

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

Q.-M. Wang¹, D. Begerow², M. Groenewald³, X.-Z. Liu¹, B. Theelen³, F.-Y. Bai^{1,3*}, and T. Boekhout^{1,3,4*}

¹State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China; ²Ruhr-Universität Bochum, AG Geobotanik, ND 03/174, Universitätsstr. 150, 44801 Bochum, Germany; ³CBS-KNAW Fungal Biodiversity Centre, Yeast Division, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands; ⁴Shanghai Key Laboratory of Molecular Medical Mycology, Changzheng Hospital, Second Military Medical University, Shanghai, China

*Correspondence: F.-Y. Bai, baify@im.ac.cn; T. Boekhout, t.boekhout@cbs.knaw.nl

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 *Malasseziomycetes*, *Moniliellomycetes* and *Ustilaginomycetes* are monophyletic, whereas *Exobasidiomycetes* in the current sense remains paraphyletic. Four new genera, namely *Dirkmeia* gen. nov., *Kalmanozyma* 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 *Golubeviaceae* fam. nov. and *Robbauerales* ord. nov. with *Robbaueraeaceae* fam. nov. are proposed to accommodate the sisterhood of *Golubevia* gen. nov. and *Robbauera* gen. nov. with other orders of *Exobasidiomycetes*. The majority of the remaining anamorphic yeast species are transferred to corresponding teleomorphic 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 tem.* 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:** *Golubeviaceae* Q.M. Wang, F.Y. Bai, Begerow, & Boekhout, *Robbaueraeaceae* 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:** *Anthracoecystis pampara* (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 acheniorum* (Buhagiar & Barnett) Begerow, Q.M. Wang, F.Y. Bai & Boekhout, *F. itapuensis* (Landell & Valente) Begerow, Q.M. Wang, F.Y. Bai & Boekhout, *F. setubalensis* (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, *Gjaerumia minor* (Nyland) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *G. penniseti* (Takashima & Nakase) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *Golubevia pallescens* (Gokhale) 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. Riaño-Pachón) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *K. fusiformata* (Buhagiar) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *K. vetiver* (Chamnanpa & Limtong) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *Langdonia jejuensis* (Seo, Um, Min, Rhee, Cho, Kim & Lee) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *Microstroma phylloplanum* (R.G. Shivas & Rodr. Mir.) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *Moesziomyces antarcticus* (Goto, Sugiyama & Iizuka) Q.M. Wang, Begerow, F.Y. Bai & Boekhout, *Mo. aphidis* (Henninger & Windisch) Q.M. Wang, Begerow, F.Y. Bai & Boekhout, *Mo. rugulosus* (Traquair, L.A. Shaw & Jarvis) Q.M. Wang, Begerow, F.Y. Bai & Boekhout, *Mo. parantarcticus* (Sugita, Takashima, Mekha & Poonwan) Q.M. Wang, Begerow, F.Y. Bai & Boekhout, *Phragmotanium dextii* (Takashima & Nakase) Q.M. Wang, Begerow, F.Y. Bai & Boekhout, *P. flavum* (Tubaki) Q.M. Wang, Begerow, F.Y. Bai & Boekhout, *P. fulvescens* (Gokhale) Q.M. Wang, Begerow, F.Y. Bai & Boekhout, *P. oryzicola* (Takashima & Nakase) Q.M. Wang, Begerow, F.Y. Bai & Boekhout, *Robbauera albescens* (Gokhale) Boekhout, Begerow, Q.M. Wang & F.Y. Bai, *Sporisorium graminicola* (W. Golubev, Sugita & N. Golubev) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *Triodiomyces crassus* (Mekha, Takashima & Sugita) Q.M. Wang, F.Y. Bai, Begerow & Boekhout, *Ustilago abaconensis* (Statzell, Scorzett & Fell) Q.M. Wang, Begerow, F.Y. Bai & Boekhout, *U. shanxiensis* (F.Y. Bai & Q.M. Wang) Q.M. Wang, Begerow, F.Y. Bai & Boekhout, *U. siamensis* (Sugita, Takashima, Poonwan & Mekha) Q.M. Wang, Begerow, F.Y. Bai & Boekhout.

Published online 10 December 2015; <http://dx.doi.org/10.1016/j.simyco.2015.10.004>. Hard copy: June 2015.

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 ustilaginomycetous fungi known from yeast states only are described as asexual 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*, *Farysizyma*, *Fereydownia*, *Jaminaea*, *Malassezia*, *Meira*, *Moniliella*, *Pseudozyma*, *Rhodotorula* (*pro*

parte), *Sympodiomyces*, *Tilletiaria* and *Tilletiopsis* (Stolk & Dakin 1966, Gokhale 1972, Boekhout 1991, 1995, Boekhout et al. 1995, 2003, 2011, Begerow et al. 2000, 2006, Inácio et al. 2008, Sipiczki & Kajdacs 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 *Microstroma*, 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 *Moesziomyces* in the *Ustilaginaceae* (*Ustilaginales*) (Begerow et al. 2000, 2006, 2014, Stoll et al. 2003, 2005, Liou et al. 2009, McTaggart et al. 2012a, b, Chamnanpa et al. 2013, Shivas et al. 2013, Oliveira et al. 2014). The genus *Farysizyma* 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 *Urocystidales* (Nasr et al. 2014). The genus *Jaminaea* represents a basal lineage in the *Microstromatales* (*Exobasidiomycetes*) based on ribosomal RNA (rRNA) gene sequence analysis (Sipiczki & Kajdacs 2009). *Sympodiomyces* is an anamorphic genus and its basidiomycetous affinity was discussed for a long time based on the ubiquinone system, type of cell wall and septal 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 *Sympodiomyces* is a member of *Exobasidiomycetes* (Suh & Sugiyama 1994, Fell et al. 2000). *Tilletiaria* is a teleomorphic genus characterised by the presence of teliospores 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 *Tilletiaceae* in the *Georgiefischeriales* (*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). *Tilletiopsis* 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 *Pucciniomycotina*, four still occur in *Ustilaginomycotina* (Fell et al. 2000, Sampaio 2011). In addition to *Rhodotorula acheniorum* which has been transferred to *Farysizyma* (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 pleomorphic 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								
Georgiefischeriales								
<i>Tilletiaria anomala</i>	CBS 436.72 ^T	AJ235284	DQ234558	AY803752	DQ234571	AY803750	DQ835991	KP323046
<i>Tilletiopsis derxii</i>	CBS 110078 ^T	AB052823	AB045707	AB045704	KP322926	KP323086	KP323138	KP323020
<i>Tilletiopsis flavus</i>	CBS 401.84 ^T	AJ235285	KP322987	KP322970	—	—	KP323126	KP323004
<i>Tilletiopsis fulvescens</i>	CBS 607.83 ^T	AJ235282	KP322988	KP322971	—	—	—	KP323045
<i>Tilletiopsis minor</i>	CBS 543.50 ^T	AJ235287	KP322989	KP322972	KP322938	KP323097	KP323114	KP323008
<i>Tilletiopsis penniseti</i>	CBS 110032 ^T	AB052825	—	KP322975	KP322917	KP323085	KP323143	KP322995
Microstromatales								
<i>Jaminaea angkorensis</i>	CBS 10918 ^T	EU587489	EU604147	EU604148	KP322907	KP323082	KP323152	KC628747
<i>Jaminaea lanaiensis</i>	CBS 10858 ^T	DQ990016	DQ990017	KP322964	—	KP323080	KP323144	KP323021
<i>Microstroma juglandis</i>	CBS 287.63	AF009867	DQ789988	DQ789987	DQ789990	DQ789989	DQ789991	—
<i>Microstroma albiziae</i>	CMW 36935	KP322982	KP322982	KP322947	—	KP323079	KP323150	KP323016
<i>Quambalaria cyanescens</i>	CBS 876.73	DQ317616	DQ317623	KF706440	—	KF706531	KF706485	KP323031
<i>Rhodotorula bacarum</i>	CGMCC 2.3190 ^T	AF190002	DQ317629	AJ496257	KP322937	KP323098	KP323120	AB040618
<i>Rhodotorula hinnulea</i>	JCM 9030 ^T	AF190003	AB038130	AB038130	KP322905	KP323062	KP323121	AB041050
<i>Rhodotorula phylloplana</i>	JCM 9035 ^T	AF190004	AB038131	AJ496258	KP322906	KP323063	KP323116	AB041051
<i>Sympodiomyces kandeliae</i>	CBS 11676	GU047881	GQ465043	KP322963	KP322925	KP323077	KP323149	KP323047
<i>Sympodiomyces paphiopedili</i>	CGMCC 2.1398 ^T	AF352054	DQ317631	DQ832239	KP322941	KP323099	KP323117	—
Tilletiales								
<i>Erratomyces patelii</i>	CBS 669.70	DQ094784	DQ846894	DQ846895	DQ846897	DQ846896	DQ846898	—
<i>Tilletia goloskokovii</i>	LMC 321	AY818998	DQ832248	DQ832247	DQ832250	DQ832249	DQ832251	—
Entylomatales								
<i>Entyloma amoseridis</i>	CBS 203.36	DQ645528	DQ911609	DQ645529	—	DQ645530	DQ645531	—
<i>Entyloma calendulae</i>	CBS 746.85	DQ663687	DQ663689	KP322948	—	DQ663690	KP323124	KP323056
<i>Entyloma ficariae</i>	CBS 480.91	AJ235295	JQ586199	KP322949	KP322944	—	KP323125	—
<i>Tilletiopsis cremea</i>	CBS 605.83 ^T	AJ235279	AB025690	KP322969	—	KP323108	KP323129	KP323006
<i>Tilletiopsis lilacina</i>	CBS 435.92 ^T	KP322984	KP322984	KP322966	—	KP323110	KP323112	KP323002
<i>Tilletiopsis washingtonensis</i>	CBS 544.50 ^T	AJ235278	DQ835994	KP322976	—	DQ835995	DQ835996	KP322997
Doassansiales								
<i>Rhamphospora nymphaeae</i>	CBS 72.38	DQ831032	DQ831034	DQ831033	—	DQ831035	DQ831036	—

(continued on next page)

Table 1. (Continued).

Species	Strains number	D1D2	ITS	SSU	RPB1	RPB2	EF1	CytB
Exobasidiales								
<i>Acaromyces ingoldii</i>	CBS 110050 ^T	AY158665	AY158671	?	KP322920	KP323078	KP323145	KP323019
<i>Exobasidium gracile</i>	DSM 4460	DQ663699	DQ663700	DQ785786	DQ663702	DQ663701	DQ663703	—
<i>Exobasidium rhododendri</i>	CBS 101457	DQ667151	DQ667153	DQ667152	DQ667155	DQ667154	DQ667156	—
<i>Exobasidium vaccinii</i>	DB 160d	KP322983	KP322983	KP866248	KP322924	KP323076	KP323146	—
<i>Meira argovae</i>	CBS 110053 ^T	AY158669	AY158675	KP322953	KP322922	KP323081	KP323139	KP323017
<i>Meira geulakonigii</i>	CBS 110052 ^T	AY158668	AY158674	KP322954	KP322919	KP323083	KP323141	KP323011
<i>Meira nashicola</i>	CBS 117161 ^T	AB185157	AB185159	KP322955	KP322921	KP323084	KP323140	KP323014
Species incertae sedis in the Exobasidiomycetes								
<i>Tilletiopsis albescens</i>	CBS 608.83 ^T	AJ235289	KP322986	KP322968	KP322942	KP323095	KP323127	KP323028
<i>Tilletiopsis pallescens</i>	CBS 364.85 ^T	AJ235292	DQ317636	KP322973	KP322943	KP323101	KP323123	KP322992
Ustilaginomycetes								
Urocystales								
<i>Urocystis colchici</i>	CBS 283.28	DQ838576	DQ839596	DQ839595	—	DQ839597	DQ839598	—
<i>Urocystis eranthidis</i>	HMK 292 ¹	JN367324	JN367299	JN367352	JN367428	—	JN367375	—
Ustilaginales								
Anthracoideaceae								
<i>Cintractia axicola</i>	MP 3490	DQ631906	DQ631908	DQ631907	—	DQ631909	DQ631910	—
<i>Cintractia limitata</i>	HAJB 10488	DQ645506	DQ645508	DQ645507	DQ645510	DQ645509	DQ645511	—
<i>Farysizyma acheniorum</i>	CGMCC 2.3198 ^T	AF190001	AB038128	AJ496256	KP322927	KP323064	KP323131	AB041047
<i>Farysizyma itapuensis</i>	CBS 10428 ^T	DQ767831	DQ767831	DQ767831	KP322915	KP323075	KP323161	KP323054
<i>Farysizyma setubalensis</i>	CBS 10241 ^T	EU002857	EU002888	KP322950	KP322913	KP323073	KP323147	KP323013
<i>Farysizyma taiwniana</i>	CBS 9927 ^T	AY551270	AY555071	KP322951	KP322914	KP323071	KP323148	KP323033
<i>Schizonella melanogramma</i>	CBS 174.42	DQ832210	DQ832212	DQ832211	DQ832214	DQ832213	DQ832215	—
<i>Ustanciosporium gigantosporum</i>	CBS 131478	JN367325	JN367300	KP322977	JN367429	KP323072	JN367376	KP322994
<i>Ustanciosporium standleyanum</i>	JAG 73	DQ846888	DQ846890	DQ846889	DQ846892	DQ846891	DQ846893	—
Ustilaginaceae								
<i>Anthracoctystis anthracoideispora</i>	HUV 18350 ¹	JN367315	JN367290	JN367344	JN367420	—	JN367367	—
<i>Anthracoctystis apludae</i>	KVU 967 ¹	JN367319	JN367294	JN367348	JN367424	—	JN367371	—
<i>Anthracoctystis walkeri</i>	KVU 975 ¹	JN367322	JN367297	JN367350	JN367426	—	JN367373	—
<i>Anthracoctystis pampara</i>	JCM 2007	KP322980	KP322980	KP322961	KP322908	KP323066	—	—
<i>Langdonia aristidae</i>	HUV 19145 ¹	JN367317	JN367292	JN367346	JN367422	—	JN367369	—
<i>Macalpinomyces eriachnes</i>	CBS 131454	JN367312	JN367287	JN367340	JN367417	KP323074	KP323142	KP323022

Table 1. (Continued).

Species	Strains number	D1D2	ITS	SSU	RPB1	RPB2	EF1	CytB
<i>Macalpinomyces spermophorus</i>	HUV 20717 ¹ /F 565	AY740171	AY740171	JN367358	JN367433	—	JN367381	—
<i>Melanopsichium pennsylvanicum</i>	UMa704 ¹	JN367313	JN367288	JN367341	JN367418	—	JN367364	—
<i>Ustilago maydis</i>	CBS 504.76	AF453938	AY854090	KP322979	KP322928	KP323090	KP323130	KP322996
<i>Ustilago maydis</i>	FB1	KP866233	KP866233	KP322952	KP322912	KP323067	KP323154	KP323003
<i>Moesziomyces bullatus</i>	CBS 425.34	DQ831011	DQ831013	DQ831012	DQ831015	DQ831014	—	—
<i>Sporisorium andropogonis</i>	CBS 192.26/KVU 841 ¹	AY740095	AY740042	KP322962	JN367419	KP323065	JN367366	—
<i>Sporisorium exsertum</i>	KVU 965 ¹	JN367318	JN367293	JN367347	JN367423	—	JN367370	—
<i>Sporisorium reilianum</i>	CBS 131460	KF706430	KF706438	KF706441	KP322910	KF706511	KF706472	KP323058
<i>Sporisorium scitamineum</i>	CBS 131463	JN367321	JN367296	KP322965	JN367425	KP323070	JN367372	KP323057
<i>Sporisorium sorghi</i>	CBS 104.17	AY745726	DQ200931	DQ234548	DQ785784	KP323105	DQ028590	KP323060
<i>Stollia bursa</i>	KVU 844 ¹	JN367316	JN367291	JN367345	JN367421	—	JN367368	—
<i>Pseudozyma abaconensis</i>	CBS 8380 ^T	FJ008047	FJ008053	KP322956	KP322916	KP323092	KP323159	KP323051
<i>Pseudozyma antarctica</i>	CBS 5955	AJ235302	AB089358	KP322960	KP322935	KP323093	KP323118	KP323048
<i>Pseudozyma flocculosa</i>	CBS 167.88 ^T	AJ235299	AF294690	AF294717	KP322931	KP323106	KP323135	KP323059
<i>Pseudozyma hubeiensis</i>	CGMCC 2.2493 ^T	DQ008953	DQ008954	KP322957	—	KP323103	KP323111	KP322990
<i>Pseudozyma parantarctica</i>	CBS 10005 ^T	AB089357	AB089356	JN940457	JN992528	KP323069	KP323151	KP322991
<i>Pseudozyma prolifica</i>	CBS 319.87 ^T	AJ235298	AF294700	AF294724	DQ352825	KP323089	DQ352831	KP323009
<i>Pseudozyma pruni</i>	CBS 10937 ^T	EU379943	EU379942	KP322958	KP322911	KP323087	KP323155	KP323050
<i>Pseudozyma rugulosa</i>	JCM 10323 ^T	JN940523	JN942670	JN940458	JN992524	KP323091	KP323133	KP323049
<i>Pseudozyma shanxiensis</i>	CGMCC 2.2523 ^T	DQ008955	DQ008956	KP866247	KP322932	KP323104	KP323113	KP323005
<i>Pseudozyma thailandica</i>	CBS 10006 ^T	AB089355	AB089354	KP322959	KP322909	KP323088	KP323157	KP322999
<i>Tranzscheliella hypodytes</i>	RK074 ¹	JN367323	JN367298	JN367351	JN367427	—	JN367374	—
<i>Tranzscheliella williamsii</i>	CBS 131475	JN367338	JN367310	KP322974	KP322923	KP323068	KP323156	KP323052
<i>Ustilago cynodontis</i>	HRK 040/MS 1	AY740168	AY740168	JN367355	JN367430	—	JN367378	—
<i>Ustilago filiformis</i>	HRK 025 ¹	JN367328	JN367302	JN367356	JN367431	—	JN367379	—
<i>Ustilago hordei</i>	CBS 131470	KF706429	KF706437	KP322978	KF706498	KF706521	KF706473	KP323055
<i>Ustilago hordei</i>	DB 1526	JN367329	JN367303	JN367357	JN367432	—	JN367380	—
<i>Ustilago striiformis</i>	HUV 18286 ¹	DQ875375	AY740172	JN367359	JN367434	—	JN367382	—
<i>Ustilago tritici</i>	CBS 669.70	DQ094784	DQ846894	DQ846895	DQ846897	DQ846896	DQ846898	—
<i>Ustilago xerochloae</i>	KVU 1000 ¹	JN367339	JN367311	JN367362	JN367436	—	JN367385	—
<i>Ustilago vetiveriae</i>	HUV 17954 ¹	JN367337	AY345011	JN367360	JN367435	—	JN367383	—

(continued on next page)

Table 1. (Continued).

Species	Strains number	D1D2	ITS	SSU	RPB1	RPB2	EF1	CytB
Malasseziomycetes								
Malasseziales								
<i>Malassezia caprae</i>	CBS 10434 ^T	AY743616	AY743656	KF706456	KF706495	KF706513	KF706467	KP323001
<i>Malassezia dermatis</i>	CBS 9169 ^T	AB070365	AY390284	KF706452	KF706490	KF706532	KF706461	KP323000
<i>Malassezia equina</i>	CBS 9969 ^T	AY743621	KF706439	KF706454	KF706492	KF706515	KP323160	KP323010
<i>Malassezia furfur</i>	CBS 1878 ^{NT}	AF063214	AY743634	KF706457	KF706497	KF706516	KF706469	KP323024
<i>Malassezia globosa</i>	CBS 7966 ^T	AF064025	AY387132	—	KF706493	KF706518	KF706465	KP323018
<i>Malassezia japonica</i>	CBS 9431 ^T	EF140672	EF140669	KF706458	—	KF706514	KP323153	KP323026
<i>Malassezia nana</i>	CBS 9558	EF140673	EF140667	KF706453	KF706491	KF706510	KF706462	KP323015
<i>Malassezia obtusa</i>	CBS 7876 ^T	AB105197	AY387137	KF706455	—	KF706519	KF706470	KP323030
<i>Malassezia pachydermatis</i>	CBS 1879 ^T	AY743605	AB118941	DQ457640	DQ785792	DQ408140	DQ028594	—
<i>Malassezia restricta</i>	CBS 7877 ^{NT}	AF064026	AY743636	EU192367	KF706496	KF706520	KF706471	KP323027
<i>Malassezia slooffiae</i>	CBS 7956 ^T CBS 9986	AJ249956	AY743633	KF706459	—	—	—	KP323025
<i>Malassezia sympodialis</i>	CBS 7222 ^T CBS 8334	AF064024	AY743632	KF706460	—	KP323094	KP323158	KP323023
<i>Malassezia yamatoensis</i>	CBS 9725 ^T	AB125263	AB125261	—	KF706494	KF706512	KF706466	KP323012
Moniliellomycetes								
Moniliellales								
<i>Moniliella acetoabutens</i>	CBS 169.66 ^T	AF335523	EU252153	KF706443	KF706500	KF706523	KF706476	KP323032
<i>Moniliella madida</i>	CBS 240.79 ^T	AF335522	—	KF706447	KF706502	KF706525	KF706478	KP323038
<i>Moniliella megachiliensis</i>	CBS 190.92 ^T	EF137916	KF706433	KF706448	KF706501	KF706524	KF706477	KP323037
<i>Moniliella mellis</i>	CBS 350.33 ^T	EU545185	—	KF706446	—	KF706528	KF706481	KP323041
<i>Moniliella nigrescens</i>	CBS 269.81 ^T	AF335527	KF706436	—	KF706504	KF706527	KF706480	KP323040
<i>Moniliella oedocephalis</i>	CBS 649.66 ^T	AF335521	KF706435	KF706449	KP322939	KP323107	KF706484	KP323042
<i>Moniliella pollinis</i>	CBS 461.67 ^T	AF335525	KF706434	KF706450	KF706505	KF706529	KF706482	KP323039
<i>Moniliella spathulata</i>	CBS 241.79 ^T	AF335526	KF706432	KF706444	KF706503	KF706526	KF706479	KP323036
<i>Moniliella suaveolens</i>	CBS 126.42 ^T	AF335520	KF706431	KF706445	—	—	KF706475	KP323043

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 Havana Jardín botánico; HMK, Herbarium Martin Kemler; HRK, Herbarium Ronny Kellner; HUV, Herbarium Ustilaginales Vánky; JAG, Herbarium J.A. Gossmann; JCM: the Japan Collection of Microorganisms (JCM); KVVU: Kálmán Vánky Ustilaginales; LMC: Herbarium L. M. Carris; MP, Herbarium Meike Piepenbring; RK, strain collection Ronny Kellner; 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, families, orders and classes are in bold.

Species	Basionym or important synonym	Strain/Herbarium number	D1/D2	ITS
Exobasidiomycetes				
Doassansiales				
Rhaphosporaceae				
Rhaphospora				
<i>Rhaphospora nymphaeae</i>		CBS 72.38	DQ831032	DQ831034
Entylomatales				
Entylomataceae				
Entyloma				
<i>E. amoseridis</i>		CBS 203.36	DQ645528	DQ911609
<i>E. calendulae</i>	<i>Protomyces calendulae</i>	CBS 746.85	DQ663687	DQ663689
<i>E. ficariae</i>		CBS 480.91	AJ235295	JQ586199
Tilletiopsis¹				
<i>T. cremea¹</i>		CBS 605.83 ^T	AJ235279	AB025690
<i>T. lilacina¹</i>		CBS 435.92 ^T	KP322984	KP322984
<i>T. washingtonensis¹</i>		CBS 544.50 ^T	AJ235278	DQ835994
Exobasidiales				
Brachybasidiaceae				
Meira¹				
<i>M. argovae¹</i>		CBS 110053 ^T	AY158669	AY158675
<i>M. geulakonigii¹</i>		CBS 110052 ^T	AY158668	AY158674
<i>M. miltonrushii¹</i>		MCA 3882 ^T	JX432962	JX432962
<i>M. nashicola¹</i>		CBS 117161 ^T	AB185157	AB185159
Cryptobasidiaceae				
Acaromyces¹				
<i>A. ingoldii¹</i>		CBS 110050 ^T	AY158665	AY158671
Laurobasidium				
<i>L. lauri</i>	<i>Exobasidium lauri</i>	MAFF238665	AB177562	AB180359
Exobasidiaceae				
Exobasidium				
<i>E. gracile</i>	<i>Exobasidium camelliae</i> var. <i>gracile</i>	DSM4460	DQ663699	DQ663700
<i>E. rhododendri</i>	<i>Exobasidium vaccinii</i> var. <i>rhododendri</i>	CBS 101457	DQ667151	DQ667153
<i>E. vaccinii</i>		TUB019109 DB160d	FJ644526 KP322983	AB180362 KP322983
Georgefischeriales				
Gjaerumiaceae				
Gjaerumia				
<i>G. penniseti</i> comb. nov. ¹	<i>Tilletiopsis penniseti¹</i>	CBS 110032 ^T	AB052825	—
<i>G. minor</i> comb. nov. ¹	<i>Tilletiopsis minor¹</i>	CBS 543.50 ^T	AJ235287	KP322989
Tilletiariaceae				
Phragmotaeonium				
<i>P. derxii</i> comb. nov. ¹	<i>Tilletiopsis derxii¹</i>	CBS 110078 ^T	AB052823	AB045707
<i>P. flavum</i> comb. nov. ¹	<i>Tilletiopsis flava¹</i>	CBS 401.84 ^T	AJ235285	KP322987
<i>P. fulvescens</i> comb. nov. ¹	<i>Tilletiopsis fulvescens¹</i>	CBS 607.83 ^T	AJ235282	KP322988
<i>P. oryzicola</i> comb. nov. ¹	<i>Tilletiopsis oryzicola¹</i>	CBS 110079 ^T	AB052825	AB045708
Tilletiaria¹				
<i>Tilletiaria anomala¹</i>		CBS 436.72 ^T	AJ235284	DQ234558
Golubeviales ord. nov. ¹				
Golubeviaceae fam. nov. ¹				

(continued on next page)

Table 2. (Continued).

Species	Basionym or important synonym	Strain/Herbarium number	D1/D2	ITS
<i>Golubevia</i> gen. nov. ¹				
<i>G. pallescens</i> comb. nov. ¹	<i>Tilletiopsis pallescens</i> ¹	CBS 111626 CBS 364.85 ^T	AY879271 AJ235292	AY879278 DQ317636
Microstromatales				
Microstromataceae				
Microstroma				
<i>M. albiziae</i>		CMW 36935	KP322982	KP322982
<i>M. album</i>	<i>Fusisporium album</i> <i>Rhodotorula bacarum</i> <i>Torulopsis bacarum</i>	RB2072 CGMCC 2.3190 ^T	AF352052 AF190002	DQ317624 DQ317629
<i>M. phylloplanum</i> comb. nov. ¹	<i>Cryptococcus phylloplanus</i> ¹ <i>Rhodotorula phylloplana</i> ¹	JCM 9035 ^T	AF190004	AB038131
	<i>Cryptococcus hinnuleus</i> ¹ <i>Rhodotorula hinnulea</i> ¹	JCM 9030 ^T	AF190003	AB038130
<i>M. juglandis</i>	<i>Fusidium juglandis</i>	CBS 287.63	AF009867	DQ789988
Volvocisporiaceae				
Volvocisporium				
<i>V. triumfeticola</i>	<i>Muribasidiospora triumfeticola</i>	RB2070	AF352053	DQ317637
Quambalariaceae				
Quambalaria				
<i>Q. cyanescens</i>	<i>Sporothrix cyanescens</i>	CBS 876.73	DQ317616	DQ317623
Microstromatales incertae sedis				
Jaminaea ¹				
<i>J. angkorensis</i> ¹		CBS 10918 ^T	EU587489	EU604147
<i>J. lanaiensis</i> ¹	<i>Sympodiomyopsis lanaiensis</i> ¹	CBS 11676 ^T	GU047881	GQ465043
Sympodiomyopsis ¹				
<i>S. kandeliae</i> ¹		CBS 10858 ^T	DQ990016	DQ990017
<i>S. paphiopedilii</i> ¹		AS 2.1398 ^T	AF352054	DQ317631
Robbaueriales ord. nov. ¹				
Robbaueraceae fam. nov. ¹				
Robbauera gen. nov. ¹				
<i>R. albescens</i> comb. nov. ¹	<i>Tilletiopsis albescens</i> ¹	CBS 608.83 ^T	AJ235289	KP322986
Tilletiales				
Tilletiaceae				
Erratomyces				
<i>E. patelii</i>	<i>Protomyopsis patelii</i>	CBS 669.70	DQ094784	DQ846894
Tilletia				
<i>T. caries</i>	<i>Uredo caries</i>	CBS 160.85	AJ235307	AY496450
<i>T. controversa</i>	<i>Tilletia controversa</i>	MP2525	DQ832244	DQ832246
<i>T. goloskokovii</i>		LMC321	AY818998	DQ832248
<i>T. iowensis</i>	<i>Neovossia iowensis</i>	BPI863664	AY818988	DQ832253
Ustilaginomycetes				
Urocystales				
Doassansiopsaceae				
Doassansiopsis				
<i>D. limnocharidis</i>	<i>Doassansia limnocharidis</i>	HUV15198	AF009850	DQ875344
Fereydouniaceae ¹				
Fereydounia ¹				
<i>F. khargensis</i> ¹		IBRCM30116 ^T	KJ490642	KJ490641
Glomosporiaceae				
Thecaphora				

Table 2. (Continued).

Species	Basionym or important synonym	Strain/Herbarium number	D1/D2	ITS
<i>T. spilanthis</i>		JAG53	DQ832241	DQ832243
Urocystaceae				
Melanoxa				
<i>M. oxalidiellae</i>		TUB 015007	EF635905	EF635906
<i>M. oxalidis</i>	<i>Melanotaenium oxalidis</i>	HUV1436	EF635908	EF635907
Mundkurella				
<i>M. kalopanacis</i>		HUV16732	AF009869	DQ875351
Urocystis				
<i>U. colchici</i>	<i>Caeoma colchici</i>	CBS 283.28	DQ838576	DQ839596
<i>U. eranthidis</i>	<i>Urocystis pompholygodes f. eranthidis</i>	hmk292	JN367324	JN367299
Ustacystis				
<i>U. waldsteiniae</i>	<i>Urocystis waldsteiniae</i>	FO38439	AF009880	DQ875356
Vankya				
<i>V. heufferi</i>	<i>Ustilago heufferi</i>	HUV15007	EF653981	EF667965
<i>V. ornithogali</i>	<i>Uredo ornithogali</i>	TUB015993	EF210712	EF635910
Ustilaginales				
Anthracoideaceae				
Cintractia				
<i>C. amazonica</i>		MP200	AJ236142	DQ875342
<i>C. axicola</i>	<i>Ustilago axicola Berk.</i>	MP3490	DQ631906	DQ631908
<i>C. limitata</i>	<i>Cintractia limitata</i>	HAB10488	DQ645506	DQ645508
Dermatosorus				
<i>D. cyperi</i>		HUV15991	AJ236157	DQ875343
Farysia				
<i>F. acheniorum</i> comb. nov. ¹	<i>Farysizyma acheniorum</i> ¹ <i>Rhodotorula acheniorum</i> ¹ , <i>Sterigmatomyces acheniorum</i> ¹	AS 2.3198 ^T	AF190001	AB038128
<i>F. chardoniana</i>		MP2062	AF009859	AY344968
<i>F. itapuensis</i> comb. nov. ¹	<i>Farysizyma itapuensis</i> ¹	CBS 10428 ^T	DQ767831	DQ767831
<i>F. setubalensis</i> comb. nov. ¹	<i>Farysizyma setubalensis</i> ¹	CBS 10241 ^T	EU002857	EU002888
<i>F. taiwaniana</i> comb. nov. ¹	<i>Farysizyma taiwniana</i> ¹	CBS 9927 ^T	AY551270	AY555071
Leucocintractia				
<i>L. leucodermoides</i>		MS482	DQ875363	DQ875346
<i>L. scleriae</i>	<i>Uredo scleriae</i>	MP2074	AJ236154	AY740025
Moreaua				
<i>M. bulbostylidis</i>		56581 (M)	DQ875366	DQ875349
<i>M. fimbriostylidis</i>		56582 (M)	DQ875367	DQ875350
Schizonella				
<i>S. melanogramma</i>	<i>Uredo melanogramma</i>	FO37174	AF009870	DQ191252
Stegocintractia				
<i>S. luzulae</i>	<i>Ustilago luzulae</i>	MP2340	AJ236148	DQ875353
Tolyposporium				
<i>T. isolepidis</i>	<i>Schizonella isolepidis</i>	HUV14720	EU246949	EU246950
<i>T. neillii</i>	<i>Sorosporium neillii</i>	HUV18533	EU246952	EU246951
<i>T. junci</i>	<i>Sorosporium junci</i>	HUV17168	AF009876	AY344994
Ustanciosporium				
<i>U. gigantosporum</i>	<i>Cintractia gigantospora</i>	HRK023	JN367325	JN367300
<i>U. standleyanum</i>	<i>Cintractia standleyana</i>	JAG73	DQ846888	DQ846890
Melanotaeniaceae				
Melanotaenium				

(continued on next page)

Table 2. (Continued).

Species	Basionym or important synonym	Strain/Herbarium number	D1/D2	ITS
<i>M. cingens</i>	<i>Ustilago cingens</i>	L.E.Kari191(M)	DQ875364	DQ875347
<i>M. endogenum</i>	<i>Protomyces endogenus</i>	CBS 481.91	DQ789979	DQ789981
<i>M. euphorbiae</i>	<i>Tilletia euphorbiae</i>	HUV17733	JN367314	JN367289
Ustilaginaceae				
Anomalomyces				
<i>A. panici</i>		BRIP46421	DQ459347	DQ459348
<i>A. yakirrae</i>		HUV 21918	KC184906	KC184907
Anthracoecystis				
<i>A. anthracoideispora</i>	<i>Sporisorium anthracoideisporum</i>	HUV18350	JN367315	JN367290
<i>A. apludae</i>	<i>Sorosporium apludae</i>	KVU967	JN367319	JN367294
<i>A. apludae-aristatae</i>	<i>Sorosporium apludae-aristatae</i>	MS287	AY740098	AY740045
<i>A. cenchri</i>	<i>Ustilago cenchri</i>	MP1974	AF453943	AY344972
<i>A. cenchri-elymoidis</i>	<i>Sporisorium cenchri-elymoidis</i>	BRIP 26491	HQ013122	HQ013094
<i>A. chrysopogonis</i>	<i>Sporisorium chrysopogonis</i>	MS135	AY740131	AY344973
<i>A. destruens</i>		Ust.exs.472 (M)	AY747077	AY344976
<i>A. elionuri</i>	<i>Ustilago elionuri</i>	MP2601 (LPB)	AY740157	AY740157
<i>A. fascicularis</i>		MS198	AY740088	AY740035
<i>A. formosana</i>	<i>Ustilago formosana</i>	Ust. Exs. 688 (M)	AY740134	AY344979
<i>A. flocculosa</i> ¹	<i>Pseudozyma flocculosa</i> ¹ <i>Sporothrix flocculosa</i> ¹	CBS 167.88 ^T	AJ235299	AF294690
<i>A. heteropogonicola</i>	<i>Sorosporium heteropogonicola</i>	BRIP51822	HQ013135	HQ013101
<i>A. hwangensis</i>	<i>Sporisorium hwangense</i>	MS267	AY740104	AY740051
<i>A. loudetiae-pedicellatae</i>	<i>Sporisorium loudetiae-pedicellatae</i>	MS252	AY740106	AY740053
<i>A. ovaria</i>	<i>Sorosporium ovarium</i>	MP1871	AJ236137	AY740020
<i>A. pampara</i> comb. nov.	<i>Ustilago pamparum</i>	JCM 2007	KP322980	KP322980
<i>A. pollinae</i>	<i>Sorosporium pollinae</i>	MS32	AY740138	AY344987
<i>A. provincialis</i>	<i>Sorosporium ellisii</i> var. <i>provincialis</i>	Ust.exs.759 (M)	AY747076	AY344988
<i>A. pseudanthistiriae</i>	<i>Sorosporium pseudanthistiriae</i>	KVU969	JN367320	JN367295
<i>A. themedae-arguentis</i>	<i>Sporisorium themedae-arguentis</i>	Ust. Exs. 855	AY740140	AY344991
<i>A. tumefaciens</i>	<i>Sorosporium tumefaciens</i>	MS139	AY740128	AY344969
<i>A. walkeri</i>	<i>Sporisorium walkeri</i>	KVU975	JN367322	JN367297
<i>Dirkmeia</i> gen. nov.¹				
<i>D. churashimaensis</i> comb. nov. ¹	<i>Pseudozyma churashimaensis</i> ¹	OK96 ^T	AB548955	AB548947
<i>Kalmanozyma</i> gen. nov.¹				
<i>K. fusiformata</i> comb. nov. ¹	<i>Pseudozyma fusiformata</i> ¹	CBS 6951 ^T	AB089367	AB089366
<i>K. brasiliensis</i> comb. nov. ¹	<i>Pseudozyma brasiliensis</i> ¹	GHG001 ^T	KF737866	KF737866
<i>K. vetiver</i> comb. nov. ¹	<i>Pseudozyma vetiver</i> ¹	DMKU-LV99 ^T	AB809649	AB809652
<i>Langdonia</i>				
<i>L. aristidae</i>	<i>Ustilago aristidae</i>	HUV19145	JN367317	JN367292
<i>L. confusa</i>	<i>Sorosporium confusum</i>	BRIP42670	HQ013132	HQ013095
<i>L. jejuensis</i> comb. nov. ¹	<i>Pseudozyma jejuensis</i> ¹	CBS 10454 ^T	FN428865	EF079966
<i>Macalpinomyces</i>				
<i>M. eragrostiellae</i>		Ust.Exs.960(M)	AY740089	AY740036
<i>M. eriachnes</i>	<i>Sorosporium eriachnes</i>	CBS 131454	JN367312	JN367287
<i>M. loudetiae</i>	<i>Sorosporium loudetiae</i>	MS250	AY740151	AY740151
<i>M. mackinlayi</i>		BRIP52549	HQ013131	GU014817
<i>M. neglectus</i>	<i>Ustilago neglecta</i>	RB2056 (TUB)	AY740109	AY740056
<i>M. spermophorus</i>		F565	AY740171	AY740171
<i>M. trichopterygis</i>		MS248	AY740092	AY740039
<i>M. tristachyae</i>		MS15	AY740164	AY740164

Table 2. (Continued).

Species	Basionym or important synonym	Strain/Herbarium number	D1/D2	ITS
<i>M. viridans</i>		BRIP 49133	HQ013125	HQ013089
Melanopsichium				
<i>M. pennsylvanicum</i>	<i>Melanopsichium pennsylvanicum</i>	HUV17548 (TUB)	AY740093	AY740040
Moesziomyces				
<i>M. antarcticus</i> comb. nov. ¹	<i>Candida antarctica</i> ¹ <i>Pseudozyma antarctica</i> ¹ <i>Trichosporon oryzae</i> ¹ <i>Vanrija antarctica</i> ¹	CBS 5955 JCM 10317 ^T	AJ235302 JN940521	AB089358 JN942668
<i>M. aphidis</i> comb. nov. ¹	<i>Pseudozyma aphidis</i> ¹	JCM 10318 CBS 517.83 ^T	JN940519 AB089363	JN942666 AF294699
M. bullatus	<i>Sorosporium bullatum</i>	CBS 425.34	DQ831011	DQ831013
<i>M. parantarcticus</i> comb. nov. ¹	<i>Pseudozyma parantarctica</i> ¹	CBS 10005 ^T	AB089357	AB089356
<i>M. rugulosus</i> comb. nov. ¹	<i>Pseudozyma rugulosa</i> ¹	CBS 170.88 ^T	JN940523	JN942670
Sporisorium				
<i>S. aegypticum</i>	<i>Ustilago aegyptiaca</i>	Ust.Exs.756(M)	AY740129	AY344970
<i>S. andropogonis</i>	<i>Uredo andropogonis</i>	MS283	AY740095	AY740042
<i>S. arthraxonis</i>	<i>Ustilago arthraxonis</i>	MS338	AY740099	AY740046
<i>S. cordobense</i>	<i>Ustilago cordobensis</i>	MS159	AY740155	AY740155
<i>S. cruentum</i>	<i>Ustilago cruenta</i>	MS14	AY740156	AY740156
<i>S. culmiperdum</i>	<i>Ustilago culmiperda</i>	MP2060	AF133580	AY344975
<i>S. dimeriae-ornithopodae</i>		Ust.exs. 472	AY740132	AY344977
<i>S. erythraeense</i>	<i>Ustilago erythraeensis</i>	Ust.Exs.849 (M)	AY740102	AY740049
<i>S. exsertum</i>	<i>Cintractia exserta</i>	KVU965	JN367318	JN367293
<i>S. fastigiatum</i>		MP1976	AY740133	AY344978
<i>S. foveolati</i>	<i>Sphacelotheca foveolati</i>	MS21	AY740103	AY740050
<i>S. graminicola</i> comb. nov. ¹	<i>Pseudozyma graminicola</i> ¹	LI20 ^T	AB180728	AB180728
<i>S. holwayi</i>	<i>Sphacelotheca holwayi</i>	MP1271	AF453941	AY344980
<i>S. lacrymae-jobi</i>	<i>Ustilago lacrymae-jobi</i>	M56611	AY740105	AY740052
<i>S. lepturi</i>	<i>Ustilago carbo</i> var. <i>lepturi</i>	Ust.exs.966 (M)	AY740135	AY344981
<i>S. manilense</i>	<i>Ustilago manilensis</i>	Ust.Exs.854 (M)	AY740112	AY740059
<i>S. modestum</i>	<i>Ustilago modesta</i>	MS237	AY740107	AY740054
<i>S. moniliferum</i>	<i>Ustilago monilifera</i>	MS 98	AF453940	AY344984
<i>S. nervosum</i>		MS241	AY740110	AY740057
<i>S. occidentale</i>	<i>Sphacelotheca occidentalis</i>	Ust.exs.758 (M)	AY740137	AY344985
<i>S. ophiuri</i>	<i>Ustilago ophiuri</i>	HB20	AJ236136	AY740019
<i>S. pseudechinolaenae</i>		Ust.exs.853 (M)	AY740139	AY344989
<i>S. puellare</i>	<i>Ustilago puellaris</i>	MP2372	AY740111	AY740058
<i>S. reilianum</i>	<i>Ustilago reiliana</i>	Ust.exs. 527	AY740163	AY740163
<i>S. scitamineum</i>	<i>Ustilago scitaminea</i>	MP541	AY740147	AY740070
S. sorghi		MP2036a	AF009872	AY740021
<i>S. trachypogonicola</i>		MP2463 (HAJB)	AY740141	AY344992
<i>S. trachypogonis-splumosi</i>		MS281	AY740113	AY740060
<i>S. veracruzianum</i>	<i>Sphacelotheca veracruziana</i>	MP960	AY740114	AY344993
<i>S. vermiculum</i>		BRIP49748	HQ013134	HQ013114
<i>S. wynaadense</i>	<i>Ustilago wynaadensis</i>	BRIP27640	HQ013124	HQ013116
Stollia				
<i>S. bursa</i>	<i>Ustilago bursa</i>	KVU844	JN367316	JN367291
S. ewartii	<i>Ustilago ewartii</i>	BRIP51818	HQ013127	HQ013087
Tranzscheliella				
<i>T. hypodytes</i>	<i>Caeoma hypodytes</i>	MS342	DQ191256	DQ191250

(continued on next page)

Table 2. (Continued).

Species	Basionym or important synonym	Strain/Herbarium number	D1/D2	ITS
<i>T. williamsii</i>	<i>Sorosporium williamsii</i>	CBS 131475	JN367338	JN367310
Triodiomyces				
<i>T. altilis</i>	<i>Ustilago altilis</i>	BRIP52543	HQ013136	AY740166
<i>T. crassus</i> comb. nov. ¹	<i>Pseudozyma crassa</i>	DMST17136 ^T	AB117962	AB117962
<i>T. triodiae</i>	<i>Ustilago triodiae</i>	HUV17662	AY740126	AY740074
Tubisorus				
<i>T. pachycarpus</i>	<i>Sorosporium pachycarpum</i>	HUV 21891	JN871718	JN871717
Ustilago				
<i>U. abaconensis</i> comb. nov. ¹	<i>Pseudozyma abaconensis</i> ¹	CBS 8380 ^T	FJ008047	FJ008053
<i>U. affinis</i>		MP692	AF133581	AY344995
<i>U. austro-africana</i>		MS316	AY740115	AY740061
<i>U. avenae</i>	<i>Uredo segetum</i> var. <i>avenae</i>	DB559	AY740117	AY740063
<i>U. bromivora</i>	<i>Ustilago carbo d bromivora</i>	MS175	AY740118	AY740064
<i>U. bullata</i>		MP2363	AF453935	AY344998
<i>U. bouriquetii</i>		MS315	—	AY740167
<i>U. calamagrostidis</i>	<i>Tilletia calamagrostidis</i>	MS314	AY740119	AY740065
<i>U. crameri</i>		MS72	AY740143	AY344999
<i>U. cynodontis</i>	<i>Ustilago carbo</i> β <i>cynodontis</i>	MS199	AY740168	AY740168
<i>U. davisii</i>		HUV19252	AY740169	AY740169
<i>U. echinata</i>		MS132	AY740144	AY345001
<i>U. esculenta</i>		Ust.exs. 540	AF453937	AY345002
<i>U. filiformis</i>	<i>Lycoperdon filiforme</i>	RB3011	AY740120	AY740066
U. hordei	<i>Uredo segetum a hordei</i>	Ust.exs. 784	AF453934	AY345003
<i>U. hordei</i>		CBS 131470	KF706429	KF706437
<i>U. ixophori</i>		MP2194 (USJ)	AY740121	AY740067
<i>U. maydis</i>	<i>Mycosarcoma maydis</i>	CBS 504.76	AF453938	AY854090
<i>U. maydis</i>		FB1	KP866233	KP866233
<i>U. maydis</i>	<i>Pseudozyma prolifica</i> ¹	CBS 319.87 ^T	AJ235298	AF294700
<i>U. nuda</i>	<i>Ustilago segetum</i> var. <i>nuda</i>	HUV17782	JN367334	JN367307
<i>U. pamirica</i>		Ust.exs.789 (M)	AY740145	AY345005
<i>U. shanxiensis</i> comb. nov. ¹	<i>Pseudozyma shanxiensis</i> ¹	AS 2.2523 ^T	DQ008955	DQ008956
<i>U. schmidtia</i>		BRIP 51848	HQ013129	HQ013121
<i>U. schroeteriana</i>		Ust.exs.887 (M)	AY740146	AY345006
<i>U. siamensis</i> comb. nov. ¹	<i>Pseudozyma siamensis</i> ¹	DMST17137 ^T	AB117963	AB117963
<i>U. sparsa</i>		KVU892	JN367335	JN367308
<i>U. striiformis</i>		HUV18286	DQ875375	AY740172
<i>U. syntherismae</i>	<i>Caecoma syntherismae</i>	Ust.Exs.998 (M)	AY740123	AY740071
<i>U. tragana</i>		MS320	AY740124	AY740072
<i>U. trichophora</i>	<i>Caecoma trichophorum</i>	MS339	AY740125	AY740073
<i>U. tritici</i>	<i>Uredo segetum</i> β <i>tritici</i>	CBS 669.70	DQ094784	DQ846894
<i>U. vetiveriae</i>		HUV17954	JN367337	AY345011
<i>U. xerochloae</i>		Ust.exs.1000 (M)	AY740150	AY345012
Species remain to be reclassified				
<i>Pseudozyma alboarmeniaca</i> pro tem. ¹		DMST17135 ^T	AB117961	AB117961
<i>P. hubeiensis</i> pro tem. ¹		AS 2.2493 ^T	DQ008953	DQ008954
<i>P. pruni</i> pro tem. ¹		CBS 10937 ^T	EU379943	EU379942
<i>P. thailandica</i> pro tem. ¹		CBS 10006 ^T	AB089355	AB089354
<i>P. tsukubaensis</i> pro tem. ¹		JCM 10324 ^T	AB089373	AB089372
Websdaneaceae				
Websdanea				

Table 2. (Continued).

Species	Basionym or important synonym	Strain/Herbarium number	D1/D2	ITS
<i>W. lyginiae</i>	<i>Ustilago lyginiae</i>	HUV 17900	AJ236159	DQ875357
Malasseziomycetes¹				
Malasseziales¹				
Malasseziaceae¹				
Malassezia¹				
<i>M. caprae¹</i>		CBS 10434 ^T	AY743616	AY743656
<i>M. cuniculi¹</i>		CBS 11721 ^T	GU733708	GU733709
<i>M. dermatis¹</i>		CBS 9169 ^T	AB070365	AY390284
<i>M. equina¹</i>		CBS 9969 ^T	AY743621	KF706439
<i>M. furfur¹</i>	<i>Microsporum furfur¹</i>	CBS 1878 ^{NT}	AF063214	AY743634
<i>M. globosa¹</i>		CBS 7966 ^T	AF064025	AY387132
<i>M. japonica¹</i>		CBS 9431 ^T	EF140672	EF140669
<i>M. nana¹</i>		CBS 9558	EF140673	EF140667
<i>M. obtusa¹</i>		CBS 7876 ^T	AB105197	AY387137
<i>M. pachydermatis¹</i>	<i>Pityrosporum pachydermatis¹</i>	CBS 1879 ^T	AY743605	AB118941
<i>M. restricta¹</i>		CBS 7877 ^{NT}	AF064026	AY743636
<i>M. slooffiae¹</i>		CBS 7956 ^T	AJ249956	AY743633
<i>M. sympodialis¹</i>		CBS 7222 ^T	AF064024	AY743632
<i>M. yamatoensis¹</i>		CBS 9725 ^T	AB125263	AB125261
Moniliellomycetes¹				
Moniellales¹				
Moniellaceae¹				
Moniella¹				
<i>M. acetoabutens¹</i>		CBS 169.66 ^T	AF335523	EU252153
<i>M. byzovii¹</i>		TBY 2041.7	KC213817	KC213818
<i>M. carnis¹</i>		KFP 246	JQ814873	—
<i>M. dehoogii¹</i>		KFP 211	JQ814874	—
<i>M. fonsecae¹</i>		ST-26	DQ400366	—
<i>M. madida¹</i>	<i>Trichosporonoides madida¹</i>	CBS 240.79 ^T	AF335522	—
<i>M. megachiliensis¹</i>	<i>Trichosporonoides megachiliensis¹</i>	CBS 190.92 ^T	EF137916	KF706433
<i>M. mellis¹</i>	<i>Zygosaccharomyces mellis¹</i>	CBS 350.33 ^T	EU545185	—
<i>M. nigrescens¹</i>	<i>Trichosporonoides nigrescens¹</i>	CBS 269.81 ^T	AF335527	KF706436
<i>M. oedocephali¹</i>	<i>Trichosporonoides oedocephalis¹</i>	CBS 649.66 ^T	AF335521	KF706435
<i>M. pollinis¹</i>	<i>Moniella tomentosa</i> var. <i>pollinis¹</i>	CBS 461.67 ^T	AF335525	KF706434
<i>M. spathulata¹</i>	<i>Trichosporonoides spathulata¹</i>	CBS 241.79 ^T	AF335526	KF706432
<i>M. suaveolens¹</i>	<i>Sachsia suaveolens¹</i>	CBS 126.42 ^T	AF335520	KF706431

¹ Yeast species.

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*, were performed as described in Wang *et al.* (2014). PCR and sequencing of the *CYT8* 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 firstly 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 Γ -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

1 000 bootstrap replicates analysis. Maximum parsimony (MP) analysis was conducted using PAUP* 4.0b10 (Swofford 2002) and the support of the branching topologies was derived from 1 000 replicates with 10 random additions. Bayesian inference (BI) analysis was conducted in MrBayes 3.2 (Ronquist et al. 2012) with parameters set to 5 000 000 generations, two runs and four chains. The chains were heated to 0.25 and a stop value of 0.01 was used. Sequences from several species of *Puccinomyces* were used as outgroups in the seven gene-based phylogenetic reconstructions.

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) confirmed that *Malasseziomyces* and *Moniliellomyces* containing only yeast species are monophyletic deep lineages as shown in Wang et al. (2014). *Ustilaginomyces* is also monophyletic, whereas *Exobasidiomyces* is polyphyletic (Figs 1, 2 and 3). The phylogenies of the latter two classes containing a mixture of yeast species and teleomorphic taxa are discussed below in detail.

Ustilaginomyces

Two orders *Ustilaginales* and *Urocystales* were recognised in this class (Boekhout et al. 2011, Begerow et al. 2014). They were resolved as monophyletic groups in the trees constructed from all the datasets analysed in this study with strong bootstrap (BP) and posterior probability (PP) support values (Figs 1, 2 and 3). The yeasts classified in the anamorphic genera *Farysia* and *Pseudozyma* (Inácio et al. 2008, Boekhout et al. 2011) were located within *Ustilaginales* and those in the genus *Fereydownia* occurred within *Urocystidales* as shown in Nasr et al. (2014). In the tree based on the ITS and LSU dataset *Fereydownia* occurred in a separated lineage distinct from the other genera in the *Urocystidales* (Fig. 2C), which is in agreement with Nasr et al. (2014). The *Farysia* species formed a monophyletic clade in the trees drawn from the seven gene and the four protein gene datasets (Figs 1 and 3) and clustered together with *Farysia chardoniana* in the tree based on the ITS and LSU dataset (Fig. 2C) as shown in Inácio et al. (2008). This clade was closely related with *Schizonella* and *Stegocintractia* species (Figs 1, 2C and 3) within *Anthracoideaceae* (Begerow et al. 2014). The genus *Farysia*, with the type species of *F. javanica*, proposed by Raciborski (1909) contained 21 species that are parasites on *Cyperaceae* (Begerow et al. 2014). The morphological characters are unique and at present there are no hints for a

polyphyletic nature of *Farysia*. Therefore, we consider *Farysia* 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) recently 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) and *Anthracoystis* (Clade 4), and proposed three new genera, *Langdonia* (Clade 8), *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), *Anthracoystis* (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 davisii* 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. prolifica*, 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. prolifica* shared identical ITS and LSU rRNA gene sequences with *Ustilago maydis* CBS 504.76, suggesting that *P. prolifica* 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

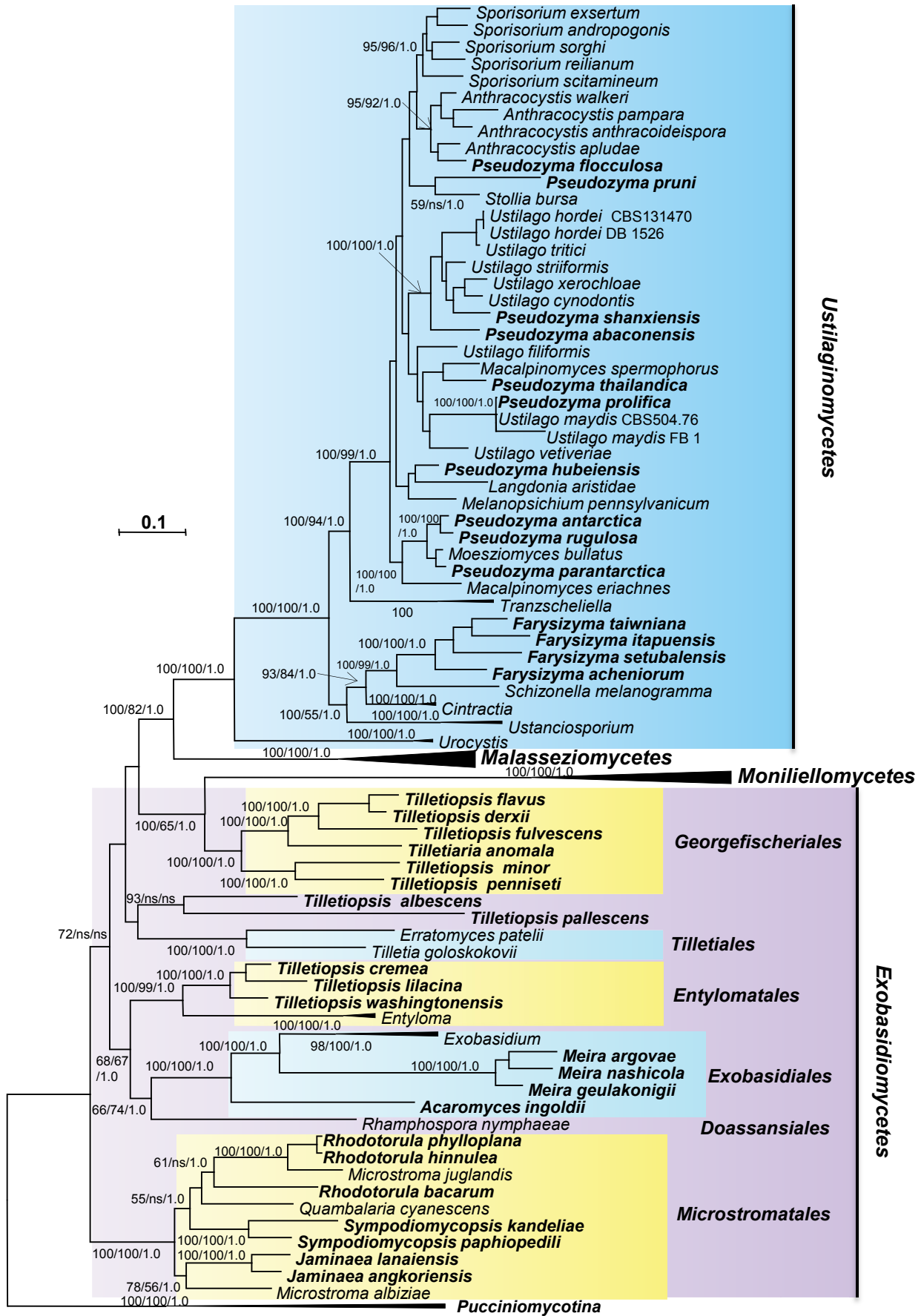


Fig. 1. Phylogenetic tree constructed using maximum likelihood analysis from combined sequences of the SSU rRNA gene, LSU rRNA D1/D2 domains, ITS1+2 regions (including 5.8S rRNA gene), *RPB1*, *RPB2*, *TEF1* and *CYTB* depicting the phylogenetic placements of yeast genera within *Ustilaginomycotina*. Branch lengths are scaled in terms of expected numbers of nucleotide substitutions per site. Bayesian posterior probabilities (PP) and bootstrap percentages (BP) from 1000 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 %).

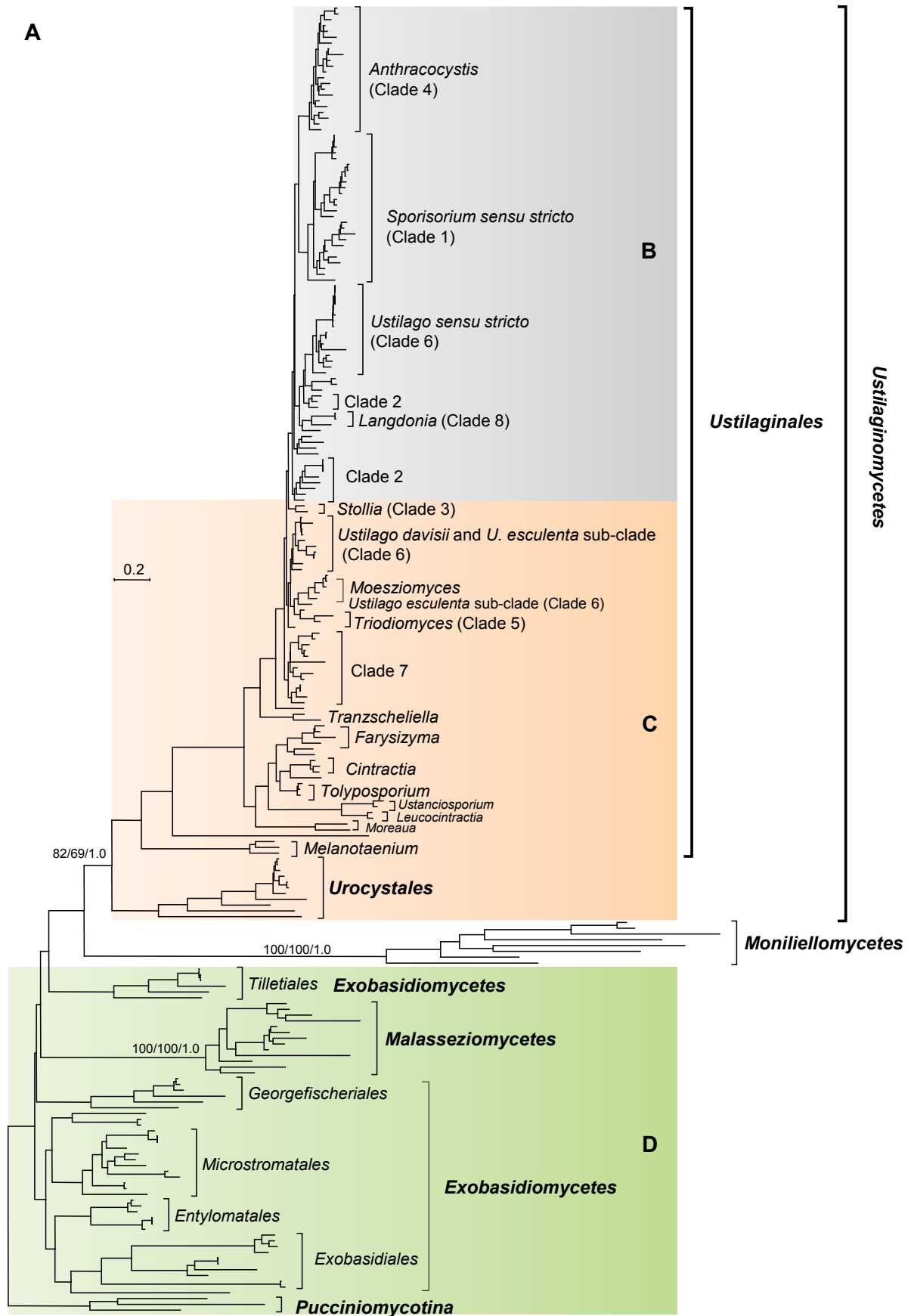


Fig. 2. Phylogenetic tree constructed using maximum likelihood analysis from the combined sequences of the LSU rRNA D1/D2 domains and ITS1+2 regions (including 5.8S rRNA gene) depicting the phylogenetic relationships of yeast taxa with teleomorphic taxa within *Ustilaginomycotina*. Branch lengths are 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 %).

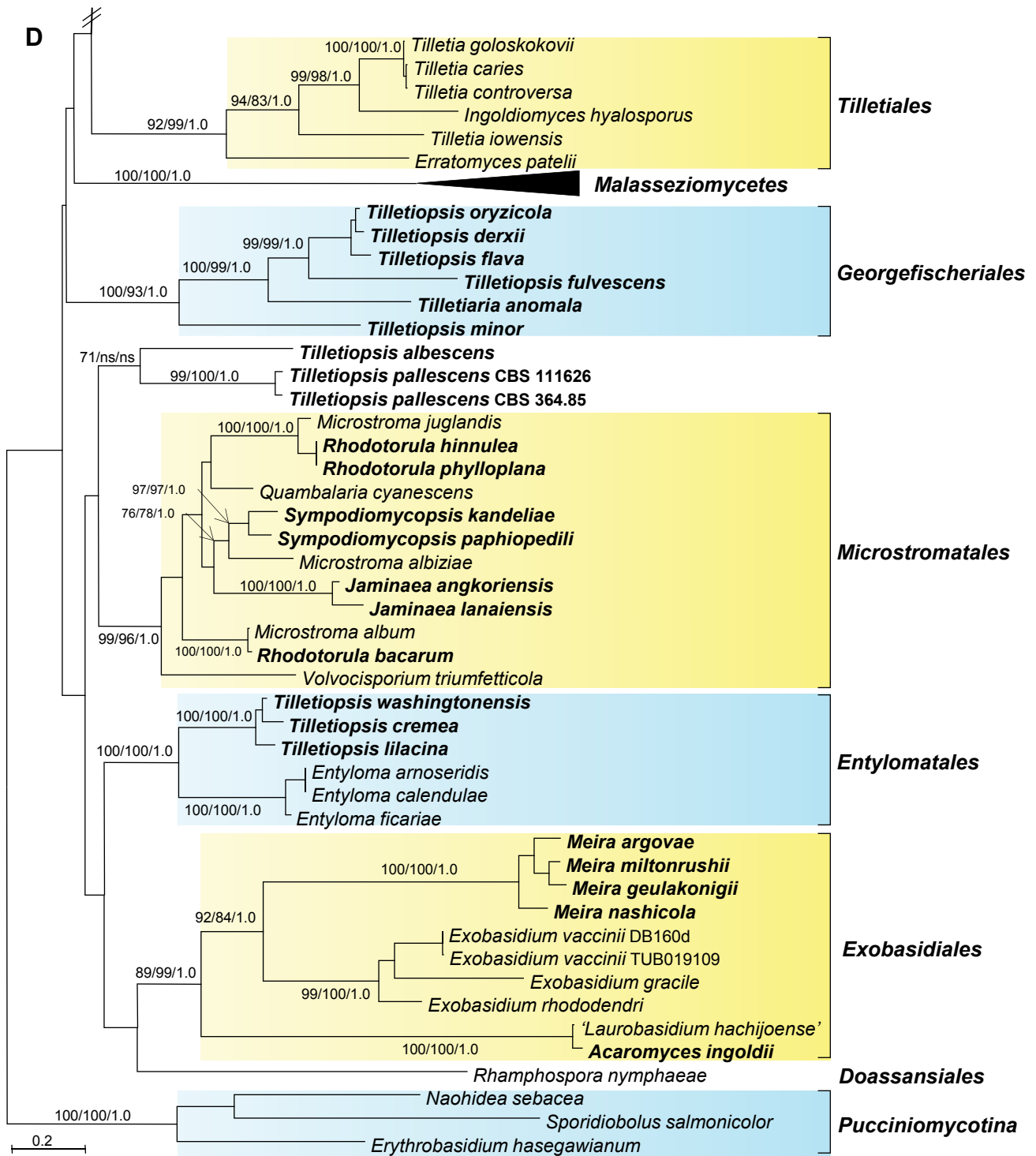


Fig. 2. (Continued).

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 *Anthracoystis apludae* was shown in the seven genes and the four protein genes based trees (Figs 1, 3). The affinity of *P. flocculosa* with *Anthracoystis* was confirmed by the phylogenetic analysis based on the ITS and LSU dataset (Fig. 2B). This species has been recently transferred into the genus *Anthracoystis* 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. altilis* with 3 and 92

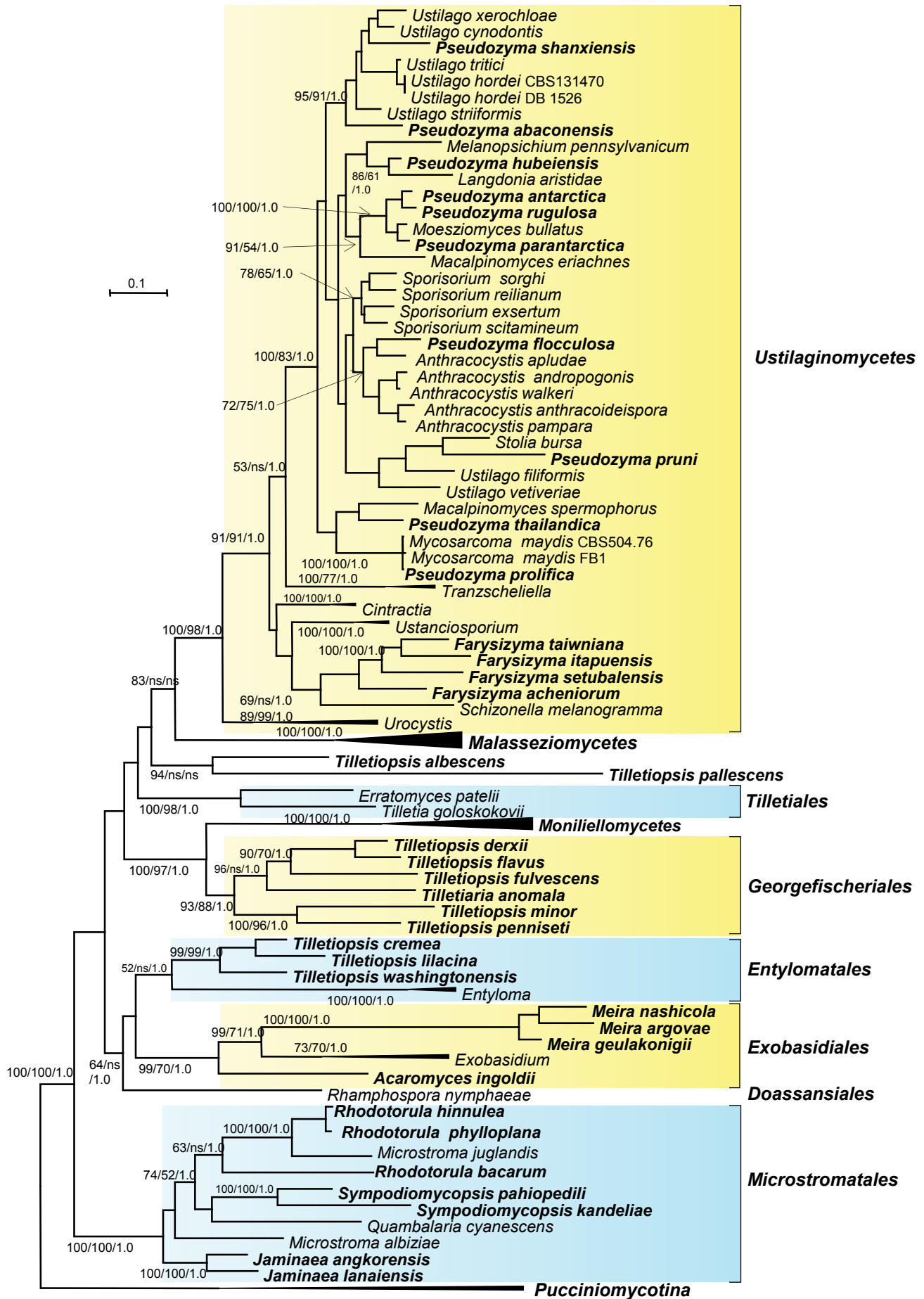


Fig. 3. Phylogenetic tree constructed from maximum likelihood analysis based on the combined sequences of protein-coding genes including *RPB1*, *RPB2*, *TEF1* and *CYT6*, showing the phylogenetic relationships of yeast genera within *Ustilaginomycotina*. Branch lengths are scaled in terms of expected numbers of nucleotide substitutions per site. Bayesian posterior probabilities (PP) and bootstrap percentages (BP) from 1000 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 %).

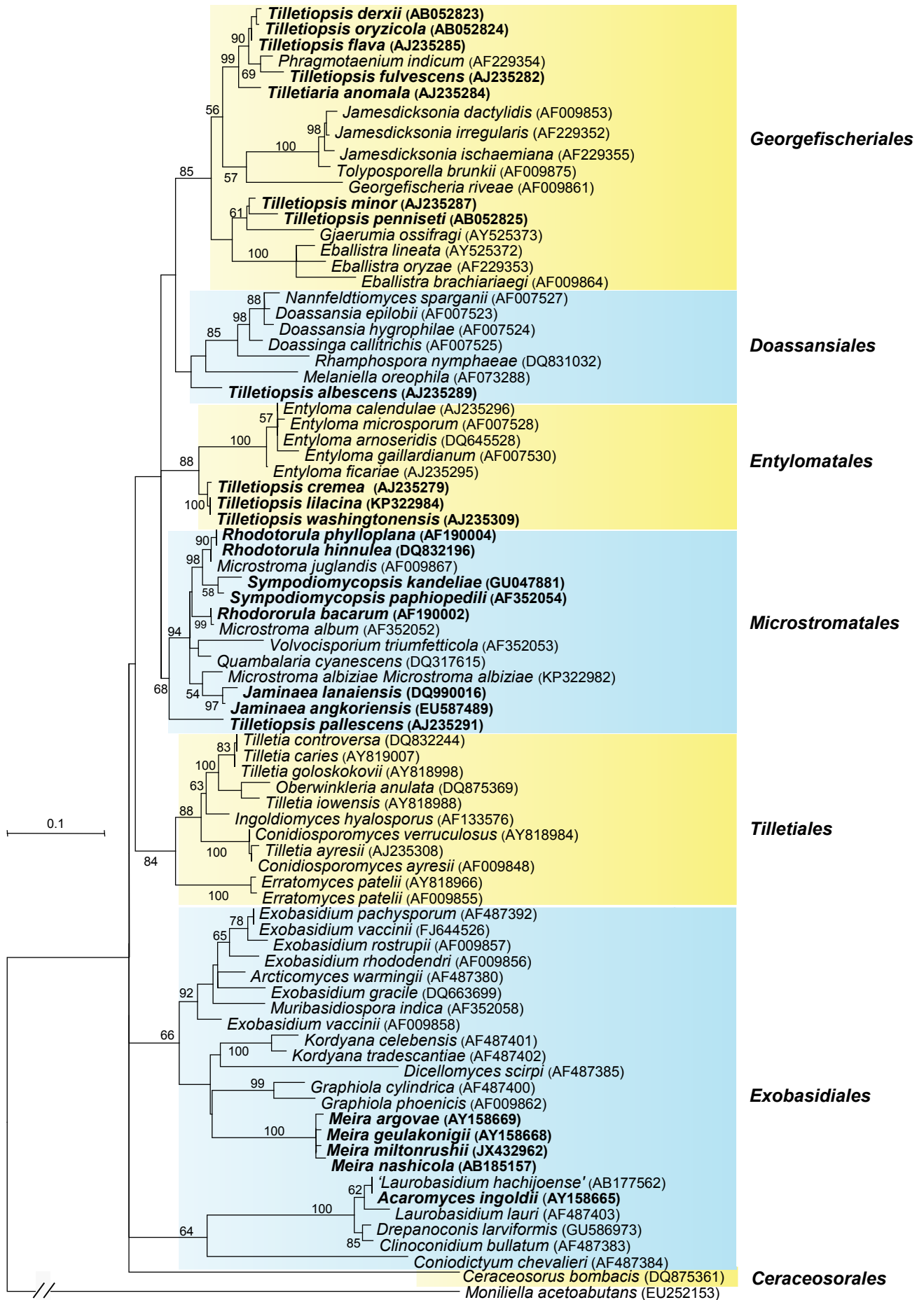


Fig. 4. Phylogenetic tree constructed from maximum likelihood analysis based on the D1/D2 domains of the LSU rRNA, showing the relationships of taxa within the Exobasidiomycetes. Bootstrap percentages over 50 % from 1000 replicates are shown. Taxa in bold are yeast and yeast-like fungi.

mismatches in the LSU rRNA gene and ITS region, respectively. The result suggests that *P. crassa* belongs to the genus *Triodiomyces*. *Pseudozyma jejuensis* 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. shanxiensis* 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. shanxiensis* 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. vetiver*, 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 phylogenetic analysis of the ITS and LSU datasets, being in agreement with Chamnanpa 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 *Ustilaginaceae* 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 *Anomalomyces yakirrae*, *Anomalomyces panici* and *Sporisorium trachypogonis-plumosi* without significant support (Fig. 2B). *P. pruni* was proposed as a close relative of *P. fusiformata* by Liou et al. (2009). The former exhibited a close affinity to *A. yakirrae* in previous studies based on sequence analysis of the ITS and LSU rRNA gene regions (Chamnanpa et al. 2013, Oliveira et al. 2014). *A. panici*, the type species of the genus *Anomalomyces*, was located in an isolated branch in the *Ustilaginales* in McTaggart et al. (2012a). *A. yakirrae* was proposed as the second member in *Anomalomyces* by Shivas et al. (2013) because it was located in the same clade with *A. panici* in the ITS and LSU rRNA gene based tree. *A. yakirrae* and *A. panici* also shared some morphological characters and occurred on closely related hosts. However, the close relationship between *A. yakirrae* and *A. panici* 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 bouriquetii*, *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 *Malasseziomycetes* to accommodate the *Malasseziales* (Wang et al. 2014), *Exobasidiomycetes* currently contains four orders, *Entylomatales*, *Exobasidiales*, *Georgefischeriales* 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 bombacis* which appeared to be closely related to a yeast-like species *Tilletiopsis albescens*. However, in the tree drawn from the LSU dataset in this study, *T. albescens* is not closely related to *C. bombacis* (Fig. 4). The phylogenetic position of *C. bombacis* and its relationship with *T. albescens* 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*, *Exobasidiales*, *Georgefischeriales* 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 *Georgefischeriales* occurred as a sister lineage to *Moniliellomycetes* with strong support (Figs 1 and 3). The orders *Entylomatales*, *Exobasidiales* 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 *Exobasidiomycetes* (Figs 1 and 3). The results confirmed that *Exobasidiomycetes* is not monophyletic, but might support the originally described superorder *Exobasidianaes* including the three orders *Entylomatales*, *Doassansiales* and *Exobasidiales* 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*, *Jaminaea*, *Meira*, *Rhodotorula* (*pro parte*), *Symptodiomyces*, *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 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, *Acaromyces ingoldii* and three *Meira* species were located together with three *Exobasidium* species in the *Exobasidiales* 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 genera *Clinoconidium*, *Coniodictyum*, *Drepanoconis* 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 '*Laurobasidium hachijoense*' (*Exobasidium hachijoense*). The name *Laurobasidium hachijoense* has not been validly published and *L. lauri* is presently the solely published species 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 teleomorphic species *Clinoconidium bullatum* and *Drepanoconis larviformis* presently classified into different genera. Therefore, the genus *Acaromyces* 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 *Exobasidiales*, 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 *Jaminaea* and *Sympodiomyopsis* species and three *Rhodotorula* species clustered in the *Microstromatales* together with teleomorphic species of *Microstroma*, *Quambalaria* and *Volvocisporium* (Figs 1, 2D and 4). The two *Jaminaea* 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 *Jaminaea* species with *Microstroma 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 *Microstroma* 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 *Jaminaea* should be remained. However, the affiliation to *Jaminea* or *Sympodiomyopsis* lacks fundamental support and further data are needed before a new combination can be proposed. Begerow *et al.* (2014) assigned *Jaminea* to the family *Quambalariaceae*, 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 *Jaminaea* as '*incertae sedis*' within *Microstromatales* as Sipiczki & Kajdacs (2009) suggested before.

The affiliation of *Sympodiomyopsis* 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 *Microstroma album*, the type species of the genus *Microstroma* (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. phylloplana*, exhibited a close relationship with *Microstroma juglandis* in all the trees constructed in this study (Figs 1, 2D, 3 and 4). *R. hinnulea* was considered a synonym of *R. phylloplana* 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. phylloplana* was located together with *M. juglandis* (Fig. 4). In the seven genes and the four protein genes based trees, the close affinity of *R. phylloplana* and *M. juglandis* with *R. bacarum* (the anamorph of *M. album*) was resolved (Figs 1 and 3). The result suggests that *R. phylloplana* represents an anamorphic species in the genus *Microstroma*.

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 *Georgiefischeriales* (Fig. 4). As shown in Boekhout *et al.* (2011), *T. dextrii*, *T. flava*, *T. fulvescens* and *T. oryzicola* formed a clade together with two teleomorphic species *Tilletiaria anomala* and *Phragmotonium 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 *Phragmotonium indicum* with 90 % ML BP support, suggesting that they belong to the genus *Phragmotonium*.

The other two *Tilletiopsis* species in the *Georgiefischeriales*, *T. minor* and *T. pennisetii*, 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. pennisetii*, and two undescribed *Tilletiopsis* species based on the Bayesian inference analysis of the LSU rRNA genes. The results support transferring *T. minor* and *T. pennisetii* 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. albescens* 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, that will offer a more robust phylogenetic analysis integrating the yeasts, are not available. It is, however, needed to make taxonomic revisions for yeast taxa at the genus level based on the phylogenetic data presented here. *Fereydounia*, *Jaminaea*, *Meira*, *Sympodiomyces* 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, *Acaromyces* will be remained at present before a taxonomic revision can be made that need to include more teleomorphic genera.

We propose to transfer the *Farysizyma* species to the genus *Farysia* and *Rhodotorula 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 *Triodiomyces*; 4) *P. graminicola* to *Sporisorium*; and 5) *P. jejuensis* to *Langdonia*. *P. brasiliensis*, *P. fusiformata*, and *P. vetiver* represent a new genus for which we propose *Kalmanozyma* 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. alboarmeniaca*, *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 *Entylomatales* by retaining the genus name for the monophyletic clade represented by the type species *T. washingtonensis*. For the taxonomic treatments of the remaining *Tilletiopsis* species, we propose to transfer *T. dextrii*, *T. flava*, *T. fulvescens* and *T. oryzicola* to the genus *Phragmotaeonium*; and *T. minor* and *T. penniseti* to *Gjaerumia*. Two new generic names, *Robbauera* gen. nov. and *Golubevia* gen. nov., are proposed for *T. albescens* 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 basidiomycetous 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: *Robbaueraceae* Boekhout, Begerow, Q.M. Wang & F.Y. Bai

Robbauera Boekhout, Begerow, Q.M. Wang & F.Y. Bai **fam. nov.** MycoBank MB812697.

Member of *Robbauerales* (*Exobasidiomycetes*). The diagnosis of the family *Robbaueraaceae* 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. Chlamydo-spores 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 *Ustilaginaceae* (*Ustilaginales*, *Ustilaginomycetes*). This genus is proposed to accommodate *Pseudozyma churashimaensis* which belongs to an isolated branch in the *Ustilaginaceae* 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 *Ustilaginaceae* (*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.

≡ *Pseudozyma fusiformata* (Buhagiar) Boekhout, J. Gen. Appl. Microbiol. 41: 363. 1995.

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. Riaño-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. Riaño-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. lilacina* 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. Chlamydo-spores 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.

Anthracocystis Bref., Unters. Gesamtgeb. Mykol. (Leipzig) 15: 53. 1912.

Type species: Anthracocystis destruens Bref.

New combination in *Anthracocystis*

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

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

= *Sphacelotheca pamparum* (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. Přírodov. Výzk. Čech. 15: 32. 1912.

= *Farysizyza* 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: Farysizyza 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: Farysizyza 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: Farysizyza 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.

= *Farysizyza 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 *Fagaceae* (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 & Rodr. Mir., Antonie van Leeuwenhoek 49: 153. 1983.

≡ *Rhodotorula phylloplana* (R.G. Shivas & Rodr. Mir.) Rodr. Mir. & Weijman, Antonie van Leeuwenhoek 54: 549. 1988.

≡ *Cryptococcus hinnuleus* R.G. Shivas & Rodr. Mir., Antonie van Leeuwenhoek 49: 155. 1983.

= *Rhodotorula hinnulea* (R.G. Shivas & Rodr. Mir.) Rodr. 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. Schröt.) 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 showed 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.

≡ *Vanrija antarctica* (Goto, Sugiyama & Iizuka) R.T. Moore, Bibl. Mycol. 108: 167. 1987.

= *Trichosporon oryzae* H. Ito, Iizuka & T. Sato, Agric. Biol. Chem. 38: 1599. 1974.

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

Basionym: *Sterigmatomyces aphidis* Henninger & Windisch, Arch. Mikrobiol. 105: 50. 1975.

≡ *Pseudozyma aphidis* (Henninger & 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.

≡ *Stephanoascus rugulosus* Traquair, L.A. Shaw & Jarvis, Can. J. Bot. 66: 929. 1988.

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

Basionym: *Pseudozyma parantarctica* Sugita, Takashima, Mekha & Poonwan, Microbiol. Immun. 47: 186. 2003.

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

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

This genus was originally proposed for a teleomorphic smut species 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 *Phragmotaeonium*

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

Basionym: *Tilletiopsis minor* Nyland var. *flava* Tubaki, Nagaoa 1: 28. 1952.

≡ *Tilletiopsis flava* (Tubaki) Boekhout, Stud. Mycol. 33: 151. 1991.

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

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

Phragmotaeonium 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.

Phragmotaeonium 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 altilis* (Syd.) McTaggart & R.G. Shivas

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. Immunol. 58: 9. 2014.

ACKNOWLEDGEMENTS

We thank Walter Gams for his nomenclatural advice. This study was supported by grants No. 31010103902, No. 30970013 and No. 31570016 from the National Natural Science Foundation of China (NSFC), grant No. 10CDP019 from the Royal Netherlands Academy of Arts and Sciences (KNAW) and No. 2012078 from the Youth Innovation Promotion Association of the Chinese Academy of Sciences. TB is supported by grant NPRP 5-298-3-086 from the Qatar National Research Fund, a member of Qatar Foundation. The authors are solely responsible for the content of this work.

REFERENCES

- Bandoni RJ, Johri BN (1972). *Tilletiaria*: a new genus in the *Ustilaginales*. *Canadian Journal of Botany* **50**: 39–43.
- Bauer R, Begerow D, Nagler A, *et al.* (2001b). The *Georgiefischeriales*: a phylogenetic hypothesis. *Mycological Research* **105**: 416–424.
- Bauer R, Lutz M, Oberwinkler F (2005). *Gjaerumia*, a new genus in the *Georgiefischeriales* (*Ustilaginomycetes*). *Mycological Research* **109**: 1250–1258.
- Bauer R, Oberwinkler F, Piepenbring M, *et al.* (2001a). *Ustilaginomycetes*. In: *The mycota, VII, Part B: systematics and evolution* (McLaughlin DJ, McLaughlin EG, Lemke PA, eds). Springer-Verlag, Berlin: 57–83.
- Bauer R, Oberwinkler F, Vánky K (1997). Ultrastructural markers and systematics in smut fungi and allied taxa. *Canadian Journal of Botany* **75**: 1273–1314.
- Begerow D, Bauer R, Boekhout T (2000). Phylogenetic placements of ustilaginomycetous anamorphs as deduced from nuclear LSU rDNA sequences. *Mycological Research* **104**: 53–60.
- Begerow D, Schäfer AM, Kellner R, *et al.* (2014). *Ustilaginomycotina*. In: *The mycota, Vol. VII, Part A: systematics and evolution* (McLaughlin DJ, Spatafora JW, eds), 2nd edn. Springer-Verlag, Berlin: 295–329.
- Begerow D, Stoll M, Bauer R (2006). A phylogenetic hypothesis of *Ustilaginomycotina* based on multiple gene analyses and morphological data. *Mycologia* **98**: 906–916.
- Boekhout T (1991). A revision of ballistoconidia-forming yeasts and fungi. *Studies in Mycology* **33**: 1–194.
- Boekhout T (1995). *Pseudozyma* Bandoni emend. Boekhout, a genus for yeast-like anamorphs of *Ustilaginales*. *The Journal of General and Applied Microbiology* **41**: 359–366.
- Boekhout T, Fell JW, O'Donnell K (1995). Molecular systematics of some yeast-like anamorphs belonging to the *Ustilaginales* and *Tilletiales*. *Studies in Mycology* **38**: 175–183.
- Boekhout T, Fonseca A, Sampaio JP, *et al.* (2011). Discussion of teleomorphic and anamorphic basidiomycetous yeasts. In: *The yeasts, a taxonomic study* (Kurtzman CP, Fell JW, Boekhout T, eds), 5th edn. Elsevier, Amsterdam: 1339–1372.
- Boekhout T, Gildemacher P, Theelen B, *et al.* (2006). Extensive colonization of apples by smut anamorphs causes a new postharvest disorder. *FEMS Yeast Research* **6**: 63–76.
- Boekhout T, Theelen B, Houbraken J, *et al.* (2003). Novel anamorphic mite-associated fungi belonging to the *Ustilaginomycetes*: *Meira geulakonigii* Gen. Nov., sp. nov., *Meira argovae* sp. nov. and *Acaromyces ingoldii* Gen. Nov., sp. nov. *International Journal of Systematic and Evolutionary Microbiology* **53**: 1655–1664.
- Boekhout T, van Gool J, van den Boogert H, *et al.* (1992). Karyotyping and G+C composition as taxonomic criteria applied to the systematics of *Tilletiopsis* and related taxa. *Mycological Research* **96**: 331–342.
- Bolano A, Stinchi S, Preziosi R, *et al.* (2001). Rapid methods to extract DNA and RNA from *Cryptococcus neoformans*. *FEMS Yeast Research* **1**: 221–224.
- Chamnanpa T, Limtong P, Srisuk N, *et al.* (2013). *Pseudozyma vetiver* sp. nov., a novel anamorphic ustilaginomycetous yeast species isolated from the phylloplane in Thailand. *Antonie van Leeuwenhoek* **104**: 637–644.
- Fell JW, Boekhout T, Fonseca A, *et al.* (2000). Biodiversity and systematics of basidiomycetous yeasts as determined by large-subunit rDNA D1/D2 domain sequence analysis. *International Journal of Systematic and Evolutionary Microbiology* **50**: 1351–1372.
- Gokhale AA (1972). Studies on the genus *Tilletiopsis*. *Nova Hedwigia* **23**: 795–809.
- Hawksworth DL (2011). A new dawn for the naming of fungi: impacts of decisions made in Melbourne in July 2011 on the future publication and regulation of fungal names. *MycKeys* **1**: 7–20.
- Hibbett DS, Binder M, Bischoff JF, *et al.* (2007). A higher-level phylogenetic classification of the fungi. *Mycology Research* **111**: 509–547.
- Inácio J, Landell MF, Valente P, *et al.* (2008). *Farysizyma* gen. nov., an anamorphic genus in the *Ustilaginales* to accommodate three novel epiphytic basidiomycetous yeast species from America, Europe and Asia. *FEMS Yeast Research* **8**: 499–508.
- Kurtzman CP, Fell JW, Boekhout T (2011). *The yeasts, a taxonomic study*, 5th edn. Elsevier, Amsterdam.
- Liou GY, Wei YH, Lin SJ, *et al.* (2009). *Pseudozyma pruni* sp. nov., a novel ustilaginomycetous anamorphic fungus from flowers in Taiwan. *International Journal of Systematic and Evolutionary Microbiology* **59**: 1813–1817.
- Matheny PB, Gossman JA, Zalar P, *et al.* (2006). Resolving the phylogenetic position of the *Wallemiomycetes*: an enigmatic major lineage of *Basidiomycota*. *Canadian Journal Botany* **84**: 1794–1805.
- McNeill J, Barrie FR, Buck WR, *et al.* (2012). *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code)*. *Regnum Vegetabile* **154**. A.R.G. Gantner Verlag KG, Ruggell, Liechtenstein, ISBN 978-3-87429-425-6. Available at: <http://www.iapt-taxon.org/nomen/main.php>.

- McTaggart AR, Shivas RG, Geering AD, *et al.* (2012a). Soral synapomorphies are significant for the systematics of the *Ustilago-Sporisorium-Macalpinomyces* complex (Ustilaginaceae). *Persoonia* **29**: 63–77.
- McTaggart AR, Shivas RG, Geering AD, *et al.* (2012b). Taxonomic revision of *Ustilago*, *Sporisorium* and *Macalpinomyces*. *Persoonia* **29**: 116–132.
- Nasr S, Soudi MR, Fazeli SAS, *et al.* (2014). Expanding evolutionary diversity in the Ustilaginomycotina: *Fereydouniaceae* fam. nov. and *Fereydounia* gen. nov., the first urocystidalean yeast lineage. *Mycological Progress* **13**: 1217–1226.
- Oliveira JV, Borges TA, Corrêa dos Santos RA, *et al.* (2014). *Pseudozyma brasiliensis* sp. nov., a xylanolytic, ustilaginomycetous yeast species isolated from an insect pest of sugarcane roots. *International Journal of Systematic and Evolutionary Microbiology* **64**: 2159–2168.
- Piątek M, Matthias Lutz M, Yorou NS (2015). A molecular phylogenetic framework for *Anthracoystis* (Ustilaginales), including five new combinations (inter alia for the asexual *Pseudozyma flocculosa*), and description of *Anthracoystis grodzinskae* sp. nov. *Mycological Progress* **14**: 88.
- Pires VM (1928). Concerning the morphology of *Microstroma* and the taxonomic position of the genus. *American Journal of Botany* **15**: 132–140.
- Posada D, Crandall KA (1998). Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**: 817–818.
- Raciborski M (1909). Parasitische und epiphytische Pilze Javas. *Bulletin International de l'Académie des Sciences de Cracovie Classe des Sciences Mathématiques et Naturelles* **3**: 346–394.
- Ronquist F, Teslenko M, van der Mark P, *et al.* (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542.
- Rush TA, Aime MC (2013). The genus *Meira*: phylogenetic placement and description of a new species. *Antonie van Leeuwenhoek* **103**: 1097–1106.
- Sampaio JP (2004). Diversity, phylogeny and classification of basidiomycetous yeasts. In: *Frontiers in basidiomycote mycology* (Agerer R, Piepenbring M, Blanz P, eds). IHW Verlag, Eching: 49–80.
- Sampaio JP (2011). *Rhodotorula* Harrison (1928). In: *The yeasts, a taxonomic study* (Kurtzman CP, Fell JW, Boekhout T, eds), 5th edn. Elsevier, Amsterdam: 1873–1927.
- Shivas RG, Lutz M, McTaggart AR, *et al.* (2013). Emended description of *Anomalomyces* (Ustilaginales), including *Anomalomyces yakirrae* sp. nov. on *Yakirra pauciflora* (Poaceae) from Australia. *Mycobiota* **1**: 17–24.
- Sipiczki M, Kajdacs E (2009). *Jaminaea angkorensis* gen. nov., sp. nov., a novel anamorphic fungus containing an S943 nuclear small-subunit rRNA group IB intron represents a basal branch of Microstromatales. *International Journal of Systematic and Evolutionary Microbiology* **59**: 914–920.
- Stamatakis A (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.
- Standley K (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.
- Stolk AC, Dakin JC (1966). *Moniliella*, a new genus of *Moniliales*. *Antonie van Leeuwenhoek* **32**: 399–409.
- Stoll M, Begerow D, Oberwinkler F (2005). Molecular phylogeny of *Ustilago*, *Sporisorium*, and related taxa based on combined analyses of rDNA sequences. *Mycological Research* **109**: 342–356.
- Stoll M, Piepenbring M, Begerow D, *et al.* (2003). Molecular phylogeny of *Ustilago* and *Sporisorium* species (Basidiomycota, Ustilaginales) based on internal transcribed spacer (ITS) sequences. *Canadian Journal of Botany* **81**: 976–984.
- Sugiyama J, Tokuoka K, Suh SO, *et al.* (1991). *Sympodiomyopsis*: a new yeast-like anamorph genus with basidiomycetous nature from orchid nectar. *Antonie van Leeuwenhoek* **59**: 95–108.
- Suh SO, Sugiyama J (1994). Phylogenetic placement of the basidiomycetous yeasts *Kondoa malvinella* and *Rhodospordium dacryoidum*, and the anamorphic yeast *Sympodiomyopsis paphiopedili* by means of 18S gene sequence analysis. *Mycoscience* **35**: 367–375.
- Swofford DL (2002). PAUP*. phylogenetic analysis using parsimony (*and other methods). Sinauer Associates, Sunderland MA. Vánky K, Lutz M, Shivas RG (2006) *Anomalomyces panici*, new genus and species of *Ustilaginomyces* from Australia. *Mycologia Balcanica* **3**: 119–126.
- Taylor JW (2011). One Fungus = One Name: DNA and fungal nomenclature twenty years after PCR. *IMA Fungus* **2**: 113–120.
- Vánky K (2002). *Illustrated genera of smut fungi*, 2nd edn. APS Press, St Paul.
- Vánky K (2012). *Smut fungi of the world*. APS Press, St. Paul.
- Wang QM, Bai FY (2008). Molecular phylogeny of basidiomycetous yeasts in the *Cryptococcus luteolus* lineage (*Tremellales*) based on nuclear rDNA and mitochondrial cytochrome *b* gene sequence analyses: proposal of *Dexomyces* gen. nov. and *Hannaella* gen. nov., and description of eight novel *Dexomyces* species. *FEMS Yeast Research* **8**: 799–814.
- Wang QM, Theelen B, Groenewald M, *et al.* (2014). *Moniliellomyces* and *Malasseziomyces*, two new classes in *Ustilaginomycotina*. *Persoonia* **33**: 41–47.
- Weiß M, Bauer R, Begerow D (2004). Spotlights on heterobasidiomycetes. In: *Frontiers in basidiomycote mycology* (Agerer R, Piepenbring M, Blanz P, eds). IHW Verlag, Eching: 7–48.