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Taxonomic revision of *Geotrichum* and *Magnusiomyces*, with the descriptions of five new *Geotrichum* species from China

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ABSTRACT

The arthroconidial yeast-like species currently classified in the asexual genera *Geotrichum* and *Saprochaete* and the sexual genera *Dipodascus*, *Galactomyces* and *Magnusiomyces* are frequently associated with dairy and cosmetics production, fruit rot and human infection. However, the taxonomic system of these fungi has not been updated to accommodate the new nomenclature code adopting the "one fungus, one name" principle. Here, we performed phylogenetic analyses of these yeast-like species based on the sequences of the internal transcribed spacer (ITS) region and the D1/D2 domain of the large subunit of the rRNA gene. Two monophyletic groups were recognised from these species. One group contained *Dipodascus*, *Galactomyces*, and *Geotrichum* species and the other *Magnusiomyces* and *Saprochaete* species. We thus assigned the species in each group into one genus and selected the genus name *Geotrichum* for the first group and *Magnusiomyces* for the second one based on the principle of priority of publication. Five new *Geotrichum* species were identified from arthroconidial yeast strains recently isolated from various sources in China. The new species are described as *Ge. dehoogii* sp. nov., *Ge. fujianense* sp. nov., *Ge. maricola* sp. nov., *Ge. smithiae* sp. nov., and *Ge. sinensis* sp. nov.

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1. Introduction

The ascomycetous yeasts or yeast-like fungi which form arthroconidia are currently assigned to the sexual genera *Dipodascus*, *Galactomyces*, and *Magnusiomyces* and the asexual genera *Geotrichum* and *Saprochaete* (de Hoog and Smith 2004, 2011b, 2011c, 2011d, 2011e). These fungi are widely distributed in nature and are commonly associated with dairy, cosmetics, infection, and the new energy industry (Marcellino et al. 2001; Ersoz et al. 2004; Kataoka et al. 2013; Arendrup et al. 2014; Banjara et al. 2015; Takei et al. 2015; Kurylenko et al. 2020). Specifically, *Ge. candidum* commonly occurs in moist substrates, including soil, plants, fruits, water, and digestive tracts of humans and other animals, and dairy products such as milk, cream, and cheese (Carmichael 1957; Spencer and Spencer 1997; Marcellino et al. 2001; Pimenta et al. 2005; Sulo et al. 2009; Alper et al. 2011; Groenewald et al. 2012; Banjara et al. 2015). *Galactomyces* fermentation filtrate (GFF) is widely used in moisturising cosmetics (Takei et al. 2015). GFF-containing moisturisers were shown to be helpful for skin protection against damage from environmental stress by increasing caspase-14 expression in epidermal cells (Kataoka et al. 2013). Infections caused by arthroconidial yeast species have been frequently reported, which may be fatal due to treatment difficulty (Ersoz et al. 2004; Lafayette et al. 2011; Özkaya-Parlakay et al. 2012; Vadkertiová et al. 2012; Fasciana et al. 2017; Shah and Mauger 2017; Tanuskova et al. 2017; Keene et al. 2019; Erman et al. 2020; Flateau et al. 2021; Noster et al. 2021; Tshisevhe et al. 2021). In agriculture, sour rot caused by *Ge. citri-aurantii* and *S. gigas* is among the common diseases of citrus fruit and grape (Butler et al. 1988; Gao et al. 2020; Wang et al. 2022). In biofuel

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production, *M. magnusii* is a promising organism for further development as a robust isobutanol producer (Kurylenko et al. 2020).

Early molecular phylogenetic studies recognised two distinct groups of arthroconidial yeasts based on sequence analyses of the partial large-subunit (LSU) (Kurtzman and Robnett 1995) and the small-subunit (SSU) (Ueda-Nishimura and Mikata 2000) of the ribosomal RNA gene (rDNA). de Hoog and Smith (2004) performed phylogenetic analyses of all arthroconidial yeasts or yeast-like fungi assigned to *Hemiascomycetes* based on sequences of the internal transcribed spacer (ITS) region of rDNA and DNA/DNA reassociation data, confirming the recognition of the two ribosomal groups Group 1 and Group 2. They consequently revised the taxonomic system of these yeasts. The species in Group 1 were kept in *Galactomyces* and *Dipodascus* with *Geotrichum* as anamorph and the species in Group 2 were transferred to *Magnusiomyces* with *Saprochaete* as anamorph. *Galactomyces* and *Dipodascus* formed two separate subclades in Group 1 (de Hoog and Smith 2011b, 2011c). A total of 32 taxa were recognised in the system proposed by de Hoog and Smith (2004), which was generally followed by subsequent taxonomic studies on arthroconidial ascomycetous yeasts or yeast-like taxa (de Hoog and Smith 2011b, 2011c, 2011d, 2011e).

The asexual genus *Geotrichum* was established by Link (1809) with *Ge. candidum* as the type species. The genus is characterised by the presence of arthroconidia that are liberated in random order and septal walls which are perforated by micropores (de Hoog and Smith 2004). de Hoog and Smith (2004) accepted eight species in the genus *Geotrichum*, *viz. Ge. candidum*, *Ge. citri-aurantii*, *Ge. decipiens*, *Ge. europaeum*, *Ge. fermentans*, *Ge. klebahnii, Ge. pseudocandidum*, and *Ge. restrictum*. Since then, a few *Geotrichum* species have been described, including *Ge. silvicola* isolated from insects (Pimenta et al. 2005), *Ge. vulgare* isolated from soft drinks factory in Turkey (Wuczkowski et al. 2006), and *Ge. bryndzae* isolated from bryndza in Slovakia (Sulo et al. 2009). Later, de Hoog and Smith (2011c) accepted *Ge. carabidarum*. *Ge. cucujoidarum* and *Ge. histeridarum* were described by Suh and Blackwell (2006) from the gut of insects. *Ge. siamensis* and *Ge. phurueaensis* were proposed by Kaewwichian et al. (2010), and *Ge. ghanense* was described by Nielsen et al. (2010). Currently, a total of 15 species are recognised in the genus *Geotrichum*.

The sexual genus *Dipodascus* was described by de Lagerheim (1892) with *D. albidus* as the type species. It is characterised by multispored asci containing eight to more than 100 ascospores (de Hoog and Smith 2004, 2011b). Nagahama et al. (2008) emended the genus to include species with asci containing four ascospores. de Hoog and Smith (2004, 2011b) accepted six species in this genus, *viz. D. aggregatus*, *D. albidus*, *D. armillariae, D. australiensis*, *D. geniculatus*, and *D. macrosporus*. Nagahama et al. (2008) introduced *D. tetrasporeus* isolated from deep-sea sediments in the Japan Trench, which was not included in de Hoog and Smith (2011b).

Redhead and Malloch (1977) emended *Endomyces* Reess (1870) to restrict the genus to species producing naked nonproliferating asci born on short pedicels, galeate ascospores, and catenulate blastoconidia. They proposed *Galactomyces* to accommodate two arthroconidial species *E. geotrichum* and *E. reessii*, which were excluded from *Endomyces*. *E. geotrichum* was initially proposed for the sexual state of *Ge. candidum* by Butler and Petersen (1972). *Galactomyces* is characterised by forming arthroconidia and subhyaline, subspherical to broadly ellipsoidal asci with one, rarely two ascospores (de Hoog and Smith 2004, 2011a; Nagahama et al. 2008). de Hoog and Smith (2004, 2011a) accepted five species in *Galactomyces*, *viz. Ga. candidus*, *Ga. citri-aurantii*, *Ga. geotrichum*, *Ga. reessii*, and *Ga. pseudocandidus*. Kwaśna and Bateman (2008) described *Ga. britannicum,* which is closely related to *Ga. geotrichum*, *Ga. reessii*, and *Ga. citri-aurantii* based on ITS sequence analysis.

The genus *Magnusiomyces* was described by Zender (1925) with *M. ludwigii* as the type species. It is characterised by hyaline, subspherical to broadly ellipsoidal asci with four ascospores (de Hoog and Smith 2011d). de Hoog and Smith (2004, 2011d) accepted seven species in this genus, *viz. M. capitatus*, *M. ingens*, *M. magnusii*, *M. ovetensis*, *M. spicifer*, *M. starmeri*, and *M. tetrasperma*.

The genus *Saprochaete* was invalidly described by Coker and Shanor (1939) as a saprophytic fungoid alga and was validated along with the validation of *S. saccharophila* as a fungus belonging to the "Fungi Imperfecti" by Wagner and Dawes (1970). de Hoog

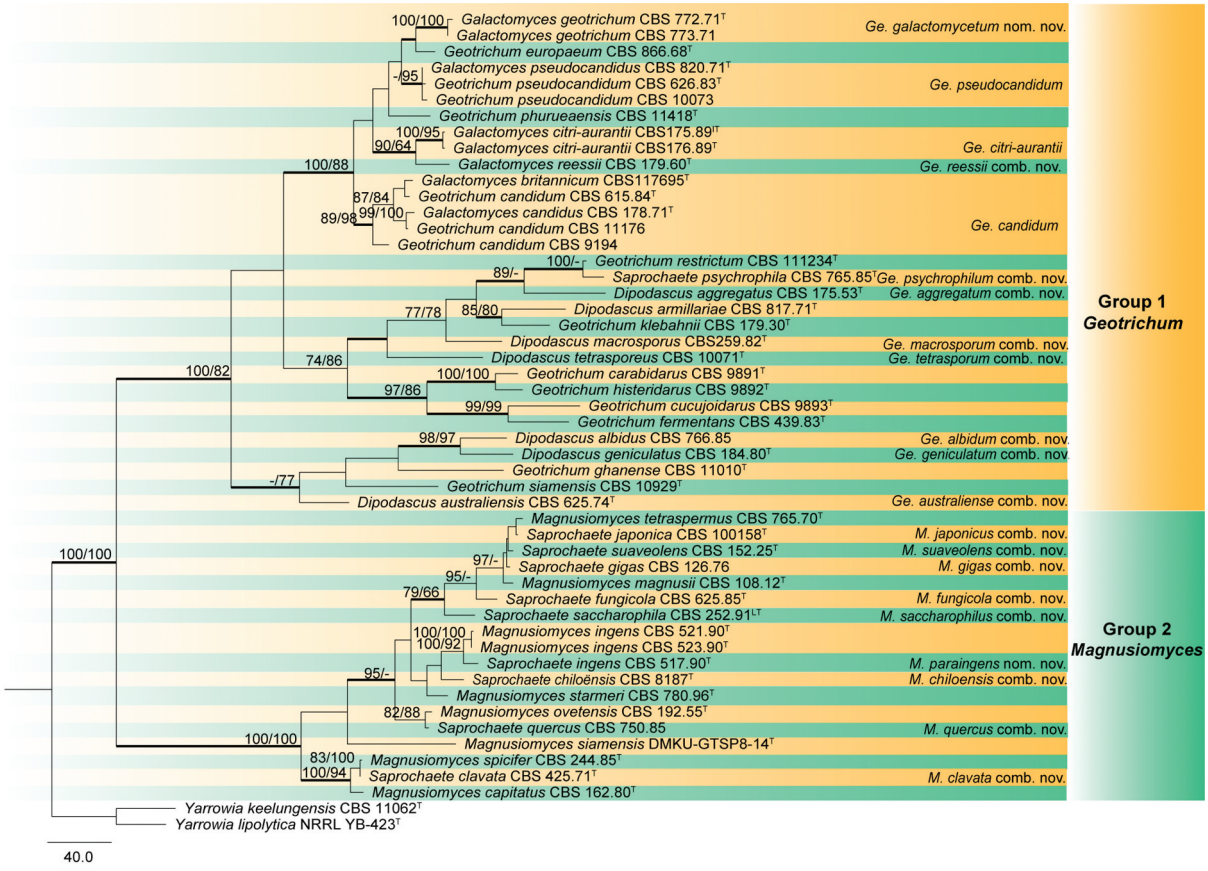

Figure 1. Phylogeny of the described arthroconidial yeast-like species based on maximum parsimony (MP) analysis of the combined ITS and D1/D2 sequences. The two *yarrowia* species were used as outgroup. The MP/maximum likelihood (ML) bootstrap support values above 70% are shown. Bold lines represent posterior probabilities above 0.95 from the Bayesian Inference (BI) test. Type strains are marked with the superscript "T". Lectotype strain is marked with the superscript "LT". Isotype strain is marked with the superscript "IT". The names of the species when changed are shown on the right.

and Smith (2004) showed that *Saprochaete* species represent asexual states of *Magnusiomyces* based on ITS sequence analyses. de Hoog and Smith (2004, 2011e) accepted 13 species in *Saprochaete*, *viz. S. capitata*, *S. chiloënsis*, *S. clavata*, *S. fungicola*, *S. gigas*, *S. ingens*, *S. japonica*, *S. ludwigii*, *S. psychrophila*, *S. quercus*, *S. saccharophila*, *S. sericea*, and *S. suaveolens*.

The new fungal nomenclature code adopting the "one fungus, one name" concept was launched in 2011 (Hawksworth 2011; Taylor 2011; McNeill et al. 2012); however, the taxonomic system of the arthroconidial ascomycetous yeasts or yeast-like fungi has not been updated to accommodate the new code. Both sexual and asexual names were used for the same species in recent studies, especially in medical research. For example, for the same pathogen, Keene et al. (2019) used the asexual name *Ge. candidum*, while Vadkertiová et al. (2012) and Flateau et al. (2021) used the sexual name *Ga. candidus*. For another species commonly associated with fungal infection in patients with various background diseases, the sexual name *M. capitatus* was used in Shah and Mauger (2017), Tanuskova et al. (2017), and Noster et al. (2021), while the anamorph name *S. capitata* was used in Liu et al. (2019). Therefore, it is necessary to emend the taxonomic system to unify the name use and consequently to eliminate or reduce the confusion caused by using different names for the same species.

In this study, we performed phylogenetic analysis of the currently accepted arthroconidial species based on sequence analyses of the ITS region and the LSU D1/D2 domain of rDNA and revised the taxonomic system of this group adopting the new International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018). We then

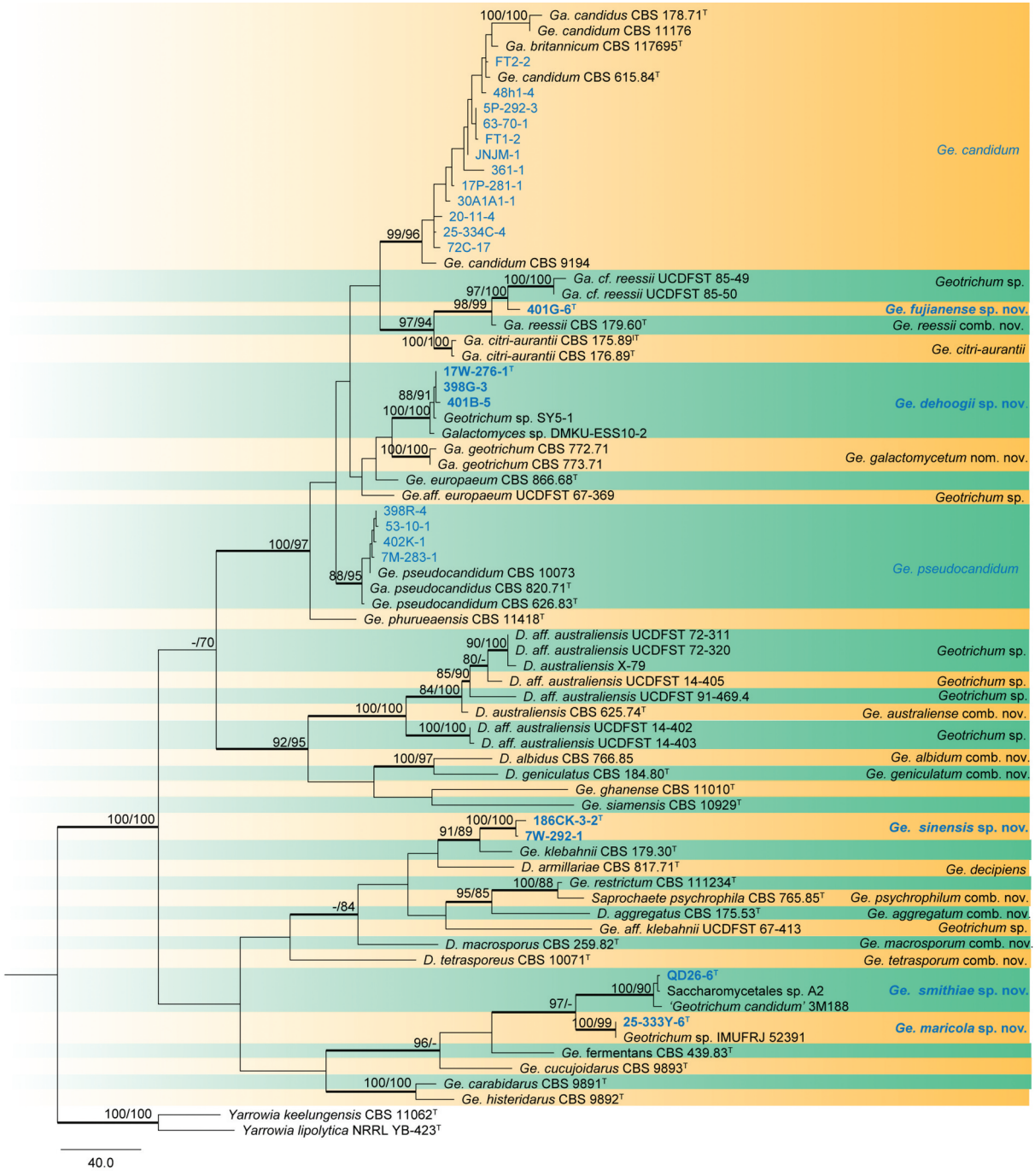

Figure 2. Phylogeny of *Geotrichum* species based on maximum parsimony (MP) analysis of the combined ITS and D1/D2 sequences. The two *yarrowia* species were used as outgroup. The MP/maximum likelihood (ML) bootstrap support values above 70% are shown. Bold lines represent posterior probabilities above 0.95 from the Bayesian Inference (BI) test. The strains isolated in this study are marked in blue. The strains represented the novel species in this study were in bold. Type strains are marked with the superscript "T". Isotype strain is marked with the superscript "IT". The names of the species when changed are shown on the right and the new species are marked in blue on the right.

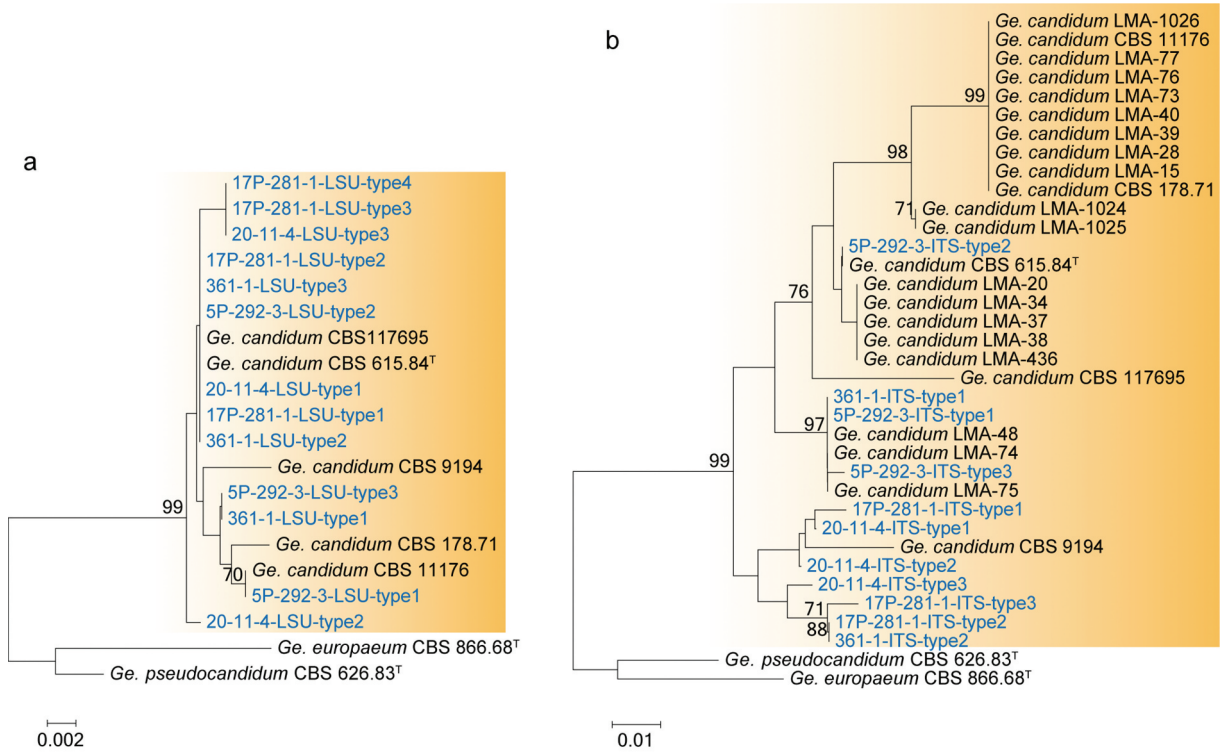

Figure 3. Intra-specific and intra-genomic polymorphisms in (a) the LSU D1/D2 domain and (b) ITS region of *Geotrichum candidum* strains. The phylograms were constructed from neighbour-joining (NJ) analyses and the bootstrap supports above 70% are shown. The other two *Geotrichum* species were used as outgroup.

performed a taxonomic study on 24 arthroconidial yeasts isolated from different substrates collected from different regions in China according to the new system. Five new species in the genus *Geotrichum* were identified, which are described in the present paper.

2. Materials and methods

2.1. Yeast strains and phenotypic characterization

The strains studied are listed in Table S1. A total of 18 new arthroconidial yeast strains were isolated from marine water and sediment samples collected from intertidal zones in different regions of China and six strains from samples associated with Chinese Baijiu fermentation environments (Table S1). The strains from marine water and sediment samples were isolated by using the method described by Zhu et al. (2023), and the strains from Baijiu fermentation environments were isolated as described by Han et al. (2023).

The morphological, physiological and biochemical characterisation was performed according to standard methods (Kurtzman et al. 2011). Assimilation of carbon compounds was conducted in liquid media, and nitrogen compounds were examined in solid media. The potential sexual cycles of new species were investigated using corn meal agar (CMA, 2.5% corn starch and 2% agar), potato dextrose agar (PDA, 20% potato infusion, 2% glucose, and 2% agar), V8 agar (10% V8 juice and 2% agar), and yeast malt agar (YM, 0.3% yeast extract, 0.3% malt extract, 0.5% peptone, 1% glucose, and 2% agar) plates which were inoculated with single and mixed strains and incubated at 25 °C for up to two months.

2.2. DNA extraction, sequencing and phylogenetic analyses

DNA of the yeast strains was extracted using the method described previously (Wang and Bai 2008). The ITS region and the LSU D1/D2 domain were amplified and sequenced using the methods described by Bai et al. (2002). For cloning sequencing, purified polymerase chain reaction (PCR) products of

the fragments covering the ITS region and the D1/D2 domain from selected strains were cloned using the ClonExpress® Ultra One Step Cloning Kit (Vazyma, China) according to the manufacturer's instructions. Ten to 12 positive clones of each strain were randomly picked for sequencing.

Novel sequences generated in this study have been deposited in GenBank (Table S1). The ITS and LSU D1/D2 sequences of the ascomycetous arthroconidial yeast species determined in previous studies (de Hoog and Smith 2004, 2011b, 2011c, 2011d, 2011e; Pimenta et al. 2005; Wuczkowski et al. 2006; Nagahama et al. 2008; Sulo et al. 2009; Kaewwichian et al. 2010; Sitepu et al. 2020; Dudhat et al. 2022) were retrieved from GenBank. The ITS and D1/D2 sequences of a few strains (Table S1) were extracted from the released genome sequences of the strains concerned (Brejová et al. 2018, 2019; Shen et al. 2018; Hodorová et al. 2019).

Sequences were aligned with MAFFT v.7 (Katoh and Standley 2013) and manually improved where necessary using MEGA v.7 (Kumar et al. 2016). Positions that were ambiguous to align were excluded using Gblocks v.0.91b (Castresana 2000). Phylogenetic analysis based on single ITS or D1/D2 sequences was performed from the evolutionary distance data calculated from Kimura's two parameter model (Kimura 1980) using the Neighbor-Joining model in MEGA v.7. Bootstrap analyses were performed on 1,000 random resampling. Maximum parsimony (MP), Bayesian Inference (BI), and maximum likelihood (ML) analyses based on the combined ITS and D1/D2 sequences were performed using PAUP v.4.0b10 (Swofford 2003), MrBayes v.3.1.2 with 1,000,000 generations (Ronquist and Huelsenbeck 2003), and RAxML-HPC 7.2.8 with 1,000 bootstrap replicates (Stamatakis 2006), respectively. The best nucleotide substitution model was estimated using Modeltest v.3.04 (Posada and Crandall 1998). The model GTR + I + G was selected for the ML and BI analyses. A bootstrap percentage (BP) above 70% and a Bayesian posterior probability (PP) above 0.95 were considered significantly supported. Phylograms were visualised in Figtree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree). The aligned matrices used for the phylogenetic analyses in this study have been deposited in TreeBASE (www.treebase.org) with accession number: S29847.

3. Results

3.1. Molecular phylogeny of known arthroconidial yeast species

We first retrieved the ITS sequences reported in de Hoog and Smith (2004) from GenBank as references for an initial phylogenetic analysis and found that the retrieved ITS sequences are all problematic. These sequences with accession numbers AY788287–AY788352 are all 163 bp in length, but de Hoog and Smith (2004) showed that the lengths of the sequences ranged from 290 to 689 bp. Furthermore, some sequences from different species, for example, AY788346 from *Magnusiomyces starmeri* CBS 780.96^T and AY788347 from *Saprochaete chiloënsis* CBS 8187^T are identical, but the trees constructed from ITS sequences in de Hoog and Smith (2004, de Hoog and Smith 2011d, 2011e) show that the two species differ remarkably. Therefore, we removed sequences AY788287–AY788352 and used the ITS sequences of the strains concerned from other sources when available or determined in this study for further analyses (Table S1).

We analysed the phylogenetic relationships of the described species of the arthroconidial yeasts based on the ITS and D1/D2 sequences. In agreement with previous studies (de Hoog and Smith 2004; Nagahama et al. 2008; Sulo et al. 2009; Kaewwichian et al. 2010), two groups were recognised from the trees constructed from the ITS and D1/D2 sequences, respectively (Figures S1 and S2) and from the combined sequences of the two regions (Figure 1). Group 1 contained the *Geotrichum*, *Galactomyces*, and *Dipodascus* species, and Group 2 contained the *Magnusiomyces* and *Saprochaete* species. However, the separation of the *Galactomyces* and the *Dipodascus* species in two subclades in Group 1 as shown in de Hoog and Smith (2011b, 2011c) was not recognised in this study. The *Galactomyces* species were limited to one subclade together with a few *Geotrichum* species, including the type species *Ge. candidum* of the genus; while the *Dipodascus* species were located in two subgroups together with the other *Geotrichum* species. These subgroups were paraphyletic and did not form a monophyletic clade. The *Magnusiomyces* and *Saprochaete* species were clustered together in Group 2 without clear separation from each other in all the trees constructed (Figures 1, S1, and S2).

In Group 1, *Ge. candidum* CBS 615.84^T, CBS 11176 and CBS 9194; *Ga. britannicum* CBS 117695^T; and *Ga. candidus* CBS 178.71^T form a strongly supported clade in the trees inferred from different datasets but exhibit remarkable sequence differences (Figures 1, S1, and S2). *Ga. candidus* CBS 178.71^T differs from *Ge. candidum* CBS 615.84^T by up to 15 nt (4.3%) and 11 nt (2.3%) in the ITS region and the D1/D2 domain, respectively. However, the former was proved to be the sexual state of the latter based on DNA-DNA reassociation data (Smith et al. 1995; de Hoog and Smith 2004). Strains CBS 11176 (previously described as *Ge. bryndzae*) and CBS 9194 (previously described as *Ge. silvicola*) differ from *Ge. candidum* CBS 615.84^T by up to 16 to 25 nt (4.7%–7.3%) in the ITS region and seven to ten nt (~2%) in the D1/D2 domain, but Groenewald et al. (2012) demonstrated that the former two were conspecific with the latter based on DNA-DNA reassociation data, mating tests and similar D1/D2 sequences with additional *Ga. candidus* strains available during that study. The significant rDNA sequence differences among the synonyms of this clade were explained by the intragenomic variation in different copies of the rDNA array observed in *Ge. candidum* strains (Alper et al. 2011).

Kwaśna and Bateman (2008) described *Ga. britannicum*, but they did not include the type strains of *Ga. candidus* or *Ge. candidum* in their study. *Ga. britannicum* located in the *Ge. candidum* clade and closely related to the type strain of the species (Figures 1, S1, and S2). Though *Ga. britannicum* CBS 117695^T differs from *Ge. candidum* CBS 615.84^T by 23 nt (6.8%) in the ITS region and six nt (1.4%) in the D1/D2 domain, the variation is within the scope of this clade and the former is unable to be clearly separated from the strains of the latter compared in the phylogenetic trees (Figures 1, S1, and S2). We therefore inferred that *Ga. britannicum* is conspecific with *Ge. candidum*.

3.2. Molecular identification of the new arthroconidial yeast strains from China

All strains isolated in this study belong to Group 1. The new strains were separated into seven clades in Group 1, representing two known and five undescribed species (Figures 2, S3, and S4). Twelve strains, namely 5P-292-3, 361-1, 48h1-4, 30A1A1-1, 25-334C-4, 72C-17, 20-9-7, 63-70-1, JNJM-1, 17P-281-1, FT1-2, and FT2-2 were nested within the *Ge. candidum* clade (Figures 2, S3, and S4). These strains differ from CBS 615.84^T by six to 24 nt (1.7%–6.9%) in the ITS region and seven to nine nt (~1.8%) in the D1/D2 domain. The sequence differences fall within the variation range of the complex (Alper et al. 2011; Groenewald et al. 2012) and hereby these strains are assigned to *Ge. candidum*. Strains 53-10-1, 7 M-283-1, 398 R-4, and 402K-1 were located in the *Ge. pseudocandidum* clade and closely related to CBS 10073 (the type strain of *Ge. vulgare*) (Figures 2, S3, and S4). Since *Ge. vulgare* was proved to be a synonym of *Ge. pseudocandidum* (Groenewald et al. 2012), we identify these four strains as *Ge. pseudocandidum*.

The remaining eight Chinese strains were unable to be classified into any known species. Strain QD26-6 formed a clade together with strain A2 isolated from wastewater in Brazil and strain 3M188 from marine water in Qatar (Figures 2, S3, and S4, Table S1). These strains differ from each other by two to five nt in the ITS region and no more than four nt in the D1/D2 domain. We thus regard them as being conspecific. Strain 25-333Y-6 possesses identical ITS and D1/D2 sequences with strain IMUFRJ 52391 isolated from marine water in Brazil. These two strains formed a clade closely related to the QD26-6 clade (Figures 2, S3, and S4). Strains QD26-6 and 25-333Y-6 differ from each other by 42 nt (8.4%) and 20 nt (5.7%) in the ITS region and D1/D2 domain, respectively, and thus represent two separate species. The QD26-6 and 25-333Y-6 clades are closely related to *Ge. cucujoidarum* and *Ge. fermentans* (Figures 2, S3, and S4). They differ from these two known species by more than 10% nt in the ITS region and the D1/D2 domain, respectively. Therefore, the QD26-6 and 25-333Y-6 clades represent two novel species.

Three strains 17W-276-1, 398 G-3, and 401B-5 isolated in this study were clustered in a distinct clade together with eight other unidentified strains with D1/D2 sequences being available in GenBank (Figure S4). The strains in this clade possess similar D1/D2 sequences with no more than three nt differences (Figure S4). When ITS data are available for comparison, strain 17W-276-1, 398 G-3, 401B-5, SY5-1, and DMKU-ESS10-2 clustered together with no more than four nt differences in the ITS region (Figure S3). This clade represented by strain 17W-276-1 is closely

related to *Ge. europaeum* and *Ge. galactomycetum* but differs from the type strains of the two known species by 12 to 14 nt (~2.8%) in the D1/D2 domain and 18 to 34 nt (~9.7%) nt in the ITS region (Figure 2). The result suggests that the 17W-276-1 clade represents another novel species in the genus *Geotrichum*.

Strain 401 G-6 formed a clade together with unidentified strains UCDFST 85-49 and UCDFST 85-50 from Puerto Rico and DMKU-Y10-2 from Thailand in the tree constructed from D1/D2 sequences (Figure S4). The strains in this clade possess similar D1/D2 sequences with no more than five nt differences (Figure S4). However, when the ITS data are available for comparison, strains UCDFST 85-49 and UCDFST 85-50 formed a distinct clade clearly separated from strain 401 G-6 (Figure S3). The former two strains differ from the latter by nine nt difference in the ITS region (Figure S3). Strain 401 G-6 is closely related to *Ge. citri-aurantii* and *Ge. reessii* (Figures 2, S3, and S4). It differs from these two species by 20 to 22 nt (~6%) in the ITS region and nine to 24 nt (1.5%–4%) in the D1/D2 domain, suggesting this strain represents one novel species. The taxonomic status of strains UCDFST 85-49, UCDFST 85-50 and DMKU-Y10-2 remains to be resolved.

Strains 186CK-2-3 and 7W-292-1 isolated in this study were clustered together in a distinct clade (Figures 2, S3, and S4). They possess similar sequences with two nt differences in the D1/D2 domain and five nt difference in the ITS region. We thus regard them as being conspecific. This clade represented by strain 186CK-3-2 is closely related to *Ge. klebahnii* and *Ge. decipiens* differs from them by 15 to 31 nt (2.5%–5%) in the D1/D2 domain and 21 to 39 nt (6%–11%) nt in the ITS region (Figure 2). The result suggests that the 186CK-2-3 clade represents another novel species in the genus *Geotrichum*.

3.3. Intragenomic rDNA sequence polymorphisms in Ge. candidum

As mentioned above, intragenomic rDNA sequence polymorphisms have been observed in *Ge. candidum* strains (Alper et al. 2011), which is considered the cause of the exceptionally high sequence variation in the ITS and D1/D2 regions of the strains within this species. We observed dual peaks in the sequencing chromatograms of ITS and LSU amplicons from some strains that were isolated and identified as *Ge. candidum* in this study. Repeated purification of the strains failed to eliminate the dual peaks, implying intragenomic rDNA polymorphisms in these strains. Thus, we selected strains 17P-281-1, 361-1, 5P-292-3, and 20-11-4 with clear dual peaks for cloning sequencing.

The fragments covering the ITS and D1/D2 regions from the four selected strains were amplified and cloned. Ten to 12 clones were randomly selected and sequenced for each strain. A total of 11 ITS types and 13 D1/D2 types were observed from the four *Ge. candidum* strains compared (Figure 3, Table S2). The ITS types differed from each other by two to 20 nt (~6%) at 26 polymorphic sites and the D1/D2 types differed from each other by one to three nt at six polymorphic sites (Figure 3). Within a single strain, two to three ITS types and three to four D1/D2 types were identified (Figure 3). Among the strains compared, the ITS types from strain 5P-292-3 showed the highest intragenomic sequence difference of ten nt (Figure 3).

A phylogenetic analysis based on the D1/D2 sequences showed that they grouped with the *Ge. candidum* CBS 615.84^T and its four synonyms (Figure 3a), a maximum of nine nt (1.8%) difference was observed in the sequences compared, suggesting a relative conservation of the D1/D2 sequences among strains in this species. Much higher variations were observed in the ITS types of the strains analysed within this species. A phylogenetic analysis based on the 11 ITS types recognised in this study and the sequences from Alper et al. (2011) showed that these sequences were divided into different subgroups (Figure 3b). The ITS sequence difference within *Ge. candidum* was substantially expanded, and a maximum of 38 nt (11%) was observed among the ITS sequences compared (Figure 3b).

3.4. Taxonomy

The distinction between Group 1 including genera *Dipodascus*, *Galactomyces*, and *Geotrichum* and Group 2 consisting of *Magnusiomyces* and *Saprochaete* as recognised in previous studies (Kurtzman and Robnett 1995; Ueda-Nishimura and Mikata 2000; de Hoog and Smith 2004) was confirmed in this study (Figures 1, S1, and S2). However, any monophyletic subclade containing species from only one of the genera was not recognised from either of the groups. We thus reclassified the genera in each group into one genus to accommodate the "one fungus, one name" principle of the currently adopted

nomenclature code for fungi (Turland et al. 2018). We select the genus name *Geotrichum* (1809) for Group 1 and *Magnusiomyces* (1925) for Group 2 based on the priority of publication principle of the code. The species in *Dipodascus* and *Galactomyces* are transferred to *Geotrichum* and the species in *Saprochaete* are transferred to *Magnusiomyces*.

Geotrichum Link, Mag. Gesell. Naturf. Freunde Berlin 3 (1): 17; 1809. *emend*. H.Y. Zhu, X.Z. Liu & F.Y. Bai.

Synonyms: Galactomyces Redhead & Malloch, Canad. J. Bot. 55: 1708; 1977.

Dipodascus Lagerh., Jb. wiss. Bot. 24: 549; 1892.

Fermentotrichon E.K. Novák & Zsolt, Acta Botanica Academiae Scientiarum Hungarica 7: 100; 1961.

Oosporoidea Sumst., Mycologia 5(2): 52; 1913.

Polymorphomyces Coupin, Revue Génerale de Botanique 26: 248; 1914.

Mycoderma Desm., Annales des Sciences Naturelles Botanique 10: 59; 1827.

Endyllium Clem., The genera of Fungi: 46, 245; 1931.

Zendera Redhead & Malloch, Can J Bot. 55 (13): 1707; 1977.

Type species: *Geotrichum candidum* Link, Mag. Gesell. naturf. Freunde, Berlin 3(1–2): 17 (1809).

Diagnosis: Asexual characteristics: Colonies are white, farinose or hairy, usually dry, and consist of true hyphae that branch at broad or right angles, have rounded apices and mostly disarticulate into arthroconidia. Budding is absent. Chlamydospores may be formed. Septa have micropores. Sexual characteristics: Gametangia are formed on opposite sides of hyphal septa, fuse at the apex and form an ascus. Asci are subhyaline to hyaline and contain one, rarely two or even eight to more than 100 ascospores. Ascospores are liberated through the apex by rupture of the firm ascus wall. Physiology/biochemistry characteristics: Fermentation is weak or absent. Xylose is assimilated. Nitrate is not assimilated. Extracellular starch is not produced, and urease activity is absent. The diazonium blue B reaction is negative.

Notes: We accept 28 species in *Geotrichum*, including nine new combinations, one novel name and five novel species proposed for the clades represented by strains 17W-276-1^T, QD26-6^T, 25-333Y-6^T, 401 G-6^T, and 186CK-3-2^T isolated in this study. The key characters of the *Geotrichum* species are listed in Table S3.

Species accepted in *Geotrichum*

Geotrichum aggregatum (Francke-Grosmann) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846376.

Basionym: *Dipodascus aggregatus* Francke-Grosm., Meddn St. SkogsförsAnst. 41: 30; 1953.

Synonym: *Dipodascus albidus* f. minor Korf, Beihefte zur Sydowia 1: 285; 1957.

Geotrichum albidum (Lagerh.) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846377.

Basionym: *Dipodascus albidus* Lagerh., Jahrb. Wiss. Bot. 24: 549; 1892.

Geotrichum australiense (Arx & J.S.F. Barker) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846378.

Basionym: Dipodascus australiensis Arx & J.S.F. Barker, Antonie van Leeuwenhoek 43: 335; 1977.

Geotrichum candidum Link, Mag. Naturf. Freunde, Berlin 9: 17; 1809.

Synonyms: *Galactomyces candidus* de Hoog & M. T. Sm., Stud. Mycol. 50: 504; 2004.

Geotrichum silvicola Pimenta, Prasad, Lachance & Rosa, Int. J. Syst. Evol. Microbiol 55: 499; 2005.

Galactomyces britannicum Kwaśna & G.L. Bateman, Sydowia 60: 77; 2008.

Geotrichum bryndzae Sulo, Laurenčík, Poláková, Minárik & Sláviková, Int. J. Syst. Evol. Microbiol. 59: 2373; 2009.

Additional synonyms are listed in de Hoog and Smith (2004).

Geotrichum carabidarum S.O. Suh & M. Blackw., Mycol. Res. 110: 221. 2006.

Synonym: *Dipodascus carabidarus* (S.O. Suh & M. Blackw.) S.O. Suh & M. Blackw., Index Fungorum 270: 1; 2015.

Geotrichum citri-aurantii (Ferraris) E.E. Butler, Mycotaxon 33: 201; 1988.

Basionyms: *Oidium citri-aurantii* Ferraris, Malpighia13: 379; 1899.

≡ *Oospora citri-aurantii* (Ferraris) Sacc. & P. Syd., Syll. fung. (Abellini)16: 1024; 1902.

Synonyms: *Geotrichum candidum* Link var. *citri-aurantii* (Ferraris) R. Ciferri & F. Ciferri, Annali Sper. agr., N.S.9: 9; 1955.

Galactomyces citri-aurantii E.E. Butler, Mycotaxon 33: 200; 1988.

Geotrichum cucujoidarum S.O. Suh & M. Blackw., Mycol. Res. 110: 224. 2006.

Synonyms: *Dipodascus cucujoidarus* (S.O. Suh & M. Blackw.) S.O. Suh & M. Blackw., Index Fungorum 270: 1; 2015.

Geotrichum decipiens (Tul. & C. Tul.) W. Gams, Sydowia 36: 50; 1983.

Synonyms: *Dipodascus armillariae* W. Gams, Sydowia 36: 50; 1983.

Geotrichum armillariae Arx, Antonie van Leeuwenhoek 43: 339; 1977.

Hypomyces decipiens Tul. & C. Tul., Select. fung. carpol. 3: 61; 1865.

Geotrichum dehoogii H.Y. Zhu, X.Z. Liu & F.Y. Bai **sp. nov.**

MycoBank: MB846373.

Etymology: The species is named in honour of G. Sybren de Hoog for his contribution to the systematics of arthroconidial yeast-like fungi.

Type: The holotype CGMCC 2.6646^{T} was isolated from a marine sediment sample collected in the Dongtan Bird National Nature Reserve, Chongming District, Shanghai Municipality, China by H.Y. Zhu, J. N. Li, and X.Z. Liu in May 2021 and has been preserved in a metabolically inactive state in the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. The ex-type culture has been deposited in the Japan Collection of Microorganisms (JCM), Koyadai, Japan, as JCM 35432 (=17W-276-1).

Culture characteristics: After 10 days on 4% malt extract/0.5% yeast extract (MEYE) agar at 20 °C, colonies are 51 mm in diameter, white, flat, dry, powdery, with finely hairy margins. Hyphae soon disarticulate into cubic arthroconidia, 3.5–4.5 × 10–18.0 µm. Hyphae and arthroconidia produce oblong blastoconidia, 3.0–5.5 × 5.0–21 µm on PDA agar after one month at 25 °C. The growth radius is 44 mm on YPD agar after one week at 25 °C (Figure 4). Sexual structures are not observed.

Physiological and biochemical characteristics: Glucose is not fermented. Glucose (latent), galactose (latent), sorbose (weak), maltose (weak), melibiose (weak), soluble starch (weak), D-xylose (latent), methanol (weak), ethanol (latent), glycerol (latent), DL-lactic acid (slowly) and succinic acid (slowly) are assimilated as sole carbon sources. Sucrose, cellobiose, trehalose, lactose, raffinose, melezitose, inulin, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-Glucosamine, erythritol, ribitol, galactitol, D-mannitol, glucitol, methyl-glucoside, salicin, D-Glucuronic acid, citric acid, inositol, hexadecane, N-acetyl-D-glucosamine, and xylitol are not assimilated as sole carbon sources. Ammonium sulphate, L-lysine, cadaverine dihydrochloride, and ethylamine hydrochloride are assimilated as sole nitrogen sources. Potassium nitrate and sodium nitrite are not assimilated as sole nitrogen sources. Growth occurs at 28 °C but not at 30 °C in a 0.5% glucose liquid medium. Growth in the vitamin-free medium is positive. Extracellular starch-like compounds are not produced. Growth does not occur on 50% (w/v) glucose-yeast extract agar. Growth occurs in 10%

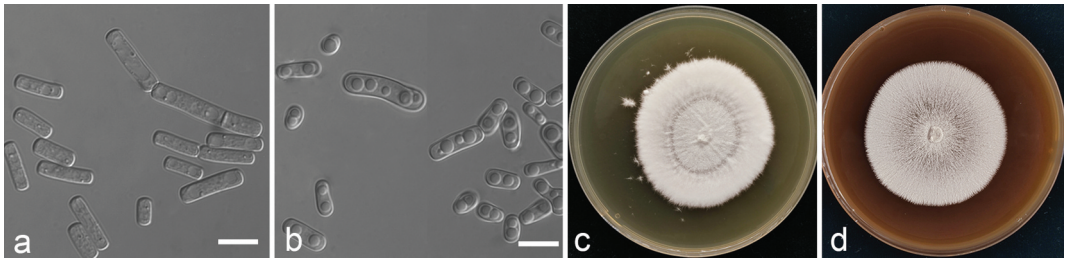

Figure 4. Morphology of *Geotrichum dehoogii* sp. nov. (strain 17W-276-1^{T}). (a) Cylindrical arthroconidia on 4% malt extract/0.5% yeast extract (MEYE) agar. (b) Blastoconidia on potato dextrose agar (PDA). (c) Colonies on yeast extract peptone dextrose (YPD) agar after one week. (d) Colonies on MEYE agar after 10 days. Scale bars: a–b = 10 µm.

(w/v) sodium chloride plus 5% (w/v) glucose liquid medium. Urease activity is negative. Diazonium Blue B reaction is negative.

Notes: Physiologically, *Ge. dehoogii* sp. nov. differs from its closely related species *Ge. europaeum*, *Ge. galctomyces*, and *Ge. phurueaensis* in its ability to assimilate maltose, D-mannitol, D-galactose, and cellobiose (Table S3). The 12 strains representing the novel species *Ge. dehoogii* sp. nov. are from marine sediment and soil collected in China, Thailand, and Russia (Table S1), suggesting the wide distribution of the new species in the world.

Geotrichum europaeum de Hoog & M.Th. Smith, Stud. Mycol.50: 502; 2004.

Geotrichum fermentans (Diddens & Lodder) Arx, Stud. Mycol. 14: 32; 1977.

Basionyms: Trichosporon fermentans Diddens & Lodder, Anaskospor. Hefen, 2. Hälfte, p. 488; 1942.

≡ *Fermentotrichon fermentans* (Diddens & Lodder) Novák & Zsolt, Acta Bot. Hung. 7: 131; 1961.

≡ *Dipodascus fermentans* (Diddens & Lodder) P.M. Kirk, Index Fungorum 270: 1; 2015.

Geotrichum fujianense H.Y. Zhu, X.Z. Liu & F.Y. Bai **sp. nov.**

MycoBank: MB846370.

Etymology: The species is named after the location where the type strain of the species was isolated: Fujian Province, China.

Type: The holotype CGMCC 2.6932^{T} was isolated from a marine sediment sample collected in Zhangzhou City, Fujian Province, China by F. Liu in April 2021 and has been preserved in a metabolically inactive state in the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. The ex-type culture has been deposited in the Japan Collection of Microorganisms (JCM), Koyadai, Japan, as JCM 36366 (=401G-6).

Culture characteristics: After 10 days on MEYE agar at 20 °C, colonies are 22 mm in diameter, white, punky, dry, powdery, with hairy margins. Hyphae soon disarticulate into cubic arthroconidia measuring 2.3–4.1 × 4.8–9.2 µm. Hyphae and arthroconidia produce oblong blastoconidia, 3.2–6.5 × 3.9–10.7 µm on PDA agar after one month at 25 °C. The growth radius is 57 mm on YPD agar after one week at 25 °C. Asci are formed on CMA agar after two months, 5.3–6.3 × 6.5–10.7 µm, and contain one ascospore. Ascospores are globose to subglobose, 3.7–5.7 µm in diameter (Figure 5). The species is homothallic.

Physiological and biochemical characteristics: Glucose is not fermented. Glucose, galactose, sorbose, maltose, melibiose (weak), soluble starch (weak), D-xylose, ethanol, glycerol, DL-lactic acid and succinic acid are assimilated as sole carbon sources. Sucrose, cellobiose, trehalose, lactose, raffinose, melezitose, inulin, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-Glucosamine, methanol, erythritol, ribitol, galactitol, D-mannitol, glucitol, methyl-glucoside, salicin, D-Glucuronic acid, citric acid, inositol, hexadecane, N-acetyl-D-glucosamine, and xylitol are not assimilated as sole carbon sources. Sodium nitrite, ammonium sulphate, L-lysine, cadaverine dihydrochloride, and ethylamine hydrochloride are assimilated as sole nitrogen sources. Potassium nitrate is not assimilated as sole nitrogen source. Growth occurs at 30 °C but not at 35 °C in a 0.5% glucose liquid medium. Growth in the vitamin-free medium is positive. Extracellular starch-like compounds are not produced. Growth does not occur on 50% (w/v) glucose-yeast extract agar and in 10% (w/v) sodium chloride plus 5% (w/v) glucose liquid medium. Urease activity is negative. Diazonium Blue B reaction is negative.

Notes: Physiologically, *Ge. fujianense* sp. nov. differs from its closely related species *Ge. citri-aurantii* and *Ge. reessii* in its ability to assimilate maltose (Table S3).

Geotrichum galactomycetum H.Y. Zhu, X.Z. Liu & F.Y. Bai **nom. nov.**

MycoBank: MB846379.

Basionyms: *Endomyces geotrichum* E.E. Butler & L.J. Petersen Mycologia, 64: 367; 1972.

≡ *Dipodascus geotrichum* (E.E. Butler & L.J. Petersen) von Arx, Antonie van Leeuwenhoek 43: 336; 1977.

≡ *Galactomyces geotrichum* (E.E. Butler & L.J. Petersen) Redhead & Malloch, Can. J. Bot.55: 1708; 1977.

Notes: To avoid a tautonym caused by the transfer of *Endomyces geotrichum* to *Geotrichum*, a new epithet "*galactomycetum*" is proposed, referring to its previous classification in the genus *Galactomyces*.

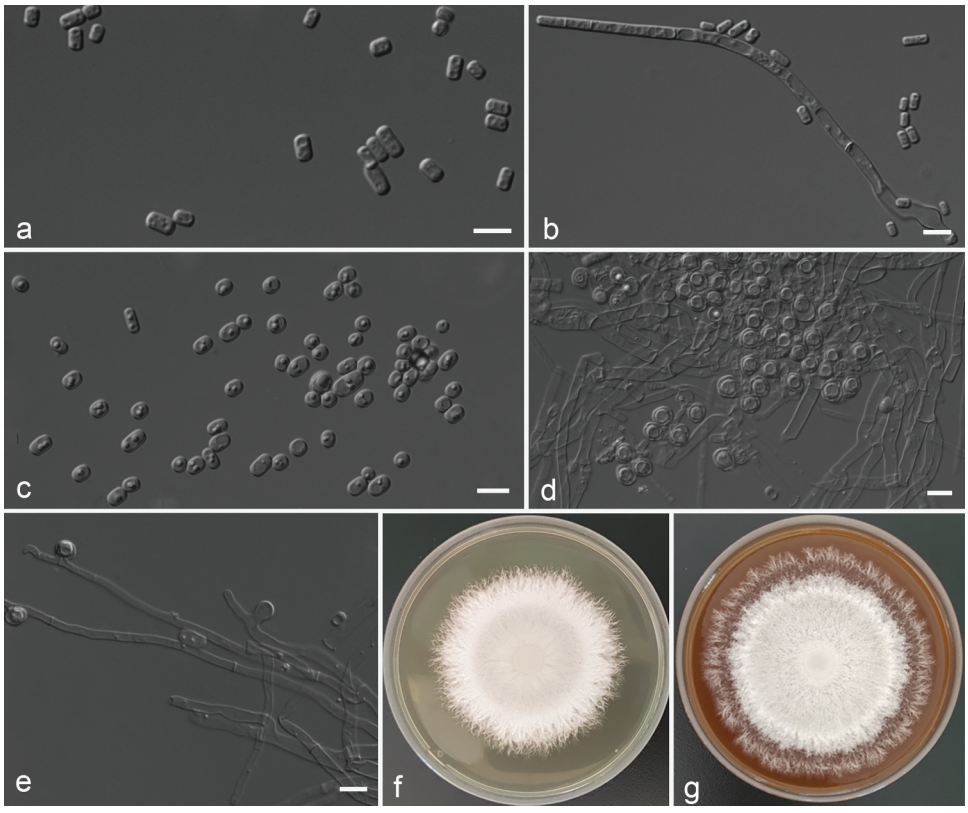

Figure 5. Morphology of *Geotrichum fujianense* sp. nov. (strain 401 G-6^T). (a) Cylindrical arthroconidia on 4% malt extract/0.5% yeast extract (MEYE) agar. (b) Hypha and arthroconidia on MEYE agar. (c) Blastoconidia on potato dextrose agar (PDA). (d–e) Asci with one ascospore on corn meal agar (CMA). (f) Colonies on yeast extract peptone dextrose (YPD) agar after one week. (g) Colonies on MEYE agar after 10 days. Scale bars: a–e = 10 µm.

Geotrichum geniculatum (de Hoog, M.Th. Smith & Guého) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846380.

Basionym: *Dipodascus geniculatus* de Hoog, M.T. Sm. & Guého, Stud. Mycol. 29: 25. 1986.

Geotrichum ghanense D.S. Nielsen, M. Jakobsen & Jespersen, Int. J. Syst. Evol. Microbiol. 60: 1463; 2010.

Synonym: *Dipodascus ghanensis* (D.S. Nielsen, M. Jakobsen & Jespersen) P.M. Kirk, Index Fungorum 270: 1; 2015.

Geotrichum histeridarum S.O. Suh & M. Blackw., Mycol. Res. 110: 224; 2006.

Synonym: *Dipodascus histeridarus* (S.O. Suh & M. Blackw.) S.O. Suh & M. Blackw., Index Fungorum 270: 1; 2015.

Geotrichum klebahnii (Stautz) Morenz, Mykol. Schriftenreihe 2: 36; 1964.

Basionym: *Trichosporon klebahnii* Stautz, Phytopath. Z. 3: 189; 1931.

Synonyms: *Endomyces lactis* (Fresen.) Windisch var. klebah-nii (Stautz) Windisch, Beitr. Biol. Pfl. 28: 125; 1951.

Trichosporon penicillatum do Carmo Sousa, Anto nie van Leeuwenhoek 31: 153; 1965.

≡ *Geotrichum penicillatum* (do Carmo Sousa) Arx, Stud. Mycol. 14: 32; 1977.

Dipodascus klebahnii (Stautz) P.M. Kirk, Index Fungorum 270: 1; 2015.

Geotrichum macrosporum (Madelin & Feest) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846381.

Basionym: *Dipodascus macrosporus* Madelin & Feest, Trans. Br. Mycol. Soc. 79: 331; 1982.

Geotrichum maricola H.Y. Zhu, X.Z. Liu & F.Y. Bai **sp. nov.**

MycoBank: MB846375.

Etymology: The specific epithet refers to marine, the inhabitant of the species.

Type: The holotype CGMCC 2.6647^T was isolated from a marine water sample collected in Zhejiang Province by H.Y Zhu, J.N. Li, and X.Z Liu in May 2021 and has been preserved in a metabolically inactive state in the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. The ex-type culture has been deposited in the Japan Collection of Microorganisms (JCM), Koyadai, Japan, as JCM 35433 (=25-333Y-6).

Culture characteristics: After 10 days on MEYE agar at 20 °C, colonies are 46 mm in diameter, beige, flat, moist, with finely hairy margins. Hyphae soon disarticulate into cubic arthroconidia, 4.0–5.0 × 7.0–16.5 µm. Hyphae and arthroconidia produce globose to subglobose blastoconidia, 6.0–10.5 µm in diameter on PDA agar after one month at 25 °C. The growth radius is 44 mm in diameter on YPD agar after one week at 25 °C (Figure 6). Sexual structures are not observed.

Physiological and biochemical characteristics: Glucose is not fermented. Glucose, galactose (weak), sorbose, maltose (weak), melibiose (weak), soluble starch (weak), D-xylose, methanol (weak), ethanol, glycerol, glucitol, DL-lactic acid, and succinic acid are assimilated as sole carbon sources. Sucrose, cellobiose, trehalose, lactose, raffinose, melezitose, inulin, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-Glucosamine, erythritol, ribitol, galactitol, D-mannitol, methyl-glucoside, salicin, D-Glucuronic acid, citric acid, inositol, hexadecane, N-acetyl-D-glucosamine, and xylitol are not assimilated as the sole carbon sources. Ammonium sulphate, L-lysine, cadaverine dihydrochloride, and ethylamine hydrochloride assimilated as sole nitrogen sources. Potassium nitrate and sodium nitrite are not assimilated as sole nitrogen sources. Growth occurs at 30 °C but not at 35 °C in a 0.5% glucose liquid medium. Growth in the vitamin-free medium is positive. Extracellular starch-like compounds are not produced. Growth occurs on 50% (w/v) glucose-yeast extract agar, but not on 60% (w/v) glucose-yeast extract agar. Growth occurs in 10% (w/v) sodium chloride plus 5% (w/v) glucose liquid medium. Urease activity is negative. Diazonium Blue B reaction is negative.

Notes: Physiologically, *Ge. maricola* sp. nov. and its three closely related species *Ge. smithiae*, *Ge. cucujoidarum*, and *Ge. fermentans* are distinguishable by the assimilation of L-sorbose, maltose, ribitol, and cellobiose; the fermentation of glucose; and the growth at 35 °C (Table S3). It seems to be associated with marine environment. The two strains representing *Ge. maricola* sp. nov. are both from marine water in China and Brazil (Table S1).

Geotrichum phurueaensis Kaewwich., Yongman., Srisuk, Fujiyama & Limtong FEMS Yeast Res. 10: 219; 2010.

Geotrichum pseudocandidum Saëz, Mycopath. Mycol. Appl. 34: 363; 1968.

Synonyms: *Galactomyces pseudocandidus* de Hoog & M. T. Sm., Stud. Mycol. 50: 503; 2004.

Geotrichum vulgare Wuczkowski, Bond & Prillinger, Int. J. Syst. Evol. Microbiol. 56: 302; 2006.

Notes: *Ga. pseudocandidus* was proposed as the sexual state of *Ge. pseudocandidum* based on DNA-DNA reassociation values (Smith et al. 1995; de Hoog and Smith 2004). *Ge. vulgare* was proved to be a synonym of *Ga. pseudocandidus* by Groenewald et al. (2012) based on D1/D2 sequence comparison and mating tests. *Ge. vulgare* is clustered together with *Ga. pseudocandidus* and *Ge. pseudocandidum* (Figure 1). *Ge. vulgare* CBS 10,073^T differs from *Ge. pseudocandidum* CBS 626.83^T by one nt in the D1/D2 domain and five nt (1.4%) in the ITS region.

Geotrichum psychrophila (de Hoog & M.T. Sm.) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846382.

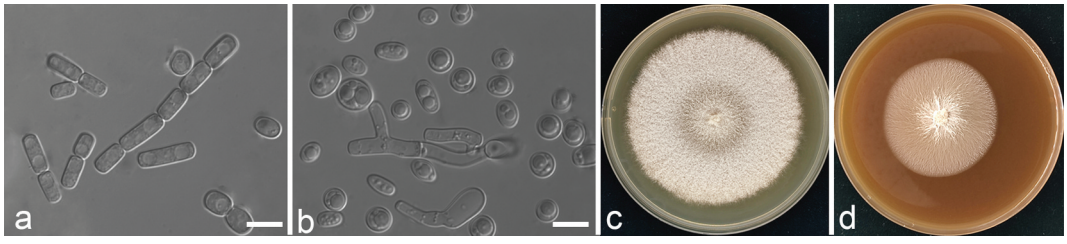

Figure 6. Morphology of *Geotrichum maricola* sp. nov. (strain 25-333Y-6^T). (a) Cylindrical arthroconidia on 4% malt extract/0.5% yeast extract (MEYE) agar. (b) Blastoconidia on potato dextrose agar (PDA). (c) Colonies on yeast extract peptone dextrose (YPD) agar after one week. (d) Colonies on MEYE agar after 10 days. Scale bars: a–b = 10 µm.

Basionym: *Saprochaete psychrophila* de Hoog & M.T. Sm., Stud. Mycol. 50: 502. 2004.

Notes: *Saprochaete psychrophila* was proposed for strain CBS 765.85 located in Group 2 based on ITS sequence analysis (de Hoog and Smith 2004). However, this strain was located in Group 1 based on D1/D2 sequence analysis (Dudhat et al. 2022). We re-determined the ITS sequence of strain CBS 765.85 and confirmed its location in Group 1, consistent with the result obtained from the D1/D2 sequence analysis (Figures S1 and S2).

Geotrichum reessii (Van der Walt) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846383.

Basionyms: *Endomyces reessii* van der Walt, Antonie van Leeuwenhoek 25: 463; 1959.

≡ *Dipodascus reessii* (van der Walt) von Arx, Antonie van Leeuwenhoek, 43: 338; 1977.

≡ *Galactomyces reessii* (van der Walt) Redhead & Malloch, Can. J. Bot. 55: 1708; 1977.

Geotrichum restrictum de Hoog & M.Th. Smith, Stud. Mycol.50: 502; 2004.

Synonym: *Dipodascus restrictus* (de Hoog & M.T. Sm.) P.M. Kirk, Index Fungorum 270: 1; 2015.

Geotrichum siamensis Limtong, Kaewwich., Yongman., Srisuk & Fujiyama FEMS Yeast Res. 10: 218; 2010.

Synonym: *Dipodascus siamensis* (Limtong, Kaewwich., Yongman., Srisuk & Fujiyama) P.M. Kirk, Index Fungorum 270: 1; 2015.

Geotrichum smithiae H.Y. Zhu, X.Z. Liu & F.Y. Bai **sp. nov.**

MycoBank: MB846372.

Etymology: The species is named in honour of Maudy Th. Smith for her contribution to the systematics of arthroconidial yeast-like fungi.

Type: The holotype CGMCC 2.6454^{T} was isolated from a marine sediment sample collected in Qingdao City, Shandong Province, China by C. Liu in August 2020 and has been preserved in a metabolically inactive state in the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. The ex-type culture has been deposited in the Japan Collection of Microorganisms (JCM), Koyadai, Japan, as JCM 35056 (=QD26-6).

Culture characteristics: After 10 days on MEYE agar at 20 °C, colonies are 50–51 mm in diameter, white, flat, dry, powdery, with finely hairy margins. Hyphae soon disarticulate into cubic arthroconidia 3.5–5 × 6.0–11.5 µm. Hyphae and arthroconidia produce oblong blastoconidia, 3.5–6.0 × 6.5–13.0 µm on PDA agar after one month at 25 °C. The growth radius is 44–52 mm on YPD agar after one week at 25 °C (Figure 7). Sexual structures are not observed.

Physiological and biochemical characteristics: Glucose is weakly fermented. Glucose, galactose, sorbose, maltose (weak), melibiose (weak), D-xylose, ethanol, glycerol (variable), DL-lactic acid, and succinic acid (weak) are assimilated as sole carbon sources. Sucrose, cellobiose, trehalose, lactose, raffinose, melezitose, inulin, soluble starch, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-Glucosamine, methanol, erythritol, ribitol, galactitol, D-mannitol, glucitol, methyl-glucoside, salicin, D-Glucuronic acid, citric acid, inositol, hexadecane, N-acetyl-D-glucosamine, and xylitol are not assimilated as sole carbon sources. Ammonium sulphate, L-lysine, cadaverine dihydrochloride, ethylamine hydrochloride are assimilated as sole nitrogen sources. Potassium nitrate and sodium nitrite are not assimilated as the sole nitrogen sources. Growth occurs at 32 °C but not at 34 °C in a 0.5% glucose liquid medium. Growth in the vitamin-free medium is positive. Extracellular starch-like compounds are not produced. Growth occurs on 50% (w/v) glucose-yeast extract agar, but not on 60% (w/v) glucose-yeast extract agar. Growth does not occur in 10% (w/v) sodium chloride plus 5% (w/v) glucose liquid medium. Urease activity is negative. Diazonium Blue B reaction is negative.

Notes: Physiologically, *Ge. smithiae* sp. nov. differs from its closely related species *Ge. maricola* in its inability to assimilate starch soluble and methanol (Table S3). The three strains representing *Ge. smithiae* sp. nov. are from diverse habitats, *viz*. marine samples in China and Qater and wastewater in Brazil (Table S1), suggesting a wide distribution of the new species in the world.

Geotrichum sinensis H.Y. Zhu, X.Z. Liu & F.Y. Bai **sp. nov.**

MycoBank: MB846371.

Etymology: The specific epithet refers to China where it was first isolated.

Type: The holotype CGMCC 2.6485^T was isolated from a marine sediment sample collected in Panjin City, Liaoning Province, China by H.Y Zhu, R.P. Zhang, X.Z. Liu, and F.Y. Bai in May 2020 and has been preserved in a metabolically inactive state in the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. The ex-type culture has been deposited in the Japan Collection of Microorganisms (JCM), Koyadai, Japan, as JCM 36365 (=186CK-3-2).

Culture characteristics: After 10 days on MEYE agar at 20 °C, colonies are 22 mm in diameter, white, dry, with hairy margins. Hyphae soon disarticulate into cubic arthroconidia, 2.6–4.2 × 5.4–17.3 µm. Hyphae and arthroconidia produce oblong blastoconidia, 3.6–6.2 × 5.3–9.2 µm on PDA agar after one month at 25 °C. The growth radius is 20 mm on YPD agar after one week at 25 °C (Figure 8). Sexual structures are not observed.

Physiological and biochemical characteristics: Glucose is weakly fermented. Glucose, galactose, sorbose, D-xylose, ethanol, glycerol, ribitol (variable), D-mannitol, D-sorbitol, DL-lactic acid, succinic acid, citric acid, and xylitol are assimilated as sole carbon sources. Sucrose, maltose, cellobiose, trehalose, lactose, melibiose, raffinose, melezitose, inulin, starch soluble, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-Glucosamine, methanol, erythritol, galactitol, glucitol, methyl-glucoside, salicin, D-Glucuronic acid, inositol, hexadecane, N-acetyl-D-glucosamine are not assimilated as sole carbon sources. Ammonium sulphate, L-lysine, cadaverine dihydrochloride, and ethylamine hydrochloride are assimilated as sole nitrogen sources. Potassium nitrate and sodium nitrite are not assimilated as sole nitrogen sources. Growth occurs at 30 °C but not at 35 °C in a 0.5% glucose liquid medium. Growth in the vitamin-free medium is positive. Extracellular starch-like compounds are not produced. Growth does not occur on 50% (w/v) glucose-yeast extract agar and in 10% (w/v) sodium chloride plus 5% (w/v) glucose liquid medium. Urease activity is negative. Diazonium Blue B reaction is negative.

Notes: Physiologically, *Ge. sinensis* sp. nov. differs from its closely related species *Ge. klebahnii* in its ability to assimilate xylitol (Table S3).

Geotrichum tetrasporum (Nagah. & Abdel-Wahab) H. Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

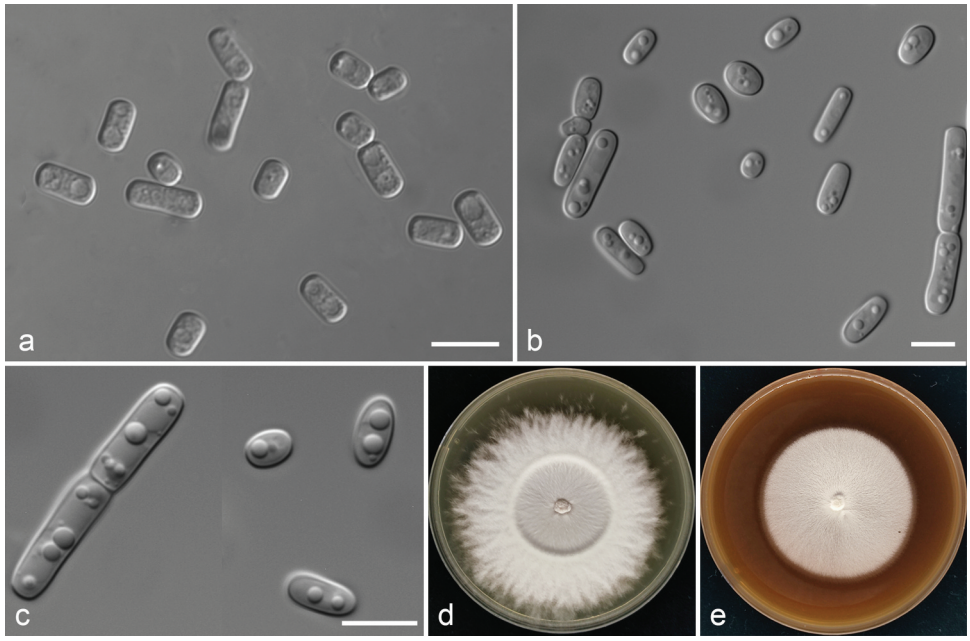

Figure 7. Morphology of *Geotrichum smithiae* sp. nov. (strain QD26–6^T). (a) Cylindrical arthroconidia on 4% malt extract/0.5% yeast extract (MEYE) agar. (b–c) Blastoconidia on potato dextrose agar (PDA). (d) Colonies on yeast extract peptone dextrose (YPD) agar after one week. (e) Colonies on MEYE agar after 10 days. Scale bars: a, c = 10 µm; b = 20 µm.

MycoBank: MB846384.

Basionym: *Dipodascus tetrasporeus* Nagah. & Abdel-Wahab, Int. J. Syst. Evol. Microbiol. 58: 1043; 2008.

Magnusiomyces Zender, Bull. Soc. Bot. Genève, Ser. 2, 17: 41; 1925. **emend**. H.Y. Zhu, X.Z. Liu & F.Y. Bai

Synonyms: *Saprochaete* Coker & Shanor, Journal of the Elisha Mitchell Scientific Society 55: 163; 1939.

Saprochaete Coker & Shanor ex D.T.S. Wagner & Dawes, Mycologia 62: 794; 1970.

Endyllium Clements, The genera of Fungi. 46: 245; 1931.

Zendera Redhead & Malloch, Canad. J. Bot. 55: 1707; 1977.

Blastoschizomyces Salkin, Gordon, Samsonoff & Rieder, Mycotaxon 22: 503; 1985.

Type species: *Magnusiomyces magnusii* (F. Ludwig) Red-head & Malloch, Can. J. Bot. 55: 1708; 1977.

Diagnosis: Asexual characteristics: Colonies are white, farinose or hairy, usually dry, and consist of true hyphae that branch at acute angles with acuminate apices and disarticulate into arthroconidia. Additional sympodial and annellidic conidiogenesis may be present. Chlamydospores are mostly absent. Septa have micropores. Sexual characteristics: Gametangia form on opposite sides of hyphal septa, become broadly ellipsoidal, soon entirely fuse and are transformed to an ascus. Asci are hyaline, subspherical to broadly ellipsoidal and contains four ascospores. Ascospores are ellipsoidal to broadly ellipsoidal, hyaline, and with smooth walls surrounded by regular slime sheaths. Ascospores are liberated by rupture at the apex of the ascus wall. Physiology/biochemistry characteristics: Assimilation of D-xylose is mostly absent. Nitrate is not assimilated. Urease is not produced. Extracellular starch is not formed. The diazonium blue B reaction is negative.

Notes: We accept 17 species in *Magnusiomyces* including seven new combinations and one novel name. The key characters of the *Magnusiomyces* species are listed in Table S4.

Species accepted in *Magnusiomyces*

Magnusiomyces capitatus (de Hoog, M.T. Sm. & Guého) de Hoog & M.Th. Smith, Stud. Mycol.50: 508; 2004.

Basionym: *Dipodascus capitatus* de Hoog, M.T. Sm. & Guého, Stud. Mycol. 29: 51; 1986.

Synonyms: *Trichosporon capitatum* Diddens & Lodder, Die anaskosporogenen Hefen, 2. Hälfte, p. 488; 1942.

≡ *Geotrichum capitatum* (Diddens & Lodder) von Arx Stud. Mycol. 14: 32; 1977.

≡ *Ascotrichosporon capitatum* (Diddens & Lodder) Kock.-Krat., E. Sláviková, Zemek & Kuniak, Proc. Fifth Int. Spec. Symp. Yeasts, Bratislava: p. 9; 1977.

≡ *Blastoschizomyces capitatus* (Diddens & Lodder) Salkin, M.A. Gordon, Sams. & Rieder, Mycotaxon 22 (2): 378; 1985.

≡ *Saprochaete capitata* (Diddens & Lodder) de Hoog & M.T. Sm., Stud. Mycol.50: 508; 2004.

Sporotrichum spicatum Delitsch, Ergebnisse der theoretischen und angewandten Mikrobiologie: Band I: Systematik der Schimmelpilze: p. 106. 1943.

Geotrichum linkii Vörös-Felkai, Acta Microbiologica Academiae Scientiarum Hungaricae 8: 99; 1961.

Blastoschizomyces pseudotrichosporon Salkin, M.A. Gordon, Sams. & Rieder, Mycotaxon 14 (2): 503; 1982.

Magnusiomyces chiloensis (C. Ramírez & A. E. González) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846395.

Basionyms: *Schizoblastosporion chiloënse* C. Ramírez & A. E. González, Mycopathologia 88: 168; 1984.

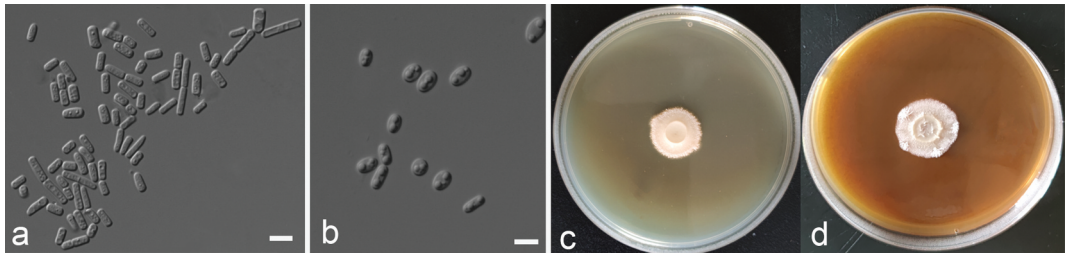

Figure 8. Morphology of *Geotrichum sinensis* (strain 186CK-3-2^T). (a) Cylindrical arthroconidia on 4% malt extract/0.5% yeast extract (MEYE) agar. (b) Blastoconidia on potato dextrose agar (PDA). (c) Colonies on yeast extract peptone dextrose (YPD) after one week. (d) Colonies on MEYE agar after 10 days. Scale bars: a–b = 10 µm.

≡ *Saprochaete chiloënsis* (C. Ramírez & A. E. González) Kurtzman, Robnett, de Hoog & M.T. Sm., Stud. Mycol.50: 509; 2004.

Magnusiomyces clavatus (de Hoog, M.T. Sm. & E. Guého) E. Kaplan, Index Fungorum 404: 1; 2019.

Basionyms: *Geotrichum clavatum* de Hoog, M.T. Sm. & E. Guého, Stud. Mycol. 29: 57; 1986.

≡ *Saprochaete clavata* (de Hoog, M.T. Smith & Guého) de Hoog & M.T. Sm., Stud. Mycol. 50: 509; 2004.

≡ *Magnusiomyces clavatus* (de Hoog, M.T. Sm. & E. Guého) E. Kaplan, Journal of Clinical microbiology 56 (1): e01427–17, 9; 2018.

Notes: Phylogenetically, *M. clavatus* is closely related to *M. spicifer* (Figures 1, S1, and S2). Because the ITS sequence of the type strain CBS 244.85^{T} of *M. spicifer* is not available, we used the ITS sequence of strain AW2 which possesses a similar D1/D2 sequence with CBS 244.85^{T} (only one nt difference) to represent the ITS sequence of *M. spicifer* in this study. *M. clavatus* and *M. spicifer* possess identical ITS sequences and similar D1/D2 sequences, thus Phaff et al. (1997) and Kurtzman and Robnett (1998) suggested that they might be conspecific. However, Smith and Poot (1998) proposed that these two species were distinct species based on DNA reassociation experiments. Ueda-Nishimura and Mikata (2001) suggested that *M. clavatus* might be a hybrid between *M. spicifer* and another species based on DNA reassociation experiments. Physiologically, *M. clavatus* differs from *M. spicifer* by its ability to grow with D-xylose (Table S4). We tentatively treat them as separate species in this study.

Magnusiomyces fungicola (de Hoog & M.T. Sm.) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846396.

Basionym: *Saprochaete fungicola* de Hoog & M.T. Sm., Stud. Mycol.50: 512; 2004.

Magnusiomyces gigas (Smit & L. Meyer) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846397.

Basionyms: *Oospora gigas* Smit & L. Meyer, Ned. Tijdschr. Microbiol. Serol.: 86; 1928.

≡ *Geotrichum gigas* (Smit & L. Meyer) M.T. Smith & Poot, Antonie van Leeuwenhoek 77: 77; 2000.

≡ *Saprochaete gigas* (Smit & L. Meyer) de Hoog & M. T. Smith, Stud. Mycol. 50: 509; 2004.

Synonyms: *Geotrichum magnum* Saëz, Microbiol. Esp.: 203; 1968.

Geotrichum rectangulatum Goto, Yamakawa & Yokotsuka, J. Agric. Chem. Soc. Japan.: 523; 1975.

Notes: In this study, we employed strain CBS 126.76 to represent *M. gigas*. The ITS and D1/D2 sequences of the type strain CBS 140.25 of the species are not available. Strain CBS 126.76 has been proved to be conspecific with strain CBS 140.25 based on DNA reassociation experiments (Smith et al. 2000).

Magnusiomyces ingens (de Hoog, M.T. Sm. & Guého) de Hoog & M.T. Sm., Stud. Mycol. 50: 510; 2004.

Basionym: *Dipodascus ingens* de Hoog, M.T. Sm. & Guého, Mycotaxon 63: 345; 1997.

Synonyms: *Pichia humboldtii* Rodr. Mir. & Török, Antonie van Leeuwenhoek 42: 343; 1976.

≡ *Zygopichia humboldtii* (Rodr. Mir. & Török) Kock.-Krat., Taxonomy of yeast and yeast-like microorganisms: p. 282; 1990.

Magnusiomyces japonicus (de Hoog & M.T. Sm.) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846398.

Synonym: *Saprochaete japonica* de Hoog & M.T. Sm., Stud. Mycol.50: 511; 2004.

Magnusiomyces magnusii (F. Ludw.) Redhead & Malloch, Can. J. Bot. 55: 1977.

Basionyms: *Endomyces magnusii* F. Ludwig, Ber. Dt. Bot. Ges. 4: 17; 1886.

≡ *Endyllium magnusii* (F. Ludw.) Clements in Clements & Shear, Gen. Fung. p. 245; 1931.

≡ *Magnusiomyces magnusii* (F. Ludw.) Zender, Bulletin de la Société Botanique de Genève 17: 299; 1926.

≡ *Dipodascus magnusii* (F. Ludw.) Arx, Antonie van Leeuwenhoek 43: 336; 1977.

Synonyms: *Oidium ludwigii* E.C. Hansen, Zentbl. Bakt. ParasitKde, Abt. 2: 185; 1901.

≡ *Oospora ludwigii* (E.C. Hansen) Sacc. & D. Sacc., Syll. Fung. 18: 500; 1906.

≡ *Geotrichum ludwigii* (E.C. Hansen) S. Fang, T.C. Yen & J.C. Yen, Acta Microbiol. Sin. 12: 69; 1966.

≡ *Saprochaete ludwigii* (E.C. Hansen) de Hoog & M. Th. Smith, Stud. Mycol.50: 508; 2004.

Magnusiomyces ludwigii Zender, Bulletin de la Société Botanique de Genève 17: 299; 1926.

≡ *Endyllium ludwigii* (Zender) Clem. & Shear, The genera of Fungi: 245; 1931.

Oospora magnusii Stautz, Phytopath. Z. 3: 185; 1931.

Magnusiomyces paraingens (van der Walt & van Kerken) H.Y. Zhu, X.Z. Liu & F.Y. Bai **nom. nov.**

MycoBank: MB846399.

Basionyms: *Candida ingens* van der Walt & van Kerken. Antonie van Leeuwenhoek 27: 285; 1961.

≡ *Geotrichum ingens* (van der Walt & van Kerken) de Hoog, M.T. Sm. & Guého, Mycotaxon 63: 346; 1997.

≡ *Saprochaete ingens* (van der Walt & van Kerken) de Hoog & M.T. Sm., Stud. Mycol. 50: 513; 2004.

Synonym: *Pichia humboldtii* Rodr. de Mir. & Török, Antonie van Leeuwenhoek 42: 343; 1976.

Notes: Since *Magnusiomyces ingens* is an existing species name, to avoid the creation of a homonym, a novel epithet "*paraingens*" is thus proposed to accommodate *Saprochaete ingens* in the genus *Magnusiomyces*. The new epithet refers to the close relationship of this species with *M. ingens* (Figures 1, S1, and S2).

Magnusiomyces quercus (de Hoog & M.T. Sm.) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846400.

Basionym: *Saprochaete quercus* de Hoog & M.T. Sm., Stud. Mycol. 50: 511; 2004.

Magnusiomyces saccharophilus (Coker & Shanor ex D.T.S. Wagner & Dawes) H.Y. Zhu, X.Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846401.

Basionym: *Saprochaete saccharophila* Coker & Shanor ex D.T.S. Wagner & Dawes, Mycologia 62: 794; 1970.

Magnusiomyces ovetensis (Pelãez & C. Ramírez) de Hoog & M.T. Sm., Stud. Mycol. 50: 507; 2004.

Basionyms: *Endomyces ovetensis* Pelãez & C. Ramírez, Micro- biol. Espagn. 9: 191; 1956.

≡ *Endomycopsis ovetensis* (Pelãez & C. Ramírez) Kreger-van Rij, Taxon. Stud. Gen. *Endomycosis*, *Pichia* and *Debaryomyces* p. 48; 1964.

≡ *Zendera ovetensis* (Pelãez & C. Ramírez) Red- head & Malloch, Canad. J. Bot. 55: 1017; 1977.

≡ *Dipodascus ovetensis* (Pelãez & C. Ramírez) von Arx, Antonie van Leeuwenhoek 43: 338; 1977.

Synonyms: *Oospora sericea* Stautz, Phytopath. Z. 3: 193; 1931.

≡ *Trichosporon sericeum* (Stautz) Diddens & Lod, der, Anaskosp. Hefen, 2. Hälfte p. 448; 1942.

≡ *Ascotrichosporon sericeum* (Stautz) Kocková-Kratochvílová, Sláviková, Zemek & Kuniak, Proc. 5th Int. Spec. Symp. Yeasts, Bratislava p. 9; 1977.

≡ *Geotrichum sericeum* (Sautz) de Hoog, M.Th. Smith & Guého, Stud. Myol. 29; 36. 1986.

≡ *Saprochaete sericea* (Stautz) de Hoog & M.Th. Smith, Stud. Mycol.50: 502; 2004.

Dipodascus ambrosiae de Hoog, M.Th. Smith & Guého, Stud. Mycol. 29: 47; 1989.

Magnusiomyces spicifer (de Hoog, M.T. Sm. & Guého) de Hoog & M.T. Sm., Stud. Mycol.50: 510; 2004.

Basionym: *Dipodascus spicifer* de Hoog, M.T. Sm. & Guého, Stud. Mycol. 29: 60; 1986.

Notes: See the notes under *Magnusiomyces clavate*.

Magnusiomyces siamensis Dudhat, Sakpuntoon, Angchuan, Kaewwich. & Srisuk, Int. J. Syst. Evol. Microbiol. 72: 005435; 2022.

Magnusiomyces starmeri (Phaff, Blue, Hagler & Kurtzman) de Hoog & M.Th. Smith, Stud. Mycol.50: 502; 2004.

Basionym: *Dipodascus starmeri* Phaff, Blue, Hagler & Kurtzman, Int. J. Syst. Bacteriol. 47: 309; 1997.

Magnusiomyces suaveolens (Krzemecki) H.Y. Zhu, X. Z. Liu & F.Y. Bai **comb. nov.**

MycoBank: MB846402.

Basionyms: *Oidium suaveolens* Krzemecki, Zentbl. Bakt. ParasitKde, Abt. 2: 577; 1913.

≡ *Geotrichum suaveolens* (Krzemecki) S.F. Fang, T.C. Yen & J.C. Yue, Acta Microbiol. Sin. 12: 68; 1966.

≡ *Saprochaete suaveolens* (Krzemecki) de Hoog & M. T. Sm., Stud. Mycol. 50: 508; 2004.

Synonyms: *Oospora fragrans* Berkhout, De Schimmelgesl. Monilia, Oidium, Oospora en Torula p. 47; 1923.

≡ *Cylindrium fragrans* (Berkhout) Burns, Iowa St. Coll. J. Sci. p. 436; 1933.

≡ *Geotrichum fragrans* (Berkhout) Morenz, Mykol. SchrReihe 1: 69; 1964.

Endomyces lactis var. *fragrans* Windisch, Beiträge zur Biologie der Pflanzen 28: 125; 1951.

Geotrichum fici Goto, Yamak. & Yokots., J. Agric. Chem. Soc. Japan 49: 522; 1975.

Magnusiomyces tetrasperma (Macy & M.W. Mill.) de Hoog & M.T. Sm., Stud. Mycol. 50: 507; 2004.

Basionyms: *Endomyces tetrasperma* Macy & M.W. Miller, J. Bact. 105: 638; 1971.

≡ *Zendera tetrasperma* (Macy & M.W. Miller) Redhead & Malloch, Can. J. Bot. 55: 1707; 1977.

≡ *Dipodascus tetrasperma* (Macy & M.W. Miller) Arx, Antonie van Leeuwenhoek 43: 338; 1977.

4. Discussion

In this study, we confirmed the recognition of two distinct monophyletic groups from the arthroconidial ascomycetous yeast species based on ITS and LSU D1/D2 sequence analyses. Group 1 contains *Dipodascus*, *Galactomyces* and *Geotrichum* species and Group 2 contains *Magnusiomyces* and *Saprochaete* species. The species from different genera within any of the groups were not clearly separated. We thus assigned the species in each group into one genus and selected the genus name *Geotrichum* for Group 1 and *Magnusiomyces* for Group 2 based on the priority of publication principle. The *Dipodascus* and *Galactomyces* species are transferred to *Geotrichum* and the *Saprochaete* species to *Magnusiomyces* to accommodate the "one fungus, one name" concept adopted in the new code of nomenclature of the fungi. Five new species *Ge. dehoogii*, *Ge. fujianense*, *Ge. maricola*, *Ge. smithiae*, and *Ge. sinensis* were then identified from the arthroconidial yeast strains recently isolated from various sources in China according to the new system. A total of 28 *Geotrichum* species and 17 *Magnusiomyces* species are currently accepted (Figure 2 and Table S1). However, some strains with ITS or D1/D2 sequences being released in GenBank cannot be assigned to any of the known species (Figures 2, S3, and S4), suggesting that more *Geotrichum* species remain to be described.

Both *Geotrichum* and *Magnusiomyces* species are characterised by forming yeast-like colonies with pronounced hyphae and septa perforated by numerous micropores, arthroconidia and asci (when formed) with ascospores covered by an even, thick gelatinous sheath (Rij and Veenhuis 1972; Kreger-van Rij and Veenhuis 1973; de Hoog et al. 1986; de Hoog and Smith 2004). In addition to the special morphological characters, the species in the two genera exhibit unique molecular characters. de Hoog and Smith (2004) observed remarkably short ITS regions with strikingly biased AT contents from the species compared. This character remains when more species are compared in this study. de Hoog and Smith (2004) observed elongated ITS regions in some species. In *Ge. albidum*, the lengths of ITS1 and ITS2 were 161 and 420 bp, respectively, being significantly longer than the 72–120 and 107–133 bp of the other species in Group 1. The elongation was caused by the insertion of AT-rich stretches (de Hoog and Smith 2004). The genome sequence of *Ge. albidum* CBS 766.85 confirmed this character of the ITS region of this species. Such elongation caused by AT-rich fragments was also observed in Group 2 species *M. capitatus*, *M. spicifer*, and *M. clavatus* by de Hoog and Smith (2004) and confirmed in this study.

Though the two groups share some morphological and molecular characteristics, they possess group specific characters. As shown in de Hoog and Smith (2004), the unique beginning sequence 5′-AACCTCCAAC-3′ of the 5.8S rDNA is shared by the Group 2/*Magnusiomyces* species. This signature 5.8S sequence of Group 2/*Magnusiomyces* has not been observed in other groups of fungi, while the Group 1 species share conserved sequence 5′-AACTTTTAAC-3′ with other groups of the fungal Kingdom (de Hoog and Smith 2004). The group specific signature rDNA sequences were confirmed in this study.

The rDNA ITS region is one of the most frequently used molecular markers in phylogeny and identification of yeasts at the species level (James et al. 1996; Montrocher et al. 1998; Sugita et al. 1999a, 1999b; Scorzetti et al. 2002; Kurtzman and Robnett 2003) and has been selected as a universal DNA barcode marker for Fungi (Schoch et al. 2012). Previous studies have claimed that conspecific yeast strains usually have fewer than 1% nucleotide differences in the ITS region overall (Nagahama et al. 1999; Sugita et al.

1999a, 1999b; Scorzetti et al. 2002; Vu et al. 2016). However, in some *Geotrichum* species, significantly higher intraspecific sequence variations in the ITS region have been observed (Groenewald et al. 2012). An extreme case is *Ge. candidum*, up to 11% base mismatches were reported among strains or synonyms of this species (Figure 3b), which were proved to be conspecific by DNA-DNA reassociation and mating tests (Groenewald et al. 2012). Alper et al. (2011) analysed rDNA polymorphisms in different *Ge. candidum* strains and intragenomic sequence variations in single strains of the species. Up to 10 (3%) and 2 (<1%) nt differences between different ITS and D1/D2 types from a single strain were observed, respectively. In this study, we also detected intragenomic rDNA sequence variations from *Ge. candidum* strains. Up to 10 nt differences were observed from different ITS types from single strain (Figure 3). Intragenomic variation in nuclear rDNA markers has been observed in different groups of fungi (Wu et al. 2016; Paloi et al. 2022), thus, caution should be taken when using the rDNA barcoding markers for yeast identification. Sufficient investigation and documentation of intraspecific variation in the barcoding markers will certainly be helpful for correct identification. Considering the exceptionally short length and intragenomic variation of the ITS region in the *Geotrichum* and *Magnusiomyces* species, we recommend the LSU D1/D2 domain as the primary barcoding marker for species identification of this group of fungi, as suggested by Groenewald et al. (2012).

Ge. candidum is a ubiquitous yeast and plays a fundamental role in the production of various cheeses (Marcellino et al. 2001; Jacques et al. 2017; Perkins et al. 2020; Bennetot et al. 2023). Recent multilocus sequence typing (MLST) and phylogenetic analyses of *Ge. candidum* revealed its genetic diversity (Alper et al. 2013; Jacques et al. 2017; Perkins et al. 2020). Perkins et al. (2020) sequenced the whole genomes of eight strains of *Ge. candidum* and provided a reliable reference for MLST scheme optimisation. Bennetot et al. (2023) conducted a comprehensive analysis of whole-genome data derived from 98 strains of *Ge. candidum*. Their findings provided evidence supporting the genuine domestication in *Ge. candidum*, which has resulted in the emergence of distinct varieties exhibiting diverse phenotypic characteristics. In this study, we isolated and collected many strains of *Ge. candidum* from intertidal zones and Chinese Baijiu fermentation environments in China, which could provide many strains from different geographical environments and substrates for future study.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability of statement

The new sequences generated in this study have been deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/) under accession numbers indicated in Table S1 and released to the public. All resulting alignments have been deposited in TreeBASE (http://www.treebase.org/) with accession number S29847. All new taxa have been registered in Mycobank (https://www.mycobank.org/). The type strains of the new species described have been deposited in the China General Microbiological Culture Collection Center (CGMCC) and the Japan Collection of Microorganisms (JCM) with strain numbers indicated in Table S1.

References

Alper I, Frenette M, Labrie S. 2011. Ribosomal DNA polymorphisms in the yeast *Geotrichum candidum*. Fungal Biol. 115 (12):1259–1269. doi: 10.1016/j.funbio.2011.09.002.

Alper I, Frenette M, Labrie S. 2013. Genetic diversity of dairy *Geotrichum candidum* strains revealed by multilocus sequence typing. Appl Microbiol Biotechnol. 97(13): 5907–5920. doi: 10.1007/s00253-013-4776-2.

Arendrup MC, Boekhout T, Akova M, Meis JF, Cornely OA, Lortholary O, Arikan-Akdagli S, Cuenca-Estrella M, Dannaoui E, van Diepeningen AD, et al. 2014. ESCMID and ECMM joint clinical guidelines for the diagnosis and management of rare invasive yeast infections. Clin Microbiol Infect. 20(S3):76–98. doi:10.1111/1469-0691.12360.

Bai FY, Zhao JH, Takashima M, Jia JH, Boekhout T, Nakase T. 2002. Reclassification of the *sporobolomyces roseus* and *Sporidiobolus pararoseus* complexes, with the description of *sporobolomyces phaffii* sp. nov. Int J Syst Evol Microbiol. 52(6):2309–2314. doi: 10.1099/00207713-52-6-2309.

Banjara N, Suhr MJ, Hallen-Adams HE. 2015. Diversity of yeast and mold species from a variety of cheese types. Curr Microbiol. 70(6):792–800. doi: 10.1007/s00284-015-0790-1.

Bennetot B, Vernadet JP, Perkins V, Hautefeuille S, Rodríguez De La Vega RC, O'donnell S, Snirc A, Grondin C, Lessard M, Peron A, et al. 2023. Domestication of different varieties in the cheese-making fungus *Geotrichum candidum*. Peer Community J. 3:e45. doi: 10.24072/pcjournal.266.

Brejová B, Lichancová H, Brázdovič F, Hegedűsová E, Forgáčová Jakúbková M, Hodorová V, Džugasová V, Baláž A, Zeiselová L, Cillingová A, et al. 2018. Genome sequence of the opportunistic human pathogen *Magnusiomyces capitatus*. Curr Genet. 65(2):539–560. doi:10.1007/s00294-018-0904-y.

Brejová B, Lichancová H, Hodorová V, Neboháčová M, Tomáška Ľ, Vinař T, Nosek J, Stajich JE. 2019. Genome sequence of an arthroconidial yeast, *Saprochaete fungicola* CBS 625.85. Microbiol Resour Announce. 8(15):e00092–19. doi: 10.1128/MRA.00092-19.

Butler EE, Fogle D, Miranda M. 1988. *Galactomyces citri-aurantii*, a newly found téleomorphe of *Geotrichum citri-aurantii* the cause of sour rot of citrus fruit. Mycotaxon. 33:197–212.

Butler EE, Petersen LJ. 1972. *Endomyces geotrichum* a perfect state of *Geotrichum candidum*. Mycologia. 64(2):365–374. doi: 10.1080/00275514.1972.12019270.

Carmichael JW. 1957. *Geotrichum candidum*. Mycologia. 49 (6):820–830. doi: 10.1080/00275514.1957.12024694.

Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Mol Biol Evol. 17:540–552. doi: 10.1093/oxfordjournals.molbev.a026334.

Coker WC, Shanor L. 1939. A remarkable saprophytic fungoid alga. J Elisha Mitchell Sci Soc. 55:152–166.

de Hoog GS, Smith MT. 2004. Ribosomal gene phylogeny and species delimitation in *Geotrichum* and its teleomorphs. Stud Mycol. 50:489–515.

de Hoog GS, Smith MT. 2011a. *Galactomyces* Redhead & Malloach (1977). In: Kurtzman C, Fell J Boekhout T, editors. The yeasts, a taxonomic study. 5th ed. Amsterdam, Netherlands: Elsevier; pp. 413–420.

de Hoog GS, Smith MT. 2011b. *Dipodascus* de Lagerheim (1892). In: Kurtzman C, Fell J Boekhout T, editors. The yeasts, a taxonomic study. 5th edn ed. Amsterdam, Netherlands: Elsevier; pp. 385–395.

de Hoog GS, Smith MT. 2011c. *Geotrichum* link: Fries (1832). In: Kurtzman C, Fell J, and Boekhout T, editors. The yeasts, a taxonomic study. 5th edn ed. Amsterdam, Netherlands: Elsevier; pp. 1279–1286.

de Hoog GS, Smith MT. 2011d. *Magnusiomyces* Zender (1977). In: Kurtzman C, Fell J Boekhout T, editors. The yeasts, a taxonomic study. 5th edn ed. Amsterdam, Netherlands: Elsevier; pp. 565–574.

de Hoog GS, Smith MT. 2011e. *Saprochaete* Coker & Shanor ex D. T. S. Wagner & Daws (1970). In: Kurtzman C, Fell J Boekhout T, editors. The yeasts, a taxonomic study. 5th edn ed. Amsterdam, Netherlands: Elsevier; pp. 1317–1327.

de Hoog GS, Smith MT, Guého E. 1986. A revision of the genus *Geotrichum* and its teleomorphs. Stud Mycol. 29:1–131.

de Lagerheim G. 1892. *Dipodascus albidus*, eine neue, Geschlechtliche Hemiascee. Jahrb Wiss Bot. 24:549–565.

Dudhat J, Sakpuntoon V, Angchuan J, Kaewwichian R, Srisuk N. 2022. *Magnusiomyces siamensis* sp. nov., a yeast-like fungus isolated from food waste. Int J Syst Evol Microbiol. 72:005435. doi: 10.1099/ijsem.0.005435.

Erman B, Fırtına S, Aksoy BA, Aydogdu S, Genç GE, Doğan Ö, Bozkurt C, Fışgın T, Çipe FE. 2020. Invasive *Saprochaete capitata* infection in a patient with autosomal recessive CARD9 deficiency and a review of the literature. J Clin Immunol. 40(3):466–474. doi: 10.1007/s10875-020-00759-w.

Ersoz G, Otag F, Erturan Z, Aslan G, Kaya A, Emekdas G, Sugita T. 2004. An outbreak of *Dipodascus capitatus* infection in the ICU: Three case reports and review of the literature. Jpn J Infect Dis. 57(6):248–252. doi: 10.1111/j.1439-0507.2005.01126.x.

Fasciana T, Giuffrè M, Calà C, Schierz IAM, Aquilina G, Pinello G, Capra G, Lipari D, Corsello G, Giammanco A. 2017. Genotyping and antifungal susceptibility of *Dipodascus capitatus* isolated in a neonatal intensive care unit of a sicilian hospital. Adv Exp Med Biol. 973:81–88. doi: 10.1007/5584_2016_195.

Flateau C, Aït-Ammar N, Angebault C, Salomon L, Matignon M, Lepeule R, Melica G, Grimbert P, Lelièvre JD, Gallien S, et al. 2021. Risk factors for intra-abdominal fungal infection after simultaneous pancreas-kidney transplantation: A single-center retrospective experience. Transpl Infect Dis. 23(2):1–10. doi: 10.1111/tid.13486.

Gao H, Yin X, Jiang X, Shi H, Yang Y, Wang C, Dai X, Chen Y, Wu X. 2020. Diversity and spoilage potential of microbial communities associated with grape sour rot in eastern coastal areas of China. PeerJ. 2020(6):1–17. doi: 10.7717/peerj.9376 .

Groenewald M, Coutinho T, Smith MT, van der Walt JP. 2012. Species reassignment of *Geotrichum bryndzae*, *Geotrichum phurueaensis*, *Geotrichum silvicola* and *Geotrichum vulgare* based on phylogenetic analyses and mating compatibility.

Int J Syst Evol Microbiol. 62(12):3072–3080. doi: 10.1099/ijs.0.038984-0.

Han PJ, Luo LJ, Han Y, Song L, Zhen P, Han DY, Wei YH, Zhou X, Wen Z, Qiu JZ, et al. 2023. Microbial community affects Daqu quality and the production of ethanol and flavor compounds in Baijiu fermentation. Foods. 12(15):2936. doi:10.3390/foods12152936.

Hawksworth D. 2011. A new dawn for the naming of fungi: Impacts of decisions made in Melbourne in July 2011 on the future publication and regulation of fungal names. MycoKeys. 1:7–20. doi: 10.3897/mycokeys.1.2062.

Hodorová V, Lichancová H, Zubenko S, Sienkiewicz K, Penir SMU, Afanasyev P, Boceck D, Bonnin S, Hakobyan S, Smyczynska U, et al. 2019. Genome sequence of the yeast *Saprochaete ingens* CBS 517.90. Microbiol Resour Announce. 8(50):6–8. doi:10.1128/mra.01366-19.

Jacques N, Mallet S, Laaghouiti F, Tinsley CR, Casaregola S. 2017. Specific populations of the yeast *Geotrichum candidum* revealed by molecular typing. Yeast. 34(4):165–178. doi: 10.1002/yea.3223.

James SA, Collins MD, Roberts IN. 1996. Use of an rRNA internal transcribed spacer region to distinguish phylogenetically closely related species of the genera *Zygosaccharomyces* and *Torulaspora*. Int J Syst Bacteriol. 46(1):189–194. doi: 10.1099/00207713-46-1-189.

Kaewwichian R, Yongmanitchai W, Srisuk N, Fujiyama K, Limtong S. 2010. *Geotrichum siamensis* sp. nov. and *Geotrichum phurueaensis* sp. nov., two asexual arthroconidial yeast species isolated in Thailand. FEMS Yeast Res. 10(2):214–220. doi: 10.1111/j.1567-1364.2009.00572.x.

Kataoka S, Hattori K, Date A, Tamura H. 2013. Human keratinocyte caspase-14 expression is altered in human epidermal 3D models by dexamethasone and by natural products used in cosmetics. Arch Dermatol Res. 305(8):683–689. doi: 10.1007/s00403-013-1359-0.

Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Mol Biol Evol. 30(4):772–780. doi: 10.1093/molbev/mst010.

Keene S, Sarao MS, McDonald PJ, Veltman J. 2019. Cutaneous geotrichosis due to *Geotrichum candidum* in a burn patient. Access Microbiol. 1(1):e000001. doi: 10.1099/acmi.0.000001.

Kimura M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. J Mol Evol. 16(2):111–120. doi: 10.1007/BF01731581.

Kreger-van Rij NJW, Veenhuis M. 1973. Spores and septa in the genus *Dipodascus*. Can J Bot. 52(6):1335–1338. doi: 10.1139/b74-173.

Kumar S, Stecher G, Tamura K. 2016. MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. Nord Hydrol. 34(4):281–294. doi: 10.1093/molbev/msw054.

Kurtzman CP, Fell JW, Boekhout T, Robert V. 2011. Methods for isolation, phenotypic characterization and maintenance of yeasts. In: Kurtzman C, Fell J Boekhout T, editors. The yeasts, a taxonomic study. 5th ed. Amsterdam, Netherlands: Elsevier; pp. 87–110.

Kurtzman CP, Robnett CJ. 1995. Molecular relationships among hyphal ascomycetous yeasts and yeastlike taxa. Can J Bot. 73(S1):S824–S830. doi: 10.1139/b95-328.

Kurtzman CP, Robnett CJ. 1998. Identification and phylogeny of ascomycetous yeasts from analysis of nuclear large subunit (26S) ribosomal DNA partial sequences. Antonie Van Leeuwenhoek. 73(4):331–371. doi: 10.1023/A:1001761008817.

Kurtzman CP, Robnett CJ. 2003. Phylogenetic relationships among yeasts of the '*Saccharomyces* complex' determined from multigene sequence analyses. FEMS Yeast Res. 3(4):417–432. doi: 10.1016/S1567-1356(03)00012-6.

Kurylenko OO, Ruchala J, Dmytruk KV, Abbas CA, Sibirny AA. 2020. Multinuclear yeast *Magnusiomyces* (*Dipodascus*, *Endomyces*) *magnusii* is a promising isobutanol producer. Biotechnol J. 15(7):1–8. doi: 10.1002/biot.201900490.

Kwaśna H, Bateman GL. 2008. A new species of *Galactomyces* and first reports of four fungi on wheat roots in the United Kingdom. Sydowia. 60(1):69–92. doi: 10.1080/02841850410005516.

Lafayette TCS, Oliveira LTO, Landell M, Valente P, Alves SH, Pereira WV. 2011. *Dipodascus capitatus* (*Geotrichum capitatum*): Infecção sistêmica fatal em paciente com leucemia mielocítica aguda. Revista Da Sociedade Brasileira de Medicina Tropical. 44(5):648–650. doi: 10.1590/S0037-86822011000500028.

Liu X, Zhou W, Jiang Y, Kuang L. 2019. Invasive fungal infection caused by *Geotrichum clavatum* in a child with acute leukemia: First documented case from mainland China. Jpn J Infect Dis. 72(2):130–132. doi: 10.7883/yoken.JJID.2018.351.

Marcellino N, Beuvier E, Grappin R, Guéguen M, Benson DR. 2001. Diversity of *Geotrichum candidum* strains isolated from traditional cheesemaking fabrications in France. Appl Environ Microbiol. 67(10):4752–4759. doi: 10.1128/AEM.67.10.4752-4759.2001.

McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, et al. 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code), adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011 (Melbourne Code). [Regnum Vegetabile no. 154]. Glashütten: Koeltz Botanical Books.

Montrocher R, Verner MC, Briolay J, Gautier C, Marmeisse R. 1998. Phylogenetic analysis of the *Saccharomyces cerevisiae* group based on polymorphisms of rDNA spacer sequences. Int J Syst Bacteriol. 48(1):295–303. doi: 10.1099/00207713-48-1-295.

Nagahama T, Abdel-Wahab MA, Nogi Y, Miyazaki M, Uematsu K, Hamamoto M, Horikoshi K. 2008. *Dipodascus tetrasporeus* sp. nov., an ascosporogenous yeast isolated from deep-sea

sediments in the Japan trench. Int J Syst Evol Microbiol. 58 (4):1040–1046. doi: 10.1099/ijs.0.65471-0.

Nagahama T, Hamamoto M, Nakase T, Horikoshi K. 1999. *Kluyveromyces nonfermentans* sp. nov., a new yeast species isolated from the deep sea. Int J Syst Bacteriol. 49:1899–1905. doi: 10.1099/00207713-49-4-1899.

Nielsen DS, Jakobsen M, Jespersen L. 2010. *Candida halmiae* sp. nov., *Geotrichum ghanense* sp. nov. and *Candida awuaii* sp. nov., isolated from Ghanaian cocoa fermentations. Int J Syst Evol Microbiol. 60(6):1460–1465. doi: 10.1099/ijs.0.016006-0.

Noster J, Köppel M, Desnos-Olivier M, Aigner M, Bader O, Dichtl K, Göttig S, Haas A, Kurzai O, Pranada AB, et al. 2021. Bloodstream infections caused by *Magnusiomyces capitatus* and *Magnusiomyces clavatus*: Epidemiological, clinical and microbiological features of two emerging yeast species. Antimicrob Agents Chemother. 66(2):e01834–21. doi:10.1128/aac.01834-21.

Özkaya-Parlakay A, Cengiz AB, Karadağ-Öncel E, Kuşkonmaz B, Saribaş Z, Kara A, Oğuz B. 2012. *Geotrichum capitatum* septicemia in a hematological malignancy patient with positive galactomannan antigen: Case report and review of the literature. Turk J Pediatr. 54(6):674–678. doi: 10.3928/00904481-20111209-06.

Paloi S, Luangsa-Ard JJ, Mhuantong W, Stadler M, Kobmoo N. 2022. Intragenomic variation in nuclear ribosomal markers and its implication in species delimitation, identification and barcoding in fungi. Fungal Biol Rev. 42:1–33. doi: 10.1016/j.fbr.2022.04.002.

Perkins V, Vignola S, Lessard MH, Plante PL, Corbeil J, Dugat-Bony E, Frenette M, Labrie S. 2020. Phenotypic and genetic characterization of the cheese ripening yeast *Geotrichum candidum*. Front Microbiol. 11:1–16. doi: 10.3389/fmicb.2020.00737.

Phaff HJ, Blue J, Hagler AN, Kurtzman CP. 1997. *Dipodascus starmeri* sp. nov., a new species of yeast occurring in cactus necroses. Int J Syst Bacteriol. 47(2):307–312. doi: 10.1099/00207713-47-2-307.

Pimenta RS, Alves PDD, Corrêa A, Lachance MA, Prasad GS, Rajaram A, Sinha BR, Rosa CA. 2005. *Geotrichum silvicola* sp. nov., a novel asexual arthroconidial yeast species related to the genus *Galactomyces*. Int J Syst Evol Microbiol. 55 (1):497–501. doi: 10.1099/ijs.0.63187-0.

Posada D, Crandall KA. 1998. Modeltest: Testing the model of DNA substitution. Bioinformatics. 14(9):817–818. doi: 10.1093/bioinformatics/14.9.817.

Redhead SA, Malloch D. 1977. The *Endomycetaceae*: New concepts, new taxa. Can J Bot. 55(13):1701–1711. doi: 10.1139/b77-198.

Rij NJW KV, Veenhuis M. 1972. Some features of vegetative and sexual reproduction in *Endomyces* species. Can J Bot. 50 (8):1691–1695. doi: 10.1139/b72-208.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics. 19:1572–1574. doi: 10.1093/bioinformatics/btg180.

Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, Levesque CA, Chen W, Chen W, Voigt K, Crous PW, et al. 2012. Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. Proc Natl Acad Sci USA. 109(16):6241–6246. doi:10.1073/pnas.1117018109.

Scorzetti G, Fell JW, Fonseca A, Statzell-Tallman A. 2002. Systematics of Basidiomycetous yeasts: A comparison of large subunit D1/D2 and internal transcribed spacer rDNA regions. FEMS Yeast Res. 2(4):495–517. doi: 10.1111/j.1567-1364.2002.tb00117.x.

Shah A, Mauger T. 2017. *Magnusiomyces capitatus*: A new and emerging pathogen linked to keratomycosis. Digit J Ophthalmol. 23(3):75–77. doi: 10.5693/djo.02.2017.04.001.

Shen XX, Opulente DA, Kominek J, Zhou X, Steenwyk JL, Buh KV, Haase MA, Wisecaver JH, Wang M, Doering DT, et al. 2018. Tempo and mode of genome evolution in the budding yeast subphylum. Cell. 175(6):1533–1545.e20. doi:10.1016/j.cell.2018.10.023.

Sitepu I, Enriquez L, Nguyen V, Fry R, Simmons B, Singer S, Simmons C, Boundy-Mills KL. 2020. Ionic liquid tolerance of yeasts in family *Dipodascaceae* and genus *Wickerhamomyces*. Appl Biochem Biotechnol. 191(4):1580–1593. doi: 10.1007/s12010-020-03293-y.

Smith MT, de Cock AWAMG, Poot A, Steensma HY. 1995. Genome comparisons in the yeastlike fungal genus *Galactomyces* redhead et malloch. Int J Syst Bacteriol. 45 (4):826–831. doi: 10.1099/00207713-45-4-826.

Smith MT, Poot GA, de Cock AWAM. 2000. Re-examination of some species of the genus *Geotrichum* link: fr. Antonie Van Leeuwenhoek. 77(1):71–81. doi: 10.1023/A:1002030518989.

Spencer JFT, Spencer DM. 1997. Ecology: Where yeasts live. In: Spencer J, and Spencer D, editors. Yeasts in natural and artificial habitats. New York, N.Y: Springer; pp. 33–58.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics. 22(21):2688–2690. doi: 10.1093/bioinformatics/btl446.

Sugita T, Cañete-Gibas CF, Takashima M, Nakase T. 1999a. Three new species of *Bullera* isolated from leaves in the Ogasawara Islands. Mycoscience. 40(6):491–501. doi: 10.1007/BF02461026.

Sugita T, Nishikawa A, Ikeda R, Shinoda T. 1999b. Identification of medically relevant *Trichosporon* species based on sequences of internal transcribed spacer regions and construction of a database for *Trichosporon* identification. J Clin Microbiol. 37 (6):1985–1993. doi: 10.1128/JCM.37.6.1985-1993.1999.

Suh SO, Blackwell M. 2006. Three new asexual arthroconidial yeasts, *Geotrichum carabidarum* sp. nov., *Geotrichum histeridarum* sp. nov., and *Geotrichum cucujoidarum* sp. nov.,

isolated from the gut of insects. Mycol Res. 110(2):220–228. doi: 10.1016/j.mycres.2005.08.008.

Sulo P, Laurenčík M, Poláková S, Minárik G, Sláviková E. 2009. *Geotrichum bryndzae* sp. nov., a novel asexual arthroconidial yeast species related to the genus *Galactomyces*. Int J Syst Evol Microbiol. 59(9):2370–2374. doi: 10.1099/ijs.0.008938-0.

Swofford DL. 2003. PAUP*: Phylogenetic analyses using parsimony. Version 4.0 beta. Sunderland, MA: Sinauer Associates.

Takei K, Mitoma C, Hashimoto-Hachiya A, Takahara M, Tsuji G, Nakahara T, Furue M. 2015. *Galactomyces* fermentation filtrate prevents T helper 2-mediated reduction of filaggrin in an aryl hydrocarbon receptor-dependent manner. Clin Exp Dermatol. 40(7):786–793. doi: 10.1111/ced.12635.

Tanuskova D, Horakova J, Svec P, Bodova I, Lengerova M, Bezdicek M, Poczova M, Koppl J, Kolenova A. 2017. First case of invasive *Magnusiomyces capitatus* infection in Slovakia. Medical Mycol Case Rep. 16:12–15. doi: 10.1016/j.mmcr.2017.03.004.

Taylor JW. 2011. One Fungus = One Name: DNA and fungal nomenclature twenty years after PCR. IMA Fungus. 2(2): 113–120. doi: 10.5598/imafungus.2011.02.02.01.

Tshisevhe V, Mitton B, Skosana L. 2021. Invasive *Geotrichum klebahnii* fungal infection: A case report. Access Microbiol. 3 (11):1–4. doi: 10.1099/acmi.0.000287.

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K, et al. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code), adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017 (Shenzhen Code). [Regnum Vegetabile no. 159]. Glashütten: Koeltz botanical books.

Ueda-Nishimura K, Mikata K. 2000. Two distinct 18S rRNA secondary structures in *Dipodascus* (*Hemiascomycetes*). Microbiology. 146(5):1045–1051. doi: 10.1099/00221287-146-5-1045.

Ueda-Nishimura K, Mikata K. 2001. Reexamination of *Dipodascus* and *Geotrichum* strains by DNA–DNA hybridization. IFO Res Commun. 20:92–96.

Vadkertiová R, Molnárová J, Vránová D, Sláviková E. 2012. Yeasts and yeast-like organisms associated with fruits and blossoms of different fruit trees. Can J Microbiol. 58 (12):1344–1352. doi: 10.1139/cjm-2012-0468.

Vu D, Groenewald M, Szöke S, Cardinali G, Eberhardt U, Stielow B, de Vries M, Verkleij GJM, Crous PW, Boekhout T, et al. 2016. DNA barcoding analysis of more than 9000 yeast isolates contributes to quantitative thresholds for yeast species and genera delimitation. Stud Mycol. 85:91–105. doi: 10.1016/j.simyco.2016.11.007.

Wagner DTS, Dawes CJ. 1970. Revision of the systematic position of *Saprochaete saccharophila*. Mycologia. 62(4):791–796. doi: 10.1080/00275514.1970.12019023.

Wang QM, Bai FY. 2008. Molecular phylogeny of basidiomycetous yeasts in the *Cryptococcus luteolus* lineage (tremellales) based on nuclear rRNA and mitochondrial cytochrome b gene sequence analyses: Proposal of *Derxomyces* gen. nov. And *Hannaella* gen. nov., and description of eight novel *Derxomyces* species. FEMS Yeast Res. 8(5):799–814. doi: 10.1111/j.1567-1364.2008.00403.x.

Wang S, Zhang H, Qi T, Deng L, Yi L, Zeng K. 2022. Influence of arginine on the biocontrol efficiency of *Metschnikowia citriensis* against *Geotrichum citri-aurantii* causing sour rot of postharvest citrus fruit. Food Microbiol. 101:103888. doi: 10.1016/j.fm.2021.103888.

Wu ZW, Wang QM, Liu XZ, Bai FY. 2016. Intragenomic polymorphism and intergenomic recombination in the ribosomal RNA genes of strains belonging to a yeast species *Pichia membranifaciens*. Mycology. 7(3):102–111. doi: 10.1080/21501203.2016.1204369.

Wuczkowski M, Bond C, Prillinger H. 2006. *Geotrichum vulgare* sp. nov., a novel asexual arthroconidial yeast. Int J Syst Evol Microbiol. 56(1):301–303. doi: 10.1099/ijs.0.63671-0.

Zender J. 1925. Sur la classification des Endomycétacées. Bulletin de la Société Botanique de Genève. 17:272–302.

Zhu HY, Han DY, Guo LC, Li JN, Wei XY, Zhang RP, Wang QM, Shang YJ, Luo LJ, Wei YH, et al. 2023. Diversity and distribution of yeasts in intertidal zones of China. Front Mar Sci. 10:1286511. doi: 10.3389/fmars.2023.1286511.