Kuthub	Percurrent	Subglobose to tetrahedral	Hyaline	Non-septate	Present	Slimy	Nawawi and Kuthubutheen 1990, Cantillo-Pérez et al. 2018
***Phaeonawawia* Goh**[ϕ]	**Percurrent**	**Tetrahedral or 3–4-armed**	**Versicolored**	**Multiseptate (staurosporous)**	**Present**	**Dry**	**This paper**
Phialosporostilbe Mercado-Sierra and Mena-Portales 1985	Absent or percurrent	Tetrahedral	Hyaline	Non-septate	Present	Slimy	Mercado-Sierra and Mena-Portales 1985; Yang et al. 2018
Polybulbophiale Goh & K.D. Hyde	Percurrent	Fusoid	Hyaline	Multiseptate (phragmosporous)	Absent	Slimy	Goh and Hyde 1998b
Polystratorictus Matsush. 1993	Percurrent	Cylindrical or fusaroid	Pale brown	Multiseptate (phragmosporous)	Absent	Slimy	Matsushima 1993
Pyrigemmula D. Magyar & Shoemaker	Absent	Elongate-ellipsoidal	Dark	Distoseptate (phragmosporous)	Absent	Dry	Magyar et al. 2011
Triposporium Corda	Percurrent	3–4-armed	Dark	Multiseptate (staurosporous)	Absent	Dry	Ellis et al. 1951

[ϕ] The new fungus is highlighted in bold

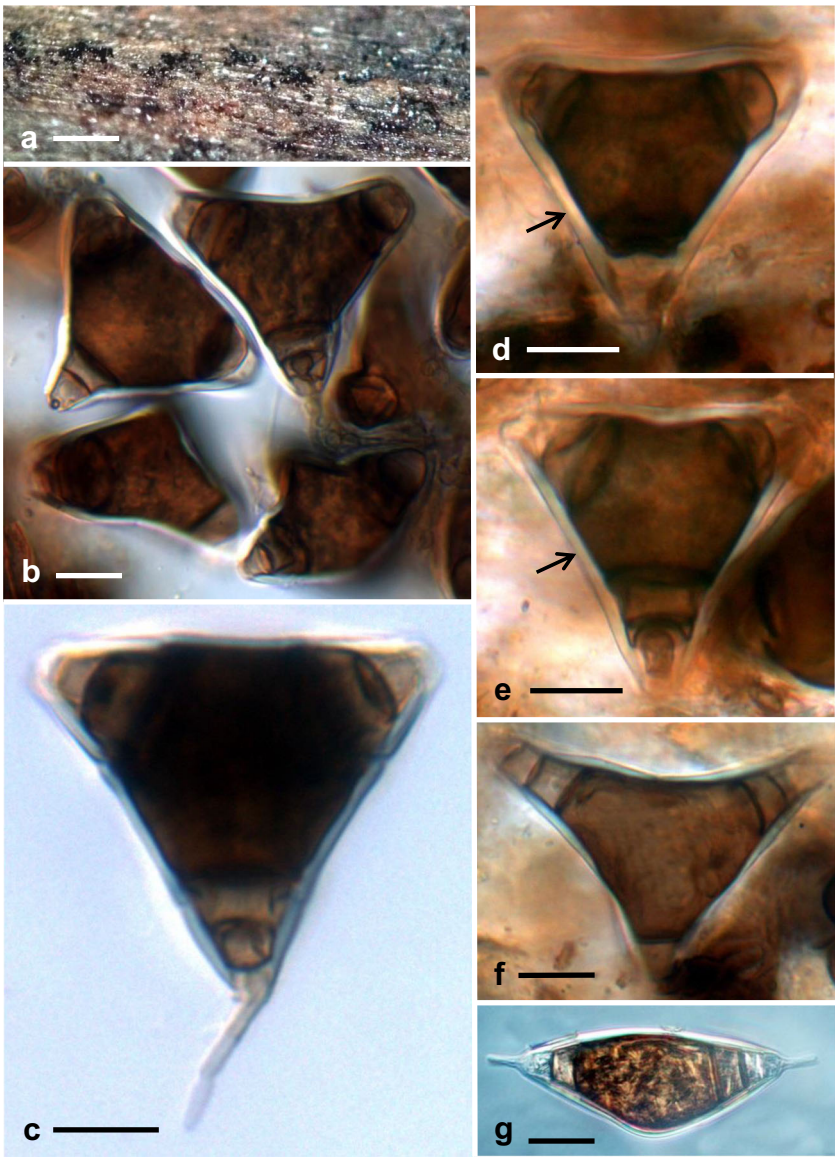


Fig. 1 *Phaeonawawia diplocladielloidea* (TNM: F0034163, holotype). **a** Colonies on the natural substratum (submerged wood). **b–f** Conidia, each with a thick hyaline sheath (arrowed in **d** and **e**). **g** An ellipsoidal conidium, bearing one hyaline appendage at each end. Scale bars: **a** = 500 μm, **b–g** = 20 μm

hyphae. Conidiophores absent or rudimentary in the form of a basal stalk (10–20 × 4–6 μm) under the single conidiogenous cell. Conidiogenous cells phialidic, discrete or integrated, sessile or incorporated terminally in the basal stalk, bulbose, doliiform or urceolate, (26.5)30–35.5 × 10–11.5 μm, with a distinct, rimmed opening (3.5–6 μm wide) at the apex, monoblastic. Sometimes regenerating percurrently. Conidia staurosporous, with 3–4 arms, broadly rounded or sometimes truncated at the tip of the arms, enteroblastic, exogenous, solitary, dry, smooth-walled, enclosed by a hyaline sheath (2–2.5 μm thick), tetrahedral to obpyramidal or occasionally ellipsoidal, mostly an equilateral triangle in surface view, with a length of (53)60–70(76.5) μm at each side and a height of 50–61 μm, multicellular, arms 2–4-euseptate, septa thick and sometimes banded, not constricted at the septa, olivaceous to medium brown and versicoloured, with the central cell darker and the arms paler, each arm bears a hyaline, aseptate, filiform appendage (25–48.5 × 2–2.5 μm); ellipsoidal conidia 75–85 × 25–30 μm, with two arms, each bearing a setula. Conidial secession schizolytic.

Teleomorph: Unknown

Conidiogenesis: Conidium ontogeny is enteroblastic, monoblastic, begins as a spherical, hyaline blown-out at the opening of the bulbose phialide. The blown-out then enlarged and becomes more or less ellipsoidal, positioning horizontally at the opening of the phialide, with its proximal side more tapering. The young conidium during the early development stages is hyaline and subsequently become more pigmented, while it continues to enlarge and finally becoming septate, setulate, and enclosed by a thick hyaline sheath. The conidium either develops into a horizontally oriented, ellipsoidal and bisetulate form, or into an obpyramidal to tetrahedral, 3–4-armed stauroform, with a hyaline setula at the end of each arm. Occasionally, the phialides may regenerate by forming

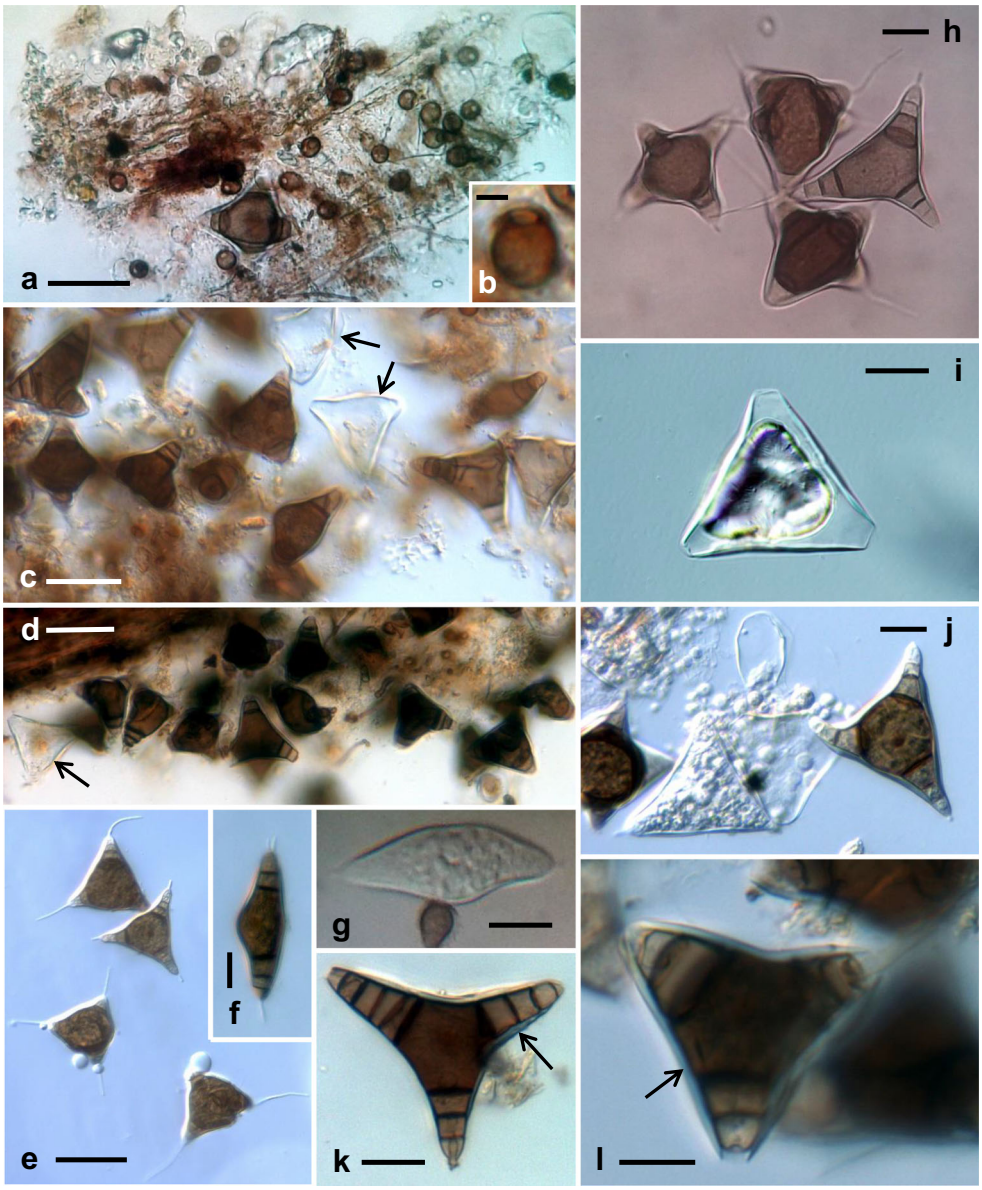


Fig. 2 *Phaeonawawia diplocladielloidea* (TNM: F0034163, holotype). **a** Squashed mount from the natural substratum showing a stauroconidium and many bulbose conidiogenous cells. **b** Close-up of a bulbose conidiogenous cell with a terminal opening. **c**, **d** Squashed mount of conidia. Arrows point to empty hyaline conidial sheaths. **e** Four conidia bearing hyaline filiform appendages, one at each arm. **f** An ellipsoidal conidium, bearing one hyaline appendage at each end. **g** A developing conidium at the opening of a bulbose conidiogenous cell. **h** Four tetrahedral or obpyramidal conidia bearing hyaline filiform appendages. **i** An empty conidial sheath. **j** Conidia beside empty conidial sheaths. **k**, **l** Conidia. Arrows point to a thick hyaline sheath enclosing the conidium. Scale bars: **a**, **c**–**e** = 50 μm, **f**–**l** = 20 μm, **b** = 5 μm

a new phialide inside or outside the old ones (Fig. 3i). The process of conidiogenesis and phialide regeneration is depicted in Fig. 5.

Specimen examined: MALAYSIA. PERAK. Menglembu, Bukit Kledang, 4.58027–101.02528, 253 m a.s.l., on submerged wood, 9 January 2014, leg. Wai-Yip Lau and Teik-Khiang Goh, UTAR-G1, Herb. no. TNM: F0034163 (holotype), NCYU-UTAR-G1 (isotype); GenBank: ITS = MT946684

Note: *Phaeonawawia diplocladielloidea* is unique in producing dematiaceous staurospores from discrete bulbose phialides. Its conidia resemble those of *Diplocladiella* species the most, especially those of *D. alta* R. Kirschner & Chee J. Chen; *D. aquatica* O.H.K. Lee, Goh & K.D. Hyde; *D. cornitumida* F.R. Barbosa, Gusmão & R.F. Castañeda; and *D. tricladioides* Nawawi, which are Y-shaped or triangular in face view, and bear filiform appendages at the end of the conidial arms. However, these species differ in having distinct conidiophores which are geniculate, cicatriced, with integrated polyblastic sympodial conidiogenous cells (Nawawi 1985b; Lee et al. 1998; Kirschner and Chen 2004; Barbosa et al. 2007). Two other fungi also have stauroconidia which are comparable with those of *P. diplocladielloidea.* In *Jerainum triquetrum* Nawawi & Kuthub., conidia are triangular in face view, muriform, bearing a single hyaline appendage at the base and several others at the distal ends. However, the conidiogenous cells are not phialides, instead, they are holoblastic, monotretic, and percurrently extending, although they are doliiform or ellipsoidal reminiscent of phialides (Nawawi and Kuthubutheen 1992). The stauroconidia of *Triposporium elegans* Corda, also resemble those of *P. diplocladielloidea* but lack filiform appendages, and also differ in

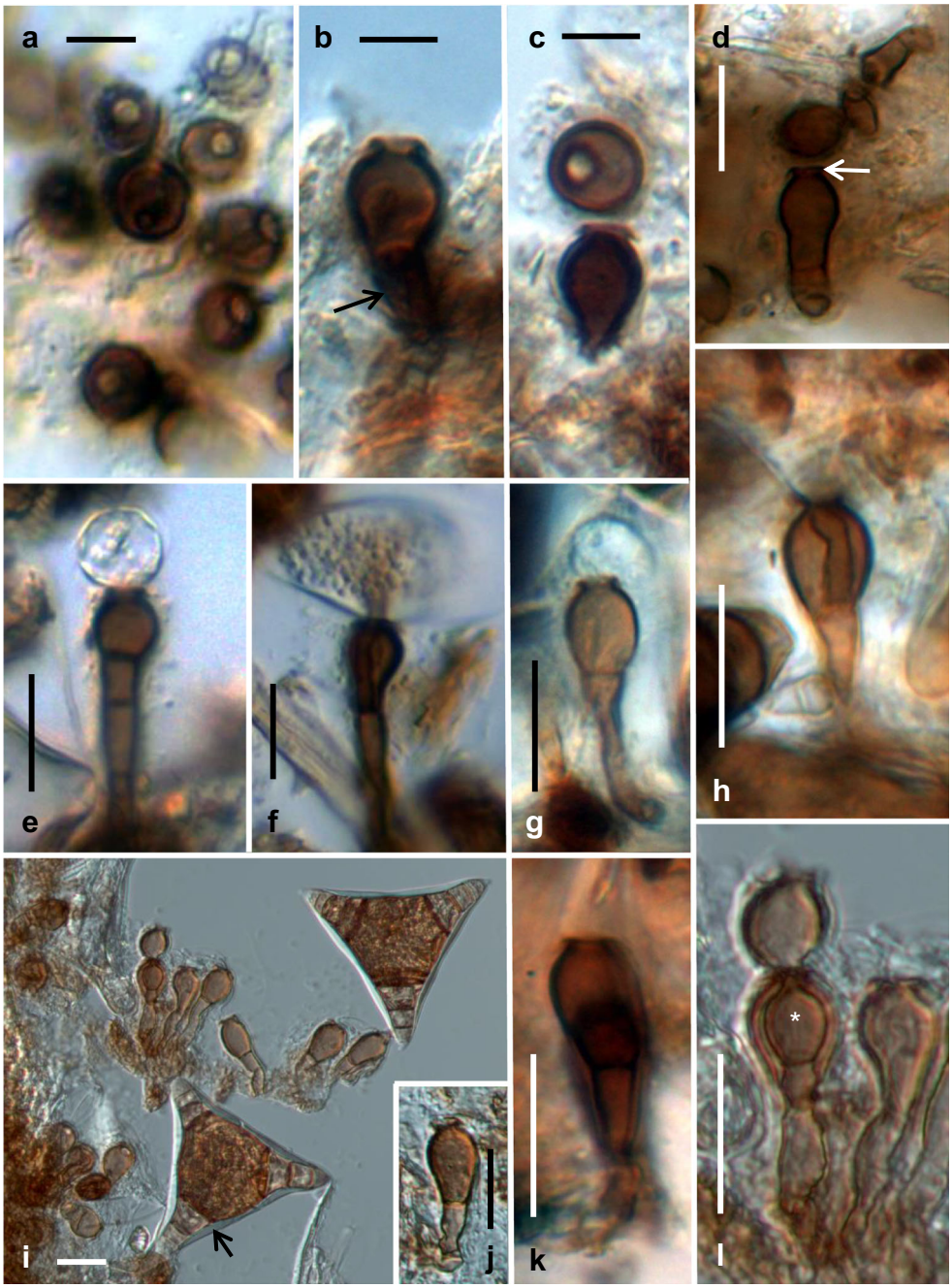


Fig. 3 *Phaeonawawia diplocladielloidea* (TNM: F0034163, holotype). **a** Several bulbose conidiogenous cells, each with a terminal opening. **b** Vertical view of a conidiogenous cell with a flared collarette at the terminal opening. Arrow points to the short basal stalk. **c** Two bulbose conidiogenous cells, one view from the top and the other from the side. **d** Vertical view of a conidiogenous cell with a short neck and flared collarette (arrowed) at the terminal opening. **e–h** Developing conidia at the opening of conidiogenous cells. **i** Two conidia and several stalked conidiogenous cells. Arrow points to the hyaline conidial sheath. **j** A stalked conidiogenous cell. **k, l** Stalked conidiogenous cells showing percurrent regenerations (highlighted by an asterisk in **l**). Scale bars: **a–c** = 10 μm, **d–l** = 20 μm

conidiogenesis, being holoblastic and non-phialidic (Corda 1837; Ellis et al. 1951). Several other hyphomycetes have discrete and/or integrated bulbose phialides similar to those of *Phaenawawia*, especially those of *Craspedodidymum* spp. (Yanna et al. 2000; Pinruan et al. 2004; Ma et al. 2011; Mel'nik et al. 2014), *Obeliospora* spp. (Nawawi and Kuthubutheen 1990; Wu and McKenzie 2003; Cantillo-Pérez et al. 2018), and *Polybulbophiale palmicola* (Goh and Hyde 1998b), but they all differ in conidial morphology. Detailed comparison of conidiogenous cells and conidial morphology is given in Table 2.

Phylogeny

Phylogenetic tree (TreeBASE TB2:S27242) inferred from aligned ITS sequences of 83 representative fungal taxa showing evolutionary relationships of *Phaeonawawia diplocladielloidea* with other fungi in the Chaetosphaeriaceae using the maximum likelihood and Bayesian inference statistical methods, with *Gelasinospora tetrasperma* CBS 178.33 (Sordariaceae) being the outgroup, is shown in Fig. 6. Molecular data revealed several branches and small clusters of taxa (designated alphabetically from A1

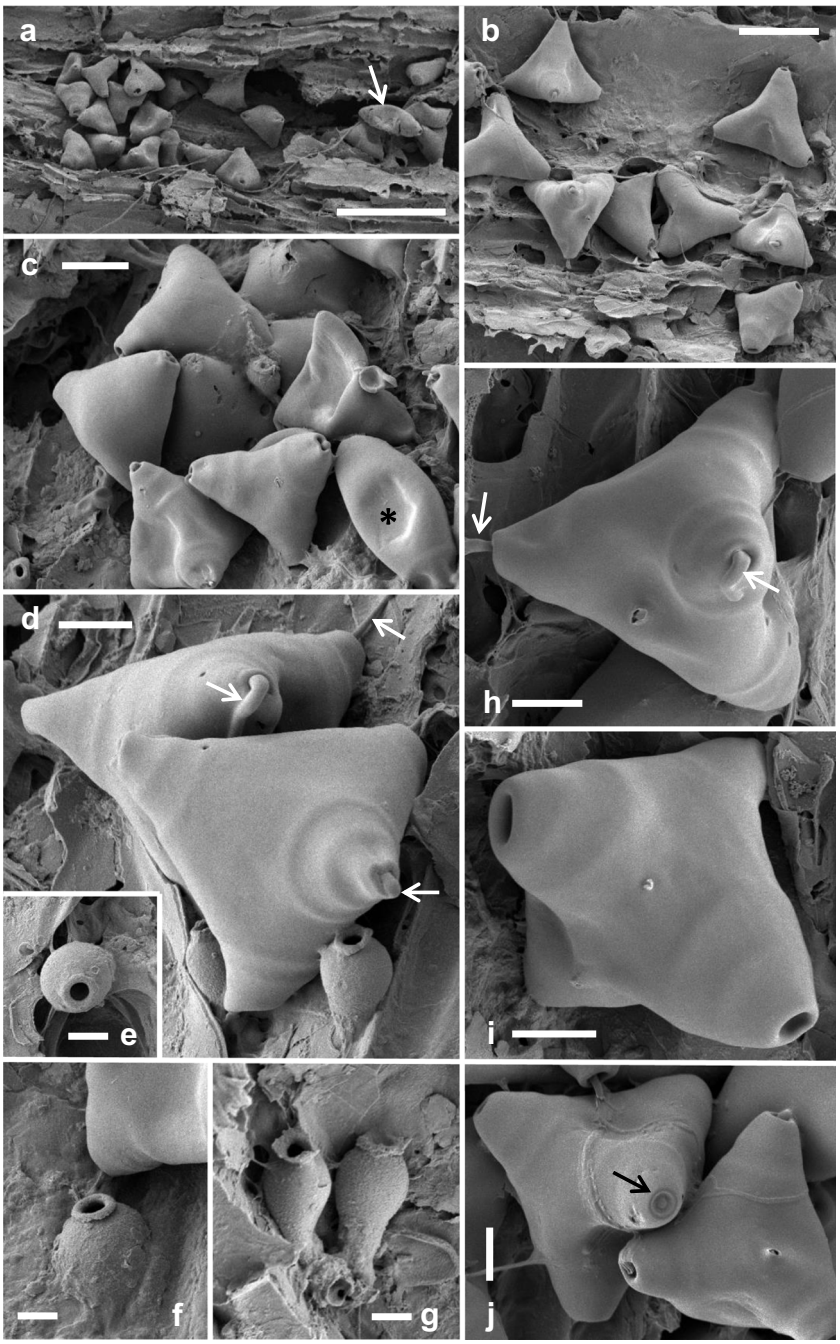


Fig. 4 *Phaeonawawia diplocladielloidea* (TNM: F0034163, holotype). Scanning electron micrographs. **a** Colony on the natural substratum. Arrows point to an ellipsoidal conidium. **b**, **c** Clumps of conidia. The asterisk denotes an ellipsoidal conidium. **d** Two tetrahedral (obpyramidal) conidia and two conidiogenous cells. Filiform appendages are visible (arrowed). **e–g** Conidiogenous cells. **h–j** Conidia. Arrows in **h** point to filiform appendages. Large pores in **i** are ends of conidial arms lacking filiform appendages. Arrow in **j** points to the basal hilum of an obpyramidal conidium. Scale bars: **a** = 100 μm; **b** = 50 μm; **c** = 20 μm; **d**, **h–j** = 10 μm, **e-g** = 5 μm

to R in Fig. 6) representing most of the anamorphic groups with phialidic conidiogenous cells in the Chaetosphaeriaceae. *Phaeonawawia diplocladielloidea* (O) did not cluster with any of the existing anamorphic groups and represents a distinct taxon in the Chaetosphaeriaceae with high bootstrap support and Bayesian inference. The tree also shows 12 major groups of fungal taxa in the family according to the spore types they produced (Table 1), which are indicated by the Roman numbers I–XII, but mostly without bootstrap support. Group I comprised three genera producing hyaline amerospores, including *Neonawawia* (A1) and *Nawawia* (A2) with setulate tetrahedral conidia, and *Zanclospora* (B) with conidia lacking appendages. Group II included *Cryptophiale* (C1) and *Cryptophialoidea* (C2), which are similar genera producing hyaline falcate or fusoid spores from groups of conidiogenous cells on the shaft of setiform conidiophores. Group III and group IV included the two major groups of anamorphic fungi: the acervular coelomycetes (D1–D5) and the hyphomycetes (E1 and E2). All taxa in these two groups produce hyaline setulate unicellular conidia (amerospores). The hyphomycete genera in these two groups belonged to the *Menispora* groups or the *Dictyochaeta* complex, which were composed of several morphologically similar genera, namely *Codinaeopsis*, *Dictyochaeta*, and

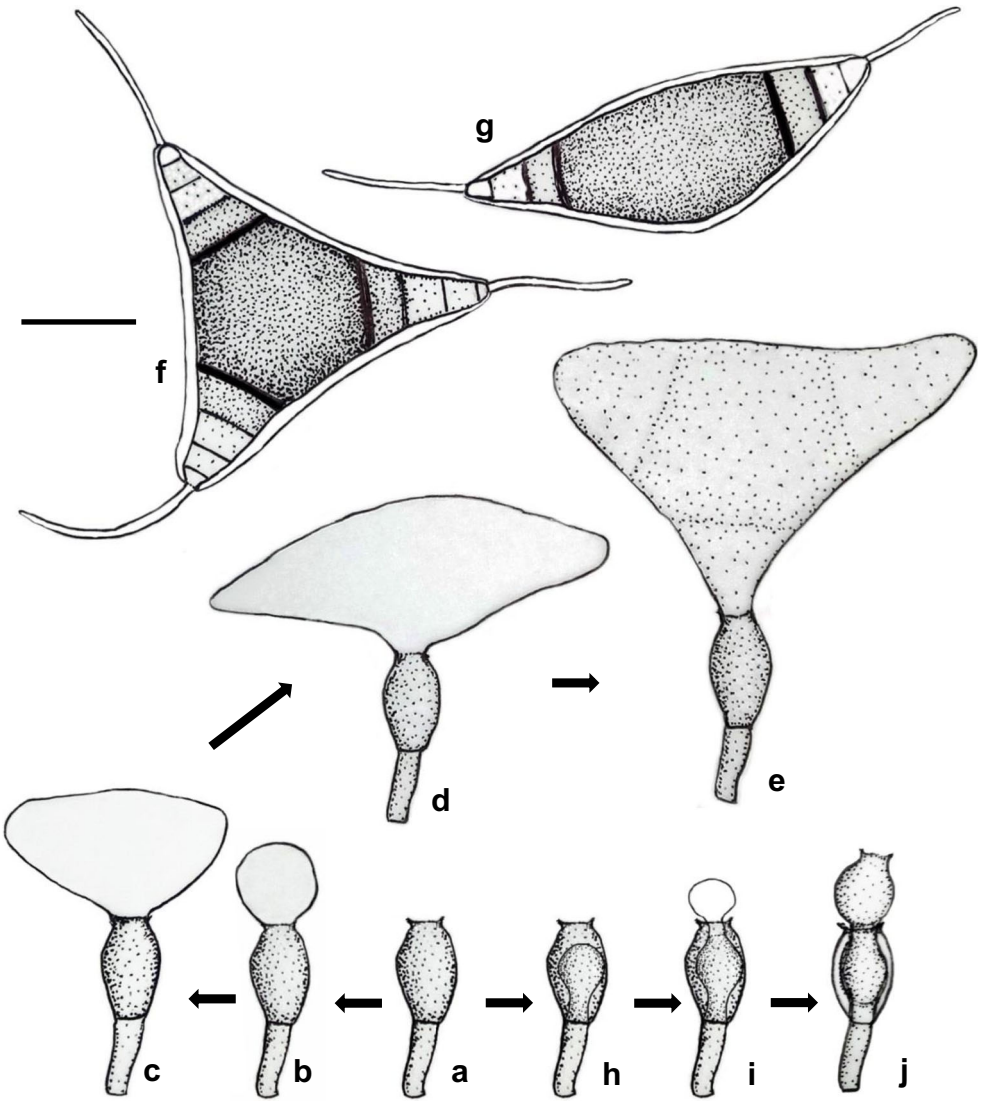
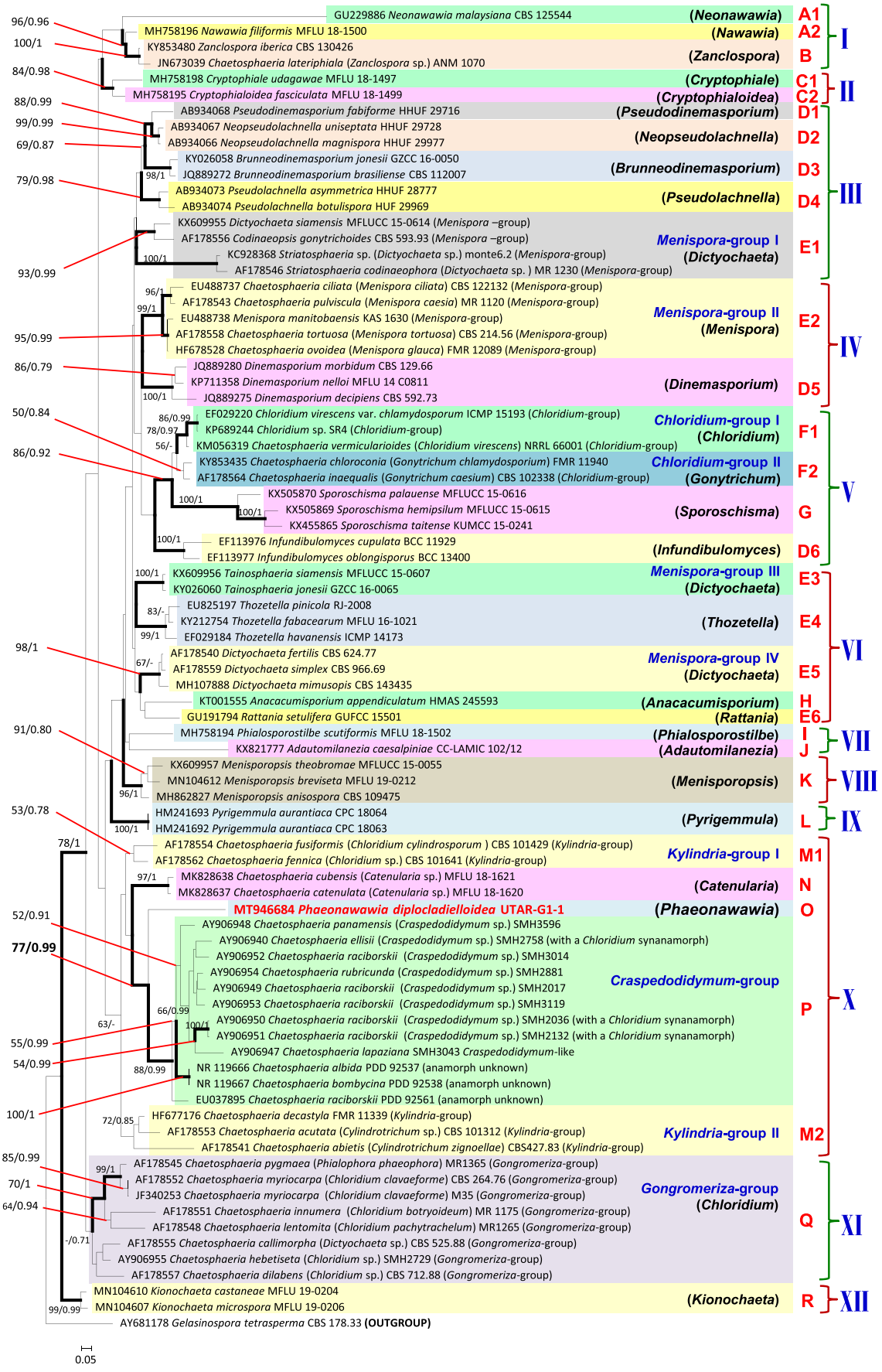


Fig. 5 *Phaeonawawia diplocladielloidea*. Diagrammatic representation of conidiogenesis. **a** A discrete phialide situated on a basal stalk. **b–e** Sequential steps of conidiogenesis. **f** A mature stauroconidium bearing a setula at the end of each arm. **g** A mature ellipsoidal conidium bearing a setula at each end. **h** An old phialide showing percurrent regeneration. **i** Conidium ontogeny from regenerated phialide. **j** Percurrent regeneration of phialides. Scale bar = 20 μm

Menispora. Group V comprised a mixture of spore types produced by various taxa. These include *Infundibulomyces* (D6), a cupulate coelomycete genus producing hyaline setulate amerospores, the *Chlorodium* complex (F1 and F2) producing subhyaline amerospores in mass, and *Sporoschisma* (G) producing catenate phaeophragmospores. Group VI comprised several similar genera belonging to the *Menispora* groups or the *Dictyochaeta* complex, producing hyaline setulate conidia (E3-E6), and the genus *Anacacumisporium* (H) which produces coloured multiseptate conidia (phaeophragmospores). Group VII comprised two morphologically distinct genera: the synnematous hyphomycete *Phialosporostilbe* (I) producing setulate hyaloconidia, and the sporodochial hyphomycetes *Adautomilanezia* (J) producing solitary phaeophragmospores. Group VIII comprised three species of *Menisporopsis* (K) producing setulate hyaloconidia from synnematous conidiophores. Group IX was represented by *Pyrigemmula aurantiaca* (L), a hyphomycete producing distoseptate phragmospores. Group X was composed of a mixture of taxa producing various spore types, including *Phaeonawawia* (O) producing solitary versicoloured staurospores, *Catenularia* (N) producing coloured cuneiform amerospores in chains, *Kylindria* complex (M1 and M2) producing septate hyalospores or phaeospores in mass, and *Craspedodidymum*

Fig. 6 Phylogenetic tree inferred from aligned ITS sequences of 83 fungal taxa showing relationships of *Phaeonawawia diplocladielloidea* and other fungi in the Chaetosphaeriaceae using the maximum likelihood and Bayesian inference in RAxML v8.2.4 and MrBayes v3.2.6. The tree was rooted with *Gelasinospora tetrasperma* (Sordariaceae). Bootstrap support values (greater than 50%) from the maximum likelihood analysis and posterior probabilities (greater than 0.7) from the Bayesian analysis are shown near each node. The tree shows branches and small clusters of taxa (designated alphabetically from A1, A2, B to R) representing most of the anamorphic groups in the Chaetosphaeriaceae. The Roman numbers I–XII indicate the major groups of fungal taxa in the family according to the spore types they produced. The anamorphic names of known *Chaetosphaeria* species were in brackets. The result shows that *P. diplocladielloidea* (in bold red) did not cluster with any of the existing anamorphic groups and represents a distinct taxon in Chaetosphaeriaceae ▶


GU229886 Neonawawia malaysiana CBS 125544 (Neonawawia) A1
MH758196 Nawawia filiformis MFLU 18-1500 (Nawawia) A2
KY853480 Zanclospora iberica CBS 130426
JN673039 Chaetosphaeria lateriphiala (Zanclospora sp.) ANM 1070 (Zanclospora) B
I
MH758198 Cryptophiale udagawae MFLU 18-1497 (Cryptophiale) C1
MH758195 Cryptophialoidea fasciculata MFLU 18-1499 (Cryptophialoidea) C2
II
AB934068 Pseudodinemasporium fabiforme HHUF 29716 (Pseudodinemasporium) D1
AB934067 Neopseudolachnella uniseptata HHUF 29728
AB934066 Neopseudolachnella magnispora HHUF 29977 (Neopseudolachnella) D2
KY026058 Brunneodinemasporium jonesii GZCC 16-0050
JQ889272 Brunneodinemasporium brasiliense CBS 112007 (Brunneodinemasporium) D3
AB934073 Pseudolachnella asymmetrica HHUF 28777
AB934074 Pseudolachnella botulispora HUF 29969 (Pseudolachnella) D4
III
KX609955 Dictyochaeta siamensis MFLUCC 15-0614 (Menispora –group)
AF178556 Codinaeopsis gonytrichoides CBS 593.93 (Menispora –group)
KC928368 Striatosphaeria sp. (Dictyochaeta sp.) monte6.2 (Menispora-group)
AF178546 Striatosphaeria codinaeophora (Dictyochaeta sp.) MR 1230 (Menispora-group)
Menispora-group I (Dictyochaeta) E1
EU488737 Chaetosphaeria ciliata (Menispora ciliata) CBS 122132 (Menispora-group)
AF178543 Chaetosphaeria pulviscula (Menispora caesia) MR 1120 (Menispora-group)
EU488738 Menispora manitobaensis KAS 1630 (Menispora-group)
AF178558 Chaetosphaeria tortuosa (Menispora tortuosa) CBS 214.56 (Menispora-group)
HF678528 Chaetosphaeria ovoidea (Menispora glauca) FMR 12089 (Menispora-group)
Menispora-group II (Menispora) E2
IV
JQ889280 Dinemasporium morbidum CBS 129.66
KP711358 Dinemasporium nelloi MFLU 14 C0811
JQ889275 Dinemasporium decipiens CBS 592.73
(Dinemasporium) D5
EF029220 Chloridium virescens var. chlamydosporum ICMP 15193 (Chloridium-group)
KP689244 Chloridium sp. SR4 (Chloridium-group)
KM056319 Chaetosphaeria vermicularioides (Chloridium virescens) NRRL 66001 (Chloridium-group)
Chloridium-group I (Chloridium) F1
KY853435 Chaetosphaeria chloroconia (Gonytrichum chlamydosporium) FMR 11940
AF178564 Chaetosphaeria inaequalis (Gonytrichum caesium) CBS 102338 (Chloridium-group)
Chloridium-group II (Gonytrichum) F2
V
KX505870 Sporoschisma palauense MFLUCC 15-0616
KX505869 Sporoschisma hemipsilum MFLUCC 15-0615
KX455865 Sporoschisma taitense KUMCC 15-0241
(Sporoschisma) G
EF113976 Infundibulomyces cupulata BCC 11929
EF113977 Infundibulomyces oblongisporus BCC 13400
(Infundibulomyces) D6
KX609956 Tainosphaeria siamensis MFLUCC 15-0607
KY026060 Tainosphaeria jonesii GZCC 16-0065
Menispora-group III (Dictyochaeta) E3
EU825197 Thozetella pinicola RJ-2008
KY212754 Thozetella fabacearum MFLU 16-1021
EF029184 Thozetella havanensis ICMP 14173
(Thozetella) E4
AF178540 Dictyochaeta fertilis CBS 624.77
AF178559 Dictyochaeta simplex CBS 966.69
MH107888 Dictyochaeta mimusopis CBS 143435
Menispora-group IV (Dictyochaeta) E5
VI
KT001555 Anacacumisporium appendiculatum HMAS 245593 (Anacacumisporium) H
GU191794 Rattania setulifera GUFCC 15501 (Rattania) E6
MH758194 Phialosporostilbe scutiformis MFLU 18-1502 (Phialosporostilbe) I
KX821777 Adautomilanezia caesalpiniae CC-LAMIC 102/12 (Adautomilanezia) J
VII
KX609957 Menisporopsis theobromae MFLUCC 15-0055
MN104612 Menisporopsis breviseta MFLU 19-0212
MH862827 Menisporopsis anisospora CBS 109475
(Menisporopsis) K
VIII
HM241693 Pyrigemmula aurantiaca CPC 18064
HM241692 Pyrigemmula aurantiaca CPC 18063
(Pyrigemmula) L
IX
AF178554 Chaetosphaeria fusiformis (Chloridium cylindrosporum) CBS 101429 (Kylindria-group)
AF178562 Chaetosphaeria fennica (Chloridium sp.) CBS 101641 (Kylindria-group)
Kylindria-group I M1
MK828638 Chaetosphaeria cubensis (Catenularia sp.) MFLU 18-1621
MK828637 Chaetosphaeria catenulata (Catenularia sp.) MFLU 18-1620
(Catenularia) N
MT946684 Phaeonawawia diplocladielloidea UTAR-G1-1 (Phaeonawawia) O
AY906948 Chaetosphaeria panamensis (Craspedodidymum sp.) SMH3596
AY906940 Chaetosphaeria ellisii (Craspedodidymum sp.) SMH2758 (with a Chloridium synanamorph)
AY906952 Chaetosphaeria raciborskii (Craspedodidymum sp.) SMH3014
AY906954 Chaetosphaeria rubricunda (Craspedodidymum sp.) SMH2881
AY906949 Chaetosphaeria raciborskii (Craspedodidymum sp.) SMH2017
AY906953 Chaetosphaeria raciborskii (Craspedodidymum sp.) SMH3119
AY906950 Chaetosphaeria raciborskii (Craspedodidymum sp.) SMH2036 (with a Chloridium synanamorph)
AY906951 Chaetosphaeria raciborskii (Craspedodidymum sp.) SMH2132 (with a Chloridium synanamorph)
AY906947 Chaetosphaeria lapaziana SMH3043 Craspedodidymum-like
NR 119666 Chaetosphaeria albida PDD 92537 (anamorph unknown)
NR 119667 Chaetosphaeria bombycina PDD 92538 (anamorph unknown)
EU037895 Chaetosphaeria raciborskii PDD 92561 (anamorph unknown)
Craspedodidymum-group P
X
HF677176 Chaetosphaeria decastyla FMR 11339 (Kylindria-group)
AF178553 Chaetosphaeria acutata (Cylindrotrichum sp.) CBS 101312 (Kylindria-group)
AF178541 Chaetosphaeria abietis (Cylindrotrichum zignoellae) CBS427.83 (Kylindria-group)
Kylindria-group II M2
AF178545 Chaetosphaeria pygmaea (Phialophora phaeophora) MR1365 (Gongromeriza-group)
AF178552 Chaetosphaeria myriocarpa (Chloridium clavaeforme) CBS 264.76 (Gongromeriza-group)
JF340253 Chaetosphaeria myriocarpa (Chloridium clavaeforme) M35 (Gongromeriza-group)
AF178551 Chaetosphaeria innumera (Chloridium botryoideum) MR 1175 (Gongromeriza-group)
AF178548 Chaetosphaeria lentomita (Chloridium pachytrachelum) MR1265 (Gongromeriza-group)
AF178555 Chaetosphaeria callimorpha (Dictyochaeta sp.) CBS 525.88 (Gongromeriza-group)
AY906955 Chaetosphaeria hebetiseta (Chloridium sp.) SMH2729 (Gongromeriza-group)
AF178557 Chaetosphaeria dilabens (Chloridium sp.) CBS 712.88 (Gongromeriza-group)
Gongromeriza-group (Chloridium) Q
XI
MN104610 Kionochaeta castaneae MFLU 19-0204
MN104607 Kionochaeta microspora MFLU 19-0206
(Kionochaeta) R
XII
AY681178 Gelasinospora tetrasperma CBS 178.33 (OUTGROUP)
0.05

species (P) producing coloured amerospores. Group XI was composed of *Chloridium*-like taxa representing the *Gongromeriza* complex (Q). Group XII was represented by two species of *Kionochaeta* (R) producing subhyaline amerospores from setiform conidiophores.

Discussion

Reflection on the hyaline conidial sheath

An outstanding feature in *Phaeonawawia diplocladielloidea* is the thick, hyaline sheath enclosing its stauroconidia. Several technical terms, namely ectosporium, endosporium, episporium, exosporium, and perisporium, have been used to describe different layers of spore walls seen in certain ascospores (Goh and Hanlin 1999; Kuhnert et al. 2016), basidiospores (Halbwachs and Bässler 2015), and teliopores (Khanna and Payak 1968).

The perisporium has been referred to be the "sheath" by several authors. It is the outermost layer of the spore and is usually thin, hyaline and sometimes fugacious (Kirk et al. 2008). Detachable perisporic sheaths have been reported in the ascospores of *Annulohypoxylon* species (Kuhnert et al. 2016) and the teliospores of certain smut fungi (Khanna and Payak 1968). Likely, the thick, hyaline, sheath-like outer covering of the conidia in *P. diplocladielloidea* is the perisporium. Empty sheaths were frequently observed in squashed mounts of the present collection (Figs. 2a–j and 3i), and they were probably the dehisced and detached perispores of the conidia. Such isolated sheaths might also be immature conidia lacking cellular content or perhaps due to an undetermined artefact of shrinking cytoplasm. However, the evidence is lacking, and these explanations remain hypothetical. A similar detachable outer coating (described as the "episporic sheath") has been reported in the didymoconidia of *Cordana abramovii* var. *seychellensis* K.D. Hyde & Goh (Hyde and Goh 1998). Such detachable sheath is, however, absent in *Cordana abramovii* var. *abramovii* Seman & Davydkina, a species which has been commonly collected worldwide (Seman and Davydkina 1983; Rao and de Hoog 1986; Zelski et al. 2014; Santos et al. 2018; Luo et al. 2019). Besides these two species, there are currently no other conidial fungi reported to have such a dehiscent or detachable "perisporic" sheath.

Diversity of anamorphic genera in Chaetosphaeriaceae

In a recent review of chaetosphaeriaceous fungi, Lin et al. (2019) recognised 49 genera in the family Chaetosphaeriaceae, among which 5 are teleomorphic names (ascomycetes) and 44 are anamorphic names (i.e. 9 are coelomycetes, 35 are hyphomycetes). The compilation of hyphomycete genera by Seifert et al. (2011) has contributed to the understanding of the diverse asexual forms of fungi, including those known to be anamorphs of *Chaetosphaeria*. Since then, several new asexual genera were added to the family (Lin et al. 2019) over the last few years. These include four coelomycete genera (Crous et al. 2012; Hashimoto et al. 2015; Hernández-Restrepo et al. 2016), namely *Brunneodinemasporium*, *Calvolachnella*, *Neopseudolachnella*, and *Pseudodinemasporium*, and six hyphomycete genera (Magyar et al. 2011; Crous et al. 2016, 2017; Ma et al. 2016; Yang et al. 2018), namely *Adautomilanezia*, *Anacacumisporium*, *Eucalyptostroma*, *Neonawawia*, *Pyrigemmula*, and *Verhulstia*. The description and illustration of *Phaeonawawia diplocladielloidea* in this paper added a unique hyphomycete genus to this family.

Addition of *Phaeonawawia* to Chaetophaeriaceae with minimal phylogenetic support

In this paper, we included a simple phylogenetic analysis to support our proposal of *Phaeonawawia* as a new genus in Chaetosphaeriaceae. Not all the known anamorphic genera in Chaetosphaeriaceae were included in the present phylogenetic study. We have excluded taxa that lack available sequences in GenBank and a few of those that are morphologically distinct from *Phaeonawawia* so that the tree was not too large lest it complicated the analysis. Since we only used the ITS sequence data to infer evolutionary relationships of taxa, some anamorphic taxa in the family that currently do not have available ITS sequences in the GenBank, such as *Exserticlava*, *Morrisiella*, and *Stanjehughesia*, were excluded from the present phylogenetic analysis. Extensive phylogenetic analyses of chaetosphaeriaceous teleomorphs and associated anamorphs are beyond our focus for the present study. This is because the specimen of *Phaeonawawia diplocladielloidea* was collected in January 2014, and we had only got its ITS sequenced. It is indeed a pity that a living ex-type culture of this new taxon is no longer available today, and therefore, no other gene sequences from it could be obtained for further phylogenetic studies. Due to this limitation in the selection of ITS gene segment for the present study, it is not suitable for large trees covering extensive phylogenetic studies of multiple taxonomic groups. However, the anamorphic genus *Phaeonawawia* is phylogenetically distinct, with outstanding morphological features in the family Chaetosphaeriaceae.

Teleomorph-anamorph connections

Species of *Chaetosphaeria* teleomorphs are generally simple and relatively homogeneous; however, their anamorphs are morphologically distinctive, complex, and diverse. Because teleomorphs of chaetosphaeriaceous fungi are hardly

distinguishable, species identification is therefore based primarily on characters of the anamorphs. Attempts to solve in part the natural status of *Chaetosphaeria* and its anamorphs have been ongoing since the 1970s (Gams and Holubová-Jechová 1976; Fernández et al. 1998; DiCosmo et al. 1983; Réblová and Gams 1999; Réblová 2000; Réblová and Winka 2000; Réblová and Seifert 2003; Fernández and Huhndorf 2005; Huhndorf and Fernández 2005; Fernández et al. 2006). Previous phylogenetic studies had revealed that species groupings within *Chaetosphaeria* are concordant with groupings based on morphological characters of their anamorphs. Certain general morphological patterns indicative of phylogenetic relationships were discerned within the family. Although *Chaetosphaeria* species appear homogeneous in morphology, phylogenetic analyses (Réblová and Winka 2000; Réblová and Seifert 2003) reveal that the genus is not monophyletic. Similar to previous findings, the result of the present phylogenetic study shows that some of the anamorphic genera associated with *Chaetosphaeria* are monophyletic, each clade with strong bootstrap support, such as *Craspedodidymum*, *Menispora*, *Menisporopsis*, *Sporoschisma*, and *Thozetella*, whereas others are polyphyletic and complex, such as *Chloridium* and *Dictyochaeta*. Réblová (2000) distinguished some of these complex anamorphs of *Chaetosphaeria* and divided them into four natural groups of taxa based on morphological, cultural, and molecular studies, namely the *Chloridium* group, the *Gongromeriza* group, the *Kylindria* group, and the *Menispora* group. However, these groupings are polyphyletic. The present phylogenetic tree (Fig. 6) inferred from aligned ITS sequences shows a similar result of groupings: the *Chloridium* group comprises species of *Chloridium* (F1) and *Gonytrichum* (F2); the *Gongromeriza* group (Q) comprises species of *Chloridium*, *Dictyochaeta*, and *Phialophora*; the *Kylindria* group comprises species of *Chloridum* (M1) and *Cylindrotrichum* (M2); and the *Menispora* group comprises species of *Codinaeopsis* (E1), *Dictyochaeta* (E1, E3, E5), and *Menispora* (E2). Based on molecular data and cultural characters, Huhndorf and Fernández (2005) recognised a group of *Chaetosphaeria* species that has teleomorph-anamorph connections with some *Craspedodidymum* species and rarely with *Chloridium*-like synanamorphs. The present phylogenetic study shows the same result, with high bootstrap support on the *Craspedodidymum* group (P).

Reflection on "one fungus = one name"

The adoption of a dual nomenclatural system for fungal species has been a tradition in mycology. When pleomorphism in fungi is encountered, confusion and frustration experienced by many practitioners of mycology and plant pathology are reckoned. The existence of synanamorphs in certain fungi further enhances the confusion with multiple fungal names. With the advent of DNA techniques and the era of molecular phylogeny in fungal systematics, mycologists nowadays have a better understanding of pleomorphism in fungi. Taylor (2011) proposed a "one fungus one name" of nomenclatural system to solve the confusion. This system has been followed by many mycologists and has particularly welcomed by the plant pathologists, as they recognised that many important plant pathogens produce the asexual forms of spores or propagules to facilitate disease dissemination and the sexual forms for overwintering (Wingfield et al. 2011; Rossman et al. 2016). Based on the concept of "one fungus one name", Réblová et al. (2016) recommended the adoption of either the sexual names or the asexual names for some taxa in the Sordariomycetes. These include the preference of adopting the anamorphic names over their teleomorphic names for several taxa in the Chaetosphaeriaceae, namely *Chloridium* (instead of *Melanopsammella* Höhn.), *Menispora* (instead of *Zignoëlla* Sacc.), *Menisporopsis* (instead of *Menisporopascus* Matsush.), *Sporoschisma* (instead of *Melanochaeta* E. Müll., Harr & Sulmont), and *Stanjehughesia* (instead of *Umbrinosphaeria* Réblová). We concur with Réblová et al. (2016) to keep these anamorphic names, as we realise that chaetosphaeriaceous fungi are relatively homogeneous in their teleomorphic forms but quite diverse in their anamorphic forms. The recognition of the various asexual forms in Chaetosphaeriaceae and the conservation of these anamorphic names may be helpful in species identification for the time being. Both the sexual and asexual names are therefore cited wherever possible in this paper (Fig. 6) to facilitate identification and examination of these fungi.

Phialides and conidial morphology in Chaetophaeriaceae

Majority of the asexual genera in Chaetosphaeriaceae have phialidic conidiogenesis (Liu et al. 2016; Lu et al. 2016; Lin et al. 2019). The phialides in these genera differ in shapes (e.g. lageniform, ampulliform, and bulbose), in conidiogenous loci (monophialidic or polyphialidic), in conidium ontogeny, and in development (e.g. solitary, catenulate, or in slimy mass). More comprehensive studies of phialides and conidial development have been given by Hughes (1953), Tubaki (1958), and Minter et al. (1982, 1983). The mechanisms of regeneration in conidiogenous cells (i.e. how a no-longer functional conidiogenous cell is replaced) are discussed in Minter et al. (1982). In certain phialidic fungi, their phialides undergo intermittent regenerations between conidiogenous episodes (Minter et al. 1983), either percurrently, as in species of *Catenularia* (Hughes 1965) and *Nawawia* (Goh et al. 2014b), or sympodially, as in species of *Codinaea* and *Dictyochaeta* (Luo et al. 2019). In the present paper, percurrent regenerations of phialides that are bulbose or urceolate in shape were observed in *Phaeonawawia*

diplocladielloidea (Fig. 3). The same manner of regeneration has also been observed in other hyphomycetes with bulbose phialides, such as *Polybulbophiale palmicola* (Goh and Hyde 1998b) and *Obeliospora microappendiculata* (Cantillo-Pérez et al. 2018). A detailed study of phialides and conidial development in *Phaeonawawia* is out of the scope of the present paper. Among the various anamorphic forms in Chaetosphaeriaceae, several genera, such as *Morrisiella* Saikia & A.K. Sarbhoy, *Stanjehughesia* Subram., and probably *Multiguttulispora* C.G. Lin & J.K. Liu, however, are not phialidic, instead, they produce holoblastic conidia from mono- or polyblastic conidiogenous cells.

Conidia of chaetosphaeriaceous anamorphs come in diverse forms, but mostly they bear hyaline appendages (Crous et al. 2012; Liu et al. 2016; Lin et al. 2019). Shenoy et al. (2006) reported some *Sporidesmium*-like taxa phylogenetically positioned in the Chaetosphaeriales, namely *Ellisembia brachypus*, *Linkosia* sp., *Morrisiella indica*, and *Stanjehughesia vermiculata*, but these hyphomycetes produce dark, obclavate or rostrate, non-setulate phragmoconidia from holoblastic conidiogenous cells. To date, *Phaeonawawia* is the only known asexual genus in the Chaetosphaeriaceae that produces versicolored setulate stauroconidia, although the setulate conidia in *Nawawia* or *Neonawawia* may be regarded as staurosporous, they are unicellular and hyaline. This genus was collected from decaying wood submerged in freshwater streams. Such stauroconidia appear to be adapted to dispersal by water and attachment to submersed substrata (Goh and Hyde 1996).

On the contrary, with evidence from many phylogenetic studies of asexual fungi based on multigene analyses in recent decades, some phialidic hyphomycetes that had been considered to belong to the Chaetosphaeriales in the past were inferred to belong to other ordinal lineages. Examples of non-chaetosphaeriaceous fungi that produce phialoconidia (Cai et al. 2009; Réblová et al. 2011; Maharachchikumbura et al. 2018) include *Monilochaetes* species (Australiascaceae, Glomerellales), the *Chalara* & *Exochalara* complex (Helotiales, Leotiomycetes), and the *Kylindria* & *Cylindrotrichum* complex (Reticulascaceae, Glomerellales).

Conclusions

This paper describes and illustrates *Phaeonawawia diplocladielloidea* from decaying wood submerged in freshwater. It is a new anamorphic taxon belonging to Chaetosphaeriaceae with phialoconidia of a unique morphology. Despite multiple efforts to study species of *Chaetosphaeria* and their anamorphs, there exist some unresolved problems in their taxonomy. One of the limitations is that until today, not all chaetosphaeriaceous taxa have their DNA sequenced. There also exist several polyphyletic taxon groups which have some of their members scattered in the Chaetosphaeriaceae and also among other fungal lineages, such as the *Chalara* complex (Cai et al. 2009), the *Chloridium* complex (Gams and Holubová-Jechová 1976), the *Dictyochaeta* complex (Wei et al. 2018; Liu et al. 2016; Lin et al. 2019) the *Kylindria* & *Cylindrotrichum* complex (DiCosmo et al. 1983; Maharachchikumbura et al. 2018); the *Phialophora* complex (Gams 2000; Réblová et al. 2011), and the *Sporidesmium* complex (Shenoy et al. 2006). Another interesting aspect for further detailed studies of chaetosphaeriaceous fungi is the phialidic conidiogenous cells of their anamorphs which exist in various forms, especially it has been over 30 years without further extensive research on the developmental biology of phialides since the contributions of Hughes (1953), Tubaki (1958), and Minter et al. (1982, 1983). Chaetosphaeriaceous fungi remain complex, especially the biology and phylogeny of the anamorphs, and await more work to resolve in the future.

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CRediT taxonomy

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- Deposition of specimens at Herbarium: Chang-Hsin Kuo
- Laboratory resources and facilities: Chang-Hsin Kuo;
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- Final proofreading: Chang-Hsin Kuo;
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Authors' contributions All authors contributed to the study conception and design. Material preparation was performed by Chang-Hsin Kuo. Identification of fungi was performed by Teik-Khiang Goh. Phylogenetic analysis was performed by Jie-Hao Ou. The first draft of the manuscript was written by the first author Teik-Khiang Goh. The other two authors (Jie-Hao Ou and Chang-Hsin Kuo) commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability The authors declare that all data and materials as well as software application or custom code support their published claims and comply with field standards.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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