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ORIGINAL ARTICLE

New species and records of *Helicosporium* sensu lato from Taiwan, with a reflection on current generic circumscription

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Abstract

This paper describes and illustrates five species of *Helicosporium* sensu lato, which represents the partial result of an investigation of fungal diversity associated with submerged wood and decaying culms *of Miscanthus floridulus* (Poaceae) from freshwater streams in Alishan area, Chiayi County, Taiwan, which was carried out during the years 2016 and 2017. *Neohelicomyces longisetosus* sp. nov. and *Helicosporium flavidum* sp. nov. are described and illustrated; the former is proposed based on molecular and morphological data, whereas the latter is based on morphology only. *Pseudohelicomyces talbotii*, a new record for Taiwan, is renamed as *Parahelicomyces talbotii* because the former genus was a homonym and thus illegitimate. The other six illegitimate *Pseudohelicomyces* species are transferred to *Parahelicomyces* as new combinations. Two other species, namely *Acanthohelicospora guianensis* and *Neohelicosporium sympodiophorum*, are also new records for Taiwan. A taxonomic key to *Helicosporium* sensu stricto is provided. Current generic circumscription of helicosporous taxa based on phylogeny is briefly discussed.

Keywords Freshwater fungi · Helicosporous hyphomycetes · Mitosporic fungi · Taxonomy · Tubeufiaceae

Introduction

Helicosporous fungi have been the subject of systematic studies because they are morphologically diverse and produce unusual but elegant conidia for reproduction (Goos 1987). *Helicoma* Corda, *Helicomyces* Link, and *Helicosporium* Nees are the three earliest erected helicosporous genera. The taxonomy of these fungi has been traditionally based on the morphology of conidiophores, conidiogenous cells, and conidia (Morgan 1892; Linder 1929, 1931; Moore 1953, 1954, 1955, 1957). According to original generic circumscriptions, distinctions between *Helicoma*, *Helicomyces*, and *Helicosporium* were often vague due to similarities in coiling of their conidia. Pirozynski (1972) suggested that the taxonomy of these three genera could put more weight on the characters of conidiogenous cells, conidial attachment position, presence of "*conidiola*" (secondary conidia), and presence of "*sclerotes pedicelées*" (stalked sclerotia). To date, more than 200 species names have been assigned to these three genera. Traditional taxonomists of these fungi generally distinguish the three genera as follows: in *Helicomyces* and *Helicosporium*, conidial filaments are relatively thin in proportion to their length and hygroscopic (Morgan 1892). Conidiophores are well-developed in *Helicosporium* (Goos 1989), whereas in *Helicomyces*, they are much reduced or lacking (Goos 1985). In *Helicoma*, conidia are non-hygroscopic, and the conidial filaments are relatively thick in proportion to their length (Goos 1986). At the specific level, *Helicoma* species are grouped into four sections according to their conidial ontogeny: Section *Helicoma*, Section *Atroseptatum*, Section *Violaceum*, and Section *Monilipes*. Details of each section within the genus *Helicoma* are given by Goos (1986) and Zhao et al. (2007).

Nowadays, molecular analysis using various gene sequences has been applied to the taxonomy of fungi. In recent years, the gene markers commonly used to infer the phylogeny of fungi are the internal transcribed spacer regions (ITS) and subunits of ribosomal DNA (SSU, LSU), certain protein-coding gene markers such as the RNA polymerase II second largest subunit (*RPB2*), the translation elongation factor 1-alpha gene (*TEF1a*), and other

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gene sequences (Hyde et al. 2016; Doilom et al. 2017; Luo et al. 2017; Lu et al. 2017a, b, 2018). Species of *Helicoma*, *Helicomyces*, *Helicosporium*, and their known teleomorphs have been shown to belong to the Tubeufiaceae (Kodsueb et al. 2006; Boonmee et al. 2011, 2014; Brahmanage et al. 2017). Tsui et al. (2006) used sequence data to revise systematics of *Helicoma*, *Helicomyces*, and *Helicosporium*; however, they found that neither of these anamorphic genera nor the four sections within the genus *Helicoma* were monophyletic. The polyphyly of helicosporous hyphomycetes has also been demonstrated by subsequent authors (Boonmee et al. 2011, 2014; Kuo and Goh 2018a, b; Lu et al. 2018). Unfortunately, to date, many helicosporous taxa remain for which marker genes are not yet sequenced, especially those published before the advent of molecular techniques. When molecular data are not available, traditional morphological characters used for distinguishing species of these fungi are certainly useful and important.

To date, there are 43 names in *Helicomyces*, 101 in *Helicosporium*, and 100 in *Helicoma* (Index Fungorum 2020), but many of these names have already been synonymized, excluded, or transferred to more appropriate genera by various authors (Goos 1985, 1986, 1987, 1989; Zhao et al. 2007; Boonmee et al. 2014; Lu et al. 2018). Recently, Lu et al. (2018) did a taxonomic reassessment of Tubeufiales based on multi-locus phylogeny and morphology, which included the analysis of various taxa of helicosporous hyphomycetes. They used a combined ITS, LSU, *RPB2*, and *TEF1a* sequence dataset in their analyses and introduced 13 new genera in the family Tubeufiaceae. Many species previously named under *Helicoma*, *Helicomyces*, *Helicosporium*, and allied genera have now been transferred to several new genera such as *Acanthohelicospora*, *Dematiohelicoma*, *Dematiohelicomyces*, *Dematiohelicosporum*, *Neohelicoma*, *Neohelicomyces*, *Neohelicosporium*, *Pleurohelicosporium*, and *Pseudohelicomyces* (Luo et al. 2017; Lu et al. 2017a, b, 2018).

Goos (1989) reviewed the status of all known species contemporarily assigned to the genus *Helicosporium* and accepted 16 species. Zhao and his colleagues further reviewed additional *Helicosporium* species which were published after Goos (1989) and accepted 21 species in their monograph (Zhao et al. 2007). Four additional species, based solely on morphological data, were subsequently added to *Helicosporium*: *H. melghatianum*, *H. myrtacearum*, *H. vesiculiferum*, and *H. xylophilum* (Cruz et al. 2009; Dharkar et al. 2010; Singh and Singh 2016). With the recent trend in molecular taxonomy, eight more species were added to the genus based on phylogeny and morphology: *H. aquaticum*, *H. flavisporum*, *H. flavum*, *H. luteosporum*, *H. setiferum*, *H. taiwanense*, *H. vesicarium*, and *H. viridiflavum* (Brahmanage et al. 2017; Lu et al. 2017a, 2018; Kuo and Goh 2018a). A majority of these *Helicosporium* sensu lato species, however, has recently been transferred to other genera based on results of multi-gene phylogenetic analyses (Lu et al. 2018). As currently circumscribed based on phylogeny and morphology, the genus *Helicosporium* sensu stricto primarily includes species whose colonies on natural substrata are yellow, conidiophores are setiferous and dark, conidiogenous cells are discrete, arising laterally as tooth-like or bladder-like protrusions from the shaft of conidiophores, and conidia are helicoid, with a narrow filament (usually not exceeding 4 μm wide), hyaline to yellowish-green. To date, only 13 species are retained in the genus *Helicosporium* sensu stricto (Lu et al. 2018). A checklist of current names for taxa previously and recently assigned to *Helicosporium* (Index Fungorum 2020) is given in Table 1.

Since the end of 2015, we have started a survey of fungal diversity in the Alishan area, Chiayi County, Taiwan. There were a few freshwater streams where some helicosporous hyphomycetes were collected, some of which have already been recorded from Taiwan (Chen 1994; Tzean et al. 2015; Taiwan Biodiversity Information Facility 2020), among which a few new taxa were recently described (Goh and Kuo 2018; Kuo and Goh 2018a, b). This paper describes and illustrates five species of *Helicosporium* sensu lato, which represents the partial result of our investigation of fungi associated with submerged wood and decaying culms of *Miscanthus floridulus* (Poaceae) from freshwater streams in the Alishan area, which was carried out during the year 2016 and 2017. Current generic concepts and nomenclature (Lu et al. 2018) are employed in describing our fungi in this paper. *Neohelicomyces longisetosus* and *Helicosporium flavidum* are described as new based on molecular and morphological data. A synopsis based on morphological features of 34 *Helicosporium* species sensu lato, following the taxonomic treatments by Goos (1989), Zhao et al. (2007), and Lu et al. (2018), is given to facilitate identification of these fungi (Table 2). A taxonomic key for the 13 accepted species in *Helicosporium* sensu stricto, the current generic concept of which is circumscribed based primarily on phylogeny (Lu et al. 2018), is provided to justify *H. flavidum*, since this species is proposed as new in this paper based on morphological data only. Morphological comparison for 9 species of *Neohelicomyces* (Luo et al. 2017; Lu et al. 2018) is given in Table 3. *Pseudohelicomyces talbotii*, a new record for Taiwan, is renamed in this paper as *Parahelicomyces talbotii* (gen. et sp. nov.) because the former genus was a homonym and thus illegitimate. The other six illegitimate *Pseudohelicomyces* species are transferred to *Parahelicomyces* as new combinations. Two other species, namely *Acanthohelicospora guianensis* (formerly *Helicosporium guianense*) and *Neohelicosporium sympodiophorum* (formerly *Helicosporium sympodiophorum*), are also new records for Taiwan.

Materials and methods

Sample collection and mycological procedures Collecting of specimens and laboratory procedures were similar to the methodology described in Kuo and Goh (2018a). Plant materials

Table 1 Current names of *Helicosporium* sensu lato

Name of taxa (Index Fungorum 2020)	Current name	References
Helicosporium abuense Chouhan & Panwar	*Neohelicosporium abuense* (Chouhan & Panwar) Y.Z. Lu & K.D. Hyde	Chouhan and Panwar 1980, Lu et al. 2018
Helicosporium albidum Grove	(Doubtful)	Goos 1989
Helicosporium albocarneum (P. Crouan & H. Crouan) Sacc.	(Doubtful)	Goos 1989
Helicosporium ambiens (Morgan) Sacc.	*Helicoma ambiens* Morgan	Morgan 1892, Goos 1986
Helicosporium ambiguum (Morgan) Sacc.	*Helicomyces ambiguus* (Morgan) Linder	Linder 1929
Helicosporium aquaticum Y.Z. Lu, J.C. Kang & K.D. Hyde	*Helicosporium aquaticum* Y.Z. Lu, J.C. Kang & K.D. Hyde	Lu et al. 2018
Helicosporium auratum Ellis	*Helicoon auratum* (Ellis) Morgan	Goos et al. 1986
Helicosporium aureum (Corda) Linder	*Acanthohelicospora aurea* (Corda) Rossman & W.C. Allen	Rossman et al. 2016
Helicosporium berkeleyi (M.A. Curtis) Sacc.	*Xenosporium berkeleyi* (M.A. Curtis) Piroz.	Deighton and Pirozynski 1966
Helicosporium binale (Berk. & M.A. Curtis) Sacc.	*Xenosporium berkeleyi* (M.A. Curtis) Piroz.	Deighton and Pirozynski 1966
Helicosporium boydii A.L. Sm. & Ramsb.	*Helicoma phaeosporum* Fresen.	Goos 1986, 1989
Helicosporium brunneolum Berk. & M.A. Curtis	*Drepanospora viridis* (Corda) Goos	Goos 1989
Helicosporium brunneum Schulzer & Sacc.	(Doubtful)	Goos 1989
Helicosporium cinereum Peck	*Neohelicosporium griseum* (Berk. & M.A. Curtis) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium citreoviride Tubaki	*Acanthohelicospora aurea* (Berk. & M.A. Curtis) Y.Z. Lu & K.D. Hyde,	Lu et al. 2018
Helicosporium coprophilum (Zukal) Sacc.	*Papulaspra coprophila* (Zukal) Hotson	Hotson 1912
Helicosporium curtisii (Berk.) Sacc.	*Thaxteriella pezizula* (Berk. & M.A. Curtis) Petr.	Petrak 1953
Helicosporium decumbens Linder	*Helicosporium decumbens* Linder	Linder 1929, Goos 1989
Helicosporium dentophorum G.Z. Zhao, Xing Z. Liu & W.P. Wu	*Tubeufia dentophora* (G.Z. Zhao, Xing Z. Liu & W.P. Wu) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium diplosporum Ellis & Everh.	*Xenosporium berkeleyi* (M.A. Curtis) Piroz.	Deighton and Pirozynski 1966
Helicosporium elinorae Linder	*Helicoma elinorae* (Linder) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium ellipticum Peck	*Helicoon ellipticum* (Peck) Morgan	Goos et al. 1986, Goos 1989
Helicosporium ellisii Cooke	(Doubtful)	Linder 1929, Goos 1989
Helicosporium fasciculatum (Berk. & M.A. Curtis) Sacc.	*Trochophora fasciculata* (Berk. & M.A. Curtis) Goos	Goos 1986
Helicosporium flavisporum Y.Z. Lu, J.C. Kang & K.D. Hyde	*Helicosporium flavisporum* Y.Z. Lu, J.C. Kang & K.D. Hyde	Lu et al. 2018
Helicosporium flavum Brahaman., Y.Z. Lu, Boonmee & K.D. Hyde	*Helicosporium flavum* Brahaman., Y.Z. Lu, Boonmee & K.D. Hyde	Brahmanage et al. 2017
Helicosporium fuckelii Fresen.	*Thaxteriella pezizula* (Berk. & M.A. Curtis) Petr.	Petrak 1953
Helicosporium fuscum Berk. & M.A. Curtis	*Helicodendron fuscum* (Berk. & M.A. Curtis) Linder	Linder 1929, Goos et al. 1985
Helicosporium gigasporum C.K.M. Tsui, Goh, K.D. Hyde & Hodgkiss	*Helicoma gigasporum* (C.K.M. Tsui, Goh, K.D. Hyde & Hodgkiss) Y.Z. Lu	Lu et al. 2018
Helicosporium gracile (Morgan) Linder	Rejected by Lu et al. (2018) and remains doubtful	Linder 1929, Goos 1989, Lu et al. 2018
Helicosporium griseum (Bonord.) Sacc.	*Helicosporium murinum* Goos	Goos 1989
Helicosporium griseum Berk. & M.A. Curtis	*Neohelicosporium griseum* (Berk. & M.A. Curtis) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium guianense Linder	*Acanthohelicospora guianensis* (Linder) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium hendrickxii Hansf.	*Hiospira hendrickxii* (Hansf.) R.T. Moore	Moore 1962
Helicosporium herbarum Sacc., E. Bommer & M. Rousseau	(Doubtful)	Linder 1929. Goos 1989
Helicosporium hiospiroides B.S. Reddy, D. Rao & G.V. Rao	Rejected by Lu et al. (2018) and remains doubtful	Reddy et al. 1970, Lu et al. 2018
Helicosporium hongkongense C.K.M. Tsui, Goh, K.D. Hyde & Hodgkiss	*Helicoma hongkongense* (C.K.M. Tsui, Goh, K.D. Hyde & Hodgkiss) Y.Z. Lu	Lu et al. 2018
Helicosporium indicum P.Rag. Rao & D. Rao		Rao and Rao 1964, Lu et al. 2018

Table 1 (continued)

Name of taxa (Index Fungorum 2020)	Current name	References
	Pseudohelicomyces indicus (P.Rag. Rao & D. Rao) Y.Z. Lu & K.D. Hyde	
Helicosporium insuetum Petr.	*Pseudocercospora insueta* (Petr.) Deighton	Deighton 1976
Helicosporium intermedium var. intermedium Penz. & Sacc.	*Helicoma intermedium* (Penz. & Sacc.) Linder	Linder 1929
Helicosporium intermedium var. *palmigenum* Penz. & Sacc.	*Helicotruncatum palmigenum* (Penz. & Sacc.) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium leptosporum Sacc.	*Neohelicosporium griseum* (Berk. & M.A. Curtis) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium limpidum (Morgan) Sacc.	*Helicoma limpidum* Morgan	Goos 1989
Helicosporium linderi R.T. Moore	*Helicoma linderi* (R.T. Moore) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium lumbricoides Sacc.	*Neohelicosporium griseum* (Berk. & M.A. Curtis) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium lumbricopsis Linder	*Helicosporium lumbricopsis* Linder	Linder 1929, Goos 1989
Helicosporium luteosporum Y.Z. Lu, Boonmee & K.D. Hyde	*Helicosporium luteosporum* Y.Z. Lu, Boonmee & K.D. Hyde	Lu et al. 2017a
Helicosporium melghatianum Hande	(Doubtful)	Dharkar et al. 2010
Helicosporium microscopicum Ellis	*Helicoma microscopium* (Ellis) Linder	Linder 1929, Goos 1989
Helicosporium monilipes (Ellis & L.N. Johnson) Sacc.	*Helicoma monilipes* Ellis & L.N. Johnson	Goos 1989
Helicosporium muelleri (Corda) Sacc.	*Helicoma muelleri* Corda	Goos 1989
Helicosporium murinum Goos	*Helicosporium murinum* Goos	Goos 1989
Helicosporium myrtacearum P.N. Singh & S.K. Singh	*Neohelicosporium myrtacearum* (P.N. Singh & S.K. Singh) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium neesii R.T. Moore	*Helicosporium vegetum* Nees/*Tubeufia cerea* (Berk. & M.A. Curtis) Höhn.	Morgan-Jones and Goos 1992, Boonmee et al. 2014
Helicosporium nematosporum Linder	*Helicoma nematosporum* (Linder) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium nizamabadense P.Rag. Rao & D. Rao	*Neohelicosporium nizamabadense* (P.Rag. Rao & D. Rao) Y.Z. Lu & K.D. Hyde	Rao and Rao 1964, Lu et al. 2018
Helicosporium nymphaearum F.V. Rand	*Dichotomophthoropsis nymphaearum* (F.V. Rand) M.B. Ellis	Ellis 1971, Goos 1989
Helicosporium obscurum Corda	*Circinotrichum obscurum* (Corda) S. Hughes	Hughes 1958
Helicosporium olivaceum Peck	*Helicosporium vegetum* Nees/*Tubeufia cerea* (Berk. & M.A. Curtis) Höhn.	Morgan-Jones and Goos 1992, Boonmee et al. 2014
Helicosporium pallidum Ces.	*Neohelicomyces pallidus* (Ces.) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium panachaeum R.T. Moore	*Helicosporium panachaeum* R.T. Moore	Moore 1954, Goos 1989
Helicosporium pannosum (Berk. & M.A. Curtis) R.T. Moore	*Helicoma pannosum* (Berk. & M.A. Curtis) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium phaeosporum (Fresen.) Sacc.	*Helicoma phaeosporum* Fresen.	Goos 1989
Helicosporium phragmitis Höhn.	*Pseudohelicomyces paludosus* (P. Crouan & H. Crouan) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium pilosum Ellis & Everh.	*Acanthohelicospora scopula* (Peck) Rossman & W.C. Allen	Rossman et al. 2016
Helicosporium politulum Schulzer	(Doubtful)	Linder 1929, Goos 1986, 1989
Helicosporium polysporum (Morgan) Sacc.	*Helicoma polysporum* Morgan	Goos 1989
Helicosporium populi (P. Crouan & H. Crouan) Sacc.	(Doubtful)	Linder 1929, Goos 1989
Helicosporium prasinum Preuss	(Doubtful)	Linder 1929, Goos 1989
Helicosporium pulvinatum var. *effusum* (Berk.) Sacc.	(Doubtful)	Linder 1929, Goos 1989
Helicosporium pulvinatum var. *pulvinatum* (Nees & T. Nees) Fr.	(Doubtful)	Linder 1929, Goos 1989
Helicosporium raghuveeri V.G. Rao & Varghese	Rejected by Lu et al. (2018) and remains doubtful	Rao and Varghese 1988, Lu et al. 2018
Helicosporium ramosum (Berk. & Sm.) Massee	*Helicoon ellipticum* (Peck) Morgan	Goos et al. 1986
Helicosporium ramosum P.H.B. Talbot		Goos 1989, Lu et al. 2018

Table 1 (continued)

Name of taxa (Index Fungorum 2020)	Current name	References
	Pseudohelicomyces talbotii (Goos) Y.Z. Lu & K.D. Hyde	
Helicosporium recurvum Petch	*Helicoma recurvum* (Petch) Linder	Linder 1929
Helicosporium repens (Morgan) Sacc.	*Helicoma repens* Morgan	Morgan 1892, Goos 1989
Helicosporium richonis Boud.	*Pleohelicoon richonis* (Boud.) Jayasiri, E.B.G. Jones & K.D. Hyde	Jayasiri et al. 2019
Helicosporium serpentinum Linder	*Helicoma serpentinum* (Linder) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium setiferum Y.Z. Lu, J.C. Kang & K.D. Hyde	*Helicosporium setiferum* Y.Z. Lu, J.C. Kang & K.D. Hyde	Lu et al. 2018
Helicosporium simplex Syd. & P. Syd.	*Trochophora fasciculata* (Berk. & M.A. Curtis) Goos	Goos 1986
Helicosporium spectabile Fautrey & Lambotte	*Helicoma phaeosporum* Fresen.	Goos 1986, 1989
Helicosporium sympodiophorum G.Z. Zhao, Xing Z. Liu & W.P. Wu	*Neohelicosporium sympodiophorum* (G.Z. Zhao, Xing Z. Liu & W.P. Wu) Y.Z. Lu & K.D. Hyde	Lu et al. 2018
Helicosporium taiwanense C.H. Kuo & Goh	*Neohelicosporium taiwanense* (C.H. Kuo & Goh) Y.Z. Lu & K.D. Hyde	Kuo and Goh 2018a, Lu et al. 2018
Helicosporium talbotii Goos	*Pseudohelicomyces talbotii* (Goos) Y.Z. Lu & K.D. Hyde	Goos 1989, Lu et al. 2018
Helicosporium thysanophorum Ellis & Harkn.	*Helicodendron fuscum* (Berk. & M.A. Curtis) Linder	Linder 1929, Goos et al. 1985
Helicosporium tiliae Peck	*Helicoma muelleri* Corda	Goos 1986, 1989
Helicosporium vegetum Nees	*Helicosporium vegetum* Nees / *Tubeufia cerea* (Berk. & M.A. Curtis) Höhn.	Morgan-Jones and Goos 1992, Boonmee et al. 2014
Helicosporium velutinum (Ellis) Sacc.	*Helicoma phaeosporum* Fresen.	Goos 1986, 1989
Helicosporium vesicarium Y.Z. Lu, J.C. Kang & K.D. Hyde	*Helicosporium vesicarium* Y.Z. Lu, J.C. Kang & K.D. Hyde	Lu et al. 2018
Helicosporium vesiculiferum A.C. Cruz & Gusmão	*Neohelicosporium vesiculiferum* (A.C. Cruz & Gusmão) Y.Z. Lu & K.D. Hyde	Cruz et al. 2009, Lu et al. 2018
Helicosporium virescens (Pers.) Sivan.	*Chaetosphaeria vermicularioides* (Sacc. & Roum.) W. Gams & Hol.-Jech.	Gams and Holubová-Jechová 1976
Helicosporium virescens sensu Sivanesan	*Tubeufia cerea* (Berk. & M.A. Curtis) Höhn.	Sivanesan 1984, Boonmee et al. 2014
Helicosporium viride (Corda) Sacc.	*Drepanospora viridis* (Corda) Goos	Goos 1989
Helicosporium viridiflavum Y.Z. Lu, J.C. Kang & K.D. Hyde	*Helicosporium viridiflavum* Y.Z. Lu, J.C. Kang & K.D. Hyde	Lu et al. 2018
Helicosporium xylophilum P.N. Singh & S.K. Singh	*Tubeufia xylophila* (P.N. Singh & S.K. Singh) Y.Z. Lu & K.D. Hyde	Lu et al. 2018

including submerged wood and decaying culms of *M. floridulus* were collected in plastic bags and returned to the laboratory where they were incubated at room temperature on moist filter paper in sterile plastic boxes. Materials were examined periodically for the presence of fungal sporulating structures under a stereomicroscope (Zeiss Discovery V8) equipped with AXIOCAM 503 Color photographic system. Fungal species were identified primarily based on morphology under a Zeiss AXIOSKOP 2 PLUS compound microscope and photographed by an AXIOCAM 506 COLOR digital camera fitted to the microscope (Carl Zeiss Co. Ltd., Hsinchu City, Taiwan). Semi-permanent slides were prepared by mounting fungal material in lactophenol and sealed by applying nail polish around the margins of coverslips. Measurements of morphological characters were made with the ZEN2 (BLUE-LITE) program. All images used for figure plates were processed with Adobe Photoshop CS3 Extended version 10.0 software (Adobe Systems, USA). Single-spore isolations were performed following Goh (1999). Specimens of fungal taxa were deposited in the Herbarium (Herbarium Code: TNM) at the National Museum of Natural Science (NMNS), Taichung, Taiwan. Fungal cultures were deposited at the Bioresource Collection and Research Centre (BCRC), Food Industry Research and Development Institute, Hsinchu, Taiwan. Other dried specimens and cultures were deposited at the Department of Plant Medicine, National Chiayi University (NCYU), Chiayi, Taiwan.

Fungal DNA extraction, polymerase chain reaction (PCR), and DNA sequencing Fungal isolates grown on PDA plates for 60 days were prepared for DNA extraction. DNA extraction was carried out following Sambrook and Russell (2001). PCR amplification and sequencing were performed according to the manufacturer's protocol (Tri-I Biotech Inc., New Taipei City, Taiwan). For the nuc rDNA barcoding, the primer set

Table 2 Comparison of *Helicosporium* sensu lato

Species[Φ]	Current genus	Colony color on natural substratum	Conidiophore size (μm)	Conidiogenous cells/conidiophores	Conidial production
H. abuense	*Neohelicosporium*	Brown	95–100 × 3.5–5.5(−7)	Cylindrical teeth on shaft	Pleurogenous
H. aquaticum	*Helicosporium*	Yellowish-green	95–170 × 2–4	Cylindrical teeth on shaft	Pleurogenous
H. aureum	*Acanthohelicospora*	Yellow to olive	390–650 × 5–7	Cylindrical teeth and bladder-like projections on shaft	Pleurogenous
H. decumbens	*Helicosporium*	Dark brown	25–200 × (3.6–)4–5	Cylindrical teeth and bladder-like projections on shaft	Pleurogenous
H. dentophorum	*Tubeufia*	White	≤ 35 × 4.5–5.5	Polyblastic denticulate at conidiophore apex	Acrogenous
H. flavidum	*Helicosporium*	Yellow to yellowish-green	184–257 × 2–3.5	Cylindrical teeth and bladder-like projections on shaft	Acro-pleurogenous
H. flavisporum	*Helicosporium*	Yellow to brown	130–180 × 3.5–6	Bladder-like projections on shaft	Pleurogenous
H. flavum	*Helicosporium*	Golden yellow	36–48 × 6.5–7.5	Sympodial with denticles	Acro-pleurogenous
H. gigasporum	*Helicoma*	Brown	170–250 × 6–7	Cylindrical teeth on shaft	Pleurogenous
H. gracile	(Doubtful)	Yellow	≤ 150 × 2.5–5	Cylindrical teeth on shaft	Acro-pleurogenous
H. griseum Berk. & Curt.	*Neohelicosporium*	Pinkish-gray	≤ 400 × 3.5–4.5	Short teeth on shaft	Acro-pleurogenous
H. guianense	*Acanthohelicospora*	Yellow	≤ 500 × 3.5–4.5	Cylindrical teeth and elongated bladder-like projections on shaft	Pleurogenous
H. hiospiroides	(doubtful)	Yellow	150–250 × 5.5–8.5	Teeth or bladder-like projections on shaft	Pleurogenous
H. hongkongense	*Helicoma*	Pale brown	130–200 × 5–6	Cylindrical teeth on shaft	Pleurogenous
H. indicum	*Pseudohelicomyces*	Brown	47–145 × 3–7.5	Cylindrical teeth on shaft	Pleurogenous
H. lumbricopsis	*Helicosporium*	Gray	25–200 × 3.5–5.5	Short teeth on shaft	Acro-pleurogenous
H. luteosporum	*Helicosporium*	Yellow	68–135 × 2.5–4	Cylindrical teeth on shaft	Pleurogenous
H. murinum	*Helicosporium*	Gray	100–250 × 3.5–4.5	Short teeth on shaft	Pleurogenous
H. myrtacearum	*Neohelicosporium*	White	80–175 × 4–8	Cylindrical teeth on shaft	Acro-pleurogenous
H. neesii	*Helicosporium*	Gray	350–400 × 4–5	Bladder-like projections on shaft	Pleurogenous
H. nizamabadense	*Neohelicosporium*	Gray	50–200 × 3–5	Cylindrical teeth on shaft	Pleurogenous
H. pallidum	*Neohelicomyces*	Gray	≤ 580 × 1.5–4	Minute teeth on shaft	Pleurogenous
H. panacheum	*Helicosporium*	White	40–70 × 4.5–6	Cluster of denticles at apex of conidiophore	Acrogenous
H. pannosum	*Helicoma*	Brown	100–250 × 5–7	Cylindrical teeth on shaft	Pleurogenous
H. phragmitis	*Pseudohelicomyces*	Brown	≤ 350 × 2.5–4.5	Minute teeth on shaft	Pleurogenous
H. raghuveeri	(Doubtful)	Brown	80–170 × 6.5–8.5	–	–
H. setiferum	*Helicosporium*	Yellowish-green	125–320 × 3–5	Cylindrical teeth on shaft	Pleurogenous
H. sympodiophorum	*Neohelicosporium*	White	10–30 × 3.5–5	Monoblastic or sympodial polyblastic, conical or truncate at the apex	Acrogenous
H. taiwanense	*Neohelicosporium*	White	100–337 × 4.7–5.4	Apical and lateral denticles on shaft	Acro-pleurogenous
H. talbotii	*Pseudohelicomyces*	White	30–240 × 3–4	Cylindrical teeth on shaft	Pleurogenous
H. vegetum	*Helicosporium*	Yellow	30–360 × 3–5	Cylindrical teeth on shaft	Acro-pleurogenous
H. vesicarium	*Helicosporium*	Yellowish-green	65–120 × 3.5–5	Bladder-like projections on shaft and also arising from creeping hyphae	Pleurogenous
H. vesiculiferum	*Neohelicosporium*	White	32.5–155 × 3–7.5	Apical and lateral denticles on shaft	Acro-pleurogenous
H. virescens (Pers.) Sivan.	*Chloridium/Chaetosphaeria*	Yellowish-brown	190–600 × 5–7	Cylindrical teeth and bladder-like projections on shaft	Pleurogenous
H. viridiflavum	*Helicosporium*	Yellowish-green	250–425 × 3–4	Cylindrical teeth on shaft	Pleurogenous
H. xylophilum	*Tubeufia*	White	16–65 × 4–6.3	Cylindrical teeth on shaft	Acro-pleurogenous

Table 2 (continued)

Species[Φ]	Conidium diam. (μm)	Conidial filament width (μm)	Conidial septa	Number of coils of conidia	Remarkable features	References
H. abuense	12–24	2–2.7	6–18	2–3.5	(None)	Chouhan and Panwar 1980
H. aquaticum	10–14	1–2	indistinct	2.5–3.5	Conidiophore setiform and attenuated towards the apex	Lu et al. 2018
H. aureum	10–20	1–2	10–20	2.5–3	Hairy colony; stiff robust bristle-like conidiophores; Conidial filaments thin	Linder 1929
H. decumbens	6–9	0.75–1.5	–	1–2	Small-sized conidia, few coils (1–2); conidiophores branched	Linder 1929
H. dentophorum	30–45	2.5–3.5	17–23	2–2.25	Short but distinct conidiophores	Zhao et al. 2007
H. flavidum	16.5–22	1.5–2	12–17(−20)	2.25–3	Pale conidiophores producing conidia acro-pleurogenously	This paper
H. flavisporum	12–15	1–2	Indistinct	2.5–3.5	(None)	Lu et al. 2018
H. flavum	18–30	6–7	5–6(−7)	1–1.5	Conidia *Helicoma*-like, tightly coiled, non-hygroscopic	Brahmanage et al. 2017
H. gigasporum	70–80	6–7	–	2–2.5	Conidiophore setiform; conidia large	Tsui et al. 2001
H. gracile	10–15	1–1.5	26–32	3–3.25	Erect conidiophores arising from repent sterile or conidiogenous hyphae	Linder 1929, Lu et al. 2018
H. griseum Berk. & Curt.	18–25	1–2.5	12–14	3–4	Conidiophores branched and anastomosing	Linder 1929
H. guianense	13–22	1.2–1.5	11–18	2–3.5	Setiform conidiophores bearing distinct bladder-like conidiogenous projections with sympodial denticles	Linder 1929, Goos 1989
H. hiospiroides	21–35	1.4–2.8	1–4	1–4	Conidiophores distinctly branched	Reddy et al. 1970, Lu et al. 2018
H. hongkongense	42–50	5–7	–	2.5–3	Conidiophore setiform, wide conidial filament	Tsui et al. 2001
H. indicum	25–36	1.4–2.5	5–12	1.5–3.5	(None)	Rao and Rao 1964
H. lumbricopsis	20–28	1.5–2.5	18–25	3–4	Conidiophore when old become branched and anastomosing	Linder 1929
H. luteosporum	17–24.5	1.5–2.5	Indistinct	1.5–3	Conidiophores arising directly from substratum	Lu et al. 2017a
H. murinum	12–15	1–1.5	–	2.5–4	Erect cylindrical pale conidiophores with distinct septa	Goos 1989, Zhao et al. 2007
H. myrtacearum	13–18.5	1.8–2	8–12	2–2.5	(None)	Singh and Singh 2016
H. neesii	13–18	1–2	–	Up to 5	Conidiophores seriform, tapering and flexuous above, bearing bladder-like protrusions at the lower portion	Moore 1957
H. nizamabadense	18–28	1.4–2.2	≤ 15	2–3.5	Conidiophores arising from repent hyphae	Rao and Rao 1964
H. pallidum	10–15	1–1.5	Indistinct	2–3.5	Colonies tufted; conidiophores pale, anastomosing at apex	Linder 1929, Zhao et al. 2007
H. panacheum	20–30	2.5–4.5	–	3–5	Pale conidiophores	Moore 1954
H. pannosum	20–50	Up to 13.5	12–60	2–2.5	Conidiophore setiform; conidia echinulate; sclerotia & 2° conidia present	Goos 1989, Zhao et al. 2007
H. phragmitis	15–18	1.5–2	–	3–4	Conidia coiled 3-4times and light pink in mass	Linder 1929
H. raghuveeri	60–85	3.5–7	–	1.5–2.5	Conidial diameter is extraordinarily wide	Rao and Varghese 1988, Lu et al. 2018
H. setiferum	13–21	1–2	Indistinct	2.5–3.5	Conidiophores setiform and occasionally branched	Lu et al. 2018
H. sympodiophorum	27–36	2.5–4.5	24–45	3–4	Short sympodial conidiophores on repent hyphae among setiform conidiophores; conidial filament coiled 3.5–4 times	Zhao et al. 2007
H. taiwanense	34.7–53	3.8–5.5	20–34	1.5–2.5	Robust polydenticulate conidiophores	Kuo and Goh 2018a
H. talbotii	19–24	1.5–2.5	14–20	1.5–2.5	Conidiophores arising from repent hyphae	Goos 1989

Table 2 (continued)

H. vegetum	10–15	1	–	2–4	Conidia intercalarily produced on erect setiform conidiophores and also from simple conidiophores on repent hyphae	Linder 1929, Morgan-Jones and Goos 1992
H. vesicarium	13–18	1.5–3	indistinct	2.5–3.75	Conidiophores robust and dark; bladder-like conidiogenous cells arising from dark robust conidiophores and also from creeping hyphae	Lu et al. 2018
H. vesiculiferum	11–18	1–1.5	10–15	2–3.5	Conidiophore bears a vesicle at apex	Cruz et al. 2009
H. virescens (Pers.) Sivan.	10–20	1–2.5	–	2–4	Conidiophores erect setiform, unbranched	Gams and Holubová-Jechová 1976, Morgan-Jones and Goos 1992
H. viridiflavum	20–23	2–3.5	13–16	2–2.5	Conidiophores slender and long (up to 425 µm), arising from repent hyphae	Lu et al. 2018
H. xylophilum	13.8–40	3.5–4.3	17–24	1.5–2.5	(none)	Singh and Singh 2016

Φ Species were selected following acceptance by Goos (1989), Zhao et al. (2007), and Lu et al. (2018)

used to amplify the ITS1-5.8S-ITS2 region was ITS5 and ITS4 (White et al. 1990). The nucleotide sequence data generated in this study were deposited in GenBank.

Phylogenetic analysis Sequence data of the ITS region were used to infer phylogenetic placement of the new taxon. Additional sequences of similar taxa within the Tubeufiaceae were selected and retrieved from GenBank according to recent publications (Brahmanage et al. 2017; Luo et al. 2017; Lu et al. 2017a, b, 2018). A total of 54 nucleotide sequences were used for the phylogenetic analysis. *Patellaria quercus* (BHI-F768exna, Patellariaceae, Dothideomycetes) was selected as the outgroup taxon. MUSCLE was used for DNA alignment (Edgar 2004). Aligned sequences were analyzed using Mega7 (Kumar et al. 2016). The evolutionary history was inferred using the maximum likelihood method based on the Tamura-Nei model (Tamura and Nei 1993). Initial trees for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the maximum composite likelihood (MCL) approach, and then selecting the topology with superior log likelihood value.

Results

Phylogeny

In this paper, we only generated a new ITS sequence for GenBank (Accession no. MT939303, 862 bp) obtained from one of the new species, *Neohelicomyces longisetosus*. Neither sequence data derived from the other new species (*Helicosporium flavidum*) nor the three fungal taxa representing new records for Taiwan were successfully generated.

The phylogenetic analysis involved a dataset comprising 54 ITS sequences representing taxa in the Tubeufiaceae, with *Patellaria quercus* (BHI-F768exna) from the Patellariaceae (Dothideomycetes) being the outgroup taxon. After alignment and trimming of uneven ends, the alignment block was 718 bp long (including gaps) for analysis, with 321 distinct alignment patterns in the final dataset. Phylogenetic analysis of the dataset using the maximum likelihood method yielded a tree (Fig. 1) with the highest log likelihood (−2641.81), showing several clusters of fungal taxa representing various generic lineages in which the overall topology agreed with the phylogenetic backbone of the Tubeufiales (Lu et al. 2018). The tree showed that fungal species were clustered accordingly into seven genera preselected for analysis, namely *Acanthohelicospora*, *Helicoma*, *Helicomyces*, *Helicosporium*, *Neohelicomyces*, *Neohelicosporium*, and *Parahelicomyces* (formerly *Pseudohelicomyces*). The new taxon *Neohelicomyces longisetosus* (NCYU-106H1-1) was positioned within the clade

Table 3 Comparison of *Neohelicomyces* species

Species	Colony color on natural substratum	Conidiophore size (µm)	Conidiogenous cell/conidiophore	Conidial production	Conidium diam. (µm)	Conidial filament width (µm)	Number of coils of conidia	Remarkable features	Reference
N. aquaticus Z.L. Luo, Bhat & K.D. Hyde	White	240–335 × 5–6	Intercalary cylindrical denticles on shaft	Pleurogenous	–	2.5–3.5	2–2.5	Conidiophores wide, pale, septa distinct; conidia guttulate	Luo et al. 2017
N. deschampsiae Crous & R.K. Schumach.	White	150–220 × 3–4	Intercalary cylindrical denticles on shaft	Pleurogenous	19–22	2–2.5	2–3	(None)	Crous et al. 2019a
N. grandisporus Z.L. Luo, Boonmee & K.D. Hyde	White	107–161 × 4–5	Polydenticulate	Acro-pleurogenous	–	4.5–5.5	1–1.5	Conidia loosely coiled, rounded at ends	Luo et al. 2017
N. hyalosporus Y.Z. Lu, J.C. Kang & K.D. Hyde	White	210–290 × 3–4	Terminal and intercalary cylindrical denticles on shaft	Acro-pleurogenous	14–20	1.5–2.5	2.5–3.75	Cylindrical conidiophores with terminal and intercalary polydenticulate conidiogenous cells	Lu et al. 2018
N. longisetosus S.Y. Hsieh, C.H. Kuo & Goh	White to grayish--brown	(14.5) 22–30.5 × (2)-3–3.5	Geniculate conidiophores bearing polydenticulate conidiogenous cells	Acro-pleurogenous	20–24	(1.5)2–3.5	2.75–4	Colony appear reticulate due to the presence of setae (150–230 µm long) and ramifying superficial hyphae bearing conidiophores	This paper
N. melaleucae Crous	Pale brown	3–4 wide; length lacking information	Mono- to polydenticulate	Pleurogenous	13–17	2	3	Conidiophores as repent hyphae, bearing cylindrical conidiogenous denticles	Crous et al. 2019b
N. pallidus Y.Z. Lu & K.D. Hyde	Gray	≤ 580 × 1.5–4	Minute teeth on shaft	Pleurogenous	10–15	1–1.5	2–3.5	Colonies tufted; conidiophores pale, anastomosing at apex	Lu et al. 2018
N. pandanicola Tibpromma & K.D. Hyde	Pinkish to pale brown	110–220 × 3–6	Polyblastic denticles on shaft	Pleurogenous	28–44	2–3	2.5–3.5	Polydenticulate conidiogenous cells on long cylindrical conidiophores	Tibpromma et al. 2018
N. submersus Z.L. Luo, Hong Y. Su & K.D. Hyde	White	172–285 × 3.5–4.5	Intercalary cylindrical denticles on shaft	Pleurogenous	–	2.5–3.5	3–3.5	Conidiophores branched	Luo et al. 2017

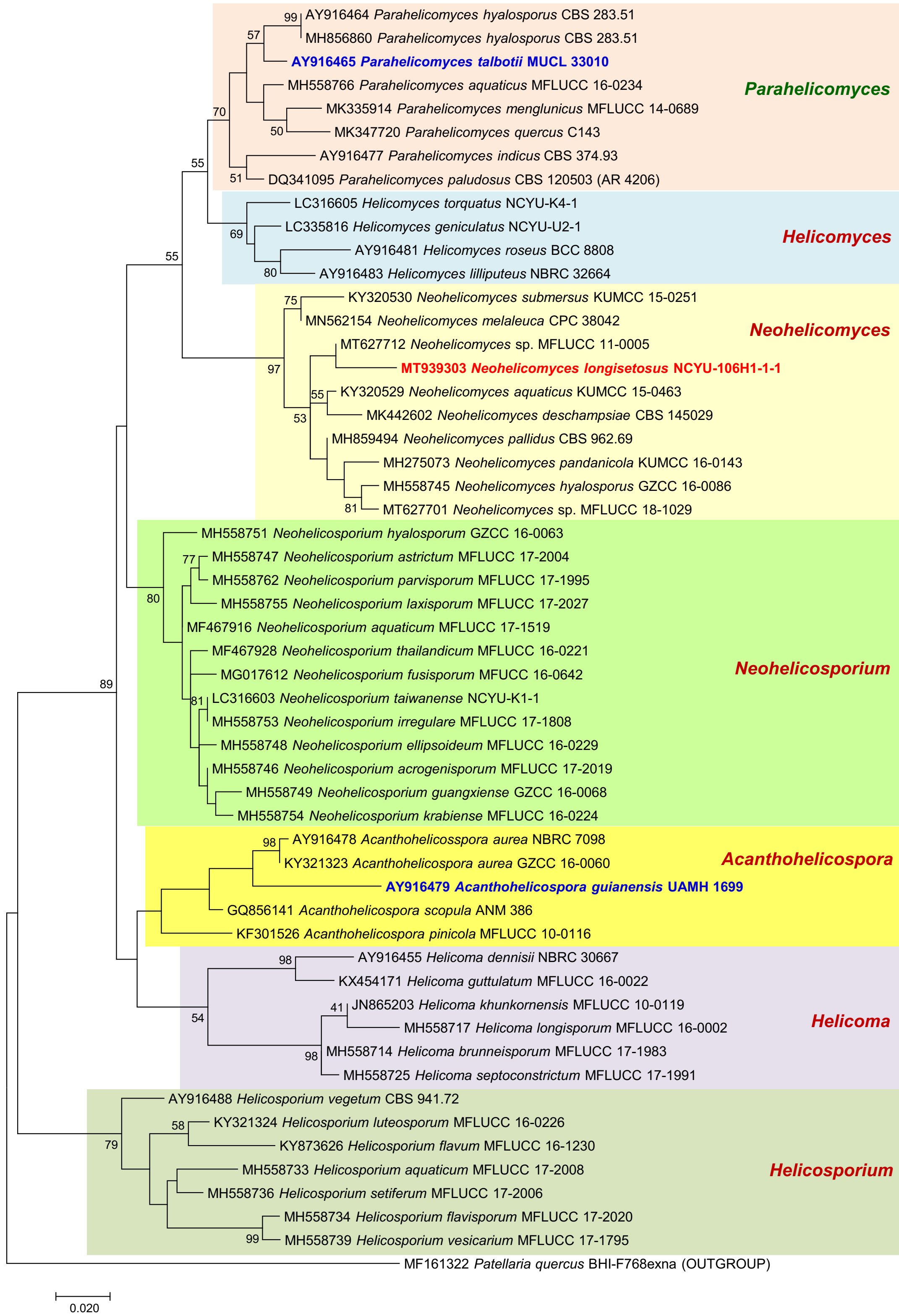

Fig. 1 Phylogenetic tree (TreeBASE TB2:S26860) inferred from ITS sequences of *Helicosporium* sensu lato and other representative helicosporous taxa from the Tubeufiaceae. The evolutionary history was inferred using the maximum likelihood method. The tree with the highest log likelihood (− 2641.81) is shown. The percentage of trees ≥ 50 in which the associated taxa clustered together is shown next to the branches. The tree is rooted with *Patellaria quercus* and drawn to scale, with branch lengths measured in the number of substitutions per site. The new taxon is highlighted in bold red, whereas the taxa representing new records for Taiwan mycoflora are in bold blue

comprising the genus *Neohelicomyces* with high bootstrap support (97%). The tree also showed that *Acanthohelicospora guianensis* (UAMH 1699) and *Parahelicomyces talbotii* (MUCL 33010), representing two of the new records for Taiwan mycoflora, were clustered accordingly with other species in their respective genera.

Taxonomy

Helicosporium flavidum S.Y. Hsieh, C.H. Kuo & Goh, sp. nov. Fig. 2.

Mycobank No.: MB 837330.

Etymology: flavidum, referring to the yellow colonies of this species.

Colonies on natural substratum effuse, yellow to yellowish-green, loose cottony layer separable from the substratum. *Mycelium* mostly superficial and partly immersed, composed of branched, septate, smooth hyphae. *Stalked-sclerotia* absent. *Conidiophores* macronematous, mononematous, erect, simple or occasionally branched near the base, straight or slightly curved, cylindrical, uniform in width, very pale brown, uniform in color, smooth-walled, distinctly 8–14-septate, sometimes slightly constricted at the septa, bearing lateral small cylindrical conidiogenous denticles or bladder-like outgrowths near the septa along the shaft, 184–257 μm long, 2–3.5 μm wide. *Conidiogenous cells* monoblastic or more commonly polyblastic, integrated, determinate or with sympodial proliferations, cylindrical, or bladder-like with denticles. *Conidia* acro-pleurogenous, hyaline, (16.5–)17–22 μm in diam, coiled (2.25–)2.5–3 times; conidial filament hygroscopic, smooth-walled, 12–17(−20)-septate, 1.5–2 μm thick, conidial secession schizolytic. *Secondary conidia* absent. *Teleomorph* unknown.

Specimen examined: TAIWAN, Chiayi County, Fanlu Township, Huoshauliao (23.48169–120.62164, 778 m a.s.l.), on a decaying culm of *Miscanthus floridulus* (Poaceae)

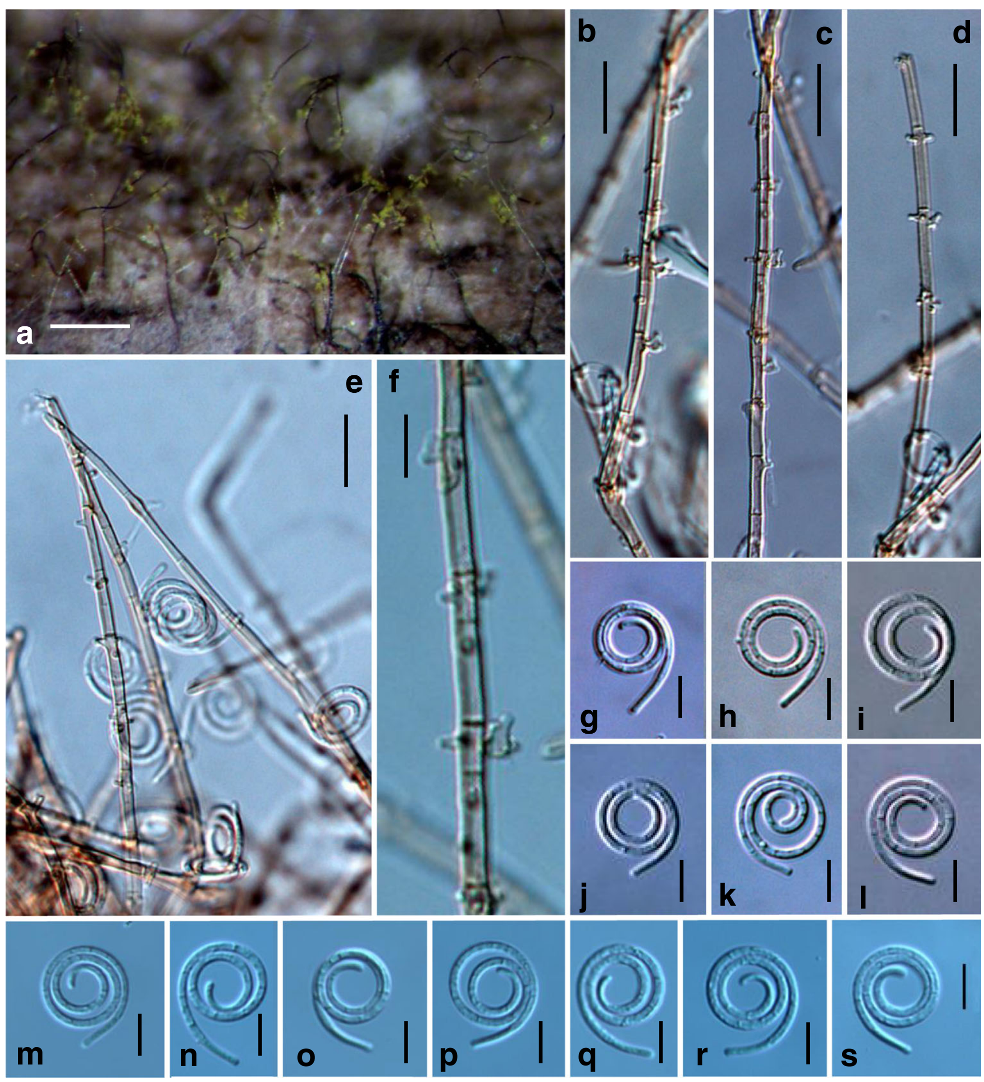

Fig. 2 *Helicosporium flavidum* (NCYU-C8-4). **a** Colonies on natural substratum. **b**–**f** Conidiophores, bearing cylindrical tooth-like or bladder-like conidiogenous projections along the shaft. **g**–**s** Conidia. Scale bar: **a** = 500 μm; **b**–**e** = 20 μm; **f**–**s** = 10 μm

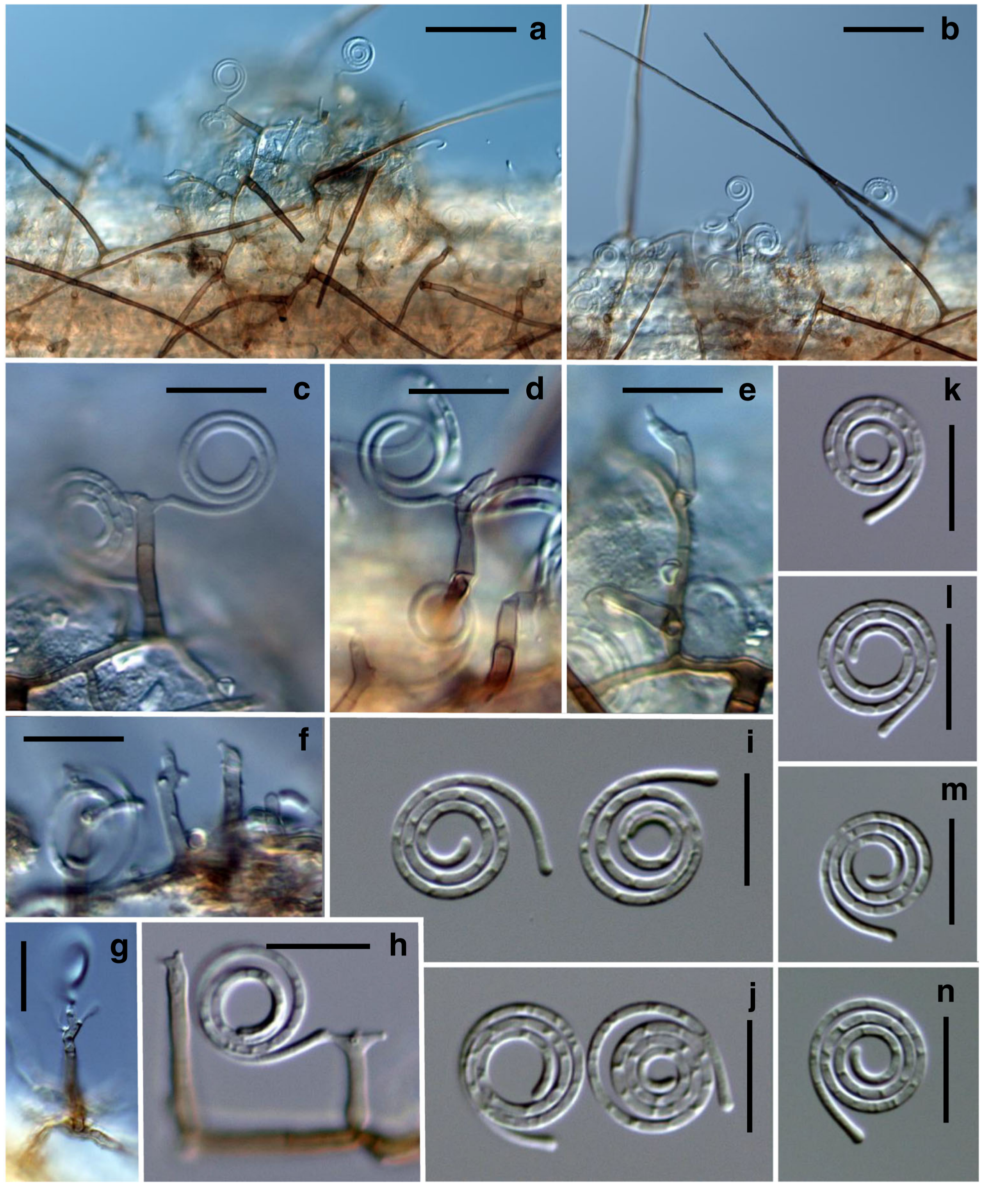

Fig. 3 *Neohelicomyces longisetosus* (NCYU-106H1-1). **a**, **b** Setae and conidiophores arising from repent hyphae. **c**–**h** Conidiophores, producing conidia sympodially from denticles. **i**–**n** Conidia. Scale bar: **a**, **b** = 50 μm; **c**–**n** = 20 μm

submerged in a freshwater stream, leg. Chang-Hsin Kuo, 13 May, 2016, NCYU-C8-4 (**holotypus**: TNM F0034160).

Known distribution: Taiwan.

Note: We have not successfully obtained a living culture of this species for DNA sequencing. Identification of this species is therefore based on morphological data. This species is distinguished from other species of *Helicosporium* sensu stricto (Lu et al. 2018) in having pale conidiophores bearing both cylindrical teeth and bladder-like conidiogenous projections along the shaft.

To facilitate identification of species based solely on morphology, a key to 14 *Helicosporium* species accepted by Goos (1989), Zhao et al. (2007), and Lu et al. (2018) is given as follows:

1. Colonies on natural substratum yellow or yellowish-green ……………………......................……………………..….. 2

1. Colonies on natural substratum white, gray or brown ……………………….......................………….…..……….. 10

2. Conidiophores 35–48 × 6.5–7.5 μm, bearing sympodial denticles at the apex; conidia acro-pleurogenous, *Helicoma*-like, non-hygroscopic, with thick filament (6–7 μm), tightly coiled 1–1.5 times, distinctly 5–6-septate…........…. *H. flavum.*

2. Conidiophores 65–425 × 2–6 μm, bearing cylindrical teeth or bladder-like projections on the shaft; conidial filaments thinner (1–3.5 μm wide), loosely coiled 1.5–3.75 times, indistinctly multiseptate …...........................……………….3

3. Conidiophores bearing bladder-like conidiogenous projections on the shaft ………………….........................…... 4

3. Conidiophores bearing cylindrical teeth on the shaft, bladder-like projections lacking 6

4. Conidiophores slender, 184–257 × 2–3.5 μm, pale, bearing both cylindrical teeth and bladder-like conidiogenous projections on the shaft; conidia acro-pleurogenous, 16.5–22 μm in diam. ………...................……………..…….. *H. flavidum.*

4. Conidiophores 65–180 × 3.5–6 μm, dark brown, primarily bearing only bladder-like projections on the shaft; conidia pleurogenous, 12–18 μm in diam. …………….............…. 5

5. Conidiophores 65–120 μm long; conidial diameter 13–18 μm, conidial filaments 1.5–3 μm wide ...... *H. vesicarium.*

5. Conidiophores 130–180 μm long; conidial diameter 12–15 μm, conidial filaments 1–2 μm wide…… *H. flavisporum.*

6. Conidia produced acro-pleurogenously from intercalary cylindrical teeth on setiform conidiophores (30–360 × 3–5 μm) and also from short lateral conidiophores on repent hyphae, 10–15 μm in diam; conidial filaments 1 μm wide and coiled 2–4 times ……………..........................… *H. vegetum.*

6. Conidia borne pleurogenously from setiform or slender conidiophores only, or combination of morphological features not as above ……..................................…………………..….. 7

7. Conidiophores 68–170 μm long …………...……….... 8

7. Conidiophore 125–425 μm long ……..........…….….. 9

8. Conidiophores 68–135 μm long; conidial diameter 17–24.5 μm, conidial filaments 1.5–2.5 μm wide, coiled 1.5–3 times ……...…………...........……………… *H. luteosporum.*

8. Conidiophores 95–170 μm long; conidial diameter 10–14 μm, conidial filaments 1–2 μm wide, coiled 2.5–3.5 times ……………...................................………….*H. aquaticum.*

9. Conidiophores setiform, 125–320 μm long, occasionally branched; conidial diameter 13–21 μm, conidial filaments 1–2 μm wide, coiled 2.5–3.5 times ……....….…. *H. setiferum.*

9. Conidiophores slender, 250–425 μm long; conidial diameter 20–23 μm, conidial filaments 2–3.5 μm wide, coiled 2–2.5 times …………………..…………….…. *H. viridiflavum.*

10. Conidial diameter up to 18 μm ……………........…... 11

10. Conidial diameter 20–30 μm …………........…….. 13

11. Colonies on natural substratum dark brown; conidiophores branched and decumbent, bearing bladder-like projections; conidia small (6–9 μm diam.), coiled 1–2 times.……..…… *H. decumbens.*

11. Colonies on natural substratum gray; conidia larger (12–18 μm diam.), coiled 2.5–5 times …........................... 12

12. Conidiophores 100–250 μm long, cylindrical with a blunt apex, bearing short cylindrical conidiogenous denticles on the shaft; conidia 12–15 μm in diameter, conidial filaments coiled 2.5–4 times ………….........…….... *H. murinum.*

12. Conidiophores 350–400 μm long, setiform, tapering and flexuous above, bearing conidiogenous bladder-like projections; conidia 13–18 μm in diameter, conidial filaments coiled up to 5 times ……………...............……… *H. neesii.*

13. Conidiophores dark, 25–200 μm long, bearing short cylindrical teeth on the shaft; conidia acro-pleurogenous; conidial filaments 1.5–2.5 μm wide …..........… *H. lumbricopsis.*

13. Conidiophores pale, 40–70 μm long, bearing clusters of minute denticles at the apex; conidia acrogenous; conidial filaments 2.5–4.5 μm wide ……....………… *H. panacheum.*

Neohelicomyces longisetosus S.Y. Hsieh, C.H. Kuo & Goh, sp. nov. Fig. 3.

Mycobank No.: MB 837331.

Etymology: longisetosus, referring to the long setae of this species.

Colonies on natural substratum effuse, white to grayish-brown, reticulate. *Mycelium* mostly superficial and partly immersed, composed of branched, subhyaline to brown, septate, smooth, 2–3 μm wide hyphae, bearing conidiophores and setae. *Stalked-sclerotia* absent. Setae anchoring on the surface of natural substratum and arising at right angle from the superficial hyphae, brown, entirely sterile, erect, stiff, unbranched, straight, multiseptate, smooth-walled, (138)150–230 μm long, (3.5)5–6.5 μm at the base, gradually attenuate towards the obtuse apex which is 1.5–3 μm wide. *Conidiophores* macronematous, mononematous, arising at right angle from the superficial hyphae, straight to flexuous or slightly geniculate, unbranched, 0–3-septate, not constricted at the septa, straight or flexuous, bearing small cylindrical conidiogenous denticles at the apex, uniformly pale grayish-brown, (14.5) 22–30.5 μm long, (2)3–3.5 μm wide, uniform in width. *Conidiogenous cells* mono-or polyblastic, integrated, with sympodial proliferations, bearing tooth-like projections; denticles distinct, cylindrical, 1.5–2 × 1–2 μm. *Conidia* hyaline, (15.5)20–24 μm diam, coiled (2.75–)3–3.5(−4) times; conidial filament hygroscopic, smooth-walled, (20)23–28-septate, (1.5)2–3.5 μm thick, conidial secession schizolytic. *Secondary conidia* absent. *Teleomorph* unknown.

Specimen examined: TAIWAN, Chiayi County, Meishan Township (23.557750–120.729100, 646 m a.s.l.), on a decaying culm of *Miscanthus floridulus* (Poaceae) submerged in a freshwater stream, leg. Chang-Hsin Kuo, 4 Aug. 2017, NCYU-106H1–1 (**holotypus**: TNM F0034161); ex-type culture: NCYU-106H1-1-1; GenBank: ITS = MT939303.

Known distribution: Taiwan.

Note: Luo et al. (2017) introduced the genus *Neohelicomyces*, segregating it from *Helicosporium* sensu lato based primarily on molecular phylogeny. The genus currently comprises 8 species (Luo et al. 2017; Tibpromma et al. 2018; Lu et al. 2018; Crous et al. 2019a, b), all of which are supported by molecular data. We have successfully obtained living cultures of this species by single-spore isolation (Goh 1999) and have sequenced its ITS rDNA region. Identification of this species is therefore based on molecular and morphological data. This species, as its species epithet suggests, is distinct among other *Neohelicomyces* species (Table 3) in having polyblastic sympodial conidiophores among distinct sterile setae which are long, straight, unbranched, stiff, and dark. Another distinct feature of this species is that its colonies on the natural substratum appear reticulate due to the presence of setae and conidiophores that arise at about right angle from the superficial repent hyphae.

Parahelicomyces Goh, gen. nov.

Mycobank No.: MB 837332.

≡ *Pseudohelicomyces* Y.Z. Lu, J.K. Liu & K.D. Hyde, nom. illegit., Art. 53.1, Fungal Diversity 92: 248 (2018); non *Pseudohelicomyces* Garnica & E. Valenz., Mycol. Res. 104: 739 (2000).

Etymology: *para*, from Greek prefix, meaning "side by side," referring to members of this genus being morphologically similar to *Helicomyces* but phylogenetically forming a separate clade adjacent to the clade comprising true *Helicomyces* species.

Type species: *Parahelicomyces talbotii* (Goos) S.Y. Hsieh, Goh & C.H. Kuo.

Note: *Pseudohelicomyces* Y.Z. Lu, J.K. Liu & K.D. Hyde, belonging to the Tubeufiaceae (Lu et al. 2018), is a later homonym of *Pseudohelicomyces* Garnica & E. Valenz., belonging to the Hymenogastraceae, (Valenzuela and Garnica 2000). A new name is therefore required for this genus.

Parahelicomyces talbotii (Goos) S.Y. Hsieh, Goh & C.H. Kuo, comb. nov. Figs. 4, 5.

Mycobank No.: MB 837333.

Basionym: Helicosporium talbotii Goos, Mycologia 81: 368 (1989).

≡ *Helicosporium ramosum* P.H.B. Talbot, Bothalia 6: 493 (1956) [non *Helicosporium ramosum* (Berk. & M.A. Curtis) Massee, 1893].

≡ *Pseudohelicomyces talbotii* (Goos) Y.Z. Lu & K.D. Hyde, Fungal Divers. 92: 252 (2018).

Colonies on natural substratum effuse, white, cottony, pulverulent. *Mycelium* mostly superficial and partly immersed, composed of branched, subhyaline to fuscous, smooth-walled, septate hyphae, 2.5–4.5 µm wide. *Stalked-sclerotia* absent. *Conidiophores* macronematous, mononematous, arising from superficial repent mycelium, branching below, anastomosing, straight or flexuous, subhyaline to very dilute brown, 3–9-septate, bearing small cylindrical conidiogenous tooth-like protuberances along the shaft near the septa, (74–)100–245 µm long, (2–)2.5–3.5(−4) µm wide. *Conidiogenous cells* cylindrical, monoblastic or rarely polyblastic, sometimes bladder-like and bearing minute tooth-like projections. *Conidia* hyaline, 16–18.5(−20) µm diam, coiled (2.5–)2.75–3.25 times; conidial filament hygroscopic, smooth-walled, indistinctly 21–23(−26)-septate, 1.5–2 µm thick, conidial secession schizolytic. *Secondary conidia* absent. *Teleomorph* unknown.

Specimens examined: TAIWAN, CHIAYI COUNTY: Fanlu Township, Huoshauliao (23.48000–120.62108, 761 m a.s.l.), on debarked wood submerged in a freshwater stream, 13 May 2016, leg. Chang-Hsin Kuo, NCYU-CC4-3. ibid. (23.47621–120.64211, 573 m a.s.l.), on a decaying culm of *Miscanthus floridulus* (Poaceae) submerged in a freshwater stream, 5 Feb 2017, leg. Chang-Hsin Kuo**,** NCYU-H3-2.

Known distribution: Japan, Mainland China, Mexico, South Africa, Taiwan, Thailand.

Note: This species is a new record for Taiwan mycoflora (Taiwan Biodiversity Information Facility 2020). We have not successfully obtained a living culture of this species collected from Taiwan for DNA sequencing. Identification of this species is therefore based on morphological data. The key identification features of this species are the white powdery colonies on natural substratum, with pale conidiophores arising from superficial repent mycelium, bearing primarily tooth-like cylindrical conidiogenous projections along the shaft.

The following six species of *Pseudohelicomyces* (Lu et al. 2018) are transferred to *Parahelicomyces* as new combinations.

Parahelicomyces aquaticus (Y.Z. Lu, Boonmee & K.D. Hyde) S.Y. Hsieh, Goh & C.H. Kuo, comb. nov.

Mycobank No.: MB 837334.

Basionym: Pseudohelicomyces aquaticus Y.Z. Lu, Boonmee & K.D. Hyde, Fungal Diversity 92: 250 (2018).

Parahelicomyces hyalosporus (Y.Z. Lu, J.K. Liu & K.D. Hyde) S.Y. Hsieh, Goh & C.H. Kuo, comb. nov.

Mycobank No.: MB 837335.

Basionym: Pseudohelicomyces hyalosporus Y.Z. Lu, J.K. Liu & K.D. Hyde, Fungal Diversity 92: 251 (2018).

Parahelicomyces indicus (P.Rag. Rao & D. Rao) S.Y. Hsieh, Goh & C.H. Kuo, comb. nov.

Mycobank No.: MB 837336.

Basionym: Helicosporium indicum P.Rag. Rao & D. Rao, Mycopath. Mycol. appl. 24: 32 (1964).

≡ *Pseudohelicomyces indicus* (P.Rag. Rao & D. Rao) Y.Z. Lu & K.D. Hyde, Fungal Diversity 92: 251 (2018).

Parahelicomyces menglunicus (J.F. Li, Rungtiwa Phookamsak & K.D. Hyde) S.Y. Hsieh, Goh & C.H. Kuo, comb. nov.

Mycobank No.: MB 837337.

Basionym: Pseudohelicomyces menglunicus J.F. Li, Rungtiwa Phookamsak & K.D. Hyde, Fungal Diversity 95: 87 (2019).

Parahelicomyces paludosus (P. Crouan & H. Crouan) S.Y. Hsieh, Goh & C.H. Kuo, comb. nov.

Mycobank No.: MB837338.

Basionym: Nectria paludosa P. Crouan & H. Crouan, Florule Finist re (Paris): 38 (1867).

≡ *Ophionectria paludosa* (P. Crouan & H. Crouan) Sacc., Michelia 1(no. 3): 323 (1878).

≡ *Tubeufia paludosa* (P. Crouan & Crouan) Rossman, Mycologia 69: 383 (1977).

≡ *Helicomyces paludosus* (P. Crouan & H. Crouan) Boonmee & K.D. Hyde [as '*paludosa*'], Fungal Diversity 68: 274 (2014).

≡ *Pseudohelicomyces paludosus* (P. Crouan & H. Crouan) Y.Z. Lu & K.D. Hyde, Fungal Diversity 92: 252 (2018).

= *Helicosporium phragmitis* Höhn., Annales Mycologici 3: 338 (1905).

= *Tubeufia coronata* Penz. & Sacc., Malpighia 11: 517 (1897).

= *Tubeufia anceps* Penz. & Sacc., Malpighia 11: 518 (1897).

≡ *Ophionectria anceps* (Penz. & Sacc.) Höhn., Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Math.-naturw. Klasse Abt. I 128: 562 (1919).

Parahelicomyces quercus (Jayasiri, E.B.G. Jones & K.D. Hyde) S.Y. Hsieh, Goh & C.H. Kuo, comb. nov.

Mycobank No.: MB 837339.

Basionym: Pseudohelicomyces quercus Jayasiri, E.B.G. Jones & K.D. Hyde, Mycosphere 10: 164 (2019).

Two other new records of *Helicosporium* sensu lato for Taiwan are described as follows:

Acanthohelicospora guianensis (Linder) Y.Z. Lu & K.D. Hyde, Fungal Diver. 92: 145 (2018) (Fig. 6).

Basionym: Helicosporium guianense Linder [as '*guianensis*'], Ann. Mo. bot. Gdn. 16: 280 (1929).

Colonies on natural substratum effuse, yellow, cottony. *Mycelium* mostly superficial and partly immersed, composed of branched, septate hyphae, 2.5–4.5 μm wide. *Stalked-sclerotia* absent. *Conidiophores* macronematous, mononematous, erect, stiff and bristle-like, unbranched or branched, anastomosing, straight or flexuous, distinctly bearing bladder-like conidiogenous projections along the shaft, uniformly brown, distinctly multiseptate, 280–495 μm long, 4.7–5.4 μm wide. *Conidiogenous cells* bladder-like, polyblastic, sympodial, bearing tooth-like projections. *Conidia* pleurogenous, hyaline, hygroscopic, 13–22 μm diam, coiled 2–3 times; conidial filament 1.2–1.5 μm wide, 11–18-septate; conidial secession schizolytic. *Secondary conidia* absent. *Teleomorph* unknown.

Specimen examined: TAIWAN, CHIAYI COUNTY: Fanlu Township, Huoshauliao (23.48169–120.62164, 778 m a.s.l.), on debarked wood submerged in a freshwater stream, 13 May 2016, leg. Chang-Hsin Kuo, NCYU-E1-1.

Known distribution: Brazil, British Guiana, Cuba, India, Mainland China, Mexico, New Guinea, Panama, Taiwan.

Note: The genus *Acanthohelicospora* was introduced by Boonmee et al. (2014) based on morphology and phylogenetic evidence. The genus currently comprises 4 species (Boonmee et al. 2014; Rossman et al. 2016; Lu et al. 2018). We have not successfully obtained a living culture of this species collected from Taiwan for DNA sequencing. Identification of this species is therefore based on morphological data. This species is distinct in having setiform conidiophores which bear distinct bladder-like conidiogenous projections with sympodial denticles.

Neohelicosporium sympodiophorum (G.Z. Zhao, Xing Z. Liu & W.P. Wu) Y.Z. Lu & K.D. Hyde, Fungal Diver. 92: 246 (2018). Fig. 7.

Basionym: Helicosporium sympodiophorum G.Z. Zhao, Xing Z. Liu & W.P. Wu, Fungal Divers. 26: 375 (2007).

Colonies on natural substratum effuse, white, velvety. *Mycelium* mostly superficial and partly immersed, composed of branched, septate hyphae, 3.5–5 μm wide. *Stalked-sclerotia* absent. *Conidiophores* macronematous, mononematous, of two types: setiform conidiophores erect, arising from superficial repent hyphae, cylindrical, with a blunt sterile apex, 140–195 μm × 4–5 μm, up to 9-septate, pale grayish-brown, straight or slightly flexuous, unbranched or bearing short geniculate conidiophores at the lower portion, scarcely bearing small intercalary cylindrical conidiogenous denticles; geniculate conidiophores cylindrical, arising as short later branches from the lower portion of the setiform conidiophores or borne directly from the superficial repent hyphae, bearing sympodially several conidiogenous denticles at the apex, uniformly pale grayish-brown, 2–3-septate, (9.5–)12–30 μm × 3.5–5. *Conidiogenous cells* mono- or more commonly polyblastic, bearing small denticles, sympodially regenerating. *Conidia* acrogenous, solitary, hyaline, smooth-walled, 26.5–31 μm diam., conidial filament 2.8–3.5 μm thick, slightly hygroscopic, 20–34-septate, coiled (2.75–)3–3.25 times, conidial secession schizolytic. *Secondary conidia* absent. *Teleomorph* unknown.

Specimen examined: TAIWAN, CHIAYI COUNTY: Fanlu Township, Huoshauliao (23.47621–120.64211, 573 m a.s.l.), on a decaying culm of *Miscanthus floridulus* (Poaceae) submerged in a freshwater stream, 5 Feb 2017, leg. Chang-Hsin Kuo, NCYU-H4-1.

Known distribution: Mainland China, Taiwan.

Note: The genus *Neohelicosporium* was established by Lu et al. (2017b) based on morphology and phylogenetic evidence. The genus currently comprises 23 species (Lu et al. 2017b, 2018). We have not successfully obtained a living culture of this species collected from Taiwan for DNA sequencing. Identification of this species is therefore based on morphological data. This species is distinct in having short sympodial conidiophores which are borne primarily on repent hyphae among setiform conidiophores, producing conidia with a thick filament that coil 3.5–4 times and distinctly septate.

Discussion

In this paper, we described five species of *Helicosporium* sensu lato from Taiwan, using current generic names proposed by Lu et al. (2018). We have only obtained a pure culture of

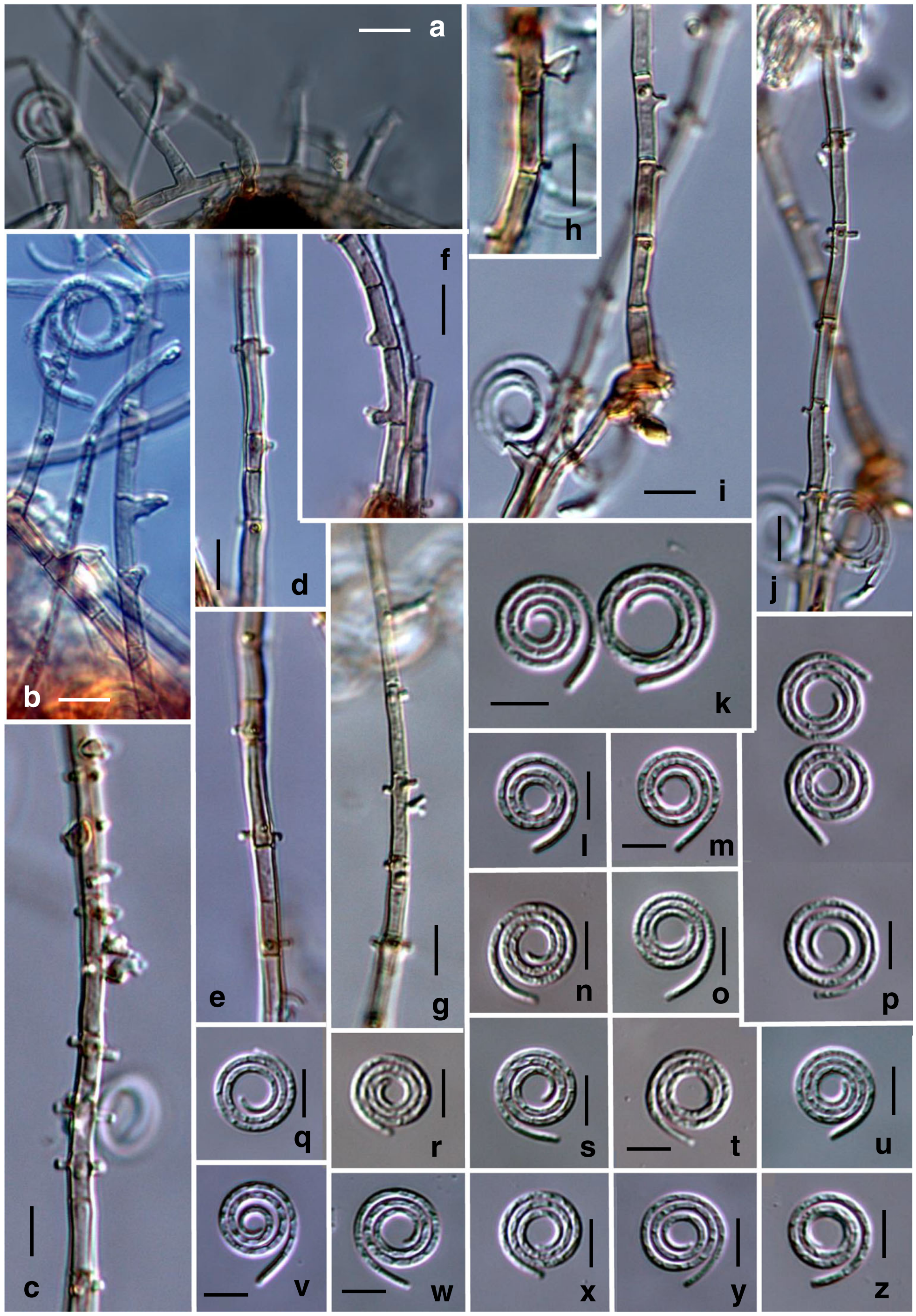

Fig. 4 *Parahelicomyces talbotii* (NCYU-CC4-3). **a** Conidiophores arising from repent hyphae. **b**–**j** Conidiophores, bearing cylindrical tooth-like conidiogenous projections along the shaft. **k**–**z** Conidia. Scale bar: **a**–**z** = 10 µm

Neohelicomyces longisetosus for DNA sequencing but we were not successful for the other four species. Despite this shortcoming, we retrieved the sequences from GenBank for *Acanthohelicospora guianensis* and *Parahelicomyces talbotii* (*Pseudohelicomyces*) and included them in our phylogenetic analysis. Unfortunately, sequence data for *Neohelicosporium sympodiophorum* are currently not available in GenBank and, therefore, could not be included in our phylogenetic tree. Likewise, we do not have sequence data for *Helicosporium flavidum*, and its identification could only be made based on morphology.

In this paper, we compiled a checklist of current names for taxa previously and recently assigned to *Helicosporium* (Table 1). We have also provided a synopsis of species accepted in *Helicosporium* sensu stricto (Table 2), with a key to these species. Lu et al. (2018) accepted 13 *Helicosporium* species; however, two of them were not included in our synopsis and key. We excluded *H. albidum* Grove (Grove 1886)

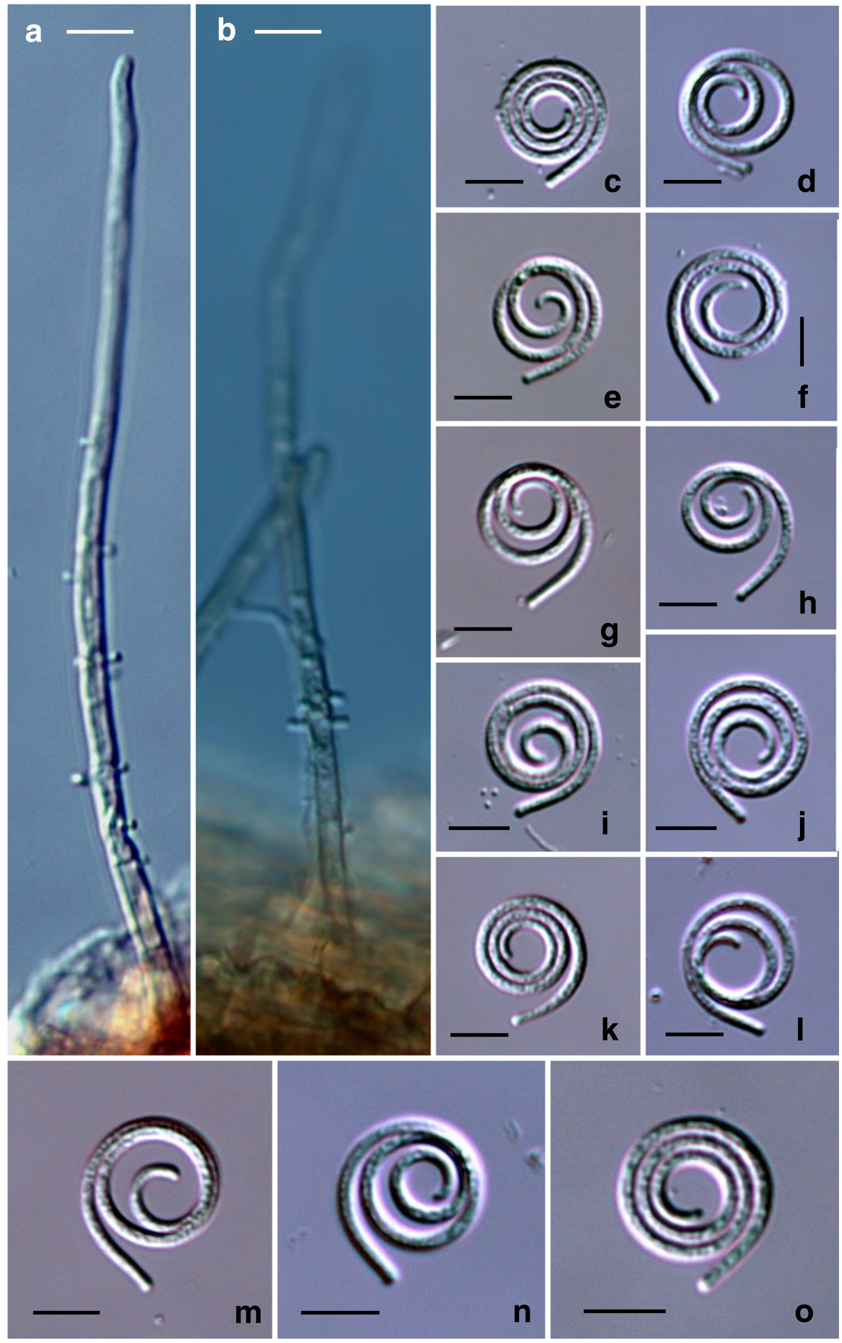

Fig. 5 *Parahelicomyces talbotii* (NCYU-H3-2). **a**, **b** Conidiophores, bearing cylindrical tooth-like conidiogenous projections along the shaft. **c**–**o** Conidia. Scale bar: **a**–**q** = 10 μm

and *H. melghatianum* Hande (Dharkar et al. 2010) due to the following reasons: *Helicosporium albidum* was regarded as "questionable" by Moore (1955) and Goos (1989) because the material of the fungus was unavailable and the description was inadequate. However, Lu et al. (2018) treated it as a valid *Helicosporium* species, by simply stating that "based on its morphological similarities to *Helicosporium*" (Lu et al. 2018, p. 217), without examining authentic material (unavailable). Moreover, it was impossible to make any logical judgement if the original description was inadequate (Moore 1955; Goos 1989). Likewise, we do not agree with Lu et al. (2018) to accept *H. melghatianum* by simply saying that "its morphology corresponds to *Helicosporium*" (Lu et al. 2018, p. 217), for which a sound basis for taxonomic judgement is lacking. We proposed to reject *H. melghatianum* because (1) the original description of this species (Dharkar et al. 2010) was too meager and incomplete; (2) the original illustration was of extremely poor quality, so the taxon could not be compared with the other species.

We have included *H. vegetum* Nees (Nees 1817), the type of the genus, and *H. neesii* R.T. Moore (Moore 1957) as two different species in the synopsis as well as the taxonomic key,

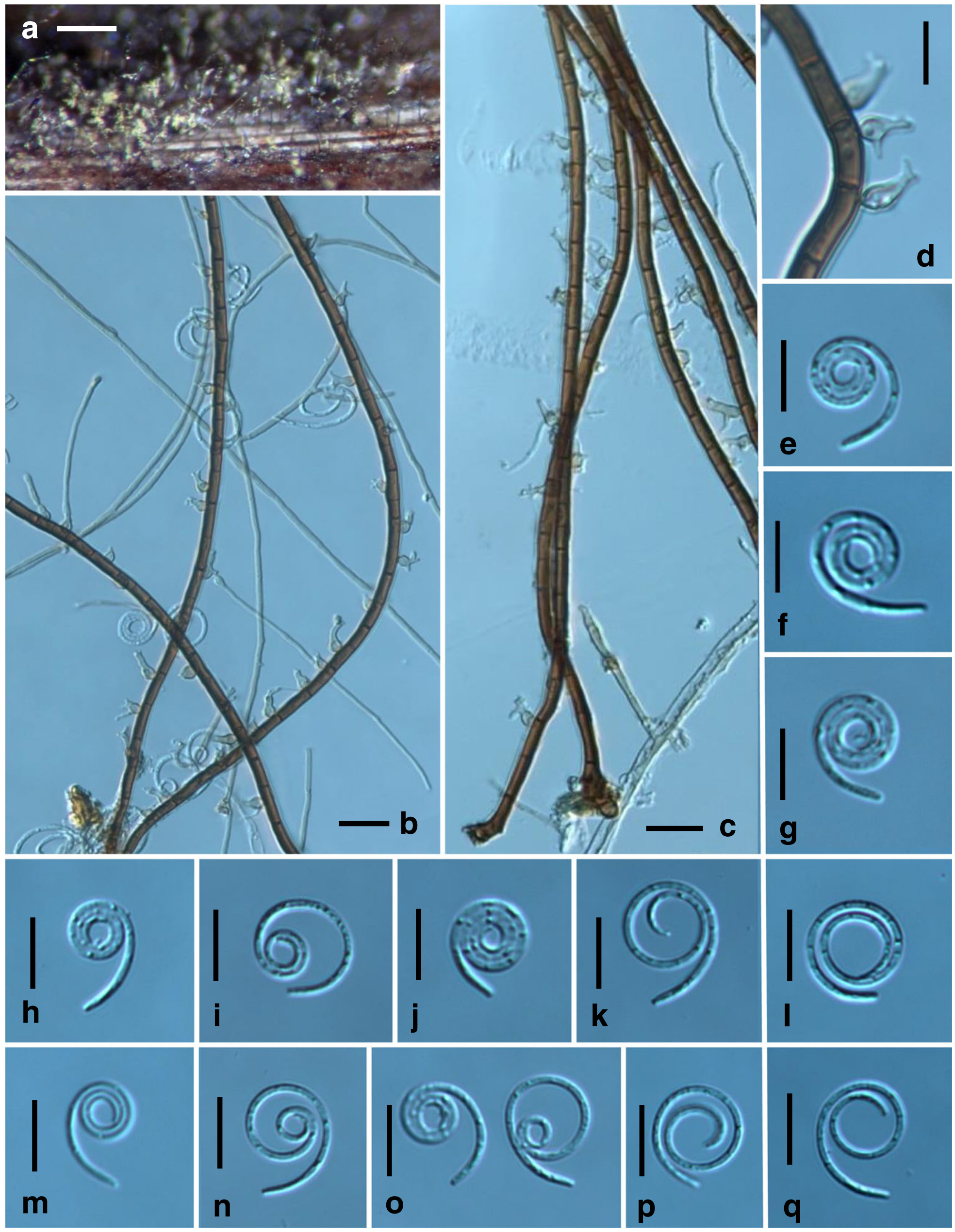

Fig. 6 *Acanthohelicospora guianensis* (NCYU-E1-1). **a** Colonies on natural substratum. **b**, **c** Conidiophores, bearing bladder-like polyblastic conidiogenous cells along the shaft. **d** Higher magnification of a part of conidiophore showing the bladder-like, polyblastic conidiogenous cells. **e**–**q** Conidia. Scale bar: **a** = 500 μm; **b**, **c** = 20 μm; **d**–**q** = 10 μm

although there have been taxonomic confusions in these two species. Both *H. vegetum* and *H. neesii* had been synonymized earlier under *H. virescens* (Pers.) Sivan. by Goos (1989). However, Morgan-Jones and Goos (1992) later synonymized *H. virescens* under *Chloridium virescens* (Pers.) W. Gams & Hol.-Jech. and listed *H. neesii* as a synonym of *H. vegetum*. Based on a careful morphological comparison between *H. neesii* and *H. vegetum*, we concur with the opinion of Lu et al. (2018) that they are two different species (Table 2), especially distinguishable in the type of conidiogenous cells (i.e., cylindrical teeth or bladder-like projections) that they have. Although molecular data are currently lacking for *H. neesii*, we agree with Lu et al. (2018) that this taxon should be restored as a valid species of *Helicosporium* sensu stricto, the current generic concept of which is circumscribed based on phylogeny and morphology (Lu et al. 2018). Morphological data used to compile the synopsis and the key in this paper for *H. neesii* were from Moore (1954), and for *H. vegetum* from Linder (1929), since the two species have been neglected and lack additional records and morphological descriptions due to the synonymies and taxonomic confusions incurred throughout the decades.

Reflection on current generic concepts in helicosporous taxa

Systematic works of helicosporous fungi have been changing tremendously in recent years due to the trend of using

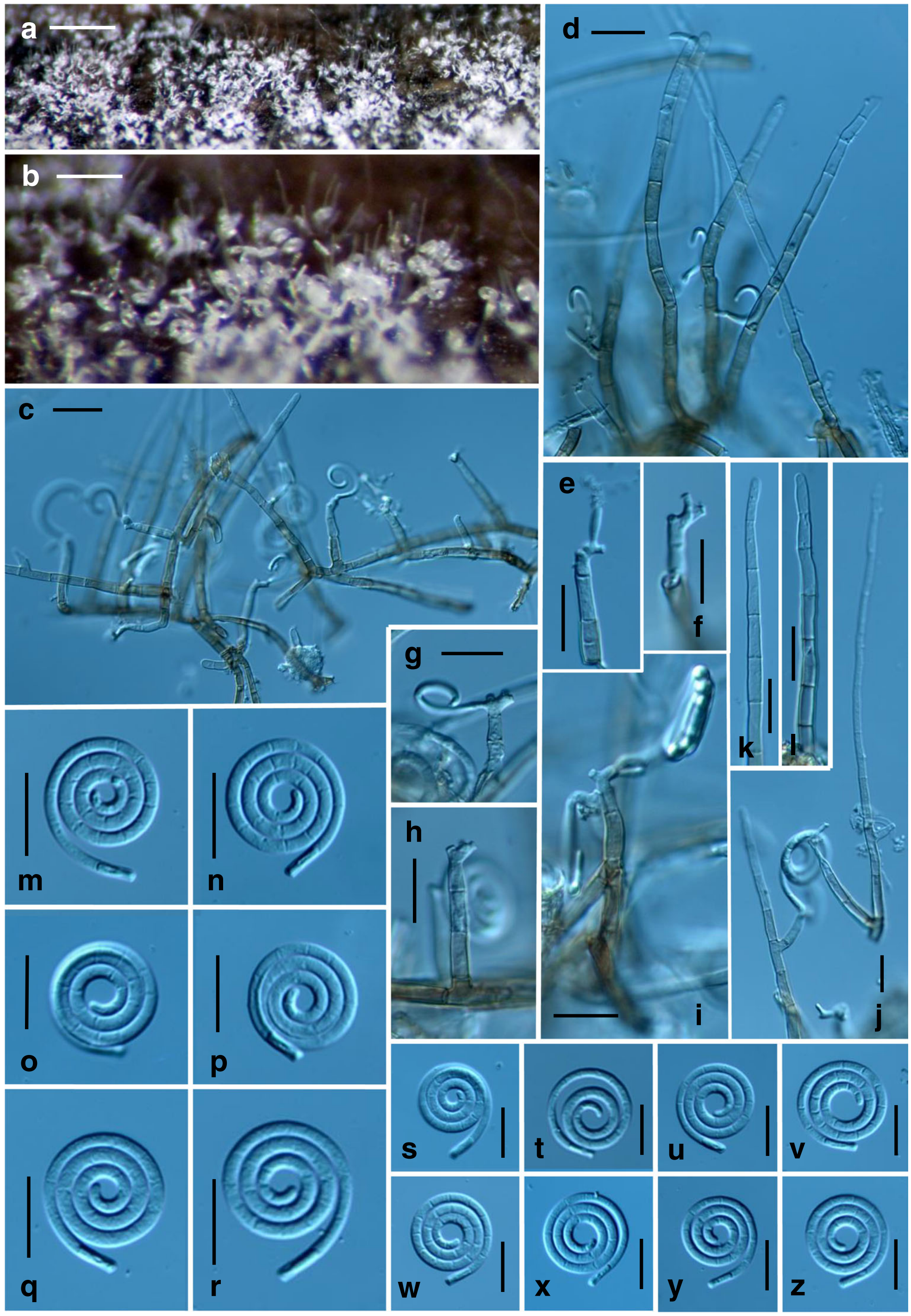

Fig. 7 *Neohelicosporium sympodiophorum* (NCYU-H4-1). **a**, **b** Colonies on natural substratum. Note the distinct erect setiform conidiophores among the white mass of helical conidia. **c** Conidiophores arising from repent hyphae, bearing developing conidia. **d** Setiform conidiophores with intercalary conidiogenous denticles and developing conidia. **e**–**i** Conidiophores that arising repent hyphae showing polyblastic sympodial conidiogenous loci at the apex. **j** Setiform conidiophores bearing shorter sympodial conidiophores at the lower portion of the shaft. **k**, **l** Upper portion of setiform conidiophores showing septation and rounded sterile apex. **m**–**z** Conidia. Scale bar: **a** = 500 µm; **b** = 200 µm; **c**–**z** = 20 µm

molecular data in taxonomy. As provoked by the problems in the polyphyly of helicosporous taxa in the Tubeufiales, many new generic names were proposed to accommodate these fungi (Boonmee et al. 2014; Brahmanage et al. 2017; Lu et al. 2018). Generic circumscriptions of traditionally well-known helicosporous taxa such as *Helicodendron*, *Helicoon*, *Helicoma*, *Helicomyces*, and *Helicosporium* (Goos 1980, 1985, 1986, 1987, 1989; Goos et al. 1985, 1986; Zhao et al. 2007) have now been largely revised based on phylogeny. The shortcoming is that species of these genera can no longer be confidently identified without knowing their phylogenetic positions. Nevertheless, until today, there remain many helicosporous taxa for which their marker genes commonly used in modern systematics are still not sequenced yet, especially those species which published in the early ages (e.g., Morgan 1892; Linder 1929; Moore 1953; Petrak 1953) and those which published in less popular journals (e.g., Rao and Rao 1964; Reddy et al. 1970; Chouhan and Panwar 1980; Rao and Varghese 1988; Dharkar et al. 2010). Moreover, scientists who work in less developed regions of the world may have problems undertaking molecular works due to the lack of essential laboratory equipment. When molecular data are not available, traditional morphological characters used for distinguishing species of these hyphomycetes are certainly useful and important. In this case, good taxonomic keys constructed using reliable morphological data that facilitate identification of species are also helpful. Many new genera and species were proposed by Lu et al. (2018) in their taxonomic reassessment of Tubeufiales to accommodate various fungi, a great contribution to fungal systematics indeed; however, taxonomic keys for the species were not given. Besides, in naming new species of helicosporous fungi, the species epithets "*aquatica*," "*aquaticum*," and "*aquaticus*" are frequently used by the authors for various similar genera. This may cause taxonomic confusions in future when making new nomenclatural combinations of taxa are needed.

In our opinion, the advent of molecular techniques is helpful towards a more natural system of fungal classification; however, identification of taxa based on morphological data is not obsolete. A combination of both approaches is important. Nowadays, new species should always be accompanied by molecular data, if possible.

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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. The sequence data generated in this study are deposited in NCBI GenBank.

Compliance with ethical standards

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

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