



# Re-evaluation of *Exserticlava* and other genera in *Chaetosphaeriaceae* with *chalara*-, *phaeostalagmus*-, *phialocephala*- and *stanjehughesia*-like morphotypes

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## Key words

*Chaetosphaeriales*  
conidiogenesis  
dematiaceous hyphomycetes  
new taxa  
phylogeny  
*Sordariomycetes*  
taxonomy  
wood-inhabiting fungi

**Abstract** In this study, we undertook a re-evaluation of species classified in genera *Exserticlava*, *Phaeostalagmus*, *Phialocephala*, and several *chalara*- and *stanjehughesia*-like fungi, whose placement has been determined within *Chaetosphaeriaceae*. They exhibit morphotypes that are either not exclusive to *Chaetosphaeriaceae* and have evolved in distantly related groups or have not been conclusively established as monophyletic within the family. Our study is based on phylogenetic reconstruction of three DNA markers and comparative morphological studies involving 21 strains, including all available ex-type strains. The non-monophyletic nature of the genus *Exserticlava* was elucidated and consequently, its generic concept has been emended, leading to the introduction of a segregate genus *Exserticlavopsis*. *Chalara*-like fungi occurred in three unrelated lineages, including a strongly supported clade comprising *Chalarosphaeria* and *Fusichalara*, a distinct lineage representing the newly introduced genus *Chalarina* gen. nov., and *Sporoschisma*, which produces the *chalara*-like synasexual morph. The genus *Stanjehughesia* is documented as a monophyletic, strongly supported clade. The notable similarity with other *stanjehughesia*-like genera is discussed. The *phialocephala*-like morphotype is infrequent within *Chaetosphaeriaceae* and is confined to two unrelated clades, specifically represented by *Chloridium* sect. *Pseudophialocephala* and *Spadicocephala* gen. nov., the latter being established to accommodate *Phialocephala fusca*. A monophyletic clade comprising members of *Phaeostalagmus* and *Sporendocladia* has been identified based on new molecular data. Since the relationship between the type species *P. cyclosporus* and *P. tenuissimus* could not be fully resolved, the clade is defined as a natural group characterized by distinct morphological patterns in conidiophore branching and aggregation of conidia. This definition is provisional, pending broader and more comprehensive taxon sampling. In this study, we introduced three new genera, two new species, and proposed six combinations. These findings emphasize the ongoing need for research to further refine the classification and enhance our understanding of the evolutionary relationships within *Chaetosphaeriaceae*.

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## INTRODUCTION

The *Chaetosphaeriaceae* is one of the largest families within the *Sordariomycetes* characterized by highly developed pleomorphism and significant variability in asexual morphological traits. The re-evaluation of the family, with the aim of achieving a fully resolved backbone phylogeny, has posed primary challenges and unresolved issues in this group in recent years. Significant progress in our understanding of *Chaetosphaeriaceae* was facilitated by obtaining living cultures and DNA sequence data from numerous species, mainly asexual morphs, whose relationship and systematic placement was previously unknown or predicted based solely on morphological characters (e.g., Crous et al. 2013, Liu et al. 2016, Ma et al. 2016, Hernández-Restrepo et al. 2017, Lin et al. 2019, Luo et al. 2019, Réblová et al. 2020b,

Wu & Diao 2022, Zhang et al. 2022, Yang et al. 2023). These studies also included discoveries of many novel species and genera. Other studies have involved revisions of genera and morphologically delimited groups, emphasizing the pivotal role of DNA sequence data in taxonomic resolution (e.g., Jeewon et al. 2009, Crous et al. 2012, Hashimoto et al. 2015, Luo et al. 2016, Yang et al. 2016, 2018, Réblová et al. 2021a–e, 2022, Réblová & Nekvindová 2023, Wu & Diao 2022). Additionally, majority of these studies focused on the identification of species complexes and cryptic species. These efforts underscore the significance of studying morphological characters in a broader context using various approaches, and recognizing their plasticity. This ongoing integrated approach contributes to the stability in the classification of *Chaetosphaeriaceae*.

The asexual morphs associated with this family are dematiaceous hyphomycetes that predominantly produce solitary conidiophores, sometimes also synnemata or sporodochia. In some cases, the conidiophores are reduced or even absent. The conidiogenous cells are mainly phialidic, typically terminal or discrete, occasionally intercalary, and seldom holoblastic. Our focus will be on fungi currently classified in the genera *Chalara* (*Cha.*), *Exserticlava* (*E.*), *Phialocephala* (*Pc.*), *Phaeostalagmus* (*P.*) and *Stanjehughesia* (*S.*), which produce phialidic or

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holoblastic conidia, and their representatives have been determined within *Chaetosphaeriaceae*. Some of these genera exhibit morphotypes that are either not exclusive to *Chaetosphaeriaceae* and have evolved in distantly related groups, or are not conclusively resolved as monophyletic within the family.

Chalara-like fungi are characterized by sessile or stalked phialides, sometimes produced on conidiophores, with a basal venter, which may abruptly taper towards a tubular and non-flaring collarette. Endogenously formed conidia on a deep-seated conidiogenous locus, whether septate or aseptate, hyaline or pigmented that usually adhere in chains, are also distinctive features. Chalara-like fungi exhibit a cosmopolitan distribution and are frequently encountered as saprobes on decomposing plant tissues (Nag Raj & Kendrick 1975). Reports of their occurrence as pathogens, endophytes, or in soil are comparatively less frequent and were recently summarized in Wu & Diao (2023). Phylogenetic relationships among numerous *Chalara* (Corda 1838, Rabenhorst 1844) and chalara-like fungi, with available molecular data, have been explored in diverse studies. These investigations offer compelling evidence indicating that the chalara-like morphotypes exhibit multiple evolutionary origins. Although the core of *Chalara* and its segregate genera, either exclusively asexually reproducing or connected to sexual morphs, are linked with the *Leotiomycetes*, similar fungi occur in different orders of the *Dothideomycetes*, *Eurotiomycetes*, and *Sordariomycetes* (e.g., Coetsee et al. 2000, Paulin & Harrington 2000, Paulin-Mahady et al. 2002, Kamgan et al. 2008, Cai et al. 2009, Réblová et al. 2011, Seifert et al. 2011, Guatimosim et al. 2016, Johnston et al. 2019, Olariaga et al. 2019, Crous et al. 2020a, 2021, Wu & Diao 2023).

Recently, Wu & Diao (2023) established the monotypic genus *Chalarosphaeria* (*Chs.*) for species exhibiting a chalara-like morphotype within *Chaetosphaeriaceae*. It was introduced to accommodate *Chaetosphaeria chalaroides* (Holubová-Jechová 1984) and its asexual morph *Chalara breviclavata* (Nag Raj & Kendrick 1975). The chalara-like morphotype is not commonly observed within *Chaetosphaeriaceae*. Besides *Chalarosphaeria*, it has been documented for *Fusichalara dingleyae*, the asexual morph of *Chaetosphaeria fusichalaroides* (Réblová 2004), and chalara-like synasexual morph of *Sporoschisma mirabile* (Müller & Samuels 1982). Several other members of *Chaetosphaeriaceae* display characters reminiscent of chalara-like fungi, particularly in terms of the anatomy of the phialide and the arrangement of conidia in chains. These fungi are classified in *Ascochalara* (Réblová 1999a) for which molecular data are currently lacking, as well as *Catenularia* (Hughes 1965, Réblová et al. 2021e, Wu & Diao 2022), *Gongromeriza* (Réblová et al. 2022, Réblová & Nekvindová 2023), *Fuscocatenula* (Li et al. 2017, Réblová et al. 2021e), and *Chaetosphaeria polygonalis* (Yang et al. 2023).

*Fusichalara*, based on *F. dimorphospora*, was introduced for a group of three species (Hughes & Nag Raj 1973). The genus was distinguished from morphologically similar *Chalara* by a convex thickening of the inner wall of the phialide at the point of transition from venter to collarette and presence of two kinds of conidia during ontogeny, which can be hyaline or versicolourous. The first-formed conidia are cylindrical, straight, about twice the length of the subsequent conidia, and contain about twice as many septa. The subsequent conidia are fusiform, straight, or somewhat sigmoid. The three core species are saprobes on decaying bark and wood and are known only from New Zealand. Currently, *Fusichalara* accommodates six species according to MycoBank ([www.mycobank.org](http://www.mycobank.org), Crous et al. 2004). However, living cultures and molecular data are available for only two of them. *Fusichalara minuta* (Gams & Holubová-Jechová 1976) was identified as belonging to the *Sclerococcales* within the *Sclerococcomycetidae* (*Eurotiomy-*

*cetes*) (Réblová et al. 2016). In the interim, our preliminary phylogenetic analysis supports the placement of *F. dingleyae* within *Chaetosphaeriaceae*.

An interesting example of conidiogenesis is exhibited by the genus *Exserticlava* (Hughes 1978), typified by *E. vasiformis* (Matsushima 1975). The terminal, integrated conidiogenous cell, which undergoes transformation during ontogeny, has become a hallmark of the genus. The outer pigmented wall of the conidiogenous cell ruptures as the hyaline, inner, thick-walled layer expands outwards, and the conidiogenous cell takes on a funnel-shaped form with a lacerate margin. The hyaline extension is initially subglobose with multiple conidiogenous loci but extends upwards into a sterile, subulate structure. The conidia are dematiaceous, ellipsoidal to obovoid and distoseptate, produced successively and adhere in brown, slimy heads. Presently, the genus *Exserticlava* includes nine species according to MycoBank, which are commonly found in tropical and subtropical regions and typically grow on decaying plant material. Tsui et al. (2001) conducted a revision of the genus and provided a key and a synopsis table of its members.

The characteristic extension of the conidiogenous cell, however, only occurs in the type species. In other members of *Exserticlava*, the inner part of the conidiogenous cell is thinner-walled and occasionally protrudes only slightly above the frayed collarette. The differences in the anatomy of the conidiogenous cells among *Exserticlava* species correlate with the variability in their sexual morphs, which were all placed in the genus *Chaetosphaeria*. The sexual-asexual connections have been established through cultural work for four *Exserticlava* species, namely *E. chlorotunicata* (Fernández & Huhndorf 2005), *E. exserticlavoides* (Réblová & Seifert 2003), *E. triseptata* (Matsushima 1985) and *E. vasiformis* (Fernández & Huhndorf 2005). The sexual morph of *E. vasiformis* produces ascomata with capitate setae and septate, cylindrical to narrowly fusiform, asymmetrical and uniformly coloured yellowish brown ascospores. In contrast, the sexual morphs of other *Exserticlava* spp. have bristle-like, dark brown ascomatal setae and septate, fusiform, symmetrical, and versicolourous ascospores with middle cells straw-coloured to pale brown and end cells hyaline.

In Subramanian's (1992) revision of the genus *Sporidesmium* (*Sp.*), a separate genus named *Stanjehughesia* was introduced to accommodate dematiaceous hyphomycetes, which are characterized by conidiophores reduced to determinate, holoblastic conidiogenous cells that produce euseptate, solitary macroconidia. Five species, including *S. hormiscioides* (Corda 1838), the generic type, were accepted in *Stanjehughesia*. The reliability of the generic diagnostic characters was questioned by Réblová (1999b) due to their variability both *in vitro* and *in vivo*, and additional variability in sexual characters in *Stanjehughesia* and the broadly perceived *Sporidesmium*. The sexual-asexual connection between *S. hormiscioides* and *Sphaeria caesariata* was proposed by Shoemaker & White (1985) based on their proximity on the natural substrate, and later experimentally verified by Réblová (1999b). Its notable morphology, including dark ascomata clothed with setae somewhat resembling capitate setae, and the presence of fusiform, septate, versicolourous ascospores, has sparked numerous taxonomic discussions. As a result, the sexual morph has undergone several reclassifications into various genera, including *Lasiosphaeria* (Saccardo 1883), *Phaeotrichosphaeria* (Barr et al. 1986), *Umbrinosphaeria* (Réblová 1999b), and *Chaetosphaeria* (Fernández & Huhndorf 2005).

As of now, *Stanjehughesia* currently comprises 21 species including synonyms according to MycoBank, which are primarily distinguished by differences in conidial traits, such as shape, size, and septation. Unfortunately, living cultures and molecular data are only available for a limited number of species. Because

*Stanjehughesia* species share a high degree of morphological similarity, morphology-based delineation of these species has proven to be challenging in the absence of molecular data. Recently, the generic characteristics have been consistently demonstrated to lack phylogenetic relevance to distinguish between stanjehughesia-like genera. *Stanjehughesia polypora* (Wu & Zhuang 2005) was classified in *Xylariales* (Shenoy et al. 2006), while three other *Stanjehughesia* species fall within *Chaetosphaeriaceae*, namely *S. hormiscioides* (Réblová & Winka 2001, Fernández et al. 2006), *S. kaohsiungensis* (Hsieh et al. 2021), and *S. vermiculata* (Cooke 1875, Shenoy et al. 2006). However, they are not congeneric. Consequently, two separate genera, *Falholtia* and *Riisgaardia*, were established to accommodate *S. kaohsiungensis* and *S. vermiculata*, respectively (Wu & Diao 2022). Furthermore, stanjehughesia-like synsexual morphs have been identified in the life cycle of members of the genus *Zanclospora* in *Chaetosphaeriaceae* (Réblová et al. 2021a).

Several genera in *Chaetosphaeriaceae* exhibit conidiophores with a complex conidiogenous apparatus reminiscent of that found in the genus *Phialocephala* (Pc.) (*Helotiales*) (Kendrick 1961). *Phialocephala* was established to accommodate species with phialidic conidial development in contrast to annellidic conidiogenesis in the morphologically similar genus *Leptographium* (Lagerberg et al. 1927, Kendrick 1962, 1963, De Beer et al. 2022). The phialocephala-like morphotype is characterised by conidiophores composed of a distinct stipe and head. The conidiogenous apparatus is compact, consisting of multiple levels of fertile branches, metulae and phialides in a mono-, bi-, ter- to quaterverticillate branching patterns. In *Chaetosphaeriaceae*, such complex structures are rare and occur in members of *Chloridium* sect. *Pseudophialocephala* (Réblová et al. 2022) and *Kionochaeta* (Kirk & Sutton 1985, Lin et al. 2019, Wu & Diao 2022), which comprises compact or loosely arranged branches. Another representative exhibiting this pattern is *Phialocephala fusca* (Kendrick 1963). The utilization of both small and large subunits rDNA (SSU and LSU) positioned this species within *Chaetosphaeriaceae* in an *incertae sedis* position (Grünig et al. 2002, Jacobs et al. 2003).

The conidiogenous apparatus can also be simplified, consisting of loosely arranged discrete phialides, which may be supported by 1–2 cells or short metulae, and confined to the apical cell of the conidiophore, as observed in *Sporendocladia* (Sn.) (Nag Raj & Kendrick 1975, Sutton 1975a, Crous & Wingfield 1994). Endogenous, cuneiform conidia arranged in false chains, along with ampulliform to lageniform phialides featuring a tubular collarette, constitute additional diagnostic traits of this genus. *Sporendocladia fumosa* (Arnaud 1954, Nag Raj & Kendrick 1975), which serves as the type species of the genus, and *Sn. beijingensis*, were recently established as members of *Chaetosphaeriaceae* by Wu & Diao (2022). The latter species produces typical 'sporendocladia' conidiophores, but also conidiophores of more arborescent appearance somewhat similar to those of *Phaeostalagmus*. *Sporendocladia* includes seven species names according to MycoBank. However, various molecular investigations have consistently confirmed its polyphyletic nature incorporating *Sn. bactrospora* in *Microascales*, and *Sn. foliicola* and *Sn. kionochaetoides* in *Leotiales* (Grünig et al. 2002, Jacobs et al. 2003, Roux et al. 2013). In response, new genera *Parasporendocladia* and *Lareunionomyces* and new combinations were introduced to accommodate the respective species (Crous et al. 2016, Wu & Diao 2022).

*Phaeostalagmus* (Gams & Holubová-Jechová 1976) displays an arrangement of phialides and the branching pattern typical of *Verticillium* (*Glomerellales*) (Nees von Esenbeck 1816, Giraldo & Crous 2019). Hughes (1951) meticulously documented two *Verticillium* species with dematiaceous conidiophores.

Gams & Holubová-Jechová (1976) recognized that these species diverged from the core characteristics of the genus and consequently introduced *Phaeostalagmus* for them, with *P. cyclosporus* as the type species, and accepted *P. tenuissimus* as a second species. *Phaeostalagmus cyclosporus* was characterised by branched conidiophores with an upper dematiaceous phialide-bearing part of an arborescent appearance, whereas *P. tenuissimus* exhibits a hyaline apical part of the conidiophore, lacks branches, and features phialides arising directly from the conidiophore in repeated verticils. Based on available rDNA sequences of *P. cyclosporus* (Vu et al. 2019), the species is classified within *Chaetosphaeriaceae*. In the phylogeny presented by Wu & Diao (2022), *Phaeostalagmus* and *Sporendocladia* were resolved as sister clades. Currently, there are eight species accepted in the genus *Phaeostalagmus* according to MycoBank, however, their placement, including that of *P. tenuissimus*, remains unknown except for *P. cyclosporus*.

The studied fungi, which exhibit morphotypes belonging to genera listed above, were placed in *Chaetosphaeriaceae* through a preliminary phylogenetic analysis. In addition, during our survey we encountered two undescribed species that align with the generic concepts of *Chalara* and *Stanjehughesia*. To investigate these fungi, a set of 21 strains comprising all available authentic strains, ex-type and other non-type isolates underwent partitioned Maximum Likelihood and Bayesian inference phylogenetic analyses of three gene markers. Additionally, detailed morphological comparisons of material from both nature and culture were conducted. The primary objectives of this study involve evaluating the diagnostic morphological characters of the studied species and delimiting the natural groups they form in correlation with molecular data. Our study aims to elucidate relationships within and among groups that share similar morphotypes, contributing to their identification in the future and stabilizing the classification of *Chaetosphaeriaceae*.

## MATERIALS AND METHODS

### Sampling and fungal strains

Fresh specimens, growing on wood in different stages of decay in terrestrial habitats were collected from diverse sites in tropical and temperate broadleaf and mixed forests in the Czech Republic, France, New Zealand, Puerto Rico, Thailand, and Ukraine. Dried specimens were deposited into the Fungarium of the Institute of Botany CAS in Průhonice, Czech Republic (PRA) and New Zealand Fungarium in Auckland, New Zealand (PDD). Cultures were accessioned in the Westerdijk Fungal Biodiversity Institute (formerly CBS-KNAW) in Utrecht, the Netherlands (CBS) and International Collection of Microorganisms from Plants in Auckland, New Zealand (ICMP). Other fungarium material and living strains were obtained from CBS, CABI-IMI Culture Collection in Egham, UK (IMI), and Fungarium of the National Museum in Prague, Czech Republic (PRM). Novel sequences generated in this study (Table 1) were deposited in GenBank at the National Centre for Biotechnology Information (NCBI) (Sayers et al. 2022). Names of newly discovered fungal taxa, and new combinations have been registered in MycoBank (Crous et al. 2004). MycoBank was also consulted for the current classification of the studied genera and their species (accessed on 15 December 2023). In addition to our collections and literature sources, information on host and geographic distribution of studied species was taken from the MyCoPortal (<http://www.mycportal.org/portal/index.php>, Miller & Bates 2017, accessed on 23 January 2024).

Since many of the generic names in this study begin with the letters 'C', 'E', 'P', and 'S', the following abbreviations will be used throughout the text: *Chaetosphaeria* (Ch.), *Chalara* (Cha.), *Chalarina* (Chl.), *Chalarosphaeria* (Chs.), *Ellisambia* (El.), *Ex-*



**Table 1** Taxa, isolate information and new sequences determined for this study; sequences in **bold** were generated in this study.

Taxon	Source	Status <sup>1</sup>	Country	Host	Substrate	GenBank accession numbers		
						ITS	LSU	<i>tef1-α</i>
<i>Chalarina hyalospora</i>	CBS 145806	T	France	<i>Buxus sempervivens</i>	decaying wood	<b>PP104310</b>	<b>PP104294</b>	<b>PP101582</b>
<i>Chalarosphaeria breviclavata</i>	CBS 148188		Czech Republic	<i>Quercus</i> sp.	decaying wood	<b>PP104311</b>	<b>PP104295</b>	<b>PP101583</b>
<i>Chalarosphaeria tubulicollaris</i>	PRM 900545	T	Thailand	<i>Quercus</i> sp.	decaying wood	<b>PP104312</b>	<b>PP104296</b>	<b>PP101584</b>
<i>Chalarosphaeria</i> sp.	S.M.H. 2018		Puerto Rico	unidentified	decaying wood	<b>PP104313</b>	AY017372 <sup>a</sup>	–
	S.M.H. 2223		Costa Rica	unidentified	decaying wood	<b>PP104314</b>	AF466063 <sup>a</sup>	–
<i>Exserticlava vasiformis</i>	S.M.H. 3239	T	Costa Rica	unidentified	decaying wood	<b>PP104315</b>	AF466061 <sup>a</sup>	–
<i>Exserticlavopsis exserticlavoides</i>	CBS 112963	T	Thailand	bamboo	decaying culm	<b>PP104316</b>	<b>PP104297</b>	<b>PP101585</b>
<i>Exserticlavopsis chlorotunicata</i>	S.M.H. 1565	T	Puerto Rico	unidentified	decaying wood	<b>PP104317</b>	AF466064 <sup>a</sup>	–
<i>Fusichalara dingleyae</i>	ICMP 15141		New Zealand	<i>Dacryodes</i> sp.	decaying wood	<b>PP104318</b>	<b>PP104298</b>	<b>PP101586</b>
	ICMP 22636		New Zealand	unidentified	decaying wood	<b>PP104319</b>	<b>PP104299</b>	<b>PP101587</b>
<i>Phaeostalagmus cyclosporus</i>	CBS 663.70		Netherlands	unidentified	decaying wood	<b>PP104320</b>	<b>PP104300</b>	<b>PP101588</b>
	IMI 63832		UK	unidentified	decaying wood	<b>PP104321</b>	<b>PP104301</b>	<b>PP101589</b>
<i>Phaeostalagmus tenuissimus</i>	CBS 145434		Czech Republic	<i>Quercus cerris</i>	decaying acorn	<b>PP104306</b>	<b>PP104290</b>	<b>PP101578</b>
	CBS 145635		Czech Republic	<i>Quercus cerris</i>	decaying acorn	<b>PP104307</b>	<b>PP104291</b>	<b>PP101579</b>
	CBS 145640		Czech Republic	<i>Quercus cerris</i>	decaying acorn	<b>PP104308</b>	<b>PP104292</b>	<b>PP101580</b>
	CBS 917.73		Netherlands	unidentified	decaying wood	<b>PP104309</b>	<b>PP104293</b>	<b>PP101581</b>
<i>Spadicocephala fusca</i>	CBS 301.85	AS	Canada	<i>Pinus strobus</i>	roof rafter	<b>PP104322</b>	<b>PP104302</b>	<b>PP101590</b>
<i>Sporendocladia fumosa</i>	CBS 518.93		Switzerland	<i>Castanea sativa</i>	cupules	<b>PP104323</b>	<b>PP104303</b>	<b>PP101591</b>
<i>Sporoschisma hemipsilum</i>	MUCL 56487		Martinique	unidentified	wood	MW987829 <sup>b</sup>	MW987824 <sup>b</sup>	<b>PP101594</b>
<i>Sporoschisma mirabile</i>	CBS 144794		France	<i>Alnus glutinosa</i>	submerged wood	MW987830 <sup>b</sup>	MW987825 <sup>b</sup>	<b>PP101595</b>
<i>Stanjehughesia hormiscioides</i>	CBS 102664		Ukraine	<i>Fagus sylvatica</i>	decaying wood	<b>PP104324</b>	<b>PP104304</b>	<b>PP101592</b>
	S.M.H. 2794		USA	<i>Betula</i> sp.	decaying wood	<b>PP104325</b>	AF466060 <sup>a</sup>	–
<i>Stanjehughesia silvana</i>	ICMP 15123	T	New Zealand	<i>Nothofagus</i> sp.	decaying wood	<b>PP104326</b>	<b>PP104305</b>	<b>PP101593</b>
<i>Verhulstia trisororum</i>	CBS 143234	T	Netherlands	n/a	soil	MG022181 <sup>c</sup>	MG022160 <sup>c</sup>	<b>PP101596</b>

<sup>1</sup> T denotes ex-type strains; AS indicates authentic strain.  
<sup>a</sup> Fernández et al. (2006).  
<sup>b</sup> Réblová et al. (2021e).  
<sup>c</sup> Hernández-Restrepo et al. (2017).

*serticlava* (*E.*), *Exserticlavopsis* (*Ex.*), *Phaeostalagmus* (*P.*), *Phialocephala* (*Pc.*), *Spadicocephala* (*Sc.*), *Sporendocladia* (*Sn.*), *Sporidesmium* (*Sp.*), and *Stanjehughesia* (*S.*).

New cultures were derived from conidia and ascospores. Conidial clusters were transferred onto the agar surface using a sterile needle tip. Ascomata were carefully cut using a sterile razor blade and a drop of sterile water was added to swell the centrum containing the asci and ascospores. The gelatinous centrum was then transferred onto agar using the tip of a sterile needle. Both ascospores and conidia were transferred to a 10 cm Petri dish containing water agar (WA) (distilled water 1 L, agar 10 g, Oxoid Limited, Hampshire, United Kingdom) and Modified Leonian's agar (MLA, Malloch 1981), incubated for 2–5 d and observed for germination. Germinating spores were transferred to a new 6 cm Petri dish containing MLA; single and multiple germinating ascospores and conidia were obtained with a single-spore isolator (Meopta, Pferov, Czech Republic). Cultures were incubated in the dark at 20–25 °C and observed periodically for sporulation.

**Morphological studies**

Dried specimens and living cultures were examined with an Olympus SZX12 dissecting microscope (Olympus America, Inc., Melville, NY, USA). Ascomata were rehydrated with tap water, and the gelatinous centrum was carefully extracted using the tip of a needle. It was then transferred to a drop of medium on a microscopic glass slide and covered with a cover slip. Conidiophores with attached conidia were either directly placed in a drop of medium on the slide or initially positioned in a drop of 90 % lactic acid to facilitate the separation of intertwined structures before being transferred into the medium. Microscopic preparations were mounted in 90 % lactic acid, tap water, and Melzer's reagent. Measurements were taken from specimens mounted in Melzer's reagent, and means ± standard deviation (SD) were calculated for sizes of asci, ascospores, and conidia, based on a minimum of 20–25 measurements. Microscopic observations were conducted using an Olympus

BX51 light microscope. Microphotographs were captured using an Olympus DP70 camera with Imaging Software Cell<sup>^</sup>D (Olympus). Colony macrophotographs were captured with a Canon EOS 77D digital camera with Canon EF 100mm f/2.8L Macro IS USM objective (Canon Europe Ltd., Middlesex, UK) with daylight spectrum 5500K 16W LED lights. Images were processed using Adobe Photoshop CS6 software (Adobe Systems, San Jose, CA, USA).

To evaluate colony characteristics, diffusible pigments, and growth patterns, fungi were cultured on various nutrient media including cornmeal dextrose agar (CMD) (Oxoid Limited; 2 % dextrose), MLA, oatmeal agar (OA), and potato-carrot agar (PCA) (Crous et al. 2019b). Colony characteristics were determined based on 5-wk-old cultures that were incubated in the dark at a temperature range of 20–23 °C. To induce sporulation, strains were also inoculated on cornmeal agar (CMA, Crous et al. 2019b) supplemented with sterile stems of *Urtica dioica*.

**Gene markers, DNA extraction, PCR amplification, and sequencing**

We performed phylogenetic analyses of three gene markers, which are well represented in *Chaetosphaeriaceae*. The internal transcribed spacer (ITS1-5.8S-ITS2) (ITS) of the nuclear rRNA cistron is the primary barcode for fungi (Schoch et al. 2012). The nuclear large subunit LSU rDNA gene (LSU) (D1–D3 domains, approximately 1800 base pairs) has demonstrated utility in investigating relationships within the Ascomycota at generic and higher taxonomic levels (e.g., Zhang et al. 2007, Schoch et al. 2009). The translation elongation factor 1-α (*tef1-α*) has been shown to be effective in distinguishing between interspecific relationships and also serves as a secondary barcode for fungi (Robert et al. 2011, Stielow et al. 2015, Meyer et al. 2019).

Total genomic DNA was extracted from 4-week-old cultures cultivated on MLA using the DNeasy® UltraClean® Microbial Kit (Qiagen GmbH, Hilden, Germany), following the manufacturer's instructions for filamentous fungi. PCR amplifications were performed in 25 µL reaction volumes using the Q5 High



**Table 2** Taxa, isolate information and sequences retrieved from GenBank.

Taxon	Strain	Status <sup>1</sup>	Country	Host	Substrate	GenBank accession numbers		
						ITS	LSU	<i>tef1-α</i>
<i>Achrochaeta rivulata</i>	CBS 148186		Australia	<i>Doryanthes excelsa</i>	dead inflorescence	OR286508	OR286551	OR326680
<i>Achrochaeta talbotii</i>	ICMP 15161		New Zealand	unknown	decaying wood	MT454480	MT454495	OL653988
<i>Adautomilanezia caesalpiniae</i>	CC-LAMIC 102/12	T	Brazil	<i>Caesalpinia echinata</i>	wood	KX821777	KU170671	–
<i>Anacacumisporium appendiculatum</i>	HMAS 245593	T	China	broad-leaved tree	dead stems	KP347129	KT001553	–
<i>Arcuatospora novae-zelandiae</i>	CBS 109474		Venezuela	<i>Nectandra</i> sp.	decaying leaf	MW984569	MW984552	OL653989
<i>Arcuatospora seorsa</i>	CBS 147510	T	Thailand	broad-leaved tree	decaying leaf	MW984572	MW984555	OL653990
<i>Aunstrupia nodipes</i>	NN043149		China	palm	leaf litter	OL627566	OL655011	–
<i>Brachydictyochaeta antillana</i>	NN058987		China	<i>Cinnamomum</i> sp.	leaf litter	OL627951	OL655147	–
<i>Brachydictyochaeta bulliformis</i>	NN076027		China	unidentified	leaf litter	OL628023	OL655155	–
<i>Brunneodinemasporium brasiliense</i>	CBS 112007	T	Brazil	unidentified	decaying leaf	JQ889272	JQ889288	–
<i>Brunneodinemasporium jonesii</i>	GZCC 16-0050	T	China	unidentified	decaying wood	KY026058	KY026055	–
<i>Cacumisporium acutatum</i>	CBS 101315	T	Czech Republic	<i>Fagus sylvatica</i>	decaying wood	OR134682	OR134626	OR130762
<i>Cacumisporium capitulatum</i>	CBS 101313		France	<i>Fagus sylvatica</i>	decaying wood	OR134683	OR134627	OR130763
<i>Caliciastrum bicolor</i>	ICMP 15136	P	New Zealand	<i>Nothofagus</i> sp.	decaying wood	OR134689	OR134633	OR130769
<i>Caligospora dilabens</i>	CBS 734.83	E	Japan	<i>Bambusa</i> sp.	culm	OR134691	OR134636	OR130771
<i>Caligospora pannosa</i>	CBS 551.89	T	Brazil	–	soil, <i>Theobroma cacao</i>	OR134692	OR134692	OR130772
<i>Calvolachnella guaviyunis</i>	CBS 134695	T	Uruguay	<i>Myrcianthes pungens</i>	bark	KJ834524	KJ834525	–
<i>Capillisphaeria crustacea</i>	CBS 145637		Czech Republic	<i>Abies alba</i>	decaying wood	OR134693	OR134638	OR130773
<i>Catenularia catenulata</i>	DLUCC 0891	T	China	unidentified	submerged wood	MK828637	MK835838	MN194088
<i>Catenularia minor</i>	PRM 900544	T <sup>a</sup>	Thailand	bamboo	bamboo culm	MW987827	MW987822	OL653993
<i>Chaetosphaeria innumera</i>	CBS 145639		Czech Republic	<i>Acer pseudoplatanus</i>	decaying wood	OP455358	OP455464	OP465036
<i>Chaetosphaeria mangrovei</i>	MCD 069	T	Thailand	mangrove	decaying wood	MG813821	MG813820	–
<i>Chaetosphaeria polygonalis</i>	GZCC 20-0438	T	China	unidentified	submerged wood	OP377861	OP377946	OP473040
<i>Chalarodes obpyramidata</i>	PDD 119364		New Zealand	<i>Nothofagus</i> sp.	decaying wood	MW987828	MW987823	OL653995
<i>Chloridium bellum</i>	CBS 709.73A	T	Germany	–	soil, wheat field	OP455360	OP455466	OP464934
<i>Chloridium caesium</i>	CBS 145633		Czech Republic	<i>Tilia cordata</i>	decaying wood	OP455367	OP455474	OP464941
<i>Chloridium gamsii</i>	CBS 667.75	T	Belgium	unidentified	decaying wood	OP455415	OP455522	OP464990
<i>Chloridium virescens</i>	CBS 145481		Czech Republic	<i>Quercus</i> sp.	decaying wood	OP455439	OP455547	OP465014
<i>Codinaea assamica</i>	CBS 139907	T <sup>b</sup>	Malaysia	<i>Acacia mangium</i>	leaf spot	OL654077	OL654134	OL653997
<i>Codinaea fertilis</i>	IMI 233824		New Zealand	<i>Betula</i> sp.	root	OL654080	OL654137	OL654000
<i>Codinaea paniculata</i>	CBS 145098	T	France	deciduous tree	submerged wood	MT118230	MT118201	OL654002
<i>Codinaeella lambertiae</i>	CBS 143419	T	Australia	<i>Lambertia formosa</i>	leaves	OL654084	OL654141	OL654009
<i>Codinaeella minuta</i>	CBS 280.59	AS	Japan	<i>Lithocarpus edulis</i>	dead leaves	OL654090	OL654147	OL654016
<i>Codinaeella parvlobata</i>	CBS 144536	T	Czech Republic	<i>Fagus sylvatica</i>	decaying cupule	OL654100	OL654157	OL654027
<i>Conicomyces pseudotransvaalensis</i>	HHUF 29956	T	Japan	<i>Machilus japonica</i>	dead twig	LC001710	LC001708	–
<i>Craspedodidymum elatum</i>	NN042874		China	unidentified	dead branch	OL627547	OL655004	–
<i>Cryptophiale udagawae</i>	GZCC 18-0047		China	unidentified	decaying wood	MN104608	MN104619	–
<i>Cryptophialoidea fasciculata</i>	MFLU 18-1499		Thailand	unknown	submerged wood	MH758195	MH758208	–
<i>Curvichaeta curvispora</i>	ICMP 15115	T	New Zealand	<i>Nothofagus</i> sp.	decaying wood	OR134705	OR134650	OR130785
<i>Dendrophoma cytisporoides</i>	CBS 144107		Germany	<i>Buxus sempervivens</i>	decaying bark	MT118234	MT118205	OL654032
<i>Dictyochaeta callimorpha</i>	ICMP 15130		New Zealand	unknown	decaying wood	MT454483	MT454498	MT454673
<i>Dictyochaeta fuegiana</i>	ICMP 15153	T <sup>c</sup>	New Zealand	unidentified	decaying wood	MT454487	EF063574	MT454677
<i>Dictyochaeta querna</i>	CBS 145503		Czech Republic	<i>Quercus cerris</i>	acorn	MT454489	MT454503	MT454679
<i>Dinemasporium cruciferum</i>	HHUF 30001		Japan	<i>Arundo donax</i>	unknown	AB900895	AB934039	AB934089
<i>Dinemasporium pseudoindicum</i>	CBS 127402	T	USA	–	soil, tallgrass prairie	JQ889277	JQ889293	–
<i>Ericsphaeria spinosa</i>	S.M.H. 2754	T	USA	<i>Betula</i> sp.	bark	MW984575	AF466079	–
<i>Eucalyptostroma eucalypti</i>	CBS 142074	T	Malaysia	<i>Eucalyptus pellita</i>	leaf spots	KY173408	KY173500	–
<i>Eucalyptostroma hongluosiense</i>	NN076613		China	<i>Fagus</i> sp.	decaying leaf	OL628127	OL655185	–
<i>Eucalyptostromiella beijingensis</i>	NN078016		China	<i>Quercus</i> sp.	decaying leaf	OL628501	OL655251	–
<i>Exserticlava vasiformis</i>	TAMA 450		Japan	unidentified	plant debris	–	AB753846	–
<i>Falholtia kaohsiungensis</i>	BCRC FU31337	T	Taiwan	unidentified	submerged wood	MT939301	MT939304	–
<i>Flectospora laminata</i>	CBS 112964	T	Thailand	unidentified	decaying wood	MW984576	MW984558	OL654034
<i>Fuscocatenula submersa</i>	MFLUCC 18-1342	T	China	unidentified	submerged wood	MK828634	MK835835	MN194085
<i>Fuscocatenula variegata</i>	NN055332		China	palm	decaying leaf	OL627817	OL655124	–
<i>Fusichloridium cylindrosporum</i>	CBS 101429	E	Czech Republic	<i>Abies alba</i>	decaying bark	OR134709	OR134653	OR130789
<i>Geniculosepta preussii</i>	CBS 145478		Czech Republic	<i>Fagus sylvatica</i>	decaying cupule	OR134714	OR134658	OR130794
<i>Gongromeriza myriocarpa</i>	CBS 264.76	N	Netherlands	unidentified	decaying wood	OP455457	OP455565	OP465028
<i>Gongromeriza pygmaea</i>	IMI 506815		Czech Republic	unidentified	decaying wood	OR134724	OR134668	OR130804
<i>Gongromerizella lignicola</i>	CBS 143.54	I	France	<i>Fagus sylvatica</i>	decaying wood	OP455460	OP455568	OP465032
<i>Gongromerizella pachytrachela</i>	CBS 645.75	T	Belgium	<i>Fagus sylvatica</i>	decaying wood	OP455461	OP455569	OP465033
<i>Gongromerizella pini</i>	CBS 146011	T	Ukraine	<i>Pinus sylvestris</i>	decaying wood	MT223787	MT223882	–
<i>Gongromerizella silvana</i>	CBS 171.76	T	Belgium	unidentified	decaying wood	OR134729	OR134673	OR130809
<i>Infundibulomyces cupulatus</i>	BCC 11929	T	Thailand	<i>Lagerstroemia</i> sp.	dead leaf	EF113976	EF113979	–
<i>Infundibulomyces oblongisporus</i>	BCC 13400	T	Thailand	unidentified angiosperm	leaf litter	EF113977	EF113980	–
<i>Kionochaeta microspora</i>	GZCC 18-0036	T	China	unidentified	decaying wood	MN104607	MN104618	–
<i>Kionochaeta ramifera</i>	MUCL 39164		Cuba	unidentified	decaying leaf	MW144421	MW144404	OL654036
<i>Kionochaetiella ivoriensis</i>	CBS 374.76	T	Ivory Coast	unidentified	bark	MH860988	MH872758	–
<i>Kylindrochaeta lignomollis</i>	S.M.H. 3015	T	Puerto Rico	unidentified	decaying wood	EU037896	AF466073	–
<i>Linkosia multiseptum</i>	CGMCC 3.20786	T	China	bamboo	dead culm	OL627557	OL655008	–
<i>Linkosia rostrata</i>	CGMCC 3.20790	T	China	bamboo	dead culm	OL627662	OL655059	–
<i>Lomaantha aquirostrata</i>	GZCC 20-0503	T	China	unidentified	submerged wood	OP377802	OP377901	OP472985

Table 2 (cont.)

Taxon	Strain	Status <sup>1</sup>	Country	Host	Substrate	GenBank accession numbers		
						ITS	LSU	<i>tef1-α</i>
<i>Lomaanthes aurantiaca</i>	CBS 126743	T	Hungary	<i>Vitis vinifera</i>	bark	HM241692	HM241692	–
<i>Lomaanthes aurea</i>	CBS 144403	T	France	<i>Sambucus nigra</i>	decaying wood	MH836375	MH836376	–
<i>Lomaanthes brachypus</i>	CBS 147396		USA	<i>Sabal minor</i>	petiole, dead leaf	OK352268	OK352269	–
<i>Lomaanthes folliculata</i>	CBS 147152		Czech Republic	<i>Carpinus betulus</i>	decaying wood	OL654105	OL654162	OL654033
<i>Lomaanthes pooga</i>	NN043946		China	bamboo	dead culm	OL627595	OL655023	–
<i>Lomaanthes reblovae</i>	CGMCC 3.20705	T	China	bamboo	dead culm	OL627632	OL655040	–
<i>Lunatochaeta shenzhenensis</i>	CGMCC 3.20757	T	China	unidentified	leaf litter	OL628577	OL655258	–
<i>Menispora caesia</i>	CBS 145022		Czech Republic	<i>Carpinus betulus</i>	decaying wood	OL654107	OL654164	OL654039
<i>Menispora ciliata</i>	CBS 122131	T <sup>d</sup>	Czech Republic	<i>Acer campestre</i>	decaying wood	EU488736	OL654165	OL654040
<i>Menispora tortuosa</i>	CBS 117553		Canada	<i>Acer</i> sp.	decaying bark	OL654111	OL654169	OL654044
<i>Menisporopsis pirozynskii</i>	MUCL 47217		Congo	unidentified	decaying leaf	MW984579	MW984561	OL654047
<i>Menisporopsis theobromae</i>	MUCL 41079		Venezuela	unidentified	decaying leaf	MW984580	MW984562	OL654048
' <i>Morrisiella indica</i> '*	NN042908		China	<i>Saccharum</i> sp.	dead culm	OL627551	OL655005	–
<i>Multiguttulispora dimorpha</i>	CBS 140002		Malaysia	<i>Eucalyptus</i> sp.	twig	MW984582	MW984564	OL654049
<i>Multiguttulispora triseptata</i>	IMI 353690		Cuba	unidentified	leaf	MW984584	MW984566	OL654050
<i>Nawawia filiformis</i>	MFLUCC 17-2394		Thailand	unidentified	decaying wood	MH758196	MH758207	–
<i>Neopseudolachnella acutispora</i>	MAFF 244358	T	Japan	<i>Pleioblastus chino</i>	dead twigs	AB934065	AB934041	AB934091
<i>Neopseudolachnella magnispora</i>	MAFF 244359	T	Japan	<i>Sasa kurilensis</i>	dead twigs	AB934066	AB934042	AB934092
<i>Nimesporella capillacea</i>	IMI 358908	T	Cote d'Ivoire	unidentified	leaf litter	OL654114	OL654171	OL654051
<i>Paliphora intermedia</i>	CBS 896.97	I	Australia	unidentified	leaf litter	MH862682	EF204501	–
<i>Papillospora hebetiseta</i>	CBS 102340	T	Ukraine	<i>Fagus sylvatica</i>	decaying wood	AF178549	AF178549	OL653994
<i>Paraceratocladia polysetosa</i>	NN044119		China	<i>Rhododendron</i> sp.	dead leaf	OL627605	OL655027	–
<i>Paraceratocladium silvestre</i>	NN055375		China	unidentified	leaf litter	OL627830	OL655132	–
<i>Paracryptophiale pirozynskii</i>	CGMCC 3.20706	T	China	unidentified	dead branch	OL627641	OL655047	–
<i>Paragaeumannomyces panamensis</i>	S.M.H. 3596	T	Panama	unidentified	decaying wood	AY906948	MT118218	–
<i>Paragaeumannomyces rubicundus</i>	S.M.H. 3221	T	Costa Rica	unidentified	decaying wood	MT118242	MT118224	–
<i>Phaeodischloridium aquaticum</i>	MFLUCC 18-1341	T	China	unidentified	submerged wood	MK828639	MK835841	MN194090
<i>Phialogeniculata guadalcanalensis</i>	MFLUCC 18-0260	T	Thailand	unidentified	decaying wood	MK828625	MK835825	MN194078
<i>Phialosporostilbe scutiformis</i>	MFLUCC 17-0227	T	China	unidentified	submerged wood	MH758194	MH758207	–
<i>Phialoturbella calva</i>	ICMP 23826	T	New Zealand	unidentified	decaying bark	MW984585	MW984567	OL654052
<i>Phialoturbella lunata</i>	MFLUCC 18-0642	T	China	unidentified	submerged wood	MK828624	MK835824	MN194077
<i>Polynema podocarp</i>	CBS 144415	T	New Zealand	<i>Podocarpus totara</i>	unknown	MH327797	MH327833	–
<i>Pseudodinemasprium fabiforme</i>	CBS 140010		Malaysia	<i>Acacia mangium</i>	leaf spots	KR611889	KR611906	–
<i>Pseudolachnea fraxini</i>	CBS 113701	T	Sweden	<i>Fraxinus excelsior</i>	unknown	JQ889287	JQ889301	AB934096
<i>Pseudolachnea hispidula</i>	MAFF 244365		Japan	<i>Morus bombycis</i>	dead twig	AB934072	AB934048	AB934098
<i>Pseudolachnella asymmetrica</i>	MAFF 244366	T	Japan	<i>Phyllostachys nigra</i> var. <i>henonis</i>	dead twig	AB934073	AB934049	AB934099
<i>Pseudolachnella scolecospora</i>	MAFF 244379		Japan	<i>Sasa</i> sp.	dead twigs	AB934086	AB934062	AB934112
<i>Pseudothozetella lunata</i>	CGMCC 3.20661	T	China	unidentified	leaf litter	OL628034	OL655157	–
<i>Psilobotrys minutus</i>	CBS 145632		Czech Republic	<i>Ulmus</i> sp.	decaying wood	OR134734	OR134678	OR130814
<i>Rattania setulifera</i>	GUFC 15501	T	India	<i>Calamus thwaitesii</i>	leaves	GU191794	HM171322	–
<i>Riisgaardia longispora</i>	CGMCC 3.20794	T	China	unidentified	rotten wood	OL627701	OL655085	–
<i>Riisgaardia obclavata</i>	CGMCC 3.20787	T	China	bamboo	dead culm	OL627568	OL655013	–
<i>Riisgaardia 'vermiculata'</i>	NN042952		China	bamboo	dead culm	OL627555	OL655007	–
<i>Spadicoccephala fusca</i>	CBS 300.85	AS	Canada	<i>Acer</i> sp.	decaying wood	MH861882	MH873570	–
<i>Spicatispora fennica</i>	CBS 101641		Ukraine	<i>Abies alba</i>	decaying wood	OR134735	OR134679	OR130815
<i>Sporendocladia beijingensis</i>	CGMCC 3.20738	T	China	<i>Quercus</i> sp.	dead cupules	OL628290	OL655217	–
<i>Sporendocladia beijingensis**</i>	NN047731		China	<i>Quercus</i> sp.	dead acorn	OL627669	OL655065	–
<i>Stilbochaeta malaysiana</i>	IMI 312436	T	Malaysia	unidentified	decaying leaf	OL654121	OL654178	OL654059
<i>Stilbochaeta novae-guineensis</i>	CBS 147515		Puerto Rico	unidentified	decaying wood	OL654122	OL654179	OL654060
<i>Stilbochaeta ramulosecula</i>	IMI 313452	E	Malaysia	unidentified	submerged leaf	OL654124	OL654181	OL654062
<i>Striatosphaeria castanea</i>	CBS 145352	T	French Guinea	woody liana	decaying periderm	MT118244	MT118229	–
<i>Striatosphaeria codinaeophora</i>	M.R. 1230		Puerto Rico	<i>Dacryodes excelsa</i>	decaying wood	AF178546	AF178546	–
<i>Tainosphaeria cecropiae</i>	CBS 101687	T	Puerto Rico	<i>Cecropia</i> sp.	decaying petiole	MW984586	MW984568	OL654064
<i>Tainosphaeria crassiparvis</i>	S.M.H. 1934	T	Puerto Rico	<i>Hymenaea</i> sp.	seed pod	MW984587	AF466089	–
<i>Tainosphaeria aquatica</i>	MFLUCC 17-2370	T	Thailand	unidentified	submerged wood	MZ161197	MZ161195	MZ170694
<i>Tainosphaeria thailandense</i>	MFLUCC 18-1282	T	Thailand	unidentified	submerged wood	MZ161198	MZ161196	MZ170695
<i>Thozetella cristata</i>	CBS 101112		Venezuela	unidentified	leaf litter	OL654126	OL654183	OL654065
<i>Thozetella tocklaiensis</i>	CBS 378.58	T	India	<i>Camellia sinensis</i>	decaying flower	OL654128	OL654185	OL654067
<i>Tracylla aristata</i>	CBS 141404	E	Australia	<i>Eucalyptus regnans</i>	leaves	OL654129	OL654186	OL654068
<i>Tracylla eucalypti</i>	CBS 144429	T	Colombia	<i>Eucalyptus urophylla</i>	leaves	OL654130	OL654187	OL654069
<i>Verhulstia biformis</i>	NN077655		China	<i>Rubus</i> sp.	dead leaf	OL628434	OL655237	–
<i>Zanclospora novae-zelandiae</i>	ICMP 15781	E	New Zealand	<i>Fuscospora cliffortioides</i>	decaying wood	MW144429	MW144411	MW147330
<i>Zanclospora ramifera</i>	ICMP 22738	T	New Zealand	unidentified	decaying wood	MW144433	MW144415	MW147334
<i>Zanclospora xylophila</i>	ICMP 22737	T	New Zealand	unidentified	decaying wood	MW144437	MW144417	MW147335

<sup>1</sup> T, E, I, N and P denote ex-type, ex-epitype, ex-isotype, ex-neotype and ex-paratype strains; AS indicates authentic strain.

<sup>a</sup> holotype of *Chaetosphaeria trianguloconidia*.

<sup>b</sup> ex-type strain of *Codinaea acaciae*.

<sup>c</sup> ex-type strain of *Chaetosphaeria fuegiana*.

<sup>d</sup> ex-type strain of *Chaetosphaeria ciliata*.

\* *Morrisiella* Saikia & A.K. Sarbhoy 1985 (Nom. illegit., Art. 53.1) non *Morrisiella* Aellen 1938 (*Chenopodiaceae*).

\*\* as *Sporendocladia fumosa sensu* Wu & Diao (2022).

Fidelity DNA polymerase kit (New England Biolabs Inc., Hitchin, UK) as per the manufacturer's protocol. Primers used for PCR amplification include: 1) V9G/LR8 primer pair (De Hoog & Gerrits van den Ende 1998, Vilgalys unpubl.) for ITS-LSU region; 2) EF1-983F/EF1-2218R primers (Rehner & Buckley 2005) to amplify the *tef1- $\alpha$*  region. PCR of ITS, LSU, and *tef1- $\alpha$*  was carried out as described in Réblová et al. (2020a). Amplicons were sequenced in both directions using the PCR and nested primers ITS5, ITS4, JS1, JS7, JS8, and LR7 (Vilgalys & Hester 1990, White et al. 1990, Landvik 1996). Automated sequencing was conducted by Eurofins Genomics Europe Sequencing Service (Cologne, Germany), and The WM Keck Center at the University of Illinois Urbana-Champaign. Analyses of raw sequence data and assembly of sequence contigs were performed using Sequencher v. 5.4.6 (Gene Codes Corp., Ann Arbor, MI, USA).

Accession numbers of sequences obtained from GenBank and previously published in other studies (Réblová & Winka 2000, Grünig et al. 2002, Huhndorf & Fernández 2005, Fernández et al. 2006, Somrithipol et al. 2008, Prabhugaonkar & Bhat 2009, Magyar et al. 2011, Crous et al. 2012, 2013, 2014, 2015, 2017, 2019a, 2020a, b, Hashimoto et al. 2015, Ma et al. 2016, Hernández-Restrepo et al. 2017, Yang et al. 2018, Lin et al. 2019, Luo et al. 2019, Vu et al. 2019, Hsieh et al. 2021, Li et al. 2021, Réblová et al. 2020b, 2021a, c–e, 2022, Réblová & Nekvindová 2023, Manawasinghe et al. 2022, Wu & Diao 2022, Fryar et al. 2023, Yang et al. 2023) are provided in Table 2.

### Phylogenetic analyses

While the majority of the studies species could be identified and appropriately classified within *Chaetosphaeriaceae* based on morphological characters, the affiliations of *Ch. tubulicollaris* and its chalara-like asexual morph, *P. tenuissimus*, and the undescribed chalara- and stanjehughesia-like species were determined through a BLASTn search (Zhang et al. 2000). All sequences newly generated in this study demonstrated similarity to members of *Chaetosphaeriaceae*. Consequently, sequences of representatives from this family were retrieved from GenBank and included in the analyses. The gene sequences were aligned using MAFFT v. 7.487 (Katoh & Standley 2013) implemented in the CIPRES Science Gateway v. 3.3 (Miller et al. 2010) and manually corrected in BioEdit v. 7.1.8 (Hall 1999), if necessary. Consensus secondary structure (2D) models acquired for the ITS1 and ITS2 of members of *Chloridium*, *Codinaea* and related taxa (Réblová et al. 2021a, d, 2022), were used to improve the alignment by comparing nucleotides at homologous positions (in helices and loops). The LSU alignment was enhanced using a predicted 2D model of this gene of *Saccharomyces cerevisiae* (Gutell et al. 1993). The GTR+I+G best-fit model of nucleotide evolution was selected for each partition (ITS, LSU, *tef1- $\alpha$* ) under Akaike information criteria using MrModeltest v. 2.4. (Nylander 2004). The final alignment of concatenated sequences (deposited in TreeBASE, study number 31095) was subjected to phylogenetic analyses.

Phylogenetic analyses based on a three-gene dataset (ITS-LSU-*tef1- $\alpha$* ) of members of *Chaetosphaeriaceae* were executed using software packages available on the CIPRES Science Gateway v. 3.3. The Maximum Likelihood (ML) analysis was performed with RAXML-HPC v. 8.2.12 (Stamatakis 2014) with a GTRCAT approximation. Statistical support for the nodes was determined by non-parametric bootstrapping (BS) with 1000 replicates. The Bayesian Inference (BI) analysis was performed with MrBayes v. 3.2.7 (Ronquist et al. 2012). Two Bayesian searches were conducted using default parameters. The B-MCMCMC (Bayesian-Metropolis-coupled Markov chain Monte Carlo) analyses lasted until the average standard deviation of split frequencies was below 0.01, with trees saved every 1000 generations with burn-in 25 %. The BI and ML phylogenetic

trees were compared visually in terms of topological conflicts between the supported clades. Nodes supported by values of  $\geq 75$  % ML Bootstrap (BS) and  $\geq 0.95$  BI Posterior Probability (PP) were deemed well-supported. *Tracylla aristata* and *T. eucalypti* (*Tracyllales*) were chosen as the outgroup, aligning with the methodology employed in prior studies by Réblová et al. (2022) and Wu & Diao (2022).

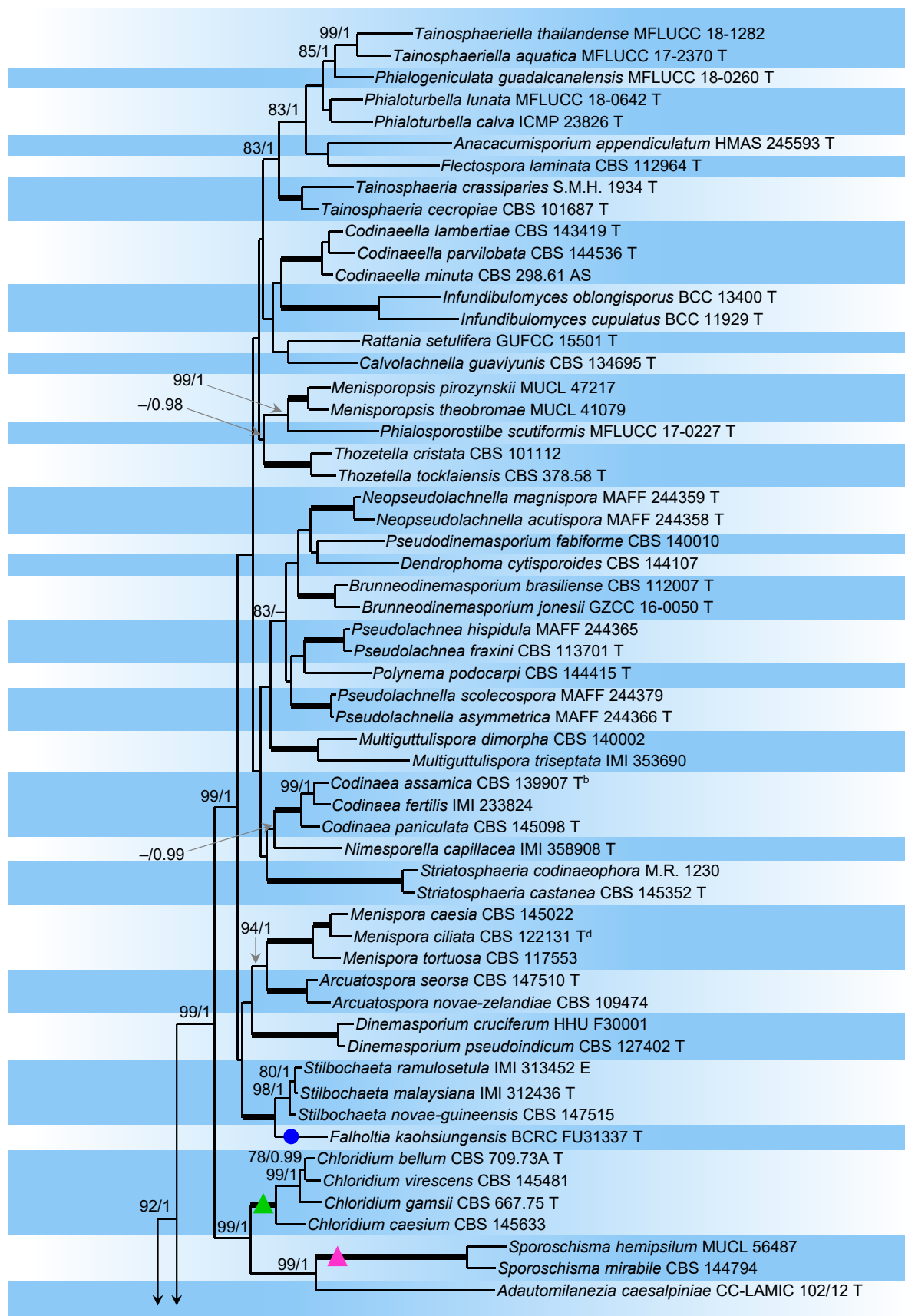
## RESULTS

To evaluate the relationships between strains of the studied species of *Chalarosphaeria*, *Exserticlava*, *Fusichalara*, *Phaeostalagmus*, *Stanjehughesia*, and two unknown fungi with members of *Chaetosphaeriaceae*, two phylogenetic analyses were conducted employing the ITS-LSU-*tef1- $\alpha$*  loci. The alignment comprised 159 strains, encompassing a total of 3512 characters, including gap regions, with 1716 unique character sites (RAXML). Eighty-nine nucleotides at the beginning of LSU were excluded from the analyses due to the incompleteness of majority of sequences retrieved from GenBank. The resulting phylogenetic trees, constructed through Bayesian Inference and Maximum Likelihood analyses, displayed a broad congruence. The ML tree is depicted in Fig. 1. Although it was difficult to fully resolve the backbone of the family tree and relationships between several genera, the deeper nodes representing individual genera received high statistical support. The phylogram yielded insights into the relationships within *Chaetosphaeriaceae*, revealing 89 supported lineages encompassing various genera and natural groups of species. Studied strains grouped in five clades (Clades A–E) in the phylogenetic tree.

Clades A, D, and the well-supported *Sporoschisma* clade (100 %/1 PP) represent fungi with a chalara-like morphotype in *Chaetosphaeriaceae*. *Chalarosphaeria* and *Fusichalara* constitute a highly supported Clade A (100/1). *Chalarosphaeria* (98/1) is represented by the reference strain of *Chs. breviclavata* CBS 148188, ex-type strain of *Chaetosphaeria tubulicollaris* PRM 900545 and two Caribbean strains of *Chalarosphaeria* sp. S.M.H. 2018 and S.M.H. 2223 isolated from ascospores and initially identified as *Chaetosphaeria chalaroides*. Based on this evidence, *Ch. tubulicollaris* is transferred to *Chalarosphaeria*. Molecular data indicate that the two Caribbean strains are not conspecific with the strain of *Chs. breviclavata* and represent a different species. *Fusichalara dingleyae*, the exclusive representative of the core of the genus *sensu* Hughes & Nag Raj (1973), grouped as a sister taxon to *Chalarosphaeria* within Clade A. Clade D represents a distinct lineage, unrelated to *Chalarosphaeria* and *Sporoschisma*, and is formally introduced as a novel genus and species, *Chalarina hyalospora*.

Clade B (100/1) comprises two morphotypes; the strongly supported *Stanjehughesia* (99/1) subclade along with three species of *Exserticlava*, distributed across two distinct lineages. Notably, *E. vasiformis*, the generic type, represented by two non-type strains (TAMA 450 from conidia and S.M.H. 3239 from ascospores), was resolved as not congeneric with the ex-type strains of *Chaetosphaeria chlorotunicata* S.M.H 1565 and *Ch. exserticlavoides* CBS 112963. Both latter species share the *Exserticlava* asexual morphology and formed a strongly supported subclade (100/1). Molecular and morphological data support the introduction of a new segregate genus, *Exserticlavopsis*, where both *Chaetosphaeria* species are transferred. The strain ICMP 15123 of the stanjehughesia-like fungus clustered as sister to *S. hormiscioides* (CBS 102664 and S.M.H. 2794), and is introduced as a novel species under the name *S. silvana* in this study. Other taxa that exhibit the stanjehughesia-like morphotype were resolved as distinct lineages, i.e., *Falhotia*, *Linkosia*, *Lomaantha*, *Morrisiella*, *Risgardia*, and *Zanclospora*.





**Fig. 1** Maximum Likelihood phylogenetic tree of members of *Chaetosphaeriaceae* based on analysis of a concatenated data set (ITS, LSU and *tef1-α*). Species names presented in **bold** represent taxonomic novelties. The newly acquired strains and those with novel sequences are highlighted in blue font. T, E, I, N, and P denote ex-type, ex-epitype, ex-isotype, ex-neotype, and ex-paratype strains. AS denotes authentic strain. Thickened branches indicate branch support with ML BS = 100 % and PP values = 1. Branch support of nodes  $\geq 75$  % ML and  $\geq 0.95$  PP is indicated above or below branches. A hyphen (–) indicates values lower than 75 % ML BS or 0.95 PP. Strains with a superscript letter 'a–d' after the accession number indicate: <sup>a</sup> holotype of *Chaetosphaeria trianguloconidia*, <sup>b</sup> ex-type strain of *Codinaea acaciae*, <sup>c</sup> ex-type strain of *Chaetosphaeria fuegiana*, and <sup>d</sup> ex-type strain of *Chaetosphaeria ciliata*. Symbols: Magenta, green, and blue triangles denote clades displaying chalaral-like (Clades A, D and *Sporoschisma*), phialocephala-like (Clade E and *Chloridium*) and stanjehughesia-like (Clade B, *Riisgaardia* and *Zanclospora*) morphotypes, respectively, while circles of the corresponding colours represent clades of various genera that are morphologically comparable to those with triangles.



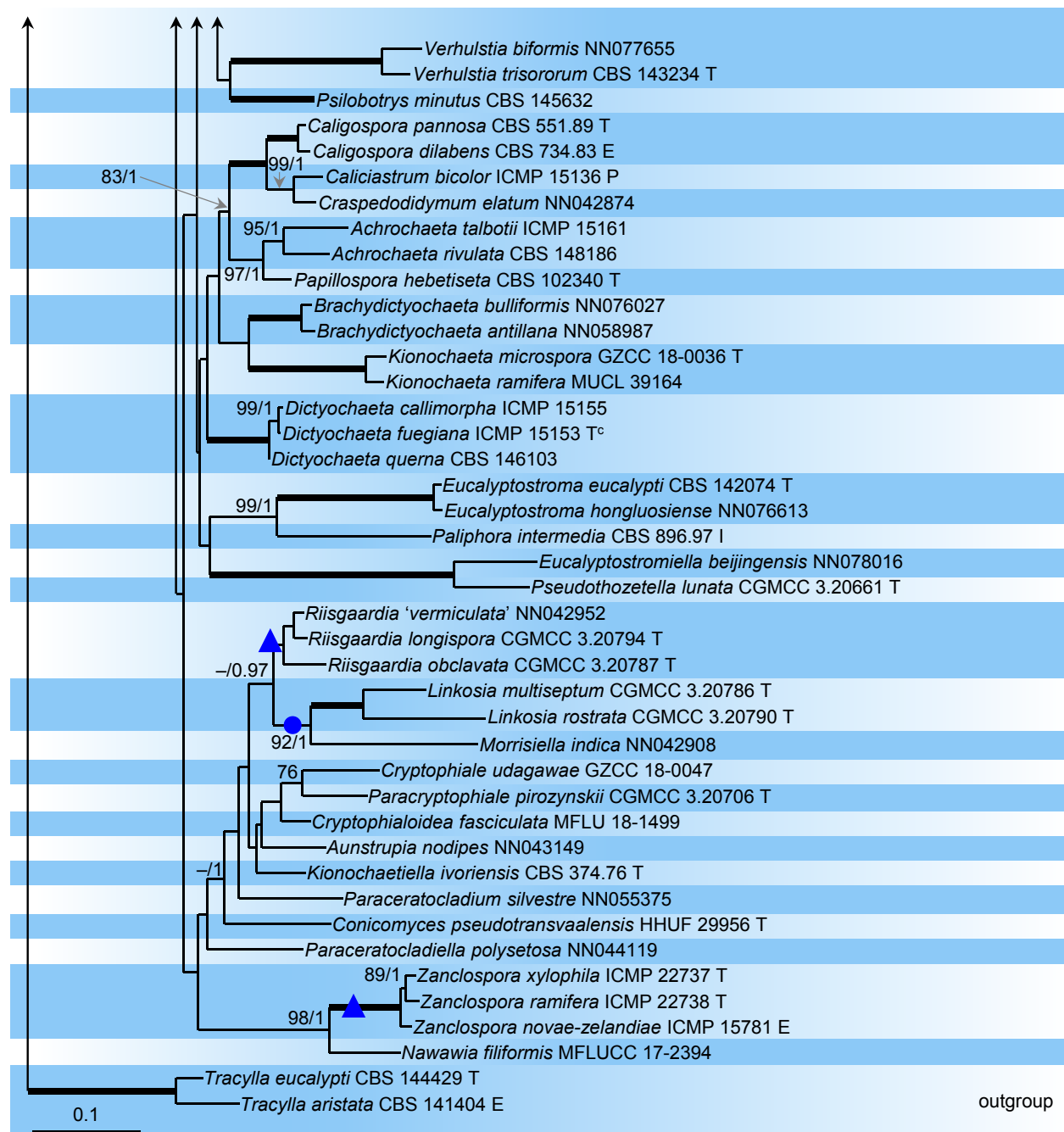


Fig. 1 (cont.)

Several species, characterized by varying degrees of penicillately and verticillately branched conidiophores, clustered within Clades C and E. Clade C (81/1) is comprised of the *Sporendocladia* subclade (100/1) and two additional subclades exhibiting the phaeostalagmus-like morphotype. These include *Phaeostalagmus cyclosporus*, represented by two non-type strains (CBS 663.70 and IMI 63832), as well as four additional strains of *P. tenuissimus* (CBS 145635, CBS 145640, CBS 145434, and CBS 917.73). The relationship between these two *Phaeostalagmus* species, distinguished mainly by the branching pattern of the conidiophores, could not be fully resolved. Therefore, Clade C is referred here as a natural group pending broader and more comprehensive taxon sampling.

Clade E (100/1) comprises two authentic strains of *Phialocephala fusca* (CBS 300.85 and CBS 301.85). The fungus displays a phialocephala-like morphotype, a characteristic previously observed only within *Chloridium* sect. *Pseudophialocephala* in *Chaetosphaeriaceae*. However, these two lineages are not phylogenetically related; instead, *Pc. fusca* was revealed to be

a sister taxon to the genus *Gongromerizella*. Consequently, a new genus, *Spadicocephala*, is proposed for *Pc. fusca*.

## TAXONOMY

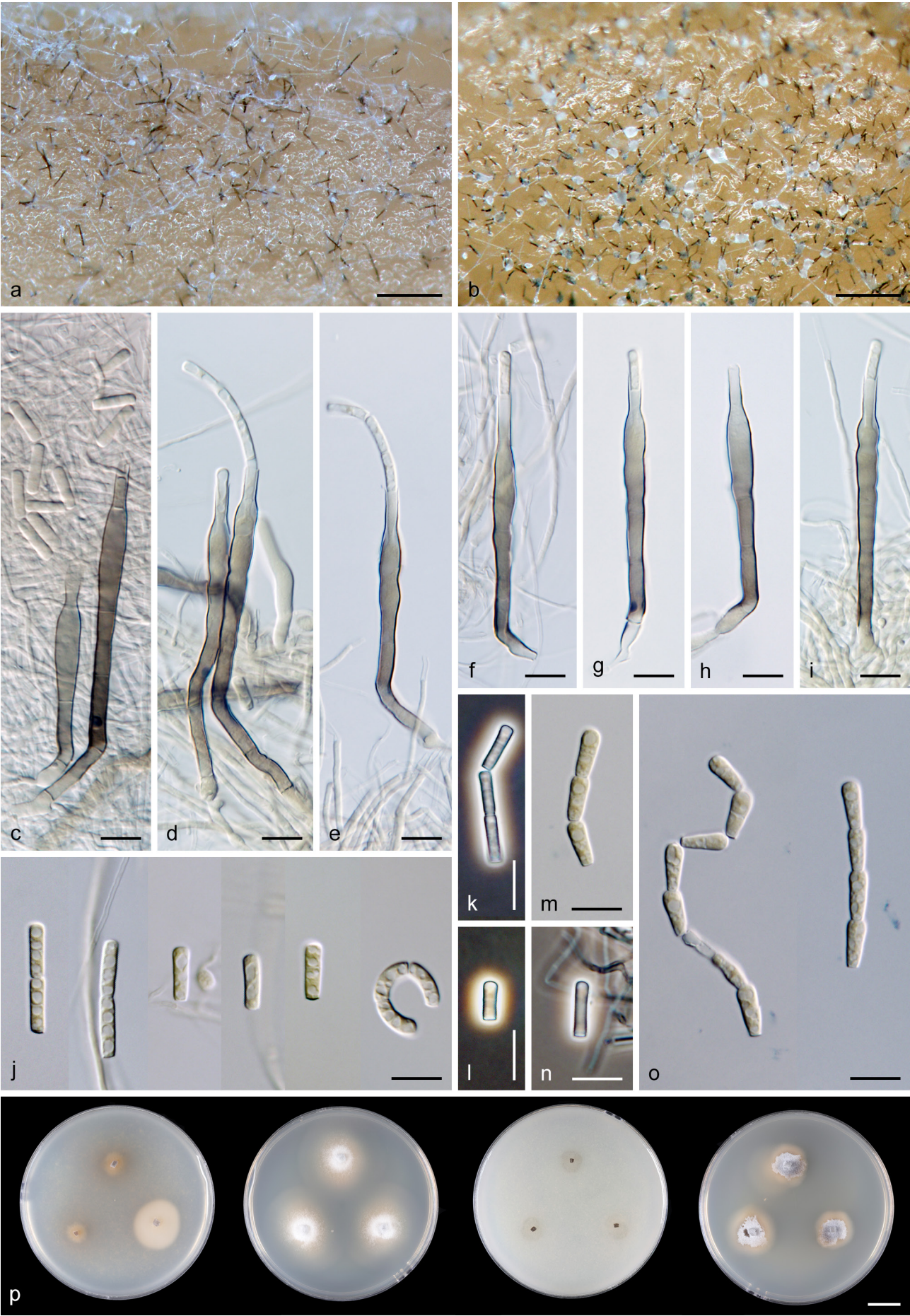
***Chalarina*** Réblová, A.N. Mill. & Hern.-Restr., *gen. nov.* — Myco-Bank MB 851460

*Etymology.* *Chalara* and *-ina* (Latin) related to, resembling; referring to the similarity of the new genus to *Chalara*.

*Type species.* *Chalarina hyalospora* Réblová, A.N. Mill. & Hern.-Restr.

*Colonies* in culture ivory, beige to pale brown, whitish to grey when sporulating, hairy, effuse. *Mycelium* aerial and submerged, septate, composed of hyaline to pale brown hyphae. *Asexual morph.* *Setae* absent. *Conidiophores* macronematous, mononematous, erect, straight, cylindrical, unbranched, pigmented, septate, sometimes reduced to stipitate conidiogenous cells. *Conidiogenous cells* phialidic, integrated, terminal, lageniform, pigmented, transition from venter to collarette abrupt; collarettes





**Fig. 2** *Chalarina hyalospora* (ex-type CBS 145806). a, b. Detail of colonies with sporulating conidiophores; c–i. conidiophores; j–o. conidia; p. colonies on CMD, MLA, OA, and PCA after 4 wk (from left to right). a–o. On MLA. — Scale bars: a, b = 500 µm, c–o = 10 µm, p = 1 cm.

narrow, tubular, shorter than the venter. *Conidia* cylindrical to subclavate, occasionally clavate, with rounded apex and truncate base bearing minute marginal frills, aseptate or with a septum, hyaline, adhering in false chains that easily collapse into colourless slimy heads. *Chlamydospores* absent. *Sexual morph* not observed.

Accepted species. *Chalarina hyalospora*.

***Chalarina hyalospora*** Réblová, A.N. Mill. & Hern.-Restr., sp. nov. — MycoBank MB 851751; Fig. 2

*Etymology.* *Hyalinus* (Latin) glassy, transparent, hyaline, *spora* (Latin); referring to the colour of conidia.

*Typus.* FRANCE, Pyrénées, Nébias, The Nature Trail and The Green Labyrinth 'Labyrinthe Vert', on decorticated twig of *Buxus sempervirens* buried in soil, 28 Sept. 2013, M. Réblová M.R. 4080 (holotype CBS H-25299 as a dried culture, culture ex-type CBS 145806).

*Colonies* on MLA effuse, hairy. *Mycelium* composed of branched, septate, hyaline to pale brown, smooth, 1–2.5 µm wide hyphae. *Asexual morph.* *Conidiophores* 63–160 × 3–4(–5) µm, macronematous, solitary, erect, cylindrical, straight, often bent in the lower part, unbranched, brown, usually paler near the base, septate, sometimes reduced to stipitate phialides. *Conidiogenous cells* 30–38 µm long, tapering just below the collarette to 2.5–3.5 µm, phialidic, integrated, terminal, lageniform, pale brown, paler upwards, occasionally proliferating percurrently; venter 20.5–29 × 5–6 µm, subcylindrical, slightly inflated and abruptly tapering to a collarette; collarettes 9–12 µm long, 2.5–3.5 µm wide, tubular, cylindrical, subhyaline to hyaline. *Conidia* 9.5–12 × 2.5–3.5 µm (mean ± se = 11.1 ± 0.6 × 2.9 ± 0.2 µm), cylindrical to long clavate, straight or curved, with rounded apex and truncate base bearing a minute marginal frill, 0–1-septate, not constricted at the septum, septum indistinct, median or submedian, smooth, adhering in false chains that easily collapse into colourless slimy heads. On OA conidia (7–)8–11.5 × 3.5–4.5 µm (mean ± se = 9.7 ± 1.0 × 3.6 ± 0.3 µm), clavate. *Chlamydospores* absent. *Sexual morph* not observed.

*Culture characteristics* (after 5 wk at 23 °C) — On CMD colonies 13–17 mm diam, circular, flat, margin entire to slightly fimbriate, sparsely velvety to cobwebby, partially mucoid, smooth, beige to ivory, reverse beige. On MLA colonies 50–52 mm diam, circular, flat to slightly convex, margin fimbriate, lanose, floccose, cobwebby at the margin, white at the centre, beige to pale brown towards the periphery, with a pale beige outer zone of submerged growth, reverse beige. On OA colonies 48–50 mm diam, circular, flat, margin entire, cobwebby to mucoid, ochre at the centre, pale brown towards the margin due to abundant formation of submerged conidiophores, reverse indistinct. On PCA colonies 23–25 mm diam, circular, flat to slightly convex, margin entire to slightly fimbriate, floccose, whitish grey becoming mucoid pale ochre towards the periphery, reverse beige. Sporulation was scarce on CMD, abundant on MLA, OA and PCA.

*Habitat & Geographical distribution* — Saprobe on decaying wood of *Buxus sempervirens*, known only from France.

*Notes* — Together with other hyphomycete obtained from a *Buxus* twig buried in soil and detritus, we also successfully isolated this species. However, no evidence of conidiophores bearing the same conidia was discernible on the original substrate (only fragments were present). It is plausible that the conidia adhered to the substrate where a piece of agar, positioned at the tip of a sterile needle, may have touched; however, other sporulating conidiophores may have been present on different twigs in the detritus, which were not within the scope of our observation. Therefore, only the description from culture is available.

The conidia of *Chl. hyalospora* displayed some variability in culture. On MLA, the conidia were mostly cylindrical to subclavate (ratio length/width approximately 3.9 : 1), whereas on OA, they appeared more clavate and wider in the upper part (ratio length/width approximately 2.7 : 1). The ratio of the length of the venter to the collarette is approximately 2.5 : 1. The trait of the longer venter serves as a distinct morphological feature that sets *Chalarina* apart from the morphologically similar genera *Nagrajchalara* and *Cylindrocephalum* from the *Leotiomyces* (Wu & Diao 2023).

***Chalarosphaeria*** W.P. Wu & Y.Z. Diao, Fungal Diversity 119: 468. 2023

*Type species.* *Chalarosphaeria breviclavata* (Nag Raj & W.B. Kendr.) W.P. Wu & Y.Z. Diao.

Description — See Wu & Diao (2023).

Accepted species. *Chalarosphaeria breviclavata*, *Cha. caribensis*, *Cha. tubulicollaris*, and *Chalarosphaeria* sp.

***Chalarosphaeria breviclavata*** (Nag Raj & W.B. Kendr.) W.P. Wu & Y.Z. Diao, Fungal Diversity 119: 468. 2023 — Fig. 3

*Basionym.* *Chalara breviclavata* Nag Raj & W.B. Kendr., A monograph of *Chalara* and allied genera: 95. 1975.

*Synonym.* *Chaetosphaeria chalaroides* Hol.-Jech., Folia Geobot. Phytotax. 19: 396. 1984.

Description — See Nag Raj & Kendrick (1975), Holubová-Jechová (1984), Wu & Diao (2023).

*Colonies* on MLA effuse, hairy. *Mycelium* composed of branched, septate, subhyaline to brown, smooth, 2–3.5 µm wide hyphae that become encrusted with age. *Asexual morph.* *Conidiophores* 34–113 × 3–4 µm, macronematous, solitary, erect, cylindrical, straight or slightly flexuous, unbranched, brown, septate, sometimes reduced to single conidiogenous cells. *Conidiogenous cells* 32–47 µm long, slightly tapering just below the collarette to 2.5–3.5 µm, monophialidic, integrated, terminal, extending percurrently, lageniform, pale brown, venter 20–35 × 4–6 µm, obclavate to subcylindrical, transition from venter to collarette more or less gradual; collarettes 11.5–14 µm long, 4–5 µm wide, subcylindrical to tubular, sometimes incurved apically, pale brown, paler towards the tip. *Conidia* 9–13.5 × 3–4 µm (mean ± se = 11 ± 0.9 × 3.5 ± 0.3 µm), cylindrical, subcylindrical to clavate, smooth, rounded or blunt at the apex, base truncate with a minute marginal frill, hyaline, aseptate, adhering in hyaline slimy heads. *Chlamydospores* absent. *Sexual morph* not observed.

*Culture characteristics* (after 5 wk at 23 °C) — On CMD colonies 20–22 mm diam, circular to irregular, flat, margin fimbriate, velvety-lanose, cobwebby at the margin, beige brown with a dark brown, somewhat irregular, outer zone of submerged growth, reverse dark grey-brown. On MLA colonies 26–27 mm diam, circular, flat, margin fimbriate, characteristics similar to those on CMD, the margin is darker brown, narrower, reverse dark grey brown. On OA colonies 48–50 mm diam, circular, flat, margin entire, floccose, mycelium thinner in the centre, olivaceous grey, dark olivaceous grey at the margin, reverse dark olivaceous grey. On PCA colonies 29–30 mm diam, circular, flat, margin fimbriate, lanose, cobwebby towards the periphery, mycelium bearing small colourless droplets of exudate, whitish beige, dark brown towards the margin, reverse dark brown with an outer pale brown ring. Sporulation was abundant on CMD and MLA, sparse on PCA, absent on OA.

*Habitat & Geographical distribution* — The species is a common saprobe on decaying wood and bark of deciduous trees, such as *Alnus glutinosa*, *Betula verrucosa*, *Betula* sp., *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Fraxinus* sp.,





**Fig. 3** *Chalarosphaeria breviclavata* (CBS 148188). a–c. Detail of colonies with sporulating conidiophores; d–g. conidiophores, phialides and conidia; h. tip of the collarette with a lacerate margin; i. phialide with conidia; j. conidia; k. colonies on CMD, MLA, OA, and PCA after 4 wk (from left to right). a, e–h, j. On natural substrate; b–d, i. on MLA. — Scale bars: a–c = 500  $\mu$ m, d–j = 10  $\mu$ m, k = 1 cm.



*Podocarpus dacrydioides*, *Populus* sp., *Quercus petraea*, *Q. robur*, *Quercus* sp., *Tilia cordata*, and other unidentified hosts. It is known from Canada, Czech Republic, China, Poland and Romania (Nag Raj & Kendrick 1975, Holubová-Jechová 1984, Wu & Diao 2023, MyCoPortal, this study).

**Materials examined.** CZECH REPUBLIC, South Moravian Region, Břeclav district, in the forest Horní les south of Lednice near Břeclav, on decaying wood of a branch of *Quercus robur*, 21 Aug. 1974, V. Holubová-Jechová (holotype of *Chaetosphaeria chalaroides* PRM 829031); *ibid.*, Lanžhot, Ranšpurk National Nature Reserve, on decaying wood of *Quercus* sp., 26 Oct. 2018, M. Réblová M.R. 4008 (PRA-21598, CBS 148188); *ibid.*, on decaying wood of *Carpinus betulus*, 26 Oct. 2018, M. Réblová M.R. 3999 (PRA-21599).

**Notes** — The asexual morph was originally described from decaying wood of a deciduous tree, likely *Fraxinus*, in Canada as *Chalara breviclavata* (Nag Raj & Kendrick 1975). The sexual morph was introduced as *Chaetosphaeria chalaroides* by Holubová-Jechová (1984) based on a collection made on *Quercus robur* in the Czech Republic, which included both morphs. *Chaetosphaeria chalaroides* is a taxonomic synonym of *Cha. breviclavata*. An isolate CBS 148188 of this species, comprising only the asexual state, found recently on *Quercus* sp. and originating from the floodplain forests in the Dyje river basin, c. 20 km away from the type locality of *Ch. chalaroides*, represents *Chs. breviclavata* in our phylogenetic analyses. Our observations of the recent specimen align closely with those of Nag Raj & Kendrick (1975) and Holubová-Jechová (1984).

Recently, two collections of *Chs. breviclavata* from China were reported by Wu & Diao (2023). Regrettably, living cultures and molecular data for these collections are unavailable. A comparison of measurements provided by Wu & Diao (2023) for these specimens showed that the collarette is longer in the Chinese material, measuring 25–40 µm, compared to 12–20 µm *vide* Holubová-Jechová (1984), 15–20 µm *vide* Nag Raj & Kendrick (1975), and 11.5–14 µm in culture and 11.5–18.5 µm from nature (CBS 148188, this study).

*Chalarosphaeria breviclavata* closely resembles *Chs. caribensis*; for comparison see notes to the latter species. It can also be compared to *Chalara nothofagi*, which was discovered on dead leaves of *Fuscospora* sp. in New Zealand (Nag Raj & Kendrick 1975) and it differs in having cylindrical, narrower conidia. *Chalara cibotti*, a species known only from Hawaii on tropical tree ferns (Nag Raj & Kendrick 1975), somewhat resembles *Chs. breviclavata*. However, the conidiophores are less distinct, and it is distinguished by its septate, cuneiform, shorter and narrower conidia.

***Chalarosphaeria caribensis*** (Hol.-Jech.) Réblová, A.N. Mill. & Hern.-Restr., *comb. nov.* — MycoBank MB 851777

**Basionym.** *Chalara caribensis* Hol.-Jech., Mycotaxon 15: 281. 1982.

**Typus.** CUBA, Santi Spiritus Province, Botanical garden in Cienfuegos near Soledad, on decaying branch of a deciduous tree, 19 Mar. 1981, V. Holubová-Jechová (holotype PRM 825414).

**Description** — See Holubová-Jechová (1982).

**Habitat & Geographical distribution** — Saprobe on decaying wood of a deciduous tree, known only from Cuba (Holubová-Jechová 1982).

**Notes** — While molecular data for this species are currently unavailable, its striking morphological similarity to *Chs. breviclavata* strongly suggests that it should be classified within the genus *Chalarosphaeria*. However, to confirm this placement, further verification with DNA sequence data is necessary. *Chalarosphaeria caribensis* is known only in its asexual form and can be differentiated from *Chs. breviclavata* by its smaller conidia (9–12.5 × 2.5 µm), shorter phialides (25–40 × 3.5–4 µm)

with a narrower venter (3.5–6 µm), shorter and narrower collar-ettes (10–12 × 3–4 µm), and slightly smaller conidia (9–12.5 × 2.5 µm) *vide* Holubová-Jechová (1982).

***Chalarosphaeria tubulicollaris*** (Réblová & Seifert) Réblová, A.N. Mill. & Hern.-Restr., *comb. nov.* — MycoBank MB 851753

**Basionym.** *Chaetosphaeria tubulicollaris* Réblová & Seifert, Sydowia 55: 337. 2003.

**Description** — See Réblová & Seifert (2003).

**Typus.** THAILAND, Nakhon Nayok Province, Khao Yai National Park NE of Bangkok, Mor Singh To trail c. 1 km SW of Khao Yai Forest Headquarters, elev. 800 m, on decaying wood of *Quercus* sp., 19 Aug. 2001, M. Réblová & N. Hywel-Jones M.R. 2037/TH 182 (holotype of *Chaetosphaeria tubulicollaris* PRM 900545).

**Habitat & Geographical distribution** — Saprobe on decaying wood of *Quercus* sp., known only from Thailand.

**Notes** — The link between the sexual and asexual morphs was experimentally confirmed by Réblová & Seifert (2003); the chalara-like conidia and conidiophores are depicted in the illustration accompanying the protologue. Regrettably, the living culture from which the DNA was extracted is no longer viable. *Chalarosphaeria tubulicollaris* resembles *Chs. breviclavata*, but it can be distinguished from the latter species by its 1–3-septate ascospores that are wider and somewhat longer in the lower range ((13–)15–17 × 4–5 µm vs 9–17 × 2.5–4 µm *vide* Holubová-Jechová 1984), shorter and wider asci (47–58 × 8.5–9(–10) µm vs 62–83 × 6.5–8 µm), and broader conidia (11–16 × 4–6 µm *in vitro* vs (7–)10–14(–16) × (2.5–)3.5–4.5 µm *in vivo*).

***Chalarosphaeria* sp.** S.M.H. 2018, S.M.H. 2223

**Habitat & Geographical distribution** — Saprobe on decaying wood, known from Costa Rica and Puerto Rico.

**Notes** — Huhndorf et al. (2001) published LSU sequences for two species collected in the Caribbean, which were identified as *Ch. chalaroides* (S.M.H. 2018 and S.M.H. 2223). Both sexual and asexual morphs were present; metadata and images without descriptions were published in Fernández et al. (2006). In our study, ITS sequences were generated from both specimens. Phylogenetic analyses indicated a close relationship of S.M.H. 2018 and S.M.H. 2223 with *Chs. breviclavata* and *Chs. tubulicollaris* within a monophyletic strongly supported clade, but they were not conspecific with the reference strain of *Chs. breviclavata* CBS 148188. The Caribbean material was not available for direct examination: COSTA RICA, Punta Arenas, Parque Internacional La Amistad, Las Alturas Biological Station, first 500 m of trail to Cerro Echandi, elev. 1580 m, on 60 cm diam log on ground, 6 May 1996, S.M. Huhndorf & F.A. Fernández S.M.H. 2223. PUERTO RICO, Bosque Estatal de Guajatasca, along Vereda Nueva, on decaying wood of a branch, 22 Jan. 1996, S.M. Huhndorf S.M.H. 2018. However, we were able to obtain measurements from existing sources: asci 50–80 × 6–8 µm, ascospores (9–)13–15(–17) × 3–4 µm, phialides with a deep collarette 9–14 × 4–5 µm, and conidia 7–18 × 3.5–5 µm (Huhndorf & Miller, unpubl. data). Based on these provided measurements, it becomes challenging to distinguish the Caribbean specimens from *Chs. breviclavata*, as the sizes of the asci, ascospores, and conidia overlap.

Based on their placement in the phylogenetic analyses, the specimens S.M.H. 2018 and S.M.H. 2223 are accepted to represent *Chalarosphaeria* sp. At present, their true identity remains unknown. Further investigation, including the acquisition of new specimens and observations in culture, is essential

to accurately identify and characterise this species. With the available data, a preliminary comparison can be made with *Chs. caribensis* (Holubová-Jechová 1982), which shares a similar geographical origin.

***Exserticlava*** S. Hughes, New Zealand J. Bot. 16: 332. 1978

*Type species. Exserticlava vasiformis* (Matsush.) S. Hughes.

**Emended description.** Colonies black, hairy, effuse, composed of conidiophores and ascomata. *Mycelium* partly immersed in the substrate, partly superficial, composed of pigmented, septate, hyphae. *Asexual morph.* Setae absent. *Conidiophores* macronematous, mononematous, erect, cylindrical, unbranched, brown, septate. *Conidiogenous cells* phialidic, integrated, terminal, funnel-shaped or cupulate, the distal outer pigmented wall ruptures as the inner, hyaline thick-walled layer expands outwards; the hyaline part bears multiple conidiogenous loci, at first it is subglobose and finally extends upwards into a subulate, hyaline, thick-walled structure; *collarettes* brown, with a frayed margin. *Conidia* broadly ellipsoidal, brown, distoseptate, thick-walled, produced successively in a cluster on the basal part of the hyaline extension, with a conidial scar, adhering in brown slimy heads. *Sexual morph.* Ascomata superficial, globose to conical, papillate, ostiolate, clothed with unbranched, usually upward bent capitate setae. *Ascomatal wall* three-layered, outer layer composed of a brightly coloured pruina covering also apices of setae, middle layer composed of brown pseudoparenchymatous cells, inner layer of hyaline, think-walled, flattened cells. *Paraphyses* hyaline, filiform, septate. *Asci* unitunicate, cylindrico-clavate, stipitate with a non-amyloid apical annulus, 8-spored. *Ascospores* cylindrical to narrowly fusiform, asymmetrical, rounded at the apical end, tapering towards the basal end, transversely septate, hyaline when young becoming yellowish brown at maturity (description of the sexual morph adopted from Sivanesan & Chang 1995, and Fernández & Huhndorf 2005).

*Accepted species. Exserticlava vasiformis.*

***Exserticlava vasiformis*** (Matsush.) S. Hughes, New Zealand J. Bot. 16: 332. 1978

*Basionym. Cordana vasiformis* Matsush., Icon. Microfung. Matsush. Lect.: 40. 1975.

*Synonym. Chaetosphaeria capitata* Sivan. & H.S. Chang, Mycol. Res. 99: 715. 1995.

**Description** — See Matsushima (1975), Hughes (1978), Sivanesan & Chang (1995), Réblová & Seifert (2003), Fernández & Huhndorf (2005), and Tsui et al. (2001).

**Habitat & Geographical distribution** — A common saprobe on decaying wood of many hosts, e.g., *Cortaderia selloana*, *Cortaderia* sp., *Brachyglottis repanda*, *Butia capitata* × *eriospatha*, *Freyinetia* sp., *Olearia rami*, *Pandanus furcatus*, *Washingtonia robusta*, and also on decayed grass culms and submerged grass, and rachides of dead leaves of *Acoelorrhaphe wrightii* and *Sabal palmetto*. It is known from Australia, Brazil, China, Costa Rica, Cuba, India, Indonesia, Japan, Malaysia, New Caledonia, New Zealand, Puerto Rico, North America, Russia, Taiwan, and USA (Matsushima 1975, 1985, Hughes 1978, Crane & Schoknecht 1982, Kuthubutheen & Nawawi 1994, Sivanesan & Chang 1995, Lu et al. 2000, Tsui et al. 2001, Heredia-Abarca et al. 2004, Fernández & Huhndorf 2005, Cruz et al. 2008, Wu & Diao 2022, MyCoPortal).

**Notes** — The species is represented by ITS and LSU sequences of two strains, S.M.H. 3239 derived from ascospores (Fernández & Huhndorf 2005) and a conidial isolate TAMA 450 (Tsuchiya et al. unpubl.). The sexual morph was initially

introduced by Sivanesan & Chang (1995) as *Ch. capitata*. The authors reported that the holotype specimen also contained two hyphomycetes, *Exserticlava vasiformis* and *Sporidesmium* sp.; however, the link between the sexual and asexual morphs could not be confirmed at that time. Fernández & Huhndorf (2005) subsequently established the sexual-asexual connection of *Ch. capitata* with *E. vasiformis* in culture. Sivanesan & Chang (1995) described the ascomata as black, although Fernández & Huhndorf (2005) reported yellow pruina covering the surface of ascomata as well as the apices of capitate setae. The coloured superficial layer may eventually fade or even become absent in aged ascomata, a phenomenon we have also observed in related *Exserticlavopsis*.

***Exserticlavopsis*** Réblová, A.N. Mill. & Hern.-Restr., *gen. nov.*  
— MycoBank MB 851462

*Etymology. Exserticlava* and *-opsis* (Greek), resembling, referring to the similarities of the new genus with the genus *Exserticlava*.

*Type species. Exserticlavopsis exserticlavoides* (Réblová & Seifert) Réblová, A.N. Mill. & Hern.-Restr.

**Colonies** on the natural substrate effuse, hairy, brown to black, greyish white when sporulating. *Mycelium* partly immersed in the substrate, partly superficial, composed of pigmented, septate hyphae. *Asexual morph.* Setae absent. *Conidiophores* macronematous, mononematous, erect, straight, solitary or caespitose, cylindrical, unbranched, usually with several percurrent proliferations, brown, septate. *Conidiogenous cells* phialidic, subcylindrical to slightly funnel-shaped, integrated, terminal, extending percurrently, the distal outer pigmented wall ruptures, hyaline, thin-walled, inner layer is sometimes protruding slightly beyond the collarette; collarettes brown, with a frayed margin. *Conidia* broadly ellipsoidal to obovoid, brown, distoseptate, thick-walled, with a minute frill around the basal scar, adhering in brown slimy heads. *Chlamydospores* absent. *Sexual morph.* Ascomata superficial, globose to conical, papillate, ostiolate, clothed with pigmented, bristle-like, acute and always sterile setae. *Ascomatal wall* three-layered, outer wall powdery, yellowish or green except the black glabrous papilla, becoming pale brown or grey, eventually disappears with age leaving the ascomata black; middle layer composed of brown pseudoparenchymatous cells; inner layer of hyaline, thin-walled, flattened cells. *Paraphyses* hyaline, filiform, septate. *Asci* unitunicate, cylindrico-clavate, stipitate, with a non-amyloid apical annulus, 8-spored. *Ascospores* fusiform, symmetrical, transversely septate, versicolorous, hyaline when young, middle cells turn subhyaline, stramineous to pale brown at maturity, end cells remain hyaline.

*Accepted species. Exserticlavopsis chlorotunicata*, *Ex. exserticlavoides*, and *Ex. hiugensis*.

***Exserticlavopsis chlorotunicata*** (F.A. Fernández & Huhndorf) Réblová, A.N. Mill. & Hern.-Restr., *comb. nov.* — MycoBank MB 851754

*Basionym. Chaetosphaeria chlorotunicata* F.A. Fernández & Huhndorf, Fungal Diversity 18: 18. 2005.

*Typus.* PUERTO RICO, Caribbean National Forest, El Verde Research Area, 16-ha Grid, Luquillo Mts, 350 to 425 m, [18.3167, -65.8167], 25 Sept. 1995, on log, S.M. Huhndorf S.M.H. 1565 (holotype of *Chaetosphaeria chlorotunicata* F).

**Description** — See Fernández & Huhndorf (2005).

**Habitat & Geographical distribution** — Saprobe on decaying wood, known from Costa Rica, Jamaica, Panama, and Puerto Rico (Fernández & Huhndorf 2005).

Notes — The asexual morph only developed in culture, originating from an ascospore isolate (Fernández & Huhndorf 2005). *Exserticlavopsis* (*Ex.*) *chlorotunicata* is closely related to *Ex. exserticlavoides* (Réblová & Seifert 2003), both species share ascomata covered by a yellowish to pale brown powdery layer except the black papilla and 3-distoseptate, brown conidia that have similar size in culture ( $22\text{--}30 \times 10\text{--}15\ \mu\text{m}$  for *Ex. chlorotunicata*,  $22.5\text{--}27 \times (10\text{--})11\text{--}12.5\text{--}(13)\ \mu\text{m}$  for *Ex. exserticlavoides*). However, they can be differentiated by the size of their asci and ascospores, which are shorter and narrower in *Ex. exserticlavoides* (*Ex. chlorotunicata*: asci  $97\text{--}127 \times 13\text{--}18\ \mu\text{m}$ , ascospores  $27\text{--}62 \times 6\text{--}9.5\ \mu\text{m}$  *vide* Fernández & Huhndorf (2005); for measurements of *Ex. exserticlavoides* see description below).

***Exserticlavopsis exserticlavoides* (Réblová & Seifert)**

Réblová, A.N. Mill. & Hern.-Restr., *comb. nov.* — MycoBank MB 851755; Fig. 4

*Basionym.* *Chaetosphaeria exserticlavoides* Réblová & Seifert, *Sydowia* 55: 316. 2003.

*Synonym.* *Exserticlava exserticlavoides* (Réblová & Seifert) W.P. Wu & Y.Z. Diao, *Fungal Diversity* 116: 340. 2022.

*Typus.* THAILAND, Nakhon Nayok Province, Khao Yai National Park, trail to Haew Suwat waterfall c. 4.5 km E of Khao Yai Forest Headquarters, N14°26' E101°25', elev. 720 m, 2 Aug. 2001, on decayed bamboo culm, *M. Réblová, G.J. Samuels & R. Nasit M.R. 2181/TH 434* (holotype of *Chaetosphaeria exserticlavoides* PRM 900540, culture ex-type CBS 112963 = DAOM 231138).

Description — See Réblová & Seifert (2003).

*Colonies* on MLA effuse, hairy. *Mycelium* composed of branched, septate, hyaline to pale brown, smooth,  $1.5\text{--}3.5\ \mu\text{m}$  wide hyphae. *Asexual morph.* *Conidiophores*  $40\text{--}202 \times 4.5\text{--}6.5\ \mu\text{m}$ , macronematous, solitary or somewhat caespitose, erect, straight or slightly flexuous, cylindrical, sometimes tapering slightly towards the base,  $4.5\text{--}5\ \mu\text{m}$  wide at the base, septate, unbranched, brown, usually with several percurrent proliferations, sometimes reduced to single conidiogenous cells. *Conidiogenous cells*  $15\text{--}30\text{--}(35) \times 5\text{--}6.5\ \mu\text{m}$ , phialidic, integrated, terminal, extending percurrently, subcylindrical, pale brown, the distal outer pigmented wall ruptures and inner, hyaline, thin-walled layer is sometimes slightly protruding beyond the collarette; collarettes  $4.5\text{--}6\ \mu\text{m}$  wide, brown, apically slightly incurved, with a frayed margin. *Conidia*  $19\text{--}26.5 \times 11\text{--}13.5\text{--}(14)\ \mu\text{m}$  (mean  $\pm$  se =  $22.8 \pm 2.1 \times 12.6 \pm 0.8\ \mu\text{m}$ ), broadly ellipsoidal to obovoidal, 3-distoseptate, with a distinct pore at each cell septum at maturity, pale brown, with a minute marginal frill around the basal scar, adhering in brown slimy heads. *Chlamydospores* absent. *Sexual morph* not observed.

*Culture characteristics* (after 5 wk at 23 °C) — On CMD colonies 8–10 mm diam, circular, raised, margin lobate, mucoid to cobwebby with funiculate projections, dark grey with white patches at the periphery, reverse grey. On MLA colonies 10–12 mm diam, circular, convex, margin entire to lobate, velvety, dark chocolate brown, reverse of the same colour. On OA colonies 8–10 mm diam, circular, slightly raised, margin lobate, floccose at the centre, partially hairy, aerial mycelium with numerous colourless exudates, becoming mucoid, dark olivaceous grey, paler at the margin, reverse of the same colour. On PCA colonies 11–12 mm diam, circular, raised, margin entire to lobate, velvety, slightly furrowed, with numerous colourless exudates, dark brown-grey with a thin isabelline ring at the margin, reverse grey, darker at the margin. Sporulation was absent on CMD, abundant on MLA, sparse to moderate on OA and PCA; conidiophores on PCA mostly submerged at the periphery of the colony.

*Habitat & Geographical distribution* — Saprobe on decaying bamboo culm, known only from Thailand.

Notes — The connection between sexual and asexual morphs was established experimentally in culture by Réblová & Seifert (2003). No asexual morph was present on the substrate in the holotype collection. The conidiogenous cells extend percurrently several times, while the meristem remains active and each proliferation is surrounded by a slimy head of adhering conidia. In cultures older than six months (grown on MLA), the conidiogenous cells extended percurrently up to nine times.

*Exserticlavopsis exserticlavoides* can be compared with *Ex. hiugensis* (Hino & Katumoto 1961, Matsushima 1975), from which it differs by its smaller ascospores ( $28\text{--}32\text{--}(33.5) \times 3.5\text{--}4.5\ \mu\text{m}$  vs  $36\text{--}43\text{--}(48) \times (6\text{--})7\text{--}7.5\text{--}(8)\ \mu\text{m}$ ), smaller asci ( $86\text{--}94 \times 11\text{--}13\ \mu\text{m}$  vs  $130\text{--}149 \times 17\text{--}22\ \mu\text{m}$ ) and slightly shorter and narrower conidia ( $22.5\text{--}27 \times (10\text{--})11\text{--}12.5\text{--}(13)\ \mu\text{m}$  vs  $25\text{--}35 \times 13\text{--}15\ \mu\text{m}$ ; measurements for both species *vide* Réblová & Seifert 2003). The degree of pigmentation in mature ascospores is less prominent in *Ex. exserticlavoides* compared to *Ex. hiugensis*. This is because the middle cells in the former species are subhyaline to straw-coloured, whereas in the latter, they are generally pale brown to mid-brown. For differences between *Ex. exserticlavoides* and the similar *Ex. chlorotunicata*, see notes under the latter species.

***Exserticlavopsis hiugensis* (I. Hino) Réblová, A.N. Mill. & Hern.-Restr., *comb. nov.* — MycoBank MB 851756**

*Basionym.* *Chaetosphaeria hiugensis* I. Hino, *Bull. Miyaz. Coll. Agr. For.* 10: 63. 1938.

*Synonyms.* *Cordana triseptata* Matsush., *Icon. Microfung. Matsush. Lect.* 39. 1975.

*Exserticlava triseptata* (Matsush.) S. Hughes, *New Zealand J. Bot.* 16: 333. 1978.

*Typus.* JAPAN, Miyazaki Prefecture (former Hyuga Province), Kibana-mura, dead stem of *Semiarundinaria fastuosa*, 11 June 1937, *I. Hino* (holotype of *Chaetosphaeria hiugensis*, location of type unknown *vide* Réblová & Seifert 2003); *ibid.*, Tottori Prefecture, Tottori City, on bamboo stem, Oct. 1966, *T. Matsushima* M.F.C. No. 1960 (holotype of *Cordana triseptata*, microscopic slide DAOM 189414).

Description — See Hino & Katumoto (1961), Matsushima (1975), Kuthubutheen & Nawawi (1994), Hernández-Gutiérrez & Mena-Portales (1995), Tsui et al. (2001), Réblová & Seifert (2003), and Cruz et al. (2008).

*Habitat & Geographical distribution* — This species is a common saprobe in terrestrial and freshwater environments. It can be found on decayed bamboo culms of *Dendrocalamus* sp., *Phyllostachydis edulis*, *Semiarundinaria fastuosa*, *Sinobambusa tootsik*, hard-wood of unidentified angiosperms, submerged woody debris, decaying leaves of a palm species *Astrocaryum* sp. and wood of various other unknown hosts. The species has been reported from Costa Rica, Cuba, China, Japan, Malaysia, Micronesia, Puerto Rico, and Seychelles (Hino & Katumoto 1961, Matsushima 1975, 1985, Kuthubutheen & Nawawi 1994, Hernández-Gutiérrez & Mena-Portales 1995, Lu et al. 2000, Tsui et al. 2001, Réblová & Seifert 2003, MyCoPortal).

*Material examined.* PUERTO RICO, Sierra de Luquillo Mts, Luquillo, Sabana, chicken farm, on decaying unidentified hard-wood, 10 June 1998, *M. Réblová M.R. 1208* (PRA-21602).

Notes — The connection between the sexual and asexual morphs, initially described as *Ch. hiugensis* (Hino 1938) and *Cordana triseptata* (Matsushima 1975), was experimentally verified by Matsushima (1985). The species was re-described by Réblová & Seifert (2003) based on a collection from Puerto Rico containing both morphs; asci:  $130\text{--}149 \times 17\text{--}22\ \mu\text{m}$ , ascospores:  $36\text{--}43\text{--}(48) \times (6\text{--})7\text{--}7.5\text{--}(8)\ \mu\text{m}$ , conidia:  $25\text{--}35 \times 13\text{--}15\ \mu\text{m}$  on the substrate. This description aligns with the observations published by Hino & Katumoto (1961) and Matsushima (1975, 1985) and study of the holotype of *Cordana triseptata* (DAOM 189414; Réblová & Seifert 2003). Although no





**Fig. 4** *Exserticlavopsis exserticlavoides* (ex-type CBS 112963). a, b. Detail of colonies with sporulating conidiophores; c. tip of the phialide having a collarette with lacerate margin; d–j. conidiophores with conidia; k. detail of the conidiogenous locus; l, m. conidia; n. colonies on CMD, MLA, OA, and PCA after 4 wk (from left to right). a–m. On MLA. — Scale bars: a, b = 500  $\mu$ m, c–m = 10  $\mu$ m, n = 1 cm.

living strain or molecular data are currently accessible for this species, its morphological resemblance to *Ex. chlorotunicata* and *Ex. exserticlavoides* is highly evident. Consequently, we suggest a new combination within the genus *Exserticlavoides*, pending confirmation through DNA sequencing.

Wu & Diao (2022) incorrectly considered *Ch. chlorotunicata* a synonym of *E. triseptata* (= *Ex. hiuensis*). *Exserticlavopsis hiuensis* is distinguished from *Ex. chlorotunicata* and *Ex. exserticlavoides* by a superficial greenish layer which turns grey with age and eventually fades leaving the ascomata black. In addition, it differs from *Ex. chlorotunicata* in longer asci and narrower conidia, and from *Ex. exserticlavoides* in having larger asci, ascospores, and conidia (for detailed measurements, refer to the notes provided for both species).

***Fusichalara*** S. Hughes & Nag Raj, New Zealand J. Bot. 11: 662. 1973

*Type species. Fusichalara dimorphospora* S. Hughes & Nag Raj, New Zealand J. Bot. 11: 663. 1973.

*Colonies* on the natural substrate effuse, bristle-like, dark brown, black or reddish brown, whitish when sporulating. *Mycelium* partly immersed in the substratum, partly superficial, composed of septate, branched, dematiaceous hyphae. *Asexual morph.* *Setae* absent. *Conidiophores* macronematous, mononematous, scattered or aggregated into compact fascicles, often tightly adhering to each other, erect, brown or reddish brown, composed of a subcylindrical septate stalk and a conidiogenous cell, sometimes with one percurrent proliferation. *Conidiogenous cells* phialidic, terminal, integrated, subcylindrical to narrowly obclavate or narrowly lageniform, glabrous, becoming verrucose with age, composed of a basal venter and a collarette, transition from venter to collarette gradual to abrupt, with a distinct thickening of the inner wall between venter and collarette; collarettes robust, tubular, cylindrical, at the apex torn and frilled. *Conidia* are of two kinds. First-formed conidia cylindrical and nearly as long as the collarette, several-septate, with the septa mostly transverse but occasionally with one or a few oblique septa, long obconical or cylindrical, rounded at the apex, sometimes tapering towards the base, truncate or obconical at the base, with or without a marginal frill, hyaline, pale brown or brown. Subsequent conidia shorter, fusiform, straight or slightly sigmoid, with less septa, hyaline or pale brown to brown with paler end cells. *Sexual morph.* *Ascomata* perithecial, superficial, subglobose, dark brown, glabrous, papillate. Ostiolar canal periphysate. *Ascomatal wall* two-layered, brittle, carbonaceous. *Paraphyses* persistent, septate, branching. *Asci* unitunicate, cylindrico-clavate, short-stipitate, with a non-amyloid apical ring, 8-spored. *Ascospores* fusiform, transversely septate, hyaline.

*Accepted species. Fusichalara dimorphospora, F. dingleyae, and F. novae-zelandiae.*

***Fusichalara dimorphospora*** S. Hughes & Nag Raj, New Zealand J. Bot. 11: 663. 1973

*Description* — See Hughes & Nag Raj (1973).

*Habitat & Geographical distribution* — On decaying bark of *Weinmannia racemosa*, known only from New Zealand (Hughes & Nag Raj 1973).

*Notes* — *Fusichalara dimorphospora* differs from the similar *F. novae-zelandiae* by larger phialides and characters of conidia. The first conidia are wider and pale brown to brown (vs subhyaline to pale brown in *F. novae-zelandiae*) except for the hyaline basal cell, and possess more septa, typically are 11–17 transversely septate but occasionally with one or a few oblique septa, the subsequent conidia are 7-septate, longer and wider with transverse septa only (Hughes & Nag Raj 1973).

***Fusichalara dingleyae*** S. Hughes & Nag Raj, New Zealand J. Bot. 11: 665. 1973 — Fig. 5

*Synonym. Chaetosphaeria fusichalaroides* Réblová, Stud. Mycol. 50: 180. 2004.

*Description* — See Hughes & Nag Raj (1973) and Réblová (2004).

*Culture characteristics* (after 5 wk at 23 °C) — On CMD colonies 8–10 mm diam, circular, flat, margin entire, cob-webby, beige to pale brown, reverse beige. On MLA colonies 12–14 mm diam, circular, convex, margin entire, lanose, aerial hyphae with numerous hyaline exudates, beige at the centre, brown towards the margin, reverse dark brown to black. On OA colonies 13–15 mm diam, circular, flat, margin entire, sparsely lanose, olivaceous brown, very pale ochre to pale brown pigment diffusing into the agar, reverse dark brown to black. On PCA colonies 8–10 mm diam, convex, margin entire to rhizoidal, lanose, floccose at the centre, brown to dark cinnamon, reverse dark brown. Sporulation was absent on CMD, moderate on MLA and PCA, abundant on OA, where conidial masses were ochre brown.

*Habitat & Geographical distribution* — Saprobe on decaying wood of *Melicitus ramiflorus*, *Olearia rani*, *Weinmannia racemosa*, and other unknown hosts, known only from New Zealand (Hughes & Nag Raj 1973, Réblová 2004, MyCoPortal, this study).

*Materials examined.* NEW ZEALAND, Auckland Province, Waitakere Ranges, Upper Piha Valley, Home Track, on decorticated wood, 9 Oct. 1963, S. Hughes (holotype of *Fusichalara dingleyae* and *Chaetosphaeria fusichalaroides* PDD 21599, isotype DAOM 93957a); *ibid.*, West Coast Province, Moeraki River valley, Paringa Cattle track c. 12 km SE of the Lake Paringa NE of Haast, on decorticated wood of a trunk of *Dacryodes* sp., 9 Mar. 2003, M. Réblová M.R. 2759/NZ 263 (PDD 78272, ICMP 15141 = CBS 113647); *ibid.*, West Coast Province, Westlands, along the Ruatapu Ross Road 6, Ross 28 km SW of Hokitika, Totara Walley Road, on decaying wood of a trunk, 12 Apr. 2005, M. Réblová M.R. 3490/NZ 778 (PDD 122548, ICMP 22636); *ibid.*, West Coast Province, Jackson River valley, a track to the Lake Ellery c. 33 km SW of Haast, on decaying wood, 10 Mar. 2003, M. Réblová M.R. 2877/NZ 394 (PDD 78275).

*Notes* — The holotype PDD 21599 contains both asexual (Hughes & Nag Raj 1973) and sexual (Réblová 2004) morphs; however, the sexual morph was not mentioned in the protologue of this species, originally described as the asexual morph. *Fusichalara dingleyae* is distinguished from the other two core species by reddish brown conidiophores, typically growing in fascicles and tightly adhering to each other, and hyaline, 7(–16)-septate conidia that possess only transverse septa, have a conspicuous marginal frill and are basally truncate. It is also the only species known so far to form a sexual morph. In culture, we observed that phialides frequently extended percurrently. In contrast, *F. dimorphospora* and *F. novae-zelandiae* have brown to dark brown conidiophores, growing either solitary or in groups. Their conidia lack a marginal frill and differ in terms of shape, size, septation (generally having more septa), and colour distribution (with pigmentation in the middle cells and one or both end cells being hyaline). Their growth in culture has not been documented.

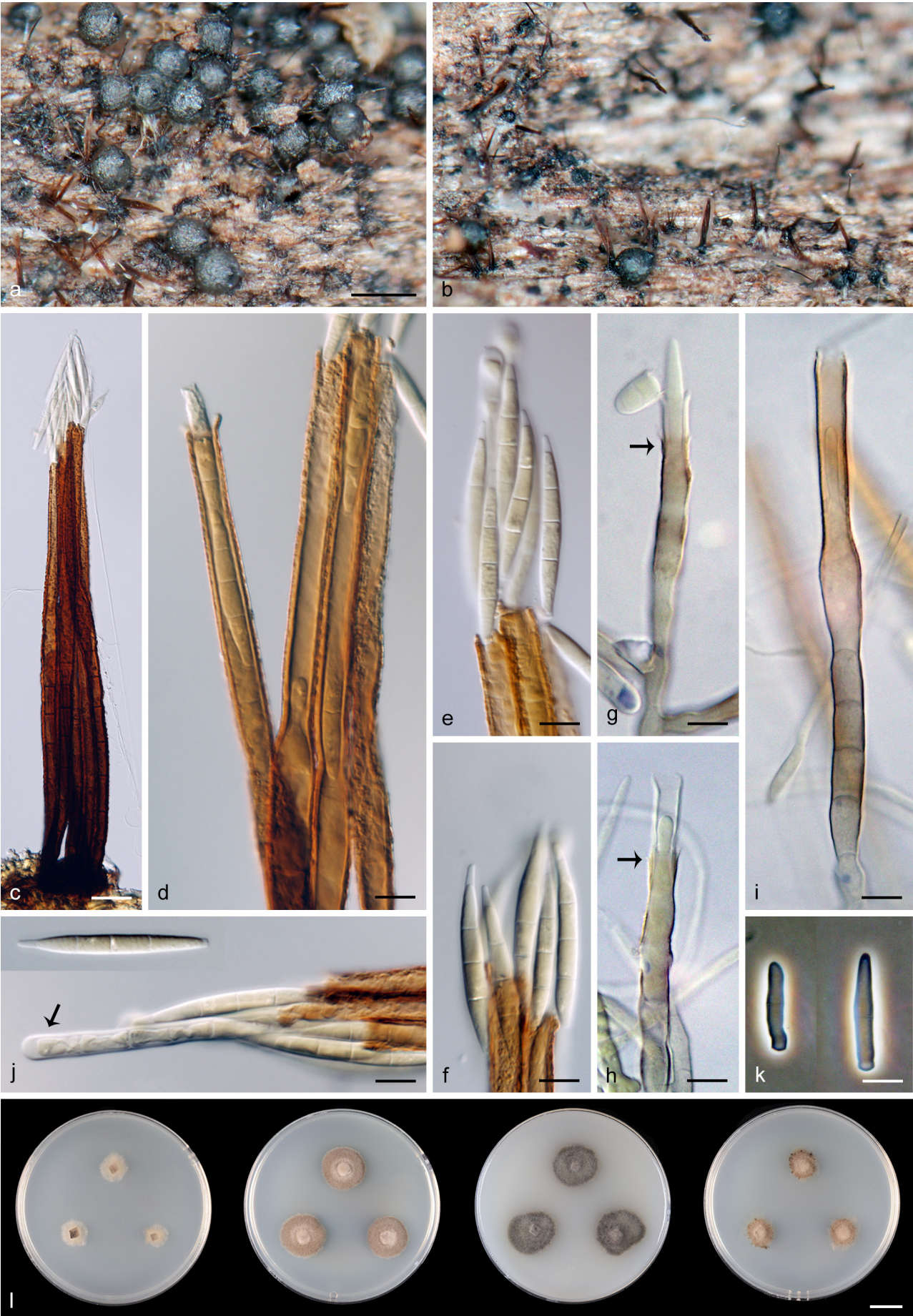
***Fusichalara novae-zelandiae*** S. Hughes & Nag Raj, New Zealand J. Bot. 11: 670. 1973

*Description* — See Hughes & Nag Raj (1973).

*Habitat & Geographical distribution* — On decaying wood of *Leptospermum scoparium*, known only from New Zealand (Hughes & Nag Raj 1973).

*Notes* — The relationships of this species are discussed in the context of *F. dimorphospora*.





**Fig. 5** *Fusichalara dingleyae* (ICMP 22636). a, b. Ascomata and conidiophores; c, g–i. conidiophores (arrows indicate percurrent extension of the phialide in culture); d. upper part of the phialide with a long tubular collarette; e, f. apical part of the collarette with adhering conidia; j. the first conidium (arrow) is long-cylindrical, septate, rounded at the apex and truncate at the base, the subsequent conidia are fusiform, septate, conical at the apex and narrowing and truncate at the base; k. 1-septate conidia; l. colonies on CMD, MLA, OA, and PCA after 4 wk (from left to right). a–f, j. On natural substrate; g–i, k. on PCA. — Scale bars: a, b = 500  $\mu$ m, c = 25  $\mu$ m, d–k = 10  $\mu$ m, l = 1 cm.





**Fig. 6** *Phaeostalagmus cyclosporus*. a, b. Detail of colonies with sporulating conidiophores; c, h–j. phialides; d–g, k. conidiophores; l, m. conidia; n. colonies on CMD, MLA, OA, and PCA after 4 wk (from left to right). a–m. On MLA. a–e, h–m. CBS 663.70; f, g. IMI 63832. — Scale bars: a = 200  $\mu$ m, b = 500  $\mu$ m, c–j, l, m = 10  $\mu$ m, k = 25  $\mu$ m, n = 1 cm.





**Fig. 7** *Phaeostalagmus tenuissimus* (CBS 145635). a, b. Detail of colonies with sporulating conidiophores; c. conidiophores; d–g. fertile part of the conidiophore with phialides in verticils; h, i. conidia; j, k. monilioid vegetative hyphae and stromatic cells; l. colonies on CMD, MLA, OA, and PCA after 4 wk (from left to right). a–e, h–k. On MLA; f, g. on natural substrate. — Scale bars: a, b = 500  $\mu$ m, c–e = 50  $\mu$ m, f, g, k = 20  $\mu$ m, h–j = 10  $\mu$ m, l = 1 cm.

***Phaeostalagmus* W. Gams, Stud. Mycol. 13: 90. 1976**

Type species. *Phaeostalagmus cyclosporus* (Grove) W. Gams.

**Colonies** on the natural substrate effuse, hairy to somewhat powdery, dark brown, whitish grey when sporulating. *Mycelium* partly immersed in the substratum, partly superficial, septate, pigmented. *Asexual morph.* *Setae* absent. *Conidiophores* macronematous, mononematous, erect, straight or slightly flexuous, cylindrical, pigmented, solitary, septate, branched, verticillate in the upper part, occasionally subverticillate or reduced to single phialides (only in culture). *Conidiogenous cells* phialidic, terminal, integrated and discrete, inserted singly in the main conidiophore stalk or in lateral branches, or forming whorls or both, with or without supporting cells, ampulliform to lageniform with a long slender neck, hyaline to lightly pigmented, with a flaring collarette. *Conidia* aseptate, ellipsoidal, ovoidal, cylindrical to subglobose, hyaline, adhering in slimy heads. *Chlamydospores* absent. *Sexual morph* not observed.

Accepted species. *Phaeostalagmus altissimus*, *P. arbusculus*, *P. cyclosporus*, *P. minimus*, *P. novae-zelandiae*, *P. peregrinus*, *P. rossicus*, and *P. tenuissimus*.

***Phaeostalagmus cyclosporus* (Grove) W. Gams, Stud. Mycol. 13: 91. 1976 — Fig. 6**

**Basionym.** *Stachylidium cyclosporum* Grove, London J. Bot. 22: 199. 1884. **Synonym.** *Verticillium cyclosporum* (Grove) E.W. Mason & S. Hughes, Mycol. Pap. 45: 19. 1951.

Description — See Hughes (1951) and Gams & Holubová-Jechová (1976).

**Colonies** on MLA effuse, powdery. *Mycelium* composed of branched, septate, hyaline to subhyaline, smooth, 2–4.5 µm wide hyphae that become pale brown and encrusted, often forming ropes. *Asexual morph.* Conidiophores, conidiogenous cells and conidia similar to those from nature (see Hughes 1951). *Conidiophores* (82–)110–390 × 2.5–4.5 µm, with a foot cell, macronematous, mononematous, erect, cylindrical, straight or slightly flexuous, dark brown, paler towards the apex, septate, sometimes subverticillate or reduced to single phialides. The upper fertile part is 42–110 µm long, composed of lateral branches and phialides; lateral branches are concolourous, positioned unilaterally or in a verticil under the septum, lower fertile part branches are longer and sometimes with secondary branches. *Conidiogenous cells* 12.5–17.5 × 2–3 µm, tapering to 1–1.5 µm just below the collarette, phialidic, integrated, terminal and discrete, born directly upon the main stalk or branches, ampulliform to lageniform, hyaline to subhyaline, venter ellipsoidal tapering into a long slender neck, often finely warted; collarettes 2–2.5 µm wide, c. 1 µm deep, flaring, hyaline. *Conidia* 2–2.5 × 1.5–2 µm (mean ± se = 2.4 ± 0.2 × 1.5 ± 0.1 µm), aseptate, ellipsoidal to ovoidal, sometimes slightly apiculate at the base, hilum often eccentric, hyaline, smooth, aggregating in hyaline, pale orange or pink slimy heads. *Chlamydospores* absent. *Sexual morph* not observed.

**Culture characteristics** (after 5 wk at 23 °C) — On CMD colonies 10–11 mm diam, circular, raised, margin entire, velvety, lanose around the centre, finely furrowed centrally, zonate, beige brown with whitish zones, reverse pale beige. On MLA colonies 28–30 mm diam, circular, convex, margin entire, velvety, floccose at the centre, somewhat funiculose, deeply furrowed, mouse grey and locally pink beige, mainly at the centre, isabelline towards the margin, reverse isabelline. On OA colonies 20–22 mm diam, circular, slightly raised, flat margin, margin entire, velvety, mucoid to cobwebby at the margin, zonate, olivaceous grey with a dark olivaceous brown outer zone and an olivaceous zone of submerged growth, reverse dark olivaceous grey. On PCA colonies 14–15 mm diam, circular, slightly convex, flat margin, margin entire, velvety, cobwebby

towards the periphery, beige pink with an olivaceous brown outer zone, reverse dark olivaceous brown. Sporulation was abundant on all media.

**Habitat & Geographical distribution** — Saprobe on decaying wood and bark of various hosts, such as *Acer pseudoplatanus*, *Acer* sp., *Alnus* sp., *Betula* sp., *Castanea sativa*, *Corylus avellana*, *Fagus sylvatica*, *Fraxinus excelsior*, *Ilex aquifolium*, *Libocedrus bidwillii*, *Pinus contorta*, *Pinus silvestris*, *Pinus* sp., *Quercus* sp., *Rhododendron* sp., *Sambucus nigra*, *Ulex europaeus*, and *Ulmus* sp. It was also recorded from soil. The species is widespread in the temperate region and is known from Canada, New Zealand, the Netherlands, and the UK (Hughes 1951, Gams & Holubová-Jechová 1976, MyCoPortal, this study).

**Material examined.** NETHERLANDS, Schovenhorst near Putten, on decaying wood, 4 June 1970, J.A. Stalpers (CBS 663.70). — UK, locality unknown, on decaying wood, 1956, A.H.S. Brown (IMI 63832).

**Notes** — The collection on decaying wood from the UK (Grove 1884) was selected by Gams & Holubová-Jechová (1976) as a neotype of *Stachylidium cyclosporum*. We examined two strains of this species, one from the Netherlands and the other from the UK, and both are fairly comparable, including the appearance of the colonies *in vitro*. In culture, especially in early stages of development, the conidiophores are subverticillate, or can be reduced to single conidiogenous cells arising from vegetative hyphae. The conidiophores that appeared later were macronematous and repeatedly verticillate but less complex than those on material from nature. The slimy heads of conidia were mostly hyaline, but they later turned pale orange and pink. Colonies on natural substrate are usually whitish grey; however, Hughes (1951) reported that some colonies were also yellowish brown, presumably due to aged-material.

*Phaeostalagmus cyclosporus* resembles *P. arbusculus* (Wang & Sutton 1982) in having conidiophores with lateral branches and warted phialides of the same size; however, the latter species is distinguished by cylindrical to allantoid, narrower conidia (2–3 × 1 µm) and the arrangement of phialides and branches on the conidiophore. In *P. arbusculus*, the branches are alternately arranged, giving a zigzag appearance, whereas those in *P. cyclosporus* are arranged oppositely and in verticils. However, in culture of *P. cyclosporus* we observed branches in both patterns, arranged alternately (especially the lower, longer branches), oppositely and in verticils.

***Phaeostalagmus tenuissimus* (Corda) W. Gams & Hol.-Jech., Stud. Mycol. 13: 93. 1976 — Fig. 7**

**Basionym.** *Verticillium tenuissimum* Corda, Icon. Fung. 1: 20. 1837. **Synonyms.** *Verticillium apicale* Berk. & Broome, Ann. Mag. Nat. Hist., Ser. 2 7: 101. 1851. *Verticicladium apicale* (Berk. & Broome) Sacc., Syll. Fung. 4: 328. 1886. **Synonymy** after Hughes (1951).

Description — See Hughes (1951) and Gams & Holubová-Jechová (1976).

**Colonies** on MLA effuse, hairy, powdery. *Mycelium* composed of branched, septate, hyaline to pale brown, smooth, 1–3 µm wide hyphae, in older cultures some hyphae become moniloid with cells 4–9 µm wide and brown. Some cells are thick-walled, stromatic, aggregating at the base of the conidiophore. *Asexual morph.* Conidiophores, conidiogenous cells and conidia similar to those from nature (see Hughes 1951). *Conidiophores* 140–400 × 3.5–5(–5.5) µm, macronematous, monone-matous, erect, cylindrical, straight or slightly flexuous, dark brown, paler towards the apex, septate, unbranched, rarely with a short branch, the upper fertile part is (30–)76–104 µm long, subhyaline to hyaline, repeatedly verticillate, bearing 5–8 whorls of phialides just below the septa and a terminal whorl; conidiophores sometimes reduced to stipitate phialides.



*Conidiogenous cells* 12.5–18 × 3.5–4 µm, tapering to 0.5–1 µm just below the collarete, phialidic, discrete, ampulliform, venter subglobose to broadly ellipsoidal, abruptly tapering into a long slender neck; collarettes 2.5–3 µm wide, 1–1.5 µm deep, hyaline, flaring. *Conidia* 2.5–3.5 × 1.5 µm (mean ± se = 3.0 ± 0.2 × 1.5 ± 0.1 µm), aseptate, ellipsoidal to oblong, sometimes slightly apiculate at the base, hyaline, smooth, aggregating in hyaline slimy heads. *Chlamydospores* absent. *Sexual morph* not observed.

**Culture characteristics** (after 5 wk at 23 °C) — On CMD colonies 23–26 mm diam, circular, raised, margin entire to weakly fimbriate, velvety-lanose, floccose at the centre, cobwebby at the margin, zonate, beige centrally, dark grey brown towards the margin, reverse dark brown. On MLA colonies 28–31 mm diam, circular, raised, margin fimbriate, velvety-lanose, floccose at the centre, furrowed, zonate, beige brown with irregular whitish patches, with dark brown and beige outer zones, reverse dark grey. On OA colonies 33–35 mm diam, circular, convex centrally, flat margin, margin entire, lanose, floccose at the centre, funiculose, mucoid towards the periphery, beige grey at the colony centre, dark olivaceous to blackish grey towards the margin, reverse dark grey. On PCA colonies 24–25 mm diam, circular, flat, slightly raised centrally, margin fimbriate, cobwebby to velvety, mucoid towards the margin, grey-brown, dark brown at the margin, with an isabelline outer zone of submerged growth, reverse dark grey to nearly black. Sporulation was present on MLA and PCA, absent on CMD and OA.

**Habitat & Geographical distribution** — Saprobe on decaying wood, bark, bud scales and woody fruits of various trees, for example *Castanea sativa*, *Fagus grandifolia*, *Fraxinus excelsior*, *Picea mariana*, *Quercus cerris*, *Quercus* sp., *Rhododendron* sp., *Salix* sp., *Sambucus* sp., decaying acorns of *Quercus* spp., unidentified coniferous wood, and also on needles of *Pinus sylvestris*. The species is distributed in the temperate region including Canada, Czech Republic, Belgium, Germany, the Netherlands, UK and USA (Hughes 1951, Sutton 1975a, Gams & Holubová-Jechová 1976, MyCoPortal, this study).

**Materials examined.** CZECH REPUBLIC, South Moravian Region, Valtice, Rendez-vous National Nature Monument, on decaying acorn of *Quercus cerris*, 28 Oct. 2018, *M. Réblová* 4028 (PRA-21600, CBS 145635); *ibid.*, *M.R. 4040B* (PRA-21601, CBS 145434); *ibid.*, *M.R. 4078* (CBS 145640). — NETHERLANDS, National Park Hoge Veluwe, on decaying wood, 7 Oct. 1973, *W. Gams* (CBS 917.73).

**Notes** — The holotype of *Verticillium tenuissimum* comes from decaying acorns of *Quercus* sp. at a locality in Central Bohemia (PRM 515139, not seen). In our study, *P. tenuissimum* is represented by four isolates, three strains were isolated from recent material collected on decaying acorns of *Q. cerris* at a site in the South Moravian Region of the Czech Republic, and one strain originating from wood from the Netherlands.

We observed some differences in the morphology of *P. tenuissimum*, depending whether the fungus grows in culture or on the natural substrate (Fig. 7). In material from nature, the conidiophores have shorter fertile part approximately 23–51 µm long, which is usually composed of 3–5 verticils, the conidia are ellipsoidal to oblong to subcylindrical and slightly longer (3–)3.5–4 × 1.5 µm. In culture, the whorls of phialides are arranged in more layers leading to a longer fertile part. The colour separation between the sterile stipe and fertile part of the conidiophore is more conspicuous in culture; the fertile part is subhyaline to hyaline compared to pale brown to subhyaline *in vivo*.

*Phaeostalagmus tenuissimus* closely resembles *Phaeostalagmus novae-zelandiae* (Hughes 1978), but the latter species differs in having branched, verticillate conidiophores that terminate in a single and narrower phialide (venter 2.5–3.5 µm wide), and larger ellipsoidal to cylindrical conidia (5–7 × 1.8–2 µm).

*Phaeostalagmus tenuissimus* may be confused with *Sporendocladia fumosa*, as both species inhabit similar substrates including woody fruits of *Castanea*, *Fagus*, and *Quercus*. However, there are several diagnostic traits that distinguish both species. In *Sn. fumosa*, the phialides are pigmented, lageniform, arranged in a more or less penicillate fashion, occasionally exhibiting mono- or biverticillate branching patterns in culture. They possess a long slender neck similar to *Phaeostalagmus* but have a tubular non-flaring collarete, and conidia are cuneiform adhering in false chains. In contrast, the phialides of *P. tenuissimus* are hyaline, lack metulae or supporting cells, they are more ampulliform in shape, featuring a conspicuous flaring collarete. Their positioning is distinctly verticillate along the upper part of the conidiophore stipe. Conidia are ellipsoidal, rounded at both ends and adhere in slimy heads. While *P. tenuissimus* also shares some resemblance with *Brachiampulla verticillata* (*Xylariales*), however, the pigmentation of all cells in conidiophores, holoblastic conidiogenous cells, and lunate conidia set the latter species apart (Réblová et al. 2021a).

***Spadicocephala* Réblová, A.N. Mill. & Hern.-Restr., gen. nov.**  
— MycoBank MB 851463

**Etymology.** *Spādix* (Latin) chestnut-coloured, *Cephalus* (Latin) derived from the Greek *Kephalos* meaning head; referring to the colouration of colonies and the conspicuous conidiogenous apparatus at the tip of the conidiophore resembling a head.

**Type species.** *Spadicocephala fusca* (W.B. Kendr.) Réblová, A.N. Mill. & Hern.-Restr.

**Colonies** in culture effuse, hairy, brown, chestnut-brown to reddish brown, dark brown to olivaceous black when sporulating with conspicuous slimy conidial masses. *Mycelium* aerial and submerged, septate, composed of subhyaline to brown hyphae. **Asexual morph.** *Setae* absent. *Conidiophores* macronematous, mononematous, mono-, bi- and terverticillate, erect, straight, cylindrical to subulate, pigmented, septate, sometimes with rhizoidal hyphae at the base, bearing a conidiogenous apparatus at the apex. *Conidiogenous apparatus* pigmented, paler than the conidiophore, composed of 1–3 series of metulae bearing phialides. *Conidiogenous cells* phialidic, terminal, integrated, lageniform, with a terminal opening, rarely with one lateral opening, with a flaring collarete, often crowded, occasionally peripheral phialides develop lateral outgrowths, repeatedly elongating or producing a single solitary phialide. *Conidia* ellipsoidal to ovoidal, sometimes slightly curved, often exhibiting a basal scar, aseptate, subhyaline to pale brown, adhering in dark brown to olivaceous black slimy heads. *Chlamydospores* absent. *Sexual morph* not observed.

*Accepted species.* *Spadicocephala fusca*.

***Spadicocephala fusca* (W.B. Kendr.) Réblová, A.N. Mill. & Hern.-Restr., comb. nov.** — MycoBank MB 851757; Fig. 8

**Basionym.** *Phialocephala fusca* W.B. Kendr., *Canad. J. Bot.* 41: 1015. 1963.

**Typus.** CANADA, Ontario, Chalk River, Petawa Forest Experiment Station, isolated from *Picea glauca* post, Oct. 1959, *K. Shields* (holotype of *Phialocephala fusca*, dried culture DAOM 75852).

**Description** — See Kendrick (1963).

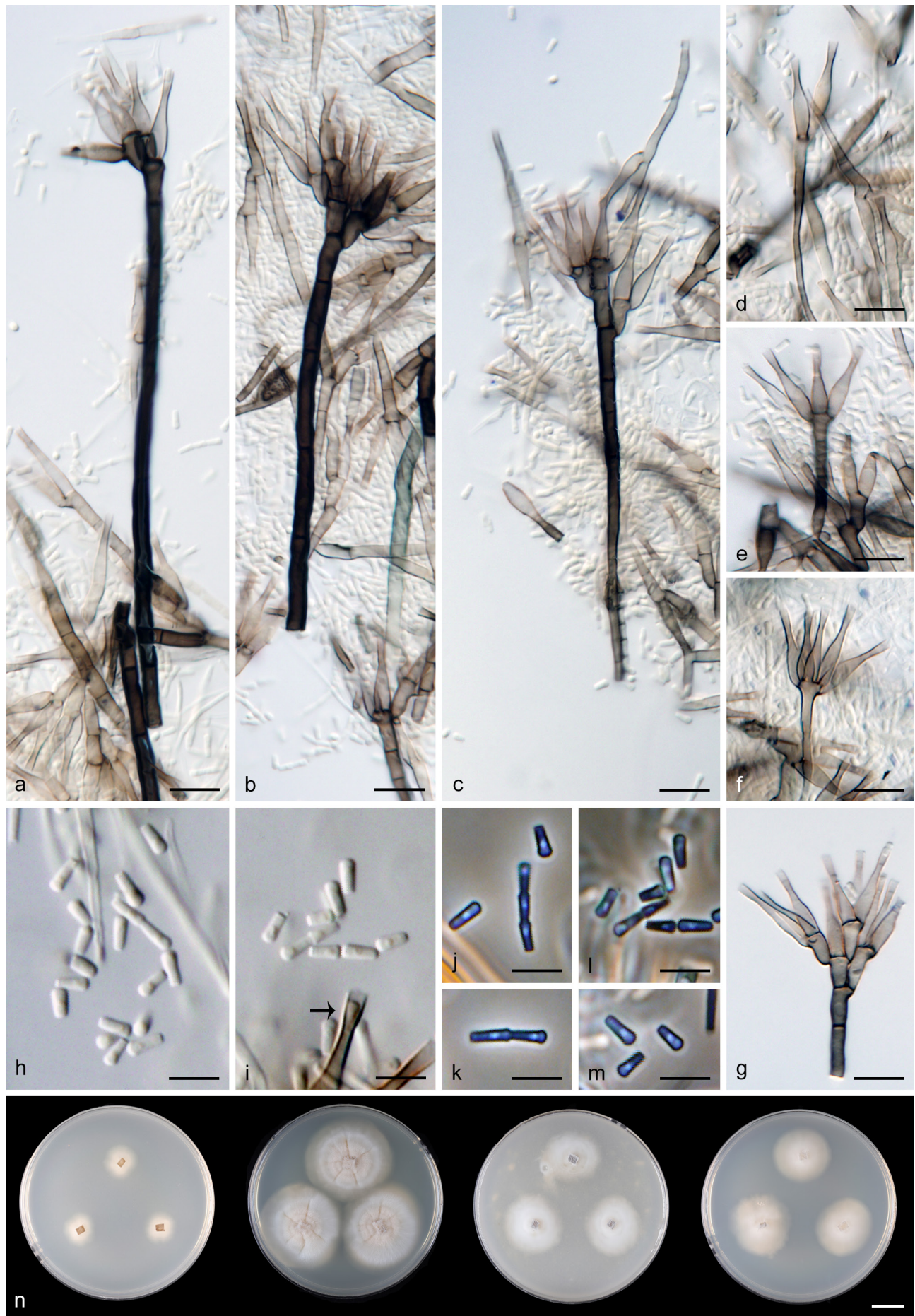
**Culture characteristics** (after 5 wk at 23 °C) — On CMD colonies 22–25 mm diam, circular, flat, margin diffuse, olivaceous brown, olivaceous cinnamon at the margin with a beige outer zone, reverse dark brown. On MLA colonies 48–53 mm diam, circular, flat, margin diffuse, velvety, zonate, dark cinnamon to dark chestnut-brown with dark brown concentric zones, beige-brown centrally with hyaline exudates, reverse dark brown to almost black. On OA colonies 54–55 mm diam, circular,





**Fig. 8** *Spadicocephala fusca* (authentic strain CBS 301.85). a–c. Detail of colonies with sporulating conidiophores; d, e. conidiophores with phialides and conidia; f, g. details of the fertile part of the conidiophore; h, j. conidia; i. basal cells of conidiophores; k. colonies on CMD, MLA, OA, and PCA after 4 wk (from left to right). a–j. On MLA. — Scale bars: a–c = 500 µm, d, e = 25 µm, f–j = 10 µm, j = 1 cm.





**Fig. 9** *Sporendocladia fumosa* (CBS 518.93). a–c. Conidiophores with phialides and conidia; d–g. detail of the fertile part of the conidiophore; h–m. conidia (arrow indicates endogenous conidium borne in a deep seated conidiogenous locus); n. colonies on CMD, MLA, OA, and PCA after 4 wk (from left to right). a–m. On MLA. — Scale bars: a–g = 10 µm, h–m = 5 µm, n = 1 cm.



flat, margin fimbriate, velvety, dark cinnamon centrally, aerial hyphae bearing numerous hyaline exudates, beige towards the periphery with a dark olivaceous grey outer zone of submerged growth, reverse dark olivaceous grey. On PCA colonies 39–43 mm diam, circular, flat, margin fimbriate, velvety to cobwebby, zonate, dark olivaceous brown at the centre with a bronze to cinnamon intermediate zone, paler towards the margin, pale pink-brown pigment diffusing into the agar, reverse dark brown. Sporulation was abundant on all media.

**Habitat & Geographical distribution** — *Spadicocephala fusca* was repeatedly isolated from lumber, post, roof rafter, and rotten wood of coniferous and deciduous woody hosts, such as *Acer* sp., *Picea glauca*, *Pinus strobus*, and *Tsuga heterophylla* in Canada, from a dead twig of thorny ornamental vine *Bougainvillea spectabilis* in Sierra Leone, and also from *Pinus* hydro picket in Canada (Kendrick 1963, MyCoPortal).

**Authentic material examined.** CANADA, Ontario, Ottawa, isolated from roof rafter of *Pinus strobus*, 19 June 1959, K. Shields (DAOM 67995 dried culture, CBS 301.85 authentic strain of *Phialocephala fusca*).

**Notes** — In our phylogeny, this species is represented by two authentic strains (CBS 300.85 and CBS 301.85). Although the fungus was isolated several times from woody substrates into axenic cultures, the wild type of *Spadicocephala fusca* is unknown as it has not yet been found fruiting on the natural substrate (Kendrick 1963). Additionally, the associated sexual morph has not yet been observed. The isolation of this species from rotten and treated wood of various hosts suggests the endophytic or saprotrophic nature of *Sc. fusca*. In culture, it formed colonies with characteristic cinnamon, olivaceous brown or dark chestnut-brown hues, especially on MLA, OA, and PCA media. This observation aligns with earlier findings by Kendrick (1963) on potato dextrose agar and malt agar.

***Sporendocladia*** G. Arnaud ex Nag Raj & W.B. Kendr., A monograph of *Chalara* and allied genera: 162. 1975

**Type species.** *Sporendocladia fumosa* (Ellis & Everh.) M.J. Wingf.

**Description** — See Nag Raj & Kendrick (1975), Sutton (1975a), Crous & Wingfield (1994).

**Accepted species.** *Sporendocladia fumosa* and *Sn. beijingensis*.

***Sporendocladia fumosa*** (Ellis & Everh.) M.J. Wingf., Trans. Brit. Mycol. Soc. 89: 515. 1987 — Fig. 9

**Basionym.** *Spicaria fumosa* Ellis & Everh., Bull. Torrey Bot. Club 10: 97. 1883. **Synonyms.** *Phialocephala fumosa* (Ellis & Everh.) Sutton, Trans. Brit. Mycol. Soc. 64: 411. 1975.

*Sporendocladia castaneae* G. Arnaud, Bull. Soc. Mycol. France 69: 279. 1954, nom. inval.

*Sporendocladia castaneae* G. Arnaud ex Nag Raj & W.B. Kendr., A monograph of *Chalara* and allied genera: 162. 1975. Synonymy adopted after Sutton (1975a).

**Description** — See Nag Raj & Kendrick (1975), Crous & Wingfield (1994).

**Accepted species.** *Sporendocladia fumosa* and *Sn. beijingensis*.

**Culture characteristics** (after 5 wk at 23 °C) — On CMD colonies 8–9 mm diam, circular, flat, margin entire, mucoid, whitish to isabelline, reverse of the same colour. On MLA colonies 24–29 mm diam, circular, raised, deeply furrowed, margin entire, whitish to isabelline, paler to translucent at the margin, with zones of dense and sparse growth, cobwebby to mucoid, partly funiculose, reverse ivory. On OA colonies 30–33 mm diam, circular, flat, margin entire, whitish, mucoid, funiculose on the inoculation block, reverse ivory. On PCA colonies 24–26 mm diam, circular, flat, margin entire, mucoid, funiculose, cobwebby at the inoculation block, whitish to isabelline, reverse isabelline. Sporulation was sparse on all media.

**Habitat & Geographical distribution** — Saprobe on dead cupules and cupular spines of *Castanea sativa*, known from France, Switzerland, UK, and the USA.

**Material examined.** SWITZERLAND, Comano, on cupules of *Castanea sativa*, May 1993, P.W. Crous, M.J. Wingfield & O. Petrini (CBS 518.93).

**Notes** — *Sporendocladia fumosa* closely resembles *P. tenuissimus*, for their comparison, refer to the notes of the latter species. In culture, we observed that the conidiophores of *S. fumosa* display a mono- to biverticillate branching pattern with metulae developed below the septum of the apical and penultimate cells. The metulae were inserted in an alternate manner and bore either a pair of phialides or 3–4 phialides in a verticil. When in a young state, the conidiogenous apparatus of *Sn. fumosa* consists of several terminal phialides in a loose arrangement; the conidiophores were occasionally reduced to single conidiogenous cells. Our examination of the strain of *Sn. fumosa* (CBS 518.93) aligns with the findings reported by Crous & Wingfield (1994).

***Stanjehughesia*** Subram., Proc. Indian Natl. Sci. Acad., B. 58(4): 184. 1992

**Synonym.** *Umbrinosphaeria* Réblová, Mycotaxon 71: 17. 1999.

**Type species.** *Stanjehughesia hormiscioides* (Corda) Subram.

**Description** — See Hughes & Illman (1974), Ellis (1976), Shoemaker & White (1985), Réblová (1999b), and Wu & Zhuang (2005).

**Accepted species.** *Stanjehughesia aquatica*, *S. caespitulosa*, *S. clavata*, *S. curviapicis*, *S. decorosa*, *S. fasciculata*, *S. floridensis*, *S. fusiformis*, *S. hormiscioides*, *S. jiangxiensis*, *S. lignicola*, *S. micheliae*, *S. minima*, *S. nigroaca*, *S. obclavorostrata*, *S. silvana*, and *S. ventricosa*.

***Stanjehughesia hormiscioides*** (Corda) Subram., Proc. Indian Natl. Sci. Acad., B. 58(4): 184. 1992 — Fig. 10

**Basionym.** *Sporidesmium hormiscioides* Corda, Icon. Fungorum 2: 6. 1838. **Synonyms.** *Sphaeria caesariata* Clinton & Peck, Ann. Rep. New York State Mus. Nat. Hist. 29: 60. 1878 [1875].

*Lasiosphaeria caesariata* (Clinton & Peck) Sacc., Syll. Fung. 2: 192. 1883. *Phaeotrichosphaeria caesariata* (Clinton & Peck) M.E. Barr, Bull. N.Y. State Mus. 459: 12. 1986.

*Umbrinosphaeria caesariata* (Clinton & Peck) Réblová, Mycotaxon 71: 18. 1999.

*Chaetosphaeria caesariata* (Clinton & Peck) F.A. Fernández & Huhndorf, Fungal Diversity 18: 49. 2005.

*Chaetosphaeria coelestinoides* Teng [as 'caelestinoides'], Sinensia 7: 502. 1936.

*Chaetosphaeria caespitulosa* Höhn., Mittell. Bot. Inst. Techn. Hochschule Wien 6: 97. 1929.

*Chaetosphaeria multiseptata* Wehm., Canad. J. Res., Sect. C, 20: 576. 1942.

*Chaetosphaeria pezizaeformis* Schulzer, Hedwigia 23: 78. 1884.

*Clasterosporium vermiculatum* Cooke, Grevillea 4(30): 69. 1875.

*Sporidesmium vermiculatum* (Cooke) M.B. Ellis, Mycol. Pap. 70: 41. 1958.

*Stanjehughesia vermiculata* (Cooke) Subram., Proc. Indian Natl. Sci. Acad., B 58(4): 184. 1992.

*Riisgaardia vermiculata* (Cooke) W.P. Wu & Y.Z. Diao *sensu* Wu & Diao, Fungal Diversity 116: 73. 2022 [non *Clasterosporium vermiculatum* Cooke 1875].

Synonymy partially adopted after Hughes (1958) and Réblová (1999b).

**Description** — See Peck (1878), Teng (1936), Wehmeyer (1942), Hughes & Illman (1974), Ellis (as *Sp. vermiculatum* 1958, 1976), Shoemaker & White (1985), Barr et al. (1986), Réblová (1999b), Réblová & Winka (2001), Wu & Diao (2022).

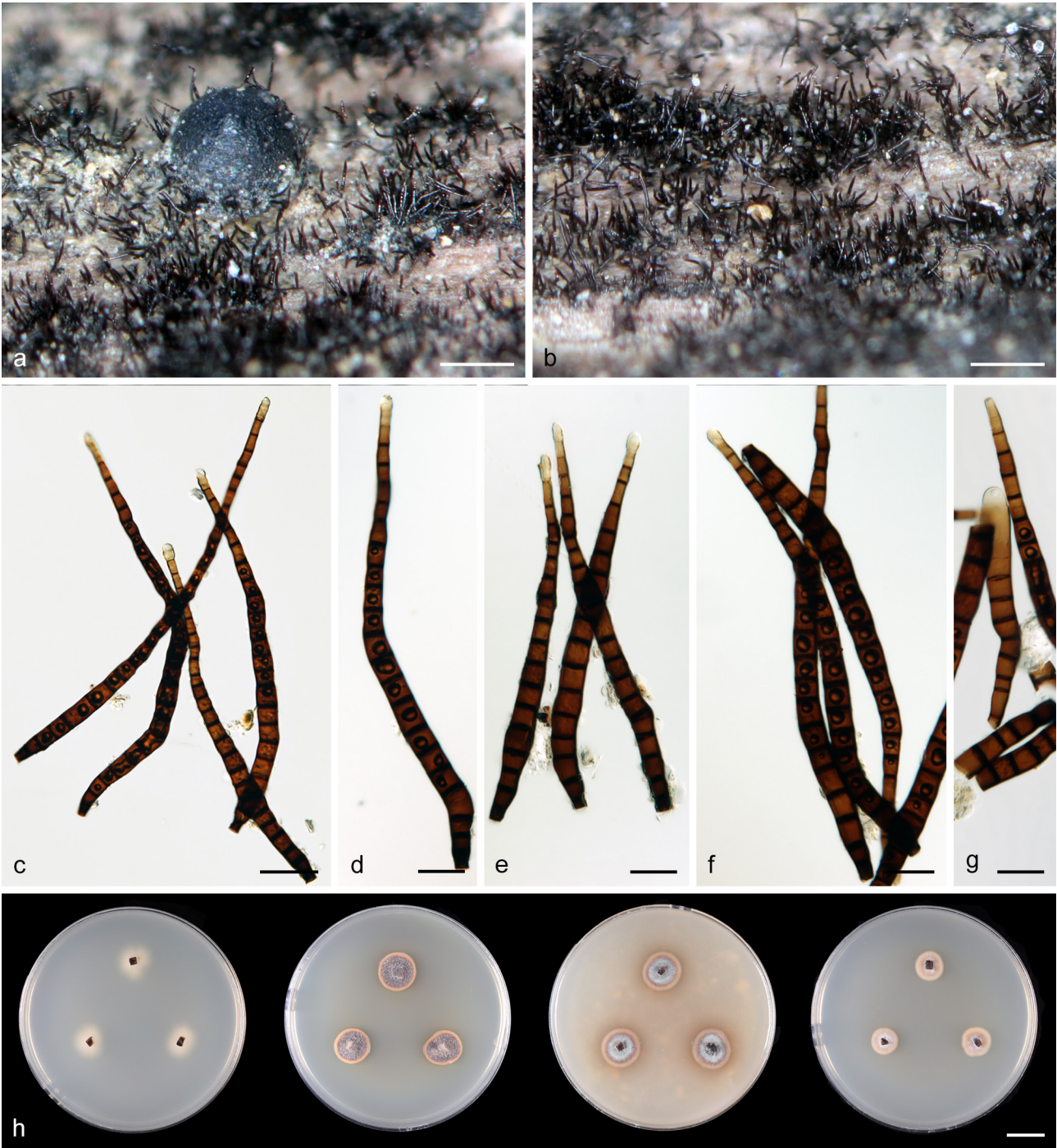
**Culture characteristics** (after 5 wk at 23 °C) — On CMD colonies 7–8 mm diam, circular, flat, margin entire, mucoid, isabelline, reverse of the same colour. On MLA colonies 9–10 mm diam, circular, convex, margin entire, furrowed, velvety, floccose at the centre, reddish brown, cinnamon at the margin with a salmon outer zone, ochre pigment diffusing into the agar, reverse reddish brown. On OA colonies 10–11 mm diam, circular,

convex, margin entire, finely furrowed, velvety, floccose at the centre, grey beige at the centre, cinnamon at the margin with a salmon outer zone, ochre pigment diffusing in to the agar, reverse dark reddish brown. On PCA colonies 8–9 mm diam, circular, slightly convex, margin entire, ochre to salmon, paler at the margin, with a pale ochre pigment diffusing into the agar, reverse cinnamon. Sporulation was absent on all media.

Habitat & Geographical distribution — The species is a saprobe on decaying bark and hard-wood of many deciduous and coniferous trees, for example *Abies alba*, *Acer pseudoplatanus*, *Alnus* sp., *Cerasus avium*, *Fagus sylvatica*, *Fraxinus excelsior*, *Populus alba*, *Quercus* sp., and other unidentified hosts. The fungus also occurs on utility wood, such as railway sleepers, conifer chips used for trails, coniferous timber, and unidentified worked wood. It is widespread in temperate regions, including

Canada, China, Czech Republic, Ukraine, the UK, and the USA (Corda 1838, Wehmeyer 1942, Hughes & Illman 1974, Ellis 1958, 1976, Shoemaker & White 1985, Barr et al. 1986, Réblová 1999b, Teng 1936, Wu & Diao 2022, MyCoPortal, this study).

**Material examined.** CZECH REPUBLIC, Šumava Mts. National Park, Spáleniště Mt near Stožec, elev. 960 m, on decaying wood of *Fagus sylvatica*, 12 Nov. 2000, M. Réblová M.R. 1740 (PRA-21603). — UKRAINE, Carpathian Mts, Massif Boržava, Pilipec, on the wooded slopes around the Tisa river, on decaying wood of *Fagus sylvatica*, 25 June 1997, M. Réblová M.R. 927 (PRA-21604); *ibid.*, M.R. 929 (PRM 843054, PRA-21605, CBS 102664); Carpathian Mts, Kvasi near Rachiv, on the wooded slopes around the Tisa river, on decaying wood, 28 June 1997, M. Réblová M.R. 950 (PRA-21606); *ibid.*, on decaying wood of *Abies alba*, 29 June 1997, M. Réblová M.R. 978 (PRA-21607); *ibid.*, Carpathian Mts, Luhv, Hoverla, a valley above the spring, on decaying wood of *Acer pseudoplatanus*, 30 June 1997, M. Réblová M.R. 961 (PRA-21608).



**Fig. 10** *Stanjehughesia hormiscioides* (PRA-21607). a. Ascoma surrounded by upright conidia; b. colony of the asexual morph; c–g. conidia; h. colonies on CMD, MLA, OA, and PCA after 4 wk (from left to right). a–g. On natural substrate. — Scale bars: a, b = 500 µm, c–g = 25 µm, h = 1 cm.

**Notes** — The identification of *S. hormiscioides* can be challenging due to the morphological variability of its conidia. Young conidia are shorter, clavate to cylindrical with the apical cell broadly rounded, whereas mature conidia are longer, fusiform, often bent (rarely more than once) and the apical subhyaline cell is narrowly rounded to subulate and sometimes slightly inflated. Hughes & Illman (1974) suggested that collections from distinct geographical regions might exhibit limited range of morphological variability with one predominant shape. For instance, some collections may mainly produce longer fusiform conidia (up to 400 µm in length), whereas others may contain primarily shorter cylindrical to clavate conidia. It appears that collections from Europe usually produce the longer fusiform conidia along with the shorter ones (Corda 1838, Réblová 1999b), whereas in material from North America or Asia, often only the shorter conidia were present (Hughes & Illman 1974, Shoemaker & White 1985, Wu & Diao 2022). The identity of these collections should be verified with molecular data to support this theory. The chloridium-like synasexual morph with phialidic conidiogenesis on single loci has been identified by Réblová & Winka (2001) and occurs only in culture. For more details, see Discussion.

Although the sexual-asexual connection of *S. hormiscioides* has been experimentally verified, the life cycle of another *Stanjehughesia* species, *S. larvata*, was based on the close proximity of both morphs on material from nature (Réblová 1999b). However, this species differs from *S. hormiscioides* in that it produces short conidiophores and a different sexual morph. Réblová (1999b) retained *S. larvata* in the genus *Sporidesmium*, and the sexual morph was proposed as a new species in the genus *Miyoshiella* (Kawamura 1929). *Miyoshiella fusi-spora*, the type species, has been linked with *Sporidesmium bambusicola*, which has distoseptate conidia (Kawamura 1929, Ellis 1958, 1976). The asexual morph was transferred to *Ellisembia* (Mena-Portales et al. 2000) and later confirmed to cluster among members of *Sporidesmium*, thus clarifying the relationship between *Stanjehughesia*, *Sporidesmium*, and *Miyoshiella* (Su et al. 2016), of which the latter represents a synonym of *Sporidesmium*. Due to the presence of short conidiophores and a sexual morph with 3-septate, hyaline ascospores, *S. larvata* is not accepted in *Stanjehughesia*. The sexual morph is morphologically similar to that of *Distoseptispora adscendens* (Shoemaker & White 1985). Regrettably, the molecular data of *S. larvata* are not available to assess its systematic placement.

***Stanjehughesia silvana* Réblová, sp. nov.** — MycoBank MB 851758; Fig. 11

**Etymology.** *Silva* (Latin) forest, wood, *-ana* (Latin) of or pertaining to, referring to the substrate and forest habitat of this species.

**Typus.** NEW ZEALAND, West Coast Province, Victoria Forest Park, Lake Stream track c. 30 km SE of Reefton, on decaying wood of *Nothofagus* sp., 27 Feb. 2003, M. Réblová M.R. 2656/NZ 142 (holotype PDD 122549, culture ex-type ICMP 15123).

**Colonies** on the natural substrate effuse, hairy, black, composed of conidiophores and ascomata. **Mycelium** partly immersed in the substrate, partly superficial, composed of pigmented, septate hyphae. **Asexual morph.** *Setae* absent. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* 10.5–14.5(–17) × 4.5–5.5 µm, holoblastic, discrete, solitary or in clusters on the substrate, ampulliform, truncate at the apex, dark brown, thick-walled, smooth. *Conidia* (70–)117–185(–230) × 8.5–11(–12) µm (mean ± se = 166.1 ± 38.1 × 10.3 ± 0.9 µm), 4–5.5 µm wide at the base, solitary, cylindrico-fusiform to lanceolate, slightly bend, base truncate, apical cell broadly or narrowly rounded, 18–22(–31)-septate, not constricted at the

septa, with dark brown, barrel-shaped septal pore in each cell septum, brown to dark reddish brown with the darkest opaque basal cell, whereas other cells are uniformly coloured, some conidia show percurrent proliferation, thick-walled, smooth. *Chlamydospores* absent. **Sexual morph.** *Ascomata* superficial, solitary or in small groups, non-stromatic, subglobose, 480–550 µm diam, 450–530 µm high, papillate, dark brown, glabrous. Ostiole periphysate. *Ascomatal wall* leathery to fragile, 35–42 µm, composed of two layers, outer layer consisting of brown, thick-walled, polyhedral cells, inner layer of thin-walled, subhyaline, flattened cells. *Paraphyses* hyaline, seldom branched septate, 2.5–4 µm wide. *Asci* 117–136 × 12–14.5 µm (mean ± SD = 124.3 ± 7.8 × 22.2 ± 27.3 µm), (75–)84–117 µm (mean ± SD = 94.9 ± 13.1 µm) long in the sporiferous part, broadly rounded to truncate at the apex, fusiform-clavate, stipitate, with a non-amyloid apical annulus c. 3.5 µm wide, 2–3 µm high, 8-spored, ascospores uniseriate. *Ascospores* 20–26(–27) × 4.5–5.5 µm (mean ± SD = 23.7 ± 2.2 × 4.9 ± 0.3 µm), fusiform, sometimes inequilateral, (3–)5-septate, not constricted at the septa, hyaline, smooth-walled, without mucilaginous sheath or appendages.

**Colonies** on MLA effuse, partially hairy. **Mycelium** composed of branched, septate, pale brown, smooth or slightly roughened, 2.5–4.5 µm wide hyphae. **Asexual morph.** *Setae* absent. *Conidiophores* micronematous, consisting of several brown cells, or reduced to conidiogenous cells. *Conidiogenous cells* 4.5–5 µm diam, 5–5.5 µm high, holoblastic, terminal, integrated, subcylindrical to doliiform, brown. *Conidia* 22.5–67.5(–82) × (6.5–)8–11.5(–13) µm (mean ± se = 44.7 ± 17.4 × 9.5 ± 2.6 µm), solitary, variable in shape, mostly clavate to cylindrico-clavate, rounded apically, truncate at the base, 1–9-septate, not constricted or slightly constricted at the septa, septal pores not seen, dark brown to blackish brown, apical cell occasionally paler. *Chlamydospores* absent. **Sexual morph** not observed.

**Culture characteristics** (after 5 wk at 23 °C) — On CMD colonies 6–8 mm diam, circular, flat, margin entire, mucoid, dark brown, whitish at the margin, reverse of the same colour. On MLA colonies 9–12 mm diam, circular, convex, margin entire or somewhat undulate, cobwebby, finely furrowed, beige-brown, grey at the centre, salmon at the margin, reverse russet. On OA colonies 9–10 mm diam, circular, slightly convex, margin entire, sparsely lanose, zonate, olivaceous grey-brown, intermediate zone whitish grey, reverse dark brown. On PCA colonies 6–7 mm diam, circular, slightly convex, margin entire, velvety, mouse grey, reverse dark brown. Sporulation was absent on CMD, OA, and PCA, moderate on MLA.

**Habitat & Geographical distribution** — Saprobe on decaying wood of *Nothofagus* sp., known only from New Zealand.

**Notes** — *Stanjehughesia silvana* is closely related to *S. hormiscioides*, but differs from it in having shorter ascospores that remain hyaline at maturity and conidial traits; conidia are shorter and slightly narrower, contain a conspicuous central pore at the septa and the apical cell does not differ in colour from other cells.

## DISCUSSION

Phylogenetic analyses employing three markers and comparative morphological analyses of 21 strains revealed that genera *Exserticlava* and *Phaeostalagmus* do not constitute monophyletic clades at the generic level. Similar observations were noted across chalara-, phialocephala-, and stanjehughesia-like morphotypes. The analysed species formed several well-supported, unrelated clades, suggesting that certain shared morphological traits can confer evolutionary advantages and result from adaptation to similar environmental challenges or ecologi-





**Fig. 11** *Stanjehughesia silvana* (ex-type ICMP 15123). a. Ascomata; b. colony of the asexual morph; c, e, f. conidia; d. conidiogenous cells; g–i. asci with ascospores; j–l. conidiogenous cells with conidia attached; m. colonies on CMD, MLA, OA, and PCA after 4 wk (from left to right). a–i. On natural substrate; j–l. on PCA. — Scale bars: a, b = 500 µm, c–l = 20 µm, m = 1 cm.

cal niches. Detailed discussions on these taxa and clades are provided below.

### Variability of *chalara-like* fungi in *Chaetosphaeriaceae*

Chalara-like fungi encompass a wide range of morphologically similar, often asexually typified fungi, initially distinguished into genera based on conidial shape, septation, and presence or absence of setae and conidiophores (e.g., Nag Raj & Kendrick 1975, McKenzie et al. 2002, Wang & Sutton 1984, Coetsee et al. 2000, Paulin & Harrington 2000). Cai et al. (2009) proposed that conidial width and septation can, to a certain extent, serve as indicators for inferring phylogenetic relationships within the broadly perceived *Chalara*. Wu & Diao (2023) presented evidence indicating that chalara-like species with septate and aseptate conidia form unrelated, strongly supported clades, whereas other morphological characters exhibit limited phylogenetic significance. Our data substantiate these observations, revealing that the three chalara-like fungi studied here delineate three distinct lineages. *Chalarosphaeria* consistently exhibits cylindrical, subcylindrical to clavate, aseptate conidia adhering in chains (Fig. 3), *Fusichalara* (represented by *F. dingleyae*) features two kinds of conidia that are long-cylindrical and fusiform, transversely septate (the first conidium); subsequent fusiform conidia adhere in readily seceding chains that soon collapse and conidia aggregate in slimy heads (Fig. 5), whereas *Chalarina* has conidia cylindrical to long clavate with 0–1 septa adhering in chains (Fig. 2).

Clade A, including *Chalarosphaeria* and *Fusichalara*, is one of the three lineages within *Chaetosphaeriaceae* that display the chalara-like morphotype. Additional chalara-like fungi are classified in the newly introduced genus *Chalarina* (Clade D), and are also associated with *Sporoschisma* as the chalara-like synasexual morph (Müller & Samuels 1982). Drawing from evidence provided by both molecular and morphological data, the genus *Chalarosphaeria* encompasses four species. These fungi are saprobic in nature, thriving on decaying wood in temperate and tropical regions. While the characters of the sexual morph, historically classified within the broadly perceived genus *Chaetosphaeria*, display high uniformity with other chaetosphaeriaceous genera with similar sexual morphs, it is the asexual characters that serve as diagnostic traits, providing a clear differentiation for this genus within the family. *Chalarosphaeria* is readily distinguishable by its robust conidiophores bearing terminal monophialides with a profound tubular collarete with frayed margin and cylindrical, subcylindrical to clavate, aseptate conidia with a minute but well discernible marginal frill. In culture, the short chains rapidly collapse, leading to the formation of mucoid droplets at the apex of the phialides. Conversely, conidia produced on natural substrates consistently exhibit adhesion in long chains.

Wu & Diao (2022, 2023) introduced *Chalarosphaeria*, typified by *Chs. breviclavata*, based on the phylogeny of LSU sequences derived from two non-type strains initially identified as *Chaetosphaeria chalaroides*, specifically S.M.H. 2018 and S.M.H. 2223, originating from Costa Rica and Puerto Rico. These sequences were sourced from GenBank, published in Huhndorf et al. (2001). Our phylogenetic analyses of *Chalarosphaeria*, incorporating also newly generated ITS sequences of the two Caribbean strains, revealed that they are not conspecific with the reference strain of *Cha. breviclavata* CBS 148188. Instead, they likely represent a different species and should be compared to *Chs. caribensis*. Morphological comparison of the Caribbean strains with *Chs. breviclavata*, based on available information (Miller & Huhndorf, unpubl.), did not reveal significant differences in sexual and asexual characters. Further research is required to fully understand this previously undocumented

lack of morphological differences for distinct genotypes, and more collections are needed for a comprehensive study.

The generic description of *Fusichalara* introduced by Hughes & Nag Raj (1973) is expanded with sexual characteristics based on the life cycle study of *F. dingleyae* (Réblová 2004). The sexual morph of *F. dimorphospora*, the type species, is unknown. Of the six species currently classified within *Fusichalara*, only three such as *F. dimorphospora*, *F. dingleyae*, and *F. novae-zelandiae*, share generic traits (i.e., convex thickening of the inner wall of the phialide and two kinds of conidia during ontogeny) and are accepted in the genus. The occurrence of conidia with a hyaline and versicolorous pattern, where the middle cells are brown and the end cells are hyaline, is acknowledged in *Fusichalara*, and is consistent with the criteria established by Hughes & Nag Raj (1973). In our recent taxonomic revisions of the genera *Chloridium* and *Cacumisporium* (both *Chaetosphaeriaceae*), we have corroborated similar observations concerning different conidial colours within the genus (Réblová et al. 2022, Réblová & Nekvindová 2023). Nevertheless, the three core *Fusichalara* species display additional differences that might warrant their future separation, if supported by molecular data. For instance, *F. dingleyae* exhibits a conspicuous marginal frill around the truncated base, while the other two species lack such a frill, and their conidia are basally tapering, appearing obconical and sometimes slightly truncated (Hughes & Nag Raj 1973). The systematic placement of *Fusichalara* needs verification through molecular data, particularly for *F. dimorphospora* and *F. novae-zelandiae*, and to confirm intrageneric morphological variability among accepted species.

Although *F. minuta*, known from decaying wood and bamboo stems in the Czech Republic and Japan (Gams & Holubová-Jechová 1976), displays conidial dimorphism, it lacks the convex thickening of the phialide. The remaining two species of *Fusichalara* lack the conidial dimorphism. These are *F. clavatispora*, collected from the dead stems of *Rubus fruticosus* in the UK (Kirk & Spooner 1984), and *F. goanensis*, found on dead wood in India (Bhat & Kendrick 1993). The placement of *F. minuta* in the *Sclerococcales* (Réblová et al. 2016) suggests that also the other two *Fusichalara* species may not be appropriately placed within the genus and could represent distinct lineages.

*Chalarina* (Clade D) represents another genus exhibiting the chalara-like morphotype in *Chaetosphaeriaceae*. A comparison with *Chalarosphaeria* reveals distinctions in conidial characteristics and morphology of phialides. *Chalarina* produces cylindrical to long clavate, straight or curved, 0–1-septate conidia. Notably, the genus displays a venter that abruptly tapers towards a narrower collarete. In contrast, the cylindrical collarete of *Chalarosphaeria* is approximately of the same width as the venter. Conidia of both genera have a minute marginal frill, which is more conspicuous in *Chalarosphaeria*. In culture, they produce conidia in false basipetal chains that are easily dispersible and conidia collapse in slimy heads. Similar chalara-like species with 1-septate conidia have been reclassified into different genera within the *Leotiomyces* based on molecular data, including *Nagrajchalara* and *Cylindrocephalum* (Wu & Diao 2023). Both genera differ from *Chalarina* in having collarettes longer than the venter, and their conidia are cylindrical and always septate. Unfortunately, molecular data and living cultures for other similar *Chalara* species with septate, hyaline conidia are not available. Wu & Diao (2023) compiled a list of these species, suggesting that they are likely members of *Nagrajchalara*.

*Chalarina* is shown as a sister to *Chaetosphaeria polygonalis* (Yang et al. 2023). Although both species exhibit terminal phialides with a deeply seated conidiogenous locus and hyaline, aseptate conidia, their relationship lacks statistical support



(32/0.94), particularly in the ML analysis. *Chaetosphaeria polygonalis* was described as a dematiaceous hyphomycete, which features hyaline, short-cuneiform conidia that aggregate in slimy masses. The images in the protologue (Yang et al. 2023: f. 59) indicate that conidia may be borne in short chains that readily collapse. *Chaetosphaeria polygonalis* is distinguishable from *Cha. hyalospora* by its collarette, which is cup- or vase-shaped compared to tubular non-flaring collarette in the latter species, and by phialides that are nearly the same width as the conidiophores and do not taper abruptly towards the collarette. *Chaetosphaeria polygonalis* is considered a candidate for inclusion in *Chalarina* pending broader and more comprehensive taxon sampling, although such fungi are currently unknown to us. *Chaetosphaeria polygonalis* is distinct from *Chaetosphaeria* based on *Ch. innumera*; the genus has recently been redefined to include fungi with a chloridium-like anamorph, originally classified under *Chloridium* sect. *Psilobotrys* (Gams & Holubová-Jechová 1976, Réblová & Nekvindová 2023). This redefinition distinguishes it as unrelated to *Ch. polygonalis*. A more appropriate classification for *Ch. polygonalis* would be within the genus *Ascochalara* (Réblová 1999a). It bears a strong resemblance to *A. gabretae*, but can be differentiated by its longer conidia.

Other morphologically comparable fungi in the family include genera *Catenularia*, *Fuscocatenula*, and *Gongromeriza*. Despite their aseptate conidia being endogenously produced and aggregating in false basipetal chains, distinctions arise in the form of erect, macronematous conidiophores with terminal phialides featuring a more or less shallow, flaring, wedge- or cup-shaped collarette. *Catenularia* exhibits dematiaceous cuneiform to obovoid conidia with an angular outline, pores, and produces capitate hyphae (Hughes 1965, Réblová et al. 2021e). *Gongromeriza* showcases hyaline, cuneiform or long clavate conidia adhering in chains, but sometimes forming heads (Gams & Holubová-Jechová 1976, Réblová et al. 2022). *Fuscocatenula* produces cuneiform to obovoid, pigmented conidia with a round outline and protracted maturation regarding the colour change from hyaline to pale brown at maturity (Luo et al. 2019, Réblová et al. 2021e).

### ***Exserticlava* and similar fungi**

*Exserticlava* serves as an illustrative example of a heterogeneous genus comprising various sexual and asexual morphotypes. In their comprehensive approach, Tsui et al. (2001) and Wu & Diao (2022) attributed significant importance and diagnostic value to asexual characters and adopted generic boundaries for *Exserticlava* to incorporate nine species, notwithstanding the morphologically distinct sexual morphs linked to some of them. Members of the genus were distinguished based only on conidial septation, shape, and colour. Despite the conspicuous heterogeneity observed, the potential non-monophyly of the genus was not taken into consideration. While molecular data is absent for most representatives of the genus, our analyses focused on nuclear and protein-coding markers derived from three *Exserticlava* species, representing two distinct morphological patterns. It was revealed that the generic description of *Exserticlava* proposed by Wu & Diao (2022) does not align with our findings.

Three species were resolved into two well-supported lineages within Clade B, identified as *Exserticlava* and *Exserticlavopsis*, each representing a holomorphic genus. Supported by molecular evidence, *Exserticlava* is now acknowledged to comprise a solitary species, namely *E. vasiformis*, and the generic description has been emended accordingly. Three additional species, morphologically similar to *E. vasiformis* but exhibiting distinct sexual morphologies, two of which possess available molecular data, have undergone reclassification within the

closely affiliated genus *Exserticlavopsis*. They were previously classified in *Chaetosphaeria* and linked with the *Exserticlava* asexual morphs, and are now recognized as *Exserticlavopsis chlorotunicata*, *Ex. exserticlavoides*, and *Ex. hiugensis*. For the remaining six *Exserticlava* species (see MycoBank), whose sexual morphs remain unknown, confirmation of their placement within either genus awaits validation through DNA sequence data. Nevertheless, considering the morphology of both their conidiogenous cells and conidia, these species appear to constitute a natural group that bears a resemblance to *Exserticlavopsis*.

*Exserticlava* and *Exserticlavopsis* share brown, distoseptate, ellipsoidal conidia and collarettes with a deeply frayed margin as a result of the rupture of the distal wall of the conidiogenous cell. However, they differ in the anatomy of the conidiogenous cell whose inner part extends above the collarette and forms a sterile subulate extension in *E. vasiformis*. The determination of whether the extension of the conidiogenous cell is a generic diagnostic trait or a species-specific characteristic remains unknown. In addition, these genera also differ in conidial morphology (presence of marginal frills in members of *Exserticlavopsis*), percurrent extension of the conidiogenous cell (one to several percurrent extensions in *Exserticlavopsis*), ascomatal setae (ascomata of *Exserticlava* are adorned with capitate setae vs bristle-like setae with pointed apices in *Exserticlavopsis*) and ascospores (asymmetrical, cylindrical to narrowly fusiform, apically rounded and tapering towards the base, and concolourous in *Exserticlava* vs symmetrical, fusiform, and versicolourous in *Exserticlavopsis*).

The conidiogenesis in both genera is characterized as phialidic, wherein conidia, upon detachment from the conidiogenous locus, adhere in slimy heads. In *Exserticlava*, conidia are produced successively from multiple growing points. However, the morphology of the conidiogenous cell in *Exserticlavopsis*, whether it features a single locus or multiple loci, has not been comprehensively determined for all species. Based on our light microscopy observations of *Ex. exserticlavoides* in culture, the conidiogenous locus appears single (Fig. 4). In contrast, in *Ex. hiugensis* (syn. *E. triseptata*), the conidiogenous locus appears to have multiple growing points. This observation is based on our material from Puerto Rico (Réblová & Seifert 2003), and illustration by Matsushima (1975, 1985), Cruz et al. (2008), and Tsui et al. (2001). In the original illustration from Matsushima (1975: pl. P349–351), the single conidia are depicted in different positions on the conidiogenous locus, indicating successive formation at multiple points. Another illustration of this species (Matsushima 1985: f. 327) shows two conidia of different age emerging simultaneously from the conidiogenous locus. Also photographs of *Ex. chlorotunicata*, as published in Fernández & Huhndorf (2005: f. 37–40), reveal conidia attached in various positions on the conidiogenous locus suggesting successive growth.

*Exserticlava* and *Exserticlavopsis* form a well-supported clade (Clade B) along with *Stanjehughesia*. The sexual morphs of *Exserticlavopsis* and *Stanjehughesia* exhibit a remarkable similarity, featuring fusiform, transversely septate, and versicolourous ascospores. However, distinct differences are evident in the morphology of the ascomatal wall, setae, and associated asexual morphs. *Exserticlavopsis* also bears resemblance to the genus *Sporoschisma* (Hughes 1966, Müller & Samuels 1982, Sivichai et al. 2000, Luo et al. 2016) due to similarities in ascospore characteristics and a three-layered ascomatal wall with a superficial coloured layer. Nevertheless, *Sporoschisma* is distinguishable by capitate setae that accompany conidiophores and also grow on ascomata, as well as morphology of the asexual and chalara-like synasexual morphs.

*Anaexserticlava caatingae* (Santa Izabel et al. 2015) exhibits a superficial resemblance to *E. vasiformis*, especially in the presence of a hyaline sterile extension of the conidiogenous cell and brown, distoseptate conidia. However, it is distinguished through features such as subcylindrical conidiogenous cells that extend percurrently, holoblastic conidiogenesis, rhexolytic conidial secession, and conidia that are pedicellate at the base.

### *Stanjehughesia* and similar genera

The family *Chaetosphaeriaceae* predominantly comprises fungi that produce phialidic conidia. Interestingly, it also accommodates several non-phialidic genera that bear a resemblance to the genus *Sporidesmium* (*Sporidesmiales*, *Sordariomycetes*) and its segregates (e.g., Subramanian 1992, Hernández-Gutiérrez & Sutton 1997, Wu & Zhuang 2005, Shenoy et al. 2006, Su et al. 2016, Yang et al. 2018, Wu & Diao 2022). They share dematiaceous, multiseptate, eu- or distoseptate structures that vary in shape and are referred to as conidia. These macroconidia, formed on holoblastic conidiogenous cells sometimes supported by conidiophores, might at first appear to be substantial resting structures that are analogous to chlamydospores in a broader sense. In *Chaetosphaeriaceae*, this morphotype can be found in several genera, such as *Aunstrupia* (Wu & Diao 2022), *Lomaantha* (Subramanian 1954), *Falholtia*, *Linkosia* (Hernández-Gutiérrez & Sutton 1997), *Morrisiella* (Saikia & Sarbhoy 1985), *Riisgaardia*, *Stanjehughesia*, and *Zanclospora*. In the case of *Stanjehughesia* and *Zanclospora*, synasexual phialidic morphs are also present in their life cycles and form only in culture (Réblová & Winka 2001, Réblová et al. 2021e). *Falholtia*, *Lomaantha*, *Stanjehughesia*, and *Zanclospora* constitute distinct and strongly supported evolutionary lineages. On the other hand, genera like *Aunstrupia*, *Linkosia*, *Morrisiella*, and *Riisgaardia* are located within a cluster of phialidic genera in a larger clade that lacks statistical support. This clade appears as sister to the clade containing *Zanclospora*, which has the *stanjehughesia*-like synasexual morph.

*Stanjehughesia* (Clade B) is characterized by absent conidiophores, determinate holoblastic, ampulliform conidiogenous cells, and dematiaceous, solitary, euseptate macroconidia that secede schizolytically. The sexual morph forms subglobose ascomata that can be adorned by sterile setae with inflated hyaline apices somewhat resembling capitate setae, cylindrical-clavate asci with a non-amyloid apical annulus and eight versicolourous, septate ascospores, which may remain hyaline in some species. Keys and a synopsis table to *Stanjehughesia* and related genera were prepared by Delgado (2008), Hsieh et al. (2021), and Wu & Diao (2022).

An intriguing characteristic observed in the conidia of *S. silvana* is the conspicuous, dark brown thickening at the centre of each septum surrounding the pore. In the side view, it is barrel-shaped and it is reminiscent of a dolipore septum occurring in basidiomycete hyphae. Similar structures were described in several other hyphomycetous and coelomycetous fungi with euseptate and distoseptate, brown conidia, for example in *Acrodictys* (Ellis 1965, Matsushima 1971), *Bactrodesmium* (Hughes & White 1983, Réblová et al. 2020a), *Canalisporium* (Nawawi & Kuthubutheen 1989), *Cancellidium applanatum* (Tubaki 1975), *Coryneum* (Sutton 1975b), *Lomaantha* (as *Ellisembia*, Kirk 1985) or *Sarcostroma* (Nag Raj 1993).

The initial taxonomic concept of *Stanjehughesia* by Subramanian (1992) included five species, such as *S. caespitulosa*, *S. hormiscioides*, *S. larvata*, *S. nigroaca*, and *S. vermiculata*. However, some of these species, still as members of the genus *Sporidesmium*, were earlier re-examined based on their holotype material by Hughes (1958), who accepted *S. hormiscioides* with *S. caespitulosa* and *S. vermiculata* as its synonyms. *Stanjehughesia hormiscioides* was originally collected from

wood of *Fagus sylvatica* in the Czech Republic (Corda 1838), *S. caespitulosa* was found on wood of *Acer* sp. in the USA (Ellis & Everhart 1889), and *S. vermiculata* was discovered on decaying wood of *Quercus* sp. in the UK (Cooke 1875). The initial synonymy of *S. hormiscioides* was primarily based on morphological observations. While *S. hormiscioides* and *S. vermiculata* produce both younger, shorter, and clavate conidia, as well as mature, longer, and fusiform conidia, *S. caespitosa* forms only the clavate conidia (Ellis 1958, Hughes 1958). In his earlier work, Ellis (1958) treated *S. caespitulosa* and *S. vermiculata* as two separate species (in the absence of *S. hormiscioides*) based on revision of their type materials. However, Ellis (1976) followed later the treatment of *S. hormiscioides* proposed by Hughes (1958). The illustration and description of *S. vermiculata*, derived from the holotype (Ellis 1958), clearly demonstrate it is identical with *S. hormiscioides*, thus corroborating Hughes's (1958) conclusions on synonymy. Hughes & Illman (1974) reported variability of conidial shapes of *S. hormiscioides* and suggested that it correlates with occurrence in different geographical regions.

Upon examining our material, we observed variability not only in conidial size but particularly in the narrowing of the upper part of conidia, which can sometimes be more abrupt. Additionally, the basal cell is not consistently darker than the other cells in different collections. In well-developed collections, we observed that young clavate conidia contain granular reddish brown substance in the apical broadly rounded cell. This characteristic persists during ontogeny and is also present in mature conidia in the much smaller apical cells. Germinating the conidia of *S. hormiscioides* *in vitro* proves challenging, and we managed to obtain only one culture (CBS 102664) from our material. The observed variability suggests the possibility of cryptic species within the *S. hormiscioides* species complex.

Shenoy et al. (2006) showed that the non-type strain of *S. vermiculata* HKUCC 10840 (= NN42952 = Wu1354g) collected on dead bamboo culm in China belongs to *Chaetosphaeriaceae*; however, it was placed on a terminal branch unrelated to *S. hormiscioides*. Based on ITS and LSU DNA sequences, Wu & Diao (2022) demonstrated that *S. vermiculata* NN42952 and two other related species constitute an independent lineage in *Chaetosphaeriaceae*, leading to the introduction of the genus *Riisgaardia*. The description of the strain NN42952 was provided by Wu & Zhuang (2005) and Wu & Diao (2022). Currently, the sexual morph of *Riisgaardia* remains unknown. Considering the characteristics of conidia and conidiogenous cells, *S. hormiscioides* and *R. vermiculata sensu* Wu & Diao (2022) are morphologically nearly indistinguishable. The only notable difference lies in the younger, shorter, and clavate conidia, which appear to be absent in *R. vermiculata*. Additionally, the fusiform conidia of *R. vermiculata* are wider at the base (7.5–9 µm *vide* Wu & Diao 2022 vs 4–7 µm *vide* Ellis 1958), and the paler apical cell is narrowly rounded and conidia appear rostrate, whereas in *S. hormiscioides*, the apical cell is usually inflated. Based on these differences and earlier studies of holotypes of both species by Ellis (1958) and Hughes (1958), *S. vermiculata* is accepted as a synonym of *S. hormiscioides*. Additionally, a new species should be proposed for the strain representing *Riisgaardia vermiculata sensu* Wu & Diao (2022) non *Clasterosporium vermiculatum* Cooke, Grevillea 4(30): 69. 1875 (= *S. hormiscioides*). The herbarium material of this species (Wu1354g) and the corresponding living strain NN42952, potentially serving as a holotype and ex-type strain, reside in a private collection and are currently inaccessible to us (Wu & Diao 2022). Despite morphological similarities between *Stanjehughesia* and *Riisgaardia* that makes both genera almost indistinguishable, molecular data provide a clear distinction between them. In the current phylogeny, the *Riisgaardia* clade did not

receive statistical support, suggesting that further investigation is necessary for this lineage.

As for *S. caespitulosa* (Ellis & Everhart 1889), despite it being suggested as another synonym of *S. hormiscioides* by Hughes (1958), it forms only shorter, apically rounded conidia and conidiogenous cells that aggregate in large fascicles. Based on these differences, we prefer to retain it as a separate species until molecular data can substantiate its relationship. The Chinese strain of *S. hormiscioides* Wu8263 given in Wu & Diao (2022) is likely a different species reminiscent of *S. caespitulosa* due to its wider clavate conidia with generally less septa and absence of the longer fusiform and somewhat bent conidia with inflated apices.

Another undescribed holomorphic species of *Stanjehughesia* was recently collected on decaying wood of *Nothofagus* sp. in New Zealand (PDD 94220, Bell & Mahoney, unpubl.). The material contains both sexual and asexual morphs, which align with the generic concept of *Stanjehughesia*. The sexual morph has hyaline, transversely 3–5-septate ascospores as observed in *S. silvana*. So far, this phenomenon has been observed only in collections from New Zealand. The asexual morph of *Stanjehughesia* sp. PDD 94220 most closely resembles *S. caespitulosa* but differs from it in having narrower and shorter conidia, 99–131 × 9–12 µm (Bell & Mahoney, unpubl.) vs 65–150 × 13–17 µm (Ellis 1958), with a dark central pore at each septum as observed in *S. silvana*. Regrettably, molecular data or a living culture of this unidentified species is currently unavailable.

Hsieh et al. (2021) utilized a limited dataset of LSU sequences to establish that the ex-type strain of *S. kaohsiungensis* BCRC FU31337, found on submerged wood in Taiwan and characterized by dark, euseptate conidia on short caespitose conidiophores, is a member of *Chaetosphaeriaceae*. It formed an independent lineage closely related to species with hyaline, falcate, and setulate conidia classified in *Codinaea* and related genera (e.g., Luo et al. 2019, Réblová et al. 2021b). Interestingly, a stanjehughesia-like morphotype has not yet been associated with taxa in this part of the phylogenetic tree. Another strain of *S. kaohsiungensis* NN050711 from China revealed additional morphological features not mentioned in the protologue, particularly synnematos conidiomata, as documented by Wu & Diao (2022). Apart from this addition, the strains shared identical morphological characteristics of conidia and conidiogenous cells. Based on molecular evidence, Wu & Diao (2022) proposed the segregation of *S. kaohsiungensis* into a new genus, *Falholtia*. However, the discrepancies in the morphology of conidiophores between the ex-type and non-type strains have not been sufficiently addressed. In a photograph featuring synnemata (Wu & Diao 2022: f. 33a, b), numerous fascicles of conidiophores were observed at a 90-degree angle along the entire length of the synnema. However, the depiction did not show the continuation of synnematos conidiophores into the diverging apices. It should not be dismissed the possibility that the synnema could pertain to another aged hyphomycete, and the mycelium with the caespitose conidiophores of *F. kaohsiungensis* might have subsequently overgrown it. The genus *Falholtia* has euseptate, obclavate conidia similar to *Stanjehughesia* but differs in the presence of short conidiophores and is clearly delimited by molecular data.

Additionally, it is challenging to distinguish *Stanjehughesia* from a group represented by *S. polypora* in the *Xylariales* (Shenoy et al. 2006), and stanjehughesia-like synasexual morphs of *Zanclospora* (*Chaetosphaeriales*) in the absence of molecular data. Furthermore, *Stanjehughesia* shares similarities with *Janetia* (*Capnodiales*), *Linkosia* (*Chaetosphaeriales*), and *Pseudostanjehughesia* (*Sordariomycetidae*). The genus *Janetia* (Ellis 1976) in-

cludes species that are typically found on the surfaces of leaves from various plants. It is characterized by having integrated, mostly intercalary, polyblastic, denticulate conidiogenous cells and dematiaceous, euseptate conidia. However, the generic concept was later expanded to encompass species with distoseptate conidia, monoblastic conidiogenous cells, and synnemata (Goh & Hyde 1996). *Linkosia* (Hernández-Gutiérrez & Sutton 1997) resembles *Stanjehughesia* in the absence of conidiophores, holoblastic ampulliform conidiogenous cells and dematiaceous, obclavate to obclavate-rostrate conidia, however the conidia are distoseptate. *Pseudostanjehughesia* (Yang et al. 2017) is a genus that bears a strong resemblance to *Stanjehughesia* in terms of lacking conidiophores and having euseptate conidia. However, molecular data indicate that it is distantly related and it is classified *incertae sedis* in *Sordariomycetidae*.

It is evident that molecular data are essential for accurately delimiting *Stanjehughesia* and morphologically similar genera. Although 17 species are accepted in *Stanjehughesia*, molecular data are available for only two of them. The affinity of other species is debatable and need to be ascertained through DNA data. The absence of living cultures and molecular data for the majority of *Stanjehughesia* species represents a significant challenge in the systematics of this group and hinders our comprehensive understanding of these fungi.

Another genus that has been delineated from *Sporidesmium* with a notable presence in *Chaetosphaeriaceae*, and is also characterized by the production of dematiaceous macroconidia, is *Ellisembia*. Subramanian (1992) introduced *Ellisembia*, typified by *E. coronata*, to encompass various *Sporidesmium* species characterized by distoseptate conidia produced on holoblastic conidiogenous cells and short conidiophores. Nevertheless, molecular data does not substantiate this proposition and *Ellisembia* has been resolved as a polyphyletic genus (Réblová & Winka 2001, Shenoy et al. 2006, Su et al. 2016, Wu & Diao 2022). Delgado et al. (2024) provided an emended description of *Ellisembia* based on a recent collection of *E. coronata*, establishing its affiliation with the *Sporidesmiales*. The strongly supported clade within *Chaetosphaeriales*, consisting of six ellisembia-like species and a non-type strain of *Lomaantha pooga*, the generic type (Subramanian 1954, Wu & Diao 2022), has been redescribed to represent the genus *Lomaantha*. Considering both molecular and morphological evidence, we endorse this taxonomic revision, acknowledging *Lomaantha* as a holomorphic genus and the correct name for this group of species.

### ***Phaeostalagmus*, *sporendocladia*, and *phialocephala*-like fungi**

Clade C encompasses *Phaeostalagmus cyclosporus*, *P. tenuissimus*, and two species of *Sporendocladia*, namely *Sn. beijingensis* and *Sn. fumosa*. Although molecular data confirm a relationship between the two *Phaeostalagmus* species, the monophyly of the genus was not supported. Within this clade (81/1), *P. tenuissimus* was identified as a sister to *Sporendocladia*, albeit without statistical support, while *P. cyclosporus* occupied a basal position. We have contemplated the possibility that Clade C could represent a single genus. Although *Phaeostalagmus* consists of eight species, these microscopic hyphomycetous fungi are infrequently collected, and their strains are rarely found in culture collections. For the time being, we consider the clade a natural group comprising two genera. Further study is required, particularly to assess whether the variations in morphological traits discussed here could represent interspecific variability. A larger pool of sampled taxa and the inclusion of additional phylogenetic markers might enhance the statistical support for this grouping.



These four species manifest three morphotypes aligning with the three lineages they represent. The studied morphotypes appear as variations on a theme in terms of the branching pattern of the conidiophores, but are distinguished by conidial features and phialide morphology. The distribution of pigments in conidiophores is another important feature and is most prominent in *P. tenuissimus*. Shared characteristics include upright, dematiaceous conidiophores, discrete and occasionally integrated, terminal phialides, and the production of endogenous, hyaline, aseptate conidia. The phialides in all three lineages are ampulliform to lageniform in shape, tapering to a slender neck, but there are variations in the collarette morphology. The conidia vary in shape and the manner in which they aggregate together. Noteworthy differences manifest in the branching system of the conidiophores, which display a varying degree of penicillately and verticillately branched conidiophores. The conidiophores of *P. tenuissimus* are characterized by simple verticils of phialides, while *P. cyclosporus* exhibits branched conidiophores, and *Sporendocladia* displays a condensed phialocephala-like conidiogenous apparatus. In addition, *Phaeostalagmus* and *Sporendocladia* exhibited temporary dimorphic conidiophores in culture; the young conidiophores were often seen as subverticillate, consisting of a stipe and one or two series of phialides. Interestingly, the existence of both penicillate and verticillate conidiophore structures, as documented for example in species such as *Clonostachys rosea* (Huang et al. 2009), can underscore the morphological variability within a single species. The morphology of conidiophores can be influenced by diverse culture conditions, and particular conidiophore morphologies have been linked to the organism's ability to infect other organisms in bioassays. This emphasizes the adaptability of conidiophore morphology and its potential functional significance in various ecological contexts. However, in *Phaeostalagmus* and *Sporendocladia*, the diagnostic conidiophore structures are linked to growth on the natural substrate and are not a product of *in vitro* environment. Although certain morphological dissimilarities in the branching dynamics of the conidiophores may initially appear subtle and were traditionally accommodated within a single genus, *Phaeostalagmus*, molecular data now provides a fresh perspective at these diagnostic characteristics.

The conidiophores of *Phaeostalagmus* are branched in their apical part. In the case of *P. cyclosporus* (Fig. 6), the type species, the conidiophores form an unbranched (sterile) stalk with a poorly differentiated foot cell at the base, which becomes well-developed in culture. The upper phialide-bearing section exhibits an arborescent morphology. The fertile part is concolourous, brown but slightly paler than the stipe, and comprises several tiers of short branches. Phialides are distinctly paler, borne in verticils on supporting cells or may also be borne directly on the conidiophore or branches. The branches are arranged alternately as well as oppositely and in verticils. In other *Phaeostalagmus* species, the conidiophores may be sparingly branched, sometimes with only discrete phialides inserted in the main stipe, e.g., *P. minutus* (Wu & Diao 2022), *P. peregrinus* (Minter & Holubová-Jechová 1981), and *P. rossicus* (Sutton & Mel'nik 1992). The collarettes are flared and funnel-shaped and conidia are ellipsoidal, oblong, cylindrical to subglobose aggregating in heads. Hughes (1951) reported that the conidia of *P. cyclosporus* are deposited in dry conidial balls that can be easily disturbed by a needle. Except for *P. tenuissimus*, species currently classified under *Phaeostalagmus* bear resemblance to *P. cyclosporus*. However, the absence of living cultures and molecular data hinders the verification of their relationship with the type species.

On the contrary, in *P. tenuissimus* (Fig. 7), the conidiophores are unbranched and the foot cell at the base is absent. The dark

brown sterile stipe and nearly hyaline fertile part of the conidiophore are well delimited. The discrete phialides are arranged in multiple verticils below the septa and in a terminal verticil. Occasionally, a short lateral branch bearing 1–2 phialides may be present and was observed only in culture. The collarettes are flared, funnel-shaped and conidia are ellipsoidal, adhering in slimy heads.

The genus *Sporendocladia*, based on *Sn. castaneae*, was originally established by Arnaud (1954) for a fungus found on old cupules of *Castanea sativa* in France. Nag Raj & Kendrick (1975) validated the name *Sporendocladia* and the name of its type species and re-described *Sporendocladia* for fungi with dematiaceous penicillate conidiophores bearing phialidic conidiogenous cells with long collarettes and aseptate conidia adhering in basipetal chains. After examining the holotype of *Spicaria fumosa* (Ellis & Everhart 1883), which was collected on cupular spines of *Castanea* sp. in Philadelphia, USA, Sutton (1975a) confirmed that it is indeed conspecific with *Sn. castaneae*. As a result, Sutton (1975a) transferred this species to *Phialocephala*, based on the presence of a simple conidiogenous apparatus at the conidiophore apex.

Wingfield et al. (1987) conducted a study on several species of *Phialocephala* that exhibit conspicuous phialides with deep set cylindrical collarettes and cylindrical conidia produced in chains, most closely resembling those found in *Chalara* and related genera (Nag Raj & Kendrick 1975). Five species displaying these traits, including *Pc. fumosa*, were subsequently separated from *Phialocephala* and placed in the genus *Sporendocladia*. The species was re-described by Crous & Wingfield (1994) based on strain CBS 518.93, which was analysed in this study. *Sporendocladia* (Fig. 9) displays a diminished conidiogenous apparatus, marked by discrete phialides grouped and inserted into the apical cell of the conidiophore, as observed in *Sn. fumosa* (Nag Raj & Kendrick 1975, Crous & Wingfield 1994, Seifert et al. 2011). The *Sporendocladia* morphotype exhibits an intermediate characteristic, bridging the gap between the branched, verticillate conidiophores of *P. cyclosporus* and unbranched, repeatedly verticillate conidiophores of *P. tenuissimus*. Interestingly, based on the study of type material, Nag Raj & Kendrick (1975) and Sutton (1975a) described *Sn. fumosa* as having cylindrical conidia that are truncate at both ends. Crous & Wingfield (1994) demonstrated that the conidia of *Sn. fumosa* are enteroblastic and have a cuneiform shape with rounded apices and truncate bases, contrary to the previous claim. Furthermore, unlike the conidia of *Chalara*, the conidia of *Sn. fumosa* adhere in false chains with only basal dehiscence scar, the chains easily collapse in culture and conidia adhere in mucous droplets at the apex of conidiophores.

Nevertheless, the morphological complexity of the conidiogenous apparatus in *Sporendocladia* may vary. In *Sn. fumosa*, the conidiogenous apparatus retains its simple structure without extensive branching and is restricted to the apical cell of the conidiophore in material from nature (Nag Raj & Kendrick 1975, Sutton 1975a). In culture, however, we occasionally observed mono- to biverticillate branching pattern and formation of short alternate branches (Fig. 9), for details see the notes under this species. On the other hand, as the conidiophores mature in *Sn. beijingensis*, they develop branching and the phialides emerge on short lateral branches in a verticillate pattern below the septa, as well as directly on the main stipe of the conidiophore. The branching pattern is identical to that displayed by *P. cyclosporus*. In *Sn. beijingensis* the branches are directed upwards, although they form a narrower angle with the main stalk compared to the 70–80 degrees observed in *P. cyclosporus*.

Despite the re-description of *Sn. fumosa* by Crous & Wingfield (1994), Wu & Diao (2022) maintained the delimitation of the

genus *Sporendocladia* with holoblastic, cylindrical conidia that are truncate at both ends and arranged in long chains. This statement is, however, in contradiction to the fact that *Sn. beijingensis*, as reported by Wu & Diao (2022) in the same publication, exhibits cuneiform conidia.

The typical phialocephala-like morphotype is infrequent within *Chaetosphaeriaceae* and is confined to two unrelated clades, specifically represented by *Chloridium* sect. *Pseudophialocephala* (Réblová et al. 2022) and the monotypic genus *Spadicocephala*, supported by molecular data to accommodate *Phialocephala fusca* (Kendrick 1963). These evolutionary lineages are distantly related to the core of the genus *Phialocephala* in the *Leotiomycetes* (Jacobs et al. 2003). While species presently classified in *Chloridium* sect. *Pseudophialocephala* exhibit phialidic conidiogenesis on multiple loci, *Sc. fusca* produces conidia on a single conidiogenous locus. *Spadicocephala* is positioned on a terminal branch as sister to the genus *Gongromerizella*; however, the latter genus is differentiated by simple conidiophores. Distinguishing *Spadicocephala* from *Phialocephala* (Kendrick 1961) and other phialocephala-like species based on morphology alone is challenging. The conidiophores of *Spadicocephala* lack a foot cell and exhibit a coloration ranging from brown to reddish brown, becoming paler in the upper fertile part. A notable characteristic appears to be the distinct cinnamon, brown, or dark chestnut-brown colour of the colonies of *Sc. fusca* in culture (Kendrick 1963, this study). However, a correct determination cannot be made without DNA sequences (e.g., Grünig et al. 2002, Jacobs et al. 2003, Day et al. 2012, Tanney et al. 2016).

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