Take-all or nothing

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Abstract: Take-all disease of *Poaceae* is caused by *Gaeumannomyces graminis* (*Magnaporthaceae*). Four varieties are recognised in *G. graminis* based on ascospore size, hyphopodial morphology and host preference. The aim of the present study was to clarify boundaries among species and varieties in *Gaeumannomyces* by combining morphology and multi-locus phylogenetic analyses based on partial gene sequences of ITS, LSU, *tef1* and *rpb1*. Two new genera, *Falciphoriella* and *Gaeumannomycella* were subsequently introduced in *Magnaporthaceae*. The resulting phylogeny revealed several cryptic species previously overlooked within *Gaeumannomyces*. Isolates of *Gaeumannomyces* were distributed in four main clades, from which 19 species could be delimited, 12 of which were new to science. Our results show that the former varieties *Gaeumannomyces graminis* var. *avenae* and *Gaeumannomyces graminis* var. *tritici* represent species phylogenetically distinct from *G. graminis*, for which the new combinations *G. avenae* and *G. tritici* are introduced. Based on molecular data, morphology and host preferences, *Gaeumannomyces graminis* var. *maydis* is proposed as a synonym of *G. radicicola*. Furthermore, an epitype for *Gaeumannomyces graminis* var. *avenae* was designated to help stabilise the application of that name.

Key words: Cryptic species, *Gaeumannomyces graminis*, *Magnaporthaceae*, Phylogeny, *Triticum*.
Taxonomic novelties: New genera: *Falciphoriella* M. Hern.-Restr. & Crous, *Gaeumannomycella* M. Hern.-Restr. & Crous; **New species:** ***Falciphoriella*** *solaniterrestris* M. Hern.-Restr. & Crous, ***Gaeumannomycella*** *caricis* M. Hern.-Restr. & Crous, ***Gaeumannomyces*** *arxii* M. Hern.-Restr. & Crous, *G. australiensis* M. Hern.-Restr. & Crous, *G. californicus* M. Hern.-Restr. & Crous, *G. ellisiorum* M. Hern.-Restr. & Crous, *G. floridanus* M. Hern.-Restr. & Crous, *G. fusiformis* M. Hern.-Restr. & Crous, *G. glycinicola* M. Hern.-Restr., G. Canning & Crous, *G. graminicola* M. Hern.-Restr. & Crous, *G. hyphopodioides* M. Hern.-Restr. & Crous, *G. oryzicola* M. Hern.-Restr. & Crous, *G. setariicola* M. Hern.-Restr. & Crous, *G. walkeri* M. Hern.-Restr. & Crous; **New combinations:** ***Gaeumannomyces tritici*** (J. Walker) M. Hern.-Restr. & Crous, ***Gaeumannomyces avenae*** (E. M. Turner) M. Hern.-Restr. & Crous; **Typification: Epitypification:** ***Gaeumannomyces graminis* var. *avenae*** (E. M. Turner) Dennis.

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INTRODUCTION

Take-all is one of the most important root diseases in cereal crops and grasses, caused by *Gaeumannomyces graminis*. Taxonomic placement of *Gaeumannomyces graminis* at the variety level has been a research topic for many decades. Based on morphology, pathogenicity and host preference, four varieties of this species can be recognised (Turner 1940, Walker 1972, Yao *et al.* 1992). The type variety *Gaeumannomyces graminis* var. *graminis* (*Ggg*) causes crown (black) sheath rot of rice, dieback in Bermuda grass, take-all root rot of St. Augustine grass or root decline of other warm-season turf grasses (Walker 1972, 1981, Elliott 1991, Ward & Bateman 1999). It is the least aggressive and is also often found as a weak pathogen or saprobe on cereals, grasses and soybeans (Walker 1980, Roy *et al.* 1982, Ward & Bateman 1999). *Gaeumannomyces graminis* var. *avenae* (Turner 1940, Dennis 1960) (*Gga*) causes take-all of oats and take-all patch of turfgrasses, although it can also infect wheat, rye and barley. *Gaeumannomyces graminis* var. *tritici* (Walker 1972) (*Ggt*) is the most aggressive variety and is known as the wheat take-all fungus. It infects mainly wheat but can also infect triticale, barley and rye as well as other cereals and grasses (Walker 1980, Ward & Bateman 1999, Freeman & Ward 2004). Take-all of wheat is the most important root disease of wheat worldwide. *Gaeumannomyces graminis* var. *maydis* (Yao *et al.* 1992) (*Ggm*) is the most recently described variety and causes take-all of maize but also can slightly infect *Sorghum* and other cereals.

The sexual morph in *Gaeumannomyces* is characterised by the production of globose or pyriform, immersed ascomata with a conical to cylindrical neck, and fusiform, multiseptate and hyaline ascospores. Asexual morphs are characterised by phialidic conidiogenous cells with refractive collarettes and lunate or phialophora-like conidia. For a long time the asexual morphs in *Gaeumannomyces* were referred to *Phialophora*, but based on morphology, Gams (2000) proposed the genus *Harpophora* to accommodate the phialidic asexual morphs in *Magnaporthaceae*. However, *Harpophora* became the later synonym of *Gaeumannomyces*, following the Melbourne code (Luo *et al.* 2015c).

Hyphopodia are commonly found in this genus and in other members of *Magnaporthaceae*. This feature has been used as a taxonomic character to differentiate some of the varieties in *G. graminis*. The asexual morph of *Ggg* has been reported to have lobed hyphopodia (Walker 1980, Ward & Bateman 1999, Freeman & Ward 2004). On the other hand *Ggt*, *Gga* and *Ggm* are characterised by the production of simple hyphopodia in the substrate (Walker 1972, Yao *et al.* 1992).

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However, differentiation among isolates of *Gaeumannomyces* based on disease symptoms, host range, cultural and/or morphological characteristics is difficult, time consuming and is in many cases inconclusive (Ulrich *et al.* 2000, Freeman & Ward 2004). Different molecular techniques have been used to identify species and varieties in *Gaeumannomyces*, for example RAPD (Wetzel *et al.* 1996, Augustin *et al.* 1999, Ulrich *et al.* 2000), RFLP (Bateman *et al.* 1992, Tan *et al.* 1994, Ward & Akrofi 1994), amplification of specific gene sequences within the ITS nrDNA (Bryan *et al.* 1995, Ward & Bateman 1999, Ulrich *et al.* 2000), or avenacinase-like genes (Rachdawong *et al.* 2002). Those studies revealed that *Ggt* and *Gga* form a monophyletic clade, whereas *Ggg* appears to be polyphyletic, with high variability among isolates (Elliott *et al.* 1993, Ward & Akrofi 1994, Fouly *et al.* 1996, Tan 1997, Ward & Bateman 1999, Fouly & Wilkinson 2000, Saleh & Leslie 2004, Sadeghi *et al.* 2012). In addition, *Ggm* is related to another maize root pathogen named *G. radicicola* (Luo *et al.* 2015c), formerly recognised as *Harpophora radicicola* and *H. zeicola* (Ward & Bateman 1999, Gams 2000). Phylogenetic studies also revealed new lineages in *Gaeumannomyces* referred to as "*Phialophora* sp. GP57" (Ward & Bateman 1999) and "group E" (Ulrich *et al.* 2000). Nevertheless, no formal names or combinations have been proposed.

The genus *Gaeumannomyces* (*Magnaporthaceae*, *Magnaporthales*), was established by von Arx & Olivier (1952) to accommodate *Ophiobolus graminis*, formerly described as *Rhaphidophora graminis*. Besides *G. graminis* and *G. radicicola*, this genus includes other root-infecting pathogens such as *G. wongoonoo*; the cause of a patch disease of *Stenotaphrum secundatum* (buffalo grass) (Wong 2002) and *G. caricis* occurring on *Carex* spp. (*Cyperaceae*) (Walker 1980). Endophytic and saprobic fungi have been found in this genus as well, for example *G. amomi*, described as endophytic in *Amomum* and *Alpinia* (*Zingiberaceae*) (Bussaban *et al.* 2001), and the saprobic *G. licualae*, an unusual *Gaeumannomyces* species collected from palm (*Licuala* sp.), known only from the type locality; Brunei Darussalam (Fröhlich & Hyde 2000).

The number of taxa in *Magnaporthaceae* with phialophora-, and harpophora-like asexual morphs has been increasing in the past 20 years, together with the introduction of new genera, e.g. *Falciphora* (Yuan *et al.* 2010, Luo *et al.* 2015c), *Magnaporthiopsis* (Luo & Zhang 2013), and *Pseudophialophora* (Luo *et al.* 2014, 2015b), with a high number of cryptic species among those genera.

Other studies relocated some species previously accommodated in *Gaeumannomyces* for example; *G. incrustans* was transferred to *Magnaporthiopsis* (Luo & Zhang 2013). *Slopeiomyces* and *Kohlmeyeriopsis* were proposed as new genera to accommodate *G. cylindrosporus* and *G. medullaris* respectively (Klaubauf *et al.* 2014).

The aims of the present study were: (1) to explore the diversity of *Gaeumannomyces* isolates, collected from diverse geographic origins and from different hosts; (2) to determine the phylogenetic relationships of the isolates using a multi-locus sequence alignment consisting of partial gene sequences of LSU (28S nrDNA), ITS (internal transcribed spacers and intervening 5.8S nrRNA gene), *tef1* (translation elongation factor 1-alpha) and *rpb1* (RNA polymerase II large subunit); (3) to resolve the taxonomy of *Gaeumannomyces* by adopting a polyphasic approach; and (4) to designate epitypes and reference sequences for species of *Gaeumannomyces*.

MATERIALS AND METHODS

Isolates and morphological analysis

A total of 83 strains identified as *Gaeumannomyces* or *Harpophora* (*Phialophora*) from different localities and hosts were examined (Table 1). Specimens were obtained from the culture collection of the CBS-KNAW Fungal Biodiversity Centre (CBS), Utrecht, The Netherlands, the Monica Elliott personal collection, University of Florida, USA, the working collection of P.W. Crous (CPC) housed at CBS, and the Rothamsted plant pathology culture collection, Department of Plant Biology and Crop Science, Rothamsted Research, Harpenden, Herts, UK.

Isolates were cultured on 2 % potato dextrose agar (PDA), 2 % malt extract agar (MEA; Oxoid) and oatmeal agar (OA; Crous *et al.* 2009), and incubated at 25 °C under daylight conditions for 1–3 wk; UV light conditions were used for some isolates to induce sporulation. After 7 d of incubation the colony diameters were measured and the colony morphologies described. Colony colours on the surface and reverse of inoculated media were assessed according to the colour charts of Rayner (1970). Micromorphological descriptions and 30 measurements of relevant features were carried out from mature cultures mounted in clear lactic acid. For ascomata, measurements were taken from 5 to 10 structures depending on availability. Observations and photomicrographs were made with a Nikon SMZ1500 stereo-microscope, and with a Nikon Eclipse N*i* microscope, using a DS-Ri2 digital camera (Nikon, Tokyo, Japan) and NIS-Elements imaging software v. 4.20. Reference strains were deposited in the CBS culture collection. Taxonomic information and nomenclature for new species were deposited in MycoBank (www.MycoBank.org; Crous *et al.* 2004).

DNA isolation, amplification and sequences alignment

Genomic DNA was extracted from fungal colonies growing on MEA using the Wizard® Genomic DNA purification kit (Promega, Madison, USA), according to the manufacturer's protocols. Procedures for amplifying and sequencing the internal transcribed spacer nrDNA including the intervening 5.8S nrDNA (ITS) and partial large subunit nrDNA (28S nrDNA; LSU), were performed as described in Hernández-Restrepo *et al.* (2016). Part of the largest subunit of the RNA polymerase II gene (*rpb1*) was amplified and sequenced as described in Klaubauf *et al.* (2014). Translation elongation factor 1-α gene (*tef1*), corresponding to the section 983–1567 bp, was amplified and sequenced as described in Rehner & Buckley (2005). Sequences were edited and consensus sequences constructed using SeqMan Pro (DNASTAR, Madison, WI, USA) and deposited in GenBank (Table 1).

To further study the phylogenetic relationships, additional homologous sequences of members of *Magnaporthales* were retrieved from GenBank and combined with those generated during the present study (Table 1). Sequence alignments were performed with MAFFT v. 7 (Katoh & Standley 2013) using the defaults settings and adjusted by hand in MEGA v. 6.06 (Tamura *et al.* 2013).

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Table 1. Isolates used in this study and their GenBank accession numbers. Newly generated sequences are indicated in **bold**.

Species	Old name/Received as	Strain number[1]	Status[2]	Country	Host, substrate	GenBank accession numbers[3]			
						LSU	ITS	RPB1	TEF1
Buergenerula spartinae	*Buergenerula spartinae*	ATCC 22848		USA	*Spartina alterniflora*, leaves	DQ341492	JX134666	JX134720	–
Bussabanomyces longisporus	*Bussabanomyces longisporus*	CBS 125232	T	Thailand	*Amomum siamense*, leaves	KM484951	KM484832	KM485046	–
Falciphora oryzae	*Harpophora oryzae*	CBS 125863, R5-6-1	T	China	*Oryza sativa*, root, endophytic	KJ026705	EU636699	KJ026706	JN857963
Falciphoriella solaniterrestris	*Gaeumannomyces* sp.	CBS 117.83	T	Netherlands	Soil in potato field	KM484959	KM484842	KM485058	–
Gaeumannomycella caricis	*Gaeumannomyces* sp.	CBS 388.81	T	UK	*Carex rostrata*	KM484960	KM484843	**KX306674**	–
	Gaeumannomyces graminis var. *graminis*	CPC 26262, CBS 141374		UK	*Carex rostrata*	**KX306548**	**KX306478**	**KX306671**	**KX306675**
Gaeumannomyces amomi	*Gaeumannomyces amomi*	CBS 109354, CMUZE0002, BCC 4066		Thailand	*Amomun* sp., endophytic in leaves	DQ341493	AY265318	–	**KX306679**
G. arxii	*Gaeumannomyces graminis* var. *graminis*	CBS 902.73, DAR 17502		Australia	*Stenotaphrum secundatum* (buffalo grass)	KM484953	KM484836	KM485052	**KX306680**
	Gaeumannomyces graminis var. *graminis*	CBS 903.73, DAR 23471	T	Australia	*Pennisetum clandestinum*, (kikuyu grass), stolon	KM484854	KM484837	KM485053	**KX306681**
	Gaeumannomyces graminis var. *avenae*	CPC 26054, CBS 141375		USA	*Stenotaphrum secundatum*	**KX306549**	**KX306479**	**KX306618**	**KX306682**
G. australiensis	*Gaeumannomyces graminis* var. *graminis*	CPC 26058, DAR 32100, CBS 141387	T	Australia	*Triticum aestivum*	**KX306550**	**KX306480**	**KX306619**	**KX306683**
G. avenae	*Gaeumannomyces graminis* var. *avenae*	CBS 187.65		Netherlands	*Avena sativa*, root	JX134680	JX134668	JX134722	JX134694
	Gaeumannomyces graminis var. *avenae*	CBS 870.73, DAR 20999		Australia	*Avena sativa*	DQ341495	KM484833	KM485048	**KX306684**
	Gaeumannomyces graminis var. *avenae*	CPC 26253		Australia	*Agrostis* (bent grass)	**KX306551**	**KX306481**	–	**KX306685**
	Gaeumannomyces graminis var. *avenae*	CPC 26254		Australia	*Agrostis* (bent grass)	**KX306552**	**KX306482**	–	–
	Gaeumannomyces graminis var. *avenae*	CPC 26255		Australia	*Agrostis* (bent grass)	**KX306553**	**KX306483**	**KX306620**	**KX306686**
	Gaeumannomyces graminis var. *avenae*	CPC 26256		UK	*Avena sativa*	**KX306554**	**KX306484**	–	–
	Gaeumannomyces graminis var. *avenae*	CPC 26257, CBS 141376		Ireland	*Avena sativa* (winter Oats)	**KX306555**	**KX306485**	**KX306621**	**KX306687**
	Gaeumannomyces graminis var. *avenae*	CPC 26258	ET	Ireland	*Avena sativa* (winter Oats)	**KX306556**	**KX306486**	**KX306622**	**KX306688**
	Gaeumannomyces graminis var. *avenae*	CPC 26259		Ireland	*Triticum aestivum* (winter wheat)	**KX306557**	**KX306487**	–	–
	Gaeumannomyces graminis var. *avenae*	CPC 26260		Ireland	Turf	**KX306558**	**KX306488**	**KX306623**	**KX306689**
	Gaeumannomyces graminis var. *avenae*	CPC 26261		UK	Turf	**KX306559**	**KX306489**	**KX306624**	**KX306690**
G. californicus	*Gaeumannomyces graminis* var. *graminis*	CPC 26044, CBS 141377	T	USA	*Stenotaphrum secundatum*	**KX306560**	**KX306490**	**KX306625**	**KX306691**
G. ellisiorum	*Gaeumannomyces graminis* var. *graminis*	CBS 387.81	T	UK	*Deschampsia caespitosa*, dead culm and sheath	KM484952	KM484835	KM485051	**KX306692**
G. floridanus	*Gaeumannomyces graminis* var. *graminis*	CPC 26037, CBS 141378	T	USA	*Stenotaphrum secundatum*	**KX306561**	**KX306491**	**KX306626**	**KX306693**
G. fusiformis	*Gaeumannomyces graminis* var. *graminis*	CPC 26068, CBS 141379	T	USA	*Oryza sativa*	**KX306562**	**KX306492**	**KX306627**	**KX306694**

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Table 1. (Continued).

Species	Old name/Received as	Strain number[1]	Status[2]	Country	Host, substrate	GenBank accession numbers[3]			
						LSU	ITS	RPB1	TEF1
Gaeumannomyces glycinicola	*Gaeumannomyces graminis* var. *graminis*	CPC 26057, DAR 28746	T	USA	*Glycine max*	**KX306563**	**KX306493**	**KX306628**	**KX306695**
	Gaeumannomyces graminis var. *graminis*	CPC 26266, CBS 141380		USA	*Glycine max*	**KX306564**	**KX306494**	**KX306629**	**KX306696**
G. graminicola	*Gaeumannomyces graminis* var. *graminis*	CBS 352.93	T	Netherlands	*Ctenanthe* sp., stem base	DQ341496	KM484834	KM485050	**KX306697**
	Gaeumannomyces graminis var. *graminis*	CPC 26025, CBS 141381		USA	*Stenotaphrum secundatum*	**KX306565**	**KX306495**	**KX306630**	**KX306698**
	Gaeumannomyces graminis var. *graminis*	CPC 26036, CBS 141382		USA	*Stenotaphrum secundatum*	**KX306566**	**KX306496**	**KX306631**	**KX306699**
	Gaeumannomyces graminis var. *graminis*	CPC 26056, CBS 141383		USA	*Eremochloa ophiuroides*	**KX306567**	**KX306497**	**KX306632**	**KX306700**
G. graminis	*Gaeumannomyces graminis* var. *graminis*	CPC 26020, CBS 141384		USA	*Cynodon dactylon* × *C. transvaalensis*	**KX306568**	**KX306498**	**KX306633**	**KX306701**
	Gaeumannomyces graminis var. *graminis*	CPC 26027		USA	*Cynodon dactylon* × *C. transvaalensis*	**KX306569**	**KX306499**	**KX306634**	**KX306702**
	Gaeumannomyces graminis var. *graminis*	CPC 26029		USA	*Cynodon dactylon* × *C. transvaalensis*	**KX306570**	**KX306500**	**KX306635**	**KX306703**
	Gaeumannomyces graminis var. *graminis*	CPC 26033, CBS 141385		USA	*Cynodon dactylon* × *C. transvaalensis*	**KX306571**	**KX306501**	**KX306636**	**KX306704**
	Gaeumannomyces graminis var. *graminis*	CPC 26035, CBS 141386		USA	*Cynodon dactylon* × *C. transvaalensis*	**KX306572**	**KX306502**	**KX306637**	**KX306705**
	Gaeumannomyces graminis var. *graminis*	CPC 26039		USA	*Cynodon dactylon* × *C. transvaalensis*	**KX306573**	**KX306503**	**KX306638**	**KX306706**
	Gaeumannomyces graminis var. *graminis*	CPC 26042		USA	*Cynodon dactylon* × *C. transvaalensis*	**KX306574**	**KX306504**	**KX306639**	**KX306707**
	Gaeumannomyces graminis var. *graminis*	CPC 26045		USA	*Cynodon dactylon* × *C. transvaalensis*	**KX306575**	**KX306505**	**KX306640**	**KX306708**
G. hyphopodioides	*Phialophora radicicola*	CBS 350.77, G6, ATCC 28234, IMI 187786	T	UK	*Zea mays*, root	**KX306576**	**KX306506**	KM009192	KM009204
	Gaeumannomyces graminis var. *tritici*	CBS 541.86		Germany	*Triticum aestivum*, seedling	**KX306577**	**KX306507**	**KX306641**	**KX306709**
	"*Phialophora* sp. lobed hyphopodia"	CPC 26247, CBS 141388		UK	*Triticum aestivum*	**KX306578**	**KX306508**	**KX306642**	**KX306710**
	"*Phialophora* sp. lobed hyphopodia"	CPC 26248		UK	*Triticum aestivum*	**KX306579**	**KX306509**	–	–
	"*Phialophora* sp. lobed hyphopodia"	CPC 26249		UK	*Triticum aestivum*	**KX306580**	**KX306510**	–	**KX306711**
	"*Phialophora* sp. lobed hyphopodia"	CPC 26250		UK	*Avena sativa*	**KX306581**	**KX306511**	–	**KX306712**
	"*Phialophora* sp. lobed hyphopodia"	CPC 26252		Poland	*Triticum aestivum*	**KX306582**	**KX306512**	**KX306643**	**KX306713**
	Gaeumannomyces graminis var. *graminis*	CPC 26264, CBS 141389		UK	*Triticum aestivum* (winter wheat)	**KX306583**	**KX306513**	**KX306644**	**KX306714**
	Gaeumannomyces graminis var. *graminis*	CPC 26265		UK	*Triticum aestivum*	**KX306584**	**KX306514**	–	**KX306715**
	Gaeumannomyces graminis var. *graminis*	CPC 26267		Australia	*Pennisetum clandestinum*	**KX306585**	**KX306515**	**KX306645**	**KX306716**
G. oryzicola	*Gaeumannomyces graminis* var. *graminis*	CPC 26063, CBS 141390	T	USA	*Oryza sativa*	**KX306586**	**KX306516**	**KX306646**	**KX306717**

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Table 1. (Continued).

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						LSU	ITS	RPB1	TEF1
Gaeumannomyces oryzinus	*Gaeumannomyces graminis* var. *graminis*	CBS 235.32		USA	*Oryza sativa*	JX134681	JX134669	KM485049	JX134695
	Gaeumannomyces graminis var. *graminis*	CPC 26030, CBS 141391		The Bahamas	*Cynodon dactylon* × *C. transvaalensis*	**KX306587**	**KX306517**	**KX306647**	**KX306718**
	Gaeumannomyces graminis var. *graminis*	CPC 26031		USA	*Oryza sativa*	**KX306588**	**KX306518**	**KX306648**	**KX306719**
	Gaeumannomyces graminis var. *graminis*	CPC 26032		USA	*Oryza sativa*	**KX306589**	**KX306519**	**KX306649**	**KX306720**
	Gaeumannomyces graminis var. *graminis*	CPC 26043, CBS 141392		USA	*Oryza sativa*	**KX306590**	**KX306520**	**KX306650**	**KX306721**
	Gaeumannomyces graminis var. *graminis*	CPC 26065		USA	*Oryza sativa*	**KX306591**	**KX306521**	**KX306651**	**KX306722**
	Gaeumannomyces graminis var. *graminis*	CPC 26066		USA	*Oryza sativa*	**KX306592**	**KX306522**	**KX306652**	**KX306723**
	Gaeumannomyces graminis var. *graminis*	CPC 26067, CBS 141393		USA	*Oryza sativa*	**KX306593**	**KX306523**	**KX306653**	**KX306724**
G. radicicola	*Phialophora zeicola*	CBS 149.85, PREM 45754		South Africa	*Zea mays*	KM484961	KM484844	KM485060	KM009205
	Phialophora radicicola	CBS 296.53, MUCL 28970	T	Canada	*Zea mays*, root	KM484962	KM484845	KM485061	KM009206
	Gaeumannomyces graminis var. *maydis*	W4066B		China	*Zea mays*	–	AJ010035	–	–
	Gaeumannomyces graminis var. *maydis*	Ggm02		–	–	–	AY120939	–	–
G. setariicola	*Gaeumannomyces graminis* var. *graminis*	CPC 26059, PRRI 4754, CBS 141394	T	South Africa	*Setaria italica*	**KX306594**	**KX306524**	**KX306654**	**KX306725**
	Gaeumannomyces graminis var. *tritici*	CBS 186.65		Netherlands	*Hordeum vulgare*	KM484955	KM484838	KM485054	**KX306726**
G. tritici	*Gaeumannomyces graminis* var. *tritici*	CBS 247.29		Netherlands	*Triticum* sp.	KM484956	KM484839	KM485055	**KX306727**
	Gaeumannomyces graminis var. *tritici*	CBS 249.29, IMI 083849		–	*Triticum aestivum*	KM484957	KM484840	KM485056	**KX306728**
	Gaeumannomyces graminis var. *tritici*	CBS 273.36		Argentina	*Triticum aestivum*	**KX306595**	**KX306525**	**KX306655**	**KX306730**
	Gaeumannomyces graminis var. *tritici*	CBS 905.73, DAR 23140		Australia	*Triticum aestivum*	KM484958	KM484841	KM485057	**KX306731**
	Gaeumannomyces graminis var. *tritici*	CBS 131293		USA	*Triticum* sp.	**KX306596**	**KX306526**	**KX306656**	**KX306729**
	Gaeumannomyces graminis var. *avenae*	CPC 26069, CBS 141395		USA	–	**KX306597**	**KX306527**	**KX306657**	**KX306732**
	Gaeumannomyces graminis var. *tritici*	CPC 26268, CBS 141396		Australia	*Triticum aestivum*	**KX306598**	**KX306528**	**KX306658**	**KX306733**
	Gaeumannomyces graminis var. *tritici*	CPC 26269, CBS 141397		Brazil	*Triticum aestivum*	**KX306599**	**KX306529**	–	–
	Gaeumannomyces graminis var. *tritici*	CPC 26270		UK	*Hordeum vulgare*	**KX306600**	**KX306530**	**KX306659**	**KX306734**
	Gaeumannomyces graminis var. *tritici*	CPC 26271		UK	*Triticum aestivum*	**KX306601**	**KX306531**	–	**KX306735**
	Gaeumannomyces graminis var. *tritici*	CPC 26272		UK	*Hordeum vulgare* (winter barley)	**KX306602**	**KX306532**	**KX306660**	**KX306736**
	Gaeumannomyces graminis var. *tritici*	CPC 26273, CBS 141398		UK	*Elymus repens* (couch grass)	**KX306603**	**KX306533**	**KX306661**	**KX306737**
	Gaeumannomyces graminis var. *tritici*	CPC 26274		Australia	–	**KX306604**	**KX306534**	**KX306662**	**KX306738**
	Gaeumannomyces graminis var. *tritici*	CPC 26275		UK	*Bromus* sp. (Brome grass)	**KX306605**	**KX306535**	**KX306663**	–
	Gaeumannomyces graminis var. *tritici*	CPC 26276		Brazil	–	**KX306606**	**KX306536**	**KX306664**	**KX306739**
	Gaeumannomyces graminis var. *tritici*	CPC 26277		UK	*Elymus repens* (couch grass)	**KX306607**	**KX306537**	**KX306665**	**KX306740**

(*continued on next page*)

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Table 1. (Continued).

Species	Old name/Received as	Strain number[1]	Status[2]	Country	Host, substrate	GenBank accession numbers[3]			
						LSU	ITS	RPB1	TEF1
Gaeumannomyces tritici	*Gaeumannomyces graminis* var. *tritici*	CPC 26278		UK	*Agropyron* sp.	**KX306608**	**KX306538**	**KX306666**	**KX306741**
	Gaeumannomyces graminis var. *tritici*	CPC 26280		UK	–	**KX306609**	**KX306539**	**KX306667**	**KX306742**
	Gaeumannomyces graminis var. *tritici*	CPC 26281		UK	–	**KX306610**	**KX306540**	**KX306668**	**KX306743**
	Gaeumannomyces graminis var. *tritici*	CPC 26282, CBS 141399		UK	*Triticum aestivum* (winter wheat)	**KX306611**	**KX306541**	–	**KX306744**
	Gaeumannomyces graminis var. *tritici*	CPC 26283		UK	*Triticum aestivum* (winter wheat)	**KX306612**	**KX306542**	**KX306669**	**KX306745**
	Gaeumannomyces graminis var. *tritici*	R3-111a-1		USA	*Triticum aestivum*	–	–	Genome	Genome
Gaeumannomyces walkeri	*Gaeumannomyces incrustans*	CPC 26028, CBS 141400	T	USA	*Stenotaphrum secundatum*	**KX306613**	**KX306543**	**KX306670**	**KX306746**
G. wongoonoo	*Gaeumannomyces wongoonoo*	BRIP 60376		Australia	Buffalo grass	KP162146	KP162137	–	–
Kohlmeyeriopsis medullaris	*Gaeumannomyces medullaris*	CBS 117849, JK5528S	T	USA	*Juncus roemerianus*	KM484968	KM484852	KM485068	–
Magnaporthiopsis incrustans	*Gaeumannomyces incrustans*	M35		–	–	JF414892	JF414843	JF710437	–
M. maydis	*Magnaporthiopsis maydis*	CBS 662.82A	T	Egypt	*Zea mays*	KM484971	KM484856	KM485072	–
	Harpophora sp.	CBS 133165, ATCC MYA-3356		Israel	*Zea mays*	**KX306614**	**KX306544**	–	–
M. poae	*Magnaporthe poae*	M48		USA	*Poa pratensis*	–	JF414837	JF710434	–
M. rhizophila	*Magnaporthe poae*	M23		–	*Poa pratensis*	JF414846	JF414834	JF710432	–
***Magnaporthiopsis* sp.**	*Gaeumannomyces graminis* var. *graminis*	CPC 26038		USA	*Cynodon dactylon* × *C. transvaalensis*	**KX306615**	**KX306545**	**KX306672**	**KX306676**
Nakataea oryzae	*Nakataea oryzae*	CBS 252.34		Burma	*Oryza sativa*	KM484976	KM484862	KM485078	–
Neogaeumannomyces bambusicola	*Neogaeumannomyces bambusicola*	MFLUCC 110390	T	Thailand	Dead culm of bamboo (*Bambusae*)	KP744492	KP744449	–	–
Omnidemptus affinis	*Omnidemptus affinis*	ATCC 200212	T	Australia	*Panicum effusum* var. *effusum*, grass leaves	KX134686	JX134674	JX134728	–
Pseudophialophora eragrostis	*Pseudophialophora eragrostis*	CM12m9	T	USA	*Eragrostis* sp.	KF689638	KF689648	KF689618	KF689628
Pyricularia grisea	*Pyricularia grisea*	BR0029		Brazil	*Digitaria sanguinalis*	KM484995	KM484880	KM485100	–
	Pyricularia grisea	CR0024		South Korea	*Lolium perenne*	KM484997	KM484882	KM485102	–
Slopeiomyces cylindrosporus	*Gaeumannomyces cylindrosporus*	CBS 609.75	T	UK	Grass root, associated with *Phialophora graminicola*	KM485040	KM484944	KM485158	–
Magnaporthaceae, incertae sedis	*Phialophora* sp.	CPC 26284, GP57, CBS 141401		UK	*Triticum aestivum*	**KX306616**	**KX306546**	–	**KX306677**
	Gaeumannomyces caricis	CPC 26245, CBS 141402		UK	*Carex acutiformis*	**KX306617**	**KX306547**	**KX306673**	**KX306678**

[1] ATCC: American Type Culture Collection, Virginia, USA; BCC: BIOTEC Culture Collection, National Center for Genetic Engineering and Biotechnology (BIOTEC), Bangkok, Thailand; BRIP: Queensland Plant Pathology Herbarium, Brisbane, Australia; CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CPC: Culture collection of Pedro Crous, housed at CBS; DAR: Plant Pathology Herbarium, Orange Agricultural Institute, Forest Road, Orange. NSW 2800, Australia; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, United Kingdom; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium; PREM: South African National Collection of Fungi (NCF), Mycology Unit, Biosystematics Division, Plant Protection Institute, Agricultural Research Council, Roodeplaat, Pretoria, South Africa.

[2] T: ex-type strain; ET: ex-epitype strain.

[3] ITS: internal transcribed spacer regions 1 & 2 including 5.8S nrRNA gene; LSU: 28S large subunit of the nrRNA gene; *rpb1*: partial RNA polymerase II largest subunit; *tef1*: partial translation elongation factor 1-α.

Phylogenetic analysis

A draft phylogeny based on the ITS sequences was first generated to infer a preliminary phylogenetic placement of the studied isolates (data not shown). Phylogenetic relationships of *Gaeumannomyces* spp. and related genera in *Magnaporthaceae* were resolved by combined analyses of ITS, LSU, *tef1*, and *rpb1* sequences. The first dataset combining LSU and *rpb1* sequences was used to infer the generic relationship among all the isolates within genera belonging to *Magnaporthaceae*. A second combined dataset based on LSU, ITS, *tef1* and *rpb1* sequences was used to resolve the taxonomy of *Gaeumannomyces sensu stricto* (*s. s.*) at species level.

Phylogenetic analyses of both individual and combined aligned data consisted of Bayesian inference (BI), Maximum Parsimony (MP), Maximum-Likelihood (ML), and neighbour-joining (NJ) analyses. Substitution models for each sequence dataset were inferred with MrModeltest2 v. 2.3 (Nylander 2004). The BI was addressed using MrBayes v. 3.2.1 (Ronquist *et al.* 2012). The Markov Chain Monte Carlo sampling (MCMC) analysis of four chains started in parallel from a random tree topology. The number of generations was set at 10 million and the run was stopped automatically when the average standard deviation of split frequencies fell below 0.01. Trees were saved each 1 000 generations. Burn-in was set at 25 % after which the likelihood values were stationary and the remaining trees were used to calculate posterior probabilities (BPP).

The ML analyses, including 1 000 bootstrap replicates, were conducted using RAxML on the CIPRES portal (www.phylo.org) using RAxML-HPC BlackBox v. 8.2.6. A general time reversible model (GTR) was applied with a gamma-distributed rate variation. The MP and NJ analyses with the Kimura 2-parameter and the HKY85 substitution model using PAUP v. 4.0b10 (Swofford 2003) were performed as described by Crous *et al.* (2006).

RESULTS

Phylogeny

The first dataset consisted of 64 aligned LSU and *rpb1* sequences of members of *Magnaporthaceae*, including the outgroup *Pyricularia grisea* represented by two strains (BR0029 and CR0024). Based on the results of MrModeltest, the GTR+I+G model with inverse gamma-distributed was selected as best fit model for BI. This dataset included 1 368 characters, from which 424 constitute unique site patterns. A total of 2 130 trees were sampled after the burn-in with a stop value of 0.01. In the MP analyses, 948 characters were constant, 66 were variable and parsimony uninformative while 354 were parsimony informative. A total of 48 equally most parsimonious trees were retained from this analysis (Tree length = 1 253, CI = 0.516, RI = 0.787, and RC = 0.407). The topology of the MP tree confirmed those of BI and ML trees for the distinction of 14 well-supported monophyletic clades, and therefore only the Bayesian tree with MP and RAxML bootstrap support values (MPBS and MLBS, respectively) and Bayesian posterior probabilities (BPP) are shown in Fig. 1. This analysis delimited 14 generic clades in *Magnaporthaceae*. The majority of the isolates cluster in *Gaeumannomyces s. s.* However one strain, CPC 26038, clustered in *Magnaporthiopsis* while CPC 26284 [=GP57 *Phialophora* sp. in Ward & Bateman (1999)], CPC 26245 (identified as *G. caricis*), CBS 117.83, and CBS 388.81 together with CPC 26262, were placed in separate clades distinct from other genera in *Magnaporthaceae*. Two new genera are introduced here (see Taxonomy section); *Falciphoriella* to accommodate CBS 117.83, and *Gaeumannomycella* to accommodate the isolates CBS 388.81 and CPC 26262. Cultures CPC 26284 and CPC 26245, identified as *Phialophora* sp. and *G. caricis* respectively, represent distinct lineages in *Magnaporthaceae*, but unfortunately these cultures proved to be sterile and thus await future taxonomic treatment until sporulating material is collected.

Gaeumannomyces s. s. was analysed in detail to calculate the phylogenetic differences among the varieties of *Gaeumannomyces* and other species included in the genus, i.e. *G. amomi*, *G. radicicola* and *G. wongoonoo*. This dataset consisted of 74 aligned sequences including two outgroups *Falciphora oryzae* (CBS 125863) and *Pseudophialophora eragrostis* (CM12m9). This dataset consisted in total of 2 634 characters (882 bp from the LSU, 719 bp from ITS, 1 041 bp from *tef1* and 1 044 bp from *rpb1*) of which 961 constitute unique site patterns. Based on the results of MrModeltest, the GTR+I+G model with inverse gamma-distributed was selected as best fit model for BI. For the multi-locus analyses, a total of 4 068 trees were sampled after the burn-in with a stop value of 0.01. In the MP analyses, 2 046 characters were constant, 322 were variable and parsimony uninformative while 266 were parsimony informative. A maximum of 1 000 equally most parsimonious trees were retained from this analysis (Tree length = 1 010, CI = 0.754, RI = 0.915, and RC = 0.690). The topology of the BI tree was congruent to that of ML and MP trees and therefore only the Bayesian tree with BPP and MPBS values are indicated in Fig. 2. *Gaeumannomyces* isolates are distributed in four main clades designated here as Graminis, Oryzinus, Radicicola, and Tritici. Naming was based on the oldest species described in the clade, except for the tritici clade which was chosen based on the most phytopathogenic important species *G. tritici* (the wheat take-all fungus). Clade tritici consists of *G. tritici*, *G. avenae* (both elevated here to species status, formerly recognised as varieties of *G. graminis*), *G. amomi* and four new species described here as *G. arxii*, *G. ellisiorum*, *G. glycinicola* and *G. walkeri*. Clade graminis consists of *G. graminis* and three new species described here as *G. californicus*, G. *australiensis* and G. *oryzicola*. Clade oryzinus consists of *G. oryzinus* and three new species described here as *G. floridanus*, *G. fusiformis* and *G. graminicola*. Clade radicicola consists of *G. radicicola*, *G. wongoonoo* and two new species described here as *G. hyphopodioides* and *G. setariicola*.

Taxonomy

Based on DNA sequence data and variation in morphology among the isolates studied, two new genera in *Magnaporthaceae* are introduced with a harpophora-like asexual morph, namely *Falciphoriella* and *Gaeumannomycella*. The *Gaeumannomyces s. s.* analysis resolved a total of 19 species, 12 of which are introduced as new species; and two new combinations are proposed. All the novelties, as well as epitypifications, are described and illustrated below. The main morphological characters of accepted species in *Gaeumannomyces* are provided in Table 2. The identity of some isolates could not be resolved in the

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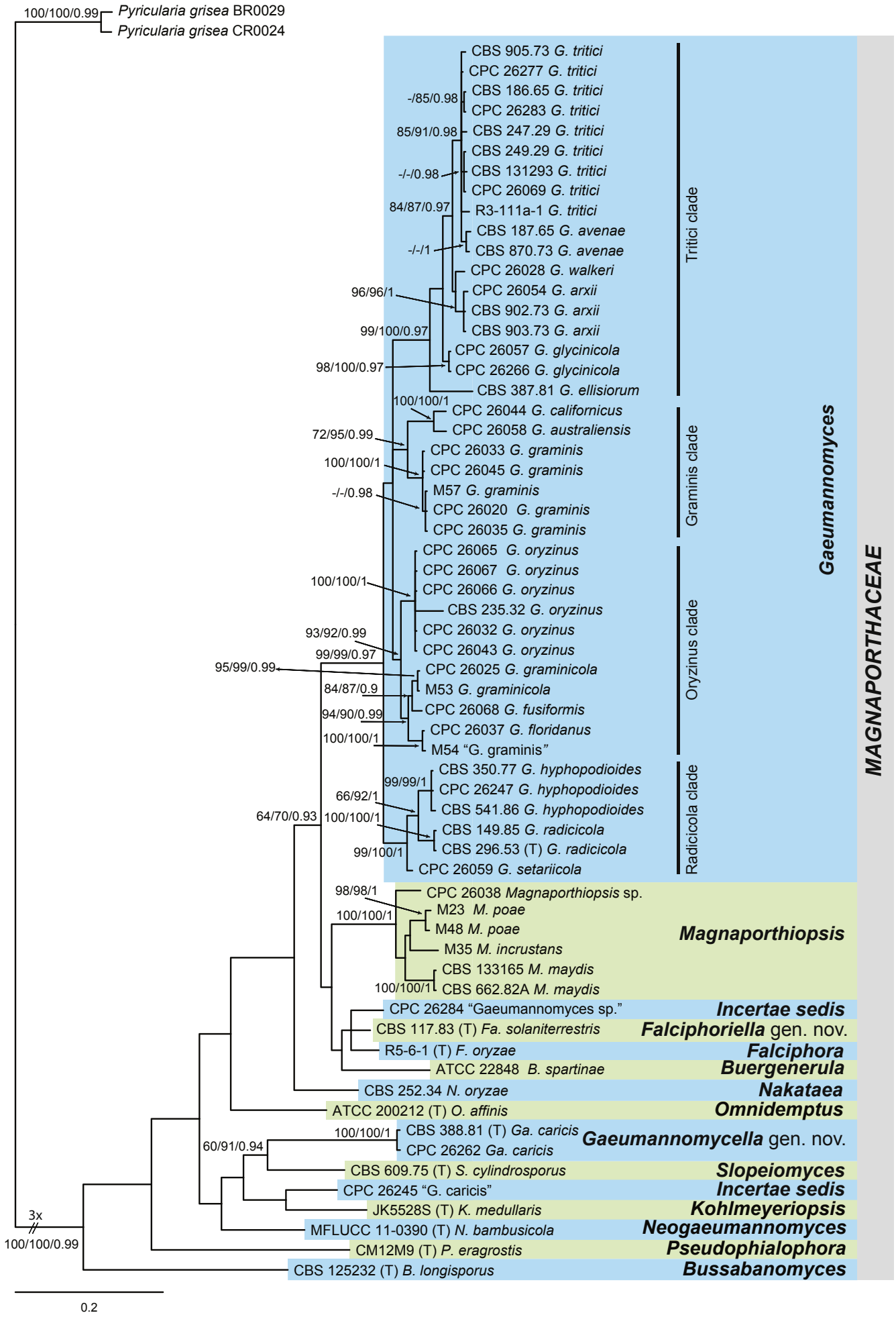

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present study, mostly because they remained sterile in culture; their identities will be resolved in future studies.

Sordariomycetes*, *Magnaporthales*, *Magnaporthaceae

Falciphoriella M. Hern.-Restr. & Crous, **gen. nov.** MycoBank MB816902.

Etymology: Morphologically similar to the genus *Falciphora*.

Mycelium consisting of septate, branched, smooth, hyaline to subhyaline. *Conidiophores* differentiated, indeterminate, branched, hyaline to pale brown. *Conidiogenous cells* phialidic, hyaline to pale brown, solitary or grouped, terminal or intercalary, cylindrical, lageniform, to conical, straight or curved with a cylindrical to funnel-shaped collarette. *Conidia* mainly fusiform sometimes obovoid, slightly curved at the ends, usually pointed base, hyaline. *Hyphopodia* not observed.

Type species: *Falciphoriella solaniterrestris* M. Hern.-Restr. & Crous

Falciphoriella solaniterrestris M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816903. Fig. 3.

Etymology: Referring to the substrate *solani* – *Solanum* the Latin generic name of potato, and *terrestris* – from soil, since this species was isolated from soil in a potato field.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to subhyaline, 1.5–4.5 µm diam hyphae. *Conidiophores* differentiated, indeterminate, branched, hyaline to pale brown. *Conidiogenous cells* phialidic, hyaline to pale brown, solitary or grouped, terminal or intercalary, cylindrical, lageniform, to conical, straight or curved, 5–29 × 1.5–3.5 µm, cylindrical to funnel-shaped collarette up to 2.5 µm, 1–2 µm diam. *Conidia* mainly fusiform sometimes obovoid, slightly curved at the ends, usually pointed base, hyaline, 5–13 × 1–2 µm. *Hyphopodia* not observed.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 35 mm diam, aerial mycelium moderate, cottony, vinaceous buff, submerged mycelium dark, margin effuse, rhizoid; reverse no change. On MEA reaching 50 mm diam, aerial mycelium abundant, dense in the centre, cottony, submerged mycelium dark, margin effuse; reverse sepia in the centre, colourless to the periphery. On OA reaching 50 mm diam, flat, aerial mycelium moderate, cottony, white, submerged mycelium pale luteous in the centre, colourless to the periphery, margin effuse; reverse colourless to yellow.

Specimen examined: **Netherlands**, Prov. Groningen, Groningen, isolated from soil in potato field, Jul. 1982, isol. by H. Nielander (**holotype**, CBS H-22572, culture ex-type CBS 117.83).

Notes: *Falciphoriella solaniterrestris* is introduced for a fungus isolated from soil in a potato field in the Netherlands. The isolate CBS 117.83, formerly identified as *Gaeumannomyces* sp. (Klaubauf *et al.* 2014), formed a separated branch distant from *Gaeumannomyces* in our phylogenetic tree (Fig. 1) and represents a new genus in *Magnaporthaceae*.

Gaeumannomycella M. Hern.-Restr. & Crous, **gen. nov.** MycoBank MB816904.

Etymology: Morphologically similar to the genus *Gaeumannomyces*.

Mycelium consisting of septate, branched, smooth, hyaline to brown, hyphae. *Conidiophores* slightly differentiated and hyaline. *Conidiogenous cells* phialidic, scarce, formed close to the hyphopodia, hyaline to pale brown, mostly grouped, terminal sometimes intercalary, ampulliform, lageniform or conical, straight or curved, with inconspicuous collarette. *Conidia* lunate or cylindrical, hyaline. *Hyphopodia* hyaline to brown when mature, lobed.

Type species: *Gaeumannomycella caricis* M. Hern.-Restr. & Crous

Gaeumannomycella caricis M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816905. Fig. 4.

Etymology: Referring to the substrate *Carex rostrata* from which the species was isolated for the first time.

Description on PDA. *Mycelium* consisting of septate, branched, smooth, hyaline to brown, 1.5–6.5 µm diam hyphae. *Conidiophores* slightly differentiated, hyaline. *Conidiogenous cells* phialidic, scarce, formed close to the hyphopodia, hyaline to pale brown, mostly grouped, terminal sometimes intercalary, ampulliform, lageniform or conical, straight or curved, 6.5–12 × 3–4 µm, inconspicuous collarette up to 1 µm long, 1 µm diam. *Conidia* lunate or cylindrical, hyaline, 6.5–9.5 × 1–2 µm. *Hyphopodia* hyaline to brown, lobed at maturity, 15–31 × 10–23 µm.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 35 mm diam, flat, aerial mycelium scarce to moderate, cottony, white, pale grey, submerged mycelium dark or white, margin effuse, rhizoid; reverse dark. On MEA reaching 36 mm diam, elevated, aerial mycelium moderate to abundant dense, cottony, white, submerged mycelium dark, margin effuse, rhizoid; reverse dark in the centre colourless to the periphery. On OA reaching 40 mm diam, elevate, aerial mycelium moderate to abundant, cottony to funiculose, submerged mycelium dark, margin effuse, rhizoid; reverse dark.

Specimens examined: **UK**, Wales, Powys, Llyn Ebyr, isolated from *Carex rostrata*, 28 May 1979, M.B. Ellis (**holotype**, CBS H-22575, culture ex-type CBS 388.81); Powys, Llyn Ebyr, isolated from *Carex rostrata*, 3 Jan. 1980, unknown collector, CPC 26262 = CBS 141374.

Notes: *Gaeumannomycella caricis* is only known occurring on *Carex rostrata*. This new species is represented by two strains

Fig. 1. Phylogenetic tree inferred from a Bayesian analysis based on a concatenated alignment of LSU and *rpb1* sequences of 64 strains representing *Magnaporthaceae* family. The Maximum Parsimony and RAxML bootstrap support values (MPBS, MLBS) and Bayesian posterior probabilities (BPP) are given at the nodes (MPBS/MLBS/BPP). Some branches were shortened to fit them to the page – these are indicated by two diagonal lines with the number of times a branch was shortened indicated next to the lines. Ex-type or ex-epitype strains are indicated as (T) and (ET) respectively. The tree was rooted with *Pyricularia grisea* (BR0029 and CR0024).

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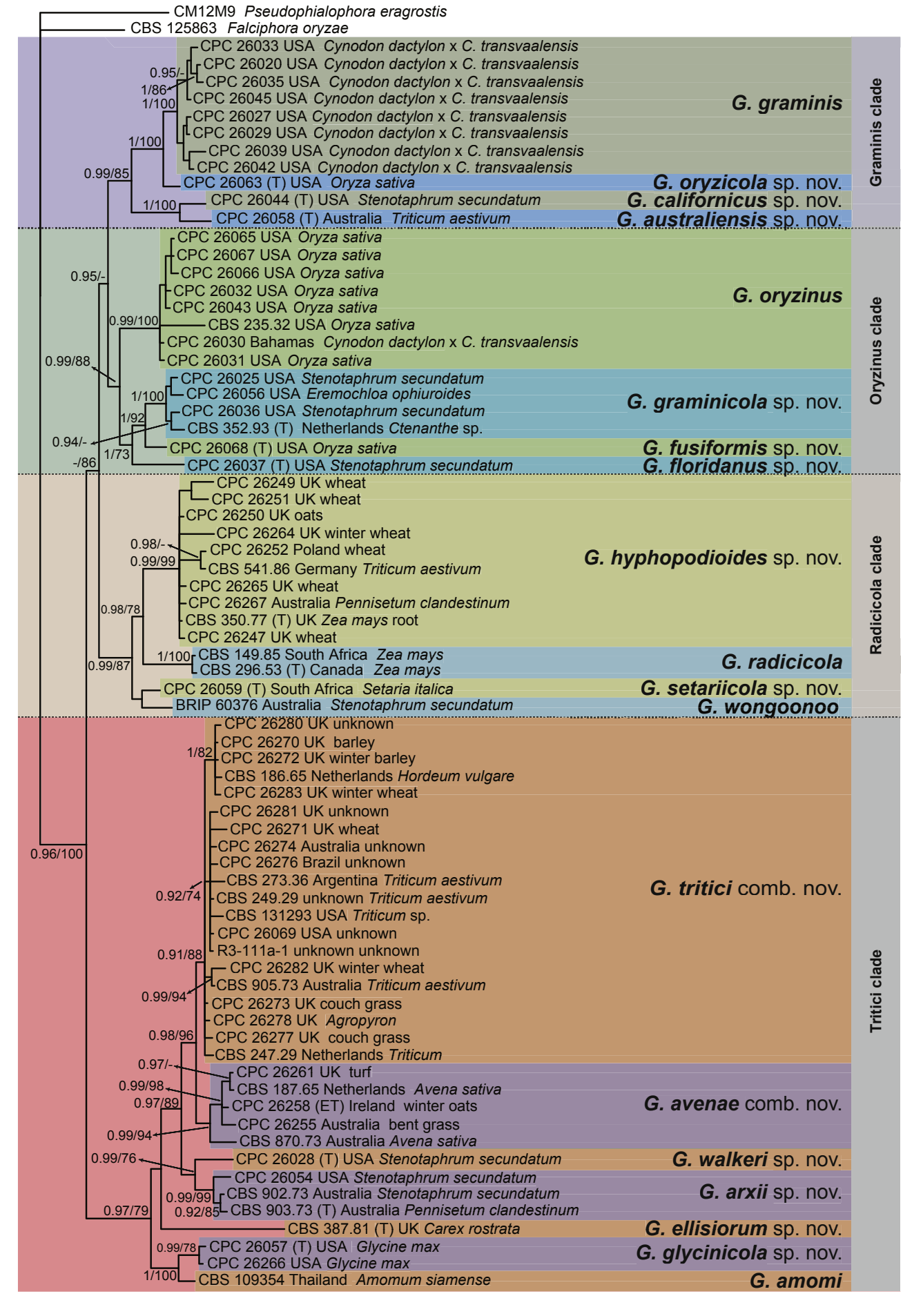

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isolated from the UK. It is morphologically similar to *Gaeumannomyces* since it produces a harpophora-like asexual state and lobed hyphopodia, but was phylogenetically considerably different. In the phylogenetic tree (Fig. 1), *Slopeiomyces* is shown to be the sister clade of *Gaeumannomycella*.

Gaeumannomyces Arx & D.L. Olivier, Trans. Br. mycol. Soc. 35: 32. 1952.

= *Rhaphidophora* Ces. & De Not., Sfer. Ital.: 79. 1863.
= *Rhaphidospora* Fr., Summa veg. Scand., Section Post. (Stockholm): 401. 1849.

Mycelium mainly immersed, consisting of branched, septate, hyaline to brown hyphae. *Sexual morph*. *Ascomata* perithecial, superficial and submerged, globose, subglobose to elliptical, with a cylindrical neck, dark brown to black. *Peridium textura epidermoidea*. *Paraphyses* hyaline, septate, often constricted at the septa, widest at the base and gradually narrow at the apex, dissolving at maturity. *Asci* numerous, unitunicate, cylindrical to elongated clavate, shortly stalked, with apical refringent ring, 8 ascospores. *Ascospores* faintly tinted yellowish in mass, hyaline to pale brown, vacuolated, slightly curved to sinuate, ends rounded, widest in the middle, tapering toward the base, septate, septa often indistinct. *Asexual morph* harpophora-, phialophora-like. *Conidiophores* branched, verticillate, indeterminate often reduced to conidiogenous cells, hyaline to brown. *Conidiogenous cells* phialidic, borne directly from the mycelium or on pale brown conidiophores, solitary or in dense clusters, individual phialides lageniform, cylindrical, straight or slightly curved tapering to a short cylindrical to funnel-shaped or hardly visible collarette. *Conidia* dimorphic (A) hyaline, ovoid to cylindrical, straight to curved, tapering to an often acute base, solitary, grouped in slimy heads and/or (B) hyaline, falcate to lunate or usually strongly curved in a semicircle with varying degrees of curvature, solitary, arranged in heads at the apex. *Hyphopodia* when present hyaline or becoming brown when mature, simple or lobed. *Sclerotia* present or absent.

Type species: *Gaeumannomyces graminis* (Sacc.) Arx & D.L. Olivier

Gaeumannomyces amomi Bussaban *et al.*, Nova Hedwigia 73: 488. 2001.

Specimen examined: **Thailand**, Chiang Mai, Doi Suthep Pui national Park, isolated from *Alpinia malaccensis*, endophytic in leaves, Aug. 1999, B. Bussaban (CBS 109354).

Notes: This species was described as an endophyte from leaves and pseudo-stem of *Amomum siamense* and *Alpinia malaccensis* in Thailand (Bussaban *et al.* 2001). It differs from *G. graminis* in having wider ascospores, more septa and being the only *Gaeumannomyces* species reported from *Zingiberaceae*.

Gaeumannomyces arxii M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816890. Fig. 5.

Etymology: Name after Josef Adolph von Arx, a distinguished mycologist who together with D.L. Olivier introduced the genus *Gaeumannomyces*.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to pale brown, 1–5 µm diam hyphae. *Conidiophores* erect, simple or branched sometimes reduced to a conidiogenous cells. *Conidiogenous cells* phialidic, terminal or intercalary, hyaline, cylindrical to lageniform, straight to curved, 6–23 × 2–5 µm, with a cylindrical to funnel-shaped, refractive collarette up to 3 µm long, 1.5–3.5 µm wide. *Conidia* lunate, fusiform, tapering to pointed base, hyaline, 4–10 × 1–2 µm. *Hyphopodia* not observed.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 72 mm, flat, mycelium mostly submerged, grey olivaceous or greyish sepia in the centre, aerial mycelium scarce and white, margin effuse to irregular, rhizoid; reverse light olivaceous to white greyish in the centre, periphery no change. On MEA reaching 64 mm, elevated, cottony to funiculose, aerial mycelium white, submerged mycelium black, and margin effuse to rhizoid; reverse centre dark, white to the periphery; or flat, velvety, mycelium aerial white, mycelium mostly submerged, margin effuse to rhizoid; reverse white. On OA reaching 70 mm, glabrous, white to colourless, submerged mycelium dark, margin effuse with rhizoid zones; reverse no change.

Specimens examined: **Australia**, New South Wales, Turramurra, isolated from *Pennisetum clandestinum* (kikuyu grass), stolon, 11 Aug. 1972, J. Walker & P. Wong (**holotype**, CBS H-22573, culture ex-type CBS 903.73); Wagga Wagga, isolated from *Stenotaphrum secundatum* (buffalo grass), 23 Jul. 1969, J. Kuiper, CBS 902.73. **USA**, California, isolated from *Stenotaphrum secundatum*, 1991, H. Wilkinson, CPC 26054 = CBS 141375.

Notes: *Gaeumannomyces arxii* is represented by two strains from *Stenotaphrum secundatum* and another one from *Pennisetum clandestinum* from USA and Australia. This species was placed in the Tritici clade with *G. walkeri* as sister species. Both species were isolated from *Stenotaphrum secundatum*. Nevertheless, *G. walkeri* had brown and lobed hyphopodia, while in *G. arxii* hyphopodia were not observed. Some minor differences in the conidial morphology were noted between these two species. *Gaeumannomyces walkeri* had cylindrical to fusiform conidia after 8 d, and at 14 d conidia were mostly lunate and longer than *G. arxii*, where conidia are mostly lunate at 8 and 14 d.

Gaeumannomyces australiensis M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816906. Fig. 6.

Etymology: Named after Australia, the country where this fungus was collected.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to subhyaline, 1–4 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, scarce, hyaline to pale brown, solitary or grouped, terminal or intercalary, cylindrical, sometimes

Fig. 2. Phylogenetic tree inferred from a Bayesian analysis based on a concatenated alignment of LSU, ITS, *tef1* and *rpb1* sequences of 74 strains of *Gaeumannomyces*. The Bayesian posterior probabilities (BPP) and Maximum Parsimony bootstrap support values (MPBS) are given at the nodes (BPP/MPBS). Ex-type or ex-epitype strains are indicated as (T) and (ET) respectively. The tree was rooted with *Falciphora oryzae* (CBS 125863) and *Pseudophialophora eragrostis* (CM19M9).

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Table 2. Overview of the main characters of *Gaeumannomyces* species.

Clade	Species	Sexual				Asexual			Hyphopodia		Reference
		Ascomata (µm)	Asci (µm)	Ascospores (µm)	# of Septa	Conidiogenous cells (µm)	Conidial size (µm)	Conidial shape[1]	Size (µm)	Shape,[2] colour	
Graminis	***G. australiensis***	Not observed				6.5–27.5 × 1.5–3	5–11 × 1–2	L, C	18.5–25 × 21.5–23	L, brown	This study
	G. californicus	Not observed				4.5–24 × 1.5–4	4–11 × 1–1.5	L, F	25–32.5 × 24–30	L, brown	This study
	G. graminis	200–300 × 150–200	80–110 × 10–13	70–110 × 2.5–4	3	–	–	–	17–27 × 20–30	S–L	Walker (1980)
		Not observed				7–30 × 1.5–4	4–10 × 1–2	L	Not observed		This study
	G. oryzicola	110–413 × 112–525	118–148 × 14–16	92.5–120 × 4–6	0–5	7.5–20.5 × 2–2.5	5–9 × 1.5–2.5	F, L	Not observed		This study
Oryzinus	***G. floridanus***	Not observed				7–14.5 × 2–3.5	5–11 × 1–1.5	L	18–27 × 14.5–26.5	L, hyaline, brown	This study
	G. fusiformis	Not observed					5–9.5 × 1.5–2	F	Not observed		This study
	G. graminicola	Not observed				5–20 × 2–4.5	5–11.5 × 1–2	L, C	16.5–24 × 15.5–23.5	L, brown	This study
	G. oryzinus	187–415	(72)87–130 × 7–16	70–112 × 2–4.6	3–5	–	–		–	–	Walker (1972) (as Ggg)
		–	113–173.5 × 14.5–24	96–116 × 3.5–5.5	0–3	5–21 × 2–5	5–11 × 1–2.5	L, F, C	19–45 × 15.5–36	L, brown	This study
Radicicola	***G. hyphopodioides***	Not observed				7–21 × 2–4	5.5–10.5 × 1–2	L, F	17–28 × 18–25	S–L, hyaline, brown	This study
	G. radicicola	200–450 diam	60–100 × 9–12	55–85 × 2.5–4		10–23 × 3–4	5–9 × 0.7–1.5	L		S–slightly L	Yao *et al.* (1992) (as Ggm), Cain (1952) (as *Phialophora*)
	G. setariicola	Not observed				6.5–28.5 × 2–4	4–12 × 1–2	L	Not observed		This study
	G. wongoonoo	300–650 × 90–160	80–140 × 10–14	36–75 × 3–5	5–8 (12)	–	5–12.5 × 3–5	–	20 diam	S–L	Wong (2002)
Tritici	***G. amomi***	500–650 × 300–400	100–130 × 12.5–15	70–100 × 4–5	3–6	–	–	–	24–34 × 30–38	L	Bussaban *et al.* (2001)
	G. arxii	Not observed				6–23 × 2–5	4–10 × 1–2	L, F	Not observed		This study
	G. avenae	300–500 × 250–400	(90)110–160 × 12–16	(85)100–130 (140) × 3–5	(3)5–13	–	–	–	7–15 × 4–8	S	Walker (1972, 1981)
	G. ellisiorum	Not observed				5–18 × 3–4	4–9 × 1–2	L	19.5–35.5 × 16.5–30	S–L, hyaline	This study
	G. glycinicola	–	–	71.6 ± 6.8 × 2.6 ± 0.5	–	–	–	–	–	–	Roy *et al.* (1982) (as Ggg)
		Not observed				Not observed			22.5–43 × 15–34	L, hyaline, brown	This study
	G. tritici	150–500	(65)90–136 × 10–15	60–118 × 3–4	(2–3)5–9 (12)	–	–	–	–	S	Walker (1972)
	G. walkeri	Not observed				6–23 × 2–3.5	5–14 × 1–1.5 (at 8 days fusiform 7.5–11 × 2–3)	F, L	20–31 × 18.5–24.5	L, brown	This study

[1] L = lobed hyphopodia, S = simple hyphopodia.

[2] L = lunate conidia, F = fusiform conidia, and C = cylindrical conidia.

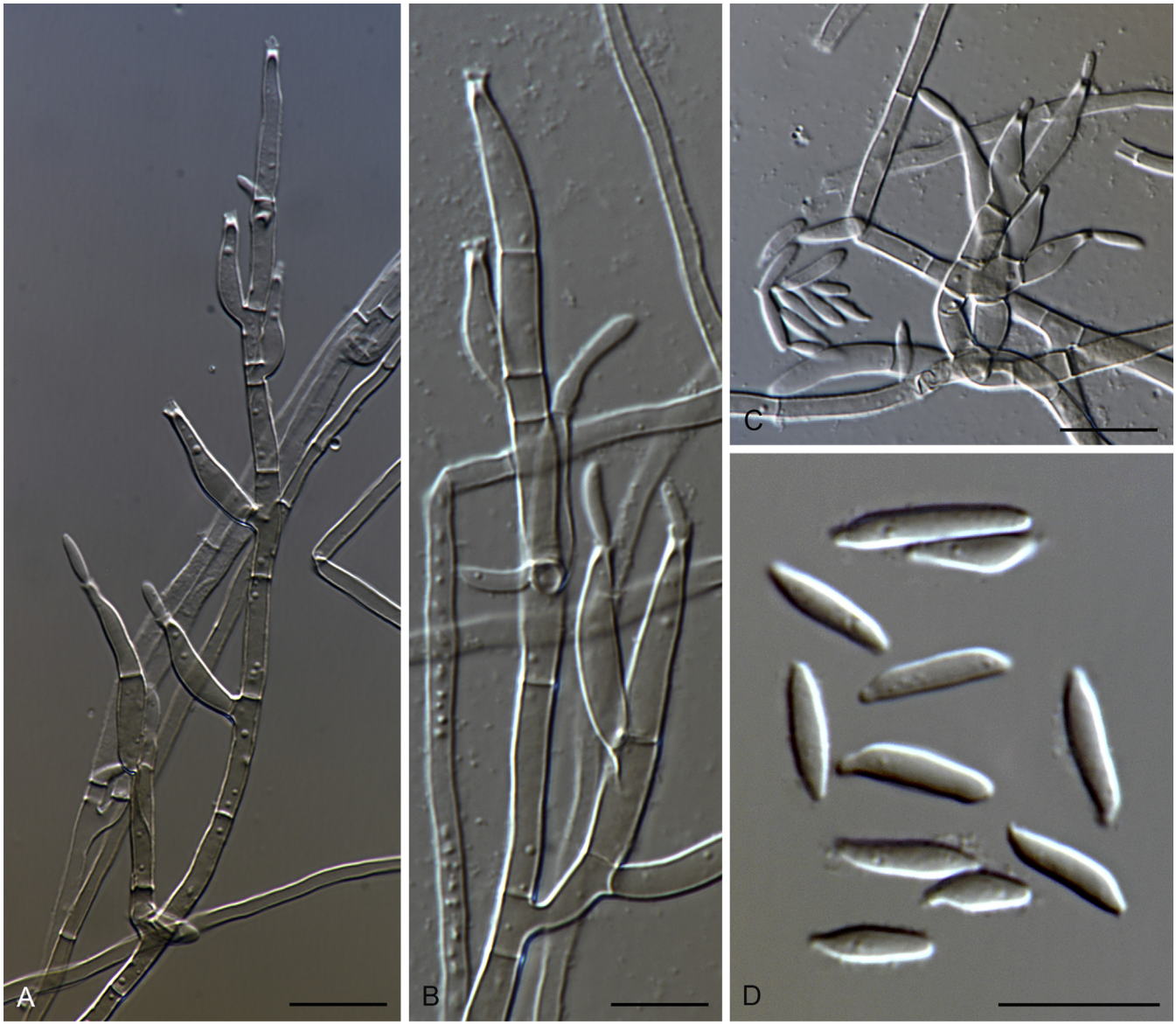

Fig. 3. *Falciphoriella solaniterrestris* (CBS 117.83). A–C. Conidiophores and conidiogenous cells. D. Conidia. Scale bars: A, C, D = 10 µm; B = 5 µm.

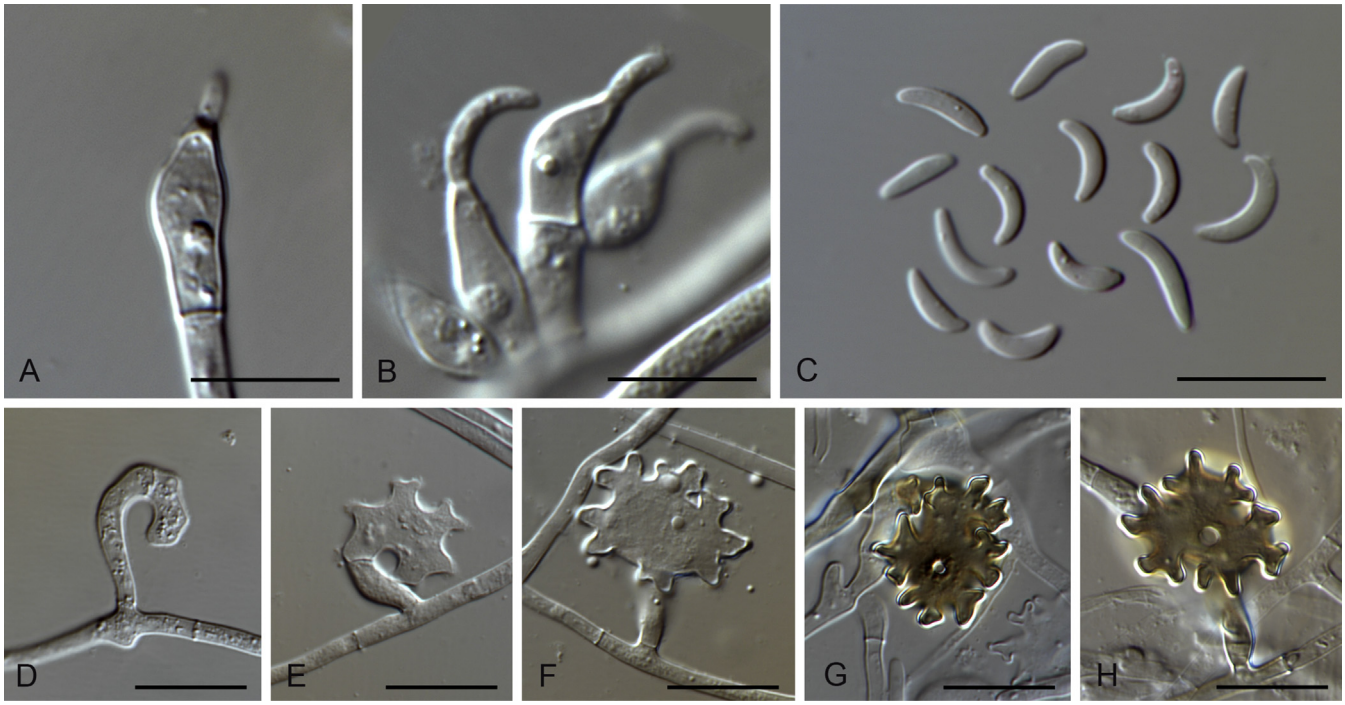

Fig. 4. *Gaeumannomycella caricis* (CBS 388.81). A, B. Conidiogenous cells. C. Conidia. D–H. Hyphopodia. Scale bars: A–H = 10 µm.

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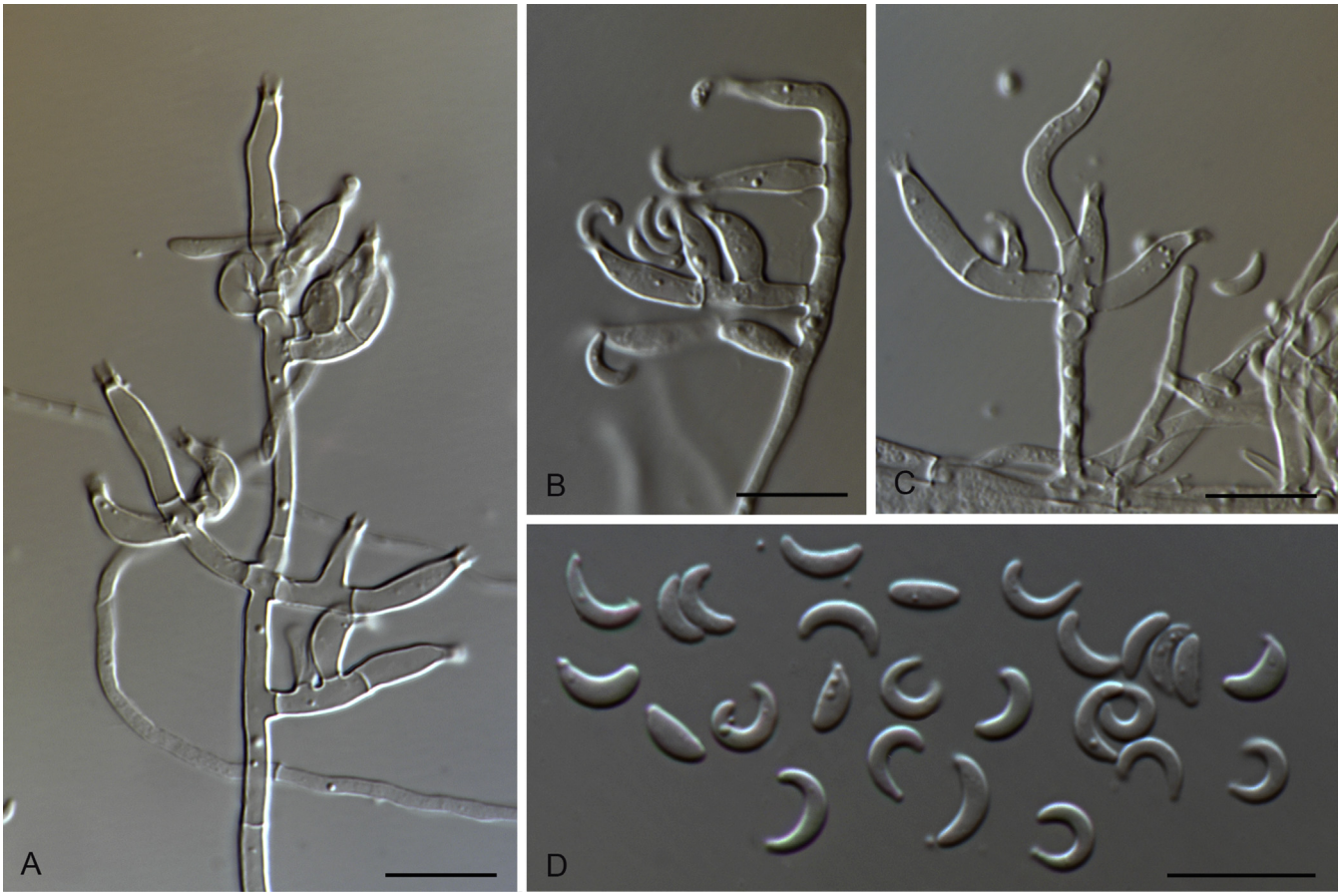

Fig. 5. *Gaeumannomyces arxii* (CBS 903.73). A–C. Conidiophores and conidiogenous cells. D. Conidia. Scale bars: A–D = 10 µm.

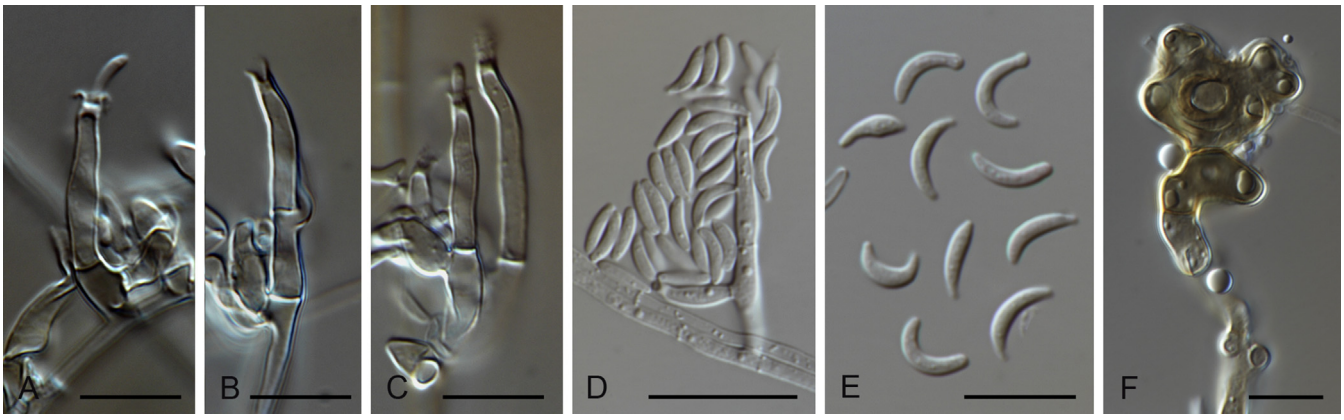

Fig. 6. *Gaeumannomyces australiensis* (CPC 26058). A–C. Conidiogenous cells. D. Conidiogenous cells and conidia. E. Conidia. F. Hyphopodium. Scale bars: A–C = 5 µm; D–F = 10 µm.

lageniform, straight or curved, 6.5–27.5 × 1.5–3 µm, cylindrical to funnel-shaped collarette up to 2.5 µm long, 1–2 µm diam. *Conidia* lunate, allantoid, hyaline, 5–11 × 1–1.5 µm. *Hyphopodia* hyaline becoming brown when mature, lobed, 18.5–25 × 21.5–23 µm.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 65 mm diam, flat, aerial mycelium scarce and white, submerged mycelium dark (isabelline), margin effuse, rhizoid; reverse no change. On MEA reaching 60 mm diam, aerial mycelium abundant, cottony, pale greenish grey, margin effuse, rhizoid; reverse centre fuscous periphery amber white to white. On OA reaching 55 mm diam, aerial mycelium white, submerged mycelium dark, smoke grey, margin effuse; reverse pale olivaceous grey.

Specimen examined: **Australia**, New South Wales, isolated from *Triticum aestivum*, unknown date, J. Walker (**holotype**, CBS H-22581, culture ex-type CBS 141387 = CPC 26058).

Notes: This is a single-isolate species collected on *Triticum* from Australia. This strain was placed in the Graminis clade with *G. californicus* as sister species (Fig. 2).

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Gaeumannomyces avenae (E.M. Turner) Hern.-Restr. & Crous, **comb. et stat. nov.** MycoBank MB816891.

≡ *Ophiobolus graminis* var. *avenae* E.M. Turner, Trans. Br. mycol. Soc. 24: 279. 1941 [1940].

= *Gaeumannomyces graminis* var. *avenae* (E.M. Turner) Dennis, British Cup Fungi & their Allies: 202. 1960.

Type details: Original collection lost. Neotype in Kew. **UK**, Scotland, Applecross, West ross, on *Avenae sativa*, 29 Sep. 1946, RWG Dennis, K(M) (slides as DAR 32104). **Ireland**, Killinick, Wexford, isolated from winter oats, 11 Sept. 1990, unknown collector (**epitype designated here**, CBS H-22587, MBT 371909, culture ex-epitype CPC 26258).

Additional specimens examined: **Australia**, New South Wales, isolated from *Agrostis* (bentgrass), 11 Nov. 1980, unknown collector, CPC 26253; CPC 26254; CPC 26255; Western Australia, 25 km W of Mt. Barker, isolated from *Avena sativa*, Dec. 1963, deposited by J. Walker, CBS 870.73. **Ireland**, Killinick, Wexford, isolated from winter oats, 11 Sept. 1990, unknown collector, CPC 26257; CPC 26259; Killarney, Kerry, isolated from turf, 11 Sep. 1990, unknown collector, CPC 26260. **Netherlands**, Oostelijk Flevoland, isolated from *Avena sativa*, root, unknown date, isol. M. Gerlagh, CBS 187.65. **UK**, England, Gleadthorpe, Notts, isolated from *Avena sativa*, 10 Jul. 1990, unknown collector CPC 26256 = CBS 141376; Macclesfield, Cheshire, isolated from turf, 11 Sep. 1990, unknown collector, CPC 26261.

Notes: In our phylogenetic tree (Fig. 2), *G. avenae* is represented by five isolates, formerly identified as *Gga*, and is placed in the Tritici clade with *G. tritici* as sister species. Isolates were collected growing on *Avenae sativa* and grasses; from Australia, Ireland, the Netherlands and the UK.

Dennis (1960) proposed *Gga* (=*Ophiobolus graminis* var. *avenae* E.M. Turner 1940) for those strains of *G. graminis* with larger ascospores and occurring on oats. This fungus causes take-all of oats and take-all patch of turfgrasses. Walker (1972, 1980) distinguished *Gga* from *Ggg* by the former producing simple hyphopodia, and distinguished *Gga* from *Ggt*, the fungus that causes wheat take-all, on the basis of longer mean ascospores length, and pathogenicity to oats. Nevertheless, *Gga* can also infect grasses and which seems to be much more important hosts than oats.

Previous studies demonstrated that oats and wheat take-all fungi are closely related but separated from *G. graminis* (Walker 1972, 1981, Bryan *et al.* 1995, Fouly & Wilkinson 2000, Saleh & Leslie 2004). *Gaeumannomyces tritici* and *G. avenae* are more virulent species and have simple hyphopodia, but ascospores are larger in *G. avenae* (Walker 1972). In addition, Rachdawong *et al.* (2002) differentiated *G. avenae* (as *Gga*) and *G. tritici* (as *Ggt*) based on sequences of avenacinase-like genes. A recent phylogenomic study by Luo *et al.* (2015a) included isolates from all three varieties, which revealed considerable differences among them. Our multi-locus analysis combining LSU, ITS, *rpb1* and *tef1* also showed differences in these two clades, and therefore we propose *G. avenae* comb. et stat. nov. to accommodate this species.

Gaeumannomyces californicus M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816892. Fig. 7.

Etymology: Named after California, the state in the USA where the sample was collected.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to brown, 1.5–4.5 µm diam hyphae. *Conidiophores* more or less differentiated, verticillate. *Conidiogenous cells* phialidic, hyaline to pale brown, solitary or grouped, terminal or intercalary, lageniform, cylindrical, straight or curved, 4.5–24 × 1.5–4 µm, cylindrical to funnel-shaped collarette up to 2.5 µm, 1–2 µm wide. *Conidia* lunate, allantoid or fusiform, hyaline, 4–11 × 1–1.5 µm. *Hyphopodia* hyaline, becoming brown when mature, lobed, 25–32.5 × 24–30 µm.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 85 mm diam, flat, aerial mycelium scarce, cottony, white, submerged mycelium grey olivaceous, margin effuse, rhizoid; reverse smoke grey. On MEA reaching 85 mm diam, aerial mycelium abundant, cottony to funiculose, white, smoke grey, submerged mycelium dark, margin effuse, rhizoid; reverse olivaceous. On OA reaching 85 mm diam, flat, aerial mycelium moderate to abundant, cottony to funiculose, white, submerged mycelium dark, olivaceous black, margin effuse, rhizoid; reverse centre no change, periphery olivaceous.

Specimen examined: **USA**, California, isolated from *Stenotaphrum secundatum*, 1992, M. Elliott (**holotype**, CBS H-22574, culture ex-type CBS 141377 = CPC 26044).

Notes: This species is represented by one strain isolated from *Stenotaphrum secundatum*, placed in the Graminis clade with *G. australiensis* as sister species (Fig. 2). In culture *G. californicus* produces long and branched conidiophores, and lunate to fusiform conidia; being different from *G. australiensis*, in which the conidiophores are mostly reduced to conidiogenous cells and conidia are lunate to cylindrical.

Gaeumannomyces ellisiorum M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816893. Fig. 8.

Etymology: Named after M.B. & J.P Ellis, who collected this fungus in the UK.

Description on PDA. *Mycelium* consisting of septate, branched, smooth, hyaline to pale brown, 1.5–3.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, scarce, terminal or intercalary, hyaline, clustered often solitary, cylindrical to lageniform, 5–18 × 3–4 µm, with a cylindrical, refractive collarette, up to 2.5 µm long, 1–2 µm diam. *Conidia* lunate, allantoid strong to slightly curved, to fusiform with one side straighter than the other, hyaline, 4–9 × 1–2 µm. *Hyphopodia* at the beginning formed as chlamydospores-like structures, globose, 1–3 cells, intercalary often terminal, hyaline, becoming lobed and pale brown hyphopodia 19.5–35.5 × 16.5–30 µm.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 80 mm diam, cottony, aerial mycelium white, submerged mycelium buff, margin effuse; reverse colourless (dark under inoculum). On MEA reaching 70 mm diam, cottony, aerial mycelium abundant, dense, and white, margin effuse; reverse apricot. On OA reaching 90 mm diam, cottony-funiculose, moderate, colourless.

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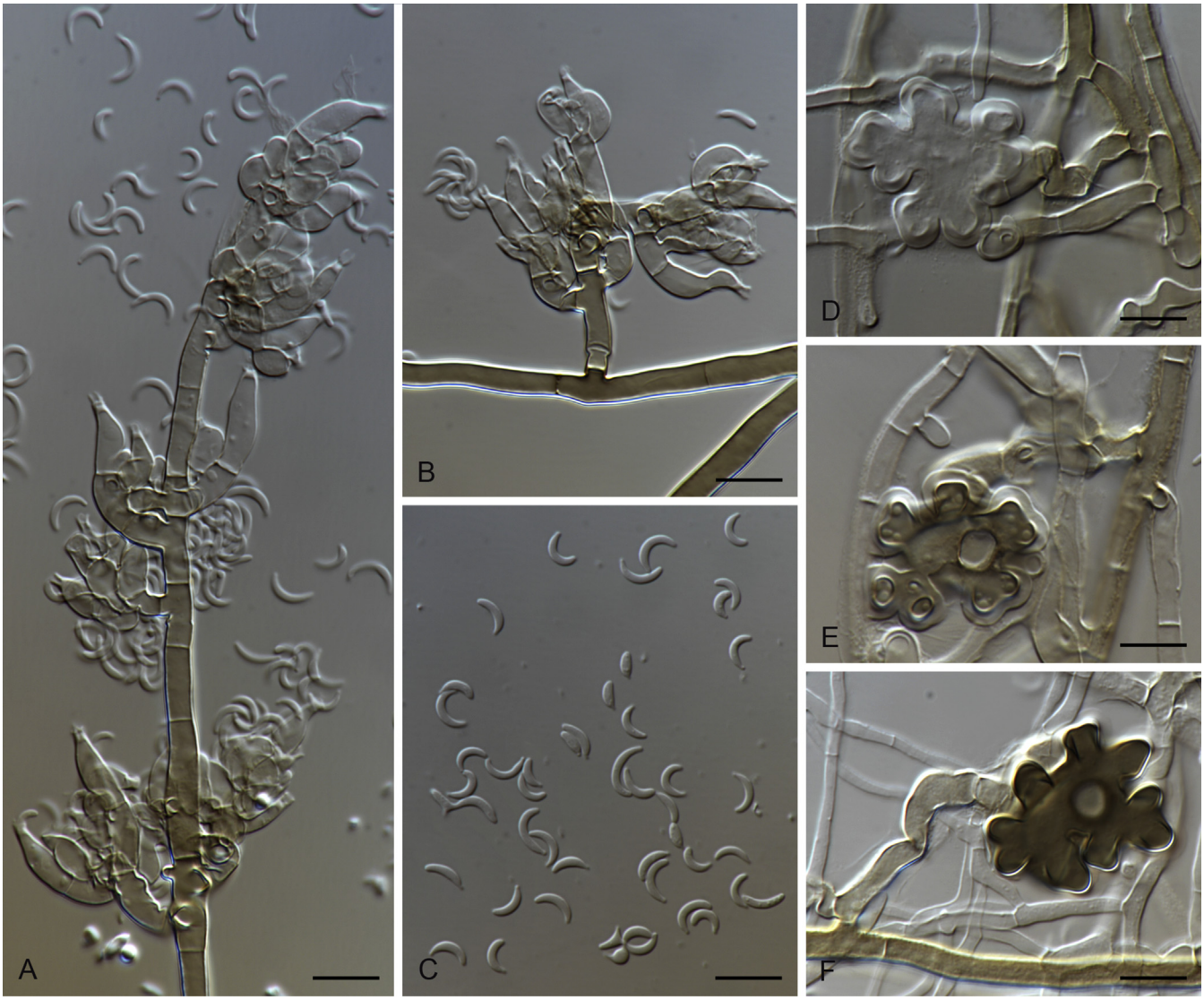

Fig. 7. *Gaeumannomyces californicus* (CPC 26044). A, B. Conidiophores and conidiogenous cells. C. Conidia. D, E. Hyphopodia. Scale bars: A–F = 10 µm.

Specimen examined: **UK**, Suffolk, Wolves Wood Reserve, isolated from *Deschampsia caespitosa*, dead culm and sheath, 9 Sep. 1979, M.B. & J.P. Ellis (**holotype**, CBS H-22576, culture ex-type CBS 387.81).

Notes: This species was previously identified as *Ggg*, and is only known from the type locality, growing on dead culms and sheaths of *Deschampsia caespitose*. In the multigene phylogeny, isolate CBS 387.81 was considerably genetically distant from other *Gaeumannomyces* species, and formed a separate branch in the Tritici clade (Fig. 2).

Gaeumannomyces floridanus M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816894. Fig. 9.

Etymology: Named after Florida, the state in the USA where the sample was collected.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to brown, 1.7–5 µm diam hyphae. *Conidiophores* more or less differentiated, simple or verticillate, hyaline to light brown. *Conidiogenous cells* phialidic, scarce, hyaline to pale brown, solitary or in groups, cylindrical, lageniform or clavate, straight or curved, 7–14.5 × 2–3.5 µm, inconspicuous collarette. *Conidia* lunate, slightly to strongly curved, hyaline, 5–11 × 1–1.5 µm. *Hyphopodia* lobed, hyaline becoming brown when mature, 18–27 × 14.5–26.5 µm.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 85 mm diam, aerial mycelium scarce, white, submerged mycelium dark (greyish sepia), margin effuse, rhizoid; reverse greyish sepia. On MEA reaching 70 mm diam, aerial mycelium abundant, cottony, submerged mycelium mouse grey, margin entire, rhizoid; reverse fuscous. On OA reaching 85 mm diam, aerial mycelium moderate, mouse grey, submerged mycelium dark, margin effuse, rhizoid; reverse mouse grey, olivaceous grey, colourless to the periphery.

Specimen examined: **USA**, Florida, isolated from *Stenotaphrum secundatum*, 1992, M. Elliott (**holotype**, CBS H-22577, culture ex-type CBS 141378 = CPC 26037).

Notes: This species is known only from the type locality, Florida (USA). It is located on a separate branch in the Oryzinus clade (Fig. 2), and is introduced here as new species.

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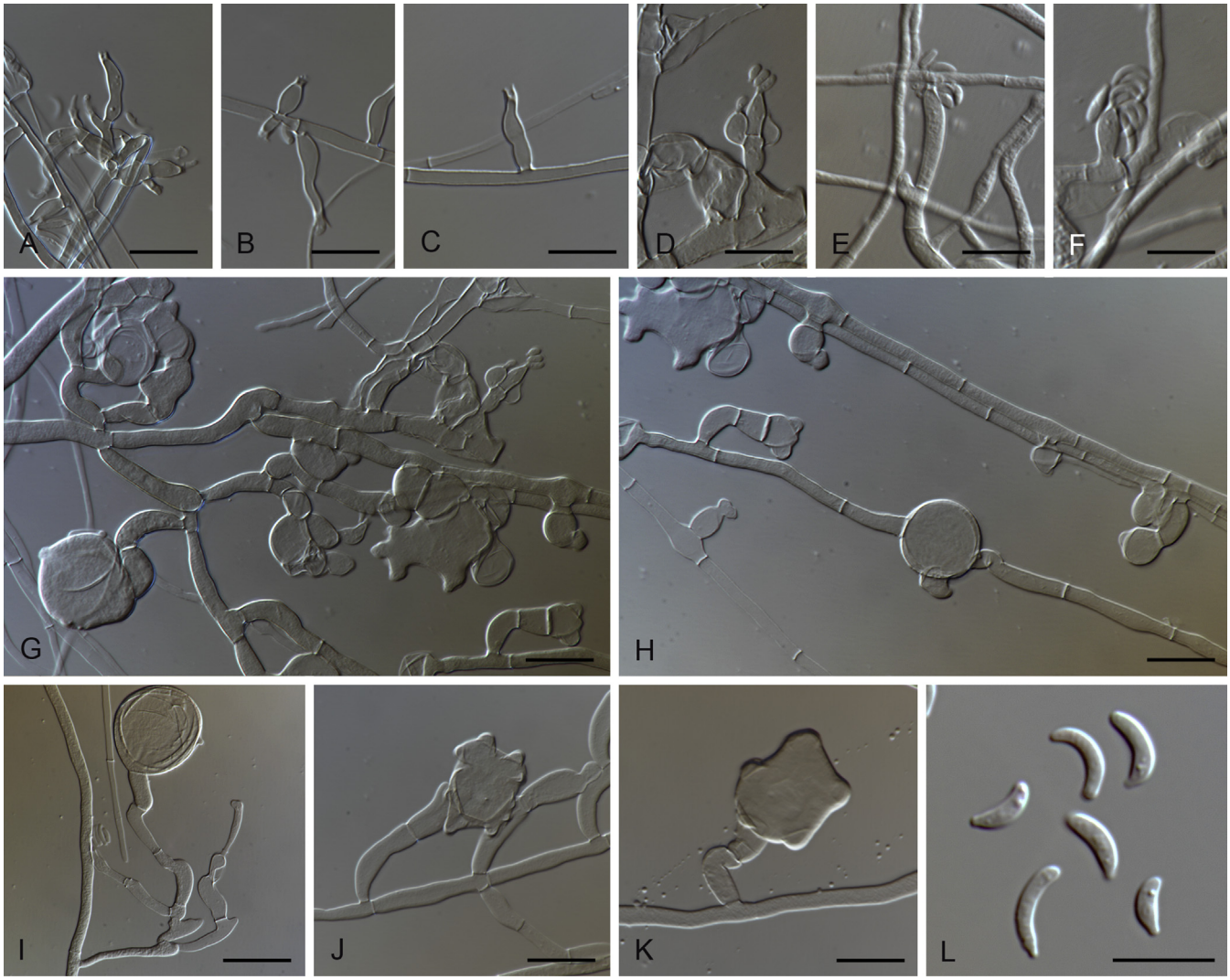

Fig. 8. *Gaeumannomyces ellisiorum* (CBS 387.81). A–F. Conidiogenous cells. G–K. Hyphopodia. L. Conidia. Scale bars: A–L = 10 µm.

The strain CPC 26037 formed a sub-clade together with *G. graminicola* and *G. fusiformis*. *Gaeumannomyces floridanus* is distinguished from *G. fusiformis* by its lunate conidia, and from *G. graminicola* in their hyphopodial pigmentation, being hyaline and brown in *G. floridanus* and brown in *G. graminicola*.

Gaeumannomyces fusiformis M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816895. Fig. 10.

Etymology: The name refers to the presence of fusiform conidia.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to brown, 1.5–5 µm diam hyphae. *Conidiophores* erect, simple or branched sometimes reduced to conidiogenous cells. *Conidiogenous cells* phialidic, terminal or intercalary, hyaline, cylindrical, straight to curved, 5–28 × 1.5–5 µm, with a cylindrical, refractive collarette, up to 2.5 µm, 1–2 µm diam. *Conidia* fusiform, tapering at the base, hyaline, 5–9.5 × 1–2.5 µm. *Hyphopodia* not observed.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 90 mm diam, aerial mycelium cottony, white, submerged mycelium rhizoid, hazel, margin rhizoid; reverse pale isabelline. On MEA reaching 60 mm diam, cottony, aerial mycelium moderate, white to grey, margin effuse; reverse umber in the centre, paler to the periphery. On OA reaching 90 mm diam, aerial mycelium scarce to moderate, cottony to funiculose, white, submerged mycelium olivaceous; reverse isabelline.

Specimen examined: **USA**, Arkansas, isolated from *Oryza sativa*, 1992, C. Rothrock G-8 (**holotype**, CBS H-22578, culture ex-type CBS 141379 = CPC 26068).

Notes: This is a single-isolate species isolated from *Oryza sativa* and phylogenetically placed in the Oryzinus clade with *G. graminicola* as sister group (Fig. 2). Morphologically it is distinct from *G. graminicola* and other species in the genus since it produces fusiform instead of lunate conidia.

Gaeumannomyces glycinicola M. Hern.-Restr., G. Canning & Crous, **sp. nov.** MycoBank MB816907. Fig. 11.

Etymology: The name refers to the host genus *Glycine*, from which this species was isolated.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, straight or flexuous, hyaline to brown, 1.5–4 µm diam

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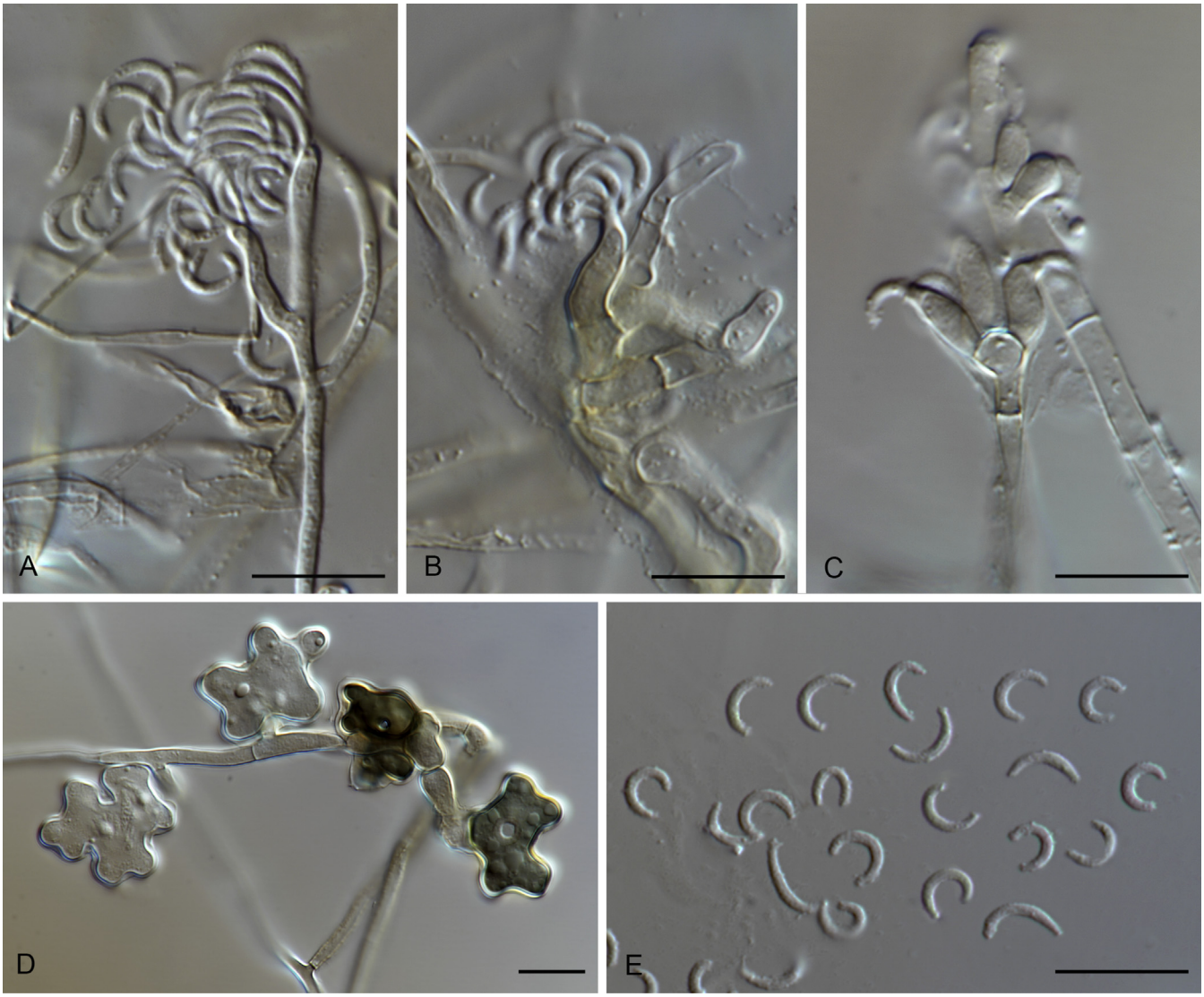

Fig. 9. *Gaeumannomyces floridanus* (CPC 26037). A, B. Conidiogenous cells and conidia. C. Conidiogenous cells. D. Hyphopodia. E. Conidia. Scale bars: A–D. = 10 µm.

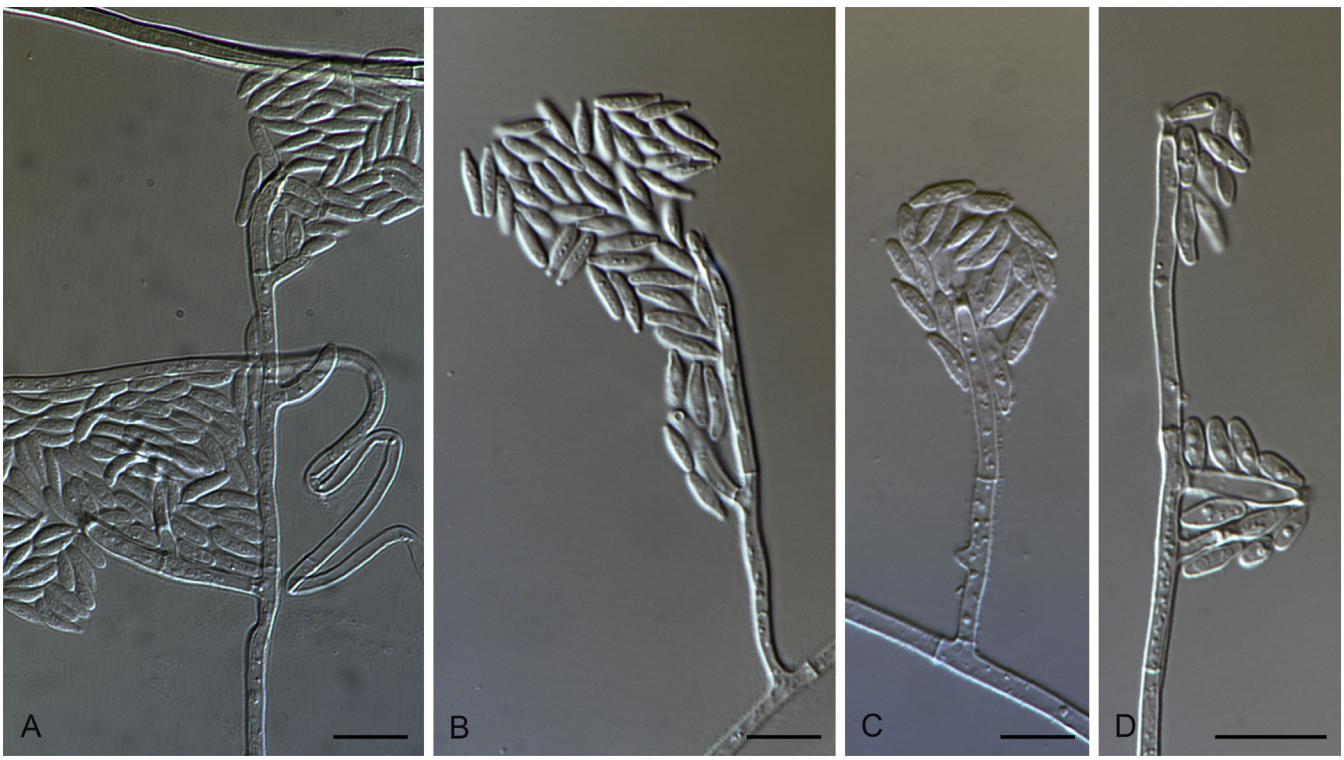

Fig. 10. *Gaeumannomyces fusiformis* (CPC 26068). A–D. Conidiophores, conidiogenous cells and conidia. Scale bars: A–D = 10 µm.

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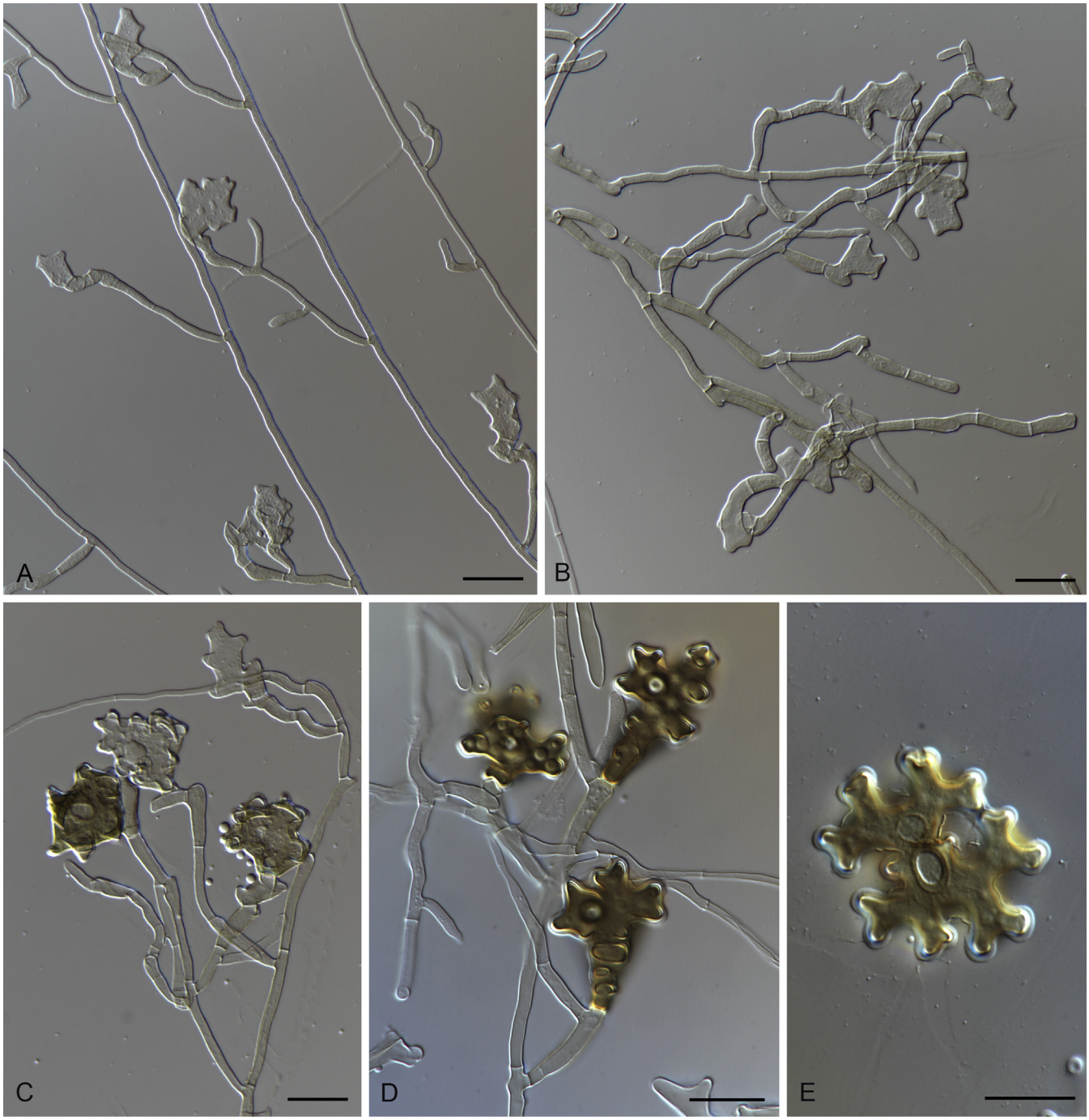

Fig. 11. *Gaeumannomyces glycinicola* (CPC 26266). A–E. Hyphopodia. Scale bars: A–E = 10 µm.

hyphae. *Hyphopodia* hyaline getting dark brown when mature, lobed, 22.5–43 × 15–34 µm diam. *Conidiophores* and *conidia* not observed.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 90 mm diam, aerial mycelium scarce, white, submerged mycelium rhizoid, pale cinnamon, margin rhizoid; reverse pale cinnamon. On MEA reaching 70 mm diam, cottony, aerial mycelium abundant, dense, white, submerged umber, margin effuse; reverse interweave, umber. On OA reaching 90 mm diam, cottony, moderate and colourless.

Specimens examined: **USA**, Indiana, isolated from *Glycine max*, 1974, D. Huber (**holotype**, CBS H-22579, culture ex-type CPC 26057 = DAR 28746); isolated from *Glycine max* (pods of soybean), 1974, unknown collector, CPC 26266 = CBS 141380.

Notes: Isolates CPC 26057 and CPC 26266, formerly classified as *Ggg*, grouped in the Tritici clade with *G. amomi* as sister group (Fig. 2). *Gaeumannomyces glycinicola* shows different ecological preferences compared to *G. amomi*. *Gaeumannomyces glycinicola* is the only *Gaeumannomyces* species reported from a dicotyledonous plant whereas *G. amomi* has been reported as an endophyte in *Amomum siamense* (Bussaban *et al.* 2001). In our study both isolates remained sterile on all media and conditions tested. Nevertheless, Roy *et al.* (1982) studied soybean isolates from Midwest USA (identified as *Ggg*) and

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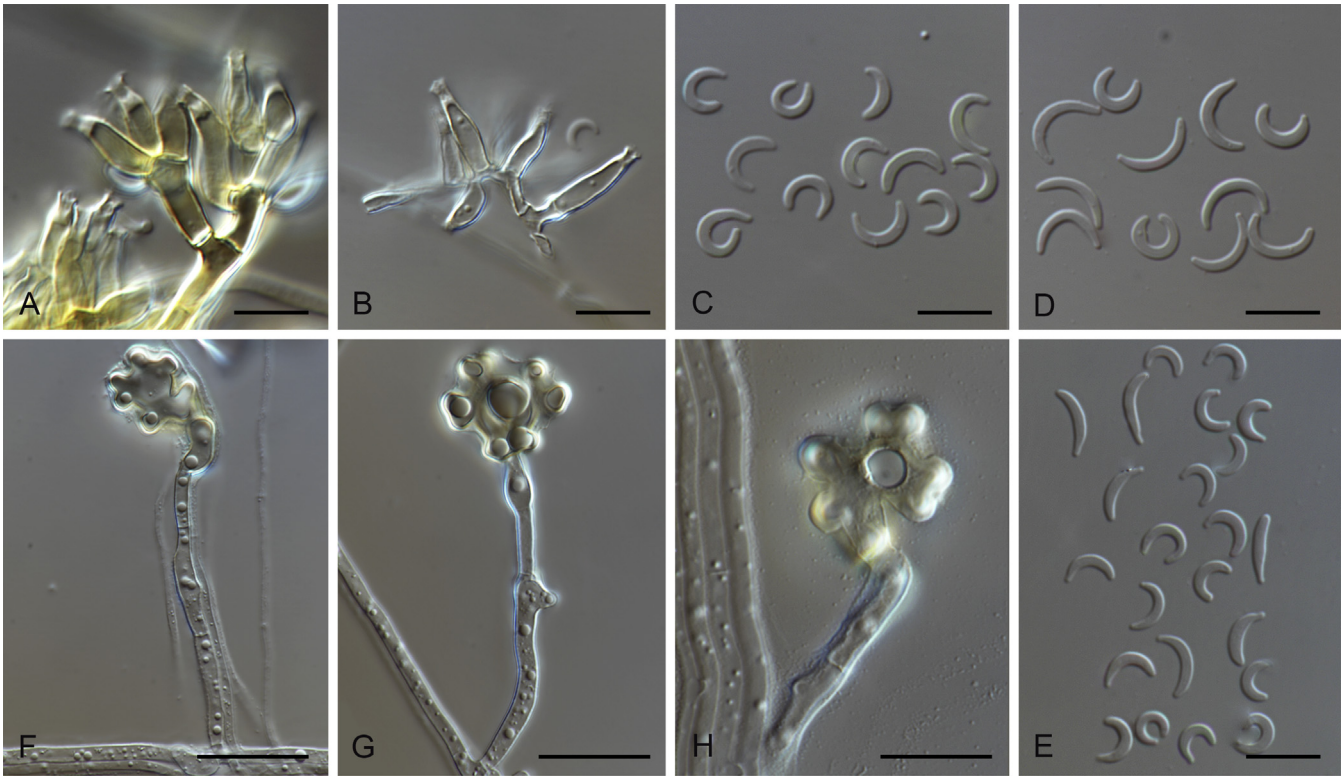

Fig. 12. *Gaeumannomyces graminicola* (CBS 352.93, CPC 26056, CPC 26025, CPC 26036). A, B. Conidiogenous cells. C–E. Conidia. F–H. Hyphopodia. Scale bars: A–H = 10 µm.

described perithecia as globose to ellipsoidal with cylindrical necks, pale to dark brown. Ascospores filiform, attenuated toward one end, measuring 71.6 ± 6.8 × 2.6 ± 0.5 µm, hyaline and multiseptate. Hyphopodia with one or more lobes, and brown. Although *G. glycinicola* is similar to *G. graminis* in hyphopodial morphology, and overlaps in ascospore dimensions, in our analyses *G. glycinicola* was phylogenetically distant from *G. graminis* (Fig. 2). Pathogenicity tests demonstrated that isolates from soybean produce the typical take-all symptoms on wheat, causing mild to severe infections, but disease symptoms were not observed on soybean leaves, stems or roots (Roy *et al.* 1982). On the other hand, *G. graminis* is not able to infect wheat. The presence of brown, lobed hyphopodia distinguishes *G. glycinicola* from *G. tritici* which produces simple hyphopodia as well as different aminopeptidase profiles (Roy *et al.* 1982).

Gaeumannomyces graminicola M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816896. Fig. 12.

Etymology: Named after the grass hosts from which it was isolated.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to brown, 1–4 µm diam hyphae. *Conidiophores* more or less differentiated, verticillate. *Conidiogenous cells* phialidic, hyaline to pale brown, solitary or grouped, terminal, sometimes intercalary, cylindrical, lageniform, 5–20 × 2–4.5 µm, collarette up to 3 µm long, 1–2.5 µm diam. *Conidia* lunate, slightly or strongly curved, hyaline, 5–11.5 × 1–2 µm. *Hyphopodia* lobed, brown, 16.5–24 × 15.5–23.5 µm.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 74 mm diam, flat, aerial mycelium scarce, cottony, white, submerged mycelium dark, in the centre hazel, grey, isabelline, olivaceous grey, buff to the periphery, margin effuse, rhizoid; reverse fuscous black, mouse grey or isabelline in the centre, no change to the periphery. On MEA reaching 76 mm diam, aerial mycelium moderate, cottony to funiculose, white, mouse grey to pale mouse grey, submerged mycelium dark (mouse grey), margin effuse, rhizoid; reverse centre fuscous, periphery amber white to white. On OA reaching 77 mm diam, flat, aerial mycelium scarce to moderate or abundant, cottony to funiculose, white, submerged mycelium dark, olivaceous grey, olivaceous black, dark mouse grey, margin effuse, rhizoid; reverse olivaceous, mouse grey, leaden grey, no change to the periphery.

Specimens examined: **Netherlands**, near Barendrecht, isolated from *Ctenanthe*, stem base, isol. J.W. Veenbaas-Rijks (**holotype**, CBS H-22580, culture ex-type CBS 352.93). **USA**, Florida, isolated from *Stenotaphrum secundatum*, 1988, M. Elliott, CPC 26022; 1990 M. Elliott, CPC 26025 = CBS 141381; 1991, M. Elliott, CPC 26036 = CBS 141382; Georgia, isolated from *Eremochloa ophiuroides*, 1994, H. Wilkinson, CPC 26056 = CBS 141383.

Notes: This species is represented by four isolates placed in the Oryzinus clade (Fig. 2). The strains were isolated from different grasses; i.e. *Ctenanthe*, *Stenotaphrum*, and *Eremochloa* from The Netherlands and USA. Formerly they were identified as *Ggg*; however the phylogenetic analyses place this species distant from *G. graminis*.

Gaeumannomyces graminis (Sacc.) Arx & Oliver, Trans. Br. mycol. Soc. 35: 32. 1952. Fig. 13.

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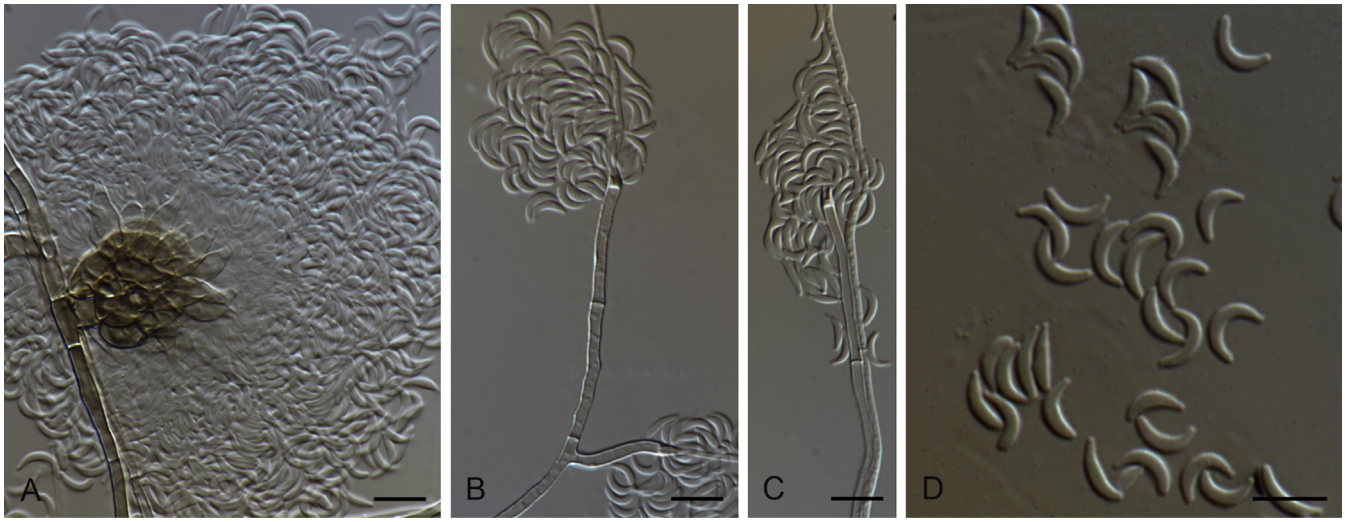

Fig. 13. *Gaeumannomyces graminis* (CPC 26035). A–C. Conidiophores, conidiogenous cells and conidia. D. Conidia. Scale bars: A–D = 10 µm.

Basionym: *Rhaphidophora graminis* Sacc., Fungi venet. nov. vel. Crit., Sér. 2: 307. 1875.

≡ *Ophiobolus graminis* (Sacc.) Sacc., Reliq. Libert 2: no. 134. 1875.
≡ *Ophiochaeta graminis* (Sacc.) Hara, Journal of Plant Protection, Tokyo 3: 342. 1916.
≡ *Gaeumannomyces graminis* (Sacc.) Arx & D.L. Olivier, Trans. Br. Mycol. Soc. 35: 32. 1952. var. *graminis*
≡ *Sphaeria cariceti* Berk. & Broome, Ann. Mag. nat. Hist., Ser. 3 7: 455. 1861.
≡ *Ophiobolus cariceti* (Berk. & Broome) Sacc., Syll. fung. (Abellini) 2: 349. 1883.
≡ *Linocarpon cariceti* (Berk. & Broome) Petr., Sydowia 6: 387. 1952.
≡ *Gaeumannomyces cariceti* (Berk. & Broome) Lar.N. Vassiljeva, Nizshie Rasteniya, Griby i Mokhoobraznye Dalnego Vostoka Rossii, Griby. Tom 4. Pirenomitsety i Lokuloaskomitsety (Sankt-Peterburg) 4: 146. 1998.

Type details: Saccardo, P.A. 1875. Fungi veneti novi vel critici. Series II. Nuovo Giornale Botanico Italiano. 7:299–329 [307–308] in PAD. Slides as DAR 21032. On *Cynodon* or *Agropyron*, Selva, Treviso, Italy, Oct. ? 1874.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to pale brown, 1–4 µm diam hyphae. *Conidiophores* differentiated, branched often verticillate, hyaline, pale brown to brown. *Conidiogenous cells* phialidic, solitary or grouped, terminal, hyaline to pale brown, cylindrical to lageniform, straight or curved, 7–30 × 1.5–4 µm, with a cylindrical to conical, refractive, collarette up to 3.5 µm long, 1–1.7 µm wide. *Conidia* lunate, allantoid, hyaline, 4–10 × 1–2 µm. *Hyphopodia* not observed.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 60 mm diam, aerial mycelium scarce to moderate, cottony, olivaceous grey, buff or isabelline, submerged mycelium darker, margin diffuse to rhizoid; reverse centre olivaceous grey, colourless to the periphery. On MEA reaching 62 mm diam, aerial mycelium abundant to moderate, cottony, pale olivaceous grey, darker to the periphery, submerged mycelium dark, margin effuse, rhizoid; reverse fuscous dark, rhizoid to the periphery. On OA reaching 62 mm diam, flat to cottony, greenish grey to grey olivaceous in the centre, white to colourless to the periphery, aerial mycelium moderate to abundant, white, submerged mycelium dark in the centre, margin effuse; reverse pale mouse grey.

Additional specimens examined: **USA**, Florida, isolated from *Cynodon dactylon* × *C. transvaalensis*, 1987, M. Elliott, CPC 26020 = CBS 141384; 1991, M. Elliott, CPC 26027; CPC 26029; CPC 26033 = CBS 141385; CPC 26035 = CBS 141386; 1992, M. Elliott, CPC 26039; CPC 26042; CPC 26045.

Notes: Isolates formerly identified as *Ggg* segregated into different species in the phylogenetic tree (Fig. 2). *Gaeumannomyces graminis*, the type species of the genus was originally described from Italy, on *Cynodon* or *Agropyron*. Unfortunately an epitype cannot be proposed at present since the isolates studied here are from a different geographic origin (USA). Based on host affinities we consider *G. graminis s. s.* as those strains isolated from *Cynodon* represented here by eight strains. The sister species was *G. oryzicola* which shows perithecia and an asexual morph in culture, characterised by conidiogenous cells scarce and cylindrical, with conidia fusiform, straight to slightly curved, while in *G. graminis* the perithecia were not observed in any of the studied isolates, and the asexual morph sometimes presents brown conidiophores with lunate conidia.

Gaeumannomyces graminis is a widespread species with a wide host range, variable pathogenicity, and high morphological and genetic diversity (Walker 1972, 1980, Bryan *et al.* 1995, Fouly et al. 1996, Ward & Bateman 1999, Saleh & Leslie 2004, Zhang *et al.* 2011, Sadeghi *et al.* 2012). *Gaeumannomyces graminis*, formerly recognised as the variety *graminis*, is characterised by perithecia immersed in culm and leaf sheath tissue, associated with a superficial mycelium producing both pale and brown hyphopodia. The asci are unitunicate, with an apical refractive ring and ascospores filiform, septate, hyaline, measuring (70–) 80–105(–110) × 2–3(–4) µm (Walker 1980). "*Phialophora* sp. (with lobed hyphopodia)" has been tentatively referred to as the asexual morph of *G. graminis* based on morphological observations of the asexual morph (Walker 1980). With the available data at that moment, Walker (1980) did not introduce a new species for "*Phialophora* sp. lobed hyphopodia". Nevertheless, in our study, strains identified as "*Phialophora*

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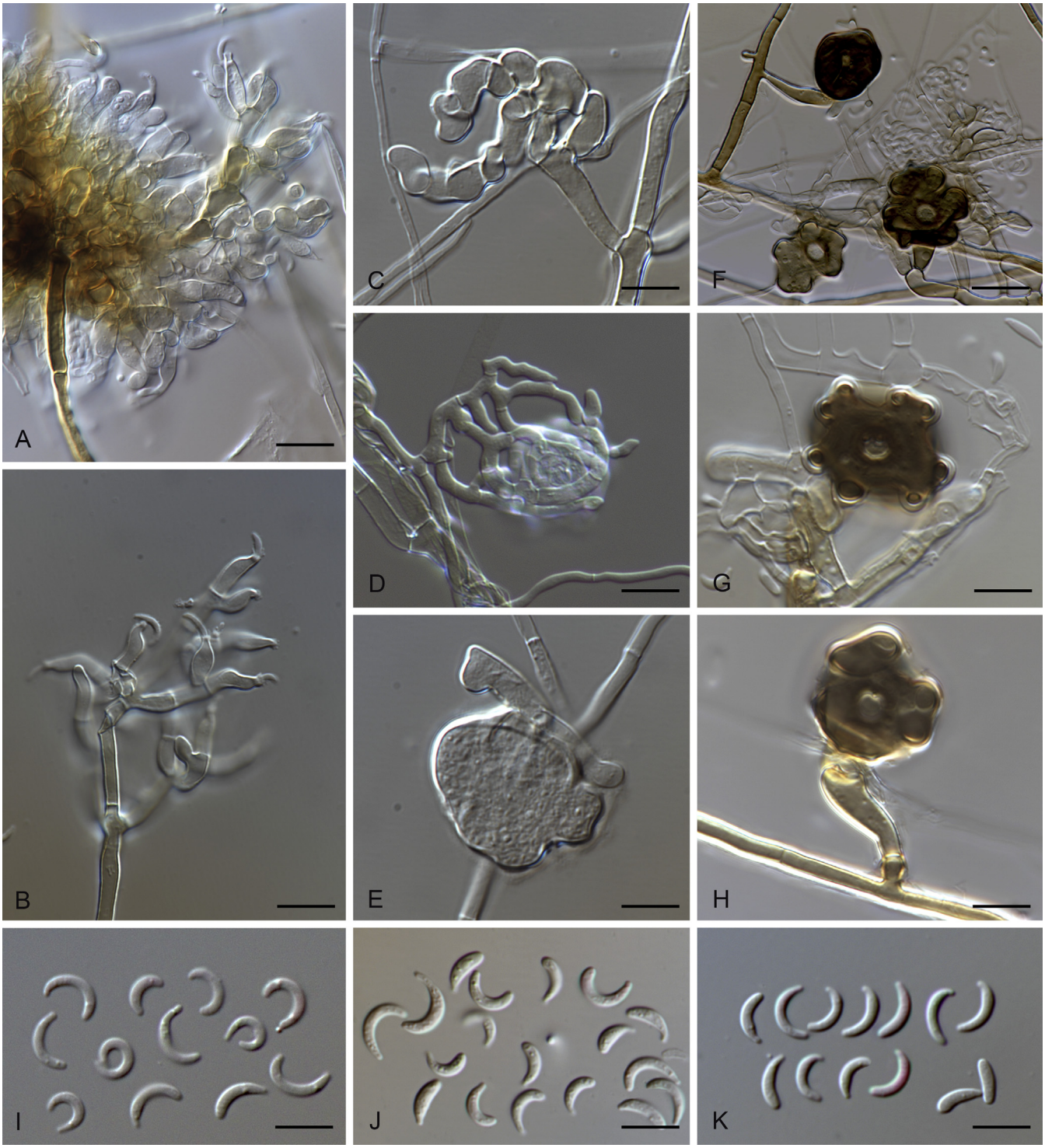

Fig. 14. *Gaeumannomyces hyphopodioides* (CBS 541.86, CBS 350.77, CPC 26248, CPC 26267) A, B. Conidiophores. C–D. Mycelium. E. Young hyphopodium. F–H. Hyphopodia. I–K. Conidia. Scale bars: A–H = 10 µm.

sp. lobed hyphopodia" from the UK, Poland, Australia and Germany were placed in the clade Radicicola (Fig. 2), and are here introduced as a new species to accommodate those isolates (see *G. hyphopodioides*).

Gaeumannomyces hyphopodioides M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816897. Fig. 14.

Etymology: hyphopodium – referring to the first approximation to this species "*Phialophora* sp. lobed hyphopodia" (Walker 1981).

= *Phialophora radicicola* var. *radicicola sensu* Deacon (1974) and subsequent British workers; NOT *P. radicicola* Cain var. *radicicola* (Cain 1952).

Description on PDA. *Mycelium* consisting of septate, branched, smooth, hyaline to red brown, 1–4 µm diam hyphae. *Conidiophores* differentiated, branched often verticillate, brown, sometimes reduced to conidiogenous cells. *Conidiogenous cells* phialidic, terminal or intercalary, hyaline to pale brown, cylindrical to lageniform, straight or curved, 7–21 × 2–4 µm, with a cylindrical to funnel-shaped collarette, up to 2.5 µm long, 1–2.5 µm

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diam. *Conidia* lunate, slightly to strongly curved, fusiform, allantoid, hyaline, 5.5–10.5 × 1–2 µm. *Hyphopodia* lobed, dark brown, 17–28 × 18–25 µm.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 85 mm diam, aerial mycelium abundant, cottony, white to grey, submerged mycelium hazel, olivaceous, dull green, margin effuse, rhizoid; reverse centre cinnamon, hazel, dark green, grey olivaceous, umber, dark olivaceous, colourless to the periphery. On MEA reaching 35–65 mm diam, aerial mycelium moderate, cottony, white to pale mouse grey, submerged mycelium grey to olivaceous grey, margin effuse; reverse dark (fuscous, olivaceous grey, dark brown). On OA reaching 20–55 mm diam, aerial mycelium scarce, white to grey, submerged mycelium grey, olivaceous black, margin effuse, rhizoid; reverse dark (olivaceous grey) or pale olivaceous, mouse grey, colourless to the periphery.

Specimens examined: **Australia**, New South Wales, isolated from *Pennisetum clandestinum*, 24 Oct. 1977, unknown collector, CPC 26267. **Germany**, Monheim, isolated from *Triticum aestivum*, seedling, unknown date, isol. A. Walz, CBS 541.86. **Poland**, Pulawy, isolated from wheat, 18 Oct. 1979, unknown collector, CPC 26252. **UK**, Butt Furlong, Woburn, Beds, isolated from oats, 27 Apr. 1983, unknown collector, CPC 26250; Essex, isolated from *Zea mays*, root, May 1972, J.W. Deacon G6 (**holotype**, CBS H-22582, culture ex-type CBS 350.77 = ATCC 28234 = IMI 187786); Hertfordshire, Fosters West, RRes, isolated from wheat, 11 Oct. 1985, unknown collector, CPC 26247 = CBS 141388; 29 Sep. 1989, unknown collector, CPC 26248; CPC 26249; West Barnfield, RRes, isolated from winter wheat, 9 Feb. 1990, unknown collector, CPC 26264 = CBS 141389; CPC 26265.

Notes: This species forms a distinct subclade in the Radicicola clade (Fig. 2) together with *G. radicicola* (ex-type culture CBS 296.53 and CBS 149.85), *G. wongoonoo* (BRIP 60376) and *G. setariicola* (CPC 26059). It is represented by strains isolated from *Zea mays*, *Triticum*, *Avena*, and *Pennisetum*, mainly from the UK, and others from Australia, Germany, and Poland.

Walker (1980) referred to this species as "*Phialophora* sp. (with lobed hyphopodia)". He found this species morphologically similar to the superficial mycelia present in *Ggg*. Nevertheless, he noticed that the isolates of "*Phialophora* sp. (with lobed hyphopodia)" from France, England and Australia from different substrates never developed perithecia. Our results show that *G. hyphopodioides* is different from *G. graminis* and is phylogenetically closer to *G. radicicola* than *G. graminis*. *Gaeumannomyces hyphopodioides* is different from *G. radicicola* in having lobed hyphopodia; McKeen (1952) described *G. radicicola* as having simple, brown hyphopodia (as chlamydospores with a pore). In addition some differences in pathogenicity are reported. *Gaeumannomyces radicicola* has been associated with root rot in corn (Cain 1952, McKeen 1952). The strain CBS 350.77 of *G. hyphopodioides* isolated from corn exhibits low virulence (Deacon 1973, Walker 1980).

Two of the isolates studied by Walker (1980) are represented in our tree as CBS 350.77 and CPC 26267. Walker (1980) found that the British (CBS 350.77), and the Australian (CPC 26267) isolates had identical serological tests. In our study those strains are placed in *G. hyphopodioides* together with other isolates from the UK, Poland and Germany.

Gaeumannomyces oryzicola M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816898. Fig. 15.

Etymology: Named after the host from which it was isolated, *Oryza*.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to brown, 2–6 µm diam hyphae. *Ascomata* perithecial, superficial and submerged, globose, subglobose to elliptical, 110–413 × 112–525 µm with a cylindrical neck, dark brown, 22–30 × 38–47 µm. *Peridium textura epidermoidea*. *Paraphyses* hyaline, septate, dissolving at maturity. *Asci* numerous, unitunicate, cylindrical to elongated clavate, shortly stalked, with apical refringent ring, 8 ascospores, 118–148 × 14–16 µm. *Ascospores* faintly tinted yellowish in mass, hyaline to pale brown, vacuolated, slightly curved to sinuate, ends rounded, 92.5–120 × 4–6, 0–5-septate, septa often indistinct. *Conidiophores* if present slightly differentiated. *Conidiogenous cells* phialidic, terminal or intercalary, hyaline, cylindrical, 7.5–20.5 × 2–2.5 µm, with a cylindrical collarette, up to 3 µm long, 1.5–2 µm diam. *Conidia* lunate, allantoid to fusiform, hyaline, 5–9 × 1.5–2.5 µm. *Hyphopodia* not observed.

Specimen examined: **USA**, Texas, isolated from *Oryza sativa*, prior to 1992, J. Krausz (**holotype**, CBS H-26063, culture ex-type CBS 141390 = CPC 26063).

Notes: *Gaeumannomyces oryzicola* is represented by a single isolate in the Graminis clade. In the phylogenetic tree (Fig. 2), it clustered as the sister species of *G. graminis*.

Gaeumannomyces oryzinus (Sacc.) Schrantz., Bull. trimest. Soc. mycol. Fr. 76: 337. 1961. Fig. 16.
Basionym: *Ophiobolus oryzinus* Sacc., Nuovo Giornale Botanico Italiano 23: 203. 1916.
≡ *Linocarpon oryzinum* (Sacc.) Petr., Sydowia 6: 387. 1952.
≡ *Gaeumannomyces oryzinus* (Sacc.) Schrantz as "*oryzinum*", Bull. trimest. Soc. mycol. Fr. 76: 337. 1961.
= *Linospora pulchella* Speg. Anal. Mus. Nac. Hist. Nat. Buenos Aires 23: 71. 1912.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to brown, 1.5–6 µm diam hyphae. *Ascomata* perithecial, superficial and submerged, globose, subglobose to elliptical, with a cylindrical neck, dark brown to black. *Peridium textura epidermoidea*. *Paraphyses* hyaline, septate, often constricted at the septa, widest at the base and gradually narrow at the apex, dissolving at maturity. *Asci* numerous, unitunicate, cylindrical to elongated clavate, shortly stalked, with apical refringent ring, 8 ascospores, 113–173.5 × 14.5–24. *Ascospores* faintly tinted yellowish in mass, hyaline to pale brown, vacuolated, slightly curved to sinuate, ends rounded, widest in the middle, tapering toward the base, 96–116 × 3.5–5.5, 0–3-septate, septa often indistinct. *Conidiophores* if present slightly differentiated. *Conidiogenous cells* phialidic, terminal or intercalary, pale brown sometimes hyaline, cylindrical to lageniform, straight or curved, 5–21 × 2–5 µm, with a cylindrical to funnel-shaped collarette, up to 2.8 µm long, 1–2 µm diam. *Conidia* lunate, allantoid to fusiform, hyaline, 5–11 × 1–2.5 µm. *Hyphopodia* if present lobed, brown, 19–45 × 15.5–36 µm diam.

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Fig. 15. *Gaeumannomyces oryzicola* (CPC 26063). A. Perithecium. B–E. Asci. F. Ascospores. G–I. Conidiogenous cells. J. Conidia. Scale bars: A, B = 50 µm; C–E = 20 µm, F–J = 10 µm.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 79 mm diam, aerial mycelium scarce to moderate, white to pale grey, submerged mycelium dark (dark to grey olivaceous, isabelline, olivaceous, smoke grey). On MEA reaching 80 mm diam, aerial mycelium moderate to abundant, cottony to funiculose, mouse grey, pale mouse grey, isabelline, pale olivaceous grey, greenish olivaceous, smoke grey, to the periphery white, submerged mycelium dark (fuscous, isabelline, mouse grey), margin effuse, rhizoid; reverse fuscous in the centre, white to the periphery or colourless. On OA reaching 85 mm diam, aerial mycelium moderate, mouse grey, submerged mycelium dark, margin effuse, rhizoid; reverse mouse grey, olivaceous grey, colourless to the periphery.

Specimens examined: **Bahamas**, New Providence, isolated from *Cynodon dactylon* × *C. transvaalensis*, 1991, M. Elliott, CPC 26030 = CBS 141391. **USA**, Arkansas, Stuttgart, isolated from *Oryza sativa*, Nov. 1931, E.C. Tullis, CBS 235.32; Florida, isolated from *Oryza sativa*, 1991, M. Elliott, CPC 26031; CPC 26032; 1992, L. Datnoff, CPC 26043 = CBS 141392; Arkansas, isolated from *Oryza sativa*, 1992, C. Rothrock, CPC 26065; CPC 26066; CPC 26067 = CBS 141393.

Notes: In our phylogenetic tree *G. oryzinus* is represented by seven isolates on *Oryza sativa* from the USA and one isolate on *Cynodon* from The Bahamas. Among the USA strains, CBS 235.32 was also studied by Walker (1972) as BRIP 3517.

Gaeumannomyces oryzinus was introduced as *Ophiobolus oryzinus* by Saccardo in 1916, growing on rotting *Oryza sativa* culms in the Philippines. Later it was treated as a synonym of *Ggg* by Walker (1972), who studied the holotypes of both species and concluded that they were the same species. Nevertheless, our phylogenetic studies demonstrate that *G. graminis* and *G. oryzinus* are distinct species.

Other species isolated from *Oryza sativa* are different from *G. oryzinus*; for instance, *G. fusiformis* has fusiform conidia and in *G. oryzicola* the ascospores are larger and have more septa (92.5–120 × 4–6 µm; 0–5 septa), and phylogenetically distant, being placed in the Graminis clade (Fig. 2).

Gaeumannomyces radicicola (Cain) J. Luo & N. Zhang, Mycologia 107: 644. 2015. Fig. 17.

Basionym: *Phialophora radicicola* Cain, Canad. J. Bot. 30: 340. 1952.

≡ *Phialophora radicicola* var. *radicicola* Cain, Canad. J. Bot. 30: 340. 1952. [NOT *Phialophora radicicola* var. *graminicola*, Deacon 1974].

= *Harpophora radicicola* (Cain) W. Gams, Stud. Mycol. 45: 192. 2000.

= *Phialophora zeicola* Deacon & D.B. Scott, Trans. Br. Mycol. Soc. 81: 256. 1983.

≡ *Harpophora zeicola* (Deacon & D.B. Scott) W. Gams, Stud. Mycol. 45: 192. 2000.

= *Gaeumannomyces graminis* var. *maydis* J.M. Yao, Yong C. Wang & Y.G. Zhu, Acta Mycol. Sin. 11: 99. 1992. [Type details. China, Province Liaoning, Tiling, *Xu Heng-wu*. On basal internodes of *Zea mays*. Shenyang Agricultural University, MHSAU 3805].

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Fig. 16. *Gaeumannomyces oryzinus* (CBS 235.32, CPC 26032, CPC 26065, CPC 26067) A. Perithecium. B–G. Asci. H–I. Ascospores. J–M, O, Q–S. Conidiogenous cells. N, P, T. Conidia. U, V. Hyphopodia. Scale bars: A–C = 50 µm; D–I = 20 µm, J–V = 10 µm.

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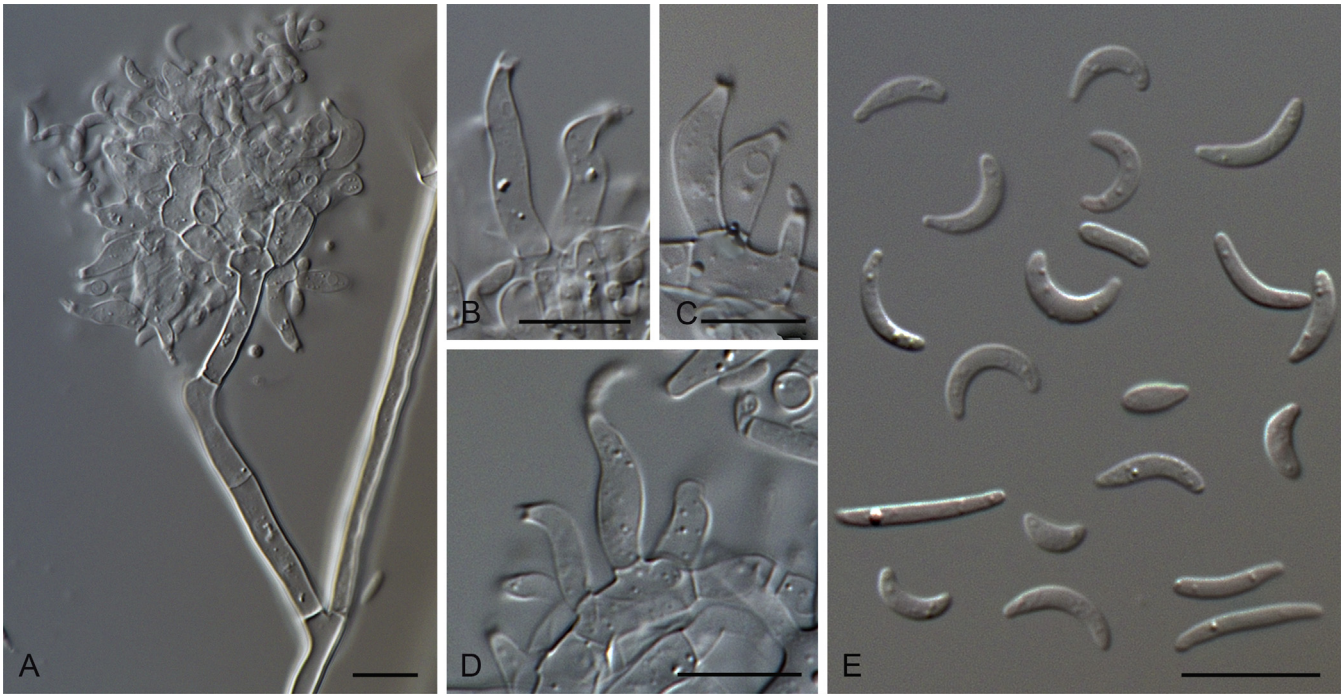

Fig. 17. *Gaeumannomyces radicicola* (CBS 296.53). A. Conidiophores. B–D. Conidiogenous cells. E. Conidia. Scale bars: A–E = 10 µm.

Specimens examined: **Canada**, Ontario, Chatham, isolated from *Zea mays*, root, 1950, R.F. Cain (**isotype** of *Phialophora radicicola* CBS H-7592, CBS H-7593, culture ex-isotype of *Phialophora radicicola*, CBS 296.53). **South Africa**, unknown locality, isolated from *Zea mays*, Feb. 1984 (**isotype** of *Phialophora zeicola* CBS H-7597, culture ex-isotype of *Phialophora zeicola*, CBS 149.85).

Notes: *Gaeumannomyces radicicola* was described as a corn root-rot pathogen in Canada (Cain 1952, McKeen 1952). Later Yao *et al.* (1992) introduce *Ggm* for the take-all fungus of maize as a new variety of *G. graminis*. Morphologically it is characterised by perithecia, asci and ascospores typical for *Gaeumannomyces*, with a phialophora-like asexual morph and simple to slightly lobed hyphopodia.

Based on ITS sequence analyses Ward & Bateman (1999) concluded that *Ggm* and *G. radicicola* (represented by isolates of *P. radicicola* and *P. zeicola*) were conspecific, but the authors did not formally propose the synonymy. Comparing those GenBank sequences with our dataset, we introduce *Ggm* as synonym of *G. radicicola*.

Gaeumannomyces setariicola M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816899. Fig. 18.

Etymology: The name refers to the host genus *Setaria*, from which this species was isolated.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to brown, 1.2–4 µm diam hyphae. *Conidiophores* simple or verticillate, often reduced to conidiogenous cells. *Conidiogenous cells* mono- or poly-phialidic, terminal or intercalary, hyaline, cylindrical to lageniform, straight to curved, 6.5–28.5 × 2–4 µm, with a cylindrical to funnel-shaped, refractive collarette, up to 3 µm long, 1.5–2.5 µm diam. *Conidia* lunate, allantoid to fusiform strong to slightly curved, tapered at the base, hyaline, 4–12 × 1–2 µm. *Hyphopodia* not observed.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 85 mm diam, flat, aerial mycelium scarce, light isabelline in the centre, smoke grey to the periphery, submerged mycelium darker, margin rhizoid; reverse isabelline. On MEA reaching 75 mm diam, cottony, aerial mycelium abundant, pale greenish grey, margin rhizoid; reverse fuscous in the centre, white-amber to the periphery. On OA reaching 65 mm diam, flat, aerial mycelium scarce, colourless, submerged mycelium with grey olivaceous "zones"; reverse similar.

Specimen examined: **South Africa**, Limpopo province, Warmbaths (current name is Bela-Bela), isolated from *Setaria italica*, 1981, D.B. Scott (**holotype**, CBS H-22584, culture ex-type CBS 141394 = PRRI 4754 = CPC 26059).

Notes: This species is represented by one strain isolated from *Setaria italica* in the Radicicola clade (Fig. 2). *Gaeumannomyces setariicola* showed the typical characteristics of harpophora-like fungi; however, hyphopodia were not observed.

Gaeumannomyces tritici (J. Walker) Hern.-Restr. & Crous, **comb. et stat. nov.** MycoBank MB816900.
Basionym: *Gaeumannomyces graminis* var. *tritici* J. Walker, Trans. Br. Mycol. Soc. 58: 439. 1972.

Type details: **Australia**, New South Wales, Dubbo, on wheat, 20 Oct. 1969, GM Murray, DAR 17916.

Additional specimens examined: **Argentina**, La Pampa, isolated from *Triticum aestivum*, 9 Feb. 1935, isol. L. Grodsinsky, CBS 273.36. **Australia**, South Australia, Mortlock, isolated from *Triticum aestivum*, 16 Dec. 1980, unknown collector, CPC 26268 = CBS 141396; Western Australia, Carnamah, isolated from *Triticum aestivum*, 28 Oct. 1970, A. Parker, DAR 23140 = CBS 905.73; unknown locality, unknown substrate, 29 Nov. 1983, unknown collector, CPC 26274. **Brazil**, Espumoso, isolated from wheat, 9

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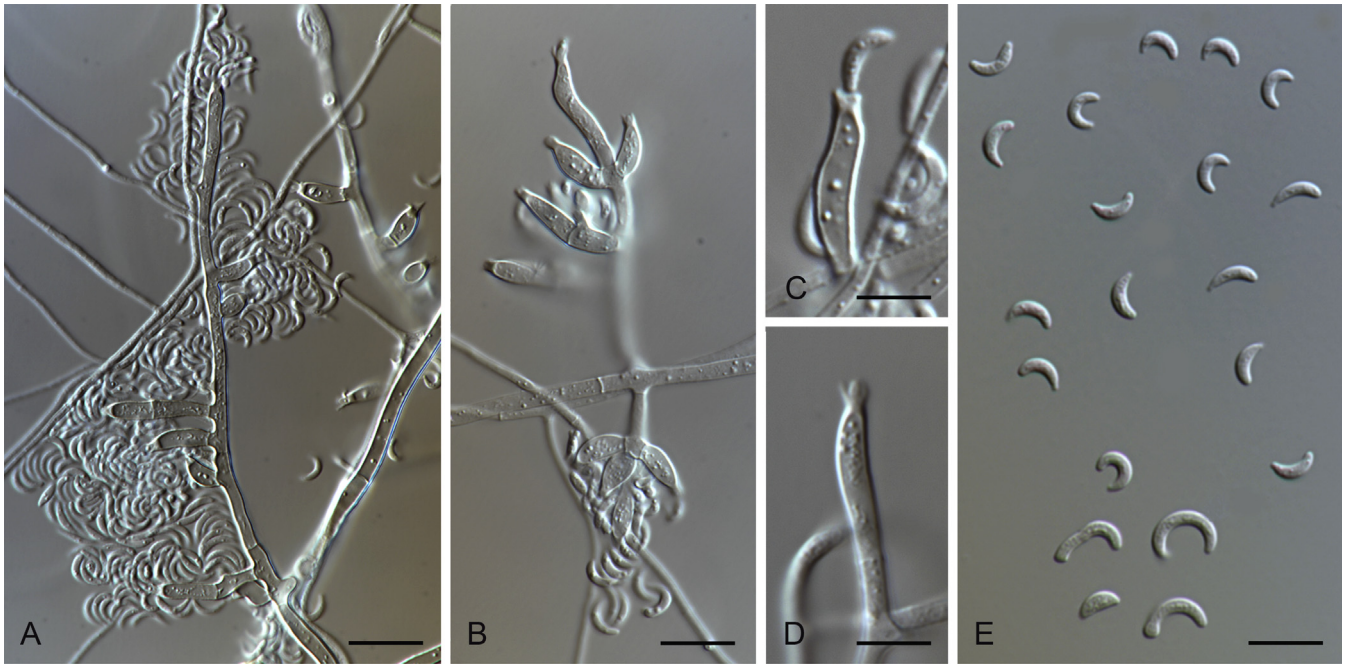

Fig. 18. *Gaeumannomyces setariicola* (CPC 26059). A–D. Conidiophores and conidia. E. Conidia. Scale bars: A–E = 10 µm.

Feb. 1982, unknown collector, CPC 26269 = CBS 141397; unknown locality, unknown substrate, 9 Feb. 1982, D. Hornby Girua, CPC 26276. **Netherlands**, Oostelijk Flevoland, isolated from *Hordeum vulgare*, isol. M. Gerlagh No. My53g, CBS 186.65; unknown locality, isolated from *Triticum*, unknown date, dep. H.A. Diddens, CBS 247.29. **UK**, Far Field II Woburn, Beds, isolated from *Elymus repens* (couch grass), 9 Jun. 1988, unknown collector, CPC 26273 = CBS 141398; Peterborough, unknown substrate, 1999, unknown collector, CPC 26280; Hertfordshire, RRes, isolated from *Bromus* sp. (brome grass), 26 Feb. 1982, unknown collector, CPC 26275; isolated from *Agropyron*, 26 Feb. 1982, unknown collector, CPC 26278; unknown substrate, 1992, unknown collector, CPC 26281; Great Harpenden, isolated from couch grass, 21 Aug. 1980, unknown collector, CPC 26277; New Zealand fields, RRes, isolated from *Triticum aestivum* (winter wheat), 1 Sept. 2012, G. Canning, CPC 26282 = CBS 141399; CPC 26283; Pastures, isolated from wheat, 24 Jun. 1988, unknown collector, CPC 26271; Summerdells, isolated from *Hordeum vulgare* (winter barley), 4 Mar. 1987, unknown collector, CPC 26272. **USA**, Montana, isolated from *Triticum* sp., unknown date, Juhnke, CBS 131293; unknown locality, unknown substrate, prior to 1987, R. Smiley, CPC 26069 = CBS 141395. **Unknown country**, unknown locality, isolated from *Triticum aestivum*, Dec. 1929, isol. C.A. Jörgensen, CBS 249.29.

Notes: *Ggt* was introduced as a variety of *G. graminis* (for a misapplied *Ophiobolus graminis*) for the wheat take-all fungus (Walker 1972). Walker (1972) distinguished *Ggt* from *Ggg* and *Gga* in their hyphopodial morphology, ascospore size and pathogenicity. In *Ggt* hyphopodia are not lobed as in *Ggg*, ascospores are shorter than in *Gga*, and *Ggt* is pathogenic to wheat. In our study, isolates received as *Ggt* grouped in a clade (Fig. 2), representing different species from *G. graminis* and *G. avenae*, and here we propose *G. tritici* comb. et stat. nov. for those isolates.

Gaeumannomyces tritici is the most aggressive species in the genus, is widespread, and found mainly on *Triticum*, but was also reported growing on other hosts as well. In our phylogenetic tree this species was represented by isolates from *Triticum*, *Hordeum, Elymus repens* and *Agropyron*.

Gaeumannomyces walkeri M. Hern.-Restr. & Crous, **sp. nov.** MycoBank MB816901. Fig. 19.

Etymology: Named after John Walker, for his contributions to understanding the taxonomy and pathology of *Gaeumannomyces*.

Description on MEA. *Mycelium* consisting of septate, branched, smooth, hyaline to brown, 1–4.5 µm diam hyphae. *Conidiophores* semi- to macronematous branched often verticillate. *Conidiogenous cells* phialidic, terminal or intercalary, hyaline, cylindrical to lageniform, straight or curved, 6–23 × 2–3.5 µm, with a funnel-shaped collarette, up to 2.5 µm long, 1–2.5 µm diam. *Conidia* initially (8 d) fusiform, 7.5–11 × 2–3 µm, becoming lunate, slightly to strongly curved, allantoid to fusiform, sinuous, hyaline, 5–14 × 1–1.5 µm. *Hyphopodia* lobed, brown, 20–31 × 18.5–24.5 µm.

Culture characteristics: After 7 d at 25 °C: On PDA reaching 65 mm diam, flat, aerial mycelium scarce, pale olivaceous in the centre, colourless to the periphery, margin effuse; reverse pale olivaceous. On MEA reaching 70 mm diam, cottony, funiculose aerial mycelium abundant, white, margin rhizoid; reverse umber, darker in the centre. On OA reaching 60 mm diam, cottony, aerial mycelium moderate, white, submerged mycelium grey olivaceous; reverse isabelline.

Specimen examined: **USA**, Alabama, isolated from *Stenotaphrum secundatum*, 1991, M. Elliott (**holotype**, CBS H-22586, culture ex-type CBS 141400 = CPC 26028 = FL156).

Note: This species is represented by one strain that is placed in the Tritici clade with *G. arxii* as sister group (Fig. 2).

Gaeumannomyces wongoonoo P. Wong, Mycol. Res. 106: 861. 2002.

Notes: This species is only known from the type locality, Australia (Wong 2002), and was placed in the Radicicola clade (Fig. 2).

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Fig. 19. *Gaeumannomyces walkeri* (CPC 26028). A–D. Conidiophores and conidiogenous cells. E, F. Hyphopodia. G. Conidia at 7 days. H. Conidia at 14 days. Scale bars: A–H = 10 µm.

Compared with the other species in the clade, *G. wongoonoo* has shorter (36–75 × 3–5 µm) ascospores than *G. radicicola* (55–85 × 2.5–4 µm), and wider conidia than other species in this clade (5–12.5 × 3–5 µm, Wong 2002).

Pathogenicity tests demonstrated that this species is pathogenic on *Stenotaphrum secundatum* (buffalo grass) causing "wongoonoo patch" and it was not pathogenic to wheat or maize (Wong 2002).

DISCUSSION

This is the first study that presents a robust phylogeny using a broad distribution of *Gaeumannomyces* isolates from different hosts and geographic origins. Based on our phylogenetic analyses two new genera with harpophora-like asexual morphs are introduced in *Magnaporthaceae*: *Falciphoriella* and *Gaeumannomycella*. By combining multi-locus data from ITS, LSU, *rpb1* and *tef1* sequences with morphological analyses, we were able to delimit 19 species in *Gaeumannomyces*, 12 of which are formally proposed as new species and two as new combinations. The taxonomic status of two unique phylogenetic lineages (CPC 26245 and CPC 26284) remains unresolved as they were only represented in our tree by single sterile isolates.

Traditionally, isolates of *G. graminis* had been classified in four varieties; *Ggg*, *Gga*, *Ggt* and *Ggm* (Turner 1940, Dennis 1960, Walker 1972, Yao *et al.* 1992). However, this classification was inconsistent with our results. Previous molecular studies had shown *Ggg* as the genetically most diverse variety (Ward & Bateman 1999, Ulrich *et al.* 2000, Freeman & Ward 2004). Ward & Bateman (1999), based on ITS sequences, recognised three groups in *Ggg*: *Ggg* I, *Ggg* II and *Ggg* III. Nevertheless, no taxonomic changes or new species were proposed by the authors. These results agree with our phylogenetic analyses; isolates formerly identified as *Ggg* presented a high genetic diversity and we find 14 cryptic species; named *G. arxii*, *G. australiensis*, *G. californicus*, *G. ellisiorum*, *G. floridanus*, *G. fusiformis*, *G. glycinicola*, *G. graminicola*, *G. graminis*, *G. hyphopodioides*, *G. oryzicola*, *G. oryzinus*, *G. setariicola* and *G. walkeri*.

Much confusion has prevailed in the naming of *Gaeumannomyces*, especially in the varieties of *G. graminis*. Walker (1972, 1980, 1981) studied type specimens and several collections of *Gaeumannomyces* in detail. He found that *Ophiobolous oryzinus* (= *Gaeumannomyces oryzinus*), described by Saccardo on rotting rice culms from the Philippines, was conspecific with *Ggg*. Nevertheless, in our phylogenetic analyses strains that were isolated from *Oryza sativa*, including the CBS 235.35 material studied by Walker (1972), formed a separate clade from *G. graminis s. s.* representing a different species; resulting in the

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resurrection of *G. oryzinus*. On the other hand, the presumed anamorph of *Ggg* was referred to as "*Phialophora* sp. with lobed hyphopodia" (Walker 1980, 1981). However, our phylogenetic analyses show that isolates identified as "*Phialophora* sp. with lobed hyphopodia", form a separate clade and we therefore introduce here as a new species *G. hyphopodioides* to accommodate those isolates.

An interesting result generated in the present study was that a well-supported clade comprising mainly of wheat and oat isolates, formerly identified as *Ggt* and *Gga*, clustered outside the *G. graminis* clade, and represent different species, *G. avenae* and *G. tritici*. This is consistent with previous studies, which indicated that *G. avenae* and *G. tritici* are more virulent pathogens than *G. graminis*. Both present simple hyphopodia and are phylogenetically related (Walker 1972, 1980, Ward & Bateman 1999, Freeman & Ward 2004, Saleh & Leslie 2004).

Ggm was introduced for a fungus with simple hyphopodia growing on maize (Yao *et al.* 1992). Based on ITS sequences (Ward & Bateman 1999) of *Ggm*, it was shown to be conspecific with *G. radicicola*, but the authors did not formally propose the synonymy. After comparing those GenBank sequences with our results, here we introduce *Ggm* as synonym of *G. radicicola*. Unfortunately no strains of *Ggm* were available to us to sequence additional loci for the combined analyses.

In the past, ascospore size, hyphopodial morphology and host preference used to be regarded as the most important criteria to discriminate species and varieties of *Gaeumannomyces* (Turner 1940, Walker 1972, 1981, Deacon 1973, 1974, Yao *et al.* 1992). Ascospores and hyphopodia produced in the natural substrate have proven to be useful in the differentiation of the varieties in *G. graminis*, but do not always develop in culture. The variability in host range within *Gaeumannomyces* is so great that grouping isolates based on host origin alone is problematic for predicting pathogenicity and genetic relatedness. Wheat isolates belong mainly to *G. tritici*, but isolates from this substrate can also be identified as *G. hyphopodioides* or *G. australiensis*. Oat isolates grouped mainly in *G. avenae*, even though one isolate was placed in *G. hyphopodioides*. *Oryza sativa* is a common substrate for *G. oryzinus*, *G. oryzicola* and *G. graminicola*. Although strains used in the present study were collected globally, the USA and UK are over-represented whereas Asia, Africa and Central and South America are less well-represented.

Gaeumannomyces spp. are morphologically difficult to distinguish because of their simple morphology, the overlapping of many features and considerable intraspecific variation. Molecular identification is mandatory to classify species in *Gaeumannomyces*. The four gene loci used in this study were chosen based on their previous use in molecular studies in *Magnaporthales* (Zhang *et al.* 2011, Klaubauf *et al.* 2014). The ITS and *rpb1* loci are more or less equal in their ability to distinguish species in this genus (17 / 19 and 15 / 17, respectively), whereas LSU and *tef1* are not very successful in distinguishing species in this genus (9 / 19 and 11 / 18, respectively). By combining ITS and *rpb1* it is possible to resolve the phylogenetic position of *G. oryzicola* as an individual species, different from *G. oryzinus* and *G. graminis*. Based on ITS sequences *G. oryzicola* is placed in the *G. oryzinus* species clade, whereas based on rpb1 sequences it is placed in *G. graminis*.

In addition to providing a phylogenetic overview of an important phytopathogenic genus, *Gaeumannomyces*, this study offers reliable sequences and cultures for future studies. The lack of type or reference strains in this genus makes the correct identification of a species difficult and confusing; this was partly addressed in the present study by designating ex-epitype culture for *G. avenae*. Unfortunately it was not possible to propose epi- or neotypes for all known species, since the geographical origins of included isolates were not the same as described in the protologues (e.g. *G. graminis* and *G. oryzinus*).

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REFERENCES

Augustin C, Ulrich K, Ward E, *et al*. (1999). RAPD-based inter- and intravarietal classification of fungi of the *Gaeumannomyces–Phialophora* complex. *Journal of Phytopathology* **147**: 109–117.

Bateman GL, Ward E, Antoniw JF (1992). Identification of *Gaeumannomyces graminis* var. *tritici* and *G. graminis* var. *avenae* using a DNA probe and non-molecular methods. *Mycological Research* **96**: 737–742.

Bryan GT, Daniels MJ, Osbourn AE (1995). Comparison of fungi within the *Gaeumannomyces–Phialophora* complex by analysis of ribosomal DNA sequences. *Applied and Environmental Microbiology* **61**: 681–689.

Bussaban B, Lumyong S, Lumyong P, *et al*. (2001). Two new species of endophytes (*Ascomycetes*) from *Zingiberaceae* sporulating in culture. *Nova Hedwigia* **73**: 487–493.

Cain RF (1952). Studies of fungi imperfecti I. *Phialophora*. *Canadian Journal of Botany* **30**: 338–343.

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.

Crous PW, Verkley GJM, Groenewald JZ, *et al*. (2009). *Fungal biodiversity*. In: *CBS laboratory manuals series 1*. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands.

Crous PW, Wingfield MJ, Mansilla JP, *et al*. (2006). Phylogenetic reassessment of *Mycosphaerella* spp. and their anamorphs occurring on *Eucalyptus*. II. *Studies in Mycology* **55**: 99–131.

Deacon JW (1973). *Phialophora radicicola* and *Gaeumannomyces graminis* on roots of grasses and cereals. *Transactions of the British Mycological Society* **61**: 471–485.

Deacon JW (1974). Further studies on *Phialophora radicicola* and *Gaeumannomyces graminis* on roots and stem bases of grasses and cereals. *Transactions of the British Mycological Society* **63**: 307–327.

Dennis RWG (1960). *British cup fungi and their allies: an introduction to the Ascomycetes*. Ray Society, London.

Elliott ML (1991). Determination of an etiological agent of Bermuda grass decline. *Phytopathology* **81**: 1380–1384.

Elliott ML, Hagan AK, Mullen JM (1993). Association of *Gaeumannomyces graminis* var. *graminis* with a St. Augustine grass root rot disease. *Plant Disease* **77**: 206–209.

Fouly HM, Wilkinson HT (2000). A group I intron in the nuclear small subunit ribosomal DNA of *Gaeumannomyces graminis*. *Current Microbiology* **40**: 291–296.

Fouly HM, Wilkinson HT, Domier LL (1996). Use of random amplified polymorphic DNA (RAPD) for identification of *Gaeumannomyces* species. *Soil Biology and Biochemistry* **28**: 703–710.

Freeman J, Ward E (2004). *Gaeumannomyces graminis*, the take-all fungus and its relatives. *Molecular Plant Pathology* **5**: 235–252.

Fröhlich J, Hyde KD (2000). *Palm microfungi*. Fungal Diversity Press, Thailand.

Gams W (2000). *Phialophora* and some similar morphologically little-differentiated anamorphs of divergent *Ascomycetes*. *Studies in Mycology* **45**: 187–199.

Hernández-Restrepo M, Groenewald JZ, Crous PW (2016). Taxonomic and phylogenetic re-evaluation of *Microdochium*, *Monographella* and *Idriella*. *Persoonia* **36**: 57–82.

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Katoh K, Standley DM (2013). MAFFT multiple sequence alignment software v. 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.

Klaubauf S, Tharreau D, Fournier E, *et al*. (2014). Resolving the polyphyletic nature of *Pyricularia* (*Pyriculariaceae*). *Studies in Mycology* **79**: 85–120.

Luo J, Qiu H, Cai G, *et al*. (2015a). Phylogenomic analysis uncovers the evolutionary history of nutrition and infection mode in rice blast fungus and other *Magnaporthales*. *Scientific Reports* **5**: 9448.

Luo J, Walsh E, Blystone D, *et al*. (2015b). Five new *Pseudophialophora* species from grass roots in the oligotrophic pine barrens ecosystem. *Fungal Biology* **119**: 1205–1215.

Luo J, Walsh E, Zhang N (2014). Four new species in *Magnaporthaceae* from grass roots in New Jersey Pine Barrens. *Mycologia* **106**: 580–588.

Luo J, Walsh E, Zhang N (2015c). Toward monophyletic generic concepts in *Magnaporthales*: species with *Harpophora* asexual states. *Mycologia* **107**: 641–646.

Luo J, Zhang N (2013). *Magnaporthiopsis*, a new genus in *Magnaporthaceae*. *Mycologia* **105**: 1019–1029.

McKeen WE (1952). *Phialophora radicicola* Cain, a corn root rot pathogen. *Canadian Journal of Botany* **30**: 338–343.

Nylander JAA (2004). *MrModeltest v2.2*. Uppsala: distributed by the author. Evolutionary Biology Centre, Uppsala University, Sweden.

Rachdawong S, Cramer CL, Grabau EA, *et al*. (2002). *Gaeumannomyces graminis* vars. *avenae*, *graminis*, and *tritici* identified using PCR amplification of avenacinase-like genes. *Plant Disease* **86**: 652–660.

Rayner RW (1970). *A mycological colour chart*. CMI and British Mycological Society, Kew, Surrey, UK.

Rehner SA, Buckley E (2005). A *Beauveria* phylogeny inferred from nuclear ITS and EF1-α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* **97**: 84–89.

Ronquist F, Teslenko M, Mark P van der, *et al*. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542.

Roy KW, Abney TS, Huber DM, *et al*. (1982). Isolation of *Gaeumannomyces graminis* var. *graminis* from soybeans in the Midwest. *Plant Disease* **66**: 822–825.

Sadeghi L, Alizadeh A, Safaie N, *et al*. (2012). Genetic diversity of *Gaeumannomyces graminis* var. *tritici* populations using RAPD and ERIC markers. *Journal of Plant Pathology and Microbiology* **3**: 143.

Saleh AA, Leslie JF (2004). *Cephalosporium maydis* is a distinct species in the *Gaeumannomyces–Harpophora* species complex. *Mycologia* **96**: 1294–1305.

Swofford DL (2003). *PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.

Tamura K, Stecher G, Peterson D, *et al*. (2013). MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* **30**: 2725–2729.

Tan MK (1997). Origin and inheritance of group I introns in 26S rRNA genes of *Gaeumannomyces graminis*. *Journal of Molecular Evolution* **44**: 637–645.

Tan MK, Wong PTW, Holley MP (1994). Characterization of nuclear ribosomal DNA (rDNA) in *Gaeumannomyces graminis* and correlation of rDNA variation with *G. graminis* varieties. *Mycological Research* **98**: 553–561.

Turner EM (1940). *Ophiobolus graminis* Sacc. var. *avenae* var. n. as the cause of take-all or white-heads in Wales. *Transactions of the British Mycological Society* **24**: 269–281.

Ulrich K, Augustin C, Werner A (2000). Identification and characterization of a new group of root-colonizing fungi within the *Gaeumannomyces–Phialophora* complex. *New Phytologist* **145**: 127–135.

von Arx JA, Olivier D (1952). The taxonomy of *Ophiobolus graminis* Sacc. *Transactions of the British Mycological Society* **35**: 29–33.

Walker J (1972). Type studies on *Gaeumannomyces graminis* and related fungi. *Transactions of the British Mycological Society* **58**: 427–457.

Walker J (1980). *Gaeumannomyces*, *Linocarpon*, *Ophiobolus* and several other genera of scolecospored *Ascomycetes* and *Phialophora* conidial states, with a note on hyphopodia. *Mycotaxon* **11**: 1–129.

Walker J (1981). Taxonomy of take-all fungi and related genera and species. In: *Biology and control of take-all* (Asher MJC, Shipton PJ, eds). Academic Press, London, UK.

Ward E, Akrofi AY (1994). Identification of fungi in the *Gaeumannomyces–Phialophora* complex by RFLPs of PCR amplified ribosomal DNAs. *Mycological Research* **98**: 219–224.

Ward E, Bateman GL (1999). Comparison of *Gaeumannomyces*- and *Phialophora*-like fungal pathogens from maize and other plants using DNA methods. *New Phytologist* **141**: 323–331.

Wetzel III HCIII, Dernoeden PH, Millner PD (1996). Identification of darkly pigmented fungi associated with turfgrass roots by mycelial characteristics and RAPD-PCR. *Plant Disease* **80**: 359–364.

Wong PTW (2002). *Gaeumannomyces wongoonoo* sp. nov., the cause of a patch disease of buffalo grass (St Augustine grass). *Mycological Research* **106**: 857–862.

Yao JM, Wang YC, Zhu YG (1992). A new variety of the pathogen of maize take-all. *Acta Mycologica Sinica* **11**: 99–104.

Yuan ZL, Lin FC, Zhang CL, *et al*. (2010). A new species of *Harpophora* (*Magnaporthaceae*) recovered from healthy wild rice (*Oryza granulata*) roots, representing a novel member of a beneficial dark septate endophyte. *FEMS Microbiology Letters* **307**: 94–101.

Zhang N, Zhao S, Shen S (2011). A six-gene phylogeny reveals the evolution of mode of infection in the rice blast fungus and allied species. *Mycologia* **103**: 1267–1276.

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