

## The hidden taxonomic novelty of anamorphic basidiomycetous yeasts in the phyllosphere and tidal flats in China

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**Citation** – Sun JQ, Du ZN, Zhu HY, Luo JZ, Zheng AK, Boekhout T, Groenewald M, Hui FL, Li AH, Stajich JE, Zang W, Bai FY, Liu XZ 2025 – The hidden taxonomic novelty of anamorphic basidiomycetous yeasts in the phyllosphere and tidal flats in China. *Mycosphere* 16(1): 3583–3672, <https://doi.org/10.5943/mycosphere/16/1/27>

### Abstract

Basidiomycetous yeasts are taxonomically and ecologically diverse. While the phyllosphere of plants in China has been the subject of extensive research on yeast biodiversity, many unique and remote habitats remain significantly underexplored for their yeast species. The objective of this study was to investigate the hidden taxonomic novelty of basidiomycetous yeasts in these distinctive niches to comprehensively refine the current phylogenetic understanding. During intensive investigations, 164 yeast strains were identified from various samples collected from the phyllosphere and tidal flats in China. These isolates underwent detailed multi-gene phylogenetic analyses combined with phenotypic characterization for taxonomic placement. The analyses revealed a remarkable level of hidden diversity. These 164 isolates represent one new order (*Sterigmoblongales*), two new families (*Sterigmoblongaceae* and *Turchettiaceae*), five new genera (*Nakasea*, *Sterigmoblongus*, *Buzzinia*, *Gracilitas*, *Turchettia*), and 37 novel basidiomycetous species. Phylogenetically, these new taxa are broadly distributed across the three major subphyla viz *Agaricomycotina*, *Pucciniomycotina*, and *Ustilaginomycotina*, including *Ballistosporomyces berchemiae*, *Bannoa hyperici*, *Bannoa lonicerae*, *Bannoa pseudoscolopiae*, *Bannoa quercus*, *Bannoa scolopiae*, *Bulleribasidium pseudosiamense*, *Bulleribasidium rhois*, *Bulleribasidium veronicastris*, *Buzzinia foliicola*, *Chrysozyma lonicerae*, *Chrysozyma rubi*, *Chrysozyma viburni*, *Chrysozyma yandangensis*, *Colacogloea woodwardiae*, *Dexomyces anmaltophilus*, *Dexomyces rhamni*, *Dexomyces spathulatus*, *Dexomyces turchettianus*, *Dioszegia maricola*, *Exobasidium cylindricum*, *Gracilitas littoralis*, *Kockovaella camelliae*, *Kockovaella malloti*, *Kockovaella rosae*, *Kondoa zhenganensis*, *Nakasea foliicola*, *Cystastrum sedimentus*, *Papiliotrema chongmingensis*, *Phyllozyma foliicola*, *Phyllozyma lyoniae*, *Rosettozyma turpiniae*, *Ruinenia pseudopyrrosiae*, *Sterigmoblongus ilicis*, *Teunia littoralis*, *Turchettia toddalia*, and *Yunzhangomyces nandinae*. Of particular note, the newly proposed order

**Submitted:** 09 March 2025; **Accepted:** 16 December 2025; **Published:** 22 December 2025

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Accepted by: Samantha C. Karunaratna

*Sterigmoblongales* ord. nov. shows unstable phylogenetic placement within *Microbotryomycetes* based on multi-gene analyses, suggesting a deep and previously undiscovered evolutionary lineage. By uncovering cryptic diversity in overlooked habitats, this study greatly expands the phylogenetic breadth of basidiomycetous yeasts. These findings emphasize the need to continue exploring undersampled environments and highlight the value of integrating taxogenomics into future studies to resolve deep and basal evolutionary divergences.

**Keywords** – *Exobasidiomycetes*, novel taxa, phylogeny, *Pucciniomycotina*, *Tremellomycetes*, yeast taxonomy

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## INTRODUCTION

Yeasts are unicellular fungi that typically propagate through budding or fission during their vegetative phase and lack enclosed fruiting structures in their sexual cycle (Kurtzman et al. 2011a). The current count of formally recognized yeast species stands at more than 2,000 in the Yeasts Trust Database ‘theyeasts.org’ lists (<https://theyeasts.org>; Boekhout et al. 2022), a rapid increase from the 1,301 species documented in the fifth edition of ‘*The Yeasts, a Taxonomic Study*’ (Kurtzman et al. 2011a). This rapid growth, however, still represents only a fraction of the estimated total yeast diversity, which is predicted to include at least 12,000 species on Earth (Boekhout et al. 2022). Using rDNA-metabarcoding or metagenomic methods has accelerated the discovery of new yeast taxa. Many studies have uncovered an underestimated biodiversity of yeast communities in both natural and human-related environments, such as soil, marine, and fermented products (Edgcomb et al. 2011, Tedersoo et al. 2014, Hao et al. 2019). Critically, culture-independent methods consistently show that, on average, over 50% of the identified yeast sequences belong to undescribed taxa across different biotopes, from boreal and tropical forests to arctic tundra (Boekhout et al. 2022). The lack of corresponding live cultures of these unidentified taxa hinders their comprehensive studies. Obtaining and preserving live cultures are necessary for performing detailed phenotypic, physiological, or metabolic characterizations, which are required to build a robust knowledge of their ecological functions and to unlock their potential for biotechnological applications. Consequently, the systematic isolation and formal description of new yeast species remain the vital foundation of contemporary ecological and metabolic research.

Yeasts are ubiquitous organisms, colonizing nearly every known ecological habitat, from natural environments to human-built structures and even the International Space Station (Péter et al. 2017, Yurkov 2017, Bijlani et al. 2020). Among these niches, plants serve as a critical reservoir of yeast diversity. Approximately one-third of the yeast strains in major culture collections worldwide and over 40% of newly described yeast species originate from plant-related materials (Groenewald et al. 2017, Boekhout et al. 2022). With its vast ecological diversity and active research community, China stands out as one of the hotspots for yeast diversity and taxonomic studies. The description of nearly 400 new yeast species from China in recent years (Boekhout et al. 2022, Li et al. 2022, Jiang et al. 2024, Chai et al. 2025, Gao et al. 2025, Liu et al. 2025, Wang et al. 2025) underscores the massive scale of undiscovered yeast resources and mandates a continued, systematic exploration. Compared with the extensive research on yeasts in plant substrates, yeast diversity in tidal zones is poorly documented, despite China having the second-largest extent of tidal flats worldwide. This lack



of knowledge is made critically urgent by two major threats: the climate crisis is driving the loss of plant diversity that will impact the biodiversity of macroscale ecosystems and the diversity of plant-related micro-diversity, including yeasts, and the massive losses of coastal ecosystems have happened in this region during the last decades (Murray et al. 2019). Therefore, the endeavor to explore and preserve the yeast diversity within these endangered and underexplored environments is highly impactful for documenting the full taxonomic wealth of yeasts.

Yeast growth forms occur in both *Ascomycota* and *Basidiomycota*. Within the latter, the basidiomycetous yeasts are distributed across three subphyla: *Agaricomycotina*, *Pucciniomycotina*, and *Ustilaginomycotina* (Hibbett et al. 2007, Boekhout et al. 2011, Liu et al. 2015a, b, Wang et al. 2015a, b, Li et al. 2021). The recognized diversity of yeast has grown significantly, increasing from 463 species in the fifth edition of ‘*The Yeasts, a Taxonomic Study*’ (Kurtzman et al. 2011a) to nearly 900 currently accepted species (<https://theyeasts.org>; Boekhout et al. 2022, Li et al. 2022, Jiang et al. 2024, Chai et al. 2025, Gao et al. 2025, Liu et al. 2025, Wang et al. 2025). Over the past ten years, China has become a dominant force in discovering this hidden diversity, accounting for over 30% of all newly documented basidiomycetous yeast species globally (Liu et al. 2015a, b, Wang et al. 2015a, b, Li et al. 2020, Li et al. 2022, Wei et al. 2022, Zhu et al. 2023), suggesting that a vast, undiscovered taxonomic reservoir remains within the country.

To systematically uncover this remaining diversity, our study conducted extensive sampling across two distinct, underexplored niches: plant substrates in subtropical forests and soil sediments and water from coastal tidal zones (Zhu et al. 2023). This work recovered a total of 5,704 strains, of which 164, representing new basidiomycetous yeast species, were isolated and identified (Zang et al. 2018, Zhu et al. 2023). In this study, we describe 38 new basidiomycetous yeast species based on multi-gene phylogenetic analyses, incorporating internal transcribed spacer (ITS), the D1/D2 domains of the large subunit rDNA (LSU), the largest subunit of RNA polymerase II (*RPB1*), the second largest subunit of RNA polymerase II (*RPB2*), translation elongation factor 1- $\alpha$  (*TEF1*), and the mitochondrial gene cytochrome b (*CYTB*), integrated with phenotypic and physiochemical characterizations. In summary, one new order, two new families, six new genera, and thirty-eight new species are proposed.

## MATERIALS AND METHODS

### Yeast strains

The yeast strains analyzed in this study were primarily isolated from plant leaves in two subtropical forests in Guizhou and Zhejiang provinces, as well as from soil sediments and marine water collected from tidal flats in 11 coastal provinces of China. All studied strains and their corresponding sampling sites are listed in Table 1 and Fig. S1. Isolates from plant leaves were obtained using the ballistoconidia-fall technique (Nakase & Takashima, 1993), while those from marine sediments and water were recovered following the protocols previously described (Zhu et al. 2023). All isolates were purified and preserved in 20% glycerol at  $-80^{\circ}\text{C}$  for further study. All yeast isolates from this study were accessioned in the Institute of Microbiology, Chinese Academy of Sciences. The holotypes of the newly described species were deposited in the China General Microbiological Culture Collection Centre (CGMCC), Beijing, China, and ex-type cultures were deposited in the Japan Collection of Microorganisms (JCM).

### DNA extraction, PCR amplification, and molecular phylogenetic analysis

Genomic DNA was extracted from actively growing yeast cultures on yeast extract peptone dextrose (YPD, 2% glucose, 1% yeast extract, 2% peptone, 2% agar) plates after approximately three days of incubation, following the protocol of Makimura et al. (1994). The sequences of two rDNA loci including the ITS region and the D1/D2 domain of the LSU rRNA gene, and partial sequences of the three nuclear protein-coding genes, *RPB1*, *RPB2*, *TEF1*, and the mitochondrial gene *CYTB* were amplified and sequenced as described by Liu et al. (2015a). We analyzed and assembled sequences using SeqMan (Lasergene 7) (DNASTAR Inc., Madison, Wisconsin, USA). Spliceosomal

intron regions were inferred from canonical splice sites (GT-AG, GC-AG, AT-AT) (Babenko et al. 2004) using sequence alignments between our data and reference cDNA sequences in GenBank. The sequences of the ITS regions and D1/D2 domains and exon sequences of the protein-encoding genes *RPB1*, *RPB2*, *TEF1*, and *CYT8* were aligned with MAFFT v. 7 using the L-INS-I algorithm (Katoh & Standley 2013). Alignments were manually edited, trimmed, and minor gaps were removed. Multiple sequence alignments of these six genes were concatenated as a combined dataset. Phylogenetic analyses were conducted using both individual and concatenated gene sequences via maximum likelihood (ML) and Bayesian analyses. The ML tree was inferred using RAxML-NG v. 1.1.0 (Kozlov et al. 2019) under the GTR model with gamma-distributed rate heterogeneity, with up to 1,000 replicates based on the autoMRE bootstrap convergence criterion. Bayesian analyses were performed using MrBayes 3.2.7 (Ronquist et al. 2012) for 5 million generations, with 4 Markov chains and sampling every 5,000 generations. The best-fit evolutionary model for individual and concatenated nucleotide datasets was assessed by the Bayesian Information Criterion (BIC) using jModeltest (Posada 2008). Furthermore, constrained ML trees were constructed using the expanded LSU rRNA (D1/D2 domains) sequence dataset, which included new species in our study and sequences of potential novel yeast species in the GenBank database, with the six-gene tree topology serving as the phylogenetic backbone.

Branches with significant support were defined as those with ML bootstrap support (BP)  $\geq$  70% and Bayesian posterior probability (PP)  $\geq$  0.95. GenBank accession numbers for all ITS regions, LSU rRNA gene D1/D2 domains, *RPB1*, *RPB2*, *TEF1*, and *CYT8* sequences analyzed in this study are listed in Table S1. Sequence alignments and phylogenetic trees were deposited in TreeBase (www.treebase.org, No. 29479).

### Phenotypical characterization

Morphological, physiological, and biochemical characteristics were determined following standard methods in yeast taxonomy (Kurtzman et al. 2011b). Assimilation of carbon compounds was assessed in liquid medium, while nitrogen compound utilization was tested on solid medium. The potential sexual cycles of all new species were investigated by culturing strains (individually and in combination) on various media, including corn meal agar (CMA, 2.5% corn starch, 2% agar), yeast malt medium (YM, 1% glucose, 0.3% yeast extract, 0.3% malt extract, 0.5% peptone, 2% agar), potato dextrose agar (PDA, 20% potato infusion, 2% glucose, 2% agar), V8 agar (10% V8 juice, 2% agar), and yeast carbon base medium (YCB, 1.17% yeast carbon base, 2% agar). Plates were incubated at 25 °C for up to two months. The ability of the newly identified species to form ballistoconidia was assessed using the inverted-plate technique (Do Carmo-Sousa & Phaff, 1962) on CMA medium incubated at 17 °C. After 3–12 days, the discharged spores were collected on a glass slide and examined under a microscope.

## RESULTS

### Yeast diversity

A total of 1,268 basidiomycetous yeast isolates were obtained from 199 plant leaves representing 108 species from tropical and subtropical forests in Zhejiang and Guizhou provinces in China. Phylogenetic screening revealed 164 strains with high sequence divergence from known taxa, which were selected for detailed taxonomic investigation. In the Yandang Mountain survey, extensive exploration of phylloplane yeast diversity covering its five areas (East, South, West, North, and Middle) yielded 1,118 isolates. Among these, 1,072 isolates were identified as known species belonging to 37 genera and 56 species based on D1/D2 sequence similarity comparisons using BLAST searches and phylogenetic analysis. The most frequently isolated genus was *Derxomyces*, accounting for 54.6% of the total isolates, followed by *Udeniomyces* at 20.0%. The other frequently isolated genera were *Sporobolomyces* (5.7%) and *Bannoa* (5.1%). Six genera, namely *Sporidiobolus*, *Symmetrospora*, *Tilletiopsis*, *Pseudozyma*, *Fellozyma*, and *Bulleribasidium*, covered 1~2% of the total isolated strains. A small subset of 46 isolates was identified as 19 putative novel species. Six

new species with clear taxonomic positions were described in this study; the others require further characterization. Compared to the wide range of exploration in Yandang Mountain, a more limited sampling effort in the Shisun peak area of Guizhou province yielded a surprisingly high novelty rate, with 142 isolates representing 26 novel species, highlighting the region's exceptional and underexplored biodiversity.

Our investigation of yeast diversity in tidal flat zones along the Chinese coastline yielded 4,436 isolates from 1,241 samples, including soil sediments in tidal flats, marine water, plants, and benthos. A total of 288 species were identified, including 39 potential novel species. The ascomycetous yeast species *Candida parapsilosis*, *Candida pseudolambica*, and *Candida tropicalis*, and the basidiomycetous yeast species *Cystobasidium minutum*, *Cystobasidium slooffiae*, and *Moesziomyces aphidis* were found to be the most frequently isolated species.

### Phylogenetic analyses

Sequences of six genes (ITS, D1/D2, *RPB1*, *RPB2*, *TEF1*, and *CYTB*) were amplified for 164 isolates representing new species in our study (Table 1). The phylogenetic positions and taxonomic affiliations of these isolates were resolved using two datasets: six-gene and concatenated rDNA sequences. To facilitate comprehensive comparisons, a constraint tree was generated from the expanded D1/D2 dataset using the six-gene tree as a phylogenetic backbone. This strategy enabled evaluation of the newly identified taxa against both their closest known counterparts and potentially uncharacterized lineages available in the GenBank database.

Phylogenetic reconstruction of *Pucciniomycotina* yeasts was performed using six molecular markers across 301 taxa (sequence per locus: ITS = 391, D1/D2 = 395, *RPB1* = 339, *RPB2* = 341, *TEF1* = 366, and *CYTB* = 297) and 5,681 characters including gaps (ITS = 1,533, D1/D2 = 651, *RPB1* = 866, *RPB2* = 1398, *TEF1* = 915, and *CYTB* = 318). The concatenated rDNA loci dataset contained 344 taxa (sequence per locus: ITS = 439, D1/D2 = 446) and 1,827 characters including gaps (ITS = 1,198, D1/D2 = 629). Both six-gene (Fig. 1) and concatenated rDNA (Fig. S2) trees generated from the ML and Bayesian methods were congruent. The expanded D1/D2 loci dataset contained 894 sequences, including 347 described taxa and 547 sequences of undescribed potential new species in the NCBI GenBank database (Fig. 2). Two species, *Ustilago maydis* and *Pseudomicrostroma phylloplanum*, were used as outgroups.

Phylogenetic reconstruction of *Tremellomycetous* yeasts was performed using six molecular markers across 344 taxa (sequence per locus: ITS = 371, D1/D2 = 371, *RPB1* = 347, *RPB2* = 346, *TEF1* = 320, and *CYTB* = 312) and 5,124 characters including gaps (ITS = 1292, D1/D2 = 635, *RPB1* = 789, *RPB2* = 1131, *TEF1* = 912, and *CYTB* = 365). The concatenated rDNA loci dataset contained 403 taxa (sequence per locus: ITS = 445, D1/D2 = 449) and 1,889 characters including gaps (ITS = 1213, D1/D2 = 676). Both six-gene (Fig. 3) and concatenated rDNA (Fig. S3) trees generated from the ML and Bayesian methods were congruent. The expanded D1/D2 loci dataset contained 754 sequences, including 457 taxa and 188 sequences of undescribed potential new species in the NCBI GenBank database (Fig. 4). Two species, *Ustilago maydis* and *Sterigmatomyces halophilus*, were used as outgroups.

Phylogenetic reconstruction of *Ustilaginomycotina* yeasts was performed using six molecular markers across 72 taxa (sequence per locus: ITS = 77, D1/D2 = 78, *RPB1* = 47, *RPB2* = 67, *TEF1* = 74, and *CYTB* = 32) and 5,203 characters including gaps (ITS = 1,096, D1/D2 = 615, *RPB1* = 818, *RPB2* = 1,204, *TEF1* = 1,041, and *CYTB* = 429). The concatenated rDNA loci dataset contained 164 taxa and 52 sequences of undescribed potential new species in the NCBI GenBank database (sequence per locus: ITS = 142, D1/D2 = 217) and 1,999 characters including gaps (ITS = 1,363, D1/D2 = 636). Both six-gene (Fig. S4) and concatenated rDNA (Fig. 5) trees generated from the ML and Bayesian methods were congruent. The expanded D1/D2 loci dataset contained 217 sequences, including 159 taxa and 52 sequences of undescribed potential new species in the GenBank database (Fig. 6). Two species, *Malassezia globosa* and *Malassezia furfur*, were used as outgroups.

**Table 1** Strain information, isolation sources, collection location, and GenBank accession numbers of the yeast strains studied.

| Species                                      | Strain numbers              | Source                              | Location                                    | GenBank accessions number |             |             |             |             |
|----------------------------------------------|-----------------------------|-------------------------------------|---------------------------------------------|---------------------------|-------------|-------------|-------------|-------------|
|                                              |                             |                                     |                                             | ITS/D1D2                  | <i>RPB1</i> | <i>RPB2</i> | <i>TEF1</i> | <i>CYT6</i> |
| <i>Pucciniomycotina</i>                      |                             |                                     |                                             |                           |             |             |             |             |
| <i>Ballistosporomyces berchemiae</i> sp. nov | CGMCC 2.6700 <sup>T</sup> = | leaf of <i>Berchemia flavescens</i> | Hexi town, Zhengan county, Zunyi            | OL853684                  | OZ363848    | OL952708    | OL952739    | OL952749    |
|                                              | JCM 35446 =                 |                                     | city, Guizhou province, China, May          |                           |             |             |             |             |
|                                              | GZ1923                      |                                     | 2020                                        |                           |             |             |             |             |
|                                              | GZ1564                      | leaf of <i>Castanea henryi</i>      | Shisun peak, Zhengan county, Zunyi          | OL853685                  | /           | PP966988    | PP862347    | PP974280    |
|                                              |                             |                                     | city, Guizhou province, China, October 2020 |                           |             |             |             |             |
| <i>Bannoa hyperici</i> sp. nov               | CGMCC 2.6710 <sup>T</sup> = | leaf of <i>Hypericum monogynum</i>  | Hexi town, Zhengan county, Zunyi            | OL853642                  | OL952688    | OL952709    | OL952729    | OL952751    |
|                                              | JCM 35449 =                 |                                     | city, Guizhou province, China, May          |                           |             |             |             |             |
|                                              | GZ2534                      |                                     | 2020                                        |                           |             |             |             |             |
|                                              | GZ1531                      | leaf of <i>Picrasma quassioides</i> |                                             | OL853643                  | PP856545    | /           | PP862346    | /           |
|                                              | GZ2924                      | leaf of <i>Lonicera japonica</i>    |                                             | OL853641                  | PP856546    | /           | PP862363    | /           |
| <i>Bannoa lonicerae</i> sp. nov              | CGMCC 2.6600 <sup>T</sup> = | leaf of <i>Lonicera japonica</i>    | Hexi town, Zhengan county, Zunyi            | OL853650                  | OZ364118    | OZ364092    | OL952728    | OL952750    |
|                                              | JCM 35425 =                 |                                     | city, Guizhou province, China, May          |                           |             |             |             |             |
|                                              | GZ2133                      |                                     | 2020                                        |                           |             |             |             |             |
|                                              | GZ0263                      | leaf of <i>Elaeagnus glabra</i>     |                                             | OL853673                  | PP856547    | PP967018    | PP862309    | PP974244    |
|                                              | GZ2943                      | leaf of <i>Lonicera japonica</i>    |                                             | OL853647                  | PP856548    | /           | PP862364    | PP974245    |
| <i>Bannoa pseudoscolopiae</i> sp. nov        | CGMCC 2.6716 <sup>T</sup> = | leaf of <i>Viburnum dilatatum</i>   | Shisun peak, Zhengan county, Zunyi          | OL853662                  | OL952684    | /           | OL952724    | OL952744    |
|                                              | JCM 36234 =                 |                                     | city, Guizhou province, China, October 2020 |                           |             |             |             |             |
|                                              | GZ0842                      |                                     |                                             |                           |             |             |             |             |
|                                              | GZ0743                      | leaf of <i>Sageretia thea</i>       |                                             | OL853671                  | PP856549    | /           | PP862323    | /           |
|                                              | GZ0745                      | leaf of <i>Sageretia thea</i>       |                                             | OL853670                  | PP856550    | PP966989    | PP862324    | /           |
|                                              | GZ0822                      | leaf of <i>Viburnum dilatatum</i>   |                                             | OL853669                  | PP856551    | /           | PP862325    | PP974252    |
|                                              | GZ0823                      | leaf of <i>Viburnum dilatatum</i>   |                                             | OL853668                  | /           | /           | /           | /           |
|                                              | GZ0825                      | leaf of <i>Viburnum dilatatum</i>   |                                             | OL853667                  | PP856552    | /           | PP862326    | PP974253    |
|                                              | GZ0827                      | leaf of <i>Viburnum dilatatum</i>   |                                             | OL853666                  | PP856553    | /           | PP862327    | PP974254    |
|                                              | GZ0833                      | leaf of <i>Viburnum dilatatum</i>   |                                             | OL853665                  | PP856554    | /           | PP862328    | /           |
|                                              | GZ0834                      | leaf of <i>Viburnum dilatatum</i>   |                                             | OL853664                  | OL952683    | OL952705    | OL952723    | OL952743    |
|                                              | GZ0835                      | leaf of <i>Viburnum dilatatum</i>   |                                             | OL853663                  | /           | /           | /           | /           |
|                                              | GZ0843                      | leaf of <i>Viburnum dilatatum</i>   |                                             | OL853661                  | PP856555    | /           | PP862330    | /           |

| Species                         | Strain numbers                                       | Source                                  | Location                                                                       | GenBank accessions number |          |          |          |          |
|---------------------------------|------------------------------------------------------|-----------------------------------------|--------------------------------------------------------------------------------|---------------------------|----------|----------|----------|----------|
|                                 |                                                      |                                         |                                                                                | ITS/D1D2                  | RPB1     | RPB2     | TEF1     | CYTB     |
| <i>Bannoa quercus</i> sp. nov   | GZ0844                                               | leaf of <i>Viburnum dilatatum</i>       | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL853660                  | PP856572 | /        | PP862331 | /        |
|                                 | GZ0847                                               | leaf of <i>Viburnum dilatatum</i>       |                                                                                | OL853659                  | PP856556 | /        | PP862332 | /        |
|                                 | GZ0853                                               | leaf of <i>Viburnum dilatatum</i>       |                                                                                | OL853657                  | PP856557 | PP967025 | PP862334 | /        |
|                                 | GZ08412                                              | leaf of <i>Viburnum dilatatum</i>       |                                                                                | OL853644                  | /        | /        | /        | /        |
|                                 | GZ0949                                               | leaf of <i>Quercus baronii</i>          |                                                                                | OL853656                  | /        | /        | /        | PP974256 |
|                                 | GZ2346                                               | leaf of <i>Ostercicum citriodorum</i>   |                                                                                | OL853648                  | PP856558 | /        | PP862360 | PP974259 |
|                                 | <b>CGMCC 2.6722<sup>T</sup> = JCM 35452 = GZ0941</b> | leaf of <i>Quercus baronii</i>          |                                                                                | OL853682                  | OL952699 | OL952706 | OL952725 | OL952745 |
|                                 | GZ0856                                               | leaf of <i>Viburnum dilatatum</i>       |                                                                                | OL853683                  | PP856559 | PP967019 | PP862335 | /        |
|                                 | GZ0942                                               | leaf of <i>Quercus baronii</i>          |                                                                                | OL853681                  | PP856560 | PP967024 | PP862336 | PP974246 |
|                                 | GZ0944                                               | leaf of <i>Quercus baronii</i>          |                                                                                | OL853680                  | /        | /        | /        | /        |
|                                 | GZ0945                                               | leaf of <i>Quercus baronii</i>          |                                                                                | OL853679                  | PP856561 | PP967023 | /        | /        |
|                                 | GZ0947                                               | leaf of <i>Quercus baronii</i>          |                                                                                | OL853678                  | PP856562 | PP967020 | PP862338 | /        |
|                                 | GZ0948                                               | leaf of <i>Quercus baronii</i>          |                                                                                | OL853677                  | /        | PP967021 | PP862339 | PP974255 |
|                                 | GZ2731                                               | leaf of <i>Pittosporum illicioides</i>  |                                                                                | OL853676                  | PP856563 | /        | PP862361 | /        |
|                                 | GZ2732                                               | leaf of <i>Pittosporum illicioides</i>  |                                                                                | OL853675                  | PP856564 | PP967022 | PP862362 | PP974257 |
| <i>Bannoa scolopiae</i> sp. nov | GZ2741                                               | leaf of <i>Pittosporum illicioides</i>  | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL853674                  | /        | /        | /        | /        |
|                                 | <b>CGMCC 2.6717<sup>T</sup> = JCM 35450 = GZ3263</b> | leaf of <i>Scolopia chinensis</i>       |                                                                                | OL853646                  | OL952689 | OL952711 | OL952732 | OL952754 |
|                                 | GZ0421                                               | leaf of <i>Kadsura longipedunculata</i> |                                                                                | OL853672                  | PP856565 | /        | PP862311 | /        |
|                                 | GZ0849                                               | leaf of <i>iburnum dilatatum</i>        |                                                                                | OL853658                  | PP856566 | PP967026 | PP862333 | /        |
|                                 | GZ2341                                               | leaf of <i>Ostercicum citriodorum</i>   |                                                                                | OL853649                  | PP856570 | /        | PP862359 | PP974284 |
|                                 | GZ3741                                               | leaf of <i>Smilax china</i>             |                                                                                | OL853645                  | PP856571 | PP967030 | PP862369 | PP974248 |
|                                 | GZ1044                                               | leaf of <i>Disporum cantoniense</i>     |                                                                                | OL853655                  | PP856567 | PP967027 | PP862340 | PP974270 |
|                                 | GZ1224                                               | leaf of <i>Millettia pachycarpa</i>     |                                                                                | OL853654                  | OL952686 | OL952707 | OL952726 | OL952747 |
|                                 | GZ1324                                               | leaf of <i>Ilex asprella</i>            |                                                                                | OL853653                  | PP856568 | PP967028 | PP862343 | PP974247 |
|                                 | GZ1425                                               | leaf of <i>Viburnum utile</i>           |                                                                                | OL853652                  | /        | /        | /        | /        |
|                                 | GZ1627                                               | leaf of <i>Pittosporum illicioides</i>  |                                                                                | OL853651                  | PP856569 | PP967029 | PP862350 | /        |

| Species                                | Strain numbers                                        | Source                                  | Location                                                                        | GenBank accessions number |          |          |          |          |
|----------------------------------------|-------------------------------------------------------|-----------------------------------------|---------------------------------------------------------------------------------|---------------------------|----------|----------|----------|----------|
|                                        |                                                       |                                         |                                                                                 | ITS/D1D2                  | RPB1     | RPB2     | TEF1     | CYTB     |
| <i>Chrysozyma lonicerae</i> sp. nov    | CGMCC 2.6709 <sup>T</sup> =<br>JCM 35448 =<br>GZ3362  | leaf of <i>Lonicera tragophylla</i>     | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020  | OL853638                  | OL952690 | OL952712 | OL952740 | OL952755 |
|                                        | GZ4032                                                | leaf of <i>Myrsine africana</i>         |                                                                                 | OL853637                  | PP862402 | PP967006 | PP862371 | PP974266 |
| <i>Chrysozyma</i> sp.                  | CGMCC 2.6804 =<br>ZJ0712                              | leaf of <i>Loropetalum chinense</i>     | Southern Yandang mountain, Wenzhou city, Zhejiang province, China, October 2016 | OL853639                  | /        | /        | /        | /        |
| <i>Chrysozyma rubi</i> sp. nov         | CGMCC 2.6608 <sup>T</sup> =<br>JCM 39290 =<br>GZ43510 | leaf of <i>Rubus innominatus</i>        | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020  | OL853640                  | OL952694 | OL952716 | OL952736 | OL952758 |
| <i>Chrysozyma viburni</i> sp. nov      | CGMCC 2.6751 <sup>T</sup> =<br>JCM 39297 =<br>GZ3831  | leaf of <i>Viburnum utile</i>           | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020  | OL853636                  | OL952692 | OL952714 | OL952734 | OL952757 |
|                                        | GZ3836                                                | leaf of <i>Viburnum utile</i>           |                                                                                 | OL853635                  | PP862400 | PP967007 | /        | PP974260 |
|                                        | GZ3838                                                | leaf of <i>Viburnum utile</i>           |                                                                                 | OL853634                  | PP862401 | /        | /        | PP974261 |
| <i>Chrysozyma yandangensis</i> sp. nov | CGMCC 2.6602 <sup>T</sup> =<br>JCM 35427 =<br>ZJ0731  | leaf of <i>Loropetalum chinense</i>     | Southern Yandang mountain, Wenzhou city, Zhejiang province, China, October 2016 | OL853632                  | OL952682 | OL952704 | OL952722 | OL952742 |
|                                        | ZJ0711                                                | leaf of <i>Loropetalum chinense</i>     |                                                                                 | OL853633                  | PP862398 | /        | /        | PP974267 |
| <i>Colacogloea woodwardiae</i> sp. nov | CGMCC 2.6601 <sup>T</sup> =<br>JCM 35426 =<br>ZJ1011  | leaf of <i>Woodwardia japonica</i>      | Southern Yandang mountain, Wenzhou city, Zhejiang province, China, October 2016 | OL853629                  | OL952685 | /        | OL952738 | OL952746 |
|                                        | FJ1442                                                | leaf of <i>Pavetta hongkongensis</i>    | Wild valley, Xiamen city, Fujian province, China, December 2019                 | OL853630                  | PP862399 | PP967008 | PP862345 | PP974268 |
| <i>Colacogloea</i> sp.                 | CGMCC 2.6705 =<br>ZJ0921                              | leaf of <i>Cryptomeria fortunei</i>     | Northern Yandang mountain, Wenzhou city, Zhejiang province, China, October 2016 | OL853631                  | /        | /        | /        | /        |
| <i>Kondoa zhenganensis</i> sp. nov     | CGMCC 2.6730 <sup>T</sup> =<br>JCM 39295 =<br>GZ04720 | leaf of <i>Kadsura longipedunculata</i> | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020  | OL853627                  | OL952681 | OL952702 | OL952720 | OL952741 |
|                                        | GZ04621                                               | leaf of <i>Kadsura longipedunculata</i> |                                                                                 | OL853628                  | /        | PP967017 | PP862312 | PP974272 |

| Species                              | Strain numbers                                  | Source                                     | Location                                                                       | GenBank accessions number |          |          |          |          |
|--------------------------------------|-------------------------------------------------|--------------------------------------------|--------------------------------------------------------------------------------|---------------------------|----------|----------|----------|----------|
|                                      |                                                 |                                            |                                                                                | ITS/D1D2                  | RPB1     | RPB2     | TEF1     | CYTB     |
| <i>Nakasea foliicola</i> sp. nov     | GZ04721                                         | leaf of <i>Kadsura longipedunculata</i>    | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL853626                  | /        | /        | /        | /        |
|                                      | GZ04730                                         | leaf of <i>Kadsura longipedunculata</i>    |                                                                                | OL853625                  | /        | /        | /        | /        |
|                                      | CGMCC 2.6737 <sup>T</sup> = JCM 35454 = GZ04620 | leaf of <i>Kadsura longipedunculata</i>    |                                                                                | OL853600                  | OZ363849 | OL952701 | OL952718 | OZ364096 |
|                                      | GZ0467                                          | leaf of <i>Kadsura longipedunculata</i>    |                                                                                | OL853603                  | PP862396 | /        | PP862314 | PP974274 |
|                                      | GZ04622                                         | leaf of <i>Kadsura longipedunculata</i>    | Hexi town, Zhengan county, Zunyi city, Guizhou province, China, May 2020       | OL853599                  | PP862395 | PP967016 | PP862313 | PP974273 |
|                                      | GZ04725                                         | leaf of <i>Kadsura longipedunculata</i>    |                                                                                | OL853598                  | PP862397 | /        | /        | PP974275 |
|                                      | GZ0861                                          | leaf of <i>Viburnum dilatatum</i>          |                                                                                | OL853602                  | /        | PP967014 | /        | PP974278 |
|                                      | GZ3034                                          | Leaf of <i>Veronicastrum stenostachyum</i> |                                                                                | OL853601                  | /        | PP967015 | /        | PP974277 |
| <i>Cystastrum sedimentus</i> sp. nov | CGMCC 2.6649 <sup>T</sup> = JCM 35434 = 278C-4  | Soil sediment from tidal flat              | Chongning district, Shanghai City, China, July, 2020                           | OR588017                  | OL952696 | OL952710 | OL952730 | OL952752 |
|                                      | CGMCC 2.6650 = JCM 35435 = 278C-5               | Soil sediment from tidal flat              |                                                                                | OR588018                  | OL952697 | /        | OL952731 | OL952753 |
| <i>Phyllozoma foliicola</i> sp. nov  | CGMCC 2.6625 <sup>T</sup> = JCM35430 = GZ3822   | leaf of <i>Viburnum utile</i>              | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL853615                  | OL952691 | OL952713 | OL952733 | OL952756 |
|                                      | GZ1631                                          | leaf of <i>Elaeagnus glabra</i>            |                                                                                | OL853622                  | PP942245 | PP967031 | PP862351 | /        |
|                                      | GZ1634                                          | leaf of <i>Elaeagnus glabra</i>            |                                                                                | OL853619                  | PP942248 | PP967042 | PP862354 | /        |
|                                      | GZ1636                                          | leaf of <i>Elaeagnus glabra</i>            |                                                                                | OL853618                  | PP942249 | PP967044 | PP862355 | /        |
|                                      | GZ1637                                          | leaf of <i>Elaeagnus glabra</i>            |                                                                                | OL853617                  | PP942250 | PP967043 | PP862356 | /        |
|                                      | GZ1638                                          | leaf of <i>Elaeagnus glabra</i>            |                                                                                | OL853616                  | PP942251 | PP967038 | PP862357 | /        |
|                                      | GZ33610                                         | leaf of <i>Lonicera tragophylla</i>        |                                                                                | OL853604                  | PP942254 | /        | PP862366 | /        |
|                                      | GZ4233                                          | leaf of <i>Nandina domestica</i>           |                                                                                | OL853613                  | PP942260 | PP967039 | PP862374 | /        |

| Species                                 | Strain numbers                                       | Source                              | Location                                                                       | GenBank accessions number |          |          |          |          |
|-----------------------------------------|------------------------------------------------------|-------------------------------------|--------------------------------------------------------------------------------|---------------------------|----------|----------|----------|----------|
|                                         |                                                      |                                     |                                                                                | ITS/D1D2                  | RPB1     | RPB2     | TEF1     | CYTB     |
|                                         | GZ4237                                               | leaf of <i>Nandina domestica</i>    |                                                                                | OL853611                  | PP942261 | PP967037 | PP862375 | /        |
|                                         | GZ4241                                               | leaf of <i>Nandina domestica</i>    |                                                                                | OL853610                  | PP942262 | /        | /        | /        |
|                                         | GZ4247                                               | leaf of <i>Nandina domestica</i>    |                                                                                | OL853606                  | PP942266 | PP967032 | PP862379 | /        |
|                                         | GZ4253                                               | leaf of <i>Nandina domestica</i>    |                                                                                | OL853605                  | PP942267 | /        | PP86238  | /        |
|                                         | GZ1632                                               | leaf of <i>Elaeagnus glabra</i>     |                                                                                | OL853621                  | PP942246 | PP967033 | PP862352 | /        |
|                                         | GZ1633                                               | leaf of <i>Elaeagnus glabra</i>     |                                                                                | OL853620                  | PP942247 | PP967034 | PP862353 | /        |
|                                         | GZ4212                                               | leaf of <i>Nandina domestica</i>    |                                                                                | OL853614                  | PP942259 | PP967035 | PP862373 | /        |
|                                         | GZ4236                                               | leaf of <i>Nandina domestica</i>    |                                                                                | OL853612                  | OL952693 | OL952715 | OL952735 | /        |
|                                         | GZ4242                                               | leaf of <i>Nandina domestica</i>    |                                                                                | OL853609                  | PP942263 | PP967040 | PP862376 | /        |
|                                         | GZ4243                                               | leaf of <i>Nandina domestica</i>    |                                                                                | OL853608                  | PP942264 | PP967036 | PP862377 | /        |
|                                         | GZ4246                                               | leaf of <i>Nandina domestica</i>    |                                                                                | OL853607                  | PP942265 | PP967041 | PP862378 | /        |
| <i>Phyllozoma lyoniae</i> sp. nov       | CGMCC 2.6603 <sup>T</sup> =<br>JCM 39289 =<br>GZ1722 | leaf of <i>Lyonia ovalifolia</i>    | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL853623                  | OL952687 | OZ364093 | OL952727 | OL952748 |
|                                         | GZ1312                                               | leaf of <i>Viburnum utile</i>       |                                                                                | OL853624                  | PP942243 | PP967045 | PP862342 | /        |
| <i>Rosettozyma turpiniae</i> sp. nov    | CGMCC 2.6626 <sup>T</sup> =<br>JCM 39294 =<br>GZ4541 | leaf of <i>Turpinia arguta</i>      | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL853573                  | OL952695 | OL952717 | OL952737 | OL952759 |
|                                         | GZ4555                                               | leaf of <i>Turpinia arguta</i>      |                                                                                | OL853572                  | PP942269 | /        | PP862382 | /        |
|                                         | GZ4521                                               | leaf of <i>Turpinia arguta</i>      |                                                                                | OL853574                  | PP942268 | PP967012 | PP862381 | /        |
|                                         | GZ3722                                               | leaf of <i>Smilax china</i>         |                                                                                | OL853576                  | PP942255 | PP967010 | PP862367 | PP974285 |
|                                         | GZ3723                                               | leaf of <i>Smilax china</i>         |                                                                                | OL853575                  | PP942256 | PP967011 | PP862368 | /        |
|                                         | GZ1277                                               | leaf of <i>Millettia pachycarpa</i> |                                                                                | OL853578                  | PP942242 | PP967009 | PP862341 | /        |
|                                         | GZ15641                                              | leaf of <i>Picrasma quassioides</i> | Hexi town, Zhengan county, Zunyi city, Guizhou province, China, May 2020       | OL853571                  | PP942244 | PP967013 | PP862348 | PP974283 |
|                                         | GZ1566                                               | leaf of <i>Picrasma quassioides</i> |                                                                                | OL853577                  | /        | /        | PP862349 | /        |
| <i>Ruinenia pseudopyrrosiae</i> sp. nov | CGMCC 2.6699 <sup>T</sup> =<br>JCM 35445 =<br>GZ0142 | leaf of <i>Viburnum utile</i>       | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL853570                  | OL952680 | OL952700 | OL952718 | OZ364098 |
| <i>Sterigmoblongus ilicis</i> sp. nov   | CGMCC 2.6623 <sup>T</sup> =<br>JCM 39293 =<br>GZ0635 | Leaf of <i>Ilex aculeolata</i>      | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL853588                  | OL952698 | OL952703 | OL952721 | OZ364097 |



| Species                                              | Strain numbers                                       | Source                                     | Location                                                                       | GenBank accessions number |          |          |          |          |
|------------------------------------------------------|------------------------------------------------------|--------------------------------------------|--------------------------------------------------------------------------------|---------------------------|----------|----------|----------|----------|
|                                                      |                                                      |                                            |                                                                                | ITS/D1D2                  | RPB1     | RPB2     | TEF1     | CYTB     |
|                                                      | GZ0143                                               | Leaf of <i>Viburnum utile</i>              |                                                                                | OL853597                  | PP942232 | PP966997 | PP862307 | /        |
|                                                      | GZ0171                                               | Leaf of <i>Viburnum utile</i>              |                                                                                | OL853596                  | PP942233 | PP967000 | PP862308 | /        |
|                                                      | GZ0344                                               | Leaf of <i>Struthiopteris eburnea</i>      |                                                                                | OL853595                  | PP942234 | PP966990 | PP862310 | /        |
|                                                      | GZ0562                                               | Leaf of <i>Myrsine africana</i>            |                                                                                | OL853594                  | PP942235 | PP967001 | PP862315 | /        |
|                                                      | GZ0563                                               | Leaf of <i>Myrsine africana</i>            |                                                                                | OL853593                  | PP942236 | PP967005 | PP862316 | /        |
|                                                      | GZ0566                                               | Leaf of <i>Myrsine africana</i>            |                                                                                | OL853592                  | PP942237 | PP967002 | PP862317 | /        |
|                                                      | GZ0631                                               | Leaf of <i>Ilex aculeolata</i>             |                                                                                | OL853591                  | PP942238 | PP966991 | PP862318 | /        |
|                                                      | GZ06310                                              | Leaf of <i>Ilex aculeolata</i>             |                                                                                | OL853580                  | /        | PP966996 | PP862319 | /        |
|                                                      | GZ0632-1                                             | Leaf of <i>Ilex aculeolata</i>             |                                                                                | OL853590                  | PP942239 | PP966993 | PP862320 | PP974251 |
|                                                      | GZ0632-2                                             | Leaf of <i>Ilex aculeolata</i>             |                                                                                | OL853589                  | PP942240 | PP966994 | PP862321 | /        |
|                                                      | GZ0638                                               | Leaf of <i>Ilex aculeolata</i>             |                                                                                | OL853587                  | PP942241 | PP966992 | PP862322 | /        |
|                                                      | GZ1965                                               | Leaf of <i>Quercus baronii</i>             |                                                                                | OL853586                  | PP942252 | PP967003 | PP862358 | PP974281 |
|                                                      | GZ2141                                               | Leaf of <i>Viburnum dilatatum</i>          |                                                                                | OL853585                  | /        | /        | /        | /        |
|                                                      | GZ2733                                               | Leaf of <i>Pittosporum illicioides</i>     |                                                                                | OL853584                  | /        | /        | /        | /        |
|                                                      | GZ2951                                               | Leaf of <i>Myrsine africana</i>            |                                                                                | OL853583                  | PP942253 | PP966999 | PP862365 | /        |
|                                                      | GZ36514                                              | Leaf of <i>Mallotus repandus</i>           |                                                                                | OL853579                  | /        | /        | /        | PP974235 |
|                                                      | GZ4031                                               | Leaf of <i>Myrsine africana</i>            |                                                                                | OL853582                  | PP942257 | PP967004 | PP862370 | /        |
|                                                      | GZ4131                                               | Leaf of <i>Symplocos sumuntia</i>          |                                                                                | OL853581                  | PP942258 | PP966998 | PP862372 | /        |
| <b><i>Tremellomycetes</i></b>                        |                                                      |                                            |                                                                                |                           |          |          |          |          |
| <b><i>Bulleribasidium pseudosiamense</i> sp. nov</b> | <b>CGMCC 2.6786<sup>T</sup> = JCM 39305 = GZ3668</b> | Leaf of <i>Mallotus repandus</i>           | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL898896                  | OL952768 | OL952779 | OM103768 | OM103777 |
| <b><i>Bulleribasidium rhois</i> sp. nov</b>          | <b>CGMCC 2.6616<sup>T</sup> = JCM 35429 = ZJ1541</b> | Leaf of <i>Rhus chinensis</i>              | East Yandang mountain, Wenzhou city, Zhejiang province, China, October 2016    | OL898898                  | OL952764 | OL952775 | OM103764 | OM103774 |
|                                                      | CGMCC 2.6648 = 0520-5-3-2                            | Unknown plant leaves in tidal flat         | Xiangshan County, Ningbo City, Zhejiang Province, May 2021                     | OR577139/ OR577143        | OR808050 | /        | OR808030 | OR808023 |
| <b><i>Bulleribasidium veronicastrum</i> sp. nov</b>  | <b>CGMCC 2.6680<sup>T</sup> = JCM 35443 = GZ4443</b> | Leaf of <i>Veronicastrum stenostachyum</i> | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL898897                  | OL952770 | OL952781 | OM103769 | OM103779 |

| Species                                 | Strain numbers                                       | Source                                     | Location                                                                       | GenBank accessions number |          |          |          |          |
|-----------------------------------------|------------------------------------------------------|--------------------------------------------|--------------------------------------------------------------------------------|---------------------------|----------|----------|----------|----------|
|                                         |                                                      |                                            |                                                                                | ITS/D1D2                  | RPB1     | RPB2     | TEF1     | CYTB     |
| <i>Buzzinia foliicola</i> sp. nov       | CGMCC 2.6779 <sup>T</sup> =<br>JCM 39302 =<br>ZJ0961 | Leaf of <i>Cryptomeria japonica</i>        | North Yandang mountain, Wenzhou city, Zhejiang province, China, October 2016   | OL898895                  | OL952763 | OL952774 | OM103763 | OM103773 |
| <i>Derxomyces anmaltophilus</i> sp. nov | CGMCC 2.6768 <sup>T</sup> =<br>JCM 39300 =<br>ZJ0372 | Leaf of <i>Sloanea sinensis</i>            | South Yandang mountain, Wenzhou city, Zhejiang province, China, October 2016   | OL898901                  | OL952760 | OL952771 | OM103761 | OM103770 |
| <i>Derxomyces rhamni</i> sp. nov        | ZJ1412                                               | Leaf of <i>Elaeocarpus decipiens</i>       |                                                                                | OL898902                  | PP942270 | PP965381 | PP862383 | /        |
|                                         | CGMCC 2.6694 <sup>T</sup> =<br>JCM 35444 =<br>GZ2213 | Leaf of <i>Rhamnus davurica</i>            | Hexi town, Zhengan county, Zunyi city, Guizhou province, China, May 2020       | OL898918                  | OL952766 | OL952777 | OM103766 | OM103775 |
|                                         | GZ1612                                               | Leaf of <i>Pittosporum illicioides</i>     |                                                                                | OL898919                  | PP942278 | PP965389 | PP862386 | /        |
|                                         | GZ2357                                               | Leaf of <i>Viburnum dilatatum</i>          |                                                                                | OL898917                  | PP942279 | PP965390 | PP862387 | PP974233 |
|                                         | GZ2533                                               | Leaf of <i>Hypericum monogynum</i>         |                                                                                | OL898915                  | PP942280 | PP965392 | PP862388 | /        |
|                                         | GZ3032                                               | Leaf of <i>Veronicastrum stenostachyum</i> |                                                                                | OL898916                  | PP942281 | PP965391 | PP862384 | PP974234 |
|                                         | GZ2851                                               | Leaf of <i>Indocalamus tessellatus</i>     | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL898920                  | /        | /        | /        | /        |
| <i>Derxomyces spathulatus</i> sp. nov   | CGMCC 2.6788 <sup>T</sup> =<br>JCM 39306 =<br>GZ0871 | Leaf of <i>Viburnum dilatatum</i>          | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL898899                  | OL952762 | OL952773 | OM103762 | OM103771 |
| <i>Derxomyces turchettianus</i> sp. nov | GZ0872                                               | Leaf of <i>Viburnum dilatatum</i>          |                                                                                | OL898900                  | /        | /        | /        | OM103772 |
|                                         | CGMCC 2.6622 <sup>T</sup> =<br>JCM 39292 =<br>GZ4354 | Leaf of <i>Rubus innominatus</i>           | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020 | OL898908                  | OL952769 | OL952780 | /        | OM103778 |
|                                         | GZ43611                                              | Leaf of <i>Rubus innominatus</i>           |                                                                                | OL898910                  | PP942272 | PP965386 | /        | PP974236 |
|                                         | GZ43613                                              | Leaf of <i>Rubus innominatus</i>           |                                                                                | OL898905                  | PP942274 | PP965387 | /        | PP974242 |
|                                         | GZ43615                                              | Leaf of <i>Rubus innominatus</i>           |                                                                                | OL898903                  | PP942275 | PP965388 | PP862391 | PP974243 |
|                                         | GZ4368                                               | Leaf of <i>Rubus innominatus</i>           |                                                                                | OL898909                  | PP942271 | PP965382 | /        | PP974237 |
|                                         | GZ4373                                               | Leaf of <i>Rubus innominatus</i>           |                                                                                | OL898907                  | /        | /        | /        | /        |
|                                         | GZ4374                                               | Leaf of <i>Rubus innominatus</i>           |                                                                                | OL898906                  | /        | /        | /        | /        |

| Species                                           | Strain numbers                                               | Source                                     | Location                                                                        | GenBank accessions number |          |          |          |          |
|---------------------------------------------------|--------------------------------------------------------------|--------------------------------------------|---------------------------------------------------------------------------------|---------------------------|----------|----------|----------|----------|
|                                                   |                                                              |                                            |                                                                                 | ITS/D1D2                  | RPB1     | RPB2     | TEF1     | CYTB     |
|                                                   | GZ44412                                                      | Leaf of <i>Veronicastrum stenostachyum</i> |                                                                                 | OL898912                  | PP942273 | PP965385 | /        | PP974238 |
|                                                   | GZ4456                                                       | Leaf of <i>Veronicastrum stenostachyum</i> |                                                                                 | OL898911                  | /        | /        | /        | PP974239 |
|                                                   | GZ4461                                                       | Leaf of <i>Veronicastrum stenostachyum</i> |                                                                                 | OL898913                  | PP942276 | PP965383 | /        | PP974241 |
|                                                   | GZ4462                                                       | Leaf of <i>Veronicastrum stenostachyum</i> |                                                                                 | OL898904                  | /        | /        | /        | /        |
|                                                   | GZ4466                                                       | Leaf of <i>Veronicastrum stenostachyum</i> |                                                                                 | OL898914                  | PP942277 | PP965384 | PP862385 | PP974240 |
| <b><i>Dioszegia maricola</i> sp. nov</b>          | <b>CGMCC 2.10014<sup>T</sup> = JCM 36245 = 17-0-2E-327-2</b> | Marine water from tidal flat               | Pudong New District, Shanghai City                                              | OR588009                  | OR588009 | OR808044 | OR808037 | OR808031 |
| <b><i>Kockovaella camelliae</i> sp. nov</b>       | <b>CGMCC 2.6642<sup>T</sup> = JCM 35431 = ZJ0541</b>         | Leaf of <i>Camellia oleifera</i>           | Southern Yandang mountain, Wenzhou city, Zhejiang province, China, October 2016 | OL898892                  | OL952761 | OL952772 | /        | OZ364099 |
| <b><i>Kockovaella malloti</i> sp. nov</b>         | <b>CGMCC 2.6706<sup>T</sup> = JCM 35447 = GZ36220</b>        | Leaf of <i>Mallotus repandus</i>           | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020  | OL898893                  | OL952767 | OL952778 | OM103767 | OM103776 |
| <b><i>Kockovaella rosae</i> sp. nov</b>           | <b>CGMCC 2.6772<sup>T</sup> = JCM 39301 = GZ1821</b>         | Leaf of <i>Rosa banksiae</i>               | Hexi town, Zhengan county, Zunyi city, Guizhou province, China, May 2020        | OL898894                  | OL952765 | OL952776 | OM103765 | /        |
| <b><i>Papiliotrema chongmingensis</i> sp. nov</b> | <b>CGMCC 2.10012<sup>T</sup> = JCM 36244 = 30A-1</b>         | Soil sediment from tidal flat              | Chongming district, Shanghai City                                               | OR588010                  | OR808045 | /        | OR808032 | /        |
| <b><i>Sirobasidium</i> sp.</b>                    | <b>CGMCC 2.7216 = 25-PDA-477-1</b>                           | Marine water from tidal flat               | Jinniwan, Dongying City, Shandong Province                                      | OR588011                  | OR808046 | OR808038 | /        | /        |
| <b><i>Solicoccozyma</i> sp.</b>                   | <b>CGMCC 2.7285 = JCM 36240 = 17-MEA-479-5</b>               | Marine water from tidal flat               | Kenli District, Dongying city, Shandong Province                                | OR588012                  | /        | /        | OR808033 | OR808025 |

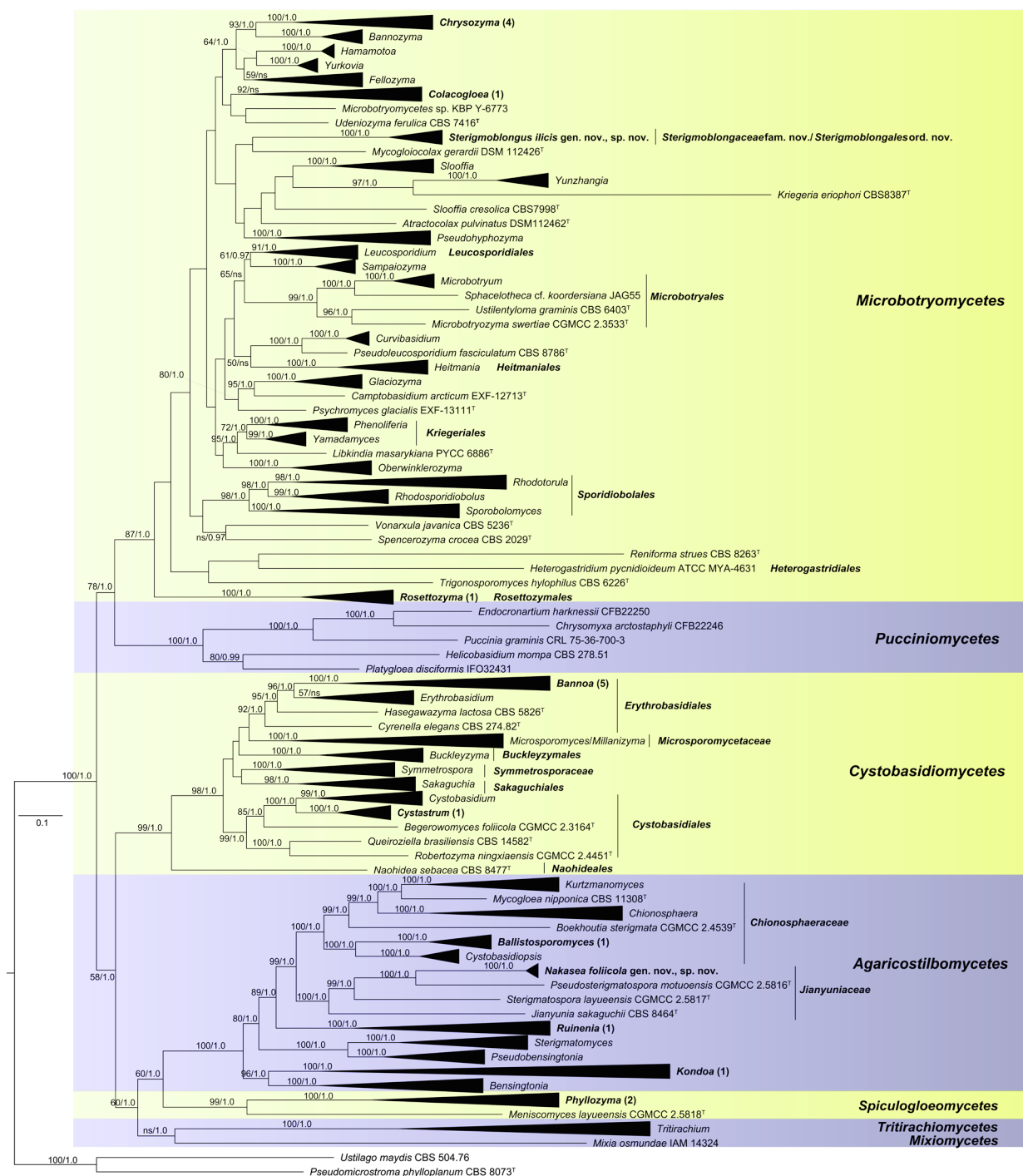
| Species                                | Strain numbers                                       | Source                             | Location                                                                          | GenBank accessions number |            |          |            |          |
|----------------------------------------|------------------------------------------------------|------------------------------------|-----------------------------------------------------------------------------------|---------------------------|------------|----------|------------|----------|
|                                        |                                                      |                                    |                                                                                   | ITS/D1D2                  | RPB1       | RPB2     | TEF1       | CYTB     |
| <i>Teunia littoralis</i> sp. nov       | CGMCC 2.6461 <sup>T</sup> =<br>JCM 35063 = 109C-2    | Soil sediment from tidal flat      | Yinhai District, Beihai City, Guangxi Zhuang Autonomous Region, China, July, 2020 | OR577141<br>/OR577145     | OR808048   | OR808040 | OR808035   | OR808027 |
|                                        | CGMCC 2.6460 =<br>JCM 35062 = 109C-1                 | Soil sediment from tidal flat      |                                                                                   | OR577140<br>/OR577144     | OR808047   | OR808039 | OR808034   | OR808026 |
|                                        | CGMCC 2.6462 =<br>JCM 35064 = 109C-3                 | Soil sediment from tidal flat      |                                                                                   | OR577142<br>/OR577146     | OR808049   | OR808041 | OR808036   | OR808028 |
| <i>Exobasidiomycetes</i>               |                                                      |                                    |                                                                                   |                           |            |          |            |          |
| <i>Exobasidium cylindricum</i> sp. nov | CGMCC 2.6728 <sup>T</sup> =<br>JCM 35453 =<br>GZ1313 | Leaf of <i>Viburnum utile</i>      | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020    | OL982304                  | OM103780   | OM103783 | OM103789   | OZ364094 |
| <i>Gracilitas littoralis</i> sp. nov   | CGMCC 2.6450 <sup>T</sup> =<br>JCM 35052 = 46D-5     | marine water                       | Xiaoshan district, Hangzhou city, Zhejiang province, China, July 2020             | OR588013                  | OZ364100   | OM103787 | OM103792   | OZ365108 |
|                                        | CGMCC 2.6451=<br>JCM 35053 = 46D-6                   | marine water                       |                                                                                   | OR588014 /                |            | OR808042 | OM103793 / |          |
|                                        | CGMCC 2.6452=<br>JCM 35054 = 46D-11                  | marine water                       |                                                                                   | OR588015 /                |            | OR808043 | OM103794 / |          |
|                                        |                                                      |                                    |                                                                                   |                           |            |          |            |          |
| <i>Doassansiales</i> sp.               | CGMCC 2.6453=<br>JCM 35055 = 45A-6                   | marine water                       | Xiaoshan district, Hangzhou city, Zhejiang province, China, July 2020             | OR588016                  | OZ364045 / |          | /          | OR808029 |
| <i>Turchettia toddaliae</i> sp. nov    | CGMCC 2.6745 <sup>T</sup> =<br>JCM 39296 =<br>GZ1871 | Leaf of <i>Toddalia asiatica</i>   | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020    | OL982307                  | OM103781   | OM103784 | OM103790 / |          |
|                                        | GZ1336                                               | Leaf of <i>Viburnum utile</i>      |                                                                                   | OL982306                  | PP942284   | PP965393 | PP862392   | PP974279 |
|                                        | CGMCC 2.6746 =<br>GZ1335                             | Leaf of <i>Viburnum utile</i>      |                                                                                   | OL982305                  | PP942283 / |          | PP862389 / |          |
|                                        |                                                      |                                    |                                                                                   |                           |            |          |            |          |
| <i>Yunzhangomyces nandinae</i> sp. nov | CGMCC 2.6604 <sup>T</sup> =<br>JCM 35428 =<br>GZ4262 | Leaf of <i>Nandina domestica</i>   | Shisun peak, Zhengan county, Zunyi city, Guizhou province, China, October 2020    | OL982310                  | OM103782   | OM103785 | OM103791   | OZ364101 |
|                                        | GZ2461                                               | Leaf of <i>Serissa serissoides</i> |                                                                                   | OL982308                  | PP942285   | PP965394 | PP862393 / |          |
|                                        | GZ2462                                               | Leaf of <i>Serissa serissoides</i> |                                                                                   | OL982309                  | PP942286   | PP965395 | PP862394 / |          |

## New taxa delimitation

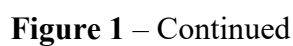
New taxa were primarily delimited using the sequence-based species concept (Boekhout et al. 2021a). Initial identification was performed via BLASTN searches against the GenBank database (Table S2). Taxa were considered novel when their ITS or D1/D2 rDNA sequences exhibited more than 1% divergence from established reference strains (Kurtzman & Robnett 1998, Fell et al. 2000, Sugita et al. 2002). This molecular screening was complemented by traditional phenotypic and physiological tests, including cell morphologies and growth properties (Kurtzman et al. 2011b). The phylogenetic analysis based on multi-locus sequences was then conducted to identify the new species. Thus, a polyphasic approach combining phenotypic characters, sequence variations, and multi-gene phylogenetic interpretations revealed a total of 38 new species distributed across 11 genera within *Pucciniomycotina*, seven genera within *Tremellomycetes* (*Agaricomycotina*), and five genera belonging to *Exobasidiomycetes* (*Ustilaginomycotina*). Sequence similarities between these new species and their closest relatives ranged from 99.5% to 92.2% (D1/D2 domains) and 99.5% to 70% (ITS regions). Notably, the sequence divergences between *Bannoa pseudoscolopiae* and *Ban. scolopiae*, as well as *Papiliotrema chongmingensis* and its close relative, were fewer than 1% in the D1/D2 domains, but 1.1% and over 6.6% in the ITS regions. The sequence divergence between *Exobasidium cylindricum* and its closely related species *Exo. siroboe* was fewer than 1% in the ITS regions, but 1.4% in the D1/D2 domains. Since six new species could not be classified within any known genera, one new order, two new families, and six new genera were proposed. The sequence similarities of these new genera, families, and orders were 92–98%, 92%, and 94.4% in the D1/D2 domains, and 77.5–92%, 92%, and 85.4% in the ITS regions. While the identification of basidiomycetous yeast genera and species in our study was guided by previously defined molecular threshold criteria (Ve et al. 2016, Boekhout et al. 2021), these thresholds are only one method for assessing the validity of new species identifications. The delimitation of new species is corroborated by other taxonomic approaches, such as morphological examination, physiological, and biochemical characters, and phylogenetic analysis using multi-locus sequences. The basis for delimiting each taxon is described below.

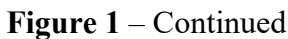
The novel genus *Sterigmoblongus* is proposed for a well-supported clade including 19 isolates represented by the strain CGMCC 2.6623. These 19 isolates from eight different plants shared identical D1/D2 domain sequences and had fewer than four nucleotide mismatches (including indels and substitutions) in the ITS regions. This clade was located at an unstable phylogenetic position in *Microbotryomycetes*, showing a weak association with *Mycogloiocolax gerardii* in the six-locus tree (Fig. 1) and with the genera *Atractocolax* and *Chrysozyma* in the concatenated rDNA tree (Fig. S2) without significant support. BLASTN comparisons revealed that the D1/D2 and ITS sequences of the representative strain CGMCC 2.6623 showed the highest similarity to *Pseudohyphozyma* (94.4%) and *Yunzhangia* (85.4%), respectively. The low sequence similarities and unstable phylogenetic position suggested that group CGMCC 2.6623 is distinct from all known orders, families, genera, and species within the *Microbotryomycetes*. Therefore, we propose a new order *Sterigmoblongales*, a new family *Sterigmoblongaceae*, a new genus *Sterigmoblongus*, and a new species *Sterigmoblongus ilicis*.

The novel genus *Nakasea* is proposed for a clade including six isolates represented by the strain CGMCC 2.6737. This clade was placed in *Jianyuniaceae* (*Agaricostilbales*) and showed a close relationship to the genus *Pseudosterigmatospora* with strong support (BP/PP = 100%/1.0) in the six-gene tree (Fig. 1). However, this clade formed a distinct branch, separate from the clade that includes *Pseudosterigmatospora motuoensis*, *Sterigmatospora layueensis*, and *Crittendenia coppinsii* in the concatenated rDNA loci-based tree (Fig. S2). BLASTN comparisons revealed that the D1/D2 sequences of the representative strain CGMCC 2.6737 matched those of *Pseudosterigmatospora motuoensis* most closely, with 92% identity and 94% coverage.



**Figure 1** – Phylogenetic relationships of *Pucciniomycotina* species based on concatenated sequences of the ITS regions, LSU rDNA D1/D2 domains, *RPB1*, *RPB2*, *TEF1*, and *CYTB*. The maximum likelihood (ML) tree was constructed using RAXML, with nodal support values indicated as follows: bootstrap percentage (BP) from 1000 replicates and Bayesian posterior probabilities (PP). Only nodes with BP  $\geq 50\%$  and PP  $\geq 0.9$  are labeled. A. The schematic tree illustrating phylogenetic relationships of genera and single-species clades within *Pucciniomycotina*. B. Section of the phylogenetic tree depicting relationships of taxa within *Microbotryomycetes*. C. Section of the phylogenetic tree depicting relationships of taxa within *Cystobasidiomycetes*, *Agaricostilbomycetes*, and *Spiculogloeomycetes*. The novel species are highlighted in bold. The scale bar represents 0.1 nucleotide substitutions per site.







The ITS sequence comparison between the strain CGMCC 2.6737 and *Pseudosterigmatospora motuoensis* showed 55% coverage and less than 85% identity. The sequence similarities fell below the threshold of 98.9% for LSU and 95.2% for ITS of basidiomycetous yeast genera proposed by Boekhout et al. (2021a). This marked molecular divergence, coupled with their distinct phylogenetic placement, provided strong support for establishing a new genus for these six isolates.

The novel genus *Buzzinia*, represented by the strain CGMCC 2.6779, formed a robust clade (BP/PP = 73%/1.0) within *Phaeotremellaceae* in the six-locus phylogeny, showing close affinity to *Gelidatrema spencermatinsiae* (Fig. 3). The strain CGMCC 2.6779 differed from *Gel. spencermatinsiae* by 47 nucleotides (~7.5%) in the D1/D2 domains and 110 nucleotide mismatches (~22.5%) in the ITS regions. A separate clade comprising ten unpublished isolates, *Cryptococcus* sp. PDD-28b-13 (HQ256884), *Cryptococcus* sp. PDD-67b-21 (KR922310), *Cryptococcus* sp. PDD-26b-3 (JF706559), *Cryptococcus* sp. PDD-28b-7 (HQ256890), *Cryptococcus* sp. NBRC 105033 (AB46341), *Phaeotremellaceae* sp. CPCCCHN\_300456 (OM980467), *Phaeotremellaceae* sp. CPCCCHN\_300457 (OM980468), *Phaeotremellaceae* sp. CPCCCHN\_300458 (OM980469), *Phaeotremellaceae* sp. CPCCCHN\_300459 (OM980470), and *Cryptococcus* sp. 46HGKG (KT970746) was also closely related to the strain CGMCC 2.6779 and *Gelidatrema* genus in both the concatenated rDNA loci-based tree (Fig. S3) and constrained D1/D2 tree (Fig. 4), corroborating and extending the findings of Kachalkin et al. (2019). Two subclades were identified among these ten strains with five to seven nucleotide differences, suggesting they represent two distinct species. The strain CGMCC 2.6779 showed greater divergence (34–40 nt, ~5.4–6.4%) from these ten unpublished isolates in the D1/D2 domains. Sequence similarities with the described species and unpublished isolates were below the thresholds of genus identification recommended by Boekhout et al. (2021a). The above analyses indicated that it was appropriate to propose a new genus to accommodate the strain CGMCC 2.6779.

The novel genus *Turchettia* is proposed for the well-supported clade including two isolates represented by the strain CGMCC 2.6745. These two isolates formed a distinct clade that is basal to *Phragmotenium*, *Jamesdicksoniain*, *Tolyposporella*, *Georgefischeria riveae*, and *Tilletiaria anomala* in *Georgefischeriales* (Fig. 5). The D1/D2 sequences analysis by BLASTN indicated that the strain CGMCC 2.6745 shared 92% identity with the described genus *Gjaerumia*. Similarly, the closest match using the ITS sequence is the genus *Gjaerumia*, with 92% identity but less than 40% coverage. These values fall below the established family-level threshold of 96.2% proposed by Vu et al. (2019) for LSU. The low coverage of ITS regions likely results in higher sequence similarity than the 88.5% threshold for ITS sequences proposed by Vu et al. (2019) for the yeast family. The sequence comparison and phylogeny supported the establishment of a novel family *Turchettiaceae*, a novel genus *Turchettia*, and a novel species *Turchettia toddaliae* to accommodate these two isolates.

The novel genus *Gracilitas* is proposed for the well-supported clade comprising three isolates represented by the strain CGMCC 2.6450 in *Doassansiaceae*. The D1/D2 and ITS sequences were analyzed by BLASTN, indicating that the strain CGMCC 2.6450 had the highest similarity to *Heterodoassansia hygrophilae*, with 98% and 89% identities, respectively. These three isolates formed a separate clade that is sister to *Pseudodermatosorus sagittariae* in the six-locus tree, without significant bootstrap or posterior probability support (Fig. 5), and match this species by only 66% coverage and 91% identity using ITS sequences. Due to the unavailability of the D1/D2 sequence of *Pse. sagittariae*, no sequence of the D1/D2 domains could be compared between the strain CGMCC 2.6450 and *Pse. Sagittarius*. Given the low sequence similarity, distinct phylogenetic position, and low support values, we propose a novel genus *Gracilitas* and a novel species *Gra. littoralis* for these three isolates.

#### **Identification of novel species within *Pucciniomycotina* *Chrysozyma* (*Chrysozymaceae*, *incertae sedis*, *Microbotryomycetes*)**

The genus *Chrysozoma* includes ten recognized species: *Chr. griseoflava*, *Chr. fushanensis*, *Chr. pseudogriseoflava*, *Chr. sambuci*, *Chr. rhododendri*, *Chr. iridis*, *Chr. sorbariae*, *Chr. fusiformis*, *Chr. cylindrica*, and *Chr. flava* (Nakase & Suzuki 1987, Nakase et al. 2005, Wang et al. 2015a, Li et al. 2020). Eight strains identified within the *Chrysozoma* clade formed four distinct groups (Fig. 1, S2). In both the six-locus and the concatenated rDNA phylogenies, group CGMCC 2.6751 clustered most closely with *Chr. Cylindrical* (Figs. 1, S2). The three strains in this group shared the identical D1/D2 and ITS sequences, showing a divergence of nine nucleotides (~1.5%) in the D1/D2 domains and 100 nucleotides (~15%) in the ITS regions compared to *Chr. cylindrica*. An unpublished strain, *Chrysozoma* sp. XZY20-10 (OP470209/OP470305), clustered the strain CGMCC 2.6751 (Fig. 2) but displayed six nucleotide differences (~1%) in the D1/D2 domains and 51 nucleotide differences (~7.5%) in ITS regions, suggesting it is likely a distinct species. Groups CGMCC 2.6709 and CGMCC 2.6608, clustered together in the six-gene phylogeny, though without an unsupported clade (Fig. 1). Group CGMCC 2.6709 occupied a basal position that separated from other *Chrysozoma* species except for *Chr. fushanensis* and *Chr. flava* in the concatenated rDNA loci tree (Fig. 1, S2). The two isolates of group CGMCC 2.6709 shared identical D1/D2 sequences with only three nucleotide variations in the ITS regions.

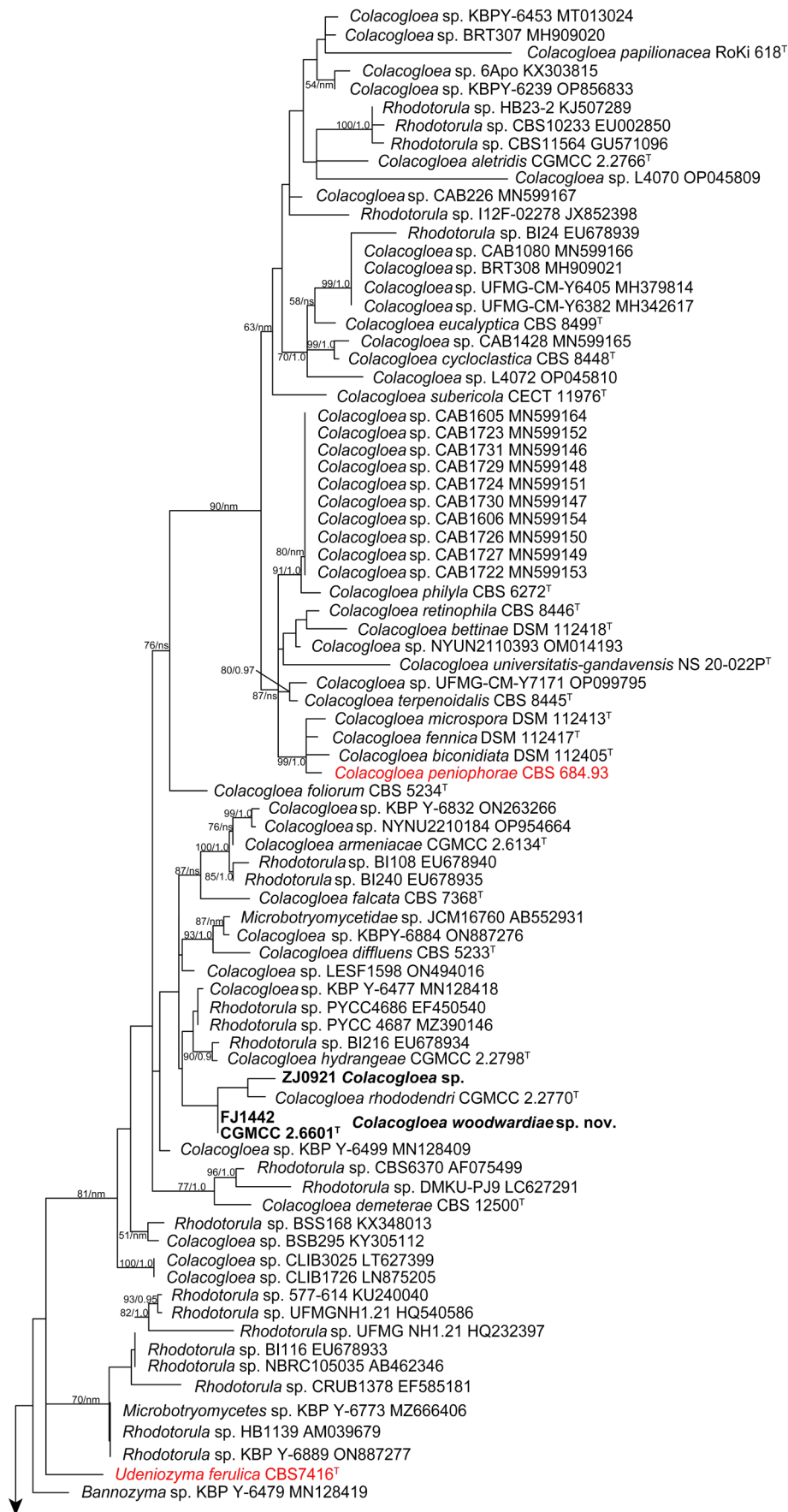
These two isolates showed sequence divergence from group CGMCC 2.6608, differing by 20 nucleotide differences (~3.2%) in the D1/D2 domains and 100 nucleotide differences (~15%) in the ITS regions. The strain CGMCC 2.6804, obtained from Yandang Mountain, was phylogenetically related to the strain CGMCC 2.6709 but was clearly distinguished by a single nucleotide substitution in the D1/D2 domains and 74–75 nucleotide mismatches (~11.2–11.4%) in the ITS regions, supporting its recognition as a distinct species. Group CGMCC 2.6608 appeared as a sister clade to group CGMCC 2.6709 in the six-locus tree, whereas it clustered with group CGMCC 2.6602 and *Chr. fushanensis* in the concatenated rDNA tree with moderate support (Figs. 1, S2). Sequence comparisons indicated divergences of 15–20 nucleotide substitutions (~2.4–3.2%) in D1/D2 domains and 100–117 nucleotide mismatches (~15.0–17.6%) in the ITS region between group CGMCC 2.6608 and related taxa. Group CGMCC 2.6602 was basal to the *Chrysozoma* genus alongside *Chr. fushanensis* in the six-gene tree (Fig. 1). The two isolates of group CGMCC 2.6602 possessed identical D1/D2 sequences with only a single mismatch in the ITS regions, yet they differed from *Chr. fushanensis* by 11 nucleotide substitutions (~1.8%) in the D1/D2 domains and 65 nucleotide mismatches (~10%) in the ITS regions. The sequence comparisons and phylogenetic placement demonstrated that the eight strains represent four previously undescribed species within the genus *Chrysozoma*.

### ***Colacogloea* (Colacogloeaceae, incertae sedis, Microbotryomycetes)**

Group CGMCC 2.6601 clustered robustly with *Col. rhododendri* in both six-locus and concatenated rDNA phylogenies (Figs. 1, S2). The two isolates in this group, collected from distinct locations, possessed identical D1/D2 and ITS sequences. Sequence comparisons revealed 12–15 nucleotide substitutions (~2%) in the D1/D2 domains and 62 nucleotide mismatches (~9.6%) in the ITS regions between group CGMCC 2.6601 and *Col. rhododendri*. The strain CGMCC 2.6705 was closely related to group CGMCC 2.6601 (Fig. S2), sharing identical ITS sequences but 15 nucleotide substitutions (~2.6%) in the D1/D2 domains, indicating it is a distinct species. Furthermore, an unpublished strain *Colacogloea* sp. KBP: Y-6499 (MN128409) from *Cladonia stellaris* in Russia clustered with group CGMCC 2.6601 (Fig. 2) but displaying four nucleotide differences in the D1/D2 domains and approximately 60 nucleotide mismatches (~10%) in the ITS regions.

### ***Sterigmoblongus* (Sterigmoblongaceae, Sterigmoblongales, Microbotryomycetes)**

The new genus *Sterigmoblongus* is represented by group CGMCC 2.6623. Nineteen isolates collected from eight different plants comprised this group. They exhibited identical D1/D2 sequences and minimal ITS variation, with fewer than four nucleotide mismatches, strongly supporting their classification as a single species, which represents the type species of the new genus.



**Figure 2** – Constrained maximum likelihood phylogeny of *Pucciniomycotina* based on LSU rDNA D1/D2 domain sequences, reconstructed using RAXML and MrBayes with a backbone constraint derived from the six-gene topology (Section A). Nodal support values indicate bootstrap percentage (BP  $\geq$  50%) from 1000 replicates and Bayesian posterior probabilities (PP  $\geq$  0.9). A–D. Section of

the phylogenetic relationships of *Microbotryomycetes*. E–F. Section of the phylogenetic relationships of *Cystobasidiomycetes*. G. Section of the phylogenetic relationships of *Agaricostilbomycetes*. H. Section of the phylogenetic relationships of *Spiculogloeomycetes*, *Tritirachiomycetes*, and *Mixiomycetes*. The novel species are highlighted in bold. The type species are highlighted in red. The scale bar represents 0.02 nucleotide substitutions per site.

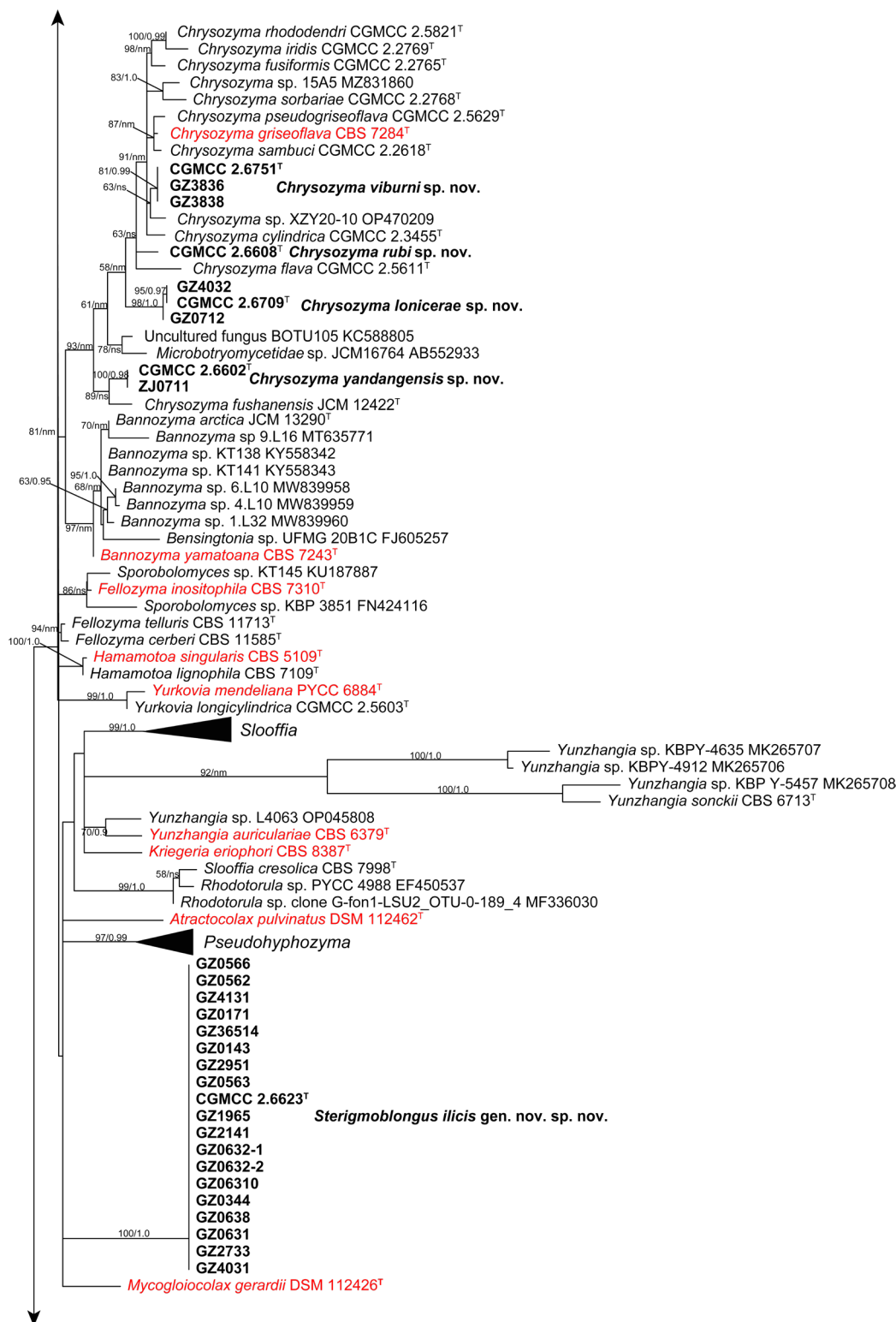


Figure 2 – Continued (Section B).

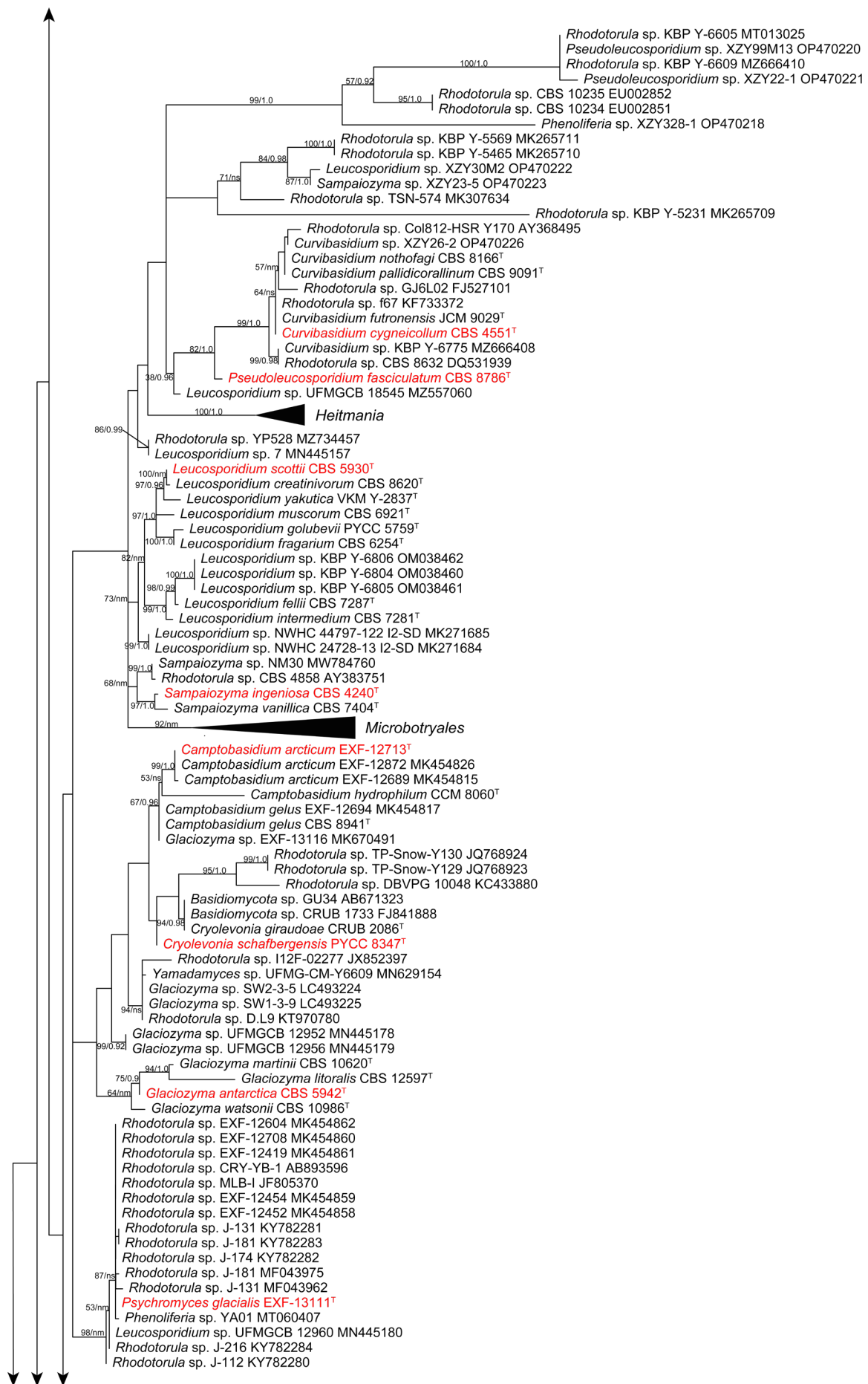


Figure 2 – Continued (Section C).



Figure 2 – Continued (Section D).



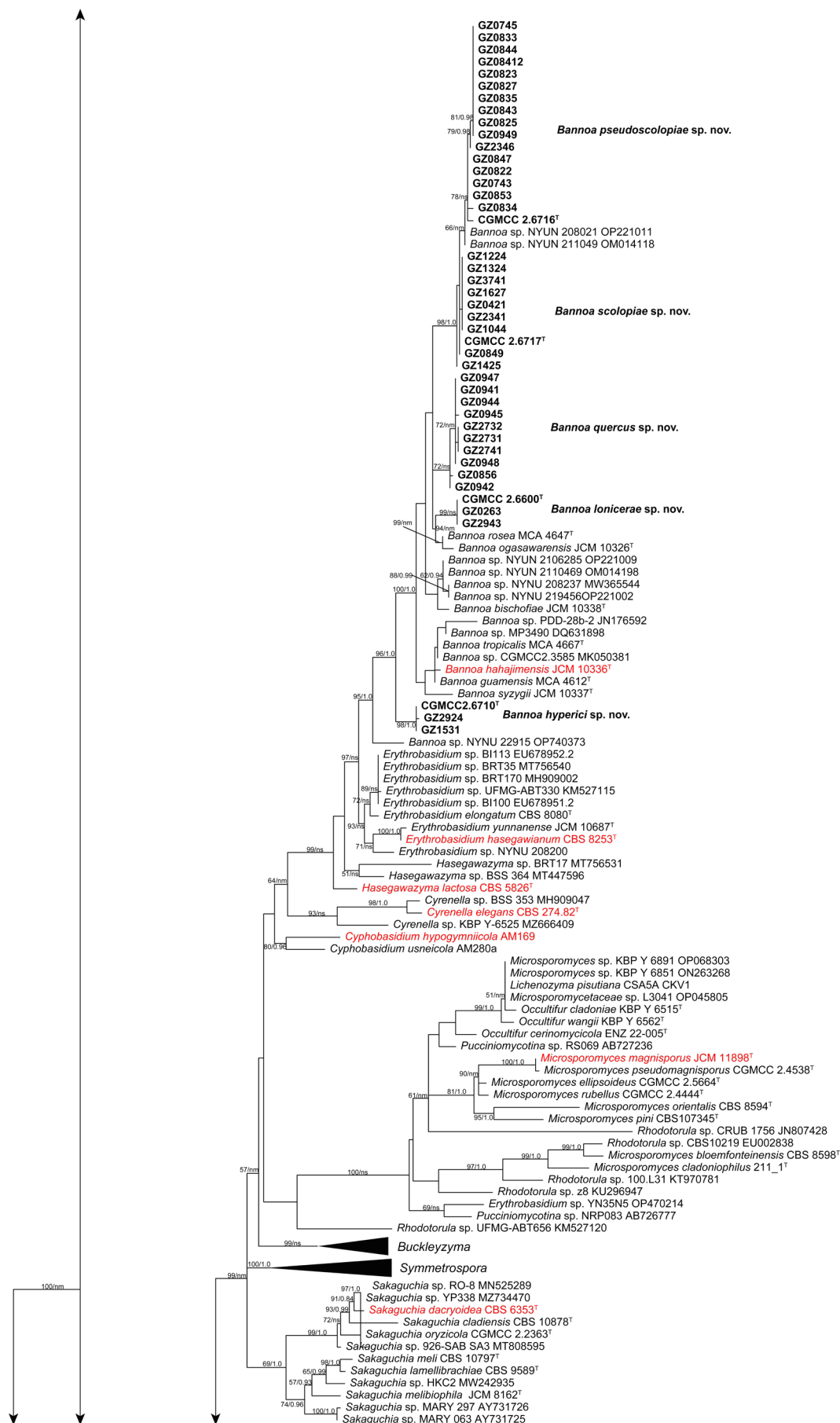


Figure 2 – Continued (Section E).

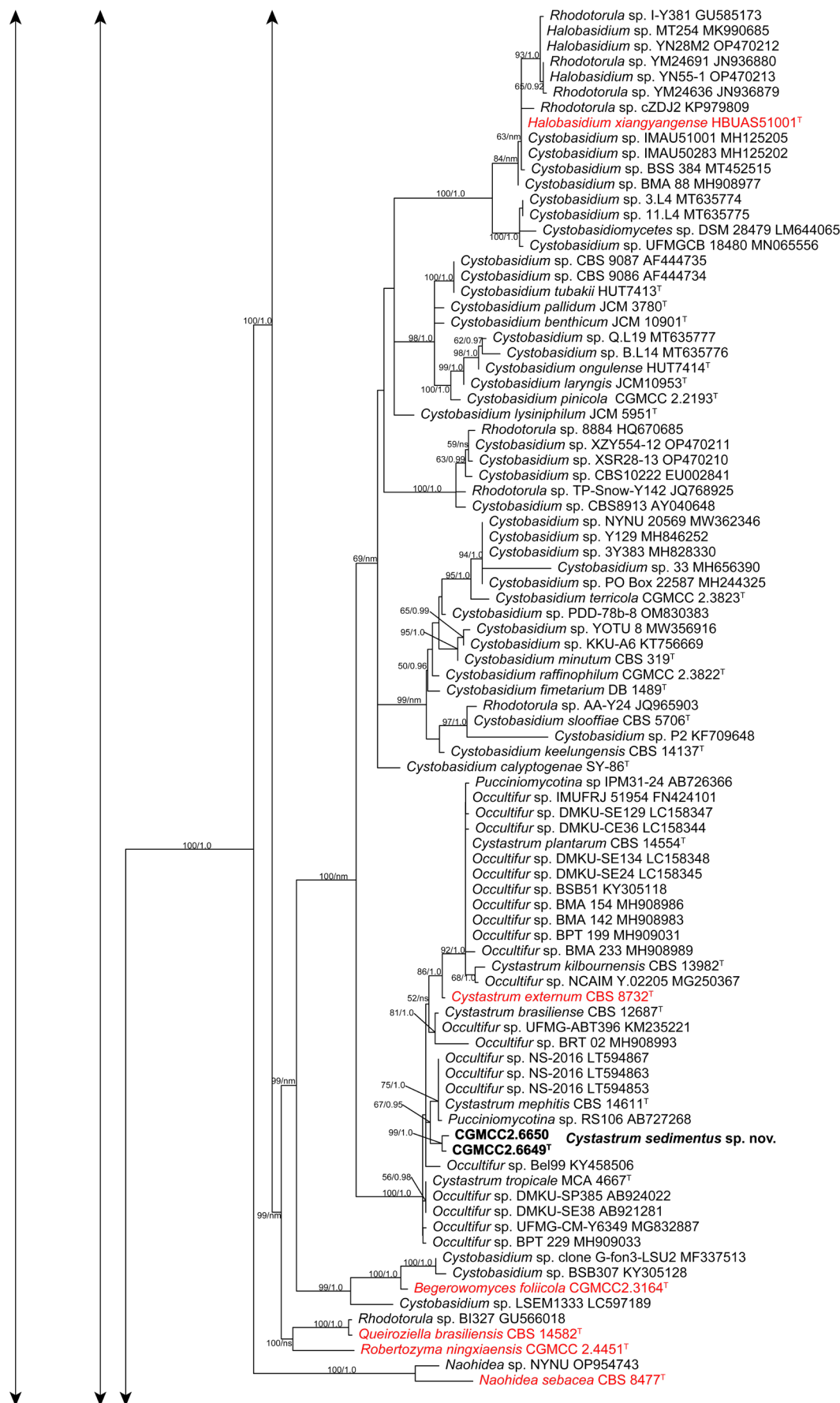


Figure 2 – Continued (Section F).



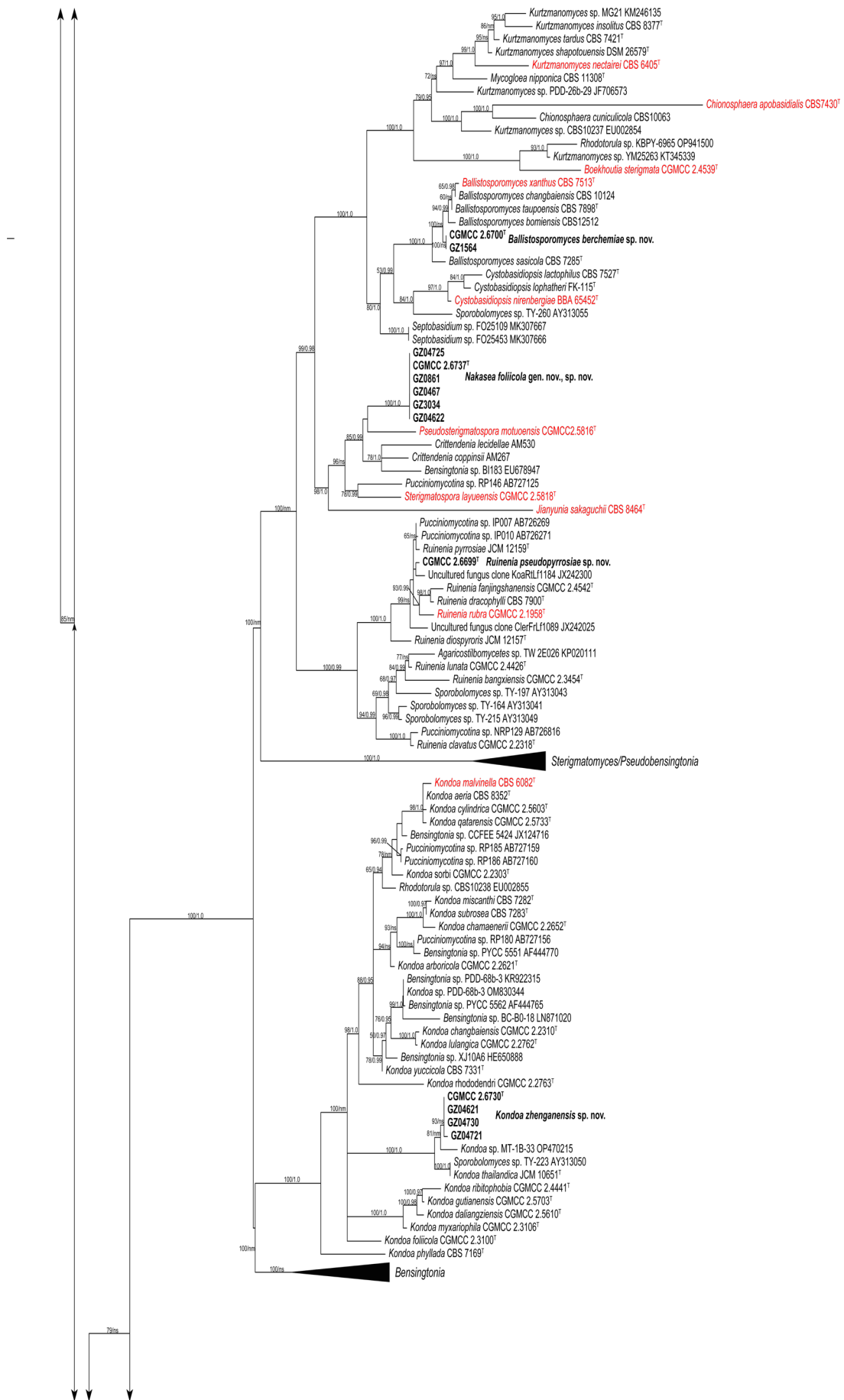
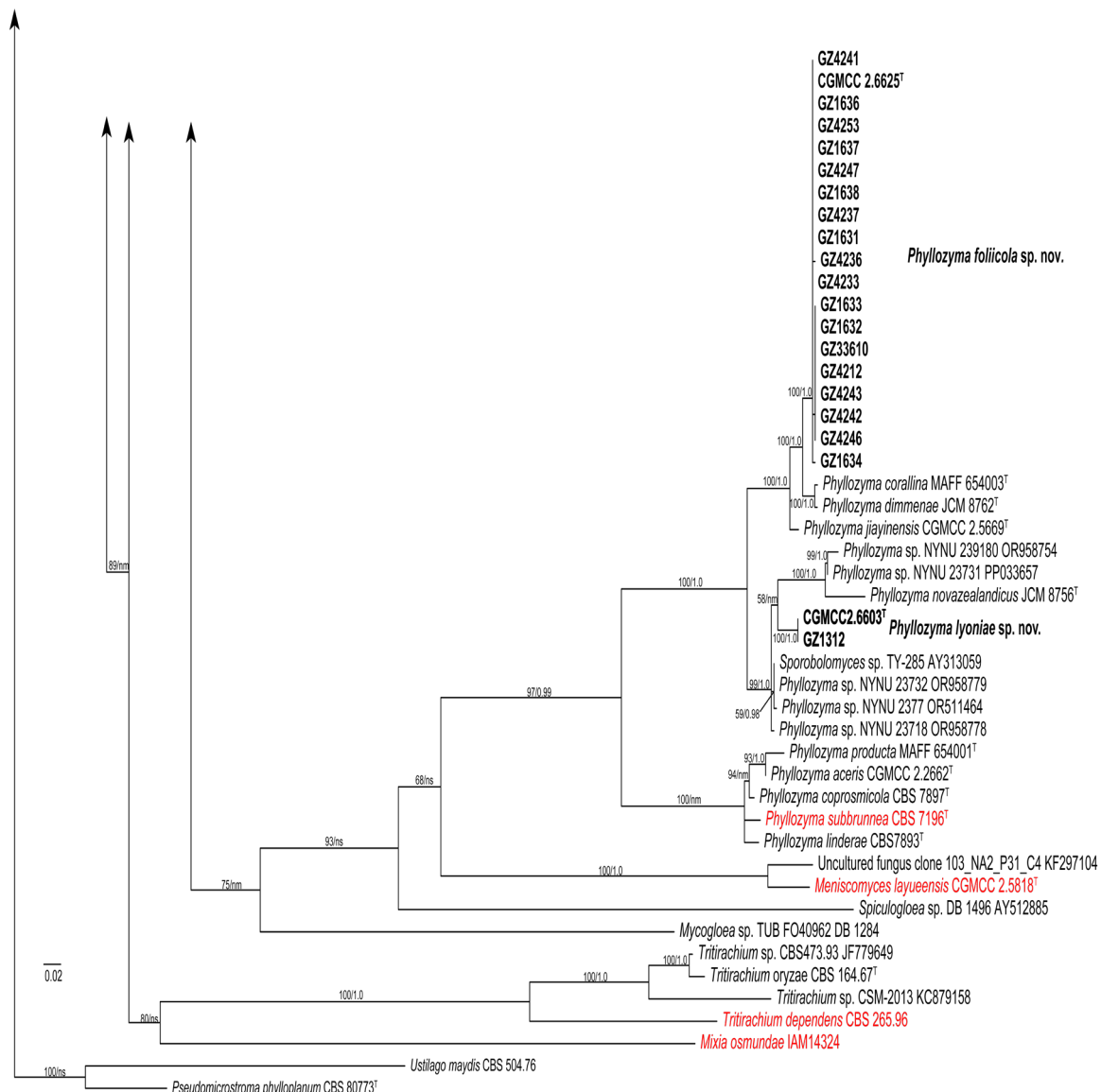


Figure 2 – Continued (Section G).



**Figure 2** – Continued (Section H).

### ***Rosetozyma* (Rosetozymaceae, Rosetozymales, Microbotryomycetes)**

The genus *Rosetozyma* was proposed as a novel genus at the base of the *Microbotryomycetes* (Li et al. 2020). This genus includes three species, namely *Ros. petaloides*, *Ros. cystopteridis*, and *Ros. motuoensis*. Group CGMCC 2.6626 clustered robustly with *Ros. motuoensis* (Fig. 1, 2, S2). Eight isolates of group CGMCC 2.6626 had identical D1/D2 sequences and minimal ITS variation, with fewer than six nucleotide mismatches. They differed from their closely related species *Ros. motuoensis* by eight nucleotide substitutions (~1.3%) in the D1/D2 domains and 12–16 nucleotide mismatches (~1.9–2.6%) in the ITS regions. We therefore propose these eight strains represent a new species of *Rosetozyma*.

### ***Bannoa* (Erythrobasidiaceae, Erythrobasidiales, Cystobasidiomycetes)**

Seven species are included in the genus *Bannoa*, namely *Ban. biscofae*, *Ban. guamensis*, *Ban. hahajimensis*, *Ban. ogasawarensis*, *Ban. rosea*, *Ban. syzygii*, and *Ban. tropicalis* (Parra & Aime 2019, Li et al. 2020). Forty-three isolates were classified into five groups within the genus *Bannoa* (Fig. 1, 2, S2). Groups CGMCC 2.6716 and 2.6717 clustered together with strong support (BP/ PP = 98%/1.0) in the six-locus tree (Fig. 1). Seventeen isolates of group CGMCC 2.6716 showed minimal intra-group variation of two nucleotide substitutions in both the D1/D2 and ITS regions. Two

unpublished isolates, *Bannoa* sp. NYUN 211049 (OM014118) and *Bannoa* sp. NYUN 208021 (OP221011), clustered with group CGMCC 2.6716 in the constrained D1/D2 tree (Fig. 2) and differed from this group by no more than two nucleotides in the D1/D2 domains and six nucleotides in the ITS regions. Ten isolates of group CGMCC 2.6717 exhibited minimal genetic variation, with only two and four nucleotide differences in the D1/D2 and ITS regions, respectively. Comparative analysis between the strain CGMCC 2.6716 and the strain CGMCC 2.6717 revealed three nucleotide substitutions (~0.5%) in the D1/D2 domains and six nucleotide substitutions (~1.1%) in the ITS regions, in addition to significant divergence in protein-coding genes (*RPB1*, *RPB2*, *TEF1*, and *CYT8*), with 30–100 nucleotide mismatches (~7.7–11.2%).

Group CGMCC 2.6722 formed a separate sister clade to the lineage, including *Ban. rosea*, *Ban. ogasawarensis*, and group CGMCC 2.6600 with moderate support (BP/PP = 60%/1.0) (Fig. 1). Ten isolates within this group displayed minimal intraspecific variation of two to three nucleotide substitutions in both the D1/D2 and ITS regions. Comparative sequence analysis showed significant divergence from their closest relatives, *Ban. ogasawarensis*, *Ban. rosea*, and group CGMCC 2.6600, with 16–17 nucleotide substitutions (~2.5–2.7%) in the D1/D2 domains and 7–14 nucleotide mismatches (~1.3–2.5%) in the ITS regions.

Group CGMCC 2.6600 appeared as a sister clade to *Ban. ogasawarensis* and *Ban. rosea* in the six-locus tree with significant support (BP/PP = 87%/1.0) (Fig. 1). Three isolates of *Ban. lonicerae*, collected from different plant leaves, exhibited identical ITS and D1/D2 sequences. This group differed from *Ban. ogasawarensis* by 14 nucleotide substitutions (~2.7%) in the D1/D2 domains and 11 nucleotide mismatches (~1.9%) in the ITS regions. While a complete D1/D2 comparison with *Ban. Rosea* was precluded by sequence truncation; significant divergence was observed with group CGMCC 2.6600 by nine nucleotide mismatches (~1.5%) in the ITS regions and ~130 nucleotide mismatches (~10.8%) in the *TEF1* regions.

Group CGMCC 2.6710 occupied a basal phylogenetic position within the *Bannoa* genus in both the six-locus and concatenated rDNA tree (Figs. 1, S2). The three isolates of *Ban. hyperici* exhibited minimal intraspecific variation with one nucleotide in the ITS and D1/D2 regions but exhibited significant divergence from other *Bannoa* type strains by ~4.0–5.7% nucleotide substitutions in the D1/D2 domains and ~10.8–14.3% nucleotide mismatches in the ITS regions.

Accordingly, we propose five novel species corresponding to groups CGMCC 2.6716, 2.6717, 2.6722, 2.6600, and 2.6710.

### ***Cystastrum* (Cystobasidiaceae, Cystobasidiales, Cystobasidiomycetes)**

Group CGMCC 2.6649 was sister to *Cystastrum mephitis* in the concatenated rDNA and constrained D1/D2 trees (Fig. 2, S2). Only *Cys. externum* is included in the six-locus phylogenetic analysis (Fig. 1) because the other *Cystastrum* species have only rDNA sequences publicly available. The two isolates in this group from tidal flat soil sediment, showed minimal intraspecific variation with 1–2 mismatches in the D1/D2 domains and ITS regions but exhibited significant divergence from *Occ. mephitis* by seven nucleotide substitutions (~1.2%) in the D1/D2 domains and 24 nucleotide mismatches (~4.1%) in the ITS regions.

### ***Ballistosporomyces* (Chionosphaeraceae, Agaricostilbales, Agaricostillbomycetes)**

Five species, namely *Bal. bomiensis*, *Bal. changbaiensis*, *Bal. sasicola*, *Bal. taupoensis*, and *Bal. xanthus*, belong to this genus (Wang et al. 2015a, Li et al. 2020). Group CGMCC 2.6700 occurred as a sister group to the clade including *Bal. bomiensis*, *Bal. changbaiensis*, *Bal. taupoensis*, and *Bal. xanthus* (Figs. 1, 2, S2). The two isolates in this group from two different plant leaves at different locations possessed identical ITS and D1/D2 sequences. They differed from *Bal. bomiensis*, *Bal. changbaiensis*, *Bal. taupoensis*, and *Bal. xanthus* by eight to ten nucleotide substitutions (~1.3–1.6%) in the D1/D2 domains and 12–24 nucleotide mismatches (~2.0–4.0%) in the ITS regions.

### ***Nakasea* (Jianyuniaceae, Agaricostilbales, Agaricostillbomycetes)**

Six isolates of group CGMCC 2.6737 from different locations and plants displayed identical D1/D2 sequences and minimal ITS variation, fewer than seven nucleotide mismatches. This group is currently the only species in the newly proposed genus *Nakasea*.

#### ***Ruinenia* (Ruineniaceae, Agaricostilbales, Agaricostillbomycetes)**

The strain CGMCC 2.6699 showed close phylogenetic affinity to *Rui. pyrrosiae* in the six-locus tree with strong support (BP/PP = 98%/1.0) and was basal to the clade containing *Rui. dracophylli*, *Rui. fanjingshanensis*, *Rui. rubra*, and *Rui. pyrrosiae* in the concatenated rDNA tree with strong support (BP/PP = 100%/1.0) (Figs. 1, S2). This isolate differed from these four species by 7–16 nucleotide mismatches (~1.2–2.5%) in the D1/D2 domains and 30–55 nucleotide mismatches (~4.7–8.6%) in the ITS regions. An uncultured fungus clone 103\_NA2\_P31\_C4 (KF297104), recovered from patterned-ground ecosystems of the North American Arctic, clustered with the strain CGMCC 2.6699 without significant support in the constrained D1/D2 tree (Fig. 2) and differed from it by seven nucleotide mismatches (~1.1%) in the D1/D2 domains, indicating that the clone represents a separate *Ruinenia* species.

#### ***Kondoa* (Kondoaaceae, Agaricostilbales, Agaricostillbomycetes)**

*Kondoa* is a large genus with recent discoveries of new plant-related species (Li et al. 2020). Phylogenetic analyses placed group CGMCC 2.6730 in a close evolutionary relationship with *Kon. thailandica* in concatenated rDNA and six-locus trees (Figs. 1, S2). The four isolates in this group shared identical D1/D2 and ITS sequences but exhibited significant divergence from *Kon. thailandica* by 15 nucleotide mismatches (~2.5%) in the D1/D2 domains and 49 nucleotide mismatches (~7.7%) in the ITS regions. An unpublished strain, MT-1B-33 (OP470215) obtained from unknown leaves in Tibet, clustered with group CGMCC 2.6730 in the constrained D1/D2 tree (Fig. 2) but displayed 12 nucleotide differences in the D1/D2 domain, confirming it as a separate *Kondoa* species.

#### ***Phyllozoma* (Spiculogloeaceae, Spiculogloeales, Spiculogloeomycetes)**

Twenty-one isolates were classified into two distinct groups within the genus *Phyllozoma* (Figs. 1, 2, S2). Group CGMCC 2.6625 showed close phylogenetic affinity to *Phy. corallina*, *Phy. dimmenae*, and *Phy. jiayinensis* (Figs. 1, 2, S2). Nineteen isolates in this group exhibited minimal sequence variation, with fewer than two and six nucleotide differences in the D1/D2 domains and ITS regions, respectively, but significant divergence from their closest relatives, *Phy. corallina*, *Phy. dimmenae*, and *Phy. Jiayinensis*, by eight to 12 nucleotide substitutions (~1.3–1.9%) in the D1/D2 domains and 17–30 nucleotide mismatches (~3.1–5.4%) in the ITS regions. Group CGMCC 2.6603 formed a sister clade to *Phy. novazealandicus* in concatenated rDNA and six-locus phylogenies (Figs. 1, S2). Two isolates in this group, collected from different plant leaves, displayed identical D1/D2 and ITS sequences but substantial divergence from *Phy. novazealandicus* by 36 nucleotide differences (~6.3%) and 70 nucleotide differences (~12.9%) in the D1/D2 domains and ITS regions. Four unpublished strains ‘*Sporobolomyces*’ sp. TY-285 (AY313059), *Phyllozoma* sp. NYNU 2377 (OR511464), *Phyllozoma* sp. NYNU 23718 (OR958778), and *Phyllozoma* sp. NYNU 23732 (OR958779) were found to be closely related to this group (Fig. 2) but differed from it by 9–10 nucleotides (~1.4–1.6%) in the D1/D2 domains, suggesting that these unpublished strains most likely belong to a different species.

#### ***Derxomyces* (Bulleribasidiaceae, Tremellales, Tremellomycetes)**

Twenty-two isolates, classified into four distinct groups, were placed within the genus *Derxomyces* (Fig. 3). Group CGMCC 2.6768 was related to *Der. wuzhishanensis* and *Der. elongatus* without significant support in the six-locus tree (Fig. 3). Two isolates in this group, collected from different plants, possessed identical D1/D2 and ITS sequences but showed substantial divergence from *Der. wuzhishanensis* and *Der. elongatus* by 13–14 nucleotide differences (~2.1–2.2%) in the D1/D2 domains and over 19% nucleotide mismatches in the ITS regions. Group CGMCC 2.6788

was related to *Der. linzhiensis* with moderate posterior probability support (PP = 0.90) in the six-locus tree (Fig. 3). Two strains in this group shared identical D1/D2 and ITS sequences while displaying significant divergence from *Der. linzhiensis* by 15 nucleotide substitutions (~2.4%) in the D1/D2 domains and 59 nucleotide mismatches (~11.4%) in the ITS regions. Group CGMCC 2.6622 grouped with *Der. longicylindricus* in the six-locus phylogeny with strong support (Fig. 3). Twelve isolates in this group exhibited high genetic uniformity, with fewer than three nucleotide differences in both the D1/D2 domains and ITS regions, while differing markedly from their nearest known relative *Der. longicylindricus* by 34–36 nucleotide differences (~5.3–6.6%) in the D1/D2 domains and over 30% nucleotide mismatches in the ITS regions. Group CGMCC 2.6694 occupied a basal phylogenetic position within *Dermomyces* and showed close affinity to *Der. anomala* in the six-locus tree (Fig. 3). Six isolates in this group displayed minimal genetic variation with one nucleotide and three nucleotide differences in the D1/D2 domains and ITS regions, while demonstrating significant divergence from *Der. anomala* by 49–50 nucleotide mismatches (~7.6–7.8%) in the D1/D2 domains and 62–65 nucleotide mismatches (~13.3–13.9%) in the ITS regions. Accordingly, we propose four novel species corresponding to groups CGMCC 2.6768, 2.6788, 2.6622, and 2.6694.

### ***Dioszegia* (Bulleribasidiaceae, Tremellales, Tremellomycetes)**

A single strain, CGMCC 2.10014, isolated from the tidal flat marine water was located as a basal clade to *Dio. changbaiensis*, *Dio. cryoxerica*, and *Dio. heilongjiangensis* with good supports in the six-locus tree (BP/PP = 92%/1.0), concatenated rDNA tree (BP/PP = 54%/1.0), and constrained D1/D2 tree (BP = 81%) (Figs. 3, 4, S3) and differed from these three species by 10–12 nucleotide mismatches (~1.6–1.9%) in the D1/D2 domains and 14–22 nucleotide mismatches (~2.9–4.6%) in the ITS regions, confirming its status as a novel *Dioszegia* species.

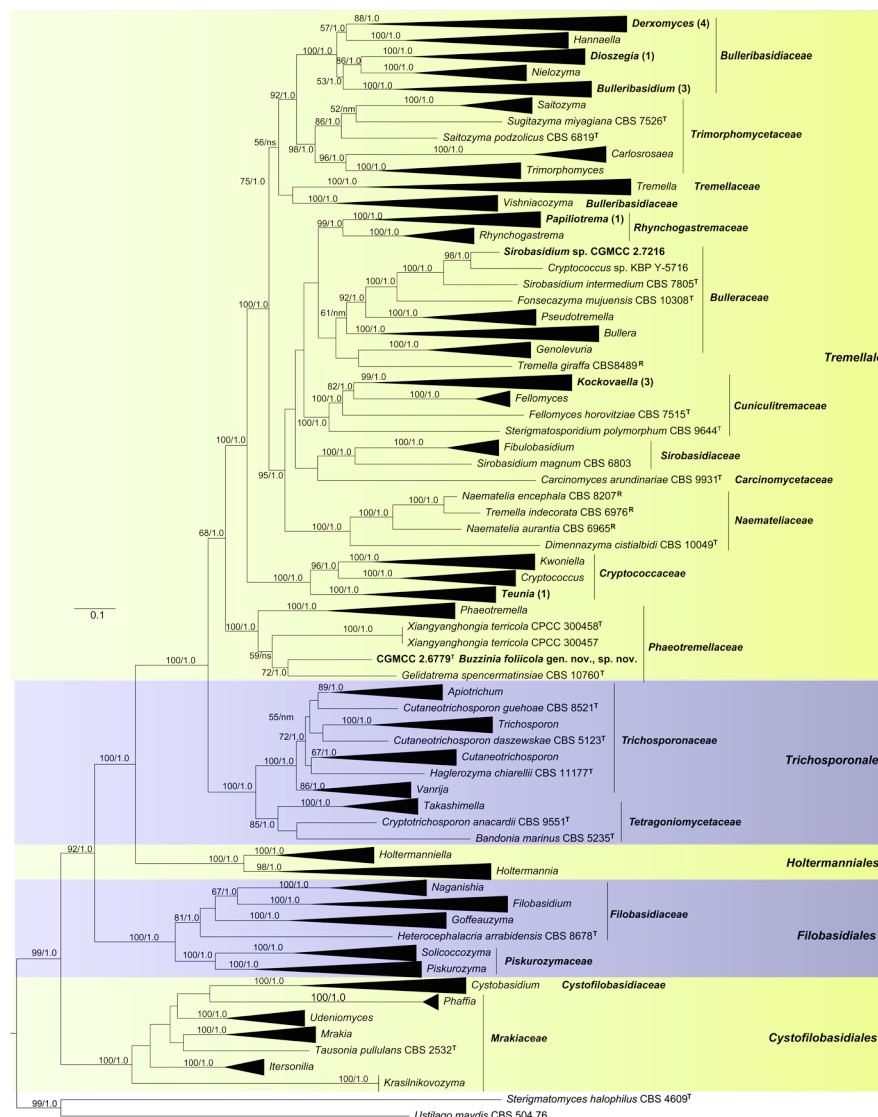
### ***Bulleribasidium* (Bulleribasidiaceae, Tremellales, Tremellomycetes)**

Four isolates were classified into three separate groups within the genus *Bulleribasidium* (Figs. 3, 4, S3). Group CGMCC 2.6616 grouped with *Bul. foliicola* and *Bul. phyllophilum* in the six-locus tree with moderate bootstrap value (BP = 63%) and strong posterior probability support (PP = 0.98) (Fig. 3). Two isolates in this group obtained from plant leaves in the forest and tidal flat, respectively, showed minimal genetic variation with a single nucleotide substitution in both D1/D2 and ITS regions but significant divergence from these two described species by 11–12 nucleotide substitutions (~1.8–1.9%) in the D1/D2 domains and 44–51 nucleotide mismatches (~8.4–9.7%) in the ITS regions. The strain CGMCC 2.6786 was closely related to *Bul. begoniae*, *Bul. panici*, *Bul. pseudopanici*, and *Bul. siamensis* (Figs. 3, S3) and differed from these four species by 6–16 nucleotide mismatches (~1.0–2.6%) in the D1/D2 domains and 28–39 nucleotide mismatches (~6.1–8.5%) in the ITS regions. The strain CGMCC 2.6680, clustered with *Bul. phyllostachydis* and *Bul. setariae* with strong supports in the six-locus tree (BP/PP = 100%/1.0) and concatenated rDNA tree (BP/PP = 91%/0.98) (Fig. 3, S3), and differed from these two species by 28–30 nucleotide differences (~4.5–4.8%) in the D1/D2 domains and 20–22 nucleotide differences (~4.5–4.9%) in the ITS regions. Accordingly, we propose three novel species corresponding to groups by CGMCC 2.6616, 2.6786, and 2.6680.

### ***Papiliotrema* (Rhynchogastremaceae, Tremellales, Tremellomycetes)**

The strain CGMCC 2.10012, isolated from tidal flat soil sediment, clustered with *Pap. rajasthanensis* and *Pap. laurentii* in the six-locus tree (Fig. 3). It differed from these two closest relatives by 6–10 nucleotide substitutions (~0.9–1.6%) in the D1/D2 domains and 36–44 nucleotide mismatches (~6.6–8.0%) in the ITS regions. Given the known heterogeneity of *Pap. laurentii* as noted by Yurkov et al. (2013), thirty *Pap. laurentii* strains deposited in the NCBI database (Fig. 4) were included in the constrained D1/D2 tree to further validate the taxonomic novelty of the group CGMCC 2.10012. Twenty-eight of these strains, including the type strain CBS 139, formed the tightly clustered core, *Pap. laurentii* clade, showing no more than two nucleotide differences (Fig. 4). The strain CGMCC 2.10012 was distinct from this core clade by 4–5 nucleotide substitutions

(~0.6–0.8%) in the D1/D2 domains and 33–36 nucleotide mismatches (~6.0–6.6%) in the ITS regions. Furthermore, two other unpublished strains, *Cryptococcus* aff. *laurentii* CBS 9007 (AF406934) and *Cryptococcus laurentii* WOOct07D(1)X-Y29 (GQ352524), along with the strain CGMCC 2.10010, and *Pap. rajasthanensis*, occurred in four separate branches sister to the core *Pap. laurentii* clade. *Cryptococcus* aff. *laurentii* CBS 9007 differed from the type strain CBS 139 by 10 nucleotide substitutions (~1.6%) in the D1/D2 domains, suggesting it may represent a different species. *Cryptococcus laurentii* WOOct07D(1)X-Y29 differed from CBS 139 by four nucleotide substitutions in the D1/D2 domains, but its phylogenetic position was separated from the core *Pap. laurentii* clade, indicating its taxonomy may require further multilocus sequence analysis. In the concatenated rDNA tree, the strain CGMCC 2.10012 grouped with *Pap. rajasthanensis*, both of which were closely related to the *Pap. laurentii* clade. The above sequence analyses and phylogenetic evidence confirm that the strain CGMCC 2.10012 represents a novel *Papiliotrema* species.



**Figure 3** – Maximum likelihood phylogeny of *Tremellomycetes* inferred from concatenated sequences of ITS regions, LSU rDNA D1/D2 domains, *RPB1*, *RPB2*, *TEF1*, and *CYT8*. The tree backbone was constructed using RAxML, with nodal support values indicated as bootstrap percentage (BP) from 1,000 replicates and Bayesian posterior probabilities (PP) (Section A). Only nodes with BP  $\geq 50\%$  and PP  $\geq 0.9$  are labeled. A. The schematic tree illustrating phylogenetic relationships of genera and single-species clades within *Tremellomycetes*. B. Section of the

phylogenetic tree depicting relationships of taxa of *Derxomyces*, *Hannaella*, *Dioszegia*, and *Nielozyma* within *Bulleribasidiaceae*, *Tremellales*. C. Section of the phylogenetic tree depicting relationships of taxa of *Bulleribasidium* within *Bulleribasidiaceae* and *Trimorphomycetaceae*, *Tremellaceae*, *Bulleribasidiaceae*, *Rhynchogastremaceae*, and *Bulleraceae* within *Tremellales*. D. Section of the phylogenetic tree depicting relationships of taxa *Cuniculitremaeae*, *Sirobasidiaceae*, *Carcinomycetaceae*, *Naemateliaceae*, and *Cryptococcaceae* within *Tremellales*. E. Section of the phylogenetic tree depicting relationships of taxa of *Phaeotremellaceae* within *Tremellales* and *Trichosporonales*, *Hotermanniales*, *Filobasidiales*, and *Cystofilocasidiales*. The novel species are highlighted in bold, with patenthetical numbers indicating the number of novel taxa per clade. The scale bar represents 0.1 nucleotide substitution per site.

### ***Kockovaella* (*Cuniculitremaeae*, *Tremellales*, *Tremellomycetes*)**

Three isolates were identified as three distinct lineages within the genus *Kockovaella* (Figs. 3, 4, S3). The strain CGMCC 2.6772 clustered with *Koc. mexicanus* and *Koc. prillingeri* with strong statistical supports (BP/PP = 97%/1.0) (Fig. 3), but differed from these two species by 10–12 nucleotide substitutions (~1.6–1.9%) in the D1/D2 domains and exceeding 6% mismatches in the ITS regions. The strain CGMCC 2.6706 showed close phylogenetic affinity to *Koc. thailandica* with strong supports in the six-locus tree (BP/PP = 100%/1.0) and constrained D1/D2 tree (BP = 100%) (Figs. 3, 4); however, it differed from this species by 10 nucleotide substitutions (~1.6%) and 25 nucleotide mismatches (~4.8%) in the D1/D2 domains and ITS regions, respectively. The strain CGMCC 2.6642 was sister to the clade including *Koc. pahffii* and *Koc. machilophila* (Figs. 3, 4) and differed from them by 16–21 nucleotide substitutions (~2.5–3.3%) in the D1/D2 domains and exceeding 8.5% mismatches in the ITS regions. Accordingly, the three lineages represented by CGMCC 2.6772, 2.6706, and 2.6642 are recognized as novel species within the genus *Kockovaella*.

### ***Teunia* (*Cryptococcaceae*, *Tremellales*, *Tremellomycetes*)**

Group CGMCC 2.6461 was closely related to *Teu. globosa* in both concatenated rDNA and six-locus analyses (Figs. 3, S3). Three isolates in this group, obtained from tidal flat soil sediment, had identical ITS and D1/D2 sequences. They showed significant sequence divergences from *Teu. globosa* by nine nucleotide mismatches (~1.4%) in the D1/D2 domains and exceeding 23% mismatches in the ITS regions. Four unpublished strains ‘*Cryptococcus*’ sp. CBS 10169 (EU002793), ‘*Cryptococcus*’ sp. GJ2L06 (FJ527075), ‘*Cryptococcus*’ sp. SJ15L08 (EU523611), and ‘*Fonsecazyma*’ sp. KT301 (MH712815) from plant leaves and litter were closely related to this group, differing from them by 7–10 nucleotide mismatches (~1.1–1.6%) in the D1/D2 domains. The sequence similarity indicates that these four unpublished isolates constitute a new species in *Teunia*.

### ***Buzzinia* (*Phaeotremellaceae*, *Tremellales*, *Tremellomycetes*)**

Taxonomic delineation of new genera confirmed that the strain CGMCC 2.6779 has been assigned to the newly proposed genus *Buzzinia* (Figs. 3, 4, S3). Consequently, we propose a novel *Buzzinia* species to accommodate this strain.

### ***Yunzhangomyces* (*Brachybasidiaceae*, *Exobasidiales*, *Exobasidiomycetes*)**

The genus *Yunzhangomyces* was recently constructed and harbors five species (Li et al. 2022). Group CGMCC 2.6604 formed a sister cluster to four described species, *Yun. clavatus*, *Yun. cylindricus*, *Yun. orchidis*, and *Yun. scirpi*, and an undescribed strain *Yunzhangomyces* sp. HLJ921 in the concatenated rDNA and six-locus trees (Figs. 5, 6, S4). The three isolates in this group had identical D1/D2 sequences and fewer than three nucleotide differences in the ITS regions. They displayed significant divergence from their closest relatives, including four described species and *Yunzhangomyces* sp. HLJ921 by 20–31 nucleotide differences (~3.3–5.1%) in the D1/D2 domains and ~17.2–18.9% mismatches in the ITS regions. An undescribed strain, ‘*Exobasidium*’ sp. NRP040 (AB726742), also clustered with group CGMCC 2.6604 (Figs. 5, 6) but showed 24 nucleotide

substitutions (~4.0%) in the D1/D2 domains, indicating that this undescribed strain likely constitutes another species. We propose a new species for group CGMCC 2.6604.

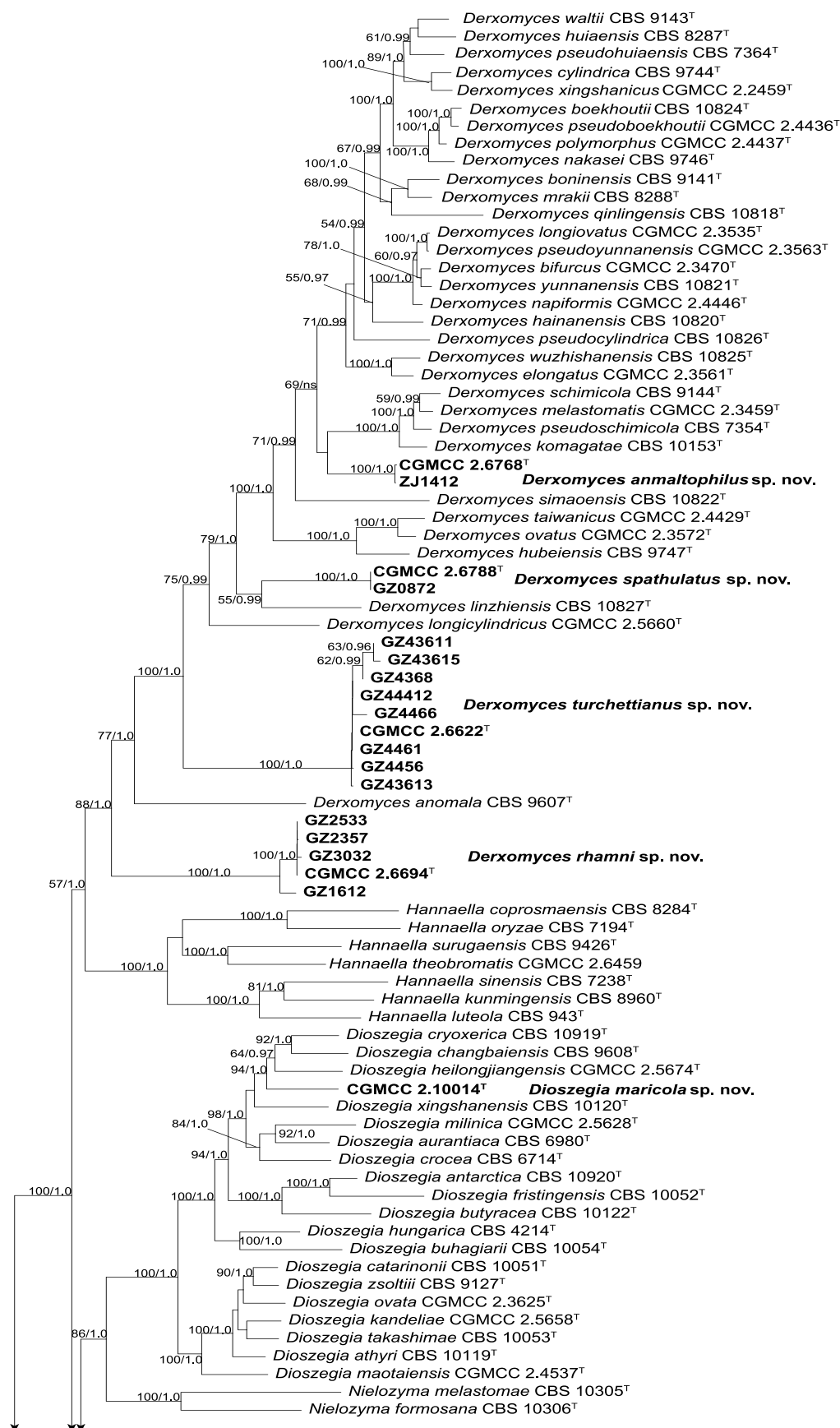


Figure 3 – Continued (Section B).





Figure 3 – Continued (Section C).

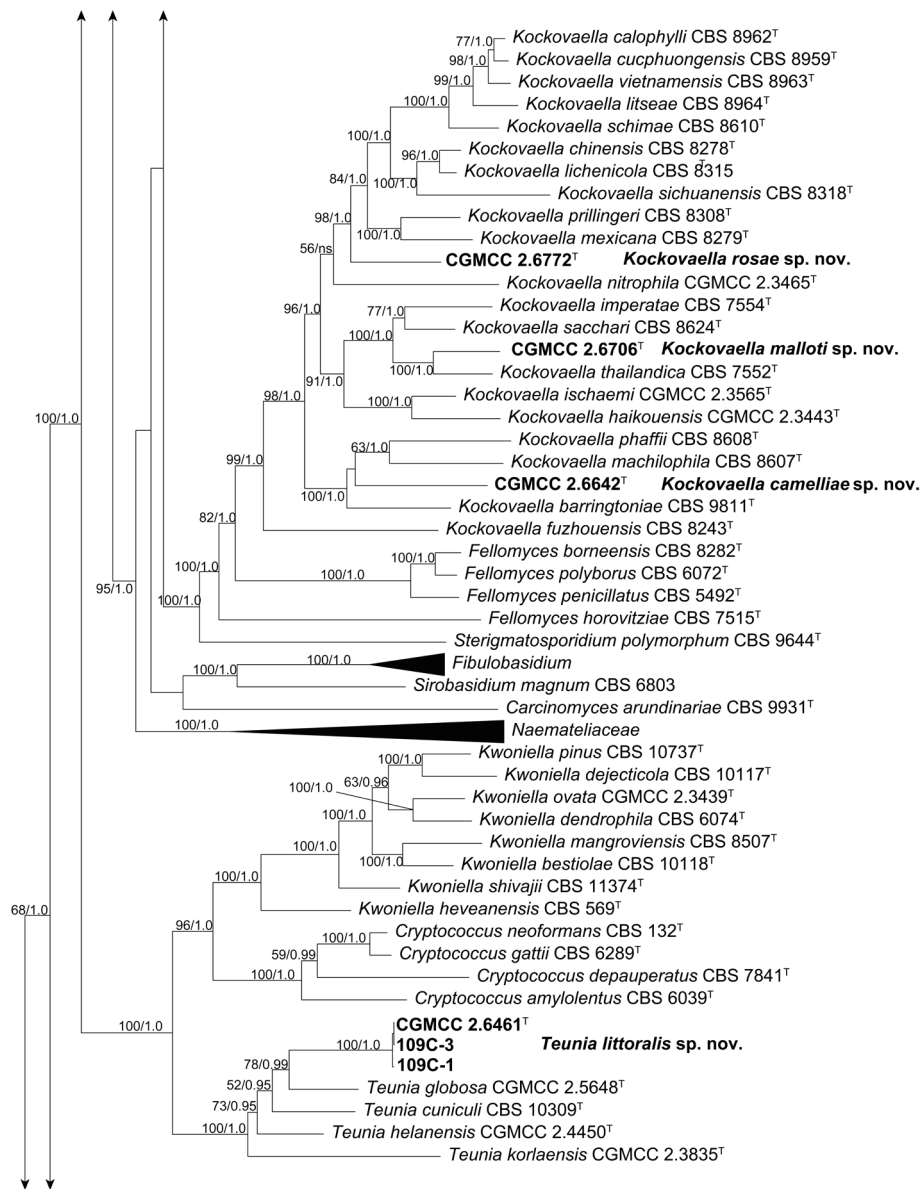


Figure 3 – Continued (Section D).

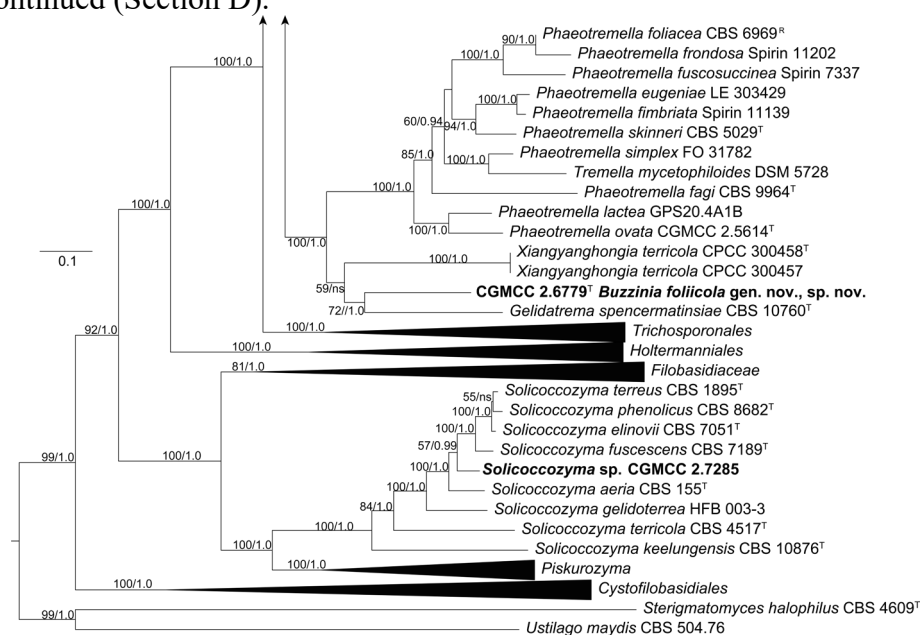
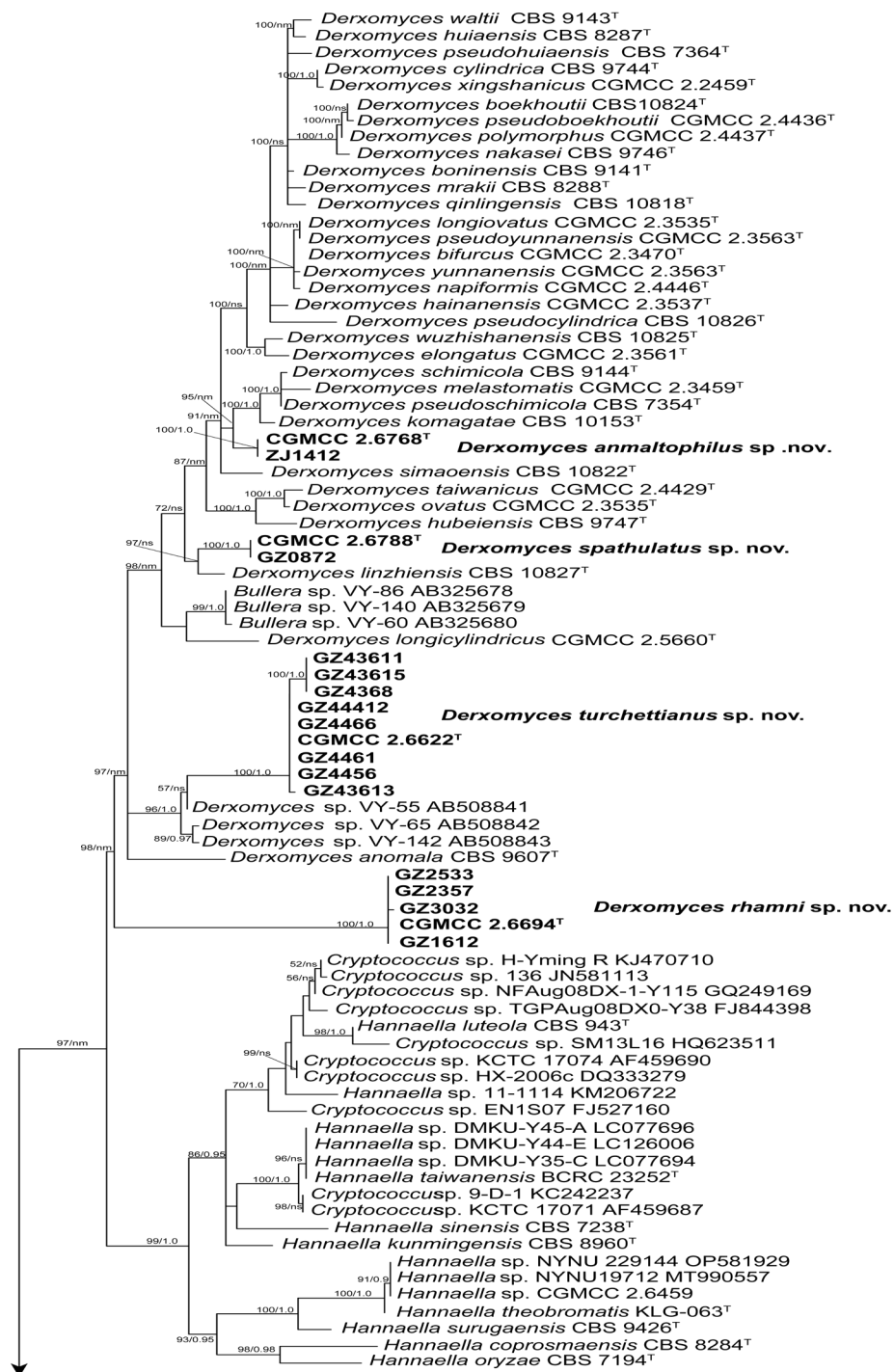


Figure 3 – Continued (Section E).



**Figure 4** – Constrained maximum likelihood phylogeny of *Tremellomycetes* based on LSU rDNA D1/D2 domain sequences, reconstructed using RAXML and MrBayes with a backbone constraint derived from the six-gene phylogeny (Section A). Nodal support values indicate bootstrap percentages (BP  $\geq 50\%$ ) from 1,000 replicates and Bayesian posterior probabilities (PP  $\geq 0.9$ ). A. Section of the phylogenetic relationships of *Derxomyces/Hannaella*. B. Section of the phylogenetic relationships of *Dioszegia/Bulleribasidium*. C. Section of the phylogenetic relationships of *Trimorphomycetaceae/Tremellaceae/Vishniacozyma*. D. Section of the phylogenetic relationships of *Rhynchogastremaceae*. E. Section of the phylogenetic relationships of *Bulleraceae/Cuniculitremaceae/Siobasidiaceae/Carcinomyetaceae/Naemateliaceae*. F. Section of the phylogenetic relationships of *Cryptococcaceae*. G. Section of the phylogenetic relationships of *Phaeotremellaceae*. H. Section of the phylogenetic relationships of *Filobasidiales*. The novel species are highlighted in bold. The scale bar represents 0.05 nucleotide substitutions per site

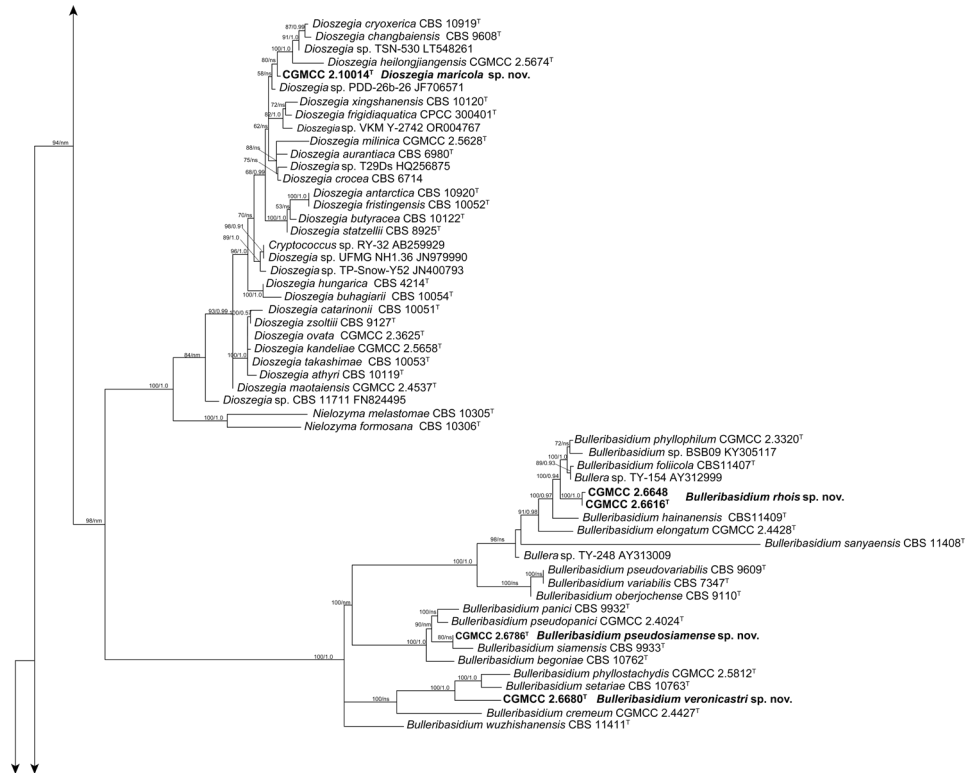


Figure 4 – Continued (Section B).

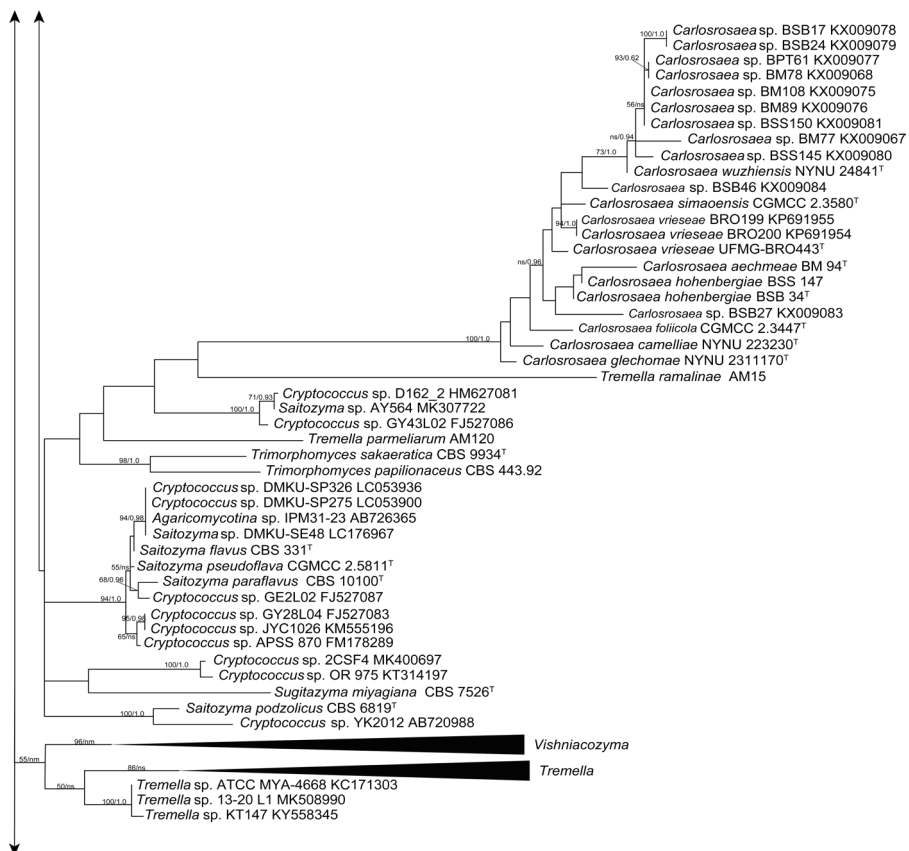


Figure 4 – Continued (Section C)

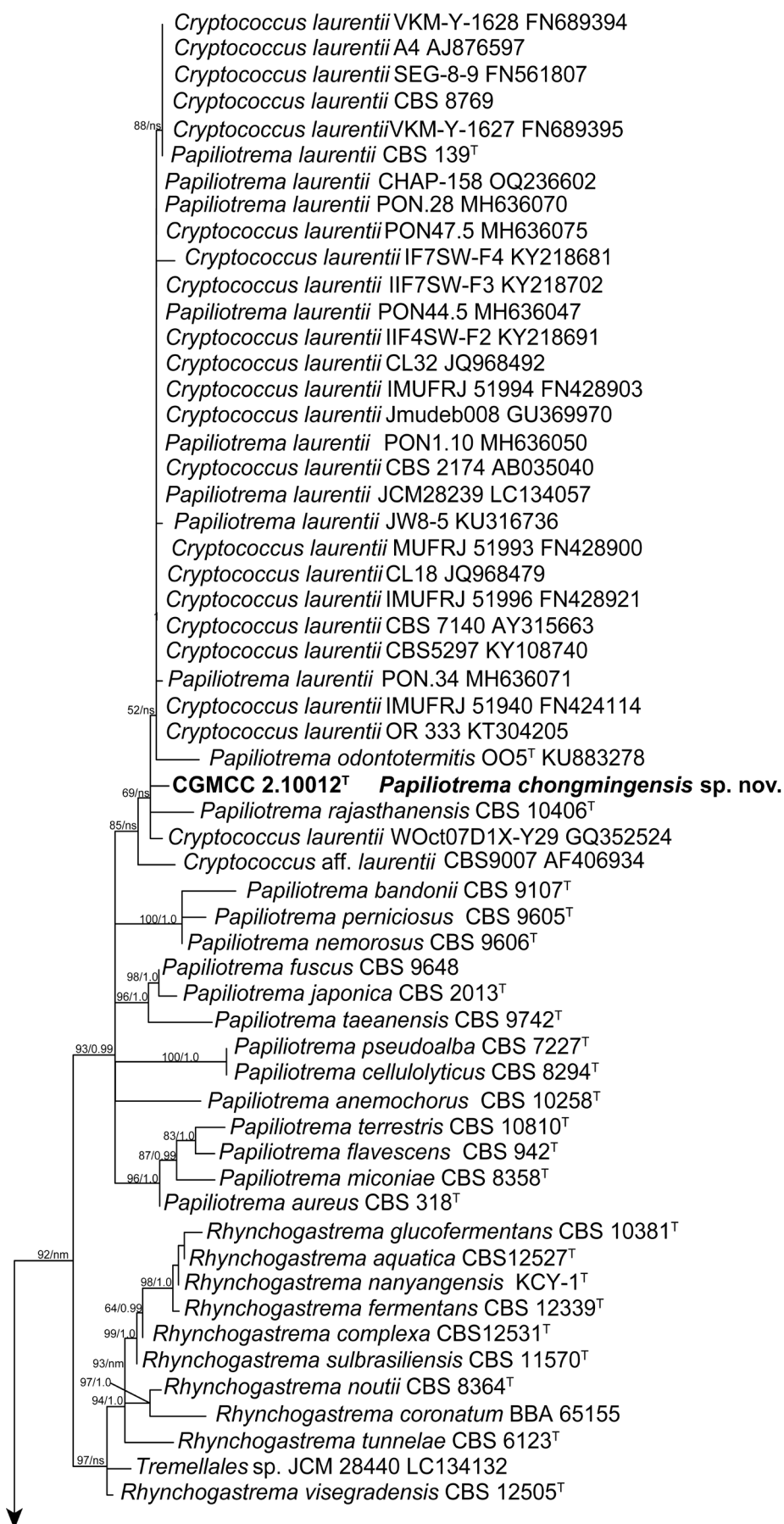


Figure 4 – Continued (Section D)



Figure 4 – Continued (Section E)

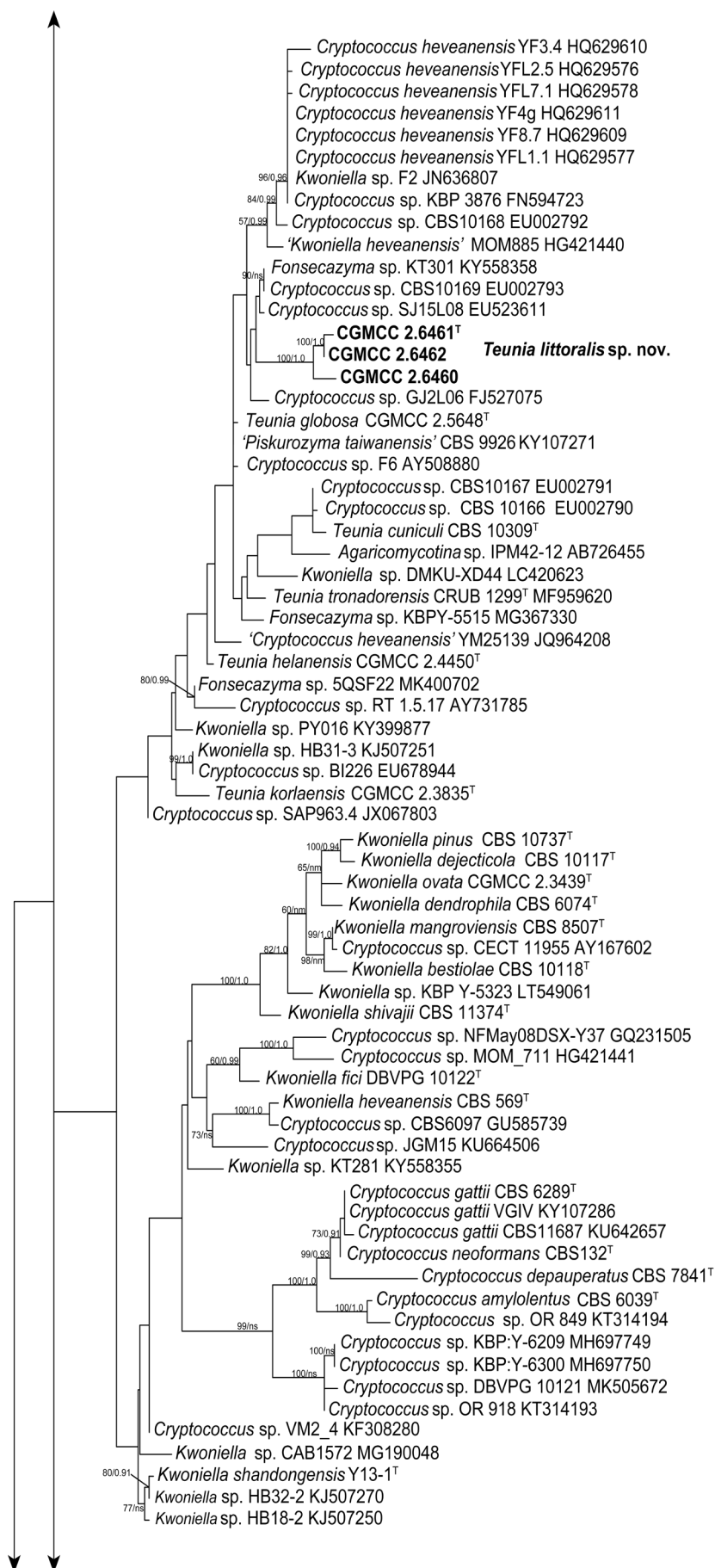


Figure 4 – Continued (Section F)

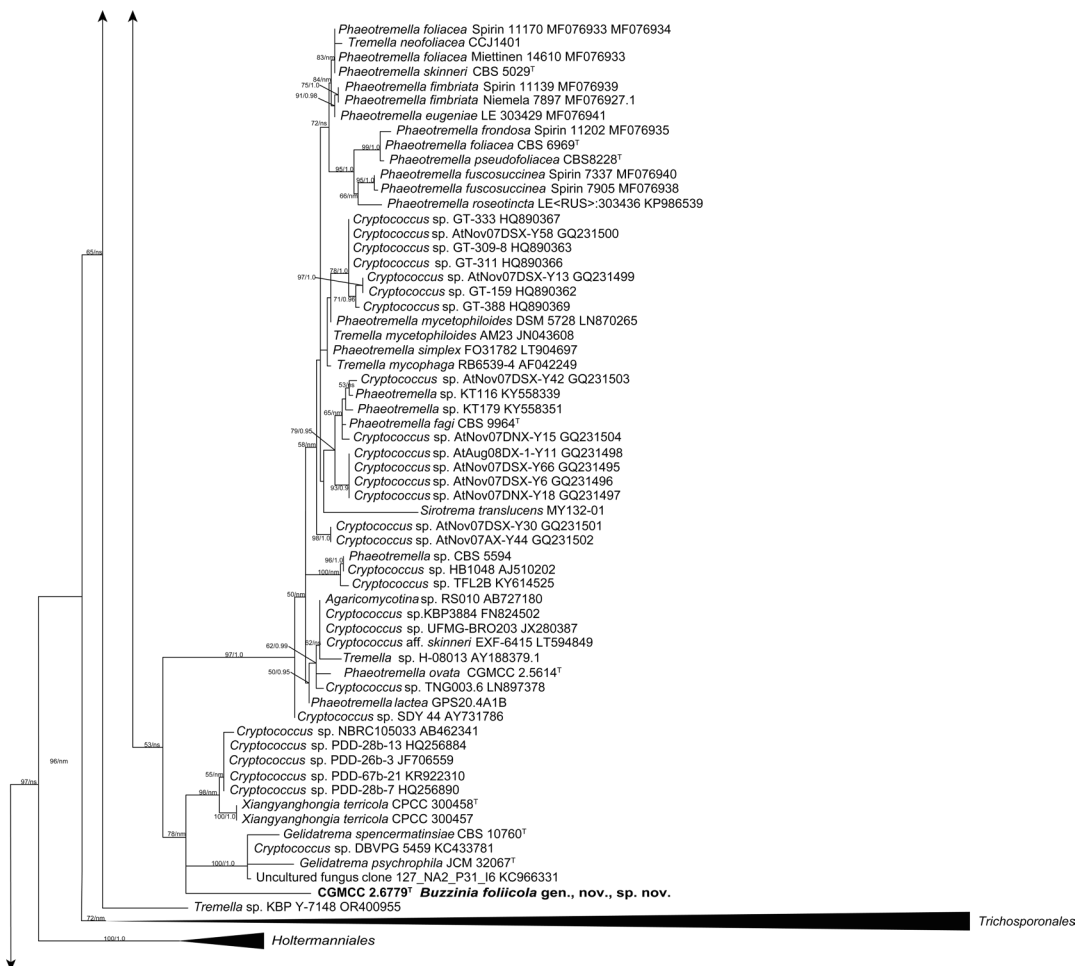


Figure 4 – Continued (Section G)

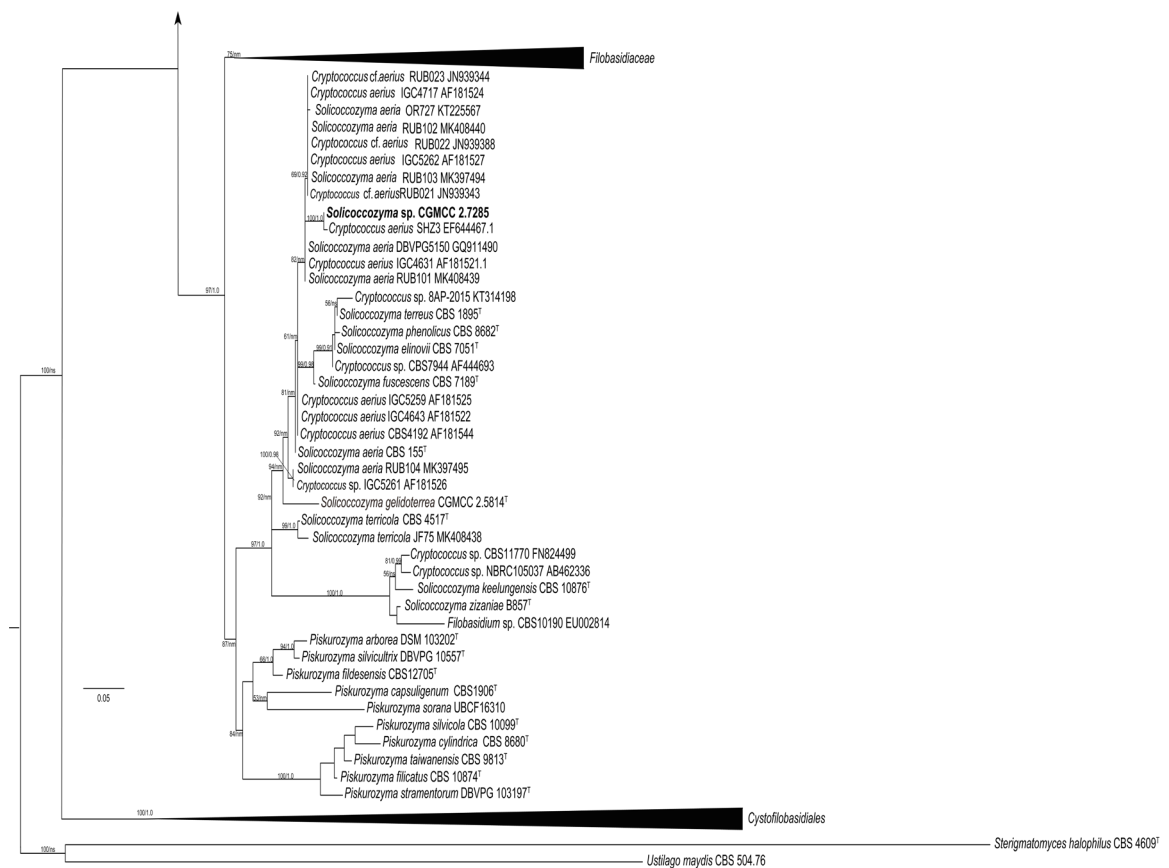
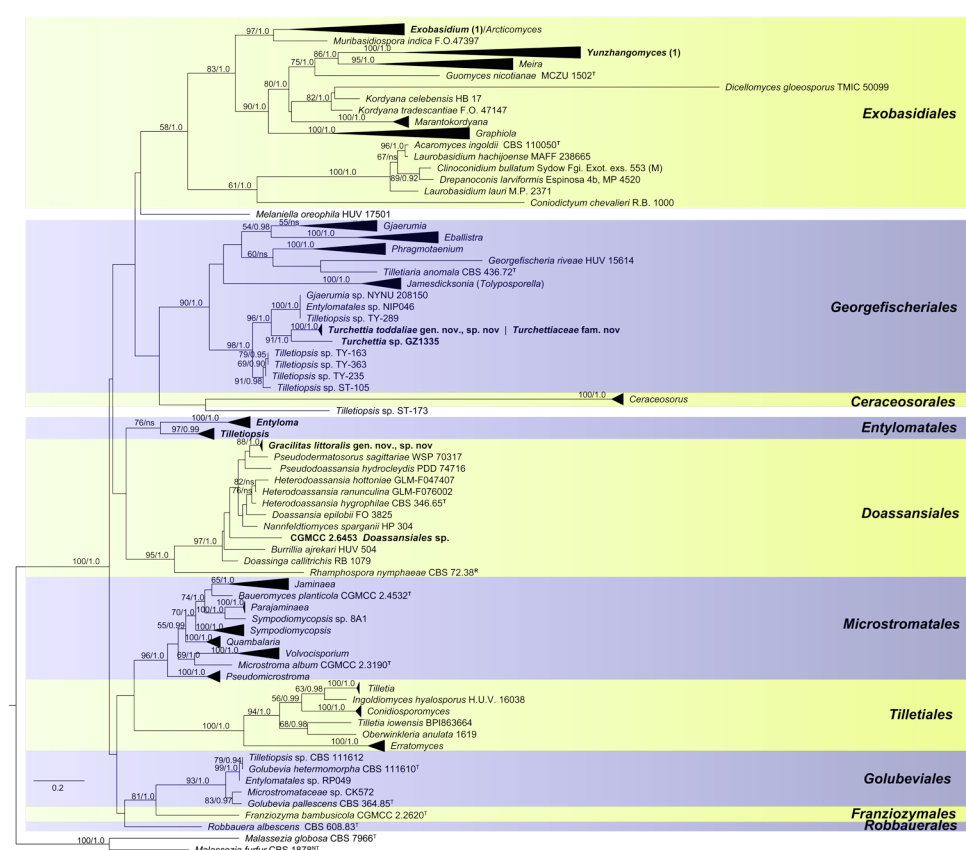


Figure 4 – Continued (Section H)



## *Exobasidium* (*Exobasidiaceae*, *Exobasidiales*, *Exobasidiomycetes*)

The genus *Exobasidium* contains approximately 50 species, which are important plant pathogenic fungi parasitizing different host families such as *Escalloniaceae*, *Ericaceae*, *Saxifragaceae*, *Symplocaceae*, and *Theaceae* (Begerow et al. 2014, Nagao & Kasuya 2023). The Nannfeldt-Sundström's species concept, based on morphological characteristics (e.g., basidiospore morphology, germination modes) and host specificity, is widely used in the taxonomy of *Exobasidium* (Sundström 1964, Nannfeldt 1981). This morphological delimitation was later supported by molecular phylogenetic studies utilizing ITS and LSU sequences (Kennedy et al. 2012, Piatek et al. 2012, Nagao & Kasuya 2023). The strain CGMCC 2.6728 was positioned on an independent lineage adjacent to *Exo. symploci-japonicae* and *Exo. siroboe* (Figs. 5, 6). It diverged from the two varieties of *Exo. symploci-japonicae* by 9–10 nucleotide mismatches (~1.4–1.6%) in the D1/D2 domains and 25–27 nucleotide mismatches (~4.0–4.3%) in the ITS regions. It differed from *Exo. siroboe* by nine nucleotides (~1.4%) in the D1/D2 domains and three nucleotide mismatches in the ITS regions. Given that several *Exobasidium* species were described exclusively via morphological characters, we need to be cautious when describing new species based solely on molecular data to avoid delimiting the species that already exist. *Exobasidium sakataniense* shows morphological similarities to *Exo. symploci-japonicae* (Nagao et al. 2003). Group CGMCC 2.6728 differed from *Exo. sakataniense* in the size of conidia. Crucially, the hosts of *Exo. symploci-japonicae* and *Exo. sakataniense* are restricted to *Symplocos*, whereas the host of group CGMCC 2.6728 is *Viburnum utile*. Additionally, *Exo. siroboe* differs from the strain CGMCC 2.6728 by having narrower conidia and the different hosts (Nagao et al. 2023). These findings justify the classification of the strain CGMCC 2.6728 as a distinct species within the genus *Exobasidium*.



**Figure 5** – Maximum likelihood phylogeny of *Exobasidiomycetes* inferred from concatenated ITS and LSU rDNA D1/D2 sequences using RAXML, with nodal support values indicated as bootstrap percentage (BP) from 1,000 replicates and Bayesian posterior probabilities (PP) (Section A). Only

nodes with BP  $\geq 50\%$  and PP  $\geq 0.9$  are labeled. The new species are highlighted in bold, with parenthetical numbers indicating the number of novel taxa per clade. A. The schematic tree illustrating phylogenetic relationships of genera and single-species clades within *Exobasidiomycetes*. B. Section of the phylogenetic tree depicting relationships of taxa within *Exobasidiales*. C. Section of the phylogenetic tree depicting relationships of taxa within *Georgefischeriales*, *Ceraceosorales*, *Entylomatales*, and *Doassansiales*. D. Section of the phylogenetic tree depicting relationships of taxa within *Microstromatales*, *Tilleiales*, *Golubeviales*, *Franzioziales*, and *Robbauerales*. The scale bar represents 0.2 nucleotide substitution per site.

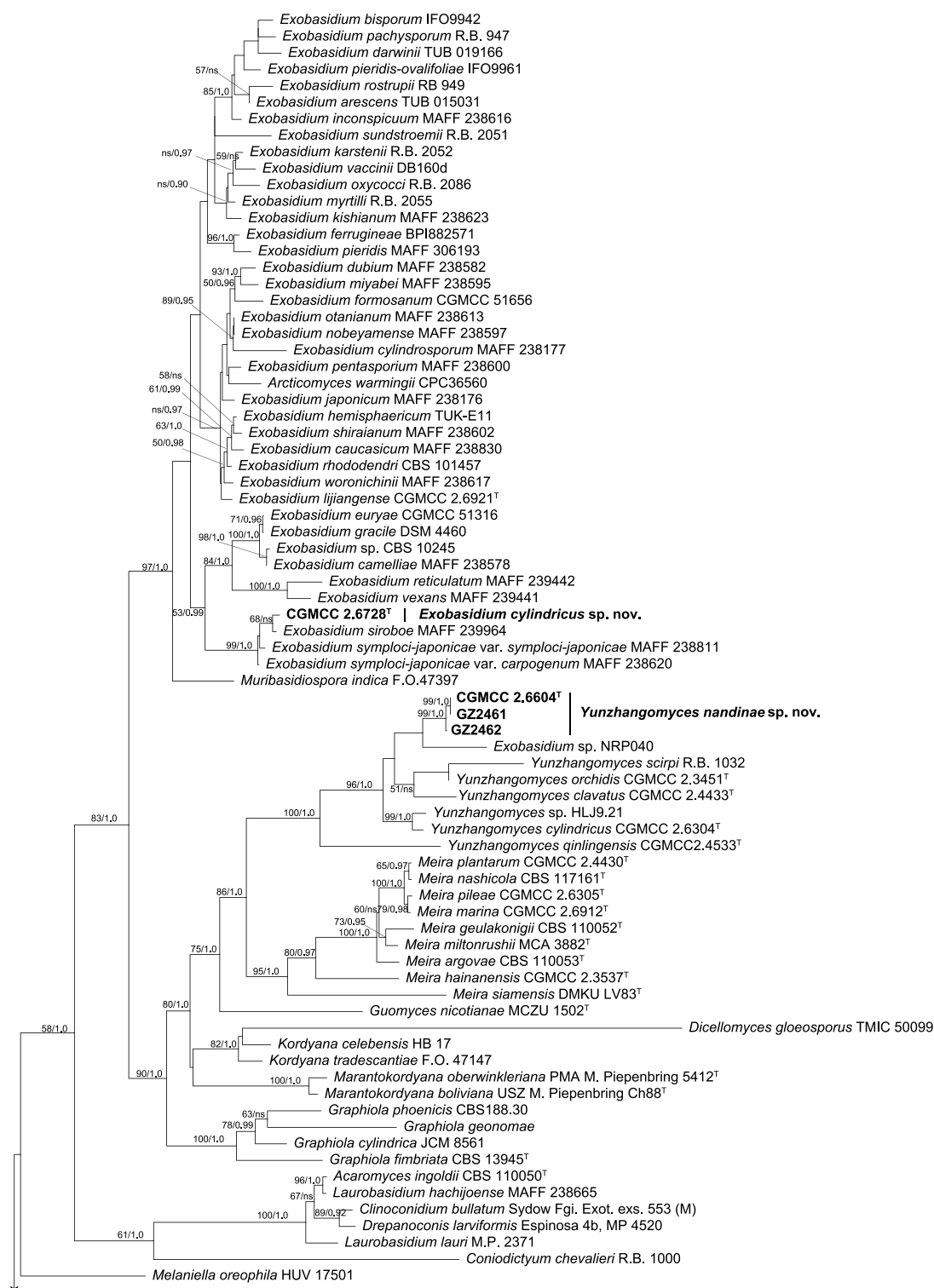


Figure 5 – Continued (Section B).

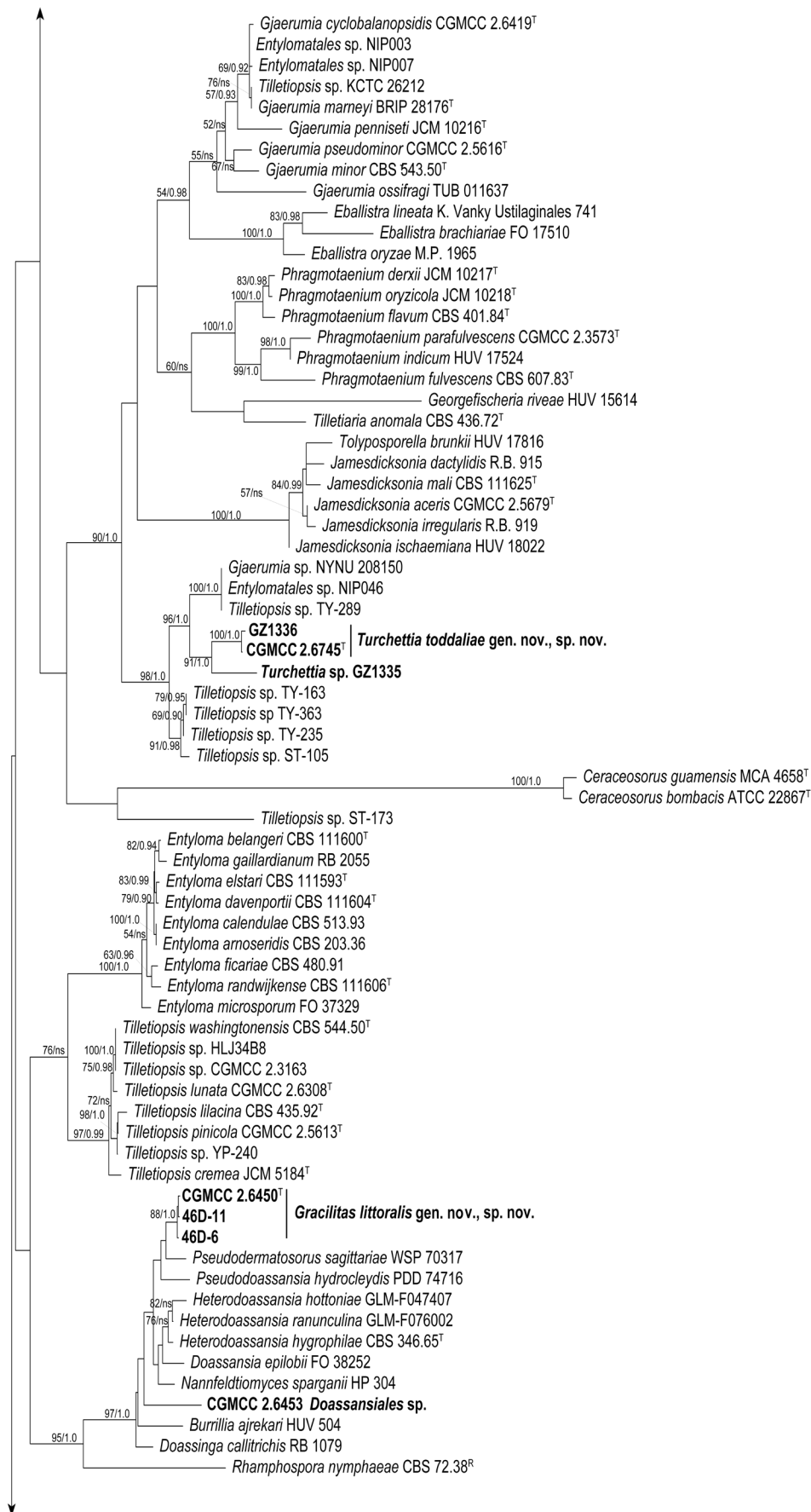
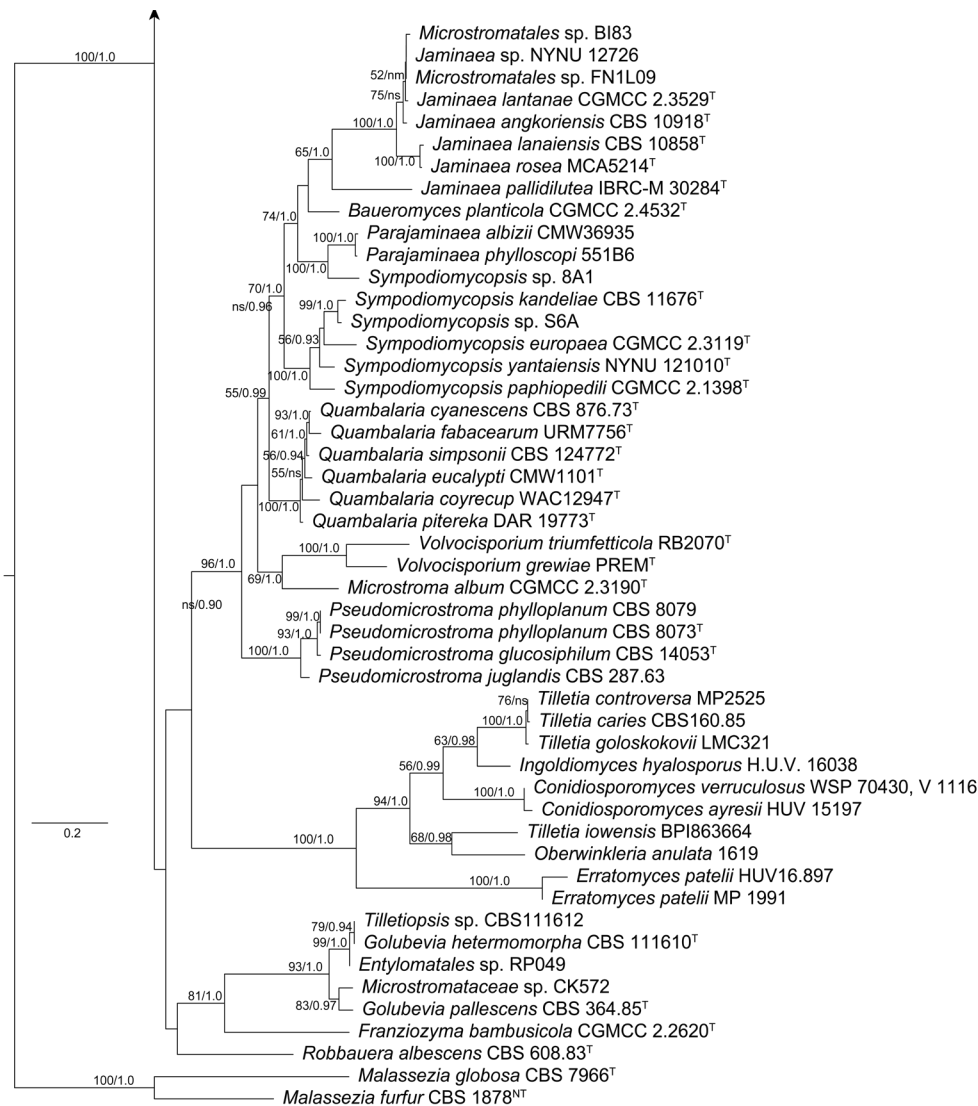


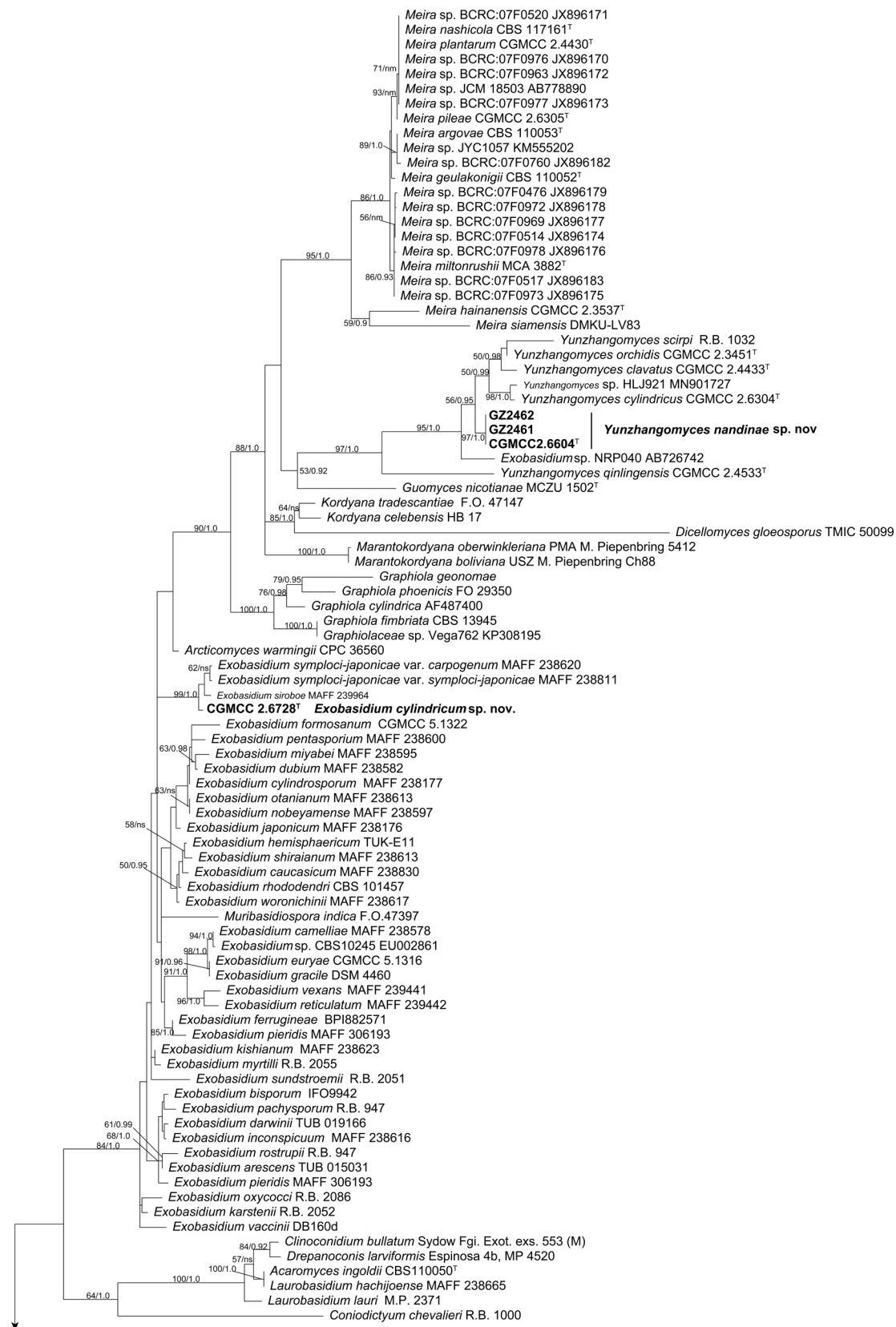
Figure 5 – Continued (Section C).



**Figure 5** – Continued (Section D).

### ***Turchettia* (Georgfischeriales, Exobasidiomycetes)**

Two isolates, CGMCC 2.6745 and GZ1336, formed a distinct basal clade within *Georgfischeriales* (Fig. 5). The isolate GZ1335 showed close phylogenetic affinity to group CGMCC 2.6745, differing by no more than five nucleotides in the D1/D2 domains and exceeding 8% mismatches in the ITS regions, implying that it represents a distinct species. Seven unpublished strains, such as *Entylomatales* sp. NIP046 (AB726628), *Gjaerumia* sp. NYNU 208150 (MW368734), *Tilletiopsis* sp. TY-289 (AY313022), *Tilletiopsis* sp. ST-105 (DQ404458), *Tilletiopsis* sp. TY-163 (AY313020), *Tilletiopsis* sp. TY-235 (AY313021), and *Tilletiopsis* sp. TY-363 (AY313023), clustered with group CGMCC 2.6745 and GZ1335 with strong supports (BP/PP = 99%/1.0) (Figs. 5, 6). These seven strains separated into two divergent subclades. The first subclade, including *Entylomatales* sp. NIP046, *Gjaerumia* sp. NYNU 208150, and *Tilletiopsis* sp. TY-289, exhibited 12 to 14 nucleotide substitutions (~2.0–2.3%) in the D1/D2 domain when compared to the group CGMCC 2.6745 and GZ1335. The second subclade, including *Tilletiopsis* sp. ST-105, *Tilletiopsis* sp. TY-163, *Tilletiopsis* sp. TY-235, and *Tilletiopsis* sp. TY-363 displayed greater sequence divergence, with 20 to 21 nucleotide mismatches (~3.3–3.5%) in the same region. The molecular distance confirmed that these seven unpublished isolates represented distinct species. Accordingly, we propose a novel species to accommodate isolates CGMCC 2.6745 and GZ1336.



**Figure 6** – Maximum likelihood phylogeny of *Exobasidiomycetes* inferred from the LSU rDNA D1/D2 domain sequences, reconstructed using RAxML and MrBayes (Section A). Nodal support values indicate bootstrap percentage (BP  $\geq$  50%) from 1,000 replicates and Bayesian posterior

probabilities (PP  $\geq$  0.9). A. Section of the phylogenetic relationships of *Exobasidiales*. B. Section of the phylogenetic relationships of *Entylomatales*, *Tilleiales*, *Doassansiales*, *Microstromatales*, *Golubeviales*, *Franzioziales*, *Ceraceosorales*, *Georgefischeriales*, and *Robbauerales*. The new species are highlighted in bold. The scale bar represents 0.02 nucleotide substitutions per site.

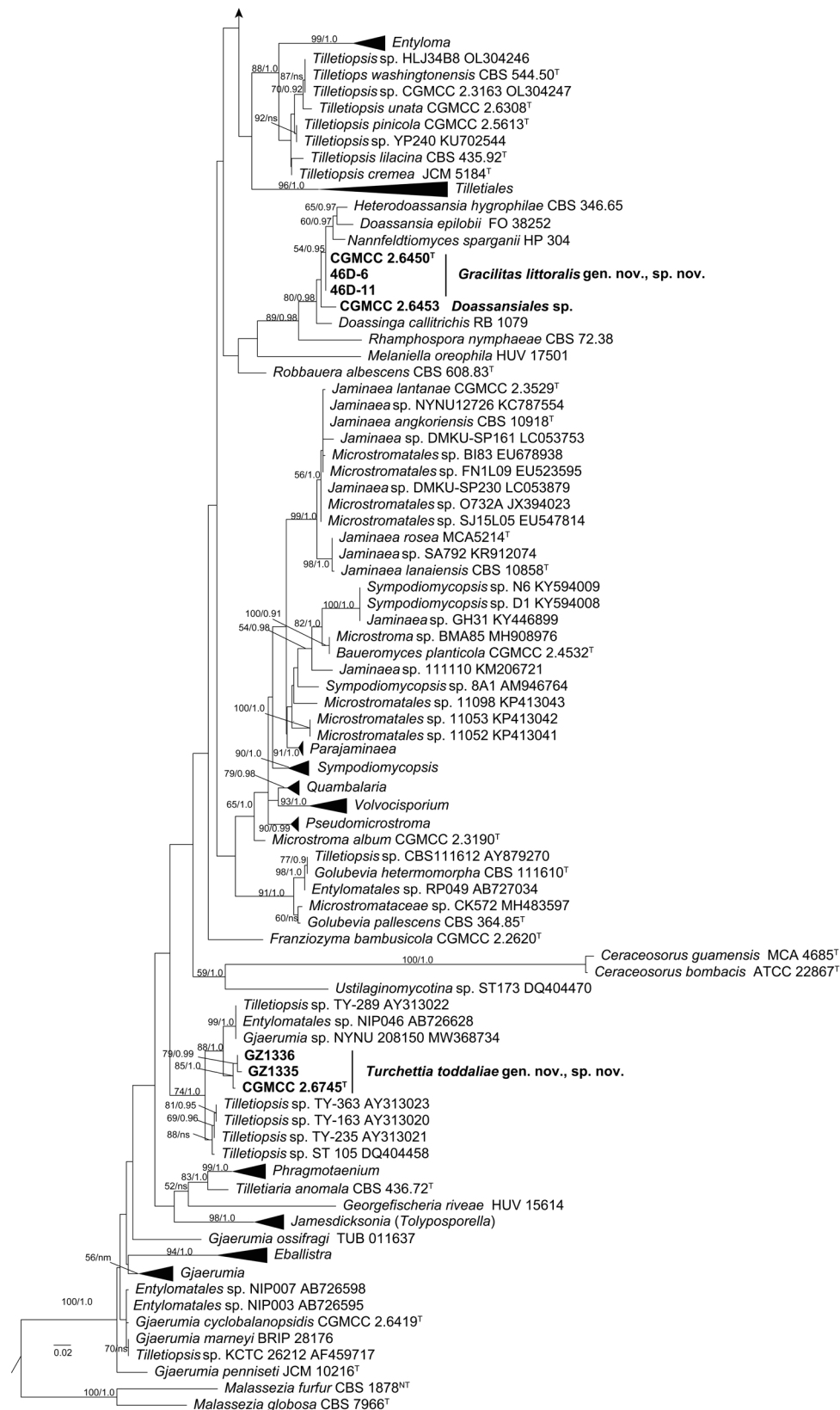


Figure 6 – Continued (Section B).

***Gracilitas* (Doassansiaceae, Doassansiales, Exobasidiomycetes)**

Three isolates, isolated from tidal flat seawater, exhibited identical D1/D2 and ITS sequences. These isolates clustered into a strongly supported lineage, justifying the establishment of a new genus, *Gracilitas*, under the family *Doassansiaceae* (Fig. 5) and the designation of a new species.

**Taxonomy**

***Pucciniomycotina, Agaricostillbomycetes, Agaricostilbales, Chionosphaeraceae***

***Ballistosporomyces berchemiae* X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.**

Fig 7a, b

MycoBank number: MB851010

Etymology – The epithet is derived from *Berchemia*, the host plant genus from which the type strain was obtained.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Hexi Town, on plant leaf of *Berchemia flavescentis*, May 2020, Z.N. Du (holotype CGMCC 2.6700, lyophilized metabolically inactive cells, ex-type culture JCM 35446 = GZ1923).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear pale-orange, butyrous, semi-glossy, and smooth with an entire margin (Fig. 7a). On YM agar incubated at 20 °C for 7 days, cells are ellipsoidal,  $2.5\text{--}4.2 \times 5.1\text{--}9.8 \mu\text{m}$ , and occur singly (Fig. 7b), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, YM, PDA, V8 and YCB. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, sucrose, maltose, cellobiose, trehalose, raffinose, soluble starch, ribitol (weak), D-mannitol, D-glucitol (delayed), and Methyl- $\alpha$ -D-glucoside (weak) as the only carbon sources. However, it does not assimilate galactose, L-sorbose, lactose, melibiose, melezitose, inulin, D-xylose, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, glycerol, erythritol, galactitol, salicin, D-glucuronic acid, DL-lactate, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, L-lysine, and cadaverine serve as the only nitrogen sources. In contrast, no assimilation occurs when potassium nitrate, sodium nitrite, or ethylamine is the sole nitrogen source. The strain does not grow in a vitamin-free medium or produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 30 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Hexi Town, on plant leaf of *Berchemia flavescentis*, May 2020, Z.N. Du (culture GZ1923); Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Castanea henryi*, Oct. 2020, Z.N. Du (culture GZ1564) (n=2).

Notes – Physiologically, *Bal. berchemiae* can be differentiated from its close relatives *Bal. taupoensis* and *Bal. xanthus* by its negative assimilation of salicin and succinate, but its capacity for growth at 30 °C (Table S3).

***Pucciniomycotina, Agaricostillbomycetes, Agaricostilbales, Kondoaceae***

***Kondoa zhenganensis* X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.**

Fig. 7c–e

MycoBank number: MB851021

Etymology – The epithet *zhenganensis* refers to the type locality, Zhengan County, Guizhou Province.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Kadsura longipedunculata*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6730, lyophilized metabolically inactive cells, ex-type culture JCM 39295 = GZ04720).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear creamish white, mucoid, smooth, and glistening with an entire margin (Fig. 7c). On YM agar incubated at 20 °C for 7 days, cells are fusiform, long ellipsoidal,  $2.5\text{--}4.3 \times 5.7\text{--}10.8 \mu\text{m}$ , and occur singly (Fig. 7d),

exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8 and YCB agar. Ballistoconidia are allantoid and reniform,  $1.4\text{--}2.2 \times 4.1\text{--}4.3$   $\mu\text{m}$  on CMA agar (Fig. 7e).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, maltose, cellobiose, trehalose, melibiose, raffinose, melezitose, soluble starch, glycerol (weak), erythritol (weak), ribitol (weak), D-mannitol (weak), and D-glucitol as the only carbon sources. However, it does not assimilate L-sorbose, lactose, inulin, D-xylose, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, galactitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, DL-lactate, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate, and ethylamine (delayed and weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when L-lysine, sodium nitrite, or cadaverine is the sole nitrogen source. The strain does not grow in a vitamin-free medium or produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature is 28 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Kadsura longipedunculata*, Oct. 2020, Z.N. Du (cultures GZ04720, GZ04621, GZ04721, GZ04730) (n=4).

Notes – Physiologically, *Kon. zhenganensis* can be differentiated from its close relative *Kon. thailandica* by its positive assimilation of erythritol and ethylamine, but its negative assimilation of citrate, galactitol, succinate, and sodium nitrite (Table S3).

#### ***Pucciniomycotina, Agaricostillbomycetes, Agaricostilbales, Ruineniaceae***

***Ruinenia pseudopyrrosiae*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 7f, g

Mycobank number: MB851026

Etymology – The epithet *pseudopyrrosiae* refers to the similar colony morphology to that of *Ruinenia pyrrosiae*.

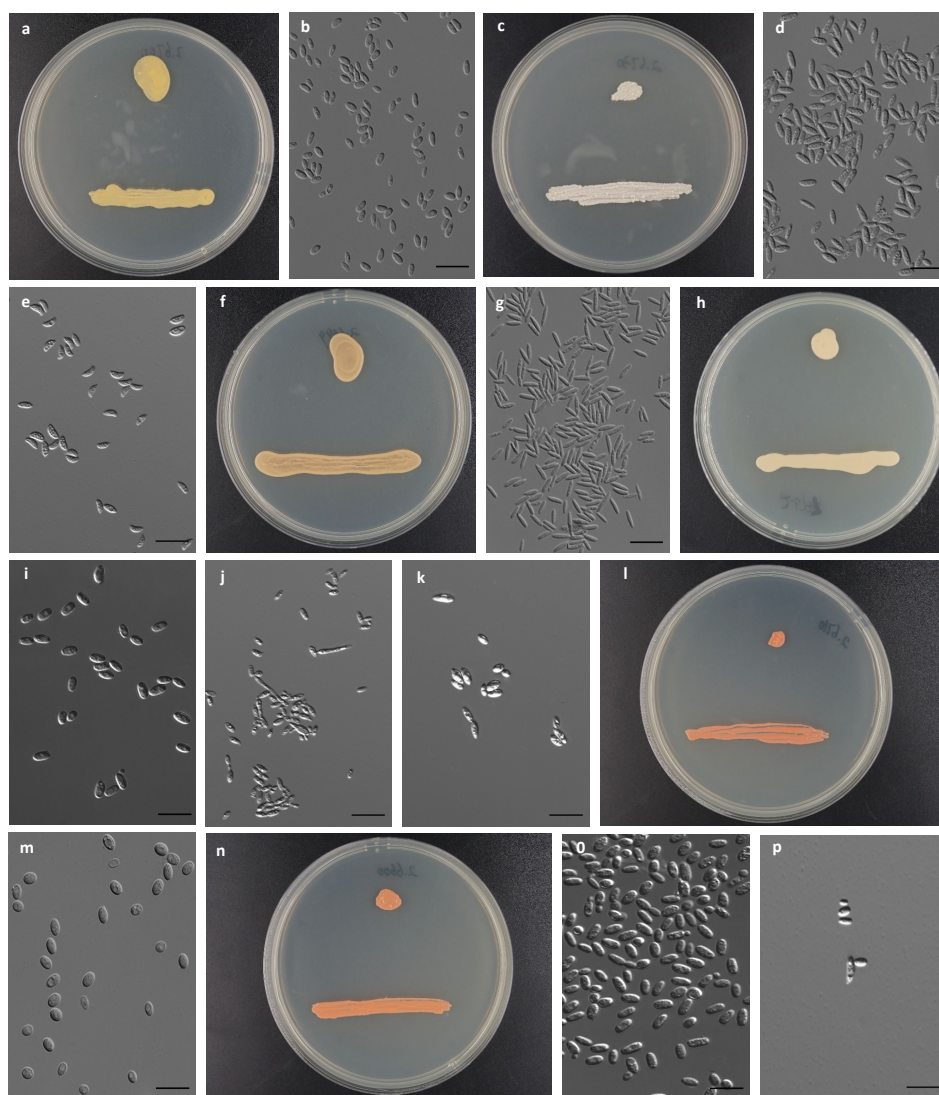
Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Viburnum utile*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6699, lyophilized metabolically inactive cells, ex-type culture JCM 35445 = GZ0142).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear pink-orange, butyrous, and smooth with an entire margin (Fig. 7f). On YM agar incubated at 20 °C for 7 days, cells are long ellipsoidal, cylindrical, or elongated fusiform,  $2.0\text{--}3.0 \times 7.0\text{--}14.1$   $\mu\text{m}$ , and occur singly (Fig. 7g), exhibiting polar budding. In YM broth incubated at 25 °C for one month, sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (weak), sucrose, cellobiose, trehalose, melibiose (weak), raffinose (weak), soluble starch, D-mannitol, D-glucitol (weak), and salicin (weak) as the only carbon sources. However, it does not assimilate L-sorbose, maltose, lactose, melezitose, inulin, D-xylose, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, glycerol, erythritol, ribitol, galactitol, Methyl- $\alpha$ -D-glucoside, D-glucuronic acid, DL-lactate, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed), L-lysine (delayed), ethylamine, and cadaverine (delayed) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain does not grow in a vitamin-free medium or produce starch-like substances. It tests for variable urease activity and is positive for the Diazonium Blue B reaction. The highest growth temperature is 29 °C.

Material examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Viburnum utile*, Oct. 2020, Z.N. Du (culture GZ0142) (n=1).





**Figure 7** – The streak culture and vegetative cells grown on YM agar for 7 days at 20 °C, and ballistoconidia formation observed on corn meal agar after 7 days at 20 °C of the new yeast species within *Pucciniomycotina*. (a, b) *Ballistosporomyces berchemiae* CGMCC 2.6700<sup>T</sup>; (c–e) *Kondoa zhenganensis* CGMCC 2.6730<sup>T</sup>; (f, g) *Ruinenia pseudopyrrosiae* CGMCC 2.6699<sup>T</sup>; (h–k) *Nakasea foliicola* CGMCC 2.6737<sup>T</sup>; (l, m) *Bannoa hyperici* CGMCC 2.6710<sup>T</sup>; (n–p) *Bannoa lonicerae* CGMCC 2.6600<sup>T</sup>. Bars = 10 μm.

Notes – Physiologically, *Rui. Pseudopyrrosiae* can be differentiated from its close relatives, *Rui. dracophylli*, *Rui. fanjingshanensis*, *Rui. pyrrosiae*, and *Rui. rubra*, by its positive assimilation of potassium nitrate and L-lysine, and negative assimilation of ribitol (Table S3).

***Pucciniomycotina*, *Agaricostillbomycetes*, *Agaricostilbales*, *Jianyuniaceae***

***Nakasea* X.Z. Liu & F.Y. Bai, gen. nov.**

Mycobank number: MB851027

Etymology – The genus name honors Dr. Takashi Nakase, formerly Director of the Japan Collection of Microorganisms, for his outstanding contributions to yeast systematics.

Type species – *Nakasea foliicola* X.Z. Liu, F.Y. Bai & J.Q. Sun.

No sexual reproduction observed. Colonies are white-cream, pale yellow to pale pink, butyrous, dull, and smooth. Vegetative reproduction occurs via budding cells and production of blastoconidia on stalk-like conidiophores. Conidiophores occur singly or in multiples, seldom bifurcated. Pseudohyphae are absent, and hyphae are rarely produced. Ballistoconidia are observed.

Accepted species – *Nakasea foliicola*

Notes – Physiologically, *Nakasea* can be differentiated from its close relatives, *Jianyunia sakaguchii*, *Sterigmatospora layueensis*, and *Pseudosterigmatospora motuoensis* by its positive assimilation of potassium nitrate and L-lysine, but negative assimilation of melibiose, D-arabinose, D-ribose, glycerol, erythritol, and DL-lactate. Moreover, *Nakasea* differs from its related genera by its capacity to hydrolyze urea (Table S3).

***Nakasea foliicola*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 7h–k

MycoBank number: MB851028

Etymology – The epithet *foliicola* refers to the leaf origin of the type strain.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Kadsura longipedunculata*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6737, lyophilized metabolically inactive cells, ex-type culture JCM 35454 = GZ04620).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear white-cream, pale yellow to pale pink, butyrous, dull, and smooth with an entire margin (Fig. 7h). On YM agar incubated at 20 °C for 7 days, cells are fusiform, ellipsoidal, or long ovoid,  $4.0\text{--}4.7 \times 4.4\text{--}10.2\ \mu\text{m}$ , and occur singly (Fig. 7i), exhibiting polar budding. Stalk-like conidiophore, single or multiple, rarely bifurcated, produces one or more conidia. In YM broth incubated at 25 °C for one month, a ring and sediment formed. No pseudohyphae observed on CMA agar. Rare hyphae are formed in the YM agar (Fig. 7j). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are allantoid or reniform,  $1.7\text{--}2.3 \times 2.5\text{--}6.2\ \mu\text{m}$  on CMA agar (Fig. 7k).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (variable), sucrose, maltose (variable), cellobiose (variable), trehalose (variable), lactose (variable), melibiose (variable), melezitose, soluble starch (variable), D-arabinose (variable), D-ribose (variable), glycerol (variable), erythritol (variable), ribitol (variable), D-mannitol (positive or weak) and DL-lactate (variable) as the only carbon sources. However, it does not assimilate L-sorbose, raffinose, inulin, D-xylose, L-arabinose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, galactitol, D-glucitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed and weak), L-lysine, ethylamine (delayed), and cadaverine serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain grows variably in a vitamin-free medium or does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature is 30 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Kadsura longipedunculata*, Oct. 2020, Z.N. Du (cultures GZ04620, GZ0467, GZ04622, GZ04725), on plant leaf of *Viburnum dilatatum*, Oct. 2020, Z.N. Du (culture GZ0861); Guizhou Province, Zunyi City, Zhengan County, Hexi Town, on plant leaf of *Veronicastrum stenostachyum*, May 2020, Z.N. Du (culture GZ3034) (n=6).

***Pucciniomycotina*, *Cystobasidiomycetes*, *Erythrobasidiales*, *Erythrobasidiaceae***

***Bannoa hyperici*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 7l, m

MycoBank number: MB851011

Etymology – The epithet *hyperici* is derived from *Hypericum*, the host plant genus from which the type strain was obtained.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Hexi Town, on plant leaf of *Hypericum monogynum*, May 2020, Z.N. Du (holotype CGMCC 2.6710, lyophilized metabolically inactive cells, ex-type culture JCM 35449 = GZ2534).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear pinkish-orange-yellow, mucoid, smooth, and glistening or dull with an entire margin (Fig. 7l). On YM agar incubated at 20 °C for 7 days, cells are subglobose or ellipsoidal,  $5.4\text{--}6.5 \times 7.4\text{--}10.5\ \mu\text{m}$ , and occur singly (Fig. 7m), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures

are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, maltose, cellobiose (variable), trehalose (positive or delayed), melezitose, soluble starch, D-xylose, L-arabinose, D-arabinose (variable), N-Acetyl-D-glucosamine (variable), glycerol (positive or delayed or weak), ribitol (variable), D-mannitol (delayed), D-glucitol (variable), and citrate (variable) as the only carbon sources. However, it does not assimilate L-sorbose, lactose, melibiose, raffinose, inulin, D-ribose, L-rhamnose, D-glucosamine, methanol, ethanol, erythritol, galactitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, DL-lactate, succinate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed), L-lysine, ethylamine, and cadaverine serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain grows positive or delayed in a vitamin-free medium and does not produce starch-like substances. It tests variably for urease activity and is positive for the Diazonium Blue B reaction. The highest growth temperature is 28 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Hexi Town, on plant leaf of *Picrasma quassioides*, May 2020, Z.N. Du (GZ1531), on plant leaf of *Lonicera japonica*, May 2020, Z.N. Du (culture GZ2924), on plant leaf of *Hypericum monogynum*, May 2020, Z.N. Du (culture GZ2534) (n=2).

Notes – Physiologically, *Ban. hyperici* can be differentiated from all other *Bannoa* species by its negative assimilation of melibiose, raffinose, and salicin. It further differs from its closet relative, *Bannoa syzygii*, by its negative assimilation of melibiose, raffinose, L-rhamnose, methyl- $\alpha$ -D-glucoside, salicin, D-gluconate, DL-lactate, and succinate, as well as its positive assimilation of ethylamine and cadaverine (Table S3).

***Bannoa lonicerae*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 7n–p

MycoBank number: MB851012

Etymology – The epithet is derived from *Lonicera*, the host plant genus from which the type strain was obtained.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Hexi Town, obtained from the plant leaf of *Lonicera japonica*, May 2020, Z.N. Du (holotype CGMCC 2.6600, lyophilized metabolically inactive cells, ex-type culture JCM 35425 = GZ2133).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear orange, mucoid, smooth, and glistening with an entire margin (Fig. 7n). On YM agar incubated at 20 °C for 7 days, cells are ellipsoidal, cylindrical, or oval,  $3.3\text{--}4.5 \times 4.7\text{--}8.7\ \mu\text{m}$ , and occur singly (Fig. 7o), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a pellicle and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are ovoidal and ellipsoidal on CMA agar,  $1.7\text{--}2.1 \times 2.3\text{--}8.1\ \mu\text{m}$  (Fig. 7p).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, L-sorbose, sucrose, maltose, cellobiose, trehalose, melibiose, raffinose, melezitose, soluble starch, D-xylose, L-arabinose, L-rhamnose (weak), glycerol (delayed or weak), ribitol, galactitol (variable), D-mannitol, D-glucitol, salicin, D-glucuronic acid, DL-lactate (weak), and succinate (variable) as the only carbon sources. However, it does not assimilate lactose, inulin, D-arabinose, D-ribose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, erythritol, Methyl- $\alpha$ -D-glucoside, citrate, myo-inositol, or hexadecane. Ammonium sulfate, L-lysine, potassium nitrate, ethylamine (delayed), and cadaverine serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain grows in the vitamin-free medium but does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 28 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Hexi Town, on plant leaf of *Elaeagnus glabra*, May 2020, Z.N. Du (culture GZ0263), on plant leaf of *Lonicera*

*japonica*, May 2020, Z.N. Du (culture GZ2943), obtained from the plant leaf of *Lonicera japonica*, May 2020, Z.N. Du (culture GZ2133) (n=3).

Notes – Physiologically, *Ban. lonicerae* can be differentiated from its close relatives *Ban. ogasawarensis* and *Ban. rosea* by its negative assimilation of lactose, myo-inositol, and grows at 29 °C, and positive assimilation of cadaverine (Table S3).

***Bannoa pseudoscolopiae*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 8a–c

MycoBank number: MB851013

Etymology – The epithet reflects its morphological resemblance to *Ban. Scolopiae* in colony appearance.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Viburnum dilatatum*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6716, lyophilized metabolically inactive cells, ex-type culture JCM 36234 = GZ0842).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear pale-orange to orange-red, mucoid, smooth, and glistening with an entire margin (Fig. 8a). On YM agar incubated at 20 °C for 7 days, cells are ellipsoidal or cylindrical,  $2.6\text{--}4.2 \times 5.0\text{--}8.3 \mu\text{m}$ , and occur singly (Fig. 8b), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are long ellipsoidal, falcate and allantoid on CMA agar,  $1.6\text{--}2.6 \times 2.5\text{--}7.1 \mu\text{m}$  (Fig. 8c).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, L-sorbose, sucrose, maltose, cellobiose, trehalose, melibiose, raffinose, melezitose, soluble starch, D-xylose, L-arabinose (weak), L-rhamnose (variable), glycerol (delayed or weak), ribitol (variable), galactitol (variable), D-mannitol, D-glucitol, salicin (weak), D-glucuronic acid, and DL-lactate (variable) as the only carbon sources. However, it does not assimilate lactose, inulin, D-arabinose, D-ribose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, erythritol, Methyl- $\alpha$ -D-glucoside, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed or weak), L-lysine (positive or delayed and weak), ethylamine (delayed or delayed and weak), and cadaverine (positive or delayed) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain grows positively or weakly in a vitamin-free medium and does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 28 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shishun Peak, on plant leaf of *Sageretia thea*, Oct. 2020, Z.N. Du (cultures GZ0743, GZ0745), on plant leaf of *Viburnum dilatatum*, Oct. 2020, Z.N. Du (cultures GZ0822, GZ0823, GZ0825, GZ0827, GZ0833, GZ0834, GZ0835, GZ0843, GZ0844, GZ0847, GZ0853, GZ08412, GZ0842), on plant leaf of *Quercus baronii*, Oct. 2020, Z.N. Du (culture GZ0949), on plant leaf of *Ostericum citriodorum*, Oct. 2020, Z.N. Du (culture GZ2346) (n=17).

Notes – *Ban. pseudoscolopiae* can be morphologically differentiated from its close relative *Ban. scolopiae* by the observation of ballistoconidia.

***Bannoa quercus*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 8d–f

MycoBank number MB 851014

Etymology – The epithet is derived from *Quercus*, the host plant genus from which the type strain was obtained.

Typus – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Quercus baronii*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6722, lyophilized metabolically inactive cells, ex-type culture JCM 35452 = GZ0941).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear cream to white, mucoid, smooth, and glistening with an entire margin (Fig. 8d). On YM agar incubated at 20 °C for 7 days, cells are ellipsoidal or cylindrical,  $3.5\text{--}4.3 \times 8.3\text{--}10.9 \mu\text{m}$ , and occur singly or in pairs (Fig.

8e), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are allantoid or reniform on CMA agar,  $1.3\text{--}2.9 \times 5.9\text{--}10.2\ \mu\text{m}$  (Fig. 8f).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, L-sorbose (weak), sucrose, maltose, cellobiose, trehalose, melibiose, raffinose, melezitose, soluble starch, D-xylose, L-arabinose, glycerol, D-mannitol (weak), D-glucitol, salicin, succinate (weak), and myo-inositol as the only carbon sources. However, it does not assimilate lactose, inulin, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, erythritol, ribitol, galactitol, Methyl- $\alpha$ -D-glucoside, D-glucuronic acid, DL-lactate, citrate, or hexadecane. Ammonium sulfate, potassium nitrate, sodium nitrite (delayed and weak), L-lysine, ethylamine, and cadaverine serve as the only nitrogen sources. The strain can grow in a vitamin-free medium and produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 30 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shishun Peak, on plant leaf of *Quercus baronii*, Oct. 2020, Z.N. Du (cultures GZ0942, GZ0944, GZ0945, GZ0947, GZ0948, GZ0941), on plant leaf of *Viburnum dilatatum*, Oct. 2020, Z.N. Du (culture GZ0856), on plant leaf of *Pittosporum illicioides*, Oct. 2020, Z.N. Du (cultures GZ2731, GZ2732, GZ2741) (n=10).

Notes – Physiologically, *Ban. quercus* can be differentiated from its close relatives, *Ban. ogasawarensis*, *Ban. rosea*, *Ban. lonicerae*, *Ban. scolopiae*, and *Ban. pseudoscolopiae* by its negative assimilation of ribitol, galactitol, D-glucuronic acid, and DL-lactate (Table S3).

***Bannoa scolopiae*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 8g–i

Mycobank number: MB851015

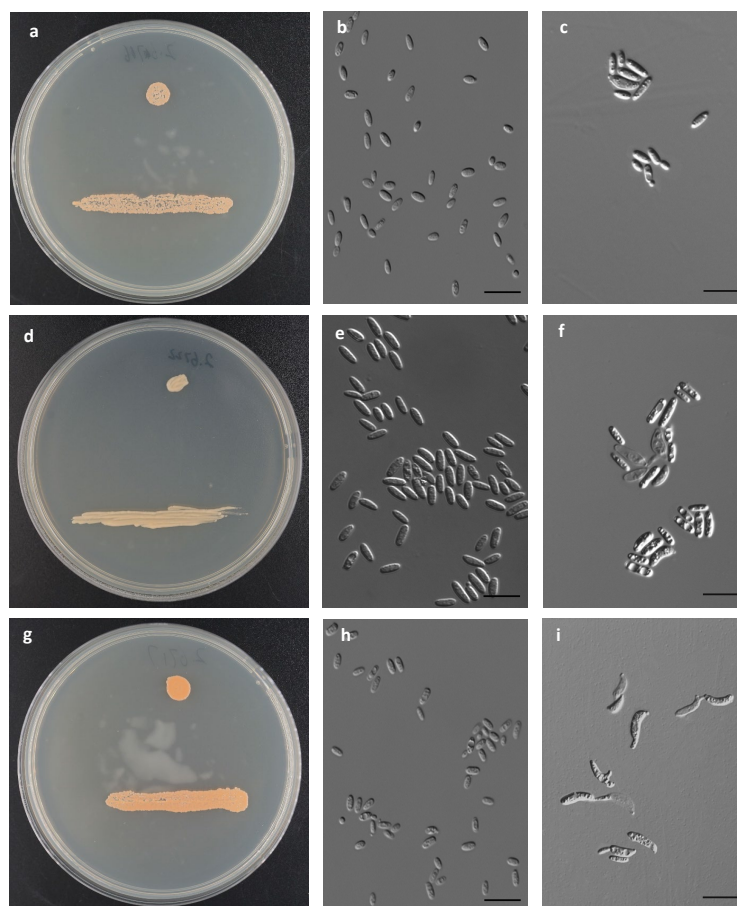
Etymology – The epithet is derived from *Scolopia*, the host plant genus from which the type strain was obtained.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shishun Peak, on plant leaf of *Lonicera japonica*, May 2020, Z.N. Du (holotype CGMCC 2.6717, lyophilized metabolically inactive cells, ex-type culture JCM 35425 = GZ3263).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear pinkish-orange-yellow, mucoid, smooth, and glistening with an entire margin (Fig. 8g). On YM agar incubated at 20 °C for 7 days, cells are ellipsoidal, cylindrical, or oval,  $2.4\text{--}3.9 \times 3.0\text{--}9.2\ \mu\text{m}$ , and occur singly (Fig. 8e), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are falcate and allantoid on CMA,  $1.2\text{--}2.4 \times 5.1\text{--}10.7\ \mu\text{m}$  (Fig. 8f).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, L-sorbose, sucrose, maltose, cellobiose, trehalose, melibiose, raffinose, melezitose, soluble starch, D-xylose, L-arabinose, L-rhamnose (positive or delayed or weak), glycerol (delayed), ribitol (positive or weak), galactitol (variable), D-mannitol, D-glucitol, salicin (positive or delayed or weak), D-glucuronic acid (positive or delayed or weak), and DL-lactate (weak) as the only carbon sources. However, it does not assimilate lactose, inulin, D-arabinose, D-ribose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, erythritol, Methyl- $\alpha$ -D-glucoside, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed), L-lysine (weak), ethylamine (delayed and weak), and cadaverine (delayed) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain grows positively or weakly in a vitamin-free medium and does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature is 28 °C.





**Figure 8** – The streak culture and vegetative cells grown on YM agar for 7 days at 20 °C, and ballistoconidia formation observed on corn meal agar after 7 days at 20 °C of the new yeast species within *Pucciniomycotina*. (a–c) *Bannoa pseudoscolopiae* CGMCC 2.6716<sup>T</sup>; (d–f) *Bannoa quercus* CGMCC 2.6722<sup>T</sup>; (g–i) *Bannoa scolopiae* CGMCC 2.6717<sup>T</sup>. Bars = 10 µm.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shishun Peak, on plant leaf of *Kadsura longipedunculata*, Oct. 2020, Z.N. Du (culture GZ0421), on plant leaf of *Viburnum dilatatum*, Oct. 2020, Z.N. Du (culture GZ0849), on plant leaf of *Ostericum citriodorum*, Oct. 2020, Z.N. Du (culture GZ2341), on plant leaf of *Smilax China*, Oct. 2020, Z.N. Du (culture GZ3741), on plant leaf of *Lonicera japonica*, May 2020, Z.N. Du (culture GZ3263); Guizhou Province, Zunyi City, Zhengan County, Hexi Town, on plant leaf of *Disporum cantoniense*, May 2020, Z.N. Du (culture GZ1044), on plant leaf of *Millettia pachycarpa*, May 2020, Z.N. Du (culture GZ1224), on plant leaf of *Ilex asprella*, May 2020, Z.N. Du (culture GZ1324), on plant leaf of *Viburnum utile*, May 2020, Z.N. Du (culture GZ1425), on plant leaf of *Pittosporum illicioides*, May 2020, Z.N. Du (culture GZ1627) (n=10).

Notes – Morphologically, *Ban. scolopiae* can be differentiated from its close relative *Ban. pseudoscolopiae* by the observation of ballistoconidia.

***Pucciniomycotina, Cystobasidiomycetes, Cystobasidiales, Cystobasidiaceae***  
***Cystastrum sedimentus* X.Z. Liu, F.Y. Bai & H.Y. Zhu, sp. nov.**

Fig. 9a–b

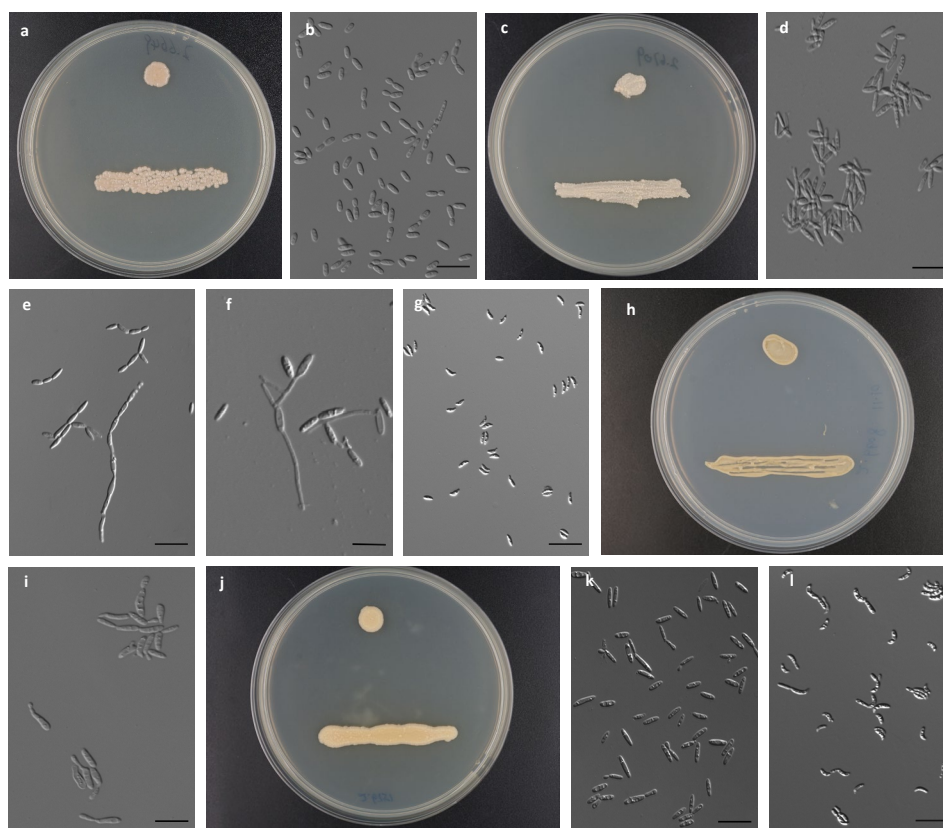
Mycobank number: MB851022

Etymology – The epithet *sedimentus* reflects the tidal flat sediment habitat of the type strain.

Typus – China, Shanghai City, Chongming District, obtained from soil sediment, July 2020, X.Z. Liu & R.P. Zhang (holotype CGMCC 2.6649, lyophilized metabolically inactive cells, ex-type culture JCM 35434 = 278C-4).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear pale pink and smooth with an entire margin (Fig. 9a). In YM broth incubated at 25 °C for one month, a sediment

and ring formed. On YM agar incubated at 20 °C for 7 days, cells are cylindrical or long ellipsoidal,  $2.0\text{--}2.6 \times 4.1\text{--}4.9\text{ }\mu\text{m}$ , and occur singly or in pairs (Fig. 9b), exhibiting polar budding. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.



**Figure 9** – The streak culture and vegetative cells grown on YM agar for 7 days at 20 °C and ballistoconidia formation observed on corn meal agar after 7 days at 20 °C of the new yeast species within *Pucciniomycotina*. (a–b) *Cystastrum sedimentus* CGMCC 2.6649<sup>T</sup>; (c–g) *Chrysozyma loniceriae* CGMCC 2.6709<sup>T</sup>; (h, i) *Chrysozyma rubi* CGMCC 2.6608<sup>T</sup>; (j–l) *Chrysozyma viburni* CGMCC 2.6751<sup>T</sup>. Bars = 10  $\mu\text{m}$ .

**Physiological and biochemical characters** – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (delayed and weak), L-sorbose (delayed or delayed and weak), sucrose (delayed), maltose (delayed), cellobiose (delayed), trehalose (delayed), lactose (delayed), melibiose (weak), melezitose, soluble starch (positive or delayed), D-xylose (delayed), L-arabinose (delayed), D-arabinose (delayed), D-glucosamine (delayed and weak), N-Acetyl-D-glucosamine, ethanol (delayed), glycerol (delayed), ribitol (delayed), D-mannitol (delayed), D-glucitol (delayed), Methyl- $\alpha$ -D-glucoside (variable), salicin (delayed or weak), D-glucuronic acid (delayed), DL-lactate (delayed and weak), succinate (delayed), and citrate (variable) as the only carbon sources. However, it does not assimilate raffinose, inulin, D-ribose, L-rhamnose, methanol, erythritol, galactitol, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed), L-lysine (delayed), ethylamine (delayed or delayed and weak), and cadaverine (delayed) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain does not grow in a vitamin-free medium or produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature is 34 °C.

**Materials examined** – China, Shanghai City, Chongming District, obtained from soil sediment, July 2020, X.Z. Liu & R.P. Zhang (cultures 278C-5, 278C-4) (n=2).

Notes – Physiologically, *Cys. sedimentus* can be differentiated from its close relative *Cystastrum mephitis* by its positive assimilation of L-sorbose, melibiose, and ethylamine and its negative assimilation of D-ribose (Table S3).

***Pucciniomycotina, Microbotryomycetes, Chrysozymaceae, incertae sedis***

***Chrysozyma lonicerae*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 9c–f

MycoBank number: MB851016

Etymology – The epithet is derived from *Lonicera*, the host plant genus from which the type strain was obtained.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Lonicera tragophylla*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6709, lyophilized metabolically inactive cells, ex-type culture JCM 35448 = GZ3362).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear creamish white, grayish-cream or yellowish, smooth, and dull with an entire margin (Fig. 9c). On YM agar incubated at 20 °C for 7 days, cells are long ellipsoidal or cylindrical,  $1.8\text{--}3.2 \times 4.8\text{--}9.3\ \mu\text{m}$ , and occur singly (Fig. 9d), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a pellicle and sediment formed. Pseudohyphae are formed in YM agar (Fig. 9e). Hyphae are formed on CMA agar,  $1\text{--}3\ \mu\text{m}$  in diameter (Fig. 9f). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are allantoid and reniform on CMA agar,  $0.8\text{--}0.9 \times 2.4\text{--}3.7\ \mu\text{m}$  (Fig. 9g).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (weak), L-sorbose (weak), sucrose, maltose, trehalose, melezitose, L-arabinose (weak), D-mannitol, D-glucitol, salicin (weak), DL-lactate (weak), and succinate (weak) as the only carbon sources. However, it does not assimilate cellobiose, lactose, melibiose, raffinose, inulin, soluble starch, D-xylose, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, glycerol, erythritol, ribitol, galactitol, Methyl- $\alpha$ -D-glucoside, D-glucuronic acid, citrate, myo-inositol, or hexadecane. Ammonium sulfate, L-lysine (weak), ethylamine (delayed), and cadaverine (weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when potassium nitrate or sodium nitrite is the sole nitrogen source. The strain does not grow in a vitamin-free medium or produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The maximum growth temperature is 28 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Myrsine Africana*, Oct. 2020, Z.N. Du (culture GZ4032), on plant leaf of *Lonicera tragophylla*, Oct. 2020, Z.N. Du (culture GZ3362); Guizhou Province, Wenzhou City, South Yandang Mountain, on plant leaf of *Myrsine africana*, Oct. 2020, Z.N. Du (culture GZ4032) (n=2).

Notes – Physiologically, *Chr. lonicerae* can be differentiated from its close relative *Chr. rubi* by its positive assimilation of L-sorbose, L-arabinose, D-glucitol, salicin, DL-lactate, succinate, and potassium nitrate, but its negative assimilation of cellobiose, soluble starch, and cadaverine, and growth in vitamin-free medium (Table S3).

***Chrysozyma rubi*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 9h, i

MycoBank number: MB851017

Etymology – The epithet is derived from *Rubus*, the host plant genus from which the type strain was obtained.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Rubus innominatus*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6608, lyophilized metabolically inactive cells, ex-type culture JCM 39290 = GZ43510).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear creamy, butyrous, smooth, partly wrinkled, and glossy with an entire margin (Fig. 9h). On YM agar incubated at 20 °C for 7 days, cells are elongate fusiform, long ellipsoidal or cylindrical,  $2.0\text{--}3.4 \times 7.2\text{--}10.7\ \mu\text{m}$ , and occur singly (Fig. 9i), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a pellicle and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar.



No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (weak), sucrose, maltose, cellobiose (weak), trehalose, melezitose, soluble starch (weak), and D-mannitol (weak) as the only carbon sources. However, it does not assimilate L-sorbose, lactose, melibiose, raffinose, inulin, D-xylose, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, glycerol, erythritol, ribitol, galactitol, D-glucitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, DL-lactate, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, L-lysine, and cadaverine serve as the only nitrogen sources. In contrast, no assimilation occurs when potassium nitrate, sodium nitrite, or ethylamine is the sole nitrogen source. The strain grows weakly in a vitamin-free medium and does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature is 28 °C.

Material examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Rubus innominatus*, Oct. 2020, Z.N. Du (culture GZ43510) (n=1).

Notes – Physiologically, *Chr. rubi* can be differentiated from its close relatives *Chr. lonicerae*, *Chr. yandangensis*, and *Chr. fushanensis* by its positive assimilation of soluble starch, but its negative assimilation of succinate (Table S3).

***Chrysozyma viburni*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 9j–l

MycoBank number: MB851018

Etymology – The epithet *viburni* is named after *Viburnum*, the genus of the source plant for the type strain.

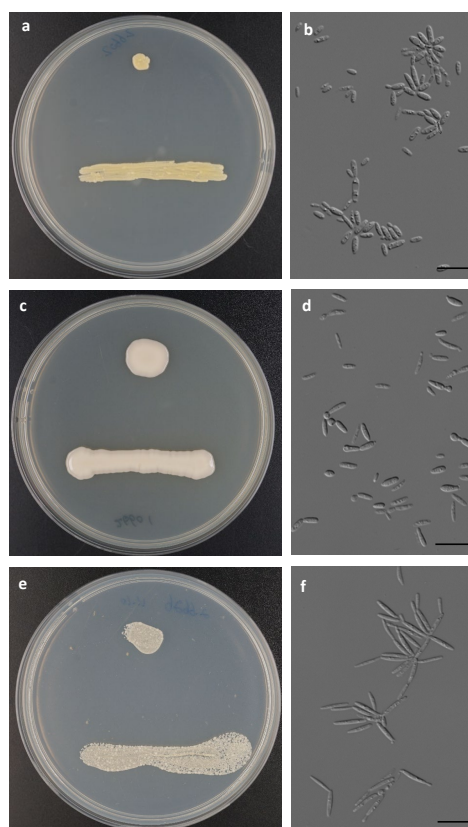
Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Viburnum utile*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6751, lyophilized metabolically inactive cells, ex-type culture JCM 39297 = GZ3831).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear yellowish-cream, smooth, and glossy with an entire margin (Fig. 9j). On YM agar incubated at 20 °C for 7 days, cells are long ellipsoidal or cylindrical,  $2.3\text{--}3.1 \times 6.0\text{--}14.2\text{ }\mu\text{m}$ , and occur singly or in pairs (Fig. 9k), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are falcate and lunate on CMA agar,  $1.1\text{--}1.6 \times 3.6\text{--}5.7\text{ }\mu\text{m}$  (Fig. 9l).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, maltose, trehalose, melezitose, soluble starch (weak), ribitol (variable), D-mannitol, and D-glucitol (weak) as the only carbon sources. However, it does not assimilate L-sorbose, cellobiose, lactose, melibiose, raffinose, inulin, D-xylose, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, glycerol, erythritol, galactitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, DL-lactate, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate, L-lysine, ethylamine, and cadaverine serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain grows weakly in a vitamin-free medium and does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 28 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Viburnum utile*, Oct. 2020, Z.N. Du (cultures GZ3836, GZ3838, GZ3831) (n=3).

Notes – Physiologically, *Chr. viburni* can be differentiated from its close relative *Chr. cylindrica* by its positive assimilation of maltose, soluble starch, and L-lysine and growth at 25 °C (Table S3).



**Figure 10** – The streak culture and vegetative cells grown on YM agar for 7 days at 20 °C, and ballistoconidia formation observed on corn meal agar after 7 days at 20 °C of the new yeast species within *Pucciniomycotina*. (a, b) *Chrysozyma yandangensis* CGMCC 2.6602<sup>T</sup>; (c, d) *Colacogloea woodwardiae* CGMCC 2.6601<sup>T</sup>; (e, f) *Rosettozyma turpiniae* CGMCC 2.6626<sup>T</sup>. Bars = 10 µm.

***Chrysozyma yandangensis*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 10a, b

MycoBank number: MB851019

Etymology – The epithet *yandangensis* refers to the type locality, Yandang Mountain.

Type – China, Zhejiang Province, Wenzhou City, Yandang Mountain, on plant leaf of *Loropetalum chinense*, Oct. 2016, Z.N. Du (holotype CGMCC 2.6602, lyophilized metabolically inactive cells, ex-type culture JCM 35427 = ZJ0731).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear creamish white, or yellowish, mucoid, smooth, and glistening with an entire margin (Fig. 10a). On YM agar incubated at 20 °C for 7 days, cells are long ellipsoidal, cylindrical, or long ovoid, 1.9–3.2 × 5.0–10.3 µm, and occur singly (Fig. 10b), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a sediment and ring formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (weak), sucrose, maltose, trehalose, lactose (variable), melibiose (variable), melezitose, N-Acetyl-D-glucosamine (variable), ethanol (variable), glycerol (variable), D-mannitol, succinate (variable), and citrate (variable) as the only carbon sources. However, it does not assimilate L-sorbose, cellobiose, raffinose, inulin, soluble starch, D-xylose, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, methanol, erythritol, ribitol, galactitol, D-glucitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, DL-lactate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate, L-lysine (delayed and weak), ethylamine, and cadaverine (delayed) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain grows weakly in a vitamin-free medium and does not produce

starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature is 28 °C.

Materials examined – China, Zhejiang Province, Wenzhou City, Yandang Mountain, on plant leaf of *Loropetalum chinense*, Oct. 2016, Z.N. Du (cultures ZJ0711, ZJ0731) (n=2).

Notes – Physiologically, *Chr. yandangensis* can be differentiated from its close relative *Ch. fushanensis* by its positive assimilation of sucrose, glycerol, potassium nitrate, and cadaverine, but its negative assimilation of cellobiose, ribitol, D-glucitol, Methyl- $\alpha$ -D-glucoside, and salicin (Table S3).

***Pucciniomycotina, Microbotryomycetes, Colacogloeaceae, incertae sedis***

***Colacogloea woodwardiae*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 10c, d

MycoBank number: MB851020

Etymology – The epithet is derived from *Woodwardia*, the genus of the source plant for the type strain.

Type – China, Zhejiang Province, Wenzhou City, South Yandang Mountain, on plant leaf of *Woodwardia japonica*, Oct. 2016, Z.N. Du (holotype CGMCC 2.6601, lyophilized metabolically inactive cells, ex-type culture JCM 35426 = ZJ1011).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear creamish white, mucoid, smooth, and glistening with an entire margin (Fig. 10c). On YM agar incubated at 20 °C for 7 days, cells are long ellipsoidal, cylindrical, or ovoid,  $1.9\text{--}3.2 \times 4.6\text{--}13.8\ \mu\text{m}$ , and occur singly (Fig. 10d), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (weak), sucrose, maltose, cellobiose, trehalose, lactose, melibiose (weak), melezitose, soluble starch (delayed weak), D-xylose (weak), D-arabinose (weak), D-ribose (weak), glycerol, erythritol (weak), ribitol (weak), D-glucuronic acid, DL-lactate, succinate, and citrate as the only carbon sources. However, it does not assimilate L-sorbose, raffinose, inulin, L-arabinose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, galactitol, D-mannitol, D-glucitol, Methyl- $\alpha$ -D-glucoside, salicin, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed), L-lysine, ethylamine, and cadaverine (weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain does not grow in a vitamin-free medium or produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature is 28 °C.

Materials examined – China, Fujian Province, Xiamen City, Wild Valley, on plant leaf of *Pavetta hongkongensis*, Dec. 2019, Z.N. Du (culture FJ1442); Zhejiang Province, Wenzhou City, South Yandang Mountain, on plant leaf of *Woodwardia japonica*, Oct. 2016, Z.N. Du (culture ZJ1011) (n=2).

Notes – Physiologically, *Col. woodwardiae* can be differentiated from its close relatives *Col. rhododendri* and *Col. hydrangeae* by its positive assimilation of lactose, melibiose, soluble starch, D-xylose, D-arabinose, D-ribose, erythritol, DL-lactate, succinate, and citrate, but its negative assimilation of D-glucosamine, ethanol, D-mannitol, and sodium nitrite (Table S3).

***Pucciniomycotina, Microbotryomycetes, Rosettozymales, Rosettozymaceae***

***Rosettozyma turpiniae*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 10e, f

MycoBank number: MB851025

Etymology – The epithet *turpiniae* is named after *Turpinia*, the genus of the source plant for the type strain.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Turpinia arguta*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6626, lyophilized metabolically inactive cells, ex-type culture JCM 39294 = GZ4541).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear whitish to cream, butyrous, smooth, and glossy with an entire margin (Fig. 10e). On YM agar incubated at 20 °C for 7 days, cells are elongated fusiform,  $2.2\text{--}3.1 \times 10.2\text{--}14.3 \mu\text{m}$ , and occur singly or in rosettes (Fig. 10f), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, sucrose, maltose, trehalose, melezitose, soluble starch (weak), D-xylose (variable), D-arabinose (variable), ethanol, glycerol, D-mannitol, D-glucitol (delayed and weak), Methyl- $\alpha$ -D-glucoside, salicin (variable), DL-lactate (weak) and citrate (variable) as the only carbon sources. However, it does not assimilate galactose, L-sorbose, cellobiose, lactose, melibiose, raffinose, inulin, L-arabinose, D-ribose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, erythritol, ribitol, galactitol, D-glucuronic acid, succinate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed), L-lysine, ethylamine, and cadaverine (weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain does not grow in a vitamin-free medium or produce starch-like substances. It tests negative for urease activity but positive for the Diazonium Blue B reaction. The highest growth temperature is 28 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Millettia pachycarpa*, Oct. 2020, Z.N. Du (culture GZ1277), on plant leaf of *Smilax China*, Oct. 2020, Z.N. Du (cultures GZ3722, GZ3723), on plant leaf of *Turpinia argute*, Oct. 2020, Z.N. Du (cultures GZ4521, GZ4555, GZ4541); Guizhou Province, Zunyi City, Zhengan County, Hexi Town, on plant leaf of *Picrasma quassioides*, May 2020, Z.N. Du (cultures GZ1566, GZ15641) (n=8).

Notes – Physiologically, *Ros. turpiniae* can be differentiated from *Ros. motuoensis* by its positive assimilation of soluble starch, D-xylose, D-arabinose, glycerol, salicin, DL-lactate, and growth at 25 °C, but its negative assimilation of succinate (Table S3).

### ***Pucciniomycotina, Microbotryomycetes***

#### ***Sterigmoblongales* X.Z. Liu & F.Y. Bai, ord. nov.**

MycoBank number: MB851007

Type family – Sterigmoblongaceae X.Z. Liu & F.Y. Bai

Within the Microbotryomycetes, the order Sterigmoblongales is taxonomically defined by its type genus, *Sterigmoblongus*, which also provides the basis for the order's nomenclature.

Accepted family – Sterigmoblongaceae X.Z. Liu & F.Y. Bai

#### ***Sterigmoblongaceae* X.Z. Liu & F.Y. Bai, fam. nov.**

MycoBank number: MB851029

Type genus – *Sterigmoblongus* X.Z. Liu & F.Y. Bai

Within the *Sterigmoblongales*, the family *Sterigmoblongaceae* is taxonomically defined by its type genus *Sterigmoblongus*, which also provides the basis for the family's nomenclature.

Accepted genus – *Sterigmoblongus* X.Z. Liu & F.Y. Bai

#### ***Sterigmoblongus* X.Z. Liu & F.Y. Bai, gen. nov.**

MycoBank number: MB851030

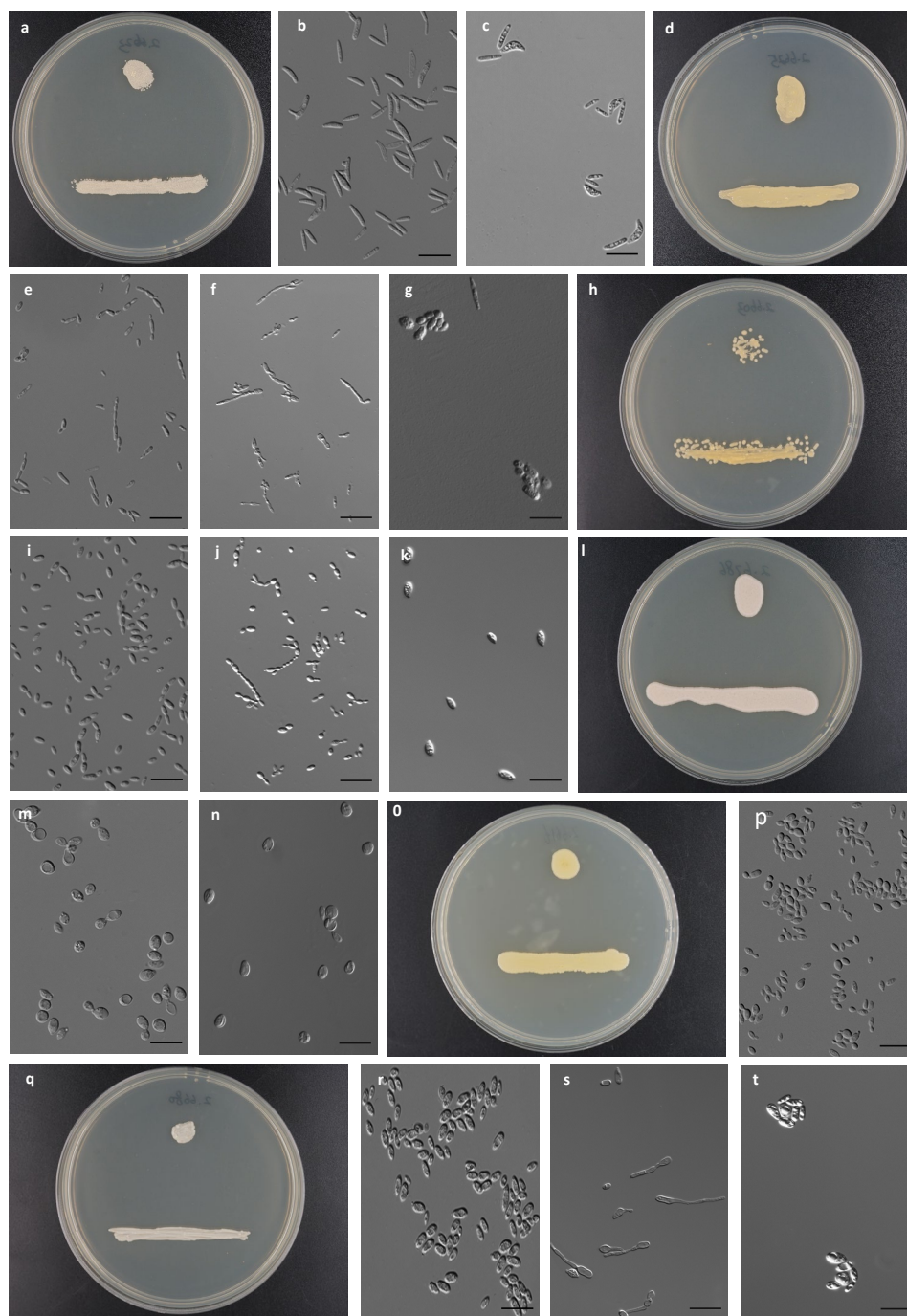
Etymology – The genus name reflects the distinctive morphology of its vegetative cells, characterized by conidia production on stalk-like and oblong-ovate conidiophores.

Type species – *Sterigmoblongus ilicis* X.Z. Liu, F.Y. Bai & J.Q. Sun.

No sexual reproduction observed. Colonies are white-cream, gray-cream, yellowish-cream, butyrous, glistening, and smooth. Budding cells are present, and blastoconidia are produced at the

end of stalk-like and oblong-ovate conidiophores. Conidiophores are single or multiple. Pseudohyphae and hyphae are absent. Ballistoconidia are observed.

Accepted species – *Sterigmoblongus ilicis*



**Figure 11** – The streak culture and vegetative cells grown on YM agar for 5 days at 20 °C and ballistoconidia formation observed on corn meal agar after 7 days at 20 °C of the new yeast species within *Pucciniomycotina*. (a–c) *Sterigmoblongus ilicis* CGMCC 2.6623<sup>T</sup>; (d–g) *Phyllozyma foliicola* CGMCC 2.6625<sup>T</sup>; (h–k) *Phyllozyma lyoniae* CGMCC 2.6603<sup>T</sup>; and within *Tremellomycetes* (l–n) *Bulleribasidium pseudosiamense* CGMCC 2.6786<sup>T</sup>; (o–p) *Bulleribasidium rhois* CGMCC 2.6616<sup>T</sup>; (q–t) *Bulleribasidium veronicastris* CGMCC 2.6680<sup>T</sup>. Bars = 10 μm.

*Sterigmoblongus ilicis* X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.  
Mycobank number: MB851031

Fig. 11a–c

**Etymology** – The epithet is derived from *Ilex*, the host plant genus from which the type strain was obtained.

**Type** – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Ilex aculeolata*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6623, lyophilized metabolically inactive cells, ex-type culture JCM 39293 = GZ0635).

**Culture characters** – On YM agar incubated at 20 °C for 7 days, colonies appear white-cream, gray-cream, yellowish-cream, butyrous, glistening, and smooth with an entire margin (Fig. 11a). On YM agar incubated at 20 °C for 7 days, cells are long ellipsoidal, elongated fusiform or falcate,  $1.8\text{--}3.3 \times 7.6\text{--}15.4 \mu\text{m}$ , and occur singly (Fig. 8b), exhibiting polar budding. Each conidiophore resembles a stalk and produces one or more conidia. Conidiophore numerous or single, typically multifurcate. In YM broth incubated at 25 °C for one month, a sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are allantoid, lunate, or cylindrical on CMA agar,  $1.2\text{--}2.1 \times 4.6\text{--}7.8 \mu\text{m}$  (Fig. 8c).

**Physiological and biochemical characters** – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (variable), sucrose (variable), maltose (variable), cellobiose (variable), trehalose (positive or delayed or delayed and weak), raffinose (variable), melezitose (variable), soluble starch (delayed or weak), D-xylose (variable), N-Acetyl-D-glucosamine (variable), ethanol (variable), glycerol (variable), D-mannitol (variable), D-glucitol (weak), salicin (variable), D-glucuronic acid (variable), DL-lactate (variable), succinate (variable) and citrate (variable) as the only carbon sources. However, it does not assimilate L-sorbose, lactose, melibiose, inulin, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, methanol, erythritol, ribitol, galactitol, Methyl- $\alpha$ -D-glucoside, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed), L-lysine (delayed), ethylamine (delayed), and cadaverine (delayed) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain grows variably in a vitamin-free medium and does not produce starch-like substances. It tests variably for urease activity and is positive for the Diazonium Blue B reaction. The highest growth temperature is 30 °C.

**Materials examined** – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Ilex aculeolata*, Oct. 2020, Z.N. Du (cultures GZ0631, GZ0632-1, GZ0632-2, GZ0638, GZ06310, GZ0635), on plant leaf of *Mallotus repandus*, Oct. 2020, Z.N. Du (culture GZ36514), on plant leaf of *Myrsine africana*, Oct. 2020, Z.N. Du (cultures GZ0562, GZ0563, GZ0566, GZ2951, GZ4031), on plant leaf of *Pittosporum illicioides*, Oct. 2020, Z.N. Du (culture GZ2733), on plant leaf of *Quercus baronii*, Oct. 2020, Z.N. Du (culture GZ1965), on plant leaf of *Struthiopteris eburnea*, Oct. 2020, Z.N. Du (culture GZ0344), on plant leaf of *Symplocos sumuntia*, Oct. 2020, Z.N. Du (culture GZ4131), on plant leaf of *Viburnum dilatatum*, Oct. 2020, Z.N. Du (culture GZ2141), on plant leaf of *Viburnum utile*, Oct. 2020, Z.N. Du (cultures GZ0143, GZ0171) (n=19).

**Notes** – Physiologically, *Sterigmoblongus ilicis* can be differentiated from its close relative *Mycogloioocolax gerardii* by its positive assimilation of sucrose, maltose, trehalose, melezitose, D-xylose, ethanol, DL-lactate, and citrate, but its negative assimilation of L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, erythritol, ribitol, galactitol, and methyl- $\alpha$ -D-glucoside (Table S3).

### ***Pucciniomycotina, Spiculogloeomycetes, Spiculogloeales, Spiculogloeaceae***

***Phyllozymba foliicola*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 11d–g

Mycobank number: MB851023

**Etymology** – The epithet *foliicola* refers to the leaf origin of the type strain.

**Type** – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Lyonia ovalifolia*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6625, lyophilized metabolically inactive cells, ex-type culture JCM 35430 = GZ3822).

**Culture characters** – On YM agar incubated at 20 °C for 7 days, colonies appear white-cream, yellowish-cream, pale orange, mucoid, smooth, glossy, or dull with an entire margin (Fig. 11d). On



YM agar incubated at 20 °C for 7 days, cells are ellipsoidal, long ellipsoidal to cylindrical,  $2.3\text{--}3.1 \times 3.9\text{--}9.5 \mu\text{m}$ , and occur singly or in pairs (Fig. 11e), exhibiting polar budding. In YM broth incubated at 25 °C for one month, sediment forms. Pseudohyphae are absent, and hyphae are formed on YM agar (Fig. 11f). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are reniform, falcate to ellipsoidal on CMA agar,  $2.4\text{--}3.6 \times 3.2\text{--}5.8 \mu\text{m}$  (Fig. 11g).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (variable), sucrose (variable), trehalose (variable), melibiose (variable), raffinose (variable), D-arabinose (variable), ribitol (variable), D-mannitol (variable), D-glucitol, DL-lactate (variable), and succinate (variable) as the only carbon sources. However, it does not assimilate L-sorbose, maltose, cellobiose, lactose, melezitose, inulin, soluble starch, D-xylose, L-arabinose, D-ribose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, glycerol, erythritol, galactitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, citrate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (weak), L-lysine (weak), and cadaverine (weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when ethylamine or sodium nitrite is the sole nitrogen source. The strain grows variably in a vitamin-free medium and does not produce starch-like substances. It tests negative for urease activity but positive for the Diazonium Blue B reaction. The highest growth temperature observed is 29 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shishun Peak, on plant leaf of *Elaeagnus glabra*, Oct. 2020, Z.N. Du (cultures GZ1631, GZ1632, GZ1633, GZ1634, GZ1636, GZ1637, GZ1638), on plant leaf of *Nandina domestica*, Oct. 2020, Z.N. Du (cultures GZ4212, GZ4233, GZ4236, GZ4237, GZ4241, GZ4242, GZ4243, GZ4246, GZ4247, GZ4253), on plant leaf of *Lonicera tragophylla*, Oct. 2020, Z.N. Du (culture GZ33610), on plant leaf of *Lyonia ovalifolia*, Oct. 2020, Z.N. Du (culture GZ3822) (n=19).

Notes – Physiologically, *Phy. foliicola* can be distinguished from its close relatives *Phy. corallina*, *Phy. dimennae* and *Phy. jiayinensis* by its positive assimilation of D-arabinose and capacity to grow in a vitamin-free medium (Table S3).

***Phyllozymba lyoniae*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 11h–k

Mycobank number: MB851024

Etymology – The epithet is derived from *Lyonia*, the host plant genus from which the type strain was obtained.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Lyonia ovalifolia*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6603, lyophilized metabolically inactive cells, ex-type culture JCM 39289 = GZ1722).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear pale yellow, mucoid, smooth, and glossy with an entire margin (Fig. 11h). On YM agar incubated at 20 °C for 7 days, cells are long ovoid and ellipsoidal,  $1.8\text{--}3.1 \times 3.5\text{--}7.6 \mu\text{m}$ , and occur singly or in pairs (Fig. 11i), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a sediment and ring formed. Hyphae are not formed on CMA and YM agar. Pseudohyphae are formed on YM agar (Fig. 11j). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are allantoid and reniform on CMA agar,  $2.1\text{--}2.7 \times 3.5\text{--}4.8 \mu\text{m}$  (Fig. 11k).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (variable), sucrose, trehalose (delayed), raffinose (weak), L-rhamnose (variable), N-Acetyl-D-glucosamine (variable), glycerol (weak), erythritol (variable), D-mannitol (weak), and D-glucitol (variable) as the only carbon sources. However, it does not assimilate L-sorbose, maltose, cellobiose, lactose, melibiose, melezitose, inulin, soluble starch, D-xylose, L-arabinose, D-arabinose, D-ribose, D-glucosamine, methanol, ethanol, ribitol, galactitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, DL-lactate, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (weak), L-lysine (weak), and cadaverine (weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite or ethylamine is the sole nitrogen source. The strain grows weakly in a vitamin-free medium and does

not produce starch-like substances. It tests negative for urease activity but positive for the Diazonium Blue B reaction. The highest growth temperature observed is 25 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Viburnum utile*, Oct. 2020, Z.N. Du (culture GZ1312), on plant leaf of *Lyonia ovalifolia*, Oct. 2020, Z.N. Du (culture GZ1722) (n=2).

Notes – Physiologically, *Phy. lyoniae* can be differentiated from its close relative *Phy. novazealandica* by its positive assimilation of L-sorbose, sucrose, raffinose, L-rhamnose, erythritol, L-lysine, and cadaverine, but its negative assimilation of succinate and citrate and hydrolysis of urea (Table S3).

#### ***Agaricomycotina, Tremellomycetes, Tremellales, Bulleribasidiaceae***

***Bulleribasidium pseudosiamense*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 11l–n

MycoBank number: MB851032

Etymology – The epithet *pseudosiamense* reflects its morphological resemblance to *Bulleribasidium siamense* in colony appearance.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Mallotus repandus*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6786, lyophilized metabolically inactive cells, ex-type culture JCM 39305 = GZ3668).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear white-cream, butyrous, glistening, and smooth with an entire margin (Fig. 11l). On YM agar incubated at 20 °C for 7 days, cells are subglobose, globose, or ovoid,  $5.2\text{--}9.8 \times 4.6\text{--}6.6\ \mu\text{m}$ , and occur singly or in pairs (Fig. 11m), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are subglobose, ellipsoidal, or somewhat kidney-shaped on CMA agar,  $1.3\text{--}3.3 \times 3.5\text{--}5.1\ \mu\text{m}$  (Fig. 11n).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, maltose, trehalose, melibiose, raffinose, melezitose (delayed), soluble starch, D-xylose, L-arabinose (weak), D-arabinose (delayed), L-rhamnose, N-Acetyl-D-glucosamine, galactitol (delayed), D-mannitol (delayed), D-glucitol, Methyl- $\alpha$ -D-glucoside (delayed), DL-lactate (weak), and myo-inositol (delayed) as the only carbon sources. However, it does not assimilate L-sorbose, sucrose, cellobiose, lactose, inulin, D-ribose, D-glucosamine, methanol, ethanol, glycerol, erythritol, ribitol, salicin, D-glucuronic acid, succinate, citrate, or hexadecane. Ammonium sulfate, L-lysine (delayed and weak), ethylamine (delayed and weak), and cadaverine (delayed and weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when potassium nitrate or sodium nitrite is the sole nitrogen source. The strain grows positively in a vitamin-free medium but does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 28 °C.

Material examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Mallotus repandus*, Oct. 2020, Z.N. Du (culture GZ3668) (n=1).

Notes – Physiologically, the species *Bul. pseudosiamense* can be differentiated from its close relatives *Bul. begoniae*, *Bul. siamensis*, *Bul. panici*, and *Bul. pseudopanici* by its negative assimilation of sucrose, cellobiose, and D-ribose (Table S3).

***Bulleribasidium rhois*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 11o–p

MycoBank number: MB851033

Etymology – The epithet is derived from *Rhus*, the host plant genus from which the type strain was obtained.

Type – China, Zhejiang Province, Wenzhou City, East Yandang Mountain, on plant leaf of *Rhus chinensis*, Oct. 2016, Z.N. Du (holotype CGMCC 2.6616, lyophilized metabolically inactive cells, ex-type culture JCM 35429 = ZJ1541).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear white-cream, butyrous, and smooth with an entire margin (Fig. 11o). On YM agar incubated at 20 °C for 7 days,



cells are ovoid, long ovoid, subglobose to ellipsoidal,  $2.1\text{--}4.6 \times 3.5\text{--}7.0\ \mu\text{m}$ , and occur singly or in pairs (Fig. 11p), exhibiting polar budding. In YM broth incubated at  $25\ ^\circ\text{C}$  for one month, a ring and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, sucrose, trehalose, melibiose, raffinose, melezitose, soluble starch, D-xylose, L-arabinose, L-rhamnose (weak), N-Acetyl-D-glucosamine, galactitol (weak), D-glucitol (weak), and succinate (weak) as the only carbon sources. However, it does not assimilate galactose, L-sorbose, maltose, cellobiose, lactose, inulin, D-arabinose, D-ribose, D-glucosamine, methanol, ethanol, glycerol, erythritol, ribitol, D-mannitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, DL-lactate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed and weak), L-lysine (delayed), ethylamine (weak), and cadaverine (delayed) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain does not grow in a vitamin-free medium or produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is  $30\ ^\circ\text{C}$ .

Materials examined – China, Zhejiang Province, Ningbo City, Xiangshan County, on an unknown plant leaf, May 2021, X.Z. Liu, H.Y. Zhu & J.N. Li (culture CGMCC 2.6648 = 0520-5-3-2); Zhejiang Province, Wenzhou City, East Yandang Mountain, on plant leaf of *Rhus chinensis*, Oct. 2016, Z.N. Du (culture ZJ1541) (n=2).

Notes – Physiologically, *Bul. rhois* can be differentiated from its close relatives *Bul. foliicola*, *Bu. phyllophilum*, and *Bul. hainanensis* by its negative assimilation of galactose, maltose, cellobiose, D-arabinose, D-mannitol, Methyl- $\alpha$ -D-glucoside, and myo-inositol, but its positive assimilation of succinate and cadaverine (Table S3).

***Bulleribasidium veronicastrum*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 11q–t

MycoBank number: MB851034

Etymology – The epithet is derived from *Veronicastrum*, the host plant genus from which the type strain was obtained.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Veronicastrum stenostachyum*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6680, lyophilized metabolically inactive cells, ex-type culture JCM 35443 = GZ4443).

Culture characters – On YM agar incubated at  $20\ ^\circ\text{C}$  for 7 days, colonies appear white-cream, butyrous, semi-glossy, and smooth with an entire margin (Fig. 11q). On YM agar incubated at  $20\ ^\circ\text{C}$  for 7 days, cells are subglobose, ellipsoidal, or ovoid,  $3.4\text{--}5.0 \times 5.2\text{--}9.9\ \mu\text{m}$ , and occur singly (Fig. 11r), exhibiting polar budding. In YM broth incubated at  $25\ ^\circ\text{C}$  for one month, a ring and sediment formed. Hyphae are formed on YM agar (Fig. 11s). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are subglobose, ellipsoidal, or ovoid on CMA agar,  $1.5\text{--}3.5 \times 4.0\text{--}5.1\ \mu\text{m}$  (Fig. 11t).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, maltose (weak), cellobiose, trehalose, melibiose (weak), raffinose, melezitose (weak), soluble starch, D-xylose (weak), L-arabinose (weak), D-arabinose (weak), N-Acetyl-D-glucosamine, D-mannitol, D-glucitol, Methyl- $\alpha$ -D-glucoside (weak) and salicin (weak) as the only carbon sources. However, it does not assimilate L-sorbose, lactose, inulin, D-ribose, L-rhamnose, D-glucosamine, methanol, ethanol, glycerol, erythritol, ribitol, galactitol, D-glucuronic acid, DL-lactate, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, L-lysine (delayed), and cadaverine (delayed) serve as the only nitrogen sources. In contrast, no assimilation occurs when ethylamine, potassium nitrate, or sodium nitrite serves as the sole nitrogen source. The strain does not grow in a vitamin-free medium or produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is  $28\ ^\circ\text{C}$ .

Material examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Veronicastrum stenostachyum*, Oct. 2020, Z.N. Du (culture GZ4443) (n=1).

Notes – Physiologically, *Bul. veronicastrum* can be differentiated from its close relatives *Bul. phyllostachydis* and *Bul. setariae* by its negative assimilation of D-ribose, L-rhamnose, D-glucosamine, galactitol, and D-glucuronic acid, but its positive assimilation of cadaverine and growth in vitamin-free medium (Table S3).

***Derxomyces anmaltophilus*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 12a–c

Mycobank number: MB851037

Etymology – The epithet reflects the inability of this species to assimilate maltose.

Type – China, Zhejiang Province, Wenzhou City, South Yandang Mountain, on plant leaf of *Sloanea sinensis*, Oct. 2016, Z.N. Du (holotype CGMCC 2.6768, lyophilized metabolically inactive cells, ex-type culture JCM 39300 =ZJ0372).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear creamish white to yellow, butyrous, and smooth with an entire margin (Fig. 12a). On YM agar incubated at 20 °C for 7 days, cells are fusiform, or long ellipsoidal,  $2.6\text{--}4.5 \times 10.6\text{--}13.0 \mu\text{m}$ , and occur singly (Fig. 12b), exhibiting polar budding or bifurcate-polar. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Hyphae are formed on CMA and YM agar (Fig. 12c). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, cellobiose (weak), trehalose, melibiose, raffinose, melezitose, soluble starch (delayed), D-xylose, L-arabinose, D-arabinose (delayed), L-rhamnose, D-glucosamine, ribitol (weak), D-mannitol (weak), D-glucitol, Methyl- $\alpha$ -D-glucoside (weak), salicin (weak), D-glucuronic acid, DL-lactate, succinate, citrate, and myo-inositol (weak) as the only carbon sources. However, it does not assimilate L-sorbose, maltose, lactose, inulin, D-ribose, N-Acetyl-D-glucosamine, methanol, ethanol, glycerol, erythritol, galactitol, or hexadecane. Ammonium sulfate, potassium nitrate (weak), L-lysine (weak), and cadaverine (weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when nitrogen, ethylamine, or sodium nitrite is the sole nitrogen source. The strain grows weakly in a vitamin-free medium and does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 29 °C.

Materials examined – China, Zhejiang Province, Wenzhou City, South Yandang Mountain, on plant leaf of *Elaeocarpus decipiens*, Oct. 2016, J.Q. Sun (culture ZJ1412), on plant leaf of *Sloanea sinensis*, Oct. 2016, Z.N. Du (culture ZJ0372) (n=2).

Notes – Physiologically, *Der. anmaltophilus* can be distinguished from all the other *Derxomyces* species by its negative assimilation of maltose (Table S3).

***Derxomyces rhamni*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

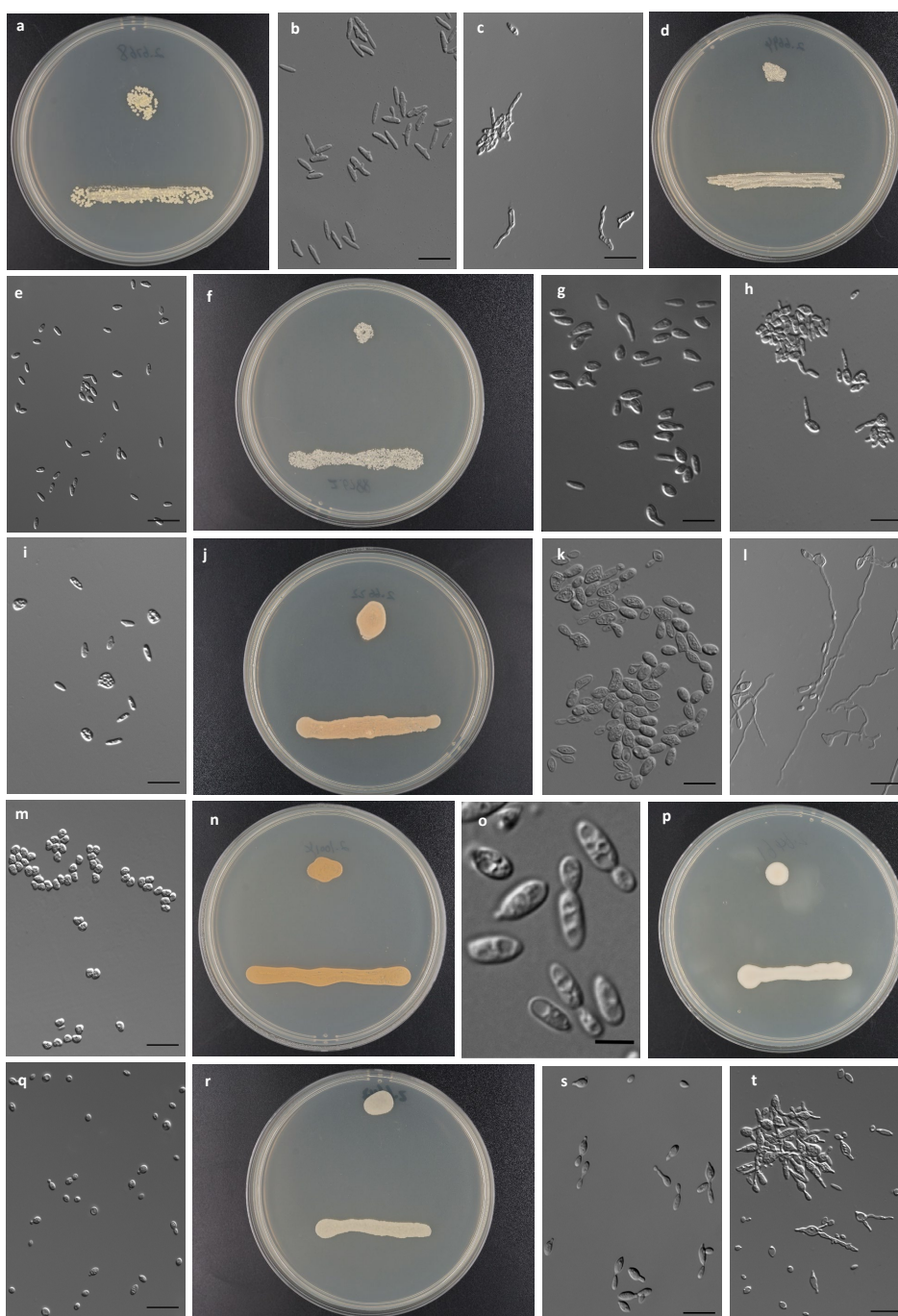
Fig. 12d, e

Mycobank number: MB851038

Etymology – The epithet is derived from *Rhamnus*, the host plant genus from which the type strain was obtained.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Hexi Town, Fenbiantang, on plant leaf of *Rhamnus davurica*, May 2020, Z.N. Du (holotype CGMCC 2.6694, lyophilized metabolically inactive cells, ex-type culture JCM 35444 = GZ2213).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear creamish white, or yellowish, butyrous, smooth, slightly wrinkled, and dull with an entire margin (Fig. 12d). On YM agar incubated at 20 °C for 7 days, cells are long ovoid or ellipsoidal,  $1.5\text{--}2.3 \times 2.5\text{--}4.1 \mu\text{m}$ , and occur singly or in pairs (Fig. 12e), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.



**Figure 12** – The streak culture and vegetative cells grown on YM agar for 5 days at 20 °C and ballistoconidia formation observed on corn meal agar after 7 days at 20 °C of the new yeast species within *Tremellomycetes*. (a–c) *Derxomyces anmaltophilus* CGMCC 2.6768<sup>T</sup>; (d, e) *Derxomyces rhamni* CGMCC 2.6694<sup>T</sup>; (f–i) *Derxomyces spathulatus* CGMCC 2.6788<sup>T</sup>; (j–m) *Derxomyces turchettianus* CGMCC 2.6622<sup>T</sup>; (n, o) *Dioszegia maricola* CGMCC 2.10014<sup>T</sup>; (p, q) *Teunia littoralis* CGMCC 2.6461<sup>T</sup>; (r–t) *Kockovaella camelliae* CGMCC 2.6642<sup>T</sup>. Bars = 10 µm except in o bar = 5 µm.

**Physiological and biochemical characters** – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, maltose, cellobiose (delayed), trehalose, melibiose, raffinose, melezitose, soluble starch, D-xylose, L-arabinose, D-arabinose (variable), D-ribose (weak), L-rhamnose, D-glucosamine (weak), N-Acetyl-D-glucosamine (weak), ribitol (variable),

galactitol (variable), D-mannitol (delayed and weak), D-glucitol, Methyl- $\alpha$ -D-glucoside, salicin (weak), D-glucuronic acid, and succinate (variable) as the only carbon sources. However, it does not assimilate L-sorbose, lactose, inulin, methanol, ethanol, glycerol, erythritol, DL-lactate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, L-lysine (weak), ethylamine (weak), and cadaverine (weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when potassium nitrate or sodium nitrite is the sole nitrogen source. The strain grows weakly in a vitamin-free medium and does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 25 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Indocalamus tessellatus*, Oct. 2020, Z.N. Du (culture GZ2851); Guizhou Province, Zunyi City, Zhengan County, Hexi Town, on plant leaf of *Pittosporum illicioides*, May 2020, Z.N. Du (culture GZ1612), on plant leaf of *Viburnum dilatatum*, May 2020, Z.N. Du (culture GZ2357), on plant leaf of *Hypericum monogynum*, May 2020, Z.N. Du (culture GZ2533), on plant leaf of *Veronicastrum stenostachyum*, May 2020, Z.N. Du (culture GZ3032); Guizhou Province, Zunyi City, Zhengan County, Hexi Town, Fenbiantang, on plant leaf of *Rhamnus davurica*, May 2020, Z.N. Du (culture GZ2213) (n=6).

Notes – Physiologically, *Der. rhamni* can be differentiated from its close relative *Der. anomala* by its positive assimilation of cellobiose, glycerol, erythritol, ribitol, salicin, citrate, and myo-inositol and growth in the vitamin-free medium, but its negative assimilation of methyl- $\alpha$ -D-glucoside, D-glucuronic acid, and inability to form starch-like compounds (Table S3).

***Derxomyces spathulatus*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 12f–i

Mycobank number: MB851039

Etymology – The epithet reflects the spathulatus cells observed in the type strain.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Viburnum dilatatum*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6788, lyophilized metabolically inactive cells, ex-type culture JCM 39306 = GZ0871).

Culture characters – On YPD agar incubated at 20 °C for 7 days, colonies appear whitish, butyrous, glistening, and smooth with an entire margin (Fig. 12f). On YM agar incubated at 20 °C for 7 days, cells are ovoid, long ovoid, fusiform, spathulatus, ellipsoidal to long ellipsoidal, 3.3–4.0  $\times$  5.5–10.2  $\mu$ m, and occur singly (Fig. 12g), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a pellicle and sediment formed. Hyphae are formed on CMA agar (Fig. 12h). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are ellipsoidal or napiform on CMA agar, 1.5–4.5  $\times$  4.0–5.2  $\mu$ m (Fig. 12i).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, maltose (variable), cellobiose (weak), trehalose (weak), melibiose, raffinose, melezitose, soluble starch, D-xylose (delayed and weak), L-arabinose (variable), N-Acetyl-D-glucosamine (weak), galactitol (weak), D-mannitol (delayed and weak), D-glucitol (delayed), and Methyl- $\alpha$ -D-glucoside as the only carbon sources. However, it does not assimilate L-sorbose, lactose, inulin, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, methanol, ethanol, glycerol, erythritol, ribitol, salicin, D-glucuronic acid, DL-lactate, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, L-lysine (weak), ethylamine (weak), and cadaverine serve as the only nitrogen sources. In contrast, no assimilation occurs when potassium nitrate or sodium nitrite is the sole nitrogen source. The strain can grow in a vitamin-free medium but does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 25 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shishun Peak, on plant leaf of *Viburnum dilatatum*, Oct. 2020, Z.N. Du (cultures GZ0872, GZ0871) (n=2).

Notes – Physiologically, *Der. spathulatus* can be differentiated from its close relatives *Der. longicylindricus*, *Der. linzhienensis*, and *Der. turchettianus* by its positive assimilation of D-ribose, D-glucosamine, ribitol, salicin, and potassium nitrate (Table S3).

***Derxomyces turchettianus*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 12j–m

MycoBank number: MB851040

Etymology – The epithet honors Prof. Benedetta Turchetti for her significant contributions to the taxonomy of extremophilic yeasts.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Rubus innominatus*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6622, lyophilized metabolically inactive cells, ex-type culture JCM 39292 = GZ4354).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear creamish white, butyrous, smooth, and wrinkled with an entire margin (Fig. 12j). On YM agar incubated at 20 °C for 7 days, cells are ovoid, long ovoid, or ellipsoidal,  $2.7\text{--}5.8 \times 4.0\text{--}10.1\text{ }\mu\text{m}$ , and occur singly or in pairs (Fig. 12k), exhibiting polar budding or bifurcate-polar. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Hyphae are formed on CMA agar (Fig. 12l). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are napiform or ellipsoidal on CMA agar,  $1.9\text{--}2.4 \times 2.8\text{--}3.4\text{ }\mu\text{m}$  (Fig. 12m).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, maltose, cellobiose (delayed), trehalose, melibiose, raffinose, melezitose, soluble starch, D-xylose, L-arabinose, D-arabinose (weak), D-ribose (weak), L-rhamnose (weak), D-glucosamine (weak), N-Acetyl-D-glucosamine (delayed), D-mannitol (weak), D-glucitol (weak), Methyl- $\alpha$ -D-glucoside (weak), salicin (weak), and succinate (weak) as the only carbon sources. However, it does not assimilate L-sorbose, lactose, inulin, methanol, ethanol, glycerol, erythritol, ribitol, galactitol, D-glucuronic acid, DL-lactate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed), L-lysine (delayed and weak), ethylamine (delayed), and cadaverine (delayed and weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain grows in a vitamin-free medium, but does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 29 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Rubus innominatus*, Oct. 2020, Z.N. Du (cultures GZ4368, GZ4373, GZ4374, GZ43611, GZ43613, GZ43615, GZ4354), on plant leaf of *Veronicastrum stenostachyum*, Oct. 2020, Z.N. Du (cultures GZ4456, GZ4461, GZ4462, GZ4466, GZ44412) (n=12).

Notes – Physiologically, *Der. turchettianus* can be differentiated from its close relatives *Der. longicylindricus* by its growth in the vitamin-free medium and positive assimilation of D-arabinose, D-ribose, D-glucosamine, N-acetyl-D-glucosamine, ribitol, galactitol, D-mannitol, salicin, and potassium nitrate, but its negative assimilation of L-sorbose and inulin (Table S3).

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

Fig. 12n, o

MycoBank number: MB851041

Etymology – The epithet *maricola* is derived from the isolation source, marine water, of the type strain.

Type – China, Shanghai City, Pudong District, obtained from marine water from the tidal flat in May 2021, H.Y. Zhu, J.N. Li, X.Z. Liu (holotype CGMCC 2.10014, lyophilized metabolically inactive cells, ex-type culture JCM 36245 = 17-0-2E-327-2).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear orange, butyrous, smooth, and glossy with an entire margin (Fig. 12n). On YM agar incubated at 20 °C for 7 days, cells are ellipsoidal or cylindric,  $3.0\text{--}4.0 \times 4.4\text{--}7.9\text{ }\mu\text{m}$ , and occur singly or in pairs (Fig. 12o), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a sediment formed. Hyphae and pseudohyphae are formed on CMA agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, L-sorbose (delayed and weak), sucrose, maltose (delayed), cellobiose, trehalose, lactose (delayed and weak), melibiose, raffinose, melezitose, inulin (delayed and weak), soluble starch (delayed and weak), D-xylose, L-arabinose, D-arabinose, D-ribose

(delayed and weak), L-rhamnose (delayed), D-glucosamine (weak), N-Acetyl-D-glucosamine (delayed), ethanol (delayed), ribitol (delayed), galactitol (delayed), D-mannitol, Methyl- $\alpha$ -D-glucoside (delayed), salicin, D-glucuronic acid (delayed), DL-lactate (delayed), succinate (delayed), citrate (delayed and weak) and myo-inositol (delayed and weak) as the only carbon sources. However, it does not assimilate methanol, glycerol, erythritol, D-glucitol, or hexadecane. Ammonium sulfate, potassium nitrate (delayed and weak), sodium nitrite (delayed and weak), L-lysine (delayed and weak), and cadaverine (delayed and weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when ethylamine is the sole nitrogen source. The strain does not grow in a vitamin-free medium but can produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 25 °C.

Material examined – China, Shanghai City, Pudong District, obtained from marine water from the tidal flat in May 2021, H.Y. Zhu, J.N. Li, X.Z. Liu (culture 17-0-2E-327-2) (n=1).

Notes – Physiologically, *Dio. maricola* can be differentiated from its close relatives *Dio. changbaiensis*, *Dio. cryoxerica*, and *Dio. heilongjiangensis* by its positive or weak assimilation of potassium nitrate, but its negative assimilation of D-glucitol (Table S3).

### ***Agaricomycotina, Tremellomycetes, Tremellales, Cryprococcaceae***

***Teunia littoralis*** X.Z. Liu, F.Y. Bai & H.Y. Zhu, sp. nov.

Fig. 12p, q

Mycobank number: MB851050

Etymology – The epithet *littoralis* is derived from the tidal flat from which the type strain originates.

Type – China, Guangxi Zhuang Autonomous Region, Beihai City, Yinhai District, obtained from soil sediment from the tidal flat in Aug. 2021, X.Z. Liu & Y.J. Shang (holotype CGMCC 2.6461, lyophilized metabolically inactive cells, ex-type culture JCM 35063 = 109C-2).

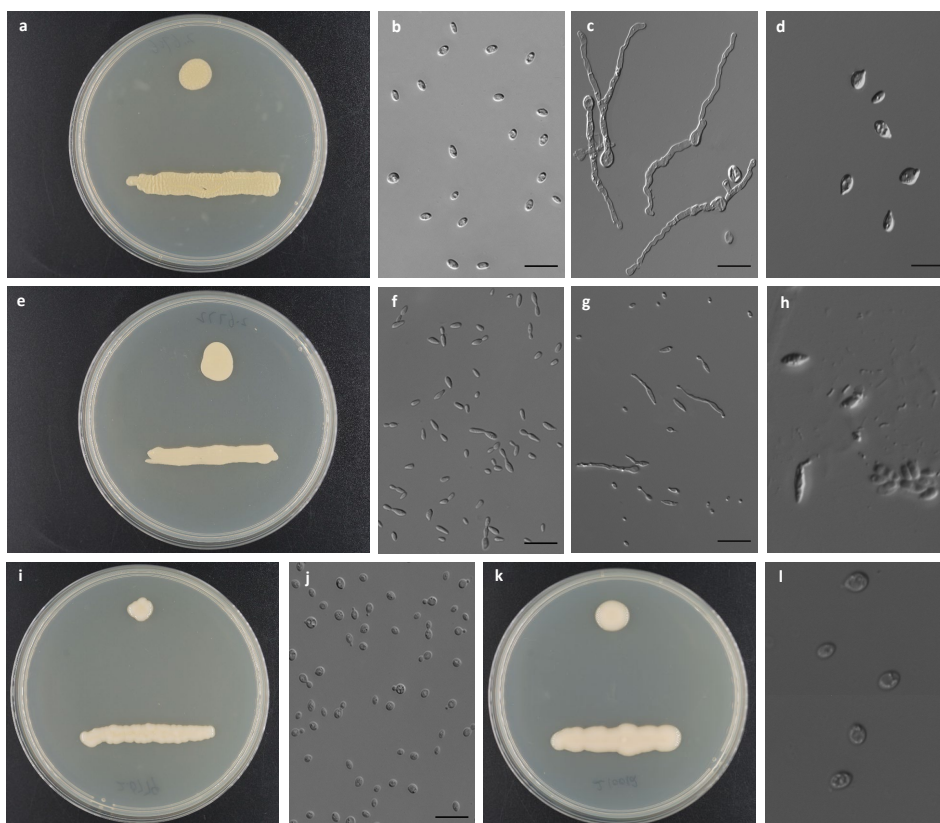
Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear white-cream, butyrous, smooth, and glistening with an entire margin (Fig. 12p). On YM agar incubated at 20 °C for 7 days, cells are ovoid, globose, or subglobose, 2.1–2.9  $\times$  2.4–3.9  $\mu$ m, and occur singly or in pairs (Fig. 12q), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (delayed or weak), L-sorbose (variable), sucrose, maltose, cellobiose (delayed), trehalose, melezitose, soluble starch, D-xylose (positive or weak), L-arabinose (delayed or weak), D-arabinose (weak), D-ribose (weak), L-rhamnose, D-glucosamine (delayed), N-Acetyl-D-glucosamine (delayed and weak), ethanol (variable), glycerol (variable), D-mannitol (weak), D-glucitol (variable), salicin (variable), D-glucuronic acid (delayed or delayed and weak), and succinate (delayed and weak) as the only carbon sources. However, it does not assimilate lactose, melibiose, raffinose, inulin, methanol, erythritol, ribitol, galactitol, Methyl- $\alpha$ -D-glucoside, L-lactate, citrate, myo-inositol, or hexadecane. Cadaverine, potassium nitrate (delayed or delayed and weak), ammonium sulfate, L-lysine, and ethylamine (delayed) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain does not grow in a vitamin-free medium or produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 29 °C.

Materials examined – China, Guangxi Zhuang Autonomous Region, Beihai City, Yinhai District, obtained from soil sediments from the tidal flat, July 2021, X.Z. Liu & Y.J. Shang (cultures CGMCC 2.6460 = 109C-1, CGMCC2.6462 = 109C-3, CGMCC 2.6461 = 109C-2) (n=3).

Notes – Physiologically, *Teu. littoralis* can be differentiated from its close relative *Teu. globosa* by its negative assimilation of L-arabinose, D-arabinose, glycerol, D-glucitol, D-glucuronic acid, and potassium nitrate, but its negative assimilation of lactose, inulin, and myo-inositol (Table S3).





**Figure 13** – The streak culture and vegetative cells grown on YM agar for 5 days at 20 °C, and ballistoconidia formation observed on corn meal agar after 7 days at 20 °C of the new yeast species within *Tremellomycetes*. (h-j) *Kockovaella malloti* CGMCC 2.6706<sup>T</sup>; (k–m) *Kockovaella rosae* CGMCC 2.6772<sup>T</sup>; (n) *Buzzinia foliicola* CGMCC 2.6779<sup>T</sup>; (o) *Papiliotrema chongmingensis* CGMCC 2.10012<sup>T</sup>

***Agaricomycotina, Tremellomycetes, Tremellales, Cuniculitremaeae***

***Kockovaella camelliae* X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.**

Fig. 12r–t

MycoBank number: MB851042

Etymology – The epithet *camelliae* is derived from *Camellia*, the host plant genus from which the strain was obtained.

Type – China, Zhejiang Province, Wenzhou City, South Yandang Mountain, on plant leaf of *Camellia oleifera*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6642, lyophilized metabolically inactive cells, ex-type culture JCM 35431 =ZJ0541).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear yellowish, butyrous, smooth, and glistening with an entire margin (Fig. 12r). On YM agar incubated at 20 °C for 7 days, cells are long ovoid or ellipsoidal,  $3.2\text{--}4.1 \times 4.3\text{--}8.2\text{ }\mu\text{m}$ , and occur singly or in pairs (Fig. 12s), exhibiting polar budding. Blastospores are produced on short stalk-like conidiophores. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Hyphae are formed on CMA agar (Fig. 12t). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, maltose, cellobiose, trehalose, lactose, melibiose, raffinose, melezitose, soluble starch, D-xylose, D-arabinose (weak), D-glucosamine, N-Acetyl-D-glucosamine (weak), galactitol (weak), D-mannitol, D-glucitol (weak), salicin (weak), D-glucuronic acid (weak), succinate (weak), and citrate (weak) as the only carbon sources. However, it does not assimilate L-sorbose, inulin, L-arabinose, D-ribose, L-rhamnose, methanol, ethanol, glycerol, erythritol, ribitol, Methyl- $\alpha$ -D-glucoside, DL-lactate, myo-inositol, or hexadecane. Cadaverine, potassium nitrate (delayed), ammonium sulfate, L-lysine (delayed), and ethylamine (delayed and

weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain grows weakly in a vitamin-free medium and does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 28 °C.

Material examined – China, Zhejiang Province, Wenzhou City, South Yandang Mountain, on plant leaf of *Camellia oleifera*, Oct. 2020, Z.N. Du (culture ZJ0541) (n=1).

Notes – Physiologically, *Koc. camelliae* can be differentiated from its close relatives *Koc. machilophila* and *Koc. phaffii* by its positive assimilation of potassium nitrate and cadaverine, but its negative assimilation of D-ribose and L-rhamnose (Table S3).

***Kockovaella malloti*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 13a–d

MycoBank number: MB851043

Etymology – The epithet *malloti* is named after *Mallotus*, the genus of the source plant for the type strain.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Mallotus repandus*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6706, lyophilized metabolically inactive cells, ex-type culture JCM 35447 =GZ36220).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear yellowish or cream, butyrous, wrinkled, and dull with an entire margin (Fig. 13a). On YM agar incubated at 20 °C for 7 days, cells are ovoid or ellipsoidal,  $3.4\text{--}5.9 \times 4.4\text{--}6.6\ \mu\text{m}$ , and occur singly (Fig. 13b), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Hyphae are formed on CMA agar (Fig. 13c). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are ovoid or ellipsoidal on CMA and YM agar,  $2.1\text{--}4.8 \times 4.4\text{--}6.2\ \mu\text{m}$  (Fig. 13d).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, maltose, cellobiose, trehalose, melibiose, raffinose (weak), melezitose, soluble starch, D-xylose, L-arabinose (delayed), D-glucosamine, and D-mannitol (weak) as the only carbon sources. However, it does not assimilate L-sorbose, sucrose, lactose, inulin, D-arabinose, D-ribose, L-rhamnose, N-Acetyl-D-glucosamine, methanol, ethanol, glycerol, erythritol, ribitol, galactitol, D-glucitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, DL-lactate, succinate, citrate, myo-inositol, or hexadecane. Ammonium sulfate, potassium nitrate (both weak and delayed), L-lysine (weak), ethylamine (delayed), and cadaverine (weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain can grow in a vitamin-free medium but does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 25 °C.

Material examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Mallotus repandus*, Oct. 2020, Z.N. Du (culture GZ36220) (n=1).

Notes – Physiologically, *Koc. malloti* can be differentiated from *Koc. thailandica* by its positive assimilation of potassium nitrate, ethylamine, and growth in the vitamin-free medium, but its negative assimilation of sucrose, lactose, D-arabinose, D-ribose, L-rhamnose, N-acetyl-D-glucosamine, ribitol, D-glucitol, and succinate (Table S3).

***Kockovaella rosae*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 13e–h

MycoBank number: MB851044

Etymology – The epithet *rosae* is derived from *Rosa*, the host plant genus from which the type strain was obtained.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Hexi Town, Fenbiantang, on plant leaf of *Rosa banksiae*, May 2020, Z.N. Du (holotype CGMCC 2.6772, lyophilized metabolically inactive cells, ex-type culture JCM 39301 = GZ1821).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear yellowish, butyrous, partly wrinkled, and glistening, and turn wrinkled after 1 month of growth with an entire



margin (Fig. 13e). On YM agar incubated at 20 °C for 7 days, cells are ovoid, fusiform, or ellipsoidal,  $2.1\text{--}2.9 \times 3.4\text{--}7.3\text{ }\mu\text{m}$ , and occur singly or in pairs (Fig. 13f), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a sediment and a pellicle formed. Hyphae are formed on CMA agar (Fig. 13g). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are ellipsoidal on CMA agar,  $2.4\text{--}3.9 \times 5.4\text{--}12.0\text{ }\mu\text{m}$  (Fig. 13h).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, maltose, cellobiose, trehalose, lactose, melibiose, raffinose, melezitose, soluble starch, D-xylose, L-arabinose, D-arabinose, D-ribose, D-glucosamine (weak), N-Acetyl-D-glucosamine, D-mannitol, D-glucuronic acid (delayed), L-lactate (weak), and myo-inositol as the only carbon sources. However, it does not assimilate L-sorbose, inulin, L-rhamnose, methanol, ethanol, glycerol, erythritol, ribitol, galactitol, D-glucitol, Methyl- $\alpha$ -D-glucoside, salicin, succinate, citrate, or hexadecane. Ammonium sulfate, potassium nitrate (weak), L-lysine (delayed), ethylamine (delayed), and cadaverine (delayed) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain can grow in a vitamin-free medium but does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 25 °C.

Material examined – China, Guizhou Province, Zunyi City, Zhengan County, Hexi Town, Fenbiantang, on plant leaf of *Rosa banksiae*, May 2020, Z.N. Du (culture GZ1821) (n=1).

Notes – Physiologically, *Koc. rosae* can be differentiated from its close relatives *Koc. mexicana* and *Koc. prillingeri* by its positive assimilation of potassium nitrate and cadaverine, but its negative assimilation of L-rhamnose, galactitol, D-glucitol, succinate, and citrate (Table S3).

#### ***Agaricomycotina, Tremellomycetes, Tremellales, Phaeotremellaceae***

##### ***Buzzinia* X.Z. Liu & F.Y. Bai, gen. nov.**

Mycobank number: MB851035

Etymology – The generic name honors Dr. Pietro Buzzini for his outstanding contributions to the biodiversity, ecology, and systematics of extremophilic yeasts.

Type species – *Buzzinia foliicola* X.Z. Liu, F.Y. Bai & J.Q. Sun.

No sexual reproduction observed. Colonies are white-cream, mucoid, smooth, glossy, and glistening. Budding cells are present. Pseudohyphae and hyphae are absent. Ballistoconidia are not observed.

Accepted species – *Buzzinia foliicola*

Notes – Physiologically, *Buzzinia* can be distinguished from its close relatives *Gelidatrema spencermartinsiae* and *Gel. psychrophila* by its negative assimilation of sucrose, lactose, melibiose, raffinose, melezitose, D-xylose, L-arabinose, D-arabinose, D-ribose, L-rhamnose, ribitol, galactitol, salicin, succinate, and myo-inositol, but its capacity to grow at 27 °C (Table S3).

##### ***Buzzinia foliicola* X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.**

Fig. 13i, j

Mycobank number: MB851036

Etymology – The epithet *foliicola* reflects the leaf origin of the type strain.

Type – China, Zhejiang Province, Wenzhou City, North Yandang Mountain, on plant leaf of *Cryptomeria japonica* var. *sinensis*, Oct. 2016, Z.N. Du (holotype CGMCC 2.6779, lyophilized metabolically inactive cells, ex-type culture JCM 39302 = ZJ0961).

Culture characters – On YPD agar incubated at 20 °C for 7 days, colonies appear white-cream, mucoid, smooth, glossy, and glistening with an entire margin (Fig. 13i). On YM agar incubated at 20 °C for 7 days, cells are globosal, subglobosal, or ovoid,  $3.0\text{--}5.7 \times 4.4\text{--}6.3\text{ }\mu\text{m}$ , and occur singly or in pairs (Fig. 13j), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a sediment and a pellicle formed. Pseudohyphae and hyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, maltose, cellobiose, trehalose, soluble starch, N-Acetyl-D-

glucosamine (weak), glycerol, D-mannitol, and D-glucitol (weak) as the only carbon sources. However, it does not assimilate L-sorbose, sucrose, lactose, melibiose, raffinose, melezitose, inulin, D-xylose, L-arabinose, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, methanol, ethanol, erythritol, ribitol, galactitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, DL-lactate, succinate, citrate, myo-inositol, or hexadecane. Cadaverine, potassium nitrate (delayed), ammonium sulfate, L-lysine, and ethylamine serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain grows weakly in a vitamin-free medium but does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 28 °C.

Material examined – China, Zhejiang Province, Wenzhou City, North Yandang Mountain, on plant leaf of *Cryptomeria japonica* var. *sinensis*, Oct. 2016, Z.N. Du (culture ZJ0961) (n=1).

***Agaricomycotina, Tremellomycetes, Tremellales, Rhynchogastremaceae***

***Papiliotrema chongmingensis* X.Z. Liu, F.Y. Bai & H.Y. Zhu, sp. nov.**

Fig. 13k, l

MycoBank number: MB851045

Etymology – The epithet *chongmingensis* refers to the type locality, Chongming District, Shanghai City.

Type – China, Shanghai City, Chongming District, obtained from soil sediment from the tidal flat, May 2021, H.Y. Zhu, J.N. Li, X.Z. Liu (holotype CGMCC 2.10012, lyophilized metabolically inactive cells, ex-type culture JCM 36244 = 30A-1).

Culture characters – On YPD agar incubated at 20 °C for 7 days, colonies appear yellowish, mucoid, and smooth with an entire margin (Fig. 13k). On YM agar incubated at 20 °C for 7 days, cells are ovoid or subglobose,  $2.2\text{--}2.8 \times 2.7\text{--}3.8 \mu\text{m}$ , and occur singly (Fig. 13l), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a sediment formed. Hyphae and pseudohyphae are absent on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, maltose, cellobiose, trehalose, lactose, melibiose (delayed and weak), raffinose, melezitose, soluble starch, D-xylose, L-arabinose, D-arabinose, D-ribose (delayed), L-rhamnose (delayed), D-glucosamine (delayed and weak), N-Acetyl-D-glucosamine, ethanol (delayed), ribitol, galactitol (delayed), D-mannitol (delayed), Methyl- $\alpha$ -D-glucoside, salicin (delayed), D-glucuronic acid (delayed), L-lactate (delayed), succinate (delayed), citrate (delayed and weak), and myo-inositol (delayed) as the only carbon sources. However, it does not assimilate L-sorbose, inulin, methanol, glycerol, erythritol, D-glucitol, or hexadecane. Ammonium sulfate, ethylamine, and cadaverine serve as the only nitrogen sources. In contrast, no assimilation occurs when potassium nitrate, sodium nitrite, or L-lysine is the sole nitrogen source. The strain can grow in a vitamin-free medium and produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 30 °C.

Material examined – China, Shanghai City, Chongming District, obtained from soil sediment from the tidal flat, May 2021, H.Y. Zhu, J.N. Li, X.Z. Liu (culture 30A-1) (n=1).

Notes – Physiologically, the taxon *Pap. chongmingensis* can be differentiated from its close relatives *Pap. rajasthanensis* and *Pap. laurentii* by its negative assimilation of L-sorbose, erythritol, and D-glucitol (Table S3).

***Ustilaginomycotina, Exobasidiomycetes, Doassansiales, Doassansiaceae***

***Gracilitas* X.Z. Liu, F.Y. Bai & H.Y. Zhu, gen. nov.**

MycoBank number: MB801051

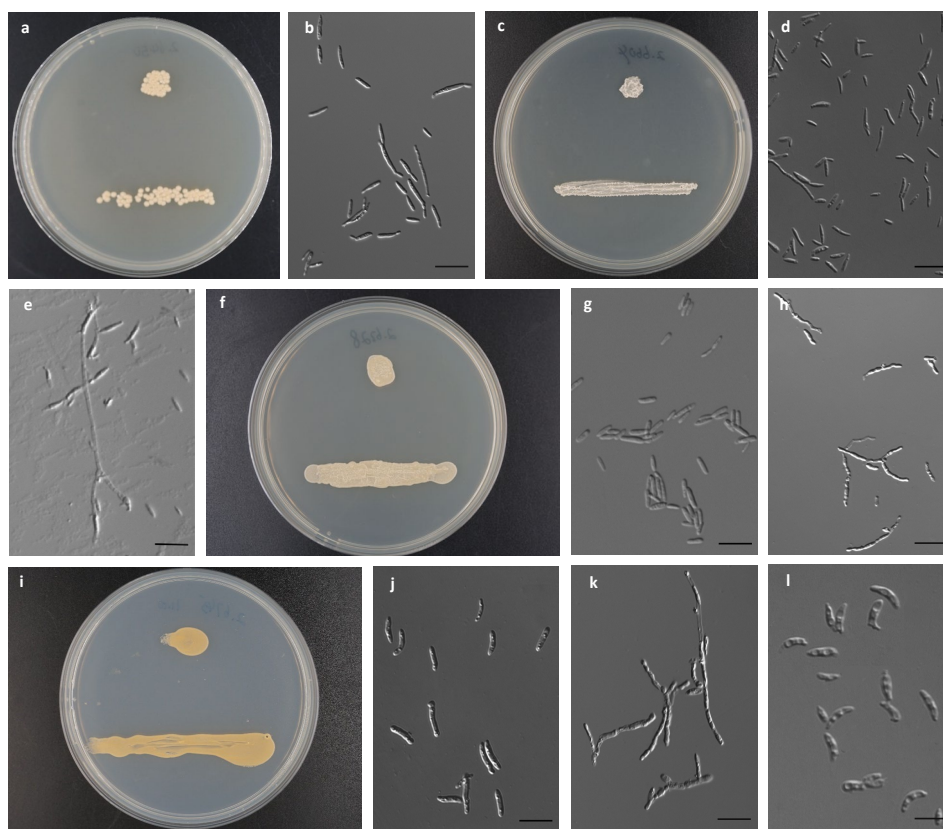
Etymology – The genus is named for the gracilis shape of the vegetative cell of the type species.

Type species – *Gracilitas littoralis* X.Z. Liu, F.Y. Bai & H.Y. Zhu.

No sexual reproduction observed. Colonies are yellow-cream, mucoid, smooth, and glossy. Budding cells are present. Pseudohyphae are absent, but not for hyphae. No ballistoconidia are detected.

Accepted species – *Gracilitas littoralis*

Notes – Physiologically, *Gracilitas* can be differentiated from its closely related yeast-like strain CGMCC 2.6453 by its positive assimilation of D-xylose, N-acetyl-D-glucosamine, ribitol, and ethylamine (Table S3).



**Figure 14** – The streak culture and vegetative cells grown on YM agar for 5 days at 20 °C, and ballistoconidia formation observed on corn meal agar after 7 days at 20 °C of the new yeast species within *Exobasidiomycetes*. (a, b) *Gracilitas littoralis* CGMCC 2.6450<sup>T</sup>; (c–e) *Yunzhangomyces nandinae* CGMCC 2.6604<sup>T</sup>; (f–h) *Exobasidium cylindricum* CGMCC 2.6728<sup>T</sup>; (i–l) *Turchettia toddaliae* CGMCC 2.6745<sup>T</sup>. Bars = 10 μm.

***Gracilitas littoralis*** X.Z. Liu, F.Y. Bai & H.Y. Zhu, sp. nov.

Fig. 14a, b

Mycobank number: MB851052

Etymology – The epithet *littoralis* is derived from the intertidal zone where the type strain was obtained.

Type – China, Zhejiang Province, Hangzhou City, Xiaoshan District, obtained from marine water, July 2020, R.P. Zhang & X.Z. Liu (holotype CGMCC 2.6450, lyophilized metabolically inactive cells, Ex-type culture JCM 35052 = 46D-5).

Culture characters – On YPD agar incubated at 20 °C for 7 days, colonies appear yellow-cream, mucoid, smooth, and glossy with an entire margin (Fig. 14a). On YM agar incubated at 20 °C for 7 days, cells are cylindrical, elongated fusiform, or long ellipsoidal,  $1.3\text{--}1.8 \times 4.3\text{--}16.7\text{ }\mu\text{m}$ , and occur singly (Fig. 14b), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Hyphae are formed on CMA and YM agar. No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, L-sorbose (delayed and weak), sucrose, maltose, cellobiose (delayed or delayed and weak), trehalose, melibiose (positive or delayed), raffinose, melezitose, soluble starch, D-xylose (delayed), D-ribose (delayed), N-Acetyl-D-glucosamine (delayed or delayed and weak), erythritol, ribitol (delayed or delayed and weak), D-mannitol (positive or delayed), D-glucitol

(positive or delayed), salicin (variable), DL-lactate, succinate (weak), and citrate (delayed and weak or weak) as the only carbon sources. However, it does not assimilate galactose, lactose, inulin, L-arabinose, D-arabinose, L-rhamnose, D-glucosamine, methanol, ethanol, glycerol, galactitol, Methyl- $\alpha$ -D-glucoside, D-glucuronic acid, myo-inositol, or hexadecane. Cadaverine, potassium nitrate, ammonium sulfate, L-lysine, and ethylamine (delayed) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain does not grow in a vitamin-free medium or produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 30 °C.

Materials examined – China, Zhejiang Province, Hangzhou City, Xiaoshan District, obtained from marine water from the tidal flat, July 2020, X.Z. Liu & R.P. Zhang (cultures 46D-6, 46D-11, 46D-5) (n=3).

***Ustilaginomycotina, Exobasidiomycetes, Exobasidiales, Brachybasidiaceae***

***Yunzhangomyces nandinae*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 14c–e

Mycobank number: MB851058

Etymology – The epithet is derived from the *Nandina*, the host plant genus from which the type strain was obtained.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Nandina domestica*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6604, lyophilized metabolically inactive cells, ex-type culture JCM 35428 = GZ4262).

Culture characters – On YPD agar incubated at 20 °C for 7 days, colonies appear pale-yellow, white-cream, wrinkled, and glistening, and turn pale-pink and wrinkled after one month of growth (Fig. 14c). On YM agar incubated at 20 °C for 7 days, cells are cylindrical,  $1.4\text{--}1.9 \times 4.8\text{--}10.0\ \mu\text{m}$ , and occur singly or in pairs (Fig. 14d). exhibiting polar budding. The margin is entire. In YM broth incubated at 25 °C for one month, a ring and sediment formed. Hyphae are formed on CMA and YM agar (Fig. 14e). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (positive or weak), sucrose, maltose (variable), trehalose, raffinose, melezitose, soluble starch (positive or weak), D-xylose, L-arabinose, D-ribose (variable), N-Acetyl-D-glucosamine (variable), ethanol (variable), glycerol (weak), erythritol (weak), D-mannitol, D-glucitol, salicin (weak), D-glucuronic acid (variable), DL-lactate (variable), succinate (variable), citrate (variable), and myo-inositol (variable) as the only carbon sources. However, it does not assimilate L-sorbose, cellobiose, lactose, melibiose, inulin, D-arabinose, L-rhamnose, D-glucosamine, methanol, ribitol, galactitol, Methyl- $\alpha$ -D-glucoside, or hexadecane. Cadaverine, potassium nitrate (delayed), sodium nitrite (delayed), ammonium sulfate, L-lysine, and ethylamine serve as the only nitrogen sources. The strain can grow in a vitamin-free medium but does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 29 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Serissa serissoides*, Oct. 2020, Z.N. Du (cultures GZ2461, GZ2462), on plant leaf of *Nandina domestica*, Oct. 2020, Z.N. Du (culture GZ4262) (n=3).

Notes – Physiologically, *Yun. nandinae* can be differentiated from all the other yeast-like species, *Yun. clavatus*, *Yun. cylindricus*, *Yun. Qinlingensis*, and *Yun. orchidis* by its positive assimilation of soluble starch and myo-inositol, but negative assimilation of L-sorbose and ribitol (Table S3).

***Ustilaginomycotina, Exobasidiomycetes, Exobasidiales, Exobasidiaceae***

***Exobasidium cylindricum*** X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.

Fig. 14f–h

Mycobank number: MB851055

Etymology – The epithet *cylindricum* reflects the cylindrical morphology of yeast cells.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Viburnum utile*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6728, lyophilized metabolically inactive cells, ex-type culture JCM 35453 = GZ1313).

Culture characters – On YPD agar incubated at 20 °C for 7 days, colonies appear pale-yellowish, partly wrinkled, and glistening with an entire margin (Fig. 14f). On YM agar incubated at 20 °C for 7 days, cells are cylindrical,  $1.8\text{--}2.2 \times 4.5\text{--}9.6\ \mu\text{m}$ , and occur singly or in pairs (Fig. 14g), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a sediment formed. Hyphae are formed on CMA agar (Fig. 14h). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are not observed on CMA and YM agar.

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose, sucrose, cellobiose, trehalose (weak), lactose (weak), melibiose (weak), raffinose, melezitose, L-arabinose (weak), glycerol (weak), and D-mannitol (weak) as the only carbon sources. However, it does not assimilate L-sorbose, maltose, inulin, soluble starch, D-xylose, D-arabinose, D-ribose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, methanol, ethanol, erythritol, ribitol, galactitol, D-glucitol, Methyl- $\alpha$ -D-glucoside, salicin, D-glucuronic acid, DL-lactate, succinate, citrate, myo-inositol, or hexadecane. Cadaverine, ammonium sulfate, potassium nitrate (weak), L-lysine, and ethylamine (weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain can grow in a vitamin-free medium but does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 30 °C.

Material examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Viburnum utile*, Oct. 2020, Z.N. Du (culture GZ1313) (n=1).

### ***Ustilaginomycotina, Exobasidiomycetes, Georgefischeriales***

#### ***Turchettiaceae* X.Z. Liu & F.Y. Bai, fam. nov.**

Mycobank number: MB851061

Type genus – *Turchettia* X.Z. Liu & F.Y. Bai

Within the *Georgefischeriales*, the family *Turchettiaceae* is taxonomically defined by its type genus *Turchettia*, which also provides the basis for the family's nomenclature.

Accepted genus – *Turchettia* X.Z. Liu & F.Y. Bai

Notes – Physiologically, *Turchettiaceae* can be differentiated from its closely related four yeast-like species, *Gja. cyclobalanopsidis*, *Gja. minor*, *Gja. penniseti*, and *Gja. pseudominor* by its positive assimilation of methanol and salicin (Table S3).

#### ***Turchettia* X.Z. Liu & F.Y. Bai, gen. nov.**

Mycobank number: MB851056

Etymology – The generic name honors Prof. Benedetta Turchetti for her outstanding contributions to understanding extremophilic yeast diversity and taxonomy.

Type species – *Turchettia toddalia* X.Z. Liu, F.Y. Bai & J.Q. Sun

No sexual reproduction observed. Colonies are white-cream to yellowish, butyrous, dull, and swollen, the surface is dry with wrinkles and has an entire margin. Budding cells are produced. Hyphae and ballistoconidia are observed.

Accepted species – *Turchettia toddaliae* X.Z. Liu, F.Y. Bai & J.Q. Sun

#### ***Turchettia toddaliae* X.Z. Liu, F.Y. Bai & J.Q. Sun, sp. nov.**

Fig. 14i–l

Mycobank number: MB851057

Etymology – The epithet is named after the *Toddalia*, the genus of the source plant for the type strain.

Type – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Toddalia asiatica*, Oct. 2020, Z.N. Du (holotype CGMCC 2.6745, lyophilized metabolically inactive cells, ex-type culture JCM 39296 = GZ1871).

Culture characters – On YM agar incubated at 20 °C for 7 days, colonies appear white-cream to yellowish, butyrous, dull, and swelled, the surface is dry with wrinkles and has an entire margin (Fig. 14i). On YM agar incubated at 20 °C for 7 days, cells are cylindrical or falcate,  $2.7\text{--}3.3 \times 8.7\text{--}16.8 \mu\text{m}$ , and occur singly (Fig. 14j), exhibiting polar budding. In YM broth incubated at 25 °C for one month, a sediment and pellicle formed. Hyphae are formed on CMA and YM agar (Fig. 14k). No sexual structures are observed on CMA, PDA, YM, V8, and YCB agar. Ballistoconidia are falcate or elongated fusiform on CMA agar,  $2.1\text{--}2.5 \times 5.3\text{--}10.1 \mu\text{m}$  (Fig. 14l).

Physiological and biochemical characters – The strain is unable to ferment glucose. It is capable of assimilating glucose, galactose (variable), sucrose (positive or delayed), maltose (positive or weak), cellobiose (delayed or weak), trehalose, melibiose (delayed), raffinose (weak), melezitose, soluble starch, D-xylose (variable), L-arabinose (variable), D-arabinose (weak), methanol (variable), ethanol (variable), glycerol (positive or weak), ribitol (variable), D-mannitol (delayed or weak), D-glucitol (delayed or weak), Methyl- $\alpha$ -D-glucoside (variable), salicin (variable), D-glucuronic acid (variable), DL-lactate (positive or weak), succinate (variable), and citrate (variable) as the only carbon sources. However, it does not assimilate L-sorbose, lactose, inulin, D-ribose, L-rhamnose, D-glucosamine, N-Acetyl-D-glucosamine, erythritol, galactitol, myo-inositol, and hexadecane. Ammonium sulfate, potassium nitrate (delayed), L-lysine (weak), ethylamine (delayed), and cadaverine (weak) serve as the only nitrogen sources. In contrast, no assimilation occurs when sodium nitrite is the sole nitrogen source. The strain can grow in a vitamin-free medium but does not produce starch-like substances. It tests positive for urease activity and the Diazonium Blue B reaction. The highest growth temperature observed is 30 °C.

Materials examined – China, Guizhou Province, Zunyi City, Zhengan County, Shisun Peak, on plant leaf of *Viburnum utile*, Oct. 2020, Z.N. Du (cultures GZ1336, GZ1335), on plant leaf of *Toddalia asiatica*, Oct. 2020, Z.N. Du (culture GZ1871) (n=3).

## DISCUSSION

In this study, nearly 200 plant leaves were collected from two subtropical forests in Zhejiang and Guizhou provinces, leading to the description of 32 new yeast species. Plant substrates are well-established reservoirs for yeast. Over one-third of the yeasts preserved in worldwide collections originated from plants (Groenewald et al. 2017), and more than 40% of new species described in the last two decades were isolated from plant materials (Boekhout et al. 2022). Our sampling efforts compared two distinct environments: the Yandang Mountain area in Zhejiang Province (southeast China), a region characterized by a developed economy and a large human population, and the Shisun Peak area in Guizhou (southwest China), a remote environment with minimal anthropogenic disturbance. Sampling in Yandang Mountain covered the entire mountain range in the east, west, north, south, and middle, yielding plant leaves from 72 species across 33 families, with the dominance of *Lauraceae* and *Fagaceae*. In contrast, sampling in Guizhou Province was concentrated on Shisun Peak and its vicinity in Zheng'an County. Here, 45 plant species from 30 families were sampled, with most families represented by a single species and the most speciose family, Caprifoliaceae, represented by only three. This pattern reflects the high taxonomic divergence often observed in relatively undisturbed mountain habitats. Notably, only nine plant species occurred simultaneously at both sites, highlighting significant differences in plant community composition. While both regions support subtropical montane flora, their dominant tropical and temperate elements differ due to distinct climatic conditions, geological histories, and levels of human impact (Ge et al. 2014, Chen et al. 2018).

Phyllosphere yeasts play crucial roles in plant-microbe interactions by driving key ecological processes, such as litter decomposition, nutrient cycling, and plant growth promotion. Furthermore, they enhance plant resilience to biotic and abiotic stresses including microbial pathogens and UV radiation, through mechanisms like induced systemic resistance, pigment production, and biofilm formation (Gouka et al. 2022). The remarkably high number of novel taxa discovered here underscores the phyllosphere as an underexplored microhabitat harbouring unexpectedly rich and specialized yeast communities. Interestingly, although the species diversity of sampling plants and



the sampling breadth in Yandang Mountain are greater than those in Shisun Peak, the latter site yielded 26 new yeast species, 20 more than those found in Yandang Mountain. This contrast suggests that phyllosphere yeast diversity is not driven solely by plant diversity but is also shaped by microclimatic, biogeographic, and habitat-specific factors. The relatively isolated montane environment of the Shisun Peak region likely provides unique microhabitats that promote lineage diversification or preserve ancient, narrowly distributed lineages. China remains a hotspot for yeast taxonomy, with at least 782 recorded yeast species and over 300 new species described recently (Boekhout et al. 2021b, Li et al. 2022). However, despite Guizhou's status as one of the most environmentally diverse provinces in China with a rich flora of 7550 vascular plant species (Liu et al. 2018), only five new species had been described from five recorded locations (Boekhout et al. 2021b, 2022). As such, targeted sampling of underexplored, remote forests like those in Guizhou province, along with ecological analyses of host-microbe associations, is essential for elucidating the full extent of the ecological functions and evolutionary histories of these yeasts.

Tidal flat zones, which serve as dynamic transitions between oceans and land, are among the most productive ecosystems on Earth (Murray et al. 2019). Beyond delivering critical ecosystemic services for humans, including storm protection, food production, carbon sequestration, and coastline stabilization, these habitats support a vast diversity of microorganisms essential for sediment and nutrient cycling (Li et al. 2016, Costello et al. 2017, Murray et al. 2019). While Jones et al. (2019) listed 220 yeast species belonging to 74 genera, 28 families, 15 orders, and nine classes from marine environments, yeasts in tidal flats remain significantly understudied compared to their deep sea, sub-seafloor, or hydrothermal vents counterparts (Richards et al. 2015, Li et al. 2016, Grossart et al. 2019). A high percentage (50%) of undescribed species have been reported in Mangrove areas, and several new species have been isolated from marine environments (Nagahama et al. 2006, Statzell-Tallman et al. 2008, Fell et al. 2011, Kachalkin 2014). Given that China has the second-largest extent of tidal flats worldwide, at 1.2 million ha, these distinctive intertidal niches represent a massive reservoir of undiscovered yeast diversity (Murray et al. 2019). Recent comprehensive surveys of yeast diversity at 161 sites in tidal flats along the Chinese coastline have begun to reveal this hidden diversity, reporting 286 species, including 39 potential novel taxa (Zhu et al. 2023). The novel species described in our study likely possess specific physiological adaptations to the fluctuating salinity, moisture, and nutrient conditions characteristic of the intertidal zone. Their discovery not only expands the inventory of marine fungi but also suggests that these specialized yeasts may play unique, niche-specific roles in the decomposition of organic matter and the maintenance of microbial networks in coastal sediments globally.

Eleven of 37 newly proposed species in our study are currently known from only a single strain. This phenomenon of single-isolate species is a common and well-documented pattern in yeast taxonomy (Yurkov et al. 2016, Kachalkin et al. 2019, Li et al. 2020, Jiang et al. 2024). In natural microbial communities, a few dominant species typically coexist with a large assemblage of ecologically rare taxa. These rare yeasts often occur at extremely low abundance due to slow growth, compete weakly for resources, or possess demanding physiological traits that reduce their chances of recovery through conventional cultivation. Consequently, obtaining only a single isolate representing a novel species is not unexpected during initial sampling. The relatively high proportion of single-isolate species observed in this study likely reflects the natural rarity or ecological specialization of certain yeast lineages rather than insufficient sampling. This interpretation is supported by a recent comprehensive study by Jiang et al. (2024), which reported that nearly half of newly discovered yeast species (49.3%) were represented by single isolates, despite intensive sampling over three years and covering 1,200 environmental samples. Such patterns indicate that rare yeasts may have narrow ecological niches, low detectability, or sporadic occurrence. Consequently, while resampling these rare taxa necessitates sustained, long-term efforts, successful re-isolation is inherently challenging and not always guaranteed (Kachalkin et al. 2019). Notably, seven of these single-strain species were isolated from Shisun Peak, compared to four from Yandang Mountain. This finding supports the notion that geographically remote locations or specialized niches promote the discovery of unique, rare lineages, for which the description of single-isolated species is generally more acceptable (Aime

et al. 2021). We believe that every new species described, especially those known from a single strain, significantly enlarges our knowledge of yeast diversity and its potential ecological significance. Genomic data are increasingly recognized as essential for refining species boundaries and elucidating evolutionary divergence among closely related taxa (Cene 2020, Boekhout et al. 2021a, Li et al. 2021). Leveraging the growing availability of high-quality reference genomes will enable higher-resolution insights into genetic divergence, evolutionary relationships, and population structure, thereby strengthening the reproducibility of taxonomic conclusions for single-isolate species. Given the current imbalance in which ascomycetous yeasts are substantially overrepresented in public databases, it is urgent to increase the genomic data for basidiomycetous yeast taxa (Libkind et al. 2020). Parallel efforts to improve the recovery of rare taxa are equally necessary. To improve the likelihood of obtaining additional isolates, we propose (i) sustained, long-term, repeated, and seasonally stratified sampling to capture temporal fluctuations in rare populations; and (ii) the application of high-throughput cultivation or network-directed isolation, guided by knowledge of microbial interactions inferred from metabarcoding data, as successfully employed in bacterial studies (Xian et al. 2020, Zhang et al. 2021).

The rapid increase in the discovery of yeast species over the last decades is filling taxonomic gaps, yet the number of known yeast species is far below the estimated 12,000 (Boekhout et al. 2022). Undersampling persists in extreme environments, such as arid, boreal, and cold-climate zones, as well as on specific substrates, including water, animals, humans, and lichens, suggesting significant potential for taxonomic novelties in future extensive sampling efforts. The higher-level taxonomy of fungi has been greatly improved with the number of fungal phyla increasing from four to 12 (James et al. 2020). The revision of basidiomycetous yeasts classification yielded an improved higher-level taxonomy, which was verified by fungal phylogeny based on genomic information (Wang et al. 2014, Liu et al. 2015b, Wang et al. 2015a, b, Li et al. 2021). The erection of new orders is of mycological importance because they likely reflect a stable clade with identifiable characteristics (Hibbett et al. 2007). Two new orders *Heitmaniales* and *Franziomyces* in *Microbotryomycetes* and *Exobasidiomycetes*, respectively, were described recently (Li et al. 2020, Li et al. 2022). The ‘Tremellales\_clade\_1’ including two species of *Phaeotremella* in the genome-scale phylogeny seems to be separated from *Tremellales* in the trees based on the genome dataset (Li et al. 2021). Our study contributes significantly to this framework by proposing a new order *Sterigmoblongales* in *Microbotryomycetes* and two new families *Sterigmoblongaceae* and *Turchettiaceae*. The foundation of high-level taxa indicates that current phylogenetic frameworks for *Basidiomycota*, particularly for the anamorphic yeast-forming lineages, are still incomplete and require significant refinement. These deep lineages represent previously uncharacterized evolutionary branches that underscore the vast, undocumented diversity at high phylogenetic nodes within *Basidiomycota*. Their findings will strengthen the resolution of current phylogeny and serve as crucial new calibration points for future systematic studies (Li et al. 2021). In terms of marker adequacy, the multi-locus dataset generally resolved most higher-level relationships. For instance, the new family *Turchettiaceae* is robustly resolved, forming a strong supported clade (BP=98, PP=1.0) with two other clades of undescribed strains (the first clade: *Gjaerumia* sp. NYNU 2018150, *Entylomatales* sp. NIP046, *Tilletiopsis* sp. TY-289; the second clade: *Tilletiopsis* sp. TY-163, *Tilletiopsis* sp. TY-363, *Tilletiopsis* sp. TY-235, *Tilletiopsis* sp. ST-105) in *Georgiomyces* within *Exobasidiomycetes*. This success confirms the adequacy of the multi-locus markers for resolving this deep evolutionary relationship. However, the unstable placement of *Sterigmoblongaceae* fam. nov./*Sterigmoblongales* ord. nov. demonstrates that multi-locus markers commonly used in yeast taxonomy are insufficient for resolving all basal phylogenetic splits. Our results therefore support the increasing consensus that definitive resolution of deep phylogenetic nodes within *Basidiomycota* requires: (i) expanding multi-locus or phylogenomic datasets, (ii) improved taxon sampling across undersampling lineages, and (iii) re-evaluation of molecular thresholds for higher-rank delimitation.

To clarify the taxonomic context of the new taxa reported in this study, it is essential to distinguish them from macrofungal lineages. Phylogenetically, macrofungi such as mushroom-forming *Agaricales* and wood-decaying *Polyporales* are predominantly distributed within the class



*Agaricomycetes*, whereas basidiomycetous yeasts are primarily restricted to the class *Tremellomycetes* (He et al. 2024). Unlike macrofungi, which possess complex multicellular fruiting bodies and occupy dominant ecological roles in wood decomposition, soil nutrient cycling, or plant symbiosis, basidiomycetous yeasts reported here exhibit strictly unicellular lifestyles with simplified morphologies. Ecologically, these newly proposed taxa inhabit mostly microhabitats, such as the phyllosphere. Furthermore, genomic features distinguish them from macrofungal lineages by generally lacking expansive suites of gene families involved in cellulose and lignocellulose decomposition, hydrophobins, and fungal lysozymes, which are essential for wood-decaying capabilities and fruiting-body development (Nagy et al. 2014). These contrasts underscore that the basidiomycetous yeasts, including newly discovered taxa, represent distinct ecological and evolutionary strategies within *Basidiomycota*.

Our study underscores the ecological and evolutionary distinctiveness of basidiomycetous yeasts, as well as the substantial challenges associated with their taxonomy. Due to the comparatively slower evolutionary rate of basidiomycetous lineages compared to their ascomycetous counterparts (Want et al. 2010), classical markers such as ITS and D1/D2 often provide insufficient resolution for many basidiomycetous yeast taxa, limiting their reliability for species delimitation when used alone. Robust species descriptions, therefore, require a multi-locus phylogenetic analysis incorporating protein-coding genes. Furthermore, taxogenomics is essential for establishing a stable and well-supported phylogenetic framework at higher taxonomic levels. An increased number of high-quality reference genomes in public databases provides crucial data support and stability for future systematic studies. To enhance data accessibility and reproducibility, the complete multi-gene dataset and genomes should be deposited in curated databases, e.g., theyeasts.org. Finally, the inherent challenges of slow growth and weak competition in these yeasts reduce isolation efficiency. Advancing culture strategies by integrating high-throughput culturomics, metagenomics, ecological data, and genomic analyses will significantly improve the detection, characterization, and understanding of their evolutionary histories and ecological roles.

## ACKNOWLEDGEMENTS

We are thankful to the MycoBank number: curator Konstanze Bensch for checking the nomenclature of the new taxa. We thank Dr. Wei Liu, Chang Liu, Dr. Da-Yong Han, Dr. Lu-Jun Luo, Ri-Peng Zhang, Yu-Jie Shang, Jun-Ning Li, Dr. Cong Sun, Dr. Bao-Zhu Fang, Zhi-Cheng Wu, and Jun-Jie Ying for their help in sampling. This study was funded by the Biological Resources Programme, Chinese Academy of Sciences (CAS-TAX-24-021), the National Science & Technology Fundamental Resources Investigation Program of China (No. 2019FY100700 and 2021FY100900) and the National Natural Science Foundation of China (No. 31870013). TB wants to acknowledge the Distinguished Scientist Fellowship Program of King Saud University, Riyadh, Saudi Arabia.

## DECLARATION OF COMPETING INTEREST

The authors declare no conflicts of interest regarding this article.

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## Supplementary Materials

**Table S1** List of yeast and the GenBank accession numbers of six generic loci used in the phylogenetic analysis. Isolates sequenced for this study are indicated in bold.

**Table S2** BLASTN results for the ITS and *RPB1* gene sequences of all strains.

**Table S3** Physiological and biochemical characters of new species and their closest relatives.

**Figure S1** – The sampling sites of yeast strains studied in China. Red cycles represent the tidal flat zones and blue cycles represent plant origin.

**Figure S2** – The phylogenetic tree of *Pucciniomycotina* species based on the concatenated sequences of ITS regions and LSU rDNA D1/D2 domains. The tree backbone was constructed using RAxML. The numbers at each node represent the bootstrap percentage (BP) of maximum likelihood over 50% from 1000 replicates. The new species are shown in bold. Scale in 0.05 substitution per nucleotide position.

**Figure S3** – The phylogenetic tree of *Tremellomycetes* species based on the concatenated sequences of ITS regions and LSU rDNA D1/D2 domains. The tree backbone was constructed using RAxML. The numbers at each node represent the bootstrap percentage (BP) of maximum likelihood over 50% from 1000 replicates. The new species are shown in bold. Scale in 0.05 substitution per nucleotide position.

**Figure S4** – The phylogenetic tree of *Exobasidiomycetes* species based on the concatenated sequences of ITS regions, LSU rDNA D1/D2 domains, *RPB1*, *RPB2*, *TEF1*, and *CYTB*. The tree backbone was constructed using RAxML. The numbers at each node represent the bootstrap percentage (BP) of maximum likelihood from 1000 replicates and Bayesian posterior probabilities (PP). BP values  $\geq 50$  and PP values  $\geq 0.9$  are plotted on the branches of the tree. The new species are shown in bold. Scale in 0.05 substitution per nucleotide position.

The supplementary materials can be accessed via Zenodo using this DOI: [10.5281/zenodo.17989984](https://doi.org/10.5281/zenodo.17989984)