Take-all or nothing

M. Hernández-Restrepo1,2,*, J.Z. Groenewald1, M.L. Elliott3, G. Canning4, V.E. McMillan4, and P.W. Crous1,2,5,6*

1CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, 3804 CT Utrecht, The Netherlands; 2Department of Microbiology and Plant Pathology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria 0002, South Africa; 3University of Florida – IFAS, Fort Lauderdale Research and Education Center, 3205 College Avenue, Fort Lauderdale (Davie), FL 33314, USA; 4Department of Plant Biology and Crop Science, Rothamsted Research, Harpenden, Herts AL5 2QJ, UK; 5Microbiology, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands; 6Wageningen University and Research Centre (WUR), Laboratory of Phytopathology, Droevendaalseweg 1, 6708 PW Wageningen, The Netherlands

*Correspondence: M. Hernández-Restrepo, m.hernandez@csb.knaw.nl; P.W. Crous, p.crous@csb.knaw.nl

Abstract: Take-all disease of Poaceae is caused by Gaeumannomyces graminis (Magnaportheaceae). 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, rpb1, and rpb2. Two new genera, Falciphoriella and Gaeumannomyccella were subsequently introduced in Magnaportheaceae. 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. avenuea and Gaeumannomyces graminicola var. tritici represent species phylogenetically distinct from G. graminis, for which the new combinations G. avenuea 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. avenuea was designated to help stabilise the application of that name.

Keywords: Cryptic species, Gaeumannomyces graminis, Magnaportheaceae, Phylogeny, Triticum.

TAXONOMIC NOVELTIES: New genera: Falciphoriella M. Hern.-Restr. & Crous, Gaeumannomyccella M. Hern.-Restr. & Crous, New species: Falciphoriella solaninterestris M. Hern.-Restr. & Crous, Gaeumannomyccella carici M. Hern.-Restr. & Crous, Gaeumannomyces axnii M. Hern.-Restr. & Crous, G. australiensis M. Hern.-Restr. & Crous, G. californicus M. Hern.-Restr. & Crous, G. elisiorum M. Hern.-Restr. & Crous, G. floridanus M. Hern.-Restr. & Crous, G. fusiformis M. Hern.-Restr. & Crous, G. glycinclica M. Hern.-Restr. & Crous, G. graminicola M. Hern.-Restr. & Crous, G. hypophodoides M. Hern.-Restr. & Crous, G. oryzicola M. Hern.-Restr. & Crous, G. setanica M. Hern.-Restr. & Crous, G. walkeri M. Hern.-Restr. & Crous; New combinations: Gaeumannomyces tritici (J. Walker) M. Hern.-Restr. & Crous, Gaeumannomyces graminis var. avenuea (E. M. Turner) M. Hern.-Restr. & Crous; Typification: Epitypification: Gaeumannomyces graminis var. avenuea (E. M. Turner) Dennis.

Available online 1 July 2016; http://dx.doi.org/10.1016/j.simyco.2016.06.002. Hard copy: xxx.

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, 1982, 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. avenuea (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, multisepitate 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 Pseudoperonospora to accommodate the phialidic asexual morphs in Magnaportheaceae. 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 Magnaportheaceae. 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).
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 avencasinase-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 path disease of Stenotaphrum secundatum (buffalo grass) (Wong 2002) and G. caricii occurring on Carex spp. (Cyperaceae) (Walker 1980). Endophytic and saprobic fungi have been found in this genus as well, for example G. amorii, described as endophytic in Amomum and Alpinia (Zingiberaceae) (Bussaban et al. 2001), and the saprobic G. licaeae, 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), Magnaportheiosis (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. incustans was transferred to Magnaportheiosis (Luo & Zhang 2013). Sloeipomycos and Kohltiemyrioperid were proposed as new genera to accommodate G. cylindrosporos 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 Ni 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-alpha 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).
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 number¹ | Status² | Country | Host, substrate | GenBank accession numbers³ |
|---------|----------------------|----------------|---------|---------|----------------|--------------------------|
| **Buergenerula spartinae** | Buergenerula spartinae | ATCC 22848 | T       | USA     | Spartina alterniflora, leaves | DQ341492 JX134666 JX134720 – |
| **Bussabamonos sp.** | Bussabamonos sp. | CBS 125232 | T       | Thailand | Amomum siamense, leaves | KM484951 KM484832 KM485046 – |
| **Falcipora oryzae** | Harpophora oryzae | CBS 125863, R5-6-1 | T       | China | Oryza sativa, root, endophytic | KJ06705 EU69699 KJ06706 JN857963 |
| **Falciporiae solaniteserrius** | Gaeumannomyces sp. | CBS 117.83 | T       | Netherlands | Soil in potato field | KM484959 KM484842 KM485058 – |
| **Gaeumannomycecaris** | Gaeumannomyces graminis var. graminis | CBS 388.81 | T       | UK | Carex rostrata | KM484960 KM484843 KX306674 – |
| **Gaeumannomyces amomi** | Gaeumannomyces amomi | CBS 109354, CMUZE0002, BCC 4066 | T       | Thailand | Amomun sp., endophytic in leaves | DQ341493 AY265318 – KX306679 |
| **G. arxii** | Gaeumannomyces graminis var. graminis | CBS 902.73, DAR 17502 | T       | Australia | Stenotaphrum secundatum (buffalo grass) | KM484953 KM484836 KM485052 KM48680 |
| **G. caespitosa** | Gaeumannomyces graminis var. graminis | CBS 903.73, DAR 23471 | T       | Australia | Pennisetum clandestinum, (kikuyu grass), stolon | KM484854 KM484837 KM485053 KM48681 |
| **G. avenae** | Gaeumannomyces graminis var. graminis | CPC 26054, CBS 141374 | T       | USA | Stenotaphrum secundatum | KM484959 KM483479 KM485068 KM48682 |
| **G. australiensis** | Gaeumannomyces graminis var. graminis | CPC 26058, DAR 32100, CBS 141387 | T       | Australia | Triticum aestivum | KM485050 KM485068 KM485069 KM48683 |
| **G. avenae** | Gaeumannomyces graminis var. graminis | CBS 870.73, DAR 20999 | T       | Australia | Avena sativa | KM485051 KM485068 KM485069 KM48684 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CPC 26253 | T       | Australia | Agrostis (bent grass) | KM485051 KM485068 KM485069 KM48685 |
| **G. gracilis** | Gaeumannomyces graminis var. graminis | CPC 26254 | T       | Australia | Agrostis (bent grass) | KM485051 KM485068 KM485069 KM48685 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CPC 26255 | T       | Australia | Agrostis (bent grass) | KM485051 KM485068 KM485069 KM48685 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CPC 26256 | T       | Australia | Avena sativa | KM485051 KM485068 KM485069 KM48685 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CPC 26257, CBS 141376 | T       | Ireland | Avena sativa (winter Oats) | KM485051 KM485068 KM485069 KM48685 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CPC 26258 | T       | Ireland | Avena sativa (winter Oats) | KM485051 KM485068 KM485069 KM48685 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CPC 26259 | T       | Ireland | Triticum aestivum (winter wheat) | KM485051 KM485068 KM485069 KM48685 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CPC 26260 | T       | Ireland | Turf | KM485051 KM485068 KM485069 KM48685 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CPC 26261 | T       | Ireland | Turf | KM485051 KM485068 KM485069 KM48685 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CPC 26044, CBS 141377 | T       | USA | Stenotaphrum secundatum | KM485051 KM485068 KM485069 KM48685 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CBS 387.81 | T       | UK | Deschampsia caespitosa, dead culm and sheath | KM485051 KM485068 KM485069 KM48685 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CPC 26037, CBS 141378 | T       | USA | Stenotaphrum secundatum | KM485051 KM485068 KM485069 KM48685 |
| **G. fusiformis** | Gaeumannomyces graminis var. graminis | CPC 26068, CBS 141379 | T       | USA | Oryza sativa | KM485051 KM485068 KM485069 KM48685 |

(continued on next page)
| Species | Old name/Received as | Strain number | Status | Country | Host, substrate | GenBank accession numbers |
|---------|---------------------|---------------|--------|---------|----------------|--------------------------|
| *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 | DO341496 KM484834 KM485050 KX306697 |
| | *Gaeumannomyces graminis var. graminis* | CPC 26025, CBS 141381 |  | USA | Stenotaphrum secundatum | KX306565 KX306495 KX306630 KX306698 |
| | *Gaeumannomyces graminis var. graminis* | CPC 26363, CBS 141382 |  | USA | Eremochloa ophiuroidis | KX306566 KX306496 KX306631 KX306699 |
| | *Gaeumannomyces graminis var. graminis* | CPC 26056, CBS 141383 |  | USA | Cynodon dactylon × C. transvaalensis | KX306567 KX306497 KX306632 KX306700 |
| | *G. 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 – KX306709 |
| | *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 |
| Species                  | Old name/Received as | Strain number | Status | Country | Host, substrate                  | GenBank accession numbers |
|-------------------------|---------------------|---------------|--------|---------|----------------------------------|--------------------------|
|                         |                     |               |        |         |                                  | LSU          | ITS           | RPB1          | TEF1          |
| Gaeumannomyces oryzinus | Gaeumannomyces      | CBS 235.32    | USA    | Oryza   |                                  | JX134681      | JX134669      | KM485049      | JX134695      |
|                         | graminis var.       | 141391        |        | sativa  |                                  | XJ306587      | XJ306517      | XJ306647      | XJ306718      |
|                         | graminis var.       | CPC 26031     | USA    | Oryza   | sativa                           | XJ306588      | XJ306519      | XJ306648      | XJ306719      |
|                         | graminis var.       | CPC 26032     | USA    | Oryza   | sativa                           | XJ306589      | XJ306549      | XJ306649      | XJ306720      |
|                         | graminis var.       | CPC 26043, CBS| USA    | Oryza   | sativa                           | XJ306590      | XJ306520      | XJ306650      | XJ306721      |
|                         | graminis var.       | CPC 26065     | USA    | Oryza   | sativa                           | XJ306591      | XJ306521      | XJ306651      | XJ306722      |
|                         | graminis var.       | CPC 26066     | USA    | Oryza   | sativa                           | XJ306592      | XJ306522      | XJ306652      | XJ306723      |
|                         | graminis var.       | CPC 26067, CBS| USA    | Oryza   | sativa                           | XJ306593      | XJ306523      | XJ306653      | XJ306724      |
|                         |                     |               |        |         |                                  |              |              |              |              |
| G. radicola             | Phialophora        | CBS 149.85, PREM | South | Zea     | mays                             | KM484061      | KM484844      | KM485060      | KM009205      |
|                         | zeicola             | 45754         |        |         |                                  |              |              |              |              |
|                         |                     | CBS 296.53, MUCL | T      | Canada  | Zea mays, root                   | KM484962      | KM484845      | KM485061      | KM009206      |
|                         |                     | 28970         |        |         |                                  | KM009206      | KM009206      | KM009206      | KM009206      |
|                         |                     | W4066B        | China  | Zea     | mays                             | –             | –             | –             | –             |
|                         |                     | Ggm02         | –      | –       |                                  | –             | –             | –             | –             |
| G. setariaicola         | Gaeumannomyces     | CPC 26059, PRRI| T      | South   | Africa Setaria italica           | XJ306594      | XJ306524      | XJ306654      | XJ306725      |
|                         | graminis var.       | 4754, CBS 141394 |        |         |                                  | XJ306595      | XJ306525      | XJ306655      | XJ306730      |
|                         | graminis var. tritici| CBS 186.65    | Netherlands | Hordeum | vulgare                         | KM484965      | KM484838      | KM485054      | XJ306726      |
|                         |                     | CBS 247.29    | Netherlands | Triticum | sp.                              | KM484956      | KM484839      | KM485055      | XJ306727      |
|                         |                     | CBS 249.29, IMI| 083849  | –       | Triticum aestivum                | KM484957      | KM484840      | KM485056      | XJ306728      |
|                         |                     | CBS 273.36    | Argentina | Triticum | aestivum                        | KM484958      | KM484841      | KM485057      | XJ306731      |
|                         |                     | CBS 905.73, DAR| 23140   | Australia | Triticum aestivum                | KM484965      | KM484838      | KM485054      | XJ306729      |
|                         |                     | CPC 131293    | USA     | Triticum | sp.                              | KM485057      | KM484838      | KM485054      | XJ306730      |
|                         |                     | CPC 26069, CBS| 141395  | –       |                                  | KM485057      | KM484838      | KM485054      | XJ306730      |
|                         |                     | CPC 26268, CBS| 141398  | Australia | Triticum aestivum                | KM485057      | KM484838      | KM485054      | XJ306730      |
|                         |                     | CPC 26269, CBS| 141397  | Brazil  | Triticum aestivum                | KM485057      | KM484838      | KM485054      | XJ306730      |
|                         |                     | CPC 26270     | UK      | Hordeum | vulgare                         | KM485057      | KM484838      | KM485054      | XJ306730      |
|                         |                     | CPC 26271     | UK      | Triticum | aestivum                        | KM485057      | KM484838      | KM485054      | XJ306730      |
|                         |                     | CPC 26272     | UK      | Hordeum | vulgare (winter barley)         | KM485057      | KM484838      | KM485054      | XJ306730      |
|                         |                     | CPC 26273, CBS| 141398  | UK      | Elymus repens (couch grass)      | KM485057      | KM484838      | KM485054      | XJ306730      |
|                         |                     | CPC 26274     | Australia | –       |                                  | KM485057      | KM484838      | KM485054      | XJ306730      |
|                         |                     | CPC 26275     | UK      | Bromus | sp. (Brome grass)               | KM485057      | KM484838      | KM485054      | XJ306730      |
|                         |                     | CPC 26276     | Brazil  | –       |                                  | KM485057      | KM484838      | KM485054      | XJ306730      |
|                         |                     | CPC 26277     | UK      | Elymus | repens (couch grass)            | KM485057      | KM484838      | KM485054      | XJ306730      |

(continued on next page)
| Species | Old name/Received as | Strain number\(^1\) | Status\(^2\) | Country | Host, substrate | GenBank accession numbers\(^3\) |
|---------|---------------------|---------------------|-------------|---------|----------------|--------------------------|
| *Gaeumannomyces tritici* | *Gaeumannomyces graminis var. tritici* | CPC 26278 | UK | Agropyron sp. | | X306608 X306538 X306666 X306741 |
| | *Gaeumannomyces graminis var. tritici* | CPC 26280 | UK | – | | X306609 X306539 X306667 X306742 |
| | *Gaeumannomyces graminis var. tritici* | CPC 26281 | UK | – | | X306610 X306540 X306668 X306743 |
| | *Gaeumannomyces graminis var. tritici* | CPC 26282, CBS 141399 | UK | Triticum aestivum (winter wheat) | | X306611 X306541 – X306744 |
| | *Gaeumannomyces walkeri* | CPC 26028, CBS 141400 | T USA | Stenotaphrum secundatum | | X306613 X306543 X306669 X306746 |
| | *G. wongoonoo* | BRIP 60376 | Australia | Buffalo grass | | KP162146 KP162137 – – |
| | *Kohlmeyeropsis medullaris* | CBS 117849, JK5528S | T USA | Juncus roemerianus | | KM484968 KM484852 KM485068 – |
| | *Magnaporthiopsis incrustans* | CPC 26038 USA | | | | |
| | *Neogaeumannomyces bambusicola* | MFLUCC 110390 | T USA | Oryza sativa | | KM484976 KM484862 KM485078 – |
| | *Omnidemptus affinis* | ATCC 200212 | T USA | Panicum effusum var. effusum, grass leaves | | KM484976 KM484862 KM485078 – |
| | *Pseudophialophora eragrostis* | CM12m9 | T USA | Eragrostis sp. | | KM484976 KM484862 KM485078 – |
| | *Pyricularia grisea* | BR0029 | Brazil | Digitaria sanguinalis | | KM484995 KM484880 KM485100 – |
| | *Slopeiomyces cylindrosporus* | CBS 609.75 | T USA | Loli um perenne | | KM484995 KM484880 KM485100 – |
| | *Magnaporthaceae, incertae sedis* | CPC 26284, GP57, CBS 141401 | UK | Triticum aestivum | | X306616 X306546 – X306777 |
| | *Magnaporthaceae, incertae sedis* | CPC 26245, CBS 141402 | UK | Carex acutiformis | | X306617 X306547 X306673 X306678 |

\(^1\) 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, Bakenham 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 *Magnaportheaceae* 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 *Magnaportheaceae*. 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 after the burn-in with a stop value of 0.01. In the MP analyses, 2,406 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, Orzyzins, 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. amoni* and four new species described here as *G. arxii*, *G. ellisorum*, *G. glycinicola* and *G. walkerii*. Clade graminis consists of *G. graminis* and three new species described here as *G. californicus*, *G. australiensis* and *G. oryzicola*. Clade oryzins 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. wongoono* and two new species described here as *G. hyphopodoides* and *G. setariicola*.

**RESULTS**

**Phylogeny**

The first dataset consisted of 64 aligned LSU and *rpb1* sequences of members of *Magnaportheaceae*, including the out-group *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 *Magnaportheaceae*. The majority of the isolates cluster in *Gaeumannomyces* s. s. However one strain, CPC 26038, clustered in *Magnaphoriphiosis* 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 *Magnaportheaceae*. Two new genera are introduced here (see Taxonomy section); *Falciphioriella* to accommodate CBS 117.83, and *Gaeumannomyccella* 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 *Magnaphoriphiosis*, 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. amoni*, *G. radicicola* and *G. wongoono*. This dataset consisted of 74 aligned sequences including two outgroups *Falcipha* *oryzae* (CBS 125863) and *Pseudophialophora eradogonis* (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, Orzyzins, 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. amoni* and four new species described here as *G. arxii*, *G. ellisorum*, *G. glycinicola* and *G. walkerii*. Clade graminis consists of *G. graminis* and three new species described here as *G. californicus*, *G. australiensis* and *G. oryzicola*. Clade oryzins 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. wongoono* and two new species described here as *G. hyphopodoides* and *G. setariicola*.

**Taxonomy**

Based on DNA sequence data and variation in morphology among the isolates studied, two new genera in *Magnaportheaceae* are introduced with a harpophora-like asexual morph, namely *Falciphioriella* and *Gaeumannomyccella*. 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
present study, mostly because they remained sterile in culture; their identities will be resolved in future studies.

**Sordariomycetes, Magnaporthales, Magnaportheaceae**

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

**Etymology:** Morphologically similar to the genus *Falciphora*.

*MycoBank MB816902.*

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 solanisterrestris* M. Hern.-Restr. & Crous

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

**Etymology:** Referring to the substrate *solanum* – 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 colourless to yellow. On MEA reaching 50 mm diam, aerial mycelium moderate, cottony, vinaceous buff, submerged mycelium dark, margin effuse, reverse sepiatone in the centre, colourless to the periphery. On OA reaching 36 mm diam, elevated, aerial mycelium moderate to abundant dense, cottony, white, submerged mycelium dark, margin effuse, reverse dark in the centre colourless to the periphery. On OA reaching 40 mm diam, elevated, aerial mycelium moderate to abundant, cottony to funiculose, submerged mycelium dark, margin effuse, rhizoid; reverse dark.

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

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

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

**Etymology:** Morphologically similar to the genus *Gaeumannomyces*.

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

*Gaeumannomyces 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, with inconspicuous collarette. **Conidia** lunate or cylindrical, hyaline. **Hyphopodia** hyaline to brown when mature, lobed.

**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, 26 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 2692 = CBS 141374.

Notes: *Gaeumannomyces caricis* is only known occurring on *Carex rostrata*. This new species is represented by two strains
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), Slopethiocereus is shown to be the sister clade of Gaeumannomycescella.

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

=Gaeumannomyces arxii Arx & D.L. Olivier, Trans. Br. mycol. Soc. 35: 1849.

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

- \( \text{Rhaphidophora Ces. & De Not., Sfrit. Ital.: 79. 1863.} \)
- \( \text{Rhaphidospora Fr., Summa veg. Scand., Section Post. (Stockholm): 401. 1849.} \)

**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, uniculate, 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. **Septa** commonly 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 (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 Anomum 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 Zingiberales.

**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 MB816806. 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

Figures 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 eradostia (CM19MI).

Please cite this article in press as: Hernandez-Restrepo M, et al., Take-all or nothing. Studies in Mycology (2016), http://dx.doi.org/10.1016/j.simyco.2016.06.002
Table 2. Overview of the main characters of *Gaeumannomyces* species.

| Clade     | Species       | Sexual | Asexual | Hyphopodia |
|-----------|---------------|--------|---------|------------|
|           |               | Ascomata (μm) | Asci (μm) | Ascospores (μm) | # of Septa | Conidiogenous cells (μm) | Conidial size (μm) | Conidial shape | Size (μm) | Shape, colour | Reference |
|           |               | 6.5–27.5 × 1.5–3 | 5–11 × 1–2 | – | – | – | – | – | 18.5–25 × 21.5–23 | L, brown | – | This study |
|           |               | 4.5–24 × 1.5–4 | 4–11 × 1–1.5 | – | – | – | – | – | 25–32.5 × 24–30 | L, brown | – | This study |
|           |               | 7–30 × 1.5–4 | 4–10 × 1–2 | – | – | – | – | – | 17–27 × 20–30 | S–L | – | Walker (1980) |
|           |               | 7.5–20.5 × 2–2.5 | 5–9 × 1.5–2.5 | – | – | – | – | – | – | – | – | This study |
|           |               | 18–27 × 14.5–26.5 | – | – | – | – | – | – | – | – | – | This study |
|           |               | 7–14.5 × 2–3.5 | 5–11 × 1–1.5 | – | – | – | – | – | – | – | – | This study |
|           |               | 5–9.5 × 1.5–2 | – | – | – | – | – | – | – | – | – | This study |
|           |               | 5–11.5 × 1–2 | – | – | – | – | – | – | 16.5–24 × 15.5–23.5 | L, brown | – | This study |
|           |               | 5–11 × 1–2.5 | – | – | – | – | – | – | 19–45 × 15.5–36 | L, brown | – | This study |
|           |               | 7–21 × 2–4 | 5.5–10.5 × 1–2 | – | – | – | – | – | 17–28 × 18–25 | S–L, hyaline, brown | – | This study |
|           |               | 10–23 × 3–4 | 5–9 × 0.7–1.5 | – | – | – | – | – | – | S–slightly L | – | This study |
|           |               | – | – | – | – | – | – | – | – | L, hyaline | – | This study |
|           |               | 6.5–28.5 × 2–4 | 4–12 × 1–2 | – | – | – | – | – | – | – | – | This study |
|           |               | 5–12.5 × 3–5 | – | – | – | – | – | – | – | – | – | This study |
|           |               | – | – | – | – | – | – | – | – | – | – | This study |
|           |               | 5–18 × 3–4 | 4–9 × 1–2 | – | – | – | – | – | 19.5–35.5 × 16.5–30 | S–L, hyaline | – | This study |
|           |               | 6–23 × 2–5 | 4–10 × 1–2 | – | – | – | – | – | – | – | – | This study |
|           |               | 7–15 × 4–8 | – | – | – | – | – | – | – | – | – | This study |
|           |               | 71.6 ± 6.8 × 2.6 ± 0.5 | – | – | – | – | – | – | – | – | – | This study |
|           |               | – | – | – | – | – | – | – | – | – | – | This study |
|           |               | 7.5–20 × 1.5–2–3 | 5–14 × 1–1.5 | – | – | – | – | – | – | – | – | 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. *Gaeumannomyces carici* (CBS 388.81). A, B. Conidiogenous cells. C. Conidia. D–H. Hyphopodia. Scale bars: A–H = 10 μm.

Please cite this article in press as: Hernández-Restrepo M., et al., Take-all or nothing, Studies in Mycology (2016), http://dx.doi.org/10.1016/j.simyco.2016.06.002
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 white, submerged mycelium dark, smoke grey, margin effuse; reverse pale olive-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).
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 Avena sativa, 11 Sep. 1990, unknown collector, CPC 26260. Ireland, Killinwick, Wexford, isolated from winter oats, 11 Oct. 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 Avena sativa, 11 Nov. 1980, unknown collector, CPC 26253; CPC 26254; CPC 26255; Western Australia, 25 km W of M. Barker, isolated from Avena sativa, Dec. 1963, deposited by J. Walker, CBS 870.73. Ireland, Killinwick, 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 Avena 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 ascosporangia and occurring on oats. This fungus causes take-all of oats and take-all patch of turfgrasses. Walker (1972, 1980) distinguished Gga from Ggt by the former producing teleomorphic stages, but ascospores are larger in G. avenae. In addition, Rachdawong et al. (2002) differentiated G. avenae (as Gga) and G. tritici (as Ggt) based on sequences of avencinase-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 tefl also showed differences in these two clades, and therefore we propose G. avenae comb. et stat. nov. to accommodate this species.

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

Etyymology: Named after California, the state in the USA where the collection was made.

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. 7.

Etyymology: 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 chlamydosporae-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.
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 caespitosa. 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.
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 36068).

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...
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.
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...
described perithecia as globose to ellipsoidal with cylindrical necks, pale to dark brown. Ascospores fIlfiform, 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, lea den 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.
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., Sytowia 6: 387. 1952.
≡ Gaeumannomyces cariceti (Berk. & Broome) Lar.N. Vassiljeva, Nizhne Rasteniya, Griby i Mokhoobraznye Dalnego Vostoka Rossii, Griby. 1998.
≡ Sphaeria cariceti (Berk. & Broome) (Sacc.) Sacc., Reliq. Libert 2: no. 134. 1875.
≡ Ophiobolus cariceti (Sacc.) Sacc., Fungi venet. nov. vel. Crit., Sér. 2: 307. 1875.
≡ Mycol. Soc. 35: 32. 1952. var. graminis
≡ Tokio 3: 342. 1916.
≡ Gaeumannomyces graminis
≡ Phialophora 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., Sytowia 6: 387. 1952.
≡ Gaeumannomyces cariceti (Berk. & Broome) Lar.N. Vassiljeva, Nizhne Rasteniya, Griby i Mokhoobraznye Dalnego Vostoka Rossii, Griby. 1998.
≡ Sphaeria cariceti (Berk. & Broome) (Sacc.) Sacc., Reliq. Libert 2: no. 134. 1875.
≡ Ophiobolus cariceti (Sacc.) Sacc., Fungi venet. nov. vel. Crit., Sér. 2: 307. 1875.
≡ Mycol. Soc. 35: 32. 1952. var. graminis
≡ Tokio 3: 342. 1916.
≡ Gaeumannomyces graminis
≡ Phialophora 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., Sytowia 6: 387. 1952.
≡ Gaeumannomyces cariceti (Berk. & Broome) Lar.N. Vassiljeva, Nizhne Rasteniya, Griby i Mokhoobraznye Dalnego Vostoka Rossii, Griby. 1998.
≡ Sphaeria cariceti (Berk. & Broome) (Sacc.) Sacc., Reliq. Libert 2: no. 134. 1875.
≡ Ophiobolus cariceti (Sacc.) Sacc., Fungi venet. nov. vel. Crit., Sér. 2: 307. 1875.
≡ Mycol. Soc. 35: 32. 1952. var. graminis
≡ Tokio 3: 342. 1916.
≡ Gaeumannomyces graminis
≡ Phialophora graminis (Sacc.) Arx & D.L. Olivier, Trans. Br. Mycol. Soc. 35: 32. 1952. var. graminis

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 dactylon (Cynodon dactylon × C. transvaalensis), 1875, 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.

Description on MEA. [307–308] conical, refractive, collarette up to 3.5 μm long, 1–1.5 μm wide. 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 G. 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 uniloculate, with an apical refractive ring and ascospores filiform, septate, hyaline, measuring (70–105×110) μm wide. “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
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).

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
**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 to olivaceous grey or pale olivaceous, mossy, 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. Watz, 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 winter wheat, 9 Feb. 1990, unknown collector, CPC 26264 = CBS 141389; CPC 26265.

**Notes**: This species forms a distinct subclade in the *Radiocilic clad* (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. gaminis* and is phylogenetically closer to *G. radicicola* than *G. gaminis*. *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 26287) 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.
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, 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. Datnof, 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 Gg 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 3605].

Please cite this article in press as: Hernandez-Restrepo M, et al., Take-all or nothing, Studies in Mycology (2016), http://dx.doi.org/10.1016/j.simyco.2016.06.002

Fig. 15. Gaeumannomyces oryzicola (CPC 26063). A. Perithecial. B–E. Asci. F. Ascospores. G–I. Conidigenous cells. J. Conidia. Scale bars: A, B = 50 μm; C–E = 20 μm, F–J = 10 μm.
Fig. 16. *Gaeumannomyces oryzae* (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.
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) introduced 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 Gen-Bank 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. Grodninsky, CBS 273.36. Australia, South Australia, Mortlock, isolated from Triticum aestivum, 16 Dec. 1980, unknown collector, CPC 28268 = 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 28274. Brazil, Espumoso, isolated from wheat, 9
**Gaeumannomyces setariicola** (CPC 26059). A–D, Conidiophores and conidia. E. Conidia. Scale bars: A–E = 10 μm.

**Fig. 18.**

**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 setariicola** 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 umbre, 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* (*Walker 1991*). *Elliott (holotype)*, CBS H-22586, culture ex-type CBS 141400 = CPC 26028 = FL-156.

**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).
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, Gpa, 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. hypopodoides, G. oryzicola, G. oryzinus, G. setanicola 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
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, hyphaloid 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. oryzae* 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 because of their simple morphology, the overlapping 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*).

**ACKNOWLEDGEMENTS**

The authors thank the technical staff, Arien van Iperen (cultures and deposit of herbarium samples), and Tríx Merx and Gerard Verkleij (deposit of isolates) for their invaluable assistance. VM was supported by the Biotechnology and Biological Sciences Research Council of the UK (BBSRC) through the Institute Strategic Programme Grant 20:20 Wheat (BB/00426X/1). GC was supported by BBSRC through the research grant “Enhancing diversity in UK wheat through a public sector pre-breeding programme” (BB/002278/1). We also thank the editors and reviewers for critically reviewing the manuscript.

**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.

Cousens 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.

Cousens PW, Verkleij GMJ, Groesewald JZ, et al. (2009). Fungal biodiversity: *In: CBS laboratory manuals series 1*, *CBS-KNAW Fungal Biodiversity Centre*, Utrecht, The Netherlands.

Cousens PW, Wingfield MJ, Mansilla JP, et al. (2006). Phylogenetic reassessment of *Mycospherella* 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 disease. *Current Microbiology* 40: 296.

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

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

Foully 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, Cousens PW (2016). Taxonomic and phylogenetic re-evaluation of *Microdochium*, *Monographella* and *Idiella*. *Persoonia* 36: 57–82.

www.studiesinmycology.org

Please cite this article in press as: Hernández-Restrepo M, et al., Take-all or nothing. Studies in Mycology (2016), http://dx.doi.org/10.1080/09137057.2016.103022
Kateh K, Standley DM (2013). MAFFT multiple sequence alignment software v. 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772–780.

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

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

Luo J, Walsh E, Blystone D, Swofford DL (2003). Four new species in Magnaporthea 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 Magnaporthea species from grass roots in New Jersey Pine Barrens. Mycologia 106: 560–588.

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

Luo J, Zhang N (2013). Magnapnorphiosis, a new genus in Magnaporthea. Mycologia 105: 1019–1029.

McKeen WE (1952). Phialophora radicina 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 var. 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-a 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, Saiaie 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.

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

Tanura 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 varietes. Mycological Research 98: 553–561.

Turner EM (1940). Ophiobolus graminis Sacc. var. avenae 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 Plant Physiologist 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 scleosporous Ascomycetes and Phialophora conidiaal 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 MJ, Shipston PJ, eds). Academic Press, London, UK.

Ward E, Akroft AY (1994). Identification of fungi in the Gaeumannomyces–Phialophora complex by RFLPs of PCR amplified ribosomal DNA sequences. 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 Phytophtora 141: 323–331.

Wetzel III HCIII, Derroeden PH, Milner PD (1996). Identification of darkly pigmented fungi associated with turfgrass root 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 (Magnaportheaceae) 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.
Author/s: Hernandez-Restrepo, M; Groenewald, JZ; Elliott, ML; Canning, G; McMillan, VE; Crous, PW

Title: Take-all or nothing

Date: 2016-03-01

Citation: Hernandez-Restrepo, M., Groenewald, J. Z., Elliott, M. L., Canning, G., McMillan, V. E. & Crous, P. W. (2016). Take-all or nothing. STUDIES IN MYCOLOGY, 83 (83), pp.19-48. https://doi.org/10.1016/j.simyco.2016.06.002.

Persistent Link: http://hdl.handle.net/11343/258253

File Description: Published version

License: CC BY-NC-ND