New genera and species with chloridium-like morphotype in the *Chaetosphaeriales* and *Vermiculariopsiellales*

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Abstract: In this study, we investigated the morphological and genetic variability of selected species belonging to the genus *Chloridium sensu lato*, some also referred to as chloridium-like asexual morphs and other undescribed morphologically similar fungi. These species do not conform to the revised generic concept and thus necessitate a re-evaluation in terms of taxonomy and phylogeny. The family *Chaetosphaeriaceae* (*Chaetosphaeriales*) encompasses a wide range of asexual morphotypes, and among them, the simplest form is represented by *Chloridium* sect. *Chloridium*. The morphological simplicity of the *Chloridium* morphotype has historically led to the amalgamation of numerous unrelated species, thereby creating a heterogeneous genus. By conducting phylogenetic reconstruction of four DNA loci and examining a set of 71 strains, including all available ex-type and other non-type strains as well as holotypes and other herbarium material, we were able to gain new insights into the relationships between these taxa. Phylogenetic analyses revealed that the studied species are distantly related to *Chloridium sensu stricto* and can be grouped into two orders in the *Sordariomycetes*. Within the *Chaetosphaeriales*, they formed nine well-separated genera in four clades, such as *Cacumisporium*, *Caliciastrum gen. nov.*, *Caligospora gen. nov.*, *Capillisphaeria gen. nov.*, and *Chloridiopsis gen. nov.* in *Vermiculariopsiellales*. Four new species and eight new combinations are proposed in these genera. Our study provides a clearer understanding of the genus *Chloridium*, its relationship to other morphologically similar fungi, and a new taxonomic treatment and molecular phylogeny to facilitate their accurate identification and classification in future research.

Key words: conidiogenesis, Chaetosphaeria, lignicolous fungi, multi-locus, new taxa, phialide

Taxonomic novelties: New genera: Caliciastrum Réblová, Caligospora Réblová, Capillisphaeria Réblová, Chloridiopsiella Réblová, Chloridiopsiella Réblová, Chloridiopsiella Réblová, Chloridiopsis Réblová, Geniculoseta Réblová, Papillospora Réblová, Spicatispora Réblová; New species: Caliciastrum bicolor Réblová, Caligospora pannosa Réblová, Chloridiopsis syzygii Réblová, Gongromerizella silvana Réblová; New combinations: Caligospora dilabens (Réblová & W. Gams) Réblová, Capillisphaeria crustacea (Sacc.) Réblová, Chloridiopsiella preussii (W. Gams & Hol.-Jech.) Réblová, Chloridiopsis constrictospora (Crous et al.) Réblová, Geniculoseta preussii (W. Gams & Hol.-Jech.) Réblová, Repillospora hebetiseta (Réblová & W. Gams) Réblová, Spicatispora carpatica (Hol.-Jech. & Révay) Réblová, Spicatispora fennica (P. Karst.) Réblová; Epitypifications (basionyms): Chaetosphaeria dilabens Réblová & W. Gams, Chloridium cylindrosporum W. Gams & Hol.-Jech.

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INTRODUCTION

The genus Chloridium (Link 1809) comprises saprobic dematiaceous hyphomycetes that are commonly found in soil and decaying plant material in both terrestrial and freshwater environments. However, the genus has been historically defined in an inconsistent manner, resulting in a heterogeneous group that includes species with varying conidiophore and conidiogenous cell morphology and conidial ontogeny. To address this disparate group, Gams & Holubová-Jechová (1976) proposed three sections to cover the wide morphological variation present in *Chloridium*. Using a wide range of methods, Réblová et al. (2022) emended Chloridium to the revised concept and established a monophyletic, polythetic genus divided into eight sections. Chloridium is delimited to phialidic dematiaceous hyphomycetes that produce conidia on multiple conidiogenous loci in sympodial manner on a central dome within the collarette. Conidia are hyaline or pale brown, aseptate, ellipsoidal, subglobose, obclavate, occasionally deltoid, adhering in slimy heads or cirrhi. They also produce mononematous, pigmented, simple, sometimes setose or penicillately branched conidiophores, 1-septate hyaline ascospores that fragment into part spores and many species form chlamydospores *in vitro*.

The family Chaetosphaeriaceae consists of numerous asexual morphotypes, among which the simplest form is represented by Chloridium sect. Chloridium. This group is characterized by unbranched conidiophores with a terminal phialide that produces minute, ellipsoidal, subglobose to obclavate conidia (Gams & Holubová-Jechová 1976, Réblová et al. 2022). In the past, the simplicity has led to taxonomic disputes where identification is mainly based on morphological features. To date, 115 species and varieties have been described historically in the genus Chloridium (MycoBank, www.mycobank.org, accessed on 28 Apr. 2023), of which 37 have been accepted in *Chloridium sensu stricto* (s. str.) (Réblová et al. 2022). Over time, several species have undergone reclassification, leading to their placement in different genera and orders across three classes. The majority of these genera are now classified within Sordariomycetes, such as Cacumisporium, Craspedodidymum, Curvichaeta, Fusichloridium, Kylindrochaeta and Phialogeniculata in Chaetosphaeriales (Wu & Diao 2022), Dischloridium and Phaeochloridium in Glomerellales (Sutton 1976, Wu & Diao 2022), Myrmecridium in Myrmecridiales (Arzanlou et al. 2007), and Rhamphoriopsis and Xylolentia in Rhamphoriales (Wu & Diao 2022, Yang et al. 2023). Within the class Dothideomycetes, Globoramichloridium is placed in the order Capnodiales (Marin-Felix et al. 2019), while Acrodontium, Mycosphaerella, Ramichloridium and Zasmidium are established in Mycosphaerellales (de Hoog 1972, 1977, Braun et al. 2003, Videira et al. 2016, 2017). Hyaloscypha is placed in Helotiales, Leotiomycetes (Fehrer et al. 2018), and Chaetopsis (Saccardo 1880) and Pleurophragmium (Ellis 1976) are listed as genera incertae sedis. The number of genera (19) associated with former Chloridium species reflects a time when species that appeared similar, were arbitrarily placed within it. Further revision and new systematic treatment are necessary for the remaining species. However, the identity of many described Chloridium species is uncertain due to missing living strains, depleted or lost type materials, and protologues that are difficult to interpret.

In our molecular and morphological study, we investigated additional species of Chloridium and chloridium-like asexual morphs that are not consistent with the current generic concept and warrant a novel systematic treatment. Their sexual morphs, if known, were assigned to the genus Chaetosphaeria (e.g. Tulasne & Tulasne 1863, Booth 1957, 1958, Gams & Holubová-Jechová 1976, Réblová & Gams 1999, 2000, Huhndorf et al. 2001, Fernández & Huhndorf 2005). The fungi in question include 71 strains of 17 known and four undescribed species. The majority of these strains represent almost 50 yr of dedicated effort to collect and isolate chloridium-like fungi in axenic cultures and gain knowledge about their taxonomy, systematics, and ecology. Many of these strains were isolated by W. Gams since the 1970s (Gams & Holubová-Jechová 1976, Réblová & Gams 2000). The other 41 strains were collected and isolated by M. Réblová between 1997 and 2018 (Réblová & Gams 1999, Réblová & Winka 2000, Réblová 2004, Réblová et al. 2022, this study). Additional strains were obtained from the CBS and FMR culture collections, allowing for a more robust and comprehensive understanding of the taxa under investigation.

Of particular interest is the relationship between *Chaetosphaeria* preussii and its presumed asexual morph *Chloridium preussii* (Gams & Holubová-Jechová 1976), which has never been fully resolved. We aimed to clarify whether these two morphs represent parts of the life cycle of a single organism. Morphological examination and preliminary phylogenetic analysis of all strains listed within the species description of *Chl. preussii* indicate that the ex-type strain CBS 230.75 is distinct from the remaining strains CBS 257.75, CBS 262.76, CBS 263.75, which, in contrast, fit within the species description and are morphologically and phylogenetically similar to the asexual morph that accompanies the ascomata of *Ch. preussii* in the holotype PRM 796750.

Chloridium constrictospora is known from a single collection on leaf litter of Syzygium cordatum in South Africa (Crous et al. 1995). Its hyaline, oblong conidia that are constricted in the middle, and formed on phialides with a single conidiogenous locus on caespitose conidiophores, make this species highly distinctive. However, such characteristics do not correspond to any known genera within Chaetosphaeriaceae or other established taxa.

Chaetosphaeria fennica (Réblová & Gams 1999) has a presumed asexual morph with pale brown, suballantoidal conidia on multiple conidiogenous loci. This rare species was recently collected for the first time since its description by Karsten (1887). It shows remarkable similarity with Chloridium carpaticum

(Holubová-Jechová & Révay 1987), which was recently transferred to *Craspedodidymum* (Wu & Diao 2022).

Chaetosphaeria crustacea (Réblová & Gams 1999) has a chloridium-like asexual morph and is commonly found on decaying wood of coniferous trees. It is strikingly similar to Chaetosphaeria curvispora (Réblová 2004), which appears to be endemic to New Zealand. Based on ribosomal DNA sequences, the latter species was transferred to a new genus, Curvichaeta, within Chaetosphaeriaceae (Wu & Diao 2022). We present seven new strains and DNA sequences of Ch. crustacea and Ch. curvispora to evaluate their relationship.

Réblová & Gams (2000) introduced two species of *Chaetosphaeria* with chloridium-like asexual morphs: *Ch. dilabens* from bamboo in Japan and *Ch. hebetiseta* from decaying wood in Ukraine. The asexual morph of *Ch. dilabens* is distinctive due to its brown, ellipsoidal to somewhat asymmetrical conidia that arise from a single conidiogenous locus within a vase-shaped collarette with more or less frayed margin. We studied four isolates of *Ch. dilabens*, which show genetic variability. The chloridium-like asexual morph of *Ch. hebetiseta* forms sparsely branched conidiophores with sympodially extending conidiogenous cells, accompanied by clavate, apically hyaline setae that also cover the ascomata. The sexual morph, with its fusiform, 3-septate hyaline ascospores and distinct setae, is similar to *Stilbochaeta brevisetula* (Réblová *et al.* 2021a).

As part of the revision of the genus *Chloridium*, Réblová *et al.* (2022) have abandoned the original classification of *Chloridium sensu* Gams & Holubová-Jechová (1976), with two former sections, *Gongromeriza* and *Psilobotrys*, reinstated at the generic level. Moreover, the reclassification of *Chloridium lignicola*, *Chl. pachytrachelum*, and *Chl. pini* to the genus *Gongromerizella*, which was supported by both morphological observations and DNA sequence analyses of their ex-type strains (Réblová *et al.* 2022), may not fully encompass the diversity within these taxa. Upon examination of additional strains and fresh specimens, it has become apparent that they likely include more than the initially recognized three species.

Our research also focuses on other species, such as Cacumisporium acutatum (formerly known as Chaetosphaeria acutata with a chloridium-like asexual morph, Réblová & Gams 1999), C. capitulatum (Corda 1838, Goos 1969), and Fusichloridium cylindrosporum (formerly Chaetosphaeria fusiformis with the Chloridium cylindrosporum asexual morph, Gams & Holubová-Jechová 1976, 1981). Recently, Wu & Diao (2022) transferred Ch. acutata to Cacumisporium based on phylogenetic analysis of ITS and LSU sequences. However, they did not revise or clarify the generic concept, and instead adopted a broadly conceived genus encompassing taxa with both phialidic and holoblastic-denticulate conidiogenesis. We provide new specimens, living strains, and novel DNA sequences of these fungal species to contribute to their classification and discussion on conidiogenesis.

During our study, we encountered three specimens of an undescribed lignicolous fungus in Canada, Germany, and New Zealand. Axenic cultures derived from two of these collections yielded chloridium-like conidiophores and conidia. The sexual morph is characterized by subglobose ascomata that collapse inwards and become cup-shaped; they are clothed with clavate, apically hyaline, sterile setae that also accompany conidiophores and the ascospores are bicolorous. The fungus is similar to *Crassochaeta fusispora* (Sivanesan 1977, Réblová 1999a), but differs by the anatomy of the setae and the inability of ascomata to collapse upon drying.

Our study aims to address the challenges associated with the genus *Chloridium*, including the presence of highly morphologically similar taxa that exhibit genetic diversity, as well as the systematic significance of conidiogenesis. The main objectives of our research are to elucidate the identity of various chloridium-like fungal strains, explore the intricate morphology of their conidiogenous cells, investigate their life cycles, and provide a comprehensive systematic classification. By undertaking these investigations, we aim to gain a deeper understanding of the complexities surrounding *Chloridium*. We gathered a significant amount of material, including all available ex-type and non-type strains, herbarium material, and freshly collected specimens. Our research is based on morphological comparative study of material from nature and culture, as well as molecular analyses such as partitioned Maximum Likelihood and Bayesian inference phylogenetic analyses of four markers.

MATERIALS AND METHODS

Sampling and fungal strains

Specimens comprising conidiophores and ascomata growing on decaying wood and bark were collected from diverse locations, including temperate broadleaf and mixed forests in Canada, Czech Republic, France, Germany, Italy, New Zealand, Spain and Ukraine.

Dried specimens were accessioned 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 deposited in Westerdijk Fungal Biodiversity Institute (formerly CBS-KNAW) in Utrecht, the Netherlands (CBS), CABI-IMI Culture Collection in Egham, UK (IMI) and International Collection of Microorganisms from Plants in Auckland, New Zealand (ICMP). Other fungarium material and living strains were obtained from CBS, Facultat de Medicina de Reus in Tarragona, Spain (FMR), University of Helsinki, Helsinki, Finland (H), Royal Botanical Gardens in Kew, UK (K), and Fungarium of the National Museum in Prague, Czech Republic (PRM). The studied strains, along with their respective sources and GenBank accession numbers for the sequences generated in this study, are provided in Table 1. Designated epitypes and newly discovered fungal taxa have been registered in MycoBank (www.mycobank.org; Crous et al. 2004). Since most of the newly introduced generic names in this study begin with the letters 'C' and 'G', the following abbreviations will be used throughout the text: Cacumisporium (C.), Caliciastrum (Cm.), Caligospora (Ca.), Capillisphaeria (Cp.), Curvichaeta (Cu.), Chaetosphaeria (Ch.), Chloridium (Chl.), Chloridiopsiella (Cha.), Chloridiopsis (Chs.), Gongromeriza (G.), Gongromerizella (Ga.) and Geniculoseta (Ge.).

Cultures derived from ascospores were established by carefully cutting the ascomata using a sterile razor blade. A drop of sterile water was added to facilitate the swelling of the centre containing the asci and ascospores. The gelatinous centre was then transferred onto agar using the tip of a sterile needle. For cultures derived from conidia, conidial clusters were transferred onto the agar surface using a needle tip. Initially, both ascospores and conidia were transferred to a 10-cm-diam Petri dish containing water agar (WA) (distilled water 1 L, agar 10 g, Oxoid Limited, Hampshire, UK) or Modified Leonian's agar (MLA) (Malloch 1981) and incubated for 2–5 d. Single and multiple ascospores and conidia were obtained with a single-spore isolator (Meopta, Přerov, Czech Republic); germinating spores were transferred to a new 6-cm-diam Petri dish containing MLA. Cultures were incubated in the dark at 20–25 °C and observed periodically for sporulation.

Morphological studies

Morphological observations were conducted on both dried specimens and living cultures. Colonies composed of conidiophores, setae and ascomata were examined with an Olympus SZX12 dissecting microscope (Olympus America, Inc., Melville, NY, USA) and rehydrated with tap water. Microscopic preparations were mounted in different media including 90 % lactic acid, tap water, or 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^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 5 500K 16 W LED lights. All colonies were photographed on a black glossy surface, with the exception of cultures with a yellow or orange diffusible pigment where also a white alabaster glossy surface was used for enhanced contrast. Images were processed using Adobe Photoshop CS6 software (Adobe Systems, San Jose, CA, USA).

Slide cultures were employed to investigate the conidial ontogeny and morphology of the conidiogenous cells. For this purpose, each strain was inoculated onto multiple small blocks of potato-carrot agar (PCA) (Crous *et al.* 2019), a nutrient-deficient agar medium. The blocks were then covered with coverslips, incubated in the dark at 20–23 °C, and monitored daily for a period of 2–3 wk. In addition, fungi were cultured on various nutrient media to assess colony characteristics, diffusible pigments, and growth patterns: cornmeal dextrose agar (CMD) (Oxoid Limited; 2 % dextrose), MLA, oatmeal agar (OA), PDA (potato-dextrose agar, Oxoid Limited) and PCA. Colony characteristics were determined based on 4-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.* 2019) supplemented with sterile stems of *Urtica dioica*.

Gene markers, DNA extraction, PCR amplification, and sequencing

We conducted sequence analyses of four gene markers. The internal transcribed spacer (ITS1-5.8S-ITS2) (ITS) of the nuclear rRNA cistron is widely used as the primary barcode for fungi (Schoch *et al.* 2012). The nuclear large subunit LSU rDNA gene (LSU) (D1-D3 domains, approximately 1 800 base pairs) is commonly employed as a marker in *Chaetosphaeriaceae* and has proven useful for studying relationships within the *Ascomycota*, providing reliable phylogenetic resolution at the generic and higher taxonomic levels in fungi (*e.g.* Zhang *et al.* 2007, Schoch *et al.* 2009). Two coding markers, the intermediate section of the translation elongation factor 1-α (*TEF1*) gene and the second largest subunit of DNA-directed RNA polymerase II (*RPB2*) gene, were also included in our analyses. These markers have been previously shown to be effective in distinguishing between interspecific relationships (Robert *et al.* 2011, Stielow *et al.* 2015, Meyer *et al.* 2019).

Accession numbers of sequences obtained from GenBank and previously published in other studies (Réblová & Winka 2000, Gruenig *et al.* 2002, Huhdorf & Fernández 2005, Fernández *et al.* 2006, Atkinson *et al.* 2007, Somrithipol *et al.* 2008, Prabhugaonkar

Taxon Cacumisporium acutatum Cacumisporium capitulatum Cacumisporium capitulatum	Source						-		
- -	Source	Status ¹	Country	Host	Substrate		Genbank acc	GenBank accession numbers	
<u> </u>						ITS	rsn	TEF1	RPB2
	CBS 101311		Ukraine	Corylus avellana	decaying wood	OR134680	OR134624	OR130760	I
	CBS 101312		France	Fagus sylvatica	decaying wood	OR134681	OR134625	OR130761	I
	CBS 101315	_	Czech Republic	Fagus sylvatica	decaying wood	OR134682	OR134626	OR130762	I
	CBS 101313		France	Fagus sylvatica	decaying wood	OR134683	OR134627	OR130763	I
	CBS 131690		Czech Republic	Quercus sp.	decaying wood	OR134684	OR134628	OR130764	I
	CBS 142445		Italy	Quercus cerris	decaying wood	OR134685	OR134629	OR130765	I
	CBS 142446		Czech Republic	Quercus sp.	decaying wood	OR134686	OR134630	OR130766	I
	PRA-21505		Czech Republic	Carpinus betulus	decaying wood	OR134687	OR134631	OR130767	I
	FMR 11339		Spain	unidentified	decaying wood	OR134688	OR134632	OR130768	I
Caliciastrum bicolor	ICMP 15136		New Zealand	Nothofagus sp.	decaying wood	OR134689	OR134633	OR130769	I
_	PRA-21507	_	Canada	Acer macrophyllum	decaying wood	I	OR134634	I	I
Caligospora dilabens	CBS 712.88		Japan	bamboo	dead stem	OR134690	OR134635	OR130770	I
	CBS 734.83	ш	Japan	Bambusa sp.	culm	OR134691	OR134636	OR130771	I
Caligospora pannosa	CBS 551.89	_	Brazil	Theobroma cacao	cultivated soil	OR134692	OR134637	OR130772	I
Capillisphaeria crustacea	CBS 145637		Czech Republic	Abies alba	decaying wood	OR134693	OR134638	OR130773	I
	CBS 144664		Czech Republic	Picea abies	decaying wood	OR134694	OR134639	OR130774	I
	CBS 144665		Czech Republic	Picea abies	decaying wood	OR134695	OR134640	OR130775	I
_	ICMP 15139		New Zealand	unidentified	decaying wood	OR134696	OR134641	OR130776	I
Chaetosphaeria abietis	CBS 427.83		Austria	Abies alba	bark	OR134697	OR134642	OR130777	I
Chaetosphaeria innumera	CBS 131270		Italy	Fagus sylvatica	decaying wood	OR134698	OR134643	OR130778	I
	M.R. 3775		Czech Republic	Fagus sylvatica	decaying wood	OR134699	OR134644	OR130779	I
Chloridiopsiella preussii	CBS 230.75	-	Netherlands	Taxus baccata	decaying wood	OR134700	OR134645	OR130780	OR135580
	CBS 247.76		Germany	unidentified	decaying wood	OR134701	OR134646	OR130781	OR135581
	CBS 265.76		Netherlands	unidentified	decaying wood	OR134702	OR134647	OR130782	OR135582
Chloridiopsis constrictospora	CBS 432.92	-	South Africa	Syzygium cordatum	leaf litter	OR134704	OR134649	OR130784	OR135584
Chloridiopsis syzygii	CBS 564.93	-	Cuba	Syzygium jambos	leaf	OR134703	OR134648	OR130783	OR135583
Curvichaeta curvispora	ICMP 15115	-	New Zealand	Nothofagus sp.	decaying wood	OR134705	OR134650	OR130785	I
-	ICMP 15118		New Zealand	Nothofagus sp.	decaying wood	OR134706	OR134651	OR130786	I
-	ICMP 18254		New Zealand	unidentified	decaying wood	OR134707	OR134652	OR130787	I
-	ICMP 18255		New Zealand	unidentified	decaying wood	OR134708	GU180636	OR130788	I
Fusichloridium cylindrosporum	CBS 101429	ш	Czech Republic	Abies alba	decaying bark	OR134709	OR134653	OR130789	I
	CBS 101430		Czech Republic	Abies alba	decaying bark	OR134710	OR134654	OR130790	I

Table 1. (Continued).									
Taxon	Source	Status ¹	Country	Host	Substrate		GenBank acc	GenBank accession numbers	
						ITS	rsn	TEF1	RPB2
Geniculoseta preussii	CBS 257.75		Germany	Fraxinus excelsior	decaying wood	OR134711	OR134655	OR130791	I
	CBS 262.76		Germany	unidentified	decaying wood	OR134712	OR134656	OR130792	I
	CBS 263.75		Netherlands	Quercus sp.	decaying wood	OR134713	OR134657	OR130793	I
	CBS 145478		Czech Republic	Fagus sylvatica	decaying cupule	OR134714	OR134658	OR130794	I
Gongromeriza myriocarpa	CBS 116.57		Italy	unidentified	unknown	OR134715	OR134659	OR130795	I
	CBS 127685		Italy	Quercus cerris	decaying wood	OR134716	OR134660	OR130796	I
	CBS 143389		Ukraine	Carpinus betulus	decaying wood	OR134717	OR134661	OR130797	I
	CBS 145805		Czech Republic	unidentified	decaying wood	OR134718	OR134662	OR130798	I
	CBS 148194		Czech Republic	unidentified	decaying wood	OR134719	OR134663	OR130799	I
Gongromeriza pygmaea	CBS 131688		Czech Republic	Fagus sylvatica	decaying wood	OR134720	OR134664	OR130800	I
	CBS 138689		Czech Republic	Fagus sylvatica	decaying wood	OR134721	OR134665	OR130801	I
	CBS 139769		Italy	Corylus avellana	decaying wood	OR134722	OR134666	OR130802	I
	CBS 149858		Czech Republic	Quercus sp.	decaying wood	OR134723	OR134667	OR130803	I
	IMI 506815		Czech Republic	unidentified	decaying wood	OR134724	OR134668	OR130804	I
	ICMP 22550		New Zealand	unidentified	decaying wood	OR134725	OR134669	OR130805	I
Gongromerizella pachytrachela	CBS 145962		Czech Republic	Fagus sylvatica	decaying wood	OR134726	OR134670	OR130806	I
	CBS 148606		Czech Republic	Fagus sylvatica	decaying wood	OR134727	OR134671	OR130807	I
Gongromerizella pini	CBS 145343		Czech Republic	Fagus sylvatica	decaying wood	OR134728	OR134672	OR130808	I
Gongromerizella silvana	CBS 171.76	-	Belgium	unidentified	decaying wood	OR134729	OR134673	OR130809	1
Psilobotrys minutus	CBS 564.74		Netherlands	unidentified	decaying wood	OR134730	OR134674	OR130810	I
	CBS 600.75B		Belgium	unidentified	decaying wood	OR134731	OR134675	OR130811	1
	CBS 629.75		Belgium	unidentified	decaying wood	OR134732	OR134676	OR130812	I
	CBS 877.73		Netherlands	Acer sp.	decaying wood	OR134733	OR134677	OR130813	I
	CBS 145632		Czech Republic	Ulmus sp.	decaying wood	OR134734	OR134678	OR130814	1
Spicatispora fennica	CBS 101641		Ukraine	Abies alba	decaying wood	OR134735	OR134679	OR130815	I
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T and E denote ex-type and ex-epitype strains.

& Bhat 2009, Magyar *et al.* 2011, Crous *et al.* 2012, 2013, 2014, 2015, 2017, 2019, 2020, Hashimoto *et al.* 2015, Ma *et al.* 2016, Yang *et al.* 2018, Lin *et al.* 2019, Luo *et al.* 2019, Vu *et al.* 2019, Li *et al.* 2021, Réblová *et al.* 2020a, 2021a–d, 2022, Hernández-Restrepo *et al.* 2022, Manawasinghe *et al.* 2022, Wu & Diao 2022, Fryar *et al.* 2023, Yang *et al.* 2023) are provided in Table 2.

Total genomic DNA was extracted from 3-4-wk-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 Fidelity DNA polymerase kit (New England Biolabs Inc., Hitchin, UK) as per the manufacturer's protocol. The ITS and LSU markers were amplified with the V9G/LR8 primer pair (de Hoog & Gerrits van den Ende 1998, Vilgalys unpubl.). The TEF1 region was amplified with the EF1-983F/EF1-2218R primers (Rehner & Buckley 2005) and segments 5-7 of RPB2 were amplified with fRPB2-5F/fRPB2-7cR primers (Liu et al. 1999). PCR of ITS, LSU, TEF1 and RPB2 was carried out as described in Réblová et al. (2020b). 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 GATC Biotech Sequencing Service (Cologne, Germany), Westerdijk Fungal Biodiversity Institute (Utrecht, the Netherlands), and Ottawa Research and Development Centre, Agriculture and Agri-Food Canada (Ottawa, Ontario, Canada). Analysis of raw sequence data and assembly of sequence contigs were performed using Sequencher v. 5.4.6 (Gene Codes Corp., Ann Arbor, MI, USA).

Phylogenetic analyses and species delimitation

The gene sequences, newly generated in this study and those obtained from GenBank, were aligned in 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, b, 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).

Through the BLASTn search (Zhang et al. 2000) our strains exhibited similarity to members of *Chaetosphaeriales* and *Vermiculariopsiellales*. Consequently, sequences of representatives of these two orders were obtained from the GenBank nucleotide database and included in the analyses. The best-fit models of nucleotide evolution for each partition (ITS, LSU, *TEF1* and *RPB2*) models under Akaike information criteria were selected using MrModeltest v. 2.4. (Nylander 2004). The GTR+I+G model was selected for all partitions. Two final alignments of concatenated sequences (deposited in TreeBASE, study number 30496) were subjected to phylogenetic analyses.

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 1 000 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 1 000 generations with burn-in set at 25 %. The BI and ML phylogenetic trees were compared visually in terms of topological conflicts between the supported clades.

The first phylogenetic analysis was based on the threegene dataset (ITS-LSU-TEF1) and included members of Chaetosphaeriaceae. The alignment comprised 179 strains representing 132 species, encompassing a total of 3 471 characters, including gap regions, with 1 782 unique character sites (RAxML). Tracylla aristata and T. eucalypti (Tracyllales), were selected as the outgroup, following the approach adopted in previous studies by Réblová et al. (2022) and Wu & Diao (2022). The second phylogenetic analysis involved a comprehensive four-gene dataset (ITS-LSU-TEF1-RPB2) that encompassed taxa from Vermiculariopsiellales. The alignment comprised 16 strains representing 14 species in five genera, encompassing a total of 4 461 characters, including gap regions, with 1 266 unique character sites (RAxML). The outgroup was selected from members of Chaetosphaeriaceae, namely Chaetosphaeria innumera, Gongromeriza pygmaea, and Menispora uncinata. This selection was made based on the known close relationship between these two groups, as indicated by the findings of Réblová et al. (2021c).

RESULTS

Phylogenetic analyses were conducted using ITS, LSU, *RPB2* and *TEF1* sequences to investigate the relationships between the set of ex-type and other non-type living strains of species originally assigned to *Chloridium* or known as chloridium-like asexual morphs and similar fungi.

In order to investigate the relationships between studied strains and members of Chaetosphaeriaceae, a phylogenetic analysis was conducted using the ITS-LSU-TEF1 loci. The resulting phylogenetic trees, generated through Bayesian Inference (BI) and Maximum Likelihood (ML) analyses, exhibited overall congruence. The ML tree is shown in Fig. 1. Nodes with support values of ≥ 75 % ML Bootstrap (BS) and ≥ 0.95 BI Posterior Probability (PP) were considered well-supported. The phylogram provided insights into the relationships within the Chaetosphaeriaceae family, uncovering 81 well-supported lineages encompassing diverse genera and natural species groups. Notably, a highly supported clade (98 % / 0.98) comprised taxa characterized by the presence of setulate conidia, including Codinaea, Menispora, Thozetella, and other genera. A strongly supported clade (100 % / 1) consisting of Chloridium s. str., Sporoschisma and Adautomilanezia was shown as its sister group. The studied strains were classified into four distinct clades (Clades A-D) that exhibited a distant relationship to Chloridium s. str.

Clade A (100 % / 1) displays a diverse array of morphotypes. It included five subclades that manifest the chloridium-like morphotype, namely *Cacumisporium*, *Curvichaeta*, *Fusichloridium*, and also *Chaetosphaeria crustacea* and *Ch. fennica* for which new genera, *Capillisphaeria* and *Spicatispora*, are introduced below. Of all species with chloridium-like morphotype, only within this group are species that exhibit conidiogenesis on multiple loci. The clade also encompasses six additional genera along with four *Chaetosphaeria* species, necessitating a new taxonomic classification.

The strongly supported Clade B (93 % / 1) comprises Achrochaeta, Craspedodidymum elatum, ex-type and other non-type strains of Chaetosphaeria dilabens and Ch. hebetiseta, and

Table 2. Taxa, isolate information and sequences retrieved from GenBank.	sequences retrieved from	GenBank.							
Taxon	Strain	Status ¹	Country	Host	Substrate		GenBank acce	GenBank accession numbers	
						ITS	rsn	TEF1	RPB2
Achrochaeta rivulata	CBS 148186		Australia	Doryanthes excelsa	dead inflorescence	OR286508	OR286551	OR326680	I
Achrochaeta talbotii	ICMP 15161		New Zealand	unknown	decaying wood	MT454480	MT454495	OL653988	I
Adautomilanezia caesalpiniae	CC-LAMIC 102/12	—	Brazil	Caesalpina echinata	wood	KX821777	KU170671	I	I
Anacacumisporium appendiculatum	HMAS 245593	—	China	broad-leaved tree	dead stems	KP347129	KT001553	I	I
Arcuatospora novae-zelandiae	CBS 109474		Venezuela	Nectandra sp.	decaying leaf	MW984569	MW984552	OL653989	I
Arcuatospora seorsa	CBS 147510	—	Thailand	broad-leaved tree	decaying leaf	MW984572	MW984555	OL653990	I
Aunstrupia nodipes	NN043149		China	palm	leaf litter	OL627566	OL655011	I	I
Brunneodinemasporium brasiliense	CBS 112007	⊢	Brazil	unidentified	decaying leaf	JQ889272	JQ889288	I	I
Brunneodinemasporium jonesii	GZCC 16-0050	⊢	China	unidentified	decaying wood	KY026058	KY026055	I	I
Caligospora dilabens	CBS 735.83	—	Japan	Bambusa sp.	stem	MH861684	ı	I	ı
Calvolachnella guaviyunis	CBS 134695	—	Uruguay	Myrcianthes pungens	bark	KJ834524	KJ834525	I	I
Catenularia angulospora	MFLUCC 18-1331		China	unidentified	submerged wood	MK828638	MK835840	MN194089	I
Catenularia catenulata	DLUCC 0891	—	China	unidentified	submerged wood	MK828637	MK835838	MN194088	I
Catenularia minor	PRM 900544	l <u>e</u>	Thailand	unidentified	bamboo culm	MW987827	MW987822	OL653993	I
Chaetosphaeria conirostris	S.M.H. 2183	—	Costa Rica	unidentified	dead branch	I	AF466066	I	I
Chaetosphaeria cylindrospora	S.M.H. 3568	—	Panama	unidentified	decorticated branch	Ι	AY017373	I	I
Chaetosphaeria guttulata	MFLUCC 17-1703	—	China	unidentified	submerged wood	MK828636	MK835837	MN194087	ı
Chaetosphaeria innumera	CBS 145639		Czech Republic	Acer pseudoplatanus	decaying wood	OP455358	OP455464	OP465036	I
Chaetosphaeria mangrovei	MCD 069	⊢	Thailand	mangrove	decaying wood	MG813821	MG813820	I	I
Chaetosphaeria metallicans	PDD 92557		New Zealand	Nothofagus sp.	decaying wood	EU037894	I	I	I
	PDD 92539	⊢	New Zealand	Nothofagus sp.	decaying wood	EU037893	EU037899	I	I
Chaetosphaeria polygonalis	GZCC 20-0438	⊢	China	unidentified	submerged wood	OP377861	OP377946	OP473040	I
Chalarodes obpyramidata	PDD 119364		New Zealand	Nothofagus sp.	decaying wood	MW987828	MW987823	OL653995	ı
Chloridium bellum	CBS 709.73A	⊢	Germany	wheat field	soil	OP455360	OP455466	OP464934	I
Chloridium caesium	CBS 145633		Czech Republic	Tilia cordata	decaying wood	OP455367	OP455474	OP464941	I
Chloridium gamsii	CBS 667.75	⊢	Belgium	unidentified	decaying wood	OP455415	OP455522	OP464990	I
Chloridium virescens	CBS 145481		Czech Republic	Quercus sp.	decaying wood	OP455439	OP455547	OP465014	1
Codinaea assamica	CBS 139907	<u>۽</u>	Malaysia	Acacia mangium	leaf spot	OL654077	OL654134	OL653997	1
Codinaea fertilis	IMI 233824		New Zealand	Betula sp.	root	OL654080	OL654137	OL654000	1
Codinaea paniculata	CBS 145098	⊢	France	deciduous tree	submerged wood	MT118230	MT118201	OL654002	I
Codinaeella lambertiae	CBS 143419	⊢	Australia	Lambertia formosa	leaves	OL654084	OL654141	OL654009	I
Codinaeella minuta	CBS 280.59	auth. strain	Japan	Lithocarpus edulis	dead leaves	OL654090	OL654147	OL654016	1

Taxon Strain Statu Codinaeella parvilobata CBS 144536 T Conicomycas pseudotransvaalensis HHUF 29956 T Conicomycas pseudotransvaalensis HHUF 29956 T Craspedodidymum elatum NN042874 T Cryptophialoidea fasciculata MFLU 18-1499 T Dictyochaeta callimorpha CBS 144107 P Dictyochaeta callimorpha CBS 144107 T Dictyochaeta callimorpha CBS 145503 T Dictyochaeta duema CBS 145503 T Dictyochaeta duema CBS 145503 T Dictyochaeta duema CBS 144403 T Ellisembia dulema CBS 144403 T Ellisembia duliculata CBS 142074 T Eucalyptostroma eucalypti CBS 142074 T Eucalyptostromiella beijingensis NN076613 T Eucalyptostromiella beijingensis NN076613 T Fuscocatenula submersa CBS 142786 T Gongromeriza pygmaea CBS 144786 T	Status,	Country Czech Republic Japan China China Thailand Germany New Zealand	Host Fagus sylvatica Machilus japonica unidentified	Substrate decaying cupule	ITS	GenBank acce LSU OL654157	GenBank accession numbers LSU TEF1	RPB2
CBS 144536 NN042874 GZCC 18-0047 MFLU 18-1499 CBS 144107 ICMP 15130 ICMP 15133 ICMP 15153 CBS 147402 CBS 127402 CBS 147403 CBS 147403 CBS 147152 S.M.H. 2754 CBS 147152 S.M.H. 2754 CBS 147152 S.M.H. 2754 CBS 147152 CBS 147162 CBS 147162 CBS 147162 CBS 147165 CBS 142074 NN076613 NN076613 NN076613 CBS 142074 NN076613 CBS 142074 CBS 142074 NN076613 CBS 142074 CBS 142074 NN076613 CBS 142074 CBS 143074 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 1443.54 CBS 143.54		Czech Republic Japan China China Thailand Germany New Zealand	Fagus sylvatica Machilus japonica unidentified	decaving cupule	ITS	LSU OL654157	TEF1	RPB2
CBS 144536 HUF 29956 NN042874 GZCC 18-0047 MFLU 18-1499 CBS 144107 ICMP 15130 ICMP 15133 ICMP 15153 CBS 144503 CBS 147402 CBS 147402 CBS 147402 CBS 147403 CBS 147403 CBS 147402 CBS 14153 CBS 142074 NN076613 NN076613 NN076613 NN076613 CBS 142074 NN076613 CBS 142074 NN056332 CBS 142074 CBS 142074 NN056332 CBS 14353 CBS 144786		Czech Republic Japan China China Thailand Germany New Zealand	Fagus sylvatica Machilus japonica unidentified	decaying cupule	01 65/100	OL654157		
HHUF 29956 NN042874 GZCC 18-0047 MFLU 18-1499 CBS 144107 ICMP 15130 ICMP 15133 ICMP 15153 CBS 147402 CBS 147402 CBS 147403 CBS 147152 S.M.H. 2754 CBS 147152 S.M.H. 2754 CBS 142074 NN076613 NN076613 NN0765332 CBS 112964 MFLUCC 18-1342 NN055332 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 16575 CBS 143.54 CBS 143.54 CBS 645.75		Japan China China Thailand Germany New Zealand	Machilus japonica unidentified		OL034 100		OL654027	I
NN042874 GZCC 18-0047 MFLU 18-1499 CBS 144107 ICMP 15130 ICMP 15153 CBS 144503 CBS 127402 CBS 127402 CBS 147152 S.M.H. 2754 CBS 147152 S.M.H. 2754 CBS 147152 S.M.H. 2754 CBS 147152 CBS 147152 CBS 147152 CBS 112964 MFLUCC 18-1342 NN055332 CBS 112964 MFLUCC 18-1342 NN055332 CBS 144786	ρ	China China Thailand Germany New Zealand	unidentified	dead twig	LC001710	LC001708	I	I
GZCC 18-0047 MFLU 18-1499 CBS 144107 ICMP 15130 ICMP 15133 CBS 145503 HHUF 30001 CBS 127402 CBS 147152 S.M.H. 2754 CBS 142074 NN076613 NN076613 NN076613 NN076613 NN076613 CBS 141.53 CBS 141.53 CBS 144786 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 645.75	ρ	China Thailand Germany New Zealand	unidentified	dead branch	OL627547	OL655004	I	I
MFLU 18-1499 CBS 144107 ICMP 15130 ICMP 15153 CBS 145503 HHUF 30001 CBS 127402 CBS 127402 CBS 147152 S.M.H. 2754 CBS 147152 S.M.H. 2754 CBS 147152 S.M.H. 2754 CBS 147152 CBS 147152 CBS 142074 NN076613 NN076613 NN076613 CBS 142074 CBS 112964 MFLUCC 18-1342 NN055332 CBS 144786	Ε	Thailand Germany New Zealand	200	decaying wood	MN104608	MN104619	I	I
CBS 144107 ICMP 15130 ICMP 15133 CBS 145503 HHUF 30001 CBS 127402 CBS 144403 CBS 142074 NN076613 NN076613 NN076613 NN0765332 CBS 141.53 CBS 141.53 CBS 144786 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 143.54 CBS 645.75	ρ	Germany New Zealand	unknown	submerged wood	MH758195	MH758208	I	I
ICMP 15130 ICMP 15153 CBS 145503 HHUF 30001 CBS 127402 CBS 147152 S.M.H. 2754 CBS 142074 NN076613 NN076613 NN076613 NN0765332 CBS 112964 MFLUCC 18-1342 NN055332 CBS 144786 CBS 144786 CBS 144786 CBS 164776 CBS 144786 CBS 164776	μ , , , ,	New Zealand	Buxus sempervivens	decaying bark	MT118234	MT118205	OL654032	I
ICMP 15153 CBS 145503 HHUF 30001 CBS 127402 CBS 127402 CBS 147152 S.M.H. 2754 CBS 142074 NN076613 NN076613 NN076613 NN0765332 CBS 112964 MFLUCC 18-1342 NN055332 CBS 141.53 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 143.54 CBS 645.75	ب ، ، ،		unknown	decaying wood	MT454483	MT454498	MT454673	I
CBS 145503 HHUF 30001 CBS 127402 CBS 144403 CBS 147152 S.M.H. 2754 CBS 142074 NN076613 NN076613 NN078016 CBS 112964 MFLUCC 18-1342 NN055332 CBS 141.53 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 143.54 CBS 645.75		New Zealand	unidentified	decaying wood	MT454487	EF063574	MT454677	I
HHUF 30001 CBS 127402 CBS 144403 CBS 147152 S.M.H. 2754 CBS 142074 NN076613 NN076613 NN076613 NN076613 NN076532 CBS 112964 MFLUCC 18-1342 NN055332 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 143.54 CBS 645.75		Czech Republic	Quercus cerris	acorn	MT454489	MT454503	MT454679	I
CBS 127402 CBS 144403 CBS 1447152 S.M.H. 2754 CBS 142074 NN076613 NN076613 NN076613 NN076613 NN076613 CBS 112964 MFLUCC 18-1342 NN055332 CBS 141.53 CBS 144786 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 143.54 CBS 645.75		Japan	Arundo donax	unknown	AB900895	AB934039	AB934089	I
CBS 144403 CBS 147152 S.M.H. 2754 CBS 142074 NN076613 NN078016 CBS 112964 MFLUCC 18-1342 NN055332 CBS 141.53 CBS 144786 CBS 144786 CBS 144786 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 143.54 CBS 645.75		USA	tallgrass prairie	soil under	JQ889277	JQ889293	I	I
CBS 147152 S.M.H. 2754 CBS 142074 NN076613 NN078016 CBS 112964 MFLUCC 18-1342 NN055332 CBS 141.53 CBS 141.53 CBS 144786 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 143.54 CBS 645.75		France	Sambucus nigra	decaying wood	MH836375	MH836376	Ι	I
S.M.H. 2754 CBS 142074 NN076613 NN078016 CBS 112964 MFLUCC 18-1342 NN055332 CBS 141.53 CBS 144.786 CBS 699.74 PRA-21531 CBS 143.54 CBS 645.75		Czech Republic	Carpinus betulus	decaying wood	OL654105	OL654162	OL654033	I
CBS 142074 NN076613 NN078016 CBS 112964 MFLUCC 18-1342 NN055332 CBS 141.53 CBS 144.53 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 645.75		USA	Betula sp.	bark	MW984575	AF466079	I	I
NN076613 NN078016 CBS 112964 MFLUCC 18-1342 NN055332 CBS 141.53 CBS 141.53 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 645.75		Malaysia	Eucalyptus pellita	leaf spots	KY173408	KY173500	I	I
NN078016 CBS 112964 MFLUCC 18-1342 NN055332 CBS 141.53 CBS 264.76 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 645.75		China	Fagus sp.	decaying leaf	OL628127	OL655185	I	I
CBS 112964 MFLUCC 18-1342 NN055332 CBS 141.53 CBS 264.76 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 143.54		China	Quercus sp.	decaying leaf	OL628501	OL655251	I	I
A MFLUCC 18-1342 NN055332 CBS 141.53 CBS 264.76 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 143.54 CBS 645.75		Thailand	unidentified	decaying wood	MW984576	MW984558	OL654034	I
NN055332 CBS 141.53 CBS 264.76 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 achela CBS 645.75		China	unidentified	submerged wood	MK828634	MK835835	MN194085	I
CBS 141.53 CBS 264.76 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 CBS 645.75		China	palm	decaying leaf	OL627817	OL655124	ı	I
CBS 264.76 CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 achela CBS 645.75	p <u>.</u>	France	Fagus sylvatica	decaying wood	OP455456	OP455564	OP465029	I
CBS 144786 CBS 699.74 PRA-21531 CBS 143.54 achela CBS 645.75	7	Netherlands	unidentified	decaying wood	OP455457	OP455565	OP465028	I
CBS 699.74 PRA-21531 CBS 143.54 CBS 645.75		Czech Republic	Fagus sylvatica	decaying wood	OP455458	OP455566	OP465030	I
	P	Netherlands	Fraxinus excelsior	decaying wood	OP455459	OP455567	OP465031	I
		Ukraine	Fagus sylvatica	decaying wood	AF178548	AF178548	I	I
		France	Fagus sylvatica	decaying wood	OP455460	OP455568	OP465032	I
		Belgium	Fagus sylvatica	decaying wood	OP455461	OP455569	OP465033	I
Gongromerizella pini CBS 146011 T		Ukraine	Pinus sylvestris	decaying wood	MT223787	MT223882	I	I
Infundibulomyces cupulatus BCC 11929 T		Thailand	Lagerstroemia sp.	dead leaf	EF113976	EF113979	I	I
Infundibulomyces oblongisporus BCC 13400 T		Thailand	unidentified angiosperm	leaf litter	EF113977	EF113980	I	I
Kionochaeta microspora GZCC 18-0036 T		China	unidentified	decaying wood	MN104607	MN104618	I	I
Kionochaeta ramifera MUCL 39164		Cuba	unidentified	decaying leaf	MW144421	MW144404	OL654036	I

lable Z. (Continued).									
Taxon	Strain	Status ¹	Country	Host	Substrate		GenBank acce	GenBank accession numbers	
						ITS	rsn	TEF1	RPB2
Kionochaetiella ivoriensis	CBS 374.76	-	Ivory Coast	unidentified	bark	MH860988	MH872758	I	I
Kylindrochaeta lignomollis	S.M.H. 3015	—	Puerto Rico	unidentified	decaying wood	EU037896	AF466073	I	I
Linkosia multiseptum	NN042961		China	bamboo	dead culm	OL627557	OL655008	I	I
Linkosia rostrata	NN047479		China	bamboo	dead culm	OL627662	OL655059	I	I
Menispora caesia	CBS 145022		Czech Republic	Carpinus betulus	decaying wood	OL654107	OL654164	OL654039	I
Menispora ciliata	CBS 122131	Ĭ-	Czech Republic	Acer campestre	decaying wood	EU488736	OL654165	OL654040	I
Menispora tortuosa	CBS 117553		Canada	Acer sp.	decaying bark	OL654111	OL654169	OL654044	I
Menispora uncinata	ICMP 15140		New Zealand	unidentified	decaying wood	OL654112	OL654170	OL654045	I
Menisporopsis pirozynskii	MUCL 47217		Congo	unidentified	decaying leaf	MW984579	MW984561	OL654047	I
Menisporopsis theobromae	MUCL 41079		Venezuela	unidentified	decaying leaf	MW984580	MW984562	OL654048	I
'orrisiella indica'*	NN042908		China	Saccharum sp.	dead culm	OL627551	OL655005	I	I
Multiguttulispora dimorpha	CBS 140002		Malaysia	Eucalyptus sp.	twig	MW984582	MW984564	OL654049	I
Multiguttulispora triseptata	IMI 353690		Cuba	unidentified	leaf	MW984584	MW984566	OL654050	I
Nawawia filiformis	MFLUCC 17-2394		Thailand	unidentified	decaying wood	MH758196	MH758209	OP473069	I
Neopseudolachnella acutispora	MAFF 244358	—	Japan	Pleioblastus chino	dead twigs	AB934065	AB934041	AB934091	I
Neopseudolachnella magnispora	MAFF 244359	—	Japan	Sasa kurilensis	dead twigs	AB934066	AB934042	AB934092	I
Nimesporella capillacea	IMI 358908	—	Cote d'Ivoire	unidentified	leaf litter	OL654114	OL654171	OL654051	ı
Paliphora intermedia	CBS 896.97	_	Australia	unidentified	leaf litter	MH862682	EF204501	I	I
Papillospora hebetiseta	CBS 102340	—	Ukraine	Fagus sylvatica	decaying wood	AF178549	AF178549	OL653994	I
	S.M.H. 2729		USA	unidentified	decaying wood	AY906955	AF466069	I	I
Paraceratocladiella polysetosa	NN044119		China	Rhododendron sp.	dead leaf	OL627605	OL655027	I	I
Paraceratocladium silvestre	NN055375		China	unidentified	leaf litter	OL627830	OL655132	I	I
Paracryptophiale pirozynskii	NN044888		China	unidentified	dead branch	OL627641	OL655047	I	I
Paragaeumannomyces panamensis	S.M.H. 3596	-	Panama	unidentified	decaying wood	AY906948	MT118218	I	I
Paragaeumannomyces rubicundus	S.M.H. 3221	—	Costa Rica	unidentified	decaying wood	MT118242	MT118224	1	I
Phaeodischloridium aquaticum	MFLUCC 18-1341	—	China	unidentified	submerged wood	MK828639	MK835841	MN194090	I
Phaeostalagmus cyclosporus	CBS 663.70		Netherlands	Quercus sp.	decaying bark	MH859892	MH871680	I	1
Phialocephala fusca	CBS 301.85	auth. strain	Canada	Pinus strobus	decaying wood	AF486122	MH873571	1	1
Phialogeniculata guadalcanalensis	MFLUCC 18-0260	—	Thailand	unidentified	decaying wood	MK828625	MK835825	MN194078	I
Phialosporostilbe scutiformis	MFLUCC 17-0227	-	China	unidentified	submerged wood	MH758194	MH758207	1	I
Phialoturbella calva	ICMP 23826	-	New Zealand	unidentified	decaying bark	MW984585	MW984567	OL654052	I

Table 2. (Continued).									
Taxon	Strain	Status ¹	Country	Host	Substrate		GenBank acc	GenBank accession numbers	
						ITS	rsn	TEF1	RPB2
Phialoturbella lunata	MFLUCC 18-0642	—	China	unidentified	submerged wood	MK828624	MK835824	MN194077	ı
Polynema podocarpi	CBS 144415	-	New Zealand	Podocarpus totara	unknown	MH327797	MH327833	I	I
Pseudodinemasporium fabiforme	CBS 140010		Malaysia	Acacia mangium	leaf spots	KR611889	KR611906	I	I
Pseudolachnea fraxini	CBS 113701	—	Sweden	Fraxinus excelsior	unknown	JQ889287	JQ889301	AB934096	I
Pseudolachnea hispidula	MAFF 244365		Japan	Morus bombycis	dead twig	AB934072	AB934048	AB934098	I
Pseudolachnella asymmetrica	MAFF 244366	⊢	Japan	Phyllostachys nigra var. henonis	dead twig	AB934073	AB934049	AB934099	I
Pseudolachnella scolecospora	MAFF 244379		Japan	Sasa sp.	dead twigs	AB934086	AB934062	AB934112	I
Pseudothozetella lunata	CGMCC 3.20661	—	China	unidentified	leaf litter	OL628034	OL655157	ı	I
Psilobotrys minutus	CBS 223.74		Netherlands	Acer pseudoplatanus	decaying wood	OP455462	OP455570	OP465034	I
	CBS 247.75		Germany	Fraxinus excelsior	decaying wood	OP455463	OP455571	OP465035	I
Pyrigemmula aurantiaca	CBS 126743	-	Hungary	Vitis vinifera	bark	HM241692	HM241692	I	I
Rattania setulifera	GUFCC 15501	⊢	India	Calamus thwaitesii	leaves	GU191794	HM171322	I	I
Riisgaardia longispora	CGMCC 3.20794	⊢	China	unidentified	rotten wood	OL627701	OL655085	I	I
Riisgaardia obclavata	CGMCC 3.20787	-	China	bamboo	dead culm	OL627568	OL655013	ı	I
Sporendocladia beijingensis	CGMCC 3.20738	-	China	Quercus sp.	dead cupules	OL628290	OL655217	I	I
Sporendocladia fumosa	NN047731		China	Quercus sp.	dead fruit	OL627669	OL655065	I	I
Sporoschisma hemipsilum	MUCL 56487		Martinique	unidentified	wood	MW987829	MW987824	I	1
Sporoschisma mirabile	CBS 144794		France	Alnus glutinosa	submerged wood	MW987830	MW987825	I	I
Stephanophorella stellata	CBS 101301	-	Nigeria	unidentified	dead leaves	MH862729	MH874336	I	MW147339
Stilbochaeta malaysiana	IMI 312436	-	Malaysia	unidentified	decaying leaf	OL654121	OL654178	OL654059	I
Stilbochaeta novae-guineensis	CBS 147515		Puerto Rico	unidentified	decaying wood	OL654122	OL654179	OL654060	I
Stilbochaeta ramulosetula	IMI 313452	ш	Malaysia	unidentified	submerged leaf	OL654124	OL654181	OL654062	I
Striatosphaeria castanea	CBS 145352	-	French Guinea	woody liana	decaying periderm	MT118244	MT118229	I	I
Striatosphaeria codinaeophora	M.R. 1230		Puerto Rico	Dacryodes excelsa	decaying wood	AF178546	AF178546	I	I
Tainosphaeria cecropiae	CBS 101687	-	Puerto Rico	Cecropia sp.	decaying petiole	MW984586	MW984568	OL654064	I
Tainosphaeria crassiparies	S.M.H. 1934	-	Puerto Rico	Hymenaea sp.	pod pees	MW984587	AF466089	I	I
Tainosphaeriella aquatica	MFLUCC 17-2370	-	Thailand	unidentified	submerged wood	MZ161197	MZ161195	MZ170694	I
Tainosphaeriella thailandense	MFLUCC 18-1282	-	Thailand	unidentified	submerged wood	MZ161198	MZ161196	MZ170695	I
Thozetella cristata	CBS 101112		Venezuela	unidentified	leaf litter	OL654126	OL654183	OL654065	I
Thozetella tocklaiensis	CBS 378.58	—	India	Camellia sinensis	decaying flower	OL654128	OL654185	OL654067	I
Tracylla aristata	CBS 141404	ш	Australia	Eucalyptus regnans	leaves	OL654129	OL654186	OL654068	I

Table 2. (Continued).									
Taxon	Strain	Status ¹	Country	Host	Substrate		GenBank acces	GenBank accession numbers	
						ITS	rsn	TEF1	RPB2
Tracylla eucalypti	CBS 144429	_	Colombia	Eucalyptus urophylla	leaves	OL654130	OL654187	OL654069	I
Tubulicolla cylindrospora	MUCL 39171		Cuba	Buchehavia capitata	fallen leaf	MT454494	EF063575	I	MT454669
Verhulstia biformis	NN077655		China	Rubus sp.	dead leaf	OL628434	OL655237	I	I
Verhulstia trisororum	CBS 143234	—	Netherlands	n/a	soil	MG022181	MG022160	I	I
Vermiculariopsiella australiensis	CBS 141499	—	Australia	Grevillea sp.	leaves	KX306772	KX306797	I	ON399361
Vermiculariopsiella eucalypticola	CBS 143442	—	Australia	Eucalyptus dalrympleana	leaves	MG386070	MG386123	I	ON399368
Vermiculariopsiella immersa	CBS 112026		Brazil	unidentified	decaying leaf	ON400773	ON400826	I	ON399364
Vermiculariopsiella pini	CBS 146009	⊢	Malaysia	Pinus tecunumanii	needles	MN562128	MN567635	I	ON399367
Vermiculariopsiella spiralis	CBS 141289	βĹ	France	Acacia heterophylla	leaves	KX228263	KX228314	I	ON399366
Vermiculariopsis castanedae	CBS 132484	—	Portugal	unidentified	leaf	MH866028	ON400828	I	ON399323
Vermiculariopsis dunnii	CBS 145538	—	Australia	Eucalyptus dunnii	leaves	MK876412	MK876452	I	ON399371
Vermiculariopsis eucalyptigena	CBS 146091	—	Australia	Eucalyptus sp.	leaves	MT223868	MT223939	I	ON399369
Vermiculariopsis lauracearum	CBS 136534		South Africa	Sideroxylon inerme	twigs	ON400778	ON400832	I	ON399322
Zanclospora novae-zelandiae	ICMP 15781	ш	New Zealand	Fuscospora cliffortioides	decaying wood	MW144429	MW144411	MW147330	I
Zanclospora ramifera	ICMP 22738	⊢	New Zealand	unidentified	decaying wood	MW144433	MW144415	MW147334	I

'T, E, I, and N denote ex-type, ex-epitype, ex-isotype and ex-neotype strains, respectively; auth. strain (authentic strain).

aholotype of Chaetosphaeria trianguloconidia.

bex-type strain of Codinaea acaciae.

ex-type strain of Chaetosphaeria fuegiana.

^dex-type strain of Catenularia heimii.

ex-type strain of Phialophora phaeophora.

'ex-type strain of *Chaetosphaeria ciliata*. 9ex-type strain of *Vermiculariopsiella acaciae*. *Morrisiella Saikia & A.K. Sarbhoy 1985 (nom. illegit, Art. 53.1) non Morrisiella Aellen 1938 (Chenopodiaceae).

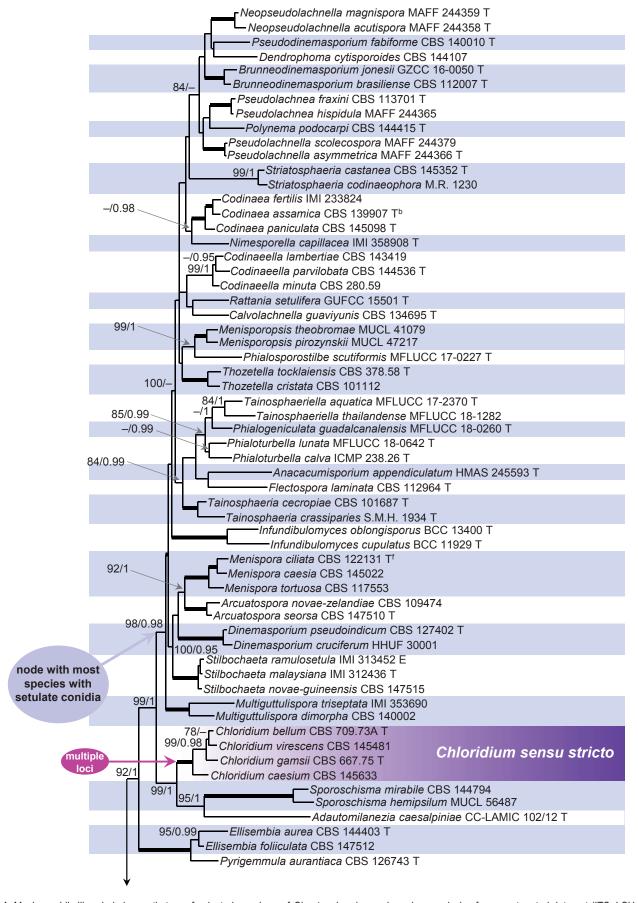


Fig. 1. Maximum Likelihood phylogenetic tree of selected members of *Chaetosphaeriaceae* based on analysis of a concatenated data set (ITS, LSU and *TEF1*). Species names given in bold are taxonomic novelties. The newly obtained strains and strains with novel sequences are printed in bold and blue font. T, E, I and N denote ex-type, ex-epitype, ex-isotype and ex-neotype strains, respectively. Thickened branches indicate branch support with ML BS = 100 % and PP values = 1. Branch support of nodes ≥ 75 % ML BS and ≥ 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 letters 'a–f' after the accession number indicate: ^a holotype of *Chaetosphaeria trianguloconidia*, ^b ex-type strain of *Codinaea acaciae*, ^c ex-type strain of *Chaetosphaeria trianguloconidia*, ^b ex-type strain of *Chaetosphaeria ciliata*.

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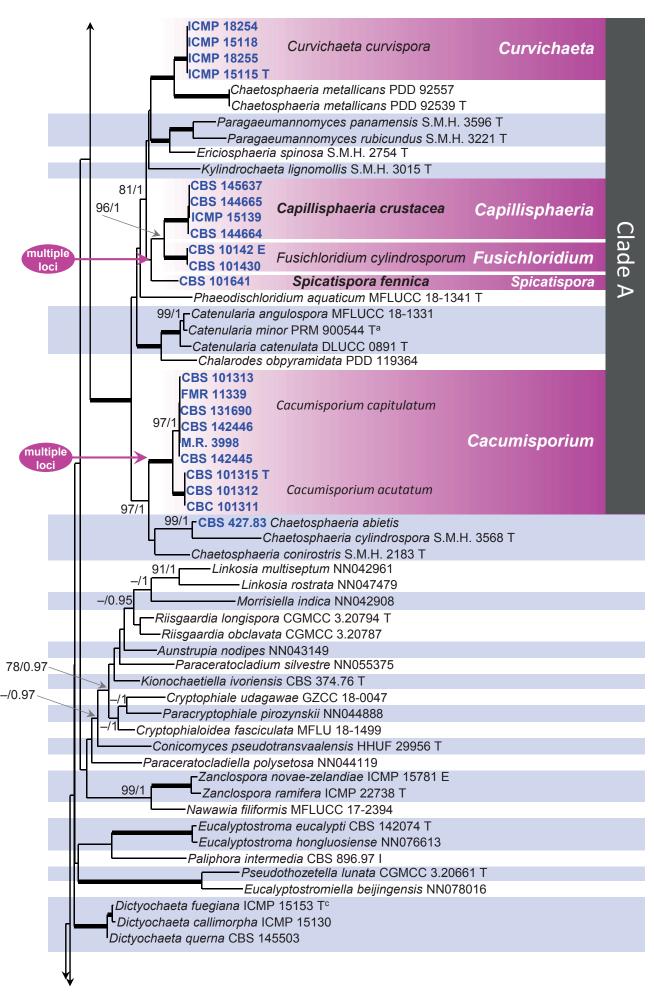


Fig. 1. (Continued).

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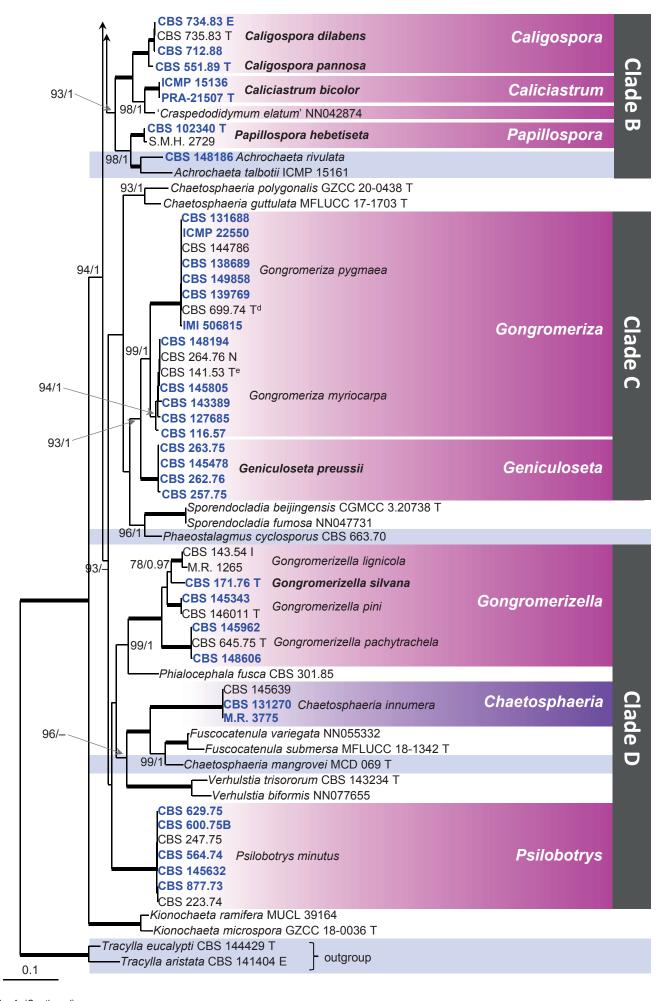


Fig. 1. (Continued).

two strains of an unknown fungus with bicolorous ascospores and a chloridium-like asexual morph. The three later taxa are introduced below as new genera *Caligospora*, *Papillospora* and *Caliciastrum*, respectively.

Clade C (93 % / 1) comprises two genera: Gongromeriza (99 % / 1) with two species, and a sister clade (100 % / 1), which includes four strains of Chaetosphaeria preussii or its chloridium-like asexual morph. To accommodate these strains, a new genus Geniculoseta is proposed. Gongromeriza myriocarpa (94 % / 1) and G. pygmaea (100 % / 1) are well represented in our phylogeny. The ex-type strain of Phialophora phaeophora, CBS 699.74, was found to form a monophyletic clade along with seven other strains of G. pygmaea that were isolated from ascospores. Similarly, the ex-type strain of Catenularia heimii, CBS 141.53, the ex-neotype strain of Sphaeria myriocarpa, CBS 264.76, and five other strains isolated from conidia or ascospores formed a well-supported monophyletic clade.

Clade D is statistically unsupported; however, it contains three chloridium-like genera, such as the monotypic *Chaetosphaeria* and *Psilobotrys*, and *Gongromerizella* (100 % / 1), which comprises four species. The strain CBS 171.76, initially classified as *Chl. lignicola*, forms a separate lineage and is introduced as a new species, *Gongromerizella silvana*.

To elucidate the relationships among chloridium-like species and other related genera within *Vermiculariopsiellales*, a comprehensive phylogenetic analysis was performed using a concatenated data set of ITS-LSU-*TEF1-RPB2* sequences. The ML and BI trees were highly congruent. The ML tree, presented in Fig. 2, illustrates the relationships within *Vermiculariopsiellales*, revealing five monophyletic lineages representing genera *Stephanophorella*, *Tubulicolla*, *Vermiculariopsiella*, and *Vermiculariopsis*. A fifth monophyletic group (86 % / 1) consisting

of five isolates, including the ex-type strains of *Chl. preussii* CBS 230.75 and *Chl. constrictospora* CBS 432.92, as well as three additional non-type strains, has been identified and proposed as two new genera, namely *Chloridiopsiella* (100 % / 1) based on *Chl. preussii*, and *Chloridiopsis* with two species (100 % / 1), *Chs. constrictospora* and *Chs. syzygii* proposed for a strain CBS 564.93 originally identified as *Chl. lignicola*. Two strains (CBS 247.76 and CBS 265.76), initially classified as *Chl. pachytrachelum*, were found to be conspecific with *Cha. preussii*.

TAXONOMY

A total of 14 genera in *Chaetosphaeriales* and *Vermiculariopsiellales* have been identified to manifest the chloridium-like morphotype. These genera were distinguished from *Chloridium* through the use of molecular and morphological studies. Their main characteristics, including arrangement of conidiophores, morphology of phialides, conidia, ascospores and presence and colour of diffusible pigments *in vitro*, are presented in the wheel diagram (Fig. 3). Epitypification is proposed for type species of *Caligospora* and *Fusichloridium*.

Chaetosphaeriales Huhndorf et al., Mycologia 96: 378. 2004.

Chaetosphaeriaceae Réblová et al., Sydowia 51: 56. 1999.

Cacumisporium Preuss, Linnaea 24: 130. 1851.

Type species: Cacumisporium capitulatum (Corda) S. Hughes, Canad. J. Bot. 36: 743. 1958.

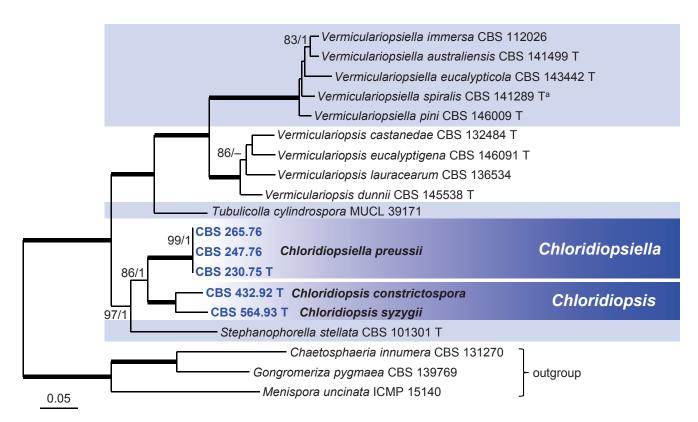


Fig. 2. Maximum Likelihood phylogenetic tree of selected members of *Vermiculariopsiellales* based on analysis of a concatenated data set (ITS, LSU, *RPB2* and *TEF1*). T denotes ex-type strains. The strain with the superscript letter 'a' after the accession number indicates ex-type strain of *Vermiculariopsiella acaciae*. The characteristics are depicted as shown in Fig. 1.

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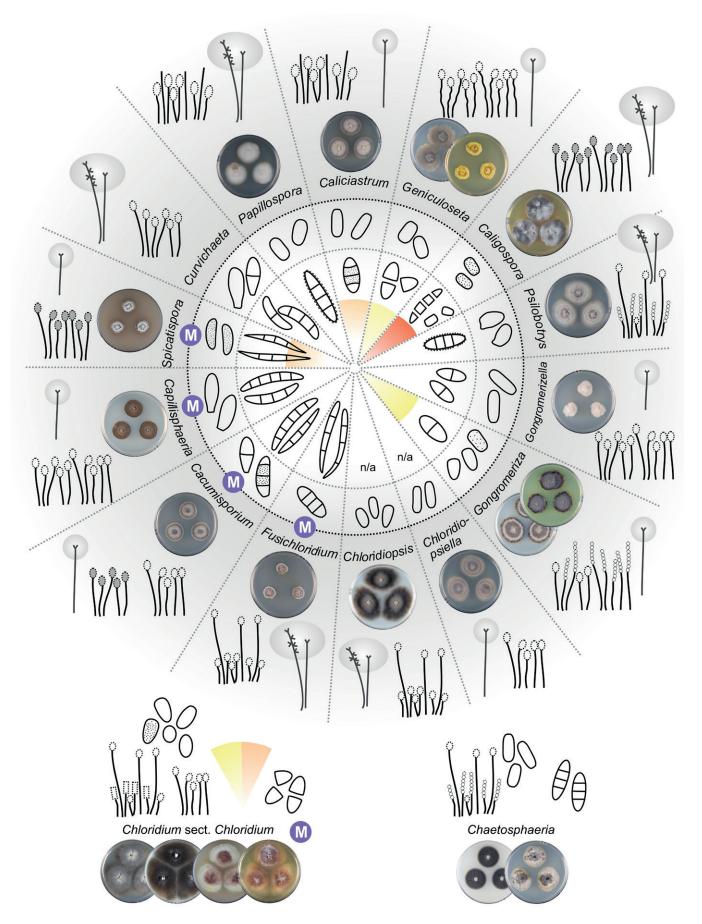


Fig. 3. A wheel diagram illustrating the morphotypes of *Chaetosphaeria*, *Chloridium* sect. *Chloridium*, and 14 chloridium-like genera. The central (white) section of the wheel diagram represents the conidia, ascospores, and pigments formed *in vitro*. The diffusible pigments produced mainly on MLA and OA media are indicated by their respective colours and colony images in the grey section. A blank space in the centre signifies the absence of pigment formation. The outer (grey) section of the wheel depicts the arrangement of conidiophores with setae (if present), the morphology of the phialides (whether they have a terminal or lateral openings), and colony characteristics. The abbreviation 'n/a' is used when specific information is not available. 'M' in bold and a purple circle indicates taxa with phialidic conidiogenesis on multiple loci.

Description: See Goos (1969) and Réblová & Gams (1999).

Accepted species: Cacumisporium acutatum, C. capitulatum, C. tropicale, C. spooneri.

Notes: The current understanding of the genus Cacumisporium (C.) (Wu & Diao 2022) is inconsistent, as it encompasses species with both phialidic and holoblastic-denticulate conidiogenesis. Further details can be found in the Discussion section.

We found two species of the genus *Cacumisporium*, namely *C. acutatum* and *C. capitulatum*. They are both holomorphic and often both sexual and asexual morphs occur together. The conidiogenous phialidic cell is characterized by percurrent extension and production of conidia on multiple conidiogenous loci within a shallow flaring collarette. The tip of the conidiogenous cell contains dense annellations. Because these structures may not always be visible on material from nature, we provide a detailed description and illustration of the conidiogenous cell *in vitro* for further clarification.

Cacumisporium acutatum (Réblová & W. Gams) W.P. Wu & Y.Z. Diao, Fungal Diversity: 116: 336. 2022. Fig. 4A–G.

Basionym: Chaetosphaeria acutata Réblová & W. Gams, Czech Mycol. 51: 9. 1999.

Description: See Réblová & Gams (1999).

Specimens examined: Czech Republic, South Bohemian region, Šumava Mts., glacial cirque of the lake Čertovo jezero near Železná Ruda, on decaying wood of Fagus sylvatica, 28 Aug. 1997, M. Réblová, M.R. 994 (holotype PRM 842979, culture ex-type CBS 101315). France, Pyréneés, Bagnères de Luchon, valle du mont du Lys, on decaying wood of Fagus sylvatica, 13 Jul. 1997, M. Réblová, M.R. 974 (PRA-21501, culture CBS 101312). Ukraine, Eastern Carpathian Mts., Kvasi near Rachiv, on the left bank of the Tisa river, on decaying wood of a branch of Corylus avellana, 26 Jun. 1997, M. Réblová, M.R. 948 (PRA-21502, culture CBS 101311.

Habitat and geographical distribution: Saprobe on decaying wood of deciduous trees, such as *Corylus avellana* and *Fagus sylvatica*, known from the Czech Republic, France, Ukraine (Réblová & Gams 1999, this study).

Notes: Cacumisporium acutatum differs from the closely related C. capitulatum in having smaller, 1-septate, hyaline conidia, (11–12.5–15.5(–16.5) × 4–5 μm and symmetrical, fusiform ascospores that are narrowly rounded at both ends. Conidia of C. capitulatum are 3-septate, bicolorous 15–20 × 5–6.5 μm , ascospores are cylindrical to cylindrical-fusiform, occasionally tapering towards one end.

Cacumisporium capitulatum (Corda) S. Hughes, Canad. J. Bot. 36: 743. 1958. Fig. 4H–M.

Basionym: Helminthosporium capitulatum Corda [as 'Helmisporium'], Icon. fung. 2: 13. 1838.

Synonyms: Acrothecium capitulatum (Corda) Ferraris, Fl. ital. crypt., Fungi 1(8): 454. 1912.

Cacumisporium tenebrosum Preuss, Linnaea 24: 130. 1851.

Acrothecium tenebrosum (Preuss) Sacc., Michelia 1: 74. 1877.

Sphaeria decastyla Cooke, Grevillea 7: 52. 1878.

Acanthostigma decastylum (Cooke) Sacc., Syll. Fung. 2: 210. 1883. Chaetosphaeria decastyla (Cooke) Réblová & W. Gams, Czech Mycol. 51: 19. 1999.

Melanomma macrosporum Sacc., Hedwigia 14: 73, May 1875; see

also Saccardo, Fungi ital. delin. 300. 1878; Michelia 1: 449. 1878. Zignoëlla macrospora (Sacc.) Sacc., Michelia 1: 346. 1878; Syll. Fung. 2: 221. 1883.

Synonymy adopted according to Hughes (1958), Réblová & Gams (1999) and Wu & Diao (2022).

Description: See Réblová & Gams (1999).

Specimens examined: Czech Republic, Central Bohemian region, Křivoklátsko Protected Landscape Area, Karlova Ves, Vysoký Tok Nature Reserve, alt. 540 m, on decaying wood of Quercus sp. associated with Menispora caesia, 29 Sep. 2012, M. Réblová, M.R. 3659 (PRA-21503, culture CBS 142446); Southern Moravian region, Milovice, Milovický les Nature Reserve, on decaying wood of a stump of Quercus sp., 18 Nov. 2010, M. Réblová, M.R. 3598 (PRA-21504, culture CBS 131690); ibid., Lanžhot, Ranšpurk National Nature Reserve, on decaying wood of Carpinus betulus, 26 Oct. 2018, M. Réblová, M.R. 3998 (PRA-21505). France, Central Pyrenees, Bagneres de Luchon, Lys valley, on decaying wood of Fagus sylvatica, 13 Jul. 1997, M. Réblová, M.R. 985 (culture CBS 101313). Italy, Lazio region, Viterbo province, Farnese, Selva di Lamone Nature Reserve, on decaying wood of Quercus cerris, 19 Mar. 2010, M. Réblová, M.R. 3138 (PRA-21506, culture CBS 142445). Spain, Galicia, A Coruña, Fragas do Eume Natural Park, on decaying wood, 13 Oct. 2010, M. Hernández-Restrepo & J. Guarro (culture FMR 11339 = MUCL 53622).

Habitat and geographical distribution: This fungus has been reported as a common saprobe on decaying wood of many hosts, for example Acer sp., Betula papyrifera, Carpinus betulus, Fagus sylvatica, Magnolia sp., Quercus cerris, Quercus sp., and others. It is known from localities in Canada, China, Czech Republic, France, Hungary, Italy, Spain, United Kingdom and the USA (Corda 1838, Rabenhorst 1908, Goos 1969, Holubová-Jechová 1979, Réblová & Gams 1999, Hernández-Restrepo et al. 2017, Wu & Diao 2022).

Notes: Cacumisporium capitulatum is distinguished by the prolonged maturation of 3-septate conidia, which start out hyaline but become partially pigmented with middle cells turning brown and end cells remaining hyaline. The conidia are arranged in slimy heads, which contain both pigmented and hyaline conidia. Molecular data support the close relationship between *C. capitulatum* and *C. acutatum*. However, the two species can be differentiated by their conidia and ascospores. For comparison, see the notes to *C. acutatum*.

Caliciastrum Réblová, gen. nov. MycoBank MB 848559.

Etymology: Calix (L) cup, -astrum (L) somewhat resembling; referring to ascomata that collapse inwards upon drying becoming cup-shaped.

Type species: Caliciastrum bicolor Réblová

Description: Colonies effuse, hairy, dark brown, whitish when sporulating, composed of setae, conidiophores and ascomata. Asexual morph. Setae erect, unbranched, cylindrical, septate, dark brown, terminal cells cylindrical to clavate to slightly inflated, subhyaline to hyaline, always sterile. Conidiophores macronematous, mononematous, solitary, erect, straight or slightly curved, cylindrical, unbranched, brown, paler upwards. Conidiogenous cells monophialidic with a single conidiogenous locus, terminal, integrated, cylindrical, paler than the conidiophores, extending percurrently (sympodially only in culture); collarettes flaring, funnel- to vase-shaped. Conidia ellipsoidal, ellipsoidaloblong to somewhat asymmetrical, hyaline, aseptate, smooth,



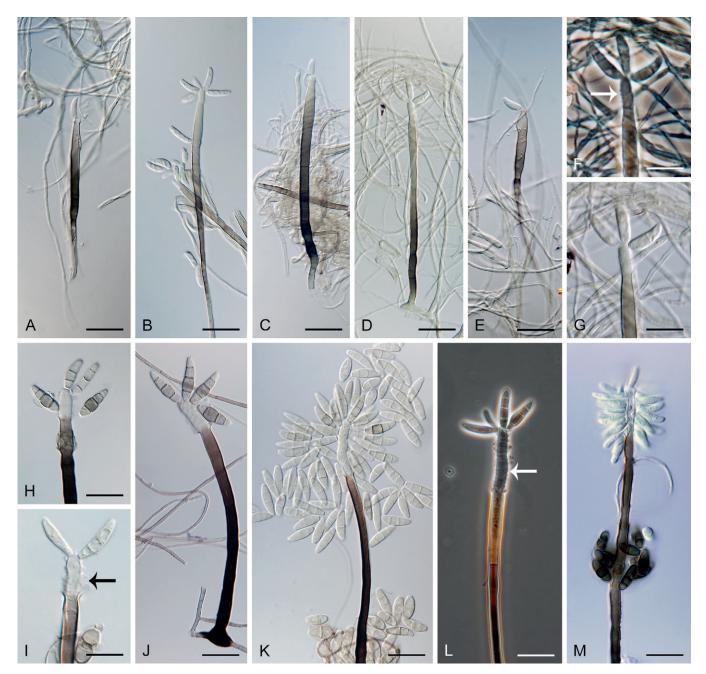


Fig. 4. Cacumisporium spp. on MLA. **A–G.** Cacumisporium acutatum (CBS 101315, ex-type culture). **A–E.** Conidiophores. **F, G.** Phialides. **H–M.** Cacumisporium capitulatum (CBS 142445; arrows indicate minute annellations along the phialide). **H, I.** Phialides. **J–M.** Conidiophores. Scale bars: A–E, J–M = 20 μm; F–I = 10 μm.

adhering in slimy heads. *Chlamydospores* absent. *Sexual morph. Ascomata* perithecial, superficial, non-stromatic, globose to subglobose, collapsing inwards upon drying and becoming cupshaped, dark brown, setose, papillate. Setae are the same as in the asexual morph. Ostiolar canal periphysate. *Ascomatal wall* two-layered, brittle to leathery, carbonaceous. *Paraphyses* persistent, branching, anastomosing. *Asci* unitunicate, cylindrical-clavate, short-stipitate, apical ring non-amyloid, 8-spored. *Ascospores* ellipsoidal-fusiform, transversely septate, hyaline when young, bicolorous at maturity, middle cells pale brown, terminal cells hyaline to subhyaline, dark brown at the septa.

Accepted species: Caliciastrum bicolor.

Notes: The genus Caliciastrum (Cm.), represented by Cm. bicolor, exhibits a close relationship with Caligospora and Craspedodidymum elatum sensu Wu & Diao (2022).

Caliciastrum can be easily distinguished from other members of the family by its distinctive characteristics. One of the key features are ascospores, which are septate and bicolorous. Additionally, the cup-shaped setose ascomata, along with the presence of a chloridium-like asexual form, further contributes to the unique identification of Caliciastrum within the family.

Caliciastrum bicolor Réblová, *sp. nov.* MycoBank MB 849178. Figs 5, 6.

Etymology: Bicolor (L) two-coloured; referring to the colour of ascospores, which are brown with subhyaline end cells.

Typus: **Canada**, British Columbia, Sidney, on decorticated wood of a fallen branch of *Acer macrophyllum*, 10 Nov. 2000, M.E. Barr, M.E.B. 10268 (**holotype** designated here PRA-21507).



Fig. 5. Caliciastrum bicolor. A, B. Ascomata with setae and conidiophores. C. Longitudinal section of the ascomatal wall. D, E. Asci with ascospores. F–J, P–R. Conidiophores. K, L. Setae. M. Conidia. N, O. Phialides (arrows indicate collarettes with a frayed margin). A, C–E. PRA-21507 (holotype). B, F–R. ICMP 15136. A–L, N, O. From nature. M, P–R. On PCA. Scale bars: A, B = 500 μm, C = 50 μm, D–R = 10 μm.

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Fig. 6. Diversity of colony morphology in Caliciastrum bicolor (ICMP 15136) on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. Scale bar = 1 cm.

Description on the natural substrate: Colonies effuse, hairy, dark brown, whitish when sporulating, composed of setae, conidiophores and ascomata. Asexual morph. Setae 80-200(-300) µm long, 4.5-5 µm wide near the bulbous base, erect, unbranched, straight or slightly flexuous, septate, dark brown, thick-walled, gradually paler upwards, cylindrical, terminal cells 16-24 × 5-6 μm, cylindrical to clavate to somewhat inflated, broadly rounded at the top, subhyaline to hyaline, thin-walled, always sterile. Conidiophores 95-200 x 4.5–6 µm, macronematous, mononematous, solitary, erect, straight or slightly curved, cylindrical, septate, unbranched, dark brown, paler upwards, with none to several percurrent proliferations. Conidiogenous cells 18-23.5 \times 4.5-5 μm tapering to 1.5-2 μm below the collarette, monophialidic with a single conidiogenous locus, integrated, terminal, extending percurrently, cylindrical, pale brown, paler towards the tip; collarettes 4-4.5 µm wide, 4-5 µm deep, flaring, funnel- to vase-shaped, pale brown. Conidia 5-6 × $2.5-3 \mu m \text{ (mean } \pm \text{ SD } = 5.6 \pm 0.5 \times 2.9 \pm 0.2 \mu m), \text{ ellipsoidal,}$ ellipsoidal-oblong to somewhat asymmetrical, sometimes slightly apiculate at the base, hyaline, aseptate, smooth, accumulating in slimy whitish heads. Sexual morph. Ascomata perithecial, superficial, non-stromatic, scattered or in groups, globose to subglobose, 175-230(-280) µm diam, 180-240(-260) µm high, collapsing inwards upon drying and becoming cup-shaped, papillate, dark brown, glossy, covered with setae and conidiophores of the asexual morph. Ostiolar canal periphysate. Ascomatal wall leathery to fragile, carbonaceous, 25-36 µm thick, two-layered; outer layer composed of polyhedral, thick-wall, dark brown cells, inner layer of more elongated and narrower, hyaline, thin-walled cells. Paraphyses persistent, 3–4 µm wide tapering to 1.5–2 µm, copious, hyaline, septate, branching sparsely near the base, longer than the asci. Asci (75–)80–93 × 8.5–10 μ m (mean \pm SD = 84.6 \pm $5.5 \times 9.4 \pm 0.6 \,\mu\text{m}$), cylindrical-clavate, obtuse at the apex, shortstipitate, apical ring non-amyloid, ca. 3 µm wide, 1–1.5 µm deep, 8-spored. Ascospores (10.5–)11.5–14 × (4.5–)5–6 μ m (mean \pm SD = $12.8 \pm 0.8 \times 5.1 \pm 0.4 \mu m$), ellipsoidal-fusiform, narrowly rounded at the ends, 3-septate, hyaline when young, bicolorous at maturity while still within the ascus, middle cells pale brown, terminal cells subhyaline, darker at the septa, smooth, obliquely 1-2-seriate in the ascus.

Culture characteristics: On CMD colonies 25–26 mm diam, convex, margin entire, mucoid-waxy, smooth, brown, isabelline at the margin, zonate, reverse pale brown. On MLA colonies 29–30 mm diam, raised, margin entire, velvety, funiculose, becoming mucoid, somewhat furrowed, ivory, pale ochre pigment diffusing into the agar, reverse pale ochre. On OA colonies 27–28 mm diam, flat, margin entire, mucoid-waxy, smooth, beige, isabelline at the margin,

reverse of the same colour. On PCA colonies 22–23 mm diam, flat, margin fimbriate, cobwebby to velvety, whitish-brown, with an outer zone of submerged growth, reverse brown. Sporulation was moderate on PCA and OA, absent on CMD and MLA.

Description in culture: On PCA, colonies effuse, hairy, vegetative hyphae 1–2.5 μm diam, branched, septate, hyaline, smooth. Asexual morph. Conidiophores, conidiogenous cells and conidia are similar to those from nature. Conidiophores 30–95 × 4–5 μm. Conidiogenous cells 20.5–30 × 4–5 μm tapering to 2–2.5 μm below the collarette, extending percurrently, in older cultures (> 4 mo) also sympodially with up to 4–5 lateral openings; collarettes 4–5 μm wide, 4–6(–7) μm deep. Conidia 3.5–6 × 2–2.5(–3) μm (mean ± SD = $4.7 \pm 0.7 \times 2.2 \pm 0.3$ μm), often with a basal scar, thick-walled. Chlamydospores absent. Sexual morph. Not observed.

Additional specimens examined: **Germany**, Baden-Würtemberg, Tübingen, Morgenstelle, on decaying wood of a branch lying on the ground, 17 Mar. 2000, R. Kirschner, Ro.Ki 630. **New Zealand**, West Coast region, Buller district, Victoria Forest Park, Big River Inanganua track *ca.* 14 km SE of Reefton, on decaying wood of a branch of *Nothofagus* sp., 6 Mar. 2003, M. Réblová, M.R. 2733 / NZ 234 (PDD 118699, culture ICMP 15136).

Habitat and geographical distribution: The species thrives on decaying wood and it is known from Canada, Germany and New Zealand.

Notes: Caliciastrum bicolor is characterized by bicolorous, fusiform 3-septate ascospores, setose cup-shaped ascomata and a chloridium-like asexual morph that produces ellipsoidal to asymmetrical conidia on a single locus. The setae have terminal cells that resemble capitate hyphae, but lack an outer gelatinous cap. While Cm. bicolor is somewhat similar to Crassochaeta fusispora (Réblová 1999a), which differs in having larger ascospores (13.5–)15.5–17.5(–19.5) × (4.5–)5–6(–7) µm, setae that are up to 200 µm long, bristle-like, pointed to slightly obtuse at the apex, and conical ascomata that never collapse.

The type collection of *Cm. bicolor* was selected from mature and well-developed material from Canada, but the living culture is no longer viable. A New Zealand specimen containing ascomata with mostly immature ascospores, but accompanied with well-developed conidiophores and conidia, was used to derive the living culture ICMP 15136. The ascospores were mostly hyaline with 1–3 septa (12.5–14.5 \times 3.5–4 μm), although several ascospores matured and were seen outside the asci. However, this material could not be considered for epitypification due to its different geographic origin. The available LSU rDNA sequences from the holotype PRA-21507 and ICMP 15136 are identical.

Caligospora Réblová, gen. nov. MycoBank MB 848560.

Etymology: Caligo (L) darkness, gloom, spora (L); in reference to pigmented conidia.

Type species: Caligospora dilabens (Réblová & W. Gams) Réblová

Description: Colonies effuse, hairy, dark brown, composed of conidiophores and ascomata. Asexual morph. Conidiophores macronematous, mononematous, solitary, erect, straight or curved, cylindrical, unbranched, brown, paler upwards. Conidiogenous cells monophialidic with a single conidiogenous locus, terminal, integrated, cylindrical to elongated lageniform, paler than the conidiophores, extending percurrently and sympodially; collarettes flaring, campanulate, often with a frayed margin. Conidia ellipsoidal to somewhat asymmetrical, pale brown, aseptate, smooth, adhering in slimy heads. Chlamydospores absent. Sexual morph. Ascomata perithecial, superficial, sitting on a thin basal stroma, globose to subglobose, dark brown, glabrous, papillate. Ostiolar canal periphysate. Ascomatal wall two-layered, brittle, carbonaceous. Paraphyses persistent, branching, anastomosing. Asci unitunicate, cylindrical-clavate, short-stipitate, apical ring nonamyloid, 8-spored. Ascospores fusiform, transversely septate, with the cells separating into part-spores at an early stage within the ascus, hyaline.

Accepted species: Caligospora dilabens, Ca. pannosa.

Notes: The genus Caligospora (Ca.) is proposed to include species with chloridium-like asexual morphs, glabrous mostly globose ascomata, hyaline, septate ascospores fragmenting into part spores and brown, ellipsoidal to somewhat asymmetrical conidia formed within a campanulate collarette on a single conidiogenous locus. Both Caligospora species produce deep orange pigment on MLA and ochre on OA. In older MLA cultures (> 3 mo), the orange colour is becoming more intense (Fig. 8). For comparison of Caligospora with similar fungi with pigmented conidia, see Discussion.

Caligospora dilabens (Réblová & W. Gams) Réblová, comb. nov. MycoBank MB 849179. Figs 7, 8.

Basionym: Chaetosphaeria dilabens Réblová & W. Gams, Mycoscience 41: 130. 2000.

Description: See Réblová & Gams (2000).

Typus: Japan, Kyoto, Daitokuji Temple, on stem of Bambusa sp., 28 Aug. 1983, W. Gams & M. Tsuda (holotype CBS H-3524, culture ex-type CBS 735.83); Kyoto, Daitokuji Temple, on stem of Bambusa sp., 28 Aug. 1983, W. Gams & M. Tsuda (epitype designated here MBT 10014168, PRA-21508 as a dried culture, culture ex-epitype CBS 734.83).

Culture characteristics: On CMD colonies 27–29 mm diam, circular, flat, margin entire, lanose to cobwebby, floccose, funiculose at the inoculation block becoming mucoid, brown, whitish-beige centrally, isabelline at the margin, reverse brown. On MLA colonies 46–50 mm diam, circular, flat, margin raised, margin entire to fimbriate, lanose, floccose, zonate, dark grey with pale grey zones, beige at the margin, aerial mycelium with numerous colourless exudates, orange pigment diffusing into the agar, reverse orange. On OA colonies 39–41 mm diam, circular, flat, margin entire, velvety, floccose, powdery, anthracite, sometimes overgrown by white aerial hyphae, with an olivaceous grey outer zone of submerged growth, ochre pigment diffusing into the agar, reverse ochre-beige. On PCA

colonies 40–41 mm diam, circular, flat, margin weakly fimbriate, powdery, dark brown to black-brown, sometimes overgrown by white aerial hyphae, pale yellow pigment diffusing into the agar, reverse isabelline to brown. Sporulation was abundant on all media.

Additional specimen examined: Japan, Kyoto, Arashiyama, on dead stem of bamboo, Aug. 1988, W. Gams (CBS-H 4389, culture CBS 712.88).

Habitat and geographical distribution: Saprobe on dead bamboo culm, known from Japan (Réblová & Gams 2000).

Notes: Caligospora dilabens closely resembles Ca. pannosa, and it is challenging to distinguish them in culture. For comparison of both species, see notes to Ca. pannosa.

Since the ex-type culture of *Ca. dilabens* CBS 735.83 is no longer available (G. Verkleij, pers. com.), an epitype strain CBS 734.83 was selected. It was collected from the same site, substrate, and date as the original ex-type strain.

Caligospora pannosa Réblová, *sp. nov.* MycoBank MB 849180. Figs 8, 9.

Etymology: Pannosus (L) ragged, frayed; referring to the frayed margin of the collarette.

Typus: **Brazil**, Pará, 200 km south-east of Belém, on washed root of *Theobroma cacao*, date unknown, L. Pfenning, R 129 (**holotype** designated here CBS H-10186, **isotype** designated here PRA-21509 as dried culture, culture ex-type CBS 551.89).

Culture characteristics: On CMD colonies 28–30 mm diam, circular, flat, margin entire, velvety-lanose, dark grey-brown, beige towards the margin, reverse of similar colour. On MLA colonies 34–35 mm diam, circular, convex, flat margin, margin entire, finely furrowed, velvety, dark grey to black, partly whitish due to sporulating conidiophores with conidial masses, with an ochre-beige outer zone of submerged growth, orange pigment diffusing into the agar, reverse ochre-beige. On OA colonies 38–39 mm diam, circular, flat, margin entire, velvety, dark grey to almost black, becoming beige-grey when sporulating, with a whitish to isabelline outer zone of submerged growth, reverse dark grey. On PCA colonies 35–36 mm diam, circular, convex centrally, margin flat, margin fimbriate, lanose, floccose, cobwebby at the margin, dark brown centrally, beige with irregular dark brown spots at the margin, reverse dark grey. Sporulation was abundant on all media.

Description in culture: On CMA with Urtica sp. stems, colonies effuse, hairy, vegetative hyphae 1.5-2.5 µm diam, branched, septate, hyaline, smooth, becoming brown and often encrusted. Asexual *morph.* Conidiophores 35–140 × 2.5–3 μm, macronematous, solitary, erect, straight or slightly flexuous, cylindrical, unbranched, brown, paler towards the apex. Conidiogenous cells 23-29 × 3.5-5 μm, tapering to ca. 1.5 μm below the collarette, monophialidic, rarely polyphialidic, with a single conidiogenous locus, integrated, terminal, extending percurrently, rarely sympodially with 1-2(-3) lateral openings, subcylindrical, slightly inflated in the upper part, pale brown, paler towards the apex; collarettes 4.5–5.5 µm wide, 3–3.5 µm deep, flaring, campanulate with a frayed margin, darker. Conidia $3.5-5 \times 2-2.5 \, \mu \text{m}$ (mean $\pm \text{SD} = 4.2 \pm 0.4 \times 2.3 \pm 0.1 \, \mu \text{m}$), ellipsoidal to oblong to somewhat asymmetrical, sometimes slightly tapering towards the base, brown, aseptate, smooth, adhering in slimy dark brown to black heads. Chlamydospores absent. Sexual morph. Not observed.

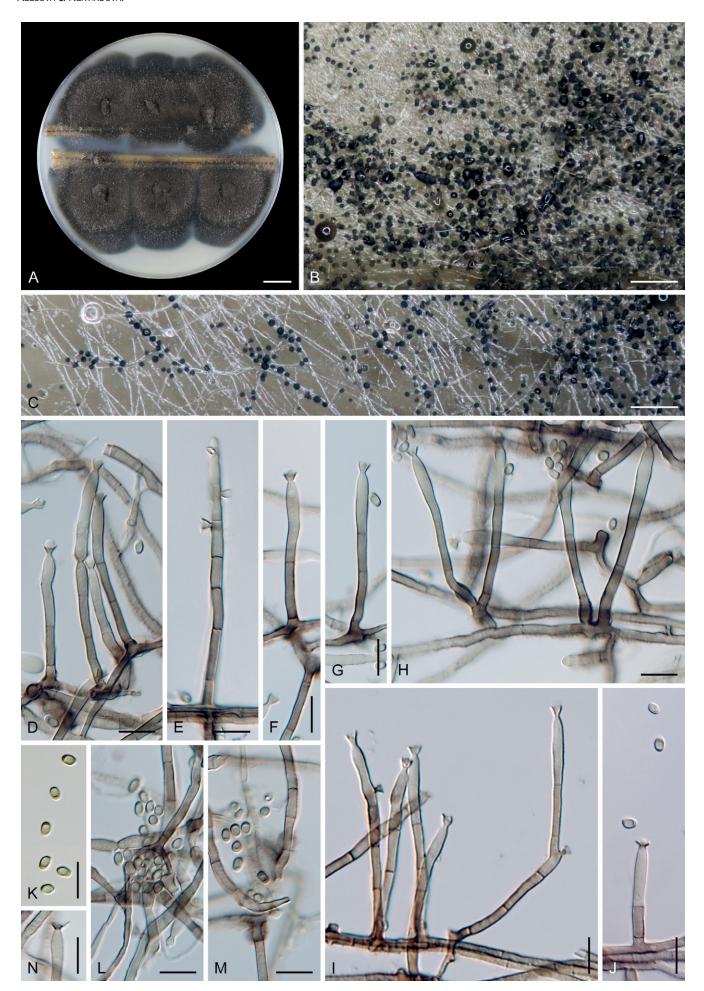


Fig. 7. Caligospora dilabens (CBS 734.83, ex-epitype culture). A. Colonies. B, C. Sporulating conidiophores. D–J. Conidiophores. K–M. Conidia. N. Upper part of the phialide with a collarette. A–C. On CMA with *Urtica* stems. D–N. On PCA. Scale bars: A = 1 cm; B, C = 500 μ m; D–N = 10 μ m.



Fig. 8. A–C. Diversity of colony morphology in *Caligospora* spp. on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. **D, E.** Colonies of *Caligospora* spp. on MLA after 3 mo showing diffusible orange pigment production. A, B, D. *Caligospora dilabens* (A, D. CBS 712.88; B. CBS 734.83, exepitype culture). C, E. *Caligospora pannosa* (CBS 551.89, ex-type culture). All cultures were photographed on a black surface except for the photos on the right of D and E, which were photographed on a white surface. Scale bar = 1 cm.

Habitat and geographical distribution: Saprobe on root of Theobroma cacao, known only from Brazil.

Notes: The strain CBS 551.89, isolated from the root of *Theobroma cacao* in Brazil, was initially included among strains of *Ca. dilabens*, which is only known to be found on dead bamboo in Japan (Réblová & Gams 2000, this study). In culture, it closely resembled *Ca. dilabens* represented by three strains (CBS 712.88, CBS 734.83, and CBS 735.83). However, CBS 551.89 forms longer conidiophores (35–140 μm *vs.* 35–72 μm), wider campanulate collarettes (4.5–5.5 μm *vs.* 3–4.5 μm) with a noticeably frayed margin and somewhat more oblong conidia, while in *Ca. dilabens* the margin is either smooth or indistinctly frayed and conidia are more ellipsoidal. Although a comparison of their ribosomal DNA sequences revealed a moderate (98.9 % in ITS) and high (99.8 % in LSU) degree of sequence identity, the sequences of the protein

coding gene differed significantly (97.8 % in *TEF1*), which indicates that CBS 551.89 is a distinct species. Therefore, we introduce this isolate as a new species and recommend that accurate identification of both *Caligospora* species can be achieved through the use of dual barcodes, namely ITS and *TEF1*.

Capillisphaeria Réblová, gen. nov. MycoBank MB 848561.

Etymology: Capillus (L) hair, bristle, sphaeria (L); referring to setose ascomata.

Type species: Capillisphaeria crustacea (Sacc.) Réblová

Description: Colonies effuse, hairy, dark brown, whitish when sporulating, composed of conidiophores and ascomata. Asexual morph. Conidiophores macronematous, mononematous, solitary,

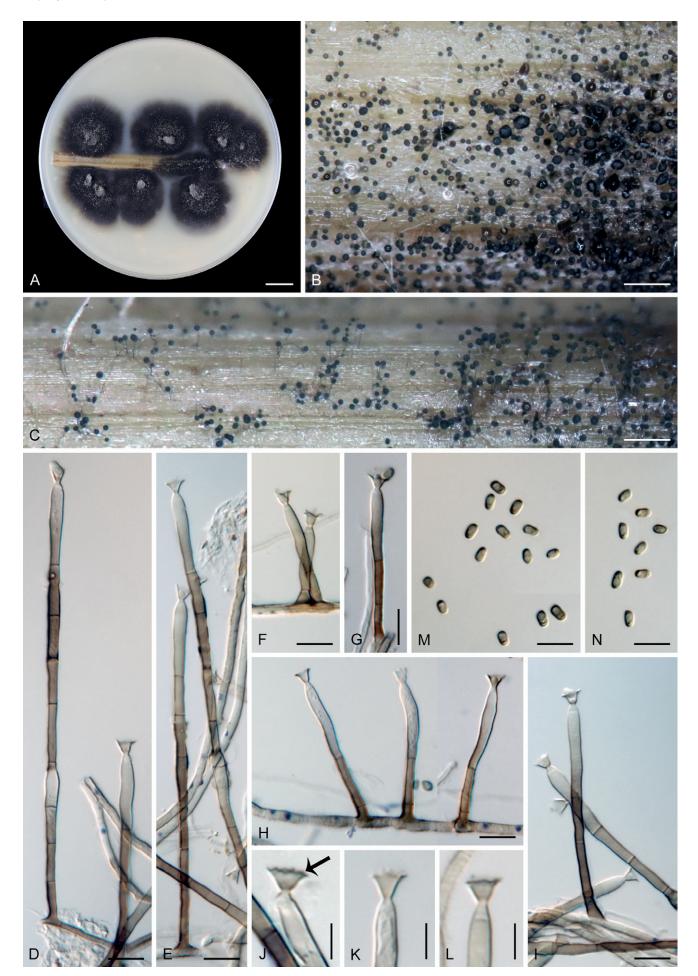


Fig. 9. Caligospora pannosa (CBS 551.89, ex-type culture). A. Colonies. B, C. Sporulating conidiophores. D–I. Conidiophores. J–L. Upper part of the conidiogenous cell with a collarette (arrow indicates collarette with a frayed margin). M, N. Conidia. A–C. On CMA with *Urtica* stem. D–N. On PCA. Scale bars: A = 1 cm; B, C = 500 μ m; D–I, M, N = 10 μ m; J–L = 20 μ m.

erect, straight or slightly flexuous, cylindrical, unbranched, brown, with percurrent proliferations. Conidiogenous cells monophialidic with a single conidiogenous locus, terminal, integrated, cylindrical, paler than the conidiophores, extending percurrently, the tip of the conidiogenous cell extends above the collarette with minute annellations; collarettes flaring, funnel-shaped, hyaline to pale brown. Conidia cylindrical-clavate or ellipsoidal-oblong, asymmetrical with a basal scar, tapering towards the base, straight or gently curved, hyaline, aseptate, smooth, adhering in slimy heads. Chlamydospores absent. Sexual morph. Ascomata perithecial, superficial, non-stromatic, globose to subglobose, dark brown, setose, papillate. Setae erect, unbranched, bristlelike, scattered, dark brown, obtuse apically, always sterile. Ostiolar canal periphysate. Ascomatal wall two-layered, brittle, carbonaceous. *Paraphyses* persistent, branching, anastomosing. Asci unitunicate, cylindrical-clavate, short-stipitate, apical ring nonamyloid, 8-spored. Ascospores cylindrical-fusiform, transversely septate, hyaline.

Accepted species: Capillisphaeria crustacea.

Notes: The genus Capillisphaeria (Cp.), based on Chaetosphaeria crustacea (Réblová & Gams 1999), accommodates fungi with setose ascomata, septate, hyaline, non-fragmenting cylindrical ascospores and hyaline, aseptate, asymmetrical conidia with a basal scar. Conidia are formed on phialides with multiple growing points, often with the protruding tip with visible annellations. Its closest relatives are Fusichloridium and Spicatispora in Clade A in Chaetosphaeriaceae.

Capillisphaeria crustacea (Sacc.) Réblová, comb. nov. MycoBank MB 849181. Fig. 10.

Basionym: Zignoëlla crustacea Sacc., Syll. Fung. 2: 220. 1883. Synonyms: Sphaeria crustacea P. Karst., Fungi fenn. exs. 865. 1869 (nom. illegit., Art. 53.1); Bidr. Kann. Finl. Nat. Folk. 23: 95. 1873. [non Sphaeria crustacea Sow., Col. Fig. Engl. Fung. 1: Tab. 372, fig. 3. Pl. 372. 1803 = Jackrogersella multiformis (Fr.) L. Wendt, Kuhnert & M. Stadler, Mycol. Prog. 17: 138. 2017.] Chaetosphaeria crustacea (Sacc.) Réblová & W. Gams, Czech. Mycol. 51: 12. 1999.

Description: See Réblová & Gams (1999).

Culture characteristics: On CMD colonies 11–15 mm diam, convex, margin entire, cobwebby, dark grey becoming whitish grey due to conidial masses, margin olivaceous grey, reverse olivaceous grey. On MLA colonies 15–18 mm diam, convex, flat margin, velvety, floccose, dark grey, margin anthracite, reverse anthracite. On OA colonies 10–14 mm diam, flat, margin somewhat undulate, velvety, brown-grey, reverse dark grey. On PCA colonies 12–14 mm diam, flat, margin undulate, cobwebby to velvety, olivaceous brown, becoming whitish-brown due to conidial masses, reverse anthracite. Sporulation was abundant on CMD, OA and PCA, absent on MLA.

Specimens examined: Czech Republic, South Bohemian region, Šumava Mts. National park, Železná Ruda, glacial cirque of the lake Černé jezero, alt. 1 025 m, on wood of *Abies alba*, 7 Nov. 1997, K. Prášil, M.R. 1169 (PRA-21510, culture CBS 101321); South Bohemian region, Šumava Mts. National park, Zátoň, Boubínský prales National nature Reserve, on decaying wood of *Picea abies*, 29 Aug. 2000, M. Réblová, M.R. 2454 (PRA-21516); South Bohemian region, Novohradské hory Mts., Dobrá voda, Hojná voda National Nature Monument, alt. 875 m, on decaying

wood of Picea abies, 29 Sep. 2017, M. Réblová, M.R. 3907 (PRA-21511, culture CBS 144664); ibid., M.R. 3923 (PRA-21512, culture CBS 144665); Pardubice region. Železné hory Mts. Protected Landscape Area. Horní Bradlo, Malá Střítež settlement, Polom National Nature Reserve, alt. 600 m, on decaying wood of Abies alba associated with Menispora caesia, Cheiromycella microscopica, 10 Nov. 2018, M. Réblová, M.R. 4065 (PRA-21513, culture CBS 145637). Finland, Ostrobottnia, Vaasa, on Pinus sylvestris, unknown collection date, P.A. Karsten (lectotype of Zignoëlla crustacea, Fung. Fenn. exsicc. 865, H). New Zealand, West Coast region, Westland district, Saltwater Forest, Wanganui River valley ca. 25 km W of Harihari, on decaying wood, 7 Mar. 2003, M. Réblová, M.R. 2750 / NZ 253 (PDD 81880, culture ICMP 15139). Ukraine, Eastern Carpathian Mts., Kvasi near Rachiv, on left bank of the river Tisa, on decaying wood of Picea abies, 26 Jun. 1997, M. Réblová & K. Prášil, M.R. 996 (PRA-21514, culture CBS 101316); Eastern Carpathian Mts., Sinevirskaja Polana Massif, Sinevir lake, on decaying wood of Picea abies, 20 Jul. 1998, M. Réblová, M.R. 1271 (PRA-21515).

Habitat and geographical distribution: Saprobe on decaying wood of coniferous trees such as Abies alba, Picea abies and Pinus sylvestris, known from the Czech Republic, Finland, New Zealand and Ukraine (Réblová & Gams 1999, this study).

Notes: Capillisphaeria crustacea is characterized by aseptate, hyaline, cylindrical-clavate, often asymmetrical conidia with a truncate base and cylindrical-fusiform, gently curved ascospores that vary in the number of septa (1–5) and setose ascomata. Its closest relative, Fusichloridium cylindrosporum (Gams & Holubová-Jechová 1976, Réblová & Gams 1999), differs in having septate conidia, conidiophores forming two layers on the natural substrate and asymmetrical ascospores, which are tapering towards the base.

Capillisphaeria crustacea and Curvichaeta (Cu.) curvispora share a striking similarity, and while they were identified as separate genera in Clade A, they have both asexual and sexual morphs that make it difficult to distinguish between them. However, there are some differences that set them apart. For example, Cu. curvispora has longer and wider ellipsoidal to oblong conidia that are formed with a delayed middle septum, $17.5-20 \times 4.5-5 \mu m$, on multiple conidiogenous loci vs. aseptate conidia $(11.5-)14.5-17(-21) \times 3-4.5 \mu m$ formed on a single locus, and shorter, wider ascospores $19-22 \times 4-5 \mu m$ vs. $(15.5-)19-26(-28) \times 3-3.5(-4) \mu m$, respectively (see also Gams & Réblová 1999, Réblová 2004). Additionally, Cu. curvispora has glabrous ascomata, while Cp. crustacea does not.

Fusichloridium W.P. Wu & Y.Z. Diao, Fungal Diversity 116: 282.

Type species: Fusichloridium cylindrosporum (W. Gams & Hol.-Jech.) Réblová

Description: See Wu & Diao (2022).

Accepted species: Fusichloridium cylindrosporum.

Fusichloridium cylindrosporum (W. Gams & Hol.-Jech.) Réblová, Stud. Mycol. 103: 198. 2022.

Basionym: Chloridium cylindrosporum W. Gams & Hol.-Jech., Stud. Mycol. 13: 46. 1976.

Synonyms: Chaetopsis cylindrospora (W. Gams & Hol.-Jech.) DiCosmo et al., Mycologia 75: 962. 1983.

Chaetosphaeria fusiformis W. Gams & Hol.-Jech., Mycotaxon 13: 257. 1981.

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Fig. 10. Capillisphaeria crustacea. A–C. Conidiophores. D–F. Phialides with a conidiogenous locus protruding above the collarette. G–I. Conidia. J. Colonies of CBS 145637 on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. A, I. CBS 144664 on MLA. B–H. ICMP 15139 on PCA. Scale bars: $A-I=10 \mu m$; J=1 cm.

Fusichloridium fusiforme (W. Gams & Hol.-Jech.) W.P. Wu & Y.Z Diao, Fungal Diversity 116: 282. 2022. Additional synonyms are listed in Réblová *et al.* (2022).

Typus: Czech Republic, Olomouc region, Hrubý Jeseník Mts., Mt. Mravenečník, alt. 1 344 m, on Abies alba, 3 Aug. 1971, V. Holubová-Jechová (holotype PRM 794008); Southern Bohemian region, Šumava Mts., Železná Ruda, glacial cirque of the lake Černé jezero, on inner surface of bark of Abies alba, 27 Aug. 1997, M. Réblová, M.R. 1048 (epitype designated here MBT 10014169, PRA-21518, culture ex-epitype CBS 101429).

Description: See Gams & Holubová-Jechová (1976) and Réblová & Gams (1999).

Additional specimen examined: **Czech Republic**, Southern Bohemian region, Šumava Mts., Železná Ruda, glacial cirque of the lake Černé jezero, on inner surface of bark of *Abies alba*, 27 Aug. 1997, M. Réblová, M.R. 1049 (PRA-21519, culture CBS 101430).

Habitat and geographical distribution: Saprobe on bark and wood of Abies alba, known from the Czech Republic (Gams & Holubová-Jechová 1976, Réblová & Gams 1999).

Notes: Fusichloridium cylindrosporum is an uncommon species found solely on decaying bark and wood of Abies alba. Its distinguishing features include cylindrical-fusiform ascospores that frequently taper towards the basal end, as well as phialides with multiple loci producing cylindrical, centrally slightly constricted,

hyaline conidia that taper towards the ends. The conidia adhere in star-like heads; they have a basal scar and possess three septa. These distinctive characteristics serve to differentiate *F. cylindrosporum* from other closely related taxa, such as *Capillisphaeria crustacea* and *Spicatispora fennica*.

Geniculoseta Réblová, gen. nov. MycoBank MB 848563.

Etymology: Geniculātus (L) derived from geniculum (little knee), bended, curved, knotty, geniculated, seta (L) bristle, hair; referring to the geniculated conidiophores.

Type species: Geniculoseta preussii (W. Gams & Hol.-Jech.) Réblová

Description: Colonies effuse, hairy, dark brown to dark reddishbrown becoming whitish to beige when sporulating, composed of ascomata and conidiophores. Asexual morph. Conidiophores macronematous, mononematous, erect, solitary, scattered, crowded, or caespitose, cylindrical, unbranched, brown to dark reddish-brown, with several percurrent proliferations. Conidiogenous cells monophialidic with a single conidiogenous locus, integrated, terminal, rarely discrete, lateral, subulate or narrowly lageniform, pale brown, paler than the conidiophores, extending percurrently; collarettes flaring, funnel-shaped. Conidia ellipsoidal to oblong, hyaline, aseptate, smooth, accumulating in slimy heads. Chlamydospores absent. Sexual morph. Ascomata perithecial, superficial, non-stromatic, subglobose, smooth, black, sometimes with a subiculum, papillate. Ostiolar canal periphysate. Ascomatal wall two-layered, fragile, carbonaceous. Paraphyses persistent, hyaline, septate, branched. Asci unitunicate, cylindrical, shortly stipitate, apical ring non-amyloid, 8-spored. Ascospores ellipsoidal to cylindrical, transversely septate, fragmenting into part spores, hyaline.

Accepted species: Geniculoseta preussii.

Notes: Four strains of Chaetosphaeria preussii were shown to be morphologically different and distantly related to its presumed asexual morph, Chloridium preussii (Gams & Holubová-Jechová 1976). Therefore, new taxonomic treatments were proposed for these two fungi. The genus Geniculoseta (Ge.) is erected for Chaetosphaeria preussii in Chaetosphaeriales, and Chl. preussii is transferred to the genus Chloridiopsiella in Vermiculariopsiellales.

Geniculoseta preussii (W. Gams & Hol.-Jech.) Réblová, comb. nov. MycoBank MB 849185. Figs 11, 12.

Basionym: Chaetosphaeria preussii W. Gams & Hol.-Jech., Stud. Mycol. 13: 34. 1976.

Description on the natural substrate: Colonies effuse, hairy, dark reddish-brown, whitish to beige when sporulating, composed of ascomata and conidiophores. Asexual morph. Conidiophores 50–157 × 2.5–3.5(–4) μm, bulbous at the base 5–10(–12) μm diam, macronematous, solitary, scattered, crowded or caespitose, erect, flexuous, subulately tapering, unbranched, brown to dark reddish-brown, paler towards the apex, with 1–5 percurrent proliferations assuming a geniculate appearance. Conidiogenous cells 11.5–20(–29) × 2.5–3.5 tapering to ca. 1.5 μm below the collarette, monophialidic with a single conidiogenous locus, integrated, terminal, rarely discrete, lateral, extending percurrently, subulate or narrowly lageniform, pale brown, paler towards the tip;

collarettes 2–3.5 µm wide, 1–1.5 µm deep, flaring, funnel-shaped, pale brown. Conidia 2.5–3.5 × 1.5–2 μ m (mean \pm SD = 2.9 \pm 0.2 \times 1.8 \pm 0.3 μ m), ellipsoidal to oblong, hyaline, aseptate, smooth, accumulating in slimy beige to pale brown heads. Sexual morph. Ascomata perithecial, superficial, non-stromatic, subglobose, papillate, smooth, black, glossy, sometimes surrounded by a dense mat of dark hyphae, 140–220 µm diam. Ostiolar canal periphysate. Ascomatal wall fragile, carbonaceous, 7-15(-18) µm thick, twolayered; outer layer composed of opaque, very thick-walled cells of textura epidermoidea, inner layer of more elongated and thin-walled hyaline cells. Paraphyses persistent, hyaline, septate, sparsely branched, 2.5–3 µm tapering to ca. 1.5 µm, longer than the asci. Asci 45–55 × 3.5–4 µm, cylindrical, shortly stipitate, apex broadly rounded, apical ring non-amyloid, 1.5–2 μm wide and ca. 1 μm high, 8-spored. Ascospores 5.5–7 \times 2–2.5 µm (mean \pm SD = 6.3 \pm $0.4 \times 2.4 \pm 0.2 \,\mu\text{m}$), cylindrical to ellipsoidal, 1-septate, fragmenting into part spores 2.5-4(-4.5) μ m long (mean \pm SD = 3.4 \pm 0.4 \times $2.2 \pm 0.2 \,\mu\text{m}$), which are sometimes slightly asymmetrical, hyaline, smooth, obliquely 1-seriate within the ascus. (Characteristics of the sexual morph were partly adopted according to Gams & Holubová-Jechová 1976).

Culture characteristics: On CMD colonies 18–20 mm diam, circular, flat to slightly convex, margin fimbriate, cobwebby to velvety-lanose, sometimes mucoid towards the periphery, whitish, beige to olivaceous grey, reverse isabelline to dark grey. On MLA colonies 24–43 mm diam, circular, slightly convex, somewhat furrowed at the centre, margin entire to fimbriate, cobwebby to velvety-lanose, floccose, whitish-grey, sometimes dark brown or with a dark brown centre, rarely yellow, occasionally a fine yellow pigment diffusing into the agar, reverse dark beige. On OA colonies 24–35 mm diam, circular, flat, margin fimbriate, velvety becoming cobwebby at the margin, beige, olivaceous grey to dark brown, reverse dark brown. On PCA colonies 20–38 mm diam, circular, flat to slightly raised, margin entire to somewhat undulate, velvety-lanose to cobwebby, ivory, beige to grey-brown, reverse grey-brown. Sporulation was abundant on CMD and PCA, moderate on OA and MLA.

Description in culture: On MLA, colonies effuse, hairy, vegetative hyphae 1–2.5 µm diam, branched, septate, hyaline to subhyaline, smooth, sometimes becoming pale brown and encrusted. Asexual morph. Conidiophores, conidiogenous cells and conidia are similar to those from nature. Conidiophores 55–153 \times 2.5–3.5 µm, often with 2–4 percurrent proliferations and with up to 6–10 percurrent proliferations in older cultures (> 6–8 wk), basal part occasionally encrusted. Conidiogenous cells 8–25(–29) \times 1.5–2.5(–3) µm tapering to ca. 1.5 µm, monophialidic, terminal, integrated; collarettes 2.5–3.5 µm wide, 0.5–1.5 µm deep, flaring, broadly funnel-shaped to almost saucer-shaped, darker than the phialide. Conidia (2–)2.5–3(–3.5) \times 1.5–2 µm (mean \pm SD = 2.7 \pm 0.3 \times 1.7 \pm 0.2 µm), adhering in slimy whitish heads. Chlamydospores absent. Sexual morph. Not observed.

Specimens examined: Czech Republic, Central Bohemian region, Lánská obora, Píně, alt. 400 m, on decaying bark of Quercus sp., 14 Apr. 1997, M. Réblová, M.R. 925 (PRA-21520); Olomouc region, Hrubý Jeseník Mts., on the northwest slopes of Mt. Mravenečník near Loučná nad Desnou, on decaying wood of Fagus sylvatica, 3 Aug. 1971, V. Holubová-Jechová (PRM 794010); South Bohemian region, Novohradské hory Mts., Dobrá voda, Hojná voda National Nature Monument, alt. 850 m, on decaying cupule of Fagus sylvatica associated with Dictyochaeta montana, 27 Sep. 2018, M. Réblová, M.R. 3959 (PRA-21521, culture CBS 145478); Ústecký region, on the slopes of Běšický chochol Mt., alt. 350 m, between villages

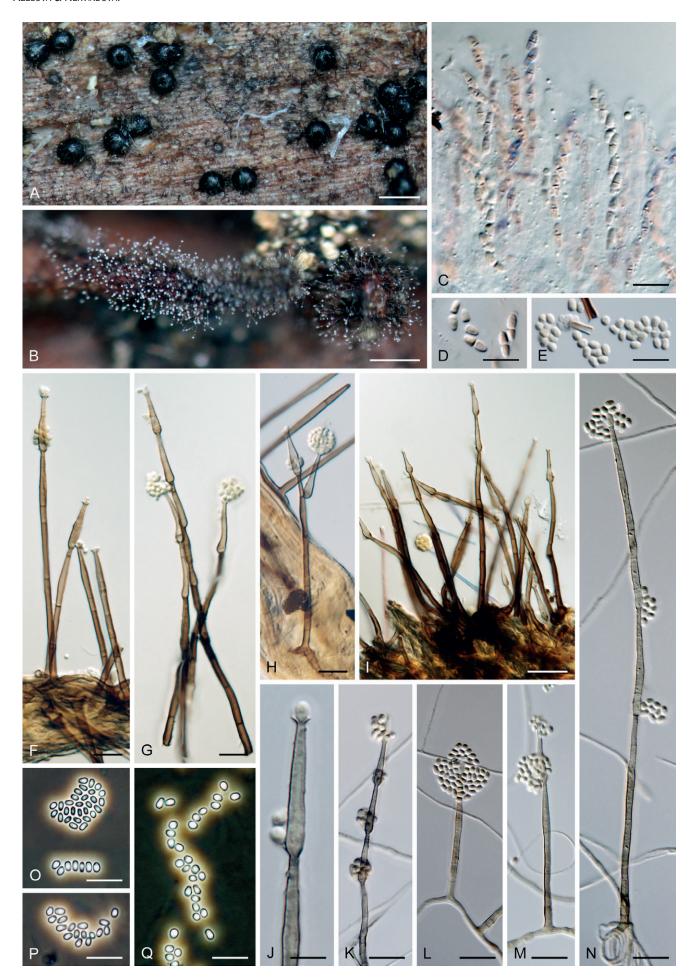


Fig. 11. Geniculoseta preussii. A. Ascomata. B. Sporulating conidiophores. C. Asci. D, E. Ascospores fragmenting into part spores. F–N. Conidiophores. O–Q. Conidia. A, C–E, I. PRM 796750, holotype of *Chaetosphaeria preussii*. B, F–H, J–Q. CBS 145478. A–I. From nature. J–Q. On PCA. Scale bars: A, B = 500 μ m; C–H, K–Q = 10 μ m; I = 20 μ m; J = 5 μ m.

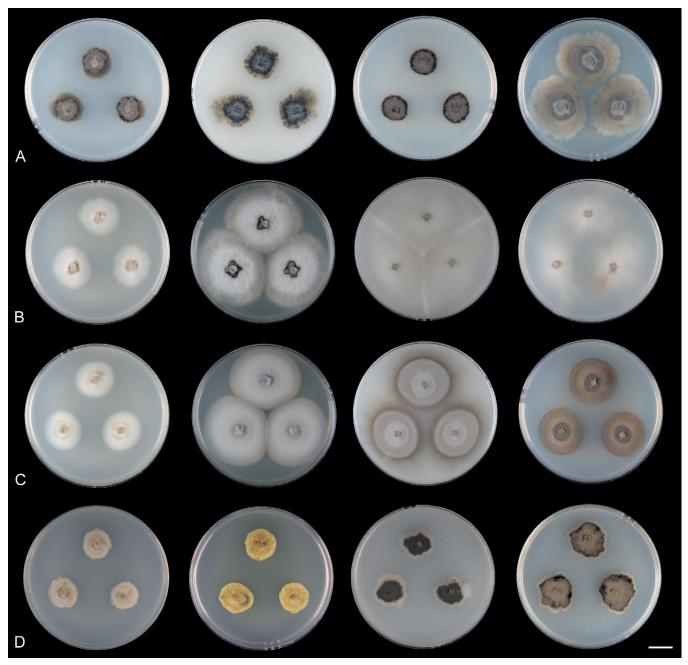


Fig. 12. Diversity of colony morphology in *Geniculoseta preussii* on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. A. CBS 257.75. B. CBS 262.76. C. CBS 263.75. D. CBS 145478. Scale bar = 1 cm.

Běšice and Prahly near Kadaň, old decaying wood of a trunk of *Quercus petraea*, 5 Jun. 1972, V. Holubová-Jechová (PRM 794057). **Germany**, Lower Saxony, Wolfenbüttel district, Elm near Schöppenstedt, on wood of *Fraxinus excelsior*, Jan. 1975, W. Gams (culture CBS 257.75); North Rhine-Westphalia, Donoper Teich near Detmold, on decaying wood, Sep. 1972, W. Gams & H. Jahn (culture CBS 262.76). **Poland**, near Kolno to the south of the city of Augustów, on decaying wood of *Alnus glutinosa*, 11 Sep. 1974, V. Holubová-Jechová (**holotype** of *Chaetosphaeria preussii* PRM 796750). **The Netherlands**, Utrecht province, Groeneveld near Baarn, on wood of *Quercus* sp., Sep. 1974, W. Gams (culture CBS 263.75).

Habitat and geographical distribution: A common saprobe on decaying wood and woody fruits of Alnus glutinosa, Fraxinus excelsior, Fagus sylvatica, Quercus petraea, Quercus sp. and other unidentified hosts, known from the Czech Republic, Germany, Hungary, Poland, and the Netherlands (Gams & Holubová-Jechová 1976, Holubová-Jechová 1979, this study).

Notes: Geniculoseta preussii is somewhat similar to Chloridiopsiella preussii, especially in the geniculate conidiophores and hyaline, ellipsoidal to oblong conidia that become beige to pale brown in mass at maturity. However, Ge. preussii differs in reddish-brown, subulately tapering conidiophores, frequently percurrently extending phialides, which are subulate or narrowly lageniform and gradually tapering upwards, and shorter conidia (2–)2.5–3(–3.5) × 1.5–2 μ m. In comparison, the conidiophores of Cha. preussii are cylindrical, phialides are subcylindrical and only slightly tapering towards the collarette and conidia are sometimes obovate to long-cuneiform, longer and wider (3–)3.5–4.5(–5) × 2–2.5 μ m.

The ascomata in the holotype PRM 796750 of *Ge. preussii* were aged and mostly empty but if the centrum was still present, the asci were partially disintegrated and difficult to separate. Conidiophores were abundantly present, but often without the conidial heads. The appearance of the colonies *in vitro* varied slightly, for example the strain CBS 257.75 showed a significant production of dark pigmented

mycelium on CMD, MLA and OA. Soluble pigments are rare in *Ge. preussii* and have only been observed in a fresh isolate CBS 148478, which has a distinct ability to produce yellow pigment on MLA.

We have considered the epitypification to clarify and stabilize the species concept of *Ge. preussii*. However, the holotype of *Ch. preussii* was collected on wood of *Alnus glutinosa* in Poland, whereas all available strains, though from Europe, are from different countries and are not suitable candidates for the epitype.

Gongromeriza Preuss, Linnaea 24: 106. 1851.

Synonym: Ejnerjensenia W.P. Wu & Y.Z. Diao, Fungal Diversity 116: 276. 2022.

Type species: Gongromeriza myriocarpa (Fr.) Réblová

Description: For generic delimitation and more information, see Réblová et al. (2022). The species descriptions and culture characteristics are provided in this study.

Accepted species: G. myriocarpa, G. pygmaea.

Gongromeriza myriocarpa (Fr.) Réblová, Stud. Mycol. 103: 199. 2022. Figs 13, 14.

Basionym: Sphaeria myriocarpa Fr., Syst. Mycol. 2(2): 459. 1823. Synonyms: Chaetosphaeria myriocarpa (Fr.) C. Booth, Mycol. Pap. 68: 5. 1957.

Rosellinia minima Fuckel & Nitschke, Jb. nassau. Ver. Naturk. 23–24: 149. 1870 [1869–70].

Sphaeria ostioloidea Cooke, Grevillea 4(31): 113. 1876. Gongromeriza clavaeformis Preuss, Linnaea 24: 106. 1851.

Catenularia heimii F. Mangenot, Rev. Gén. Bot. 59: 445. 1952. (Rech. méth. Champ. Bois Décomp. p. 25. 1952.)

Additional synonyms listed in Booth (1957) and Réblová et al. (2022).

Description: See Booth (1957), Gams & Holubová-Jechová (1976) and Wu & Diao (2022).

Culture characteristics: On CMD colonies 60–63 mm diam, circular, convex, flat margin, margin entire, lanose, floccose, mucoid towards the periphery, beige, occasionally dark brown, whitish centrally, pale brown at the margin, reverse olivaceous brown. On MLA colonies 58–60 mm diam, circular, convex, margin entire, lanose, floccose, whitish-grey, olivaceous grey at the margin, reverse dark olivaceous grey. On OA colonies 44–47 mm diam, circular, flat, margin entire, velvety, mucoid towards the periphery, anthracite to olivaceous grey, reverse dark grey. On PCA colonies 34–36 mm diam, circular, convex, flat margin, margin slightly fimbriate, velvety, cobwebby towards the periphery, beige, often dark olivaceous brown at the margin, reverse dark olivaceous grey. Sporulation was abundant on PCA, sparse on MLA and OA, absent on CMD.

Specimens examined: Czech Republic, Pardubice region, Železné hory Mts. Protected Landscape Area, Horní Bradlo, Malá Střítež settlement, Polom national Nature Reserve, on decaying wood, 10 Nov. 2018, M. Réblová, M.R. 4060 (PRA-21522, culture CBS 145805); *ibid.*, on decaying wood associated with *Menispora ciliata, M. caesia*, 10 Nov. 2018, M. Réblová, M.R. 4070B (PRA-21523, culture CBS 148194). France, locality unknown, on dead wood of *Fagus sylvatica*, date unknown, F. Mangenot (an authentic strain of *Catenularia heimii* culture CBS 141.53 = IMI 061296 = UPSC 3464); Massif de Ste. Baume, near Marseille, on decaying wood, Oct. 1974, W. Gams, No. F5 (culture CBS 241.75B). Italy, Lazio region, Viterbo province, Farnese, Nature Reserve Selva di Lamone, on decayed

wood of *Quercus cerris*, 19 Mar. 2010, M. Réblová & W. Gams, M.R. 3138 (PRA-21506, culture CBS 127685); locality, date and substrate unknown, A. Rambelli (culture CBS 116.57). **The Netherlands**, Utrecht province, Pijnenburg, on decaying wood, 19 Aug. 1972, W. Gams, No. Pij 4 (culture ex-neotype of *Sphaeria myriocarpa* CBS 264.76 = UPSC 3465). **Ukraine**, Ternopil region, Zalischyky district, Dniester Canyon, on decaying wood of *Carpinus betulus*, 5 Oct. 2016, A. Akulov (culture CBS 143389).

Habitat and geographical distribution: A common saprobe on decaying wood of many deciduous trees, for example Acacia, Acer, Alnus, Betula, Carpinus betulus, Cedrus, Fagus sylvatica, Populus, Quercus robur, Sorbus, bamboo and other unknown hosts, and also stromata of Hypoxylon, Diatrype and Diatrypella. This species is widespread in the temperate zone. It is known in Belgium, China, Czech Republic, France, Hungary, Italy, Netherlands, Slovak Republic, Sweden, Ukraine, United Kingdom and USA (Fries 1823, Booth 1957, Gams & Holubová-Jechová 1976, Holubová-Jechová 1979, Crous et al. 2018a, b, Luo et al. 2019, Wu & Diao 2022).

Notes: The association between the sexual and asexual morphs was initially established through experimental investigations by Brefeld in 1891. Subsequently, Booth (1957, 1958) and Gams & Holubová-Jechová (1976) independently confirmed these findings. The asexual morph was described as Catenularia heimii (Mangenot 1952) and also Gongromeriza clavaeformis (Preuss 1851), which was later transferred to the genus Chloridium (Gams & Holubová-Jechová 1976). In the phylogenetic analysis, the ex-type strains of Cat. heimii and the ex-neotype strain of G. myriocarpa were confirmed to be conspecific. For a detailed comparison of G. myriocarpa with the closely related G. pygmaea, refer to the notes provided for the latter species.

Gongromeriza pygmaea (P. Karst.) Réblová, Stud. Mycol. 103: 199. 2022. Figs 15, 16.

Basionym: Sphaeria pygmaea P. Karst., Fungi Fenniae Exsiccati, Fasc. 9: no. 875. 1869.

Synonyms: Zignoëlla pygmaea (P. Karst.) Sacc., Michelia 1: 346. 1878.

Phialophora phaeophora W. Gams, Stud. Mycol. 13: 65. 1976. Additional synonyms listed in Réblová et al. (2022).

Description: See Gams & Holubová-Jechová (1976) and Constantinescu et al. (1995).

Culture characteristics: On CMD colonies 20–23 mm diam, circular, flat, margin entire, cobwebby, mucoid towards the periphery, pale pink-beige, creamy towards the margin, reverse creamy. On MLA colonies 24–31 mm diam, circular, convex, flat margin, margin fimbriate, lanose, floccose, funiculose centrally, cobwebby towards the periphery, whitish-beige, dark brown at the margin, reverse of the same colours. On OA colonies 24–30 mm diam, circular, flat, margin fimbriate, funiculose at the inoculation block, cobwebby, mucoid towards the periphery, russet becoming tawny, light gold towards the periphery, reverse russet. On PCA colonies 30–39 mm diam, circular, flat, margin fimbriate, cobwebby, mucoid towards the periphery, whitish-beige with a pale brown outer zone of submerged growth, reverse of the same colours. Sporulation was abundant on MLA, OA, PCA, absent on CMD.

Specimens examined: Czech Republic, South Bohemian region, Novohradské hory Mts., Žofín National Nature Reserve, on decaying wood of Fagus sylvatica, 6 Aug. 1997, M. Réblová, M.R. 967 (PRA-21524, culture CBS 144786); South Bohemian region, Novohradské hory

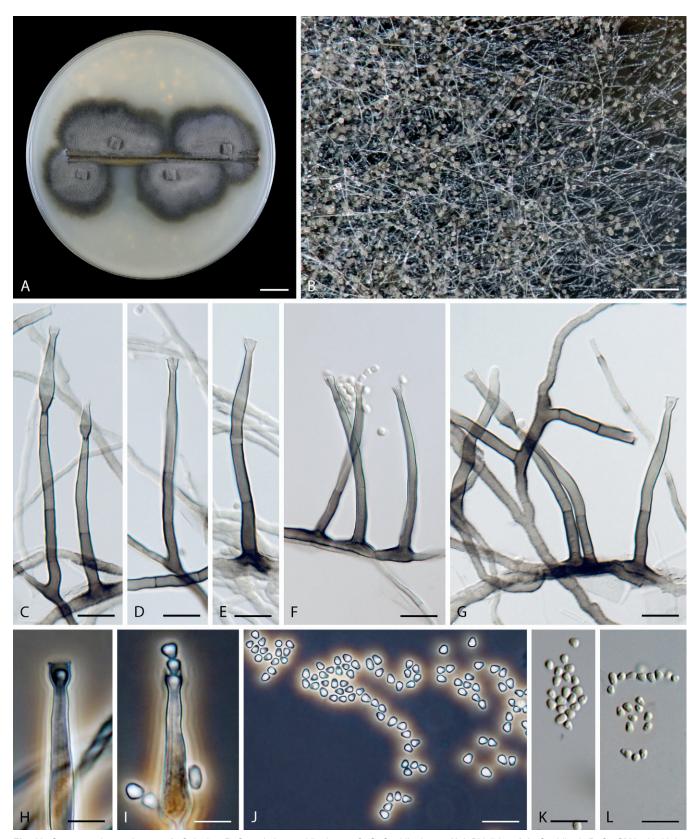


Fig. 13. Gongromeriza myriocarpa. A. Colonies. B. Sporulating conidiophores. C–G. Conidiophores. H, I. Phialides. J–L. Conidia. A, B. On CMA with *Urtica* stem. C–I. On MLA. J–L. On PCA. A–I. CBS 145805. J–L. CBS 148194. Scale bars: A = 1 cm; B = 500 µm; C–G, J–L = 10 µm; H, I = 5 µm.

Mts., Dobrá voda, Hojná voda National Nature Monument, on decaying wood of *Fagus sylvatica*, 13 Oct. 2003, M. Réblová, M.R. 3814A (PRA-21525, culture CBS 138689); *ibid.*, on decaying wood, 10 Oct. 2016, M. Réblová, M.R. 3894 (PRA-21526, culture IMI 506815); South Bohemian region, Šumava Mts. National Park, Železná Ruda, glacial cirque of the Čertovo jezero lake, on decaying wood of *Fagus sylvatica*, 28 Aug. 1998, M. Réblová, M.R. 1365 (PRA-21527); South Bohemian region, Šumava

Mts. National Park, Stožec, Oslí les, alt. 950 m, on decaying wood of *Fagus sylvatica*, 16 Sep. 2007, M. Réblová, M.R. 3009 (PRA-21528, culture CBS 131688); South Moravian region, Hodonín district, Mikulčice oppidum, Mikulčický luh Nature Park, Malá Pinuška, on decaying wood of *Quercus* sp., 7 Nov. 2017, M. Réblová, M.R. 3935 (PRA-21529, culture CBS 149858). *Italy*, Tuscany region, Grosseto province, San Quirico near Pitigliano, on decaying wood of *Corylus avellana*, 8 Apr. 2014, M.



Fig. 14. Diversity of colony morphology in *Gongromeriza myriocarpa* on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. **A.** CBS 264.76, ex-neotype culture of *Sphaeria myriocarpa*. **B.** CBS 141.53, authentic strain of *Catenularia heimii*. **C.** CBS 145805. **D.** CBS 148194. Scale bar = 1 cm.

Réblová, M.R. 3853 (PRA-21530, culture CBS 139769). **New Zealand**, Otago region, Queenstown-Lakes district, Mount Aspiring National Park, Makarora Bush Walk, on decaying wood, 30 Mar. 2005, M. Réblová, M.R. 3405 / NZ 685 (culture ICMP 22550). **Sweden**, Skåne, Äsphult parish, Linderödsåsen, *ca.* 700 m SW of Olarp, 8 Jul. 1978, K. & L. Holm, 1401b (duplicate ex UPS). **The Netherlands**, Utrecht province, Berenkuil near Utrecht, on decaying twig of *Fraxinus excelsior*, May 1974, W. Gams (culture ex-type of *Phialophora phaeophora* CBS 699.74 = UPSC 3466); Baarn, Maarschalksbos, on old, empty *Diatrypaceae*, on fallen twig (*Fagus*?), 4 Sep. 1970, H.A. van der Aa (culture CBS 878.70).

Habitat and geographical distribution: A common saprobe on decaying wood of various hosts, for example *Corylus avellana*, *Fagus sylvatica*, *Picea glauca*, *Quercus* sp., or old stromatic ascomycetes, known from the Czech Republic, Finland, Italy, Netherlands, New Zealand and Sweden (Gams & Holubová-Jechová 1976, Costantinescu *et al.* 1995, this study).

Notes: Gongromeriza pygmaea resembles *G. myriocarpa*, but it can be distinguished by shorter conidiophores, usually reduced to single phialides in culture, non-flaring cup-shaped collarettes and somewhat narrower, hyaline, mostly dacryoid conidia with a less truncate base (2–3 × 1.5–2 µm *fide* Gams & Holubová-Jechová 1976). On the other hand, *G. myriocarpa* has longer, geniculate conidiophores with several percurrent proliferations, flaring, funnel-shaped collarettes and slightly wider, light pigmented, short-cuneate conidia (2.3–3 × 1.6–2.5 µm *fide* Gams & Holubová-Jechová 1976).

The culture characterization is based on the ex-type strain CBS 699.74 of *Phialophora phaeophora*, a species initially erected for the asexual morph. However, we observed considerable variability among strains *in vitro*. The ex-type isolate displays a varying degree of reduced pigmented hyphae on OA and PCA, akin to one of our recent strains, CBS 138689. Colonies grown on these media

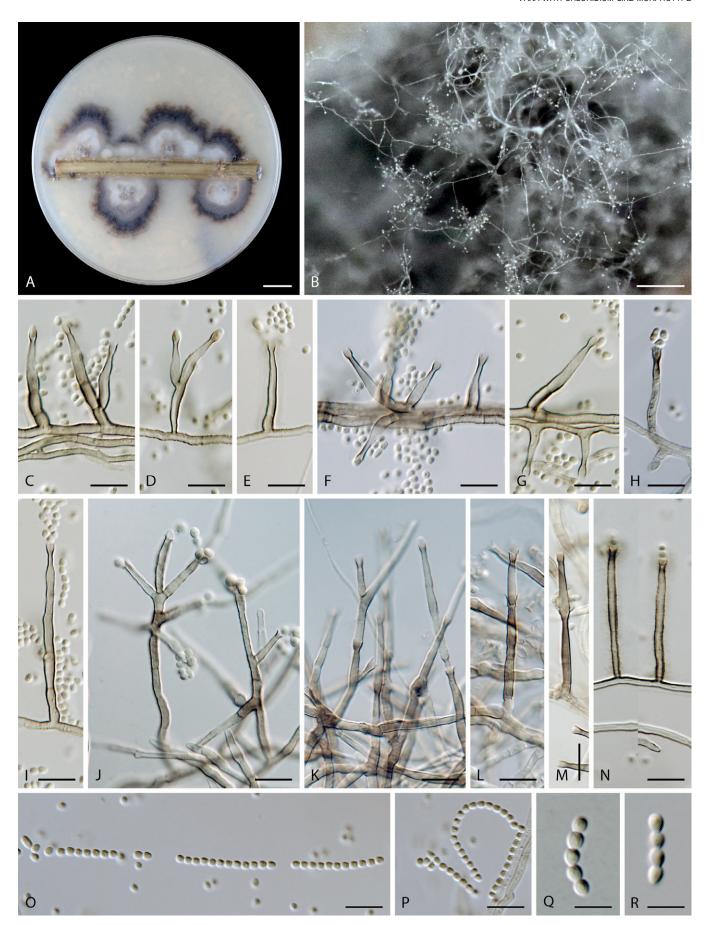


Fig. 15. *Gongromeriza pygmaea*. **A.** Colonies. **B.** Aerial mycelium with sporulating conidiophores. **C–N.** Conidiophores and solitary phialides. **O–R.** Conidia. A, B. On CMA with *Urtica* stem. C–R. On MLA. A, B, K–M. IMI 506815. C–I, N–P. CBS 144786. J, Q, R. CBS 139769. Scale bars: A = 1 cm; B = 500 μ m; C–P = 10 μ m; Q, R = 5 μ m.

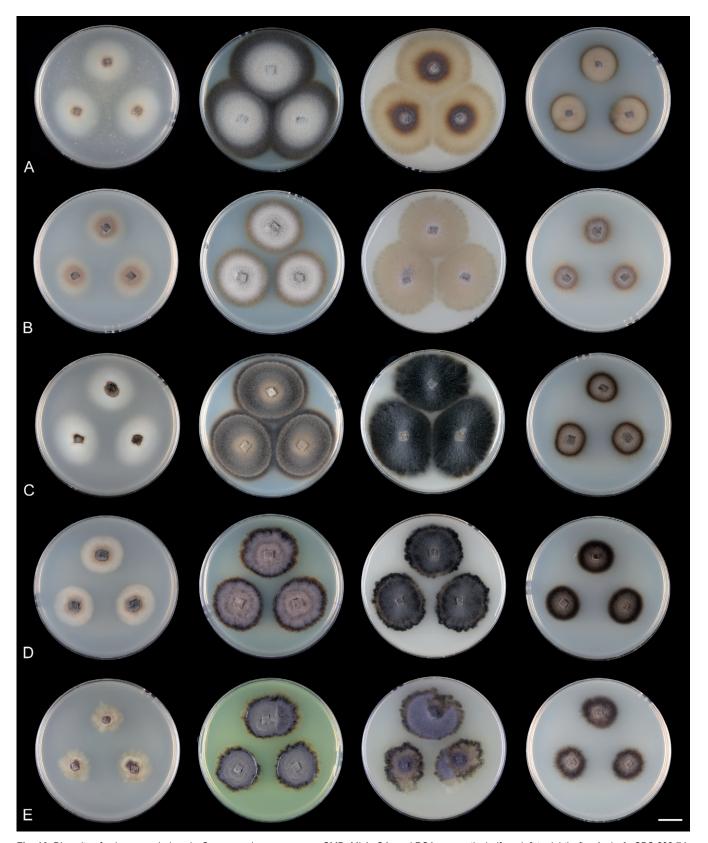


Fig. 16. Diversity of colony morphology in *Gongromeriza pygmaea* on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. **A.** CBS 699.74, ex-type culture of *Phialophora phaeophora*. **B.** CBS 138689. **C.** CBS 144786. **D.** CBS 139769. **E.** IMI 506815. Scale bar = 1 cm.

exhibit a different range of colours, ranging from russet to tawny to light gold, in contrast to the dark brown to anthracite observed in other strains. Several strains also produced diffusible yellow pigment *in vitro* (Fig. 17). For further details, see Discussion.

Gongromerizella Réblová, Stud. Mycol. 103: 199. 2022.

Description: For generic delimitation and more information, see Réblová et al. (2022).

Accepted species: Gongromerizella lignicola, Ga. pachytrachela, Ga. pini, Ga. silvana.

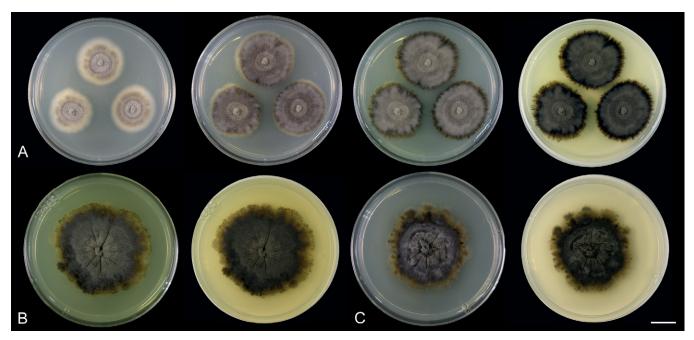


Fig. 17. Colonies of *Gongromeriza pygmaea* (IMI 506815) on MLA and PDA showing production of diffusible yellow pigment. **A.** Colonies on MLA after 4 wk, one wk apart. **B.** Colony on MLA after 5 wk. **C.** Colony on PDA after 5 wk. All cultures were photographed on a black surface except for the right-most photos of A, B and C, which were photographed on a white surface. Scale bar = 1 cm.

Notes: The genus Gongromerizella (Ga.) (Réblová et al. 2022) was proposed to accommodate species segregated from Chloridium sect. Gongromeriza. The sexual morph is known only for Ga. pachytrachela. Gongromerizella differs from Chloridium s. str. by ascospores that do not fragment into part spores, robust, bristle-like conidiophores and phialides with a single conidiogenous locus, sometimes elongating sympodially in culture.

Gongromerizella lignicola (F. Mangenot) Réblová, Stud. Mycol. 103: 199. 2022. Figs 18, 19.

Basionym: Bisporomyces lignicola F. Mangenot, Rev. Mycol. 18: 136. 1953.

Synonym: Chloridium lignicola (F. Mangenot) W. Gams & Hol.-Jech., Stud. Mycol. 13: 37. 1976.

Description on the natural substrate: Colonies effuse, hairy, black, whitish when sporulating, composed of conidiophores. Asexual morph. Conidiophores (86–)175–285 × (4.5–)5.5–8 μm, macronematous, solitary or gregarious, erect, straight or slightly flexuous, cylindrical to somewhat subulately tapering, somewhat bulbous at the base, unbranched, with several percurrent proliferations, dark brown, paler towards the apex. Conidiogenous cells $17.5-45 \times 4-5 \mu m$ tapering to ca. $2.5-3 \mu m$ below the collarette, monophialidic with a single conidiogenous locus, integrated, terminal, extending percurrently, subcylindrical, pale brown, paler towards the tip; collarettes 5.5-7.5 µm wide, 4.5-5.5 µm deep, flaring, funnel-shaped, hyaline to subhyaline, with conspicuous periclinal thickening. Conidia (5.5-)6-7.5 × 2.5-3.5 µm (mean \pm SD = 6.7 \pm 0.5 \times 3.1 \pm 0.3 μ m), ellipsoidal to oblong, hyaline, becoming pale brown with age, aseptate, smooth, accumulating in slimy white heads. Sexual morph. Unknown.

Culture characteristics: On CMD colonies 23–24 mm diam, circular, flat, margin entire, mucoid, funiculose centrally, whitish to isabelline, reverse of the same colour. On MLA colonies 39–40 mm diam, circular, convex, margin entire, lanose, funiculose, floccose, whitish, pale brown at the margin, with a beige outer zone of

submerged growth, reverse isabelline. On OA colonies 32–33 mm diam, circular, flat, margin entire, lanose at the centre becoming mucoid towards the periphery, cobwebby at the margin, white-beige, with an outer pale brown zone of submerged growth, reverse of the same colour. On PCA colonies 25–26 mm diam, circular, flat, margin entire, mucoid, cobwebby at the centre, funiculose at the inoculation block, brown, whitish centrally, reverse pale brown. Sporulation was delayed on CMD, PCA and OA, absent on MLA.

Description in culture: See Gams & Holubová-Jechová (1976).

Specimens examined: France, Argonne, Vallée Grand Rû, on the rotten trunk of Fagus sylvatica, 1953, F. Mangenot (culture ex-isotype of Bisporomyces lignicola CBS 143.54 = LCP 88.3536 = MUCL 1149). Ukraine, Carpathian Mts., Boržava Massif, Pilipec, on decaying wood of Fagus sylvatica, 17 Jul. 1998, M. Réblová, M.R. 1265 (PRA-21531).

Habitat and geographical distribution: Saprobe on decaying wood of Fagus sylvatica, known from Belgium, Canada, France, Ukraine and USA (Mangenot 1953, Gams & Holubová-Jechová 1976, this study).

Notes: Gams & Holubová-Jechová (1976) previously reported that the ex-isotype strain of *Ga. lignicola* CBS 143.54 exhibits longer conidia (3.5–5 × 1.5–2 μ m) compared to other specimens assigned by them to this species. Mangenot (1953) also documented slightly longer conidia in the holotype (3.8–8.0 × 1.5–2.7 μ m) (material from nature), which aligns with our observations of the ex-isotype strain in culture (on OA and PCA). Additionally, we noted that conidial size in the ex-isotype strain varies within the range of 3.5–6.5(–8) × 1.5–2.5 μ m *in vitro*.

Apart from the ex-type strain and three herbarium specimens listed by Gams & Holubová-Jechová (1976) as part of the species description of *Ga. lignicola*, another strain, CBS 171.76, was included. Comparative examination of the DNA sequences and morphological data of these specimens revealed that they actually represent two distinct species. Therefore, the isolate CBS 171.76

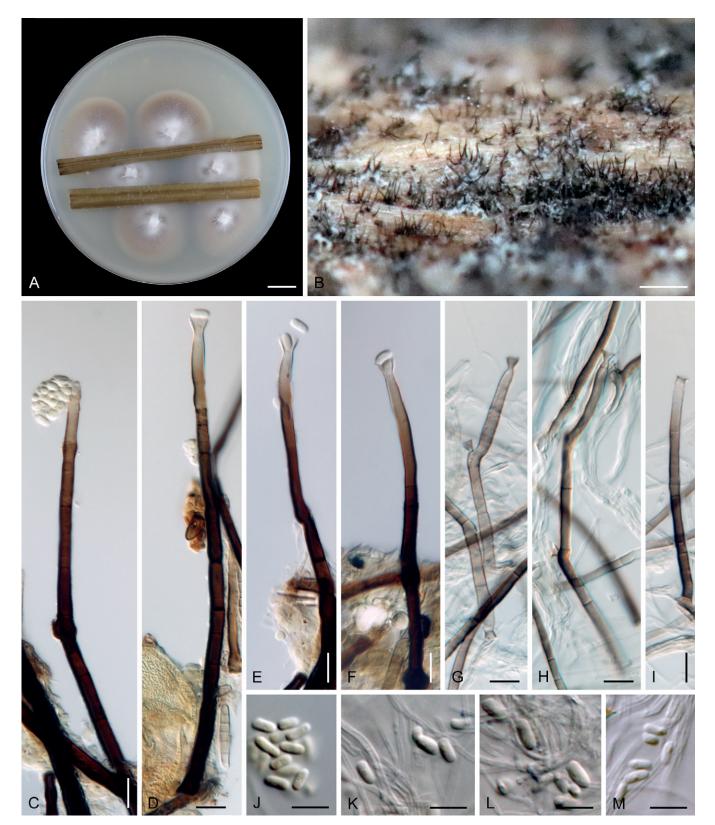


Fig. 18. *Gongromerizella lignicola*. **A.** Colonies. **B.** Sporulating conidiophores. **C–I.** Conidiophores. **J–M.** Conidia. A. On CMA with *Urtica* stems. B–F, J. From nature. G–I, K–M. On PCA. A, G–I, K–M. CBS 143.54, ex-isotype culture of *Bisporomyces lignicola*. B–F, J. PRA-21531. Scale bars: A = 1 cm; B = 500 μm; C–M = 10 μm.

is described as a novel species, *Ga. silvana*. Further details and information regarding this new species are presented below.

Gongromerizella lignicola exhibits remarkable similarities to Ga. pachytrachela, yet they can be distinguished by certain characteristics. Gongromerizella pachytrachela displays darker and shorter conidiophores (146–210 \times 4.5–6 μm), wider conidia (7–8.5 \times 3–4 μm), and larger funnel- to beaker-shaped collarettes (4–6.5 μm wide, 3–4.5 μm deep). Based on the observed similarities, the

collection M.R. 1265 (PRA-21531) was initially identified as *Ga. pachytrachela* (as *Chl. pachytrachelum*, Réblová & Winka 2000). This identification was made by comparing the material from nature with the reference material available in culture, as described in Gams & Holubová-Jechová (1976). However, the variable conidial size of *Ga. lignicola in vitro* can sometimes cause difficulties during identification. Phylogenetic analysis showed that this specimen is conspecific with the isotype strain of *Ga. lignicola*.

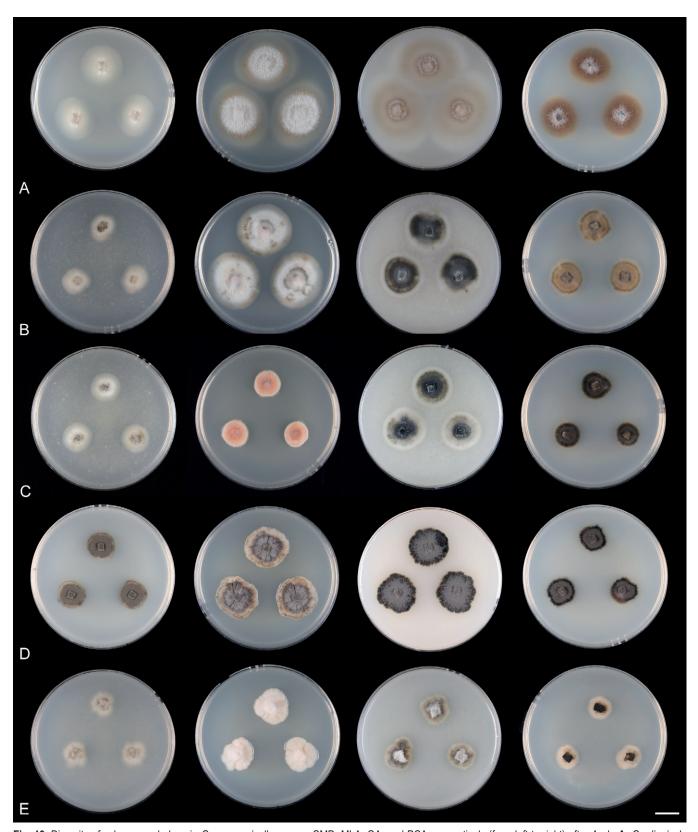


Fig. 19. Diversity of colony morphology in *Gongromerizella* spp. on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. **A.** *Ga. lignicola* (CBS 143.54, ex-isotype culture of *Bisporomyces lignicola*). **B.** *Ga. silvana* (CBS 171.76, ex-type culture). **C–E.** *Ga. pachytrachela* (C. CBS 645.75, ex-type culture of *Chaetosphaeria lentomita* and *Chloridium pachytrachelum*. D. CBS 145962. E. CBS 148606). Scale bar = 1 cm.

Gongromerizella pachytrachela (W. Gams & Hol.-Jech) Réblová, Stud. Mycol. 103: 199. 2022. Figs 19, 20.

Basionym: Chloridium pachytrachelum W. Gams & Hol.-Jech., Stud. Mycol. 13: 26. 1976.

Synonyms: Chaetosphaeria lentomita W. Gams & Hol.-Jech., Stud. Mycol. 13: 24. 1976.

Chaetosphaeria innumera Berk. & Br. ex Tul. & C. Tul. sensu C.

Booth, Mycol. Pap. 68: 2. 1957 [non Ch. innumera Berk. & Br. ex Tul. & C. Tul., Select. fung. carpol. 2: 252. 1863].

Description on the natural substrate: Colonies effuse, hairy, dark brown to black, whitish when sporulating, composed of conidiophores and ascomata. Asexual morph. Conidiophores 146–210 × 4.5–6 µm, macronematous, solitary, scattered, erect, straight or slightly

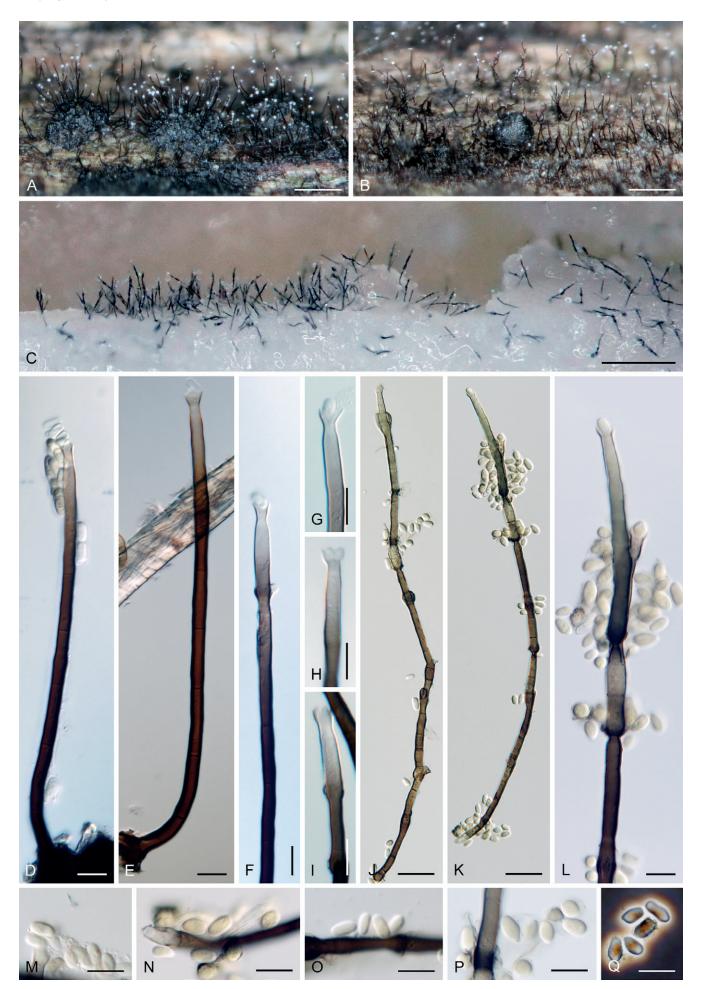


Fig. 20. Gongromerizella pachytrachela (CBS 148606). A, B. Sporulating conidiophores on old ascomata of an ascomycete. C–F, J–L. Conidiophores. G–I. Phialides. M–Q. Conidia. A, B, D–M. From nature. C, N–Q. On MLA. Scale bars: A–C = 500 μ m; D–I, L–Q = 10 μ m; J, K = 25 μ m.

bent near the base, cylindrical, bulbous or lobate, unbranched, with several percurrent proliferations, dark brown, paler towards the apex. Conidiogenous cells 25.5-56 × 4-5.5 µm tapering to ca. 2.5–3.5 µm below the collarette, monophialidic with a single conidiogenous locus, integrated, terminal, extending percurrently, rarely sympodially, subcylindrical or narrowly lageniform, pale brown to subhyaline, paler towards the tip; collarettes 4-6.5 μm wide, 3-4.5 μm deep, flaring, funnel- to beaker-shaped, subhyaline to pale brown, with periclinal thickening. Conidia 7-8.5 \times 3–4 µm (mean ± SD = 7.4 ± 0.5 \times 3.7 ± 0.4 µm), ellipsoidal to oblong, sometimes tapering towards the base, with a basal scar, hyaline, becoming pale brown with age and after release from the conidiogenous locus, aseptate, smooth, accumulating in slimy white heads. Sexual morph. Ascomata perithecial, non-stromatic, superficial, subglobose to conical, 150-265 µm diam, broadly attached to the substrate, without subiculum, papillate, smooth, appearing slightly pruinose. Ostiolar canal periphysate. Ascomatal wall 15-22(-30) µm thick, two-layered; outer layer composed of rather wide (3-5 µm diam), very thick-walled, pigmented cells of textura epidermoidea or angularis, the outermost layer or at least some superficial cells hyaline; inner layer composed of elongated, hyaline cells. Paraphyses 1.2–1.5 µm wide, at the tip slightly swollen to 2.2 μ m. Asci 65–75 \times 6–7.5 μ m, cylindrical, with a thin apical plate, thin-walled, 8-spored. Ascospores 8–14 × 3.5–4 µm, fusiform with rounded ends, hyaline, finely roughened, at maturity 2-celled, not constricted at the septum, each cell 1-2-guttulate, obliquely uniseriate in the ascus. (Characteristics of the sexual morph were partly adopted according to Gams & Holubová-Jechová 1976).

Culture characteristics: On CMD colonies 14–18 mm diam, circular, convex, margin entire, sparsely lanose, funiculose centrally, mucoid towards the periphery, whitish-brown, isabelline at the margin, reverse isabelline. On MLA colonies 15–18 mm diam, circular, raised, margin entire to weakly fimbriate, sparsely lanose, velvety at the margin, salmon pink, white-pink at the margin, reverse beige. On OA colonies 18–20 mm diam, circular, convex, flat margin, margin entire, velvety to cobwebby, dark grey centrally, olivaceous grey towards the periphery, with an isabelline outer zone, reverse olivaceous grey. On PCA colonies 17–19 mm diam, circular, convex, margin entire to fimbriate, velvety, dark olivaceous brown with a beige-pink outer zone of submerged growth, reverse olivaceous brown. Sporulation was abundant on CMD, OA and PCA, absent on MLA.

Description in culture: On MLA, colonies effuse, hairy, vegetative hyphae 1.5–3 µm diam, branched, septate, hyaline, and smooth, becoming pale brown and encrusted. Asexual morph. Conidiophores, conidiogenous cells and conidia similar to those from nature. Conidiophores 106–178 × 3.5–4.5 µm, with 1–6 percurrent proliferations, geniculate, occasionally branched. Conidiogenous cells 17–35(–40) × 4.5–6 µm, tapering to 2.5–3.5 µm below the collarette, extending percurrently, rarely sympodially with 1–2(–3) lateral openings formed along the conidiophore; collarettes 5–8 µm wide, 2.5–3.5 µm deep. Conidia 5–8.5(–9) × 3–4.5 µm (mean \pm SD = 6.6 \pm 0.9 × 3.8 \pm 0.4 µm), variable in shape, ellipsoidal or ellipsoidal-oblong to somewhat obclavate, sometimes with a basal scar, accumulating in slimy whitish heads. Chlamydospores absent. Sexual morph. Not observed.

Specimens examined: **Belgium**, Ardennes, near Neupont, on decaying wood of *Fagus sylvatica*, Sep. 1975, W. Gams (culture ex-type of *Chaetosphaeria lentomita* and *Chloridium pachytrachelum* CBS 645.75).

Czech Republic, Olomouc region, Hrubý Jeseník Mts., valley of Hučivá Desná, on decaying wood of Fagus sylvatica, 6 August 1971, V. Holubová-Jechová (PRM 794021); Olomouc region, Hrubý Jeseník Mts., forest Bučina on slopes above the hunting house Františkova myslivna near Kouty nad Desnou, on decaying wood of a trunk of Fagus sylvatica, 4 Aug. 1971, V. Holubová-Jechová (PRM 794016); Olomouc region, Rychlebské hory Mts., forest in the Bučínský potok valley opposite the village Žulová near Javorník, on roots of Picea abies, 10 Aug. 1971, V. Holubová-Jechová (PRM 794023); South Bohemian region, Novohradské hory Mts., Dobrá voda, Hojná voda National Nature Monument, alt. 850 m, on decaying wood of Fagus sylvatica, 27 Sep. 2018, M. Réblová, M.R. 3962 (PRA-21532, culture CBS 148606); South Bohemian region, Novohradské hory Mts., Pohoří na Šumavě, Myslivna Mt., alt. 1 040 m, on decaying wood of Fagus sylvatica, 3 Oct. 2018, M. Réblová, M.R. 3971A (PRA-21533, culture CBS 145962). Slovak Republic, Trenčín region, Maká Fatra Mts., between Mt. Kľak and Mt. Revan near Nitrianske Pravno, on decaying wood of Fagus sylvatica, 14 Jul. 1976, V. Holubová-Jechová (PRM 796748).

Habitat and geographical distribution: Saprobe on decaying wood of Fagus sylvatica and Picea abies, known from Belgium, Czech Republic, Hungary and the Slovak Republics (Gams & Holubová-Jechová 1976, Holubová-Jechová 1979, this study).

Notes: In addition to the ex-type strain CBS 645.75 of *Ga. pachytrachela*, Gams & Holubová-Jechová (1976) documented four additional strains of this species: CBS 247.76, CBS 260.75B, CBS 260.75C, and CBS 265.76 (strains CBS 260.75B and CBS 260.75C are no longer available). Upon our examination, it was determined that CBS 247.76 and CBS 265.76 are not actually related to *Ga. pachytrachela*; instead, they were confirmed to be conspecific with the ex-type strain CBS 230.75 of *Chloridiopsiella preussii*.

Our phylogenetic analysis includes three strains of *Ga. pachytrachela*. The culture characteristics were based on the extype strain CBS 645.75. Some variability in colony appearance was observed, with CBS 645.75 forming salmon pink colonies on MLA, CBS 148606 forming whitish-pink colonies, and CBS 145962 producing brown mycelium. *Gongromerizella pachytrachela* can be distinguished from other species within the genus by its larger conidia (7–8.5 × 3–4 μ m) and robust conidiophores, which are among the widest (4.5–6 μ m). While it bears a close resemblance to *Ga. lignicola*, specific distinctions between the two species are provided in the notes accompanying the description of *Ga. lignicola*.

Gongromerizella pini (Crous & Akulov) Réblová, Stud. Mycol. 103: 200. 2022. Fig. 21.

Basionym: Chloridium pini Crous & Akulov, Fungal Syst. Evol. 6: 182. 2020.

Description on the natural substrate: Colonies effuse, hairy, dark brown to black, whitish when sporulating, composed of conidiophores. Asexual morph. Conidiophores 55–185 \times 2.5–3.5 μm , base bulbous 5.5–8.5(–10) μm wide, macronematous, solitary or fasciculate, erect, straight or slightly flexuous, cylindrical, wider towards the base, unbranched, dark brown, paler towards the apex, sometimes with 1–2 percurrent proliferations. Conidiogenous cells 17.5–36 \times 2.5–4 μm tapering to ca. 1.5(–2) μm below the collarette, monophialidic with a single conidiogenous locus, integrated, terminal, extending percurrently, subcylindrical or narrowly lageniform, brown or pale brown; collarettes 3.5–4 μm wide, 2.5–3.5(–4) μm deep, flaring, funnel-shaped, subhyaline. Conidia (2.5–)3–4.5 \times 1.5–2.5 μm (mean \pm SD = 3.5 \pm 0.5 \times 1.9 \pm 0.2 μm), ellipsoidal, irregularly ellipsoidal to oblong with bluntly



Fig. 21. *Gongromerizella pini* (CBS 145343). **A, B.** Colonies of sporulating conidiophores. **C–F.** Conidiophores (arrows indicate abrupt colour transition between the upper part of the phialide and the collarette). **G, H.** Conidia. A–D. From nature. E–H. On MLA. Scale bars: A, B = 500 μm; C–H = 10 μm.

rounded to truncate ends, hyaline, aseptate, smooth, accumulating in slimy whitish heads. *Sexual morph*. Unknown.

Description in culture: See Crous et al. (2020).

Specimen examined: **Czech Republic**, South Bohemian region, Novohradské hory Mts., Pohoří na Šumavě, Myslivna Mt., alt. 1 040 m, on decaying wood of *Fagus sylvatica*, 3 Oct. 2018, M. Réblová, M.R. 3971B (PRA-21533, culture CBS 145343).

Habitat and geographical distribution: Saprobe on decaying wood of Fagus sylvatica and Pinus sylvestris, known from the Czech Republic and Ukraine (Crous et al. 2020, this study).

Notes: Gongromerizella pini exhibits the closest resemblance to Ga. silvana; however, the latter species can be distinguished by its longer conidiophores, which percurrently proliferate in vitro. Additionally, Ga. silvana differs in having pale brown phialides that gradually become paler towards the shallow, funnel- to vase-shaped, subhyaline to pale brown collarette. In contrast, Ga. pini shows brown phialides that contrast with subhyaline collarettes (Fig. 21C, D). The distinct species trait of Ga. pini lies in the abrupt colour transition between the upper part of the phialide and the collarette. The paleness of the entire phialide in relation to the conidiophore is occasionally observed. This characteristic is particularly noticeable in material from nature.

Gongromerizella silvana Réblová, **sp. nov.** MycoBank MB 849186. Figs 19, 22.

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

Typus: **Belgium**, Ardennes, near Neupont, on decaying wood, Sep. 1975, W. Gams (**holotype** designated here PRA-21534 as dried culture, culture ex-type CBS 171.76).

Culture characteristics: On CMD colonies 16–20 mm diam, circular, flat, margin entire, mucoid, funiculose centrally, whitish to isabelline, reverse of the same colour. On MLA colonies 28–30 mm diam, circular, convex, margin entire, lanose, floccose, funiculose, whitish, pale brown at the margin, with an outer beige zone of submerged growth, reverse isabelline. On OA colonies 38–45 mm diam, circular, flat, margin entire, lanose at the centre, mucoid towards the periphery, cobwebby at the margin, beige, white-beige centrally, with an outer pale brown zone of submerged growth, reverse of the same colour. On PCA colonies 24–26 mm diam, circular, flat, margin entire, cobwebby at the centre, mucoid towards the periphery, funiculose at the inoculation block, cinnamon, whitish centrally, reverse pale brown. Sporulation was absent on CMD and PCA, moderate on MLA and OA.

Description in culture: On MLA, colonies effuse, hairy, vegetative hyphae 1-3 µm diam, branched, septate, hyaline to subhyaline, smooth, pale brown in older cultures. Asexual morph. Conidiophores $(30-)100-550 \times (2-)2.5-3.5 \mu m$, macronematous, solitary or fasciculate, erect, straight or slightly flexuous, cylindrical, septate. unbranched, brown, somewhat darker at the base of original phialide, gradually paler towards the apex, in older cultures with numerous percurrent proliferations, geniculate. Conidiogenous cells 20.5-35.5(-41) \times 3.5-5 μ m, tapering to 1-1.5 μ m below the collarette, monophialidic with a single conidiogenous locus, integrated, terminal, rarely intercalary, extending percurrently, occasionally sympodially, subulate to lageniform, pale brown, older phialide often with an inner septum (becoming encrusted on PCA); collarettes 3-4.5 µm wide, 1.5-2 µm deep, flaring, funnel- to vaseshaped, subhyaline to pale brown. Conidia (3–)3.5–5 × 1.5–2.5 μm (mean \pm SD = 3.8 \pm 0.4 \times 1.9 \pm 0.2 μ m), oblong to long-cuneate, obtusely rounded at the distal end, slightly truncate at the proximal end, hyaline, aseptate, smooth, adhering in slimy whitish heads. Chlamydospores absent. Sexual morph. Not observed.

Habitat and geographical distribution: Saprobe on decaying wood of an unknown host in Belgium.

Notes: The strain CBS 171.76 was initially reported as *Chloridium lignicola* in the species description by Gams & Holubová-Jechová (1976), but our subsequent investigations utilizing both morphological and molecular data have revealed that this isolate is not conspecific with the ex-isotype strain CBS 143.54. Comparative analysis of their DNA sequences revealed the following similarities: 94.9 % in ITS, 99.4 % in LSU, and 96 % in *TEF1*, indicating that they should be considered distinct at the species level. Morphologically, the two isolates also exhibit distinguishing characteristics. The conidia of *Ga. lignicola* are oblong-ellipsoidal to allantoid, measuring $3.5-6.5(-8) \times 1.5-2.5 \, \mu m$, while those of CBS 171.76 are oblong to long-cuneate and shorter, rarely exceeding 4.5 $\, \mu m$ in length. *In vitro*, the conidiophores of CBS 171.76 often form fascicles, with the conidiogenous cells frequently extending percurrently in older

cultures. Moreover, the conidiophores can reach lengths of up to 550 μ m and exhibit conspicuous geniculation. In contrast, the conidiophores of *Ga. lignicola* undergo only slight elongation. Based on these observed differences and genetic distinction in ITS and *TEF1* loci, the strain CBS 171.76 is proposed as a new species.

Papillospora Réblová, gen. nov. MycoBank MB 848564.

Etymology: Papilla (L) a nipple-like protuberance, a small projection, spora (L); referring to verrucose ascospores of the type species.

Type species: Papillospora hebetiseta (Réblová & Gams) Réblová

Description: Colonies effuse, hairy, brown, whitish when sporulating, composed of ascomata, setae and conidiophores. Asexual morph. Setae erect, unbranched, cylindrical, septate, brown, terminal cells cylindrical, clavate or inflated, subhyaline to hyaline, broadly rounded apically, always sterile. Conidiophores macronematous, mononematous, solitary, erect, straight or gently curved, cylindrical, unbranched or sparsely branched, brown. Conidiogenous cells monophialidic or polyphialidic with a single conidiogenous locus, terminal, integrated or intercalary, extending sympodially; collarettes narrow, not flared, hyaline. Conidia ellipsoidal to somewhat asymmetrical, hyaline, aseptate, smooth, adhering in slimy heads. Chlamydospores absent. Sexual morph. Ascomata perithecial, non-stromatic, superficial, globose to subglobose, setose, setae similar to those accompanying conidiophores. Ostiolar canal periphysate. Ascomatal wall brittle, carbonaceous, two-layered. Paraphyses persistent, branching, anastomosing. Asci unitunicate, cylindrical to clavate, shortstipitate, apical ring non-amyloid, 8-spored. Ascospores fusiform, transversely septate, hyaline.

Accepted species: Papillospora hebetiseta.

Notes: The genus Papillospora is placed in a strongly supported Clade B as a sister to Achrochaeta (Réblová et al. 2021b) and is related to Caliciastrum and Caligospora.

Papillospora hebetiseta (Réblová & W. Gams) Réblová, comb. nov. MycoBank MB 849187.

Basionym: Chaetosphaeria hebetiseta Réblová & W. Gams, Mycoscience 41: 133. 2000.

Description: See Réblová & Gams (2000).

Specimen examined: **Ukraine**, Eastern Carpathian Mts., Kvasi near Rachiv, on the right bank of the Tisa river, on decaying wood of *Fagus sylvatica*, 29 Jun. 1997, M. Réblová, M.R. 938 (**holotype** CBS-H 6566, culture ex-type CBS 102340).

Habitat and geographical distribution: Saprobe on decaying wood of Fagus sylvatica and other unidentified host, known from Ukraine and USA (Réblová & Gams 2000, Huhndorf & Fernández 2005).

Notes: Papillospora hebetiseta exhibits a striking resemblance to Stilbochaeta brevisetula (Hughes & Kendrick 1968, Réblová et al. 2021). Both species share dark brown ascomata adorned with sterile setae, which are also present alongside conidiophores. These setae terminate in broadly rounded hyaline to subhyaline cells, and both species produce 3-septate, hyaline, fusiform ascospores of comparable size. However, there are distinguishing



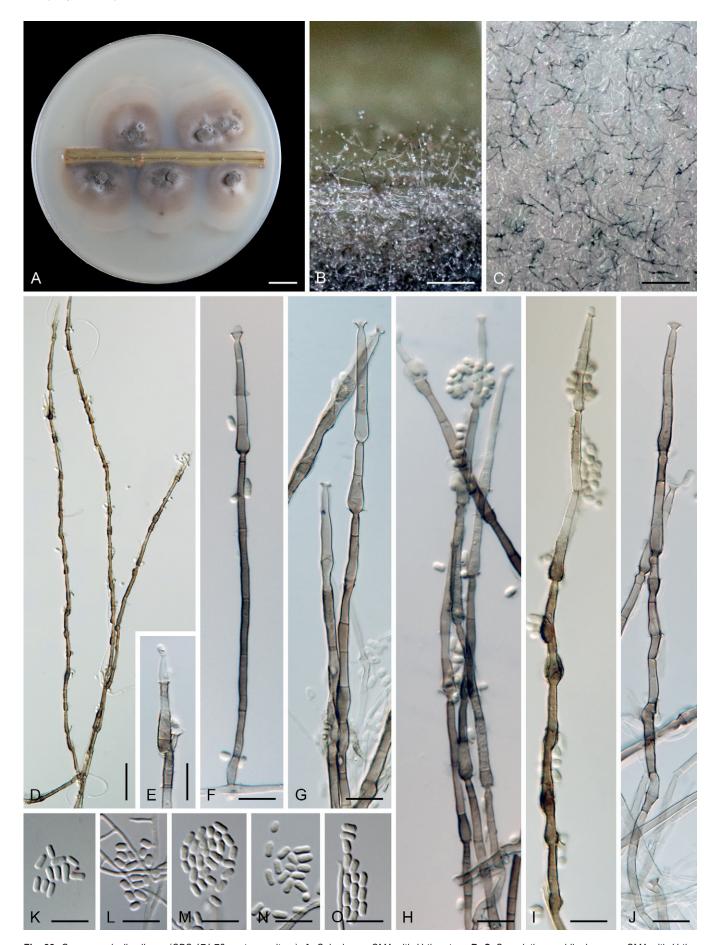


Fig. 22. Gongromerizella silvana (CBS 171.76, ex-type culture). A. Colonies on CMA with Urtica stem. B, C. Sporulating conidiophores on CMA with Urtica stem. D–J. Conidiophores on PCA. K–O. Conidia on MLA. Scale bars: A = 1 cm; B, C = 500 μ m; D–O = 10 μ m.

features that set *S. brevisetula* apart. Specifically, *S. brevisetula* possesses smooth-walled ascospores, while those of *P. hebetiseta* are verrucose. Additionally, the asexual characters of the two species differ. The asexual morph of *Stilbochaeta* produces simple conidiophores growing in tufts with setae and falcate, septate conidia adorned with terminal setulae. In contrast, *Papillospora* produces sparsely branched conidiophores scattered among setae and non-setulate, ellipsoidal conidia. Our phylogenetic analysis demonstrates that these two genera are distantly related. It is worth noting that *Caliciastrum*, which also possesses morphologically similar setae growing on the outer ascomatal wall and accompanying the conidiophores of the asexual morph, falls within the same clade as *Papillospora*.

Psilobotrys (Sacc.) Sacc., Michelia 1: 538. 1879.

Synonyms: Rhinotrichum Corda sect. Psilobotrys Sacc., Michelia 1: 87. 1877.

Chloridium Link sect. Psilobotrys (Sacc.) W. Gams & Hol.-Jech., Stud. Mycol. 13: 39. 1976.

Type species: Psilobotrys minutus (Sacc.) Sacc. [as 'minuta']

Description: For generic delimitation and more information, see Réblová et al. (2022).

Accepted species: Psilobotrys minutus.

Psilobotrys minutus (Sacc.) Sacc. [as 'minuta'], Michelia 1: 538. 1879. Figs 23, 24.

Basionym: Rhinotrichum minutum Sacc., Michelia 1: 87. 1877. Fungi ital. autogr. del. Tab. 62. 1877.

Synonyms: Chloridium minutum (Sacc.) Sacc., Syll. Fung. 4: 321. 1886

Chloridium botryoideum var. minutum (Sacc.) W. Gams & Hol.-Jech., Stud. Mycol. 13: 43. 1976.

Description on the natural substrate: Colonies effuse, hairy, dark brown to black, whitish when sporulating, composed of conidiophores and ascomata. Asexual morph. Conidiophores macronematous, forming two layers; longer conidiophores 100-165 × 3-4.5 μm, base bulbous to somewhat lobate 6.5-11(-14) µm, setiform, solitary, crowded or caespitose, erect, straight or slightly curved, cylindrical, septate, unbranched, dark brown, paler upwards, with several percurrent proliferations; they are accompanied by smaller and slightly paler conidiophores 27-96 × 2-2.5 µm. Conidiogenous cells 12-23.5 \times 2.5-3.5 μ m tapering to 1-1.5 μ m below the collarette, monophialidic with a single conidiogenous locus, rarely polyphialidic with 1(-2) phialidic apertures, integrated, terminal, or intercalary, extending percurrently and sympodially, cylindrical, pale brown, hyaline towards the tip; collarettes 1.5–2.5 µm wide, 1-2 µm deep, flaring, narrowly funnel-shaped, hyaline, disintegrate soon. Conidia $(2.5-)3-4 \times 2-3 \mu m$ (mean $\pm SD = 3.3 \pm 0.3 \times 2.4 \pm 0.3 \times 2.4$ 0.3 µm), short ellipsoidal to subglobose, obliquely apiculate at the base, sometimes tapering towards both ends, hyaline, aseptate, smooth, adhering in whitish, imbricate chains or slimy heads. Sexual morph. Ascomata perithecial, superficial, non-stromatic, scattered or in small groups, subglobose, 150-220 µm diam, 170-220 µm high, papillate, dark brown, glossy. Ostiolar canal periphysate. Ascomatal wall two-layered, fragile, carbonaceous, 14–28 µm thick; outer layer composed of polyhedral, thick-wall, dark brown cells, inner layer of more elongated and narrower, hyaline, thin-walled cells. Paraphyses persistent, 2-3.5 µm wide,

hyaline, septate, longer than the asci. Asci 79–95(–108) × 8.5–9.5 μ m (mean \pm SD = 88.3 \pm 9.9 × 8.9 \pm 0.6 μ m), cylindrical-clavate, rounded at the apex, short-stipitate, apical ring non-amyloid, 3–3.5 μ m wide, $ca.1~\mu$ m deep, 8-spored. $Ascospores~(10–)11–14.5~\times~3.5–4.5~\mu$ m (mean \pm SD = 12.4 \pm 1.2 × 4.1 \pm 0.3 μ m), ellipsoidal-fusiform, 3-septate, hyaline, finely verrucose, obliquely 1–2-seriate in the ascus.

Culture characteristics: On CMD colonies 24–25 mm diam, circular, flat to slightly raised, margin entire, mucoid to sparsely lanose, grey-brown, darker in the middle, reverse dark grey-brown. On MLA colonies 36–38 mm diam, convex with flat margin, margin entire, velvety-lanose, floccose, funiculose, white-beige, sometimes with dark grey concentric rings, finely furrowed, reverse white-beige. On OA colonies 26–28 mm diam, flat, margin entire, partly mucoid, cobwebby to velvety, dark brown, white-brown centrally, with a creamy outer zone of submerged growth, reverse of the same colour. On PCA colonies 23–25 mm diam, flat, margin entire, lanose, whitish to grey-brown centrally, olivaceous brown towards the periphery, reverse dark olivaceous brown. Sporulation was sparse on CMD, MLA and OA, absent on PCA.

Description in culture: On MLA, colonies effuse, hairy, vegetative hyphae 1.5–2.5 μm diam, sometimes monilioid, 4.5–9.5 μm diam, branched, septate, hyaline, smooth. Asexual morph. Conidiophores, conidiogenous cells and conidia are similar to those from nature. Conidiophores 55–205 × 2–3.5 μm, sometimes sparsely branched, proliferating percurrently in older cultures (> 2 mo), sometimes arising from melanized monilioid hyphae. Conidiogenous cells 14–29 × 2.5–3.5 μm tapering to 1(–1.5) μm below the collarette, collarettes 1.5–2 μm wide, 1.5–2 μm deep. Conidia 2.5–3.5(–4) × 1.5–2.5 μm (mean ± SD = 3.1 ± 0.3 × 2.1 ± 0.2 μm). Chlamydospores absent. Sexual morph. Not observed.

Specimens examined: Belgium, Ardennes, near Abbaye de St. Rémy, on decaying wood, Sep. 1975, W. Gams (culture CBS 600.75B); ibid., (culture CBS 629.75). Czech Republic, South Moravian region, Břeclav district, Lanžhot, Ranšpurk National Nature Reserve, on decaying wood of Ulmus sp., 26 Oct. 2018, M. Réblová, M.R. 4000B (PRA-21535, culture CBS 145632); Olomouc Region, Rychlebské hory Mts., Vápenná near Jeseník, in forest on the valley of Ztracený potok, on decaying wood of Fagus sylvatica, 9 Aug. 1971, V. Holubová-Jechová (PRM 794025). Germany, Lower Saxony, Wolfenbüttel district, Elm near Schöppenstedt, on decaying twig of Fraxinus excelsior, Jan. 1975, W. Gams & K.H. Domsch (culture CBS 247.75). Italy, Province of Treviso, Veneto region, forests of Montello Mt., on decaying wood of Quercus sp., Sep. 1874, P.A. Saccardo (holotype of Rhinotrichum minutum PAD, not seen; microscopic slide ex holotype DAOM 41259); locality unknown, on decaying wood of Populus nigra subsp. nigra 'Italica', date unknown, P.A. Saccardo (DAOM 41258). The Netherlands, Friesland province, Isle of Ameland, near Buren, on dead twig of Acer sp., Nov. 1973, W. Gams (culture CBS 877.73); ibid., on dead twig of Acer pseudoplatanus, 28 Oct. 1973, W. Gams (culture CBS 223.74); Limburg province, Schaesberg, on decaying wood, Jun. 1974, W. Gams (culture CBS 564.74). Slovak Republic, Bratislava, Kováčová near Podunajské Biskupice, in forest Kopáč, on decaying wood of Cornus sanguinea, V. Holubová-Jechová (PRM 794105); Velký Krtíš, Cerovo, in the valley of Litavica river on slopes of Čabrad Mt., alt. 248 m, on decaying wood of Acer pseudoplatanus, 12. Aug. 1975, V. Holubová-Jechová (PRM 794079); Velký Krtíš, in the valley of Csurgo river near Opava and Kosihovce, alt. 340 m, on decaying wood of Robinia pseudoacacia, 12. Aug. 1975, V. Holubová-Jechová (PRM 796742); Vihorlat Mts., Remetské Hámre, in the forest on slopes of Mt. Veža near Morské Oko lake, on decaying wood of Fagus sylvatica, 10 Aug. 1972, V. Holubová-Jechová (PRM 794054); ibid., Kremnické pohorie Mts., Badín near Bánská Bystrica, in the forest Badínský prales in the valley of Badínský potok stream, on



Fig. 23. *Psilobotrys minutus.* **A.** Ascomata associated with conidiophores. **B, C.** Sporulating conidiophores. **D.** Asci. **E.** Ascospores. **F.** Paraphyses. **G, M.** Conidia. **H–L.** Conidiophores. A, D–J. From nature. B, C, K–M. On MLA. A, D–F. PRM 794079. B. CBS 145632. C, L. CBS 629.75. G. PRM 794039. H–J. PRM 794025. K. CBS 247.75. M. CBS 877.73. Scale bars: A, B = 500 μm; C = 200 μm; D–G, M = 10 μm; H–L = 20 μm.

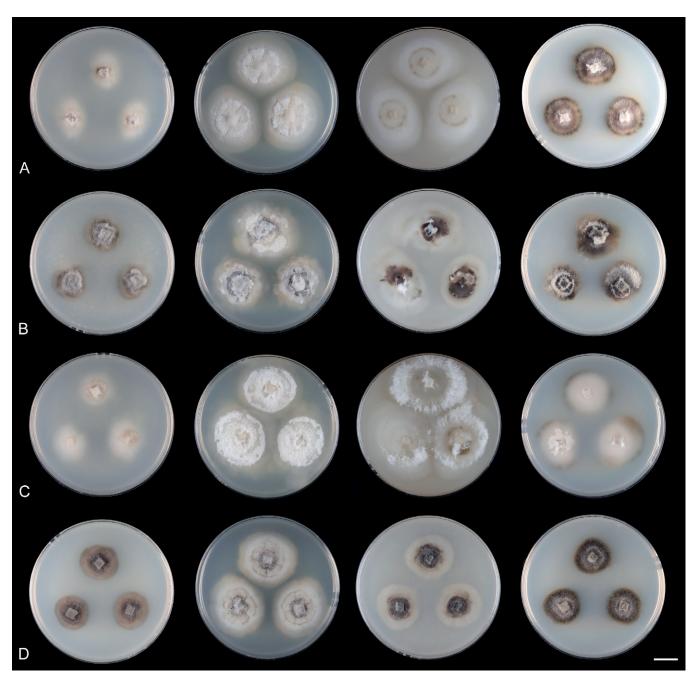


Fig. 24. Diversity of colony morphology in *Psilobotrys minutus* on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. A. CBS 247.75. B. CBS 600.75B. C. CBS 877.73. D. CBS 145632. Scale bar = 1 cm.

decaying wood of *Fagus sylvatica*, 9. Aug. 1969, V. Holubová-Jechová (PRM 794039). **UK**, England, Somerset, Batheaston, on decaying wood of *Ulmus* sp., 30 Mar. 1865, C.E. Broome (K(M) 264818); Somerset, St Catherine, on decaying wood, 30 Mar. 1871, C.E. Broome (K(M)264817); Greater London, Kew, arboretum, on decaying wood, Aug. 1880, collector unknown (K(M) 85524).

Habitat and geographical distribution: This species is a common saprobe on decaying wood of various hosts, for example Abies alba, Acer sp., Acer pseudoplatanus, Betula verrucosa, Carpinus betulus, Cornus sanguinea, Fagus sylvatica, Fraxinus excelsior, Eucalyptus sp., Populus alba, Populus nigra subsp. nigra 'Italica', Quercus petraea, Q. robur, Robinia pseudacacia, Sorbus aucuparia and Ulmus sp. It is known from Austria, Belgium, Czech Republic, France, Italy, Netherlands, Slovak Republic, United Kingdom and USA (Saccardo 1877, Gams & Holubová-Jechová 1976, this study).

Notes: Psilobotrys minutus is a holomorphic species that bears a strong resemblance to Ch. innumera. However, there are several distinguishing features that set P. minutus apart. Firstly, P. minutus exhibits conidia that are short ellipsoidal to subglobose and obliquely apiculate at the base, whereas Ch. innumera produces elongate-ellipsoidal to cylindrical conidia, sometimes obliquely apiculate at the base. Additionally, the conidiophores of P. minutus terminate into a short narrowly funnel-shaped collarette, whereas in Ch. innumera, the conidiophores taper to a very narrow phialidic tip with a short tubular collarette. Although both species produce conidiophores in two layers. P. minutus has conidiophores of the lower layer shorter with monophialides that rarely extend sympodially, while Ch. innumera possesses shorter conidiophores with regularly sympodially extending polyphialides. Another distinguishing feature lies in the ascospore ornamentation, with P. minutus displaying a finely verrucose surface, whereas Ch. innumera has smooth ascospores.

All strains displayed comparable morphology *in vitro*, with only moderate variability observed. Notably, strain CBS 877.73 exhibited either a lack of pigmented mycelium or a reduction in aerial hyphae on different media.

Spicatispora Réblová, gen. nov. MycoBank MB 848565.

Etymology: Spicatus (L) pointed, *spora* (L); referring to ascospores that are tapering strongly towards the ends.

Type species: Spicatispora fennica (P. Karst.) Réblová

Description: Colonies effuse, hairy, dark brown, whitish when sporulating, composed of conidiophores and ascomata. Asexual morph. Conidiophores macronematous, mononematous, solitary, erect, straight or slightly flexuous, cylindrical, unbranched, dark brown, paler upwards. Conidiogenous cells monophialidic with a multiple conidiogenous locus, terminal, integrated, cylindrical to narrowly lageniform, paler than the conidiophores, extending percurrently, the tip with minute annellations often protruding beyond the collarette; collarettes flaring, funnel-shaped. Conidia ellipsoidal-oblong to suballantoid, with a pore at one or both ends, brown, aseptate, smooth, adhering in slimy heads. Chlamydospores absent. Sexual morph. Ascomata perithecial, superficial, non-stromatic, subglobose, dark brown, glabrous, papillate. Ostiolar canal periphysate. Ascomatal wall two-layered, brittle, carbonaceous. Paraphyses persistent, branching, anastomosing. Asci unitunicate, cylindrical, short-stipitate, apical ring non-amyloid, 8-spored. Ascospores elongate-fusiform, tapering strongly towards the ends immediately after the middle septum, transversely septate, hvaline.

Accepted species: Spicatispora carpatica, S. fennica.

Notes: Spicatispora is a holomorphic genus comprising two species, S. carpatica and S. fennica. Phylogenetic analyses demonstrate its close relationship with Fusichloridium and Capillisphaeria. When compared to other genera that have been segregated from Chaetosphaeria and Chloridium, Spicatispora is notably set apart by its brown, ellipsoidal to suballantoidal conidia with a pore present at one or both ends. Furthermore, it can be distinguished by its septate, elongate-fusiform ascospores, which taper strongly towards the ends immediately after the median septum. The sexual morph has been observed only in S. fennica.

Spicatispora carpatica (Hol.-Jech. & Révay) Réblová, *comb.* **nov.** MycoBank MB 849188.

Basionym: Chloridium carpaticum Hol.-Jech. & Révay, Acta bot. hung. 33: 63. 1987.

Synonyms: Craspedodidymum carpaticum (Hol.-Jech. & Révay) W.P. Wu & Y.Z. Diao, Fungal Diversity 116: 274. 2022.

Craspedodidymum guatemalense Figueroa et al., Mycotaxon 133: 316. 2018.

Description: See Holubová-Jechová & Révay (1987), Figueroa et al. (2018) and Wu & Diao (2022).

Specimens examined: Czech Republic, South Bohemian region, Šumava Mts. National Park, Stožec, Spáleniště Mt., on inner side of the decaying bark of *Sorbus aucuparia* and on old ascomata of *Lasiosphaeria* sp., 28 Aug. 2000, M. Réblová, M.R. 1689 (PRA-21536); *ibid.*, M.R. 2094 (PRA-21537).

Habitat and geographical distribution: Saprobe on decaying wood and bark of Fagus sylvatica, Quercus sp., Sorbus aucuparia and other unknown hosts, known from China, Czech Republic, Guatemala and Hungary (Holubová-Jechová & Révay 1987, Figueroa et al. 2018, Wu & Diao 2022, this study).

Notes: Spicatispora carpatica bears a strong resemblance to *S. fennica*, but can be differentiated by its larger conidia, measuring (9.5–)10–14 × 3.5–5.5 µm fide Holubová-Jechová & Révay (1987), 8–12.5 × 4–5 µm fide Wu & Diao (2022), and (9.5–)10–12 × 4–5 µm (as observed in this study). In comparison, *S. fennica* displays shorter conidia measuring 8.5–9.5(–10) × 3–4.5 µm (holotype, Réblová & Gams 1999), and 8–9.5(–11) × 3–3.5(–4) µm (this study).

Spicatispora fennica (P. Karst.) Réblová, **comb. nov.** MycoBank MB 849189. Fig. 25.

Basionym: Lasiosphaeria britzelmayri Sacc. subsp. fennica P. Karst., Rev. Mycol. 9: 160. 1887.

Synonyms: Acanthostigma fennicum (P. Karst.) Berlese, Icon. Fung. 1: 102. 1894.

Chaetosphaeria fennica (P. Karst.) Réblová & W. Gams, Czech Mycol. 51: 24. 1999.

Additional synonyms listed in Réblová & Gams (1999).

Description: See Réblová & Gams (1999).

Culture characteristics: On CMD colonies 9–10 mm diam. circular. slightly raised, margin irregular to lobate, velvety, finely furrowed, furrows obscured by aerial mycelium, isabelline-beige on the inoculation block, white towards the margin with irregular moist brown spots due to pigmented submerged mycelium, reverse dark brown. On MLA colonies 11-12 mm diam, circular, convex, weakly undulate, velvety, floccose, furrowed, beige centrally, isabellinegrey towards the periphery, white at the margin, reverse dark brown. On OA colonies 12-13 mm diam, circular, raised, margin entire, velvety, moist at the margin, developing deep cracks at the centre, white with a pale yellow to yellow-grey outer zone, pale ochre pigment diffusing into the agar, reverse brown. On PCA colonies 11-12 mm diam, circular, flat, margin entire, velvety, mucoid and smooth towards the periphery, whitish centrally, light ochre-beige with an orange-ochre zone, reverse pale ochre-beige. Sporulation was sparse on PCA, absent on other media, on MLA conidiophores appeared after prolonged incubation (6–8 wk). Pale ochre pigment diffusing into agar on CMD, MLA, PCA, ochre-brown diffusible pigment was formed on OA.

Description in culture: On MLA, colonies effuse, hairy, vegetative hyphae 1.5–3.5(–4) μm diam, branched, septate, hyaline, smooth. Asexual morph. Conidiophores, conidiogenous cells and conidia are similar to those from nature. Conidiophores 38–182 × 2.5–4.5 μm, macronematous, solitary, erect, straight or slightly flexuous, cylindrical, unbranched, with several percurrent proliferations, dark brown, paler towards the apex. Conidiogenous cells 14.5–26.5 × 3.5–4.5(–5) μm, tapering to 1.5–2 μm below the collarette, monophialidic with multiple conidiogenous loci, extending percurrently, the tip often protruding beyond the collarette and with minute annellations, integrated, terminal, cylindrical to elongated lageniform, pale brown, hyaline to subhyaline towards the apex; collarettes 2.5–4 μm wide, 2–3.5 μm deep, flaring, shortly funnel-shaped, hyaline. Conidia 3.5–5.5(–6.5) × 1.5–2.5 μm (mean ± SD = 4.6 ± 0.5 × 2.1 ± 0.2 μm), ellipsoidal-oblong to suballantoidal,

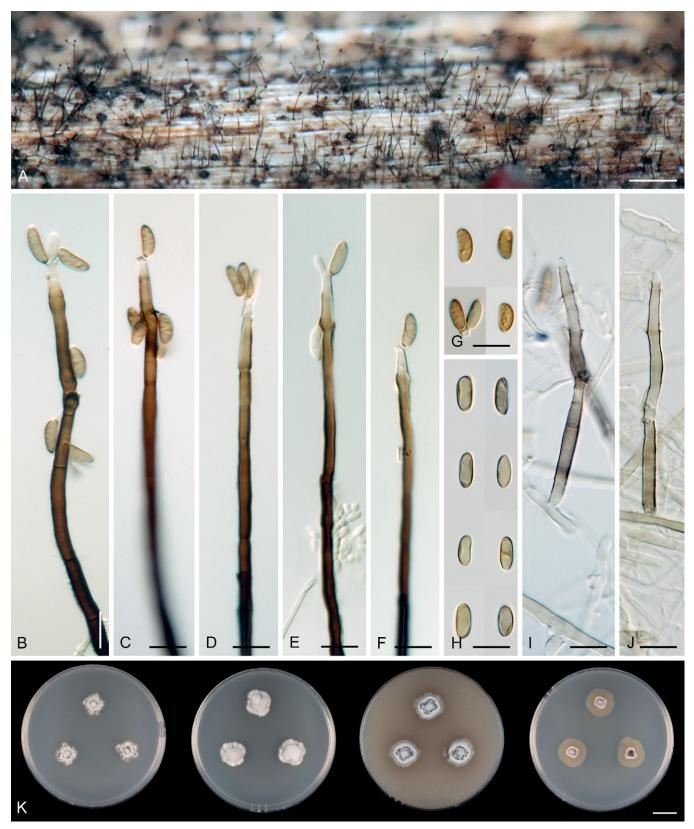


Fig. 25. Spicatispora fennica. **A.** Colony of sporulating conidiophores. **B–F, I, J.** Conidiophores. **G, H.** Conidia. **K.** Colonies on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. A–G. PRA-21538. H–J. CBS 101641. Scale bars: A = 500 μm; B–J = 10 μm; K = 1 cm.

hyaline, pale brown at maturity, aseptate, smooth, with a pore at one or both ends, adhering in slimy brown heads. *Chlamydospores* absent. *Sexual morph*. Not observed.

Specimens examined: Czech Republic, South Bohemian region, Šumava Mts. National Park, Modrava, Studená hora Mt., on decaying wood under the bark of *Picea abies*, 25 Aug. 2000, M. Réblová, M.R. 1767 (PRA-

21538); *ibid.*, M.R. 2524 (PRA-21539). **Finland**, Mustiala Myllypera, on old stromata of *Eutypa* sp. on decaying bark of *Betula* sp., 28 Jul. 1887, P.A. Karsten, 929 (**holotype** of *Lasiosphaeria britzelmayri* subsp. *fennica*, H). **Ukraine**, Eastern Carpathian Mts., Boržava Massif, Guklivij, on decaying wood of *Abies alba*, 21 Jul. 1998, M. Réblová, M.R. 1343 (PRA-21540, culture CBS 101641).

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Habitat and geographical distribution: Saprobe on decaying wood of Abies alba, Picea abies and old stromata of Eutypa sp., known from the Czech Republic, Finland and Ukraine (Karsten 1887, this study).

Notes: Spicatispora fennica is a rare species, characterized by brown, suballantoidal to ellipsoidal-oblong conidia with a pore at one or both ends formed on multiple conidiogenous loci, and elongate-fusiform 3-septate ascospores that taper strongly towards the ends. It can be confused with Cacumisporium acutatum by its ascospores, but the ascospores in latter species are much less tapered towards the ends and somewhat shorter (28–)30.5–38(–44) × 3–4(–5) µm vs. (34.5–)36.5–42(–43) × (3.5–)4(–4.5) µm fide Réblová & Gams (1999). Moreover, conidia of C. acutatum remain hyaline at maturity; they are 1-septate and cylindrical-clavate.

The chloridium-like asexual morph has been first observed by Réblová & Gams (1999) in the holotype of *S. fennica* (Karsten 1887), and the sexual-asexual connection has been suggested by the joint occurrence of conidiophores and ascomata. In this study, we experimentally confirmed this relationship. In the recently collected material, conidiophores from nature were 155–250 × 3.5–5 μm , 11–12.5 μm wide at the bulbous base, phialides 11–21 ×3.5–4 μm , the conidiogenous tip with multiple loci extended beyond the collarette, collarette 3.5–4.5 μm wide, 1.5–2 μm deep, conidia 8–9.5(–11) × 3–3.5(–4) μm . These morphological structures are well comparable with those in the holotype.

Spicatispora fennica is very similar to S. carpatica; for comparison, see notes to the latter species.

Vermiculariopsiellales Hern.-Restr. *et al.*, Stud. Mycol. 86: 91. 2017.

Vermiculariopsiellaceae Hern.-Restr. et al., Stud. Mycol. 86: 91. 2017

Chloridiopsiella Réblová gen. nov. MycoBank MB 849139.

Etymology: Chloridiopsis and -ella (L) diminutive; here referring to similarity to the genus Chloridiopsis.

Type species: Chloridiopsiella preussii (W. Gams & Hol.-Jech.) Réblová

Description: Colonies effuse, hairy, brown, whitish to beige or pale brown when sporulating. Asexual morph. Conidiophores macronematous, mononematous, forming a single layer, solitary, scattered, erect, straight or flexuous, cylindrical, unbranched, with several percurrent proliferations, brown. Conidiogenous cells monophialidic with a single conidiogenous locus, terminal, integrated, extending percurrently, subcylindrical, paler than the conidiophores; collarettes flaring, funnel-shaped. Conidia oblong to obovate to long-cuneiform, hyaline, with protracted maturation, becoming beige to pale brown upon aging (in culture), aseptate, smooth, accumulating in slimy heads. Chlamydospores absent. Sexual morph. Unknown.

Accepted species: Chloridiopsiella preussii.

Notes: The genus Chloridiopsiella (Cha.) is proposed within the order Vermiculariopsiellales for a single species, Cha. preussii, which was originally classified under the genus Chloridium. It is introduced for fungi with aseptate, oblong to obovate to long-cuneiform, hyaline conidia that may become beige to pale brown

in mass at maturity. The phialides extend only percurrently and conidiophores are pale brown, never setiform, forming a single layer. It is closely related to *Chloridiopsis*.

Chloridiopsiella preussii (W. Gams & Hol.-Jech.) Réblová, *comb. nov.* MycoBank MB 849182. Figs 26, 27.

Basionym: Chloridium preussii W. Gams & Hol.-Jech., Stud. Mycol. 13: 35. 1976.

Synonyms: ?Acrostalagmus geniculatus Preuss, Linnaea 24: 125. 1851.

Acrostalagmus (?Stachylidium) geniculatus (Preuss) Sacc., Syll. Fung. 4: 164. 1886.

Stachylidium geniculatum (Preuss) Lindau, Rabenh. Krypt.-Fl. 1(8): 740. 1906.

Synonymy adopted from Gams & Holubová-Jechová (1976).

Culture characteristics: On CMD colonies 24–25 mm diam, circular, flat, margin entire, mucoid-waxy, glossy, smooth, or finely wrinkled, pink-beige with an outer creamy zone of submerged growth, reverse beige. On MLA colonies 35–37 mm diam, circular, convex, margin entire to fimbriate, sparsely lanose, floccose, funiculose, zonate, beige with dark brown concentric zones, reverse beige, zonate. On OA colonies 39–40 mm diam, circular, flat, margin fimbriate, cobwebby to mucoid, zonate, beige to pale brown, with dark brown and olivaceous brown concentric zones at the margin, reverse beige. On PCA colonies 33–34 mm diam, circular, flat, margin fimbriate, velvety, cobwebby at the margin, beige, pale brown towards the periphery with an outer isabelline zone of submerged growth, reverse beige, creamy at the margin. Sporulation was sparse on CMD and OA, abundant on MLA and PCA.

Description in culture: On MLA, colonies effuse, hairy, vegetative hyphae 1.5–2.5 µm diam, branched, septate, hyaline, smooth. Asexual morph. Conidiophores 32–113 × 3.5–4.5 µm, macronematous, solitary, erect, straight or flexuous, cylindrical, septate, unbranched, brown, with 1-4 percurrent proliferations, sometimes reduced to single conidiogenous cells. Conidiogenous cells 12.5–29 \times 3–4 μ m, tapering to 1.5–2 μ m below the collarette, monophialidic with a single conidiogenous locus, integrated, terminal, extending percurrently, subcylindrical, pale brown to subhyaline, paler towards the tip; collarettes 3-4.5 µm wide, 2-4 µm deep, flaring, funnel- to cup-shaped, subhyaline. Conidia (3-) $3.5-4.5(-5) \times 2-2.5 \mu m$ (mean \pm SD = $4.0 \pm 0.4 \times 2.2 \pm 0.2 \mu m$), ellipsoidal, oblong to obovate to long-cuneiform, hyaline, aseptate, smooth, accumulating in slimy whitish (on CMD, OA) or beige to pale brown (on MLA, PCA) heads. Chlamydospores absent. Sexual morph. Unknown.

Specimens examined: **Germany**, North Rhine-Westphalia, Neuenheerse, Teutoburger Wald, on decaying wood, Sep. 1972, W. Gams (culture CBS 247.76). **The Netherlands**, Utrecht province, Groeneveld near Baarn, on wood of *Taxus baccata*, 17 Dec. 1972, H.A. van der Aa (culture ex-type CBS 230.75); Utrecht province, Baarn, estate Pijnenburg, on decaying wood, Aug. 1972, W. Gams (culture CBS 265.76).

Habitat and geographical distribution: Saprobe on decaying wood of *Taxus baccata* and other unidentified hosts, known from Germany and the Netherlands (Gams & Holubová-Jechová 1976).

Notes: Our molecular analysis confirmed that the ex-type strain of *Chl. preussii*, CBS 230.75, is not conspecific with its presumed sexual morph *Chaetosphaeria preussii*. Additionally, *Chl. preussii* is not related to the genera *Chloridium* and *Chaetosphaeria* (both

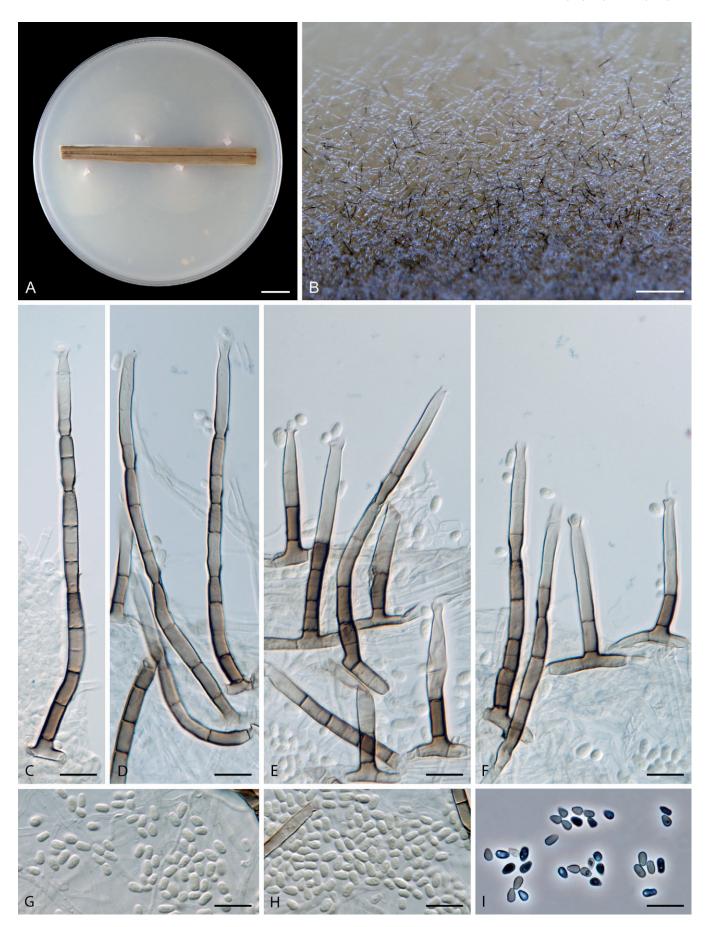


Fig. 26. Chloridiopsiella preussii. A. Colonies. B–F. Conidiophores. G–I. Conidia. A, B. On CMA with Urtica stem. C–I. On MLA. A–H. CBS 230.75, ex-type culture. I. CBS 247.76. Scale bars: A = 1 cm; B = 500 μ m; C–I = 10 μ m.

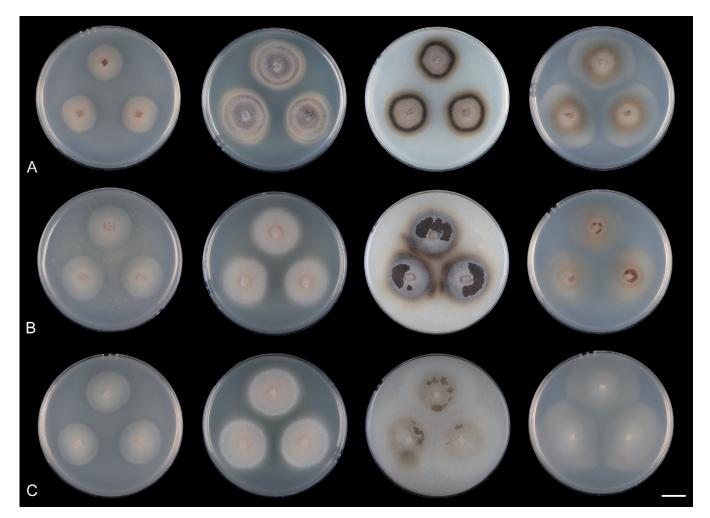


Fig. 27. Diversity of colony morphology in *Chloridiopsiella preussii* on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. **A.** CBS 230.75, ex-type culture. **B.** CBS 247.76. **C.** CBS 265.76. Scale bar = 1 cm.

members of *Chaetosphaeriales*), but it was resolved as a sister to *Chloridiopsis* in *Vermiculariopsiellales*, and consequently transferred to the new genus *Chloridiopsiella*. For more information and morphological comparison with similar species, see notes to *Geniculoseta preussii* and also Discussion.

Chloridiopsis Réblová, gen. nov. MycoBank MB 848562.

Etymology: Chloridium and -opsis (Greek) resemblance; referring to its similarity to the genus Chloridium.

Type species: Chloridiopsis constrictospora (Crous et al.) Réblová

Description: Colonies effuse, hairy, dark brown, whitish when sporulating. Asexual morph. Conidiophores macronematous, mononematous, forming two layers, setiform, mostly fasciculate, sometimes solitary, erect, straight or flexuous, cylindrical, unbranched, with several percurrent proliferations, brown. Conidiogenous cells monophialidic with a single conidiogenous locus, terminal, integrated, rarely discrete (only in culture), extending percurrently and sympodially (only in culture), subcylindrical to lageniform, pale brown to subhyaline; collarettes flaring, funnel-shaped. Conidia oblong to cylindrical, constricted in the middle, hyaline, aseptate, smooth, accumulating in slimy heads. Chlamydospores absent. Sexual morph. Unknown.

Accepted species: Chloridiopsis constrictospora, Chs. syzygii.

Notes: The genus Chloridiopsis (Chs.) harbours two species, one of which was originally placed in Chloridium, as Chs. constrictospora, the second species is Chs. syzygii described as new to science. Its closest relative is Chloridiopsiella and they form a moderately supported clade in Vermiculariopsiellales.

Chloridiopsis constrictospora (Crous *et al.*) Réblová, **comb. nov.** MycoBank MB 849183. Fig. 28.

Basionym: Chloridium constrictospora Crous et al., Canad. J. Bot. 73: 228. 1995.

Culture characteristics: On CMD colonies 48–52 mm diam, circular, flat, margin entire to fimbriate, cobwebby to sparsely lanose, floccose, pink beige with a brown outer zone of submerged growth, reverse dark brown. On MLA colonies 80–84 mm diam, circular, slightly convex, margin entire, lanose, finely furrowed, whitish, olivaceous brown at the margin, reverse dark brown. On OA colonies 98–104 mm diam, circular, flat, margin entire, velvety-lanose, funiculose at the inoculation block, partially mucoid at the margin, grey to whitish-grey, mosaic brown to yellow brown at the periphery, reverse dark grey-brown. On PCA colonies 88–90 mm diam, circular, flat, margin entire, cobwebby, floccose, funiculose, white-beige with irregular brown spots, olivaceous beige towards the periphery, reverse beige-brown. Sporulation was abundant on MLA and OA, sparse on PCA, absent on CMD.

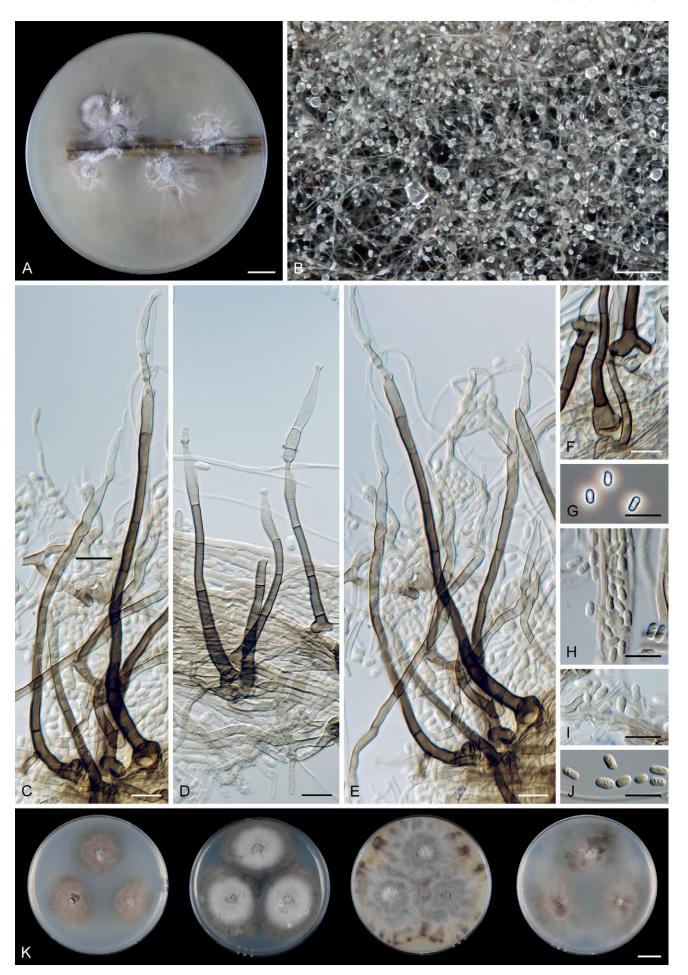


Fig. 28. Chloridiopsis constrictospora (CBS 432.92, ex-type culture). **A.** Colonies. **B.** Sporulating conidiophores. **C–E.** Conidiophores. **F.** Base of conidiophores. **G–J.** Conidia. **K.** Colonies on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. A, B. On CMA with *Urtica* stem. C–J. On OA. Scale bars: A, K = 1 cm; B = 500 μ m; C–J = 10 μ m.

Description in culture: On MLA, colonies effuse, hairy, vegetative hyphae 1.5-2.5 µm diam, sparsely branched, septate, hyaline to subhyaline, pale brown in mass, smooth. Asexual morph. Conidiophores macronematous, forming two layers; longer conidiophores 100-182 × 3.5-6 µm, base bulbous or lobate 5.5-10.5 µm wide, setiform, solitary or fasciculate, erect, straight or flexuous, cylindrical, septate, unbranched, dark brown, gradually paler towards the apex, with 1-6 percurrent proliferations; they are accompanied by smaller and paler conidiophores 36-92 × 2.5-3.5 µm, which are sometimes reduced to single conidiogenous cells. Conidiogenous cells 14-29 × 3.5-4.5(-5.5) µm, tapering to 1.5-2 µm below the collarette, monophialidic with a single conidiogenous locus, integrated, terminal, extending percurrently, sometimes sympodially, subcylindrical to lageniform, pale brown to subhyaline; collarettes 2.5-4 µm wide, 2-3.5(-4.5) µm deep, flaring, funnelshaped, subhyaline to pale brown. *Conidia* 3.5–5.5(–6.5) × 1.5–2.5 μ m (mean \pm SD = 4.6 \pm 0.5 \times 2.1 \pm 0.2 μ m), oblong to cylindrical, slightly constricted in the middle, sometimes tapering and truncate at the base, which can be slightly eccentric, hyaline, aseptate, smooth, accumulating in slimy whitish heads. Chlamydospores absent. Sexual morph. Unknown.

Specimen examined: **South Africa**, KwaZulu-Natal province, Kwambonambi, leaf litter of *Syzygium cordatum*, Feb. 1992, M.J. Wingfield (**holotype** PREM 51688, culture ex-type CBS 432.92 = CPC 508).

Habitat and geographical distribution: Saprobe on leaf litter of Syzygium cordatum, known from South Africa.

Notes: Chloridiopsis constrictospora is well distinguished by oblong to cylindrical conidia that are slightly constricted in the middle. In culture, setiform, dark brown conidiophores grow in bundles with shorter and paler conidiophores, which is consistent with the observations from nature (Crous et al. 1995). This species is very similar to Chs. syzygii, but the two species are well distinguished by genetic distances in ITS, TEF1 and RPB2 genes; for comparison, see notes to Chs. syzygii.

Chloridiopsis syzygii Réblová, *sp. nov.* MycoBank MB 849184. Fig. 29.

Etymology: Syzygium; referring to the host plant.

Typus: **Cuba**, locality unknown, on a leaf of *Syzygium jambos*, 6 May 1993, R.F. Castañeda-Ruiz (**holotype** designated here PRA-21517 as dried culture, culture ex-type CBS 564.93 = INIFAT C93/218-1).

Culture characteristics: On CMD colonies 64–66 mm diam, circular, flat, margin entire to fimbriate, cobwebby, somewhat mucoid at the margin, brown-grey, pale brown towards the periphery, whitish-grey on the inoculation block, reverse brown. On MLA colonies 84–90 mm diam, circular, raised, flat margin, lanose, floccose, beige, dark brown to cinnamon brown at the margin, reverse dark brown. On OA colonies 100–106 mm diam, circular, flat, margin entire to fimbriate, partially mucoid, cobwebby at the periphery, dark brown with beige spots, grey-brown at the margin, reverse of the same colour. On PCA colonies 80–86 mm diam, circular, flat, margin fimbriate to rhizoidal, velvety to cobwebby, mucoid towards the margin, beige-brown, with a dark brown outer zone of submerged growth, reverse dark brown. Sporulation was abundant on MLA, OA, sparse on PCA, absent on CMD.

Description in culture: On MLA, colonies effuse, hairy, vegetative hyphae 1.5-2 µm diam, branched, septate, hyaline, sometimes pale brown, some hyphae monilioid. Asexual morph. Conidiophores macronematous, forming two layers; longer conidiophores 97-213 × 4.5–5.5 μm, setiform, base bulbous or somewhat lobate 6.5–12 µm wide, solitary or fasciculate, erect, straight or slightly flexuous, cylindrical, septate, unbranched, dark brown, gradually paler towards the tip, with several percurrent and sympodial proliferations; they are accompanied by smaller and paler conidiophores 28-89 × 2.5–4 µm, base bulbous 4.5–6 µm wide, sometimes reduced to single conidiogenous cells. Conidiogenous cells 17.5-26 × 3-4 μm, tapering to 1–2 μm below the collarette, monophialidic with a single conidiogenous locus, seldom polyphialidic, integrated, terminal, extending percurrently and sympodially, lageniform to subcylindrical, pale brown to subhyaline; collarettes 2.5-3 µm wide, 2-2.5 µm deep, flaring, funnel-shaped, subhyaline. Conidia $3.5-4.5(-5) \times 1.5-2 \mu m \text{ (mean } \pm \text{SD} = 4.1 \pm 0.3 \times 1.7 \pm 0.1 \mu m),$ oblong to cylindrical or slightly asymmetrical, sometimes tapering towards one end, some conidia slightly constricted in the middle. base may be somewhat eccentric, apiculate, hyaline, aseptate, smooth, accumulating in slimy whitish heads. Chlamydospores absent. Sexual morph. Unknown.

Habitat and geographical distribution: Saprobe on leaf litter of Syzygium jambos, known from Cuba.

Notes: Chloridiopsis syzygii is the closest relative to Chs. constrictospora. They represent sibling species in a strongly supported monophyletic clade. It is challenging to distinguish them in culture, both species form dark setiform conidiophores accompanied by smaller and paler conidiophores, and share oblong to cylindrical hyaline conidia with overlapping size. The conidia of Chs. constrictospora are regularly constricted in the middle, while the conidia of Chs. syzygii seldom show a similar constriction on both sides. Both species are saprobes on leaf litter of Syzygium spp. Comparison of their DNA showed that the sequence identity in ITS and two protein coding genes supports their specific distinction (90.5 % sequence identity in ITS, 88 % in TEF1 and 96.5 % in RPB2).

DISCUSSION

The revised concept of Chloridium, as presented by Réblová et al. (2022), provided a new perspective on this genus. In addition to the simplest morphological form exhibited by members of the sect. Chloridium, the genus now also includes species distributed in other sections and displaying gonytrichum-like (Nees & Nees 1818, Gams & Holubová-Jechová 1976) and phialocephala-like (Kendrick 1961) characteristics. Despite the initial classification of examined fungi within the genus Chloridium and their occurrence in similar ecological niches by predominantly colonizing decaying plant tissues, they deviate from its defined characteristics and necessitate a re-evaluation in terms of taxonomy and phylogeny. The phylogenetic analyses, based on four loci (ITS, LSU, TEF1 and RPB2), unveiled that the studied species are distributed among nine genera within Chaetosphaeriales (Fig. 1). Additionally, they constitute two strongly supported clades proposed as two new genera within Vermiculariopsiellales (Fig. 2). For accurate identification of the examined species, especially in cases where two sibling species exhibit a high degree of morphological similarity, the use of dual barcodes, ITS and TEF1, supported by RPB2 in one



Fig. 29. Chloridiopsis syzygii (CBS 564.93, ex-type culture). **A.** Colonies. **B.** Sporulating conidiophores. **C, D.** Conidiophores. **E.** Phialides. F–H. Conidia. **I.** Colonies on CMD, MLA, OA, and PCA, respectively (from left to right) after 4 wk. A, B. On CMA with *Urtica* stem. C–E. On OA. F–H. On MLA. Scale bars: A, I = 1 cm; B = 500 μm; C–H = 10 μm.

case, is recommended. This approach is particularly relevant for distinguishing between species such as *Caligospora dilabens* and *Ca. pannosa*, as well as *Chloridiopsis constrictospora* and *Chs. syzygii*.

A comprehensive morphological analysis of sexual and asexual characteristics reinforced the findings of our phylogenetic investigations. Gams & Holubová-Jechová (1976) and Réblová et al. (2022) have emphasized the importance of conidiogenous cell morphology and conidial ontogeny in Chloridium. The production of conidia on single or multiple loci has been highlighted as a key characteristic for identifying taxa at the section and genus levels, building upon important contributions in this field by Hughes (1953), Tubaki (1958), Barron (1968), Kendrick (1971), and Cole & Samson (1979). Present phylogenetic analyses of species exhibiting conidiogenesis on either single or multiple loci support these conclusions and provide evidence against their inclusion within a single genus. The elongation pattern of phialides, whether percurrent or sympodial, can sometimes exhibit variability in response to environmental factors. Under laboratory conditions, species within Caliciastrum and Gongromerizella have demonstrated the ability to produce both types of elongations, with sympodial elongation present only in culture. Furthermore, the presence or absence of septation in conidia represents another significant characteristic; species belonging to a particular genus possess either aseptate or septate conidia, sometimes the septum development can be delayed. Notably, the coloration of conidia holds significance in distinguishing between species, such as in the case of the closely related Gongromeriza myriocarpa and G. pygmaea, or in instances when conidia exhibit protracted maturation, gradually turning brown with age or display bicolorous characteristics, e.g. Cacumisporium acutatum vs. C. capitulatum. Furthermore, the sexual features can serve as a critical factor in distinguishing closely related genera with chloridium-like asexual morphs that show minimal variation. Among these characteristics, ascospores are particularly intriguing. Although ascospores are typically hyaline and septate, their ability of separation into part spores differs and serves as a distinct generic characteristic, as observed in genera like Geniculoseta and Caligospora.

We discuss the accepted species and genera, along with their taxonomy and phylogeny, below. Our findings provide valuable insights into the classification and diversity of these genera, with implications for future studies.

Clade A: Cacumisporium and its relatives

Clade A is a robust assemblage of several genera. It comprises former Chloridium and Chaetosphaeria species with chloridium-like asexual morphs, which are now accommodated in five genera, such as Cacumisporium (Preuss 1851, Hughes 1958), Curvichaeta (Wu & Diao 2022), Fusichloridium (Wu & Diao 2022), Capillisphaeria and Spicatispora (this study). In addition to Chloridium s. str., this clade is the only one within the family that comprises genera exhibiting conidial ontogeny on multiple loci, i.e. Cacumisporium, Capillisphaeria, Exserticlava (not included in the analyses due to fragmentary LSU sequence data, see phylogram in Réblová et al. 2020), Fusichloridium, and Spicatispora. Interestingly, all genera that grouped in Clade A, including Catenularia, Ericiosphaeria, Kylindrochaeta, Paragaeumannomyces and also four species of Chaetosphaeria incertae sedis, are characterized by sexual morphs with long fusiform, cylindrical-fusiform, cylindrical to filiform, transversely septate, hyaline ascospores that may have asymmetrical ends and do not fragment into part spores.

Wu & Diao (2022) attempted to clarify the concept of Cacumisporium, but the authors proposed a largely heterogeneous genus with conidia produced from both phialidic and holoblasticdenticulate conidiogenous cells. In contrast, C. capitulatum, the generic type, produces monophialidic conidiogenous cells with a tip protruding above the shallow collarette. Both the phialide and the conidiogenous tip elongate percurrently, and as a result, the tip bears minute, densely aggregated annellations with multiple growing points, on which arise conidia in a sympodial succession (Fig. 4H–M). The unique conidiogenesis of C. capitulatum was first described by Goos (1969). A similar anatomy of the conidiogenous cell, the so-called sympodulo-phialide, has also been documented for members of Chloridium s. str. (Hammill 1972, Sivasithamparam 1975, Gams & Holubová-Jechová 1976, Onofri et al. 1994, Réblová et al. 2022) but is rare outside the genus and is known only in Chaetosphaeriaceae.

Of the nine species assigned to *Cacumisporium* (MycoBank), only *C. acutatum* (Réblová & Gams 1999), *C. capitulatum*, *C. tropicale* (Castañeda-Ruiz *et al.* 2007a) and *C. spooneri* (Kirk 1992) conform to this pattern. Although the conidia are truncated at the base, indicating a wide attachment site, there are no visible conidial scars at the tip of the phialide. Conidia with a basal scar were also observed in related genera *Capillisphaeria* and *Fusichloridium*, and in *Curvichaeta* also from Clade A, indicating a similarity in conidial morphology among these genera.

The other Cacumisporium species, such as C. fusiforme (Xu et al. 2019), C. pleuroconidiophorum (Castañeda-Ruiz et al. 2007b), C. rugosum (Tsui et al. 2001), C. sigmoideum (Mercado Sierra & Castañeda-Ruiz 1987), and C. uniseptatum (Wongsawas et al. 2009), also form conidia in a sympodial manner but exhibit a different mode of conidiogenesis, and the conidia are holoblastic. In C. rugosum, the tip of the conidiogenous cell contains conidial scars visible in scanning electron microscopy, and the annellides are absent. After detachment, conidia possess basal frills, and the frills of the conidial wall also remain on conidiogenous cells. In the other four species, conidiogenesis is similar, although the collarettes and conidial frills may be absent. These species represent further morphological variation and expand the generic concept of Cacumisporium. Unfortunately, DNA sequences and living strains of only *C. acutatum* and *C. capitulatum* with phialides are available. To refine the current generic concept and consolidate taxonomy, new material and strains of additional species of Cacumisporium with different conidial ontogeny should be obtained.

Within Clade A, three previous Chaetosphaeria species with chloridium-like asexual morphs were found to be closely related, each exhibiting distinct morphological patterns and genetic variation that justify their classification at the genus level. Fusichloridium is a monotypic genus that was proposed for Ch. fusiformis and its Chloridium cylindrosporum asexual morph (Wu & Diao 2022). Fusichloridium cylindrosporum has hyaline, septate conidia that taper towards rounded or truncate ends, they are sometimes slightly constricted in the middle and arranged in star-like heads on conidiophores that form two distinct layers. The ascospores are septate, fusiform, asymmetrical, and taper at the basal end. Capillisphaeria is based on Ch. crustacea (Réblová & Gams 1999) and differs from similar Fusichloridium in having aseptate, cylindrical-clavate to asymmetrical conidia with a truncate base adhering in slimy heads, and conidiophores forming a single layer. The ascospores are septate, cylindrical-fusiform, symmetrical, often gently curved. Spicatispora is introduced for Ch. fennica (Réblová & Gams 1999) and characterized by aseptate, pale brown, ellipsoidal-oblong conidia with a germ pore at one of both ends, conidiophores of a single layer and septate, fusiform ascospores that abruptly taper towards both ends. Interestingly, all three genera inhabit the bark and wood of coniferous trees.

The genus Spicatispora comprises two species. Spicatispora carpatica was initially classified within Chloridium (Holubová-Jechová & Révay 1987) and subsequently transferred to Craspedodidymum (Wu & Diao 2022), but without a comprehensive study of conidiogenesis and in the absence of molecular data. The examination of conidiogenous cell morphology and conidial ontogeny unveiled that conidia of Chl. carpaticum develop sympodially from multiple growing points located at the tip of the phialidic conidiogenous cell. Furthermore, these conidia possess pores at either one or both ends. In contrast, Craspedodidymum elatum, the generic type (Holubová-Jechová 1972), demonstrates conidiogenesis on a single conidiogenous locus, and its conidia lack pores. Morphologically, Chl. carpaticum is nearly identical to S. fennica, with the primary difference being the size of the conidia. As a result, we proposed a new combination for Chl. carpaticum in the genus Spicatispora. Regrettably, its DNA sequence data are currently unavailable. Thus, confirmation by molecular data is required for the transfer.

Other related and morphologically similar species initially described in the genus *Chaetosphaeria* that grouped in Clade A include *Ch. abietis* (Gams & Holubová-Jechová 1976), *Ch. cylindrospora* (Huhndorf *et al.* 2001), *Ch. conirostris* (Fernández & Huhndorf 2005), and *Ch. metallicans* (Atkinson *et al.* 2007). Apart from *Ch. metallicans* (asexual morph unknown), they are characterized by phialides with a single conidiogenous locus. However, information on them is limited, as they have been documented in only a few instances, with cultures being absent except for *Ch. abietis*. Additional material and molecular data are required to study their conidiogenesis in detail and establish their relationships.

We examined the lectotype of *Ch. abietis* (K 49555!) and our own material of this species from the Czech Republic, France, and Ukraine, but the ascospores never germinated *in vitro*. The only available living strain, CBS 427.83, remained sterile after cultivation on various media used in this study. It is unclear whether CBS 427.83 was isolated from ascospores or conidia. Although the sexual-asexual relationship between *Ch. abietis* and *Cylindrotrichum zignoëllae* has been suggested based on their juxtaposition on a natural substrate (Gams & Holubová-Jechová 1976), it needs to be experimentally verified. Hawksworth & Minter (1980) addressed this issue and concluded that *Cy. zignoëllae*, as defined by Gams and Holubová-Jechová (1976), may include two taxa belonging to different sexual morphs.

Other asexual morphotypes found within Clade A exhibit considerable variability and are characterized by phialidic conidiogenesis on a single locus. One of these is Paragaeumannomyces (Huhndorf & Fernández 2005, Réblová et al. 2020a), which has recently been linked to the hyphomycete genus Obeliospora (Nawawi & Kuthubutheen 1990) by Wu & Diao (2022). Obeliospora was originally described from freshwater habitats and is characterized by the presence of setae, doliiform phialides with a deep collarette, and hyaline, appendaged conidia. Another morphotype is exemplified by Kylindrochaeta lignomollis (Fernández & Huhndorf 2005), whose asexual morph features dematiaceous conidiophores with terminal polyphialides possessing numerous lateral openings and producing cylindrical, hyaline and septate conidia. Catenularia and Chalarodes (Saccardo 1886, McKenzie 1991, Réblová et al. 2021d) form a well-supported subclade and exhibit an asexual morphotype characterized by simple conidiophores with terminal monophialides, sometimes accompanied with capitate hyphae, and hyaline or brown, both setulate and non-setulate, aseptate, cuneiform to rounded-obconic conidia with an angular outline, arranged in chains. *Phaeodischloridium* (Matsushima 1975, Wu & Diao 2022), on the other hand, forms cylindrical, bicolorous phialidic conidia within a shallow collarette on a single conidiogenous locus on a terminal monophialide.

Clade B: Caligospora and similar fungi with brown and hyaline conidia

The well-supported Clade B comprises five genera with high variation in sexual and asexual characters, such as *Achrochaeta* (Réblová *et al.* 2021b), *Craspedodidymum* (Holubová-Jechová 1972) and three newly proposed genera for species with the chloridium-like morphotype, *i.e. Caliciastrum*, *Caligospora* and *Papillospora*.

The genus *Craspedodidymum* is represented in our phylogeny by *Cr. elatum* isolate NN042874 from China (Wu & Diao 2022). However, it differs from the type collection of *Cr. elatum* (PRM 704057!, Holubová-Jechová 1972). *Craspedodidymum elatum sensu* Wu & Diao (2022) has simple, stout, erect, dark brown conidiophores, collarettes with a smooth margin and almost triangular to widely obovoid conidia often truncate at the base. The holotype PRM 704057 of *Cr. elatum*, on the other hand, contains a fungus with dichotomously branched olivaceous brown to olivaceous grey conidiophores, the collarettes have a frayed margin and conidia are ellipsoidal with a small basal papilla (Holubová-Jechová 1972). We question the identity of the Chinese isolate of *Cr. elatum*, as it appears to belong to a distinct species, and possibly even a different genus.

Caliciastrum, Caligospora and 'Cr. elatum' form a strongly supported subclade characterized by asexual morphs with widely open, vase-shaped collarettes and brown or hyaline conidia. Caligospora is characterized by hyaline, fusiform, septate ascospores fragmenting into part spores at the septa and brown, simple conidiophores and ellipsoidal to somewhat asymmetrical conidia formed on subcylindrical, slightly inflated mono- rarely polyphialides.

The hyaline ascospores separating into part spores are not unusual among members of *Chaetosphaeriaceae* and occur in several distantly related genera, such as *Chloridium s. str.* (Gams & Holubová-Jechová 1976, Réblová *et al.* 2022) and *Geniculoseta. Ascochalara* (Réblová 1999b) is another genus placed in the family on the basis of morphology; it has hyaline, long-fusiform ascospores that are transversely septate and separate into more or less cubic part spores at an early stage within the ascus. *Caligospora* also resembles *Craspedodidymum*. Both genera share brown conidia adhering in dark brown to black slimy heads, and phialides with a flaring collarette with a frayed margin. *Craspedodidymum elatum* differs by conspicuously inflated, amphora-like phialides and dichotomously branched conidiophores; its sexual morph is unknown.

The pale brown conidia of *Caligospora* occur in several other chloridium-like species, *i.e. Chl. phaeosporum* and its two varieties (Gams & Holubová-Jechová 1976, Holubová-Jechová 1987), *Spicatispora fennica* and *S. carpatica. Spicatispora* exhibits distinctive phialide morphology compared to *Caligospora*, forming conidia on multiple conidiogenous loci. *Chloridium phaeosporum* resembles *Caligospora* in its conidiophores with percurrently extending phialides and brown, ellipsoidal conidia on a single

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conidiogenous locus. However, var. *phaeosporum* is distinct in having basally truncate conidia and a darker basal hilum, while var. *cubense* has ellipsoidal conidia with rounded ends and a conspicuously darker basal hilum. Recently, the type variety of *Chl. phaeosporum* has been transferred to a new genus, *Phaeochloridium* in *Glomerellales* (Wu & Diao 2022).

Caliciastrum is a holomorphic genus that represents a new phenotype in Chaetosphaeriaceae. It is characterized by its glossy, collapsing ascomata clothed with brown, apically clavate and hyaline, always sterile setae, 3-septate bicolorous ascospores, and the chloridium-like asexual morph. Based on ascospore morphology, Caliciastrum can be compared to Sporoschisma within Chaetosphaeriaceae; however, there are distinct differences between the two. Sporoschisma is characterized by non-collapsing ascomata covered with a light-coloured (whitish to pale blue) superficial layer and capitate hyphae. The asexual morph of Sporoschisma consists of robust, heavily melanized conidiophores with a tubular collarette and dark brown or bicolorous, septate macroconidia arranged in chains; the chalara-like synasexual morph forms rectangular to cuboidal, pale brown conidia (Müller et al. 1969, Müller & Samuels 1982, Sivichai et al. 2000).

Papillospora is erected for *P. hebetiseta*, which was originally placed in *Chaetosphaeria* (Réblová & Gams 2000). It is differentiated from other species with chloridium-like asexual morphs by its dark brown setae terminating in cylindrical to club-shaped, almost hyaline apical cells, sparsely branched conidiophores with polyphialides and hyaline, ellipsoidal, aseptate conidia and verrucose, hyaline, septate ascospores. In the absence of the asexual morph, it may be challenging to distinguish it from *Stilbochaeta brevisetula* (Hughes & Kendrick 1968, Réblová *et al.* 2021a). For their comparison, see the notes to *P. hebetiseta*.

Clade C: Gongromeriza

In Clade C, the studied isolates are distributed among two genera. Gongromeriza comprises two species, G. myriocarpa and G. pygmaea, which are common fungi on decaying plant material. This genus is characterized by glabrous ascomata, fusiform, 1-septate, hyaline ascospores, and conidia that are short-cuneate or dacryoid with a truncate base, hyaline to lightly pigmented, aseptate, and mostly adhere in chains, sometimes in slimy heads. The conidia are formed on phialides with a single conidiogenous locus. In older cultures, the phialides usually regenerate percurrently. Interestingly, while G. myriocarpa seems to be more common in nature in the asexual state (in the literature known under the former name *Chloridium clavaeforme*), G. pygmaea occurs mostly as the sexual morph. It is common for no conidiophores to grow together with ascomata on the natural substrate. Our observations are consistent with the findings of Constantinescu et al. (1995), who reported that no asexual morph was found in the isotype and three other authentic specimens of G. pygmaea collected by Karsten (1869), nor in the other 14 specimens examined by them. However, the asexual morph is regularly produced in axenic culture derived from the ascospores. The asexual morph of G. pygmaea was initially described as Phialophora phaeophora (Gams & Holubová-Jechová 1976) and latter considered a miniature Chloridium (Réblová et al. 2011); the DNA sequences of the ex-type strain CBS 699.74 of P. phaeophora and other strains derived from ascospores of G. pygmaea are identical or nearly identical. Our observations of G. myriocarpa and G. pygmaea colonies in culture have revealed previously undescribed variability, including the production

of diffusible pigments in *G. pygmaea*. Of the studied strains, three (CBS 138689, CBS 139769, IMI 506815) produced yellow pigment diffusing into the agar (Figs 16, 17).

Members of *Gongromeriza* can be compared to *Chaetosphaeria polygonalis*, a recently introduced dematiaceous hyphomycete with an unknown sexual morph (Yang *et al.* 2023). It is characterized by erect conidiophores and terminal phialides with a cylindrical to deep cup-like collarettes, producing endogenous, cuneiform, hyaline conidia. The accompanying illustration (Yang *et al.* 2023: fig. 59) shows that conidia have a basal scar and tend to adhere in false chains that collapse into a mucous mass. *Chaetosphaeria polygonalis* grouped as a sister to Clade C containing *Gongromeriza* and *Geniculoseta*.

The genus Geniculoseta is the closest relative to Gongromeriza and is distinguished by ascospores that fragment into part spores, the conidiophores that are strongly geniculate with numerous percurrent proliferations as a result of frequently extending phialides, and ellipsoidal to oblong conidia that only adhere in slimy heads. Chaetosphaeria preussii and its asexual morph Chloridium preussii (ex-type strain was isolated from conidia from a different specimen than the holotype of Ch. preussii), were described by Gams & Holubová-Jechová (1976) and proposed to belong to a single organism. Our analyses showed that the sexual and asexual morphs represent two different species belonging to different genera in two orders. Upon examination of the ex-type and additional material of Chl. preussii, it was discovered that the protologue did not originate from the ex-type strain CBS 230.75, but instead from three other strains, namely CBS 257.75, CBS 262.76, and CBS 263.75, which were listed as part of the species description. These three strains were found to be identical to the asexual morph growing adjacent to the ascomata of Ch. preussii in the holotype PRM 796750. They were also confirmed to be conspecific with our specimens CBS 145478 and PRA-21520, which solely contain the asexual morph. Based on molecular data and morphology, it was determined that these five strains represent the newly established genus Geniculoseta in Chaetosphaeriaceae. Phylogenetic analyses of ITS, LSU, RPB2, and TEF1 markers demonstrated that the ex-type strain CBS 230.75 of Chl. preussii should be accommodated in a separate genus Chloridiopsiella in Vermiculariopsiellales.

Clade D: Gongromerizella and Psilobotrys

Clade D consists of three highly supported subclades encompassing former Chloridium species, namely Chaetosphaeria, Gongromerizella and Psilobotrys. The genus Gongromerizella (Réblová et al. 2022) comprises saprobic chloridium-like fungi, with Ga. lignicola serving as the designated type species. These fungi exhibit distinctive characteristics, including the production of dark brown, unbranched, robust, bristle-like conidiophores, phialides with a single conidiogenous locus and hyaline, oblong to ellipsoidal-oblong conidia adhering in slimy heads. Réblová et al. (2022) recognized three species within this genus: Ga. lignicola, Ga. pachytrachela, and Ga. pini. In this study, we conducted phylogenetic and morphological analyses, utilizing ex-type strains, other living strains, and herbarium material to provide a comprehensive understanding of the genus. Additionally, we present a new species, Ga. silvana, which demonstrates intermediate morphological features between Ga. lignicola and Ga. pachytrachela. Although all four Gongromerizella species exhibit high similarity, they can be distinguished by the morphology of their conidiophores, conidia, and collarettes. In culture, it is characteristic for *Ga. lignicola*, *Ga. pachytrachela* and *Ga. pini* to exhibit sympodial growth, with phialides extending laterally; lateral collarettes or short phialides remain active along the main conidiophore axis.

Psilobotrys is a monotypic genus based on P. minutus and recently separated from Chloridium and Chaetosphaeria. It was previously treated as a variety of Chloridium botryoideum, the asexual morph of Chaetosphaeria innumera (Gams & Holubová-Jechová 1976). Gams & Holubová-Jechová (1976) suggested that both conidial varieties of Chl. botryoideum were derived from ascospore isolates of the same sexual morph. However, recent molecular and morphological analyses have shown that the two varieties represent distinct species in two genera, leading to the reinstatement of the name Psilobotrys (Réblová et al. 2022). In our study, we analyzed six out of the 11 strains of P. minutus listed in Gams & Holubová-Jechová (1976, as Chl. botryoideum var. minutum), including the strain CBS 629.75, which was derived from an ascospore isolate. All these strains and our isolate CBS 145632 formed a strongly supported, monophyletic clade *Psilobotrys* within Chaetosphaeriaceae, which is unrelated to Ch. innumera. Since the existing literature's description of P. minutus is inadequate for precise determination, this study provides a comprehensive characterization, illustrations on the natural substrate and in culture, and relevant discussion.

This clade also encompasses other genera that exhibit variation in conidiophore structure. For instance, *Verhusltia* (Crous et al. 2017) form setose sporodochia, while *Phialocephala fusca* (Kendrick 1963) possesses penicillately branched conidiophores. These taxa produce aseptate, ellipsoidal to cylindrical conidia on terminal monophialides, which adhere in slimy heads. The recently proposed genus *Fuscocatenula* (Réblová et al. 2021d) includes asexually reproducing catenularia-like fungi, characterized by aseptate, cuneiform to obovoid, pigmented conidia with a round outline and protracted maturation, which adhere in a basipetal chain.

Chloridiopsiella and Chloridiopsis

Several species displaying the chloridium-like morphotype but producing conidia on a single conidiogenous locus, clustered within *Vermiculariopsiellales*. The phylogenetic analyses support the recognition of two closely related genera, *Chloridiopsiella* and *Chloridiopsis*. Although superficially similar, they exhibit clear morphological distinctions in conidiophores, phialides and conidia between them. The sexual morphology has not been documented for any of the species currently recognized in them.

Chloridiopsiella preussii CBS 230.75, the generic type, displays a single layer of solitary conidiophores and ellipsoidal, oblong to obovate to long-cuneiform conidia that undergo a colour change to beige or pale brown as they age. In culture, the colonies are often mucoid, cobwebby to sparsely lanose, creamy, beige to pale brown. In contrast, members of Chloridiopsis, Chs. constrictospora CBS 432.92 and Chs. syzygii CBS 564.93, display conidiophores in fascicles arranged in two layers (of which the upper layer is formed by setiform conidiophores) and produce oblong to cylindrical hyaline conidia sometimes constricted in the middle. Their phialides can extend sympodially in culture. In vitro, the mycelium is dark brown; colonies often appear velvety-lanose, sometimes cobwebby. Further investigation with additional strains may provide more evidence to confirm the separation of these similar genera.

Interestingly, a non-type strain of Gongromerizella lignicola and two isolates of Ga. pachytrachela, originally listed under

respective species of *Chloridium* by Gams & Holubová-Jechová (1976), were found to belong to *Chloridiopsiella* and *Chloridiopsis* in *Vermiculariopsiellales* and are conspecific with *Cha. preussii* and *Chs. syzygii*, respectively. *Gongromerizella pachytrachela* can be differentiated from *Cha. preussii* by its dark brown, stout and bristle-like conidiophores, slightly tapering phialides, thick-walled collarette, and larger conidia (5–8.5(–9) × 3–4.5 μ m). On the other hand, *Ga. lignicola* produces conidia of variable size that are never constricted in the middle, and its conidiophores are scattered rather than caespitose.

Within Vermiculariopsiellales, Chloridiopsis exhibits striking similarities to Tubulicolla (Réblová et al. 2021). Both genera share the characteristic of caespitose conidiophores forming two layers, with the presence of taller, darker, setiform conidiophores bearing fertile apices, accompanied by shorter, paler conidiophores. In T. stipitocolla (Kuthubutheen & Nawawi 1991), the setiform conidiophores are replaced by setae with pointed and always sterile apices. Tubulicolla can be clearly distinguished from Chloridiopsis by the presence of a tubular neck between the funnel-shaped collarette and the conidiogenous cell, cylindrical to subcylindrical conidia, as well as conidiogenous cells that elongate sympodially in vitro and collarettes that are sometimes branched dichotomously or form a cascade of openings as a result of several dense percurrent elongations.

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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