

Towards an integrated phylogenetic classification of the *Tremellomycetes*

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Abstract: Families and genera assigned to *Tremellomycetes* have been mainly circumscribed by morphology and for the yeasts also by biochemical and physiological characteristics. This phenotype-based classification is largely in conflict with molecular phylogenetic analyses. Here a phylogenetic classification framework for the *Tremellomycetes* is proposed based on the results of phylogenetic analyses from a seven-genes dataset covering the majority of tremellomycetous yeasts and closely related filamentous taxa. Circumscriptions of the taxonomic units at the order, family and genus levels recognised were quantitatively assessed using the phylogenetic rank boundary optimisation (PRBO) and modified general mixed Yule coalescent (GMYC) tests. In addition, a comprehensive phylogenetic analysis on an expanded LSU rRNA (D1/D2 domains) gene sequence dataset covering as many as available teleomorphic and filamentous taxa within *Tremellomycetes* was performed to investigate the relationships between yeasts and filamentous taxa and to examine the stability of undersampled clades. Based on the results inferred from molecular data and morphological and physiochemical features, we propose an updated classification for the *Tremellomycetes*. We accept five orders, 17 families and 54 genera, including seven new families and 18 new genera. In addition, seven families and 17 genera are emended and one new species name and 185 new combinations are proposed. We propose to use the term *pro tempore* or *pro tem.* in abbreviation to indicate the species names that are temporarily maintained.

Key words: Jelly fungi, Morphology, Multigene phylogeny, Ranks, Taxonomy, *Tremellomycetes*, Yeasts.

Taxonomic novelties: **New families:** *Bulleraceae* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Bulleribasidiaceae* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Mrakiacae* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Naemateliaceae* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Phaeotremellaceae* A.M. Yurkov & Boekhout, *Piskurozymaceae* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Trimorphomycetaceae* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout; **New genera:** *Bandonia* A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Carlosrosaea* A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cutaneotrichosporon* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Dimennazyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Effuseotrichosporon* A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Fonsecazyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Gelidatrema* A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Genolevuria* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Goffeazyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Haglerozyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Krasilnikovozyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nielozyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Piskurozyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pseudotremella* X.Z. Liu, F.Y. Bai, A.M. Yurkov, M. Groenew. & Boekhout, *Saitozyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Sugitazyma* A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Solicoccozyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Vishniacozyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout; **New species:** *Kockovaella prillingeri* (Prillinger, G. Kraep. & Lopandic) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout; **New combinations:** *Apiotrichum brassicae* (Nakase) A.M. Yurkov & Boekhout, *A. cacaoliposimilis* (J.L. Zhou, S.O. Suh & Gujjari) Kachalkin, A.M. Yurkov & Boekhout, *A. dehoogii* (Middelhoven, Scorzetti & Fell) A.M. Yurkov & Boekhout, *A. domesticum* (Sugita, A. Nishikawa & Shinoda) A.M. Yurkov & Boekhout, *A. dulcicum* (Boekhout) A.M. Yurkov & Boekhout, *A. gamsii* (Middelhoven, Scorzetti, Sigler & Fell) A.M. Yurkov & Boekhout, *A. gracile* (Weigmann & A. Wolff) A.M. Yurkov & Boekhout, *A. laibachii* (Windisch) A.M. Yurkov & Boekhout, *A. lignicola* (Diddens) A.M. Yurkov & Boekhout, *A. loubieri* (Morenz) A.M. Yurkov & Boekhout, *A. montevidense* (L.A. Queiroz) A.M. Yurkov & Boekhout, *A. mycotoxinivorans* (O. Molnár, Schatzm. & Prillinger) A.M. Yurkov & Boekhout, *A. scarabaeorum* (Middelhoven, Scorzetti & Fell) A.M. Yurkov & Boekhout, *A. siamense* (Nakase, Jindam., Sugita & H. Kawas.) Kachalkin, A.M. Yurkov & Boekhout, *A. sporotrichoides* (van Oorschot) A.M. Yurkov & Boekhout, *A. vadense* (Middelhoven, Scorzetti & Fell) A.M. Yurkov & Boekhout, *A. veenhuisii* (Middelhoven, Scorzetti & Fell) A.M. Yurkov & Boekhout, *A. wieringae* (Middelhoven) A.M. Yurkov & Boekhout, *A. xylopinii* (S.O. Suh, Lee, Gujjari & Zhou) Kachalkin, A.M. Yurkov & Boekhout, *Bandonia marina* (van Uden & Zobel) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Bulleribasidium begoniae* (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Bu. foliicola* (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Bu. hainanense* (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Bu. panici* (Fungsin, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Bu. pseudovariabile* (F.Y. Bai, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Bu. sanyaense* (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Bu. setariae* (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Bu. siamense* (Fungsin, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Bu. variabile* (Nakase & M. Suzuki) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Bu. wuzhishanense* (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Carcinomyces arundinariae* (Fungsin, M. Takash. & Nakase) A.M. Yurkov, *Carc. polyporina* (D.A. Reid) A.M. Yurkov, *Carlosrosaea vrieseae* (Landell, Brandão, Safar, Gomes, Félix, Santos, Pagani, Ramos, Broetto, Mott, Valente & Rosa) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cryptococcus depauperatus* (Petch) Boekhout, Liu, Bai & M. Groenew., *Cr. luteus* (Roberts) Boekhout, Liu, Bai & M. Groenew., *Cutaneotrichosporon arboriformis* (Sugita, M. Takash., Sano, Nishim., Kinebuchi, S. Yamag. & Osanai) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. curvatus* (Diddens & Lodder) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. cutaneum* (de Beurmann, Gougerot & Vaucher) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. cyanovorans* (Motaung, Albertyn, J.L.F. Kock et Pohl) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. daszewskae* (Takash., Sugita, Shinoda & Nakase) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. debeurmannianum* (Sugita, Takash., Nakase & Shinoda) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. dermatis* (Sugita, Takash., Nakase, Ichikawa, Ikeda & Shinoda) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. guehoae* (Middelhoven, Scorzettii & Fell) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. haglerorum* (Middelhoven, Á. Fonseca, S.C. Carreiro, Pagnocca & O.C. Bueno) X.Z. Liu, F.Y. Bai, M. Groenew. &

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Boekhout, *Cu. jirovecii* (Frágner) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. moniliiforme* (Weigmann & A. Wolff) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. mucoides* (E. Guého & M.T. Smith) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. oleaginosus* (J.J. Zhou, S.O. Suh & Gujari) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. smithiae* (Middelhoven, Scorzetti, Sugita & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Cu. terricola* (Sugita, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Dimennazyma cistialbidi*** (Á. Fonseca, J. Inácio & Spenc.-Mart.) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Effuseotrichosporon vanderwaltii*** (Motaung, Albertyn, Kock, C.F. Lee, S.O. Suh, M. Blackwell & C.H. Pohl) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Filobasidium chernovii*** (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Fil. magnum* (Lodder & Kreger-van Rij) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Fil. oerense* (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Fil. stepposum* (Golubev & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Fil. wieringae* (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Fonsecazyma betulae*** (K. Sylvester, Q.M. Wang, C. T. Hittinger) A.M. Yurkov, A.V. Kachalkin & Boekhout, *Fon. mujuensis* (K.S. Shin & Y.H. Park) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Fon. tronadorensis* (V. De Garcia, Zalar, Brizzio, Gunde-Cim. & van Brook) A.M. Yurkov, ***Gelidatrema spencermartinsiae*** (Garcia, Brizzio, Boekhout, Theelen, Libkind & van Broock) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Genolevuria amylolytica*** (Á. Fonseca, J. Inácio & Spenc.-Mart.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Gen. armeniaca* (Á. Fonseca & J. Inácio) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Gen. bromelium* (Landell & P. Valente) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Gen. tibetensis* (F.Y. Bai & Q.M. Wang) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Goffeuzyma aciditolerans*** (Gadanhó & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Gof. agrionensis* (Russo, Libkind, Samp. & van Broock) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Gof. gastrica* (Reiersöl & di Menna) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Gof. gilvescens* (Chernov & Babeva) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Gof. iberica* (Gadanhó & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Gof. metallitolerans* (Gadanhó & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Haglerozyma chiarellii*** (Pagnocca, Legaspe, Rodrigues & Ruivo) A. M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Heterocephalacria arrabidensis*** (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Het. bachmannii* (Diederich & M.S. Christ.) Millanes & Wedin, *Het. physciacearum* (Diederich) Millanes & Wedin, ***Itersonilia pannonica*** (Niwata, Takash., Tornai-Lehoczki, T. Deák & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Kockovaella chinensis*** (Prillinger, G. Kraep. & Lopandic) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Ko. distylii* (Hamam., Kuroy. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Ko. fuzhouensis* (J.Z. Yue) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Ko. lichenicola* (Prillinger, G. Kraep. & Lopandic) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Ko. mexicana* (Lopandic, O. Molnár & Prillinger) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Ko. ogasawarensis* (Hamam., Kuroy. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Ko. sichuanensis* (Prillinger, G. Kraep. & Lopandic) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Krasilnikovozyma huempii*** (C. Ramírez & A. E. González) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Kr. tahquamenonensis* (Wang, Hulfachor, Sylvester and Hittinger) A.M. Yurkov, ***Kwoniella bestiolae*** (Thanh, Hai & Lachance) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Kw. dejecticola* (Thanh, Hai & Lachance) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Kw. dendrophila* (Van der Walt & D.B. Scott) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Kw. pini* (Golubev & Pfeiffer) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Kw. shivajii* (S.R. Ravella, S.A. James, C.J. Bond, I.N. Roberts, K. Cross, Retter & P.J. Hobbs) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Mrakia aquatica*** (E.B.G. Jones & Slooff) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *M. cryoconitii* (Margesin & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *M. niccombsii* (Thomas-Hall) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Naematelia aurantialba*** (Bandoni & M. Zang) Millanes & Wedin, *Naem. microspora* (Lloyd) Millanes & Wedin, ***Naganishia adeliensis*** (Scorzetti, I. Petrescu, Yarrow & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nag. albida* (Saito) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nag. albidosimilis* (Vishniac & Kurtzman) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nag. antarctica* (Vishniac & Kurtzman) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nag. bhutanensis* (Goto & Sugiy.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nag. cerealis* (Passoth, A.-C. Andersson, Olstorpe, Theelen, Boekhout & Schnürer) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nag. diffluens* (Zach) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nag. friedmannii* (Vishniac) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nag. liquefaciens* (Saito & M. Ota) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nag. onofrii* (Turchetti, Selbmann & Zucconi) A.M. Yurkov, *Nag. randhawae* (Z.U. Khan, S.O. Suh, Ahmad, F. Hagen, Fell, Kowshik, Chandy & Boekhout) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nag. uzbekistanensis* (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Nag. vaughanmartiniae* (Turchetti, Blanchette & Arenz) A.M. Yurkov, *Nag. vishniacii* (Vishniac & Hempfling) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Nielozyma formosana*** (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Niel. melastomae* (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Papiliotrema anemochoreius*** (C.H. Pohl, Kock, P.W.J. van Wyk & Albertyn) F.Y. Bai, M. Groenew. & Boekhout, *Pap. aspenensis* (K. Ferreira-Paim, T.B. Ferreira, L. Andrade-Silva, D.J. Mora, D.J. Springer, J. Heitman, F.M. Fonseca, D. Matos, M.S.C. Melhem & M.L. Silva-Vergara) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. aurea* (Saito) M. Takash., Sugita, Shinoda & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. baii* (A.M. Yurkov, M.A. Guerreiro & Á. Fonseca) A.M. Yurkov, *Pap. flavescens* (Saito) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. fonsecae* (V. de Garcia, Zalar, Braizzio, Gunde-Cim. & van Brollck) A.M. Yurkov, *Pap. frias* (V. de Garcia, Zalar, Braizzio, Gunde-Cim. & van Brollck) A.M. Yurkov, *Pap. fuscus* (J.P. Samp., J. Inácio, Fonseca & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. hoabinhensis* (D.T. Luong, M. Takash., Ty. Dung & Nakase) A.M. Yurkov, *Pap. japonica* (J.P. Samp., Fonseca & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. laurentii* (Kuff.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. mangalensis* (Fell, Statzell & Scorzett) A.M. Yurkov, *Pap. nemorosus* (Golubev, Gadanhó, J.P. Samp. & N.W. Golubev) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. perniciosus* (Golubev, Gadanhó, J.P. Samp. & N.W. Golubev) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. pseudoalba* (Nakase & M. Suzuki) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. rajasthanensis* (Saluja & G.S. Prasad) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. ruineniae* (A.M. Yurkov, M.A. Guerreiro & Á. Fonseca) A.M. Yurkov, *Pap. taeanensis* (K.S. Shin & Y.H. Park) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. terrestris* (Crestani, Landell, Faganello, Vainstein, Vishniac & P. Valente) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pap. wisconsinensis* (Crestani, Landell, Faganello, Vainstein, Vishniac & P. Valente) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Phaeotremella fagi*** (Middelhoven & Scorzetti) A.M. Yurkov & Boekhout, *Ph. mycetophiloides* (Kobayaci) Millanes & Wedin, *P. mycophaga* (G.W. Martin) Millanes & Wedin, *Ph. neofoliacea* (Chee J. Chen) Millanes & Wedin, *Ph. simplex* (H.S. Jacks. & G.W. Martin) Millanes & Wedin, *Ph. skinneri* (Phaff & Carmo Souza) A.M. Yurkov & Boekhout, ***Pseudotremella allantoinivorans*** (Middelhoven) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Ps. lacticolor* (Satoh & Makimura) A.M. Yurkov, *Ps. moriformis* (Berk.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Ps. nivalis* (Chee J. Chen) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Piskurozyma capsuligena*** (Fell, Statzell, I.L. Hunter & Phaff) A.M. Yurkov, *Pis. cylindrica* (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pis. fildesensis* (T. Zhang & L.-Y. Yu) A.M. Yurkov, *Pis. filicatus* (Golubev & J.P. Samp.) Kachalkin, *Pis. silvicola* (Golubev & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Pis. sorana* (Hauerslev) A.M. Yurkov, *Pis. taiwanensis* (Nakase, Tsuzuki & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Rhynchogastrema aquatica*** (Brandao, Valente, Pimenta & Rosa) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, *R. complexa* (Landell, Pagnocca, Sette, Passarini, Garcia, Ribeiro, Lee, Brandao, Rosa & Valente) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, *R. fermentans* (Lee) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, *R. glucofermentans* (S.O. Suh & Blackwell) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, *R. nanyangensis* (F.L. Hui & Q.H. Niu) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, *R. noutii* (Boekhout, Fell, Scorzett & Theelen) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, *R. tunnelae* (Boekhout, Fell, Scorzetti & Theelen) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, *R. visegradensis* (Peter & Dlačhy) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, ***Saitozyma flava*** (Saito) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Sait. ninhbinhensis* (Luong, Takash., Dung & Nakase) A.M. Yurkov, *Sait. paraflava* (Golubev & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Sait. podzolica* (Babeva & Reshetova) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Solicoccozyma aerea*** (Saito) A.M. Yurkov, *Sol. fuscescens* (Golubev) A.M. Yurkov, *Sol. keelungensis* (C.F. Chang & S.M. Liu) A.M. Yurkov, *Sol. phenolicus* (Á. Fonseca, Scorzetti & Fell) A.M. Yurkov, *Sol. terreus* (Di Menna) A.M. Yurkov, *Sol. terricola* (T.A. Pedersen) A.M. Yurkov, ***Sugitazyma miyagiana*** (Nakase, Itoh, Takem. & Bandoni) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Tausonia pullulans*** (Lindner) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, ***Tremella yokohamensis*** (Alshahni, Satoh & Makimura) A.M. Yurkov, ***Trimorphomyces sakaeraticus*** (Fungsin, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, ***Vanrija fragicola*** (M. Takash., Sugita, Shinoda & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Van. meifongana* (C.F. Lee) Kachalkin, A.M. Yurkov & Boekhout, *Van. nantouana* (C.F. Lee) Kachalkin, A.M. Yurkov & Boekhout, *Van. thermophila* (Vogelmann, Chaves & Hertel) Kachalkin, A.M. Yurkov & Boekhout, ***Vishniacozyma carnescens*** (Verona & Luchetti) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Vis. dimennae* (Fell & Phaff) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Vis. foliicola* (Q.M. Wang & F.Y. Bai) A.M. Yurkov, *Vis. globispora* (B.N. Johri & Bandoni) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Vis. heimaeyensis* (Vishniac) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Vis. nebularis*

(Vishniac) A.M. Yurkov, *Vis. peneaus* (Phaff, Mrak & O.B. Williams) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Vis. psychrotolerans* (V. de García, Zalar, Brizzio, Gunde-Cim. & van Broock) A.M. Yurkov, *Vis. taibaiensis* (Q.M. Wang & F.Y. Bai) A.M. Yurkov, *Vis. tephrensensis* (Vishniac) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Vis. victoriae* (M.J. Montes, Belloch, Galiana, M.D. García, C. Andrés, S. Ferrer, Torr.-Rodr. & J. Guinea) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

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INTRODUCTION

Tremellomyces is a class of *Agaricomycotina* (Hibbett *et al.* 2007, Boekhout *et al.* 2011a) and encompasses yeasts, dimorphic taxa and species that form hyphae and/or complex fruiting bodies. Five orders, namely *Cystofilobasidiales*, *Filobasidiales*, *Holtermanniales*, *Tremellales* and *Trichosporonales*, are currently recognised in *Tremellomyces* based on phenotypic and phylogenetic properties (Fell *et al.* 2000, Scorzetti *et al.* 2002, Boekhout *et al.* 2011a, Wuczkowski *et al.* 2011, Weiss *et al.* 2014, Liu *et al.* 2015). However, the separation of *Trichosporonales* from *Tremellales* remains a matter of debate (Hibbett *et al.* 2007, Millanes *et al.* 2011).

Basidiomycetous yeasts, like ascomycetous yeasts, were conventionally classified based on morphological features, including sexual and asexual reproductive structures and morphology; chemotaxonomic criteria, including cell-wall composition data and ubiquinone types; and physiological properties characterised by standardised tests on the assimilation and fermentation of carbon and nitrogen compounds, production of starch-like compounds, and other growth tests (Lodder & Kreger-van Rij 1952, Van der Walt 1970, Van der Walt & Yarrow 1984, Boekhout *et al.* 1993, 2011a, Kurtzman *et al.* 2011b, Prillinger *et al.* 1993, McLaughlin *et al.* 1995, Sampaio & Fonseca 1995, Nguyen *et al.* 1998, Yarrow 1998, Takashima *et al.* 2000, Bauer *et al.* 2006, Celio *et al.* 2006). Basidiocarp-forming *Tremellomyces* were mainly classified using morphological features, such as form and consistency of the fruiting bodies, and details of hyphae, basidia, basidiospores etc. The classification based on these phenotypical features, however, was in many cases not consistent with the results obtained from molecular phylogenetic analyses. This non-concordance is one of the most prominent problems in the classification of this group of fungi, as illustrated by the polyphyletic nature of many currently recognised genera. *Bullera* and *Cryptococcus* are just two examples of genera that are highly polyphyletic with species belonging to more than one order of *Tremellomyces* (Boekhout *et al.* 2011b, Fonseca *et al.* 2011). Further discovery of new species belonging to these genera not only worsened the problem of systematics of *Tremellomyces*, but also impeded the communication of researchers from different fields. For instance, a large number of environmental sequences have been obtained by microbial ecologists and were identified to species belonging to these polyphyletic genera. The NCBI GenBank database (<http://www.ncbi.nlm.nih.gov/>) is the most widely used tool to identify these molecular reads, but the taxon names presented in the results from GenBank searches are often confusing because they refer to such non-monophyletic groups or genera.

Molecular phylogenetic analyses of multiple genes have become an effective approach to reconstruct fungal phylogenies. As the result of the Assembling the Fungal Tree of Life (AFTOL) project, James *et al.* (2006) used a six-gene dataset to resolve a kingdom-wide fungal phylogeny and Hibbett *et al.* (2007) proposed a comprehensive phylogenetic re-classification of the

fungi down to the ordinal level. Yeast species formed only a small part of the nearly 200 fungal species involved in the AFTOL project. The majority of teleomorphic ascomycetous yeast taxa have independently been reclassified based on results obtained from multigene phylogenetic studies (Kurtzman 2003, Kurtzman & Robnett, 2003, 2007, Kurtzman *et al.* 2007, 2008), but most basidiomycetous yeast taxa remain to be studied. In the fifth edition of 'The Yeasts, a Taxonomic Study' (Kurtzman *et al.* 2011a) many of the basidiomycetous yeast genera included are still highly polyphyletic.

The recent changes in the dual nomenclature for pleomorphic fungi prompted us to modify the classification of *Tremellomyces* to fulfil the "One Fungus = One Name" principle (McNeill *et al.* 2012). As is the case in other groups of fungi, many species of this class have separate teleomorphic and anamorphic names. A further change in the new nomenclature is that electronic publication of new taxa and their names is permitted from 1 January 2012 in the absence of a printed hard copy (Knapp *et al.* 2011). So far, approximately 190 new fungal species have been e-published in Index Fungorum since then (<http://www.indexfungorum.org/>). The e-publication rule will accelerate the description of new fungal species, and this further urges us to revise the taxonomy of the *Tremellomyces* in order to provide a stable taxonomic framework that reflects our knowledge of the phylogenetic diversity and relationships of these fungi.

Several studies across the eukaryotic tree of life have shown that there is poor equivalence of taxonomic ranks across the groups studied (Johns & Avise 1998, Avise & Johns 1999, Castresana 2001, Lumbsch 2002, Avise & Liu 2011, Talavera *et al.* 2013). Clades of the same rank often show high variance with regard to genetic distances and temporal aspects. Despite the arbitrary nature of taxonomic ranks above the species level, they have importance in an evolutionary framework for cataloguing and communicating about biological diversity and, hence, taxonomic decisions should be made on a consistent basis (Holt & Jonsson 2014). Different methods have been suggested to level off ranks within taxonomic groups, including a temporal approach (Hennig 1966, Farris 1976, Avise & Johns 1999, Holt & Jonsson 2014), but they have not commonly been applied in botany, mycology and zoology (Vences *et al.* 2013). In bacteriology, a quantitative interpretation of ranks is much more common, particularly by means of traditional (Tindall *et al.* 2010) or digital (Meier-Kolthoff *et al.* 2013) DNA:DNA hybridisation thresholds for species and 16S rRNA gene thresholds for higher ranks (Yarza *et al.* 2014). However, thresholds for pairwise (dis-)similarities are not a phylogenetic criterion (Wiley & Lieberman 2011) and can yield inconsistencies (Meier-Kolthoff *et al.* 2014). Moreover, the method used by Yarza *et al.* (2014) to estimate similarity thresholds does not guarantee maximum agreement with the existing assignment to ranks, which could be obtained using clustering optimisation (Göker *et al.* 2009, 2010, Stielow *et al.* 2011). Another question regarding Linnaean classification is whether higher taxa are real; this has usually been denied in the literature (Wiley & Lieberman

2011, Vences *et al.* 2013), but recent studies found statistical tests to identify evolutionary significant units above the species level (Humphreys & Barraclough 2014, Barraclough & Humphreys 2015).

Recently, we reconstructed the phylogeny of tremellomycetous yeasts and related dimorphic and filamentous *Tremellomyces* by analysing sequences from seven genes (Liu *et al.* 2015), resulting in a relatively robust framework that allows us to update the taxonomic system of the *Tremellomyces*. Here, we employed two quantitative methods, namely a phylogenetic variant of clustering optimisation (Göker *et al.* 2009, 2010, Stielow *et al.* 2011) and the iterative application of a modified general mixed Yule coalescent (GMYC) (Humphreys & Barraclough 2014), to test and circumscribe the taxonomic units at the order, family and genus levels recognised from this multi-gene phylogeny. Results of either method were not followed strictly, however, but were modified where necessary to decrease the number of new taxa to be introduced. Moreover, a comprehensively sampled LSU rRNA gene phylogeny, including taxa that were not studied in the seven-gene phylogeny, was constructed for *Tremellomyces* integrating both yeasts and filamentous fungi, incorporating information from the seven-gene phylogeny by using backbone constraints. An updated taxonomic system for *Tremellomyces* is consequently proposed based on the integrated phylogenetic evidence combined with morphological and physiological criteria.

MATERIALS AND METHODS

Organisms

A total of 294 tremellomycetous yeast strains, including the type strains of 286 currently recognised species and varieties as listed in Table 1 of Liu *et al.* (2015), were employed in this study. In addition, 47 tremellomycetous yeast species which were published too late to be included in the study of Liu *et al.* (2015) and 47 more fruiting body forming species from the genera *Tremella*, *Syzygospora*, *Rhynchogastrea*, *Tetragoniomyces* and *Trimorphomyces* were employed in this study (Table 1). Additionally, 23 novel but undescribed species retrieved from the public dataset were also included. Five *Cryptococcus* species recently described by Hagen *et al.* (2015) were listed in Table 1 of accepted species names but not included in the phylogenetic analyses. Large ribosomal subunit (LSU) rRNA gene sequences were additionally sampled specifically from related and filamentous taxa in Tremellomycetes, for which no culture material or other nucleotide data are available. All together, a total of 435 taxa were compared in this study.

Phylogenetic analysis

The phylogenetic analysis used for the taxonomic backbone in this study was presented in Liu *et al.* (2015). The phylogeny was inferred from a seven-gene dataset comprising nucleotide sequences of the internal transcribed spacer region (ITS) rRNA gene, the D1/D2 domains of the large subunit (LSU or 26S) rRNA gene, the small subunit (SSU or 18S) rRNA gene, two subunits of RNA polymerase II (*RPB1* and *RPB2*), translation elongation factor 1- α (*TEF1*) and cytochrome *b* (*CYTB*), using Bayesian inference, maximum likelihood (ML) and neighbour-

joining (NJ) analyses (Liu *et al.* 2015). The supplementary LSU rRNA gene (D1/D2 domains) sequence dataset containing newly published tremellomycetous yeast species and additional filamentous teleomorphic taxa was constructed and subjected to constrained maximum likelihood (ML) and maximum parsimony (MP) analyses based on the topology of a seven-genes dataset taken from Liu *et al.* (2015). The LSU sequences were aligned with MAFFT version 7 and the G-INS-i option. Constrained phylogenetic analyses were only enforced for species previously analysed using seven DNA loci. Only bipartitions that received at least 85 % bootstrap support during fast bootstrapping of the seven-genes dataset (Liu *et al.* 2015) conducted with Pthreads-parallelised RAxML version 8.1.24 (Stamatakis 2014) were used as a backbone constraint for LSU phylogenetic inference. Fast bootstrapping in conjunction with the autoMRE bootstopping criterion (Pattengale *et al.* 2009) and subsequent search for the best tree (Stamatakis *et al.* 2008) were conducted using the GTRCAT model approximation. MP bootstrapping with 1000 replicates was conducted with TNT version 1.1/June 2015 (Goloboff *et al.* 2008).

Quantitative assessment of taxonomic ranks

Two methods were used for the assessment of taxonomic ranks on the basis of the maximum likelihood tree obtained from the concatenated sequences of the seven genes (Liu *et al.* 2015). Firstly, we used a phylogeny-based variant of clustering optimisation called phylogenetic rank boundary optimisation (PRBO). The goal of clustering optimisation (Göker *et al.* 2009, 2010, Stielow *et al.* 2011) is to detect distance thresholds (and clustering parameters) that yield non-hierarchical clusterings that are in maximal agreement with a given reference clustering (such as a classification into taxa of a single rank). The limitations of the approach are that it is rather a clustering method than a phylogenetic approach, even though the resulting clusters are often monophyletic, and that it estimates the boundaries for each taxonomic rank separately. PRBO instead is based on rooted phylogenies. It measures the divergence of each clade as maximum subtree height (MaSH). Taxonomic ranks are made quantitatively comparable by assigning an upper MaSH boundary to each rank, which also serves as the lower MaSH boundary of the next higher rank. Using an existing classification as template, these MaSH ranges for each rank are chosen so as to minimise the number of taxa whose MaSH is outside the MaSH range of their respective rank. Clades to which no taxon is assigned can also enter the optimisation, because their MaSH value must be higher than the upper boundary for the rank of any taxon they contain but lower than the upper boundary for the rank of the taxon assigned to the closest parent clade. This allows for estimating the boundaries for all ranks from an entire tree in a single run. Confidence intervals for the boundaries can be obtained by bootstrapping the set of clades that enters the boundary estimation. Afterwards taxa that did not enter the calculation can be judged as too large or too small, as long as their MaSH values are on the same scale.

The implementation used is the one of the forthcoming MaSH package for the R statistical software environment (R core team 2015). The boundary optimisation is done using the rpart package (Therneau *et al.* 2015) with the MaSH values of each clade as dependent and the rank as independent variable. One hundred bootstrap replicates were applied to obtain 95 %

Table 1. List of accepted tremellomycetous yeast and dimorphic taxa.

Taxon	Basionym or important synonym	Strain	LSU D1D2
Cystofilobasidiales			
Cystofilobasidiaceae emend.			
Cystofilobasidium			
<i>C. bisporidii</i>		CBS 6346 ^T	EU085532
<i>C. capitatum</i> ^T	<i>Rhodosporidium capitatum</i>	CBS 6358 ^T	AF075465
<i>C. ferigula</i>		CBS 7202 ^T	CBS database
<i>C. infirmominiatum</i>		CBS 323 ^T	AF075505
<i>C. lacus-mascardii</i>		CBS 10642 ^T	AY158642
<i>C. macerans</i>	<i>Cryptococcus macerans</i>	CBS 10757 ^T	EU082225
Mrakiaceae fam. nov.			
Itersonilia emend.			
<i>I. pannonicus</i> comb. nov.	<i>Udeniomyces pannonicus</i>	CBS 9123 ^T	AB077382
<i>I. perplexans</i> ^T		CBS 363.85 ^T	AJ235274
Krasilnikovozyma gen. nov.			
<i>K. huempii</i> ^T comb. nov.	<i>Candida huempii</i> <i>C. huempii</i> <i>Mrakia curviuscula</i>	CBS 8186 ^T	AF189844
<i>K. tahquamenonensis</i> comb. nov.	<i>C. tahquamenonensis</i>	CBS 13897 ^T	KM408125
Mrakia emend.			
<i>M. aquatica</i> comb. nov.	<i>Mrakiella aquatica</i>	CBS 5443 ^T	AF075470
<i>M. blollopis</i>		CBS 8921 ^T	AY038814
<i>M. cryoconiti</i> comb. nov.	<i>M. cryoconiti</i>	CBS 10834 ^T	GQ911524
<i>M. frigida</i> ^T	<i>Leucosporidium frigidum</i>	CBS 5270 ^T	AF075463
<i>M. gelida</i>	<i>L. gelidum</i>	CBS 5272 ^T	AF189831
<i>M. niccombsii</i> comb. nov.	<i>M. niccombsii</i>	CBS 8917 ^T	AY029345
<i>M. psychrophila</i>		CBS 10828 ^T	EU224266
<i>M. robertii</i>		CBS 8912 ^T	AY038811
Phaffia emend.			
<i>P. rhodozyma</i> ^T	<i>Xanthophyllomyces</i> <i>X. dendrorhous</i>	CBS 5905 ^T	AF189871
Tausonia emend.			
<i>T. pamirica</i> ^T		CBS 8428 ^T	EF118825
<i>T. pullulans</i> comb. nov.	<i>Guehomyces pullulans</i>	CBS 2532 ^T	EF551318
Udeniomyces			
<i>U. kanasensis</i>		CBS 12488 ^T	JQ002681
<i>U. megalosporus</i>		CBS 7236 ^T	AF075510
<i>U. puniceus</i>		CBS 5689 ^T	AF075519
<i>U. pyricola</i> ^T		CBS 6754 ^T	AF075507
Filobasidiales			
Filobasidiaceae emend.			
Filobasidium emend.			
<i>F. chernovii</i> comb. nov.	<i>C. chernovii</i>	CBS 8679 ^T	AF181530
<i>F. elegans</i>		CBS 7640 ^{EXT}	AF181548
<i>F. floriforme</i> ^T		CBS 6241 ^{EXT}	AF075498
<i>F. globisporum</i>		CBS 7642 ^{EXT}	AF075495
<i>F. magnum</i> comb. nov.	<i>C. magnum</i>	CBS 140 ^T	AF181851
<i>F. oeirensis</i> comb. nov.	<i>C. oeirensis</i>	CBS 8681 ^T	AF181519
<i>F. stepposus</i> comb. nov.	<i>C. stepposus</i>	CBS 10265 ^T	DQ222456
<i>F. uniguttulatum</i>		CBS 1730 ^T	AF075468
<i>F. wieringae</i> comb. nov.	<i>C. wieringae</i>	CBS 1937 ^T	AF181541

(continued on next page)

Table 1. (Continued).

Taxon	Basionym or important synonym	Strain	LSU D1D2
Goffeauzyma gen. nov.			
<i>G. aciditolerans</i> comb. nov.	<i>Cryptococcus aciditolerans</i>	CBS 10872 ^T	AY731790
<i>G. agrionensis</i> comb. nov.	<i>C. agrionensis</i>	CBS 10799 ^T	EU627786
<i>G. gastricus</i> ^T comb. nov.	<i>C. gastricus</i>	CBS 2288 ^T	AF137600
<i>G. gilvescens</i> comb. nov.	<i>C. gilvescens</i>	CBS 7525 ^T	AF181547
<i>G. ibericus</i> comb. nov.	<i>C. ibericus</i>	CBS 10871 ^T	AY731791
<i>G. metallitolerans</i> comb. nov.	<i>C. metallitolerans</i>	CBS 10873 ^T	AY731789
Heterocephalacria emend.			
<i>H. arrabidensis</i> comb. nov.	<i>C. arrabidensis</i>	CBS 8678 ^T	AF181535
<i>H. bachmannii</i> comb. nov.	<i>Syzygospora bachmannii</i>	AM72	JN043613
<i>H. physciacearum</i> comb. nov.	<i>S. physciacearum</i>	AM17	JN043614
<i>H. solida</i>	<i>S. solida</i>		
Naganishia emend.			
<i>N. adeliensis</i> comb. nov.	<i>C. adeliensis</i>	CBS 8351 ^T	AF137603
<i>N. albidia</i> comb. nov.	<i>C. albidus</i>	CBS 142 ^T	AF075474
<i>N. albidosimilis</i> comb. nov.	<i>C. albidosimilis</i>	CBS 7711 ^T	AF137601
<i>N. antarctica</i> comb. nov.	<i>C. antarcticus</i>	CBS 7687 ^T	AF075488
<i>N. bhutanensis</i> comb. nov.	<i>C. bhutanensis</i>	CBS 6294 ^T	AF137599
<i>N. cerealis</i> comb. nov.	<i>C. cerealis</i>	CBS 10505 ^T	FJ473376
<i>N. diffluens</i> comb. nov.	<i>C. diffluens</i>	CBS 160 ^T	AF075502
<i>N. friedmannii</i> comb. nov.	<i>C. friedmannii</i>	CBS 7160 ^T	AF075478
<i>N. globosa</i> ^T	<i>C. saitoi</i>	CBS 5106 ^T	AF181539
<i>N. liquefaciens</i> comb. nov.	<i>C. liquefaciens</i>	CBS 968 ^T	AF181515
<i>N. onofrii</i> comb. nov.	<i>C. onofrii</i>	DBVPG 5303 ^T	KC433831
<i>N. randhawae</i> comb. nov.	<i>C. randhawai</i>	CBS 10160 ^T	AJ876599
<i>N. uzbekistanensis</i> comb. nov.	<i>C. uzbekistanensis</i>	CBS 8683 ^T	AF181508
<i>N. vaughanmartinae</i> comb. nov.	<i>C. vaughanmartinae</i>	DBVPG4736 ^T	KF861779
<i>N. vishniacii</i> comb. nov.	<i>C. vishniacii</i>	CBS 7110 ^T	AF075473
Syzygospora			
<i>S. alba</i> ^T		AM147	JN043616
<i>S. pallida</i>		FO31621	AJ406403
Piskurozymaceae fam. nov.			
Piskurozyma gen. nov.			
<i>P. capsuligenum</i> comb. nov.	<i>Filobasidium capsuligenum</i>	CBS 1906 ^T	AF363642
<i>P. cylindricus</i> ^T comb. nov.	<i>C. cylindricus</i> ^T	CBS 8680 ^T	AF181534
<i>P. fildesensis</i> comb. nov.	<i>C. fildesensis</i>	CBS12705	KC894161
<i>P. filicatus</i> comb. nov.	<i>C. filicatus</i>	CBS 10874 ^T	EU433983
<i>P. silvicola</i> comb. nov.	<i>C. silvicola</i>	CBS 10099 ^T	AY898955
<i>P. sorana</i> comb. nov.	<i>S. sorana</i>	UBC_F16310	EU541305
<i>P. taiwanensis</i> comb. nov.	<i>Bullera taiwanensis</i>	CBS 9813 ^T	AB079065
Solicoccozyma gen. nov.			
<i>S. aerius</i> ^T comb. nov.	<i>C. aerius</i>	CBS 155 ^T	AF075486
<i>S. fuscescens</i> comb. nov.	<i>C. fuscescens</i>	CBS 7189 ^T	AF075472
<i>S. keelungensis</i> comb. nov.	<i>C. keelungensis</i>	CBS 10876 ^T	EF621562
<i>S. phenolicus</i> comb. nov.	<i>C. phenolicus</i>	CBS 8682 ^T	AF181523
<i>S. terreus</i> comb. nov.	<i>C. terreus</i>	CBS 1895 ^T	AF075479
<i>S. terricola</i> comb. nov.	<i>C. terricola</i>	CBS 4517 ^T	AF181520

Table 1. (Continued).

Taxon	Basionym or important synonym	Strain	LSU D1D2
Holtermanniales			
Holtermannia			
<i>H. corniformis</i>		CBS 6979 ^R	AF189843
Holtermanniella			
<i>H. festucosa</i>	<i>Cryptococcus festucosus</i>	CBS 10162 ^T	AY462119
<i>H. mycelialis</i>	<i>C. mycelialis</i>	CBS 7712 ^T	AJ311450
<i>H. nyarrowii</i>	<i>C. nyarrowii</i>	CBS 8804 ^T	AY006480
<i>H. takashimae</i> ^T		CBS 11174 ^T	FM242574
<i>H. wattica</i>	<i>C. watticus</i>	CBS 9496 ^T	AY138478
Tremellales			
Bulleraceae fam. nov.			
Bullera emend.			
	<i>Bulleromyces</i>		
<i>B. alba</i> ^T	<i>B. albus</i>	CBS 501 ^T	AF075500
<i>B. hanna</i>		CBS 8286 ^T	AF363661
<i>B. penniseticola</i>		CBS 8623 ^T	AF363649
<i>B. unica</i>		CBS 8290 ^T	AF075524
Fonsecazyma gen. nov.			
<i>F. betulae</i> comb. nov.	<i>Kwoniella betulae</i>	CBS 13896 ^T	KM408130
<i>F. mujuensis</i> ^T comb. nov.	<i>C. mujuensis</i>	CBS 10308 ^T	DQ333884
<i>F. tronadorensis</i> comb. nov.	<i>C. tronadorensis</i>	CBS 12691 ^T	GU560003
Genolevuria gen. nov.			
<i>G. amylolyticus</i> ^T comb. nov.	<i>C. amylolyticus</i>	CBS 10048 ^T	AY562134
<i>G. armeniacus</i> comb. nov.	<i>C. armeniacus</i>	CBS 10050 ^T	AY562140
<i>G. bromeliarum</i> comb. nov.	<i>C. bromeliarum</i>	CBS 10424 ^T	DQ784566
<i>G. tibetensis</i> comb. nov.	<i>C. tibetensis</i>	CBS 10456 ^T	EF363143
Pseudotremella gen. nov.			
<i>P. allantoinivorans</i> comb. nov.	<i>C. allantoinivorans</i>	CBS 9604 ^T	AY315662
<i>P. lacticolor</i> comb. nov.	<i>C. lacticolor</i>	CBS 10915 ^T	AB375775
<i>P. moriformis</i> ^T comb. nov.	<i>Tremella moriformis</i>	CBS 7810 ^R	AF075493
<i>P. nivalis</i> comb. nov.	<i>T. nivalis</i>	CBS 8487 ^R	AF042232
Tremella Clade I (Millanes <i>et al.</i> 2011)			
<i>Cryptococcus cuniculi</i> pro tem		CBS 10309 ^T	DQ333885
<i>Sirobasidium brefeldianum</i>		AM71	JN043578
<i>S. intermedium</i>		CBS 7805	AF075492
<i>Tremella caloplacae</i>		AM31	JN043573
<i>T. candelariellae</i>		AM34	JN043575
<i>T. christiansenii</i>		AM36	JN043577
<i>T. dendrographae</i>		AM39	JN043576
<i>T. exigua</i>		RB6623-15	AF042248
Tremella Clade III (Millanes <i>et al.</i> 2011)			
<i>Biatoropsis usnearum</i>		Sweden, Hagner s.n. (S-F92134)	JN043592
<i>Tremella cetraricicola</i>		Finland, Suija s.n. (S-F102413)	JN043596
<i>T. coppinsii</i>		UK, Diederich 15628 (S-F102414)	JN043601
<i>T. everniae</i>		USA, 2005, Kneiper s.n. (S)	JN043599
<i>T. giraffa</i>		CBS 8489 ^R	AF042271
<i>T. huuskonenii</i>		Canada, B.C., Goward 11-50 (UBC), L321S/L321	KR857095
<i>T. hypogymniae</i>		Sweden, Wedin 6892 (UPS)	JN043590

(continued on next page)

Table 1. (Continued).

Taxon	Basionym or important synonym	Strain	LSU D1D2
<i>T. lichenicola</i>		Germany, John & Diederich s.n. (UPS-256878)	JN043611
<i>T. pertusariae</i>		France, Diederich 16331 (S-F102502)	JN043600
<i>T. tuckerae</i>		Mexico, Tucker 37335 (SBBG)	JN043588
<i>T. wirthii</i>		The Netherlands, 1996, Herk s.n. (herb. Diederich)	JN043598
Single-species lineages			
<i>Tremella</i> 'indecorata' l pro tem		AM5	JN043610
<i>Tremella haematommatis</i> pro tem		AM41	JN043617
<i>Tremella ramalinae</i> pro tem		Spain, Etayo s.n. (UPS 158799)	JN043619
Bulleribasidiaceae fam. nov.			
Bulleribasidium emend.	<i>Mingxiaea</i>		
<i>B. begoniae</i> comb. nov.	<i>Bullera begoniae</i>	CBS 10762 ^T	AB119462
<i>B. foliicola</i> comb. nov.	<i>M. foliicola</i>	CBS 11407 ^T	GQ438834
<i>B. hainanense</i> comb. nov.	<i>M. hainanensis</i>	CBS 11409 ^T	GQ438828
<i>B. oberjochense</i> ^T		CBS 9110 ^T	AF416646
<i>B. panici</i> comb. nov.	<i>B. panici</i>	CBS 9932 ^T	AY188387
<i>B. pseudovariabile</i> comb. nov.	<i>B. pseudovariabilis</i>	CBS 9609 ^T	AF544247
<i>B. sanyaense</i> comb. nov.	<i>M. sanyaensis</i>	CBS 11408 ^T	GQ438831
<i>B. setariae</i> comb. nov.	<i>B. setariae</i>	CBS 10763 ^T	AB119463
<i>B. siamense</i> comb. nov.	<i>B. siamensis</i>	CBS 9933 ^T	AY188388
<i>B. variabile</i> comb. nov.	<i>B. variabilis</i>	CBS 7347 ^T	AF189855
<i>B. wuzhishanense</i> comb. nov.	<i>M. wuzhishanensis</i>	CBS 11411 ^T	GQ438830
Derxomyces			
<i>D. amylogenes</i>		CBS 12233 ^T	HQ890372
<i>D. anomala</i>	<i>B. anomala</i>	CBS 9607 ^T	EF682504
<i>D. bambusicola</i>		CBS 12234 ^T	HQ890376
<i>D. boekhoutii</i>		CBS 10824 ^T	EU517057
<i>D. boninensis</i>	<i>B. boninensis</i>	CBS 9141 ^T	AY487568
<i>D. corylopsis</i>		CBS 12259 ^T	HQ890374
<i>D. cylindrica</i>	<i>B. cylindrica</i>	CBS 9744 ^T	AY487563
<i>D. hainanensis</i>		CBS 10820 ^T	EU517056
<i>D. hubeiensis</i>	<i>B. hubeiensis</i>	CBS 9747 ^T	AY487566
<i>D. huiaensis</i>	<i>B. huiaensis</i>	CBS 8287 ^T	AB118870
<i>D. komagatae</i>	<i>B. komagatae</i>	CBS 10153 ^T	AF544249
<i>D. linzhiensis</i>		CBS 10827 ^T	EU517058
<i>D. mrakii</i> ^T	<i>B. mrakii</i>	CBS 8288 ^T	AB118871
<i>D. nakasei</i>	<i>B. nakasei</i>	CBS 9746 ^T	AY487564
<i>D. pseudocylindrica</i>		CBS 10826 ^T	EU517059
<i>D. pseudohuiaensis</i>	<i>B. pseudohuiaensis</i>	CBS 7364 ^T	AF544250
<i>D. pseudoschimicola</i>	<i>B. pseudoschimicola</i>	CBS 7354 ^T	AF416647
<i>D. qinlingensis</i>		CBS 10818 ^T	EU517060
<i>D. schimicola</i>	<i>B. schimicola</i>	CBS 9144 ^T	AY487570
<i>D. simaoensis</i>		CBS 10822 ^T	EU517062
<i>D. waltii</i>	<i>B. waltii</i>	CBS 9143 ^T	AY487569
<i>D. wuzhishanensis</i>		CBS 10825 ^T	EU517063
<i>D. yunnanensis</i>		CBS 10821 ^T	EU517064
Dioszegia			
<i>D. antarctica</i>		CBS 10920 ^T	FJ640575
<i>D. athyri</i>		CBS 10119 ^T	EU070931

Table 1. (Continued).

Taxon	Basionym or important synonym	Strain	LSU D1D2
<i>D. aurantiaca</i>	<i>Bullera aurantiaca</i>	CBS 6980 ^T	AB104689
<i>D. buhagiarii</i>		CBS 10054 ^T	AY562151
<i>D. butyracea</i>		CBS 10122 ^T	EU070929
<i>D. catarinonii</i>		CBS 10051 ^T	AY562142
<i>D. changbaiensis</i>		CBS 9608 ^T	AY242819
<i>D. crocea</i>	<i>B. crocea</i>	CBS 6714 ^T	AF075508
<i>D. cryoxerica</i>		CBS 10919 ^T	FJ640562
<i>D. fristingensis</i>		CBS 10052 ^T	AY562146
<i>D. hungarica</i> ^T	<i>Cryptococcus hungaricus</i>	CBS 4214 ^T	AF075503
<i>D. rishiriensis</i>		CBS 11844 ^T	AB545810
<i>D. statzelliae</i>		CBS 8925 ^T	AY029341
<i>D. takashimae</i>		CBS 10053 ^T	AY562149
<i>D. xingshanensis</i>		CBS 10120 ^T	EU070928
<i>D. zsolttii</i>		CBS 9127 ^T	AF544245
Hannaella			
<i>H. coprosmaensis</i>	<i>B. coprosmae</i>	CBS 8284 ^T	AF363660
<i>H. kunmingensis</i>	<i>B. kunmingensis</i>	CBS 8960 ^T	AB109558
<i>H. luteola</i>	<i>C. luteolus</i>	CBS 943 ^T	AF075482
<i>H. oryzae</i>	<i>B. oryzae</i>	CBS 7194 ^T	AF075511
<i>H. pagnoccae</i>		CBS 11142 ^T	FJ828959
<i>H. phetchabunensis</i>		CBS 13386 ^T	AB922849
<i>H. phyllophila</i>		CBS 13921 ^T	AB934929
<i>H. siamensis</i>		CBS 13533 ^T	AB922844
<i>H. sinensis</i> ^T	<i>B. sinensis</i> , <i>B. deroxii</i>	CBS 7238 ^T	AF189884
<i>H. surugaensis</i>	<i>C. surugaensis</i>	CBS 9426 ^T	AB100440
Nielozyma gen. nov.			
<i>N. formosana</i> comb. nov.	<i>B. formosana</i>	CBS 10306 ^T	AB119465
<i>N. melastomae</i> ^T comb. nov.	<i>B. melastomae</i>	CBS 10305 ^T	AB119464
Vishniacozyma gen. nov.			
<i>V. carnescens</i> ^T comb. nov.	<i>Torulopsis carnescens</i> <i>C. carnescens</i>	CBS 973 ^T	AB035054
<i>V. dimennae</i> comb. nov.	<i>C. dimennae</i>	CBS 5770 ^T	AF075489
<i>V. foliicola</i> comb. nov.	<i>C. foliicola</i>	CBS 9920 ^T	AY557599
<i>V. globispora</i> comb. nov.	<i>B. globispora</i>	CBS 6981 ^T	AF075509
<i>V. heimaeyensis</i> comb. nov.	<i>C. heimaeyensis</i>	CBS 8933 ^T	DQ000317
<i>V. nebularis</i> comb. nov.	<i>Trimorphomyces nebularis</i>	CBS12283	EU266921
<i>V. peneaus</i> comb. nov.	<i>Rhodotorula peneaus</i> <i>C. peneaus</i>	CBS 2409 ^T	AB035051
<i>V. psychrotolerans</i> comb. nov.	<i>C. psychrotolerans</i>	CBS 12690 ^T	JN193445
<i>V. taibaiensis</i> comb. nov.	<i>C. taibaiensis</i>	CBS 9919 ^T	AY557601
<i>V. tephrensensis</i> comb. nov.	<i>C. tephrensensis</i>	CBS 8935 ^T	DQ000318
<i>V. victoriae</i> comb. nov.	<i>C. victoriae</i>	CBS 8685 ^T	AF363647
Carcinomycetaceae emend.			
Carcinomyces emend.			
<i>C. arundinariae</i> comb. nov.	<i>B. arundinariae</i>	CBS 9931 ^T	AF547661
<i>C. effibulatus</i> ^T	<i>Syzygospora effibulata</i>	AM6	JN043605
<i>C. polyporinus</i> comb. nov.	<i>Tremella polyporina</i>	AM20	JN043607
Tremella Clade II (Millanes <i>et al.</i> 2011)			
<i>Tremella cladoniae</i>		AM125	JN043583

(continued on next page)

Table 1. (Continued).

Taxon	Basionym or important synonym	Strain	LSU D1D2
<i>T. leptogii</i>		AM81	JN043582
<i>T. lobariacearum</i>		AM80	JN043579
<i>T. nephromatis</i>		AM133	JN043581
<i>T. phaeophysciae</i>		AM98	JN043585
Cryptococcaceae emend.			
Cryptococcus emend.			
<i>C. amylolentus</i>	<i>Candida amyloenta</i> <i>Filobasidiella amyloenta</i> <i>Tsuchiyaea wingfieldii</i> <i>Sterigmatomyces wingfieldii</i>	CBS 6039 ^T	AF105391
<i>C. bacillisporus</i>	<i>F. bacillispora</i>	CBS 6955 ^T	JN939485
<i>C. decagattii</i>		CBS 11687 ^T	
<i>C. deneoformans</i>	<i>F. neoformans</i> <i>F. neoformans</i> var. <i>neoformans</i>	CBS 6900 ^T	
<i>C. depauperatus</i> comb. nov.	<i>F. depauperata</i>	CBS 7841 ^T	FJ534911
<i>C. deuterogattii</i>		CBS 10514 ^T	FJ534907
<i>C. gattii</i>		CBS 6289 ^T	AF075526
<i>C. luteus</i> comb. nov.	<i>F. lutea</i>		
<i>C. neoformans</i> ^T	<i>Cryptococcus neoformans</i> var. <i>grubii</i>	CBS 8710 ^T	FJ534909
<i>C. tetragattii</i>		CBS 10101 ^T	
Kwoniella emend.			
<i>K. bestiolae</i> comb. nov.	<i>C. bestiolae</i>	CBS 10118 ^T	FJ534903
<i>K. botswanensis</i>		CBS 12716 ^T	HF545769
<i>K. dejecticola</i> comb. nov.	<i>C. dejecticola</i>	CBS 10117 ^T	AY917102
<i>K. dendrophila</i> comb. nov.	<i>Bullera dendrophila</i>	CBS 6074 ^T	AF189870
<i>K. europaea</i>		CBS 12714 ^T	AY167602
<i>K. heveanensis</i>	<i>C. heveanensis</i>	CBS 569 ^T	AF075467
<i>K. mangroviensis</i> ^T		CBS 8507 ^T	AF444742
<i>K. newhampshirensis</i>		CBS 13917 ^T	KM408127
<i>K. pinus</i> comb. nov.	<i>C. pinus</i>	CBS 10737 ^T	EF672245
<i>K. shandongensis</i>		CBS 12478 ^T	JN160602
<i>K. shivajii</i> comb. nov.	<i>C. shivajii</i>	CBS 11374 ^T	FM212446
Cuniculitremaceae			
Fellomyces			
<i>F. borneensis</i>		CBS 8282 ^T	AF189877
<i>F. horovitziae</i>		CBS 7515 ^T	AF189856
<i>F. penicillatus</i>		CBS 5492 ^T	AF177405
<i>F. polyborus</i> ^T		CBS 6072 ^T	AF189859
Kockovaella emend.			
<i>K. barringtoniae</i>		CBS 9811 ^T	AB292854
<i>K. calophylli</i>		CBS 8962 ^T	AB292852
<i>K. chinensis</i> comb. nov.	<i>Fellomyces chinensis</i>	CBS 8278 ^T	AF189878
<i>K. cucphuongensis</i>		CBS 8959 ^T	AB292853
<i>K. distylii</i> comb. nov.	<i>F. distylii</i>	CBS 8545 ^T	AF363652
<i>K. fuzhouensis</i> comb. nov.	<i>F. fuzhouensis</i>	CBS 8243 ^T	AF363659
<i>K. imperatae</i>		CBS 7554 ^T	AF189862
<i>K. lichenicola</i> comb. nov.	<i>F. lichenicola</i>	CBS 8315 ^T	AF363643
<i>K. litseae</i>		CBS 8964 ^T	AB292850
<i>K. machilophila</i>		CBS 8607 ^T	AF363654
<i>K. mexicanus</i> comb. nov.	<i>F. mexicanus</i>	CBS 8279 ^T	AJ627906

Table 1. (Continued).

Taxon	Basionym or important synonym	Strain	LSU D1D2
<i>K. ogasawarensis</i> comb. nov.	<i>Fellomyces ogasawarensis</i>	CBS 8544 ^T	AF363651
<i>K. phaffii</i>		CBS 8608 ^T	AF363655
<i>K. prillingeri</i> sp. nov.	<i>F. thailandicus</i>	CBS 8308 ^T	AF363644
<i>K. sacchari</i>		CBS 8624 ^T	AF363650
<i>K. schimae</i>		CBS 8610 ^T	AF363656
<i>K. sichuanensis</i> comb. nov.	<i>F. sichuanensis</i>	CBS 8318 ^T	AF189879
<i>K. thailandica</i> ^T		CBS 7552 ^T	AF075516
<i>K. vietnamensis</i>		CBS 8963 ^T	AB292851
Sterigmatosporidium	<i>Cuniculitrema</i>		
<i>S. polymorphum</i> ^T	<i>C. polymorpha</i>	CBS 9644 ^T	AY032662
Naemateliaceae fam. nov.			
Dimennazyma gen. nov.			
<i>D. cistialbidi</i> ^T comb. nov.	<i>Cryptococcus cistialbidi</i>	CBS 10049 ^T	AY562135
Naematelia			
<i>N. aurantia</i>	<i>Tremella aurantia</i>	CBS 6965 ^R	AF189842
<i>N. aurantialba</i> comb. nov.	<i>T. aurantialba</i>	strain9102	EF010939
<i>N. encephala</i> ^T	<i>T. encephala</i>	CBS 8207 ^R	AF042220
<i>N. microspora</i> comb. nov.	<i>T. microspora</i>	BPI702328	AF042253
Single-species lineage			
<i>Tremella 'indecorata'</i> Il pro tem.		CBS 6976 ^R	AF042250
Phaeotremellaceae fam. nov.			
Gelidatrema gen. nov.			
<i>G. spencermartinsiae</i> ^T comb. nov.	<i>C. spencermartinsiae</i>	CBS 10760 ^T	DQ513279
Phaeotremella emend.			
<i>P. fagi</i> comb. nov.	<i>C. fagi</i>	CBS 9964 ^T	DQ054535
<i>P. mycetophiloides</i> comb. nov.	<i>T. mycetophiloides</i>	AM23	JN043608
<i>P. mycophaga</i> comb. nov.	<i>T. mycophaga</i>	RB6539-4	AF042249
<i>P. neofoliacea</i> comb. nov.	<i>T. neofoliacea</i>	CBS 8475 ^R	AF042236
<i>P. pseudofoliacea</i> ^T	<i>T. foliacea</i>	CBS 6969 ^R	AF189868
<i>P. simplex</i> comb. nov.	<i>T. simplex</i>	FO31782	AF042246
<i>P. skinneri</i> comb. nov.	<i>C. skinneri</i>	CBS 5029 ^T	AF189835
Rhynchogastremaceae emend.			
Papiliotrema emend.			
<i>P. anemochoreius</i> comb. nov.	<i>C. anemochoreius</i>	CBS 10258 ^T	DQ384929
<i>P. aspenensis</i> comb. nov.	<i>C. aspenensis</i>	CBS 13867 ^T	KC485500
<i>P. aureus</i> comb. nov.	<i>Torula aurea</i> <i>C. aureus</i>	CBS 318 ^T	AB035041
<i>P. baii</i> comb. nov.	<i>C. baii</i>	PYCC 6523 ^T	LK023766
<i>P. bandonii</i> ^T		CBS 9107 ^T	AF416642
<i>P. flavescens</i> comb. nov.	<i>T. flavescens</i> <i>C. flavescens</i>	CBS 942 ^T	AB035042
<i>P. fonsecae</i> comb. nov.	<i>C. fonsecae</i>	CBS 12692 ^T	JN193447
<i>P. frias</i> comb. nov.	<i>C. frias</i>	CBS 12693 ^T	LK023834
<i>P. fuscus</i> comb. nov.	<i>Auriculibuller fuscus</i>	CBS 9648	AF444763
<i>P. hoabinhensis</i> comb. nov.	<i>Bullera hoabinhensis</i>	JCM 10835 ^T	AB193347
<i>P. japonica</i> comb. nov.	<i>B. japonica</i>	CBS 2013 ^T	AF444760
<i>P. laurentii</i> comb. nov.	<i>C. laurentii</i>	CBS 139 ^T	AF075469
<i>P. mangaliensis</i> comb. nov.	<i>C. mangaliensis</i>	CBS 10870 ^T	FJ008046
<i>P. nemorosus</i> comb. nov.	<i>C. nemorosus</i>	CBS 9606 ^T	AF472625

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Table 1. (Continued).

Taxon	Basionym or important synonym	Strain	LSU D1D2
<i>P. perniciosus</i> comb. nov.	<i>Cryptococcus perniciosus</i>	CBS 9605 ^T	AF472624
<i>P. pseudoalba</i> comb. nov.	<i>Bullera pseudoalba</i>	CBS 7227 ^T	AF075504
<i>P. rajasthanensis</i> comb. nov.	<i>C. rajasthanensis</i>	CBS 10406 ^T	AM262324
<i>P. ruineniae</i> comb. nov.	<i>C. ruineniae</i>	PYCC 6170 ^T	LK023764
<i>P. siamense</i>		CBS 13330 ^T	AB909023
<i>P. taeenensis</i> comb. nov.	<i>C. taeenensis</i>	CBS 9742 ^T	AY422719
<i>P. terrestris</i> comb. nov.	<i>C. terrestris</i>	CBS 10810 ^T	EF370393
<i>P. wisconsinensis</i> comb. nov.	<i>C. wisconsinensis</i>	CBS 13895 ^T	KM408131
Rhynchogastrema emend.			
<i>R. aquatica</i> comb. nov.	<i>Bandoniozyma aquatica</i>	CBS 12527 ^T	JN979992
<i>R. complexa</i> comb. nov.	<i>B. complexa</i>	CBS 11570 ^T	GU321090
<i>R. coronatum</i> ^T		BBA 65155 ^T	KJ170152
<i>R. fermentans</i> comb. nov.	<i>B. fermentans</i>	CBS 12399 ^T	HM461720
<i>R. glucofermentans</i> comb. nov.	<i>B. glucofermentans</i>	CBS 10381 ^T	AY520334
<i>R. nanyangensis</i> comb. nov.	<i>C. nanyangensis</i>	CBS 12474 ^T	JN564592
<i>R. noutii</i> comb. nov.	<i>B. noutii</i>	CBS 8364 ^T	AF444700
<i>R. tunnelae</i> comb. nov.	<i>B. tunnelae</i>	CBS 6123 ^T	AF444687
<i>R. visegradensis</i> comb. nov.	<i>B. visegradensis</i>	CBS 12505 ^T	GU195658
Sirobasidiaceae			
Fibulobasidium			
<i>F. inconspicuum</i>		CBS 8237 ^R	AF363641
<i>F. murrhardtense</i>		CBS 9109 ^T	AF416648
<i>F. sirobasidioides</i>		RJB12787	AF416644
Single-species lineages			
<i>Sirobasidium japonicum</i> pro tem.		MY111_05	LC016573
<i>Sirobasidium magnum</i> pro tem.		CBS 6803	AF075475
Tremellaceae			
Tremella			
<i>T. brasiliensis</i>		CBS 6966 ^R	AF189864
<i>T. cinnabarina</i>		CBS 8234 ^R	AF189866
<i>T. coalescens</i>		CBS 6967 ^R	AF189865
<i>T. flava</i>		CBS 8471 ^R	AF042221
<i>T. fuciformis</i>		CBS 6970 ^R	AF075476
<i>T. globispora</i>		CBS 6972 ^R	AF189869
<i>T. laurisilvae</i>		TFC Mic.24580	
<i>T. mesenterica</i> ^T		CBS 6973 ^R	AF075518
<i>T. resupinata</i>		CBS 8488 ^R	AF042239
<i>T. taiwanensis</i>		CBS 8479 ^R	AF042230
<i>T. tropica</i>		CBS 8483 ^R	AF042251
<i>T. yokohamensis</i> comb. nov.	<i>C. yokohamensis</i>	JCM 16989 ^T	HM222927
Trimorphomycetaceae fam. nov.			
Carlosrosaea gen. nov.			
<i>C. vrieseae</i> ^T comb. nov.	<i>B. vrieseae</i>	CBS 13870 ^T	JX280388
Saitozyma gen. nov.			
<i>S. flava</i> ^T comb. nov.	<i>C. flavus</i>	CBS 331 ^T	AF075497
<i>S. ninhbinhensis</i> comb. nov.	<i>B. ninhbinhensis</i>	JCM 10836 ^T	AB261011
<i>S. parafflava</i> comb. nov.	<i>C. parafflavus</i>	CBS 10100 ^T	AY395799
<i>S. podzolica</i> comb. nov.	<i>C. podzolicus</i>	CBS 6819 ^T	AF075481

Table 1. (Continued).

Taxon	Basionym or important synonym	Strain	LSU D1D2
Sugitazyma gen. nov.			
<i>S. miyagiana</i> ^T comb. nov.	<i>Bullera miyagiana</i>	CBS 7526 ^T	AF189858
Trimorphomyces emend.			
<i>T. papilionaceus</i> ^T		CBS 443.92	AF075491
<i>T. sakaeratica</i> comb. nov.	<i>B. sakaeratica</i>	CBS 9934 ^T	AY211546
<i>Incertae sedis</i>			
<i>Tremella diploschistina</i> pro tem.		AM199 ^T	JN790588
<i>Tremella parmeliarum</i> pro tem.		Spain, Diederich 16574 (S-F102497)	JN043618
Trichosporonales			
Tetragonomycetaceae emend.			
Bandonia gen. nov.			
<i>B. marina</i> ^T comb. nov.	<i>Cryptococcus marinus</i>	CBS 5235 ^T	AF189846
Cryptotrichosporon			
<i>C. anacardii</i> ^T		CBS 9551 ^T	AY550002
<i>C. tibetense</i>		CBS 10455 ^T	KP020115
Takashimella			
<i>T. formosensis</i> ^T	<i>B. formosensis</i>	CBS 9812 ^T	AY787858
<i>T. koratensis</i>	<i>B. koratensis</i>	CBS 10484 ^T	AY313006
<i>T. lagerstroemiae</i>	<i>B. lagerstroemiae</i>	CBS 10483 ^T	AY313010
<i>T. tepidarius</i>	<i>C. tepidarius</i>	CBS 9427 ^T	AB094046
Tetragonomycetes			
<i>T. uliginosus</i> ^T	<i>Tremella uliginosa</i>	AM186	JN043621
Trichosporonaceae emend.			
Apiotrichum emend.			
<i>A. brassicae</i> comb. nov.	<i>Trichosporon brassicae</i>	CBS 6382 ^T	AF075521
<i>A. cacaoliposimilis</i> comb. nov.	<i>T. cacaoliposimilis</i>	ATCC 20505 ^T	HM755978
<i>A. dehoogii</i> comb. nov.	<i>T. dehoogii</i>	CBS 8686 ^T	AF444718
<i>A. domesticum</i> comb. nov.	<i>T. domesticum</i>	CBS 8280 ^T	AF075512
<i>A. dulciturum</i> comb. nov.	<i>Oospora dulciturum</i> <i>T. dulciturum</i>	CBS 8257 ^T	AF075517
<i>A. gamsii</i> comb. nov.	<i>T. gamsii</i>	CBS 8245 ^T	AF444708
<i>A. gracile</i> comb. nov.	<i>Oidium gracile</i> <i>T. gracile</i>	CBS 8189 ^T	AF105399
<i>A. laibachii</i> comb. nov.	<i>Endomyces laibachii</i> <i>T. laibachii</i> <i>T. multisporum</i>	CBS 5790 ^T	AF075514
<i>A. lignicola</i> comb. nov.	<i>Hyalodendron lignicola</i> <i>T. lignicola</i>	CBS 219.34 ^T	AY370685
<i>A. loubieri</i> comb. nov.	<i>Geotrichum loubieri</i> <i>T. loubieri</i>	CBS 7065 ^T	AF075522
<i>A. montevideense</i> comb. nov.	<i>Endomycopsis montevideensis</i> <i>T. montevideense</i>	CBS 6721 ^T	AF105397
<i>A. mycotoxinivorans</i> comb. nov.	<i>T. mycotoxinivorans</i>	CBS 9756 ^T	AJ601388
<i>A. porosum</i> ^T	<i>T. porosum</i>	CBS 2040 ^T	AF189833
<i>A. scarabaeorum</i> comb. nov.	<i>T. scarabaeorum</i>	CBS 5601 ^T	AF444710
<i>A. siamense</i> comb. nov.	<i>T. siamense</i>	JCM 12478 ^T	AB164370
<i>A. sporotrichoides</i> comb. nov.	<i>T. sporotrichoides</i>	CBS 8246 ^T	AF189885
<i>A. vadense</i> comb. nov.	<i>T. vadense</i>	CBS 8901 ^T	AY093426
<i>A. veenhuisii</i> comb. nov.	<i>T. veenhuisii</i>	CBS 7136 ^T	AF105400
<i>A. wieringae</i> comb. nov.	<i>T. wieringae</i>	CBS 8903 ^T	AY315666

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Table 1. (Continued).

Taxon	Basionym or important synonym	Strain	LSU D1D2
<i>A. xylopinii</i> comb. nov.	<i>Trichosporon xylopinii</i>	CBS 11841 ^T	HQ005757
Cutaneotrichosporon gen. nov.			
<i>C. arboriformis</i> comb. nov.	<i>Cryptococcus arboriformis</i>	CBS 10441 ^T	AB260936
<i>C. curvatus</i> comb. nov.	<i>C. curvatus</i>	CBS 570 ^T	AF189834
<i>C. cutaneum</i> ^T comb. nov.	<i>Oidium cutaneum</i> <i>T. cutaneum</i>	CBS 2466 ^T	AF075483
<i>C. cyanovorans</i> comb. nov.	<i>C. cyanovorans</i>	CBS 11948 ^T	JF680899
<i>C. daszewskae</i> comb. nov.	<i>C. daszewskae</i>	CBS 5123 ^T	AB126588
<i>C. debeurmannianum</i> comb. nov.	<i>T. debeurmannianum</i>	CBS 1896 ^T	AY143554
<i>C. dermatis</i> comb. nov.	<i>T. dermatis</i>	CBS 2043 ^T	AY143555
<i>C. guehoae</i> comb. nov.	<i>T. guehoae</i>	CBS 8521 ^T	AF105401
<i>C. hagleorum</i> comb. nov.	<i>C. hagleorum</i>	CBS 8902 ^T	AF407276
<i>C. jirovecii</i> comb. nov.	<i>T. jirovecii</i>	CBS 6864 ^T	AF105398
<i>C. moniliiforme</i> comb. nov.	<i>O. moniliiforme</i> <i>T. moniliiforme</i>	CBS 2467 ^T	AF105392
<i>C. mucoides</i> comb. nov.	<i>T. mucoides</i>	CBS 7625 ^T	AF075515
<i>C. oleaginosus</i> comb. nov.	<i>T. oleaginosus</i>	ATCC 20509 ^T	HM802135
<i>C. smithiae</i> comb. nov.	<i>T. smithiae</i>	CBS 8370 ^T	AF444706
<i>C. terricola</i> comb. nov.	<i>T. terricola</i>	CBS 9546 ^T	AB086382
Effuseotrichosporon gen. nov.			
<i>E. vanderwaltii</i> comb. nov.	<i>T. vanderwaltii</i>	CBS 12124 ^T	JF680903
Haglerozyma gen. nov.			
<i>H. chiarellii</i> ^T comb. nov.	<i>T. chiarellii</i>	CBS 11177 ^T	EU030272
Trichosporon			
<i>T. aquatile</i>		CBS 5973 ^T	AF075520
<i>T. asahii</i>		CBS 2479 ^T	AF105393
<i>T. asteroides</i>		CBS 2481 ^T	AF075513
<i>T. caseorum</i>		CBS 9052 ^T	AJ319757
<i>T. coremiiforme</i>		CBS 2482 ^T	AF139983
<i>T. dohaense</i>		CBS 10761 ^T	FJ228471
<i>T. faecale</i>		CBS 4828 ^T	AF105395
<i>T. inkin</i>		CBS 5585 ^T	AF105396
<i>T. insectorum</i>		CBS 10422 ^T	AY520383
<i>T. japonicum</i>		CBS 8641 ^T	AF308657
<i>T. lactis</i>		CBS 9051 ^T	AJ319756
<i>T. ovooides</i> ^T		CBS 7556 ^T	AF075523
Vanrija			
<i>V. albida</i>	<i>Sporobolomyces albidus</i>	CBS 2839 ^T	AB126584
<i>V. fragicola</i> comb. nov.	<i>C. fragicola</i>	CBS 8898 ^T	AB126585
<i>V. humicola</i> ^T	<i>Torula humicola</i> <i>Candida humicola</i>	CBS 571 ^T	AF189836
<i>V. longa</i>	<i>C. longus</i>	CBS 5920 ^T	AB126589
<i>V. meifongana</i> comb. nov.	<i>Asterotremella meifongana</i>	CBS 11424 ^T	EU289356
<i>V. musci</i>	<i>C. musci</i>	CBS 8899 ^T	AB126586
<i>V. nantouana</i> comb. nov.	<i>Asterotremella nantouana</i>	CBS 10890 ^T	EF653952
<i>V. pseudolongus</i>	<i>C. pseudolongus</i>	CBS 8297 ^T	AB126587
<i>V. thermophila</i> comb. nov.	<i>C. thermophilus</i>	CBS 10687 ^T	AM746982

Table 2. PRBO results showing the divergences, if any, of the proposed taxa (except for the families) from the optimal range of divergences for their rank as inferred from the selected reference taxa.

Taxa	Rank	MaSH	Deviation	Sigdev
Cystofilobasidiales	Order	0.7211	-0.1226	0
<i>Cystofilobasidium</i> *	Genus	0.2518	0	0
<i>Krasilnikovozyma</i> (huempii clade)	Genus	0.0003	0	0
<i>Itersonilia</i>	Genus	0.0672	0	0
<i>Mrakia</i> *	Genus	0.2071	0	0
<i>Phaffia</i>	Genus	0.1028	0	0
<i>Tausonia</i>	Genus	–	–	–
<i>Udeniomyces</i> *	Genus	0.1326	0	0
Filobasidiales	Order	0.5866	-0.2570	-0.1242
<i>Filobasidium</i>	Genus	0.2465	0	0
<i>Naganishia</i> (albidus clade)	Genus	0.1835	0	0
<i>Goffeauzyma</i> (gastricus clade)	Genus	0.3281	0	0
<i>Solicoccozyma</i> (aerius clade)	Genus	0.2537	0	0
<i>Piskurozyma</i> (cylindricus clade)	Genus	0.1235	0	0
<i>Cryptococcus arrabidensis</i>	Genus	–	–	–
<i>Filobasidium capsuligenum</i>	Genus	–	–	–
Holtermanniales	Order	0.4607	0	0
<i>Holtermanniella</i> *	Genus	0.1832	0	0
<i>Holtermannia</i>	Genus	–	–	–
Tremellales	Order	0.9475	0	0
<i>Naematelia</i> (aurantia clade and <i>C. cistialbidi</i>)	Genus	0.3098	0	0
<i>Rhynchogastrema</i>	Genus	0.1336	0	0
<i>Bulleribasidium</i> *	Genus	0.3380	0	0
<i>Bullera</i> (<i>Bullera</i> and <i>hannae</i> clades)	Genus	0.4009	0.0597	0.0476
<i>Cryptococcus</i>	Genus	0.2325	0	0
<i>Derxomyces</i> *	Genus	0.6263	0.2851	0.2730
<i>Dioszegia</i> *	Genus	0.3296	0	0
<i>Genolevuria</i> (amylolyticus clade)	Genus	0.1985	0	0
<i>Fellomyces</i>	Genus	0.3096	0	0
<i>Fibulobasidium</i> *	Genus	0.0971	0	0
<i>Phaeotremella</i> (foliacea clade)	Genus	0.2697	0	0
<i>Hannaella</i> *	Genus	0.2876	0	0
<i>Kockovaella</i>	Genus	0.3573	0.0161	0.0040
<i>Kwoniella</i>	Genus	0.3335	0	0
<i>Papiliotrema</i> (<i>aureus</i> , <i>Auriculibuller</i> , <i>Papiliotrema</i> , <i>pseudoalba</i> , <i>laurentii</i> clades)	Genus	0.3345	0	0
<i>Pseudotremella</i> (<i>moriformis</i> clade and <i>C. allantoinivorans</i>)	Genus	0.2068	0	0
<i>C. mujuensis</i> and <i>S. intermedium</i>	Genus	0.2123	0	0
<i>Saitozyza</i> (<i>flavus</i> clade)	Genus	0.3187	0	0
<i>Nielozyma</i> (<i>melastomae</i> clade)	Genus	0.1478	0	0
<i>Tremella</i>	Genus	0.4809	0.1397	0.1276
<i>Vishniacozyma</i> (<i>dimennae</i> clade)	Genus	0.3674	0.0262	0.0141

Table 2. (Continued).

Taxa	Rank	MaSH	Deviation	Sigdev
Trichosporonales	Order	0.4386	-0.4050	-0.2722
<i>Cutaneotrichosporon</i> (<i>cutaneum</i> clade and <i>haglerorum</i> clade)	Genus	0.2107	0	0
<i>Takashimella</i> (<i>formosensis</i> clade)	Genus	0.1490	0	0
<i>Apiotrichum</i> (<i>gracile/brassicae</i> and <i>porosum</i> clade)	Genus	0.2377	0	0
<i>Trichosporon</i> *	Genus	0.2250	0	0
<i>Vanrija</i> (<i>humicola</i> clade)	Genus	0.1955	0	0
<i>Cryptotrichosporon</i>	Genus	–	–	–

Note. MaSH: Maximum Subtree Height; Deviation: deviation from the point estimate for the upper (positive value) or lower (negative value) threshold of the rank of the taxon; Sigdev: significant deviation, i.e. a deviation even outside the upper or lower 95 % confidence band of the upper or lower threshold, respectively. Zero indicates taxa with the appropriate divergence, negative values indicate taxa that are too small, positive values taxa that are too large. An asterisk (*) indicates the well-established taxa that were used as a reference classification for PRBO. A dash (–) indicates taxa that are monotypic in the investigated sampling, for which MaSH is not calculated. Numbers in bold indicate significant deviation from the range defined by the optimal boundaries calculated for the rank.

confidence intervals. A taxon was regarded as too large or too small in a strict sense when its MaSH was outside the MaSH range of its rank, and as deviating in even a relaxed sense (i.e. significantly deviating) when its MaSH was not even located within the outer confidence bounds. Ten genera (Table 2) of tremellomycetous yeasts and their parent taxa were chosen as references. These genera are considered as being well delimited phenotypically and phylogenetically because they were resolved as strongly supported monophyletic clades with stable positions in the trees derived from different datasets using different algorithms (Liu *et al.* 2015) and the species in each genus exhibit similar morphological or physiological properties. The resulting optimal MaSH thresholds and their 95 % confidence intervals were then applied to the entire dataset.

In addition, we used a modified GMYC (generalised mixed Yule coalescent) method designed to identify evolutionary significant units (Humphreys & Barraclough 2014). The GMYC method was originally developed for species delimitation (Pons *et al.* 2006, Monaghan *et al.* 2009) and subsequently extended for identifying higher taxonomic units, also called evolutionary significant units (Humphreys & Barraclough 2014). The method allows, without prior expectations, locating independently evolving lineages as a transition from intra- to intertaxa relationships on a phylogenetic tree. It aims at detecting shifts in branching rates between relationships within and among evolutionary significant units. The most recent common ancestral node at the transition point is interpreted as distinguishing taxa at a specific level. Within a likelihood framework it uses chronograms to compare two models: a) a null model under which the whole sample derives from a single evolutionary significant unit and b) an alternative GMYC model. The latter combines equations that separately describe branching patterns within and among evolutionary units. A likelihood ratio test (LRT) is used to evaluate whether the null model can be significantly rejected. If the GMYC model fits the data significantly better than the null model, the threshold T allows estimating the number of evolutionary significant units (to be interpreted as higher taxa) present in the dataset. Outgroup samples were excluded from the dataset using the drop.tip command in ape (Paradis 2006). A

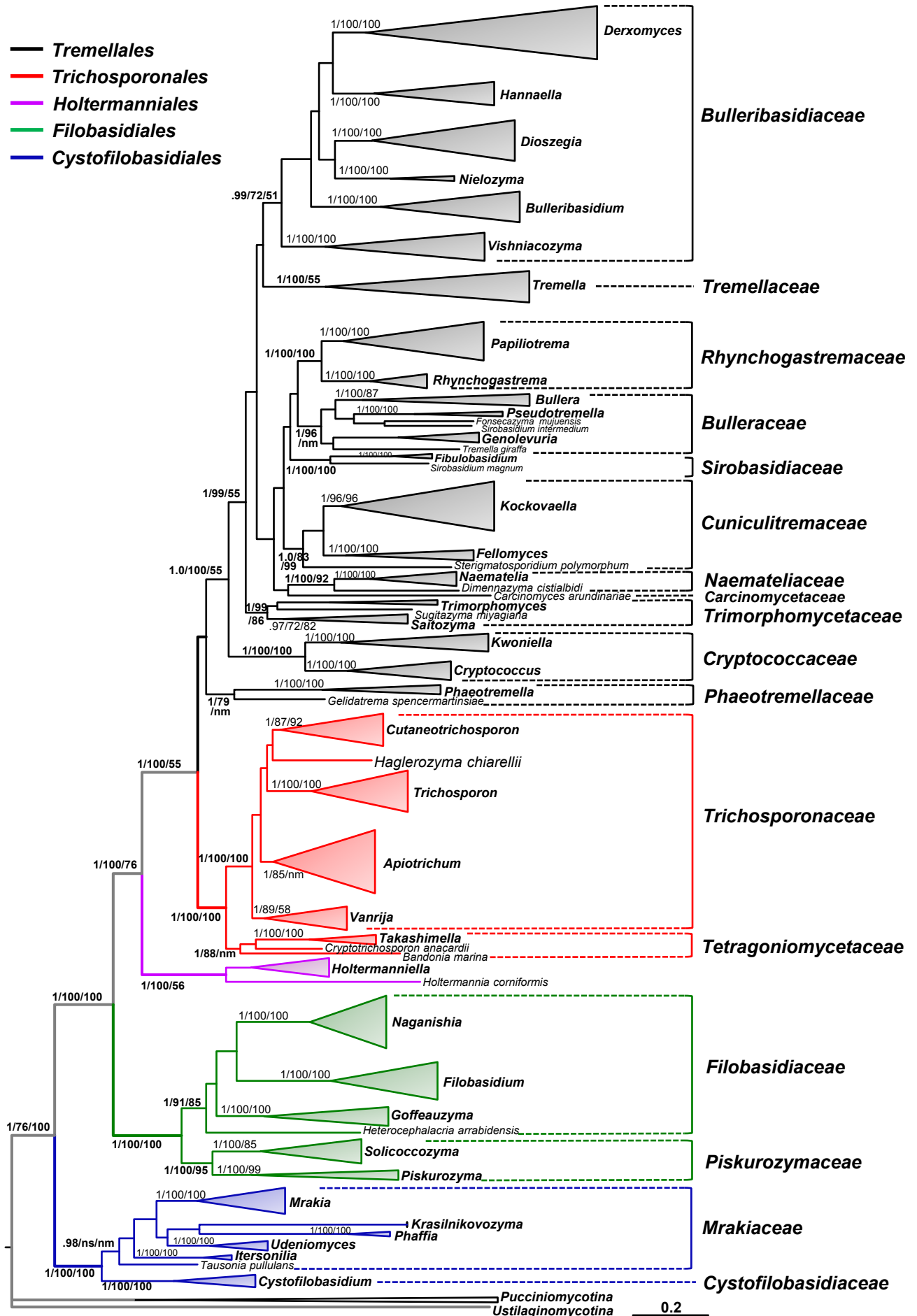


Fig. 1. A taxonomic framework of genera and higher levels in *Tremellomycetes* based on the seven-genes phylogeny (Liu et al. 2015). The tree backbone is constructed using Bayesian analysis and branch lengths are scaled in terms of expected numbers of nucleotide substitutions per site. The Bayesian posterior probabilities (PP) and bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1 000 replicates are shown respectively from left to right on the deep and major branches resolved. Note: ns, not supported (PP < 0.9 or BP < 50 %); nm, not monophyletic.

chronogram was calculated from the ML tree using the penalised likelihood method (Sanderson 2002) as implemented in the `chronopl` function in `ape` (Paradis 2006). The chronogram was then analysed using a modified GMYC package in `SPLITS` in `R` (R core team 2015) version 2.10, using the single-threshold method. Since the method identifies order units, we subsequently performed nested analyses for each major order to identify evolutionary significant units. That is, the modified GMYC model was applied iteratively to subtrees identified as evolutionary significant units in the respective last step.

The major differences in perspective between the two approaches are as follows. The modified GMYC method presupposes an ultrametric tree but is independent of an existing classification. When using the single-threshold approach, the modified GMYC method is capable of identifying taxa of a similar divergence, measured as evolutionary age. If applied iteratively, however, there is no guarantee even under the single-threshold model that the thresholds of all taxa obtained in the second, third etc. iteration are at a comparable level of divergence, because the thresholds are independently estimated for each tree obtained by splitting the tree of the last iteration. The iteratively applied modified GMYC method is ideal for obtaining taxa of several ranks that correspond to evolutionarily significant units in the sense of Humphreys & Barraclough (2014). It does not guarantee to obtain taxa of the same rank that are quantitatively comparable and cannot minimise the deviations from an existing classification.

In contrast, PRBO is independent of a molecular clock (can be applied to either ultrametric or non-ultrametric trees) but as used here it assumes an existing classification for at least some of the organisms under study. Boundaries for missing ranks could be derived by interpolation but this was not applied in this study. It is capable of obtaining taxa of the same rank that are quantitatively comparable, measured as evolutionary age or just as maximum subtree height, because the boundaries of all ranks are inferred from the entire dataset at once. It is also able to minimise the deviations from an existing classification, but only as the secondary criterion. Moreover, PRBO often allows the taxonomist, within the limits set by the estimated boundaries, several choices for delineating taxa. It does not guarantee, however, to find taxa that are “real” or evolutionary significant units.

It must be emphasised, however, that none of the two methods was followed strictly in the current study, even where they agreed on taxon boundaries. As far as possible, broader circumscriptions of taxa were chosen to lower the number of suggested names, particularly if these taxa were newly introduced, had strong branch support, or showed diagnostic phenotypical features. These principles will be illustrated by examples given below.

RESULTS AND DISCUSSION

Taxonomic units assessed by PRBO and a modified GMYC approach

A taxonomic framework was firstly proposed based on the seven-genes phylogeny (Liu *et al.* 2015) as shown in Fig. 1, which was the basis for further taxonomic unit assessment and expanded LSU dataset analysis. Based on the PRBO analysis

including 286 taxa represented by 294 strains of tremellomycetous yeasts, strong delimitation evidence was found for the orders *Cystofilobasidiales*, *Holtermanniiales* and *Tremellales*, which showed no significant deviation from the range defined by the optimal boundaries calculated for their rank (Table 2). The demarcation of orders *Filobasidiales* and *Trichosporonales* showed a small negative, significant deviation (Sigdev = -0.1242 and -0.2722, respectively), i.e. these orders were judged too small, most likely because of the overlap between the divergences of taxa of distinct ranks. The recognition of *Filobasidiales* as a distinct monophyletic lineage in *Tremellomycetes* is consistent in many studies (Fell *et al.* 2000, Scorzetti *et al.* 2002, Weiss *et al.* 2004, Hibbett *et al.* 2007, Boekhout *et al.* 2011a, Millanes *et al.* 2011, Liu *et al.* 2015). Therefore, and for reasons of conservatism we keep it as a single order. The recognition of *Trichosporonales* remains a matter of debate. Some authors placed this order within *Tremellales* (Weiss *et al.* 2004, Hibbett *et al.* 2007, Millanes *et al.* 2011), while others accepted it as a sister group to *Tremellales* (Scorzetti *et al.* 2002, Boekhout *et al.* 2011a, Weiss *et al.* 2014). The problem was probably caused by the unstable phylogenetic position of the **foliacea** clade. It appeared as an early branching clade of the *Tremellales* in the Bayesian tree but posterior probability (PP) support for this positioning was lacking. In the ML and NJ tree, the **foliacea** clade was branching before the *Trichosporonales* and the *Tremellales* lineages with strong to moderate bootstrap support values (data not shown). When the **foliacea** clade was considered as an independent lineage as implied by the results shown above, the monophyly of both *Trichosporonales* and *Tremellales* was resolved by Bayesian and ML analyses of a seven-genes dataset with 1.0 posterior probability and 100 % bootstrap support (Liu *et al.* 2015). In the LSU tree the node delimiting *Tremellales* was not originally constrained and received poor to moderate support in ML and MP analyses, respectively, while other nodes in *Tremellales* received lower support (Fig. 2). This implies that undersampling may substantially influence the delimitation of clades, and, therefore, we presently consider *Trichosporonales* as a distinct order based on its phylogenetic position and phenotypic characters.

Ten genera or clades of tremellomycetous yeasts which were consistently resolved as monophyletic groups with strong statistical support in the trees constructed using different datasets and algorithms (Liu *et al.* 2015) were used as references in the PRBO test (Table 2). Six of these genera, *Bulleribasidium* emend., *Deroxomyces*, *Dioszegia*, *Fibulobasidium*, *Hannaella* and *Holtermanniella*, have been accepted as well-established genera based on their distinct morphological characters and phylogenetic positions (Bandoni 1979, Wang & Bai 2008, Wang *et al.* 2011, Wuczowski *et al.* 2011). Of the 44 monotypic genera or clades identified in this study based on the multigene phylogeny (Liu *et al.* 2015), the majority (34 genera) was in agreement with the PRBO results (Table 2). Five genera showed significant deviation from the optimal range calculated for the genus rank, namely *Bullera* emend., *Deroxomyces*, *Kockovaella* emend., *Tremella* sensu stricto and *Vishniacozyma* gen. nov. (i.e. the **dimennae** clade). The emended genus *Bullera* contains four species that were located in two clades (i.e. **Bulleromyces** and **hannae** clades) in Liu *et al.* (2015). The GC contents of the species in the **Bulleromyces** and **hannae** clades are 53.3–55.4 % and 42.7–44.5 %, respectively. These data support the significant deviation of the four species assigned to a single genus. We nevertheless propose to keep them in the

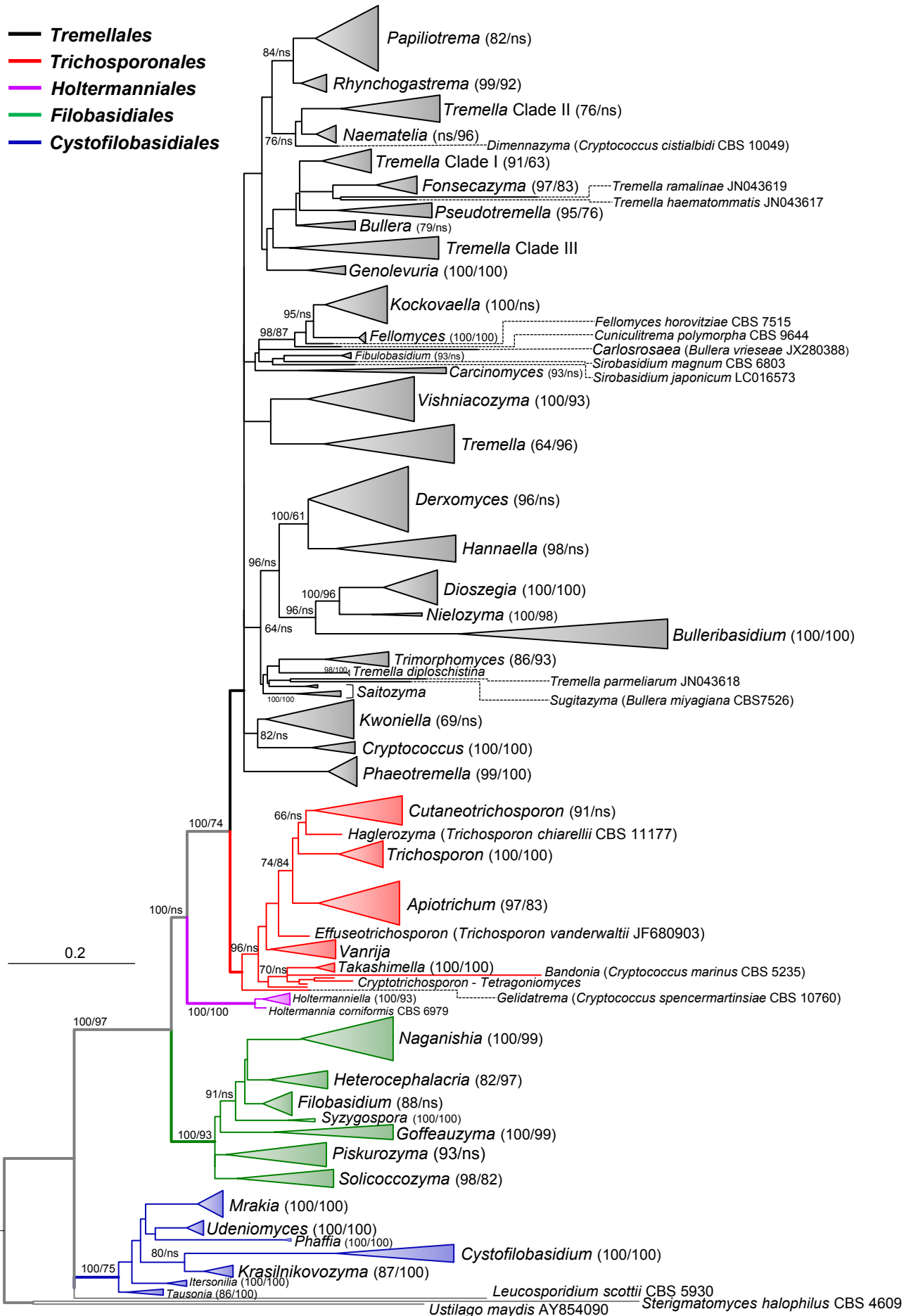


Fig. 2. Phylogenetic relationships of yeasts and related taxa in *Tremellomycetes* (major lineages) obtained by maximum-likelihood analysis of LSU (D1/D2 domains) rRNA gene. Tree topology was backbone-constrained with the well-supported (>85 %) bipartitions of the topology of the seven-genes tree (Liu et al. 2015). Bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1000 replicates are shown respectively from left to right on the deep and major branches resolved and in brackets following recognised clades. Note: ns, not supported (BP < 50 %).

Table 3. The family identification using single thresholds model in mixed Yule coalescent method (GMYC) and its comparison with the taxonomic units delimited according to phylogeny and morphological characters.

Order	Genus (or single-species clade)	GMYC ST	PP/BP ¹ / BP ²	Accepted	PP/BP ¹ / BP ²
Cystofilobasidiales	<i>Cystofilobasidium</i>	new family 1	1.0/100/100	<i>Cystofilobasidiaceae</i>	1.0/100/100
	<i>Tausonia</i>	new family 2	0.98/ns/nm	<i>Mrakiaceae</i>	0.98/ns/nm
	<i>Krasilnikovozyma</i>				
	<i>Itersonilia</i>				
	<i>Mrakia</i>				
	<i>Udeniomyces</i>				
	<i>Xanthophyllomyces</i>				
Filobasidiales	<i>Piskurozyma</i>	new family 3	1.0/100/99	<i>Piskurozymaceae</i>	1.0/100/95
	<i>Filobasidium capsuligenum</i>				
	<i>Solicoccozyma</i>	new family 4	1.0/100/85		
	<i>Goffeauzyma</i>	new family 5	1.0/100/100	<i>Filobasidiaceae</i>	1.0/91/85
	<i>Filobasidium</i>	new family 6	1.0/100/100		
	<i>Fonsecazyma</i>	new family 7	1.0/100/100		
	<i>Cryptococcus arrabidensis</i>	Single-species clade	/		
Tremellales	<i>Phaeotremella</i>	new family 8	1.0/79/nm	<i>Phaeotremellaceae</i>	1.0/79/nm
	<i>C. spencermartinsiae</i>				
	<i>Cryptococcus</i>	new family 9	1.0/100/100	<i>Cryptococcaceae</i>	1.0/100/100
	<i>Kwoniella</i>	new family 10	1.0/100/100		
	<i>Naematelia</i>	new family 11	ns/nm/nm	<i>Naemateliaceae</i>	ns/nm/nm
	<i>B. arundinariae</i>				
	<i>Rhynchogastrema</i>	new family 12	1.0/100/100	<i>Rhynchogastremaceae</i>	1.0/100/100
	<i>Papiliotrema</i>	new family 13	1.0/100/100		
	<i>Bullera</i>	new family 14	nm/nm/nm	<i>Bulleraceae</i>	1.0/96/nm
	<i>Genolevuria</i>				
	<i>Pseudotremella</i>				
	<i>Cryptococcus mujuensis, Sirobasidium intermedium, Tremella giraffa</i>				
	<i>Fibulobasidium</i>			<i>Sirobasidiaceae</i>	1.0/100/99
	<i>Sirobasidium magnum</i>				
	<i>Fellomyces</i>	new family 15	1.0/83/99	<i>Cuniculitremaeae</i>	1.0/83/99
	<i>Kockovaella</i>				
	<i>Cuniculitrema polymorpha</i>				
	<i>Tremella</i>	new family 17	1.0/100/55	<i>Tremellaceae</i>	1.0/100/55
	<i>Saitozyma</i>	new family 18	1.0/99/86	<i>Trimorphomycaceae</i>	1.0/99/86
	<i>Bullera miyagiana, B. sakaeratica, Trimorphomyces papilionaceus</i>				
	<i>Vishniacozyma</i>	new family 16	1.0/100/100	<i>Bulleribasidiaceae</i>	.99/72/51
	<i>Derxomyces</i>	new family 19	1.0/100/100		
	<i>Hannaella</i>	new family 20	1.0/100/100		
<i>Bulleribasidium</i>	new family 21	1.0/100/100			
<i>Dioszegia</i>	new family 22	1.0/91/nm			
<i>Nielozyma</i>					
Trichosporonales	<i>Takashimella</i>	new family 23	1.0/88/nm	<i>Tetragonimycetaceae</i>	1.0/88/nm
	<i>Cryptotrichosporon anacardii, Cryptococcus marinus</i>				
	<i>Cutaneotrichosporon</i>	new family 24	1.0/100/100	<i>Trichosporaceae</i>	1.0/100/100
	<i>Apiotrichum</i>				
	<i>Haglerozyma</i>				
	<i>Trichosporon Vanrija</i>				

Note. GMYC ST: the family delimitation using GMYC for single thresholds (ST) model across seven-gene ML tree; PP, Bayesian posterior probability; BP¹ and BP², bootstrap values from the maximum likelihood and neighbour-joining analyses, respectively; nm: not monophyletic; ns, not supported (PP < 0.9 or BP < 50 %).

emended genus *Bullera* at present to accommodate their phenotypic similarity and to avoid suggesting a new genus with only two species. The significant deviation of the genus *Dexomyces* resulted from the inclusion of the early branching species *D. anomala*, which showed a remarkable divergence from the other species of the genus in the tree inferred from the seven genes (Liu et al. 2015). We prefer to maintain the current taxonomic status of this species to avoid creating a single-species clade or a monotypic genus without specific phenotypic characters. The significant deviation of the genus *Kockovaella* emend. was caused by the inclusion of *Fellomyces fuzhouensis* in this genus. This species branches first within the *Kockovaella* clade with strong support (Liu et al. 2015) and is morphologically similar to the other species of the genus by forming conidia on stalks (Lopandic et al. 2011). Thus, at present we prefer to assign this species to the emended genus *Kockovaella*. The new genus *Vishniacozyma* is proposed for the strongly supported **dimennae** clade (Table 1, Fig. 1) (i.e. **vic-toriae** clade in Fonseca et al. 2011) including one *Bullera* and six *Cryptococcus* species in the seven-genes tree (Fig. 1). Two strongly supported sub-clades containing two and five species, respectively, were recognised in this clade (Liu et al. 2015). The combination of these two sub-clades into a single genus is due to the consideration that they are phenotypically indistinguishable. The *Tremella sensu stricto* clade (i.e. the **mesenterica** clade in Boekhout et al. 2011a) exclusively contains *Tremella* species, including the type species of the genus, *T. mesenterica*, together with other representatives of the **mesenterica** and **fuciformis** subclades as distinguished by Chen (1998) and Liu et al. (2015). Several ecological and morphological features can be used to distinguish both subclades (Chen 1998): 1) basidiocarps are frequently associated with fungi of Russulales (*Peniophora*) in the **mesenterica** subclade, and with fungi of Xylariaceae (*Hypoxilon* or *Xylaria*) in the **fuciformis** subclade; 2) hymenial and subhymenial structures are loose in the **mesenterica** subclade in contrast to firm with numerous anastomoses present in the **fuciformis** subclade; 3) hyphidia are present in the **mes-entherica** subclade but lacking in the **fuciformis** subclade; and 4) haustorial hyphae are not branched in the **mesenterica** subclade in contrast to those of the species in the **fuciformis** subclade. The genus *Tremella* containing approximately 90 species (Kirk et al. 2008) is highly polyphyletic and remains to be recircumscribed (Millanes et al. 2011, Weiss et al. 2014, Liu et al. 2015). We propose to keep the species in the *Tremella sensu stricto* clade in this genus at present. We also caution against the use of the generic name *Tremella* for newly described species outside that clade.

Phylogenetic demarcation of families in the Fungi is usually difficult due to the lack of molecular data from many taxa (Hibbett et al. 2007). This is also the case for *Tremellomycetes* at present because the rRNA gene sequences of many filamentous members of this class are not yet available for an integrated phylogenetic analysis (e.g. Millanes et al. 2011, Lindgren et al. 2015). The boundaries of the existing families within *Tremellomycetes* have not been subjected to robust phylogenetic analyses based on sufficient taxon sampling, thus family boundaries could only be derived by PRBO via interpolation, which was not applied here because the number of established genera is also small. The modified GMYC approach (Humphreys & Barraclough 2014), which does not need the reference information, was used to assign families, and the resulting taxa were then assessed using PRBO. The LRT test resulted in the

recognition of two families in *Cystofilobasidiales*, five in *Filobasidiales*, 15 in *Tremellales* and two in *Trichosporonales* (Table 3). Some of the families identified in *Filobasidiales* and *Tremellales* using the GMYC approach lacked phylogenetic support. Therefore, we adjusted the family boundaries from a conservative point of view and a combined consideration on phylogenetic and phenotypic criteria, resulting in the proposal of two families in *Filobasidiales* and ten in *Tremellales* (Table 3).

The two families recognised in *Cystofilobasidiales* by the GMYC test are accepted here. Family 1 is equivalent to *Cystofilobasidiaceae* (Fell et al. 1999) and *Mrakiaceae* fam. nov. is proposed to accommodate family 2. They are supported phenotypically by the morphology and size of basidia and phylogenetically by the seven-genes Bayesian analysis. The former usually produces long and slender (up to 65 µm) holobasidia, while the teleomorphic taxa of the latter usually form short and tubular (8–12 µm) holo- or phragmometabasidia. The two families recognised in *Trichosporonales* by the GMYC test are also accepted and are assigned to *Trichosporonaceae* (family 23) and *Tetragoniomycetaceae* (family 24). The majority of the taxa in the former can produce arthroconidia while the latter can not. Each of them also received strong phylogenetic support (Table 3).

The five clades resolved in the *Filobasidiales* obtained from the seven-genes phylogeny (Liu et al. 2015) were recognised as representing a family each (families 3–7) by the GMYC test (Table 3). However, discriminative phenotypic criteria among these clades were difficult to find from the morphological, biochemical and physiological characters that have been investigated (Kurtzman et al. 2011b). From a practical point of view, we suggest to combine families 3 and 4 (i.e. the **aerius** and **cylindricus** clades in Fonseca et al. 2011 and Liu et al. 2015) into a single new family *Piskurozymaceae* fam. nov. and combine families 5–7 together with the single-species lineage *Cryptococcus arrabidensis* into *Filobasidiaceae*.

The family recognition in the order *Tremellales* was more complicated and five (families 8, 11, 15, 17 and 18) of the 15 families recognised by the GMYC test are accepted as well delimited families with phenotypic and phylogenetic support (Table 3). The genera *Cryptococcus sensu stricto* (i.e. the **Filobasidiella** clade in Fonseca et al. 2011) and *Kwoniella* were identified as representing two separate families (families 9 and 10) by the GMYC test, but we suggest to combine them as a single family *Cryptococcaceae* in view of their close phylogenetic relationship with strong support (Liu et al. 2015) and both contain human or arthropod-associated species (Findley et al. 2009). We propose to combine families 12 and 13 (Table 3) identified by the GMYC test into a single family *Auriculibulleraceae*, which is phylogenetically strongly supported (Liu et al. 2015). Family 14 determined by the GMYC analysis was a paraphyletic group in the seven-genes tree (Liu et al. 2015), thus we divided it into two separate families, namely *Bulleraceae* and *Sirobasidiaceae*. The **dimennae**, **Dexomyces**, **Hannaella**, **Bulleribasidium** and **Dioszegia** (together with the melostomae clade) clades were recognised as representing a family each (families 16 and 19–22) by the GMYC test (Table 3). These clades consist of species previously belonging to the genera *Bullera* or *Cryptococcus* (Wang & Bai 2008, Fonseca et al. 2011, Wang et al. 2011), suggesting their phenotypic similarity. Therefore, we propose to combine these five clades into a single family *Bulleribasidiaceae*, which showed good support values in the seven-genes analyses, both in Bayesian and ML trees (Fig. 1).

Taxonomic impact of the expanded LSU rDNA sequence dataset analysis

The phylogenetic analysis using the seven-genes sequence dataset contained limited teleomorphic and filamentous species of Tremellomycetes. For a better understanding of the phylogenetic relationships between anamorphic (mostly well represented in the analysis in Liu *et al.* 2015) and teleomorphic species in Tremellomycetes, more teleomorphic species were added to the expanded LSU rDNA dataset. In public databases these taxa are often known from a limited number of rRNA gene sequences derived from herbarium specimens. Furthermore, several recently published yeast species were also added to the LSU dataset. The constrained ML analysis of the expanded LSU dataset was used to place species known from LSU sequences in the phylogenetic clades previously recognised in the analysis of the seven genes (Fig. 1). Results from the LSU analysis were not used to challenge the results of multi-gene studies (Findley *et al.* 2009, Millanes *et al.* 2011, Liu *et al.* 2015), but to enlarge undersampled clades in Liu *et al.* (2015) and to investigate the stability of these clades.

In agreement with the few available multigene studies (Findley *et al.* 2009, Millanes *et al.* 2011, Liu *et al.* 2015), our results showed that LSU alone is not sufficient to resolve many clades in Tremellomycetes and the topology of the best tree from the unconstrained ML analysis (data not shown) differed from the seven-genes tree in Liu *et al.* (2015). Enforcing topological constraints and enlarging step-wise the dataset from 396 (data not shown) to 435 taxa, resulted in a slightly altered topology and, on average, acceptable bootstrap values (Fig. 2). Sequences containing ambiguities and missing data (e.g. from herbarium specimens) and species with unclear phylogenetic placement resulted in decreased average bootstrap values from 79.04 % in the 396-taxa-dataset (data not shown) to 69.05 % in the 435-taxa-dataset, respectively. In particular, support values of the **aurantia** clade comprised by *Tremella aurantia*, *T. indecorata* and *T. encephala* and strongly supported in Liu *et al.* (2015) decreased substantially, while support values for the clade containing *Cryptococcus mujuensis* increased. The constrained ML tree obtained from the expanded LSU rRNA gene sequence dataset did not change the main taxonomic conclusions (Fig. 2). Among the clades supported in Liu *et al.* (2015) poor or no support was observed for the clade (*Saitozyma*) comprised by *C. flavus*, *C. parafflavus* and *C. podzolicus* (Figs 1 and 2).

The addition of the supplemental species or strains resulted in the enlargement of several clades, especially single-species lineages recognised in the seven-genes tree, e.g. *Bullera arundinariae*, *Cryptococcus arrabidensis*, *C. mujuensis*, *Filobasidium capsuligenum*, and *Tremella giraffa* (Fig. 2). In addition, a few new clades were identified (Fig. 2, Table 1). The addition of the recently described species *Cryptococcus tahquamenonensis* (Sylvester *et al.* 2015) to the monotypic **huempii** clade recognised in the seven-genes dataset in the *Cystofilobasidiales* supports the proposal of a new genus (*Krasilnikovozyma* gen. nov.) for this clade (Fig. 3). Thirteen of the supplemental sequences corresponding to nine species were located in the Filobasidiales (Fig. 4). The single-species clade represented by *Cryptococcus arrabidensis* in the seven-genes tree was expanded to contain eight species including two *Syzygospora* and five undescribed *Cryptococcus* species with high (82 % in ML and 97 % in MP, respectively) bootstrap support (Fig. 4),

confirming that this clade represents a distinct genus, for which the older name *Heterocephalacria* is reinstated (Fig. 4, see **Taxonomy** section). The **cylindricus** clade containing two *Cryptococcus* species recognised in the seven-genes tree (Liu *et al.* 2015) was expanded to include *Syzygospora sorana*, *Filobasidium capsuligenum* and three additional *Cryptococcus* species. The expanded clade received 93 % and 92 % bootstrap support in the ML and MP trees, respectively (Fig. 4). The teleomorphic species *Christiansenia pallida* and *Syzygospora alba*, the type species of the genus *Syzygospora*, formed a distinct new clade with 100 % bootstrap support (Fig. 4). This result supports the transfer of *C. pallida* to the genus *Syzygospora* as proposed previously by Ginns (1986) and shown by Millanes *et al.* (2011). The remaining four clades recognised in the Filobasidiales in Liu *et al.* (2015) remain unchanged (Figs 1, 2 and 4).

In the Tremellales, the majority of the newly added *Tremella* species were located in the *Tremella*-containing clades recognised previously, including clades I, II and III, which were distinguished by Millanes *et al.* (2011) for lichenicolous taxa. These three clades exclusively or mainly contained *Tremella* species (Fig. 5A, B). The strongly supported **aurantia** clade in the seven-genes tree, comprising *T. aurantia*, *T. indecorata* and *T. encephala*, was extended with two species, namely *T. aurantialba* and *T. microspora* (Fig. 5A). The phylogenetic position of *T. indecorata* in the LSU tree was controversial because the support for this clade was decreasing with increasing dataset size and because sequences representing this taxon appeared to be separated in the tree. Nucleotide sequences of *T. indecorata* derived from strains CBS 6976 (used in Liu *et al.* 2015) and DSM 5727 grouped together, while a sequence derived from a herbarium specimen (used in Millanes *et al.* 2011) was placed close to *T. moriformis* (Fig. 5B). The latter sequence was also identical to the sequence of *T. subanomala* strain NBRC 9308 (collected by R.J. Bandoni), which is available in the online catalogue of the NBRC collection (NITE, Japan). Thus additional sampling is needed to assess the phylogenetic position of *T. indecorata*. We recognise the resolving power of multi-gene trees and despite lack of support in the LSU phylogeny, the **aurantia** clade will be treated as a separate genus, for which the name *Naematelia* is available (Fig. 5A). The **foliaceae** clade formed by one *Tremella* and two *Cryptococcus* species recognised previously (Liu *et al.* 2015) was expanded to include four more *Tremella* species represented by eight strains with high (99 % in ML and 100 % in MP) bootstrap support (Fig. 5C). This clade will also receive generic rank and the available name *Phaeotremella* will be assigned. The single-species clade *Tremella moriformis* recognised in Liu *et al.* (2015) was expanded to include three *Tremella* and two *Cryptococcus* species with moderate bootstrap support (95 % and 76 % in ML and MP analyses, respectively) and the new genus *Pseudotremella* is proposed to accommodate these fungi (Fig. 5B). *Bullera arundinariae*, which was placed in an isolated position in the seven-genes tree (Liu *et al.* 2015), joined a well-supported clade together with *Tremella polyporina* and *Syzygospora effibulata* (syn. *Carcinomyces effibulatus*) in the LSU analysis, for which the genus *Carcinomyces* is resurrected (Fig. 5D). *Tremella exigua* together with *Sirobasidium brefeldianum* and *Sirobasidium intermedium* formed a strongly supported new clade with a close relationship to clade I in Millanes *et al.* (2011). The remaining five *Tremella* species (*T. diploschistina*, *T. haematommatis*, *T. ramalinae*, *T. parmeliarum*, and *T. phaeophysciae*) newly added to the LSU tree were located in independent branches in the

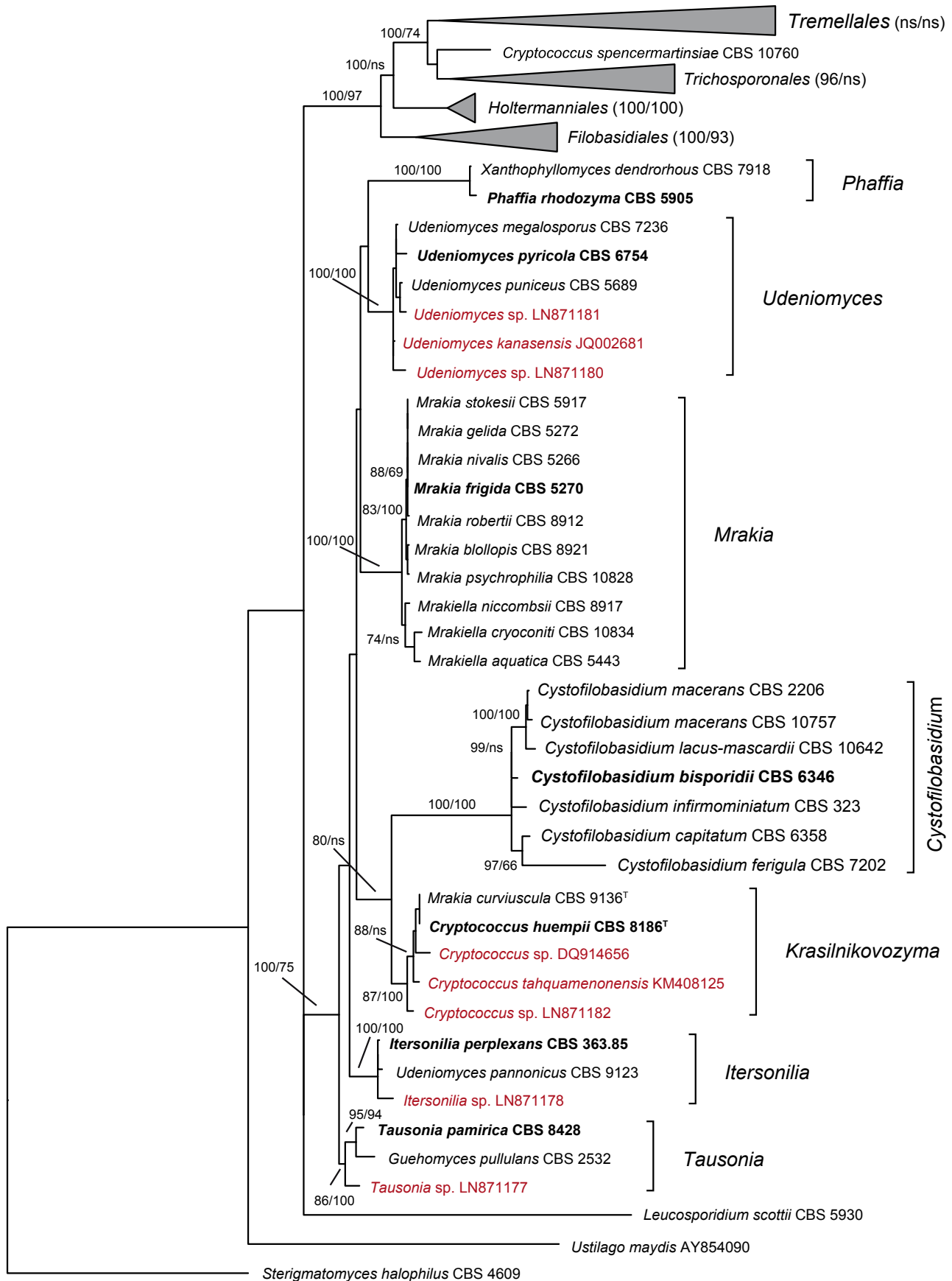


Fig. 3. Phylogenetic relationships of yeasts and related taxa from the order Cystofilobasidiales in Tremellomycetes obtained by maximum-likelihood analysis of LSU (D1/D2 domains) rRNA gene. Tree topology was backbone-constrained with the well-supported (>85 %) bipartitions of the topology of the seven-genes tree (Liu et al. 2015). Bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1 000 replicates are shown respectively from left to right on the deep and major branches resolved and in brackets following recognised clades. The type species of accepted genera are in bold and the taxa not included in the seven-genes dataset (Liu et al. 2015) are in red. Note: ns, not supported (BP < 50 %).

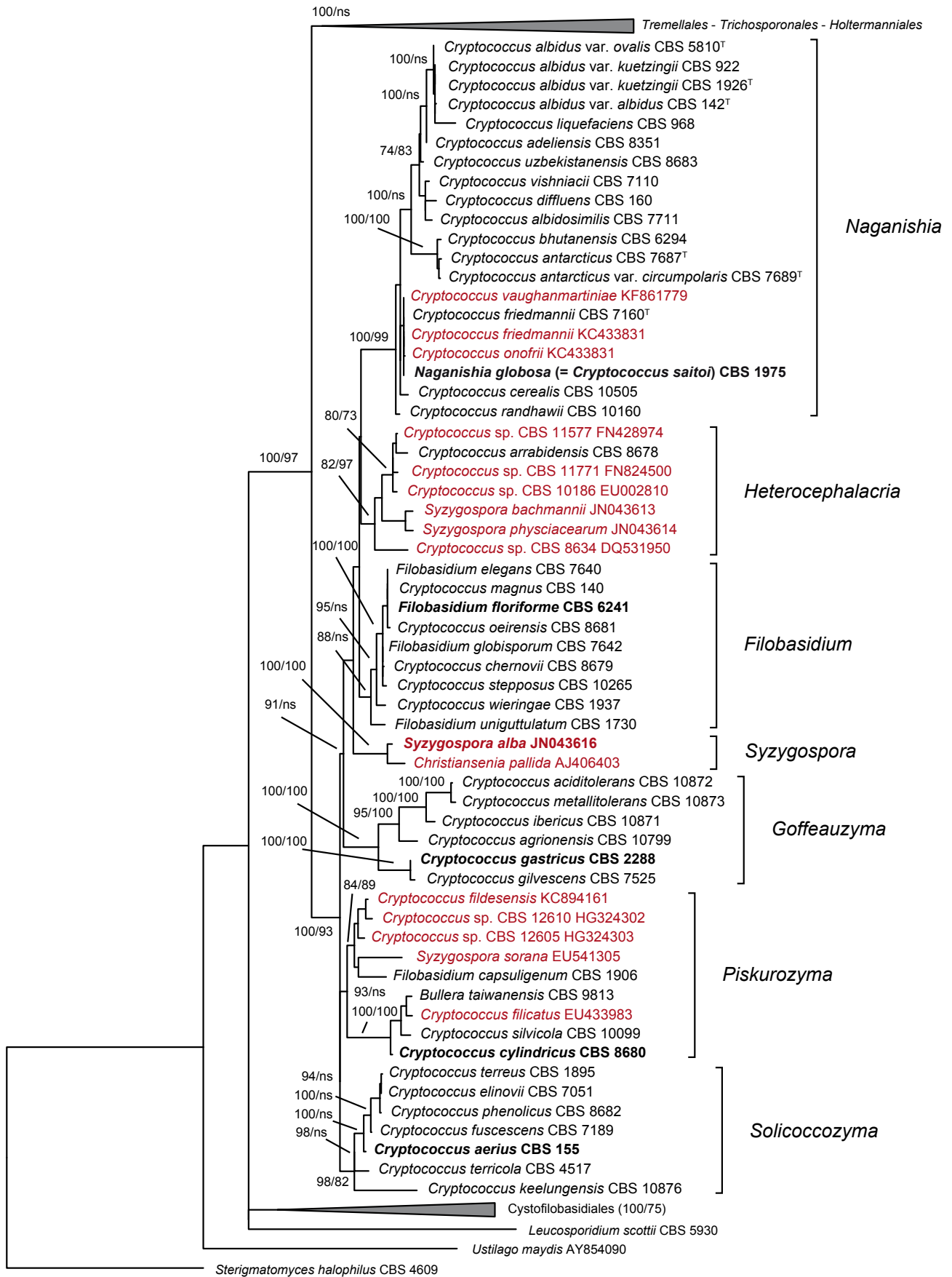


Fig. 4. Phylogenetic relationships of yeasts and related taxa from the order *Filobasidiales* in *Tremellomycetes* obtained by maximum-likelihood analysis of LSU (D1/D2 domains) rRNA gene. Tree topology was backbone-constrained with the well-supported (>85 %) bipartitions of the topology of the seven-genes tree (Liu *et al.* 2015). Bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1 000 replicates are shown respectively from left to right on the deep and major branches resolved and in brackets following recognised clades. The type species of accepted genera are in bold and the taxa not included in the seven-genes dataset (Liu *et al.* 2015) are in red. Note: ns, not supported (BP < 50 %).

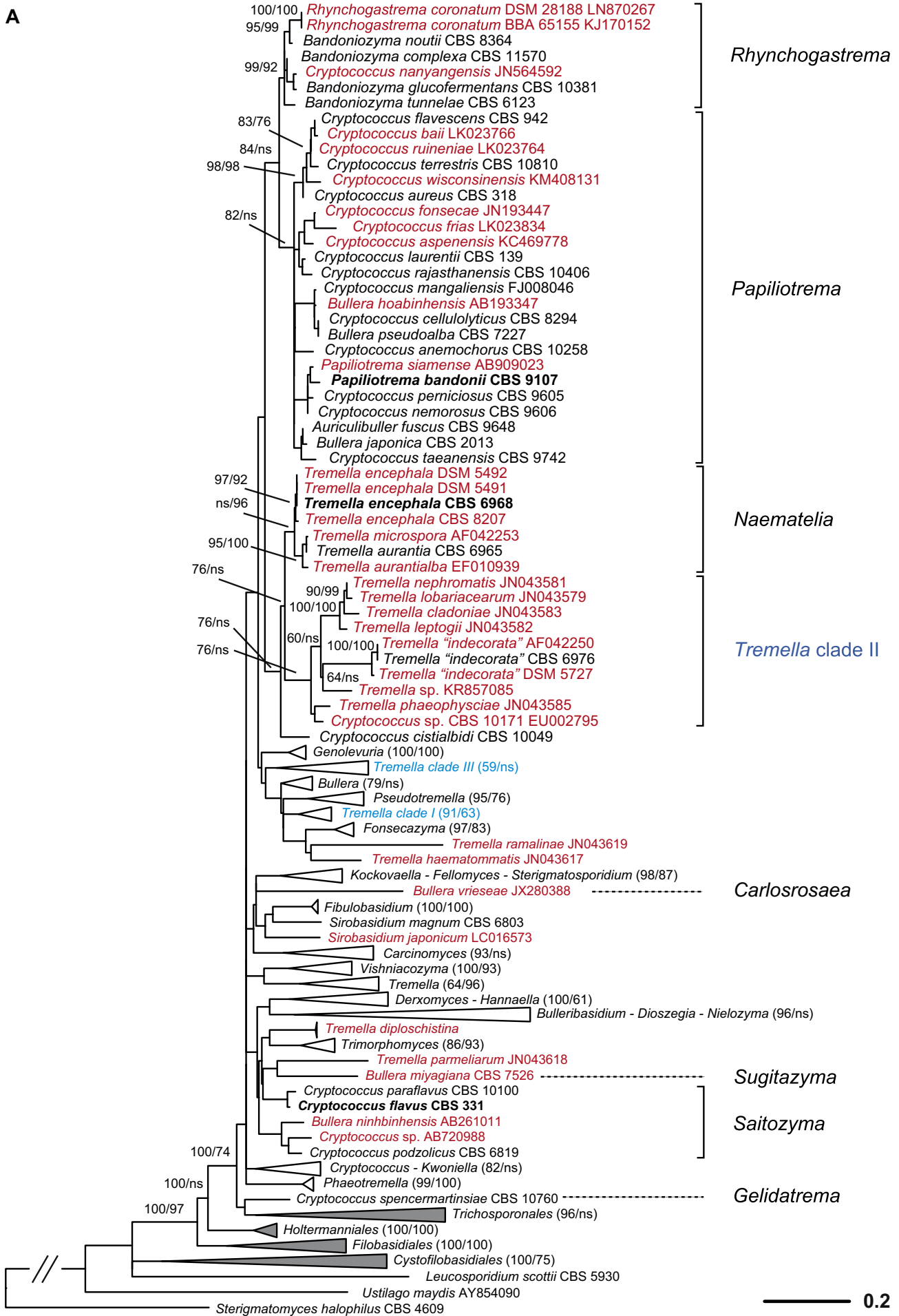


Fig. 5. Phylogenetic relationships of yeasts and related taxa from the order *Tremellales* in *Tremellomycetes* obtained by maximum-likelihood analysis of LSU (D1/D2 domains) rRNA gene. Tree topology was backbone-constrained with the well-supported (>85 %) bipartitions of the topology of the seven-genes tree (Liu *et al.* 2015). Bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1000 replicates are shown respectively from left to right on the deep and major branches resolved and in brackets following recognised clades. The type species of accepted genera are in bold and the taxa not included in the seven-genes dataset (Liu *et al.* 2015) are in red. Note: ns, not supported (BP < 50 %).

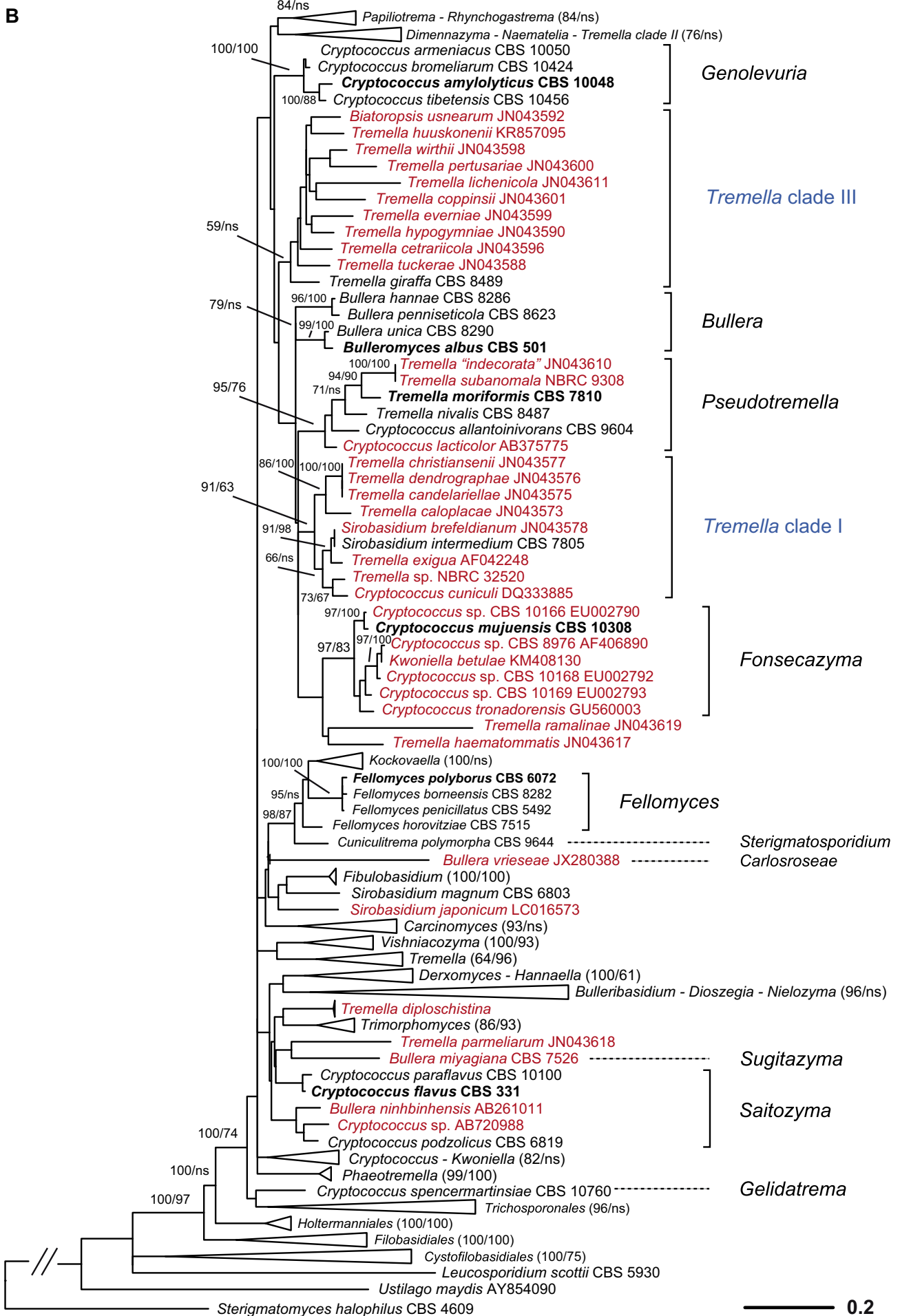


Fig. 5. (Continued).

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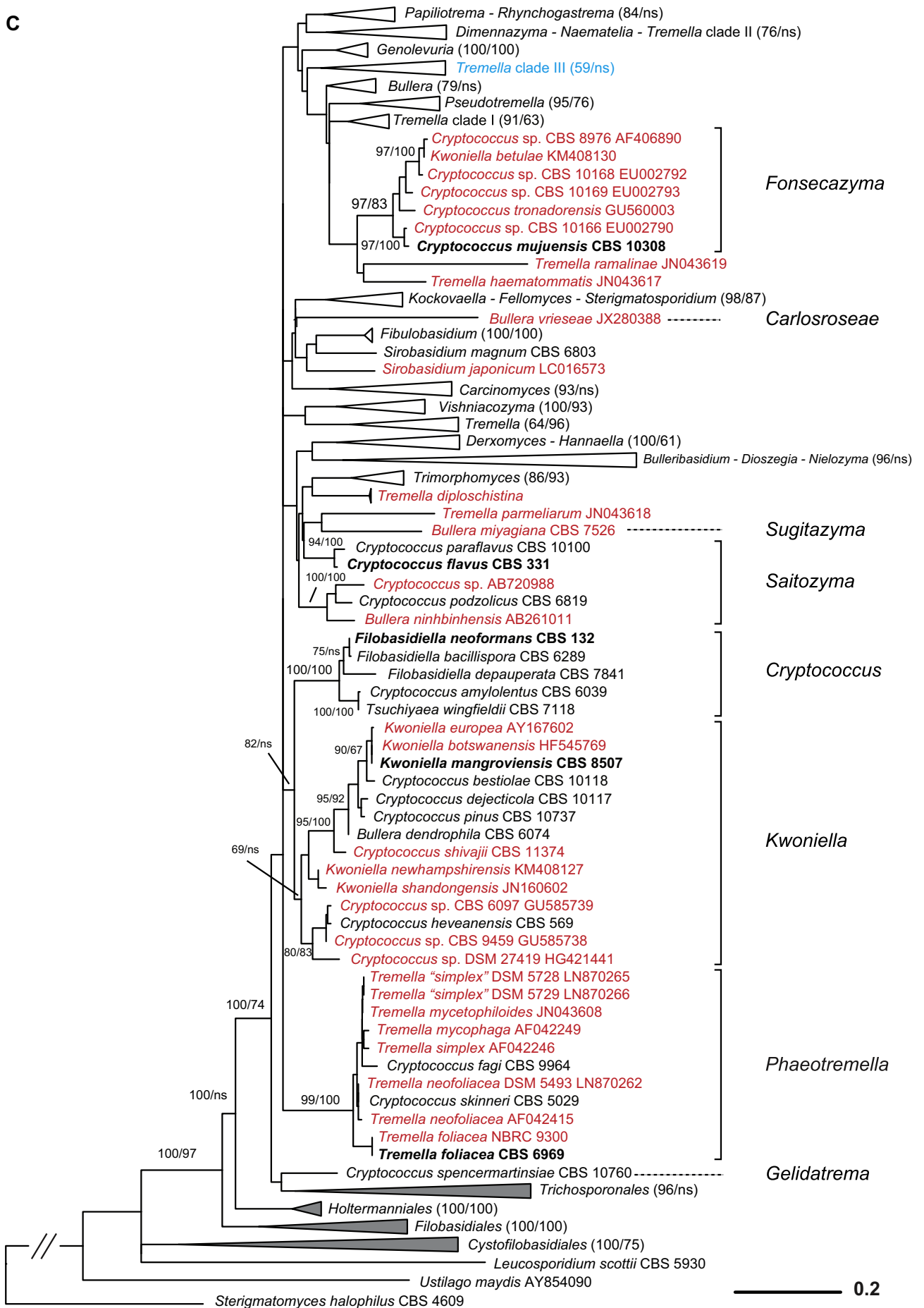


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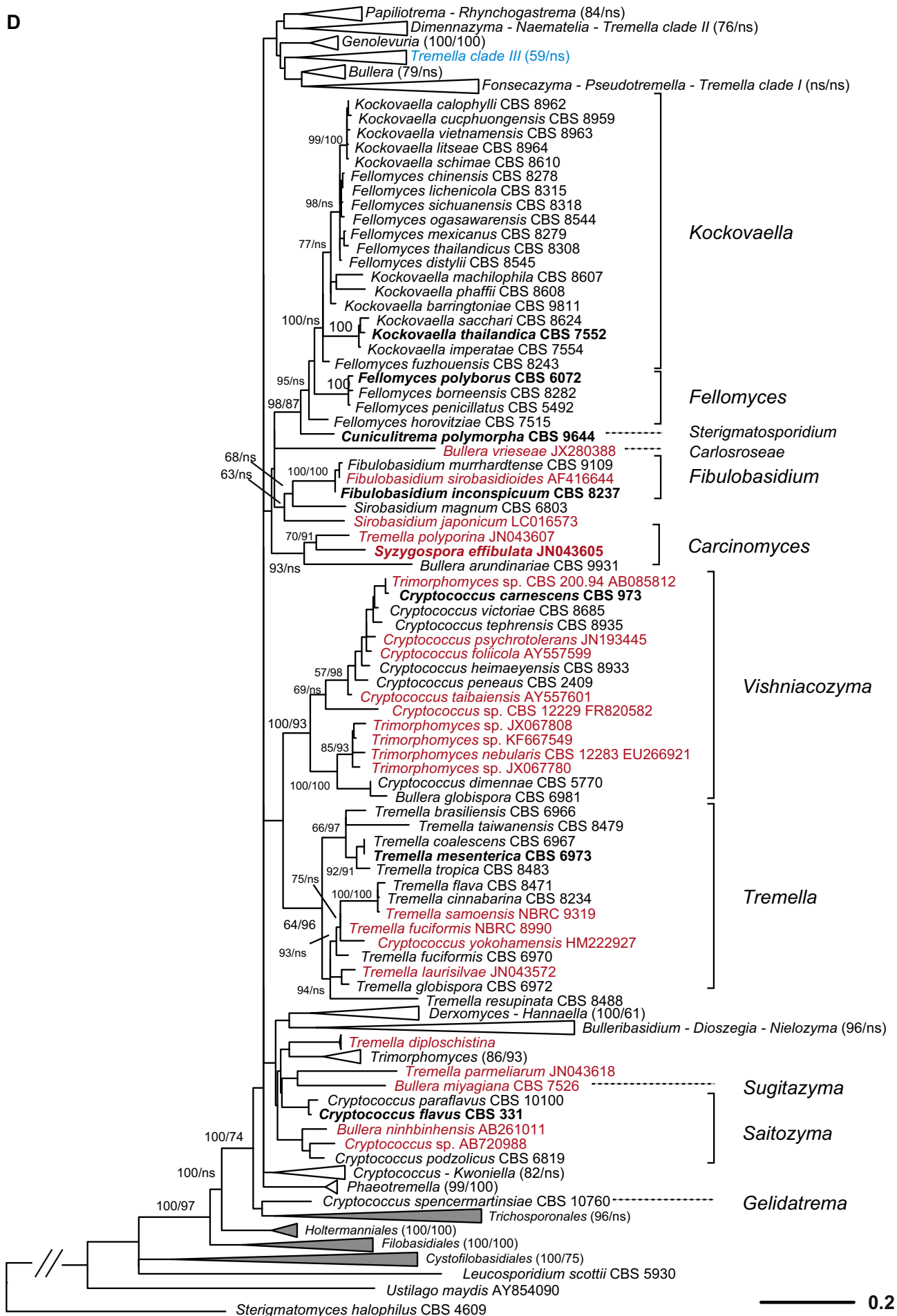


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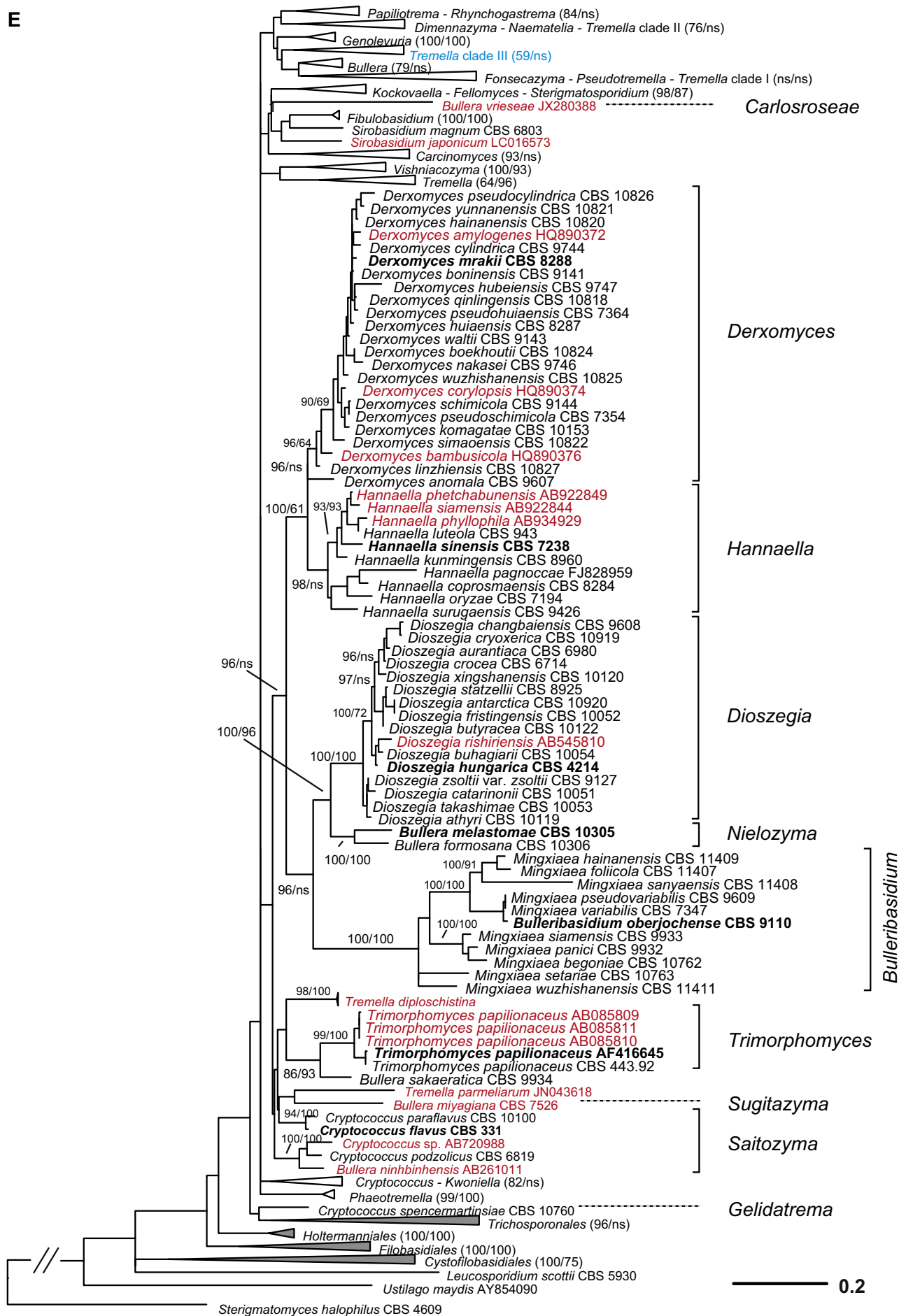


Fig. 5. (Continued).

Tremellales. The *Tremella sensu stricto* clade resolved in Liu *et al.* (2015) (i.e. the **mesenterica** clade in Boekhout *et al.* 2011a) containing the type species of the genus, *T. mesenterica*, was also revealed in the LSU tree and received moderate bootstrap support (64 % and 96 % in ML and MP analyses, respectively) (Fig. 5D).

The **Bandoniozyma** clade recognised in the seven-genes tree was expanded to include the sexual species *Rhynchogastrema coronatum* and a recently described *Cryptococcus* species with strong bootstrap support (99 % and 92 % in ML and MP analyses, respectively) (Fig. 5A). Hence, the *Bandoniozyma* species will be renamed as *Rhynchogastrema*.

Our analysis also cautions against the description of new species in the genus *Kwoniella* solely based on LSU sequence data. The support for this rapidly growing clade was low in all ML analyses and varied from 70 % to 64 % (data not shown). From the recently described asexual species placed in the genus based on the similarity to known *Kwoniella* species, *K. newhampshirensis* and *K. shandongensis* were grouped close to *K. heveanensis* (Fig. 5C). However, two other recently described anamorphic species, *Cryptococcus tronadorensis*, which was assigned to the **Kwoniella** clade by de Garcia *et al.* (2012) and *K. betulae* described by Sylvester *et al.* (2015) formed a separate clade together with *Cryptococcus mujuensis* with high bootstrap support (97 % in ML and 93 % in MP analyses) (Fig. 5C). These taxa were in isolated positions in Liu *et al.* (2015). The affinity of this clade with the **Kwoniella** clade was not supported in this study, therefore a new genus *Fonsecazyma* is proposed to accommodate these species (Fig. 5C).

The five strains of *Trimorphomyces papilionaceus*, which is the type species of the genus, clustered together and were found to be closely related to *Bullera sakaeratica* with bootstrap support values of 86 % and 93 % in the ML and MP analyses, respectively (Fig. 5E). The close relationship of *T. papilionaceus* and *B. sakaeratica* was also resolved in the seven-genes tree (Liu *et al.* 2015), suggesting that *B. sakaeratica* has to be transferred to the genus *Trimorphomyces*. The other additional *Trimorphomyces* species employed here were placed in another well supported clade (100 % and 93 % in ML and MP analyses, respectively) with some *Cryptococcus* and *Bullera* species (Fig. 5D). This clade is also referred to as **vicioriae** clade (Fonseca *et al.* 2011) or **dimennae** clade (Liu *et al.* 2015) and is not closely related to *T. papilionaceus*. The result suggests that the H-shaped conidia, as a morphological character of the genus *Trimorphomyces*, can be found in different phylogenetic clades. Thus different yeast-like taxa in *Tremellomycetes* may have a *Trimorphomyces*-like morph in their life cycles. In addition to the two *Trimorphomyces* strains, the **dimennae** clade originally holding six *Cryptococcus* and one *Bullera* species as recognised from the seven-genes tree (Liu *et al.* 2015) was expanded to contain four more *Cryptococcus* species in the tree constructed from the LSU dataset (Fig. 5D). The new *Trimorphomyces* strains were located in two subgroups in the **dimennae** clade, indicating that this clade may have a trimorphomyces-like sexual state and might be mycoparasitic.

Ten of the supplemental sequences were located in the *Trichosporonales* (Fig. 6). Two *Asterotremella* species and one recently described species *Cryptococcus thermophilus* (Vogelmann *et al.* 2012) clustered in the **Vanrija** clade. The

teleomorphic species, *Tetragoniomyces uliginosus*, was located in this order with a phylogenetic position being in agreement with that obtained by Millanes *et al.* (2011) based on the combined rRNA analysis. The present and previous results suggest that *Tetragoniomyces* holds an early-branching position in *Trichosporonales* together with the genera *Cryptotrichosporon* (Okoli *et al.* 2007) and *Takashimella* (Wang & Wang 2015). Three of the four newly added *Trichosporon* species were scattered in different clades formed by other species of the genus; the other species, *T. wanderwaltii*, formed a single species lineage (Fig. 6).

TAXONOMY

Based on 1) the multigene phylogenetic framework presented by in Liu *et al.* (2015), 2) the quantitative assessment of taxonomic units using the PRBO approach as well as the iterative modified GMYC tests, 3) a further phylogenetic analysis on an expanded LSU rRNA (D1/D2 domains) gene sequence dataset containing as many as available teleomorphic and filamentous taxa within *Tremellomycetes*, and finally 4) phenotypical criteria, we propose to update the taxonomic system for tremellomycetous yeasts and related filamentous taxa (Table 1). The phylogenetic classification includes five orders, 17 families and 54 genera. Among the genera accepted here, 18 are newly described and 18 are emended (Table 1, Figs 1 and 2). Seven of the families are newly proposed and seven are emended from existing ones. Among the accepted species, one is newly proposed and 185 are new combinations. The new and emended families and genera and new combinations are described and discussed within their respective orders. We propose to use the term *pro tempore* or *pro tem.* in abbreviation to indicate the species names that are temporarily maintained.

Order Cystofilobasidiales Fell, Roeijmans & Boekhout, Int. J. Syst. Bacteriol. 49: 911. 1999.

The order *Cystofilobasidiales* was proposed for teleomorphic yeasts with teliospores, holobasidia and septa with dolipores, but without parenthesomes (Fell *et al.* 1999). This order was accepted as family *Cystofilobasidiaceae* in *Filobasidiales* by Wells & Bandoni (2001). Our phylogenetic analysis demonstrated the rationality of its taxonomic rank as an order (Liu *et al.* 2015). Accordingly a new family *Mrakiaceae* is described and family *Cystofilobasidiaceae* is emended to accommodate the two major lineages recognised in the order. A new genus *Krasilnikovozyma* is described and four genera are emended.

Mrakiaceae X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB812173.

Etymology: In reference to the name of the type genus *Mrakia*.

This new family is proposed for the monophyletic group formed by the **Mrakia**, **huempii**, **Phaffia**, **Udeniomyces**, **Itersonilia** and **Tausonia** clades recognised in the trees constructed from the Bayesian and ML analyses of the seven-gene dataset (Liu *et al.* 2015) as shown in Fig. 1 of this study.

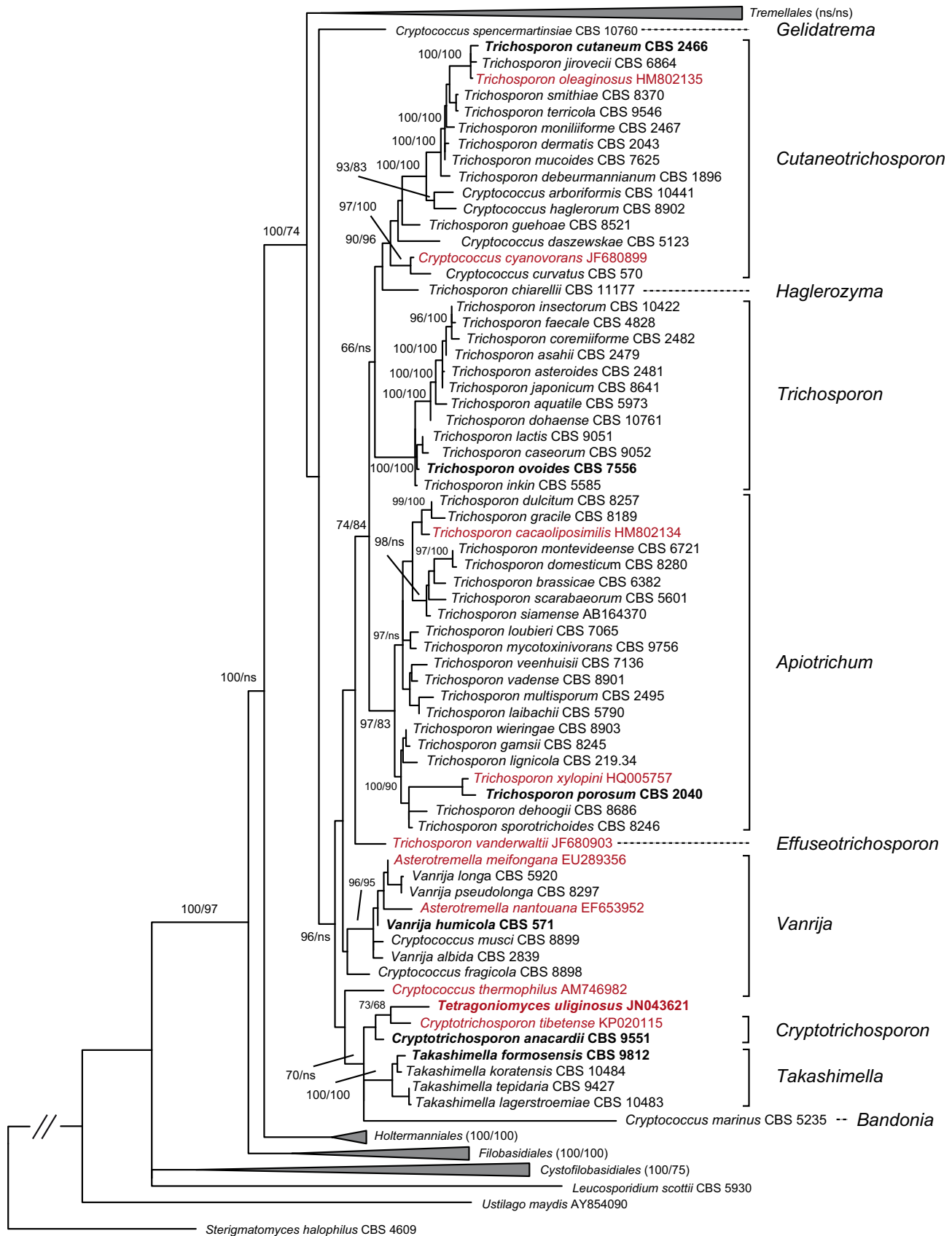


Fig. 6. Phylogenetic relationships of yeasts and related taxa from the orders Trichosporonales in Tremellomycetes obtained by maximum-likelihood analysis of LSU (D1/D2 domains) rRNA gene. Tree topology was backbone-constrained with the well-supported (>85 %) bipartitions of the topology of the seven-genes tree (Liu et al. 2015). Bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1 000 replicates are shown respectively from left to right on the deep and major branches resolved and in brackets following recognised clades. The type species of accepted genera are in bold and the taxa not included in the seven-genes dataset (Liu et al. 2015) are in red. Note: ns, not supported (BP < 50 %).

Type genus: Mrakia Y. Yamada & Komag. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

Genera accepted: Mrakia emend., *Krasilnikovozyma* gen. nov., *Phaffia* emend., *Udeniomyces*, *Itersonilia* emend. and *Tausonia* emend.

Mrakia Y. Yamada & Komag., J. Gen. Appl. Microbiol. 33: 456. 1987. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

= *Mrakiella* Margesin & Fell, Int. J. Syst. Evol. Microbiol. 58: 2980. 2008.

This genus is emended to accommodate the ***Mrakia*** clade recognised in Liu *et al.* (2015) which includes five *Mrakia* and two *Mrakiella* species in the seven-genes tree.

Basidiocarps absent. Pseudohyphae occasionally produced, branched. True hyphae occasionally produced. Clamp connections present. Sexual reproduction observed in some species. Teliospores terminal or intercalary produced, developing directly from a single cell; teliospores germination by formation of short (8–12 µm), tubular holometabasidia or phragmobasidia. Budding cells present. Chlamydoconidia and ballistoconidia may be present. Glucose and sucrose may be fermented. Nitrate and nitrite usually utilised. Major CoQ systems CoQ-8, CoQ-9 or CoQ-10.

Type species: Mrakia frigida (Fell, Statzell, I.L. Hunter & Phaff) Y. Yamada & Komag., J. Gen. Appl. Microbiol. 33: 457. 1987.

Notes: Mrakia curviuscula is excluded from the emended genus *Mrakia* because this species forms a distinct clade together with the anamorph species *Cryptococcus huempfi* (Liu *et al.* 2015). The genus *Mrakiella* was proposed for anamorphic species closely related to *Mrakia* (Margesin & Fell 2008). The three *Mrakiella* species are transferred here to the genus *Mrakia*. The affinity of *Mrakiella cryoconiti*, which was not included in the seven-genes phylogeny, to *Mrakia* is shown in the trees obtained from the LSU rRNA gene sequences in this study (Fig. 3) as well as in Boekhout *et al.* (2011a) and Weiss *et al.* (2014). The emended genus *Mrakia* currently contains eight species (Table 1).

New combinations for *Mrakia*

Mrakia aquatica (E.B.G. Jones & Slooff) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812175.

Basionym: Candida aquatica E.B.G. Jones & Slooff, Antonie van Leeuwenhoek 32: 223. 1966.

= *Mrakiella aquatica* (E.B.G. Jones & Slooff) Margesin & Fell, Int. J. Syst. Evol. Microbiol. 58: 2981. 2008.

Mrakia cryoconiti (Margesin & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812176.

Basionym: Mrakiella cryoconiti Margesin & Fell, Int. J. Syst. Evol. Microbiol. 58: 2981. 2008.

Mrakia niccombsii (Thomas-Hall) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812177.

Basionym: Mrakiella niccombsii Thomas-Hall, Extremophiles 14: 56. 2010.

Krasilnikovozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB812178.

Etymology: The genus is named in honour of the Russian microbiologist N. A. Krasil'nikov for his contribution to the ecology and systematics of yeasts.

This genus is proposed for the **huempfi** clade containing *Mrakia curviuscula*, its anamorph *Cryptococcus huempfi* (Liu *et al.* 2015) and the recently described *Cryptococcus tahquamenonensis* (Sylvester *et al.* 2015).

Basidiocarps absent. Pseudohyphae and true hyphae occasionally produced. Sexual reproduction observed in some species. Teliospores with pseudoclamps terminal produced; teliospores germination by formation of holometabasidia or hyphal structures. Budding cells present. Chlamydoconidia may be present. Fermentation absent. D-glucose, D-galactose, cellobiose, lactose, D-xylose, and citric acid are usually utilised. Glycerol and low-weight aromatic compounds are not utilised. Nitrate and nitrite usually utilised. Starch-like compounds can be produced. Major CoQ system CoQ-8.

Type species: Krasilnikovozyma huempfi (C. Ramírez & A. E. González) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

Notes: Mrakia curviuscula was considered to be the teleomorph of *C. huempfi* based on similar physiological and biochemical characters (Bab'eva *et al.* 2002) and identical D1/D2 LSU rRNA gene sequences (Boekhout *et al.* 2011a, Weiss *et al.* 2014). Liu *et al.* (2015) showed that they also exhibited similar protein-coding gene sequences, confirming their conspecificity. *Cryptococcus tahquamenonensis* was recently described as a close relative of *Mrakia curviuscula* and *Cryptococcus huempfi* (Sylvester *et al.* 2015). This relationship was confirmed in this study by the ML analysis of the D1/D2 sequence dataset (Fig. 3). Thus, *C. tahquamenonensis* is transferred here to *Krasilnikovozyma* gen. nov. Phenotypically, the species in *Krasilnikovozyma* can grow at 25 °C and thus differ from the species of the genus *Mrakia* emend., which are psychrophilic with a maximum growth temperature below 20 °C (Fell 2011). *Krasilnikovozyma* currently contains two species (Table 1) and two additional sequences representing potential new species were obtained from public databases (Fig. 3).

New combinations for *Krasilnikovozyma*

Krasilnikovozyma huempfi (C. Ramírez & A. E. González) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812179.

Basionym: Candida huempfi C. Ramírez & A. E. González, Mycopathologia 88: 167. 1984.

= *Mrakia curviuscula* Bab'eva, Lisichk., Reshetova & Danilev., Microbiology, Moscow 71: 450. 2002.

Krasilnikovozyma tahquamenonensis (Q.M. Wang, A.B. Hulfachor, K. Sylvester & C.T. Hittinger) A.M. Yurkov, **comb. nov.** MycoBank MB813656.

Basionym: Cryptococcus tahquamenonensis Wang *et al.*, FEMS Yeast Res. 15: <http://dx.doi.org/10.1093/femsyr/fov002>. 2015.

Phaffia M.W. Mill., Yoney. & Soneda, *Int. J. Syst. Bacteriol.* 26: 287. 1976. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. = *Xanthophyllomyces* Golubev, *Yeast* 11: 105. 1995.

The genus *Phaffia* is emended to include the teleomorphic species *Xanthophyllomyces dendrorhous* (Golubev 1995) based on molecular phylogenetic analyses (Fell *et al.* 2000, Scorzetti *et al.* 2002, Boekhout *et al.* 2011a, David-Palma *et al.* 2014, Weiss *et al.* 2014, Liu *et al.* 2015).

Basidiocarps absent. Cultures often pigmented and pink to orange due to carotenoid pigments. Holobasidia slender cylindrical with apical basidiospores. True hyphae not produced. Rudimentary pseudohyphae occasionally produced. Budding cells present. Ballistoconidia not produced. Fermentation present. Nitrate and nitrite not utilised. Major CoQ system CoQ-10.

Type species: Phaffia rhodozyma M.W. Miller, Yoneyama & Soneda, *Int. J. Syst. Bacteriol.* 26: 287. 1976.

Notes: The teleomorphic genus *Xanthophyllomyces* (Golubev 1995) was described later than the anamorphic genus *Phaffia* (Miller *et al.* 1976), thus the name *Phaffia* has priority according to the code of nomenclature (McNeill *et al.* 2012). *Phaffia rhodozyma* was regarded as the anamorph of *X. dendrorhous* because the type strains of the two species had similar D1/D2 sequences (Fell *et al.* 2007, 2011). However, ITS and IGS sequence analyses generated by Fell & Blatt (1999) and protein-coding gene sequence comparisons performed in Liu *et al.* (2015) suggest that they may represent different species. A recent analysis performed by David-Palma *et al.* (2014) showed a rather complex population structure within the species *P. rhodozyma*. These authors also observed that the type strain of *P. rhodozyma* contains genetic material from two different populations. Thus, DNA sequencing attempts may result in two different PCR-products for marker genes, which show a substantial nucleotide difference (David-Palma *et al.* 2014, Liu *et al.* 2015). It has been suggested to consider sexual and asexual strains in a single species with four genetic lineages, and we adopt this proposal in the present study. The genus currently contains one species (Table 1) and the discovery of two more potential novel species was recently reported by David-Palma *et al.* (2014).

Itersonilia Derx, *Bull. bot. Gdns Buitenz.* 17: 471. 1948. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus is emended to include the *Itersonilia* clade recognised from the rRNA and multigene sequence analyses (Niwata *et al.* 2002, Boekhout *et al.* 2011a, Weiss *et al.* 2014, Liu *et al.* 2015) and to incorporate a species previously assigned to the genus *Udeniomyces*.

Basidiocarps absent. Dikaryotic hyphae occasionally produced, regularly branched, inflated cells may be present. Monokaryotic hyphae may be present. Clamp connections present. Septa with dolipores lacking parenthesomes. Pseudohyphae without clamp connections occasionally present. Sexual reproduction not observed. Budding (monokaryotic) cells may be present. Ballistoconidia present. Chlamydospores occasionally produced.

Fermentation absent. Low-weight aromatic compounds not utilised. Nitrate and nitrite utilised. Starch-like compounds may be produced. The major CoQ system CoQ-9 or CoQ-10.

Type species: Itersonilia perplexans Derx., *Bull. Bot. Gdns Buitenz.* 17: 471. 1948.

Notes: The species *Udeniomyces pannonicus* was separated from the *Udeniomyces* clade and located together with *Itersonilia perplexans* based on molecular data (Niwata *et al.* 2002, Boekhout *et al.* 2011a, Weiss *et al.* 2014, Liu *et al.* 2015). *I. perplexans* and *U. pannonicus* are phenotypically similar by forming grayish to yellowish colonies, whereas the other *Udeniomyces* species form pinkish-white to orange-white colonies. The emended genus *Itersonilia* currently contains two species (Table 1) and an additional sequence representing a potential new species was obtained from public databases (Fig. 3).

New combination for *Itersonilia*

Itersonilia pannonica (Niwata, Tornai-Leh., T. Deák & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812189.

Basionym: Udeniomyces pannonicus Niwata *et al.*, *Int. J. Syst. Evol. Microbiol.* 52: 1890. 2002.

Tausonia Babeva, *Mikrobiologiya* 67: 231. 1998. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

= *Guehomyces* Fell & Scorzetti, *Int. J. Syst. Evol. Microbiol.* 54: 997. 2004.

This genus is emended to include the monotypic genus *Guehomyces* based on rRNA sequence analyses (Boekhout *et al.* 2011a, Fell & Guého-Kellermann 2011, Sampaio 2011b, Liu *et al.* 2015).

Basidiocarps absent. Cultures may be pigmented and pinkish. Hyphae disarticulate into arthroconidia. Chlamydospores occasionally produced. Sexual reproduction not observed. Budding cells present. Fermentation absent. Nitrate and nitrite utilised. Major CoQ system CoQ-9.

Type species: Tausonia pamirica Bab'eva, *Mikrobiologiya* 67: 232. 1998.

Notes: *Guehomyces pullulans* (formerly *Trichosporon pullulans*) and *T. pamirica* were located together in a well-supported clade named *Guehomyces* based on rRNA sequence analyses (Boekhout *et al.* 2011a, Fell & Guého-Kellermann 2011, Sampaio 2011b, Liu *et al.* 2015). *Tausonia* (Bab'eva 1998) has nomenclatural priority over *Guehomyces* (Fell & Scorzetti 2004). The two species are phenotypically similar in producing arthroconidia. The genus currently contains two species (Table 1) and an additional sequence representing a potential new species was obtained from public databases (Fig. 3).

New combination for *Tausonia*

Tausonia pullulans (Lindner) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812190.

Basionym: *Oidium pullulans* Lindner, Mikrosk. Betriebsk. Gahrung. 3te Aufl.: 286. 1901.

- ≡ *Trichosporon pullulans* (Lindner) Diddens & Lodder, Die anaskosporogenen Hefen, II Halfte: 410. 1942. MycoBank MB291595.
- ≡ *Guehomyces pullulans* (Lindner) Fell & Scorzetti, Int. J. Syst. Evol. Microbiol. 54: 997. 2004.

Cystofilobasidiaceae K. Wells & Bandoni, The Mycota 7(B): 113. 2001. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This family is emended to include the **Cystofilobasidium** clade recognised from the seven-gene phylogeny (Liu *et al.* 2015).

Basidiocarps absent. Cultures often pink to orange due to carotenoid pigments. True hyphae produced. Pseudohyphae occasionally produced. Clamp connections may be present. Sexual reproduction observed in some species. Teliospores terminal or intercalary produced; teliospores germination by holobasidia. Budding cells present. Fermentation absent. Aromatic compounds weakly or not utilised. Nitrate and nitrite utilised. Major CoQ system CoQ-8.

Type genus: *Cystofilobasidium* Oberw. & Bandoni.

Genus accepted: *Cystofilobasidium*.

Notes: The family *Cystofilobasidiaceae* was originally proposed within the order *Filobasidiales* mainly based on the morphological features of the holobasidia. Three genera *Cystofilobasidium*, *Mrakia*, and *Xanthophyllomyces* were included in this family (Wells & Bandoni 2001). Phylogenetic analyses suggest that this family represents an order independent of *Filobasidiales* (Fell *et al.* 1999, Fell *et al.* 2000, Scorzetti *et al.* 2002, Boekhout *et al.* 2011a, Weiss *et al.* 2014, Liu *et al.* 2015) and support the proposal of *Cystofilobasidiales* by Fell *et al.* (1999). The family *Cystofilobasidiaceae* is emended here to include only the **Cystofilobasidium** clade (Fig. 1). The species in this family produce much longer (up to 65 µm) holobasidia (Fell *et al.* 1999, Sampaio 2011a, Weiss *et al.* 2014) than those (8–12 µm) produced by the teleomorphic species in the other family *Mrakia*-*ceae* within *Cystofilobasidiales*.

Order Filobasidiales Julich, Bibl. Mycol. 85: 324. 1981.

The order *Filobasidiales* was originally introduced to accommodate yeasts lacking basidiocarps and having holobasidia with passively released basidiospores (Julich 1981). Three families, namely *Filobasidiaceae*, *Cystofilobasidiaceae* and *Rhynchogastremaceae* were included in this order by Wells & Bandoni (2001). As discussed above, the *Cystofilobasidiaceae* sensu Wells & Bandoni (2001) represents a distinct order and this family is emended in this study to include only the genus *Cystofilobasidium*. *Rhynchogastremaceae* was monotypic, including only *Rhynchogastrema coronatum* (Metzler *et al.* 1989). LSU rRNA sequence analyses assigned this dimorphic mycoparasite to the *Tremellales* as shown in Weiss *et al.* (2014) and this study (Fig. 5A). Molecular phylogenetic analyses showed that the order *Filobasidiales* without *Cystofilobasidiaceae* and *Rhynchogastremaceae* represents a monophyletic lineage, which includes species from the

teleomorphic genera *Filobasidium* and *Syzygospora* and the anamorphic genus *Cryptococcus* (Fell *et al.* 2000, Scorzetti *et al.* 2002, Boekhout *et al.* 2011a, Millanes *et al.* 2011, Weiss *et al.* 2014, Liu *et al.* 2015). Three families, namely *Filobasidiaceae*, *Syzygosporaceae* and *Christianseniaceae* have been proposed in this order. However, they were not resolved as separate groups in the previous and present molecular phylogenetic analyses. Therefore, the families and genera within this order are recircumscribed in this study based on the phylogenetic analyses of the seven-genes (Fig. 1) and the LSU rRNA datasets (Figs 2 and 4), resulting in the recognition of two families and seven genera (Table 1).

Filobasidiaceae L.S. Olive, J. Elisha Mitchell Scient. Soc. 84: 261. 1968. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This family is circumscribed to accommodate a monophyletic group containing the **Filobasidium**, **albidus**, **gastricus**, **Cryptococcus arrabidensis** and **Syzygospora** clades resolved in the trees from the seven-gene dataset (Liu *et al.* 2015) and the expanded LSU rRNA dataset (Figs 1 and 2).

Basidiocarps waxy to gelatinous in lichenicolous species, absent in cultures. Hyphae with clamp connection and haustorial branches may be present. Holobasidia tubular or long with terminally sessile basidiospores. Pseudohyphae and true hyphae occasionally produced. Sexual reproduction present in some species. Budding cells present. Ballistoconidia absent. Fermentation absent. Nitrate utilised by several species. The major CoQ system CoQ-9 or CoQ-10.

Type genus: *Filobasidium* L.S. Olive. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

Genera accepted: *Filobasidium*, *Goffeauzyma*, *Heterocephalacria*, *Naganishia*, and *Syzygospora*.

Notes: The family *Filobasidiaceae* was proposed by Olive (1968) to accommodate the species *Filobasidium floriforme*. Three teleomorphic genera, namely *Filobasidium*, *Filobasidiella* and *Cystofilobasidium*, were then included in this family (Kwon-Chung 1987). These genera share the presence of long slender holobasidia, sessile terminal basidiospores and dolipore-like septa without parenthesomes (Kwon-Chung 1987). The genera *Filobasidiella* and *Cystofilobasidium* were transferred to the *Tremellales* and *Cystofilobasidiales*, respectively, based on molecular phylogenetic analyses (Fell *et al.* 2000, Scorzetti *et al.* 2002). Phylogenetic analysis of the expanded LSU rRNA dataset showed that four *Syzygospora* species were closely related to the taxa assigned to *Filobasidiaceae* (Fig. 4). Therefore, the *Filobasidiaceae* is emended here to include *Filobasidium*, *Naganishia* (i.e. the **albidus** clade), *Goffeauzyma* gen. nov. (i.e. the **gastricus** clade), *Heterocephalacria* (i.e. the **Cryptococcus arrabidensis** clade) and *Syzygospora*.

Filobasidium L.S. Olive, J. Elisha Mitchell Scient. Soc. 84: 261. 1986. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus is emended to accommodate the species in the **Filobasidium** clade (**floriforme** clade sensu Fonseca *et al.*

2011) circumscribed by the phylogenetic analyses of seven genes (Liu *et al.* 2015).

Basidiocarps absent. Cultures often pigmented and pinkish-white. Sexual reproduction present in some species. Hyphae with clamp connections and haustorial branches may be present. Holobasidia tubular with terminal, sessile basidiospores. Pseudohyphae occasionally produced. Budding cells present. Fermentation absent. L-malic, saccharic, protocatechuic and p-hydroxybenzoic acids often utilised. Nitrate may or may not be utilised. Starch-like compounds usually produced. The major CoQ system CoQ-9 or CoQ-10.

Type species: Filobasidium floriforme L.S. Olive, J. Elisha Mitchell scient. Soc. 84: 261. 1968.

Notes: Filobasidium capsuligenum is excluded from this genus because it is located outside the **Filobasidium** clade and is closely related to the **cylindricus** clade (i.e. *Piskurozyma* gen. nov.). The genus *Filobasidium* currently contains nine species (Table 1).

New combinations for *Filobasidium*

Filobasidium chernovii (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812191.

Basionym: Cryptococcus chernovii Á. Fonseca *et al.*, Can. J. Microbiol. 46: 20. 2000.

Filobasidium magnum (Lodder & Kreger-van Rij) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812192.

Basionym: Cryptococcus laurentii var. *magnum* Lodder & Kreger-van Rij, Yeast, a taxonomic study, [Edn 1]: 670. 1952.

Filobasidium oeirensis (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812193.

Basionym: Cryptococcus oeirensis Á. Fonseca *et al.*, Can. J. Microbiol. 46

Filobasidium stepposum (Golubev & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812194.

Basionym: Cryptococcus stepposus Golubev & J.P. Samp. Mycol. Res. 110: 960. 2006.

Filobasidium wieringae (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812195.

Basionym: Cryptococcus wieringae Á. Fonseca *et al.*, Can. J. Microbiol. 46: 25. 2000.

Naganishia S. Goto, J. Ferment. Technology 41: 461. 1963. **emend.** A.M. Yurkov & T. Boekhout.

This genus is resurrected and emended here to accommodate the **albidus** clade comprised of 15 species that previously belonged to *Cryptococcus* (Fell *et al.* 2000, Scorzetti *et al.* 2002, Fonseca *et al.* 2011, Liu *et al.* 2015).

Basidiocarps absent. Hyphae and pseudohyphae usually absent. Sexual reproduction not observed. Budding cells present. Ballistoconidia absent. Fermentation absent. L-malic, vanillic, ferulic, caffeic, p-coumaric protocatechuic and hydroxybenzoic acids often utilised. Nitrate utilised. Starch-like compounds usually produced. Major CoQ system CoQ-9 or CoQ-10.

Type species: Naganishia globosa S. Goto, J. Ferment. Technology 41: 461. 1963. MycoBank MB335061.

= *Cryptococcus saitoi* Á. Fonseca, Scorzetti & Fell, Can. J. Microbiol. 46: 24. 2000. MycoBank MB464349.

Notes: The genus *Naganishia* was described to accommodate the yeast *Naganishia globosus* (Goto 1963), which was later synonymised with *Cryptococcus saitoi* based on rRNA sequence data (Fonseca *et al.* 2011). Some of the other species comprising this clade were described earlier than *N. globosus*, but they were originally classified in the genera *Torula*, *Torulopsis* and *Rhodotorula*. Since type species of these genera are placed outside Tremellomycetes, none of them can be used to reclassify the **albidus** clade. The generic name *Naganishia* also appears to be the oldest in the clade where the type species of the genus is specified and a type strain is preserved. *Cryptococcus onofrii* and *C. vaughanmartinae* were recently described as cold-adaptive species in the **albidus** clade (Turchetti *et al.* 2015). Their affinity to the **albidus** clade was confirmed in this study by ML analysis using the expanded LSU rRNA gene sequence dataset (Fig. 4). Thus, these two *Cryptococcus* species are transferred to the genus *Naganishia* together with the *Cryptococcus* species included in the **albidus** clade in the seven-genes dataset (Liu *et al.* 2015). Fifteen species are presently accepted in the genus *Naganishia* (Table 1).

New combinations for *Naganishia*

Naganishia adeliensis (Scorzetti, I. Petrescu, Yarrow & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813139.

Basionym: Cryptococcus adeliensis Scorzetti *et al.*, Antonie van Leeuwenhoek 77: 155. 2000.

Naganishia albidosimilis (Vishniac & Kurtzman) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813140.

Basionym: Cryptococcus albidosimilis Vishniac & Kurtzman, Int. J. Syst. Bacteriol. 42: 550. 1992.

Naganishia albida (Saito) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813140.

Basionym: Torula albida Saito, Jap. J. Bot. 1: 43. 1922.

Naganishia antarctica (Vishniac & Kurtzman) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813145.

Basionym: Cryptococcus antarcticus Vishniac & Kurtzman, Int. J. Syst. Bacteriol. 42: 548. 1992.

Naganishia bhutanensis (Goto & Sugiy.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813165.

Basionym: Cryptococcus bhutanensis Goto & Sugiy., Can. J. Bot. 48: 2097. 1970.

Naganishia cerealis (Passoth, A.-C. Andersson, Olstorpe, Theelen, Boekhout & Schnürer) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813167.

Basionym: Cryptococcus cerealis Passoth *et al.*, Antonie van Leeuwenhoek 96: 641. 2009.

Naganishia diffluens (Zach) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813172.

Basionym: Torulopsis diffluens Zach, Wolfram & Zach, Arch. Derm. Syph. 170: 690. 1934.

Naganishia friedmannii (Vishniac) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813175.

Basionym: Cryptococcus friedmannii Vishniac, Mycologia 77: 150. 1985.

Naganishia liquefaciens (Saito & M. Ota) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813177.

Basionym: Torulopsis liquefaciens Saito & M. Ota, Jozogaku Zasshi 12: 167. 1934.

Naganishia onofrii (Turchetti, Selbmann & Zucconi) A.M. Yurkov, **comb. nov.** MycoBank MB813182.

Basionym: Cryptococcus onofrii Turchetti *et al.*, Extremophiles 19: 149–159. 2015.

Naganishia randhawae (Z.U. Khan, S.O. Suh, Ahmad, F. Hagen, Fell, Kowshik, Chandy & Boekhout) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813246.

Basionym: Cryptococcus randhawae Z.U. Khan *et al.*, Antonie van Leeuwenhoek 97: 256. 2010.

Naganishia uzbekistanensis (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813248.

Basionym: Cryptococcus uzbekistanensis Á. Fonseca *et al.*, Can. J. Microbiol. 46: 25. 2000.

Naganishia vaughanmartinae (Turchetti, Blanchette & Arenz) A.M. Yurkov, **comb. nov.** MycoBank MB813249.

Basionym: Cryptococcus vaughanmartinae Turchetti *et al.*, Extremophiles 19: 157. 2015.

Naganishia vishniacii (Vishniac & Hempfling) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813250.

Basionym: Cryptococcus vishniacii Vishniac & Hempfling, Int. J. Syst. Bacteriol. 29: 155. 1979.

Goffeauzyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813251.

Etymology: The genus is named in honour of the yeast biologist and geneticist André Goffeau, who was the initiator and coordinator of the genome sequence project of *Saccharomyces cerevisiae*.

The new genus is proposed for the **gastricus** clade recognised from the seven-genes tree (Liu *et al.* 2015), which consists of six species previously belonging to *Cryptococcus*.

Basidiocarps absent. True hyphae and pseudohyphae not observed. Sexual reproduction not observed. Budding cells present. Ballistoconidia absent. Fermentation absent. Low-weight aromatic compounds often not utilised. Nitrate usually not utilised. Major CoQ system CoQ-9.

Type species: Goffeauzyma gastrica (Reiersöl & di Menna) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout **comb. nov.**

Notes: The **gastricus** clade recognised in Liu *et al.* (2015) consists of *C. gastricus* and *C. gilvescens* isolated from soil (Fell *et al.* 2000, Boekhout *et al.* 2011a, Fonseca *et al.* 2011); *C. aciditolerans*, *C. ibericus* and *C. metallitolerans* in the **ARD ecoclade** that were obtained from acid rock drainage (Gadanhó & Sampaio 2009); and *C. agrionensis* from acidic water of a volcanic environment (Russo *et al.* 2010). Though the species of the **ARD ecoclade** clustered together, they did not form a significantly supported clade in the seven-genes tree (Liu *et al.* 2015) and in the LSU rRNA gene tree (Fig. 4). The PRBO test indicated that the six species of the **gastricus** clade did not show significant deviation compared to the species in the reference clades (Table 2). Thus they are assigned to a single genus at present which currently contains six species (Table 1).

New combinations for *Goffeauzyma*

Goffeauzyma aciditolerans (Gadanhó & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813252.

Basionym: Cryptococcus aciditolerans Gadanhó & J.P. Samp., Int. J. Syst. Evol. Microbiol. 59: 2378. 2009.

Goffeauzyma agrionensis (Russo, Libkind, Samp. & van Broock) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813253.

Basionym: Cryptococcus agrionensis Russo *et al.*, Int. J. Syst. Evol. Microbiol. 60: 998. 2010.

Goffeauzyma gastrica (Reiersöl & di Menna) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813254.

Basionym: Cryptococcus gastricus Reiersöl & di Menna, Antonie van Leeuwenhoek 24: 28. 1958.

Goffeauzyma gilvescens (Chernov & Babeva) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813255.

Basionym: Cryptococcus gilvescens Chernov & Babeva, Mikrobiologiya 57: 1032. 1988.

Goffeauzyma iberica (Gadanhó & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813256.

Basionym: Cryptococcus ibericus Gadanhó & J.P. Samp., Int. J. Syst. Evol. Microbiol. 59: 2378. 2009.

Goffeauzyma metallitolerans (Gadanhó & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813257.

Basionym: Cryptococcus metallitolerans Gadanhó & J.P. Samp., Int. J. Syst. Evol. Microbiol. 59: 2379. 2009.

Heterocephalacria Berthier, Mycotaxon 12: 114. 1980. **emend.** A. M. Millanes, M. Wedin & A.M. Yurkov.

This genus is resurrected and emended to accommodate the clade represented by *Cryptococcus arrabidensis* recognised in the seven-genes tree (Liu *et al.* 2015) and was expanded to include two *Syzygospora* and five undescribed *Cryptococcus* species in this study (Fig. 4). The type of *Heterocephalacria*, *H. solida* (Berthier 1980), is morphologically similar to these two lichenicolous “*Syzygospora*” species, viz. basidia with up to four sterigmata, spores obliquely attached to sterigmata, both spores and sterigmata refractive at the point of attachment, and most likely belongs here.

Basidiocarps waxy to gelatinous in lichenicolous species. Hyphae thin-walled with clamp connections and haustorial branches. Holobasidia tubular or long with terminal sessile basidiospores. Sexual reproduction not observed in culture. True hyphae and pseudohyphae absent in culture. Budding cells present. Fermentation absent. Nitrate utilised. Starch-like compounds usually not produced. Major CoQ system not known.

Type species: Heterocephalacria solida Berthier, Mycotaxon 12: 114. 1980.

≡ *Syzygospora solida* (Berthier) Ginns, Mycologia 78: 632. 1986.

Notes: The genus *Heterocephalacria* with one species, *H. solida*, was described by Berthier (1980) for a capitata clavarioid fungus with partially cruciately septate apices of the basidia and secondary spores (i.e. conidia). This genus was treated as a synonym of the genus *Syzygospora* by Ginns (1986) based on the morphological similarity of *H. solida* with *Syzygospora* species. The type species of *Syzygospora*, *S. alba*, is located in a separate clade (Fig. 4). The emended genus *Heterocephalacria* currently contains four described species (Table 1) and four additional sequences representing potential new species were obtained from public databases (Fig. 4).

New combinations for *Heterocephalacria*

Heterocephalacria arrabidensis (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813258.

Basionym: *Cryptococcus arrabidensis* Á. Fonseca *et al.*, Can. J. Microbiol. 46: 20. 2000.

Heterocephalacria bachmannii (Diederich & M.S. Christ.) Millanes & Wedin, **comb. nov.** MycoBank MB813259.

Basionym: *Syzygospora bachmannii* Diederich & M.S. Christ., Bibl. Lichenol. 61: 30. 1996.

Heterocephalacria physciacearum (Diederich) Millanes & Wedin, **comb. nov.** MycoBank MB813260.

Basionym *Syzygospora physciacearum* Diederich, Bibl. Lichenol. 61: 38. 1996.

Syzygospora G.W. Martin, J. Wash. Acad. Sci. 27: 112. 1937.
= *Christiansenia* Hauerlev, Friesia 9: 43. 1969.

This genus is restricted to include the species in the clade represented by *Syzygospora alba*, the type species of the genus, as recognised in the tree drawn from the LSU D1/D2 dataset (Fig. 4).

Basidiocarps thin, gelatinous, subhyaline on the hymenial surface of the host or a cerebriform mass up to 12 cm diam. Hyphae

with clamp connections present. Haustorial branches rather frequent, typically subglobose, arising from clamp connections. Basidia suburniform to cylindrical or clavate, 50–120 × 6–8 µm, holobasidiate or incompletely septate. Basidiospores broadly ellipsoid. Zygoconidia develop as two swellings, one on each side of the transverse septum in the conidiogenous cells.

Type species: Syzygospora alba G.W. Martin, J. Wash. Acad. Sci. 27: 112. 1937.

Notes: *Syzygospora* proved to be polyphyletic (Sampaio 2004, Millanes *et al.* 2011). The phylogenetic analysis of the expanded LSU rRNA gene sequence dataset in this study showed that *Syzygospora effibulata* formed a strongly supported clade with *Tremella polyporina* in Tremellales, while the other species of *Syzygospora* studied occurred in three separate clades in the Filobasidiales. *Syzygospora bachmannii* and *S. physciacearum* were assigned to the emended genus *Heterocephalacria* as discussed above. *Syzygospora sorana* was located in a different clade together with *Cryptococcus fildesensis* and *Filobasidium capsuligenum* (see below). The type of the genus, *S. alba*, formed a well supported clade with *Christiansenia (Syzygospora) pallida* (Fig. 4). Both species form zygoconidia and are mycoparasitic on the hymenial surface of *Corticaceae* (aphyllophorean fungi) differing from the hosts of other *Syzygospora* species (Ginns 1986). Thus, the genus *Syzygospora* currently includes only *S. alba* and *S. pallida* (Table 1).

Piskurozymaceae X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB812196.

Etymology: In reference to the name of the type genus *Piskurozyma* gen. nov.

This family is proposed for a strongly supported monophyletic lineage including the **aerius** (*Solicoccozyma* gen. nov.) and **cylindricus** (*Piskurozyma* gen. nov.) clades and a single-species clade *Filobasidium capsuligenum* in *Filobasidiales* resolved by the seven-gene dataset analysis (Fig. 1).

Basidiocarps absent. Pseudohyphae and true hyphae may be present. Clamp connections on dikaryotic hyphae occasionally present. Haustorial branches not present. Sexual reproduction with holobasidia. Budding cells present. Ballistoconidia absent. Fermentation usually absent. Nitrate usually utilised. The major CoQ system CoQ-10.

Type genus: Piskurozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

Genera accepted: Piskurozyma gen. nov. and *Solicoccozyma* gen. nov.

Piskurozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB812206.

Etymology: The genus is named in honour of the late Jure Piškur for his contribution to yeast genetics, physiology and evolutionary biology.

This genus is proposed for the **cylindricus** clade (Liu *et al.* 2015) containing three species previously classified in the genera

Cryptococcus or *Bullera* as shown in the trees obtained from the seven-genes dataset. Phylogenetic analysis of the extended LSU rRNA gene dataset suggests close relationships with the teleomorphic species *Filobasidium capsuligenum* and *Syzygospora sorana*, and two recently described cryptococci, *C. filicatus* and *C. fildensis* (Fig. 4).

Basidiomes, if present, within the hymenium of the host. Dikaryotic hyphae with clamp connections. Haustoria not reported. In culture true hyphae occur occasionally. Pseudohyphae absent. Sexual reproduction observed for some species. Holobasidia slender with terminal sessile basidiospores. Budding cells present. Ballistoconidia may be present. Fermentation occasionally present. Nitrate may be utilised. Starch-like compounds usually produced. Major CoQ system CoQ-10.

Type species: Piskurozyma cylindrica (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

Notes: Filobasidium capsuligenum was regarded as a single-species clade because of its unique fermentative ability. However, the close relationship of this species with the **cylindricus** clade was resolved in the seven-genes tree with strong support (Liu *et al.* 2015). In the constrained ML tree from the expanded LSU rRNA sequence dataset, *F. capsuligenum* clustered together with a fungicolous species, *Syzygospora sorana*, and two recently published *Cryptococcus* species, namely *C. filicatus* (Golubev & Sampaio 2009) and *C. fildensis* (Zhang *et al.* 2014). Therefore these species are assigned to the genus *Piskurozyma* gen. nov. This genus currently contains seven described species (Table 1) and two additional sequences representing potential new species were obtained from public databases (Fig. 4).

New combinations for *Piskurozyma*

Piskurozyma capsuligena (Fell, Statzell, I.L. Hunter & Phaff) A.M. Yurkov, **comb. nov.** MycoBank MB813122.

Basionym: Leucosporidium capsuligenum Fell *et al.*, *Antonie van Leeuwenhoek* 35: 444. 1969.

Piskurozyma cylindrica (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812208.

Basionym: Cryptococcus cylindricus Á. Fonseca *et al.*, *Can. J. Microbiol.* 46: 22. 2000.

Piskurozyma fildensis (T. Zhang & L.-Y. Yu) A.M. Yurkov, **comb. nov.** MycoBank MB813124.

Basionym: Cryptococcus fildensis T. Zhang & L.Y. Yu, *Int. J. Syst. Evol. Microbiol.* 64: 675–679. 2013.

Piskurozyma filicatus (Golubev & J.P. Samp.) Kachalkin, **comb. nov.** MycoBank MB814788.

Basionym: Cryptococcus filicatus Golubev & J.P. Sampaio, *J. Gen. Appl. Microbiol.* 55: 445. 2009.

≡ *Cryptococcus filicatus* var. *filicatus* Golubev & J.P. Sampaio, *J. Gen. Appl. Microbiol.* 55: 445. 2009.

≡ *Cryptococcus filicatus* var. *pelliculosus* Golubev & J.P. Sampaio, *J. Gen. Appl. Microbiol.* 55: 445. 2009.

Piskurozyma silvicola (Golubev & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812209.

Basionym: Cryptococcus silvicola Golubev & J.P. Samp., *Antonie van Leeuwenhoek* 89: 48. 2006.

Piskurozyma sorana (Hauerslev) A.M. Yurkov, **comb. nov.** MycoBank MB813129.

Basionym: Syzygospora sorana Hauerslev, *Op. bot.* 100: 113. 1989.

Piskurozyma taiwanensis (Nakase, Tsuzuki & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812207.

Basionym: Bullera taiwanensis Nakase *et al.*, *J. Gen. Appl. Microbiol.* 48: 349. 2002.

Solicoccozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB812197.

Etymology: In reference to the ecological origin of the species in this genus that are mostly isolated from soils.

This genus is proposed for the **aerius** clade (Fonseca *et al.* 2011, Liu *et al.* 2015) containing six anamorphic species previously belonging to the genus *Cryptococcus* (Liu *et al.* 2015).

Basidiocarps absent. Sexual reproduction with holobasidia may be present. Pseudohyphae and true hyphae occasionally produced. Clamp connections may be present on dikaryotic hyphae. Haustorial branches not observed. Budding cells present. Ballistoconidia absent. Fermentation absent. Nitrate utilised. Starch-like compounds usually not produced. The major CoQ system CoQ-10.

Type species: Solicoccozyma aerea (Saito) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

Notes: The **aerius** clade on which the new genus is based was consistently resolved and strongly supported in the trees using different datasets (Fonseca *et al.* 2011, Liu *et al.* 2015, this study). The species of this genus are usually obtained from soils (Botha 2006, Fonseca *et al.* 2011, Yurkov *et al.* 2012). They frequently produce thick polysaccharide capsules and accumulate substantial amount of lipids (Tanimura *et al.* 2014). They have a pronounced ability to assimilate aldaric acids and low-weight aromatic compounds, such as L-malic, L-tartaric, saccharic, mucic, caffeic, gentisic, p-coumaric, protocatechuic and hydroxybenzoic acids (Fonseca *et al.* 2011). This genus currently contains six described species (Table 1).

New combinations for *Solicoccozyma*

Solicoccozyma aerea (Saito) A.M. Yurkov, **comb. nov.** MycoBank MB812198.

Basionym: Torula aerea Saito, *Jap. J. Bot.* 1: 41. 1922.

Solicoccozyma fuscescens (Golubev) A.M. Yurkov, **comb. nov.** MycoBank MB812201.

Basionym: Cryptococcus fuscescens Golubev, *J. Gen. Appl. Microbiol.* 39: 428. 1984.

Solicoccozyma keelungensis (C.F. Chang & S.M. Liu) A.M. Yurkov, **comb. nov.** MycoBank MB812202.

Basionym: Cryptococcus keelungensis C.F. Chang & S.M. Liu, *Int. J. Syst. Evol. Microbiol.* 58: 2974. 2008.

Solicoccozyma phenolicus (Á. Fonseca, Scorzetti & Fell) A.M. Yurkov, **comb. nov.** MycoBank MB812203.

Basionym: *Cryptococcus phenolicus* Á. Fonseca et al., Can. J. Microbiol. 46: 24. 2000.

Solicoccozyma terreus (Di Menna) A.M. Yurkov, **comb. nov.** MycoBank MB812204.

Basionym: *Cryptococcus terreus* Di Menna, J. Gen. Microbiol. 11: 195. 1954.

= *Cryptococcus himalayensis* Goto & Sugiyama, Can. J. Bot. 48: 2099. 1970.

= *Cryptococcus elinovii* Golubev, Mikol. Fitopatol. 13: 466. 1979.

Solicoccozyma terricola (T.A. Pedersen) A.M. Yurkov, **comb. nov.** MycoBank MB812205.

Basionym: *Cryptococcus terricola* T.A. Pedersen, Bull. Jard. Bot. État Brux. 31: 101. 1958.

Order Holtermanniales Libkind, Wuczkowski, Turchetti & Boekhout, Int. J. Syst. Evol. Microbiol. 61: 685. 2011.

This order was proposed by Wuczkowski et al. (2011) to include the monotypic teleomorphic genus *Holtermannia* and the anamorphic genus *Holtermanniella*. The latter was proposed to accommodate four *Cryptococcus* species and a new anamorphic species closely related to *Holtermannia corniformis* (Wuczkowski et al. 2011). The order *Holtermanniales* was confirmed to be a distinct lineage in the trees from the seven-gene and the expanded LSU datasets with strong support values (Figs 1 and 2). The five anamorphic *Holtermanniella* species clustered together in a robust clade separate from the teleomorphic species *Holtermannia corniformis* (Figs 1 and 2). Therefore, the two genera *Holtermannia* with one species and *Holtermanniella* with five species are accepted here (Table 1).

Order Tremellales Fries, Syst. mycol. 1: 2. 1821.

Tremellales is the largest order in *Tremellomycetes* and six families, namely *Cuniculitremaeae*, *Tremellaceae*, *Sirobasidiaceae*, *Tetragoniomycetaceae*, *Phragmoxenidiaceae* and *Rhynchogastremaceae* containing yeast and yeast-like taxa have been proposed within this order (Metzler et al. 1989, Bandoni 1995, Wells & Bandoni 2001, Kirschner et al. 2001). This taxonomic concept included only teleomorphic species and was circumscribed based on basidial morphology, septal pore anatomy and ballistospore production (Bandoni 1995). The monotypic family *Phragmoxenidiaceae* was tentatively assigned to the *Tremellales* by Oberwinkler et al. (1990). The inclusion of this family in the order is still uncertain because molecular data are not available from this family (Bandoni 1995, Wells & Bandoni 2001). The *Phragmoxenidiaceae* species is therefore not included in this study. Previous phylogenetic analyses showed the paraphyletic nature of the families in *Tremellales* after the inclusion of anamorphic yeast and yeast-like taxa (Fell et al. 2001, Scorzetti et al. 2002, Sampaio 2004). We re-circumscribed the families and genera in *Tremellales* based on the multigene phylogeny (Liu et al. 2015) and the PRBO test performed in this study. A total of 11 families and 28 genera are accepted in *Tremellales* here (Table 1, Figs 1, 2 and 5).

Bulleribasidiaceae X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB812215.

Etymology: In reference to the name of the type genus *Bulleribasidium*.

This family is proposed to accommodate the monophyletic lineage containing the *Bulleribasidium*, *Deroxomyces*, *Dioszegia*, *Hannaella*, *melastomae* and *dimennae* clades in the tree obtained from the seven genes (Liu et al. 2015).

Basidiocarps not present. Pseudohyphae and true hyphae may be present. Septal pore a dolipore with poorly developed parenthosome-like structures. Sexual reproduction observed in some species. Basidia cylindrical or occasionally globose, two-celled, with transverse and occasionally longitudinal septa, and globose basidiospores. Budding cells present. Ballistoconidia occasionally present. Fermentation absent. Nitration usually not utilised. Starch-like compounds usually produced. Major CoQ system CoQ-9 or CoQ-10.

Type genus: *Bulleribasidium* J.P. Sampaio. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

Genera accepted: *Bulleribasidium*, *Deroxomyces*, *Dioszegia*, *Hannaella*, *Nielozyma* gen. nov., and *Vishniacozyma* gen. nov.

Notes: Except for one teleomorphic species, *Bulleribasidium oberjochense*, all the species included in this family are known from the asexual states only.

Bulleribasidium J.P. Sampaio., M. Weiss & R. Bauer, Mycologia 94: 874. 2002. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus *Bulleribasidium* is emended to accommodate the *Bulleribasidium* clade containing *B. oberjochense* and ten anamorphic species previously belonging to *Mingxiaea* (Liu et al. 2015).

Basidiocarps not present. Pseudohyphae and true hyphae may be present. Septa with dolipores with poorly developed parenthosome-like structures. Sexual reproduction observed in some species. Basidia cylindrical or occasionally globose, two-celled, with transverse and occasionally longitudinal septa, with globose basidiospores. Budding cells present. Ballistoconidia rotationally symmetrical.

Type species: *Bulleribasidium oberjochense* J.P. Samp., Gadanho, M. Weiss & R. Bauer, Mycologia 94: 875. 2002.

Notes: The teleomorphic genus name *Bulleribasidium*, which was proposed in 2002 (Sampaio et al. 2002) has nomenclatural priority over the anamorphic genus name *Mingxiaea* proposed in 2011 (Wang et al. 2011). The species of the latter are, therefore, transferred to the genus *Bulleribasidium*. Eleven species are currently accepted in this genus (Table 1, Fig. 5E).

New combinations for *Bulleribasidium*

Bulleribasidium begoniae (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812218.

Basionym: Bullera begoniae Nakase *et al.*, Mycoscience 45: 290. 2004.

≡ *Mingxiaea begoniae* (Nakase *et al.*) Q.-M. Wang *et al.*, Int. J. Syst. Evol. Microbiol. 61: 213. 2011.

Bulleribasidium foliicola (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812232.

Basionym: Mingxiaea foliicola Q.M. Wang *et al.*, Int. J. Syst. Evol. Microbiol. 61: 217. 2011.

Bulleribasidium hainanense (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813261.

Basionym: Mingxiaea hainanensis Q.M. Wang *et al.*, Int. J. Syst. Evol. Microbiol. 61: 215. 2011.

Bulleribasidium panici (Fungsin, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813262.

Basionym: Bullera panici Fungsin *et al.*, Microbiol. Culture Coll. 19: 27. 2003.

≡ *Mingxiaea panici* (Fungsin *et al.*) Q.-M. Wang *et al.*, Int. J. Syst. Evol. Microbiol. 61: 213. 2011.

Bulleribasidium pseudovariabile (F.Y. Bai, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813263.

Basionym: Bullera pseudovariabilis F.Y. Bai *et al.*, Antonie van Leeuwenhoek 83: 261. 2003.

≡ *Mingxiaea pseudovariabilis* (F.Y. Bai *et al.*) Q.-M. Wang *et al.*, Int. J. Syst. Evol. Microbiol. 61: 214. 2011.

Bulleribasidium sanyaense (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813264.

Basionym: Mingxiaea sanyaensis Q.M. Wang *et al.*, Int. J. Syst. Evol. Microbiol. 61: 214. 2011.

Bulleribasidium setariae (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813265.

Basionym: Bullera setariae Nakase *et al.*, Mycoscience 45: 292. 2004.

≡ *Mingxiaea setariae* (Nakase *et al.*) Q.-M. Wang *et al.*, Int. J. Syst. Evol. Microbiol. 61: 213. 2011.

Bulleribasidium siamense (Fungsin, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813266

Basionym: Bullera siamensis Fungsin *et al.*, Microbiol. Culture Coll. 19: 29. 2003.

≡ *Mingxiaea siamensis* (Fungsin *et al.*) Q.-M. Wang *et al.*, Int. J. Syst. Evol. Microbiol. 61: 214. 2011.

Bulleribasidium variabile (Nakase & M. Suzuki) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813267.

Basionym: Bullera variabilis Nakase & M. Suzuki, J. Gen. appl. Microbiol. 33: 350. 1987.

≡ *Mingxiaea variabilis* (Nakase & Suzuki) Q.-M. Wang *et al.*, Int. J. Syst. Evol. Microbiol. 61: 214. 2011.

Bulleribasidium wuzhishanense (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813268.

Basionym: Mingxiaea wuzhishanensis Q.M. Wang *et al.*, Int. J. Syst. Evol. Microbiol. 61: 218. 2011.

Nielozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813269.

Etymology: The genus is named in honour of C.B. van Niel for his pioneering contributions to the study of ballistoconidium-forming yeasts.

This genus is proposed for the **melastomae** clade recognised from the seven-genes phylogeny (Liu *et al.* 2015).

Basidiocarps not present. Colonies usually yellowish to brownish. Pseudohyphae and true hyphae not observed. Sexual reproduction not observed. Budding cells present. Ballistoconidia present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type species: Nielozyma melastomae (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

Notes: *Nielozyma* gen. nov. is closely related to the genus *Dioszegia* (Nakase *et al.* 2004, Liu *et al.* 2015). *Nielozyma* species usually form yellowish to brownish colonies (Nakase *et al.* 2004), being distinct from those of *Dioszegia* species that usually are orange-coloured (Wang & Bai 2008). This genus currently contains two described species (Table 1, Fig. 5E).

New combinations for *Nielozyma*

Nielozyma formosana (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813270.

Basionym: Bullera formosana Nakase *et al.*, Syst. Appl. Microbiol. 27: 562. 2004.

Nielozyma melastomae (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813271.

Basionym: Bullera melastomae Nakase *et al.*, Syst. Appl. Microbiol. 27: 560. 2004.

Vishniacozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813272.

Etymology: The genus is named in honour of the American microbiologist Helen S. Vishniac for her contributions to the study of microbial diversity and yeast ecology, especially of cold-adapted yeasts.

This genus is proposed for the **victoriae** (sensu Fonseca *et al.* 2011) and **dimennae** clades recognised in Boekhout *et al.* (2011a) and Liu *et al.* (2015).

Basidiocarps gelatinous, mycoparasitic. Hyphae thin-walled with clamp connections. H-shaped conidia (e.g. zygoconidia) may be present. Haustoria not known. Basidia subglobose to ellipsoidal or clavate, with basal clamp connections, two- to four-celled, longitudinally or obliquely septa, with ellipsoidal basidiospores. Cultures are often pigmented, pinkish-white, orange-white or yellowish-white. Hyphae not observed in culture. Poorly developed pseudohyphae present. Sexual reproduction not observed in culture. Budding cells present. Ballistoconidia occasionally present. Fermentation absent. Nitrate not utilised. Starch-like compounds weakly produced or not produced. Major CoQ system CoQ-9 or CoQ-10.

Type species: Vishniacozyma carnescens (Verona & Luchetti) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

Notes: The **victoriae** clade (sensu [Fonseca et al. 2011](#)) coincides with the **dimennae** clade as recognised in [Boekhout et al. \(2011a\)](#) and [Liu et al. \(2015\)](#) and consists of six *Cryptococcus* and one *Bullera* species. In the tree derived from the expanded LSU rRNA gene sequence dataset, two teleomorphic mycoparasites *Trimorphomyces nebularis* and *Trimorphomyces* sp. CBS 200.94 ([Takashima et al. 2003](#), [Kirschner & Chen 2008](#)) and three recently published *Cryptococcus* species were also located in this clade ([Fig. 5D](#)). Yeasts of this genus are widespread eurybionts and are often found associated with plant material ([Fonseca & Inácio 2006](#), [Fonseca et al. 2011](#), [Yurkov et al. 2015](#)). A possible mycoparasitic nature has been suggested for these yeasts, which may have sexual trimorphomyces-like morphs ([Kirschner & Chen 2008](#)). This genus currently contains eleven described species ([Table 1](#)) and four additional sequences representing potential new species were obtained from public databases ([Fig. 5D](#)).

New combinations for *Vishniacozyma*

Vishniacozyma globispora (B.N. Johri & Bandoni) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813273.

Basionym: *Bullera globispora* B.N. Johri & Bandoni, in Subramanian (ed.), Taxonomy of Fungi, (Proc. int. Symp. Madras, 1973) Part 2 (Madras) 2: 539. 1984.

Vishniacozyma carnescens (Verona & Luchetti) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813274.

Basionym: *Torulopsis carnescens* Verona & Luchetti, Boll. R. Istituto Superiore Agrario di Pisa 12: 280. 1936.

≡ *Cryptococcus carnescens* (Verona & Luchetti) M. Takash et al., Int. J. Syst. Evol. Microbiol. 53: 1192. 2003.

Vishniacozyma dimennae (Fell & Phaff) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813275.

Basionym: *Cryptococcus dimennae* Fell & Phaff, Antonie van Leeuwenhoek 33: 467. 1967.

Vishniacozyma foliicola (Q.M. Wang & F.Y. Bai) A.M. Yurkov, **comb. nov.** MycoBank MB813277.

Basionym: *Cryptococcus foliicola* Q.M. Wang & F.Y. Bai, J. Gen. Appl. Microbiol. 57: 287. 2011.

Vishniacozyma heimaeyensis (Vishniac) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813278.

Basionym: *Cryptococcus heimaeyensis* Vishniac, Can. J. Microbiol. 48: 464. 2002.

Vishniacozyma nebularis (Vishniac) A.M. Yurkov, **comb. nov.** MycoBank MB813279.

Basionym: *Trimorphomyces nebularis* R. Kirschner & Chee J. Chen, Nova Hedwigia 87: 448. 2008.

Vishniacozyma psychrotolerans (V. de García, Zalar, Brizzio, Gunde-Cim. & van Broock) A.M. Yurkov, **comb. nov.** MycoBank MB813281.

Basionym: *Cryptococcus psychrotolerans* V. de García et al., FEMS Microbiol. Ecol. 82: 535. 2012.

Vishniacozyma peneaus (Phaff, Mrak & O.B. Williams) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813282.

Basionym: *Rhodotorula peneaus* Phaff et al., Mycologia 44: 438. 1952.

≡ *Cryptococcus peneaus* (Phaff et al.) M. Takash. et al., Int. J. Syst. Evol. Microbiol. 53: 1192. 2003.

Vishniacozyma taibaiensis (Q.M. Wang & F.Y. Bai) A.M. Yurkov, **comb. nov.** MycoBank MB813283.

Basionym: *Cryptococcus taibaiensis* Q.M. Wang & F.Y. Bai, J. Gen. Appl. Microbiol. 57: 5. 2011.

Vishniacozyma tephrensensis (Vishniac) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813284.

Basionym: *Cryptococcus tephrensensis* Vishniac, Can. J. Microbiol. 48: 466. 2002.

Vishniacozyma victoriae (M.J. Montes, Belloch, Galiana, M.D. García, C. Andrés, S. Ferrer, Torr.-Rodr. & J. Guinea) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813285.

Basionym: *Cryptococcus victoriae* M.J. Montes et al., Syst. Appl. Microbiol. 22: 104. 1999.

Tremellaceae Fr., Syst. mycol. 1: lv. 1821.

This family is re-delimited to accommodate only the ***Tremella sensu stricto*** (= **mesenterica**) clade circumscribed by the phylogenetic analyses of seven genes ([Liu et al. 2015](#)) and consists of ten *Tremella* species previously included in the mesenterica and fuciformis groups as distinguished by [Chen \(1998\)](#). Additionally, *Cryptococcus yokohamensis* is included in this family based on previous phylogenetic results by [Alshahni et al. \(2011\)](#) and results from the analysis of the expanded LSU rRNA gene sequence dataset ([Fig. 5D](#)).

The diagnosis of the family is based on the description of the genus *Tremella* as recircumscribed below.

Type genus: *Tremella* Pers. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

Genus accepted: *Tremella*.

Notes: This family was created by [Fries \(1821\)](#) to include fungi with gelatinous fruitbodies and was later restricted by [Patouillard](#)

(1900) to genera with tremelloid basidia. Bandoni (1984) made a major revision of this family based on the ultrastructure of the septal pore and restricted the *Tremellaceae* to the genera *Holtermannia*, *Tremella* and *Trimorphomyces*. Later, three other genera, *Bulleromyces*, *Sirotrema* and *Xenolachne*, were also included in this family (Bandoni 1995, Wells & Bandoni 2001). Phylogenetic analyses indicated that the genera assigned to the *Tremellaceae* did not form a monophyletic group but occurred scattered in different lineages (Bandoni 1984, Fell *et al.* 2000, Scorzetti *et al.* 2002, Sampaio 2004, Boekhout *et al.* 2011a, Millanes *et al.* 2011, Weiss *et al.* 2014, Liu *et al.* 2015). This family is, therefore, re-defined here to include only the ***Tremella sensu stricto*** clade as presented in Liu *et al.* (2015) and as shown in Fig. 1.

Tremella Pers., Neues Mag. Bot. 1: 111. 1794. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus is re-delimited to include the species in the ***Tremella sensu stricto*** clade (= ***mesenterica*** clade) including the type species of the genus, *T. mesenterica*. This clade is circumscribed based on the seven-genes phylogeny (Liu *et al.* 2015).

Basidiocarps minute (0.3–0.5 cm in diameter) to large (to 5–10 cm high). Basidiocarps variable in colour, ranging from whitish-yellow, cream, yellowish-orange to brown, reddish or black. Clamp connections and haustorial branches present in dikaryotic hyphae. Basidia globose, subglobose, ellipsoid, oval, clavate or pyriform, two- or four-celled with longitudinal or oblique septa, occasionally with transverse septa. Basidiospores globose to ellipsoid. Budding cells originate from germinating basidiospores. Fermentation absent in yeast states. Nitrate not utilised. Major CoQ systems CoQ-9 or CoQ-10.

Type species: Tremella mesenterica (Schaeff.) Retz.

Notes: The genus *Tremella* as traditionally circumscribed is the largest polyphyletic genus in the order *Tremellales* (Weiss *et al.* 2014). Molecular phylogenetic analyses based on LSU rRNA gene sequences showed that *Tremella* species occurred in several distantly related clades (Fell *et al.* 2000, Scorzetti *et al.* 2002, Sampaio 2004, Bandoni & Boekhout 2011b, Boekhout *et al.* 2011a, Millanes *et al.* 2011, Weiss *et al.* 2014, Liu *et al.* 2015, also see Fig. 2 of this study) and should be re-classified. Here we re-define the genus *Tremella* to include only the species in the ***Tremella sensu stricto*** clade as recognised in the tree derived from seven genes (Liu *et al.* 2015). As discussed above, the ***Tremella sensu stricto*** clade showed a significant deviation from the reference thresholds in the PRBO analysis (Table 2) and two subclades, ***mesenterica*** and ***fuciformis***, with distinguishable morphological characters could be identified within the clade as shown in Chen (1998) and Liu *et al.* (2015). These data imply that the ***Tremella sensu stricto*** clade probably can be reclassified into two genera in the future. At present, we prefer to keep them in the genus *Tremella*. The reclassification of the entire *Tremella* genus is unfeasible at present because even the D1/D2 LSU rRNA gene sequences are only available from less than half of the described *Tremella* species (Millanes *et al.* 2011, Weiss *et al.* 2014, Liu *et al.* 2015, this study).

An anamorphic yeast species, *Cryptococcus yokohamensis*, was recently described and showed a close relationship to the

Tremella species in the ***Tremella sensu stricto*** clade (Alshahni *et al.* 2011). This species exhibits phenotypic characteristics similar to those of the yeast states of *Tremella*. Specifically, *C. yokohamensis* has two major coenzymes CoQ-9 and CoQ-10, being similar to *T. mesenterica* and *T. coalescens* (Alshahni *et al.* 2011). Thus, *C. yokohamensis* represents a yeast state of a species in the ***Tremella sensu stricto*** clade and is transferred to *Tremella*. The re-defined genus *Tremella* currently contains twelve species (Table 1, Fig. 5D).

New combination for *Tremella*

Tremella yokohamensis (Alshahni, Satoh & Makimura) A.M. Yurkov, **comb. nov.** MycoBank MB813286.

Basionym: *Cryptococcus yokohamensis* Alshahni *et al.*, Int. J. Syst. Evol. Microbiol. 61: 3069. 2011.

Rhynchogastremataceae (Oberw. & B. Metzler) Syst. Appl. Microbiol. 12: 283. 1989. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov.

This family is emended to accommodate the well supported monophyletic lineage consisting of the ***aureus***, ***Auriculibuller***, ***Bandoniozyma***, ***Papiliotrema***, ***pseudoalba*** and ***laurentii*** clades as recognised in Liu *et al.* (2015).

Basidiocarps if present, minute. Sexual reproduction present in some species. Dikaryotic hyphae with clamp connections and haustorial branches. Basidia transversely septate, cylindrical, and in small clusters. Basidiospores globose or allantoid. In culture pseudohyphae and true hyphae occasionally present. Budding cells present. Ballistoconidia may be present. Fermentation present in some species. Nitrate not utilised. Starch-like compounds usually produced. Major CoQ system CoQ-10 as far as known.

Type genus: Rhynchogastrema B. Metzler & Oberw. emend. X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov

Genera accepted: *Rhynchogastrema* emend. and *Papiliotrema* emend.

Notes: The family *Rhynchogastremataceae* was originally proposed for a heterobasidiomycetous species *Rhynchogastrema coronatum* (Metzler *et al.* 1989). The expanded LSU rRNA gene sequence analysis located this species in the ***Bandoniozyma*** clade (Fig. 5A). Therefore, the *Rhynchogastremataceae* is expanded here to include the species in the ***Bandoniozyma*** and closely related clades that formed a 100 % supported monophyletic lineage (Liu *et al.* 2015) as shown in Fig. 1.

Papiliotrema J. P. Sampaio., M. Weiss & R. Bauer, Mycologia 94: 875. 2002. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, MycoBank MB813287.

This genus is emended to accommodate a well-supported monophyletic clade containing teleomorphic *Papiliotrema* and *Auriculibuller* species (Liu *et al.* 2015) as well as anamorphic yeasts including 16 *Cryptococcus* and three *Bullera* species (Table 1, Fig. 5A).

Basidiocarps, if present, minute, ca. 0.5 mm in diameter. Dikaryotic hyphae with clamp connections and haustorial branches. Basidia cylindrical and transversely septate. Cultures pale to brownish yellow. Pseudohyphae and true hyphae may be present. Budding cells present. Ballistoconidia may be present. Sexual reproduction observed in some species. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type species: Papiliotrema bandonii J. P. Sampaio., Gadanho, M. Weiss & R. Bauer, *Mycologia* 94: 875. 2002.

Notes: The species assigned to the emended genus *Papiliotrema* here were located in the **aurus**, **Auriculibuller**, **laurentii**, **Papiliotrema** and **pseudoalba** clades in the seven-genes phylogenetic tree (Liu *et al.* 2015). In order to avoid creating genera for these small clades, we decided to combine them in a single genus. The PRBO test did not show significant deviation for the emended *Papiliotrema* generic concept (Table 2), supporting this taxonomic treatment. The genus *Papiliotrema* was proposed in 2002 (Sampaio *et al.* 2002), thus having nomenclature priority over *Auriculibuller*, which was proposed in 2004 (Sampaio *et al.* 2004). The genera *Auriculibuller* and *Papiliotrema* are morphologically similar and their sexual states form clavate basidia with transverse septa, differing clearly from those formed by *Tremella* species (Sampaio *et al.* 2002, 2004, Sampaio 2011c). Twenty-two species are currently accepted in the emended genus *Papiliotrema* (Table 1, Fig. 5A).

New combinations for *Papiliotrema*

Papiliotrema anemochoreius (C.H. Pohl, Kock, P.W.J. van Wyk & Albertyn) Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813287.

Basionym: *Cryptococcus anemochoreius* C.H. Pohl *et al.*, *Int. J. Syst. Evol. Microbiol.* 56: 2705. 2006.

Papiliotrema aurea (Saito) M. Takash., Sugita, Shinoda & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813288.

Basionym: *Torula aurea* Saito, *Mitt. Jpn. J. Bot.* 1: 44. 1922.
= *Cryptococcus aureus* (Saito) M. Takash. *et al.*, *Int. J. Syst. Evol. Microbiol.* 53: 1192. 2003.

Papiliotrema aspenensis (K. Ferreira-Paim, T.B. Ferreira, L. Andrade-Silva, D.J. Mora, D.J. Springer, J. Heitman, F.M. Fonseca, D. Matos, M.S.C. Melhem & M.L. Silva-Vergara) X.Z. Liu, F.Y. Bai, A.M. Yurkov & Boekhout **comb. nov.** MycoBank MB814710.

Basionym: *Cryptococcus aspenensis* K. Ferreira-Paim *et al.*, *PLoS ONE* 9: e108633. 2014.

Papiliotrema baii (A.M. Yurkov, M.A. Guerreiro & Á. Fonseca) A.M. Yurkov, **comb. nov.** MycoBank MB813648.

Basionym: *Cryptococcus baii* A.M. Yurkov *et al.*, *PLoS One* 10: e0120400. 2015.

Papiliotrema flavescens (Saito) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813289.

Basionym: *Torula flavescens* Saito, *Jap. J. Bot.* 1: 43. 1922.

= *Cryptococcus flavescens* (Saito) C.E. Skinner, *Am. Midl. Nat.* 43: 249. 1950.

Papiliotrema fonsecae (V. de García, Zalar, Braizzio, Gunde-Cim. & van Brollck) A.M. Yurkov, **comb. nov.** MycoBank MB813290.

Basionym: *Cryptococcus fonsecae* V. de García *et al.*, *FEMS Microbiol. Ecol.* 82: 536. 2012.

Papiliotrema frias (V. de García, Zalar, Braizzio, Gunde-Cim. & van Brollck) A.M. Yurkov, **comb. nov.** MycoBank MB813292.

Basionym: *Cryptococcus frias* V. de García *et al.*, *FEMS Microbiol. Ecol.* 82: 537. 2012.

Papiliotrema fuscus (J.P. Samp., J. Inácio, Fonseca & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813432.

Basionym: *Auriculibuller fuscus* J.P. Samp. *et al.*, *Int. J. Syst. Evol. Microbiol.* 54: 989. 2004.

Papiliotrema hoabinhensis (D.T. Luong, M. Takash., Ty. Dung & Nakase) A.M. Yurkov, **comb. nov.** MycoBank MB813293.

Basionym: *Bullera hoabinhensis* D.T. Luong *et al.*, *J. Gen. Appl. Microbiol.* 51: 340. 2005.

Papiliotrema japonica (J.P. Samp., Fonseca & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813294.

Basionym: *Bullera japonica* J.P. Samp. *et al.*, *Int. J. Syst. Evol. Microbiol.* 54: 990. 2004.

Papiliotrema laurentii (Kuff.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813295.

Basionym: *Torula laurentii* Kuff., *Ann. Soc. Roy. Sci. Méd. Natur. Brux.* 74: 38. 1920.

= *Cryptococcus laurentii* (Kuff.) C.E. Skinner, *Am. Midl. Nat.* 43: 249. 1950.

Papiliotrema mangalensis (Fell, Statzell & Scorzett) A.M. Yurkov, **comb. nov.** MycoBank MB813296.

Basionym: *Cryptococcus mangalensis* Fell *et al.*, *Antonie van Leeuwenhoek* 99: 548. 2011.

Papiliotrema nemorosus (W.I. Golubev, Gadanho, J.P. Samp. & N.W. Golubev) X.Z. Liu, F.Y. Bai, A.M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813298.

Basionym: *Cryptococcus nemorosus* W.I. Golubev *et al.*, *Int. J. Syst. Evol. Microbiol.* 53: 907. 2003.

Papiliotrema perniciosus (W.I. Golubev, Gadanho, J.P. Samp. & N.W. Golubev) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813299.

Basionym: *Cryptococcus perniciosus* W.I. Golubev *et al.*, *Int. J. Syst. Evol. Microbiol.* 53: 910. 2003.

Papiliotrema pseudoalba (Nakase & M. Suzuki) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813300.

Basionym: *Bullera pseudoalba* Nakase & M. Suzuki, *J. Gen. Appl. Microbiol.* 32: 131. 1986.

= *Cryptococcus cellulolyticus* Nakase *et al.*, *J. Gen. Appl. Microbiol.* 9. 1996.

Papiliotrema ruineniae (A.M. Yurkov, M.A. Guerreiro & Á. Fonseca) A.M. Yurkov, **comb. nov.** MycoBank MB813649.
Basionym: *Cryptococcus ruineniae* A.M. Yurkov *et al.*, PLoS One 10: e0120400. 2015.

Papiliotrema rajasthanensis (Saluja & G.S. Prasad) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813301.

Basionym: *Cryptococcus rajasthanensis* Saluja & G.S. Prasad, Int. J. Syst. Evol. Microbiol. 57: 417. 2007.

Papiliotrema taeenensis (K.S. Shin & Y.H. Park) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813302.

Basionym: *Cryptococcus taeenensis* K.S. Shin & Y.H. Park, Int. J. Syst. Evol. Microbiol. 55: 1367. 2005.

Papiliotrema terrestris (Crestani, Landell, Faganello, Vainstein, Vishniac & P. Valente) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813303.

Basionym: *Cryptococcus terrestris* Crestani *et al.*, Int. J. Syst. Evol. Microbiol. 59: 635. 2009.

Papiliotrema wisconsinensis (K. Sylvester, Q.M. Wang & C.T. Hittinger) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB815284.

Basionym: *Cryptococcus wisconsinensis* K. Sylvester *et al.*, FEMS Yeast Res. 15: 7. 2015.

Rhynchogastrema B. Metzler & Oberw., Syst. Appl. Microbiol. 12: 281. 1989. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov.

This genus is emended to include species classified in the anamorphic genus *Bandoniozyma* and is based on the phylogenetic analyses of the seven-gene (Liu *et al.* 2015) and the expanded LSU rRNA gene datasets (Fig. 5A).

Basidiocarps not present. Dikaryotic hyphae thin-walled with clamp connections and haustorial branches. Septa with dolipores and parenthesomes of cup-shaped vesicles of the Tremella-type. Sexual reproduction observed in some species. Basidium with basally swollen probasidium, elongated to subglobose, with apex of the neck partly cruciately septate. Budding cells present, globose, subglobose, ovoid or ellipsoidal. Ballistoconidia not produced. Pseudohyphae and true hyphae with clamp connections may be present in cultures. Fermentation of glucose usually present. Nitrate not utilised. Starch-like compounds are usually formed. Major CoQ system not known.

Type species: *Rhynchogastrema coronatum* B. Metzler & Oberw., Syst. Appl. Microbiol. 12: 281. 1989.

Notes: The species of the recently described anamorphic genus *Bandoniozyma* (Valente *et al.* 2012) formed a well-supported clade in the trees obtained from the analyses of the rRNA ITS (Valente *et al.* 2012) and the sequences of seven genes studied (Liu *et al.* 2015). Sequences of the D1/D2 region of the LSU rRNA gene of *Rhynchogastrema coronatum*, the type species of the

telemorphic genus (Metzler *et al.* 1989), were independently obtained for the type specimen BBA 65155 (GenBank KJ170152) by Weiss *et al.* (2014) and the ex-type culture DSM 28188 (deposited in DSMZ collection by Bertold Metzler) by Andrey Yurkov (GenBank LN870267). The sequences derived from both sources are identical. Phylogenetic analysis showed that *Rhynchogastrema coronatum* was nested within the genus *Bandoniozyma* with 99 % and 92 % bootstrap support in ML and MP analyses, respectively (Fig. 5A), suggesting that *Bandoniozyma* species represent yeast stages of *Rhynchogastrema* species. Based on the nomenclatural priority principle, the name *Rhynchogastrema* is selected for this genus. A fermentative species, *Cryptococcus nanyangensis*, was described by Hui *et al.* (2012). This species was closely related to a group of unnamed *Cryptococcus* strains, which were assigned to the genus *Bandoniozyma* by Valente *et al.* (2012). The ML tree from the expanded LSU rRNA dataset confirmed that *C. nanyangensis* clustered together with *Bandoniozyma* and *Rhynchogastrema* species (Fig. 5A). The former is therefore transferred to the genus *Rhynchogastrema*. Nine species are currently accepted in this genus (Table 1, Fig. 5A). The yeast states of most species of this genus can ferment glucose, which is an unusual trait among basidiomycetous yeasts.

New combinations for *Rhynchogastrema*

Rhynchogastrema aquatica (Brandao, Valente, Pimenta & Rosa) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, **comb. nov.** MycoBank MB813305.

Basionym: *Bandoniozyma aquatica* Brandao *et al.*, PLoS One 7: e46060. 2012.

Rhynchogastrema complexa (Landell, Pagnocca, Sette, Passarini, Garcia, Ribeiro, Lee, Brandao, Rosa & Valente) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, **comb. nov.** MycoBank MB813306.

Basionym: *Bandoniozyma complexa* Landell *et al.*, PLoS One 7: e46060. 2012.

Rhynchogastrema fermentans (Lee) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, **comb. nov.** MycoBank MB813307.

Basionym: *Bandoniozyma fermentans* C.F. Lee, PLoS One 7: e46060. 2012.

Rhynchogastrema glucofermentans (S.O. Suh & Blackwell) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, **comb. nov.** MycoBank MB813308.

Basionym: *Bandoniozyma glucofermentans* S.O. Suh & Blackwell, PLoS One 7: e46060. 2012.

Rhynchogastrema nanyangensis (F.L. Hui & Q.H. Niu) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, **comb. nov.** MycoBank MB813309.

Basionym: *Cryptococcus nanyangensis* F.L. Hui & Q.H. Niu, Curr. Microbiol. 65: 619. 2012.

Rhynchogastrema noutii (Boekhout, Fell, Scorzett & Theelen) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, **comb. nov.** MycoBank MB813304.

Basionym: Bandoniozyma noutii Boekhout et al., PLoS One 7: e46060. 2012.

Rhynchogastrema tunnelae (Boekhout, Fell, Scorzetti & Theelen) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, **comb. nov.** MycoBank MB813310.

Basionym: Bandoniozyma tunnelae Boekhout et al., PLoS One 7: e46060. 2012.

Rhynchogastrema visegradensis (Peter & Dlačny) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, **comb. nov.** MycoBank MB813311.

Basionym: Bandoniozyma visegradensis Peter & Dlačny, PLoS One 7: e46060. 2012.

Bulleraceae X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB813328.

Etymology: In reference to the name of the type genus *Bullera*.

This family is proposed to accommodate a monophyletic lineage formed by the **amylolyticus** (i.e. *Genolevuria* gen. nov.), **Bulleromyces** and **hannae** (i.e. *Bullera* emend.), and **moriformis** clades and four single-species lineages, namely *Cryptococcus allantoinivorans* (*Pseudotremella*), *C. mujuensis* (*Fonsecazyma*), *Sirobasidium intermedium* and *Tremella giraffa* in the tree obtained from the seven-genes dataset (Liu et al. 2015).

Basidiocarps tremella-like, 1–2 cm in diameter. Dikaryotic hyphae with clamp connections and haustorial branches. Sexual reproduction observed in some species. Basidia transversely, obliquely or longitudinally septate. Basidiospores globose, fusiform to narrowly clavate. Budding cells present. Pseudohyphae occasionally present. Ballistoconidia may be present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10 as far as known.

Type genus: Bullera Derx emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

Genera accepted: Bullera emend., *Fonsecazyma* gen. nov., *Genolevuria* gen. nov., and *Pseudotremella* (Table 1, Fig. 1).

Notes: In the constrained ML tree inferred from the expanded LSU rRNA gene dataset, the *Tremella* species in Clade I of Millanes et al. (2011) were assigned to the new family *Bulleraceae* though bootstrap support was lacking (Figs 2 and 5B). *Cryptococcus allantoinivorans* was incorporated into the **moriformis** clade together with two newly added species. A new genus *Pseudotremella* is proposed for this expanded clade (Fig. 5B). *Cryptococcus mujuensis* and the recently described species *Cryptococcus tronadorensis* and *Kwoniella betulae* formed a well supported clade for which a new genus *Fonsecazyma* is proposed (Fig. 5B). The *Sirobasidium intermedium* lineage was expanded to contain two more species, namely *Sirobasidium brefeldianum* and *Tremella exigua*, which correspond to **Tremella clade I** in Millanes et al. (2011). The *Tremella giraffa* lineage was expanded with eight *Tremella* species corresponding to **Tremella clade III** in Millanes et al. (2011). We recommend reclassifying *Sirobasidium* and *Tremella* species in this family, as well as *Biatoropsis* (Fig. 5B) when additional molecular data are available from all or the majority of the species of these three basidiocarp-forming genera.

Cryptococcus cuniculi was described by Shin et al. (2006) as a member of the **Kwoniella** clade showing some relatedness to *Kwoniella* (*Cryptococcus*) *heveanensis* as well as *Cryptococcus tronadorensis* in de Garcia et al. (2012). These results were not supported in our analyses, and *C. cuniculi* clustered close to **Tremella clade I** in Millanes et al. (2011) in the expanded LSU rRNA gene analysis (Fig. 5B). In our opinion, this species should be re-classified together with respective species of *Biatoropsis*, *Sirobasidium* and *Tremella*. Currently, we propose to keep it unclassified as *Cryptococcus cuniculi* pro tem. until additional molecular data is available. Similarly, two *Tremella* species were not assigned to any clade in the expanded LSU rRNA gene analysis (Fig. 5B) as well as in the combined rRNA genes analysis (Millanes et al. 2011). Thus, we recommend keeping them unclassified as *Tremella haematommatis* pro tem. and *Tremella ramalinae* pro tem. until additional molecular data are available.

Bullera Derx, Anns Mycol. 28: 11. 1930. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

= *Bulleromyces* Boekhout & Á. Fonseca, Antonie van Leeuwenhoek 59: 91. 1991.

This genus is emended to include the species in the **Bulleromyces** and **hannae** clades recognised from the multigene phylogeny (Liu et al. 2015).

Basidiocarps absent. Sexual reproduction observed in some species. Dikaryotic hyphae with clamp connections and haustorial branches. Basidia subglobose, clavate or ovoid, and transversely, obliquely or longitudinally septated. Budding cells present. Ballistoconidia rotationally or bilaterally symmetrical. Pseudohyphae not observed. Fermentation absent. Nitrate not utilised. Starch-like compounds usually produced. Major CoQ system CoQ-10.

Type species: Bullera alba (W.F. Hanna) Derx.

Notes: The genus *Bullera* as circumscribed by Boekhout et al. (2011b) contained more than 40 species, which occurred distributed in many different clades of different orders (Fell et al. 2000, Scorzetti et al. 2002, Boekhout et al. 2011a, Weiss et al. 2014, Liu et al. 2015). The sexual state of the type species *Bullera alba* was discovered by Boekhout et al. (1991) and *Bulleromyces albus* as the teleomorph of this species was consequently described. According to the “One fungus = One name” principle implemented in the *Code of Nomenclature for algae, fungi, and plants* (McNeill et al. 2012), the genus name *Bullera* has nomenclatural priority over *Bulleromyces*. The genus *Bullera* emend. currently includes four species (Table 1, Fig. 5B), which were located into two closely related clades in the tree obtained from the seven-genes dataset (Liu et al. 2015). Though these species show a significant deviation from the reference threshold (Table 2), they are kept in the genus *Bullera* at present to accommodate their phenotypic similarity and close phylogenetic relationship and to minimise name changes.

Fonsecazyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813136.

Etymology: The genus is named in honour of the Portuguese mycologist Álvaro Fonseca, for his contributions to the study of diversity and systematics of basidiomycetous yeasts.

This genus is proposed for the clade represented by *Cryptococcus mujuensis*, which was resolved as a single-species lineage in the seven-genes tree (Liu *et al.* 2015) and was supplemented by two newly described species *Cryptococcus tronadorensis* (de Garcia *et al.* 2012) and *Kwoniella betulae* (Sylvester *et al.* 2015) in the LSU rRNA gene tree (Fig. 5C).

Basidiocarps unknown. Sexual reproduction has not been observed. Pseudohyphae and true hyphae have not been observed. Budding cells present. Ballistoconidia are not formed. Fermentation is absent. Nitrate is not utilised. Major CoQ system is CoQ-10.

Type species: Fonsecazyma mujuensis (K.S. Shin & Y.H. Park) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout *comb. nov.*

Notes: The phylogenetic analysis of the seven-gene dataset in Liu *et al.* (2015) indicated that *Cryptococcus mujuensis* was closely related to *Sirobasidium intermedium*. *Cryptococcus tronadorensis* was originally described as a new species related to the *Kwoniella* clade based on the LSU rRNA gene sequences similarity in de Garcia *et al.* (2012). Similarly, the recently described *Kwoniella betulae* (Sylvester *et al.* 2015) was also placed in this clade. Unfortunately, *Cr. mujuensis* was not employed in these studies. In the tree obtained from the expanded LSU rRNA gene dataset, *Cr. mujuensis*, *Cr. tronadorensis* and *K. betulae* formed a strongly supported clade, which was only distantly related to the *Kwoniella* and the *S. intermedium* clades (Fig. 5C). Thus, the new genus *Fonsecazyma* is proposed to accommodate these three species (Table 1). Other sequences obtained from public databases belong to a mislabelled *K. heveanensis* (GenBank AF406890) and three undescribed *Cryptococcus* species (Fig. 5C).

New combinations for *Fonsecazyma*

Fonsecazyma betulae (K. Sylvester, Q.M. Wang, C. T. Hittinger) A.M. Yurkov, A.V. Kachalkin & Boekhout, **comb. nov.** MycoBank MB814752.

Basionym: *Kwoniella betulae* K. Sylvester *et al.*, FEMS Yeast Res. 15: 7. 2015.

Fonsecazyma mujuensis (K.S. Shin & Y.H. Park) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813341.

Basionym: *Cryptococcus mujuensis* K.S. Shin & Y.H. Park, Int. J. Syst. Evol. Microbiol. 56: 2243. 2006.

Fonsecazyma tronadorensis (V. De Garcia, Zalar, Brizzio, Gunde-Cim. & van Brook) A.M. Yurkov, **comb. nov.** MycoBank MB813342.

Basionym: *Cryptococcus tronadorensis* V. De Garcia *et al.*, FEMS Microbiology Ecology. 82: 536. 2012.

Genolevuria X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813329.

Etymology: The genus is named in honour of the French yeast genomics consortium “Genolevures” that produced high-quality yeast genome data.

This genus is proposed for the **amylolyticus** clade comprising four *Cryptococcus* species in the tree derived from the seven-genes dataset (Liu *et al.* 2015).

Basidiocarps not present. Colonies usually orange-coloured. Pseudohyphae occasionally present. True hyphae not observed. Budding cells present. Ballistoconidia not observed. Fermentation absent. Nitrate not utilised. Starch-like compounds weakly produced or not produced at all. Major CoQ system CoQ-10.

Type species: Genolevuria amylolytica (Á. Fonseca, J. Inácio & Spenc.-Mart.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

Notes: The species of this genus have orange-coloured colonies (Inácio *et al.* 2005, Wang *et al.* 2007, Landell *et al.* 2009, Liu *et al.* 2015), which is not a common characteristic among tremellaceous yeasts (Fonseca *et al.* 2011). Four species are currently accepted in this genus (Table 1, Fig. 5B).

New combinations for *Genolevuria*

Genolevuria amylolytica (Á. Fonseca, J. Inácio & Spenc.-Mart.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813330.

Basionym: *Cryptococcus amylolyticus* Á. Fonseca *et al.*, FEMS Yeast Res. 5: 1177. 2005.

Genolevuria armeniaca (Á. Fonseca & J. Inácio) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813331.

Basionym: *Cryptococcus armeniacus* Á. Fonseca & J. Inácio, FEMS Yeast Res. 5(12): 1177. 2005.

Genolevuria bromeliarum (Landell & P. Valente) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813332.

Basionym: *Cryptococcus bromeliarum* Landell & P. Valente, Int. J. Syst. Evol. Microbiol. 59: 911. 2009.

Genolevuria tibetensis (F.Y. Bai & Q.M. Wang) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813333.

Basionym: *Cryptococcus tibetensis* F.Y. Bai & Q.M. Wang, J. Gen. Appl. Microbiol., Tokyo 53: 282. 2007.

Pseudotremella X.Z. Liu, F.Y. Bai, A.M. Yurkov, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813334.

Etymology: In reference to the tremella-like basidiocarp and basidium morphology.

This genus is proposed for the moriformis lineage recognised by Chen (1998) and Liu *et al.* (2015), which was expanded with two *Cryptococcus* species in the tree obtained from the analysis of the LSU rRNA gene dataset (Fig. 5B).

Basidiocarps pustulate, erumpent or tuberculate on wood, pulvinate, hemispherical-moriform to cerebriform, white to pinkish or cream, amber to dark reddish-brown, drying brownish to black. Dikaryotic hyphae hyaline to brown or reddish, with clamp

connections and occasionally haustorial branches. Basidia globose, ellipsoidal, obovoid, pyriform or capitate; four-celled with longitudinal to oblique septa. Budding cells sometimes present. Poorly developed pseudohyphae sometimes present. Fermentation absent. Nitrate not utilised. Major CoQ system unknown.

Type species: Pseudotremella moriformis (Berk.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

Notes: In the tree obtained from the seven-genes dataset, *Tremella moriformis* and *Cryptococcus allantoinivorans* clustered together with strong BP and PP support values, though they were regarded as representing single-species lineages (Liu et al. 2015). In the tree from the expanded LSU rRNA gene dataset (Fig. 5B), the *Tremella* species in the **moriformis** clade recognised in Chen (1998) and *Cryptococcus allantoinivorans* formed a monophyletic clade together with a recently described species, *Cryptococcus laticolor* (Satoh et al. 2013). Thus, we propose the new genus *Pseudotremella* to accommodate this clade. Four species are currently accepted in this genus (Table 1, Fig. 5B).

It should be noted that a sequence of *Tremella indecorata* AM5 derived from specimen Santos s.n. was located in the **moriformis** clade, being in agreement with Millanes et al. (2011). However, three strains obtained from different specimens of the species from different origin and hosts, CBS 6976, originated from *Salix* sp., HBZ194 and DSM 5727 (both from *Diatrype* sp. growing on *Sorbus aucuparia* twigs, Germany), constituted a separate clade distantly related to the **moriformis** clade (Fig. 5A). However, strain CBS 6976 is placed with support closely related to *Pseudotremella* in an unconstrained LSU-based tree – together also with strains HBZ194 and DSM 5727 (data not shown). This represents a conflict with the placement of CBS 6976 in the seven-genes tree (Liu et al. 2015), where it is located in the **aurantia** clade (= *Naemate-llia*). This conflict should be further investigated in the future. Specimen AM5 and strain CBS 6976 are in any case not conspecific. Strain AM5 differs from strain HBZ194 by 7 % (42/613 bp) nucleotide divergence in the LSU rRNA gene sequence, which suggest that *Tremella indecorata* constitutes a species complex. A taxonomic revision for *T. indecorata* cannot be made until the species concept of this species and the strains and sequences belonging to it are verified. Thus, we keep this species unassigned to any lineage as *Tremella indecorata* pro tem. (Table 1).

New combinations for *Pseudotremella*

Pseudotremella allantoinivorans (Middelhoven) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813335.

Basionym: Cryptococcus allantoinivorans Middelhoven, Antonie van Leeuwenhoek 87: 103. 2004.

Pseudotremella laticolor (Satoh & Makimura) A.M. Yurkov, **comb. nov.** MycoBank MB813337.

Basionym: Cryptococcus laticolor Satoh & Makimura, Antonie van Leeuwenhoek 104: 90. 2013.

Pseudotremella moriformis (Berk.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813338.

Basionym: Tremella moriformis Berk., in Smith, Engl. Fl., Fungi (Edn 2) (London) 34: tab. 2446. 1836.

Pseudotremella nivalis (Chee J. Chen) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813340.

Basionym: Tremella nivalis Chee J. Chen, Bibl. Mycol. 174: 101. 1998.

Sirobasidiaceae Lindau, Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1: 89. 1897.

The family *Sirobasidiaceae* was proposed by Möller (1895) and validated by Lindau to accommodate the genus *Sirobasidium*. *Fibulobasidium* was the second genus assigned to this family (Bandoni 1979, Bandoni 1995, Wells & Bandoni 2001). *Sirobasidiaceae* are characterised by basidia arranged in linear chains (*Sirobasidium*) or in clusters (*Fibulobasidium*), which form passively released basidiospores. Phylogenetic studies indicated that the *Fibulobasidium* species formed a well-supported monophyletic clade while *Sirobasidium* species belonged to divergent lineages in the *Tremellales* (Bandoni et al. 2011, Liu et al. 2015). *Sirobasidium magnum* and *S. japonicum* formed a monophyletic lineage with the genus *Fibulobasidium* (Fig. 5B), whereas *S. brefeldianum* and *S. intermedium* grouped with *Tremella exigua* in the *Bulleraceae* (Millanes et al. 2011, Weiss et al. 2014, Liu et al. 2015, Fig. 5B). The phylogenetic position of the type species of *Sirobasidium*, *S. sanguineum*, is unknown because sequence data were not available for this species. Therefore, it is difficult to re-delimitate the genus *Sirobasidium* at present. We suggest to maintain the family *Sirobasidiaceae* for the monophyletic lineage formed by the genus *Fibulobasidium* and the two *Sirobasidium* species (Figs 1 and 5B).

Cuniculitremaceae J.P. Sampaio., R. Kirschner & M. Weiss, Antonie van Leeuwenhoek 80: 155. 2001

Type genus: Cuniculitrema J.P. Sampaio. & R. Kirschner, Antonie van Leeuwenhoek 80: 155. 2001 (synonym of *Sterigmatosporidium*).

Genera accepted: Fellomyces, Kockovaella and *Sterigmatosporidium* (Table 1, Fig. 1).

Notes: The family *Cuniculitremaceae* was proposed by Kirschner et al. (2001) to accommodate the teleomorphic genus *Cuniculitrema* and two anamorphic genera, *Fellomyces* and *Kockovaella*, based on their close phylogenetic relationship and the common morphological feature of producing conidia on stalks. *Cuniculitrema* was described for the teleomorph of *Sterigmatosporidium* (Kirschner et al. 2001). The latter was proposed by Kraepelin & Schulze (1982) and has nomenclatural priority over the former. Therefore, *Cuniculitrema* is treated as a synonym of *Sterigmatosporidium* here.

Fellomyces Y. Yamada & I. Banno, J. Gen. Appl. Microbiol., Tokyo 30: 524. 1984.

This genus is restricted to accommodate the ***Fellomyces*** clade as recognised in Liu et al. (2015) based on the analysis of the seven-genes dataset.

Basidiocarps unknown. Sexual reproduction not observed. Pseudohyphae and true hyphae may be present. Blastoconidia at the top of stalk-like conidiophores. Budding cells present. Ballistoconidia not present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type species: Fellomyces polyborus (D.B. Scott & Van der Walt) Y. Yamada & I. Banno, J. Gen. Appl. Microbiol. 30: 524. 1984.

Notes: This genus as previously delimited contained twelve species (Lopandic *et al.* 2011) but the **Fellomyces** clade recognised in Liu *et al.* (2015) included only four *Fellomyces* species. The support for the affinity of *F. horovitziae* to this clade in the seven-genes tree was weak (Liu *et al.* 2015). This species differs in physiological characteristics when compared to other *Fellomyces* species (Lopandic *et al.* 2011). We maintain this species in the emended genus *Fellomyces* for the time being to avoid creating a monotypic genus. This genus currently contains four species (Table 1, Fig. 5D).

Kockovaella Nakase, I. Banno & Y. Yamada, J. Gen. Appl. Microbiol., Tokyo 37: 178. 1991. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus is emended to accommodate the **Kockovaella** clade as recognised in Liu *et al.* (2015), which includes non-ballistoconidium-forming species previously belonging to the genus *Fellomyces*.

Basidiocarps unknown. Sexual reproduction not observed. Pseudohyphae absent or poorly developed. True hyphae not observed. Blastoconidia separate from the parental cells at the distal end of stalk-like conidiophores. Budding cells present. Ballistoconidia may be present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type species: Kockovaella thailandica Nakase, I. Banno & Y. Yamada, J. Gen. Appl. Microbiol. 37: 178. 1991.

Notes: The **Kockovaella** clade recognised in Liu *et al.* (2015) includes eight *Fellomyces* species and all currently recognised eleven *Kockovaella* species (Takashima & Nakase 2011). As previously circumscribed, the genus *Kockovaella* was differentiated from the genus *Fellomyces* only by the production of ballistoconidia (Takashima & Nakase 2011), a property that has since long been shown to be an unstable character (Nakase *et al.* 1993). The PRBO test, however, indicated that the genus is significantly more divergent than the genera that fit into the optimal boundaries (Table 2), discouraging us to merge this clade with the **Fellomyces** clade into a single genus, which will significantly expand the deviation of the genus further. Nineteen species are currently accepted in the genus *Kockovaella* (Table 1, Fig. 5D).

New combinations for **Kockovaella**

Kockovaella chinensis (Prillinger, G. Kraep. & Lopandic) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813343.

Basionym: Fellomyces chinensis Prillinger *et al.*, Syst. Appl. Microbiol. 20: 579. 1997.

Kockovaella distylii (Hamam., Kuroy. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813344.

Basionym: Fellomyces distylii Hamam. *et al.*, Int. J. Syst. Bacteriol. 48: 290. 1998.

Kockovaella fuzhouensis (J.Z. Yue) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813345.

Basionym: Sterigmatomyces fuzhouensis J.Z. Yue, Acta Mycol. Sin. 1: 81. 1982.

= *Fellomyces fuzhouensis* (J.Z. Yue) Y. Yamada & I. Banno, J. Gen. Appl. Microbiol. 34: 506. 1988.

Kockovaella lichenicola (Prillinger, G. Kraep. & Lopandic) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813346.

Basionym: Fellomyces lichenicola Prillinger *et al.*, Syst. Appl. Microbiol. 20: 582. 1997.

Kockovaella mexicana (Lopandic, O. Molnár & Prillinger) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813347.

Basionym: Fellomyces mexicanus Lopandic *et al.*, Microbiol. Res. 160: 8. 2005.

Kockovaella ogasawarensis (Hamam., Kuroy. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813348.

Basionym: Fellomyces ogasawarensis Hamam. *et al.*, Int. J. Syst. Bacteriol. 48: 289. 1998.

Kockovaella sichuanensis (Prillinger, G. Kraep. & Lopandic) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813349.

Basionym: Fellomyces sichuanensis Prillinger *et al.*, Syst. Appl. Microbiol. 20: 582. 1997.

Kockovaella prillingeri X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **sp. nov.** MycoBank MB813350 Holotype: CBS 7552.

= *Fellomyces thailandicus* Prillinger *et al.*, Syst. Appl. Microbiol. 20: 583. 1997.

Notes: The name *Kockovaella thailandica*, which is the type species of the genus *Kockovaella*, already exists. Thus a new name *Kockovaella prillingeri* is proposed for *Fellomyces thailandicus* as this species has to be transferred to the genus *Kockovaella* and a new combination using the epithet 'thailandicus' is not possible in this genus. The new name is proposed in honour of Hansjörg Prillinger who discovered and described the species *Fellomyces thailandicus*.

Sterigmatosporidium G. Kraep. & U. Schulze, Antonie van Leeuwenhoek 48: 479. 1983.

= *Cuniculitrema* J. P. Sampaio & R. Kirschner, Antonie van Leeuwenhoek 80: 155. 2001.

Notes: The name *Sterigmatosporidium* was described before *Cuniculitrema* and thus has nomenclatural priority. The genus has only one species, *S. polymorphum* with the name *C. polymorpha* listed as synonym (Table 1).

Naemateliaceae X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB813351.

Etymology: In reference to the name of type genus *Naematelia*.

This family is proposed to accommodate a monophyletic lineage consisting of the **aurantia** clade formed by four *Tremella* species and a single-species clade represented by *Cryptococcus cistialbidi* as resolved in the seven-genes tree (Liu et al. 2015).

Basidiocarps when formed caespitose, tuberculate or spherical to thick foliaceous or crumpled, ivory, yellow, bright orange, reddish. Basidia subglobose, globose to ovoid, four-celled and with vertical or occasionally transverse septa. Orange-pigmented colonies may be present. True hyphae with clamp connections and haustorial branches sometimes present. Budding cells present. Ballistoconidia sometimes present. Fermentation absent. Nitrate and nitrite not utilised. Major CoQ system CoQ-10.

Type genus: *Naematelia* Fr.

Genera accepted: *Naematelia* and *Dimennazyma*.

Notes: The species *Bullera arundinariae* branched before the **aurantia** clade and *Cryptococcus cistialbidi* in the seven-genes Bayesian tree, but this phylogenetic relationship was not supported (Liu et al. 2015). Thus, it is not included in the new family *Naemateliaceae*. *C. cistialbidi* occurred at different positions in the ML and NJ trees obtained from the seven-genes dataset (Liu et al. 2015). Possible relationship of the **Tremella Clade II** species (e.g. *T. cladoniae*, *T. leptogii*, *T. phaeophysciae*) with the **aurantia** clade was shown in the analyses of rRNA genes (Millanes et al. 2011, Liu et al. 2015, Fig. 5A in this study), but the affinity lacked support in rRNA gene analyses. The taxonomic assignment of the Clade II species remains to be determined. A strain representing *T. indecorata* in Liu et al. (2015) was placed close to Clade II species in the expanded LSU rRNA gene tree (Fig. 5A).

Naematelia Fr., Obs. Myc. 2: 370. 1818.

This genus is resurrected to accommodate species in the **aurantia** clade (Chen 1998, Millanes et al. 2011, Liu et al. 2015).

Basidiocarps caespitose, tuberculate or spherical to thick foliaceous or crumpled, ivory, yellow, bright orange, reddish. Basidia subglobose, globose to ovoid, four-celled and with vertical or occasionally transverse septa. True hyphae with clamp connections and haustorial branches present. Budding cells present. Ballistoconidia sometimes present. Fermentation absent. Nitrate and nitrite not utilised. Major CoQ system CoQ-10.

Type species: *Naematelia encephala* (Pers.) Fr., Observ. mycol. (Havniae) 2: 370. 1818.

Basionym: *Tremella encephala* Pers., Syn. meth. fung. (Göttingen) 2: 623. 1801.

Notes: The genus contains four species previously classified as *Tremella* (Chen 1998, Millanes et al. 2011, Liu et al. 2015). These species formed a strongly supported monophyletic clade in the

trees from the seven-genes (Liu et al. 2015) and expanded LSU datasets (Fig. 5A), and also in an unconstrained LSU tree (data not shown).

New combinations for *Naematelia*

Naematelia aurantialba (Bandoni & M. Zang) Millanes & Wedin, **comb. nov.** MycoBank MB813352.

Basionym: *Tremella aurantialba* Bandoni & M. Zang, Mycologia 82: 270. 1990.

Naematelia microspora (Lloyd) Millanes & Wedin, **comb. nov.** MycoBank MB813357.

Basionym: *Tremella microspora* Lloyd, Mycol. Writ. 6 (Letter 64): 991. 1920.

Dimennazyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813339.

Etymology: The genus is named in honour of M. E. di Menna for her pioneering work on yeast ecology and diversity.

This genus is proposed to accommodate the single-species lineage *Cryptococcus cistialbidi* in the tree derived from the seven-genes dataset (Liu et al. 2015).

Basidiocarps not present. Colonies usually orange-coloured. Pseudohyphae occasionally present. True hyphae not observed. Budding cells present. Ballistoconidia not observed. Fermentation absent. Nitrate not utilised. Starch-like compounds weakly produced or not produced. Major CoQ system CoQ-10.

Type species: ***Dimennazyma cistialbidi*** (Á. Fonseca, J. Inácio & Spenc.-Mart.) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout **comb. nov.** MycoBank MB814753.

Basionym: *Cryptococcus cistialbidi* Á. Fonseca et al., FEMS Yeast Res. 5: 1177. 2005.

Notes: The species *Cryptococcus cistialbidi* formed a single-species branching before the **aurantia** clade (i.e. *Naematelia* gen. nov.) with strong support in the seven-genes tree (Liu et al. 2015). This species produces orange-coloured colonies as emphasised by Inácio et al. (2005), which is different from the yeast stage of the *Naematelia* species that have yellowish brown colonies. Thus *C. cistialbidi* is not assigned to *Naematelia*. The colony colour of *C. cistialbidi* is similar to those produced by the genus *Genolevuria* (i.e. the **amylolyticus** clade in Fonseca et al. 2011). However, *C. cistialbidi* was distantly related to *Genolevuria* in the seven-genes tree (Liu et al. 2015). Therefore, we propose a new genus for this single-species lineage.

Carcinomycetaceae Oberw. & Bandoni, Nordic JI Bot. 2: 507. 1982. **emend.** A.M. Yurkov.

Basidiocarps mycoparasitic, forming a thin layer on the surface of host. Basidia subglobose or cylindrical, longitudinally or cruciately septated, with four sterigmata. Budding cells present. Ballistoconidia occasionally present. Pseudohyphae and true hyphae not observed in culture. Sexual reproduction not

observed in culture. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type genus: *Carcinomyces* Oberw. & Bandoni.

Genus accepted: *Carcinomyces*.

Notes: Oberwinkler & Bandoni (1982) proposed the family *Carcinomycetaceae* to accommodate three mycoparasitic genera *Carcinomyces*, *Christiansenia* and *Syzygospora*. While the type genus of this family is placed in the order Tremellales, two other genera are phylogenetically related to *Filobasidiales* (Millanes *et al.* 2011, Fig. 2 of this study). A close relationship between the genus *Carcinomyces* (*Syzygospora effibulata*) and *Tremella polyporina* was shown previously in the analysis of the combined rRNA dataset (Millanes *et al.* 2011). In the present study a well-supported clade formed by *Bullera arundinariae*, *Syzygospora effibulata* and *Tremella polyporina* was resolved in the expanded LSU rRNA gene tree (Fig. 5D). The species *B. arundinariae* was the only member of this clade included in the seven-genes phylogenetic analysis in Liu *et al.* (2015). *B. arundinariae* branched before the **aurantia** clade (i.e. *Naematelia*) and *Cryptococcus cistialbidi* (i.e. *Dimennazyma*) in the seven-genes Bayesian tree, but this phylogenetic relationship was not supported (Liu *et al.* 2015). Thus, we prefer to classify these genera into two different families, *Naemateliaceae* (*Naematelia* and *Dimennazyma*) and *Carcinomycetaceae* (*Carcinomyces*).

Carcinomyces Oberw. & Bandoni, *Nordic JI Bot.* 2: 507. 1982. **emend.** A.M. Yurkov.

This genus is resurrected and emended to accommodate a well-supported clade formed by *Bullera arundinariae*, *Syzygospora effibulata* and *Tremella polyporina* in the expanded LSU rRNA gene tree (Figs 2 and 5D). The diagnosis of *Carcinomyces* is based on the description of the family *Carcinomycetaceae*.

Type species: *Carcinomyces effibulatus* (Ginns & Sunhede) Oberw. & Bandoni, *Nordic Journal of Botany* 2: 509. 1982.

≡ *Christiansenia effibulata* Ginns & Sunhede, *Bot. Notiser* 131: 168. 1978.

≡ *Syzygospora effibulata* (Ginns & Sunhede) Ginns, *Mycologia* 78: 626. 1986.

Notes: *Carcinomyces* was proposed by Oberwinkler & Bandoni (1982) to accommodate two species transferred from *Christiansenia*, namely *Ch. mycetophila* and *Ch. effibulata*, with the latter being the type species. Ginns (1986) treated *Carcinomyces*, *Christiansenia* and *Heterocephalacria* as synonyms of *Syzygospora*. Molecular phylogenetic analyses showed that the genus *Syzygospora* sensu Ginns (1986) was polyphyletic (Millanes *et al.* 2011, also see Fig. 2 of this study). As discussed above, *S. alba* (type of *Syzygospora*) and *Ch. pallida* (type of *Christiansenia*) were located in a clade within the *Filobasidiales*, while *S. effibulata* (= *Ch. effibulata*) was located in a well supported clade together with *Bullera arundinariae* and *Tremella polyporina* in the *Tremellales* (Fig. 2). Therefore, the genus *Carcinomyces* is resurrected here for this clade. The taxonomic assignment of the genus *Carcinomyces* in *Tremellales* remains to be determined as discussed above. The affinity of *Carcinomyces* (*Christiansenia*) *mycetophila* with this genus needs to be confirmed using molecular data.

New combinations for *Carcinomyces*

Carcinomyces arundinariae (Fungsin, M. Takash. & Nakase) A.M. Yurkov, **comb. nov.** MycoBank MB813361.

Basionym: *Bullera arundinariae* Fungsin *et al.*, *Microbiol. Culture Coll.* 18: 86. 2002.

Carcinomyces polyporina (D.A. Reid) A.M. Yurkov, **comb. nov.** MycoBank MB813362.

Basionym: *Tremella polyporina* D.A. Reid, *Trans. Br. Mycol. Soc.* 55: 416. 1970.

Trimorphomycetaceae X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB813363.

Etymology: In reference to the name of the type genus *Trimorphomyces*.

This family is proposed for a well-supported monophyletic lineage including the **flavus** clade and *Trimorphomyces papilionaceus*, *Bullera miyagiana* and *B. sakaeratica* (Liu *et al.* 2015).

Basidiocarps minute, pustulate up to 2 mm diameter, watery-gelatinous, milky to faintly greenish. H-shaped dikaryotic conidia form dikaryotic hyphae with clamp connections and haustorial branches. Alternatively, these conidia germinate with paired blastogenous conidia. Basidia tremella-like, narrowly clavate, pyriform to stalked capitate, and four-celled. Basidiospores bud or form ballistoconidia. In culture, true hyphae may form extensively. Budding cells present, with polar or multilateral budding. Ballistoconidia occasionally present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type genus: *Trimorphomyces* Bandoni & Oberw.

Genera accepted: *Trimorphomyces*, *Carlosrosaea*, *Saitozyma* and *Sugitazyma*.

Notes: The species assigned to *Trimorphomycetaceae* also formed a monophyletic lineage in the tree obtained from the expanded LSU rRNA gene dataset, but bootstrap support was lacking (Fig. 5D). Two lichenicolous *Tremella* species (*T. diploschistina* and *T. parmiliarum*) are only loosely connected with other species and we therefore refrain from including them in any family until additional molecular data are available. Contrarily, *Bullera ninhbinhensis* clustered together with *Cryptococcus podzolicus* with strong support (Fig. 5E) and we thus suggest to include this species in the family. In the original description *Bullera vrieseae* (Landell *et al.* 2015) was placed together with *Bullera sakaeratica* and *B. miyagiana* in a well-supported clade, which is resolved in this study as members of the family *Trimorphomycetaceae* (Fig. 5E). Relationships between the three *Bullera* species were not supported in our analyses. *Bullera sakaeratica* was closely related to *Trimorphomyces papilionaceus* with strong support, while *B. miyagiana* and *B. vrieseae* were located in significantly diverged branches with unresolved positions (Fig. 5E), suggesting that they represent independent lineages in the family *Trimorphomycetaceae*. Thus, we propose new genera for *B. vrieseae* and *B. miyagiana*. The phylogenetic relationships of *Tremella diploschistina* and *T. parmiliarum* with other species were also not resolved in our analyses. We do not reclassify the two sexual species and leave

them temporary as *T. diploschistina* pro tem and *T. parmeliarum* pro tem.

Trimorphomyces Bandoni & Oberw., Syst. Appl. Microbiol. 4: 106. 1983. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov.

This genus is emended to include an anamorphic yeast species *Bullera sakaeratica*, which is closely related to the type species of *Trimorphomyces* (Liu *et al.* 2015, Fig. 5E in this study).

Basidiocarps mycoparasitic, small, watery-gelatinous. Hyphae with clamp connections and haustorial branches may be present. Basidia narrow clavate, pyriform to capitate, four-celled, longitudinally or obliquely septa. Basidiospores subglobose. H-shaped zygoconidia may be present. Budding cells present. Ballistoconidia occasionally present. Sexual reproduction not observed in culture. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type species: Trimorphomyces papilionaceus Bandoni & Oberw., Syst. Appl. Microbiol. 4: 106. 1983.

Notes: The close relationship between *T. papilionaceus* and *B. sakaeratica* was shown in different studies (Boekhout *et al.* 2011a, Weiss *et al.* 2014, Liu *et al.* 2015). As discussed above, these species were treated as two single-species lineages in Liu *et al.* (2015) due to the consideration that the former is morphologically unique (Bandoni & Boekhout 2011a). The separation of *Trimorphomyces* species in distantly related clades and the close relationships of some *Trimorphomyces* species with some *Cryptococcus* and *Bullera* species as shown in the tree obtained from the expanded LSU rRNA gene dataset (Fig. 5D, E) suggested that the phenotypically circumscribed genus *Trimorphomyces* is polyphyletic and that *Trimorphomyces* species may have a common yeast stage. Therefore, we transfer *B. sakaeratica* to the genus *Trimorphomyces* here. Another described *Trimorphomyces* species, *T. nebularis* (Kirschner & Chen 2008), is transferred to the genus *Vishniacozyma* gen. nov. *Trimorphomyces papilionaceus* forms zygoconidia from a single conidiogenous cell, differing from *T. nebularis* (*Vishniacozyma nebularis* comb. nov.) which produces zygoconidia from two neighbouring conidiogenous cells (Bandoni & Oberwinkler 1983, Kirschner & Chen 2008). The genus *Trimorphomyces* currently contains two species (Table 1, Fig. 5E).

New combinations for *Trimorphomyces*

Trimorphomyces sakaeraticus (Fungsini, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, **comb. nov.** MycoBank MB813365.

Basionym: Bullera sakaeratica Fungsini *et al.*, Microbiol. Culture Coll. 19: 37. 2003.

Saitozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813367.

Etymology: The genus is named in honour of the Japanese yeast taxonomist Masuyoshi Saito.

This genus is proposed for the **flavus** clade containing three species previously assigned to the genus *Cryptococcus* (Liu *et al.* 2015).

Basidiocarps not known. Cultures can be pigmented and pale to brownish-yellow in colour. Pseudohyphae and true hyphae may be present. Sexual reproduction not observed in culture. Budding cells present. Ballistoconidia occasionally present. Fermentation absent. Nitrate not utilised. Starch-like compounds weakly produced or not formed. Major CoQ system CoQ-10.

Type species: Saitozyma flava (Saito) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813368.

Basionym: Torula flavus Saito, Jap. J. Bot. 1: 45. 1922.

Notes: The **flavus** clade delimited in Liu *et al.* (2015) based on multiple genes is equivalent to the **podzolicus** clade in Boekhout *et al.* (2011a), which was based on the analysis of LSU rRNA gene (D1/D2 domains) sequences, even though this clade received no bootstrap support. In the tree from the expanded LSU rRNA gene dataset, the close relationship between *C. podzolicus* and *Bullera ninhbinhensis* was confirmed, but they did not form a monophyletic clade with the other two species, *C. flavus* and *C. paraflavus*, in the **flavus** clade (Fig. 5E). Since the affinity of *C. podzolicus* with the **flavus** clade was strongly supported in the trees obtained both from the seven genes and the three rRNA gene datasets (Liu *et al.* 2015), we assign these species to *Saitozyma* gen. nov. Four species are currently accepted in this new genus (Table 1) and an additional sequence representing a potential new species was obtained from public databases (Fig. 5E).

New combinations for *Saitozyma*

Saitozyma ninhbinhensis (Luong, M. Takash., Dung & Nakase) A.M. Yurkov, **comb. nov.** MycoBank MB813370.

Basionym: Bullera ninhbinhensis Luong *et al.*, J. Gen. Appl. Microbiol. 6: 335–342. 2002.

Saitozyma paraflava (Golubev & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813372.

Basionym: Cryptococcus paraflavus Golubev & J.P. Samp., J. Gen. Appl. Microbiol. 50: 68. 2004.

Saitozyma podzolica (Babeva & Reshetova) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813373.

Basionym: Candida podzolica Babeva & Reshetova, Mikrobiologiya, Seriya B 44: 333. 1975.

Sugitazyma A. M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB814754.

Etymology: The genus is named in honour of the Japanese yeast taxonomist Takashi Sugita.

This genus is proposed for the single-species lineage *Bullera miyagiana* resolved in the tree inferred from seven genes (Liu *et al.* 2015) and the expanded LSU rRNA gene dataset (Fig. 5E).

Basidiocarps not known. Pseudohyphae and true hyphae may be present. Sexual reproduction not observed in culture. Budding cells present. Ballistoconidia may be present. Fermentation

absent. Nitrate not utilised. Starch-like compounds produced. Major CoQ system CoQ-10.

Type species: Sugitazyma miyagiana (Nakase, Itoh, Takem. & Bandoni) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb nov.** Mycobank MB814755.

Basionym: Bullera miyagiana Nakase *et al.*, J. Gen. Appl. Microbiol. 36: 35. 1990.

Notes: Relationships between *Bullera miyagiana* and other *Trimorphomycataceae* remained unclear in the expanded analysis of the LSU rRNA gene sequences (Fig. 5E). We propose to erect a new genus for this single-species lineage to restrict the genus *Bullera* to the type lineage in the family *Bulleraceae*. The genus *Sugitazyma* currently contains one species (Table 1).

Carlosrosaea A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB814756.

Etymology: The genus is named in honour of the Brazilian yeast taxonomist and ecologist Carlos A. Rosa.

This genus is proposed for the single-species lineage *Bullera vrieseae* resolved in the tree inferred from the expanded LSU rRNA gene dataset (Fig. 5E).

Basidiocarps not known. Pseudohyphae and true hyphae not observed in culture. Sexual reproduction not observed in culture. Budding cells present. Ballistoconidia may be present. Fermentation absent. Nitrate sometimes utilised. Starch-like compounds not produced. Major CoQ system unknown.

Type species: Carlosrosaea vrieseae (Landell, Brandão, Safar, Gomes, Félix, Santos, Pagani, Ramos, Broetto, Mott, Valente & Rosa) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb nov.** Mycobank MB814757.

Basionym: Bullera vrieseae Landell *et al.*, Int. J. Syst. Evol. Microbiol. 65: 2469. 2015.

Notes: Relationships between *Bullera vrieseae* and other *Trimorphomycataceae* remained unclear in the expanded analysis of the LSU rRNA gene sequences (Fig. 5E). *B. vrieseae* was distantly related to *B. miyagiana* (*Sugitazyma* gen. nov.) and showed additionally distinct phenotypic characters (Landell *et al.* 2015). We propose to erect a new genus for this single-species lineage to restrict the genus *Bullera* emend. to the type lineage in the family *Bulleraceae*. The genus *Carlosrosaea* contains currently one species (Table 1) and an additional sequence representing a potential new species (LSU: GenBank KJ690943) was found in public databases.

Cryptococcaceae Kütz. ex Castell. & Chalm., Man. Trop. Med., 3rd Edn: 1070. 1919. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This family is emended here to accommodate the monophyletic lineage consisting of the **Cryptococcus** and **Kwoniella** clades (Fig. 1) as recognised in Liu *et al.* (2015).

Basidiocarps not known. Pseudohyphae and true hyphae present or not, but present after mating. Basidia one-celled, cylindrical, clavate, capitate with four chains of acropetal basidiospores, or globose to ovoid with longitudinal and transverse septa. Basidiospores passively released, variably shaped, smooth or somewhat rough bacilliform, ellipsoid, globose, oblong-pentagonal or obpyriform to cylindrical. Budding cells usually present, but may be absent. Fermentation absent. Nitrate not utilised. Starch-like compounds usually produced. Major CoQ system CoQ-9 or CoQ-10.

Type genus: Cryptococcus Vuillemin

Genera accepted: Cryptococcus and *Kwoniella*.

Notes: The family *Cryptococcaceae* was originally established to contain anamorphic tremellomycetous yeasts, including the genera *Bullera*, *Cryptococcus*, *Fellomyces*, *Kockovaella*, *Trichosporon*, *Tschuchiyaea* and *Udeniomyces* (Kützing 1833, Van der Walt 1987). Molecular phylogenetic studies indicated that this family and most of the genera assigned to it are not monophyletic (Wells 1994, Fell *et al.* 2000, Scorzetti *et al.* 2002, Sampaio 2004, Liu *et al.* 2015). Based on the seven-genes phylogeny (Liu *et al.* 2015), the family *Cryptococcaceae* is emended here to accommodate only two emended genera *Cryptococcus* and *Kwoniella* (Tables 1 and 2, Fig. 1).

Cryptococcus Vuillemin, Rev. Gén. Sci. Pures Appl. 12: 741. 1901. Nomen Cons. (McNeil *et al.* 2006), **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

= *Filobasidiella* Kwon-Chung, Mycologia 67: 1198. 1975.

= *Tsuchiyaea* Yamada, Kawasaki, Itoh, Banno et Nakase, J. Gen. Appl. Microbiol. 34: 509. 1988.

This genus is emended to accommodate the **Cryptococcus** clade described in Findley *et al.* (2009), Liu *et al.* (2015) and the LSU rRNA gene tree (Fig. 5C), and includes the species belonging to the *C. neoformans/C. gattii* complex, *Filobasidiella depauperata* and *F. lutea*.

Basidiocarps not present. True hyphae may be present, but present after mating. Basidia one-celled, slender, cylindrical sphaeropedunculate. Basidiospores in four long basipetal chains, smooth, or somewhat rough bacilliform, ellipsoid, globose, oblong-pentagonal or obpyriform. Haustorial branches present or not. Budding cells usually present, but in some species also absent. Thick polysaccharide capsules may be present. Fermentation absent. Nitrate and nitrite not utilised. Starch-like compounds usually produced. Major CoQ system CoQ-9 or CoQ-10.

Type species: Cryptococcus neoformans (Sanfelice) Vuillemin, Rev. Gén. Sci. Pures Appl. 12: 747–750. 1901.

Notes: The generic name *Cryptococcus* was originally created by Kützing (1833) for an organism placed among the algae and only one species *C. mollis* was included, but the description of this species was not presented. Vuillemin (1901) recircumscribed *Cryptococcus* to include pathogenic yeasts and transferred *Saccharomyces neoformans* to this genus. The genus *Cryptococcus* has been conserved with *C. neoformans* as the type species as proposed by Fell *et al.* (1989). Many molecular

phylogenetic studies have shown that *Cryptococcus* as circumscribed until now (Fonseca *et al.* 2011) is a highly artificial genus that contains species distributed in all five major lineages of *Tremellomycetes* (Takashima & Nakase 1999, Fell *et al.* 2000, Scorzetti *et al.* 2002, Sampaio 2004, Fonseca *et al.* 2011, Weiss *et al.* 2014, Liu *et al.* 2015). The teleomorphic genus *Filobasidiella* was described by Kwon-Chung (1975) for the perfect state of *C. neoformans*. Four species are currently accepted in the genus *Filobasidiella* (Kwon-Chung 2011). *Filobasidiella bacillispora* was described for the sexual stage of serotypes B and C of *C. neoformans* (Kwon-Chung 1976). Two other *Filobasidiella* species, *F. depauperata* and *F. lutea*, are mycoparasites but lack ontogenetic yeast states. The affinity of *F. depauperata* with the **Cryptococcus/Filobasidiella** clade has been shown in different studies (Sivakumaran *et al.* 2002, Findley *et al.* 2009, Rodriguez-Carres *et al.* 2010, Boekhout *et al.* 2011a, Weiss *et al.* 2014, Liu *et al.* 2015). Sequence analyses of the ITS regions and SSU rRNA gene showed that *F. lutea* belongs to the **Cryptococcus/Filobasidiella** clade (Sivakumaran *et al.* 2002). Unfortunately, the sequence data from this species are neither available from GenBank, nor from other databases, nor from these authors. *Filobasidiella xianghuijun* is the fifth species described in the genus (Zang 1999), but the taxonomic and phylogenetic position of this species remains to be confirmed by molecular means (Kwon-Chung 2011). Recently, a sexual cycle with a tetrapolar mating system was found in *C. amyloletus* (Findley *et al.* 2012). So far, all the species in the **Cryptococcus/Filobasidiella** clade have been shown to have similar sexual forms. The *C. neoformans/C. gattii* complex was recently revised and presently contains seven species (Hagen *et al.* 2015). In that paper it was also suggested that the anamorph name *Cryptococcus* should have priority over the teleomorph name *Filobasidiella* (Kwon-Chung 1975) as the former has nomenclatural priority, is much more commonly used and, importantly, refers to the name of an important infectious disease, cryptococcosis, that is caused by species of this genus (Heitman *et al.* 2011). Thus, the *Filobasidiella* species without a yeast state are transferred here to *Cryptococcus*. Fonseca *et al.* (2011) considered *Tsuchiyaea wingfieldii* (basionym *Sterigmatomyces wingfieldii*) a synonym of *C. amyloletus* because of similar SSU, ITS and LSU D1/D2 sequences. This point of view is supported by similar sequences of four protein-coding genes (Liu *et al.* 2015). Phylogenetic analysis of four MAT related genes, *STE3*, *STE20*, *SXI1a* and *LPD1* indicated minor differences between *T. wingfieldii* and *C. amyloletus* (Findley *et al.* 2012). Thus, further studies are needed to fully understand the taxonomic relationship between these two species. Ten species are currently accepted in this genus (Table 1).

New combinations for *Cryptococcus*

Cryptococcus depauperatus (Petch) Boekhout, Liu, Bai & M. Groenew., **comb. nov.** MycoBank MB813376.

Basionym: *Aspergillus depauperatus* Petch, Trans. Br. Mycol. Soc. 16: 245. 1932 ('1931').

= *Filobasidiella depauperata* (Petch) Samson *et al.*, Antonie van Leeuwenhoek 49: 454. 1983.

= *Filobasidiella arachnophila* Malloch *et al.*, Can. J. Bot. 56: 1823. 1978.

Notes: The close relatedness between this species and *C. neoformans* (cited as *F. neoformans*) was shown by SSU rRNA gene sequence analysis (Kwon-Chung *et al.* 1995).

Multilocus phylogenetic analysis using ITS, *TEF-1 alpha* and *RPB1* sequences corroborated these conclusions and found the species related to *C. neoformans* (cited as var. *grubii*), *C. deneoformans* (cited as var. *neoformans*), *C. gattii* (cited as VGI) and *C. deuteroformans* (cited as VGII) (Rodriguez-Carres *et al.* 2010). Another study using six genes (the above with addition of *RPB2*, mitSSU and the D1/D2 domains of LSU rDNA) showed that also *Tsuchiyaea wingfieldii* and *Cryptococcus amyloletus* were phylogenetically related (Findley *et al.* 2009).

Cryptococcus luteus (Roberts) Boekhout, Liu, Bai & M. Groenew., **comb. nov.** MycoBank MB814758.

Basionym: *Filobasidiella lutea* Roberts, Mycotaxon 60, 198. 1997.

Notes: This species could not be studied by molecular means due to the absence of a culture. The close relatedness between this species, *C. neoformans* (cited as *Filobasidiella neoformans*) and *C. depauperatus* (cited as *Filobasidiella depauperata*) was shown by sequence analysis of ITS and SSU rRNA gene fragments (Sivakumaran *et al.* 2002).

Kwoniella Statzell-Tallman & Fell, FEMS Yeast Res. 8: 107. 2008. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus is emended to include the species of the ***Kwoniella*** clade containing *K. mangroviensis* and six anamorphic species previously classified in *Bullera* and *Cryptococcus* (Liu *et al.* 2015).

Basidiocarps unknown. Sexual reproduction with tetrapolar mating system observed in some species. Basidia polymorphic, lageniform, globose to ovoid with longitudinal and transverse septa. Basidiospores passively released, globose, ovoid to cylindrical. Pseudohyphae and true hyphae may be present. Budding cells present. Ballistoconidia occasionally present. Fermentation absent. Nitrate not utilised. Starch-like compounds are usually produced. Major CoQ system CoQ-10.

Type species: *Kwoniella mangroviensis* Statzell, Belloch & Fell, FEMS Yeast Res. 8: 107. 2008.

Notes: The genus *Kwoniella* was proposed for a teleomorphic yeast *K. mangroviensis* isolated from mangrove habitats (Statzell-Tallman *et al.* 2008). The second species of the genus, *K. heveanensis*, was proposed for the teleomorph of *Cryptococcus heveanensis* (Sun *et al.* 2011). Recently, two teleomorphic species, *K. europaea* and *K. botswanensis*, closely related to *K. mangroviensis* were described (Guerreiro *et al.* 2013). All sexual species displayed a tetrapolar mating system (Guerreiro *et al.* 2013). Since the use of a dual nomenclature for classification of sexual and asexual morphs of fungi was recently terminated, three asexual species were described in the genus *Kwoniella*, *K. shandongensis* (Chen *et al.* 2012), *K. newhampshirensis* and *K. betulae* (Sylvester *et al.* 2015). The ***Kwoniella*** clade was consistently resolved in different studies (Findley *et al.* 2009, Boekhout *et al.* 2011a, Guerreiro *et al.* 2013, Weiss *et al.* 2014, Liu *et al.* 2015). However, the affinity of *Cryptococcus cuniculi* to this clade remains controversial. Boekhout *et al.* (2011a) and Weiss *et al.* (2014) showed that this species belonged to the ***Kwoniella*** clade according to LSU rRNA gene sequence analyses, but Liu *et al.* (2015)

showed that *C. cuniculi* branched before the **Cryptococcus** and **Kwoniella** clades in an analysis of combined SSU, ITS and LSU rRNA gene sequences. In the tree obtained from the expanded LSU rRNA gene dataset in this study, *C. cuniculi* was located in a branch distantly related to the **Kwoniella** clade (Fig. 5B, C). Thus, the final phylogenetic position of *C. cuniculi* remains to be determined. The recently described *K. betulae* was also placed outside the genus *Kwoniella* in a well-supported clade (i.e. *Fonsecazyma* gen. nov.) containing *C. mujuensis* and *C. tronadorensis* (Fig. 5C). Eleven species are accepted in *Kwoniella* emend. in this study (Table 1) and three sequences representing potential new species were obtained from public databases (Fig. 5C). *Kwoniella* species are usually saprobic and differ from the closely aligned pathogenic yeasts in the genus *Cryptococcus* emend. by their inability to grow at 37 °C (Findley et al. 2009).

New combinations for *Kwoniella*

Kwoniella dendrophila (Van der Walt & D.B. Scott) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813381.

Basionym: *Bullera dendrophila* Van der Walt & D.B. Scott, Antonie van Leeuwenhoek 36: 384. 1970.

Kwoniella bestiolae (Thanh, Hai & Lachance) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813383.

Basionym: *Cryptococcus bestiolae* Thanh et al., FEMS Yeast Res. 6: 301. 2006.

Kwoniella dejecticola (Thanh, Hai & Lachance) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813384.

Basionym: *Cryptococcus dejecticola* Thanh et al., FEMS Yeast Res. 6: 303. 2006.

Kwoniella pini (Golubev & Pfeiffer) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813387.

Basionym: *Cryptococcus pinus* Golubev & Pfeiffer, Int. J. Syst. Evol. Microbiol. 58: 1970. 2007.

Kwoniella shivajii (S.R. Ravella, S.A. James, C.J. Bond, I.N. Roberts, K. Cross, Retter & P.J. Hobbs) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813389.

Basionym: *Cryptococcus shivajii* S.R. Ravella et al., Curr. Microbiol. 60: 14. 2010.

Phaeotremellaceae A.M. Yurkov & Boekhout, **fam. nov.** MycoBank MB813390.

Etymology: In reference to the name of the type genus *Phaeotremella*.

This family is proposed to accommodate the **foliaceae** clade and a single-species lineage, *Cryptococcus spencermartinsiae* (Liu et al. 2015).

Basidiocarps, if present, foliaceous with caespitose lobes, gelatinous, tan to cinnamon or light brown when fresh, drying dark brown to black. Hyphae with clamp connections; haustorial branches occasionally present. Basidia globose, subglobose,

ovoid or ellipsoidal, four-celled and with longitudinal to diagonal or transverse septa. Basidiospores subglobose to broadly ellipsoidal. Budding cells present in culture. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type genus: *Phaeotremella* Rea

Genera accepted: *Phaeotremella* and *Gelidatrema*.

Notes: The **foliaceae** clade was resolved as early branching *Tremellales* in the seven-genes Bayesian tree without PP support; however, in the seven-genes ML and NJ trees, this clade was branching prior to the **Tremellales** and **Trichosporonales** lineages (Liu et al. 2015). The **foliaceae** clade was also resolved as a well-supported monophyletic group in the trees constructed from rRNA genes datasets, but its position varied. In the tree from the combined SSU, ITS-5.8S and LSU datasets, the **foliaceae** clade is branching before the **Tremellales** and **Trichosporonales** lineages in Millanes et al. (2011), but between these two lineages in Liu et al. (2015). In the trees from the LSU rRNA gene datasets containing more filamentous fruitbody-forming taxa, this clade located within the *Tremellales* (Boekhout et al. 2011a, Weiss et al. 2014), but as a group (equivalent to *Phaeotremella*) branching before the order in this study (Fig. 1). The affinity of *Cryptococcus spencermartinsiae* to *Phaeotremellaceae* fam. nov. remains to be confirmed. It branches before the **foliaceae** clade with strong to moderate support in the Bayesian and ML trees obtained from the seven-genes dataset, but it occurred in a branch distantly related to this clade in the combined rRNA genes tree (Liu et al. 2015). In the tree from the expanded LSU dataset, *C. spencermartinsiae* branched more early than the **foliaceae** (*Phaeotremella*) clade, but without bootstrap support (Fig. 5C). Furthermore, this species is not able to grow above 25 °C in contrast to the other species in the **foliaceae** clade (*Phaeotremella* gen. nov.) that can grow at 30 °C. Thus, we propose to accommodate it in the new genus *Gelidatrema* gen. nov.

Phaeotremella Rea, Trans. Br. Mycol. Soc. 3: 377. 1912. **emend.** A.M. Yurkov & Boekhout.

Type species: *Phaeotremella pseudofoliacea* Rea, Trans. Br. Mycol. Soc. 3: 377. 1912.

= *Tremella foliacea* Pers., Observationes mycologicae 2: 98. 1800.

This genus is resurrected and emended to accommodate the **foliaceae** clade (Chen 1998, Boekhout et al. 2011a, Millanes et al. 2011, Weiss et al. 2014, Liu et al. 2015, also see Fig. 5B).

Basidiocarps, if present, foliaceous with caespitose lobes, gelatinous, tan to cinnamon or light brown when fresh, drying dark brown to black. Hyphae with clamp connections; haustorial branches occasionally present. Basidia globose, subglobose, ovoid or ellipsoidal, four-celled and with longitudinal to diagonal or transverse septa. Basidiospores subglobose to broadly ellipsoidal. In culture budding cells sometimes present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Notes: *Phaeotremella* was described by Rea (1912) including only *Phaeotremella pseudofoliacea*, which was considered a synonym of *Tremella foliacea* (Roberts 1999). As discussed

above, the **foliacea** clade was consistently resolved as a well supported clade in different studies using various datasets, though its phylogenetic position varied (Chen 1998, Boekhout et al. 2011a, Millanes et al. 2011, Weiss et al. 2014, Liu et al. 2015, this study Fig. 1). Seven species, including two *Cryptococcus* and five *Tremella* species were included in this clade with 100 % bootstrap support (Fig. 1) and therefore are transferred to *Phaeotremella* (Table 1).

New combinations for *Phaeotremella*

Phaeotremella fagi (Middelhoven & Scorzetti) A.M. Yurkov & T. Boekhout, **comb. nov.** MycoBank MB813391.

Basionym: *Cryptococcus fagi* Middelhoven & Scorzetti, Antonie van Leeuwenhoek 90: 63. 2006.

Phaeotremella simplex (H.S. Jacks. & G.W. Martin) Millanes & Wedin, **comb. nov.** MycoBank MB813392.

Basionym: *Tremella simplex* H.S. Jacks. & G.W. Martin, Mycologia 32: 687. 1940.

Phaeotremella skinneri (Phaff & Carmo Souza) A.M. Yurkov & T. Boekhout, **comb. nov.** MycoBank MB813393.

Basionym: *Cryptococcus skinneri* Phaff & Carmo Souza, Antonie van Leeuwenhoek 28: 205. 1962.

Phaeotremella mycetophiloides (Kobayasi) Millanes & Wedin, **comb. nov.** MycoBank MB813394.

Basionym: *Tremella mycetophiloides* Kobayasi, Sci. Rep. Tokyo Bunrika Daig., Sect. B 4: 13. 1939.

Phaeotremella mycophaga (G.W. Martin) Millanes & Wedin, **comb. nov.** MycoBank MB813395.

Basionym: *Tremella mycophaga* G.W. Martin, Mycologia 32: 686. 1940.

Phaeotremella neofoliacea (Chee J. Chen) Millanes & Wedin, **comb. nov.** MycoBank MB813396.

Basionym: *Tremella neofoliacea* Chee J. Chen, Bibl. Mycol. 174: 135. 1998.

Gelidatrema A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB814759.

Etymology: In reference to the origin of this psychrophilic yeast and its phylogenetic relatedness to the order *Tremellales*.

This genus is proposed for the single-species lineage *Cryptococcus spencermartinsiae* as resolved in the seven-genes tree (Liu et al. 2015) and the expanded LSU rRNA gene tree (Fig. 5C).

Basidiocarps not know. Pseudohyphae and true hyphae not observed in culture. Sexual reproduction not observed in culture. Budding cells present. Ballistoconidia absent. Fermentation absent. Nitrate not utilised. Starch-like compounds not produced. Major CoQ system unknown.

Type species: *Gelidatrema spencermartinsiae* (Garcia, Brizzio, Boekhout, Theelen, Libkind & van Broock) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB814760.

Basionym: *Cryptococcus spencermartinsiae* Garcia et al., Int. J. Syst. Evol. Microbiol. 60: 710. 2010.

Notes: Relationships between *Cryptococcus spencermartinsiae* and *Phaeotremella* remained unclear in phylogenetic analyses. *Cryptococcus spencermartinsiae* branched earlier than the **foliacea** (*Phaeotremella*) clade, but without bootstrap support in the expanded LSU rRNA gene tree (Fig. 5C) and with moderate support in the tree inferred from seven genes (Liu et al. 2015). Additionally, *C. spencermartinsiae* showed phenotypic characters distinct from other members of the **foliacea** clade (de Garcia et al. 2010). Thus, we propose to erect a new genus for this single-species lineage. The genus *Gelidatrema* currently contains one species (Table 1), but a few additional sequences representing potential new species (ITS: GenBank KC455886, DQ242634) were found in public databases.

Order *Trichosporonales* Boekhout & Fell, FEMS Yeast Res. 1: 265–270. 2001.

The order *Trichosporonales* was introduced to accommodate arthroconidia-producing *Trichosporon* species that formed a clade in a sequence analysis of the D1/D2 domains of LSU rRNA gene (Fell et al. 2000). The distinction of this order from the order *Tremellales* was supported by the seven-genes phylogeny (Liu et al. 2015). Several *Bullera* and *Cryptococcus* species were included in this order although they do not produce arthroconidia (Takashima et al. 2001, Fungsin et al. 2006, Boekhout et al. 2011a, Weiss et al. 2014, Liu et al. 2015). In view of physiological, morphological and molecular data, two families, namely *Trichosporaceae* emend. and *Tetragonomycetaceae* emend. and ten genera, including one emended and four new genera are accepted in this order (Table 1).

Trichosporonaceae Nann. [as 'Trichosporaceae'], Repert. mic. uomo: 285. 1934. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

= *Asterotremellaceae* Prillinger et al., J. Gen. Appl. Microbiol. 53: 174. 2007.

This family is emended to accommodate the monophyletic lineage comprising the **brassicae/gracile**, **cutaneum**, **haglerorum**, **porosum**, ***Trichosporon*** and ***Vanrija*** clades, and four single-species lineages comprising three *Cryptococcus* and one *Trichosporon* species as recognised in multigene phylogenies (Liu et al. 2015).

Basidiocarps unknown. Sexual reproduction not known. Septate hyphae with arthroconidia usually present. Pseudohyphae may be present. Budding cells usually present. Fermentation absent. Nitrate not utilised. This family has a pronounced ability to assimilate aromatic compounds. Major CoQ system CoQ-9 or CoQ-10.

Type genus: *Trichosporon* Behrend.

Genera accepted: *Trichosporon*, *Apiotrichum* emend., *Cutaneotrichosporon* gen. nov., *Effuseotrichosporon* gen. nov., *Haglerozyma* gen. nov., and *Vanrija*.

Notes: *Trichosporonaceae* was introduced to include the *Trichosporon* species that were assigned to *Geotrichoides* and *Proteomyces* (Nannizzi 1934). The scope of this family has been expanded by the discovery of more *Trichosporon* species

(Sugita & Nakase 1998, Colombo *et al.* 2011), but was also reduced by the exclusion of the genus *Geotrichum*, an ascomycetous genus that also forms arthroconidia (Weijman 1979). Some *Cryptococcus* species also belonged to this clade. Thus, this family is emended to accommodate a monophyletic lineage consisting of the **brassicae/gracile, cutaneum, haglerorum, humicola** (i.e. *Vanrija* pro parte), **porosum**, and ***Trichosporon*** clades, as well as four single-species clades of three *Cryptococcus* species and one *Trichosporon* species as recognised in Liu *et al.* (2015).

Trichosporon Behrend, Berliner Klin. Wochenschr. 21: 464. 1890.

This genus is re-defined to accommodate only the species in the ***Trichosporon*** clade recognised in the seven-genes phylogeny (Liu *et al.* 2015).

Basidiocarps not known. Septate hyphae with arthroconidia usually present. Sexual reproduction not observed. Budding cells present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-9.

Type species: Trichosporon ovooides Behrend

Notes: Pleurococcus beigelii Küchenmeister & Rabenhorst (Rabenhorst 1867) was probably the first fungus representing the current genus *Trichosporon*. The name *Pleurococcus* was rejected by Guého *et al.* (1992a) as it concerned a poorly described species and no material was preserved. The name *Trichosporon* was introduced to include only one species, *T. ovooides*, isolated from an infected moustache hair from Germany (Behrend 1890). Guého *et al.* (1992a) selected a neotype for *T. ovooides*, CBS 7556 isolated from capital white piedra occurring on a Caucasian, a habitat that agreed with the original description of the species by Behrend. These authors also rejected the neotypification of *T. beigelii* with ATCC 28592 (= CBS 2466) as proposed by McPartland & Goff (1991), but they selected this strain as neotype for *T. cutaneum* when using a more narrow species concept for this taxon. A major contribution to the taxonomy of the genus *Trichosporon* was made by Guého *et al.* (1992b) by recircumscribing several species using rRNA sequence analysis, nutritional physiology, electron microscopy of septal pores, and the analysis of the G+C content of the DNA and DNA–DNA hybridisation experiments. Using sequence analysis of the D2 domain of the 26S rRNA, five clusters of species were observed: 1) *T. sporotrichoides*, *T. dulcitum*, *T. gracile*, *T. multisporum*, *T. laibachii*, and *T. loubieri*; 2) *T. cutaneum*, *T. jirovecii*, *T. mucoides*, and *T. moniliiforme*; 3) *T. coremiiforme*, *T. aquatile*, *T. faecale*, *T. asahii*, *T. asteroides* and *Fissurella filamenta*; 4) *T. ovooides* and *T. inkin*; and 5) *T. brassicae* and *T. montevidense* (Guého *et al.* 1992b). It is interesting to note that this clustering is fully congruent with our results from the analyses of multiple genes.

Recently, many new *Trichosporon* species have been described or have been transferred to this genus from other genera (Guého *et al.* 1998, Colombo *et al.* 2011, Sugita 2011). According to the latest monographic treatment (Sugita 2011) the genus contains 37 species. The *Trichosporon* species are distributed over five clades, namely brassicae, cutaneum, gracile, porosum and *Trichosporon* (Middelhoven *et al.* 2004, Sugita *et al.* 2004, Sugita 2011), which are similar to those observed before in analyses

of partial LSU rRNA sequences (Guého *et al.* 1992b). Serological characteristics correlate well with these clades and therefore were applied as a taxonomic marker in this group (Tsuchiya *et al.* 1974, Sugita 2011). The genus is restricted here to accommodate only the *Trichosporon* clade, including the neotype species *T. ovooides* (Liu *et al.* 2015). Species belonging to this newly circumscribed genus *Trichosporon* have serotype II. Twelve species are accepted in this genus (Table 1, Fig. 6).

Cutaneotrichosporon X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813397.

Etymology: In reference to the specific epithet of the type species in this genus.

This genus is proposed for the well supported monophyletic group consisting of the cutaneum and haglerorum clades together with *Trichosporon guehoae*, *Cryptococcus curvatus*, *Cr. cyanovorans* and *Cr. daszewskae* (Liu *et al.* 2015, Fig. 6 of this study).

Basidiocarps not known. Sexual reproduction not observed. True hyphae disarticulate into ovoid, cylindrical or cubic arthroconidia. Pseudohyphae abundant or not. Budding cells present. Fermentation absent. Nitrate not utilised, nitrite utilised or not. Major CoQ system CoQ-10.

Type species: Cutaneotrichosporon cutaneum (Beurm., Gougerot & Vaucher bis) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** Mycobank MB13398.

Notes: Close relationships between the cutaneum and haglerorum clades were supported in recent phylogenetic studies (Sugita 2011, Liu *et al.* 2015, Takashima *et al.* 2015, Fig. 6 of this study). The next well-supported node clustered with cutaneum and haglerorum clades with *T. guehoae*, *Cr. curvatus*, *Cr. cyanovorans* and *Cr. daszewskae* (Fig. 6). Since this expanded clade received strong support in multi-gene studies by Liu *et al.* (2015) and Takashima *et al.* (2015) as well as the extended LSU rRNA gene phylogeny (Fig. 6), we propose to classify the cutaneum and haglerorum clades together with *T. guehoae*, *Cr. curvatus*, *Cr. cyanovorans* and *Cr. daszewskae* (Fig. 6) in a single genus *Cutaneotrichosporon* gen. nov., in order to avoid proposing several small genera with only one or two species. The genus *Cutaneotrichosporon* currently contains 15 species (Table 1).

New combinations for *Cutaneotrichosporon*

Cutaneotrichosporon arboriformis (Sugita, M. Takash., Sano, Nishim., Kinebuchi, S. Yamag. & Osanai) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813407.

Basionym: Cryptococcus arboriformis Sugita *et al.*, Microbiol. Immunol. 51: 544. 2007.

Cutaneotrichosporon curvatus (Diddens & Lodder) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB814761.

Basionym: Candida heveanensis Diddens & Lodder var. *curvata* Diddens & Lodder, Beitr. Monogr. Hefenarten. II Teil. Die anaskoprogenen Hefen: 310. 1942.

= *Cryptococcus curvatus* (Diddens & Lodder) Golubev, Mikol. Fitopatol. 15: 467. 1981.

Cutaneotrichosporon cutaneum (de Beurmann, Gougerot & Vaucher) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813398.

Basionym: *Oidium cutaneum* de Beurmann *et al.*, Bull. Mém. Soc. Méd. Hôpit. Paris 18: 52. 1910.

= *Trichosporon cutaneum* (de Beurmann *et al.*) M. Ota, Anns Parasit. hum. comp. 4: 12. 1926.

Cutaneotrichosporon cyanovorans (Motaung, Albertyn, J. L. F. Kock et Pohl) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB814762.

Basionym: *Cryptococcus cyanovorans* Motaung *et al.*, Int. J. Syst. Evol. Microbiol. 62: 1211. 2012.

Cutaneotrichosporon daszewskae (M. Takash., Sugita, Shinoda & Nakase) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB814763.

Basionym: *Cryptococcus daszewskae* M. Takash. *et al.*, Int. J. Syst. Evol. Microbiol. 51: 2204, 2001.

Cutaneotrichosporon debeurmannianum (Sugita, M. Takash., Nakase & Shinoda) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813399.

Basionym: *Trichosporon debeurmannianum* Sugita *et al.*, Int. J. Syst. Evol. Microbiol. 51: 1221–1228. 2001.

Cutaneotrichosporon dermatis (Sugita, M. Takash., Nakase, Ichikawa, Ikeda & Shinoda) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813400.

Basionym: *Trichosporon dermatis* Sugita *et al.*, Int. J. Syst. Evol. Microbiol. 51: 1221. 2001.

Cutaneotrichosporon guehoae (Middelhoven, Scorzettii & Fell) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB814764.

Basionym: *Trichosporon guehoae* Middelhoven *et al.*, Can. J. Microbiol. 45: 687. 1999.

Cutaneotrichosporon jirovecii (Frágner) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813401.

Basionym: *Trichosporon jirovecii* Frágner, Česká Mykol. 23: 160. 1969.

Cutaneotrichosporon haglerorum (Middelhoven, Á. Fonseca, S.C. Carreiro, Pagnocca & O.C. Bueno) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813408.

Basionym: *Cryptococcus haglerorum* Middelhoven *et al.*, Antonie van Leeuwenhoek 83: 168. 2003.

Cutaneotrichosporon moniliiforme (Weigmann & A. Wolff) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813403.

Basionym: *Oidium moniliiforme* Weigmann & A. Wolff, Zentbl. Bakt. Parasitkde, Abt. II 22: 668. 1909.

= *Trichosporon moniliiforme* (Weigmann & A. Wolff) E. Guého & M.T. Smith, Antonie van Leeuwenhoek 61: 309. 1992.

Cutaneotrichosporon mucooides (E. Guého & M.T. Smith) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813402.

Basionym: *Trichosporon mucooides* E. Guého & M.T. Smith, Antonie van Leeuwenhoek 61: 312. 1992.

Cutaneotrichosporon oleaginosus (J.J. Zhou, S.O. Suh & Gujjari) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB815305.

Basionym: *Trichosporon oleaginosus* J.J. Zhou *et al.*, Mycologia 103: 1115. 2011.

Cutaneotrichosporon smithiae (Middelhoven, Scorzetti, Sugita & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813404.

Basionym: *Trichosporon smithiae* Middelhoven *et al.*, Int. J. Syst. Evol. Microbiol. 54: 979. 2004.

Cutaneotrichosporon terricola (Sugita, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813405.

Basionym: *Trichosporon terricola* Sugita *et al.*, J. Gen. Appl. Microbiol. 48: 295. 2002.

Haglerozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813406.

Basionym: *Trichosporon chiarellii* Pagnocca, Legaspe, Rodrigues & Ruivo, Int. J. Syst. Evol. Microbiol. 60: 1457. 2010.

Etymology: The genus is named in honour of Allen N. Hagler for his work on yeast ecology and physiology.

This genus is proposed for the single-species lineage *Trichosporon chiarellii*, which showed some phylogenetic relatedness to the genus *Cutaneotrichosporon* in the seven-genes tree (Liu *et al.* 2015).

Basidiocarps not known. Sexual reproduction not observed. True hyphae sometimes disarticulate into arthroconidia. Pseudohyphae abundant or not. Budding cells present. Fermentation absent. Nitrate and nitrite not utilised. The major CoQ system unknown.

Type species: *Haglerozyma chiarellii* (Pagnocca, Legaspe, Rodrigues & Ruivo) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** Mycobank MB814765.

Notes: *Trichosporon chiarellii* was branching earlier than the genus *Cutaneotrichosporon* in the seven-genes tree with strong posterior probability support from Bayesian analysis but without bootstrap support from ML and NJ analyses (Liu *et al.* 2015). In the expanded LSU rRNA gene analysis, *T. chiarellii* was located in the same position without statistical support (Fig. 6), suggesting the species represents a distinct lineage. The genus currently contains one species (Table 1).

Apiotrichum Stautz, Phytopath. Z. 3: 209. 1931. **emend.** A.M. Yurkov & Boekhout.

= *Hyalodendron* Diddens, Centbl. Bakt. Parasitkde, Abt. II 90: 316. 1934.

= *Protendomycopsis* Windisch, Beitr. Biol. Pfl. 41: 355, 1965.

The genus *Apiotrichum* is resurrected and emended here for the gracile/brassicae and **porosum** clades containing 18 *Trichosporon* species (Middelhoven *et al.* 2004, Sugita 2011, Liu *et al.* 2015). Close relationships between these clades were resolved in multi-gene studies by Liu *et al.* (2015) and Takashima *et al.* (2015) as well as an extended LSU rRNA gene phylogeny (Fig. 6). Several genus names are available

for species contained in this clade. The genus *Apiotrichum* was described for *Apiotrichum (Trichosporon) porosum* by Stautz (1931) and *Hyalodendron* was proposed by Diddens (1934) to accommodate *Hyalodendron (Trichosporon) lignicola*. The former name has nomenclature priority over the latter. Therefore, *Hyalodendron* is treated as a synonym of *Apiotrichum*.

Basidiocarps not known. Sexual reproduction not observed. Septate and branched hyphae present that form arthroconidia. Catenate or lateral conidia occasionally present. Pseudohyphae present. Budding cells present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-9.

Type species: Apiotrichum porosum Stautz, *Phytopath. Z.* 3: 209. 1931

Notes: The genus *Apiotrichum* was proposed with *A. porosum* as the type species (Stautz 1931). Though this species could not produce fragmenting mycelium, viz. arthroconidia, it was transferred to the genus *Trichosporon* based on rRNA gene sequence analysis and a similar physiology with other *Trichosporon* species (Middelhoven *et al.* 2001). Species belonging to this genus have serotype I and III, and their major coenzyme Q system is Q-9 (Sugita 2011, Takashima *et al.* 2015). Close relationships between these three clades received strong support in multi-gene studies by Liu *et al.* (2015) and Takashima *et al.* (2015) as well as the extended LSU rRNA gene phylogeny (Fig. 1). For reasons of conservatism we combine the three clades into a single genus *Apiotrichum*. The genus currently contains 20 species (Table 1).

New combinations for *Apiotrichum*

Apiotrichum brassicae (Nakase) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813409.

Basionym: *Trichosporon brassicae* Nakase, *J. Gen. Appl. Microbiol.* 17: 417. 1971.

Apiotrichum cacaoliposimilis (J.L. Zhou, S.O. Suh & Gujjari) Kachalkin, A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB814766.

Basionym: *Trichosporon cacaoliposimilis* J.L. Zhou *et al.*, *Mycologia* 103: 1114. 2011.

Apiotrichum dehoogii (Middelhoven, Scorzetti & Fell) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813410.

Basionym: *Trichosporon dehoogii* Middelhoven *et al.*, *Int. J. Syst. Evol. Microbiol.* 54: 979. 2004.

Apiotrichum domesticum (Sugita, A. Nishikawa & Shinoda) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813411.

Basionym: *Trichosporon domesticum* Sugita *et al.*, *J. Gen. Appl. Microbiol.* 41: 431. 1995.

Apiotrichum dulcimum (Berkhout) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813412.

Basionym: *Oospora dulcita* Berkhout, *Consid. Vég. Vosges:* 50–51 + pl. 3. 1923.

≡ *Trichosporon dulcimum* (Berkhout) Weijman, *Antonie van Leeuwenhoek* 45: 126. 1979.

Apiotrichum gamsii (Middelhoven, Scorzetti, Sigler & Fell) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813413.

Basionym: *Trichosporon gamsii* Middelhoven *et al.*, *Int. J. Syst. Evol. Microbiol.* 54: 982. 2004.

Apiotrichum gracile (Weigmann & A. Wolff) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813414.

Basionym: *Oidium gracile* Weigmann & A. Wolff, *Zentbl. Bakt. ParasitKde, Abt. II* 22: 668. 1909.

≡ *Trichosporon gracile* (Weigmann & A. Wolff) E. Guého & M.T. Smith, *Antonie van Leeuwenhoek* 61: 307. 1992.

Apiotrichum laibachii (Windisch) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813415.

Basionym: *Endomyces laibachii* Windisch, *Beitr. Biol. Pfl.* 41: 356. 1965.

≡ *Trichosporon laibachii* (Windisch) E. Guého & M.T. Smith, *Antonie van Leeuwenhoek* 61: 302. 1992.

Apiotrichum lignicola (Diddens) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813416.

Basionym: *Hyalodendron lignicola* Diddens, *Zentbl. Bakt. ParasitKde, Abt. II* 90: 317. 1934.

≡ *Trichosporon lignicola* (Diddens) Fell & Scorzetti, *Int. J. Syst. Evol. Microbiol.* 54: 997. 2004.

Apiotrichum loubieri (Morenz) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813417.

Basionym: *Geotrichum loubieri* Morenz, *Mykologische Schriftenreihe, Leipzig* 2: 46. 1964.

≡ *Trichosporon loubieri* (Morenz) Weijman, *Antonie van Leeuwenhoek* 45: 126. 1979.

Apiotrichum montevidense (L.A. Queiroz) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813418.

Basionym: *Endomyces montevidensis* L.A. Queiroz, *Mycopath. Mycol. Appl.* 51: 311. 1973.

≡ *Trichosporon montevidense* (L.A. Queiroz) E. Guého & M.T. Smith, *Antonie van Leeuwenhoek* 61: 301. 1992.

Apiotrichum mycotoxinivorans (O. Molnár, Schatzm. & Prillinger) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813420.

Basionym: *Trichosporon mycotoxinivorans* O. Molnár *et al.*, *Syst. Appl. Microbiol.* 27: 664. 2004.

Apiotrichum siamense (Nakase, Jindam., Sugita & H. Kawas.) Kachalkin, A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB814767.

Basionym: *Trichosporon siamense* Nakase *et al.*, *Mycoscience* 47: 107. 2006.

Apiotrichum scarabaeorum (Middelhoven, Scorzetti & Fell) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813421.

Basionym: *Trichosporon scarabaeorum* Middelhoven *et al.*, *Int. J. Syst. Evol. Microbiol.* 54: 981. 2004.

Apiotrichum sporotrichoides (van Oorschot) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813422.

Basionym: *Trichosporiella sporotrichoides* van Oorschot, *Stud. Mycol.* 20: 66. 1980.

Apiotrichum vadense (Middelhoven, Scorzetti & Fell) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813423.

Basionym: *Trichosporon vadense* Middelhoven *et al.*, Int. J. Syst. Evol. Microbiol. 54: 976. 2004.

Apiotrichum veenhuisii (Middelhoven, Scorzetti & Fell) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813424.

Basionym: *Trichosporon veenhuisii* Middelhoven *et al.*, Int. J. Syst. Evol. Microbiol. 50: 382. 2000.

Apiotrichum wieringae (Middelhoven) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813425.

Basionym: *Trichosporon wieringae* Middelhoven, Antonie van Leeuwenhoek 86: 331. 2004.

Apiotrichum xylopinii (S.O. Suh, Lee, Gujjari & Zhou) Kachalkin, A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB814768.

Basionym: *Trichosporon xylopinii* S.O. Suh *et al.*, Int. J. Syst. Evol. Microbiol. 61: 2540. 2010.

Vanrija R.T. Moore, Bot. Mar. 23: 367. 1980.

= *Asterotremella* H.J. Prillinger, K. Lopandic, K. Sterflinger, E. Metzger & R. Bauer, ScienceWeek@Austria: 11. 1993. Nomen nudum. (Note: The name *Asterotremella* is introduced as a nomen nudum as a description, a diagnosis, and information on a type were not provided).

= *Asterotremella* Prillinger, Lopandic & Sugita, J. Gen. Appl. Microbiol. 53: 171. 2007.

The concept of this genus as emended by Weiss *et al.* (2014) is accepted.

Basidiocarps not known. Sexual reproduction not observed. Pseudohyphae and true hyphae present. Arthroconidia usually not present. Budding cells present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-9 or CoQ-10.

Type species: *Vanrija humicola* (Dasz.) R.T. Moore

Notes: The genus *Vanrija* was proposed with *V. humicola* as the type strain (Moore 1980). Following suggestions made by Okoli *et al.* (2007) and Fonseca *et al.* (2011), Weiss *et al.* (2014) emended this genus to accommodate the **humicola** clade, including five *Cryptococcus* species, namely *C. ramirezgomezianus* (= *Vanrija albida*, basionym *Sporobolomyces albidus*), *C. humicola*, *C. longa*, *C. musci*, and *C. pseudolongus* (Takashima *et al.* 2001), but they did not present an emended diagnosis for the genus. The genus *Asterotremella* and family Asterotremellaceae based on the study of yeasts isolated from *Asterophora* basidiocarps has been introduced by Prillinger *et al.* (1993) and later described (Prillinger *et al.* 2007), indicating in both cases close relationships with the species *C. humicola*, the type species of the genus *Vanrija* (Moore 1980). However, *Vanrija* has nomenclatural priority over *Asterotremella*. Two species, which were described as *Asterotremella*, namely *A. meifongana* and *A. nantouana* were placed in the **humicola** clade in the expanded LSU rRNA gene tree with high bootstrap support (Fig. 6). *Cryptococcus fragicola*, which did not cluster in the **Vanrija** clade in Weiss *et al.* (2014), was shown to be closely related to this clade in the Bayesian and ML trees based on the seven-genes dataset with strong PP and BP support (Liu *et al.* 2015) as well as in the combined rRNA genes analysis in Wang & Wang (2015). *Cryptococcus thermophilus* was not included in the phylogenetic analysis performed by Weiss *et al.* (2014) and

clustered loosely with the *Vanrija* core group in the LSU rRNA gene tree in Takashima *et al.* (2015) and Wang & Wang (2015). This species, however, clustered inside the clade delimited with *Cr. fragicola* in Takashima *et al.* (2015) and in the expanded LSU rRNA gene tree (Fig. 6). Therefore, we transfer these four species to the genus *Vanrija*. The genus currently contains nine species (Table 1).

New combinations for *Vanrija*

Vanrija fragicola (M. Takash., Sugita, Shinoda & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813426.

Basionym: *Cryptococcus fragicola* M. Takash. *et al.*, Int. J. Syst. Evol. Microbiol. 51: 2205. 2001.

Vanrija meifongana (C.F. Lee) Kachalkin, A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB814769.

Basionym: *Asterotremella meifongana* C.F. Lee, Antonie van Leeuwenhoek 99: 647. 2011.

Vanrija nantouana (C.F. Lee) Kachalkin, A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB814770.

Basionym: *Asterotremella nantouana* C.F. Lee, Antonie van Leeuwenhoek 99: 648. 2011.

Vanrija thermophila (Vogelmann, Chaves & Hertel) Kachalkin, A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB814772.

Basionym: *Cryptococcus thermophilus* Vogelmann *et al.*, Int. J. Syst. Evol. Microbiol. 62: 1719. 2012.

Effuseotrichosporon A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB814773.

Etymology: In reference to the widespread distribution (Lat. effuse) of the species.

This genus is proposed for the single-species lineage formed by *Trichosporon vanderwaltii* in *Trichosporonaceae* (Figs 2 and 6).

Basidiocarps not known. Sexual reproduction not observed. True hyphae disarticulate into arthroconidia. Pseudohyphae abundant or not. Budding cells present. Fermentation absent. Nitrate and nitrite sometimes utilised. The major CoQ system unknown.

Type species: *Effuseotrichosporon vanderwaltii* (Motaung, Albertyn, Kock, C.F. Lee, S.O. Suh, M. Blackwell & C.H. Pohl) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MB814774.

Basionym: *Trichosporon vanderwaltii* Motaung *et al.*, Antonie van Leeuwenhoek. 103: 315. 2013.

Notes: *Trichosporon vanderwaltii* was described for a group of strains from different sources (Motaung *et al.* 2013). These strains formed a sister clade to the **brassicae/porosum** clades (i.e. *Apiotrichum* gen. nov.) in the tree drawn from the ITS and LSU D1/D2 sequences but statistical support for this phylogeny was lacking (Motaung *et al.* 2013). The affinity of *T. vanderwaltii* to the family Trichosporonaceae was resolved in this study but its phylogenetic relationships to other clades of the family remained

unclear (Fig. 6). This species showed wide geographic distribution and we expect more species to be described in the future. Currently the genus contains one species (Table 1).

Tetragonomycetaceae Oberw. & Bandoni, Can. J. Bot. 59: 1039. 1981. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

This family is emended to accommodate the monophyletic lineage comprising *Tetragonomycetes*, *Takashimella* (i.e. the **formosensis** clade), *Cryptotrichosporon* and *Cryptococcus marinus* recognised in Liu *et al.* (2015) and the present study (Figs 1, 2 and 6).

Basidiocarps not known or growing as a thin film on sclerotia of a basidiomycetous host. Sexual reproduction unknown or by basidia that occur terminally on hyphae; initially thin-walled, ellipsoid to globose, becoming thick-walled and four-celled; mature basidia deciduous, rhomboidal; germination by dikaryotic hyphae or germ tubes that may conjugate. In culture pseudohyphae and true hyphae present or not. Budding cells present or absent. Ballistoconidia bilaterally symmetrical. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type genus: *Tetragonomycetes* Oberw. & Bandoni

Genera accepted: *Bandonia*, *Cryptotrichosporon*, *Takashimella* and *Tetragonomycetes*.

Notes: The family *Tetragonomycetaceae* was established for a single species, *Tetragonomycetes uliginosus* (Oberwinkler & Bandoni 1981). This species produces unusual deciduous basidia that germinate directly into a filamentous phase and does not have a unicellular yeast phase. Molecular phylogenetic analysis indicated that *T. uliginosus* is an early-branching member of Trichosporonales with loose connection to *Cryptotrichosporon anacardii* (Millanes *et al.* 2011, Weiss *et al.* 2014). The latter is branching before the **formosensis** clade (i.e. *Takashimella*) with strong support in the Bayesian and ML trees obtained from the seven-genes dataset (Liu *et al.* 2015). The tree inferred from the expanded LSU rRNA gene dataset confirmed this phylogenetic relationship (Fig. 6). A new *Cryptotrichosporon* species, *C. tibetense* that is able to form ballistoconidia was described recently and the genus description emended consequently (Wang & Wang 2015). The close phylogenetic relationship between *Cryptotrichosporon* and *Tetragonomycetes* was supported in Wang & Wang (2015). The genus *Tetragonomycetes* remains monotypic and the genera *Cryptotrichosporon* (Okoli *et al.* 2007) and *Takashimella* (Wang & Wang 2015) contain two and four species, respectively (Table 1). *Cryptococcus marinus* was branching more early than this family in the Bayesian and ML trees derived from the seven-genes dataset, but its position was not resolved in the seven-genes NJ tree and the combined rRNA genes tree (Liu *et al.* 2015). In all molecular phylogenetic studies performed to date this species occurred as a single species long-branch lineage (Fell *et al.* 2000, Scorzetti *et al.* 2002). Below we propose a new genus *Bandonia* to accommodate this species.

Bandonia A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB814775.

Etymology: In honour of Robert J. Bandoni for his valuable contribution to the studies of *Tremellomycetes*.

The genus is proposed to accommodate the single-species lineage *Cryptococcus marinus*, which was placed in *Tetragonomycetaceae* (Liu *et al.* 2015, Fig. 6 of this study).

Basidiocarps not known. Sexual reproduction not observed. Pseudohyphae present or not. Budding cells present or absent. Ballistoconidia not observed. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type species: *Bandonia marina* (van Uden & Zobell) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB814776.

Basionym: *Candida marina* van Uden & Zobell, Antonie van Leeuwenhoek. 28: 278. 1962.

Notes: The phylogenetic position of *Cryptococcus marinus* in Tremellomycetes remained unclear (e.g. Fonseca *et al.* 2011) before the seven-genes phylogenetic analysis (Liu *et al.* 2015). The latter analysis placed the species in Trichosporonales with some affinity to the genera *Cryptotrichosporon* and *Takashimella*. The species is known from a single strain only and is characterised by several unusual physiological properties (Fonseca *et al.* 2011).

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