Multigene phylogeny and taxonomic revision of yeasts and related fungi in the *Ustilaginomycotina*

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Abstract: The subphylum *Ustilaginomycotina* (Basidiomycota, *Fungi*) comprises mainly plant pathogenic fungi (smuts). Some of the lineages possess cultivable unicellular stages that are usually classified as yeast or yeast-like species in a largely artificial taxonomic system which is independent from and largely incompatible with that of the smut fungi. Here we performed phylogenetic analyses based on seven genes including three nuclear ribosomal RNA genes and four protein coding genes to address the molecular phylogeny of the ustilaginomycetous yeast species and their filamentous counterparts. Taxonomic revisions were proposed to reflect this phylogeny and to implement the ‘One Fungus = One Name’ principle. The results confirmed that the yeast-containing classes Malasseziales, Moniliellales and *Ustilaginomycotina* are monophyletic, whereas Exobasidiomycetes in the current sense remains paraphyletic. Four new genera, namely Dirkmeia gen. nov., Kalma- nozyma gen. nov., Golubevia gen. nov. and Robbauera gen. nov. are proposed to accommodate *Pseudozyma* and *Tilletiopsis* species that are distinct from the other smut taxa and belong to clades that are separate from those containing type species of the hitherto described genera. Accordingly, new orders Golubeviales ord. nov. with Golubeviaeaceae fam. nov. and Robbauerales ord. nov. with Robbaueraeaceae fam. nov. are proposed to accommodate the sisterhood of *Golubevia* gen. nov. and Robbauer gen. nov. with other orders of Exobasidiomycetes. The majority of the remaining anamorphic yeast species are transferred to corresponding teleomorph genera based on strongly supported phylogenetic affinities, resulting in the proposal of 28 new combinations. The taxonomic status of a few *Pseudozyma* species remains to be determined because of their uncertain phylogenetic positions. We propose to use the term *pro tempore* or *pro tm* in abbreviation to indicate the single-species lineages that are temporarily maintained.

Keywords: Fungi, Molecular phylogeny, Smuts, Taxonomy, Yeasts.

Taxonomic novelties: New orders: *Golubeviales* Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *Robbauerales* Boekhout, Begerow, Q.M. Wang & F.Y. Bai; New families: *Golubeviaeae* Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *Robbaueraeae* Boekhout, Begerow, Q.M. Wang & F.Y. Bai; New genera: *Dirkmeia* F.Y. Bai, Q.M. Wang, Begerow & Boekhout, *Golubevia* Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *Robbauera* Boekhout, Begerow, Q.M. Wang & F.Y. Bai, *Kalmanozyma* Q.M. Wang, F.Y. Bai, Begerow & Boekhout; New combinations: *Anthracocystis* parmpara (Speg.) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *Dirkmeia* churashimaensis (T. Morita, Y. Ogura, M. Takash., N. Hirose, Fukuoka, Imura, Y. Kondo & Kitamoto) F.Y. Bai, Q.M. Wang, Begerow & Boekhout, *Farysia* achenorium (Buhagiar & Barnett) F.Y. Bai, Q.M. Wang, Begerow & Boekhout, *F. itapuensis* (Landelli & Valente) Begerow, Q.M. Wang, F.Y. Bai & Boekhout, *F. setulabalis* (Fonseca & Inácio) Begerow, Q.M. Wang, F.Y. Bai & Boekhout, *F. taiwaniana* (P.-H. Wang, Y.-T. Wang & S.-H. Yang) Begerow, Q.M. Wang, F.Y. Bai & Boekhout, *Gjerencia* minor (Nyland) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *Kalmanozyma* brasiliensis (J.V.C. Oliveira, T.A. Borges, R.A.C. Santos, L.F.D. Freitas, C.A. Rosa, G.H. Goldman & D.M. Ria). The majority of remaining anamorphic yeast species are transferred to corresponding teleomorph genera based on strongly supported phylogenetic affinities, resulting in the proposal of 28 new combinations. The taxonomic status of a few *Pseudozyma* species remains to be determined because of their uncertain phylogenetic positions. We propose to use the term *pro tempore* or *pro tm* in abbreviation to indicate the single-species lineages that are temporarily maintained.

INTRODUCTION

The subphylum *Ustilaginomycotina* (Basidiomycota, *Fungi*) comprises mainly plant pathogenic fungi usually known as smuts, which are mostly dimorphic and present a yeast stage during part of their life cycle (Bauer et al. 2001a, Begerow et al. 2014). As this yeast stage sometimes not only consists of unicellular budding cells, but also includes cultures that might eventually produce hyphae or divide in other modes than budding, these fungi are often summarised as yeasts or yeast-like fungi. For simplicity of reading we will refer to ‘yeasts’ only, as long a differentiation is not necessary. A considerable number of *Ustilaginomycotina* fungi known from yeast stages only are described as assexual yeast species that are currently classified into 12 genera with 71 species (Boekhout et al. 2011, Begerow et al. 2014, Nasr et al. 2014, Wang et al. 2014). These genera are *Acaromyces*, *Farysizyge*, *Fereydounia*, *Jaminiaea*, *Malassezia*, *Meira*, *Moniliella*, *Pseudozyma*, *Rhodotorula* (pro
parte), **Sympodiomycopsis**, **Tilletia** and **Tilletiosis** (Stolk & Dakin 1966, Gokhale 1972, Boekhout 1991, 1995, Boekhout et al. 1995, 2003, 2011, Begerow et al. 2000, 2006, Inácio et al. 2008, Sipiczki & Kajdacsi 2009, Nasr et al. 2014, Wang et al. 2014). Species of these 12 genera occur in four classes currently recognised in **Ustilaginomycotina**, namely **Exobasidiomycetes**, **Malasseziomycetes**, **Moniliellomycetes** and **Ustilaginomycetes** (Bauer et al. 2001a, Begerow et al. 2006, 2014, Hibbett et al. 2007, Nasr et al. 2014, Wang et al. 2014). Many of ustilaginomycetous genera described from teleomorphic stages are cultivable, like members of **Ustilago**, **Exobasidium** and **Microstoma**, but their yeast stages have not been studied with respect to their physiological characteristics in depth as it is typically done for yeasts.

The genera **Acaromyces** and **Meira** contain probably mite-associated species, which are morphologically similar to **Pseudozyma** species, but phylogenetically belong to different lineages within **Exobasidiomycetes** (Boekhout et al. 2003, 2011, Rush & Aime 2013). The genus **Pseudozyma** is a polyphyletic anamorphic genus with species occurring in various clusters together with teleomorphic species of **Ustilago**, **Sporisorium** and **Moeszziomyces** in the **Ustilaginales** (**Ustilaginaceae**) (Begerow et al. 2000, 2006, 2014, Stoll et al. 2003, 2005, Liou et al. 2009, McTaggart et al. 2012a, b, Chamanpao et al. 2013, Shivas et al. 2013, Oliveira et al. 2014). The genus **Faryszyma** is an anamorphic genus in the **Anthracoideaceae** (**Ustilaginales**) described by Inácio et al. (2008) that clusters with teleomorphic species of the genus **Farysia** containing dimorphic smut fungi. The genus **Fereydounia** represents the first yeast lineage within **Urocystidiales** (Nasr et al. 2014). The genus **Jaminiaea** represents a basal lineage in the **Microstromatales** (**Exobasidiomycetes**) based on ribosomal RNA (rRNA) gene sequence analysis (Sipiczki & Kajdacsi 2009). **Sympodiomycopsis** is an anamorphic genus and its basidiomycetous affinity was discussed for a long time based on the ubiquinone system, type of cell wall and sepal pore ultrastructure (Sugiyama et al. 1991). Sequence analyses of the small subunit ribosomal RNA (SSU rRNA) and the large subunit rRNA (LSU rRNA) D1/D2 domains indicated that **Sympodiomycopsis** is a member of **Exobasidiomycetes** (Suh & Sugiyama 1994, Fell et al. 2000). **Tilletiaria** is a teleomorphic genus characterised by the presence of telospores and narrow hyphae without clamp connections (Bandoni & Johri 1972). This genus was tentatively placed in the **Tilletiales** (Boekhout et al. 1992), but was later proposed to represent the family **Tilletiariaceae** in the **Georgefisicherales** (**Exobasidiomycetes**) based on molecular phylogenetic analyses and morphology of its basidium (Begerow et al. 2006, Boekhout et al. 2006, Hibbett et al. 2007, Boekhout et al. 2011). **Tilletiosis** species occur in different orders of **Exobasidiomycetes** and this genus was often used as a ‘catch all’ genus for anamorphic members of **Exobasidiomycetes** (Begerow et al. 2000, 2006, 2014, Fell et al. 2000, Boekhout et al. 2011). Although most **Rhodotorula** species belong to **Puccinicipynomentina** (Fell et al. 2000, Sampaio 2011). In addition to **Rhodotorula acheniorum** which has been transferred to **Faryszyma** (Inácio et al. 2008), three other **Rhodotorula** species are located in the **Microstromatales** (**Exobasidiomycetes**) (Sampaio 2004, 2011, Boekhout et al. 2011, Begerow et al. 2014). Recently, multiple gene sequence analyses showed that the genera **Malassezia** and **Moniliella** represent two deeply rooted lineages within **Ustilaginomycotina** and, subsequently, two classes **Malasseziomycetes** and **Moniliellomycetes** were proposed to accommodate them (Wang et al. 2014).

Based on several studies, it has been clear that many anamorphic yeast species are phylogenetically closely related with teleomorphic smut fungi and that some of the former represent a saprophytic stage of the latter (Begerow et al. 2000, 2014, Boekhout et al. 2011). However, as is the case in other groups of **Basidiomycota**, ustilaginomycetous yeasts have been conventionally classified mainly based on physiological and biochemical criteria, resulting in a taxonomic system independent from, and largely incompatible with that of the smut fungi, which were classified mainly based on morphological characters and host range of the teleomorphic stage (Boekhout 1991, Boekhout et al. 2011, Begerow et al. 2014). Additionally, although many species of smut fungi are cultivable only very few teleomorphic species are available as reference cultures. Integrated taxonomic revisions of **Ustilaginomycotina** unifying anamorphic and teleomorphic taxa have been made in recent years based on molecular data (Begerow et al. 2000, 2006, 2014, Bauer et al. 2001a, Weiß et al. 2004, Matheny et al. 2006, Boekhout et al. 2011). The process is, however, hampered by the lack of a robust and integrated phylogenetic analysis and by use of the dual nomenclature code for teleomorphic fungi. Recent studies have shown that the **Exobasidiomycetes** may not represent a monophyletic group (Begerow et al. 2006, 2014, Hibbett et al. 2007, Boekhout et al. 2011, Wang et al. 2014) and a considerable number of currently recognised genera of both yeasts and dimorphic smut fungi in **Ustilaginomycotina** are polyphyletic (Begerow et al. 2000, 2014, Boekhout et al. 2011, McTaggart et al. 2012a, b). The fine phylogenetic relationships between the yeast and filamentous taxa remain to be resolved. Here we used phylogenetic analyses of seven genes to address the phylogenetic relationships of ustilaginomycetous yeast species with each other and with their filamentous counterparts. Consequently, taxonomic revisions for the majority of the ustilaginomycetous yeasts employed were proposed according to the ‘One Fungus = One Name’ principle (Hawksworth 2011, Taylor 2011, McNeill et al. 2012).

**MATERIALS AND METHODS**

**Taxon sampling**

All ustilaginomycetous yeast species listed in the 5th edition of *The Yeasts, A Taxonomic Study* (Kurtzman et al. 2011) were employed (Tables 1 and 2). The yeast and smut culture strains used came from the CBS Fungal Biodiversity Centre (CBS-KNAW), Utrecht, Netherlands; the China General Microbiological Culture Collection Center (CGMCC), Institute of Microbiology, Chinese Academy of Sciences, Beijing, China; and Ruhr-Universität Bochum, AG Geobotanik, Germany.

**PCR and DNA sequencing**

Genomic DNA was extracted from cultures grown on yeast extract peptone dextrose (YPD) plates using the method described by Bolano et al. (2001). Seven loci were selected, including four protein-coding genes, namely the two RNA polymerase II subunits (**RPB1** and **RPB2**), the translation elongation factor 1-α (**TEF1**) and the mitochondrial cytochrome b (**CYTB**); and three rRNA
Table 1. Taxa and sequence accession numbers employed in the combined seven genes sequence analysis (those in bold are determined in this study).

| Species                  | Strains number | D1D2     | ITS      | SSU      | RPB1      | RPB2      | EF1      | CytB     |
|--------------------------|----------------|----------|----------|----------|-----------|-----------|----------|----------|
| **Exobasidiomycetes**    |                |          |          |          |           |           |          |          |
| Tilletiaria anomala      | CBS 436.72     | AJ235284 | DQ234558 | AY803752 | DQ234571  | AY803750  | DQ835991 | KP323046 |
| Tilletiopsis derrxi       | CBS 110078 T   | AB052823 | AB045707 | AB045704 | KP322926  | KP323086  | KP323138 | KP323020 |
| Tilletiopsis flavus       | CBS 401.84 T   | AJ235285 | KP322987 | KP322970 | —         | —         | KP323126 | KP323004 |
| Tilletiopsis fulvescens   | CBS 607.83 T   | AJ235282 | KP322988 | KP322971 | —         | —         | —        | KP323045 |
| Tilletiopsis minor        | CBS 543.50 T   | AJ235287 | KP322989 | KP322972 | KP322938  | KP323097  | KP323114 | KP323008 |
| Tilletiopsis penniseti    | CBS 110032 T   | AB052825 | —        | KP322975 | KP322917  | KP323085  | KP323143 | KP322995 |
| **Microstromatales**      |                |          |          |          |           |           |          |          |
| Jaminia angkorensis       | CBS 10918      | EJ587489 | EJ604147 | EJ604148 | KP322907  | KP323082  | KP323152 | KC628747 |
| Jaminia lanaiensis        | CBS 10858  T   | DQ990016 | DQ990017 | KP322964 | —         | KP323080  | KP323144 | KP323021 |
| Microstoma juglandidis    | CBS 287.63     | AF09867  | DQ789988 | DQ789987 | DQ789990  | DQ789991  |          | —        |
| Microstoma albizae        | CMV 36935      | KP322982 | KP322982 | KP322947 | —         | KP323079  | KP323150 | KP323016 |
| Quambalaria cyanescens    | CBS 876.73     | DQ317616 | DQ317623 | KF706440 | —         | KP706845  | KP323031 | —        |
| Rhodotorula bacarum       | CGMCC 2.3190 T | AF190002 | DQ317629 | AJ496257 | KP322937  | KP323098  | KP323120 | AB040618 |
| Rhodotorula hinnulae      | JCM 9030 T     | AF190003 | AB038130 | AB038130 | KP322905  | KP323062  | KP323121 | AB041050 |
| Rhodotorula phylloplana   | JCM 9035 T     | AF190004 | AB038131 | AJ496258 | KP322906  | KP323063  | KP323116 | AB041051 |
| Sympodiomycopsis kandeliae| CBS 11676      | GU047881 | GQ465043 | KP322963 | KP322925  | KP323077  | KP323149 | KP323047 |
| Sympodiomycopsis papilipes| CGMCC 2.1398 T | AF352054 | DQ317631 | KP322941 | KP323099  | KP323117  | —        | —        |
| **Tilletiales**           |                |          |          |          |           |           |          |          |
| Erratomyces patellii      | CBS 669.70     | DQ094784 | DQ846894 | DQ846895 | DQ846897  | DQ846896  | DQ846898 | —        |
| Tilletia goloskokovii     | LMC 321        | AY818998 | DQ32248 | DQ32247  | DQ832250  | DQ832249  | DQ832251 | —        |
| **Entylomatales**         |                |          |          |          |           |           |          |          |
| Entyloma amoseridis       | CBS 203.36     | DQ645528 | DQ911699 | DQ645529 | —         | DQ645530  | DQ645531 | —        |
| Entyloma calendulae       | CBS 74.85      | DQ663687 | DQ663689 | KP322948 | —         | DQ663690  | KP323124 | KP323056 |
| Entyloma ficariae         | CBS 480.91     | AJ235295 | JQ86199  | KP322949 | KP322944  | —         | KP323125 | —        |
| Tilletiopsis creema       | CBS 605.83 T   | AJ235279 | AB025690 | KP322969 | —         | KP323108  | KP323129 | KP323006 |
| Tilletiopsis lilacina     | CBS 435.92 T   | KP322984 | KP322966 | —         | KP323110  | KP323112  | KP323002 | —        |
| Tilletiopsis washingtonensis| CBS 544.50 T  | AJ235278 | DQ835994 | KP322976 | —         | DQ835995  | DQ835996 | KP322997 |
| **Doassansiales**         |                |          |          |          |           |           |          |          |
| Rhamphospora nymphaeae    | CBS 72.38      | DQ831032 | DQ831034 | DQ831033 | —         | DQ831035  | DQ831036 | —        |

(continued on next page)
| Species | Strains number | D1D2 | ITS | SSU | RPB1 | RPB2 | EF1 | CytB |
|---------|----------------|------|-----|-----|------|------|-----|------|
| Exobasidiales | | | | | | | | |
| Acaromyces ingoldii | CBS 110050 T | AY158665 | AY158671 | ? | KP322920 | KP323078 | KP323145 | KP323019 |
| Exobasidium gracile | DSM 4460 | DQ663699 | DQ663700 | DQ785786 | DQ663702 | DQ663701 | DQ663703 | — |
| Exobasidium rhododendri | CBS 101457 | DQ667151 | DQ667153 | DQ667152 | DQ667155 | DQ667154 | DQ667156 | — |
| Exobasidium vaccini | DB 160d | KP322983 | KP322983 | KP322984 | KP322924 | KP323076 | KP323146 | — |
| Meira argoae | CBS 110053 T | AY158669 | AY158675 | KP322953 | KP322922 | KP323081 | KP323139 | KP323017 |
| Meira geulakonigii | CBS 110052 T | AY158668 | AY158674 | KP322954 | KP322919 | KP323083 | KP323141 | KP323011 |
| Meira nashicola | CBS 117161 T | AB185157 | AB185159 | KP322955 | KP322921 | KP323084 | KP323140 | KP323014 |
| Species incertae sedis in the Exobasidiomycetes | | | | | | | | |
| Tilletiopsis alsbescens | CBS 608.83 T | AJ235289 | KP322986 | KP322968 | KP322942 | KP323095 | KP323127 | KP323028 |
| Tilletiopsis pallescens | CBS 364.85 T | AJ235292 | DQ317636 | KP322973 | KP322943 | KP323075 | KP323123 | KP323092 |
| Ustilaginomycetes | | | | | | | | |
| Urocystales | | | | | | | | |
| Urocystis colchici | CBS 283.28 | DQ838576 | DQ839596 | DQ839595 | — | DQ839597 | DQ839598 | — |
| Urocystis pallescens | CBS 364.85 T | AJ235292 | DQ317636 | KP322973 | KP322943 | KP323075 | KP323123 | KP323092 |
| Ustilaginales | | | | | | | | |
| Anthracocystis axicola | MP 3490 | DQ631906 | DQ631908 | DQ631907 | — | DQ631909 | DQ631910 | — |
| Cintractia axicola | HAJB 10488 | DQ645506 | DQ645508 | DQ645507 | DQ645510 | DQ645509 | DQ645511 | — |
| Cintractia limitata | CGMCC 2.3198 T | AF190001 | AB038128 | AJ496256 | KP322927 | KP323064 | KP323131 | AB041047 |
| Farysizyma acheniorum | CBS 10428 T | DQ767831 | DQ767831 | DQ767831 | KP322915 | KP323075 | KP323161 | KP323054 |
| Farysizyma itapuensis | CBS 10241 T | EU002887 | EU002888 | KP322950 | KP322913 | KP323073 | KP323147 | KP323013 |
| Farysizyma taiwianica | CBS 9927 T | AY551270 | AY555071 | KP322951 | KP322914 | KP323071 | KP323148 | KP323033 |
| Schizonella melanogramma | CBS 174.42 | DQ832210 | DQ832211 | DQ832211 | DQ832214 | DQ832213 | DQ832215 | — |
| Ustanciosporium gigantosporum | CBS 131478 | JN367325 | JN367329 | JN367352 | JN367428 | — | JN367375 | — |
| Ustanciosporium standleyanum | JAG 73 | DQ846888 | DQ846890 | DQ846892 | DQ846891 | DQ846893 | — | — |
| Anthracocystis anthracoidespora | HUV 18350 | JN367315 | JN367290 | JN367344 | JN367420 | — | JN367367 | — |
| Anthracocystis apludae | KVU 967 | JN367319 | JN367294 | JN367348 | JN367424 | — | JN367371 | — |
| Anthracocystis walkeri | KVU 975 | JN367322 | JN367297 | JN367390 | JN367426 | — | JN367373 | — |
| Anthracocystis pampera | JCM 2007 | KP322980 | KP322980 | KP322961 | KP322908 | KP323066 | — | — |
| Langdonia aristidae | HUV 19145 | JN367317 | JN367292 | JN367346 | JN367422 | — | JN367369 | — |
| Macalpinomyces eraschnes | CBS 131454 | JN367312 | JN367287 | JN367340 | JN367417 | KP323074 | KP323142 | KP323022 |
Table 1. (Continued).

| Species                        | Strains number | D1D2          | ITS           | SSU            | RPB1           | RPB2           | EF1            | CytB            |
|--------------------------------|----------------|---------------|---------------|----------------|----------------|----------------|----------------|----------------|
| Macalpinomyces spermophorus    | HUV 20717/F 565| AY740171      | AY740171      | JN367358       | JN367433       | —              | JN367381       | —              |
| Melanopichium pennsylvanicum   | UMa704         | JN367313      | JN367288      | JN367341       | JN367418       | —              | JN367364       | —              |
| Ustilago maydis                | CBS 504.76     | AF453938      | AY854090      | KP322979       | KP322928       | KP323090       | KP323130       | KP322996       |
| Ustilago maydis                | FB1            | KP866233      | KP866233      | KP322952       | KP322912       | KP323067       | KP323154       | KP323003       |
| Moeszziomyces bullatus         | CBS 425.34     | DQ831011      | DQ831012      | DQ831015       | DQ831015       | —              | —              | —              |
| Sporisorium andropogonis      | CBS 192.26/KVU 841 | AY740095      | AY740042      | KP322962       | JN367419       | KP323065       | JN367366       | —              |
| Sporisorium exertum            | KVU 965        | JN367318      | JN367293      | JN367437       | JN367423       | —              | JN367370       | —              |
| Sporisorium reilianum          | CBS 131460     | KF706430      | KF706438      | KF322910       | KF706511       | KF706472       | KP323058       | —              |
| Sporisorium sotamineum         | CBS 131463     | JN367321      | JN367296      | KP322965       | JN367425       | KP323070       | JN367372       | —              |
| Sporisorium sorghi             | CBS 104.17     | AY745726      | DQ200931      | KP323105       | DQ285784       | KP323060       | —              | —              |
| Stollia bursa                  | KVU 844        | JN367316      | JN367291      | JN367345       | JN367421       | —              | JN367368       | —              |
| Pseudozyma abaconensis         | CBS 6380       | FJ008047      | FJ008053      | KP322956       | KP322916       | KP323092       | KP323159       | KP323051       |
| Pseudozyma antarctica          | CBS 5955       | AJ235302      | AB089358      | KP322960       | KP322935       | KP323093       | KP323118       | KP323048       |
| Pseudozyma flocculosa          | CBS 167.88 T   | AJ235299      | AF294690      | KP322931       | KP323016       | —              | JN367368       | —              |
| Pseudozyma hubeiensis          | CGMC 2.2493 T  | DQ008953      | DQ008954      | KP322957       | —              | KP323103       | KP323111       | KP322990       |
| Pseudozyma parantarctica       | CBS 10005 T    | AB089357      | AB089356      | JN904507       | JN992528       | KP323093       | KP323151       | KP322991       |
| Pseudozyma prolifica           | CBS 319.87 T   | AJ235298      | AF294700      | AF294724       | DQ352825       | KP323089       | KP323093       | KP323009       |
| Pseudozyma prinii              | CBS 10937 T    | EU379943      | EU379942      | KP322958       | KP322911       | KP323087       | KP323155       | KP323050       |
| Pseudozyma rugulosa            | JCM 10323 T    | JN405423      | JN405458      | KP323091       | KP323133       | KP323049       | —              | —              |
| Pseudozyma shaxiensis          | CGMC 2.2523 T  | DQ008955      | DQ008956      | KP322932       | KP323014       | KP323113       | KP323005       | —              |
| Pseudozyma thailandica         | CBS 10069 T    | AB089355      | AB089354      | KP322959       | KP322909       | KP323088       | KP323157       | KP322999       |
| Tranzscheliella hypodytes      | RK074 T        | JN367323      | JN367298      | JN367351       | JN367427       | —              | JN367374       | —              |
| Tranzscheliella williamssii    | CBS 131475     | JN367338      | JN367310      | KP322974       | KP322923       | KP323068       | KP323156       | KP323052       |
| Ustilago cyanodontis           | HRK 040/MS 1   | AY740168      | AY740168      | JN367355       | JN367430       | —              | JN367378       | —              |
| Ustilago filiformis            | HRK 025 T      | JN367328      | JN367302      | JN367356       | JN367431       | —              | JN367379       | —              |
| Ustilago hordei                | CBS 131470     | KF706429      | KF706437      | KP322978       | KF706498       | KF706521       | KF706473       | KP323055       |
| Ustilago hordei                | DB 1526        | JN367329      | JN367303      | JN367357       | JN367432       | —              | JN367380       | —              |
| Ustilago striiformis           | HUV 18286 T    | DQ875375      | AY740172      | JN367359       | JN367434       | —              | JN367382       | —              |
| Ustilago tritici               | CBS 669.70     | DQ948784      | DQ846894      | DQ846895       | DQ846897       | DQ846896       | —              | —              |
| Ustilago xerochloae            | KVU 1000 T     | JN367339      | JN367311      | JN367362       | JN367436       | —              | JN367385       | —              |
| Ustilago vetiveriae            | HUV 17954 T    | JN367337      | AY345011      | JN367360       | JN367435       | —              | JN367383       | —              |

(continued on next page)
### Table 1. (Continued).

| Species Strains number | D1D2   | ITS    | SSU    | RPB1   | RPB2   | EF1   | CytB   |
|------------------------|--------|--------|--------|--------|--------|-------|--------|
| **Malasseziomycetes**  |        |        |        |        |        |       |        |
| **Malasseziales**      |        |        |        |        |        |       |        |
| Malassezia caprae      | CBS 10434 T | AY743616 | AY743656 | KF706456 | KF706495 | KF706513 | KF706467 | KP323001 |
| Malassezia dermatis    | CBS 9169 T | AB070365 | AY390284 | KF706452 | KF706490 | KF706532 | KF706461 | KP323000 |
| Malassezia equina      | CBS 9969 T | AY743621 | KF706439 | KF706454 | KF706492 | KF706515 | KP323100 |
| Malassezia furfur       | CBS 1878 T | AF063214 | AY743634 | KF706457 | KF706497 | KF706516 | KF706469 | KP323024 |
| Malassezia globosa      | CBS 7966 T | AF064025 | AY387132 | —        | KF706493 | KF706518 | KF706465 | KP323018 |
| Malassezia japonica    | CBS 9431 T | EF140672 | EF140669 | KF706458 | —        | KF706514 | KF323153 | KP323026 |
| Malassezia nana        | CBS 9558 T | EF140673 | EF140667 | KF706453 | KF706491 | KF706510 | KF706462 | KP323015 |
| Malassezia obtusa       | CBS 7876 T | AB105197 | AY738137 | KF706455 | —        | KF706519 | KF706470 | KP323030 |
| Malassezia pachydermatis | CBS 1879 T | AY743605 | AB118941 | DQ457640 | DQ785792 | DQ408140 | —        | —        |
| Malassezia restricta   | CBS 787 T | AF064026 | AY743636 | EU192367 | KF706496 | KF706520 | KF706471 | KP323027 |
| Malassezia slooffiae    | CBS 9966 T | AJ249956 | AY743633 | KF706459 | —        | —        | —        | —        |
| Malassezia sympodialis | CBS 722 T | AF064024 | AY743632 | KF706460 | —        | KP323094 | KP323158 | KP323023 |
| Malassezia yamatoensis | CBS 9725 T | AB125263 | AB125261 | KF706494 | KF706512 | KF706466 | KP323012 |
| **Moniliellomycetes**  |        |        |        |        |        |       |        |
| **Moniliellales**      |        |        |        |        |        |       |        |
| Moniliella acetoabutens | CBS 169.66 T | AF335523 | EU252153 | KF706443 | KF706500 | KF706523 | KF706476 | KP323032 |
| Moniliella madda       | CBS 240.79 T | AF335522 | —        | KF706447 | KF706502 | KF706525 | KF706478 | KP323038 |
| Moniliella megachiliensis | CBS 190.92 T | EF137916 | KF706433 | KF706448 | KF706501 | KF706524 | KF706477 | KP323037 |
| Moniliella melis        | CBS 350.33 T | EU545185 | —        | KF706446 | —        | KF706528 | KF706481 | KP323041 |
| Moniliella nigrescens   | CBS 269.81 T | AF335527 | KF706436 | —        | KF706504 | KF706527 | KF706480 | KP323040 |
| Moniliella oedocephalis | CBS 649.66 T | AF335521 | KF706435 | KF706449 | —        | KP323039 | KP323107 | KP323042 |
| Moniliella pollinis     | CBS 461.67 T | AF335525 | KF706434 | KF706450 | KF706505 | KF706529 | KF706482 | KP323039 |
| Moniliella spathulata   | CBS 241.79 T | AF335526 | KF706432 | KF706444 | KF706503 | KF706526 | KF706479 | KP323036 |
| Moniliella suaveolens   | CBS 126.42 T | AF335520 | KF706431 | KF706445 | —        | —        | —        | —        |

1 Cultures and herbarium specimen are available from the respective collections (CBS, Centraalbureau voor Schimmelcultures; CGMCC, the China General Microbiological Culture Collection Center; CMW, DB, DSM, and FB, Dominik Begerow, Ruhr-Universität Bochum; F, Herbarium Franz Oberwinkler; HAJB, Herbarium Havanna Jardin botánico; HMK, Herbarium Martin Kemler; HRK, Herbarium Ronny Kelner; HUV, Herbarium Ustilaginales Vanký; JAG, Herbarium J.A. Gossmann; JCM: the Japan Collection of Microorganisms (JCM); KVU: Kálmán Vánky Ustilaginales; LMC: Herbarium L. M. Carris; MP, Herbarium Meike Piepenbring; RK, strain collection Ronny Kelner; UMa, Marco Thines).
Table 2. Overview of the classification of the ustilaginomycetous yeasts and related fungi in the Ustilaginomycotina. Only the species compared in this study are included. For the details on the taxonomy of teliomorphs see Vanky (2012) and Begerow et al. (2014). Type species of genera, genera, families, orders and classes are in bold.

| Species                | Basionym or important synonym | Strain/Herbarium number | D1/D2 | ITS         |
|------------------------|--------------------------------|-------------------------|-------|-------------|
| **Exobasidiomycetes**  |                                 |                         |       |             |
| Doassansiales          |                                 |                         |       |             |
| **Rhamphosphoraceae**  |                                 |                         |       |             |
| *Rhamphospora*         | *Rhamphospora nymphaeae*        | CBS 72.38               | DQ831032 | DQ831034   |
| **Entylomatales**      |                                 |                         |       |             |
| **Entylomataceae**     |                                 |                         |       |             |
| *Entyloma*             |                                 | CBS 203.36              | DQ645528 | DQ911609   |
| *E. calendulae*        | *Protomyces calendulae*         | CBS 746.85              | DQ663687 | DQ663689   |
| *E. ficariae*          |                                 | CBS 480.91              | AJ235295 | JQ561999   |
| **Tilletiopsis**       |                                 | CBS 605.83              | AJ235279 | AB025690   |
| *T. cremaea*           |                                 | CBS 435.92              | KP322984 | KP322984   |
| *T. washingtonensis*   |                                 | CBS 544.50              | AJ235278 | DQ835994   |
| **Exobasidiales**      |                                 |                         |       |             |
| **Brachybasidiaceae**  |                                 |                         |       |             |
| *Meira*                |                                 | CBS 110053              | AY158669 | AY158675   |
| *M. argovae*           |                                 | CBS 110052              | AY158668 | AY158674   |
| *M. geulakonigii*      |                                 | MCA 3882                | JX432962 | JX432962   |
| *M. miltonrushii*      |                                 | CBS 117161              | AB185157 | AB185159   |
| *Cryptobasidiaceae*    |                                 |                         |       |             |
| *Acaromyces*           |                                 | CBS 110050              | AY158665 | AY158671   |
| **Laurobasidium**      |                                 |                         |       |             |
| *L. lauri*             | *Exobasidium lauri*             | MAFF238685              | AB177562 | AB180359   |
| **Exobasidiaceae**     |                                 |                         |       |             |
| *Exobasidium*          |                                 |                         |       |             |
| *E. gracile*           | *Exobasidium camelliae var. gracile* | DSM4460 | DQ663690 | DQ663700   |
| *E. rhododendri*       | *Exobasidium vaccinii var. rhododendri* | CBS 101457 | DQ667151 | DQ667153   |
| *E. vaccinii*          |                                   | TUB019109              | FJ644526 | AB180362   |
| **Georgefischeriales** |                                 |                         |       |             |
| **Gjaerumia**          |                                 |                         |       |             |
| *G. penniseti*         | *Tilletiopsis penniseti*         | CBS 110032              | AB052825 | —           |
| *G. minor*             | *Tilletiopsis minor*             | CBS 543.50              | AJ235287 | KP322989   |
| **Tilletiariaceae**    |                                 |                         |       |             |
| **Phragmotaenium**     |                                 |                         |       |             |
| *P. derrxi*            | *Tilletiopsis derrxi*            | CBS 110078              | AB052823 | AB045707   |
| *P. flavum*            | *Tilletiopsis flavum*            | CBS 401.84              | AJ235285 | KP322987   |
| *P. fulvescens*        | *Tilletiopsis fulvescens*        | CBS 607.83              | AJ235282 | KP322988   |
| *P. oryzicola*         | *Tilletiopsis oryzicola*         | CBS 110079              | AB052825 | AB045708   |
| **Tilletiaria**        |                                 | CBS 436.72              | AJ235284 | DQ234558   |
| **Golubeviales**       |                                 |                         |       |             |
| **Golubeviae**         |                                 |                         |       |             |
| (continued on next page) |                                |                         |       |             |
| Species | Basionym or important synonym | Strain/Herbarium number | D1/D2 | ITS |
|---------|-------------------------------|-------------------------|-------|-----|
| **Golubevia gen. nov.¹** | | | | |
| G. pallescens comb. nov.¹ | Tilletopsis pallescens¹ | CBS 111626 | AY879271 | AY879278 |
| | | CBS 364.85¹ | AJ235292 | DQ317636 |
| **Microstromatales** | | | | |
| **Microstromataceae** | | | | |
| M. albiziae | | CMW 36935 | KP322982 | KP322982 |
| M. album | Fusisporium album | RB2072 | AF352052 | DQ317624 |
| | Rhodotorula bacarum | CGMCC 2.3190¹ | AF190002 | DQ317629 |
| | Tilletopsis bacarum | | | |
| M. phlyloplanum comb. nov.¹ | Cryptococcus phlyloplanus¹ | JCM 9035¹ | AF190004 | AB038131 |
| | Rhodotorula phlyloplana¹ | | | |
| | Cryptococcus hinnuleus¹ | JCM 9030¹ | AF190003 | AB038130 |
| | Rhodotorula hinnulea¹ | | | |
| M. juglandis | Fusidium juglandis | CBS 287.63 | AF009867 | DQ789988 |
| **Volvocisporiaceae** | | | | |
| **Volvocisporium** | | | | |
| V. triumfetticola | Munbasidiospora triumfetticola | RB2070 | AF352053 | DQ317637 |
| **Quambalariaeae** | | | | |
| Q. cyanescens | Sporothrix cyanescens | CBS 876.73 | DQ317616 | DQ317623 |
| **Microstromatales incertae sedis** | | | | |
| **Jaminiae¹** | | | | |
| J. angkorensis¹ | | CBS 10918¹ | EU587499 | EU604147 |
| J. lanaiensis¹ | Sympodiomycopsis lanaiensis¹ | CBS 11676¹ | GU047881 | GQ465043 |
| **Sympodiomycopsis¹** | | | | |
| S. kandelliae¹ | | CBS 10858¹ | DQ990016 | DQ990017 |
| S. paphiopedilii¹ | | AS 2.1398¹ | AF352054 | DQ317631 |
| **Robbaueraceae ord. nov.¹** | | | | |
| **Robbaueraceae fam. nov.¹** | | | | |
| Robbauer a gen. nov.¹ | | | | |
| R. albescens comb. nov.¹ | Tilletopsis albescens¹ | CBS 608.83¹ | AJ235289 | KP322986 |
| **Tilletiales** | | | | |
| **Tilletiaceae** | | | | |
| E. patelli | Protomyces patelli | CBS 669.70 | DQ94784 | DQ846894 |
| **Tilletia** | | | | |
| T. caries | Uredo caries | CBS 160.85 | AJ235307 | AY496450 |
| T. controversa | Tilletia controversa | MP2525 | DQ832244 | DQ832246 |
| T. goloskokovii | | LMC321 | AY819998 | DQ832248 |
| T. iowensis | Neovossia iowensis | BP1863664 | AY819988 | DQ832253 |
| **Ustilaginomycetes** | | | | |
| **Urocystales** | | | | |
| **Doassansiopsaceae** | | | | |
| Doassansiops transformis | Doassansa limbocaridis | HUV15198 | AF09850 | DQ873544 |
| **Fereydouniaceae¹** | | | | |
| Fereydounia | | | | |
| F. khargensis¹ | | IBRCM30116¹ | KJ490642 | KJ490641 |
| **Glomosporiaceae** | | | | |
| **Thecaphora** | | | | |

¹: Authors' synonyms or basionyms.
Table 2. (Continued).

| Species                          | Basionym or important synonym                  | Strain/Herbarium number | D1/D2 ITS |
|----------------------------------|------------------------------------------------|-------------------------|-----------|
| *T. spilanthis*                  |                                               | JAG53                   | DQ832241  DQ832243 |
| **Urocystaceae**                 | **Melanoxa**                                   |                         |           |
| *M. oxalidiella*                 |                                               | TUB 015007              | EF635905  EF635906 |
| *M. oxalidis*                    | Melanotaenium oxalidis                        | HUV1436                 | EF635908  EF635907 |
| **Mundkurella**                  | *M. kalopanacis*                              | HUV16732                | AF009869  DQ875351 |
| **Urocystis**                    | *U. colchici*                                  | CBS 283.28              | DQ838576  DQ839596 |
|                                  | *U. eranthidis*                                | hmk292                  | JN367324  JN367299 |
| **Ustacystis**                   | *U. waldsteiniæ*                              | FO38439                 | AF009880  DQ875356 |
| **Vankyta**                      | *V. heufleri*                                  | HUV15007                | EF653981  EF667965 |
|                                  | *V. ornithogali*                               |                         |           |
| **Ustilaginales**                | **Anthracoideaceae**                           |                         |           |
| **Cintractia**                   | *C. amazonica*                                 | MP200                   | AJ236142  DQ875342 |
|                                  | *C. axicola*                                   | MP3490                  | DQ631906  DQ631908 |
|                                  | *C. limitata*                                  | HAJB10488               | DQ645506  DQ645508 |
| **Dermatosorus**                 | *D. cypér*                                     | HUV15991                | AJ236157  DQ875343 |
| **Farysia**                      | *F. acheniorum comb. nov.*                    | AS 2.3198T              | AF190001  AB038128 |
|                                  | *F. chardoniana*                               | MP2062                  | AF009859  AY344968 |
|                                  | *F. itapuensis comb. nov.*                    | CBS 10428T              | DQ767831  DQ767831 |
|                                  | *F. setubalensis comb. nov.*                   | CBS 10241T              | EU002857  EU002888 |
|                                  | *F. taiwaniana comb. nov.*                     | CBS 992T                | AY551270  AY555071 |
| **Leucocintractia**              | *L. leucodermoides*                            | MS482                   | DQ875363  DQ875346 |
|                                  | *L. scleriae*                                  | MP2074                  | AJ236154  AY740025 |
| **Moreaua**                      | *M. bulbostylidis*                             | 56581 (M)               | DQ875366  DQ875349 |
|                                  | *M. fimbristyldis*                             | 56582 (M)               | DQ875367  DQ875350 |
| **Schizonella**                  | *S. melanogramma*                              |                         |           |
|                                  | *S. luzulæ*                                    |                         |           |
| **Stegocintractia**              | *Ustilago luzulæ*                              | MP2340                  | AJ236148  DQ875353 |
| **Tolyposporium**                | *T. isolepidis*                                | HUV14720                | EU246949  EU246950 |
|                                  | *T. neillii*                                   | HUV18533                | EU246952  EU246951 |
|                                  | *T. junci*                                     | HUV17168                | AF009876  AY344994 |
| **Ustanciosporium**              | *Cintractia gigantospora*                      | HRK023                  | JN367325  JN367300 |
|                                  | *Cintractia standleyana*                       | JAG73                   | DQ846888  DQ846890 |
| **Melanotaeniaceae**             | **Melanotaenium**                             |                         |           |

(continued on next page)
Table 2. (Continued).

| Species | Basionym or important synonym | Strain/Herbarium number | D1/D2 | ITS |
|---------|--------------------------------|-------------------------|-------|-----|
| M. cingens | Ustilago cingens | L.E.Kari191(M) | DQ875364 | DQ875347 |
| M. endogenum | Protomyces endogenus | CBS 481.91 | DQ789979 | DQ789981 |
| M. euphorbiae | Tilletia euphorbiae | HUV17733 | JN367314 | JN367289 |
| **Ustilaginaceae** | | | | |
| **Anomalomyces** | | | | |
| A. panici | | BRIP46421 | DQ459347 | DQ459348 |
| A. yakirrae | | HUV 2198 | KC184906 | KC184907 |
| **Anthracocystis** | | | | |
| A. anthracoidespora | Sporisorium anthracoidespora | HUV18350 | JN367315 | JN367290 |
| A. apulidae | Sorosporium apulidae | KVU967 | JN367319 | JN367294 |
| A. apulidae-aristatae | Sorosporium apulidae-aristatae | MS287 | AY740098 | AY740045 |
| A. cenchri | Ustilago cenchri | MP1974 | AF453943 | AY344972 |
| A. cenchri-elymoidis | Sorosporium cenchri-elymoidis | BRIP 26491 | HCO13122 | HCO13094 |
| A. destruens | Ust. exs. 472 (M) | UST74077 | AY344976 |
| A. elionuri | Ustilago elionuri | MP2601 (LPB) | AY740157 | AY740157 |
| A. fasicularis | | MS198 | AY740088 | AY740035 |
| A. formosana | Ustilago formosana | Ust. Exs. 688 (M) | AY740134 | AY344979 |
| A. flocculosa | Pseudozyma flocculosa | CBS 167.88 | AJ235299 | AF294690 |
| A. heteropogonica | Sorosporium heteropogonica | BRIP51822 | HCO13135 | HCO130101 |
| A. hwangensis | Sorosporium hwangense | MS267 | AY740104 | AY740051 |
| A. loudetiae-pedicellatae | Sorosporium loudetiae-pedicellatae | MS252 | AY740106 | AY740053 |
| A. ovaria | Sorosporium ovarium | MP1871 | AJ236137 | AY740020 |
| A. pampara comb. nov. | Ustilago pamparum | JCM 2007 | AY740088 | AY740056 |
| A. polliniae | Sorosporium polliniae | MS32 | AY740138 | AY344987 |
| A. provincialis | Sorosporium elisii var. provinciale | Ust.exs.759 (M) | AY747078 | AY344988 |
| A. pseudanthistriatae | Sorosporium pseudanthistriatae | KVU967 | JN367320 | JN367285 |
| A. themedae-argentei | Sorosporium themedae-argentei | Ust. Exs. 855 | AY740140 | AY344991 |
| A. tumefaciens | Sorosporium tumefaciens | MS139 | AY740128 | AY344969 |
| A. walkeri | Sorosporium walkeri | KVU975 | JN367322 | JN367297 |
| **Dirkmeia gen. nov.** | | | | |
| D. churashimensis comb. nov. | Pseudozyma churashimensis | OK98 | AB548955 | AB548947 |
| **Kalmanolza gen. nov.** | | | | |
| K. fusiformata comb. nov. | Pseudozyma fusiformata | CBS 6951 | AB089367 | AB089366 |
| K. brasiliensis comb. nov. | Pseudozyma brasiliensis | GHG001 | KF737866 | KF737866 |
| K. vetiver comb. nov. | Pseudozyma vetiver | DMKU-LV99 | AB809649 | AB809652 |
| **Langdonia** | | | | |
| L. aristidae | Ustilago aristidae | HUV19145 | JN367317 | JN367292 |
| L. confusa | Sorosporium confusum | BRIP42670 | HCO13132 | HCO13095 |
| L. jejuensis comb. nov. | Pseudozyma jejuensis | CBS 10454 | FN286865 | EF079966 |
| **Macalpinomyces** | | | | |
| M. eragrostiellae | | Ust.Exs.960(M) | AY740089 | AY740036 |
| M. eriachnes | Sorosporium eriachnes | CBS 131454 | JN367312 | JN367287 |
| M. loudetiae | Sorosporium loudetiae | MS250 | AY740152 | AY740151 |
| M. mackinlayi | Sorosporium mackinlayi | BRIP50249 | HCO13131 | GU014817 |
| M. neglectus | Ustilago neglecta | RB0256 (TUB) | AY740109 | AY740056 |
| M. spermophorus | | F565 | AY740171 | AY740171 |
| M. trichophyta | | MS248 | AY740092 | AY740039 |
| M. tristachyae | | MS15 | AY740164 | AY740164 |
| Species | Basionym or important synonym | Strain/Herbarium number D1/D2 | ITS |
|---------|-------------------------------|-------------------------------|-----|
| *M. viridans* | *Melanopsichium pennsylvanicum* | BRIP 49133 | HQ013125 HQ013089 |
| *M. pennsylvanicum* | *Melanopsichium pennsylvanicum* | HUV17548 (TUB) | AY740093 AY740040 |
| *M. antarcticus* comb. nov.| *Candida antarctica* | CBS 5865 | AJ235302 AB089358 |
| *M. aphidis* comb. nov.| *Pseudozyma aphidis* | JCM 10317 | JN940521 JN942668 |
| *M. bullatus* | *Sorosporium bullatum* | CBS 425.34 | DQ931011 DQ931013 |
| *M. parantarcticus* comb. nov.| *Pseudozyma parantarctica* | CBS 10005 | AB089357 AB089356 |
| *M. rugulosus* comb. nov.| *Pseudozyma rugulosa* | CBS 170.88 | JN940523 JN942670 |
| *S. aegypticum* | *Ustilago aegyptica* | Ust.Exs.756(M) | AY740129 AY344970 |
| *S. andropogonis* | *Uredo andropogonis* | MS283 | AY740095 AY740042 |
| *S. arthraxonis* | *Ustilago arthraxonis* | MS338 | AY740099 AY740046 |
| *S. cordobense* | *Ustilago cordobensis* | MS159 | AY740155 AY740155 |
| *S. cruentum* | *Ustilago cruenta* | MS14 | AY740156 AY740156 |
| *S. culmipерdum* | *Ustilago culmipерd* | MP2060 | AF135860 AY344975 |
| *S. dimeniae-ornithopodae* | *Ustilago* | Ust.exs. 472 | AY740132 AY344977 |
| *S. erythraeense* | *Ustilago erythraeensis* | Ust.Exs.849 (M) | AY740102 AY740049 |
| *S. exsertum* | *Cintractia exserta* | KV0965 | JN963718 JN976293 |
| *S. fastigiatum* | *Sphacelotheca fastigiatum* | MS21 | AY740133 AY344978 |
| *S. foveolati* | *Sphacelotheca foveolati* | MS283 | AY740095 AY740042 |
| *S. graminicola* comb. nov.| *Pseudozyma graminicola* | LII0 | AB108728 AB108728 |
| *S. holwayii* | *Sphacelotheca holwayii* | MP1271 | AY453941 AY344990 |
| *S. lacrymae-jobi* | *Ustilago lacrymae-jobi* | MS6611 | AY740105 AY740052 |
| *S. lepturi* | *Ustilago carbo var. lepturi* | Ust.exs.966 (M) | AY740135 AY344981 |
| *S. manilense* | *Ustilago manilensis* | Ust.Exs.854 (M) | AY740112 AY740059 |
| *S. modestum* | *Ustilago modesta* | MS337 | AY740107 AY740054 |
| *S. moniliferum* | *Ustilago monilifera* | MS 98 | AY453940 AY344984 |
| *S. nervosum* | *Ustilago nervosa* | MS241 | AY740110 AY740057 |
| *S. occidentale* | *Sphacelotheca occidentalis* | Ust.exs.758 (M) | AY740137 AY344985 |
| *S. ophiuri* | *Ustilago ophiuri* | HB20 | AY740019 AY740019 |
| *S. pseudochinolaenae* | *Ustilago pseudochinolaenae* | Ust.exs.853 (M) | AY740139 AY344989 |
| *S. puellare* | *Ustilago puellaris* | MP2372 | AY740111 AY740058 |
| *S. reilianum* | *Ustilago reiliana* | Ust.exs. 527 | AY740163 AY740163 |
| *S. sclatamineum* | *Ustilago sclataminea* | MP541 | AY740147 AY740070 |
| *S. sorghi* | *Ustilago sorghi* | MP2036a | AY740141 AY344992 |
| *S. trachypogonicola* | *Sphacelotheca trachypogonicola* | MS283 | AY740113 AY740060 |
| *S. trachypogonis-splumosi* | *Sphacelotheca trachypogonis-splumosi* | MS283 | AY740113 AY740060 |
| *S. veracruzanum* | *Sphacelotheca veracruzanum* | MP960 | AY740104 AY344993 |
| *S. vermiculum* | *Ustilago vermiculums* | BRIP49748 | HQ013134 HQ013114 |
| *S. wynaadens* | *Ustilago wynaadensis* | BRIP27640 | HQ013124 HQ013116 |
| *Stollia* | *Ustilago bursa* | KVU844 | JN967316 JN967291 |
| *S. ewartii* | *Ustilago ewartii* | BRIP51818 | HQ013127 HQ013087 |
| *Tranzscheliella* | *Caeoma hypodytes* | MS342 | DQ191256 DQ191250 |
| *T. hypodytes* | *Caeoma hypodytes* | MS342 | DQ191256 DQ191250 |

(continued on next page)
| Species               | Basionym or important synonym               | Strain/Herbarium number | D1/D2 | ITS       |
|-----------------------|---------------------------------------------|-------------------------|-------|-----------|
| T. williamsii         | Sorosporium williamsii                      | CBS 131475              | JN367338 | JN367310 |
| **Triodiomyces**      |                                             |                         |       |           |
| T. altillis           | Ustilago altillis                           | BRIP52543               | H0013136 | AY740166 |
| T. crassus comb. nov. | Pseudozyma crassa                           | DMST17136               | A1117962 | A1117962 |
| T. trioides           | Ustilago trioides                           | HUV17662                | AY740128 | AY740074 |
| **Tubisorus**         |                                             |                         |       |           |
| T. pachycarpus        | Sorosporium pachycarpum                     | HUV 21891               | JN871718 | JN871717 |
| **Ustilago**          |                                             |                         |       |           |
| U. abaconensis comb. nov. | Pseudozyma abaconensis                      | CBS 8380               | FJ008047 | FJ008053 |
| U. affinis            |                                            | MP982                   | A133581 | AY344995 |
| U. austro-africana    |                                            | MS316                   | AY740115 | AY740061 |
| U. avaneae            | Ustilago carbo var. avaneae                 | DB559                   | AY740117 | AY740063 |
| U. bromivora          | Ustilago carbo d bromivora                  | MS175                   | AY740118 | AY740064 |
| U. bullata            |                                            | MP2363                  | AY453935 | AY344998 |
| U. bouquetii          |                                            | MS315                   | A740167 |
| U. calamagrostidis    | Tileta calamagrostidis                      | MS314                   | AY740119 | AY740065 |
| U. crameri            |                                            | MS72                    | AY740143 | AY344999 |
| U. cynodontis         | Ustilago carbo b cynodontis                 | MS199                   | AY740168 | AY740168 |
| U. davisi             |                                            | HUV19252                | AY740169 | AY740169 |
| U. echinata           |                                            | MS132                   | AY740144 | AY345001 |
| U. esculenta          |                                            | Ust.exs. 540            | A453937 | AY345002 |
| U. filiformis         | Lycoperdon filiforme                        | RB3011                  | AY740120 | AY740066 |
| U. hordei             | Uredo segetum a hordei                      | Ust.exs. 784            | A453934 | AY345003 |
| U. hordei             |                                            | CBS 131470              | KF706429 | KF706437 |
| U. ixophori           |                                            | MP2194 (USJ)            | AY740121 | AY740067 |
| U. maydis             | Mycosarcoma maydis                          | CBS 504.76              | A453938 | AY854090 |
| U. maydis             |                                            | FB1                     | K866233 | K866233 |
| U. maydis             | Pseudozyma prolifica                        | CBS 319.87              | A235298 | AF294700 |
| U. nuda               | Ustilago segetum var. nuda                  | HUV17782                | JN367324 | JN367307 |
| U. pamirica           |                                            | Ust.exs.789 (M)         | AY740145 | AY345005 |
| U. shanxiensis comb. nov. | Pseudozyma shanxiensis                      | AS 2.2523               | D008955 | D008956 |
| U. schmidtae          |                                            | BRIP1848                | HQ013129 | HQ013121 |
| U. Schroeteriana      |                                            | Ust.exs.887 (M)         | AY740146 | AY345006 |
| U. siamensis comb. nov. | Pseudozyma siamensis                        | DMST17137               | A1117963 | A1117963 |
| U. sparsa             |                                            | KUV892                  | JN367335 | JN367308 |
| U. striiformis         |                                            | HUV18286                | D8753175 | AY740172 |
| U. synthetismae       | Caeoma synthetismae                         | Ust.Exs.998 (M)         | AY740123 | AY740071 |
| U. tragana            |                                            | MS320                   | AY740124 | AY740072 |
| U. trichophora        | Caeoma trichophorum                         | MS336                   | AY740125 | AY740073 |
| U. tritici            | Uredo segetum & tritici                     | CBS 669.70              | DQ094784 | DQ846894 |
| U. vetiveriae         |                                            | HUV17954                | JN367337 | JN345501 |
| U. xerocloae          |                                            | Ust.exs.1000 (M)        | AY740150 | AY345012 |
| **Species remain to be reclassified** |                                        |                         |       |           |
| Pseudozyma alboarmeniaca pro tem. |                                  | DMST17135               | A1117961 | A1117961 |
| P. hubeiensis pro tem. |                                              | AS 2.2493               | D008953 | D008954  |
| P. pruni pro tem.     |                                            | CBS 10937               | EU379943 | EU379942 |
| P. thaiandica pro tem. |                                              | CBS 10006               | AB089355 | AB089354 |
| P. tsukubaensis pro tem. |                                            | JCM 10324               | AB089373 | AB089372 |

**Websdaneaceae**

**Websdanea**

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gene regions, namely the small subunit nuclear ribosomal RNA (SSU or 18S rRNA), the D1/D2 domains of the large subunit (LSU or 26S rRNA) and the ITS 1+2 regions (including 5.8S rRNA). PCR and sequencing of the three rRNA gene regions and three protein genes, \( RPB1 \), \( RPB2 \) and \( TEF1 \), we performed as described in Wang et al. (2014). PCR and sequencing of the CYTB gene were performed according to Wang & Bai (2008).

Cycle sequencing was performed using the ABI BigDye cycle sequencing kit (Applied Biosystems, Foster, California). Electrophoresis was done using an ABI PRISM 3730 DNA sequencer.

Molecular phylogenetic analyses

Five data sets consisting of the D1/D2 domains of the LSU rRNA gene, the combined ITS (including 5.8S rRNA gene) and D1/D2 domains of the LSU rRNA gene, the combined three rRNA regions, the combined four protein coding genes, and the combined seven genes, respectively, were constructed. Introns were deleted from all sequences before the alignment performed. Sequences of those data sets were aligned with the MAFFT program (Standley 2013). The alignments of different genes were concatenated in the respective analyses. The alignment data sets were first analysed with Modeltest version 3.04 (Posada & Crandall 1998) using the Akaike information criterion (AIC) to find the most appropriate model of DNA substitution. A general time-reversible model of DNA substitution additionally assuming a percentage of invariable sites and \( \Gamma \)-distributed substitution rates at the remaining sites (GTR + I + G) was selected for further analyses. Maximum likelihood (ML) analysis was conducted in RAxML-HPC2 7.2.8 (Stamatakis 2006) using

Table 2. (Continued).

| Species       | Basionym or important synonym | Strain/Herbarium number | D1/D2  | ITS             |
|---------------|-------------------------------|-------------------------|--------|-----------------|
| \( W. \) \( l y g i n i e \) | \( Ustilago \) \( l y g i n i e \) | HUV 17900                | AJ23619 | DQ875357       |
| Malasseziomycetes\(^1\) | \( Malassezia\) | \( CBS 10434\)\(^2\) | \( AY743616 \) \( AY743656 \) |
| \( M. \) \( c a p r a e \)\(^1\) | \( CBS 11721\)\(^3\) | \( GU733708 \) \( GU733709 \) |
| \( M. \) \( d e r m a t i s \)\(^1\) | \( CBS 9169\)\(^7\) | \( AB070365 \) \( A390284 \) |
| \( M. \) \( e q u i n a \)\(^1\) | \( CBS 9969\)\(^7\) | \( AY743621 \) \( KF706439 \) |
| \( M. \) \( f u r f u r \)\(^1\) | \( Microsporum \) \( f u r f u r \)\(^1\) | \( CBS 1878\)\(^X\) | \( AFO65324 \) \( AY743634 \) |
| \( M. \) \( g l o b o s a \)\(^1\) | \( CBS 7966\)\(^7\) | \( AFO64025 \) \( A387132 \) |
| \( M. \) \( j a p o n i c a \)\(^1\) | \( CBS 9431\)\(^7\) | \( EF140672 \) \( EF140669 \) |
| \( M. \) \( n a n a \)\(^1\) | \( CBS 9558 \) | \( EF140673 \) \( EF140667 \) |
| \( M. \) \( o b l u s a \)\(^1\) | \( CBS 7878\)\(^7\) | \( AB105197 \) \( A387137 \) |
| \( M. \) \( p a c h y d e r m a t i s \)\(^1\) | \( Pityosporum \) \( p a c h y d e r m a t i s \)\(^1\) | \( CBS 1879\)\(^7\) | \( AY743605 \) \( A118941 \) |
| \( M. \) \( r e s t r i c t a \)\(^1\) | \( CBS 7877\)\(^X\) | \( AFO64026 \) \( AY743636 \) |
| \( M. \) \( s l o c i f i a e \)\(^1\) | \( CBS 7956\)\(^7\) | \( A249956 \) \( AY743633 \) |
| \( M. \) \( s y m p o d i a l i s \)\(^1\) | \( CBS 7222\)\(^7\) | \( AFO64024 \) \( AY743632 \) |
| \( M. \) \( y a m a t o e n t i s \)\(^1\) | \( CBS 9725\)\(^7\) | \( AB125263 \) \( AB125261 \) |

\(^1\) Yeast species.
RESULTS AND DISCUSSION

Based on the sequences determined in this study and those retrieved from GenBank (http://www.ncbi.nlm.nih.gov/genbank) two datasets comprising concatenated sequences of the seven genes and of the four protein-coding genes solely were constructed for the analysis of the phylogeny of yeast and representative teleomorphic taxa and to visually examine the topological concordance of the trees generated using different algorithms. In order to further examine the fine phylogenetic relationships of yeast species with teleomorphic taxa, a dataset consisting of the combined ITS (including 5.8S rRNA gene) and LSU rRNA gene sequences and a dataset consisting of only LSU rRNA gene sequences were constructed and analysed.

The analysis of the combined seven genes, the combined ITS and LSU rRNA genes and the four protein genes (Figs 1, 2 and 3) were recognised in Nasr et al. (2011), proposed by Farysia species representing anamorphic stages of the genus Farysia. Therefore, we consider Farysizyma species representing anamorphic stages of the genus Farysia.

The Pseudozyma species were located mainly in various clades together with teleomorphic species from the so called Ustilago-Sporisorium-Macalpinomyces complex (McTaggart et al. 2012a, b) in the trees made from the seven gene and the four protein gene datasets (Figs 1 and 3), being in agreement with previous studies based on rRNA gene sequence analysis (Boekhout et al. 2011). The three teleomorphic genera were also found to be polyphyletic (Stoll et al. 2003, 2005), McTaggart et al. (2012a) reconstructed the phylogeny of the complex using four nuclear loci including ITS, LSU rRNA gene, GAPDH and TEF1 and defined eight groups, Clade 1 to Clade 8. Each of the clades was also characterised by host specificity and soral synapomorphies (McTaggart et al. 2012a). Consequently, the authors re-classified the complex by emending the genera Sporisorium (Clade 1), Stollia (Clade 3), Anthracocystis (Clade 4), Triodiomyces (Clade 5), Langdonia (Clade 8) and Stollia (Clade 3) and Triodiomyces (Clade 5) to reflect morphological synapomorphies (McTaggart et al. 2012b).

The fine phylogenetic relationships of the Pseudozyma species with the teleomorphic taxa in the Ustilaginales are shown in the tree constructed from the ITS and LSU dataset which contained the species employed in McTaggart et al. (2012a, b) and other smut fungi (Fig. 2). Sporisorium (Clade 1), Stollia (Clade 3), Anthracocystis (Clade 4), Triodiomyces (Clade 5), Langdonia (Clade 8) and Clade 7 were resolved as well supported monophyletic clades here, being in agreement with McTaggart et al. (2012a, b). However, Clade 2 and Clade 6 as defined by McTaggart et al. (2012a) were shown to be polyphyletic in this study (Fig. 2A). Species from Clade 2 were located in two different subgroups and those from Clade 6 in three subgroups (Fig. 2A). The phylogenetic relationships among these subgroups were not resolved due to the lack of support. The statistical support values for Clade 2 and Clade 6 were weak in the previous study (McTaggart et al. 2012a). Clade 2 lacked Bayesian PP support and Clade 6 with three sub-clades lacked both ML BP and Bayesian PP support. The Ustilago davisi and Ustilago esculenta sub-clades defined by McTaggart et al. (2012a) in Clade 6 also lacked statistical support.

As shown in previous studies based on rRNA gene sequence analyses (Fell et al. 2000, Boekhout et al. 2011), the type species of the genus Pseudozyma, P. proliifica, clustered together with Ustilago maydis in the trees reconstructed from the seven gene, the four protein gene and the two rRNA genes datasets (Figs 1, 2B and 3). The type strain of P. proliifica shared identical ITS and LSU rRNA gene sequences with Ustilago maydis CBS 504.76, suggesting that P. proliifica represents the saprobic asexual stage of Ustilago maydis and should be treated as a synonym of the latter according to the new nomenclature for fungi (McNeill et al. 2012). As a consequence, the genus name Pseudozyma is not available any more.

Four Pseudozyma species, namely P. antarctica, P. aphidis, P. parantarctica and P. rugulosa, clustered together with Moesziomyces bullatus, the sole described species of this teleomorphic genus (Begerow et al. 2014) with strong BP and PP support values in the tree constructed from the ITS and LSU dataset (Fig. 2C). The close affinity of the four Pseudozyma species with Moesziomyces bullatus was also resolved and strongly supported in the trees made from the seven genes and the four protein genes datasets (Figs 1 and 3). Another
Fig. 1. Phylogenetic tree constructed using maximum likelihood analysis from combined sequences of the SSU rRNA gene, LSU rRNA D1/D2 domains, ITS1+2 regions (including 5.8S rRNA gene), RPB1, RPB2, TEF1 and CYTB depicting the phylogenetic placements of yeast genera within Ustilaginomycotina. Branch lengths are scaled in terms of expected numbers of nucleotide substitutions per site. Bayesian posterior probabilities (PP) and bootstrap percentages (BP) from 1 000 replicates of maximum likelihood and maximum parsimony analyses are shown respectively from left to right on the deep and major branches resolved. Taxa in bold are yeast and yeast-like fungi. Note: nm, not monophyletic; ns, not supported (PP < 0.9 or BP < 50 %).
Fig. 2. Phylogenetic tree constructed using maximum likelihood analysis from the combined sequences of the LSU rRNA D1/D2 domains and ITS1+2 regions (including 5.8S rRNA gene) depicting the phylogenetic relationships of yeast taxa with teleomorphic taxa within Ustilaginomycotina. Branch lengths are scaled in terms of expected numbers of nucleotide substitutions per site. Bayesian posterior probabilities (PP) and bootstrap percentages (BP) from 1 000 replicates of maximum likelihood and maximum parsimony analyses are shown respectively from left to right on the deep and major branches resolved. A. The outline of the tree showing the phylogenetic relationships of the genera or clades within Ustilaginomycotina. B. A part of the tree showing the phylogenetic relationships of a part of taxa within the Ustilaginales. C. A part of the tree showing the phylogenetic relationships of another part the taxa within the Ustilaginales and the taxa in the Urocystales. D. A part of the tree showing the phylogenetic relationships of the taxa within Exobasidiomycetes. Taxa in bold are yeast and yeast-like fungi. Notes: nm, not monophyletic; ns, not supported (PP < 0.9 or BP < 50%).
B

Fig. 2. (Continued).
Stollia ewartii  Stollia bursa  Ustilago trichophora  Ustilago schroeteriana  Ustilago davisii  Ustilago filiformis  Ustilago tragana  Melanopsisichium pennsylvanicum  Sporisorium aegypticum  Sporisorium modestum  Ustilago schmidtiae  Ustilago esculenta  Pseudozyma rugulosa  Pseudozyma aphidis  Pseudozyma antarctica  Pseudozyma parantarctica  U. davisii sub-clade  U. esculenta sub-clade  (Clade 6)  Moesziomyces  Farysizyma taiwaniana  Farysizyma chardoniana  Farysizyma acheniorum  Schizonella melanogramma  Stegocintractia luzulae  Cintractia axicola  Cintractia amazonica  Dermatosorus cypri  Tolypoosporium nelli  Tolypoosporium isolepidis  Tolypoosporium juncl  Farysizyma itapuensis  Ustanciosporium standleyanum  Ustanciosporum gigantosporum  Leucocintractia scleriae  Leuconectria leucodermoides  Moreaua fimbriystilids  Moreaua bulbostyliids  Websdanea lyginiae  Fereydounia khargensis  Doassansiops limnocharidis  Thecaphora splantihs  

Fig. 2. (Continued).
teleomorphic species, *Macalpinomyces eriachnes*, occurred as a basal branch to the *Moesziomyces* clade (Figs 1 and 3). The close phylogenetic relationship of the four *Pseudozyma* species with the monotypic genus *Moesziomyces* suggests that the former represent anamorphic and culturable stages of *Moesziomyces* species and can be transferred to the genus *Moesziomyces*.

*Pseudozyma graminicola* clustered in the recently emended genus *Sporisorium* (McTaggart et al. 2012b). The closest relative of this species was *S. holwayii* (Fig. 2B). *P. graminicola* differed from *S. holwayii* by 47 (7 %) and 6 (1 %) mismatches in the ITS and LSU rRNA gene regions, respectively, suggesting that the former represents a distinct species in the genus *Sporisorium* and a new combination is proposed.

The close relationship between *Pseudozyma flocculosa* and *An thracocystis apludae* was shown in the seven genes and the four protein genes based trees (Figs 1, 3). The affinity of *P. flocculosa* with *An thracocystis* was confirmed by the phylogenetic analysis based on the ITS and LSU dataset (Fig. 2B). This species has been recently transferred into the genus *Anthracocystis* by Piątek et al. (2015).

*Pseudozyma crassa* occurred in the *Triodiomyces* clade with 75–89 % BP and 1.0 PP support values (Fig. 2C). *P. crassa* was most closely related to *T. altillis* with 3 and 92
Fig. 3. Phylogenetic tree constructed from maximum likelihood analysis based on the combined sequences of protein-coding genes including RPB1, RPB2, TEF1 and CYTB, showing the phylogenetic relationships of yeast genera within Ustilaginomycotina. Branch lengths are scaled in terms of expected numbers of nucleotide substitutions per site. Bayesian posterior probabilities (PP) and bootstrap percentages (BP) from 1 000 replicates of maximum likelihood and maximum parsimony analyses are shown respectively from left to right on the deep and major branches resolved. Taxa in bold are yeast and yeast-like fungi. Note: nm, not monophyletic; ns, not supported (PP < 0.9 or BP < 50 %).
Fig. 4. Phylogenetic tree constructed from maximum likelihood analysis based on the D1/D2 domains of the LSU rRNA, showing the relationships of taxa within the Exobasidiomycetes. Bootstrap percentages over 50 % from 1000 replicates are shown. Taxa in bold are yeast and yeast-like fungi.
mismatches in the LSU rRNA gene and ITS region, respectively. The result suggests that *P. crassa* belongs to the genus *Triodiotomyces*. *Pseudozyma jejuniensis* was located in the *Langdonia* clade with 56–58 % BP and 0.99 PP support values (Fig. 2B), indicating that this species can be transferred to the genus *Langdonia*.

*Pseudozyma abaconensis*, *P. sharxiensis* and *P. siamensis* occurred in the *Ustilago sensu stricto* sub-clade (Clade 6) containing *U. hordei*, the type species of *Ustilago* (McTaggart et al. 2012a), with strong BP (90–95 %) and PP (1.0) support values (Fig. 2B). *P. siamensis* branched first in the *Ustilago sensu stricto* sub-clade while the phylogenetic positions of *P. abaconensis* and *P. sharxiensis* within this sub-clade were not resolved. The *Ustilago sensu stricto* sub-clade was also resolved as a strongly supported monophyletic group by McTaggart et al. (2012a). Due to the presence of *U. hordei*, the generic type, the genus name *Ustilago* will be used for this sub-clade. Therefore, it is reasonable to transfer these three *Pseudozyma* species to the genus *Ustilago*.

Three *Pseudozyma* species, including *P. brasiliensis*, *P. fusiformata* and *P. vetiveri*, clustered together in an independent clade with 79–87 % BP and 1.0 PP support values (Fig. 2B). The phylogenetic relationship of this clade with other clades in the *Ustilaginales* were not resolved based on the phylogenetical analysis of the ITS and LSU datasets, being in agreement with Chamanapa et al. (2013) and Oliveira et al. (2014). The result suggests that this clade represents a distinct genus. *Pseudozyma churashimaensis* occurred in an isolated deep branch within *Ustilaginaeae* in the tree drawn from the ITS and LSU dataset (Fig. 2C). The affinity of this species to any teleomorphic taxa was not resolved, suggesting that this species represents another genus.

Three *Pseudozyma* species, including *P. alboarmeniaca*, *P. thailandica* and *P. tsukubaensis* clustered in Clade 7 recognised by McTaggart et al. (2012a) with 73 % ML BP and 1.0 PP support values (Fig. 2C). This clade containing mixed smut species from the genera *Macalpinomyces*, *Sporisorium* and *Ustilago*, was also resolved by Stoll et al. (2003, 2005). *P. thailandica* was most closely related to *Macalpinomyces viridians*; *P. tsukubaensis* had identical LSU rRNA gene sequences with *Ma. spermophorus*; and *P. alboarmeniaca* showed close affinity to *Ustilago austro-africana, Ma. spermophorus* and *P. tsukubaensis*. Because of the taxonomic confusion between the teleomorphic genera, the taxonomic treatment of these three *Pseudozyma* species should be made together with the taxonomic revision of the teleomorphic species in this clade.

*Pseudozyma pruni* clustered together with the teleomorphic species *Anomalomycetes yakirae*, *Anomalomycetes panicii* and *Sporisorium trachypogonis-plumosii* without significant support (Fig. 2B). *P. pruni* was proposed as a close relative of *P. fusiformata* by Liu et al. (2009). The former exhibited a close affinity to *A. yakirae* in previous studies based on sequence analysis of the ITS and LSU rRNA gene regions (Chamanapa et al. 2013, Oliveira et al. 2014). *A. panicii*, the type species of the genus *Anomolomycetes*, was located in an isolated branch in the *Ustilaginales in McTaggart et al. (2012a)*. *A. yakirae* was proposed as the second member in *Anomalomycetes* by Shivas et al. (2013) because it was located in the same clade with *A. panicii* in the ITS and LSU rRNA gene based tree. *A. yakirae* and *A. panicii* also shared some morphological characters and occurred on closely related hosts. However, the close relationship between *A. yakirae* and *A. panicii* was not confidently resolved in this study and was only weakly supported by previous molecular data compared in Shivas et al. (2013). Thus, a more robust phylogenetic analysis using more genes will be required for a taxonomic treatment of *P. pruni* and related teleomorphic species.

In the tree based on the seven genes dataset (Fig. 1), the position of *Pseudozyma hubeiensis* remained uncertain probably because of the limited sampling of teleomorphic taxa. In the ITS and LSU dataset based tree, this species was located in Clade 2 (McTaggart et al. 2012a) together with *Ustilago maydis*, *Ustilago boucheti*, *Tubisorus pachycarpus*, *Ustilago vetiveriae* and *Macalpinomyces mackinlayi*, but the phylogeny lacked statistical support (Fig. 2B). Thus, the taxonomic position of *P. hubeiensis* remains to be determined.

**Exobasidiomycetes**

Eight orders were previously proposed in this class (Begerow et al. 2006, 2014, Boekhout et al. 2011). After the proposal of class *Malasseziomycales* to accommodate the *Malasseziales* (Wang et al. 2014), *Exobasidiomycetes* currently contains four orders, *Entylomatales*, *Exobasiales*, *Georgoschleriales* and *Microstromatales*, that have species with a yeast state and three orders, *Ceraceosorales*, *Doassansiales* and *Tilletiales*, that do not have any known yeast species (Boekhout et al. 2011). Begerow et al. (2006) proposed the order *Ceraceosorales* for *Ceraceosorus bombaci* which appeared to be closely related to a yeast-like species *Tilletiopsis ablescens*. However, in the tree drawn form the LSU dataset in this study, *T. ablescens* is not closely related to *C. bombaci* (Fig. 4). The phylogenetic position of *C. bombaci* and its relationship with *T. ablescens* remain controversial (Hibbett et al. 2007, Boekhout et al. 2011, Begerow et al. 2014).

In the trees constructed from the seven genes, the four protein coding genes and the two rRNA genes, each of the four yeast containing orders, *Entylomatales*, *Exobasiales*, *Georgoschleriales* and *Microstromatales*, was resolved as a strongly supported monophyletic clade. The three orders without yeast species were also resolved as separate clades in these analyses (Figs 1–4). However, these orders assigned to *Exobasidiomycetes* did not form a monophyletic lineage. In the trees drawn from the seven genes and the four protein coding genes, the *Georgoschleriales* occurred as a sister lineage to *Moniliellomycetes* with strong support (Figs 1 and 3). The orders *Entylomatales*, *Exobasiales* and *Doassansiales* formed a monophyletic lineage together but with weak BP support; while *Microstromatales* and *Tilletiales* formed distinct lineages with paraphyletic relationships to the other orders in *Exobasidiomycales* (Figs 1 and 3). The results confirmed that *Exobasidiomycetes* is not monophyletic, but might support the originally described superorder *Exobasidiana* including the three orders *Entylomatales*, *Doassansiales* and *Exobasiales* based on morphological similarities of the interaction apparatus as suggested by Bauer et al. (1997).

Seven genera of yeasts or yeast-like fungi, namely *Acaromyces*, *Jaminiaea*, *Meira*, *Rhodotorula* (*pro parte*), *Symposiumycopsis*, *Tilletiaria* and *Tilletiopsis* are currently included in the *Exobasidiomycetes*. Since the protein coding gene and even the SSU and ITS rRNA gene sequences of many teleomorphic taxa of *Exobasidiomycetes* are not available at present, a supplementary dataset containing only LSU rRNA gene sequences was not attempted.
sequences was used for analysing the phylogenetic relationships of yeast species with teleomorphic species in the *Exobasidiomycetes*.

In the trees drawn from the seven genes, the four protein genes and the ITS dataset, *Acaramyces ingoldii* and three *Meira* species were located together with three *Exobasidiales* in the *Exobasidiomycetes* with strong support (Figs 1, 2D and 3), being in agreement with Boekhout et al. (2011). However, in the tree made from the LSU dataset containing more teleomorphic species, the taxa of *Exobasidiales* as defined by Begerow et al. (2014) were separated into two clades (Fig. 4). *Ac. ingoldii* occurred in a well supported clade together with species of the teleomorphic genus *Conicinodium*, *Conidiotrichum*, *Drepanosporis* and *Laurobasidium*. *Ac. ingoldii* was closely related with *Laurobasidium lauri* and shared an identical LSU rRNA gene sequence with a GenBank entry (AB177562) labelled as ‘Laurobaedium hachijoense’ (*Exobasidium hachijoense*). The name *Laurobasidium hachijoense* has not been validly published and *L. lauri* is presently the solely species published in the genus *Laurobasidium* (Begerow et al. 2014). It is not sure whether *Ac. ingoldii* represents an anamorphic species of *Laurobasidium* because the ML BP support for a close affinity of *Ac. ingoldii* and *L. lauri* remained weak (62 %) (Fig. 4). Besides, the sequence difference between *Ac. ingoldii* and *L. lauri* appeared greater than that between the two teleomorph species *Conicinodium bullatum* and *Drepanosporis larviformis* presently classified into different genera. Therefore, the genus *Acaramyces* will be maintained at present. In the LSU rRNA gene-based tree, the *Meira* species were located in another clade together with teleomorphic species from *Exobasidium* and other genera of the *Exobasidiomycetes*, including *Dicellomyces*, *Graphiola* and *Kordyana* (Fig. 4). In this clade, the four *Meira* species formed a distinct sub-clade with 100 % ML BP value, supporting the recognition of this genus.

The *Jamineae* and *Sympodiomycopsis* species and three *Rhodotorula* species clustered in the *Microstromatales* together with teleomorphic species of *Microstoma*, *Quambalaria* and *Volvocisporium* (Figs 1, 2D and 4). The two *Jamineae* species formed a first branched clade in the *Microstromatales* in the seven genes and the four protein genes based trees (Figs 1 and 3). A close relationship of the *Jamineae* species with *Microstoma albiziae* was shown in the trees drawn from the combined seven gene sequences (Fig. 1) and the LSU rRNA gene sequences alone (Fig. 4), but not supported in the combination of ITS and LSU datasets (Fig. 2D). The genus *Microstoma* is polyphyletic as shown previously (Begerow et al. 2006, 2014, Boekhout et al. 2011) and in the present study. *M. albiziae* is not the type species of the genus, and, therefore, the genus *Jamineae* should be remained. However, the affiliation to *Jaminea* or *Sympodiomycopsis* lacks fundamental support and further data are needed before a new combination can be proposed. Begerow et al. (2014) assigned *Jaminea* to the family *Quambaliariaceae*, but the close relationship of this genus with the teleomorphic species *Quambalaria cyanescens* was not shown in any of the trees constructed in this study. Therefore and due to the lack of other *Quambalaria* species in our dataset, it is preferred to treat *Jaminea* as ‘incertae sedis’ within *Microstromatales* as Spiczki & Kajdacsi (2009) suggested before.

The affiliation of *Sympodiomycopsis* species within the *Microstromatales* was confirmed in this study, but the relationship of this genus with the other members of the order was not resolved (Figs 1, 2D, 3 and 4), being in agreement with Begerow et al. (2014) who treated the genus as ‘incertae sedis’ in the *Microstromatales*.

Among the three *Rhodotorula* species belonging to the *Microstromatales*, *R. bacarum* had almost identical ITS and LSU rRNA gene sequences with *Microstoma album*, the type species of the genus *Microstoma* (Figs 2D and 4). As commented by Sampaio (2011), *R. bacarum* should be regarded as representing the asexual stage of *M. album* and thus should be treated as a synonym of the latter. The other two *Rhodotorula* species, *R. hinnulea* and *R. phyllolopa*, exhibited a close relationship with *Microstoma juglandis* in all the trees constructed in this study (Figs 1, 2D, 3 and 4). *R. hinnulea* was considered a synonym of *R. phyllolopa* in Sampaio (2011) because of identical ITS and LSU rRNA gene sequences. In this study we showed that the type strains of the two species also shared similar protein gene sequences (Fig. 3), supporting their assumed conspecificity (Fig. 2D). In the LSU rRNA gene based tree, *R. phyllolopa* was located together with *M. juglandis* (Fig. 4). In the seven genes and the four protein genes based trees, the close affinity of *R. phyllolopa* and *M. juglandis* with *R. bacarum* (the anamorph of *M. album*) was resolved (Figs 1 and 3). The result suggests that *R. phyllolopa* represents an anamorphic species in the genus *Microstoma*.

In agreement with previous studies (Fell et al. 2000) the genus *Tilletiopsis* was shown to be polyphyletic in this study. Three *Tilletiopsis* species, including the type species of the genus, *T. washingtonensis*, formed a well supported (100 % BP and 1.0 PP) clade in the *Entylomales* in all the trees constructed using different datasets (Figs 1, 2D, 3 and 4). This clade was resolved as a sister group of the genus *Entyloma*. The result suggests that this clade represents a distinct genus which should keep the name *Tilletiopsis*.

Six *Tilletiopsis* species belonged to the *Georgenfischeriales* (Fig. 4). As shown in Boekhout et al. (2011), *T. derxii*, *T. flava*, *T. fulvescens* and *T. oryzicola* formed a clade together with two teleomorphic species *Tilletiaria anomala* and *Phragmotaenia indicum* in the tree constructed from the LSU rRNA gene sequences (Fig. 4). The latter two teleomorphic species differ remarkably in the morphology of teliospores (Bauer et al. 2001b) and the genetic distance between them is similar with those between other genera, suggesting they represent two different genera. *Tilletiaria anomala* formed a basal position in this clade. The four *Tilletiopsis* species were resolved to be more closely related to *Phragmotaenia indicum* with 90 % ML BP support, suggesting that they belong to the genus *Phragmotaenum*.

The other two *Tilletiopsis* species in the *Georgenfischeriales*, *T. minor* and *T. penniseti*, formed another clade with a teleomorphic species *Gjaerumia ossifragi*, the type of the genus, as a basal branch with 61 % ML BP support (Fig. 4). Bauer et al. (2005) also showed that *G. ossifragi* formed a statistically supported cluster with *T. minor*, *T. penniseti*, and two undescribed *Tilletiopsis* species based on the Bayesian inference analysis of the LSU rRNA genes. The results support transferring *T. minor* and *T. penniseti* into *Gjaerumia*.

Two *Tilletiopsis* species, *T. albescens* and *T. pallescens*, could not be assigned to any recognised orders in the *Exobasidiomycetes*. In the ML trees constructed from the seven gene and four protein gene datasets, they clustered together in a deep lineage with 93 % and 94 % BP support, but their
phylogenetic relationship with other lineages of Exobasidiomycetes was not resolved. The MP and BI analyses of the two datasets did not support a close relationship between the two Tilletiopsis species (Figs 1 and 3). In the trees generated from the other datasets, these two species formed independent deep branches with uncertain phylogenetic positions (Figs 2D and 4). These two Tilletiopsis species were also treated as 'incertae sedis' in the Exobasidiomycetes by Begerow et al. (2006, 2014) and Hibbett et al. (2007). Our results suggested that T. abescens and T. pallescens represent two separate genera belonging to two different orders.

**Taxonomy**

The phylogenetic analyses described above confirm that the class Exobasidiomycetes is polyphyletic. However, it is immature to redefine this class at present because molecular data, especially protein gene sequences from the majority of the teleomorphic taxa in this class, will offer a more robust phylogenetic analysis integrating the yeasts, are not available. It is, however, needed to make taxonomic revisions for yeasts taxa at the genus level based on the phylogenetic data presented here. Fereydounia, Jaminiaea, Meira, Sympodiomycopsis and Tilletiaria together with Malassezia and Moniliella as shown in Wang et al. (2014) and Nasr et al. (2014) are monophyletic genera. In order to avoid possible name changes in the future, Acaromycetes will be remained at present before a taxonomic revision can be made that need to include more teleomorphic genera.

We propose to transfer the Farysyzma species to the genus Farysia and Rhodorotula phylloplana to Microstroma. For the Pseudozyma species, it is clear that P. prolifica, the type species of the genus, is a synonym of Ustilago maydis. We propose to transfer 1) P. abaconensis, P. shanxiensis and P. siamensis to the genus Ustilago; 2) P. antarctica, P. aphidis, P. parantarctica and P. rugulosa to Moesziomyces; 3) P. crassa to Triodiyomycetes; 4) P. graminicola to Sporisorium; and 5) P. jeuenensis to Langdonia. P. brasiilensis, P. fusiformata, and P. vetiver represent a new genus for which we propose Kalmanoxzyma gen. nov. Pseudozyma churashimaensis represents another new genus for which Dirkmeia gen. nov. is proposed. The taxonomic treatment for the remaining Pseudozyma species, including P. aboam endeavour, P. thailandica, P. tsukubaensis, P. hubeiensis and P. pruni remains to be determined. These species are embedded in groups with lots of teleomorphic species, where only very few specimens have been sequenced so far, thus we expect, that they probably have already a synonym, which we just did not identify so far. Because the genus name Pseudozyma is not available any more, we suggest to use 'pro tempore' or 'pro tem.' in abbreviation to indicate that these species names are temporarily remained.

We propose to emend the genus Tilletiopsis in the order Entylomatoidales by retaining the genus name for the monophyletic clade represented by the type species T. tungstenensis. For the taxonomic treatment of the remaining Tilletiopsis species, we propose to transfer T. derxii, T. vata, T. fulvescens and T. oryzae to the genus Phragmatozoon; and T. minor and T. penisseli to Gjaerumia. Two new generic names, Robbauera gen. nov. and Golubevia gen. nov., are proposed for T. abescens and T. pallescens, respectively. Two new orders are also proposed for them to accommodate the sisterhood of these two new genera with other orders of Exobasidiomycetes.

**Golubeviales** Q.M. Wang, F.Y. Bai, Begerow & Boekhout ord. nov. MycoBank MB812083.

Member of Exobasidiomycetes. The diagnosis of the order Golubeviales is based on the description of the genus Golubevia. The nomenclature of the order is based on the genus Golubevia.

**Type family:** Golubeviaceae Q.M. Wang, F.Y. Bai, Begerow & Boekhout

**Golubeviaceae** Q.M. Wang, F.Y. Bai, Begerow, & Boekhout fam. nov. MycoBank MB812692.

Member of Golubeviales (Exobasidiomycetes). The diagnosis of the family Golubeviaceae is based on the description of the genus Golubevia. The nomenclature of the family is based on the genus Golubevia.

**Type genus:** Golubevia Q.M. Wang, F.Y. Bai, Begerow & Boekhout

**Golubevia** Q.M. Wang, F.Y. Bai, Begerow & Boekhout gen. nov. MycoBank MB812694.

**Etymology:** The genus is named in honour of W.I. Golubev for his pioneering contributions to the taxonomic of basidiomycetaceous yeasts.

This genus is proposed for the single species clade formed by Tilletiopsis pallescens as resolved by multiple gene sequence analyses. It occurred as a sister lineage of the other orders within Exobasidiomycetes (Figs 1, 2D, 3 and 4).

Sexual reproduction unknown, but chlamydospore-like structures germinating with a holobasidium-like structure that forms ballistospores on the apex, have been observed (Begerow et al. 2000). Colonies pale yellowish-brown or cream and have an eroded margin. Budding cells present. Hyphae regularly branched, narrow and cylindrical, and with retraction septa, but lack clamp connections. Chlamydospores may occur terminally or intercalarily. Ballistoconidia present. Xylose absent, but glucose, galactose and mannose present in whole-cell hydrolysates. The major ubiquinone Q-10. Starch-like compounds are not produced.

**Type species:** Golubevia pallescens (Gokhale) Q.M. Wang, F.Y. Bai, Begerow & Boekhout comb. nov. MycoBank MB812695.

**Robbauerales** Boekhout, Begerow, Q.M. Wang & F.Y. Bai ord. nov. MycoBank MB812696.

Member of Exobasidiomycetes. The diagnosis of the order Robbauerales is based on the description of the genus Robbauera. The nomenclature of the order is based on the genus Robbauera.

**Type family:** Robbaueraeaceae Boekhout, Begerow, Q.M. Wang & F.Y. Bai
**Robbauerae** Boekhout, Begerow, Q.M. Wang & F.Y. Bai fam. nov. MycoBank MB812697.

Member of Robbauerales (Exobasidiomycetes). The diagnosis of the family Robbaueraceae is based on the description of the genus Robbauera. The nomenclature of the family is based on the genus Robbauera.

Type genus: **Robbauera** Boekhout, Begerow, Q.M. Wang & F.Y. Bai

**Robbauera** Boekhout, Begerow, Q.M. Wang & F.Y. Bai gen. nov. MycoBank MB812698.

**Etymology:** The genus is named in honour of Robert Bauer for his contributions to the taxonomy and ultrastructure of smuts.

This genus is proposed for the single species clade formed by *Tilletiopsis albescens* as resolved by multiple gene sequence analyses. It occurred as a sister lineage of the other orders within Exobasidiomycetes (Figs 1, 2D, 3 and 4).

Sexual reproduction unknown. Colonies are whitish-cream and with an eroded margin. Hyphae regularly branched, narrow, with retraction septa, but lack clamp connections. Chlamydospores may be present. Ballistoconidia present. Xylose absent, but glucose, galactose and mannose present in whole-cell hydrolysates. The major ubiquinone Q-10. Starch-like compounds not produced.

Type species: **Robbauera albescens** (Gokhale) Boekhout, Begerow, Q.M. Wang & F.Y. Bai comb. nov. MycoBank MB812699.

Basionym: *Tilletiopsis albescens* Gokhale, Nova Hedwigia 23: 803. 1972.

**Dirkmeia** F.Y. Bai, Q.M. Wang, Begerow & Boekhout gen. nov. MycoBank MB812700.

**Etymology:** the genus is named in honour of Dirk van der Mei who was a former director of CBS Fungal Biodiversity Centre (CBS-KNAW).

Member of Ustilaginaeae (Ustilaginales, Ustilaginomycetes). This genus is proposed to accommodate *Pseudozyma churashimaensis* which belongs to an isolated branch in the Ustilaginomycetes based on the combined ITS and LSU rRNA gene sequence analysis (Fig. 2C).

Sexual reproduction unknown. Colonies cream-coloured, shiny, smooth, and with an eroded margin. Budding cells present. Ballistoconidia absent. Cell carbohydrates not determined. The major ubiquinone unknown. Starch-like compounds not produced.

Type species: **Dirkmeia churashimaensis** (T. Morita, Y. Ogura, M. Takash., N. Hirose, Fukuoka, Imura, Y. Kondo & Kitamoto) F.Y. Bai, Q.M. Wang, Begerow & Boekhout comb. nov. MycoBank MB812727.

Basionym: *Pseudozyma churashimaensis* T. Morita, Y. Ogura, M. Takash., N. Hirose, Fukuoka, Imura, Y. Kondo & Kitamoto, J. Biosci. Bioeng. 112: 142. 2011.

**Kalmanozyma** Q.M. Wang, F.Y. Bai, Begerow & Boekhout gen. nov. MycoBank MB812702.

**Etymology:** The genus is named in honour of Kálmán Vánky for his contributions to the taxonomy of smuts.

Member of Ustilaginaeae (Ustilaginales, Ustilaginomycetes). This genus is proposed to accommodate *Pseudozyma fusiformata*, *Pseudozyma brasiliensis* and *Pseudozyma vetiver* that form a distinct clade in the Ustilaginaceae based on the phylogenetic analysis of the ITS and LSU rRNA gene sequences (Fig. 2B).

Sexual reproduction unknown. Colonies whitish, cream to light salmon, shiny, smooth, and with an eroded margin. Budding cells present. Ballistoconidia absent. Pseudomycelium and true mycelium may be formed. Cell carbohydrates not determined. The major ubiquinone Q-10. Starch-like compounds not produced.

Type species: **Kalmanozyma fusiformata** (Buhagiar) Q.M. Wang, F.Y. Bai, Begerow & Boekhout comb. nov. MycoBank MB812703.

Basionym: *Candida fusiformata* Buhagiar, J. Gen. Microbiol. 110: 95. 1979.

New combinations in *Kalmanozyma*

**Kalmanozyma brasiliensis** (J.V.C. Oliveira, T.A. Borges, R.A.C. Santos, L.F.D. Freitas, C.A. Rosa, G.H. Goldman & D.M. Riano-Pachón) Q.M. Wang, F.Y. Bai, Begerow & Boekhout comb. nov. MycoBank MB812704.

Basionym: *Pseudozyma brasiliensis* J.V.C. Oliveira, T.A. Borges, R.A.C. Santos, L.F.D. Freitas, C.A. Rosa, G.H. Goldman & D.M. Riano-Pachón, Int. J. Syst. Evol. Microbiol. 64: 2159. 2013.

**Kalmanozyma vetiver** (Chamnanpa & Limtong) Q.M. Wang, F.Y. Bai, Begerow & Boekhout comb. nov. MycoBank MB812735.

Basionym: *Pseudozyma vetiver* Chamnanpa & Limtong, Antonie van Leeuwenhoek 104: 637. 2013.

**Tilletiopsis** Derx, Bulletin du Jardin Botanique de Buitenzorg 17: 471. 1948. emend. Begerow, Q.M. Wang, F.Y. Bai & Boekhout.

Member of Entylomatales (Exobasidiomycetes). This genus is emended to include only the species in the clade represented by *T. washingtonensis*, *T. lilacinax* and *T. cremea*.

Sexual reproduction unknown. Colonies cream coloured and with an entire or eroded margin. Budding cells present. Hyphae narrow, with retraction septa, but lack clamp connections. Chlamydospores may be present. Ballistoconidia present. Xylose in cell wall hydrolysate absent. The major ubiquinone Q-10. Starch-like compounds not produced.

Type species: *Tilletiopsis washingtonensis* Nyland, Mycologia 42: 488. 1950.
This genus was originally described for teleomorphic smut fungi occurring on Cyperaceae plants and was redefined Vánky (2002, 2012). Here it is emended to include free-living yeast species with unknown sexual states as shown by molecular phylogenetic analysis (Fig. 2C).

New combinations in Anthracocystis

*Anthracocystis pampara* (Speg.) Q.M. Wang, F.Y. Bai, Begerow & Boekhout comb. nov. MycoBank MB812705.

*Basionym:* Ustilago pamparana Speg., Boln Acad. nac. Cienc. Córdoba 11: 28. 1887.

≡ Sphacelotheca pamparana (Speg.) G.P. Clinton, J. Mycol. 8: 140. 1902.

*Farysia* Racib., Bull. int. Acad. Sci. Lett. Cracovie, Cl. sci. math. nat. Sér. B, sci. nat. 3: 354. 1909. *emend.* Q.M. Wang, F.Y. Bai, Begerow & Boekhout.

≡ Elateromyces Bubák, Arch. Prírodov. Výzk. Čech. 15: 32. 1912.

≡ Farysizyma A. Fonseca, FEMS Yeast Res. 8: 505. 2008.

Type species: *Farysia butleri* (H. & P. Sydow) H. & P. Sydow.

This genus was originally described for teleomorphic smut fungi occurring on Cyperaceae plants and was redefined Vánky (2002, 2012). Here it is emended to include free-living yeast species with unknown sexual states as shown by molecular phylogenetic analysis (Fig. 2C).

New combinations in *Farysia*

*Farysia itapuensis* (Landell & Valente) Begerow, Q.M. Wang, F.Y. Bai & Boekhout comb. nov. MycoBank MB812706.

*Basionym:* Farysizyma itapuensis Landell & Valente, FEMS Yeast Res. 8: 506. 2008.

*Farysia taiwaniana* (P.-H. Wang, Y.-T. Wang & S.-H. Yang) Begerow, Q.M. Wang, F.Y. Bai & Boekhout comb. nov. MycoBank MB812707.

*Basionym:* Farysizyma taiwaniana P.-H. Wang, Y.-T. Wang & S.-H. Yang, FEMS Yeast Res. 8: 506. 2008.

*Farysia setubalensis* (Fonseca & Inácio) Begerow, Q.M. Wang, F.Y. Bai & Boekhout comb. nov. MycoBank MB812708.

*Basionym:* Farysizyma setubalensis Fonseca & Inácio., FEMS Yeast Res. 8: 507. 2008.

*Farysia acheniorum* (Buhagiar & Barnett) Begerow, Q.M. Wang, F.Y. Bai & Boekhout comb. nov. MycoBank MB812709.

*Basionym:* Sterigmatomyces acheniorum Buhagiar & Barnett., J. Gen. Microbiol. 77: 78. 1973.

≡ Farysizyma acheniorum (Buhagiar & Barnett) Fonseca, FEMS Yeast Res. 8: 499. 2008.

≡ Rhodotorula acheniorum (Buhagiar & Barnett) Rodrigues de Miranda, Stud. Mycol. 14: 28. 1977.

*Gjaerumia* R. Bauer, M. Lutz & Oberw., Mycol. Res. 109: 1257. 2005. *emend.* Q.M. Wang, F.Y. Bai, Begerow & Boekhout.

*Type species:* *Gjaerumia ossifragi* (Rostr.) R. Bauer, M. Lutz & Oberw.

This genus was originally proposed for teleomorphic smut fungi occurring on Asparagaceae, Melanthiaceae and Xanthorrhoeaceae (Bauer et al. 2005) and is emended to include free-living yeast species with unknown sexual states as shown by molecular phylogenetic analysis (Fig. 4).

New combinations in *Gjaerumia*

*Gjaerumia minor* (Nyland) Q.M. Wang, F.Y. Bai, Begerow & Boekhout comb. nov. MycoBank MB812710.

*Basionym:* Tilletiopsis minor Nyland, Mycologia 42: 489. 1950.

*Gjaerumia penniseti* (Takashima & Nakase) Q.M. Wang, F.Y. Bai, Begerow & Boekhout comb. nov. MycoBank MB812711.

*Basionym:* Tilletiopsis penniseti Takashima & Nakase, Antonie van Leeuwenhoek 80: 43. 2001.

*Langdonia* McTaggart & R.G. Shivas, Persoonia, 29: 130. 2012. *emend.* Q.M. Wang, F.Y. Bai, Begerow & Boekhout.

Type species: *Langdonia fraseriana* (Syd.) McTaggart & R.G. Shivas.

This genus was originally proposed for teleomorphic smut fungi occurring on Poaceae (McTaggart et al. 2012b) and is emended to include free-living yeast species with unknown sexual states as shown by molecular phylogenetic analysis (Fig. 2B).

New combination in *Langdonia*

*Langdonia jejuensis* (Seo, Um, Min, Rhee, Cho, Kim & Lee) Q.M. Wang, F.Y. Bai, Begerow & Boekhout comb. nov. MycoBank MB812712.

*Basionym:* Pseudozyma jejuensis H.S. Seo, H.J. Um, J. Min, S.K. Rhee, T.J. Cho, Y. H. Kim & J. Lee, FEMS Yeast Res. 7: 1039. 2007.

*Microstroma* Niessl, Öst. bot. Z. 11: 250. 1861. *emend.* Q.M. Wang, F.Y. Bai, Begerow & Boekhout.

Type species: Microstroma album (Desm.) Sacc.

This genus was originally proposed for teleomorphic smut fungi occurring on Juglandaceae, Fabaceae and Fagaceaeas (Begerow et al. 2014) as defined by Pires (1928) and is emended to include free-living yeast species with unknown sexual states as shown by molecular phylogenetic analysis (Fig. 2D).

New combinations in *Microstroma*

*Microstroma phylloplanum* (R.G. Shivas & Rodr. Mir.) Q.M. Wang, F.Y. Bai, Begerow & Boekhout comb. nov. MycoBank MB812713.
**Basionym:** Cryptococcus phylloplanus R.G. Shivas & Rostr. Mir.,
Antonie van Leeuwenhoek 49: 153. 1983.
≡ Rhodotorula phyloplana (R.G. Shivas & Rostr. Mir.) Rostr. Mir. &
Weijman, Antonie van Leeuwenhoek 54: 549. 1988.
≡ Cryptococcus hinnuleus R.G. Shivas & Rostr. Mir., Antonie van
Leeuwenhoek 49: 155. 1983.
≡ Rhodontorula hinnulea (R.G. Shivas & Rostr. Mir.) Rostr. Mir. &
Weijman, Antonie van Leeuwenhoek 54: 549. 1988.

**Moesziomyces** Vánky, Bot. Notiser 130: 133. 1977. **emend.**
Q.M. Wang, Begerow, F.Y. Bai & Boekhout.

**Type species:** Moesziomyces bullatus (J. Schrötl.) Vánky

This genus was originally proposed for a teleomorphic smut fungus
occurring on Poaceae as defined by Vánky (2002, 2012) and is
emended to include free-living yeast species with unknown sexual
states as shown by molecular phylogenetic analysis (Fig. 2C).

**New combinations in Moesziomyces**

*Moesziomyces antarcticus* (Goto, Sugiyama & Iizuka) Q.M.
Wang, Begerow, F.Y. Bai & Boekhout **comb. nov.** MycoBank
MB812714.

*Basionym:* Sporobolomyces antarcticus Goto, Sugiyama &
Iizuka, Mycologia 61: 759. 1969.
≡ Pseudozyma antarctica (Goto, Sugiyama & Iizuka) Boekhout, J. Gen.
Appl. Microbiol. 41: 364. 1995.
≡ Candida antarctica (Goto, Sugiyama & Iizuka) Kurtzman, M.J. Smiley,
C.J. Johnson & M.J. Hoffman, Yeasts: Characteristics and Identification
(Cambridge): 86. 1983.
≡ Vaniija antarctica (Goto, Sugiyama & Iizuka) R.T. Moore, Bibl. Mycol.
108: 167. 1987.
≡ Trichosporon oryzicola H. Ito, Iizuka & T. Sato, Agric. Biol. Chem. 38: 1599. 1974.

*Moesziomyces aphidis* (Henning & Windisch) Q.M.
Wang, Begerow, F.Y. Bai & Boekhout **comb. nov.** MycoBank
MB812715.

*Basionym:* Sterigmatomyces aphidis Henning & Windisch,
Arch. Mikrobiol. 105: 50. 1975.
≡ Pseudozyma aphidis (Henning & Windisch) Boekhout, J. Gen. Appl.
Microbiol. 41: 364. 1995.

*Moesziomyces rugulosus* (Traquair, L.A. Shaw & Jarvis) Q.M.
Wang, Begerow, F.Y. Bai & Boekhout **comb. nov.** MycoBank
MB812716.

*Basionym:* Sporothrix rugulosa Traquair, L.A. Shaw & Jarvis,
Can. J. Bot. 66: 929. 1988.
≡ Pseudozyma rugulosa (Traquair, L.A. Shaw & Jarvis) Boekhout &
Traquair, J. Gen. Appl. Microbiol. 41: 364. 1995.
≡ Stephaniomyces rugulosus Traquair, L.A. Shaw & Jarvis, Can. J. Bot.
66: 929. 1988.

*Moesziomyces parantarcticus* (Sugita, Takashima, Mekha &
Poornwan) Q.M. Wang, Begerow, F.Y. Bai & Boekhout **comb. nov.**
MycoBank MB812717.

*Basionym:* Pseudozyma parantarctica Sugita, Takashima,
Mekha & Poornwan, Microbiol. Immun. 47: 156. 2003.

**Phragmotaenium** R. Bauer, Begerow, A. Nagler & Oberw.,
Mycol. Res. 105: 423. 2001. **emend.** Q.M. Wang, Begerow, F.Y.
Bai & Boekhout.

**Type species:** Phragmotaenium indicum (Vánky, M.S. Patil &
N.D. Sharma) R. Bauer, Begerow, A. Nagler & Oberw.

This genus was originally proposed for a teleomorphic smut
fungus occurring on Poaceae (Bauer et al. 2001b) and is
emended to include free-living yeast species with unknown sexual
states as shown by molecular phylogenetic analysis (Fig. 4).

**New combinations in Phragmotaenium**

**Phragmotaenium flavum** (Tubaki) Q.M. Wang, Begerow, F.Y.
Bai & Boekhout **comb. nov.** MycoBank MB812726.

*Basionym:* Tilletiopsis minor Nyland var. flava Tubaki, Nagaoka 1:
28. 1952.
≡ Tilletiopsis flavida (Tubaki) Boekhout, Stud. Mycol. 33: 151. 1991.

**Phragmotaenium derxii** (Takashima & Nakase) Q.M. Wang,
Begerow, F.Y. Bai & Boekhout **comb. nov.** MycoBank MB812718.

*Basionym:* Tilletiopsis derxii Takashima & Nakase, Antonie van
Leeuwenhoek 80: 43. 2001.

**Phragmotaenium oryzicola** (Takashima & Nakase) Q.M.
Wang, Begerow, F.Y. Bai & Boekhout **comb. nov.** MycoBank
MB812719.

*Basionym:* Tilletiopsis oryzicola Takashima & Nakase, Antonie van
Leeuwenhoek 80: 43. 2001.

**Phragmotaenium fulvescens** (Gokhale) Q.M. Wang, Begerow,
F.Y. Bai & Boekhout **comb. nov.** MycoBank MB812720.

*Basionym:* Tilletiopsis fulvescens Gokhale, Nova Hedwigia 23:
805. 1972.

**Sporisorium** Ehrenb. ex Link, in Willdenow, Sp. pl., Edn 4 6: 86.
1825. **emend.** Q.M. Wang, F.Y. Bai, Begerow & Boekhout.

**Type species:** Sporisorium sorghi Ehrenb. ex Link

This genus was originally proposed for teleomorphic smut fungi
occurring on Poaceae. It was emended by McTaggart et al.
(2012b) to include only the **Sporisorium sensu stricto** clade.
Here it is emended further to include free-living yeast species
with unknown sexual states as shown by molecular phylogenetic
analysis (Fig. 2B).

**New combination in Sporisorium**

**Sporisorium graminicola** (W. Golubev, Sugita & N. Golubev)
Q.M. Wang, F.Y. Bai, Begerow & Boekhout **comb. nov.** MycoBank
MB812721.

*Basionym:* Pseudozyma graminicola W. Golubev, Sugita & N.
Golubev, Mycoscience 48: 30. 2007.

**Triodiomyces** McTaggart & R.G. Shivas, Persoonia 29: 131.
2012. **emend.** Q.M. Wang, F.Y. Bai, Begerow & Boekhout.

**Type species:** Triodiomyces altillis (Syd.) McTaggart & R.G. Shivas

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PHYLOGENY AND TAXONOMY OF USTILAGINOMYCETOUS YEASTS
This genus was originally proposed to accommodate a group of teleomorphic smut fungi occurring on grasses of the genus Triodia (McTaggart et al. 2012b) and is emended to include free-living yeast species with unknown sexual states as shown by molecular phylogenetic analysis (Fig. 2C).

New combination in Triodiomyces

Triodiomyces crassus (Mekha, Takashima & Sugita) Q.M. Wang, F.Y. Bai, Begerow & Boekhout comb. nov. MycoBank MB812722.

**Basionym**: Pseudozyma crassa Mekha, Takashima & Sugita, Microbiol. Immunol. 58: 9. 2014.

New combinations in Ustilago (Pers.) Roussel, Fl. Calvados, Edn 2: 47. 1806.

**Type species**: Ustilago hordei (Pers.) Lagerh.

The genus Ustilago is polyphyletic and remains to be redefined (McTaggart et al. 2012a, b). It is immature to emend this genus at present but it is reasonable to transfer the three Pseudozyma species to this genus because they are located in the monophyletic Ustilago sensu stricto clade containing the type species of the genus (Fig. 2B). Thus the genus Ustilago also contains anamorphic fungi.

Ustilago abaconensis (Statzell, Scorzetti & Fell) Q.M. Wang, Begerow, F.Y. Bai & Boekhout comb. nov. MycoBank MB812723.

**Basionym**: Pseudozyma abaconensis Statzell, Scorzetti & Fell, Int. J. Syst. Evol. Microbiol. 60: 1983. 2010.

Ustilago shanxiensis (F.Y. Bai & Q.M. Wang) Q.M. Wang, Begerow, F.Y. Bai & Boekhout comb. nov. MycoBank MB812724.

**Basionym**: Pseudozyma shanxiensis F.Y. Bai & Q.M. Wang, Int. J. Syst. Evol. Microbiol. 56: 292. 2006.

Ustilago siamensis (Sugita, Takashima, Poonwan & Mekha) Q.M. Wang, Begerow, F.Y. Bai & Boekhout comb. nov. MycoBank MB812725.

**Basionym**: Pseudozyma siamensis Sugita, Takashima, Poonwan & Mekha, Microbiol. Immun. 58: 9. 2014.

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