

# Phylogeny and taxonomic revision of *Microascaceae* with emphasis on synnematosus fungi

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**Abstract:** The taxonomy of the synnematosus genera *Cephalotrichum*, *Doratomyces* and *Trichurus*, and other related genera *Gamsia*, *Wardomyces* and *Wardomyopsis*, has been controversial and relies mainly on morphological criteria. These are microascaceous saprobic fungi mostly found in air and soil and with a worldwide distribution. In order to clarify their taxonomy and to delineate generic boundaries within the *Microascaceae*, we studied 57 isolates that include clinical, environmental and all the available ex-type strains of a large set of species by means of morphological, physiological and molecular phylogenetic analyses using DNA sequence data of four loci (the ITS region, and fragments of rDNA LSU, translation elongation factor 1 $\alpha$  and  $\beta$ -tubulin). The results demonstrate that *Cephalotrichum*, *Doratomyces* and *Trichurus* are congeneric and the genus *Cephalotrichum* is accepted here with *Echinobotryum* as a further synonym. The genera *Acaulium* and *Fairmania*, typified by *A. albonigrescens* and *F. singularis*, respectively, are distinct from *Microascus* and *Scopulariopsis*, *Gamsia* is distinct from *Wardomyces*, and *Wardomyopsis* is confirmed as a separate genus in the *Microascaceae*. Two new species of *Cephalotrichum* are described as *C. brevistipitatum* and *C. hinnuleum*. Nine new combinations are proposed, i.e. *Acaulium acremonium*, *A. caviariforme*, *Cephalotrichum asperulum*, *C. columnare*, *C. cylindricum*, *C. dendrocephalum*, *C. gorgonifer*, *Gamsia columbina* and *Wardomyces giganteus*. A neotype is designed for *C. stemonitis*. Lectotypes and epitypes are designated for *A. acremonium*, *A. albonigrescens*, *C. gorgonifer*, *C. nanum* and *W. anomalus*. *Cephalotrichum cylindricum*, *C. microsporum*, *F. singularis* and *Gamsia columbina* are also epitypified with new specimens. Descriptions of the phenotypic features and dichotomous keys for identification are provided for accepted species in the different genera.

**Key words:** *Cephalotrichum*, *Doratomyces*, *Gamsia*, *Trichurus*, *Wardomyces*, *Wardomyopsis*, *Microascales*, Multigene phylogeny, Taxonomy.

**Taxonomic novelties:** **New species:** *Cephalotrichum brevistipitatum* Sandoval-Denis, Guarro & Gené, *Cephalotrichum hinnuleum* Sandoval-Denis, Guarro & Gené; **New combinations:** *Acaulium acremonium* (Delacr.) Sandoval-Denis, Guarro & Gené, *Acaulium caviariforme* (Malloch & Hubart) Sandoval-Denis, Guarro & Gené, *Cephalotrichum asperulum* (J.E. Wright & S. Marchand) Sandoval-Denis, Guarro & Gené, *Cephalotrichum columnare* (H.J. Swart) S.P. Abbott, *Cephalotrichum cylindricum* (Clem. & Shear) S.P. Abbott, *Cephalotrichum dendrocephalum* (Udagawa, Y. Horie & Abdullah) S.P. Abbott, *Cephalotrichum gorgonifer* (Bainier) Sandoval-Denis, Gené & Guarro, *Gamsia columbina* (Demelius) Sandoval-Denis, Guarro & Gené, *Wardomyces giganteus* (Malloch) Sandoval-Denis, Guarro & Gené; **Typification:** **Epitypification (basionyms):** *Acaulium albonigrescens* Sopp, *Fairmania singularis* Sacc., *Monilia acremonium* Delacr., *Periconia nana* Ehrenb., *Stysanus microsporus* Sacc., *Trichurus cylindricus* Clem. & Shear, *Trichurus gorgonifer* Bainier, *Trichosporum columbinum* Demelius, *Wardomyces anomalus* F.T. Brooks & Hansf.; **Lectotypification (basionyms):** *Acaulium albonigrescens* Sopp, *Monilia acremonium* Delacr., *Periconia nana* Ehrenb., *Trichurus gorgonifer* Bainier, *Wardomyces anomalus* F.T. Brooks & Hansf.; **Neotypification:** *Isaria stemonitis* Pers.: Fr.

Available online 29 July 2016; <http://dx.doi.org/10.1016/j.simyco.2016.07.002>.

## INTRODUCTION

The family *Microascaceae*, as established by Luttrell (Malloch 1970a), currently accommodates a morphologically heterogeneous group of fungi, comprising saprobic and plant pathogenic species. Some species of *Microascaceae* are opportunistic pathogens of humans and show intrinsic resistance to antifungal agents (de Hoog *et al.* 2011, Sandoval-Denis *et al.* 2013, 2016, Lackner *et al.* 2014).

Recent molecular studies have demonstrated that the *Microascaceae* contains several closely related genera that are difficult to separate morphologically (Sandoval-Denis *et al.* 2016). Members of the family are characterised by the presence of mostly annellidic asexual morphs with dry aseptate conidia and by sexual morphs that form cleistothecial or perithecial, carbonaceous ascomata producing reniform, lunate or triangular ascospores with or without germ pores. The most studied genera

are *Microascus*, *Scedosporium* and *Scopulariopsis*, primarily because of their clinical importance (Sandoval-Denis *et al.* 2013, Lackner *et al.* 2014). Lackner *et al.* (2014) delimited phylogenetic boundaries among genera of the *Scedosporium* clade by means of 28S large subunit (LSU) and internal transcribed spacer (ITS) sequence analyses. Recently, three of the most debated genera of the family, *Microascus*, *Scopulariopsis* and *Pithoascus* were revised through a detailed morphological study combined with a four-gene phylogeny (Sandoval-Denis *et al.* 2016). As a result, several taxa were excluded from these genera and still remain in an uncertain taxonomic position. For instance, the genus *Acaulium*, previously considered a synonym of *Scopulariopsis* was suggested to be a distinct genus, while *Microascus singularis*, the type species of the genus *Fairmania*, currently a synonym of *Microascus* (Curzi 1931, Barron *et al.* 1961, Udagawa & Awao 1969, von Arx *et al.* 1988), appeared as a new lineage within the *Microascaceae* (Sandoval-Denis *et al.* 2016). Furthermore,

the phylogeny and taxonomy of several lesser-known genera of the *Microascaceae* are still unresolved. Current concepts of the synnematos genera *Cephalotrichum*, *Doratomyces* and *Trichurus*, and the related genera *Gamsia*, *Wardomyces* and *Wardomyopsis*, having conidia with germ slits, are based exclusively on morphological criteria. Ex-type cultures are unavailable for several species of these genera and DNA sequences are scarce or of doubtful quality.

*Cephalotrichum* Link (1809) is tied to *C. stemonitis* (formerly *Periconia stemonitis*) after it was lectotypified by Hughes (1958). It is characterised by the production of dry conidia in basipetal chains from percurrently extending (annellidic) conidiogenous cells that arise on the upper part of large dark pigmented synnemata (Abbott 2000). According to Index Fungorum *Cephalotrichum* currently comprises 68 species, 25 of them of uncertain application. *Doratomyces* (Sturm 1829), typified by *D. neesii*, currently includes 22 species, five of them of uncertain application and shares morphological characteristics with *Cephalotrichum*. Since the application of *Cephalotrichum* was unclear to them, Morton & Smith (1963) considered the former as a possible synonym of *Doratomyces* whereas other authors, following the lectotypification of the genus by Hughes (1958), considered *Cephalotrichum* as the correct name for this genus (Carmichael et al. 1980, von Arx 1981, Abbott 2000, Jiang et al. 2011, Seifert et al. 2011, de Beer et al. 2013). *Cephalotrichum* was sanctioned by Fries (1832), and it is currently included in the proposed List of Protected Fungal Generic Names (Kirk et al. 2013). *Trichurus* (Clements 1896) is typified by *T. cylindricus* and currently comprises five species. It is also morphologically similar to *Cephalotrichum* and *Doratomyces*, but distinguished by the presence of setae on the upper part of the synnemata (Morton & Smith 1963). However, detailed ultrastructural studies on the synnematal morphogenesis suggested that the sole presence of setae might not support their distinction as a different genus (Hasselbring 1896, Swart 1964, Hammill 1977, Abbott 2000). Abbott (2000) studied a large set of strains belonging to these fungi and concluded that the three genera were congeneric, which led to numerous proposed new combinations, but they were not formally published.

*Wardomyces* (*W.*), typified by *W. anomalus*, is characterised by polyblastic conidiogenous cells borne on undifferentiated hyphae and dark, 0–1-septate conidia with characteristic longitudinal germ slits. The generic concept was expanded with the inclusion of *W. columbinus*, showing a secondary type of conidia formed on annellides (Hennebert 1968) and with the addition of *W. aggregatus*, *W. dimerus* and *W. simplex*, all having septate annelloconidia (Gams 1968, Sugiyama et al. 1968, Malloch 1970b). *Wardomyces columbinus* and *W. ovalis* were transferred to the genus *Hennebertia* and *W. dimerus* to *Gamsia*, typified with *G. dimera* (Morelet 1969), but these transfers were not widely accepted (Domsch et al. 2007, Seifert et al. 2011, Whitton et al. 2012). Although lacking synnemata, *Wardomyces* has been shown to be phylogenetically related to *Cephalotrichum* (Issakainen et al. 2003, Lackner et al. 2014, Sandoval-Denis et al. 2016). *Wardomyopsis* (*Ws.*), typified by *Ws. inopinata* (Udagawa & Furuya 1978), is similar to *Wardomyces* in the presence of dark conidia with longitudinal germ slits, but differs in that the conidia are borne on annellidic conidiogenous cells and are arranged in short chains. Its phylogenetic position is still unresolved, although it has been shown that *Wardomyopsis* species cluster as a distinct and well-supported lineage within the *Microascaceae* (Sandoval-Denis et al. 2016).

In this study a polyphasic approach is carried out, using phenotypic features and DNA sequence data for all available living type material and several authentic and reference strains from public collections, to resolve the taxonomy of main genera of *Microascaceae* including *Cephalotrichum*, *Doratomyces* and *Trichurus*, characterised by the production of synnemata, and *Gamsia*, *Wardomyces* and *Wardomyopsis* characterised by dark conidia with germ slits.

## MATERIALS AND METHODS

### Isolates

Fifty-six isolates belonging to 29 species of *Cephalotrichum*, *Doratomyces*, *Gamsia*, *Microascus*, *Scopulariopsis*, *Trichurus*, *Wardomyces* and *Wardomyopsis* were examined, including all the available ex-type cultures for the mentioned species. Type material was obtained from the collections of the CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands (CBS); Facultat de Medicina, Universitat Rovira I Virgili, Reus, Spain (FMR), Institute of Hygiene and Epidemiology-Mycolology Laboratory, Brussels, Belgium (IHEM), UAMH Centre for Global Microfungal Biodiversity, University of Toronto, Canada (UAMH) and the University of Texas Health Science Center at San Antonio, Texas, USA (UTHSCSA) (Table 1), and from different herbaria for which acronyms are listed according to Index Herbariorum (<http://sweetgum.nybg.org/science/ih/>).

### Phenotypic characters

The isolates were grown on oatmeal agar (OA; 30 g of filtered oat flakes, 20 g of agar, 1 L of distilled water), potato-carrot agar (PCA; 20 g each of filtered potatoes and carrots, 20 g of agar, 1 L of distilled water) and potato dextrose agar (PDA, Pronadisa, Spain), incubated in the dark at different temperatures (5–40 °C at intervals of 5 °C) and examined at 7, 14 and 28 d to determine colony growth rates. Cultural and micro-morphological characteristics were recorded after 14 d of incubation at 25 °C on OA. Colour notations were from Kornerup & Wanscher (1978). Measurements and descriptions of microscopic structures were made using an Olympus CH2 light microscope (Olympus Corporation, Tokyo, Japan). Photographs were made using a Zeiss Axio Imager M1 light microscope (Zeiss, Oberkochen, Germany) with a mounted DeltaPix Infinity X digital camera using Nomarski differential interference contrast and phase contrast optics or using an Olympus SZ61 stereomicroscope with a mounted Olympus SC30 digital camera (Olympus, Tokyo, Japan). Cardinal temperatures were determined using PDA plates incubated at temperatures ranging from 5 to 40 °C at 5 °C intervals, including 37 °C.

### DNA extraction, sequencing and PCR amplification

Total genomic DNA was extracted from fresh mycelia using FastPrep (MP Biomedicals, Santa Ana, California, USA) following the manufacturer's protocol. DNA was quantified using Nanodrop 3000 (Thermo Scientific, Madrid, Spain).

Four nuclear DNA regions were amplified by PCR following previously described conditions (Sandoval-Denis et al. 2016).

**Table 1.** Strains and sequence accession numbers included in this study.

Current name	Original name	Strain number <sup>1</sup>	Source <sup>2</sup>	Origin	Sequence accession number <sup>3</sup>			
					LSU	ITS	TEF	TUB
<i>Acaulium acremonium</i>	<i>Scopulariopsis danica</i>	CBS 290.38 (Ex-type)	Skin of a horse	Denmark	LN851001	LM652456	HG380362	LN851108
	<i>Scopulariopsis acremonium</i>	MUCL 8274 (Ex-epitype)	Wheat field soil	Germany: Schleswig-Holstein	LN851002	LM652457	LN851056	LN851109
	<i>Scopulariopsis acremonium</i>	MUCL 8409	Soil	Germany: Schleswig-Holstein	LN851003	LM652458	LN851057	LN851110
<i>A. albonigrescens</i>	<i>Microascus albonigrescens</i>	IHEM 18560 (Ex-epitype)	Litter treated with urea	Japan: Nemuro-shi	LN851004	LM652389	LN851058	LN851111
<i>A. caviariforme</i>	<i>Microascus caviariformis</i>	CBS 536.87 (Ex-type)	Decaying meat	Belgium: Flemalle	LN851005	LM652392	LN851059	LN851112
<i>Cephalotrichum asperulum</i>	<i>Doratomyces asperulus</i>	CBS 127.22	Seed	Netherlands: Wageningen	LN851006	LN850959	LN851060	LN851113
	<i>Doratomyces asperulus</i>	CBS 582.71 (Ex-isotype)	Soil	Argentina: Buenos Aires	LN851007	LN850960	LN851061	LN851114
	<i>Doratomyces</i> sp.	UTHSCSA D114-62; FMR 13443	BAL	USA	LN851008	LN850961	LN851062	LN851115
	<i>Doratomyces</i> sp.	UTHSCSA D114-65; FMR 13446	BAL	USA	LN851009	LN850962	LN851063	LN851116
<i>C. brevistipitatum</i>	<i>Doratomyces purpureofuscus</i>	CBS 157.57 (Ex-type)	Tuber	Netherlands: Wageningen	LN851031	LN850984	LN851084	LN851138
<i>C. columnare</i>	<i>Doratomyces columnaris</i>	CBS 159.66 (Ex-type)	Dung of hare	South Africa: Johannesburg	LN851010	LN850963	LN851064	LN851117
<i>C. cylindricum</i>	<i>Trichurus terrophilus</i>	CBS 448.51	Timber	South Africa: Bekker	LN851011	LN850964	LN851065	LN851118
	<i>Trichurus cylindricum</i>	UAMH 1348 (Ex-epitype)	Seed of sorghum	USA: Kansas	LN851012	LN850965	LN851066	LN851119
<i>C. dendrocephalum</i>	<i>Trichurus dendrocephalus</i>	CBS 528.85 (Ex-isotype)	Cultivated soil	Iraq: Basrah	LN851013	LN850966	LN851067	LN851120
<i>C. gorgonifer</i>	<i>Trichurus spiralis</i>	CBS 131.08	Unknown	Unknown	LN851021	LN850974	–	LN851128
	<i>Trichurus terrophilus</i>	CBS 368.53	Treated wood	South Africa	LN851023	LN850976	LN851076	LN851130
	<i>Trichurus spiralis</i>	CBS 635.78 (Ex-epitype)	Hair	Netherlands	LN851024	LN850977	LN851077	LN851131
	<i>Trichurus spiralis</i>	UAMH 3585	Mushroom compost	Canada: Alberta	LN851025	LN850978	LN851078	LN851132
	<i>Doratomyces</i> sp.	UTHSCSA D114-63; FMR 13444	BAL	USA	LN851026	LN850979	LN851079	LN851133
	<i>Doratomyces microsporus</i>	UTHSCSA D114-64; FMR 13445	BAL	USA	LN851027	LN850980	LN851080	LN851134
	<i>Doratomyces</i> sp.	UTHSCSA D114-69; FMR 13450	BAL	USA	LN851028	LN850981	LN851081	LN851135
	<i>Doratomyces purpureofuscus</i>	UTHSCSA D114-71; FMR 13452	Maxillary sinus fluid	USA	LN851029	LN850982	LN851082	LN851136
	<i>Trichurus spiralis</i>	UTHSCSA D114-75; FMR 13456	BAL	USA	LN851030	LN850983	LN851083	LN851137
	<i>C. hinnuleum</i>	<i>Doratomyces stemonitis</i>	CBS 289.66 (Ex-type)	Dung of deer	Australia: Tasmania	LN851032	LN850985	LN851085
<i>C. microsporum</i>	<i>Doratomyces purpureofuscus</i>	CBS 523.63 (Ex-epitype)	Wheat field soil	Germany: Schleswig-Holstein	LN851014	LN850967	LN851068	LN851121
	<i>Cephalotrichum microsporum</i>	UAMH 9365	Indoor air	Canada: Alberta	LN851015	LN850968	LN851069	LN851122
<i>C. nanum</i>	<i>Doratomyces nanus</i>	CBS 191.61 (Ex-epitype)	Dung of deer	England: Surrey	LN851016	LN850969	LN851070	LN851123
	<i>Cephalotrichum nanum</i>	UAMH 9126	Dung of bison	Canada: Alberta	LN851017	LN850970	LN851071	LN851124
<i>C. purpureofuscum</i>	<i>Cephalotrichum purpureofuscum</i>	UAMH 9209	Indoor air	Canada: British Columbia	LN851018	LN850971	LN851072	LN851125
<i>C. stemonitis</i>	<i>Doratomyces stemonitis</i>	CBS 103.19 (Ex-neotype)	Seed	Netherlands: Wageningen	LN850952	LN850951	LN850953	LN850954

(continued on next page)

Table 1. (Continued)

Current name	Original name	Strain number <sup>1</sup>	Source <sup>2</sup>	Origin	Sequence accession number <sup>3</sup>			
					LSU	ITS	TEF	TUB
	<i>Doratomyces stemonitis</i>	CBS 180.35	Unknown	Unknown	<b>LN851019</b>	<b>LN850972</b>	<b>LN851073</b>	<b>LN851126</b>
	<i>Cephalotrichum stemonitis</i>	UAMH 1532	Unknown	Unknown	<b>LN851020</b>	<b>LN850973</b>	<b>LN851074</b>	<b>LN851127</b>
<i>C. verrucisporum</i>	<i>Doratomyces asperulus</i>	CBS 187.78	Sand dune soil	Netherlands: Katijk	<b>LN851033</b>	<b>LN850986</b>	<b>LN851086</b>	<b>LN851140</b>
<i>Fairmania singularis</i>	<i>Microascus singularis</i>	CBS 249.64	Unknown	Canada: Toronto	<b>LN851034</b>	<b>LN850987</b>	<b>LN851087</b>	<b>LN851141</b>
	<i>Microascus singularis</i>	CBS 414.64	Laboratory contaminant	Japan: Tokyo	<b>LN851035</b>	LM652442	<b>LN851088</b>	<b>LN851142</b>
	<i>Microascus singularis</i>	CBS 505.66 (Ex-epitype)	Barrel bottom	USA: Maine	<b>LN851036</b>	<b>LN850988</b>	<b>LN851089</b>	<b>LN851143</b>
<i>Gamsia aggregata</i>	<i>Wardomyces aggregatus</i>	CBS 251.69 (Ex-isotype)	Dung of carnivore	USA	<b>LN851037</b>	LM652378	<b>LN851090</b>	<b>LN851144</b>
<i>G. columbina</i>	<i>Wardomyces columbinus</i>	CBS 230.82	Sandy soil	Netherlands: Wageningen	<b>LN851038</b>	<b>LN850989</b>	<b>LN851091</b>	<b>LN851145</b>
	<i>Wardomyces columbinus</i>	CBS 233.66 (Ex-epitype)	Sandy soil	Germany: Giessen	<b>LN851039</b>	<b>LN850990</b>	<b>LN851092</b>	<b>LN851146</b>
	<i>Wardomyces dimerus</i>	CBS 235.66 (Ex-type)	Wheat field soil	Germany: Schleswig-Holstein	<b>LN851040</b>	<b>LN850991</b>	<b>LN851093</b>	<b>LN851147</b>
	<i>Wardomyces simplex</i>	CBS 546.69 (Ex-type)	Milled <i>Oryza sativa</i>	Japan	<b>LN851041</b>	LM652379	<b>LN851094</b>	<b>LN851148</b>
<i>Scopulariopsis brevicaulis</i>	<i>Microascus brevicaulis</i>	MUCL 40726 (Ex-type)	Indoor air	Canada: Alberta	<b>LN851042</b>	LM652465	HG380363	LM652672
<i>Microascus longirostris</i>	<i>Microascus longirostris</i>	CBS 196.61 (Ex-neotype)	Wasp's nest	USA: Maine	<b>LN851043</b>	LM652421	LM652566	LM652634
<i>Wardomyces anomalus</i>	<i>Wardomyces anomalus</i>	CBS 299.61 (Ex-epitype)	Air cell of egg	Canada: Ontario	<b>LN851044</b>	<b>LN850992</b>	<b>LN851095</b>	<b>LN851149</b>
<i>W. giganteus</i>	<i>Microascus giganteus</i>	CBS 746.69 (Ex-type)	Insect frass in dead log	Canada: Ontario	<b>LN851045</b>	LM652411	<b>LN851096</b>	<b>LN851150</b>
<i>W. humicola</i>	<i>Wardomyces humicola</i>	CBS 369.62 (Ex-isotype)	Soil in tropical greenhouse	Canada: Ontario	<b>LN851046</b>	<b>LN850993</b>	<b>LN851097</b>	<b>LN851151</b>
<i>W. inflatus</i>	<i>Wardomyces hughesii</i>	CBS 216.61 (Ex-isotype)	Wood, <i>Acer</i> sp.	Canada: Québec	<b>LN851047</b>	LM652496	<b>LN851098</b>	<b>LN851152</b>
	<i>Wardomyces inflatus</i>	CBS 367.62 (Ex-neotype)	Greenhouse soil	Belgium: Heverlee	<b>LN851048</b>	<b>LN850994</b>	<b>LN851099</b>	<b>LN851153</b>
<i>W. moseri</i> <sup>4</sup>	<i>Wardomyces moseri</i>	CBS 164.80 (Ex-isotype)	Dead petiole	Colombia: Dep. Meta	<b>LN851049</b>	<b>LN850995</b>	<b>LN851100</b>	<b>LN851154</b>
<i>W. ovalis</i>	<i>Wardomyces ovalis</i>	CBS 234.66 (Ex-type)	Wheat field soil	Germany: Schleswig-Holstein	<b>LN851050</b>	<b>LN850996</b>	<b>LN851101</b>	<b>LN851155</b>
<i>W. pulvinatus</i>	<i>Wardomyces papillatus</i>	CBS 112.65 (Ex-type)	Salt-marsh	England: Cheshire	<b>LN851051</b>	<b>LN850997</b>	<b>LN851102</b>	<b>LN851156</b>
<i>Wardomyces humicola</i>	<i>Scopulariopsis humicola</i>	CBS 487.66 (Ex-isotype)	Soil	Canada: Ontario	LM652554	LM652497	<b>LN851103</b>	<b>LN851157</b>
	<i>Wardomyces humicola</i>	FMR 3993	Sediment of Ter river	Spain: Girona	<b>LN851052</b>	<b>LN850998</b>	<b>LN851104</b>	<b>LN851158</b>
	<i>Wardomyces</i> sp.	FMR 13592	Soil	Spain: Reus	<b>LN851053</b>	<b>LN850999</b>	<b>LN851105</b>	<b>LN851159</b>
<i>Ws. inopinata</i>	<i>Wardomyces inopinata</i>	FMR 10305	Soil	Myanmar	<b>LN851054</b>	LM652498	<b>LN851106</b>	<b>LN851160</b>
	<i>Wardomyces inopinata</i>	FMR 10306	Soil	Myanmar	LN850956	LN850955	LN850957	LN850958
<i>Ws. litoralis</i>	<i>Wardomyces litoralis</i>	CBS 119740 (Ex-type)	Beach soil	Spain: Castellón	<b>LN851055</b>	<b>LN851000</b>	<b>LN851107</b>	<b>LN851161</b>

<sup>1</sup> CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; FMR: Facultad de Medicina i Ciències de la Salut, Reus, Spain; IHEM: Biomedical Fungi and Yeasts Collection, Scientific Institute of Public Health, Belgium; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium; UAMH: UAMH Centre for Global Microfungal Biodiversity, University of Toronto, Canada; UTHSCSA: Fungus Testing Laboratory, Department of Pathology, University of Texas Health Science Center, San Antonio, USA.

<sup>2</sup> BAL: bronchoalveolar lavage fluid.

<sup>3</sup> ITS: Internal transcribed spacer regions of the rDNA and 5.8S region; LSU: partial large subunit of the rDNA; EF-1 $\alpha$ : partial translation elongation factor gene; TUB: partial beta-tubulin gene.

<sup>4</sup> Excluded or doubtful species name. Sequences newly generated in this study are indicated in bold.

The ITS region (ITS) of nuclear rDNA (nrDNA), spanning the ITS1, 5.8S and ITS2 regions, was amplified using the primer pair ITS5/ITS4 (White *et al.* 1990). LSU nrDNA region, spanning the variable domains D1–D3, was amplified using the primer pair LR5/LR0R (Vilgalys & Hester 1990, Vilgalys & Sun 1994). In addition, two protein coding genes were also used. Partial fragments of the translation elongation factor 1 $\alpha$  (*EF-1 $\alpha$* ) and  $\beta$ -tubulin (*TUB*) genes were amplified using the primer pairs 983F/2218R (Rehner & Buckley 2005) and BT2a/BT2b (Glass & Donaldson 1995), respectively. Sequencing was made in both directions with the same primers used for amplification at Macrogen Europe (Macrogen Inc. Amsterdam, The Netherlands). Consensus sequences were obtained using SeqMan v. 7.0.0 (DNASTAR Lasergene, Madison, WI, USA). Sequences newly generated in this study and their GenBank accession numbers are shown in Table 1.

### Sequence alignment and phylogenetic analysis

Alignments of individual genes were created in MEGA v. 6 (Tamura *et al.* 2013), using the ClustalW function and refined in the same platform manually or using Muscle (Edgar 2004). The best-fit models of evolution for the four genes tested (GTR+I+G for LSU, ITS and *EF-1 $\alpha$* ; and HKY+I+G for *TUB*) were selected following the Akaike criterion (AIC) (Posada & Buckley 2004) implemented in MrModelTest v. 2.3 (Nylander 2004). *Microascus longirostris* (CBS 196.61) and *Scopulariopsis brevicaulis* (MUCL 40726) were used as outgroups. Maximum likelihood (ML) analyses were performed using MEGA v. 6 with Nearest-Neighbour-Interchange as a heuristic method. Gaps were treated as partial deletions with a 95 % site coverage cut-off. Robustness of the branches was estimated using a bootstrap analysis of 1000 replicates (Felsenstein 1985). Bootstrap values  $\geq 70$  % were considered significant. Bayesian (BI) analyses were conducted on MrBayes v. 3.2 (Huelsenbeck & Ronquist 2001) and involved two parallel runs of four incrementally heated Markov Chains starting from a random tree topology. The analyses lasted for 5 M generations with a sampling frequency of every 100 generations. The 50 % majority rule consensus trees and posterior probabilities (pp) were calculated after discarding 25 % of the initial trees for burn-in. Posterior probability values equal or above 0.95 were considered significant. The resulting trees were plotted using FigTree v. 1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree/>). Individual datasets of ITS, LSU, *EF-1 $\alpha$*  and *TUB* were assessed for potential incongruence before being concatenated into a combined dataset. If conflict between clades with significant ML and BI support was observed, the individual phylogenies were considered to be incongruent (Mason-Gamer & Kellogg 1996, Wiens 1998). However, since no incongruences were found, all genes were combined for the final phylogenetic analyses. The alignments originated in this study have been deposited in TreeBASE (<http://www.treebase.org>) and taxonomic novelties in MycoBank (Crous *et al.* 2004).

## RESULTS

The final dataset comprised 2595 characters (819 characters for LSU, 504 for ITS, 772 for *EF-1 $\alpha$*  and 500 for *TUB*) and

included 584 parsimony-informative positions (74 for LSU, 119 for ITS, 162 for *EF-1 $\alpha$*  and 229 for *TUB*) from 56 isolates. The resulting ML phylogenetic tree (Fig. 1) resolved 27 well-supported terminal clades distributed in six main lineages (I–VI), which corresponded to six different genera, i.e. *Acaulium*, *Cephalotrichum*, *Fairmania*, *Gamsia*, *Wardomyces* and *Wardomyopsis*.

Lineage I corresponded to the genus *Cephalotrichum* which encompassed 12 terminal clades (C1–C12); nine of which included an ex-type, ex-neotype or ex-epitype strain of a known species. Two clades (C4 and C10) corresponded to new species described here as *C. brevistipitatum* and *C. hinnuleum*, and clades C5 and C7 included a single strain which were identified respectively as *C. purpureofuscum* and *C. verrucisporum* (see notes on those species). The species phylogenetically attributed to *Cephalotrichum* are characterised by forming synnematous conidiophores with or without sterile distal setae and annellidic conidiogenesis producing smooth or rough conidia arranged in basipetal chains.

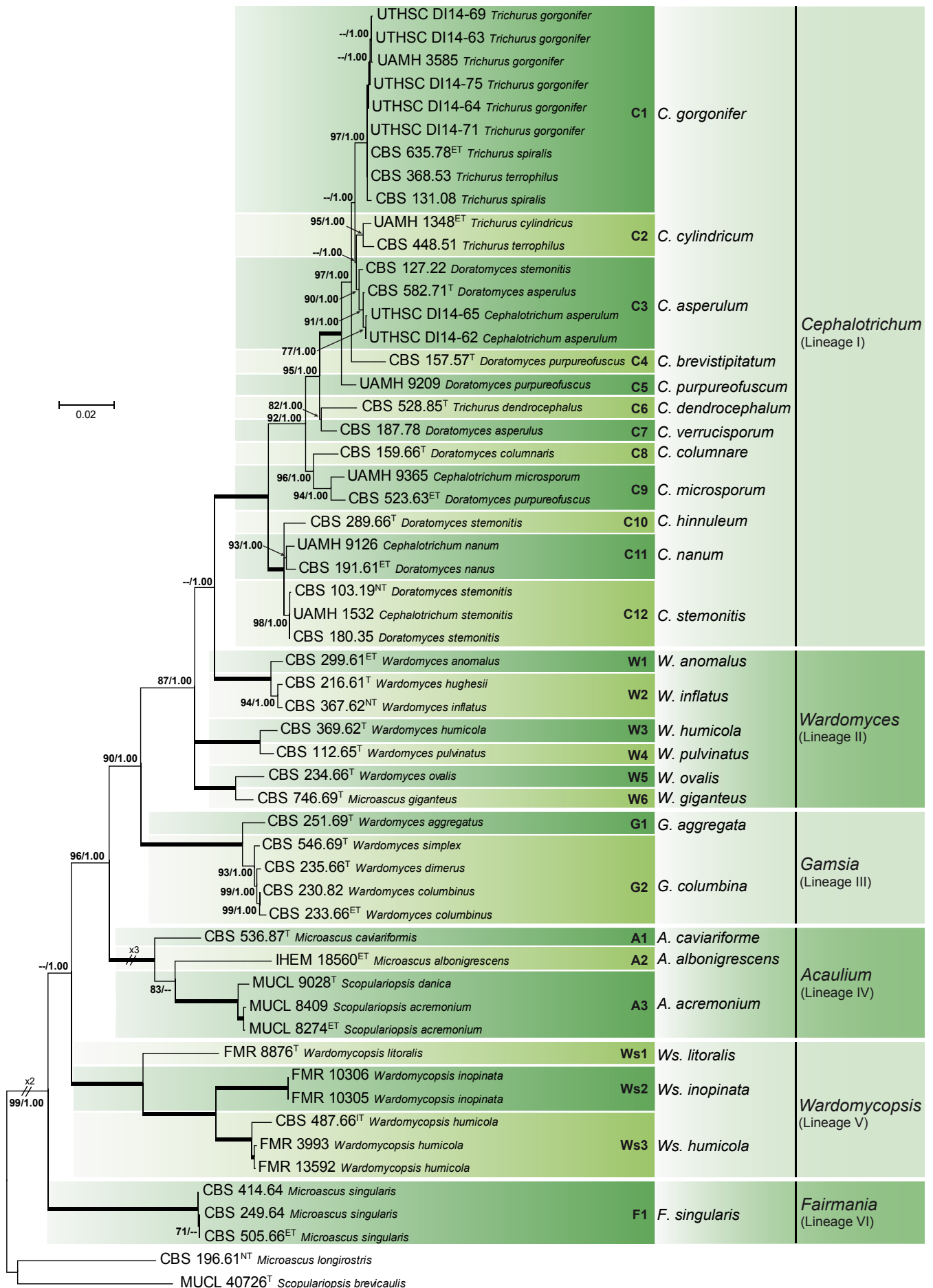
Lineage II showed considerable phylogenetic diversity among species of *Wardomyces* that grouped into six clades distributed into three paraphyletic sublineages. Each of these six clades (W1–W6) included an ex-type or authentic strain for the species. Members of this lineage are characterised by the formation of usually branched conidiophores with polyblastic conidiogenous cells producing solitary, dark 1–2-celled conidia bearing a germ slit. An exception is *W. ovalis* (clade W5) that presented secondary annellidic, hyaline, 1-celled conidia arranged in chains. Given the lack of clear morphological differences, we interpreted these six clades as belonging to *Wardomyces sensu lato*.

Lineage III corresponded to the genus *Gamsia* and comprised two terminal clades (G1 and G2), which represented two known species. Members of this lineage are characterised by usually unbranched conidiophores bearing polyblastic conidiogenous cells, and 1-celled, dark, solitary conidia provided with germ slits, and secondary, 1–2-celled, hyaline annelloconidia in long chains.

Lineage IV comprised three terminal clades (A1–A3), each of which included an ex-type or a reference strain of a known species. One of them, *Microascus albonigrescens*, is the type species of the obscure genus *Acaulium*, which is reintroduced here. *Acaulium* is characterised by annellidic conidiogenesis, guttulate conidia and mycelium forming abundant hyphal fascicles.

Lineage V included three clades (Ws1–Ws3) corresponding to the genus *Wardomyopsis* and the currently accepted species *Ws. litoralis*, *Ws. humicola* and *Ws. inopinata*. Although the ex-type strain of *Ws. inopinata*, the type species of the genus, was unavailable for study, specimens in clade Ws2 were considered representative of that species in that they match morphologically with the protologue of *Ws. inopinata* (Udagawa & Furuya 1978). Members of *Wardomyopsis* are characterised by hyaline annellidic conidiogenous cells producing conidia in short chains; the conidia are darkly pigmented and have a single longitudinal germ slit.

Lineage VI corresponded to the obscure genus *Fairmania*, which is reintroduced here. This lineage included a single terminal clade (F1), which comprises three strains of *F. singularis* characterised by dark, 1-celled conidia with 1–5 longitudinal paler bands.



**Fig. 1.** Maximum likelihood (ML) tree obtained from the combined LSU, ITS, EF-1 $\alpha$  and TUB sequences of 57 representative taxa of the *Microascaceae*. Numbers on the branches are ML bootstrap values (bs) above 70 %, followed by Bayesian posterior probabilities (pp) above 0.95. Fully supported branches (100 % bs/1.0 pp) are indicated in bold. Branch lengths are proportional to distance. The tree is rooted to *Microascus longirostris* (CBS 196.61) and *Scopulariopsis brevicaulis* (MUCL 40726). <sup>T</sup>, Ex-type; <sup>ET</sup>, Ex-epitype; <sup>NT</sup>, Ex-neotype; A, *Acaulium*; C, *Cephalotrichum*; F, *Fairmania*; G, *Gamsia*; W, *Wardomyces*; Ws, *Wardomycopsis*.

## TAXONOMY

***Acaulium*** Sopp, Skr. VidenskSelsk. Christiania, Kl. I, Math.-Natur. 11: 42. 1912.

*Colonies* expanding, often membranous at first, becoming velvety, lanose or funiculose, flat, white to pale grey. *Hyphae* hyaline, thin- and smooth-walled, often forming fascicles. *Conidiophores* mononematous, rarely synnematos, branched or unbranched, hyaline. *Conidiogenous cells* annellidic, cylindrical, smooth-walled. *Conidia* obovoid to cylindrical, hyaline or subhyaline, smooth- and thick-walled, truncate at the base. *Ascospores* superficial or immersed, scattered, perithecial and papillate or cleistothecial, black, with scattered setae. *Asci* evanescent, 8-spored, subglobose to globose. *Ascospores* 1-celled, lunate, pale orange to red-brown, smooth-walled, with a single apical germ pore.

*Type species:* *Acaulium albonigrescens* Sopp.

*Notes:* Species currently included in *Acaulium* were recently excluded from *Microascus* and *Scopulariopsis* on the basis of DNA phylogenetic analysis (Sandoval-Denis *et al.* 2016). Although the morphological distinction among the three genera is difficult, *Acaulium* is characterised by the formation of pale colonies with dense hyphal fascicles and the presence of abundant oil drops in the mycelium, conidia and ascospores, showing a guttulate appearance. In addition, species of *Acaulium* are able to grow at low temperature, sporulating abundantly at 15 °C,

whereas in *Microascus* and *Scopulariopsis*, sporulation is markedly reduced at temperatures below 25 °C.

***Acaulium acremonium*** (Delacr.) Sandoval-Denis, Guarro & Gené, **comb. nov.** MycoBank MB814571. Fig. 2.

*Basionym:* *Monilia acremonium* Delacr., Bull. Soc. Mycol. France 13: 114. 1897.

*Synonyms:* *Scopulariopsis acremonium* (Delacr.) Vuill. Bull. Soc. Mycol. France. 27: 148. 1911.

*Scopulariopsis communis* Bainier, Bull. Soc. Mycol. France. 23: 125. 1907.

*Penicillium brevicaulis* Sacc. var. *glabrum* Thom, Bull. Off. Exp. Sta. U. S. D. A. 118: 48. 1910.

*Scopulariopsis brevicaulis* (Sacc.) Bainier var. *glabra* (Thom) Thom in The Penicillia: 250. 1930.

*Oospora glabra* Hanzawa, J. Coll. Agric. Tohoku Imp. Univ. 4: 1912.

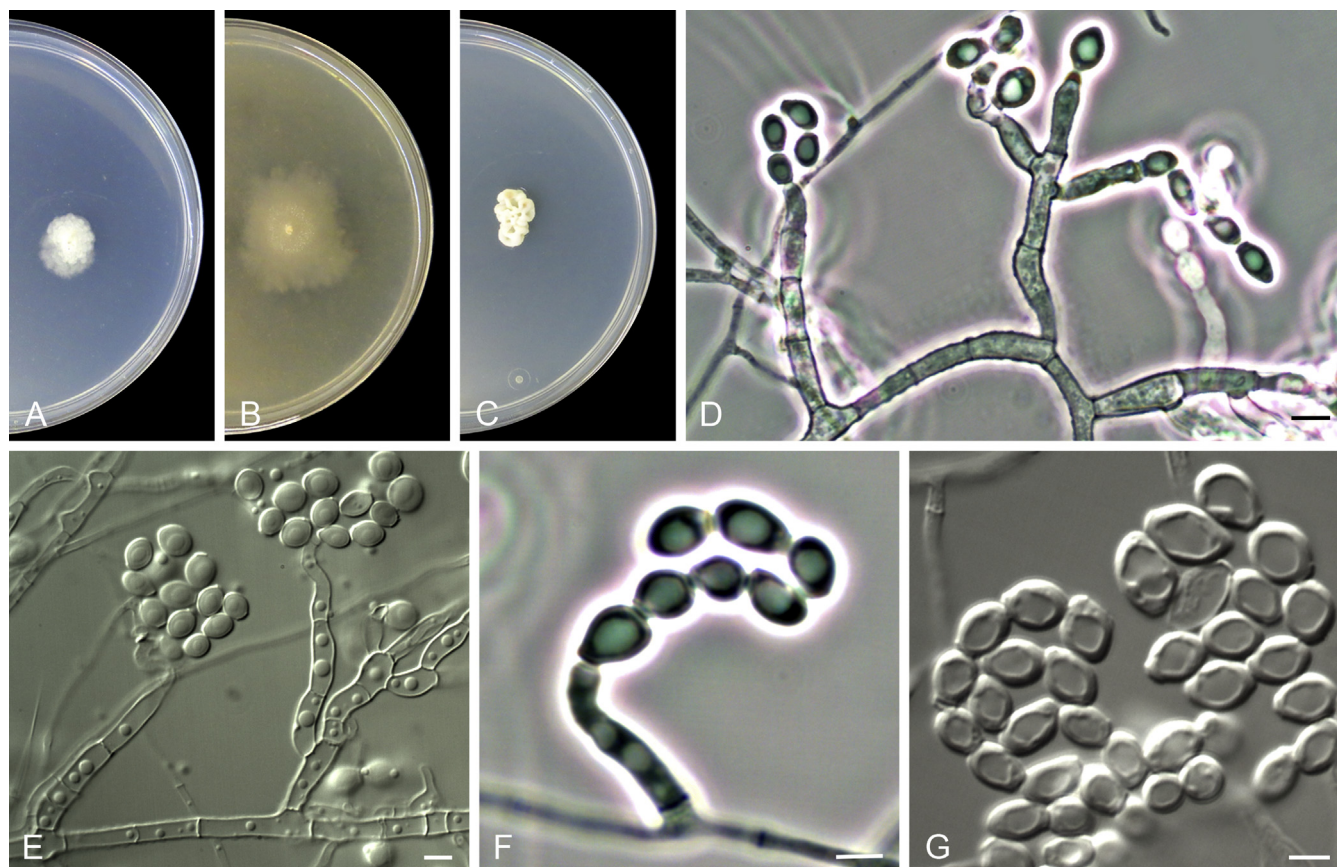
*Penicillium scopulariopsis* Sacc., Syll. Fung. 22: 1275. 1913.

*Scopulariopsis candelabrum* Loubière, Rech. struct. Mucor., (Thesis), Paris: 63. 1924.

*Scopulariopsis danica* F.H. Beyma, Zentralbl. Bakteriol. Parasitenk., Abt. 2. 99: 390. 1939.

*Scopulariopsis communis* Bainier var. *lunzinensis* S zilvinyi., Zentralbl. Bakteriol. Parasitenk., Abt. 2. 103: 173. 1941.

*Material examined:* **Lectotype designated here:** T. XIII, plate IX in Delacroix EG. 1897. Quelques espèces nouvelles. Bulletin de la Société Mycologique de France 13: 114–127, MBT-372234. **Denmark,** from skin of a horse infected with *Trichophyton* sp., 1938, C. Werdelin (ex-type culture of *Scopulariopsis danica* MUCL 9028). **Epitype designated here:** Germany, Schleswig-Holstein, Kiel



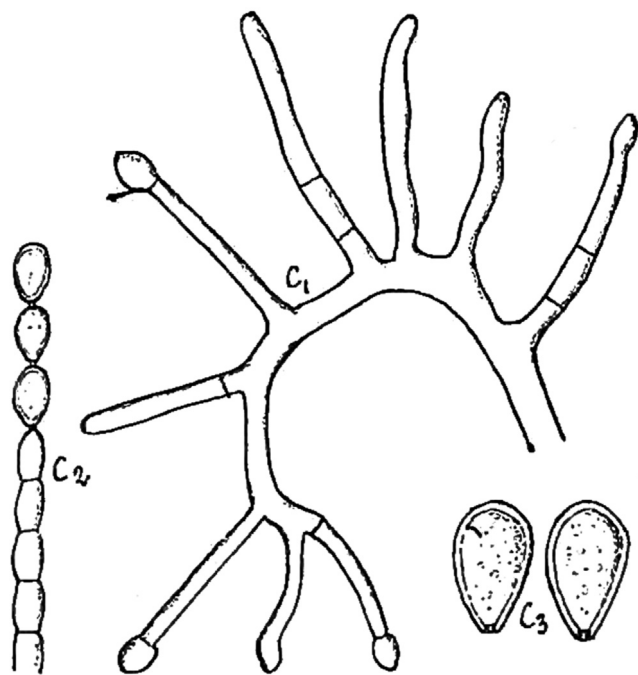
**Fig. 2.** *Acaulium acremonium* (ex-epitype MUCL 8274). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–G. Conidiophores, annellides and conidia. Scale bars: D–G = 10 µm.

Kitzeberg, from wheat field soil, 1963, W. Gams, MBT-202769 (culture ex-epitype MUCL 8274 = CBS 104.65); Schleswig-Holstein, Kiel-Kitzeberg, from soil, 1965, W. Gams (MUCL 8409).

**Description and illustrations:** Morton & Smith (1963).

**Notes:** Delacroix (1897) described *Monilia acremonium* from rotten paper found in garbage, but no type material is known. The ex-type strain of *Scopulariopsis danica*, studied here and considered a heterotypic synonym of *S. acremonium*, can be still recognised by its morphological features, although, as previously documented, this culture is in bad condition with poor sporulation (Morton & Smith 1963). Holotype material is unavailable for this species. However, the protologue contains an illustration that serves as lectotype, which is designated and reproduced here (Fig. 3). Given that only a limited number of strains of *A. acremonium* exist and in order to fix the use of the name, we have selected the strain MUCL 8274 as epitype. Although it has conidia slightly smaller ( $5\text{--}12 \times 3\text{--}6 \mu\text{m}$ ) than those described in the protologue of *M. acremonium*, their size ranges are close to that given by Morton & Smith (1963) for *S. acremonium*. A number of additional North American isolates from soil and clinical sources examined by one of us (Abbott 2000) are consistent with *S. acremonium* as circumscribed by Morton & Smith (1963) and support the epitypification proposed here.

This species has been reported as causing skin and nail infections in humans (de Hoog et al. 2011); however, its identification from cases of proven clinical infection has not been confirmed by molecular methods (Sandoval-Denis et al. 2013). *Acaulium acremonium* is only known by its asexual morph characterised by large, often pointed ovate conidia produced on long cylindrical and somewhat curved annellides borne on branched or unbranched conidiophores. The closely related species *A. albonigrescens* produces smaller ( $5.5\text{--}8 \times 2\text{--}3.5 \mu\text{m}$ ), clavate to cylindrical conidia with rounded apices, formed on straight cylindrical annellides and the species further differs by showing a sexual morph.



**Fig. 3.** Reproduction of the original drawings by Delacroix (1897) illustrating *Monilia acremonium* (original numbers are maintained to indicate the different structures). C1. Conidiogenous cells and conidia. C2. Conidial chain. C3. Conidia.

***Acaulium albonigrescens*** Sopp, Skr. Vidensk.-Selsk. Christiania Math.-Nat. Kl. 11: 70. 1912. Fig. 4.

**Synonyms:** *Microascus albonigrescens* (Sopp) Curzi, Boll. Staz. Patol. Veg. Roma 11: 60. 1931.

*Penicillium albonigrescens* (Sopp) Sacc. [as '*alba-nigrescens*'], Syll. Fung. 25: 670. 1931.

**Material examined:** **Lectotype designated here:** plates VI–VII in Sopp OJ. 1912. Monographie der Pilzgruppe *Penicillium* mit besonderer Berücksichtigung der in Norwegen gefundenen Arten. Videnskaps Selskaps Skrifter. 1. Mat-Naturv Klasse 11: 1–207, MBT-372235; **Epitype designated here:** Japan, Nemuro-shi, Hokkaido, from litter treated with urea, 1967, S. Udagawa, MBT-202737 (CBS H-22334, culture ex-epitype IHEM 18560 = CBS 109.69).

**Description and illustrations:** Barron et al. (1961).

**Notes:** Although no authentic material exists and Morton & Smith (1963) list the species as “unidentifiable”, the modern concept of this taxon (as *Microascus albonigrescens*) was based in herbarium material and a living isolate described by Barron et al. (1961). The protologue of the species includes numerous drawings and aquarels which are thus proposed here as lectotype (Fig. 5). The isolate studied and proposed as epitype (IHEM 18560) conforms with the morphological characteristics of descriptions of *M. albonigrescens* by Barron et al. (1961), Udagawa & Awao (1969), von Arx et al. (1988), and Lumley et al. (2000). *Acaulium albonigrescens* forms white colonies, guttulate, cylindrical to clavate, hyaline conidia ( $5.5\text{--}8 \times 2\text{--}3.5 \mu\text{m}$ ), and has a sexual morph characterised by lunate ascospores with rounded ends. *Acaulium caviariforme*, the other species of the genus producing a sexual morph, has darker colonies, shorter, obovoid to ellipsoidal, brown conidia ( $5\text{--}7 \times 3\text{--}5 \mu\text{m}$ ) and fusiform ascospores. *Acaulium albonigrescens* is a well-circumscribed species described from soil, dung and wood in northern areas (Scandinavia, northern North America and Japan).

***Acaulium caviariforme*** (Malloch & Hubart) Sandoval-Denis, Guarro & Gené **comb. nov.** MycoBank MB814573. Fig. 6.

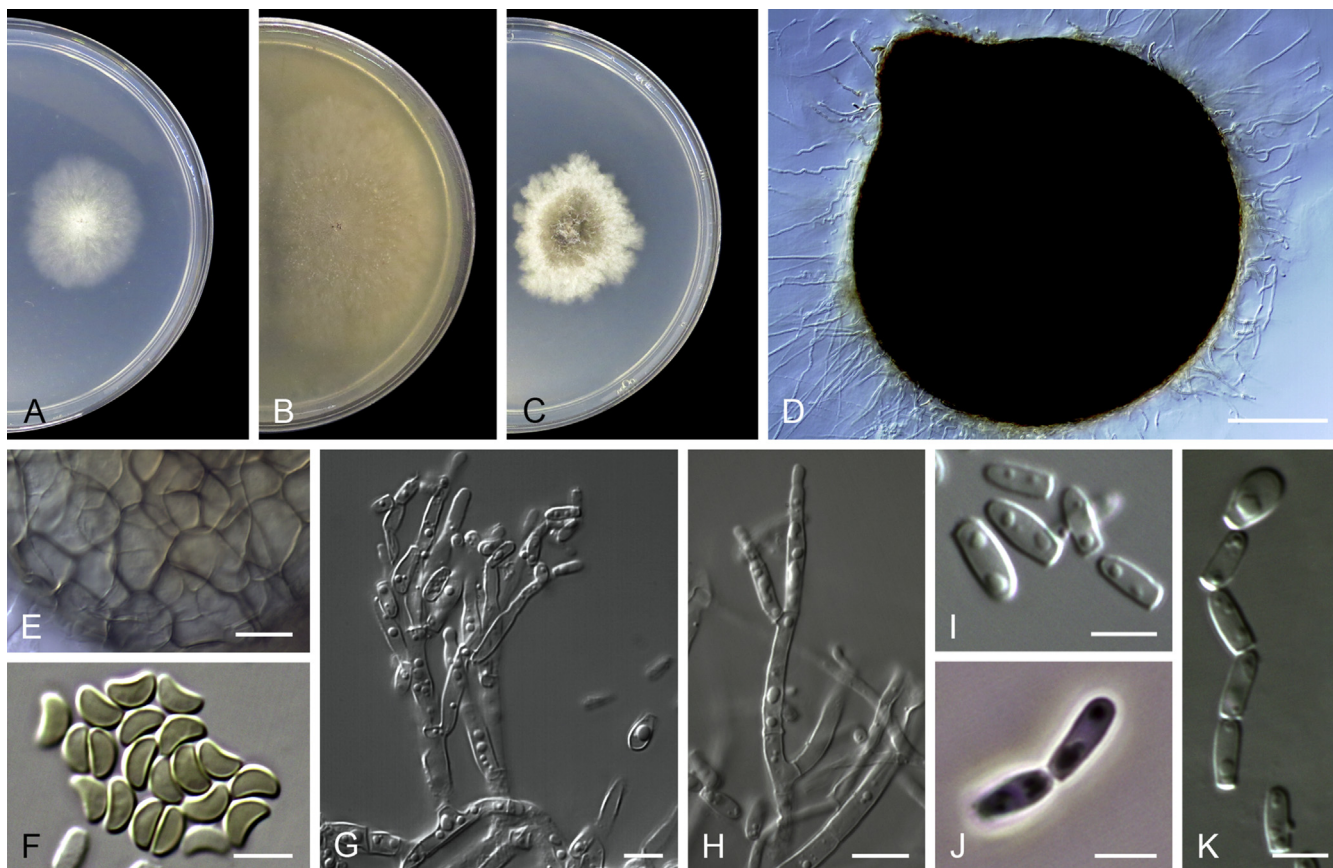
**Basionym:** *Microascus caviariformis* Malloch & Hubart, Canad. J. Bot. 65: 2384. 1987.

**Material examined:** Belgium, Prov. de Liège, Flemalle, Cave de Ramioul, from decaying meat, 1985, D.W. Malloch (**Holotype** TRTC 50940; culture ex-type CBS 536.87).

**Description and illustrations:** Malloch & Hubart (1987).

**Notes:** This species was originally placed in *Microascus* based on morphological features of the well developed sexual morph (Malloch & Hubart 1987). Phylogenetic analyses have demonstrated, however, that it grouped in a lineage separate from the above mentioned genus (Issakainen et al. 2003, Sandoval-Denis et al. 2016). In our phylogenetic analysis, the ex-type culture of *A. caviariforme* grouped with high statistical support with species of *Acaulium*. *Acaulium caviariforme* is morphologically similar to *A. albonigrescens*; both species produce sexual and asexual morphs in culture. However, *A. caviariforme* has fusiform, pale orange to copper-red ascospores, measuring  $6\text{--}9 \times 2\text{--}3 \mu\text{m}$ , and brown, obovoid to ellipsoidal conidia,  $5\text{--}7 \times 3\text{--}5 \mu\text{m}$ ; ascospores of *A. albonigrescens* are smaller ( $3.5\text{--}5.5 \times 2\text{--}3.5 \mu\text{m}$ ), lunate and red-brown, and its conidia are clavate to cylindrical, hyaline and narrower ( $5.5\text{--}8 \times 2\text{--}3.5 \mu\text{m}$ ).





**Fig. 4.** *Acaulium albonigrescens* (ex-epitype IHEM 18560). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D. Ascoma. E. Ascomatal peridium. F. Ascospores. G–H. Conidiophores and conidiogenous cells. I–K. Conidia. Scale bars: D = 100 µm; E–K = 5 µm.

*Acaulium caviariforme* appears to occupy a unique niche, having been isolated from meat in caves in Europe and North America.

***Cephalotrichum*** Link, Mag. Ges. Naturf. Freunde Berlin 3: 20. 1809.

*Synonyms:* *Doratomyces* Corda, Sturm, Deutschl. Fl., Abt. 3 (Pilze Deutschl.) 2: 65. 1829.

*Stelechotrichum* Ritgen 1831 *nom. inval.* Publication not traced (Seifert *et al.* 2011).

*Echinobotryum* Corda, in Sturm, Deutschlands Flora, Abt. 3 (Pilze) 3: 51.1831.

*Stysanus* Corda, Icon. fung. (Prague) 1: 21. 1837.

*Synpenicillium* Costantin, Bull. Soc. Mycol. France. 4: 62. 1888.

*Trichurus* Clem. [ & Shear], in Pound & Clements, Bot. Surv. Nebr. 4: 7. 1896.

*Berkeleyna* Kuntze, Revis. gen. pl. (Leipzig) 3: 447. 1898.

*Stysanopsis* Ferraris, Ann. Mycol. 7: 281. 1909.

*Capnostysanus* Speg., Physis 4: 295. 1918.

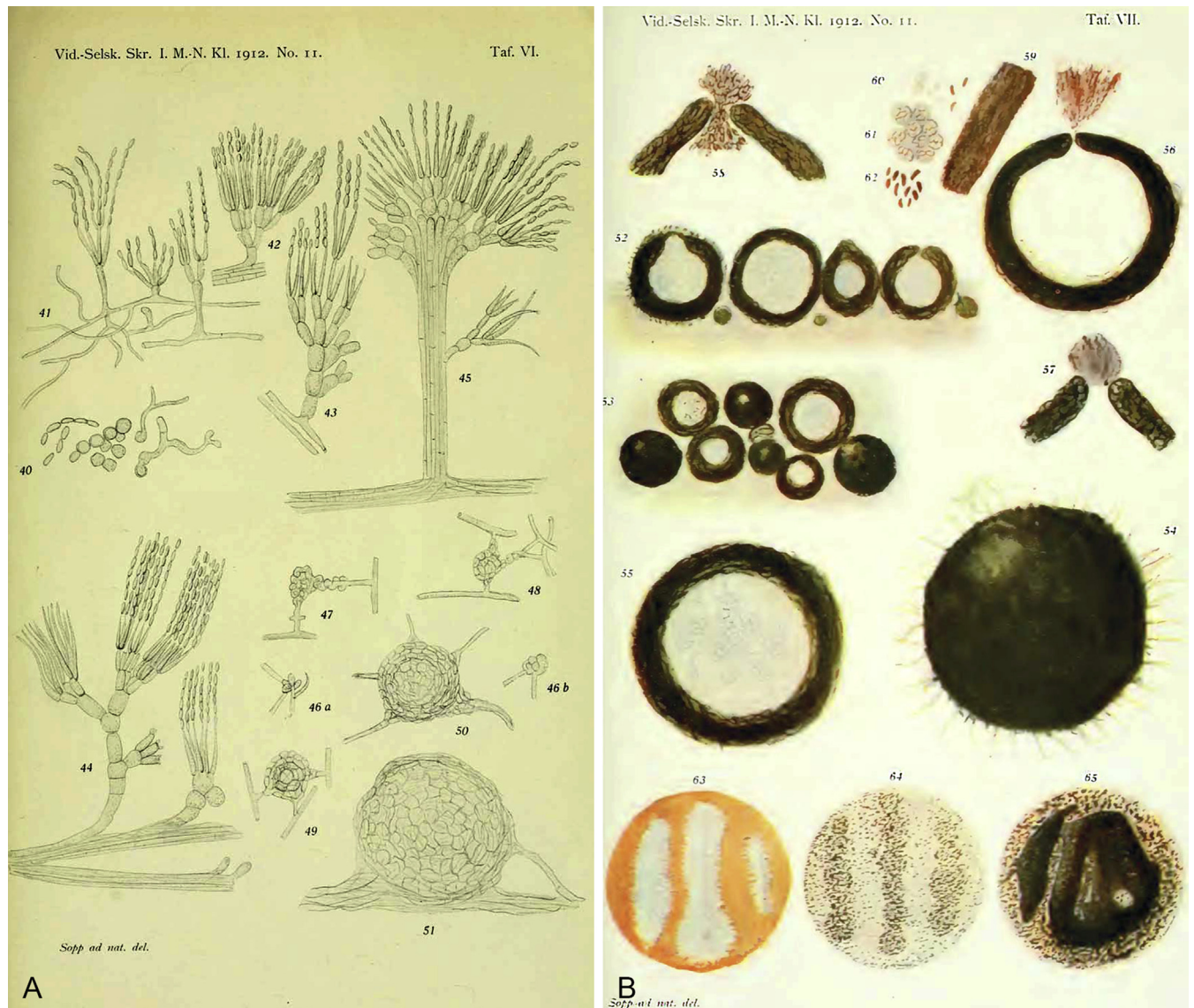
*Colonies* growing slowly to moderately fast, velvety, powdery, floccose, funiculose or fasciculate, flat, white, becoming pale to dark grey. *Hyphae* subhyaline to dark brown, rarely hyaline, thin- and smooth-walled. *Conidiophores* arising from the substratum or from the aerial mycelium, branched or unbranched, septate, smooth or finely ornamented, often aggregated in synnemata. *Conidiogenous cells* commonly penicillately arranged, annellidic, flask-shaped, subhyaline to dark brown and smooth-walled. *Conidia* basipetal, catenate, dry, 1-celled, obovoid, ellipsoidal, globose to subglobose broadly truncate at the base, hyaline or subhyaline, thin- or thick-walled, smooth or distinctly verrucose.

*Synnemata* with a pale brown to black stipe and fertile at the upper portion forming a rounded to cylindrical sporulating head; sterile setae can be formed at the upper part of the synnemata, septate, long, cylindrical, branched or unbranched, straight or coiled. A second asexual state (referred as echinobotryum-like synasexual morph) can be present: *conidiogenous cells* polyblastic, borne solitary or on short penicillate conidiophores on the hyphae or on the synnemata; *conidia* grouped in clusters, oval to fusiform, often with a pointed apex, dark brown, verrucose and thick-walled.

*Type species:* *Cephalotrichum stemonitis* Link.

*Notes:* *Cephalotrichum* and other genera of the *Microascaceae* such as *Microascus*, *Scopulariopsis* and the recently proposed genus *Fuscoannellis* (Jagielski *et al.* 2016) have very similar conidiogenous apparatus, and asexual morphs of the genera could be hardly distinguished from each other, especially when isolates grow on rich culture media like PDA. However, although conidiophores in the three latter genera can arise from dense hyphal mycelial fascicles, they never form synnemata. Other genera of *Microascaceae* having synnematos conidiophores include *Parascedosporium*, *Petriella* and *Scedosporium*, but the conidia of these genera are produced in slimy masses and sexual morphs are produced in many species (Lackner *et al.* 2014). *Cephalotrichum* produces conidia in dry basipetal chains and sexual morphs are unknown.

***Cephalotrichum asperulum*** (J.E. Wright & S. Marchand) Sandoval-Denis, Guarro & Gené, **comb. nov.** MycoBank MB814577. [Fig. 7](#)



**Fig. 5.** Reproduction of the original drawings by Sopp (1912) illustrating *Acaulium albonigrescens* (original numbers are maintained to indicate the different structures). A. Asexual morph: 40. Germinating conidia. 41–44. Conidiophores, conidiogenous cells and conidia. 45. Synnematal conidiophores. 46–51. Diverse phases of perithecial development, the first stages are seen in 46a and b. B. Sexual morph: 52. Sections of perithecia showing the ostiole development. 53. Horizontal section of perithecia embedded in the mycelium. 54. Mature perithecium. 55. Cross section of an immature perithecium. 56. Cross section of a fully mature perithecium, completely emptied through the ostiole. 57. Cross section of an empty perithecial ostiole. 58. Cross section of a perithecial ostiole during the liberation of ascospores. 59–60. Free ascospore masses. 61. Asci. 62. Ascospores. 63–65. Macroscopic features.

**Basionym:** *Doratomyces asperulus* J.E. Wright & S. Marchand, Bol. Soc. Argent. Bot. 14: 308. 1972.

**Material examined:** **Argentina**, Buenos Aires, Arroyo Las Viboras, humus-rich soil in low grassland, 1971, J.E. Wright (**Holotype** BAFC 2135; culture ex-isotype CBS 582.71). **The Netherlands**, Wageningen, from seed, 1922, C.M. Doyer (CBS 127.22 as *Doratomyces stemonitis*). **USA**, from bronchoalveolar lavage fluid, unknown date, D.A. Sutton (UTHSCSA D114-62 = FMR 13443); from bronchoalveolar lavage fluid, unknown date, D.A. Sutton (UTHSCSA D114-65 = FMR 13446).

**Description and illustrations:** Wright & Marchand (1972).

**Notes:** This clade includes isolates obtained from different environmental sources, as well as from clinical human specimens mainly from lower respiratory tract. However, its inability to grow at 37 °C (Table 2) suggests that its isolation from clinical samples could represent environmental contamination.

Abbott (2000) considered this species a synonym of *C. purpureofuscum* s. lat. based on a broad range of variation in

the ornamentation patterns of the conidia seen by light microscopy and SEM. Our phylogenetic results, however, showed that the two are not conspecific and can be easily differentiated by the morphology of their conidia. The conidia of *C. asperulum* (CBS 582.71) are apically pointed and coarsely roughened with a spiral-sculpted appearance, while those of *C. purpureofuscum* (UAMH 9209) are smooth to finely roughened with a slender pointed apex.

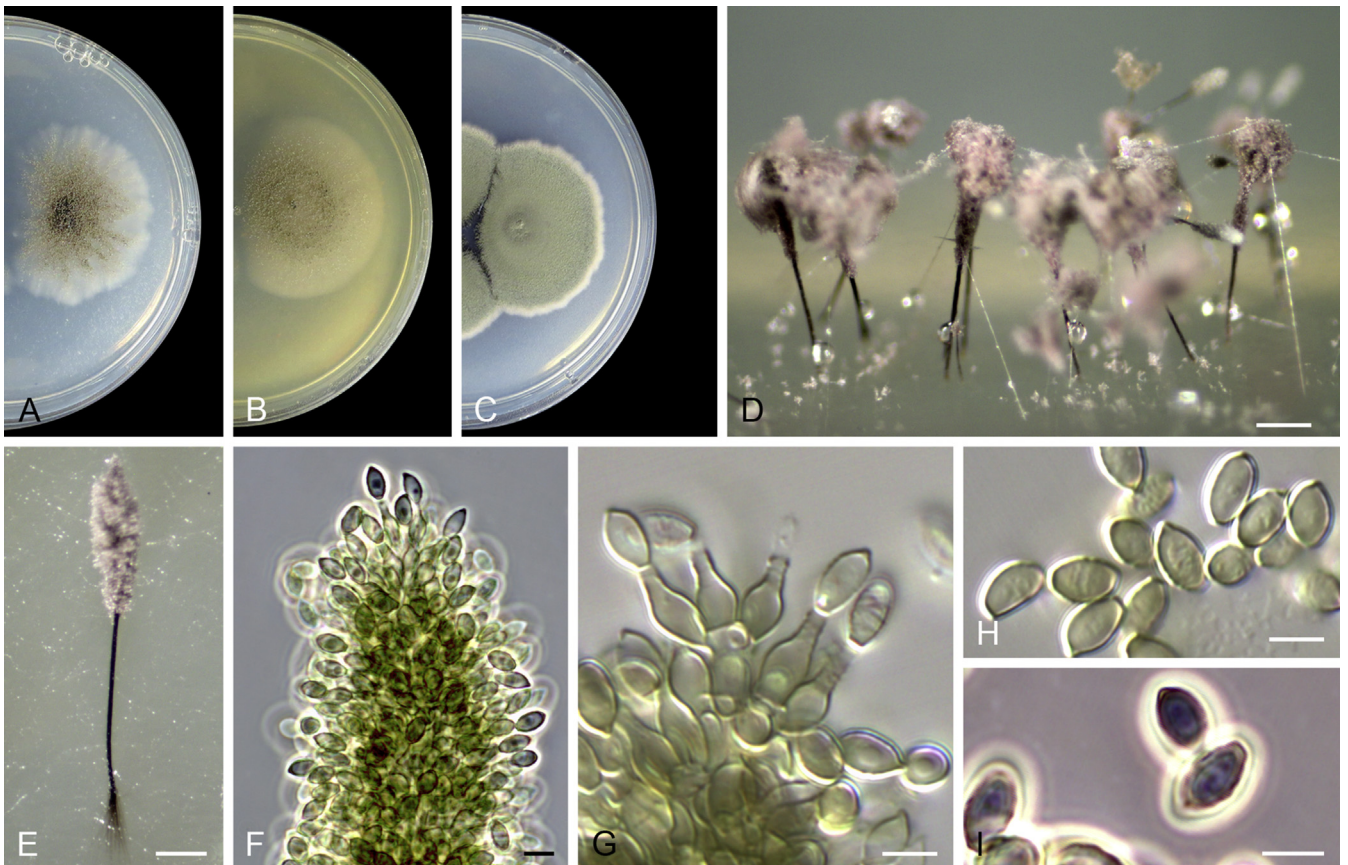
***Cephalotrichum brevistipitatum*** Sandoval-Denis, Guarro & Gené, sp. nov. MycoBank MB814530. Fig. 8.

**Etymology:** From the Latin words *brevis*-small and *stipes*-tree trunk, “short-stiped”, referring to the short synnemata.

**Colonies** on OA and PCA reaching 47–50 mm diam in 14 d at 25 °C, flat, velvety with scarce aerial mycelium, front and reverse golden grey (4C2). On PDA reaching 31–33 mm diam in 14 d at 25 °C, radially folded, velvety to felty, olive-brown (4D3/4E3), with regular margin; reverse olive-brown (4D3). **Hyphae** septate, hyaline to pale brown, smooth- and thin-walled, 1.5–4 µm wide.



**Fig. 6.** *Acaulium caviariforme* (ex-type CBS 536.87). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–G. Conidiophores and conidiogenous cells. H–I. Conidia. Scale bars: D–I = 5 µm.



**Fig. 7.** *Cephalotrichum asperulum* (ex-isotype CBS 582.71). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–E. Synnemata. F. Apical portion of a synnema. G. Conidiogenous cells. H–I. Conidia. Scale bars: D–E = 200 µm; F–I = 5 µm.

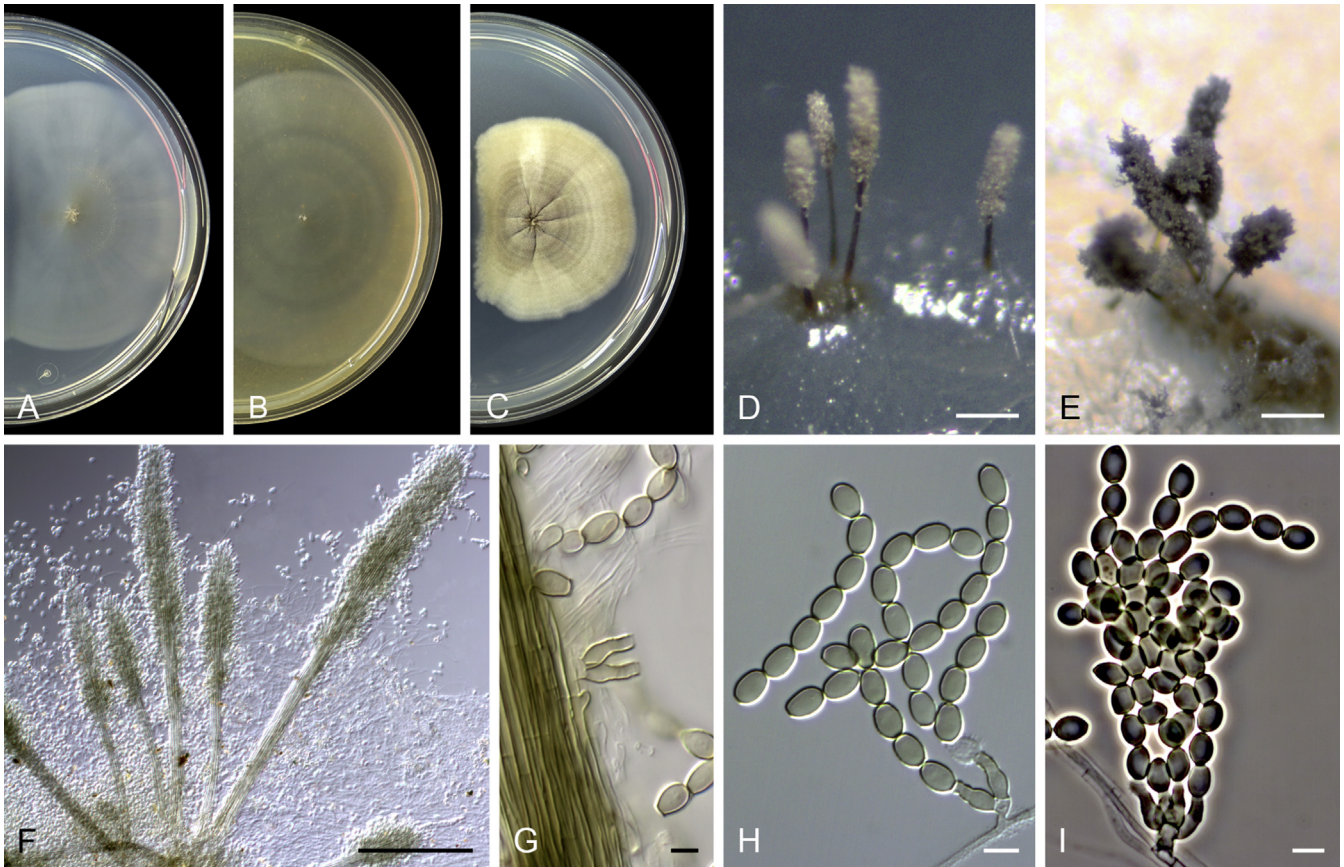
**Table 2.** Relevant phenotypic features of members of *Acaulium*, *Cephalotrichum*, *Fairmania*, *Gamsia*, *Wardomyces* and *Wardomycopsis*.

Species	Sexual morph	Asexual morph	Ascospore		Synnemata size (µm)	Anneloconidia		Solitary conidia		Growth at (°C)					
			Size (µm)	Shape		Size (µm)	Shape, surface and colour	Size (µm)	Shape, surface and colour	5	15	25	30	35	37
<i>Acaulium</i>															
<i>A. acremonium</i>	-	+	n/a	n/a	n/a	5–12 × 3–6	Obovate, smooth and hyaline	n/a	n/a	+	+	+	+	+	-
<i>A. albonigrescens</i>	+	+	3.5–5.5 × 2–3.5	Lunate	n/a	5.5–8 × 2–3.5	Cylindrical to clavate, smooth and hyaline	n/a	n/a	+	+	+	+	-	-
<i>A. caviariforme</i>	+	+	6–9 × 2–3	Fusiform	n/a	5–7 × 3–5	Obovoid to ellipsoidal/ smooth/brown	n/a	n/a	+	+	+	+	-	-
<i>Cephalotrichum</i>															
<i>C. asperulum</i>	-	+	n/a	n/a	120–1 000	5–8.5 × 3–4	Oval to ellipsoidal, rough, pale brown	n/a	n/a	+	+	+	+	+	-
<i>C. brevistipitatum</i>	-	+	n/a	n/a	300–500	6–7 × 3.5–4	Ellipsoidal, smooth to finely roughened, pale brown	n/a	n/a	-	+	+	+	+	-
<i>C. columnare</i>	-	+	n/a	n/a	50–500	5.5–7.5 × 2.5–4	Oval to ellipsoidal, assymetrical, smooth, brown-black	n/a	n/a	+	+	+	+	+	+
<i>C. cylindricum</i>	-	+	n/a	n/a	450–700	4.5–6 × 2.5–3.5	Oval to ellipsoidal, smooth, pale green	n/a	n/a	+	+	+	+	+	+
<i>C. dendrocephalum</i>	-	+	n/a	n/a	1 000–2 000	5–7 × 2.5–3.5	Oval to ellipsoidal, smooth, grey-brown	n/a	n/a	+	+	+	+	+	-
<i>C. gorgonifer</i>	-	+	n/a	n/a	500–1 000	4–8 × 2.5–4	Oval to ellipsoidal, smooth, pale brown	n/a	n/a	+	+	+	+	+	+
<i>C. hinnuleum</i>	-	+	n/a	n/a	800–1 600	6–7.5 × 2.5–4	Subglobose to ellipsoidal, smooth, pale brown	8.5–10 × 5.5–7	Oval to navicular, warted, brown	+	+	+	+	-	-
<i>C. microsporium</i>	-	+	n/a	n/a	500–1 000	3.5–5 × 2–3	Oval to ellipsoidal, smooth, green-brown	n/a	n/a	-	+	+	+	-	-
<i>C. nanum</i>	-	+	n/a	n/a	500–2 000	6–8.5 × 4.5–7.5	Subspherical to oval, coarsely warted, grey-brown	n/a	n/a	+	+	+	+	-	-
<i>C. purpureofuscum</i>	-	+	n/a	n/a	800–1 600	5–8 × 3–4.5	Oval to ellipsoidal, smooth or slightly roughened, green-brown	n/a	n/a	+	+	+	+	+	-
<i>C. stemonitis</i>	-	+	n/a	n/a	2 000–3 000	6–9 × 4–5	Ellipsoidal to cylindrical, smooth, pale green-brown	8–19 × 6–7.5	Fusoid, coarsely warted, dark-brown	+	+	+	+	-	-

Table 2. (Continued)

Species	Sexual morph	Asexual morph	Ascospore		Synnemata size (µm)	Anelloconidia		Solitary conidia		Growth at (°C)					
			Size (µm)	Shape		Size (µm)	Shape, surface and colour	Size (µm)	Shape, surface and colour	5	15	25	30	35	37
<i>C. verrucisporum</i>	-	+	n/a	n/a	1 000–3 000	6–9 × 3–5.5	Globose to oval, rough, dark brown	n/a	n/a	+	+	+	+	-	-
<i>Fairmania</i>															
<i>F. singularis</i>	+	+	4.5–7 × 4–6	Heart shaped	n/a	4–7.5 × 3–5	Obovate to clavate, finely striate, pale brown	n/a	n/a	+	+	+	+	-	-
<i>Gamsia</i>															
<i>G. aggregata</i>	-	+	n/a	n/a	n/a	8–10.5 × 3.5–5	Ellipsoidal, rounded or appiculate/hyaline (2-celled)	4–7.5 × 3.5–5	Oval to broadly ellipsoidal, smooth, dark brown	+	+	+	+	-	-
<i>G. columbina</i>	-	+	n/a	n/a	n/a	5–10.5 × 2.5–5.5	Oval, smooth/hyaline (1–2-celled)	6–13 × 3.5–6.5	Oval to ellipsoidal, smooth, dark brown	+	+	+	+	-	-
<i>Wardomyces</i>															
<i>W. anomalus</i>	-	+	n/a	n/a	n/a	n/a	n/a	4–8 × 3.5–6	Oval, smooth, dark brown	+	+	+	+	-	-
<i>W. giganteus</i>	+	+	4–5.5 × 3.5–4	Reniform (2 germ pores)	n/a	n/a	n/a	6.5–14 × 3.5–5	Ellipsoidal, smooth, dark brown	+	+	+	-	-	-
<i>W. humicola</i>	-	+	n/a	n/a	n/a	n/a	n/a	9–12 × 2.5–5.5	Navicular, smooth, dark brown	n/d	n/d	n/d	n/d	n/d	n/d
<i>W. inflatus</i>	-	+	n/a	n/a	n/a	n/a	n/a	6–8 × 3.5–5	Ellipsoidal to cylindrical, smooth, dark brown	+	+	+	+	-	-
<i>W. ovalis</i>	-	+	n/a	n/a	n/a	5.5–10 × 3.5–6	Oval, smooth/hyaline to subhyaline (1-celled)	7–11 × 4–5	Ellipsoidal, smooth, dark brown	+	+	+	+	-	-
<i>W. pulvinatus</i>	-	+	n/a	n/a	n/a	n/a	n/a	5.5–10 × 3–4.5	Navicular, smooth, dark brown	+	+	+	+	-	-
<i>Wardomycopsis</i>															
<i>Ws. humicola</i>	-	+	n/a	n/a	n/a	4–5 × 2.5–3	Ovate to cylindrical, smooth, smokey brown	n/a	n/a	-	+	+	+	-	-
<i>Ws. inopinata</i>	+	+	3–3.5 × 2.5–3	Reniform to triangular (1 germ pore)	n/a	4–5.5 × 4–5.5	Globose to subglobose, smooth, olive-brown	n/a	n/a	n/d	n/d	n/d	n/d	n/d	n/d
<i>Ws. litoralis</i>	-	+	n/a	n/a	n/a	5–7 × 3–4.5	Obovoid to broadly ellipsoidal, smooth, dark olive brown,	n/a	n/a	-	+	+	+	+	+

n/a, not available; n/d, not determined.



**Fig. 8.** *Cephalotrichum brevistipitatum* (ex-type CBS 157.57). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–F. Synnemata. G. Conidiogenous cells. H–I. Conidia. Scale bars: D–F = 100 µm; G–I = 5 µm.

*Conidiophores* unbranched or sparingly branched, often consisting of single annellides borne sessile on the aerial hyphae or in groups of 2–3 annellides on short basal cells, 4–5 × 3–4 µm, pale brown, smooth- and thin-walled, usually forming synnemata. *Synnemata* 300–500 µm high, stipes pale brown to brown, 9–14 µm wide, conidial heads brown, subglobose, ellipsoidal or short clavate; setae absent. *Annellides* ampulliform, 6–9 × 2.5–3.5 µm, subhyaline to pale brown, smooth- and thin-walled. *Conidia* ellipsoidal, 6–7 × 3.5–4 µm, with truncate base and rounded apex, pale brown, smooth- and thin-walled, arranged in long chains.

Cardinal temperatures for growth — Optimum 25–30 °C, maximum 35 °C, minimum 15 °C.

*Material examined:* The Netherlands, Wageningen, from *Solanum tuberosum*, 1957, PD A-1379 (Holotype CBS H-22332; culture ex-type CBS 157.57).

*Notes:* *Cephalotrichum brevistipitatum* is morphologically similar to *C. purpureofuscum*. However, the latter species has larger synnemata (800–1600 µm high) with compact black stipes and apically pointed conidia. *Cephalotrichum brevistipitatum* has conidia with rounded apices and small synnemata, up to 500 µm high, with brown stipes formed by somewhat loose, pale brown hyphae.

***Cephalotrichum columnare*** (H.J. Swart) S.P. Abbott, **comb. nov.** MycoBank MB814969. Fig. 9.

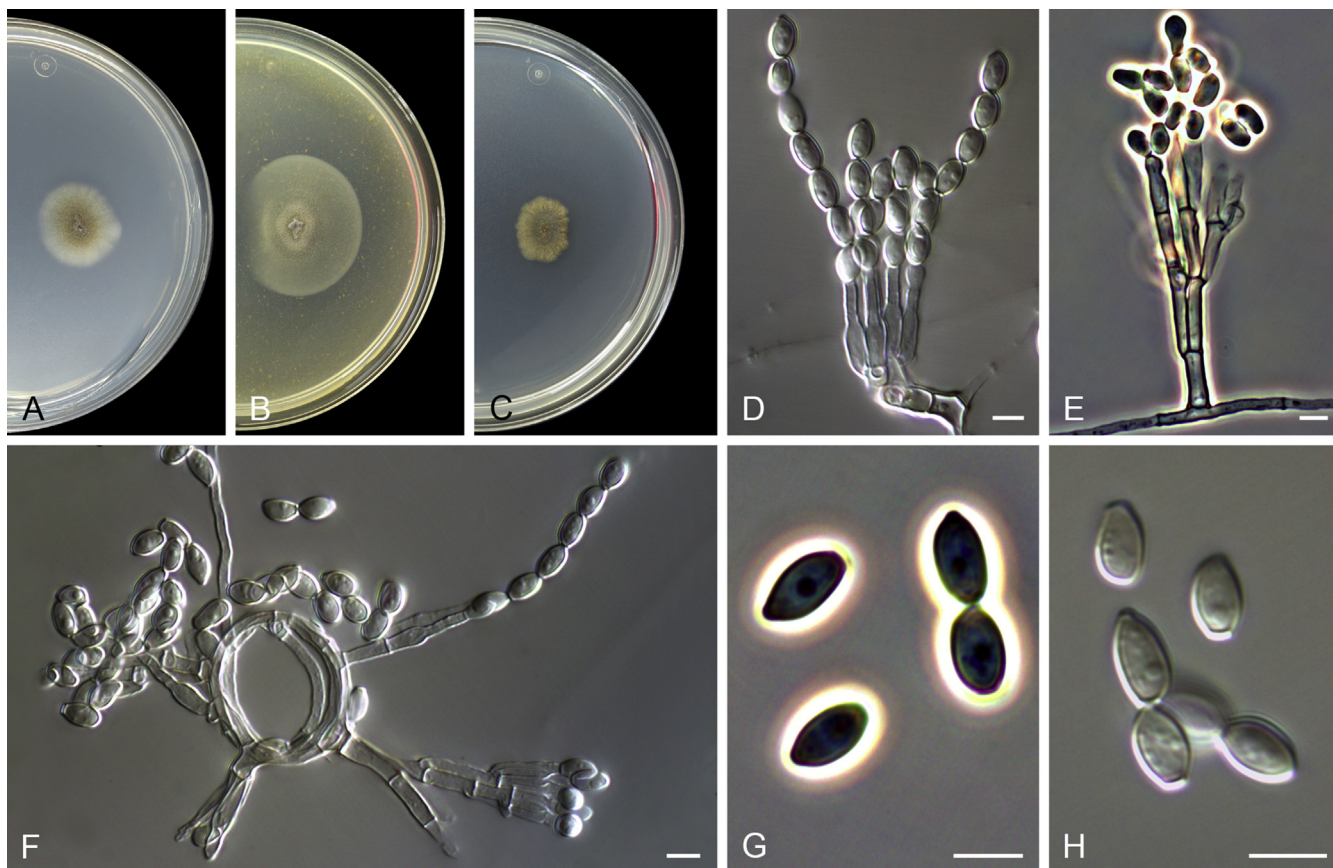
*Basionym:* *Doratomyces columnaris* H.J. Swart, Acta Bot. Neerl. 15: 521. 1967.

*Material examined:* South Africa, Johannesburg, Melville Koppies Nature Reserve, from dung of *Lepus*, 1964, H.J. Swart (Holotype IMI 116691; culture ex-type CBS 159.66).

*Descriptions and illustrations:* Swart (1967), Abbott (2000).

*Notes:* Synnemata are more reduced than in most other species of *Cephalotrichum*. Abbott (2000) suggested a morphological similarity to synnemata seen in asexual morphs of *Kernia* species (described as *Scopulariopsis* morphs) and some *Graphium* species, but molecular data confirm a close relationship between *C. columnare* and other species in *Cephalotrichum* (Fig. 1). In the study of Abbott (2000), several isolates of *C. columnare* did not produce synnemata in culture and recent isolations of this species from indoor environments show a propensity of synnema production to be reduced or disappear after primary isolation and overall sporulation to be sparse. We were also unable to obtain synnemata from the ex-type culture (CBS 159.66) in this study; however, the isolate produced dry conidia in chains characteristic of *Cephalotrichum* instead to conidia in slimy heads typical of *Graphium* and *Kernia* asexual morphs (Lackner et al. 2014).

*Cephalotrichum columnare* morphologically resembles *C. brevistipitatum* and *C. microsporum*. However, the conidia of *C. brevistipitatum* are pale brown and smooth to finely roughened (6–7 × 3.5–4 µm), while those of *C. microsporum* are brown and smaller (3.5–5 × 2–3 µm). In addition, these two species have colonies with a faster growth rate (47–50 mm and 26–37 mm diam, respectively, in 14 d at 25 °C). By contrast, *C. columnare* produces asymmetrical, dark brown, smooth-walled conidia



**Fig. 9.** *Cephalotrichum columnare* (ex-type CBS 159.66). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–E. Conidiophores. F–H. Conidiogenous cells and conidia. Scale bars: D–H = 5 µm.

(5.5–7.5 × 2.5–4 µm) and slow-growing colonies (18–19 mm diam in 14 d at 25 °C) with poorly developed synnemata.

***Cephalotrichum cylindricum*** (Clem. & Shear) S. P. Abbott, **comb. nov.** MycoBank MB814970, [Fig. 10](#).

*Basionym:* *Trichurus cylindricus* Clem. & Shear, in Pound & Clements, Bot. Surv. Nebr. 4: 7. 1896.

*Synonym:* *Trichurus terrophilus* Swift & Povah, Mycologia 21: 214. 1929, non *Cephalotrichum terricola* Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 221. 2011.

*Material examined:* **USA**, Lincoln, Nebraska, on decaying seeds of *Cucurbita maxima*, 1895, collector unknown (**Holotype** NEB0041953). **Epitype designated here:** **USA**, Kansas, seed of *Sorghum*, 1955, C.T. Rogerson, MBT-203075 (culture ex-epitype UAMH 1348). **South Africa**, Bekker, timber of *Eucalyptus saligna*, 1951, TRL8-FPRL (CBS 448.51).

*Description and illustrations:* [Swift \(1929\)](#), [Abbott \(2000\)](#).

*Notes:* Our phylogenetic and morphological results support the designation of the epitype culture selected by [Abbott \(2000\)](#), which is formally proposed here. Only three species of *Cephalotrichum* produce setae in the upper part of the synnemata, i.e., *C. cylindricum*, *C. dendrocephalum*, and *C. gorgonifer*. *Cephalotrichum cylindricum* can be differentiated by the production of straight, unbranched or branched setae on synnemata 450–700 µm tall with brown stipes. By contrast, *C. dendrocephalum* and *C. gorgonifer*, produce undulating and spirally twisted setae, respectively, and synnemata >1 000 µm tall with dark brown to black stipes.

***Cephalotrichum dendrocephalum*** (Udagawa, Y. Horie & Abdullah) S.P. Abbott, **comb. nov.** MycoBank MB814971. [Fig. 11](#)  
*Basionym:* *Trichurus dendrocephalus* Udagawa, Y. Horie & Abdullah, Mycotaxon 23: 253. 1985.

*Material examined:* **Iraq**, near Basrah, cultivated soil from date palm plantation, 1983, S.K. Abdullah (**Holotype** NHL 2927; culture ex-isotype CBS 528.85).

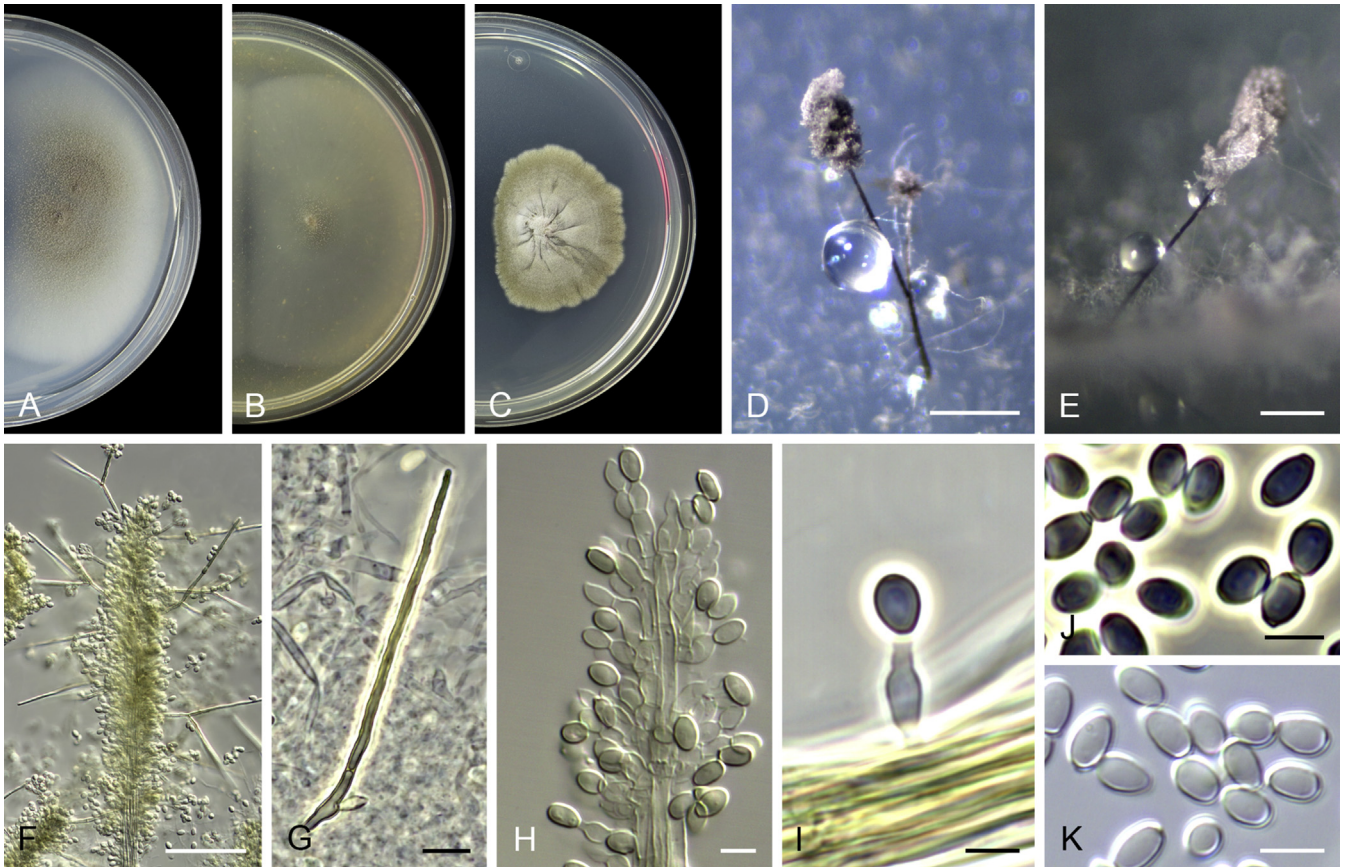
*Description and illustrations:* [Udagawa et al. \(1985\)](#), [Abbott \(2000\)](#).

*Notes:* The presence of characteristic undulating branched setae on large synnemata is a distinctive morphological characteristic of this species (see notes on *C. cylindricum*). In the absence of setae, *C. dendrocephalum* can be confused with *C. purpureofuscum*. However, *C. dendrocephalum* exhibits brown to grey conidia, measuring 5–7 × 2.5–3.5 µm, with rounded or pointed apex, and grey colonies with a growth rate 18–39 mm diam in 14 d at 25 °C; while *C. purpureofuscum* produces somewhat larger (5–8 × 3–4.5 µm) green-brown pointed conidia, and dark grey to black colonies with a faster growth rate (44–56 mm diam in 14 d at 25 °C).

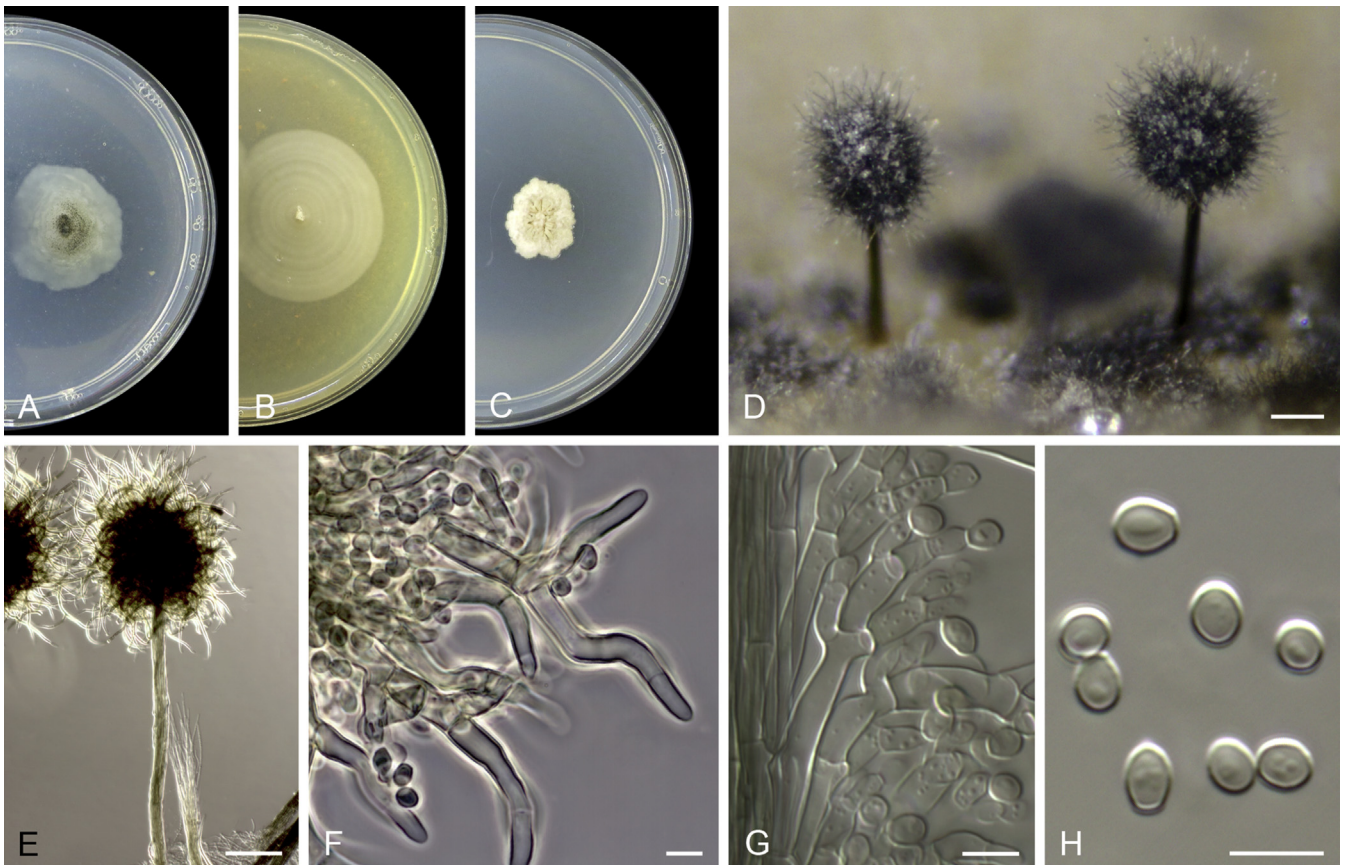
***Cephalotrichum gorgonifer*** (Bainier) Sandoval-Denis, Gené & Guarro, **comb. nov.** MycoBank MB817599. [Fig. 12](#).

*Basionym:* *Trichurus gorgonifer* Bainier, Bull. Soc. Mycol. France. 23: 230. 1907.

*Synonyms:* *Trichurus spiralis* Hasselbr., Bot. Gaz. 29: 321. 1900. *Cephalotrichum heliciforme* T.Y. Zhang, Mycosystema 33: 948. 2014, non *Cephalotrichum spirale* H.M. Liu, H.Q. Pan & T.Y. Zhang, Mycotaxon 117: 220. 2011.

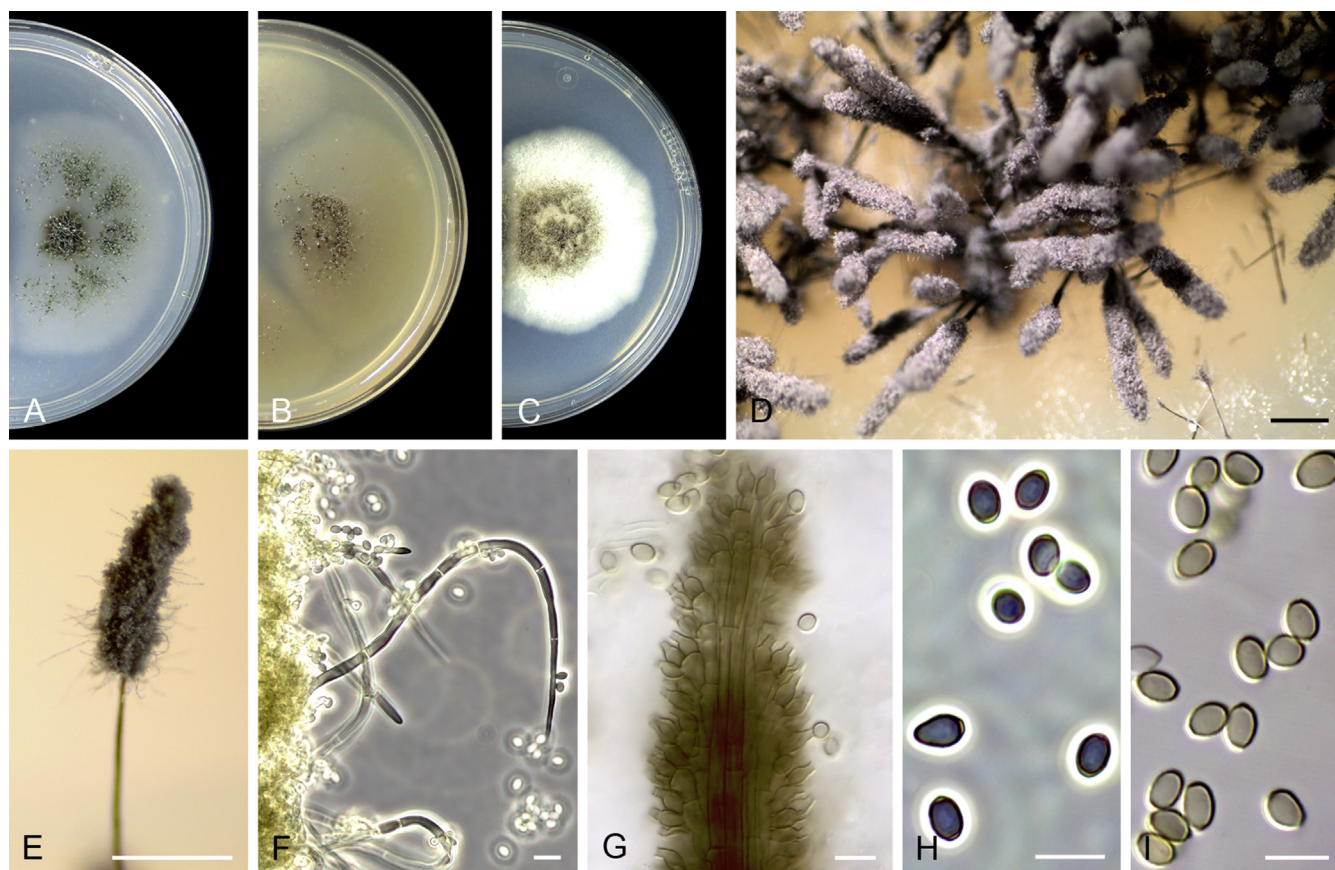


**Fig. 10.** *Cephalotrichum cylindricum* (ex-epitype UAMH 1348). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–E. Synnemata. F. Detail of the apical part of a synnema. G. Detail of a synnemal seta. H–I. Conidiogenous cells. J–K. Conidia. Scale bars: D–E = 200  $\mu$ m; F = 100  $\mu$ m; G = 20  $\mu$ m; H–K = 5  $\mu$ m.



**Fig. 11.** *Cephalotrichum dendrocephalum* (ex-isotype CBS 528.85). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–E. Synnemata. F. Detail of synnemal setae. G. Conidiogenous cells. H. Conidia. Scale bars: D–E = 200  $\mu$ m; F–H = 5  $\mu$ m.





**Fig. 12.** *Cephalotrichum gorgonifer* (ex-epitype CBS 635.78). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–E. Synnemata. F. Detail of a synnemal seta. G. Conidiogenous cells. H–I. Conidia. Scale bars: D–E = 200 µm; F–I = 10 µm.

**Material examined:** **Lectotype designated here:** T. XXXIII, plate XXV in Bainier G. Mycothèque de l'École de Pharmacie, XXI–XXIII. Bulletin de la Société Mycologique de France, 1907, 23: 218–241, MBT-372236. **Canada,** Alberta, Spruce Grove, steamed decomposing mushroom compost, unknown date, L. Sigler (UAMH 3585). **South Africa,** from unknown origin, 1953, unknown collector (CBS 368.53). **Epitype designated here:** **The Netherlands,** from human hair, 1978, S.S.D.Z Delft, MBT-203078 (CBS H-22697, culture ex-epitype CBS 635.78). **USA,** from unknown origin, 1908, A.F. Blakeslee (CBS 131.08); from bronchoalveolar lavage fluid, unknown date, D.A. Sutton (UTHSCSA DI14-63 = FMR 13444); from bronchoalveolar lavage fluid, unknown date, D.A. Sutton (UTHSCSA DI14-64 = FMR 13445); from bronchoalveolar lavage fluid, unknown date, D.A. Sutton (UTHSCSA DI14-69 = FMR 13450); from maxillary sinus fluid, unknown date, D.A. Sutton (UTHSCSA DI14-71 = FMR 13452); from bronchoalveolar lavage fluid, unknown date, D.A. Sutton (UTHSCSA DI14-75 = FMR 13456).

**Description and illustrations:** Ellis (1971), Domsch *et al.* (2007).

**Notes:** Zhang *et al.* (2014) proposed *Cephalotrichum heliciforme* as *nomen novum* for *Trichurus spiralis* Hasselbr. to avoid nomenclatural conflict with the recently described species *Cephalotrichum spirale* by Jiang *et al.* (2011), which was characterised by the spiral pattern of roughness on the conidial surface. However, according to the International Code of Nomenclature (ICN) for algae, fungi and plants, a new combination is required for *C. heliciforme* as there is an older epithet available for this species (*Trichurus gorgonifer*). Therefore, the new combination *C. gorgonifer* is proposed and *C. heliciforme* is reduced to a synonym. Because type material for *T. gorgonifer* is nonexistent, an illustration included in the protologue reproduced here (Fig. 13) serves as lectotype of *C. gorgonifer*. In addition, to assure the availability of information for modern identification, an epitype culture is designated.

The widespread species *C. gorgonifer* has been commonly known as *T. spiralis*, and it is a common inhabitant of soil and decaying vegetable material. However, the majority of isolates included in this study were from human clinical samples, mainly hair and respiratory specimens. Although *C. gorgonifer* is able to grow at human physiological temperature, the potential pathogenic role of this species is uncertain since no clinical data are available.

*Cephalotrichum gorgonifer* is morphologically similar to *C. cylindricus* and *C. dendrocephalus*, but it is easily recognisable by its spirally coiled setae. Strains with poorly developed or lacking synnematal setae could be confused with *C. purpureofuscum*, however the conidia of the latter species are brown with slightly pointed apices, while those of *C. gorgonifer* are grey-brown with rounded apices.

***Cephalotrichum hinnuleum*** Sandoval-Denis, Guarro & Gené, **sp. nov.** MycoBank MB814531. Fig. 14.

**Etymology:** From the Latin *hinnuleus*-fawn, referring to the brown “fawn” colour of the colony reverse.

**Colonies** on OA and PCA reaching 32–38 mm diam in 14 d at 25 °C, flat, velvety to floccose with a regular margin, obverse and reverse brown-grey to olivebrown (4F2/4F3). On PDA reaching 29–30 mm diam in 14 d at 25 °C, velvety to felty, golden grey to brown-grey (4C2/D2) with regular margin; reverse at first golden grey to brown-grey (4C2/D2), turning pale brown to brown (6D7/6E7) with age by the production of a non-diffusible pigment. **Hyphae** septate, subhyaline to pale brown, smooth- and thin-walled, 2–4 µm wide. **Conidiophores**

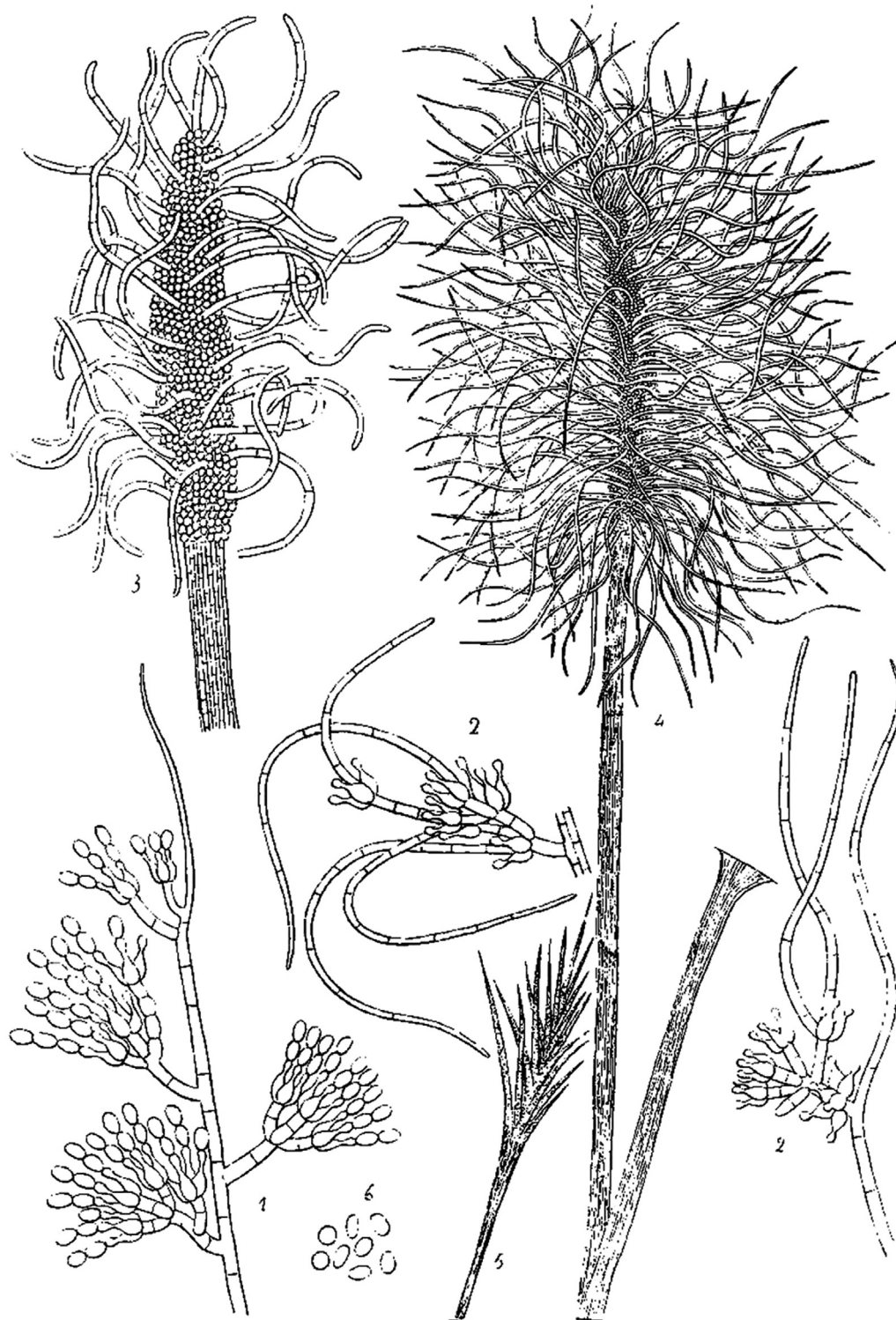


Fig. 13. Reproduction of the original drawings by Bainier (1907) illustrating *Trichurus gorgonifer* (original numbers are maintained to indicate the different structures). 1–2. Hyphae and penicillate conidiophores. 3. Young synnema showing setae. 4. Mature synnemata. 5. Abnormal synnema. 6. Conidia.

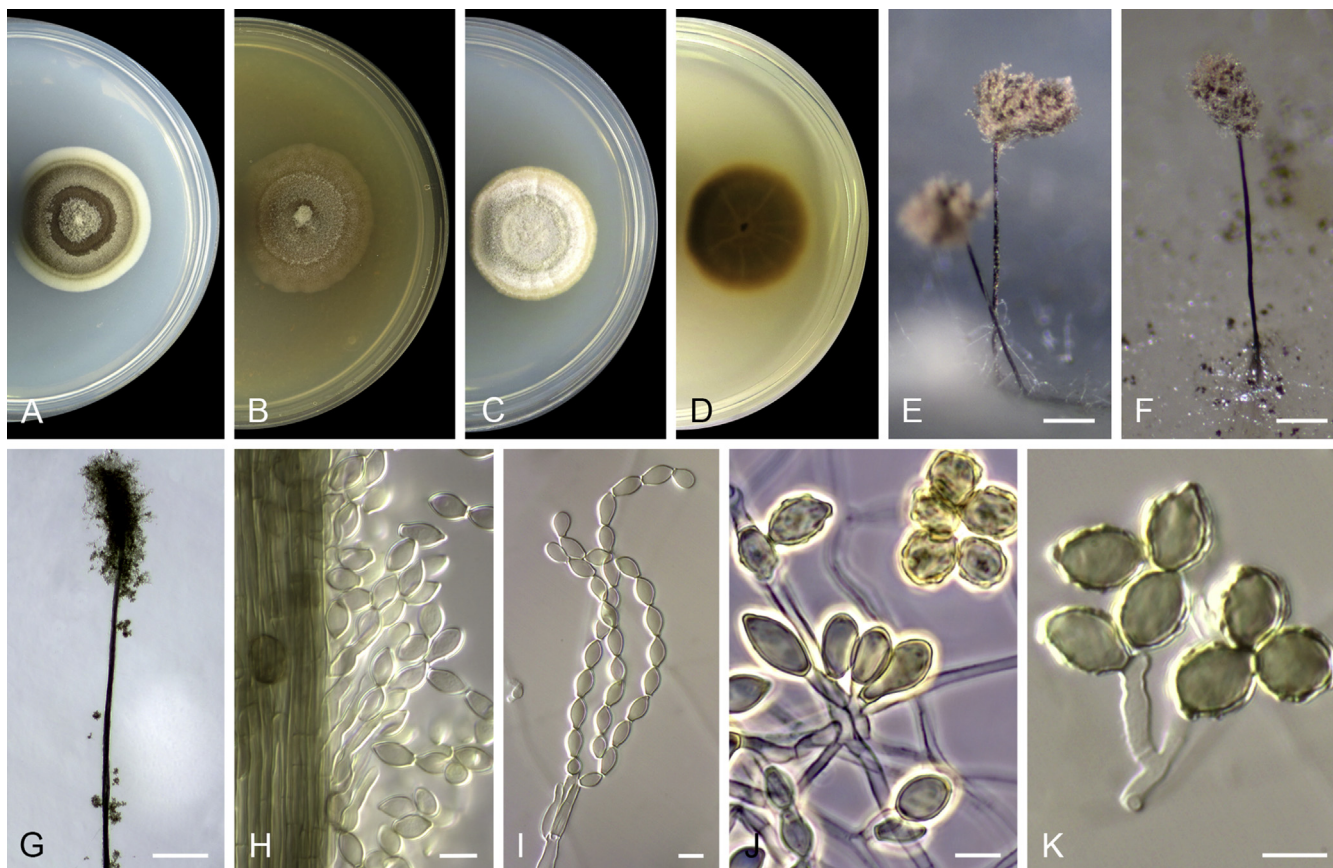
branched, septate,  $12\text{--}19 \times 2\text{--}3 \mu\text{m}$ , pale brown, smooth- and thin-walled, commonly aggregated in dense synnemata. *Synnemata*  $800\text{--}1600 \mu\text{m}$  high, stipes compact, dark brown to black,  $10\text{--}30 \mu\text{m}$  wide, conidial heads grey, clavate to ellipsoidal; setae absent. *Anellides* ampulliform to cylindrical,  $5.5\text{--}9 \times 2\text{--}3.5 \mu\text{m}$ , subhyaline to pale brown, smooth- and thin-walled. *Conidia* subglobose to ellipsoidal,  $6\text{--}7.5 \times 2.5\text{--}4 \mu\text{m}$  with truncate base and pointed apex, pale brown, smooth- and thin-walled, arranged in long chains. An echinobotryum-like synasexual morph can be present, producing conidia from short penicillate conidiophores,  $10\text{--}15 \times 2.5\text{--}3 \mu\text{m}$ , on the top

of synnemata or on the hyphae; *conidia* oval to navicular,  $8.5\text{--}10 \times 5.5\text{--}7 \mu\text{m}$ , with truncate base and pointed apex, dark brown, coarsely verrucose, thick-walled.

Cardinal temperatures for growth — Optimum  $15\text{--}25 \text{ }^\circ\text{C}$ , maximum  $30 \text{ }^\circ\text{C}$ , minimum  $5 \text{ }^\circ\text{C}$ .

*Material examined:* Australia, Tasmania, from dung of deer, 1963, K. Tubaki (Holotype CBS H-22333; culture ex-type CBS 289.66).

*Notes:* *Cephalotrichum hinnuleum* and *C. stemonitis* are the only species of the genus producing an echinobotryum-like



**Fig. 14.** *Cephalotrichum hinnuleum* (ex-type CBS 289.66). A–D. Colonies on PCA, OA and PDA, respectively, and pigment production on PDA after 14 d at 25 °C. E–G. Synnemata. H. Detail of the apical portion of a synnema. I. Annelidic conidiogenous cells and conidia. J–K. Polyblastic conidiogenous cells and conidia. Scale bars: E–G = 200 µm; H–K = 5 µm.

synasexual morph. The former species is easily distinguished by its smaller ( $8\text{--}10 \times 5.5\text{--}7 \mu\text{m}$  versus  $8\text{--}19 \times 6\text{--}7.5 \mu\text{m}$  in *C. stemonitis*) and unbeaked, echinobotryum-like conidia. In addition, the most striking feature of this new species is the presence of a non-diffusible brown pigment in the colony reverse on PDA.

***Cephalotrichum microsporum*** (Sacc.) P.M. Kirk, Kew Bull. 38: 578. 1984. Fig. 15.

*Basionym:* *Stysanus microsporus* Sacc., Michelia. 1: 274. 1878.  
*Synonyms:* *Doratomyces microsporus* (Sacc.) F.J. Morton & G. Sm., Mycol. Pap. 86: 77. 1963.

*Graphium graminum* Cooke & Massee, Grevillea. 16: 11. 1887.  
*Graphium pistillarioides* Speg., Revista Fac. Agron. Univ. Nac. La Plata 2: 254. 1896.

? *Cephalotrichum inflatum* Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 213. 2011.

? *Cephalotrichum ovoideum* Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 217. 2011.

? *Cephalotrichum robustum* Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 218. 2011.

*Material examined:* **Canada**, Alberta, near Peace River, indoor air of home, 1998, S.P. Abbott (UAMH 9365). **Epitype designated here:** **Germany**, Schleswig-Holstein, Kiel-Kitzeberg, wheat-field soil, 1963, W. Gams, MBT-203079 (CBS H-12123, culture ex-epitype CBS 523.63). **Italy**, Selva, in rotting trunk of *Robinia pseudacacia*, Aug. 1875, P.A. Saccardo (**Holotype** PAD 663).

*Descriptions and illustrations:* Morton & Smith (1963), Ellis (1971), Domsch et al. (2007).

*Notes:* This is one of the most commonly isolated species of *Cephalotrichum* and has been studied as a potential source of keratinases for industrial applications (Gradisar et al. 2000, Hublin et al. 2002). Abbott (2000) examined numerous isolates of this species from diverse geographical origins and its morphological observations agree with ours. In order to fix the name of this taxon, we have selected the strain CBS 523.63 as epitype. *Cephalotrichum microsporum* is morphologically similar to *C. purpureofusum*. However, *C. microsporum* produces synnemata 500–1000 µm long, smooth conidia measuring  $3.5\text{--}5 \times 2\text{--}3 \mu\text{m}$ , and grey colonies, while *C. purpureofusum* has larger synnemata (up to 1600 µm long), smooth to finely roughened, larger conidia ( $5\text{--}8 \times 3\text{--}4.5 \mu\text{m}$ ) and has dark grey to black colonies.

***Cephalotrichum nanum*** (Ehrenb.) S. Hughes, Canad. J. Bot. 36: 744. 1958. Fig. 16.

*Basionym:* *Periconia nana* Ehrenb., Sylv. mycol. berol. (Berlin) 13: 24. 1818.

*Synonyms:* *Stilbum nanum* (Ehrenb.) Spreng., Syst. veg., Edn 16. 4: 547. 1827.

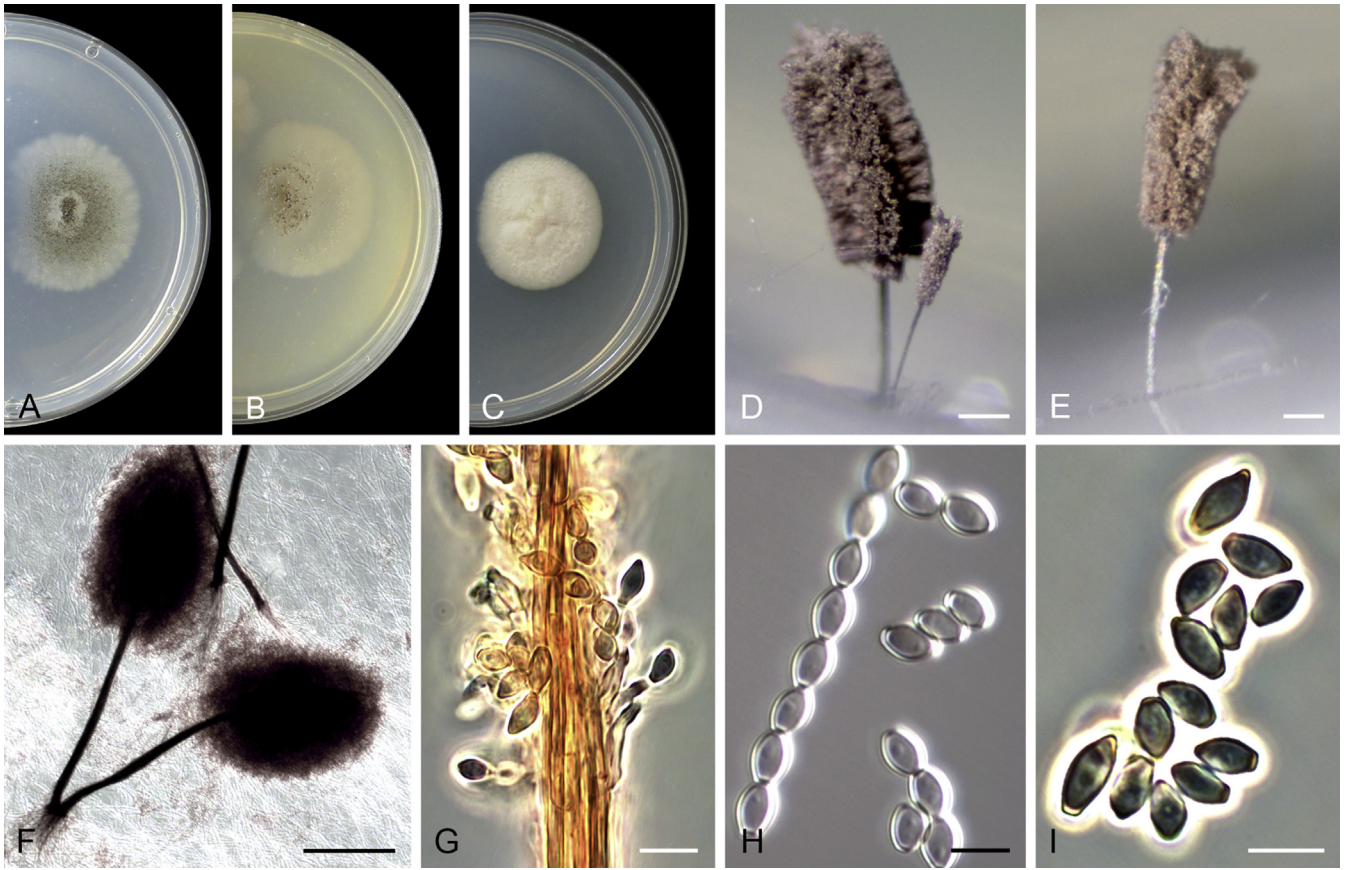
*Graphium nanum* (Ehrenb.) Sacc., Syll. Fung. 4: 616. 1886.

*Doratomyces nanus* (Ehrenb.) F.J. Morton & G. Sm., Mycol. Pap. 86: 80. 1963.

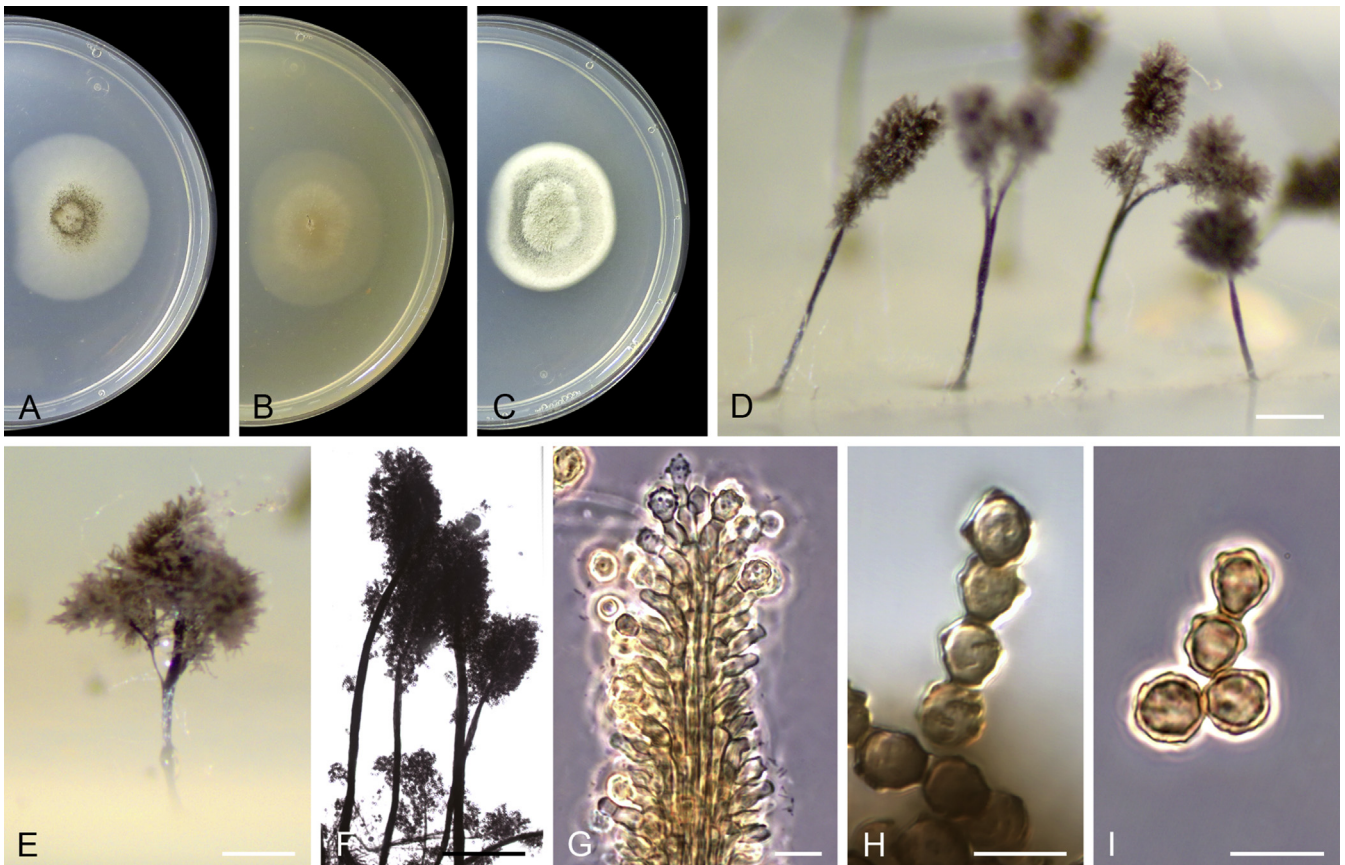
*Stysanus stemonitis* (Pers.: Fr.) var. *fimetarius* P. Karst. [as 'stemonites'], Meddel. Soc. Fauna Fl. Fenn. 14: 93. 1887.

*Stysanus fimetarius* (P. Karst.) Massee & E.S. Salmon, Ann. Bot. 16: 86. 1902.

*Stysanus verrucosus* Oudem., Ned. Kruidk. Arch. 2: 923. 1903.



**Fig. 15.** *Cephalotrichum microsporum* (ex-epitype CBS 523.63). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–F. Synnemata. G. Detail of the apical portion of synnema. H–I. Conidia. Scale bars: D–F = 200 µm; G–I = 5 µm.



**Fig. 16.** *Cephalotrichum nanum* (ex-epitype CBS 191.61). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–F. Synnemata. G. Detail of the apical portion of synnema. H–I. Conidia. Scale bars: D–F = 200 µm; G–I = 10 µm.

**Material examined:** Canada, Alberta, Elk Island National Park, dung of bison, 1997, S.P. Abbott (UAMH 9126). **Lectotype designated here:** Unknown country, on leaves of *Pinus strobus*, unknown date, C.G. Ehrenberg, MBT-372237 (L0111516). **Epitype designated here:** England, Surrey, Richmond Park, dung of deer, 1956, J. Hawkins, MBT-203082 (CBS H-22698, culture ex-epitype CBS 191.61).

**Descriptions and illustrations:** Morton & Smith (1963), Ellis (1971), Domsch *et al.* (2007).

**Notes:** *Cephalotrichum nanum* is a common species on dung. This species is distinguished by its large, globose to subglobose and coarsely warted conidia, 6–8.5 × 4.5–7.5 µm, which resemble those of *Scopulariopsis brevicaulis*, from which it clearly differs in the colony colour (dark grey-brown, turning black-grey in *C. nanum*, tan in *S. brevicaulis*) and in the production of well-developed, black synnemata. *Cephalotrichum asperulum* is a further similar species, but its conidia are narrower (5–8.5 × 3–4 µm), oval to ellipsoidal and finer roughening.

According to Hughes (1958) and Seifert (1985), Ehrenberg's herbarium material of *Periconia nana* was deposited in B, DAOM and L. However, material in B does not exist anymore as is presumed to be lost during the Second World War (Dr. Robert Lücking, pers. comm.). Original material was located in L and, in order to stabilise the use of the name, it is designated here to serve as lectotype. In addition, the species is epitypified with the strain CBS 191.61, which matches with the species concept by Hughes (1958).

***Cephalotrichum purpureofuscum*** (Schwein.: Fr.) S. Hughes, *Canad. J. Bot.* 36: 744. 1958. Fig. 17.

**Basionym:** *Aspergillus purpureofuscus* Schwein., *Trans. Amer. Philos. Soc.* 4: 282. 1832: Fr., *Syst. mycol.* (Lundae) 3: 388, Index: 53. 1832.

**Synonyms:** *Stysanus purpureofuscus* (Schwein.) S. Hughes, *Canad. J. Bot.* 31: 615. 1953.

*Doratomyces purpureofuscus* (Schwein.) F.J. Morton & G. Sm., *Mycol. Pap.* 86: 74. 1963.

*Stilbum pusillum* Wallr., *Fl. crypt. Germ. (Norimbergae)* 2: 326. 1833.

*Graphium pusillum* (Wallr.) Sacc., *Syll. Fung.* 4: 614. 1886.

*Ceratopodium pusillum* (Wallr.) Kuntze, *Revis. gen. pl. (Leipzig)* 2: 847. 1891.

*Stilbum brevipes* Wallr., *Fl. crypt. Germ. (Norimbergae)* 2: 326. 1833.

*Sporocybe brevipes* (Wallr.) Sacc., *Syll. Fung.* 4: 607. 1886.

*Cephalotrichum brevipes* (Wallr.) Kuntze, *Revis. gen. pl. (Leipzig)* 3: 453. 1898.

*Cephalotrichum leucocephalum* Wallr., *Fl. crypt. Germ. (Norimbergae)* 2: 330. 1833.

*Graphium leucocephalum* (Wallr.) Sacc., *Syll. Fung.* 4: 615. 1886.

*Pachnocybe grisea* Berk., in Smith, *Engl. Fl., Fungi (Edn 2)* (London) 5: 334. 1836.

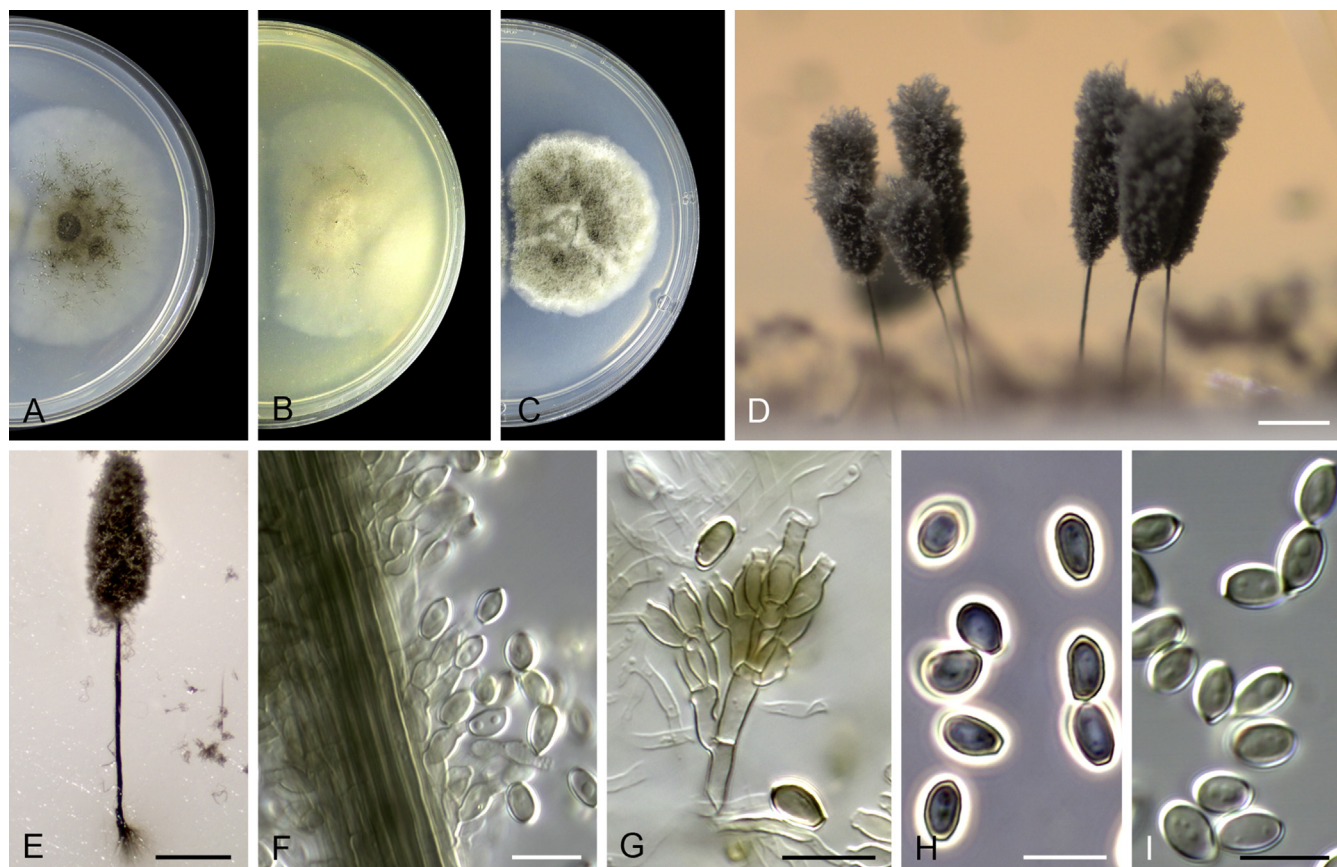
*Graphium griseum* (Berk.) Sacc., *Syll. Fung.* 4: 616. 1886.

*Periconia fusca* Corda, *Icon. fung. (Prague)* 1: 19. 1837.

*Stysanus fuscus* (Corda) E.W. Mason & M.B. Ellis, *Mycol. Pap.* 56: 31. 1953.

*Stysanus mandlii* Mont., *Ann. Sci. Nat., Bot.* 4: 365. 1845.

*Stysanus stemonitis* (Pers.) Corda *formae mandlii* (Mont.) Guég., *Bull. Soc. Mycol. France.* 19: 219. 1903.



**Fig. 17.** *Cephalotrichum purpureofuscum* (UAMH 9209). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–E. Synnemata. F. Detail of the apical portion of synnema. G. Conidiophores and conidiogenous cells. H–I. Conidia. Scale bars: D–E = 200 µm; F–I = 10 µm.

*Periconia discolor* Corda, Icon. fung. (Prague) 3: 13. 1839.  
*Periconia brassicicola* Berk. & Broome [as '*brassicaecola*'], Ann. Mag. Nat. Hist. 15: 33. 1875.  
*Sporocybe brassicicola* (Berk. & Broome) Sacc. [as '*brassicaecola*'], Syll. Fung. 4: 606. 1886.  
*Cephalotrichum brassicicola* (Berk. & Broome) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.  
*Stysanus medius* Sacc., Michelia 2: 300. 1881.  
*Stysanopsis media* (Sacc.) Ferraris, Ann. Mycol. 7: 281. 1909.  
*Cephalotrichum medium* (Sacc.) S. Hughes, Canad. J. Bot. 36: 744. 1958.  
*Pycnostysanus medius* (Sacc.) Bat. & Peres, Nova Hedwigia 2: 469. 1960.  
*Doratomyces medius* (Sacc.) Matsush., Matsush. Mycol. Mem. 1: 33. 1980.  
*Sporocybe byssoides* (Pers.) Bon.: Sacc., Syll. Fung. 4: 606. 1886.  
*Sporocybe sacchari* Speg., Revista Fac. Agron. Univ. Nac. La Plata 2: 253. 1896.  
? *Cephalotrichum longicollum* Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 213. 2011.  
? *Cephalotrichum macrosporum* Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 214. 2011.  
? *Cephalotrichum oblongum* J.J. Xu & T.Y. Zhang, Mycotaxon 117: 216. 2011.  
? *Cephalotrichum terricola* Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 221. 2011.

*Material examined:* Canada, British Columbia, Pemberton, Indoor air of school library, 1998, S.P. Abbott (UAMH 9209).

*Descriptions and illustrations:* Morton & Smith (1963), Ellis (1971), Domsch et al. (2007).

*Notes:* No single morphological feature distinguishes this commonly reported species, and it can more easily be described as lacking distinctive characters than defined by recognisable features such as setae, echinobotryum-like synasexual morph roughened conidia, or spores of particularly large or small dimensions. Not surprisingly, it has been described in the literature on a number of occasions. Here, of the four isolates originally received as *C. purpureofuscum* (Table 1), only that studied by Abbott (2000) could correspond to such species (UAMH 9209); the other three have been reidentified as *C. brevistipitatum*, *C. gorgonifer* and *C. microsporium*. *Cephalotrichum purpureofuscum* is morphologically similar to *C. cylindricum* and *C. gorgonifer*, all having similar oval to ellipsoidal, brown conidia, and synnemata of similar size. However, the absence of setae is the most relevant distinctive feature of *C. purpureofuscum*. Also, its conidia are slightly larger ( $5\text{--}8 \times 3\text{--}4.5 \mu\text{m}$ ) and smooth to finely roughened, while those of *C. cylindricum* and *C. gorgonifer* are always smooth and measure  $4.5\text{--}6 \times 2.5\text{--}3.5 \mu\text{m}$  and  $4\text{--}8 \times 2.5\text{--}4 \mu\text{m}$ , respectively. The absence of an echinobotryum-like state easily separates this species from *C. stemonitis*.

Several recently described species (i.e., *C. longicollum*, *C. macrosporum*, *C. oblongum* and *C. terricola*) are here considered probable synonyms of *C. purpureofuscum* based on their morphological similarity and molecular comparisons of ITS sequences available in GenBank (see notes on doubtful species).

Abbott (2000) studied a large set of isolates of *C. purpureofuscum* from different substrates and geographic origins, and selected a putative ex-epitype culture, however, it was not formally proposed. The species concept presented and illustrated here centres on UAMH 9209, which was also characterised based on DNA sequence data. However, considering that we have not had access to the type material (BPI) and that the species seems not to be properly characterised, no epitype is designated at the moment until additional isolates can be morphologically and molecularly analysed for a correct circumscription of the species.

***Cephalotrichum stemonitis*** (Pers.: Fr.) Nees, Mag. Ges. Naturf. Freunde Berlin 3: 20. 1809. Fig. 18.

*Basionym:* *Isaria stemonitis* Pers., Comm. fung. clav. (Lipsiae): 234. 1797.

*Synonyms:* *Periconia stemonitis* (Pers.) Pers., Syn. meth. fung. (Göttingen) 2: 687. 1801.

*Cephalotrichum stemonitis* (Pers.: Fr.) Link, Mag. Ges. Naturf. Freunde Berlin 3: 20. 1809.

*Stysanus stemonitis* (Pers.: Fr.) Corda, [as '*stemonites*'], Icon. fung. (Prague) 1: 22. 1837.

*Doratomyces stemonitis* (Pers.) F.J. Morton & G. Sm., Mycol. Pap. 86: 70. 1963.

*Periconia stemonitis* (Pers.) Pers. var. *communis* Alb. & Schwein., Consp. fung. (Leipzig): 358. 1805.

*Periconia stemonitis* (Pers.) Pers. var. *pusilla* Alb. & Schwein., Consp. fung. (Leipzig): 358. 1805.

*Periconia subulata* Nees, Nova Acta Acad. Leop. Carol. Ac. Naturf. Fo. 9: tab. 5, fig. 8. 1818.

*Stilbum subulatum* (Nees) Spreng., Syst. veg., 16th ed. 4: 547. 1827.

*Pachnocybe subulata* (Nees) Berk., In Smith, Engl. Fl., Fungi, 2nd ed., 5: 333. 1836.

*Graphium subulatum* (Nees) Sacc., Syll. Fung. 4: 612. 1886. [nom. illegit., Art. 53.1, non Pass. & Beltrani 1882]

*Ceratopodium subulatum* (Nees) Kuntze, Rev. Gen. Pl. 2: 847. 1891.

*Doratomyces neesii* Corda, Sturm, Deutschl. Fl., Abt. 3 (Pilze Deutschl.) 2: 65. 1829.

*Echinobotryum atrum* Corda, Sturm, Deutschl. Fl., 3 Abt. (Pilze Deutschl.) 3: 51. 1831.

*Stilbum setosum* Wallr., Fl. crypt. Germ. (Norimbergae) 2: 329. 1833.

*Periconia setosa* (Wallr.) Rabenh., Deutschl. Krypt.-Fl. (Leipzig) 1: 118. 1884.

*Sporocybe setosa* (Wallr.) Sacc., Syll. Fung. 4: 607. 1886.

*Cephalotrichum setosum* (Wallr.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Stilbum typhinum* Wallr., Fl. crypt. Germ. (Norimbergae) 2: 330. 1833.

*Graphium typhinum* (Wallr.) Sacc., Syll. Fung. 4: 617. 1886.

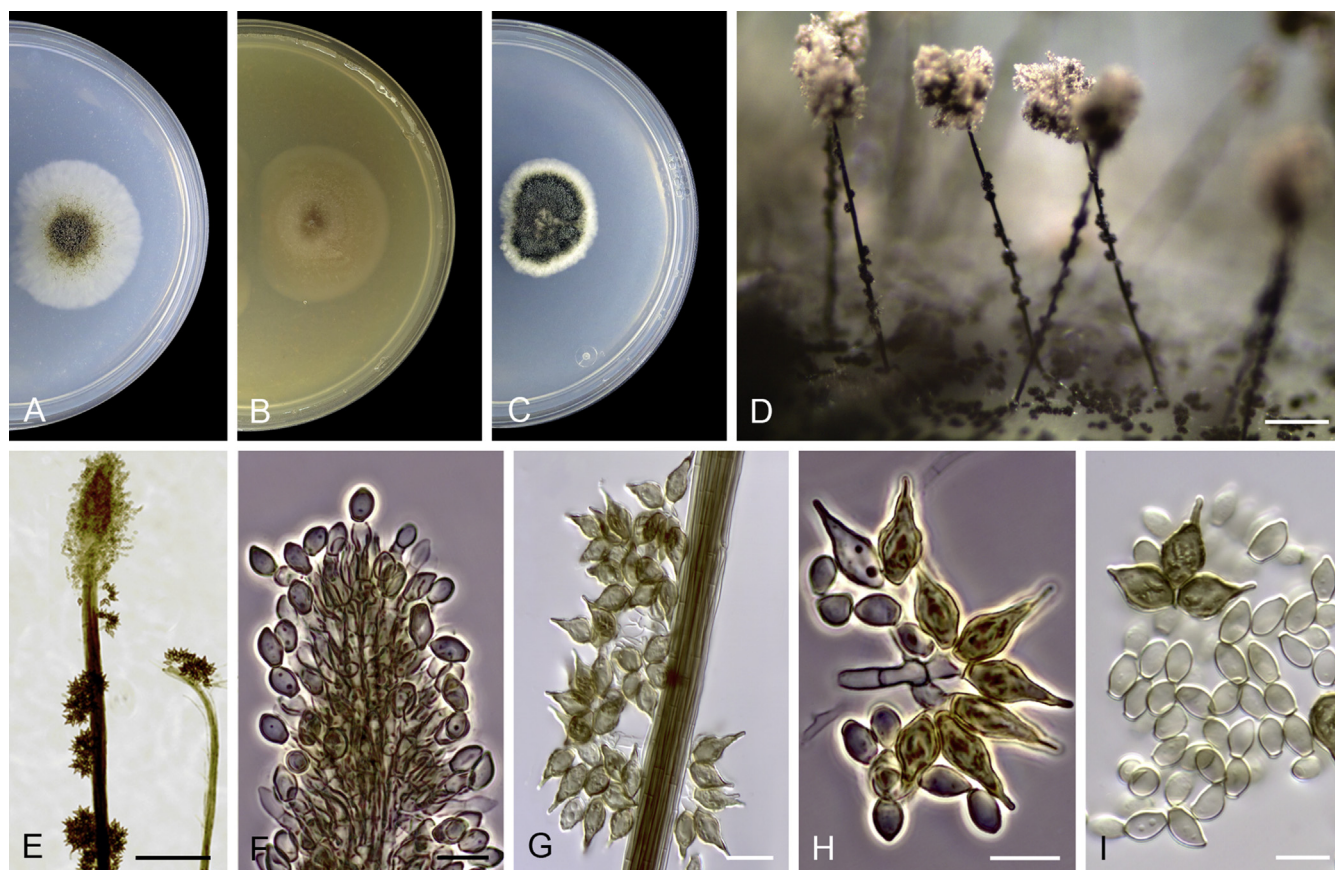
*Ceratopodium typhinum* (Wallr.) Kuntze, Revis. gen. pl. (Leipzig) 2: 847. 1891.

*Echinobotryum parasitans* Corda, Pracht-Flora. 17: 1839.

*Stysanus capitatus* Reinke & Berthold, Die Zersetzung der Kartoffel durch Pilze. 37. 1879.

*Stysanus ramifer* Rolland, Bull. Soc. Mycol. France. 6: 106. 1890.

*Stysanus tubericola* Ellis & Dearn., Proc. Canad. Inst. 1: 90. 1897.



**Fig. 18.** *Cephalotrichum stemonitis* (ex-neotype CBS 103.19). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–E. Synnemata. F. Tip of synnema with annelidic conidiogenous cells and conidia. G–H. Polyblastic conidiogenous cells and conidia. I. Conidia of both kinds. Scale bars: D–E = 500 µm; F–I = 10 µm.

*Stysanus stemonitis* (Pers.) Corda var. *ramosa* Pim., Trans. Brit. mycol. Soc. 1. 65: 1899.

*Doratomyces stemonitis* (Pers.) F.J. Morton & G. Sm var. *keratinolyticus* Dominik & Majchr. [as '*keratinolytica*'], Ekol. Pol. 13: 434. 1965.

**Material examined:** Canada, Ontario, near Guelph, soil, 1961, G.L. Barron, (UAMH 1532). **Unknown country**, unknown substratum, 1935, N.F. Conant (CBS 180.35). **Neotype designated here:** The Netherlands, Wageningen, from seed, 1919, C.M. Doyer, MBT-203081 (CBS H-12129, culture ex-neotype CBS 103.19).

**Descriptions and illustrations:** Morton & Smith (1963), Domsch *et al.* (2007).

**Notes:** The main distinguishing morphological characteristic of this species is the presence of an echinobotryum-like synasexual morph with fusiform, coarsely warted and apically beaked conidia, 8–19 × 6–7.5 µm (Abbott 2000). The other species exhibiting an echinobotryum-like morph is *C. hinnuleum*, but *C. stemonitis* is different by robust synnemata of 2 000–3 000 µm tall, smooth conidia measuring 6–9 × 4–5 µm, and the shape and size of the echinobotryum-like conidia. *Cephalotrichum hinnuleum* has shorter synnemata 800–1 600 µm tall, narrower (6–7.5 × 2.5–4 µm), smooth to finely verruculose conidia, and the echinobotryum-like morph exhibits smaller (8.5–10 × 5.5–7 µm), oval to navicular verrucose and slightly pointed conidia. In addition, the latter species produces a non-diffusible, pale brown to brown (6D7/E7) pigment on PDA.

Only four specimens were located in the herbarium Persoon in L. However, all four are labelled as *P. stemonitis*, and none of

them is regarded as type. Since the holotype of *Isaria stemonitis* seems to be lost, a neotype specimen and an ex-neotype culture are designated here to fix the use of the name.

***Cephalotrichum verrucisporum*** (Y.L. Jiang & T.Y. Zhang) Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 224. 2011. Fig. 19

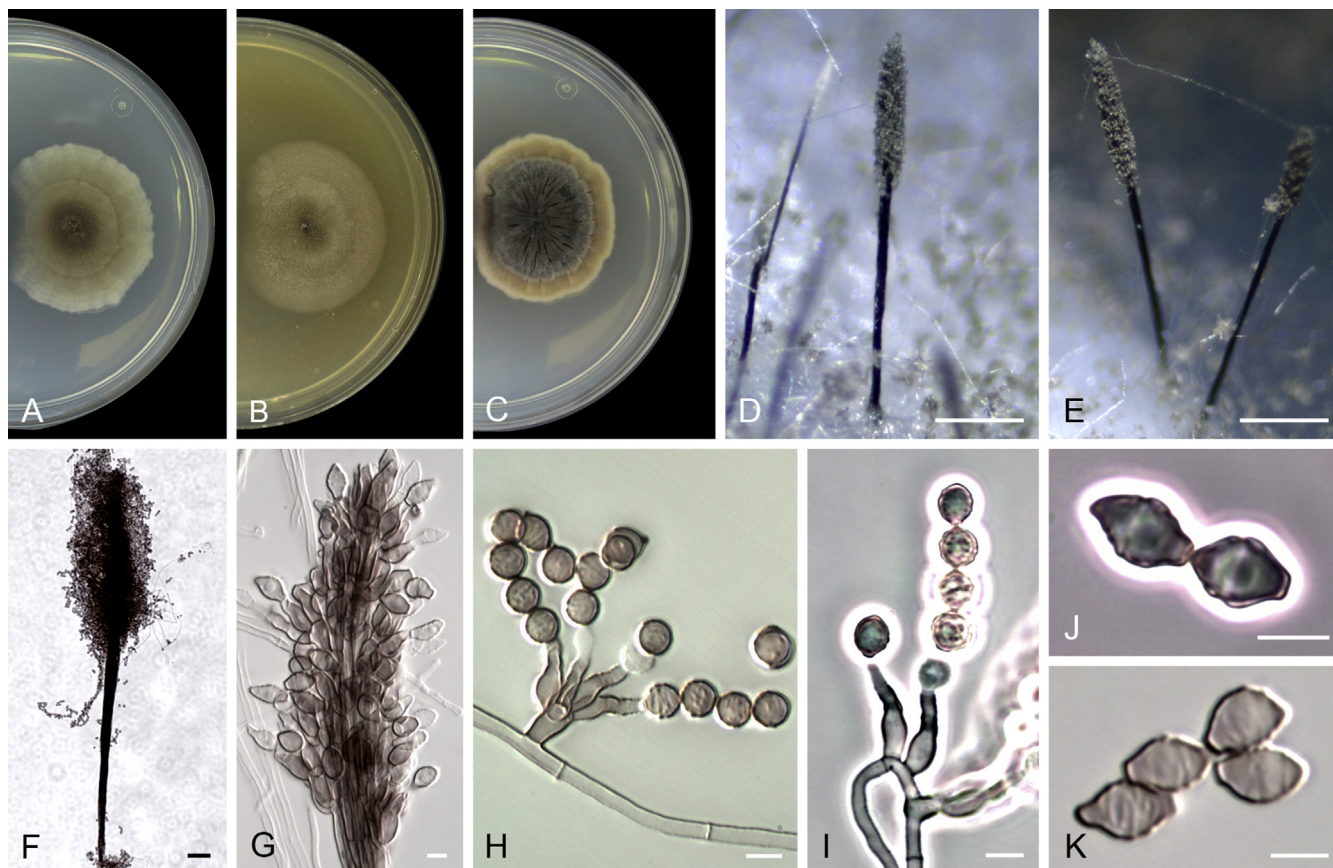
**Basionym:** *Doratomyces verrucisporus* Y.L. Jiang & T.Y. Zhang, Mycotaxon 104: 133. 2008.

**Material examined:** The Netherlands, Katwijk, from sand dune soil, 1978, W. Gams (CBS 187.78).

**Description and illustration:** Jiang & Zhang (2008).

**Notes:** Although the holotype of *C. verrucisporum* (HSAUP<sub>05</sub>1029, preserved at the Herbarium of the Shandong Agricultural University: Plant Pathology, China) was not available for morphological comparison, in GenBank there was an ITS sequence from the ex-type strain (accession number JX537968), which had 100 % similarity with the strain CBS 187.78 examined here. The molecular and morphological data confirm this taxon as a distinct species of *Cephalotrichum*.

*Cephalotrichum verrucisporum* is morphologically similar to *C. asperulum*. Both species produce rough-walled conidia with a spiral-sculpted ornamentation. However, synnemata are up to 3 000 µm tall and the conidia are ovoid and darker in *C. verrucisporum*, whereas synnemata are up to 1 000 µm tall and conidia are oval to ellipsoidal and pale brown in *C. asperulum*. The latter species is also able to grow at 35 °C, whereas, according to our data, the maximum temperature for growth in *C. verrucisporum* is 30 °C.



**Fig. 19.** *Cephalotrichum verrucisporum* (CBS 187.78). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–F. Synnemata. G. Detail of the apical part of synnema. H–I. Conidiogenous cells and conidia. J–K. Conidia. Scale bars: D–E = 500 µm; F = 100 µm; G–K = 5 µm.

**Fairmania** Sacc., Ann. Mycol. 4: 276. 1906.

Colonies restricted, velvety to felty with granular centre, flat, white, becoming grey-white with dark centre. *Hyphae* hyaline, thin- and smooth-walled. *Conidiophores* undifferentiated, usually unbranched and borne laterally on the hyphae, hyaline. *Conidiogenous cells* annelidic, short-cylindrical, subhyaline to pale brown, smooth-walled. *Conidia* obovoid to cylindrical, dark brown, smooth- and thick-walled with one to several longitudinal striations. *Ascospores* 1-celled, broadly lunate, golden yellow, pale brown in mass, smooth, with a single germ pore.

*Type species:* *Fairmania singularis* Sacc.

**Notes:** This monotypic genus differs from the other members of *Microascaceae* by its conidia with several longitudinal striations. Whether these striations participate in conidial germination has been controversial (Barron 1966). However, our observations showed that germination actually occurs laterally from the striations, confirming the observations by Barron (1966), that they function as germ slits.

**Fairmania singularis** Sacc., Ann. Mycol. 4: 276. 1906. **Fig. 20.** **Synonyms:** *Microascus singularis* (Sacc.) Malloch & Cain, Canad. J. Bot. 49: 859. 1971.

*Microascus doguetii* Moreau, Rev. Mycol. (Paris). 18: 174. 1953.

**Material examined:** USA, Lyndonville, New York, on rotten wood of *Fagi americanae*, C.E. Fairman (**Holotype** PAD1239). **Epitype designated here:** USA,

Maine, Kittery Point, from barrel bottom, 1966, R. Thaxter, MBT-202772 (culture ex-epitype CBS 505.66). **Canada,** Toronto, from unknown substrate, 1964, M. Corlett (CBS 249.64). **Japan,** Tokyo, laboratory contaminant, 1962, S. Udagawa (CBS 414.64).

**Descriptions and illustrations:** Barron et al. (1961), Udagawa (1963), von Arx et al. (1988).

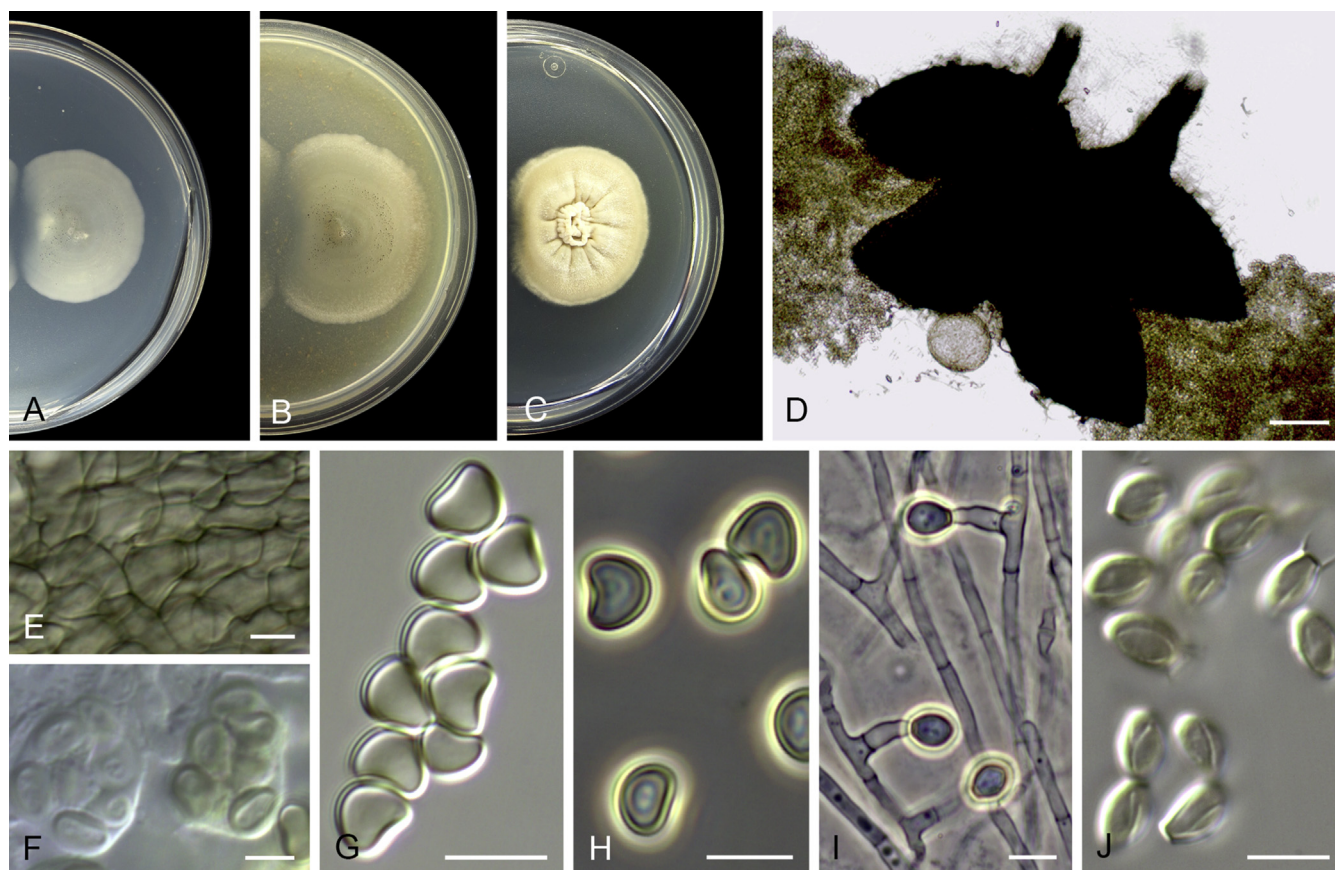
**Notes:** Malloch & Cain (1971) studied Saccardo's original material of *F. singularis* and concluded that it is morphologically identical to *M. doguetii*. Both species were then synonymised and placed in *Microascus*, *M. singularis* having priority. This synonymy was also accepted by von Arx et al. (1988).

However, the longitudinal striations in the conidial wall and presence of erect and thick-walled annelides are singular features of this species, which are absent in all genera of *Microascaceae*, and considered here of taxonomic value for the reintroduction of this obscure genus. Previous phylogenetic analyses supported such morphological differences (Issakainen et al. 2003, Sandoval-Denis et al. 2016).

**Gamsia** M. Morelet, Ann. Soc. Sci. Nat. Archéol. Toulon Var 21: 105. 1969.

Colonies grey to black, compact and slow growing. *Hyphae* mostly superficial, hyaline, thin- and smooth-walled. *Conidiophores* mostly undifferentiated, unbranched or sometimes once or twice branched, borne laterally on the hyphae, septate, hyaline, smooth-walled. *Conidiogenous cells* and *conidia* of two types: i) *conidiogenous cells* polyblastic, cylindrical with a swollen apical part, hyaline, smooth-walled; *conidia* borne





**Fig. 20.** *Fairmania singularis* (ex-epitype CBS 505.66). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D. Ascomata. E. Ascomatal peridium. F. Asci. G–H. Ascospores. I. Conidiogenous cells. J. Conidia. Scale bars: D = 20 µm; E–J = 5 µm.

solitary in lateral succession and forming large apical clusters, 1-celled, ovoid to broadly ellipsoidal, flat at the base, brown to black, smooth- and thick-walled, often with a longitudinal germ slit; ii) *conidiogenous cells* annelidic, sometimes grouped in sporodochia, subulate to cylindrical, hyaline, smooth-walled; *conidia* catenate, 1–2-celled, oval to ellipsoidal, truncate at the base, hyaline, smooth- and thin-walled.

*Type species:* *Gamsia columbina* (Demelius) Sandoval-Denis, Guarro & Gené.

*Notes:* The genera *Gamsia* and *Hennebertia* were simultaneously erected to accommodate those *Wardomyces* species that have 1-septate annelloconidia (Morelet 1969), being competing synonyms. The selection of *Gamsia* was posteriorly settled when Ellis (1976) took up only this name. However, our morphological study demonstrated that the conidial septation is not a constant character in this genus. In contrast, the lack of well-differentiated conidiophores, and the conidial arrangement with large apical clusters which resemble the echinobotryum-like synasexual morphs of *Cephalotrichum* more than those of *Wardomyces*, justifies the separation of the two genera, which is also supported by phylogenetic results.

***Gamsia aggregata*** (Malloch) Kiffer & M. Morelet, Ann. Soc. Sci. Nat. Archéol. Toulon Var 47: 93. 1995. Fig. 21.

*Basionym:* *Wardomyces aggregatus* Malloch, Can. J. Bot. 48: 883. 1970.

*Synonym:* ? *Gymnodochium fimicola* Masee & Salmon, Ann. Bot. 16: 89. 1902.

*Material examined:* USA, Michigan, Emmet Co., Wycamp Lake, from dung of carnivore, 1967, D.W. Malloch (**Holotype** TRTC 45325; culture ex-isotype CBS 251.69).

*Description and illustrations:* Malloch (1970b).

*Notes:* This species can be easily recognised by its broadly ellipsoidal to ovoid solitary conidia, measuring 4–7.5 × 3.5–5 µm, and having a rounded apex. It also produces abundant sporodochia composed of annelides bearing 2-celled, hyaline, ellipsoidal conidia of 8–10.5 × 3.5–5 µm. The other species of the genus, *G. columbina*, has larger (6–13 × 3.5–6.5 µm), oval to ellipsoidal, solitary conidia with slightly pointed apices, its annelides are solitary or grouped in sporodochia, and form 1–2-celled, oval annelloconidia of 5–10.5 × 2.5–5.5 µm.

***Gamsia columbina*** (Demelius) Sandoval-Denis, Guarro & Gené, **comb. nov.** MycoBank MB814578, Fig. 22.

*Basionym:* *Trichosporum columbinum* Demelius, Verh. Zool.-Bot. Ges. Wien 72: 105. 1923.

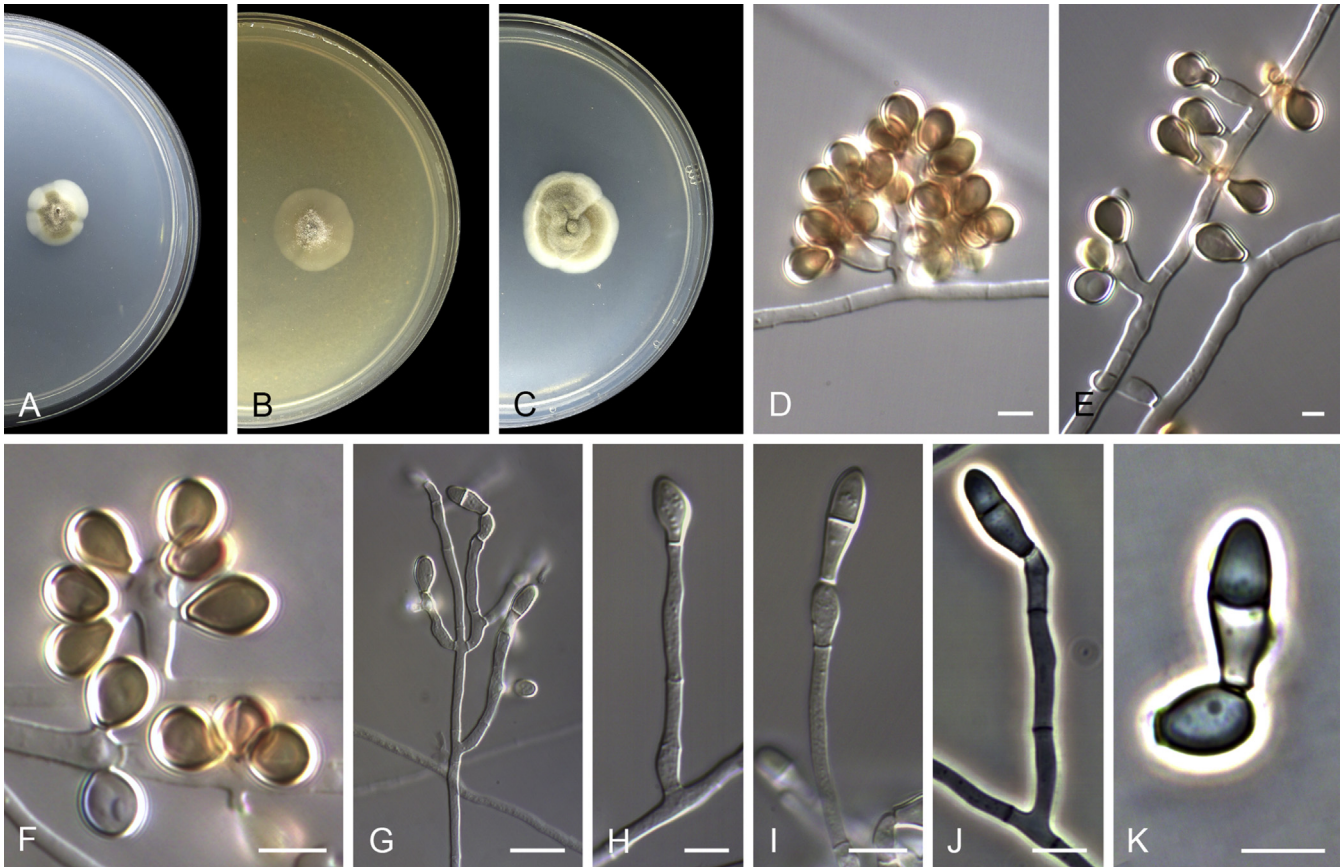
*Synonyms:* *Wardomyces columbinus* (Demelius) Hennebert, Trans. Brit. mycol. Soc. 51: 753. 1968.

*Hennebertia columbina* (Demelius) M. Morelet, Ann. Soc. Sci. Nat. Archéol. Toulon Var 21: 104. 1969.

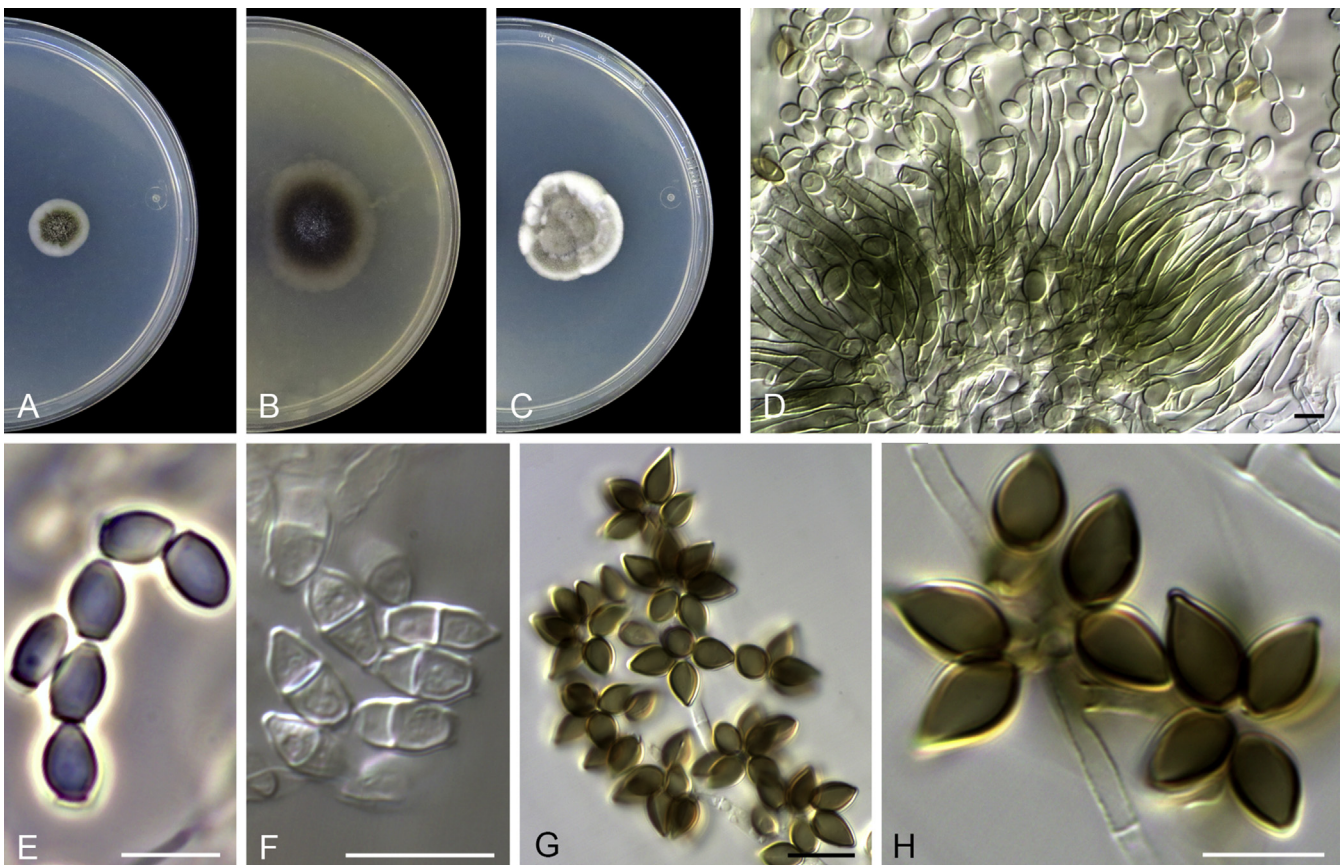
*Wardomyces simplex* Sugiy., Y. Kawas. & H. Kurata, Bot. Mag. Tokyo 81: 244. 1968.

*Gamsia simplex* (Sugiy., Y. Kawas. & H. Kurata) Arx, Gen. Fungi Sporul. Cult., Edn 3: 340. 1981.

*Wardomyces dimerus* W. Gams, Trans. Brit. mycol. Soc. 51: 800. 1968.



**Fig. 21.** *Gamsia aggregata* (ex-isotype CBS 251.69). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–F. Conidiophores, polyblastic conidiogenous cells and conidia. G–K. Conidiophores, annelidic conidiogenous cells and conidia. Scale bars: D–K = 5  $\mu$ m.



**Fig. 22.** *Gamsia columbina* (ex-epitype CBS 233.66). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D. Sporodochium and annelidic conidiogenous cells. E. Aseptate annelloconidia. F. Septate annelloconidia from CBS 546.69. G–H. Polyblastic conidiogenous cells and conidia. Scale bars: D–H = 10  $\mu$ m.

*Gamsia dimera* (W. Gams) M. Morelet, Ann. Soc. Sci. Nat. Archéol. Toulon Var 21: 105. 1969.

*Material examined:* Austria, Vienna, in plum gelatin, Mar. 1917, P. Demelius (Holotype W1134). **Epitype designated here:** Germany, Giessen, from sandy soil, 1964, A. von Klopotek, MBT-202773 (culture ex-epitype CBS 233.66); Schleswig-Holstein, Kiel-Kitzeberg, from wheat-field soil, 1966, W. Gams (ex-type culture of *Wardomyces dimerus* CBS 235.66). Japan, Osaka Region, from milled *Oryza sativa*, 1968, J. Sugiyama (ex-isotype culture of *Wardomyces simplex* CBS 546.69). **The Netherlands**, Wageningen, from sandy soil, 1982, J.A. van Veen (CBS 230.82).

*Descriptions and illustrations:* Gams (1968), Hennebert (1968) and Sugiyama *et al.* (1968, 1969).

*Notes:* This species has been isolated from air, soil and decaying wood (Gams 1968, Ellis 1976, Domsch *et al.* 2007), and was associated with loss of weight and tensile strength in maple-wood (Domsch *et al.* 2007).

Several authors have discussed the relationship between the species originally included in *Wardomyces*, i.e. *W. columbinus*, *W. dimerus*, *W. ovalis* and *W. simplex* (Hennebert 1968, Gams 1968, Morelet 1969, Sugiyama *et al.* 1969), all forming two types of conidia in culture: one dark, thick-walled and with a longitudinal germ slit, arising singly on the conidiogenous cells, and the other with hyaline, thin-walled scopulariopsis-like annelloconidia. Morelet (1969) proposed the genera *Gamsia* and *Hennebertia* to include species with septate and aseptate annelloconidia, respectively. Nevertheless, neither *Gamsia* nor *Hennebertia* have been widely accepted (Ellis 1971, 1976, Domsch *et al.* 2007, Whitton *et al.* 2012). Of these two competing simultaneously published synonyms only *Gamsia* was taken up, e.g. by Ellis (1971). Our molecular phylogeny shows that *W. columbinus*, a species described with only aseptate annelloconidia, belongs to the same clade as *W. dimerus* and *W. simplex*. Moreover, Gams (1968) and Sugiyama *et al.* (1969) reported both aseptate and septate annelloconidia in cultures of *W. dimerus* and *W. simplex*. Conidial septation thus is not a reliable criterion for generic delimitation of *Gamsia*. The species name *W. columbinus* has priority over the latter *W. dimerus* and *W. simplex*, and since only dried type material is available for this species we have selected an ex-epitype culture from the authentic material of *W. columbinus* studied by Hennebert (1968).

*Gamsia columbina* is morphologically very similar to *G. aggregata*, but can be distinguished by having larger and pointed solitary conidia (see notes on *G. aggregata*).

***Wardomyces*** F.T. Brooks & Hansf., Trans. Brit. mycol. Soc. 8: 137. 1923.

*Type species:* *Wardomyces anomalus* F.T. Brooks & Hansf.

*Descriptions and illustrations:* Brooks & Hansford (1923), Dickinson (1964), Domsch *et al.* (2007).

*Notes:* Judging from our phylogenetic results, the species of *Wardomyces* do not form a monophyletic group, being scattered in three closely related lineages. The small genetic distances and inconsistent morphological differences observed between the three groups do not support the proposal of a generic status for the lineages.

To date, only *Wardomyces giganteus* has been described with a sexual morph, which closely resembles those observed in *Microascus* and *Scopulariopsis*. However, it can be differentiated by significantly larger ascospores with two germ pores and dark, solitary conidia with a longitudinal germ slit, features that are never present in the other two genera *sensu stricto*.

***Wardomyces anomalus*** F.T. Brooks & Hansf., Trans. Brit. mycol. Soc. 8: 137. 1923. Fig. 23.

*Material examined:* **Lectotype designated here:** England, on meat of *Oryctolagus cuniculus*, 1918, J.F. Brooks and C.G. Handsford, MBT-372238 (IMI 25846). **Epitype designated here:** Canada, Ottawa, air cell of egg in cold storage in salt solution, 1947, W.I. Illman, MBT-202776 (culture ex-epitype CBS 299.61).

*Descriptions and illustrations:* Brooks & Hansford (1923), Hennebert (1962).

*Notes:* This species has been isolated from frozen stored meat and eggs, and from soil and marine environments (Dickinson 1964), and is associated with the production of antioxidant compounds (Abdel-Lateff *et al.* 2003). This is the type species of *Wardomyces*, however, no holotype material was cited in the protologue and neither is present in the different herbaria we checked (BPI, BR, CGE, E, or K) and therefore, it is presumed lost. Isotype dry material was deposited in IMI (Kew, England) and is proposed here as lectotype. Since an ex-type or ex-isotype culture does not exist, we selected an epitype culture from the authentic material referenced in Brooks & Hansford (1923) and studied here.

*Wardomyces anomalus* is similar to *W. inflatus* exhibiting hyaline, inflated to barrel shaped conidiogenous cells and similar conidial size. However, the conidia of the former species are ovoid with pointed apex and measure 4.5–8 × 3.5–6 µm, while those of *W. inflatus* are ellipsoidal to cylindrical with a rounded apex and measure 6–8 × 3.5–5 µm.

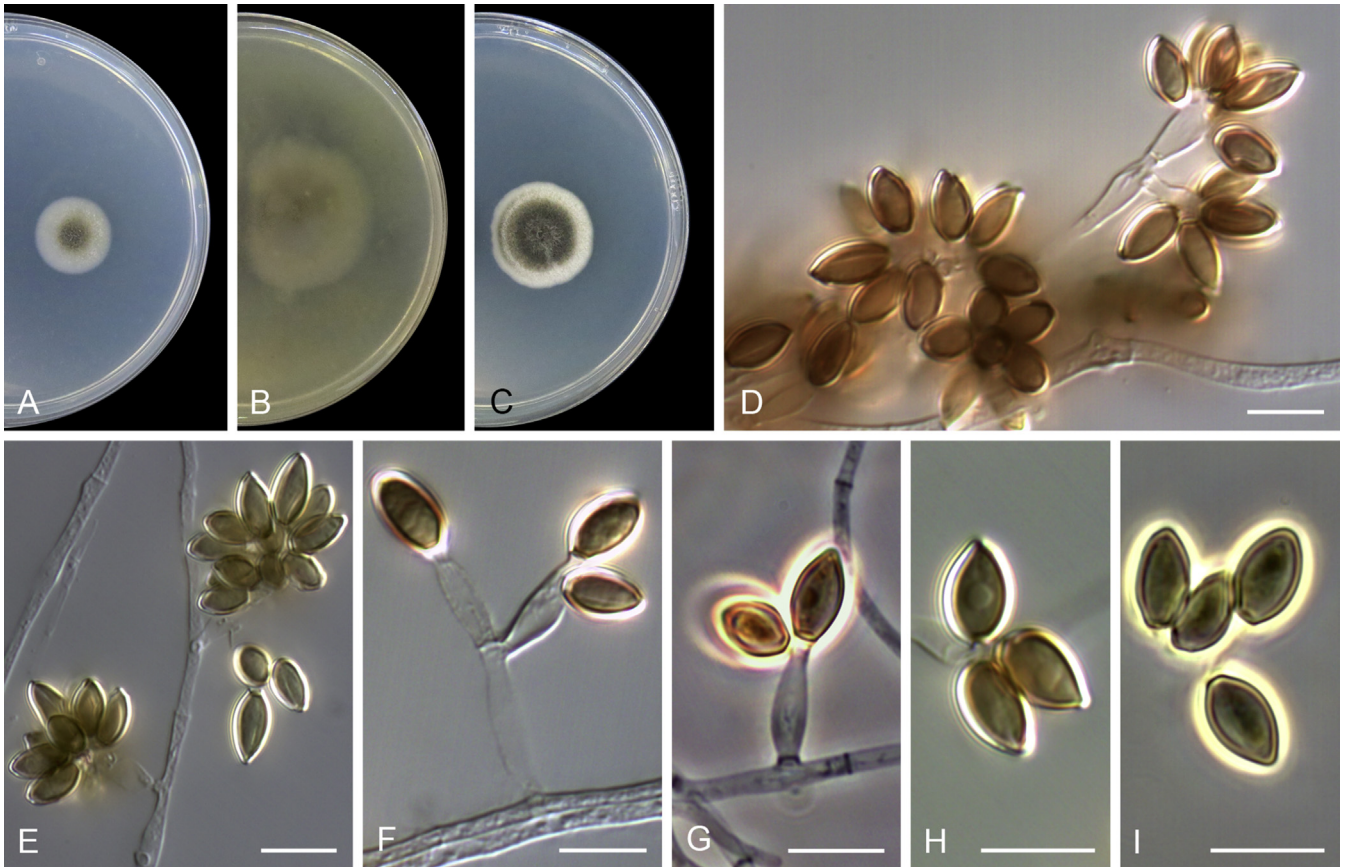
***Wardomyces giganteus*** (Malloch) Sandoval-Denis, Guarro & Gené, **comb. nov.** MycoBank MB814579. Fig. 24  
*Basionym:* *Microascus giganteus* Malloch, Mycologia 62: 731. 1970.

*Material examined:* Canada, Ontario, Simcoe Co., insect frass in dead log, 1968, D.W. Malloch (Holotype TRTC 45434; culture ex-type CBS 746.69).

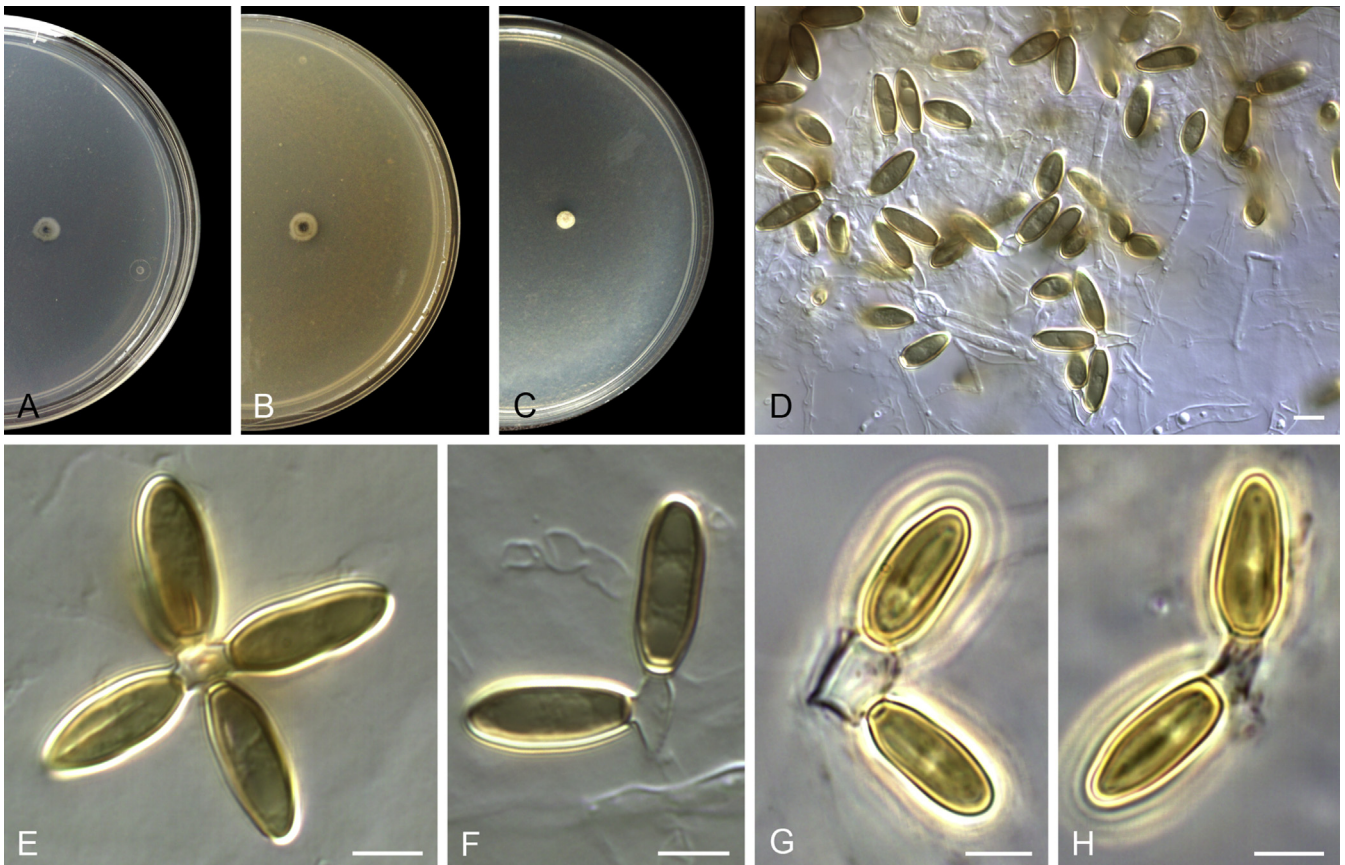
*Descriptions and illustrations:* Malloch (1970a), Guarro *et al.* (2012).

*Notes:* This species was originally described in *Microascus* because of the characters of its sexual morph. However, the morphology of the asexual morph, with polyblastic conidiogenous cells and dark, thick-walled conidia with a longitudinal germ slit does not match with the morphological characteristics of the asexual morphs of *Microascus* or *Scopulariopsis*. In addition, the morphology of its sexual morph is slightly different from *Microascus*; *W. giganteus* has large hairy ascospores and reniform ascospores with two polar germ pores. Several phylogenetic studies (Issakainen *et al.* 2003, Sandoval-Denis *et al.* 2016) point toward *Wardomyces*, which also agrees with the morphological evidences.

*Wardomyces giganteus* morphologically resembles *W. humicola* and *W. pulvinatus*, mainly in the characters of the asexual morph. However, in addition to the presence of a sexual



**Fig. 23.** *Wardomyces anomalus* (ex-epitype CBS 299.61). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–G. Conidiophores. H–I. Conidia. Scale bars: D–I = 5  $\mu$ m.



**Fig. 24.** *Wardomyces giganteus* (ex-type CBS 746.69). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D. Conidiophores. E–H. Polyblastic conidiogenous cells and conidia. Scale bars: D–H = 5  $\mu$ m.

morph in *W. giganteus*, this species has 1-celled, ellipsoidal and pointed conidia 6.5–14 × 3.5–5 µm, borne from hyaline, mostly solitary conidiogenous cells. In contrast, *W. humicola* exhibits 2-celled, ellipsoidal to navicular conidia, slightly smaller (9–12 × 2.5–5.5 µm), while the conidia of *W. pulvinatus* are 1-celled, smaller (5.5–10 × 3–4.5 µm), typically papillate and formed on pale brown conidiogenous cells.

***Wardomyces humicola*** Hennebert & G.L. Barron, *Canad. J. Bot.* 40: 1209. 1962. Fig. 25.

*Material examined:* Canada, Ontario, Guelph, Ontario Agricultural College, soil in tropical greenhouse, 1961, G.L. Barron (Holotype DAOM 75655; culture ex-isotype CBS 369.62).

*Description and illustrations:* Hennebert (1962).

*Notes:* This fungus was isolated from soil in Africa, Asia, Europe and North America (Hennebert 1962, Domsch *et al.* 2007). It is phylogenetically and morphologically similar to *W. pulvinatus*; both species producing penicillate conidiophores and pointed conidia. However, the conidia of *W. humicola* are 2-celled, measuring 9–12 × 2.5–5.5 µm and are formed on hyaline, barrel-shaped conidiogenous cells, while those of *W. pulvinatus* are 1-celled, 5.5–10 × 3–4.5 µm, and are formed on pale brown conidiogenous cells.

***Wardomyces inflatus*** (Marchal) Hennebert, *Trans. Brit. mycol. Soc.* 51: 755. 1968. Fig. 26.

*Basionym:* *Trichosporum inflatum* Marchal, *Champ. copr. Belg.* 7: 142. 1896.

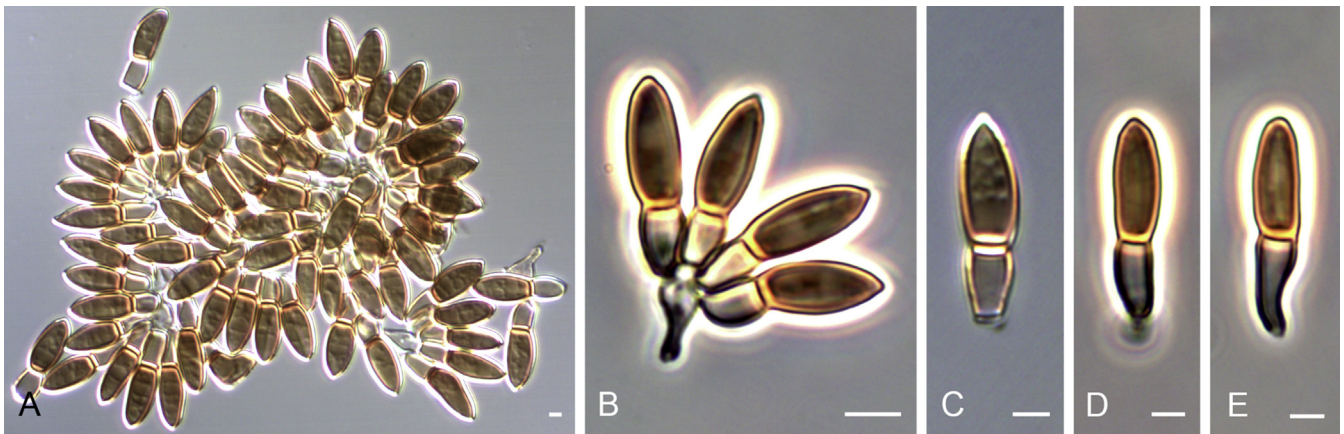


Fig. 25. *Wardomyces humicola* (ex-isotype CBS 369.62). A. Conidiophores. B–E. Polyblastic conidiogenous cells and conidia. Scale bars: A–E = 2 µm.

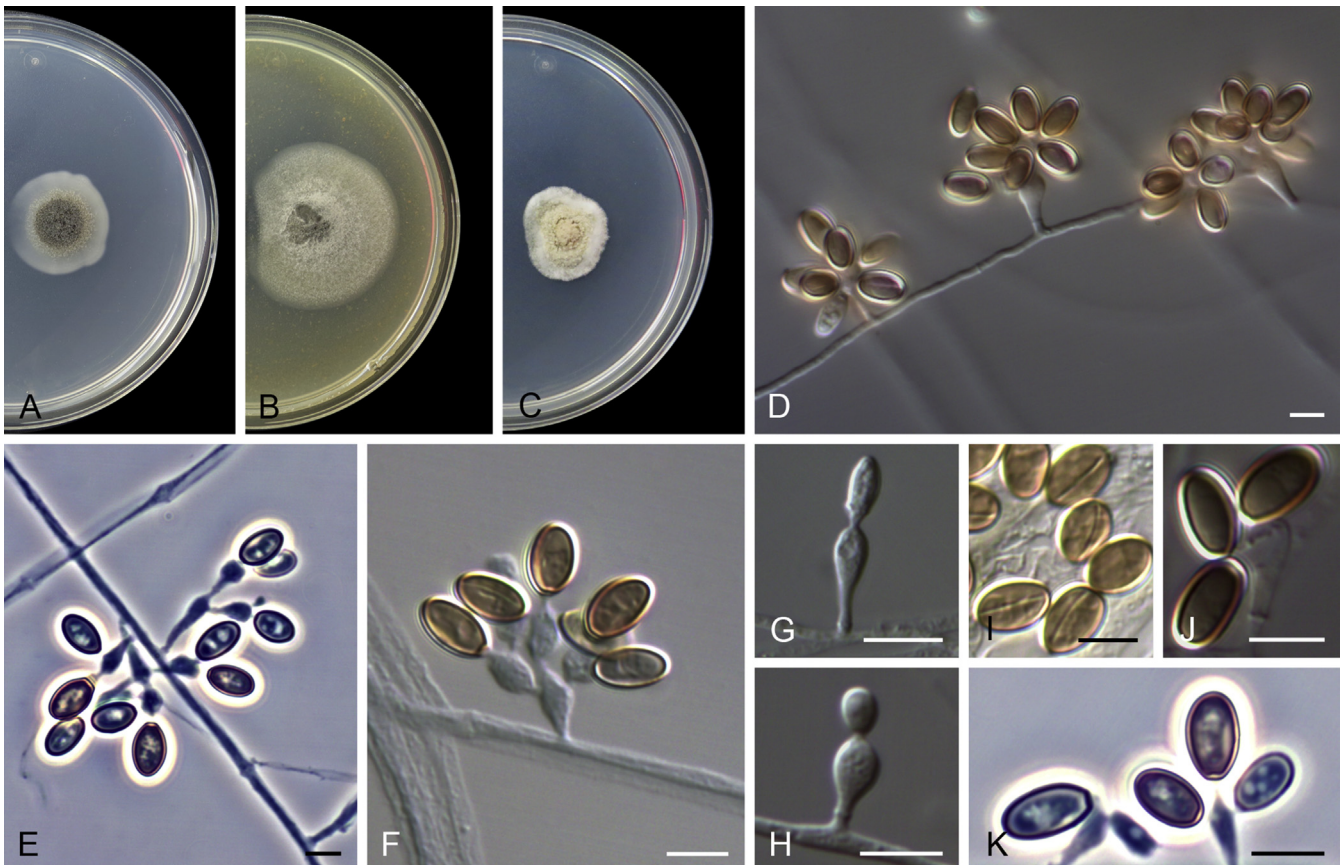


Fig. 26. *Wardomyces inflatus* (ex-neotype CBS 367.62). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–F. Conidiophores. G–H. Polyblastic conidiogenous cells. I–K. conidia. Scale bars: D–K = 5 µm.

**Synonym:** *Wardomyces hughesii* Hennebert, *Canad. J. Bot.* 40: 1207. 1962.

**Material examined:** **Belgium**, Heverlee, greenhouse soil under *Lycopersicon esculentum*, 1959, G.L. Hennebert & E. Delvaux (culture ex-neotype CBS 367.62). **Canada**, Quebec, Gatineau County, Ste Cécile de Masham, from decayed wood, 1960, G.L. Hennebert (culture ex-isotype of *Wardomyces hughesii* CBS 216.61).

**Descriptions and illustrations:** Hennebert (1962, 1968).

**Notes:** Hennebert (1968) discussed the morphological similarity between *W. hughesii* and *Trichosporum inflatum* and, despite some morphological discrepancies, they were considered as conspecific. Our molecular results confirm this synonymy.

The morphological features of the conidiogenous cells (markedly constricted at the septum) and conidia (ellipsoidal to cylindrical with rounded apices,  $6\text{--}8 \times 3.5\text{--}5 \mu\text{m}$ ) in *W. inflatus* clearly differentiate this species from the other members of the genus. *Wardomyces anomalus*, its closest phylogenetic and morphological relative, has barrel-shaped conidiogenous cells and somewhat smaller ( $4.5\text{--}8 \times 3.5\text{--}6 \mu\text{m}$ ), ovoid and pointed conidia.

***Wardomyces ovalis*** W. Gams, *Trans. Brit. mycol. Soc.* 51: 798. 1968. Fig. 27.

**Synonym:** *Hennebertia ovalis* (W. Gams) M. Morelet, *Ann. Soc. Sci. Nat. Archéol. Toulon Var* 21: 105. 1969.

**Material examined:** **Germany**, Schleswig-Holstein, Kiel-Kitzeberg, wheat-field soil, 1963, W. Gams (culture ex-type CBS 234.66).

**Description and illustrations:** Gams (1968).

**Notes:** *Wardomyces ovalis* resembles *W. anomalus* and *W. inflatus*. However, it is unique in the genus by the production of additional scopulariopsis-like conidiation, which is characterised by hyaline to subhyaline, 1-celled, smooth-walled conidia ( $5.5\text{--}10 \times 3.5\text{--}6 \mu\text{m}$ ) from hyaline, cylindrical annellides ( $6\text{--}10 \times 2\text{--}4 \mu\text{m}$ ).

***Wardomyces pulvinatus*** (Marchal) C.H. Dickinson, *Trans. Brit. mycol. Soc.* 49: 521. 1966. Fig. 28.

**Basionym:** *Echinobotryum pulvinatum* Marchal, *Bull. Soc. Roy. Bot. Belgique* 34: 139. 1895.

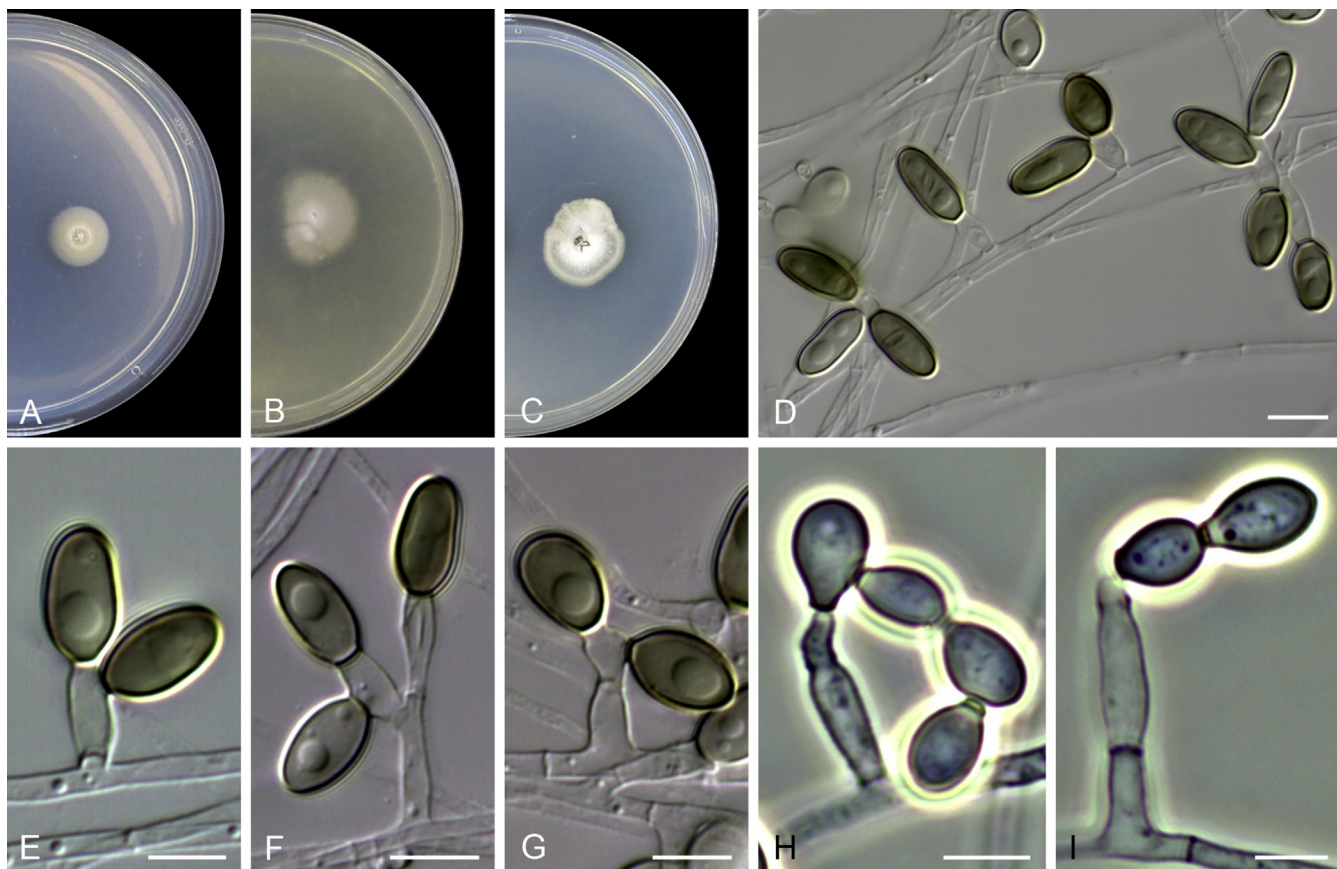
**Synonym:** *Wardomyces papillatus* C.H. Dickinson, *Trans. Brit. mycol. Soc.* 47: 321. 1964.

**Material examined:** **England**, Cheshire, Parkgate, salt-marsh mud under *Halimione portulacoides*, 1962, C.H. Dickinson (culture ex-isotype CBS 112.65).

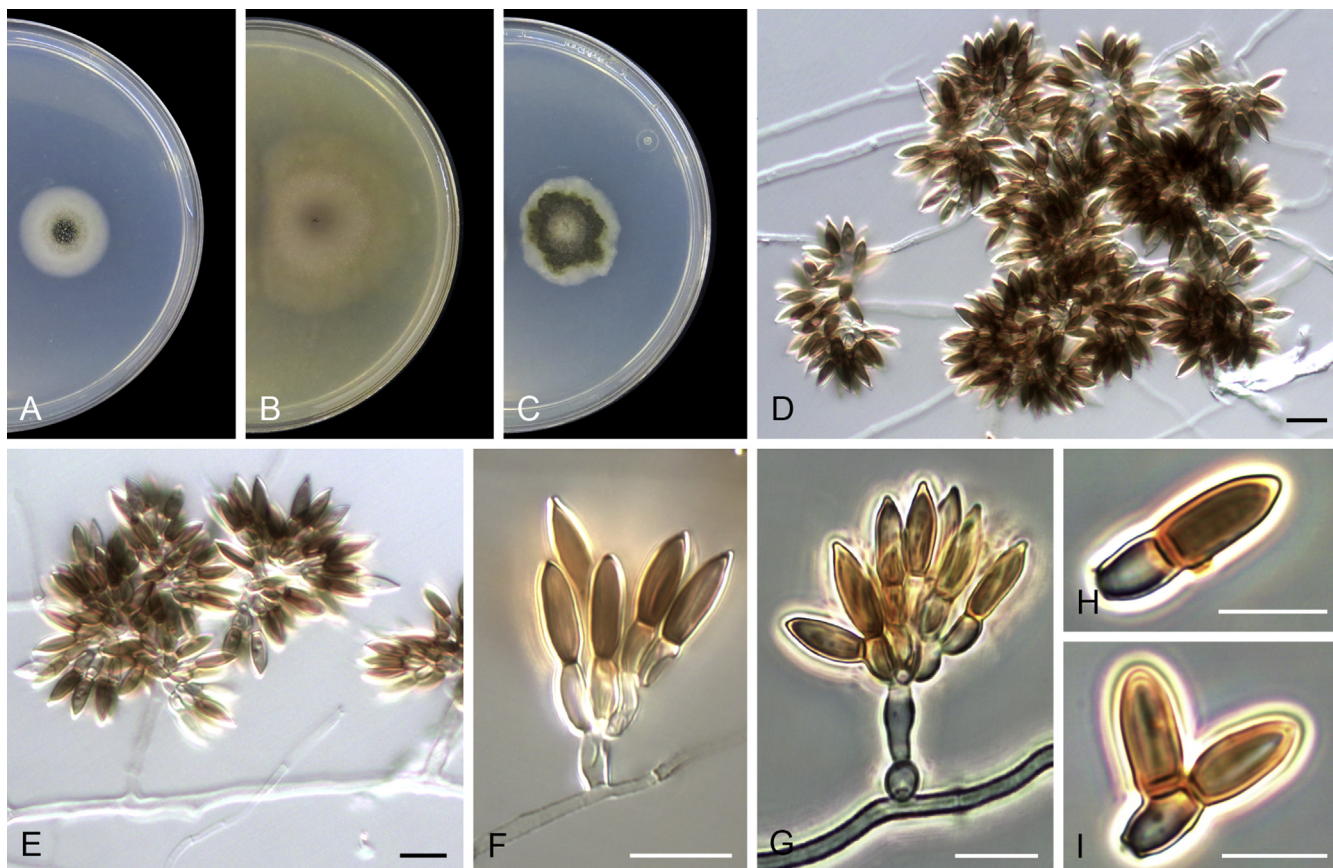
**Descriptions and illustrations:** Dickinson (1964, 1966), Ellis (1971).

**Notes:** This species has been isolated from soil and on decaying leaves of *Pandanus tectorius* (Dickinson 1966, Whitton et al. 2012).

*Wardomyces pulvinatus* strongly resembles *W. humicola*, both having navicular and pointed solitary conidia on barrel-shaped conidiogenous cells and mostly penicillately branched conidiophores. However, the conidia of *W. pulvinatus* are  $5.5\text{--}10 \times 3\text{--}4.5 \mu\text{m}$ , 1-celled, typically papillate at the apex and



**Fig. 27.** *Wardomyces ovalis* (ex-type CBS 234.66). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–G. Conidiophores, polyblastically conidiogenous cells and conidia. H–I, Annellidic conidiogenous cells and conidia. Scale bars: D–I = 5 μm.



**Fig. 28.** *Wardomyces pulvinatus* (ex-type CBS 112.65). A–C. Colonies on PCA, OA and PDA respectively, after 14 d at 25 °C. D–E. Conidiophores. F–G. Conidiogenous cells. H–I. Conidia. Scale bars: D–I = 5 µm.

commonly secede, carrying a portion of the conidiogenous cell. In addition, that species is the only one in the genus forming sporodochia in culture. In contrast, the conidia of *W. humicola* are slightly larger (9–12 × 2.5–5.5 µm), non-papillate and 2-celled.

***Wardomyopsis*** Udagawa & Furuya, Mycotaxon 7: 92. 1978.

*Type species:* *Wardomyopsis inopinata* Udagawa & Furuya.

*Descriptions and illustrations:* Barron (1966), Udagawa & Furuya (1978).

*Notes:* *Wardomyopsis* closely resembles *Wardomyces*, especially in the early stages of conidiation, both genera forming darkly pigmented conidia with a single longitudinal germ slit (Barron 1966). However, the conidiogenesis and arrangement of conidia in *Wardomyopsis* are more similar to those of *Scopulariopsis* and *Fairmania* species (i.e., formation of basipetal conidial chains on annellidic conidiogenous cells) rather than to *Wardomyces* species (i.e., formation of solitary conidia on polyblastic conidiogenous cells). The conidia of *Scopulariopsis* spp. are arranged in long chains and lack germ slits, while those of *Fairmania* present numerous (1–5) longitudinal striations.

***Wardomyopsis humicola*** (G.L. Barron) Udagawa & Furuya, Mycotaxon 7: 96. 1978. Fig. 29.

*Basionym:* *Scopulariopsis humicola* G.L. Barron, Antonie van Leeuwenhoek 32: 294. 1966.

*Material examined:* Canada, Ontario, Guelph, from soil, 1964, G.L. Barron (Holotype OAC 10260; culture ex-isotype CBS 487.66). Spain, Girona, Pals,

from sediments of Ter River, 1991, C. Ulfig & J. Gené (FMR 3993); Reus, Institut Salvador Vilaseca, from garden soil, 2014, M. Repollés & J. Gené (FMR 13592).

*Description and illustrations:* Barron (1966).

*Notes:* *Wardomyopsis humicola* is a soil-borne, seldom observed species. It is phylogenetically close to *Ws. inopinata*, but differs in its pale brown, ovate to cylindrical conidia (4–5 × 2.5–3 µm) and absence of sexual morph. By contrast, *Ws. inopinata* has olivaceous brown, globose to subglobose conidia (4–5.5 × 4–5.5 µm) and can produce ascomata in culture (Udagawa & Furuya 1978).

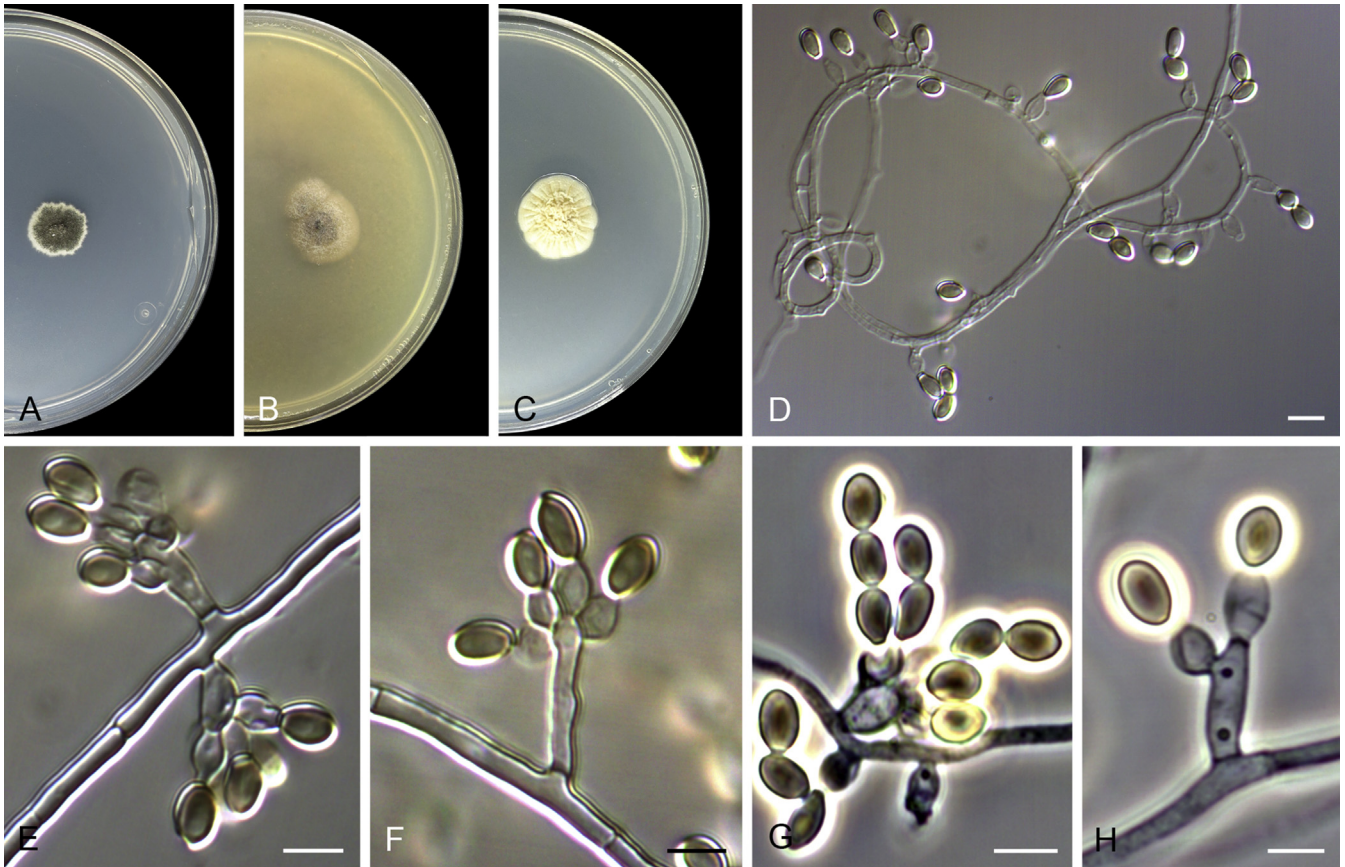
***Wardomyopsis inopinata*** Udagawa & Furuya, Mycotaxon 7: 92. 1978. Fig. 30

*Synonym:* *Microascus inopinatus* Udagawa & Furuya, Mycotaxon 7: 91. 1978.

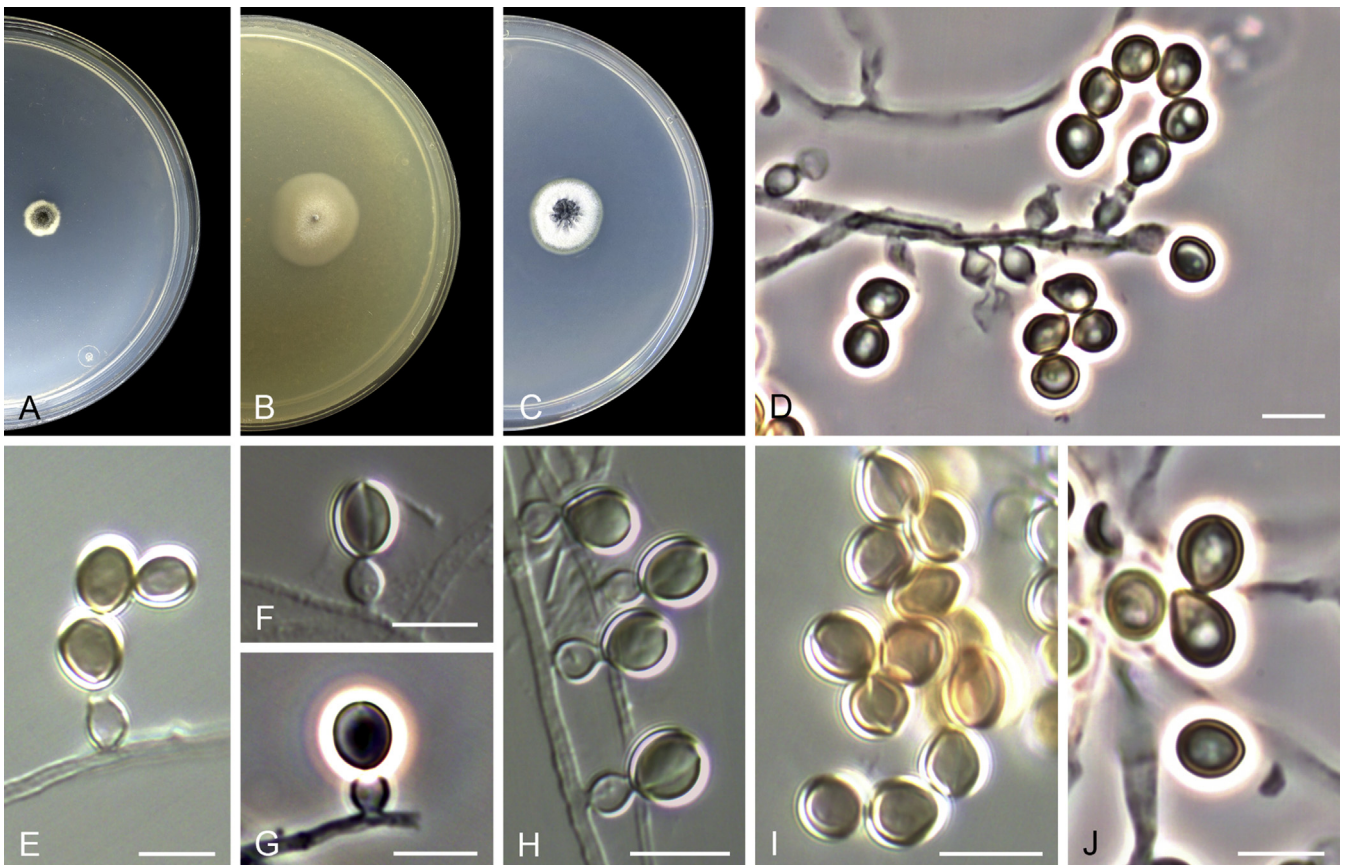
*Material examined:* Myanmar, from soil, 2008, C. Hartung (FMR 10305); from soil, 2008, C. Hartung (FMR 10306).

*Descriptions and illustrations:* Udagawa & Furuya (1978).

*Notes:* This is the only species of the genus for which a sexual morph has been described. It is characterised by slowly forming ostiolate ascomata (up to 350 µm diam) and straw-coloured, reniform to triangular ascospores (3–3.5 × 2.5–3 µm) with a single germ pore. Nonetheless, the sexual morph was not observed in either of two isolates studied here. Although the holotype (NHL 2767, preserved at the National Institute of Hygienic Sciences, Tokyo, Japan) or ex-type cultures of *Ws.*



**Fig. 29.** *Wardomyopsis humicola* (ex-isotype CBS 487.66). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–G. Conidiophores, conidiogenous cells and conidia. Scale bars: D–G = 5 μm.



**Fig. 30.** *Wardomyopsis inopinata* (FMR 10305). A–C. Colonies on PCA, OA and PDA, respectively, after 14 d at 25 °C. D–H. Conidiogenous cells. I–J. Conidia. Scale bars: D–J = 5 μm.



*inopinata* are unavailable for comparison, the morphology of the asexual morph of the soil isolates investigated from Myanmar agrees with that of the protologue of *Ws. inopinata*, which was based on a soil isolate from Thailand (Udagawa & Furuya 1978). The phylogenetic analysis confirmed this taxon as different from the previous three species accepted in the genus. *Wardomycesopsis inopinata* is characterised by globose to subglobose, olivaceous brown conidia, measuring 4–5.5 × 4–5.5 µm, on flask-shaped or cylindrical, 2.5–3 µm wide annellides; *Ws. humicola* produces narrower ovoid to cylindrical, smoky brown conidia (4–5 × 2.5–3 µm) on barrel-shaped annellides (1.5–2.5 µm wide); and *Ws. litoralis* has obovoid to broadly ellipsoidal, dark olive conidia (5–7 × 3–4.5 µm) and wider ampulliform annellides (3.5–5 µm wide).

***Wardomycesopsis litoralis*** Silvera *et al.*, Mycotaxon 105: 197. 2008. Fig. 31.

**Material examined:** Spain, Vinarós, Castelló, from soil, 2004, A. Stchigel (Holotype IMI 394093; culture ex-type CBS 119740 = IMI 394093 = FMR 8876).

**Description and illustrations:** Silvera-Simón *et al.* (2008).

**Notes:** *Wardomycesopsis litoralis* was originally described on the basis of morphological features and ITS sequence analysis (Silvera-Simón *et al.* 2008). Our polyphasic approach confirms this taxon as a distinct phylogenetic species of *Wardomycesopsis*, being characterised by dark olive brown, obovoid to broadly ellipsoidal and smooth, short-catenate conidia (5–7 × 3–4.5 µm) borne on hyaline to subhyaline ampulliform annellides (5.5–7.5 × 3.5–5 µm).

## DISCUSSION

This work adds relevant data to build a more natural taxonomy of the *Microascales*, and particularly of the *Microascaceae*. Previous studies have reviewed the molecular phylogenetic relationships among members of this family (Lackner & de Hoog 2011, Lackner *et al.* 2014, Sandoval-Denis *et al.* 2016), providing a broad phylogenetic backbone through a molecular overview of this group of fungi. It was demonstrated that this family shows an intricate phylogenetic structure composed of several genera that share similar ecological and morphological features (Lackner & de Hoog 2011, Lackner *et al.* 2014, Jagielski *et al.* 2016, Sandoval-Denis

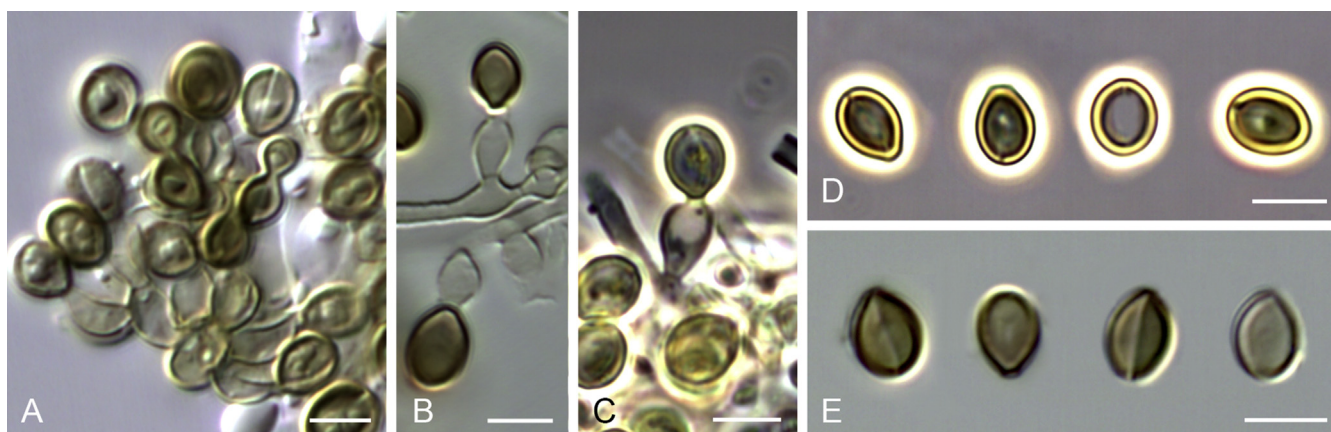
*et al.* 2016). Due to the lack of DNA sequences in public databases and the paucity of phylogenetic studies, several genera of the family, particularly those with synnematos conidiophores or conidia with germ slits were still of uncertain affinities. We studied a large set of isolates, including all the available living type material, of the synnematos genera *Cephalotrichum*, *Doratomyces*, *Trichurus*, their closest phylogenetic relatives *Wardomyces* and *Wardomycesopsis*, and several related taxa of uncertain taxonomic position.

The morphology of the sexual morphs is very homogeneous in *Microascaceae* and particularly among *Acaulium*, *Fairmania*, *Fuscoannellis*, *Microascus*, *Pithoascus*, *Pseudoscopulariopsis*, *Scopulariopsis*, *Wardomyces* and *Wardomycesopsis*; this explains the former placement of most of these genera as synonyms of *Microascus* (Morton & Smith 1963, Guarro *et al.* 2012). However, our current and recent phylogenetic results (Sandoval-Denis *et al.* 2016, Jagielski *et al.* 2016) showed the above-mentioned genera to comprise distinct lineages. Their genetic diversity correlates with subtle morphological differences, such as the presence or absence of hyaline or pigmented annellidic conidiogenous cells, unicellular or septate annelloconidia and/or solitary conidia with or without germ slits (Table 2).

Interestingly, our study revealed that the genus *Wardomyces* is paraphyletic. Its species are distributed in three closely related lineages, with two species each. The morphological differences between these species (i.e., presence/absence of annelloconidia and/or septate solitary conidia) have previously led to the proposal to segregate *Wardomyces* into different genera (Morelet 1969). However, we could demonstrate that these morphological features are not constant and thus we preferred to maintain *Wardomyces s. lat.* until more taxa can be investigated and the morphological evidence is properly understood.

Another controversial issue has been the current status of the genus *Gamsia*, which has been considered a synonym of *Wardomyces* by most authors (Domsch *et al.* 2007, Seifert *et al.* 2011, Whitton *et al.* 2012). However, our results demonstrated that *Gamsia* constitutes a genetically distinct lineage basal to *Wardomyces s. lat.*, being morphologically distinguished by the complexity of its conidiophores.

The genera *Acaulium* and *Fairmania*, with three and one species, respectively, have been reintroduced in this study. The phylogenetic data provided here agree with significant morphological differences for maintaining *Acaulium* and *Fairmania* as different from *Microascus* and *Scopulariopsis*, respectively, from which both genera had been previously considered synonyms.



**Fig. 31.** *Wardomycesopsis litoralis* (ex-type CBS 119740). A. Conidiophores. B–C. Conidiogenous cells. D–E. Conidia. Scale bars: A–E = 5 µm.

The decision about the most appropriate name for the synnematus genera *Cephalotrichum* and *Doratomyces*, considered synonyms by numerous authors, has been a matter of discussion for a long time (Hughes 1958, Morton & Smith 1963, Abbott 2000, Domsch et al. 2007), while *Trichurus* has been until recently considered as a different genus (Domsch et al. 2007). However, phylogenetic inference resolved a lineage comprising the *Cephalotrichum* lectotype suggested by Hughes (1958), and followed by subsequent authors (Abbott 2000, Seifert et al. 2011, de Beer et al. 2013). It also demonstrated that *Trichurus* species belong to the same lineage hence being congeneric with *Cephalotrichum*, as it was suggested by several authors based on morphological criteria (Hasselbring 1896, Abbott 2000). Our phylogenetic results confirm most of the species synonymies previously proposed by Abbott (2000) and also corroborate the chosen epitypes for several taxa.

Although *Cephalotrichum* has not been regarded as a human pathogen, several of the isolates included in this study

were from clinical origin, particularly those belonging to *C. asperulum* and *C. gorgonifer*, mostly isolated from respiratory specimens. However, given the lack of clinical data concerning such isolates, no information on the actual pathogenic role of these isolates can be provided. Given the origin of the isolates and the common airborne dispersal method of these fungi, it is most likely that they were in fact colonisers or mere sample contaminants.

It is important to highlight the large number of reported taxa that could not be studied because of the lack of living cultures and consequently considered uncertain species. Given the usefulness and importance of combining morphological data with molecular phylogenetic studies to adhere to the requirements of the ICN (McNeill et al. 2012), it is crucial for the progress of science to encourage all authors of fungal names to deposit live material in international culture collections for future studies.

## KEY TO TAXA INCLUDED IN THIS STUDY

1a	Synnemata present in culture .....	<b><i>Cephalotrichum</i></b>
1b	Synnemata usually lacking .....	2
2a	Conidia hyaline to brown, guttulate, smooth, without slits or striations .....	<b><i>Acaulium</i></b>
2b	Conidia pale to dark brown, with longitudinal slits or striations .....	3
3a	Conidia with a longitudinal germ slit present .....	4
3b	Conidia with 1–5 longitudinal striations .....	<b><i>Fairmania singularis</i></b>
4a	Conidia of one type, dark, with a longitudinal germ slit, formed on annellidic conidiogenous cells and arranged in short chains .....	<b><i>Wardomycopsis</i></b>
4b	Conidia of two types can be present, i) dark, with a longitudinal germ slit arising solitary and forming groups on polyblastic conidiogenous cells, ii) hyaline, arranged in chains on annellidic conidiogenous cells .....	5
5a	Conidiophores undifferentiated; dark conidia forming dense clusters on the top of the conidiogenous cells .....	<b><i>Gamsia</i></b>
5b	Conidiophores well differentiated, branched; dark conidia borne apically and laterally in groups of 2–3 on the top of the conidiogenous cells .....	<b><i>Wardomyces</i></b>

## Key to *Acaulium* species

1a	Conidia hyaline, obovate, cylindrical or clavate .....	2
1b	Conidia pale brown to brown, obovate .....	<b><i>A. caviariforme</i></b>
2a	Sexual morph absent; conidia obovate up to 12 µm long .....	<b><i>A. acremonium</i></b>
2b	Sexual morph present; conidia cylindrical to clavate up to 8 µm long .....	<b><i>A. albonigrescens</i></b>

## Key to *Cephalotrichum* species

1a	Setae present on the upper part of the synnemata .....	2
1b	Setae absent .....	4
2a	Setae straight, branched or unbranched .....	<b><i>C. cylindricum</i></b>
2b	Setae curved or flexuous .....	3
3a	Setae flexuous, coiled, unbranched .....	<b><i>C. gorgonifer</i></b>
3b	Setae undulate and dichotomously branched .....	<b><i>C. dendrocephalum</i></b>
4a	Echinobotryum-like synasexual morph present .....	5
4b	Echinobotryum-like synasexual morph absent .....	6
5a	Synnemata up to 3 000 µm tall; annelloconidia ellipsoidal to cylindrical, 5–9 × 4–5 µm with rounded apices .....	<b><i>C. stemonitis</i></b>
5b	Synnemata up to 1 600 µm tall; annelloconidia subglobose to ellipsoidal, 6–7.5 × 2.5–4 µm with slightly pointed apices .....	<b><i>C. hinnuleum</i></b>
6a	Conidia distinctively rough .....	7
6b	Conidia smooth or finely ornamented .....	9
7a	Synnemata up to 1 000 µm tall; conidia oval to ellipsoidal .....	<b><i>C. asperulum</i></b>
7b	Synnemata often higher; conidia globose to ovoid .....	8

8a	Conidia 4.5–7.5 µm wide, coarsely warted, grey-brown .....	<i>C. nanum</i>
8b	Conidia 3–5.5 µm wide, spirally sculpted, dark brown .....	<i>C. verrucisporum</i>
9a	Conidia 3.5–5 × 2–3 µm; no growth at 35 °C .....	<i>C. microsporum</i>
9b	Conidia larger; growth at 35 °C .....	10
10a	Synnemata up to 500 µm tall; conidia with rounded apex, pale to dark brown .....	11
10b	Synnemata higher; conidia with finely pointed apex, green-brown .....	<i>C. purpureofuscum</i>
11a	Conidia asymmetrical, dark brown, 5.5–7.5 × 2.5–4 µm .....	<i>C. columnare</i>
11b	Conidia symmetrical, pale brown, 6–7 × 3.5–4 µm .....	<i>C. brevistipitatum</i>

### Key to *Gamsia* species

1a	Dark conidia 4–7.5 × 3.5–5 µm with rounded apices; annelloconidia ellipsoidal, 2-celled, 8–10.5 × 3.5–5 µm .....	<i>G. aggregata</i>
1b	Dark conidia 6–13 × 3.5–6.5 µm with slightly pointed apices; annelloconidia oval, 1–2-celled, 5–10.5 × 2.5–5.5 µm .....	<i>G. columbina</i>

### Key to *Wardomyces* species

1a	Annelloconidia present: hyaline to subhyaline, 5.5–10 × 3.5–6 µm, 1-celled; solitary dark conidia ellipsoidal, 7–11 × 4–5 µm .....	<i>W. ovalis</i>
1b	Annelloconidia absent, only solitary dark conidia present .....	2
2a	Conidia 1-celled .....	3
2b	Conidia 2-celled .....	<i>W. humicola</i>
3a	Conidia ellipsoidal with rounded apex, 6–8 × 3.5–5 µm .....	<i>W. inflatus</i>
3b	Conidia oval to ellipsoidal with pointed apex .....	4
4a	Conidia navicular, 5.5–10 × 3–4.5 µm, papillate, often seceding with a portion of the conidiogenous cell .....	<i>W. pulvinatus</i>
4b	Conidia otherwise .....	5
5a	Conidia oval, up to 8 µm long; sexual form absent .....	<i>W. anomalus</i>
5b	Conidia ellipsoidal, up to 14 µm long; sexual morph if present with reniform ascospores, 4–5.5 × 3.5–4 µm, with two germ pores .....	<i>W. giganteus</i>

### Key to *Wardomyopsis* species

1a	Conidia globose to subglobose; sexual morph if present with reniform to triangular ascospores, 3–3.5 × 2.5–3 µm .....	<i>Ws. inopinata</i>
1b	Conidia otherwise; sexual morph absent .....	2
2a	Conidia 4–5 × 2.5–3 µm, ovate to cylindrical .....	<i>Ws. humicola</i>
2b	Conidia 5–7 × 3–4.5 µm, obovoidal to broadly ellipsoidal .....	<i>Ws. litoralis</i>

### LIST OF UNCERTAIN OR EXCLUDED SPECIES

***Cephalotrichum acutisporum*** J.J. Xu & T.Y. Zhang, Mycotaxon 117: 208. 2011.

*Notes:* The original description and illustration of this species morphologically resemble *C. columnare*. However, *C. acutisporum* has slightly longer synnemata (120–820 µm tall) with dark, compact stipes. Synnemata in *C. columnare* are up to 500 µm tall with very narrow stalks. Type material or DNA sequence data were unavailable for study.

***Cephalotrichum album*** (Costantin) Seifert, CBS Biodiversity Series 12: 309. 2013.

*Basionym:* *Synpenicillium album* Costantin, Bull. Soc. Mycol. France. 4: 62. 1888.

*Synonyms:* *Coremium album* (Costantin) Sacc. & Traverso, Syll. fung. 19: 428. 1910.

*Penicillium costantinii* Bain. [as ‘*costantini*’], Bull. Soc. Mycol. France. 22: 205. 1906.

*Scopulariopsis costantinii* (Bain.) Dale, Ann. Mycol. 12: 57. 1914.

*Notes:* This species was recently included in *Cephalotrichum* as a new combination for one of the two different fungi present in the holotype of *Stysanus putredinis* Corda (de Beer *et al.* 2013).

The species is well circumscribed as “*Doratomyces putredinus*” in Morton and Smith (1963) and “*Cephalotrichum putredinus*” by Abbott (2000) for a white synnematosus fungus exhibiting long chains of hyaline conidia. However, recently, Lackner & de Hoog (2011) designated an epitype for *S. putredinis* to fix this epithet under the new combination *Parascedosporium putredinis*, a

fungus producing larger conidia in slimy masses, and previously regarded as conspecific with *Graphium cuneiferum* by other authors (Hughes 1958, Seifert 1985, Abbott 2000). Thus, as indicated above, given the confuse application of the epithet “*putredinis*” under two different fungal concepts, de Beer et al. (2013) were forced to choose a different epithet for the white fungus described by Morton & Smith (1963) and now listed in *Cephalotrichum*.

Morphologically, *C. album* is dissimilar from other members of *Cephalotrichum* s. str., with white to pallid colonies lacking dematiaceous pigments and poorly developed, white synnemata. It is likely that it is related to another lineage of *Microasceae*, and has considerable morphological similarity to species of *Acaulium*. However, no molecular sequence data is currently available for this species.

***Cephalotrichum antarcticum*** (Speg.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Sporocybe antarctica* Speg., Bol. Acad. Nac. Ci. 11: 63. 1887.

*Note:* Carmarán & Novas (2003) studied the holotype of *S. antarctica* (LSP 33139) and considered this specimen to be a lichen.

***Cephalotrichum aterrimum*** (Rabenh.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Periconia aterrima* Rabenh., Deutschl. Krypt.-Fl. (Leipzig) 1: 118. 1844.

*Synonym:* *Sporocybe aterrima* (Rabenh.) Sacc., Syll. Fung. 4: 607. 1886.

*Notes:* No type specimen was found to be examined and no comment on this taxon was included in the revision of the genus *Periconia* by Mason & Ellis (1953). The description of this species is too vague for a correct identification of fresh isolates.

***Cephalotrichum atrofusum*** (Mont.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Stilbum atrofusum* Mont., J. Linn. Soc., Bot. 10: 358. 1868.

*Synonym:* *Sporocybe atrofusca* (Mont.) Sacc., Syll. fung 4: 605. 1886.

*Notes:* This species was poorly described and considered a *nomen dubium* by Seifert (1985) since type and isotype material preserved in K only contained sterile structures.

***Cephalotrichum bulbosum*** (Schwein.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Periconia bulbosa* Schwein., Trans. Amer. Philos. Soc. 4: 304. 1832.

*Notes:* No comment on this taxon was included in the revision of *Periconia* by Mason & Ellis (1953) and no living material is available for a proper morphological characterisation of the species. There is not certainty about the identity of the holotype material. Two different specimens are available in PH and regarded as “probable types”.

***Cephalotrichum caespitosum*** Demelius, Verh. Zool.-Bot. Ges. Wien 72: 99. 1923.

*Notes:* No type specimen was found for examination. The original description shows a fungus with catenate conidia borne on polyblastic and denticulate conidiogenous cells, which seems to indicate that it does not correspond to a *Cephalotrichum* species.

***Cephalotrichum carneum*** (Richon) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Sporocybe carnea* Richon, Cat. champ. Marne: no. 2088.

*Note:* The original description is too vague for its recognition.

***Cephalotrichum castaneum*** (Y.L. Jiang & T.Y. Zhang) Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 224. 2011.

*Basionym:* *Doratomyces castaneus* Y.L. Jiang & T.Y. Zhang, Mycotaxon 104: 131. 2008.

*Notes:* The protologue describes a species of *Cephalotrichum* characterised by spherical to subspherical, thick-walled conidia (4–6 µm diam.). Type material was unavailable for study; however, the analysis of an ITS sequence of the ex-type (GenBank, FJ914681) had a sequence similarity of 99.2 % with *C. dendrocephalum*. Further studies involving more informative loci are needed to clarify the taxonomy of this species.

***Cephalotrichum cellare*** (Peck) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Sporocybe cellaris* Peck, Annual Rep. New York St. Mus. Nat. Hist. 42: 129. 1889.

*Note:* The description of this species is too vague for a proper identification.

***Cephalotrichum clavulatum*** (Sacc.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Sporocybe clavulata* Sacc., Syll. Fung 4: 604. 1886.

*Note:* The original description of this species is too vague for a proper identification.

***Cephalotrichum commune*** Demelius, Verh. zool.-bot. Ges. Wien 72: 98. 1923.

*Notes:* The original description point toward a species of *Cladosporium* rather than *Cephalotrichum*. Type material or living strains were not found for confirmation.

***Cephalotrichum concentricum*** (Schwein.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Coremium concentricum* Schwein., Proc. Am. Phil. Soc. Phila. 4: 282. 1832.

*Synonym:* *Sporocybe concentrica* (Schwein.) Sacc., Syll. Fung. 4: 608. 1886.

*Notes:* Seifert & Samson (1985) studied the type material of *Coremium concentricum* and reported the presence of only immature or decapitated conidiomata of what may be a *Mycosphaerella* asexual morph, rendering this taxon to a *nomen dubium*.

***Cephalotrichum corticale*** (Cooke & Peck) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Periconia corticalis* Cooke & Peck, in Peck, Annual Rep. New York St. Mus. Nat. Hist. 29: 52. 1878.

*Synonyms:* *Sporocybe corticalis* (Cooke & Peck) Sacc., Syll. Fung. 4: 604. 1886.

*Didymobotryum corticale* (Cooke & Peck) Dearn. & House, Bull. New York State Mus. 266: 98. 1925.

*Notes:* No comment on this species was included in the revision of *Periconia* by Mason & Ellis (1953), and no living material is available for a better morphological characterisation of the species.

***Cephalotrichum cylindrosporum*** Y.L. Zhang & T.Y. Zhang, Mycotaxon 117: 209. 2011.

*Notes:* The ITS sequence of the ex-type culture of this species (GenBank FJ914686) has a similarity of 100 % with the ex-epitype strain of *C. stemonitis*. However, these results do not match with the morphological characteristics described in the protologue of *C. cylindrosporum*, which has smooth conidia (5–6.2 × 2.5–3.2 µm) and lack of an echinobotryum-like synsexual morph. Unfortunately, the type material could not be examined after repeated request to the authors, and further studies are needed to assess the taxonomic position of this fungus. In any case, the epithet “*cylindrosporum*” can create confusion with the previously described species *C. cylindricum*.

***Cephalotrichum ellipsoideum*** H.Q. Pan & T.Y. Zhang, Mycotaxon 117: 211. 2011.

*Notes:* The protologue describes a fungus morphologically similar to *C. purpureofuscum*. However, in *C. ellipsoideum* the conidia are wider and have rounded apices (6–8.5 × 3.5–6 µm versus 5–8 × 3–4.5 µm with slightly pointed apices in *C. purpureofuscum*). Type material was unavailable for study.

***Cephalotrichum epiphyllum*** (Schwein.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Periconia epiphylla* Schwein., Trans. Amer. Philos. Soc. 4: 304. 1832.

*Synonym:* *Sporocybe epiphylla* (Schwein.) Sacc. Syll. fung. 4: 608. 1886.

*Notes:* Description too vague for a correct identification and no comment on this species was included in the revision of *Periconia* by Mason & Ellis (1953). A specimen deposited by Schweinitz and dated 1828 is available in PH, although it is unknown if it corresponds to the holotype for the species.

***Cephalotrichum fasciculatum*** (Schwein.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Periconia fasciculata* Schwein., Trans. Amer. Philos. Soc. 4: 304. 1832.

*Synonym:* *Sporocybe fasciculata* (Schwein.) Sacc., Syll. Fung. 4: 607. 1886.

*Notes:* Description rather imprecise for a correct identification. A herbarium sheet exists in PH, although it is not known if it represents the holotype of this species.

***Cephalotrichum flavovirens*** (Alb. & Schwein.) Nees, Syst. Pilze (Würzburg) 87: 1817.

*Basionym:* *Periconia flavovirens* Alb. & Schwein., Consp. fung. (Leipzig): 357. 1805.

*Synonyms:* *Stilbum flavovirens* (Alb. & Schwein.) Link, Sp. pl., 4: 111. 1825.

*Ceratopodium flavovirens* (Alb. & Schwein.) Corda, Icon. fung. (Prague) 1: 19. 1837.

*Graphium flavovirens* (Alb. & Schwein.) Sacc., Syll. Fung. 4: 618. 1886.

*Notes:* The protologue does not include any measurements to accurately identify the species. Although considered previously a *Periconia* species, no further data on this fungus has been found in Mason & Ellis (1953).

***Cephalotrichum gracile*** (Schwein.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Periconia gracilis* Schwein., Trans. Amer. Philos. Soc. 4: 304. 1832.

*Synonym:* *Sporocybe gracilis* (Schwein.) Sacc. Syll. fung. 4: 608. 1886.

*Notes:* Description too vague for a correct identification. No data on this fungus has been found in Mason & Ellis (1953). A herbarium specimen is preserved in PH but regarded as a “possible type”.

***Cephalotrichum gramineum*** (P. Karst.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Sporocybe graminea* P. Karst., Rev. Mycol. (Toulouse) 1888.

*Notes:* The description of this species is too vague for a correct identification.

***Cephalotrichum inflatum*** Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 213. 2011.

*Notes:* The protologue describes a species morphologically similar to *C. microsporum*, but differentiated by its conidiophores composed of distinctively inflated cells. An ITS sequence of the ex-type culture available in GenBank (FJ914676) showed 99.5 % sequence similarity with the ex-epitype strain of *C. microsporum*. Further studies are needed to clarify the taxonomy of this taxon; however, type material was not made available for study.

***Cephalotrichum lagerheimii*** Pat., Bull. Soc. Mycol. France. 9: 8. 1893.

*Notes:* The original description does not include any measurements to allow for accurate species recognition.

***Cephalotrichum longicollum*** Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 213. 2011.

*Notes:* The protologue of the species refers to a fungus closely resembling *C. purpureofuscum*, although with slightly shorter conidia (4.5–5.5 × 2.5–4 µm) and synnemata (340–750 µm tall) versus 5–8 × 3–4.5 µm and 800–1 600 µm tall, respectively, in *C. purpureofuscum*. The analysis of the ITS sequence of the ex-type strain of *C. longicollum* (FJ914672) showed 100 % of similarity with the reference strain of *C. purpureofuscum*. Type material was unavailable for study.

***Cephalotrichum lycopersici*** (Plowr.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Sporocybe lycopersici* Plowr., Fung. Dis. Tom 3: 4. 1881.

*Notes:* Description too vague for a correct identification.

***Cephalotrichum macrocephalum*** Corda, Icon. fung. (Prague) 1: 19. 1837.

*Synonym:* *Sporocybe macrocephala* (Corda) Sacc., Syll. Fung. 4: 605. 1886.

*Notes:* The original description and illustration show a fungus similar to *C. dendrocephalum*, with thick stipitate synnemata with spherical heads and flexuous and branched sterile hairs, but with distinct globose and dark conidia with verrucose walls. Although the holotype (PRM 155400b) is preserved in the National Museum of the Czech Republic in Prague, it was unavailable for examination. Since no ex-type culture was deposited nor any strain of the species exists in any public culture collection for further study, the taxonomy of this fungus remains unclear.

***Cephalotrichum macrosporum*** Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 214. 2011.

*Notes:* According to the protologue, this fungus closely resembles *C. purpureofuscum* morphologically, from which it differs by its somewhat larger conidia ( $5.5\text{--}12 \times 2.5\text{--}4.5 \mu\text{m}$ ) and smaller synnemata ( $200\text{--}600 \mu\text{m}$  long) versus  $5\text{--}8 \times 3\text{--}4.5 \mu\text{m}$  and  $800\text{--}1\ 600 \mu\text{m}$  long, respectively, in *C. purpureofuscum*. The analysis of an ITS sequence of the ex-type strain of *C. macrosporum* (FJ914675) showed 100 % similarity with the reference strain of *C. purpureofuscum*. Type material was not made available for study.

***Cephalotrichum maculare*** (Schwein.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Periconia macularis* Schwein., Trans. Amer. Philos. Soc. 4: 304. 1832.

*Synonym:* *Sporocybe macularis* (Schwein.) Sacc., Syn. Amer. bor. no. 3050.

*Notes:* Description too vague for a correct identification.

***Cephalotrichum minimum*** (Fr.) Sacc., Syll. Fung. 11: 612. 1895.

*Basionym:* *Actinocladium minimum* Fr., Syst. mycol. (Lundae) 3: 353. 1832.

*Notes:* Description too vague for a correct identification.

***Cephalotrichum monilioides*** (Alb. & Schwein.) Link, Sp. Pl. 6: 112. 1825.

*Basionym:* *Isaria monilioides* Alb. & Schwein., Consp. fung. (Leipzig): 362. 1805.

*Synonyms:* *Stysanus monilioides* (Alb. & Schwein.) Corda, Icon. fung. (Prague) 2: 17. 1838.

*Coremium monilioides* (Alb. & Schwein.) Pound & Clem., Minn. Bot. Stud. 1: 729. 1897.

*Notes:* The protologue lacks of microscopic details necessary for the identification of the fungus. However, the macroscopic

features in the description and illustrations (i.e. white to yellowish mycelium and white synnemata) seem to match with the current concept of the genus *Isaria* (de Hoog 1972, Hodge et al. 2005).

***Cephalotrichum oblongum*** J.J. Xu & T.Y. Zhang, Mycotaxon 117: 216. 2011.

*Notes:* The protologue describes a fungus morphologically similar to *C. purpureofuscum*, the most important difference being its narrower conidia ( $2\text{--}2.5 \mu\text{m}$  wide versus  $3\text{--}4.5 \mu\text{m}$  wide in *C. purpureofuscum*). An ITS sequence of the ex-type strain of *C. oblongum* available in GenBank (FJ914667) showed 100 % similarity with the reference strain of *C. purpureofuscum*. Type material was unavailable for study.

***Cephalotrichum ovoideum*** Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 217. 2011.

*Notes:* The protologue of *C. ovoideum* shows a fungus that morphologically matches *C. microsporum*. The most important distinctive morphological feature of *C. ovoideum* being the formation of synnemata with branched stipes. However, we observed branched stipes in several *Cephalotrichum* species, including *C. dendrocephalum*, *C. microsporum* and *C. nanum*, thus not a reliable feature for species delimitation. An ITS sequence of the ex-type strain of *C. ovoideum* (GenBank FJ914662) showed 99.5 % similarity with the ex-epitype of *C. microsporum* and 100 % similarity with the ex-type strains of *C. inflatum* and *C. robustum*. Type material was not made available for study.

***Cephalotrichum parasiticum*** (Peck) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Periconia parasitica* Peck, Annual Rep. New York St. Mus. Nat. Hist. 33: 28. 1883.

*Synonym:* *Sporocybe parasitica* (Peck) Sacc., Syll. Fung. 4: 605. 1886, non *Periconia parasitica* Tilak, Mycopathol. Mycol. Appl. 9: 195. 1958.

*Notes:* The description of this species is too vague for a correct identification.

***Cephalotrichum rhois*** (Berk. & M.A. Curtis) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym:* *Stilbum rhois* Berk. & M.A. Curtis [as '*rhoidis*'], in Berkeley, Grevillea 3: 64. 1874.

*Synonyms:* *Sporocybe rhois* (Berk. & M.A. Curtis) Sacc., Syll. Fung. 4: 605. 1886.

*Calicium rhois* (Berk. & M.A. Curtis) Farl., in Thaxter, Mycologia 14: 103. 1922.

*Notes:* This is the asexual morph of the well-known fungus *Amphiporthel/Cryptodiaportha aculeans* (Seifert 1985).

***Cephalotrichum rigescens*** Link, Mag. Ges. Naturf. Freunde Berlin 3: 20. 1809.

*Synonym:* *Sporocybe rigescens* (Link) Sacc., Syll. Fung. 4: 605. 1886.

*Notes:* The original description is too vague for a correct identification and probably refers to a myxomycete (Domsch et al. 2007). This settled the basis for the confusion regarding *Cephalotrichum* and *Doratomyces*, as being the first species

described in *Cephalotrichum*, *C. rigescens* was assumed to be the type of the genus. However, Hughes (1958) designated *C. stemonitis* as the lectotype of *Cephalotrichum*, which makes the application of the name very clear. According to Morton & Smith (1963), there is not type material available for this species.

***Cephalotrichum robiniae*** (Schwein.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym*: *Periconia robiniae* Schwein., Schriften Naturf. Ges. Leipzig. 1: 125. 1822.

*Synonym*: *Sporocybe robiniae* (Schwein.) Fr., Syst. mycol. (Lundae) 3: 342. 1832.

*Notes*: The original description of this species was very poor for a proper identification.

***Cephalotrichum robustum*** Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 218. 2011.

*Notes*: Based on the protologue, *C. robustum* closely resembles *C. microsporum*. However, *C. robustum* exhibits slightly larger conidia (5–7 × 3–5 µm versus 3.5–5 × 2.5–3 µm in *C. microsporum*). An ITS sequence of the ex-type strain of *C. robustum* (GenBank accession number FJ914674) shows 99.5 % similarity with the ex-epitype of *C. microsporum* and 100 % similarity with the ex-type strains of *C. inflatum* and *C. ovoideum*. Type material was not made available.

***Cephalotrichum septatum*** Demelius, Verh. zool.-bot. Ges. Wien 72: 102. 1923.

*Notes*: The original illustration shows a dematiaceous fungus with simple, septate conidiophores forming ramoconidia that resemble a species of *Cladosporium* rather than *Cephalotrichum*. No material was found in the type collection, general herbarium nor in the Petrak collection in W nor WU (pers. comm.).

***Cephalotrichum spirale*** H.M. Liu, H.Q. Pan & T.Y. Zhang, Mycotaxon 117: 220. 2011.

*Notes*: The protologue describes a fungus morphologically similar to *C. stemonitis*, *C. nanum* and *C. verrucisporum*, the four species with ovoid to ellipsoidal verrucose conidia with somewhat overlapping sizes. An ITS sequence of the ex-type culture of *C. spirale* (GenBank accession number FJ914705) shows 99.5 % of similarity with the ex-type strain of *C. verrucisporum*. Type material was not made available.

***Cephalotrichum terricola*** Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 221. 2011.

*Notes*: The protologue describes a fungus morphologically similar to *C. purpureofuscum*. The most important difference being is its smooth and slightly smaller conidia with rounded ends (4.5–7 × 2.5–3.5 µm versus 5–8 × 3–4.5 µm in *C. purpureofuscum*). An ITS sequence of the ex-type strain of *C. terricola* (GenBank accession number FJ914677) shows 100 % similarity with the reference strain of *C. purpureofuscum*. Type material was not made available for study.

***Cephalotrichum tessulatum*** (Sacc.) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym*: *Sporocybe tessulata* Sacc., Michelia 2: 299. 1881.

*Notes*: The original description of this species is very poor for a correct identification. However, it seems a quite unique synnematosus fungus forming cubical conidia with a tiny apiculate base. The holotype (on stems of *Dianthus armeria*) is available in PAD, and includes a hand draw that clearly depicts the mentioned conidial shape. Because living strains are not available for a molecular characterisation, the taxonomy of this fungus remains uncertain.

***Cephalotrichum truncatum*** (Cooke & Peck) Kuntze, Revis. gen. pl. (Leipzig) 3: 453. 1898.

*Basionym*: *Periconia truncata* Cooke & Peck, in Peck, Annual Rep. New York St. Mus. Nat. Hist. 29: 51. 1878.

*Synonym*: *Sporocybe truncata* (Cooke & Peck) Sacc., Syll. Fung. 4: 604. 1886.

*Notes*: Description too vague for a correct identification.

***Cephalotrichum verrucipes*** Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 223. 2011.

*Notes*: Original material of this fungus was unavailable for study. The protologue suggests a species of *Cephalotrichum*; however, it differs considerably from members of this genus by its verrucose conidiophores with a distinctive irregular ramification pattern.

***Doratomyces albus*** (Szilvinyi) Dominik, Ekol. Pol. 18: 595. 1970.

*Basionym*: *Scopulariopsis alba* Szilv., Zentralbl. Bakteriolog. Parasitenk., Abt. 2. 103: 172. 1941.

*Notes*: This species is unidentifiable according to Morton & Smith (1963), but listed as a synonym of *Doratomyces putredinus* by Abbott (2000). See additional notes under *Cephalotrichum album*. The original description matches with a *Cephalotrichum* species, the most distinctive features are the white to yellow-white colonies. However, further studies are necessary to clarify the taxonomy of these white cephalotrichum-like fungi.

***Doratomyces eichhorniae*** Conway & Kimbr. [as 'eichhornius'], Mycotaxon 2: 128. 1975.

*Notes*: This taxon was excluded from *Cephalotrichum* by Abbott (2000) after examination of the ex-type culture (ATCC 28418), based on its particular macroscopic features (i.e., brown colonies with white tufts and abundant dark brown diffusible pigment) and the absence of annellidic conidiogenous cells. In addition, the original description and illustration showed conidia truncate at both ends.

***Doratomyces phillipsii*** (Berk. & Leight.) F.J. Morton & G. Sm., Mycol. Pap. 86: 82. 1963.

*Basionym*: *Periconia phillipsii* Berk. & Leight., in Berkeley & Broome, Ann. Mag. Nat. Hist. 15: 33. 1875.

*Synonyms*: *Sporocybe phillipsii* (Berk. & Leight.) Sacc., Syll. Fung. 4: 609. 1886.

*Stysanus phillipsii* (Berk. & Leight.) E.W. Mason & M.B. Ellis, Mycol. Pap. 56: 40. 1953.

*Cephalotrichum phillipsii* (Berk. & Leight.) S. Hughes, *Canad. J. Bot.* 36: 744. 1958.

*Leightonimyces phillipsii* (Berk. & Leight.) D. Hawksw. & B. Sutton, *J. Linn. Soc., Bot.* 75: 204. 1977.

**Notes:** This taxon became the type species of the genus *Leightonimyces*, erected to accommodate algicolous/lichenicolous fungi morphologically distinct from *Cephalotrichum/Doratomyces*. It is recognised by the shape and scar of the conidia, which are produced solitary from annellidic conidiogenous cells and tend to become markedly verrucose at maturity (Hawksworth 1977).

*Doratomyces putredinis* (Corda) F.J. Morton & G. Sm., *Mycol. Pap.* 86: 83. 1963. (See notes in *Cephalotrichum album*).

*Doratomyces sambuci* P. Crouan & H. Crouan, *Florule Finistère* (Paris): 15. 1867.

**Notes:** Original description inadequate for species recognition (Morton & Smith 1963).

*Doratomyces tenuis* Corda, *Icon. fung.* (Prague) 1: 19. 1837.

**Notes:** The description of this species was incomplete for its recognition (Morton & Smith 1963).

*Doratomyces viridis* Corda, *Weitenweber's Beitr. Nat.* 1: tab. 5: 262B. 1837.

**Notes:** Morton & Smith (1963) examined the type specimen and concluded that it does not belong to *Cephalotrichum* (as *Doratomyces*). However, its identity was not determined.

*Wardomyces moseri* W. Gams, *Sydowia Beih.* 10: 67. 1995.

**Material examined:** Colombia, Department of Meta, from *Mauritia minor*, 1980, W. Gams (culture ex-isotype CBS 164.80).

**Notes:** Although this fungus forms sporodochium-like structures and its conidia are usually aggregated in slimy masses, it was originally included in *Wardomyces* (Gams 1995). Our analysis of the LSU and ITS sequences of the ex-type culture showed that this taxon does not belong to *Wardomyces*, clustering among the *Xylariales*, and related to members of the *Amphisphaeriaceae* and *Clypeosphaeriaceae* (data not shown).

*Wardomyces trachycarpicola* Joanne E. Taylor *et al.*, *Fungal Diversity Res. Ser.* 12: 370. 2003.

**Notes:** According to the original description this species seems to be morphologically close to *Wardomycesopsis*. However, while species of this genus produce catenate conidia on annellidic conidiogenous cells, *Ws. trachycarpicola* produces only solitary conidia. According to Silvera-Simón *et al.* (2008), this species is only known from the type specimen. Because living strains are not available for a molecular characterisation, the taxonomy of this fungus remains uncertain.

## ACKNOWLEDGEMENTS

The authors are very grateful to the members of the following institutions: Ann Bogaerts (BR), Anton Igersheim (W), Bryn Dentinger and Lee Davies (K),

Christine Bartram (CGE), Elana Benamy (PH), Jan Holec (PRM), Lisa A. Castlebury (BPI), Nicolien Sol (L), Robert Lücking (B), Rossella Marcucci (PAD) and Walter Till (WU). We also thank to Keith Seifert and an anonymous reviewer for their valuable comments and suggestions to improve the content of the manuscript. This study was supported by the Spanish Ministerio de Economía y Competitividad, grants CGL 2011-27185 and CGL2013-43789-P.

## REFERENCES

- Abbott SP (2000). *Holomorph studies of the Microascaceae*. Ph.D. dissertation. Department of Biological Sciences, University of Alberta, Canada.
- Abdel-Lateff A, Klemke C, König GM, *et al.* (2003). Two new xanthone derivatives from the algicolous marine fungus *Wardomyces anomalus*. *Journal of Natural Products* 66: 706–708.
- Arx JA von (1981). *The genera of fungi sporulating in pure culture*, 3rd edn. Verlag J. Cramer, Vaduz, Liechtenstein.
- Arx JA von, Figueras MJ, Guarro J (1988). Sordariaceae ascomycetes without ascospore ejaculation. *Beihefte zur Nova Hedwigia* 94: 1–104.
- Bainier G (1907). Mycothèque de l'École de Pharmacie, XXI–XXIII. *Bulletin de la Société Mycologique de France* 23: 218–241.
- Barron GL (1966). A new species of *Scopulariopsis* from soil. *Antonie van Leeuwenhoek* 32: 293–298.
- Barron GL, Cain RF, Gilman JC (1961). The genus *Microascus*. *Canadian Journal of Botany* 39: 1609–1631.
- Beer ZW de, Seifert KA, Wingfield MJ (2013). The ophiostomatoid fungi: their dual position in the *Sordariomycetes*. In: *The ophiostomatoid fungi: expanding frontiers* (Seifert KA, de Beer ZW, Wingfield MJ, eds), *CBS biodiversity series* 12. CBS-KNAW Fungal Biodiversity Centre, The Netherlands: 1–19.
- Brooks FT, Hansford CG (1923). Mould growths upon cold-store meat. *Transactions of the British Mycological Society* 8: 113–142.
- Carmarán CC, Novas MV (2003). A review of Spegazzini taxa of *Periconia* and *Sporocybe* after over 115 years. *Fungal Diversity* 14: 67–76.
- Carmichael JW, Kendrick W, Connors IL, *et al.* (1980). *Genera of Hyphomycetes*. The University of Alberta Press, Canada.
- Clements FE (1896). Report on collections made in 1894–95. *Botanical Survey of Nebraska* 4: 1–48.
- Crous PW, Gams W, Stalpers JA, *et al.* (2004). MycoBank: an online initiative to launch mycology into the 21st century. *Studies in Mycology* 50: 19–22.
- Curzi M (1931). Rapporti fra i generi *Microascus* Zukal e *Scopulariopsis* Bainier. *Bollettino della Stazione di Patologia Vegetale di Roma* 11: 55–60.
- Delacroix EG (1897). Quelques espèces nouvelles. *Bulletin de la Société Mycologique de France* 13: 114–127.
- Dickinson CH (1964). The genus *Wardomyces*. *Transactions of the British Mycological Society* 47: 321–325.
- Dickinson CH (1966). *Wardomyces pulvinata* comb. nov. *Transactions of the British Mycological Society* 49: 521–522.
- Domsch KH, Gams W, Anderson TH (2007). *Compendium of soil fungi*, 2nd edn. IHW Verlag, Eching, Germany.
- Edgar RC (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.
- Ellis MB (1971). *Dematiaceous Hyphomycetes*. Commonwealth Mycological Institute, Kew, England.
- Ellis MB (1976). *More Dematiaceous Hyphomycetes*. Commonwealth Mycological Institute, Kew, England.
- Felsenstein J (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
- Fries EM (1832). *Systema mycologicum: sistens fungorum ordines, genera et species, huc usque cognitae, quas ad normam methodi naturalis determinavit*. Lundae.
- Gams W (1968). Two new species of *Wardomyces*. *Transactions of the British Mycological Society* 51: 798–802.
- Gams W (1995). An unusual species of *Wardomyces* (Hyphomycetes). *Beihefte zur Sydowia* 10: 67–72.
- Glass NL, Donaldson GC (1995). Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous ascomycetes. *Applied and Environmental Microbiology* 61: 1323–1330.
- Gradisar H, Kern S, Friedrich J (2000). Keratinase of *Doratomyces microsporus*. *Applied Microbiology and Biotechnology* 53: 196–200.
- Guarro J, Gené J, Stchigel AM, *et al.* (2012). *Atlas of soil ascomycetes*. In: *CBS biodiversity series* 10. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands.



- Hammill TM (1977). Transmission electron microscopy of annellides and conidiogenesis in the synnematal hyphomycete *Trichurus spiralis*. *Canadian Journal of Botany* **55**: 233–244.
- Hasselbring H (1896). Comparative study of the development of *Trichurus spiralis* and *Stysanus stemonitis*. *Botanical Gazette Crawfordville* **29**: 312–322.
- Hawksworth DL (1977). Three new genera of lichenicolous fungi. *Botanical Journal of the Linnean Society* **75**: 195–209.
- Hennebert GL (1962). *Wardomyces* and *Asteromyces*. *Canadian Journal of Botany* **40**: 1203–1216.
- Hennebert GL (1968). *Echinobotryum*, *Wardomyces* and *Mammaria*. *Transactions of the British Mycological Society* **51**: 749–762.
- Hodge KT, Gams W, Samson RA, et al. (2005). Lectotypification and status of *Isaria* Pers.: Fr. *Taxon* **54**: 5–9.
- Hoog GS de (1972). The genera *Beauveria*, *Isaria*, *Tritirachium* and *Acrodontium* gen. nov. *Studies in Mycology* **1**: 1–41.
- Hoog GS de, Guarro J, Gené J, Figueras MJ (2011). *Atlas of clinical fungi*. CD-ROM version 3.1. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands.
- Hublin A, Gradisar H, Friedrich J, et al. (2002). Stability and stabilisation of *Doratomyces microsporus* keratinase. *Biocatalysis and Biotransformation* **20**: 329–336.
- Huelsenbeck JP, Ronquist F (2001). MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.
- Hughes SJ (1958). Revisiones hyphomycetum aliquot cum appendice de nominibus rejiciendis. *Canadian Journal of Botany* **36**: 727–836.
- Issakainen J, Jalava J, Hyvönen J, et al. (2003). Relationships of *Scopulariopsis* based on LSU rDNA sequences. *Medical Mycology* **41**: 31–42.
- Jagielski T, Sandoval-Denis M, Yu J, et al. (2016). Molecular taxonomy of scopulariopsis-like fungi with description of new clinical and environmental species. *Fungal Biology* **120**: 586–602.
- Jiang YL, Xu JJ, Wu YM, et al. (2011). Studies on *Cephalotrichum* from soils in China — twelve new species and two new combinations. *Mycotaxon* **117**: 207–225.
- Jiang YL, Zhang TY (2008). Two new species of *Doratomyces* from soil. *Mycotaxon* **104**: 131–134.
- Kirk PM, Stalpers JA, Braun U (2013). A without-prejudice list of generic names of fungi for protection under the International Code of Nomenclature for algae, fungi, and plants. *IMA Fungus* **4**: 381–443.
- Kornerup A, Wanscher JH (1978). *Methuen handbook of colour*, 3rd edn. Methuen, London, England.
- Lackner M, Hoog GS de (2011). *Parascedosporium* and its relatives: phylogeny and ecological trends. *IMA Fungus* **21**: 39–48.
- Lackner M, Hoog GS de, Yang L, et al. (2014). Proposed nomenclature for *Pseudallescheria*, *Scedosporium* and related genera. *Fungal Diversity* **67**: 1–10.
- Link HF (1809). Observations in ordines plantarum naturales. *Dissertatio I. Magazin der Gesellschaft Naturforschender Freunde Berlin* **3**: 3–42.
- Lumley TC, Abbott SP, Currah RS (2000). Microscopic ascomycetes isolated from rotting wood in the boreal forest. *Mycotaxon* **74**: 395–414.
- Malloch D (1970a). New concepts in the *Microascaceae* illustrated by two new species. *Mycologia* **62**: 727–740.
- Malloch D (1970b). *Wardomyces aggregatus* sp. nov. and its possible relationship to *Gymnodochium fimicolum*. *Canadian Journal of Botany* **48**: 883–885.
- Malloch D, Cain RF (1971). The genus *Kernia*. *Canadian Journal of Botany* **49**: 855–867.
- Malloch D, Hubart JM (1987). An undescribed species of *Microascus* from the Cave of Ramioul. *Canadian Journal of Botany* **65**: 2384–2388.
- Mason EW, Ellis MB (1953). British species of *Periconia*. *Mycological Papers* **56**: 1–127.
- Mason-Gamer R, Kellogg E (1996). Testing for phylogenetic conflict among molecular data sets in the tribe *Triticeae* (*Gramineae*). *Systematic Biology* **45**: 524–545.
- McNeill J, Barrie FF, Buck WR, et al. (eds) (2012). *International Code of Nomenclature for algae, fungi and plants (Melbourne Code)*. A.R.G. Ganter Verlag KG [Regnum Vegetabile no. 154].
- Morelet M (1969). Micromycètes du var et d'ailleurs (2me Note). *Annales de la Société des Sciences Naturelles et d'Archéologie de Toulon et du Var* **21**: 104–106.
- Morton FJ, Smith G (1963). The genera *Scopulariopsis* Bainier, *Microascus* Zukal, and *Doratomyces* Corda. *Mycological Papers* **86**: 1–96.
- Nylander JA (2004). *MrModeltest v2. Program distributed by the author*. Evolutionary Biology Centre, Uppsala University, Sweden.
- Posada D, Buckley TR (2004). Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology* **53**: 793–808.
- Rehner SA, Buckley E (2005). A *Beauveria* phylogeny inferred from nuclear ITS and EF1- $\alpha$  sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* **97**: 84–98.
- Sandoval-Denis M, Gené J, Sutton DA, et al. (2016). Redefining *Microascus*, *Scopulariopsis* and allied genera. *Persoonia* **36**: 1–36.
- Sandoval-Denis M, Sutton DA, Fothergill AW, et al. (2013). *Scopulariopsis*, a poorly known opportunistic fungus: spectrum of species in clinical samples and *in vitro* responses to antifungal drugs. *Journal of Clinical Microbiology* **51**: 3937–3943.
- Seifert KA (1985). A monograph of *Stilbella* and some allied *Hyphomycetes*. *Studies in Mycology* **27**: 1–235.
- Seifert KA, Morgan-Jones GA, Gams W, Kendrick WB (2011). *The genera of Hyphomycetes*. In: *CBS biodiversity series 9*. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands.
- Seifert KA, Samson RA (1985). The genus *Coremium* and the synnemalous *Penicillia*. In: *Advances in Penicillium and Aspergillus systematics* (Samson RA, Pitt JI, eds). Plenum Press, New York: 143–154.
- Silvera-Simón C, Gené J, Cano J, et al. (2008). *Wardomycopsis litoralis*, a new soil-borne hyphomycete from Spain. *Mycotaxon* **105**: 195–202.
- Sopp OJ (1912). Monographie der Pilzgruppe *Penicillium* mit besonderer Berücksichtigung der in Norwegen gefundenen Arten. *Skrifter udgivne af Videnskabs-Selskabet i Christiania. Mathematisk-Naturvidenskabelig Klasse* **11**: 1–208.
- Sturm J (1829). Deutschlands Flora, Abt. III. *Die Pilze Deutschlands* **2**: 1–136.
- Sugiyama J, Kawasaki Y, Kurata H (1968). *Wardomyces simplex*, a new hyphomycete from milled rice. *The Botanical Magazine, Tokyo* **81**: 243–250.
- Sugiyama J, Kawasaki Y, Kurata H (1969). *Wardomyces simplex* (Hyphomycetes) and its annellospores. *The Botanical Magazine, Tokyo* **82**: 353–358.
- Swart HJ (1964). A study of the production of coremia in three species of the genus *Trichurus*. *Antonie van Leeuwenhoek* **30**: 257–260.
- Swart HJ (1967). *Doratomyces columnaris* sp. nov. *Acta Botanica Neerlandica* **15**: 521–523.
- Swift ME (1929). Contributions to a mycological flora of local soils. *Mycologia* **21**: 204–221.
- Tamura K, Stecher G, Peterson D, et al. (2013). MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* **30**: 2725–2729.
- Udagawa S (1963). *Microascaceae* in Japan. *The Journal of General and Applied Microbiology* **9**: 137–148.
- Udagawa S, Awa T (1969). Notes on some Japanese Ascomycetes. VIII. *Transactions of the Mycological Society of Japan* **10**: 1–8.
- Udagawa S, Furuya K (1978). A new species of *Microascus* and its peculiar conidial state. *Mycotaxon* **7**: 91–96.
- Udagawa S, Horie Y, Abdullah S (1985). *Trichurus dendrocephalus* sp. nov., from Iraqi soil. *Mycotaxon* **23**: 253–259.
- Vilgalys R, Hester M (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**: 4238–4246.
- Vilgalys R, Sun BL (1994). Ancient and recent patterns of geographic speciation in the oyster mushroom *Pleurotus* revealed by phylogenetic analysis of ribosomal DNA sequences. *Proceedings of the National Academy of Sciences of the United States of America* **91**: 4599–4603.
- White TJ, Bruns T, Lee S, et al. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: a guide to methods and applications* (Innis MA, Gelfand DH, Sninsky JJ, et al., eds). Academic Press, New York, USA: 315–322.
- Whitton SR, McKenzie EHC, Hyde KD (2012). *Fungi associated with Pandanaceae*. In: *Fungal diversity research series*. Springer Science & Business Media, The Netherlands.
- Wiens JJ (1998). Testing phylogenetic methods with tree congruence: phylogenetic analysis of polymorphic morphological characters in phrynosomatid lizards. *Systematic Biology* **47**: 427–444.
- Wright JE, Marchand S (1972). Micoflora del suelo de la Argentina. III. Dos interesantes géneros sinemáticos: *Trichurus* y *Doratomyces*. *Boletín de la Sociedad Argentina de Botánica* **14**: 305–310.
- Zhang YL, Wu YM, Zhang TY (2014). Notes on soil dematiaceous hyphomycetes from Hainan Province China I. *Mycosystema* **33**: 945–953.