






Da Vinci's yeast: *Blastobotrys davincii* f.a., sp. nov

Cobus M. Visagie^{1,2}  | Teun Boekhout^{3,4}  | Bart Theelen³  |
Jan Dijksterhuis³ | Neriman Yilmaz^{1,2}  | Keith A. Seifert^{2,5} 

¹Department of Biochemistry, Genetics and Microbiology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa

²Ottawa Research and Development Centre, Agriculture & Agri-Food Canada, Ottawa, Ontario, Canada

³Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands

⁴Institute of Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam, The Netherlands

⁵Department of Biology, Carleton University, Ottawa, Ontario, Canada

Correspondence

Cobus M. Visagie, Department of Biochemistry, Genetics and Microbiology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa.
Email: cobus.visagie@fabi.up.ac.za

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Abstract

A new species of the yeast genus *Blastobotrys* was discovered during a worldwide survey of culturable xerophilic fungi in house dust. Several culture-dependent and independent studies from around the world detected the same species from a wide range of substrates including indoor air, cave wall paintings, bats, mummies, and the iconic self-portrait of Leonardo da Vinci from ca 1512. However, none of these studies identified their strains, clones, or OTUs as *Blastobotrys*. We introduce the new species as *Blastobotrys davincii* f.a., sp. nov. (holotype CBS H-24879) and delineate it from other species using morphological, phylogenetic, and physiological characters. The new species of asexually (anamorphic) budding yeast is classified in *Trichomonascaceae* and forms a clade along with its associated sexual state genus *Trichomonascus*. Despite the decade-old requirement to use a single generic name for fungi, both names are still used. Selection of the preferred name awaits a formal nomenclatural proposal. We present arguments for adopting *Blastobotrys* over *Trichomonascus* and introduce four new combinations as *Blastobotrys allociferii* (\equiv *Candida allociferii*), *B. fungorum* (\equiv *Sporothrix fungorum*), *B. mucifer* (\equiv *Candida mucifera*), and *Blastobotrys vanleenenianus* (\equiv *Trichomonascus vanleenenianus*). We provide a nomenclatural review and an accepted species list for the 37 accepted species in the *Blastobotrys/Trichomonascus* clade. Finally, we discuss the identity of the DNA clones detected on the da Vinci portrait, and the importance of using appropriate media to isolate xerophilic or halophilic fungi.

KEYWORDS

Arxula, nomenclature, phylogeny, *Sporothrix*, taxonomy, xerophilic fungi

1 | INTRODUCTION

Humans spend $\pm 90\%$ of their time in the built environment (Höppe & Martinac, 1998). We share this space with invisible microbial communities in what is arguably one of the most important

human-microbe interfaces. Built environments are usually well regulated to ensure moderate temperatures and low humidity, while they contain recalcitrant and nonrecalcitrant carbon sources (e.g., building materials, textiles, food, and dust). When fungi grow, they typically release billions of airborne spores and fragments that can

Taxonomic novelties: New species: *Blastobotrys davincii* Visagie, Boekhout, Theelen, Yilmaz & Seifert; New combinations: *Blastobotrys allociferii* (Ueda-Nishimura & Mikata) Visagie & Boekhout; *Blastobotrys ciferii* (M.T. Sm., Van der Walt & Johannsen) Visagie & Boekhout; *Blastobotrys fungorum* (de Hoog & G.A. de Vries) Visagie & Boekhout; *Blastobotrys mucifer* (Kock.-Krat. & E. Sláviková) Visagie & Boekhout; *Blastobotrys vanleenenianus* (M. Groenew. & M.T. Sm.) Visagie & Boekhout.

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affect humans as allergens (Horner et al., 1995; Osborne et al., 2015) or pathogens (de Hoog et al., 2014), spoil food (Pitt & Hocking, 2009; Samson et al., 2019), or cause structural damage to building materials or artifacts of significant historical value (Cavka et al., 2010; Chunduri, 2014; Gabriel & Švec, 2017; Kausrud et al., 2007; Ljaljevic-Grbic et al., 2013; Piñar et al., 2013, 2015, 2020; Pinheiro, Mesquita, et al., 2019; Pinheiro, Sequeira, et al., 2019; Schmidt, 2007; Sklenář et al., 2017; Trovão et al., 2020).

The impact of indoor fungal communities on personal and public health makes them important to study but addressing complex research questions presents challenges. Traditional culture-dependent approaches are often subject to bias (e.g., easily culturable and fast-growing fungi, growth media that are selective, and so forth), labor intensive and expertise-dependant, especially when compared with culture-independent approaches like high-throughput sequencing (HTS). Culture-based fungal surveys of the built environment suggest a community of perhaps several hundred species (Flannigan & Miller, 2011; Samson et al., 2019). HTS surveys reveal more diverse microbial populations, which are greatly influenced by outdoor fungal community composition and external variables like climate (Adams et al., 2013a, 2013b; Amend et al., 2010; Hanson et al., 2016; Pitkäranta et al., 2008; Rocchi et al., 2017; Weigl et al., 2016). However, it is difficult to distinguish which species in HTS surveys are nonviable, uncultured, or unculturable residents and which may be transients that do not function as part of the ecosystem (Carini et al., 2016; Nilsson et al., 2019; Wutkowska et al., 2018).

These powerful HTS approaches require reliable, comprehensive, and accurate DNA reference sequence databases, which have mainly been derived from culture-dependent studies. Curated reference datasets that aim to limit incorrectly named or low-quality sequences currently still have significant taxonomic gaps (Abarenkov et al., 2016; Kõljalg et al., 2005, 2013; Nilsson et al., 2015, 2018; Schoch et al., 2014). Also, the large number of undescribed fungi (Boekhout et al., 2021; Hawksworth & Lücking, 2017; Lücking et al., 2021) and lack of resolution in sequences of the internal transcribed spacer rDNA region (ITS), the usual marker employed, for many fungi like *Aspergillus*, *Cladosporium*, *Fusarium*, *Penicillium*, and so forth (Schoch et al., 2012) suggest that species-level identifications will remain problematic with current HTS approaches. A common feature of many such surveys is a high proportion of unidentified taxa. Some of these are the consequence of incompletely or incorrectly classified or misidentified reference data (Kõljalg et al., 2013).

For the better part of a decade, closing the knowledge gap between uncultured and cultured fungi has been a focus for ecologists and taxonomists, especially those working on endophytes or mycorrhizal fungi symbiotic with plants (e.g., Arnold et al., 2021; Tanney & Seifert, 2018). Our coordinated microbiological and HTS surveys in the built environment yielded thousands of fungal strains, many of them now accessioned in culture collections. These were identified using modern taxonomic concepts, resulting in the description of many new species and the release of thousands of newly generated reference sequences on GenBank

Take-away

- *Blastobotrys davincii* is introduced as a new species.
- Surveys have detected this species, but could never correctly identify or name it.
- The species was found on the da Vinci portrait, mummies and other substrates.
- A nomenclature review and an accepted species list for the *Blastobotrys/Trichomonascus* clade is provided.
- Appropriate isolation media are important to allow for growth of specific fungi.

(Bensch et al., 2018; Hirooka et al., 2016; Nguyen et al., 2015; Tanney et al., 2017; Visagie et al., 2014; Wang et al., 2016; Woudenberg, Meijer, et al., 2017; Woudenberg, Sandoval-Denis, et al., 2017).

Here, we focus on yeasts and yeast-like fungi isolated during a house dust survey that targeted xerophilic/osmotolerant fungi from Canada and Hawaii. This survey was an extension of the original IM-BOL project that surveyed fungi from house dust collected around the world (Amend et al., 2010). We introduce *Blastobotrys davincii*, a species detected in several HTS surveys (most notably on the only surviving self-portrait of Leonardo da Vinci (Figure 1),



FIGURE 1 Self-portrait of Leonardo da Vinci, red chalk on paper, ca 1512, public domain, Wikipedia (https://en.wikipedia.org/wiki/Portrait_of_a_Man_in_Red_Chalk); original in the Royal Library of Turin, Italy, inventory number 15571.

drawn in ca 1512 using red chalk on paper) but never classified using morphology, physiology and/or multigene sequence data. *Blastobotrys* (= *Arxula*) is a genus of asexual (anamorphic) budding yeasts classified with *Diddensiella*, *Groenewaldozyma*, *Spenceriella*, *Sugiyamaella*, *Wickerhamiella*, *Trichomonascus*, and *Zygoascus* in the family *Trichomonascaceae*. *Trichomonascus* is the sexual state (teleomorph) genus of *Blastobotrys*, with which it forms a cohesive clade. After the abandonment of dual nomenclature and move to the One Fungus = One Name concept in 2012 (McNeill et al., 2012), no formal decision was made on which generic name to accept for this group. Consequently, over the past decade, new species were introduced in both *Blastobotrys* and *Trichomonascus* (Barretto et al., 2018; Chai et al., 2020; Groenewald et al., 2018; Nouri et al., 2018). In a move towards nomenclatural stability, we review the described species and genera, present arguments for adopting *Blastobotrys* over *Trichomonascus*, and provide a list of currently accepted species.

2 | MATERIALS AND METHODS

2.1 | Sampling and isolations

House dust samples were collected from various homes across Canada and Hawaii, and a modified dilution-to-extinction method (Collado et al., 2007), as described by Visagie et al. (2014), was used to isolate cultures. Isolation media included media targeting xerophilic and osmotolerant fungi Dichloran 18% Glycerol agar (DG18; Hocking & Pitt, 1980), Malt extract yeast extract 10% glucose 12% NaCl agar (MY10-12), and Malt extract yeast extract 50% glucose agar (MY50G) (Samson et al., 2019). Isolates were preserved in 10% glycerol stored at -80°C in the KAS working collection at the Ottawa Research and Development Centre (ORDC) of Agriculture and Agri-Food Canada (AAFC), Ottawa, Canada. Selected strains were also deposited into DAOMC (Canadian Collection of Fungal Cultures housed at ORDC), CMW (internal culture collection of the Forestry and Agricultural Biotechnology Institute [FABI], University of Pretoria, Pretoria, South Africa), and CBS (Westerdijk Institute, Utrecht, the Netherlands).

2.2 | DNA extraction, sequencing, and phylogenetic analysis

DNA was extracted from 7 d old colonies grown on malt extract agar (MEA) using the Ultraclean™ Microbial DNA Isolation Kit (MoBio Laboratories Inc.). The internal transcribed spacer (ITS1-5.8S-ITS2) rDNA region (ITS) and large subunit (LSU) were amplified with primer pairs V9G & LS266 (de Hoog & van den Ende 1998; Masclaux et al., 1995) and LR5 & LROR (Vilgalys & Hester, 1990). Polymerase chain reaction (PCR) amplification employed an initial denaturing at 95°C for 5 min; 35 cycles at the following conditions: 95°C for 45 s, 55°C for 45 s, 72°C for 60 s; and final extensions at 72°C for 4 min. Sequencing reactions were set up using the BigDye Terminator Cycle

Premix Kit (Applied Biosystems) using the same primer pairs used for PCR amplification. Sequences were determined on an ABI PRISM 3730xl genetic analyser. Sequence contigs were assembled in Geneious Prime 2022 (Biomatters Ltd.) and newly generated sequences submitted to GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>).

A reference sequence data set was compiled using previously deposited sequences obtained from the NCBI nucleotide database (<https://www.ncbi.nlm.nih.gov/nucleotide/>), mainly based on a core set of DNA reference sequences recommended by Smith et al. (2011a) and Smith et al. (2011b) (also accessible at <https://theyeasts.org>). Additional sequences were added based on similar sequences revealed by BLAST. Table 1 lists strains used for phylogenetic comparisons.

ITS and LSU datasets were aligned in MAFFT v. 7.453 (Katoh & Standley, 2013) using the L-INS-I option. Alignments were trimmed, adjusted, and concatenated in Geneious Prime 2022. The most appropriate nucleotide substitution model for each partition was selected based on the Akaike information criterion (Akaike, 1974) using partitionfinder v. 2.1 (Lanfear et al., 2017). Phylogenies were calculated using Maximum Likelihood (ML) and Bayesian tree Inference (BI). ML was performed using IQtree v. 2.1.3 (Minh et al., 2020; Nguyen et al., 2015) with bootstrap analyses performed with 1000 replicates. BI analyses were performed in MrBayes v. 3.2.7 (Ronquist et al., 2012) with three sets of four chains (one cold and three heated) and were stopped using the stoprule option at an average standard deviation for split frequencies of 0.01. Trees were visualised using TreeViewer v. 2.0.1 (<https://treeviewer.org/>) and edited in Affinity Publisher 1.9.3 (Serif (Europe) Ltd.). ML and BI tree topologies did not differ and thus ML trees were used to present results with both bootstrap values and posterior probabilities shown for supported branches. Alignments and trees were deposited in TreeBase as Study ID: 27413.

2.3 | Morphology and physiology

Strains were characterised from growth on MEA (Oxoid), glucose yeast peptone agar (GYPA), DG18, 5% glucose in yeast nitrogen broth, and Dalmau plates on yeast morphology agar. Plates were incubated at 25°C for 7 d. Microscopic observations and measurements were made using an Olympus SZX12 dissecting microscope and Olympus BX50 light microscopes. These were equipped with an Evolution MP digital microscope camera and ImagePro v. 6.0 software. Colony close-ups were captured using extended depth of field and micrographs were stacked using Helicon Focus v. 7.5.4 (HeliconSoft). Low-temperature scanning electron microscopy (SEM) was performed by cutting out 5×5 mm agar blocks from colonies on Yeast Morphology agar (Difco) after 5–7 d of growth using a surgical blade and transferring into a copper cup (10 mm diam, 8 mm deep). The agar blocks were glued to the copper cup using KP-Cryoblock frozen tissue medium (Klinipath) mixed with one-part colloidal graphite (Agar Scientific). The copper cup was placed in a wet agar plate to prevent the sample from drying. The sample was snap-frozen in nitrogen slush and immediately transferred to a JEOL 5600LV scanning electron microscope (JEOL) equipped with

TABLE 1 Strains used for phylogenetic analyses

Taxon name	Strain	Location	Source	GenBank: ITS	GenBank: LSU
<i>Blastobotrys adeninivorans</i>	CBS 7350	The Netherlands	Maize	n.a.	LR031516
<i>Blastobotrys adeninivorans</i>	CBS 7766	Sweden	Liver and intestines of a Gila monster (<i>Heloderma suspectum</i>)	n.a.	LR031517
<i>Blastobotrys adeninivorans</i>	CBS 8244 = NRRL Y-17692 IFO 10858 = IGC 4638 = PYCC 4638 (ex-type)	The Netherlands: Wageningen	Soil	KY101746	DQ442697
<i>Blastobotrys allociferii</i>	CBS 5165 = IFO 10193	The Netherlands	Fence post	KY101922	KY106285
<i>Blastobotrys allociferii</i>	CBS 5166 = NBRC 10194 = IFO 10194 (ex-type)	Germany	Human	LC158134	LC158143
<i>Blastobotrys americanus</i>	CBS 10337 = NRRL Y-6844 = LRB 70B3 (ex-type)	USA: Kansas	Unknown	KY101748	DQ442699
<i>Blastobotrys arbuscula</i>	CBS 227.83 = NRRL Y-17585 (ex-type)	Finland	Indoor air	OL772655	DQ442689
<i>Blastobotrys aristatus</i>	CBS 521.75 = NRRL Y-17579 = ATCC 34215 = CCM F-410 = HFM 2672 = UAMH 4665 (ex-type)	Czech Republic	Moldy plaster	OL772656	DQ442686
<i>Blastobotrys attinorum</i>	CBS 9734 = NRRL Y-27639 = UNESP-S156 (ex-type)	Brazil: Sao Paulo	Fungal garden of nests of the leaf-cutting ant (<i>Atta sexdens</i>)	KY101749	AY442294
<i>Blastobotrys baotianmanensis</i>	CBS 16024 = CICC 33083 (ex-type)	China: Henan Province, Baotianman Nature Reserve	Gut of ground beetle (<i>Pterostichus gebleri</i>)	KU128710	KU128725
<i>Blastobotrys bombycis</i>	CBS 15274 (ex-type)	India: Dharwad	Silkworm (<i>Bombyx mori</i>)	OL772657	OL772653
<i>Blastobotrys buckinghamii</i>	CBS 13900 = NRRL Y-63727 = yHAB 196 (ex-type)	USA: Michigan, Tahquamenon Falls State Park	Mushroom associated with American beech (<i>Fagus grandifolia</i>)	OL772658	OL772654
<i>Blastobotrys capitulata</i>	CBS 287.82 = NRRL Y-17573 (ex-type)	South Africa	Flower, decaying tissue of candelabra tree (<i>Euphorbia ingens</i>)	OL772659	DQ442688
<i>Blastobotrys chiropterorum</i>	CBS 6064 = NRRL Y-17071 (ex-type)	Columbia	Liver of bat (<i>Mormoops megalophylla</i>)	KY101750	DQ442682
<i>Blastobotrys ciferrii</i>	CBS 5295 = NRRL Y-10943 = ATCC 58443 = CCRC 21427 = Goto TH-26 = IFO 1854 = IGC 4164 = IMI 344641 = JCM 7621 (ex-type)	The Netherlands	Pig	AY493435	DQ442681
<i>Blastobotrys davincii</i>	CBS 16861 = DAOMC 251467 = CMW 56638 = CN 002G3 = KAS 5710 (ex-type)	Canada: Ontario, Stittsville	House dust	MW367648	MW367634
<i>Blastobotrys davincii</i>	CBS 16862 = DAOMC 251468 = CMW 56639 = CN 002G4 = KAS 5711	Canada: Ontario, Stittsville	House dust	MW367649	MW367635
<i>Blastobotrys davincii</i>	clone CII-K12	Italy: Turin	Leonardo da Vinci's self-portrait	KP828180	n.a.
<i>Blastobotrys davincii</i>	clone CMH052	USA: Missouri, Kansas City	Indoor air	KF800143	n.a.
<i>Blastobotrys davincii</i>	clone F9-K24	Italy: Capuchin Catacombs of Palermo	Stuffing material from mummies	KC535143	n.a.

TABLE 1 (Continued)

Taxon name	Strain	Location	Source	GenBank: ITS	GenBank: LSU
<i>Blastobotrys davincii</i>	MJ4F-1A	China	Cave painting surface	KY412159	n.a.
<i>Blastobotrys davincii</i>	NWHC 45698-845_3LNA	USA: Washington	Bat (<i>Eptesicus fuscus</i>)	MK782473	n.a.
<i>Blastobotrys davincii</i>	NWHC 45701-677_1LNA	USA: California	Bat (<i>Myotis yumanensis</i>)	MK782430	n.a.
<i>Blastobotrys elegans</i>	CBS 530.83A = NRRL Y-17572 (ex-type)	Finland	Indoor air	OL772660	DQ442687
<i>Blastobotrys farinosus</i>	CBS 140.71 = NRRL Y-17593 = IGC 4592 = JCM 2935 (ex-type)	The Netherlands	Fruiting body of <i>Hirneola auricula-judae</i>	OL772661	DQ442685
<i>Blastobotrys fungorum</i>	CBS 259.70 = CMW 17165 = UAMH 3678 (ex-type)	Germany	Old <i>Fomes fomentarius</i> basidiome	KX590837	KX590883
<i>Blastobotrys illinoisensis</i>	CBS 10339 = NRRL YB-1343 (ex-type)	USA: Illinois, Marion, Wohlwend farm	Tree	KY101751	DQ442696
<i>Blastobotrys indianensis</i>	CBS 9600 = NRRL YB-1950 (ex-type)	USA: Indiana, Spencer, McCormick's Creek State Park	White fungus associated with pine	KY101752	DQ442692
<i>Blastobotrys malaysiensis</i>	CBS 10336 = NRRL Y-6417 = EMMONS S3.539A (ex-type)	Malaysia	Cave soil	KY101753	DQ442695
<i>Blastobotrys meliponae</i>	CBS 14100 = URM7224 (ex-type)	Brazil: Pernambuco, Recife	Honey	KT448719	KR779217
<i>Blastobotrys mokoensis</i>	CBS 8435 = NRRL Y-27420 (ex-type)	South Africa	Soil	KY101754	DQ442694
<i>Blastobotrys mucifer</i>	CBS 7409 = CCY 29-170-1 = IFO 10918 (ex-type)	Brazil: Manaus	Liver of toad (<i>Rhinella granulosa</i>)	KY102217	KY106587
<i>Blastobotrys muscicola</i>	CBS 10338 = NRRL Y-7993 (ex-type)	USA: Louisiana, near New Orleans	Moss on fallen log	KY101755	DQ442680
<i>Blastobotrys navarrensis</i>	CBS 139.77 = ATCC 36955 = IJFM 2642 = UAMH 4664 (ex-type)	Spain: Pampelona	Black pepper (<i>Piper nigrum</i>)	OK623478	OK623486
<i>Blastobotrys nivea</i>	CBS 163.67 = NRRL Y-17581 = ATCC 18420 = HFM 26 = UAMH 4663 = MUCL 6078 (ex-type)	Germany	Municipal compost	OL772662	DQ442690
<i>Blastobotrys parvus</i>	CBS 6147 = NRRL Y-10004 (ex-type)	Antarctic Ocean	Seawater	KY101757	DQ442693
<i>Blastobotrys peoriensis</i>	CBS 10340 = NRRL YB-2290 (ex-type)	USA: Illinois, Peoria	Unknown	KY101758	DQ442700
<i>Blastobotrys persicus</i>	CBS 14259 = IBRC-M30238 (ex-type)	Iran: Ilam	Soil	OL772663	KU659141
<i>Blastobotrys proliferans</i>	CBS 522.75 = NRRL Y-17577 = ATCC 34216 = CCM F-493 = HFM 2673 = UAMH 4666 (ex-type)	Brazil	Mite-infested nut (<i>Bertholletia excelsa</i>)	EU343812	DQ442684
<i>Blastobotrys raffinosifermentans</i>	CBS 6800 = NRRL Y-27150 (ex-type)	Unknown	Unknown	KY101759	DQ442698
<i>Blastobotrys robertii</i>	CBS 10106 = NRRL Y-27775 (ex-type)	The Netherlands: Wageningen forest	Rotten pine wood (<i>Pinus sylvestris</i>)	KY101760	DQ839395

(Continues)

TABLE 1 (Continued)

Taxon name	Strain	Location	Source	GenBank: ITS	GenBank: LSU
<i>Blastobotrys serpentis</i>	CBS 10541 = NRRL Y-48249 = MTCC 8332 = W113A = YS W113A (ex-type)	India: Hyderabad City	Trinket snake gut	KY101761	AM410667
<i>Blastobotrys</i> sp.	clone Cl-K20	Italy: Turin	Leonardo da Vinci's self-portrait	KP828159	n.a.
<i>Blastobotrys</i> sp.	clone ClI-K33	Italy: Turin	Leonardo da Vinci's self-portrait	KP828174	n.a.
<i>Blastobotrys</i> sp.	clone ClI-K35	Italy: Turin	Leonardo da Vinci's self-portrait	KP828173	n.a.
<i>Blastobotrys</i> sp.	clone F9-K2	Italy: Capuchin Catacombs of Palermo	Stuffing material from mummies	KC535141	n.a.
<i>Blastobotrys</i> sp.	clone F9-K27	Italy: Capuchin Catacombs of Palermo	Stuffing material from mummies	KC535144	n.a.
<i>Blastobotrys</i> sp.	clone F9-K49	Italy: Capuchin Catacombs of Palermo	Stuffing material from mummies	KC535146	n.a.
<i>Blastobotrys</i> sp.	NCAIMY.01950	Unknown	Unknown	n.a.	GU195655
<i>Blastobotrys</i> sp.	UFMG-CM-Y6482	Brazil: Caxiuana National Forest	Gut from fruit fly (<i>Hirtodrosophila</i> sp.)	n.a.	MK130971
<i>Blastobotrys</i> sp.	BG98-12-9-2-1	Unknown	Gut of ciid beetle	n.a.	AY242297
<i>Blastobotrys</i> sp.	BG00-7-5-1-2-1	Unknown	Gut of tenebrionid beetle	n.a.	AY242247
<i>Blastobotrys</i> sp.	BG01-7-21-005C-1-4	Unknown	Gut of scarabaeid beetle	n.a.	AY242291
<i>Blastobotrys</i> sp.	BG01-7-21-001A-1-1	Unknown	Gut of anthribid beetle	n.a.	AY242321
<i>Blastobotrys</i> sp.	BG01-7-24-002F-2-1	Unknown	Gut of endomychid beetle	n.a.	AY242286
<i>Blastobotrys</i> sp.	BG01-7-22-001B-1-1	Unknown	Gut of erotylid beetle	n.a.	AY242276
<i>Blastobotrys</i> sp.	BG01-7-22-018A-1-1	Unknown	Gut of endomychid beetle	n.a.	AY242285
<i>Blastobotrys</i> sp.	BG01-7-24-002C-Egg-1-1	Unknown	Gut of erotylid beetle	n.a.	AY242272
<i>Blastobotrys</i> sp.	BG99-11-14-1-4-1	Unknown	Gut of mycetophagid beetle	n.a.	AY242316
<i>Blastobotrys</i> sp.	BG01-7-26-005A-2-1	Unknown	Gut of nitidulid beetle	n.a.	AY242313
<i>Blastobotrys</i> sp.	BG01-7-21-010A-4-1	Unknown	Gut of tenebrionid beetle	n.a.	AY242251
<i>Blastobotrys</i> sp.	BG00-6-26-2-2-1	Unknown	Gut of tenebrionid beetle	n.a.	AY242248
<i>Blastobotrys</i> sp.	BG01-7-23-021A-4-1	Unknown	Gut of tenebrionid beetle	n.a.	AY242250
<i>Blastobotrys</i> sp.	KBP-Y6879	Russia	Tunnels under the bark of oak tree		ON887274
<i>Blastobotrys terrestris</i>	CBS 7376 = NRRL Y-17704 = CSIR Y914 = IFO 10859 = IGC 5133 = PYCC 5133 (ex-type)	South Africa: Barberton	Soil	KY101762	DQ442683

TABLE 1 (Continued)

Taxon name	Strain	Location	Source	GenBank: ITS	GenBank: LSU
<i>Blastobotrys vanleenenianus</i>	CBS 14902 (ex-type)	The Netherlands	Soil	MG986487	MG986492
<i>Blastobotrys xishuangbannaensis</i>	CBS 16044 = CICC 33360 (ex-type)	China: Yunnan Province, Jinghong	Rotting wood	MK682811	MK682809
<i>Trichomonascus apis</i>	CBS 10922 = NRRL Y-48475 = NCAIM Y.01848 (ex-type)	Hungary	Mouldy honeycomb	KY105699	EU790643
<i>Trichomonascus apis</i>	CBS 10923 = NRRL Y-48476 = NCAIM Y.01849	Hungary	Mouldy honeycomb	KY105700	KY109912
<i>Trichomonascus ciferrii</i>	CBS 215.79 = CMW 17161 (ex-type of <i>Sporothrix catenata</i>)	Romania	Calf skin	KX590833	KX590879
<i>Trichomonascus petasosporus</i>	CBS 9602 = NRRL Y-B2092 (ex-type)	USA: Missouri, Salem	White Oak (<i>Quercus</i> sp)	KY105704	DQ442691
<i>Wickerhamiella domercqiae</i>	CBS 4351 = NRRL Y-6692 (ex-type)	South Africa	Wine vat	DQ911463	DQ438240

an Oxford CT1500 Cryo station for cryo-electron microscopy (cryoSEM). The sample was sputter-coated with a gold target for three times 90 s, arranging the sample at different angles for optimal coating. Electron micrographs were acquired with the F4 scan at 4 kV.

The physiological growth profile of the isolates was assessed using methods commonly used in yeast taxonomy. The utilization of carbon compounds was assessed using liquid media, nitrogen compounds were tested using auxanograms, and growth at different temperatures was assessed on glucose yeast peptone agar medium (GYPA) agar plates placed in incubators for 1 week.

3 | RESULTS

3.1 | Isolations

Isolations targeting xerophilic and osmotolerant fungi from Canadian and Hawaiian house dust yielded 1038 fungal strains. *Aspergillus* (at 29% of the total), *Penicillium* (23%), *Cladosporium* (9%), and *Wallemia* (5%) were the most frequently isolated genera. Yeasts were also commonly encountered during this survey, especially the black yeasts *Aureobasidium* and several others that morphologically resembled *Aureobasidium*, which were treated in Humphries et al. (2017). A similar trend in fungal community structure was observed during the worldwide house dust survey employing both culture-dependent and -independent approaches (Amend et al., 2010). The yeast and yeast-like fungi we isolated and identified from Canada using media targeting xerophilic or osmotolerant fungi were *Aureobasidium melanogenum*, *Aureobasidium pullulans*, *Candida parapsilosis*, *Cystobasidium slooffiae*, *Debaryomyces hansenii*, *Exophiala dermatitidis*, *Exophiala xenobiotica*, *Rhizosphaera pini*, *Rhodotorula* cf. *toruloides*, *Rhodotorula diobovata*, *Rhodotorula mucilaginosa*, *Sterigmatomyces halophilus*, *Sydowia polyspora* and *Vishniacozyma carnescentis* with *A. melanogenum* and *Hortaea werneckii* isolated from Hawaii (see Supporting Information: Table S1).

In Amend et al. (2010) an OTU identified as *S. halophilus* was found to be one of the most common species, however, it was not recovered during isolations from the same house dust when MEA and 20% sucrose MEA were used as isolation media. In our survey, six strains of this species were isolated when the high NaCl medium MY10-12 was used, indicating the importance of selecting appropriate media to allow for the growth of for example halophilic fungi.

Two other filamentous yeast strains were isolated and found to represent a new *Blastobotrys* species, described below. Similarity searches revealed several identical unnamed sequences previously deposited in GenBank.

3.2 | Species delineation and phylogenetic placement of *B. davincii* sp. nov

Our phylogenetic analyses based on ITS and LSU included all species currently accepted in *Blastobotrys* and *Trichomonascus* (Figure 2). The aligned datasets were 624 bp long for ITS and 590 bp long for LSU.

The most appropriate nucleotide substitution model for ITS was TVM+I+G and for LSU was GTR+G+I. House dust strains of the new species resolved in a distinct, well-supported clade along with several sequences obtained from GenBank. These included clones obtained from indoor air (KF800143, Kansas, USA), stuffing material from a mummy (KC535143, Palermo, Italy) and the Leonardo da Vinci self-portrait drawn in ca 1512 (KP828180, Italy) (Piñar et al., 2013; Piñar et al., 2015; Rittenour et al., 2014). Additional unpublished sequences

were derived from cultures isolated from a cave wall painting (KY412159, Maijishan Grottoes in China) and from bat caves (MK782473, MK782430, USA). The new species resolved closest to a clade containing *Blastobotrys aristatus*, *Blastobotrys bombycis*, and *Blastobotrys elegans*, with *Blastobotrys farinosus* and *Blastobotrys fungorum* more distantly related. Generally, the *Blastobotrys* clade had poor backbone support. Similarities between *B. davincii* (DAOMC 251468T) and its closest relatives were low with LSU sequences that

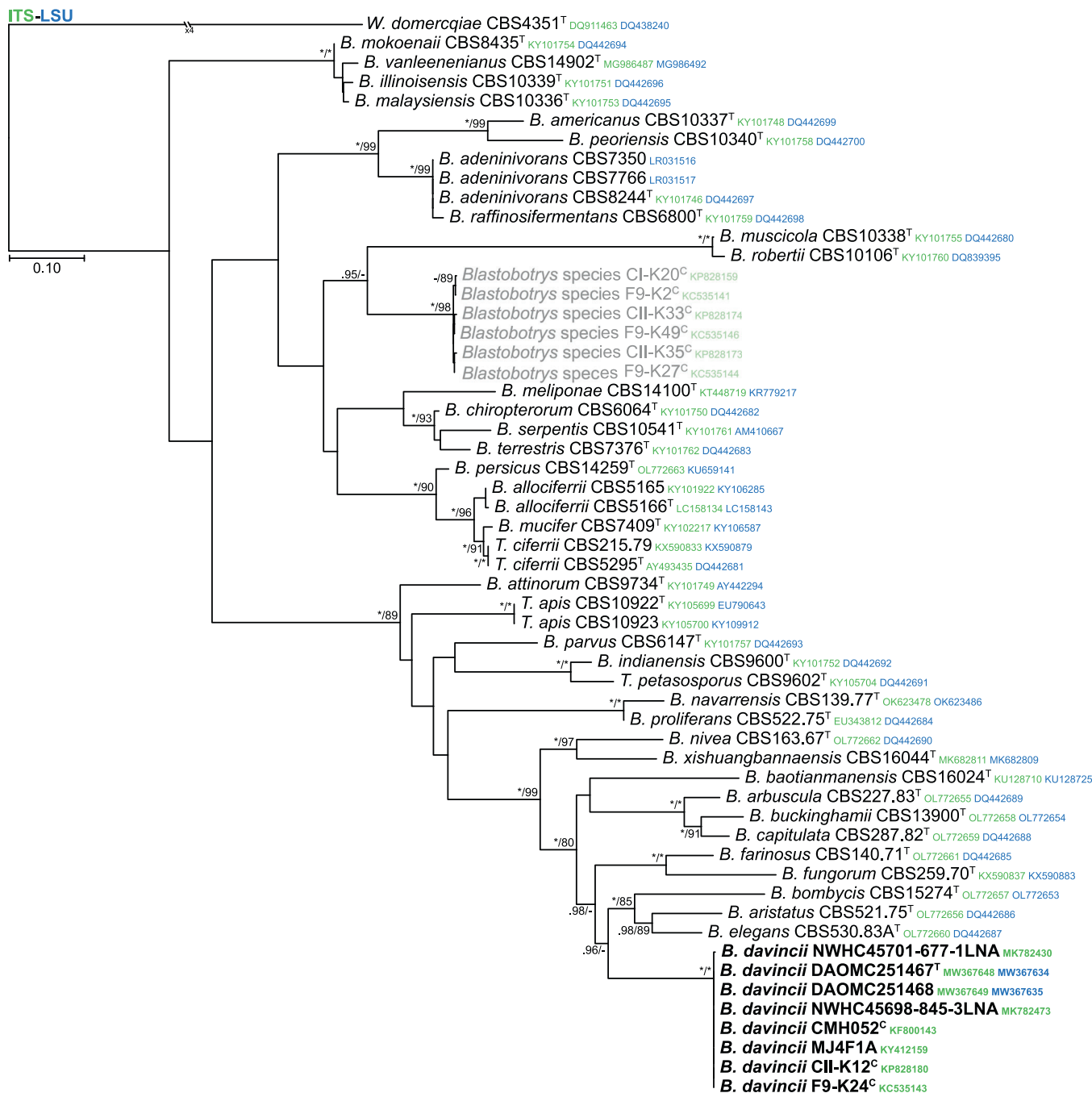


FIGURE 2 Combined phylogenetic tree of described *Blastobotrys* and *Trichomonascus* species based on ITS and LSU. The tree is rooted to *Wickerhamiella domercqiae* CBS3451^T. Posterior probabilities (≥ 0.95) and Bootstrap support values ($\geq 80\%$) are given above branches. The new species is indicated in bold text, unnamed sequences are indicated by grey text, ^T = ex-type strain, ^c = sequence from cloned DNA fragment, and GenBank accession numbers are shown in a smaller font (ITS = green; LSU = blue).

differs by 44 or more substitutions (based on alignment from 5'-AAACCAACAGGGATTGCCTC-3' to 5'-GGTTCCTGCCGAAGTT-3'), while ITS differed by 99 or more substitutions (based on alignment from 5'-AAGGATCATTA-3' to 5'-TAAGCATATCA-3').

The new species displayed the typical morphology of *Blastobotrys*, with branched conidiophores ending in conidiogenous cells producing blastoconidia (Figure 3). Morphologically the species is similar to its closest relatives, with no characters able to distinguish among them.

Our phylogenies also indicate that Piñar et al. (2013, 2015) detected another new *Blastobotrys* species (GenBank accession numbers: KP828173, KC535141, KP828159, KC535146, KC535144, and KP828174) during their cloning survey from both Capuchin catacomb mummies and the Leonardo da Vinci self-portrait, but no strains were isolated. Using UNITE's Species Hypothesis approach (Köljalg et al., 2013), this species refers to SH1142619.08FU at a 3% threshold, or SH2126732.08FU at a 0% threshold. BLAST searches and a subsequent phylogenetic analysis revealed several strains that represent potential new species (Supporting Information: Figure 1), including one closely related to *B. davincii*. Most of these strains were isolated from beetle guts (Suh et al., 2004), with one unpublished sequence generated from a fruit fly gut isolate (UFMG-CM-Y6482: MK130971), one from tunnels under the bark of an oak tree from Russia (KBP-Y6879: ON887274) and one from an unknown source (NCAIM Y.01950: AY242316).

The nutritional growth requirements of strains DAOMC251467^T and DAOMC251468 are presented in Table 2 and can be summarized as follows: the strains have fermentative capabilities, a character that distinguishes them from all close relatives; they utilize most of the tested carbon sources, although with weak and slow growth for some; they utilize both nitrate and nitrite; they are mesophilic and do not grow at 35°C; they do not produce starch or starch-like compounds; and they do not grow in media with elevated sugar concentrations.

Here we use a phylogenetic species concept to delineate our new species and formally describe it below as *B. davincii*.

4 | TAXONOMY

Blastobotrys davincii Visagie, Boekhout, Theelen, Yilmaz & Seifert, *sp. nov.* MycoBank MB 843366 (Figure 3).

4.1 | Etymology

Latin, *da.vin.ci'i*, named after Leonardo da Vinci, the famous Italian painter, draughtsman, engineer, scientist, theorist, sculptor, and architect. The species was first detected during a culture-independent survey of fungi associated with his famous self-portrait.

4.2 | Typus

Canada, Stittsville, from house dust collected from vacuum cleaner by Keith A. Seifert, isolated by Cobus M. Visagie, December 2014, Holotype

CBS H-24879 (metabolically inactive state), culture ex-type DAOMC 251467 = CBS 16861 = CMW 56638 = CN 002G3.

4.3 | Additional strains examined

Canada, Stittsville, from house dust collected from vacuum cleaner by Keith A. Seifert, isolated by Cobus M. Visagie, December 2014, dried specimen CBS H-24880, culture DAOMC 251468 = CBS 16862 = CMW 56639 = CN 002G4.

4.4 | Barcode sequences

ITS = MW367648, MW367649. LSU = MW367634, MW367635.

4.5 | UNITE species hypothesis

SH2279294.08FU/https://unite.ut.ee/bl_forw_sh.php?sh_name=SH2279294.08FU

4.6 | Description

Growth in 5% glucose in yeast nitrogen broth: After 2 weeks at 25°C, white flocks present at the bottom of the tube. Yeast cells not observed. Irregularly branched, hyaline, septate hyphae present, 2–3 µm in diameter, and with thick-walled inflated cells 7–14 × 6–12 µm. Growth on yeast morphology agar: After 2 weeks at 25°C, colony ca. 5–8 mm wide, somewhat elevated, tough, strongly irregular and ridged, dull, whitish cream, and with an entire margin. Hyphae branched, hyaline, 1.5–2.5 µm wide, with inflated regions 5–13 × 5–11 µm. Dalmau plate on yeast morphology agar: Extensive hyphae and yeast cells present. Growth on GYP and MEA: After 2 weeks at 25°C, colony 15–18 mm wide, dull, whitish, tough, strongly irregular, crateriform, and ridged, with a fine velvety appearance, and an entire margin. On MEA colony with clear central and peripheral parts. Hyphae abundant, 10–35(–50) × 1–3 µm, with broadened, ellipsoidal, subglobose, or clavate tips, ca. 6–7.5 µm wide, on which several subglobose to ellipsoidal blastoconidia, 2–3 × 1.5–3 µm, form on short denticles, 1.5–3.5 × 1–2.5 µm. Blastoconidia germinate by producing secondary blastoconidia. Blastoconidia also occur on short denticles near septa in the hyphae. Growth on DG18: After 10 d at 25°C, colonies 3–5 mm, white to cream, folded, powdery, margins crenulate.

4.7 | Physiology

For the complete data on fermentative and assimilative growth on carbon and nitrogen compounds see Tables 2 and 3.

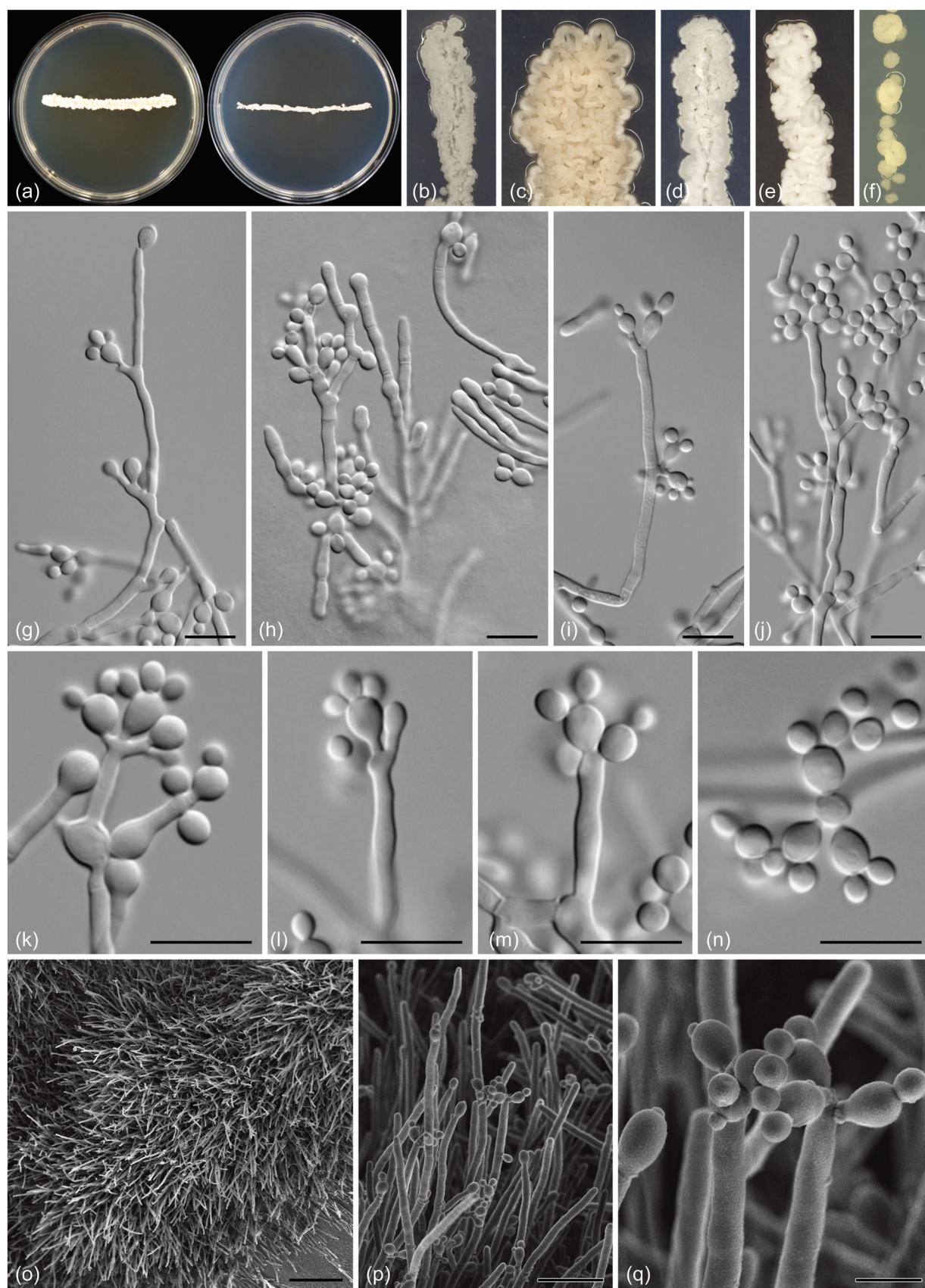


FIGURE 3 *Blastobotrys davincii* (DAOMC 251467^T). (a) Colonies on, from left to right, MEA and YPGA. (b–f) Colony close-ups on: (b) MEA, (c) YPGA, (d) PDA, (e) DG18, and (f) YMA. (g–n) Fertile conidiophores and conidia observed under a light microscope. (o–q) Hyphae and fertile conidiophores observed using cryo-SEM. Scale bars: (g–n) = 10 μ m, o = 100 μ m, p = 20 μ m, and q = 5 μ m.

TABLE 2 *Blastobotrys davincii* physiological characters (+, growth; –, no growth; d, delayed growth; w, weak growth)

	DAOMC251467	DAOMC251468		DAOMC251467	DAOMC251468
Growth carbon compounds			Fermentation		
D-Glucose	+	+	D-Glucose	+	+
D-Galactose	+	+	D-Galactose	dw	dw
L-Sorbose	+	+	Maltose	dw	dw
D-Glucosamine	–	w	Sucrose	dw	dw
D-Ribose	+	+	Trehalose	dw	dw
D-Xylose	+	+	Actose	dw	dw
L-Arabinose	+	+	Raffinose	dw	dw
D-Arabinose	d	+	D-Xylose	dw	dw
L-Rhamnose	d	+			
Sucrose	+	+	Growth nitrogen compounds		
Maltose	+	+	Nitrate	+	+
α,α trehalose	+	+	Nitrite	+	+
Methyl α-glucoside	+	+	Ethylamine	+	+
Cellobiose	+	+	L-lysine	+	+
Salicin	+	+	Cadaverine	+	+
Arbutin	+	+	Creatine	–	–
Melibiose	+	+	Creatinine	–	–
Lactose	+	+	Glucosamine	–	–
Raffinose	+	+	Imidazole	–	–
Melezitose	d	+			
Inuline	d	+	Growth temperatures		
Soluble starch	+	+	4°C	–	–
Glycerol	dw	+	10°C	+	+
Meso erythritol	+	+	15°C	+	+
Ribitol	+	+	20°C	+	+
Xylitol	+	+	25°C	+	+
L-Arabinitol	+	+	30°C	+	+
D-Glucitol	+	+	35°C	–	–
D-Mannitol	+	+			
Galactitol	+	d	Other tests		
myo-inositol	+	+	0.01% Cycloheximide	–	–
Glucono D-lactone	–	–	0.1% Cycloheximide	–	–
2-Keto-D-gluconate	d	d	1% Acetic acid	–	–
D-Gluconate	+	d	50% Glucose	–	–
D-Glucuronate	w	+	Starch production	–	–
D-Galacturonate	–	–	Urea test	–	–
DL-Lactate	–	+	DBB reaction	–	–
Succinate	–	–			
Citrate	–	–			

(Continues)

TABLE 2 (Continued)

	DAOMC251467	DAOMC251468	DAOMC251467	DAOMC251468
Methanol	–	+		
Ethanol	–	–		
Propane-1,2-diol	dw	+		
Butane-2,3-diol	–	v		
Quinic acid	–	–		
Saccharate	dw	dw		
Galactonic acid	dw	dw		

Blastobotrys Klopotek, Archiv für Mikrobiologie 58: 92 (1967) [MB 7384], generic type *Blastobotrys nivea*.

= *Trichomonascus* H.S. Jacks., Mycologia 39 (6): 712 (1947) [MB 5562], generic type *Trichomonascus mycophagus*.

= *Sympodiomyces* Fell & Statzell, Antonie van Leeuwenhoek 37 (3): 361 (1971) [MB 5321], generic type *Sympodiomyces parvus* (fide Kurtzman and Robnett 2007).

= *Stephanoascus* M.T. Sm. et al., Antonie van Leeuwenhoek 42 (1–2): 125 (1976) [MB 5209], generic type *Stephanoascus ciferrii* (fide Kurtzman and Robnett 2007).

= *Arxula* Van der Walt, M.T. Sm. & Y. Yamada, Antonie van Leeuwenhoek 57: 60 (1989) [MB 11246], generic type *Arxula terrestris* (fide Kurtzman and Robnett 2007).

Arxula adenivorans: see under ***Blastobotrys adenivorans***.

Arxula terrestris: see under ***Blastobotrys terrestris***.

Blastobotrys adenivorans (Middelhoven, Hoogk. Niet & Kreger-van Rij) Kurtzman & Robnett, FEMS Yeast Research 7 (1): 149 (2007) [MB 530150]. Holotype CBS 8244. Ex-type strains CBS 8244 = NRRL Y-17692 = IFO 10858 = IGC 4638 = PYCC 4638. Barcode sequences: ITS KY101746; LSU DQ442697.

Basionym: *Trichosporon adenivorans* Middelhoven, Hoogk. Niet & Kreger, Antonie van Leeuwenhoek 50: 373 (1984), (published as (*Trichosporon adeninovorans*)) [MB 374736].

= *Arxula adenivorans* (Middelhoven, Hoogk. Niet & Kreger) Van der Walt, M.T. Sm. & Y. Yamada, Antonie van Leeuwenhoek 57: 60 (1990) [MB 126538].

Blastobotrys allociferii (Ueda-Nishimura & Mikata) Visagie & Boekhout **comb. nov.** [MB 844756]. Holotype CBS 5166. Ex-type strains CBS 5166 = NBRC 10194 = IFO 10194. Barcode sequences: ITS LC158134; LSU LC158143.

Basionym: *Candida allociferii* Ueda-Nishim. & Mikata, International Journal of Systematic and Evolutionary Microbiology 52 (2): 469 (2002) [MB#374338].

Blastobotrys americanus Kurtzman, International Journal of Systematic and Evolutionary Microbiology 57 (5): 1157 (2007),

(published as "*Blastobotrys americana*") [MB 626960]. Holotype CBS 10337, NRRL Y-6844. Ex-type strains CBS 10337 = NRRL Y-6844 = LRB 70B3. Barcode sequences: ITS KY101748; LSU DQ442699.

Blastobotrys arbuscula de Hoog, Rant.-Leht. & M.T. Sm., Antonie van Leeuwenhoek 51 (1): 93 (1985) [MB 105101]. Holotype CBS 227.83. Ex-type strains CBS 227.83 = NRRL Y-17585. Barcode sequences: ITS OL772655; LSU DQ442689.

Blastobotrys aristatus Marvanová, Transactions of the British Mycological Society 66 (2): 221 (1976), (published as "*Blastobotrys aristata*") [MB 626931]. Holotype BRNU 445 810. Ex-type strains CBS 521.75 = NRRL Y-17579 = ATCC 34215 = CCM F-410 = HFM 2672 = UAMH 4665. Barcode sequences: ITS OL772656; LSU DQ442686.

Blastobotrys attinorum (Carreiro, Pagnocca, C.A. Rosa & Lachance) Kurtzman & Robnett, FEMS Yeast Research 7 (1): 149 (2007) [MB 530151]. Holotype UNESP-S156. Ex-type strains CBS 9734 = NRRL Y-27639 = UNESP-S156. Barcode sequences: ITS KY101749; LSU AY442294.

Basionym: *Sympodiomyces attinorum* Carreiro, Pagnocca, C.A. Rosa & Lachance, International Journal of Systematic and Evolutionary Microbiology 54: 1893 (2004) [MB 369148].

Blastobotrys baotianmanensis F.L. Hui & Huang, International Journal of Systematic and Evolutionary Microbiology 70 (7): 4222 (2020) [MB 834577]. Holotype NYNU 1581. Ex-type strain CBS 16024 = CICC 33083. Barcode sequences: ITS KU128710; LSU KU128725.

Blastobotrys bombycis D.A. Barretto, Avchar, C. Carvalho, J.P. Samp., Vootla & Baghela, International Journal of Systematic and Evolutionary Microbiology 68 (8): 2642 (2018) [MB 825095]. Holotype RAAB001. Ex-type strain CBS 15274. Barcode sequences: ITS OL772657; LSU OL772653.

Blastobotrys buckinghamii Q.M. Wang, Hulfachor, K. Sylvester & Hittinger, FEMS Yeast Research 15 (3): 9 (2015), [MB 809708]. Holotype yHAB 196. Ex-type strains CBS 13900 = NRRL Y-63727 = yHAB 196. Barcode sequences: ITS OL772658; LSU OL772654.

*Note: MycoBank lists this as an invalid name (Art. 40.7 [Melbourne Code]). However, an argument was recently made against invalidating certain yeast names by the strict interpretation of Art. 40.7, which pertains to the need to indicate a single repository as the holder of the holotype (Yurkov et al., 2021).

Blastobotrys capitulata de Hoog, Rant.-Leht. & M.T. Sm., *Antonie van Leeuwenhoek* 51 (1): 91 (1985) [MB 105102]. Holotype CBS 287.82. Ex-type strains CBS 287.82 = NRRL Y-17573. Barcode sequences: ITS OL772659; LSU DQ442688.

Blastobotrys chiropterorum (Grose & Marink.) Kurtzman & Robnett, *FEMS Yeast Research* 7 (1): 149 (2007) [MB 530154]. Holotype Colombia et positus in herbario mycologico universitatis specimen 6031. Ex-type strains CBS 6064 = NRRL Y-17071. Barcode sequences: ITS KY101750; LSU DQ442682.

Basionym: *Candida chiropterorum* Grose & Marink., *Mycopathologia et Mycologia Applicata* 36: 225 (1968) [MB 327425].

Blastobotrys davincii Visagie, Boekhout, Theelen, Yilmaz & Seifert [MB 843366]. Described here.

Blastobotrys elegans de Hoog, Rant.-Leht. & M.T. Sm., *Antonie van Leeuwenhoek* 51 (1): 95 (1985) [MB 105103]. Holotype CBS 530.83A. Ex-type strains CBS 530.83A = NRRL Y-17572. Barcode sequences: ITS OL772660; LSU DQ442687.

Blastobotrys farinosus de Hoog, Rantio-Lehtimäki & M.T. Sm.: 79–109 (1985) [MB 581155] Holotype CBS 140.71. Ex-type strains CBS 140.71 = NRRL Y-17593 = IGC 4592 = JCM 2935. Barcode sequences: ITS OL772661; LSU DQ442685.

= *Stephanoascus farinosus* de Hoog, Rant.-Leht. & M.T. Sm., *Antonie van Leeuwenhoek* 51 (1): 102 (1985) [MB 105809].

= *Trichomonascus farinosus* (de Hoog, Rant.-Leht. & M.T. Sm.) Kurtzman & Robnett, *FEMS Yeast Research* 7 (1): 149 (2007) [MB 530084].

?= *Blastobotrys gigas* de Hoog, Rant.-Leht. & M.T. Sm., *Antonie van Leeuwenhoek* 51 (1): 97 (1974) [MB 105104] (fide Kurtzman et al., 2011).

Blastobotrys fungorum (de Hoog & G.A. de Vries) Visagie, Seifert & Boekhout *comb. nov.* [MB 844758]. Holotype CBS 259.70. Ex-type strains CBS 259.70 = CMW 17165 = UAMH 3678. Barcode sequences: ITS KX590837; LSU KX590883.

Basionym: *Sporothrix fungorum* de Hoog & G.A. de Vries, *Antonie van Leeuwenhoek* 39 (3): 518 (1973) [MB#323932].

*Note: De Hoog and de Vries (1973) introduced *Sporothrix fungorum* noting similarities in morphology with the then only species in *Blastobotrys*, *B. nivea*. In a subsequent study, de Hoog et al. (1985) introduced *St. farinosus* for CBS 140.71, a strain considered to be the yeast-like representative of *Sp. fungorum* that produced a *Stephanoascus* sexual state. DNA sequences for the ex-type strain (CBS 259.70) revealed that *Sp. fungorum* is a distinct species in *Blastobotrys*.

Blastobotrys gigas: see under *Blastobotrys farinosus*.

Blastobotrys illinoisensis Kurtzman, *International Journal of Systematic and Evolutionary Microbiology* 57 (5): 1157 (2007) [MB 505837]. Holotype NRRL YB-1343. Ex-type strains CBS 10339 = NRRL YB-1343. Barcode sequences: ITS KY101751; LSU DQ442696.

Blastobotrys indianensis (Kurtzman) Kurtzman & Robnett, *FEMS Yeast Research* 7 (1): 149 (2007), (published as "*Blastobotrys indianaensis*") [MB 529419]. Holotype NRRL YB-1950. Ex-type strains CBS 9600 = NRRL YB-1950. Barcode sequences: ITS KY101752; LSU DQ442692.

Basionym: *Sympodiomyces indianensis* Kurtzman, *Antonie van Leeuwenhoek* 85 (4): 303 (2004), (published as "*Sympodiomyces indianaensis*") [MB 529418].

Blastobotrys malaysiensis Kurtzman, *International Journal of Systematic and Evolutionary Microbiology* 57 (5): 1160 (2007) [MB 505835]. Holotype NRRL Y-6417. Ex-type strain NRRL Y-6417 = CBS 10336 = EMMONS S3,539A. Barcode sequences: ITS KY101753; LSU DQ442695.

Blastobotrys meliponae R.N. Barbosa, Boekhout, G.A. Silva, Souza-Motta & N. Oliveira, *Persoonia* 36: 443 (2016) [MB 812601]. Holotype URM 7224. Ex-type strains CBS 14100 = URM 7224. Barcode sequences: ITS barcode KT448719; LSU KR779217.

Blastobotrys mokoena (Mokwena, E. Jansen & Myburgh) Kurtzman & Robnett, *FEMS Yeast Research* 7 (1): 149 (2007) [MB 530156]. Holotype CBS 8435. Ex-type strains CBS 8435 = NRRL Y-27120. Barcode sequences: ITS KY101754; LSU DQ442694.

Basionym: *Candida mokoena* Mokwena, E. Jansen & Myburgh, *Antonie van Leeuwenhoek* 77 (1): 44 (2000) [MB 464317].

Blastobotrys muscicola Kurtzman, *International Journal of Systematic and Evolutionary Microbiology* 57 (5): 1160 (2007) [MB 505838]. Holotype NRRL Y-7993. Ex-type strains CBS 10338 = NRRL Y-7993. Barcode sequences: ITS KY101755; LSU DQ442680.

Blastobotrys mucifer (Kock.-Krat. & E. Sláviková) Visagie & Boekhout *comb. nov.* [MB 844757]. Holotype CBS 7409. Ex-type strains CBS 7409 = CCY 29-170-1 = IFO 10918. Barcode sequences: ITS KY102217; LSU KY106587.

Basionym: *Candida mucifera* Kock.-Krat. & E. Sláviková, *Journal of Basic Microbiology* 28 (9–10): 613 (1988) [MB#125429].

Blastobotrys navarrensis Sesma & C. Ramírez, *Mycopathologia* 63 (1): 41 (1978) [MB 309585]. Holotype CBS 139.77. Ex-type strains CBS 139.77 = ATCC 36955 = IJFM 2642 = UAMH 4664. Barcode sequences: ITS OK623478; LSU OK623486.

*Note: Considered a synonym of *B. proliferans* by Smith et al. (2011b), but recently considered distinct by Palma et al. (2022) based on DNA sequence comparisons.

TABLE 3 Physiological characters of *Blastobotrys* and *Trichomonascus* species (+, growth; -, no growth; w, weak; v, variable; n, not done)

	<i>B. davincii</i>	<i>B. elegans</i>	<i>B. aristatus</i>	<i>B. bombycis</i>	<i>B. farinosus</i>	<i>B. fungorum</i>	<i>B. arbuscula</i>	<i>B. buckinghamii</i>	<i>B. capitulata</i>	<i>B. baotianmenensis</i>	<i>B. nivea</i>	<i>B. xishuangbannaensis</i>	<i>B. navarensis</i>
	TYTS5th	TYTS5th	10.1099/ ijsem.0.002890	TYTS5th	10.1007/ BF00444231	TYTS5th	10.1093/ femsyr/fov002	TYTS5th	10.1099/ ijsem.0.004275	TYTS5th	10.1099/ ijsem.0.004275	10.1099/ ijsem.0.005388/ doi.org/10.1007/ BF00473158	
F glucose	-	+	+	+	n	+	+	+	-	+	+	+	+
F galactose	w	v	+	v	n	+	+	+	-	+	+	+	+
F sucrose	w	-	-	-	n	-	-	-	-	-	-	-	-
F maltose	w	+	-	v	n	+	w	v	-	+	-	-	-
F lactose	w	-	-	v	n	-	-	-	-	-	-	-	-
F raffinose	w	-	-	-	n	-	-	-	-	-	-	-	-
F trehalose	w	+	+	v	n	+	+	v	+	+	+	+	+
G glucose	+	+	+	+	n	+	+	+	+	+	+	+	+
G galactose	+	+	+	+	n	+	n	+	+	+	+	+	+
G L-sorbose	+	+	+	+	n	+	w	+	+	+	+	+	+
G D-glucosamine	-/w	+	-	v	n	+	n	+	+	+	+	+	n
G D-ribose	+	+	+	v	n	+	w	+	+	+	+	+	-
G D-xylose	+	+	+	v	n	+	w	+	+	+	+	+	+
G L-arabinose	+	v	+	v	n	+	n	+	+	+	+	+	+
G D-arabinose	+	-	-	v	n	-	w	v	-	+	+	+	-
G L-rhamnose	v	v	-	-	n	-	n	+	+	-	+	+	+
G sucrose	+	+	-	-	n	-	n	v	+	v	+	+	+
G maltose	+	+	+	v	n	+	+	v	-	+	+	+	+
G trehalose	+	+	+	+	n	+	n	+	+	+	+	+	+
G methyl- α -D-glucoside	+	-	n	v	n	v	n	-	-	v	+	+	+
G cellobiose	+	+	+	+	n	+	+	+	+	+	+	+	+
G salicin	+	v	-	v	n	-	n	+	+	+	+	+	+
G arbutin	+	n	n	v	n	n	n	n	+	n	+	n	n
G melibiose	+	-	+	v	n	-	n	-	-	+	+	+	+
G lactose	+	+	-	v	n	-	n	v	+	+	+	+	-
G raffinose	+	-	-	v	n	-	n	v	-	-	+	+	+
G melezitose	+	-	-	-	n	-	n	-	-	-	+	+	+
G inulin	+	v	-	v	n	v	n	v	+	v	+	+	-
G soluble starch	+	v	-	v	n	+	n	+	-	+	+	+	-
G glycerol	+	+	+	+	n	+	+	+	-	+	+	w	+
G erythritol	+	+	+	v	n	+	+	+	+	+	+	+	+
G ribitol	+	+	v	+	n	+	n	+	+	+	+	+	+
G xylitol	+	n	n	n	n	n	n	n	-	n	+	+	+
G L-arabinitol	+	n	n	n	n	n	n	n	-	n	+	+	n
G D-glucitol	+	+	-	+	n	+	n	+	-	+	+	+	+
G D-mannitol	+	+	+	+	n	+	n	+	-	+	+	+	+
G galactitol	+	v	+	v	n	+	n	+	-	+	+	+	+
G myo-inositol	+	-	+	+	n	-	-	+	-	+	+	+	n
G 2-keto-D-gluconate	n	n	n	n	n	n	n	n	-	n	+	+	n
G 5-keto-D-gluconate	n	n	n	n	n	n	n	n	+	n	-	-	n
G D-gluconate	v	+	+	-	n	n	n	n	-	n	+	+	v
G DL-lactate	v	-	-	-	n	v	n	-	-	-	-	+	v
G succinate	-	+	+	+	n	+	n	+	-	+	+	+	n

TABLE 3 (Continued)

	<i>B. davincii</i>	<i>B. elegans</i>	<i>B. aristatus</i>	<i>B. bombycis</i>	<i>B. farinosus</i>	<i>B. fungorum</i>	<i>B. arbuscula</i>	<i>B. buckinghamii</i>	<i>B. capitulata</i>	<i>B. baotianmenensis</i>	<i>B. nivea</i>	<i>B. xishuangbannaensis</i>	<i>B. navarrensis</i>
	TYTS5th	TYTS5th	TYTS5th	10.1099/ ijsem.0.002890	TYTS5th	10.1007/ BF00444231	TYTS5th	10.1093/ femsyr/fov002	TYTS5th	10.1099/ ijsem.0.004275	TYTS5th	10.1099/ ijsem.0.004275	10.1099/ ijsem.0.005388/ doi.org/10.1007/ BF00473158
G citrate	-	+	V	+	V	n	-	w	V	-	+	+	V
G methanol	V	n	n	n	n	n	n	n	n	-	n	-	n
G ethanol	-	+	-	-	V	n	-	+	+	-	+	-	-
G propane 1,2 diol	-/w	n	n	n	n	n	n	n	n	n	n	n	n
G butane 2,3 diol	V	n	n	n	n	n	n	n	n	n	n	n	n
G saccharate	w	n	n	n	n	n	n	n	n	n	n	n	n
G N-acetyl-D-glucosamine	n	+	n	+	n	n	n	n	n	n	n	n	n
G hexadecane	n	n	n	-	n	n	n	n	n	n	n	n	n
G nitrate	+	-	-	-	-	-	-	-	-	-	-	+	n
G nitrite	+	n	n	n	n	n	n	-	n	-	n	+	n
G ethylamine	+	n	n	n	n	n	n	n	n	-	n	-	n
G L-lysine	+	n	n	n	n	n	+	+	n	+	n	+	n
G cadaverine	+	n	n	n	n	n	n	n	n	+	n	-	n
G creatinine	-	n	n	n	n	n	n	n	n	-	n	-	n
G vitamin free	n	-	-	-	-	n	-	n	-	+	-	+	n
G 50% glucose	-	n	n	n	n	n	-	-	n	n	n	n	+
G 10% NaCl/5% glucose	n	n	n	+	n	n	n	n	n	-	n	+	n
Starch formation	-	n	n	n	n	n	n	n	n	-	n	-	n
Urease	-	n	n	n	n	n	n	n	n	n	n	n	n
Gelatin liquefaction	n	n	n	n	n	n	n	n	n	n	n	n	n
G cycloheximide	-	n	n	+	n	n	n	n	+	+	n	+	+
G cycloheximide 0.01%	-	n	n	+	n	n	n	n	+	n	n	n	+
G cycloheximide 0.1%	n	+	+	n	+	n	+	n	+	n	+	n	n
G 19°C	+	+	+	n	+	n	+	n	+	n	+	n	n
G 25°C	+	+	+	n	+	n	+	n	+	n	+	n	n
G 30°C	+	+	+	+	+	n	+	+	+	+	+	+	n
G 35°C	-	n	n	+	+	n	+	+	+	+	+	+	n
G 37°C	-	n	-	-	n	n	-	+	+	-	+	+	n
G 40°C	-	-	-	n	-	n	-	n	n	n	n	-	V
G 45°C	-	-	-	n	-	n	-	n	n	n	n	n	n
CoQ	n	n	n	n	9	n	n	n	n	n	n	n	n
Mol% G+C	n	n	n	n	49, 2	n	n	n	n	n	n	n	n
DBB	-	-	-	n	-	n	-	n	-	n	-	n	n
	<i>B. proliferans</i>	<i>B. indianensis</i>	<i>T. petasosporus</i>	<i>B. parvus</i>	<i>T. apis</i>	<i>B. attinorum</i>	<i>B. chiropterorum</i>	<i>B. meliponae</i> 10.3767/ 003158516x692185	<i>B. terrestris</i>	<i>B. serpentina</i>	<i>T. ciferrii</i>	<i>B. allociferii</i>	<i>B. mucifer</i>
	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	003158516x692185	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th
F glucose	+	+	+	-	+	+	-	+	-	-	-	-	-
F galactose	+	+	+	-	+	-	-	+	-	-	-	-	-
F sucrose	+	-	-	-	-	-	-	+	-	-	-	-	-
F maltose	+	+	+	-	-	V	-	-	-	-	-	-	-
F lactose	-	-	-	-	-	-	-	n	-	-	-	-	-
F raffinose	+	-	-	-	-	-	-	-	-	-	-	-	-
F trehalose	V	+	+	-	-	-	-	n	-	-	-	-	-

(Continues)

TABLE 3 (Continued)

	<i>B. proliferans</i>	<i>B. indianensis</i>	<i>T. petasosporus</i>	<i>B. parvus</i>	<i>T. apis</i>	<i>B. attinorum</i>	<i>B. chiropterorum</i>	<i>B. meliponae</i> 10.3767/ 003458516x692485	<i>B. serpentis</i>	<i>B. terrestris</i>	<i>T. ciferrii</i>	<i>B. allociferii</i>	<i>B. mucifer</i>
	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th		TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th
G glucose	+	+	+	+	+	+	+	+	+	+	+	+	+
G galactose	+	+	+	+	+	+	+	+	+	+	+	+	+
G L-sorbose	+	+	+	-	+	+	+	+	+	+	+	+	+
G D-glucosamine	+	+	+	+	n	+	+	-	+	-	-	-	w
G D-ribose	v	-	-	v	+	+	+	n	+	+	v	v	+
G D-xylose	+	+	+	+	+	+	+	+	+	+	+	+	+
G L-arabinose	+	+	+	+	+	+	+	+	+	+	+	+	+
G D-arabinose	+	+	+	v	+	+	+	n	+	+	+	+	+
G L-rhamnose	v	-	-	+	+	+	+	n	+	+	+	+	+
G sucrose	+	-	-	+	+	-	+	n	+	+	+	+	-
G maltose	+	+	+	+	+	+	+	+	+	+	+	+	+
G trehalose	+	+	+	+	-	-	+	n	+	+	+	+	+
G methyl-α-D-glucoside	v	+	+	-	+	+	+	n	n	+	v	v	-
G cellobiose	+	+	+	+	+	+	+	n	+	+	v	v	-
G salicin	+	-	+	-	+	+	+	n	+	+	v	v	-
G arbutin	n	n	n	n	v	n	+	n	n	n	v	v	n
G melibiose	+	+	+	-	+	-	-	-	+	-	v	v	-
G lactose	+	-	-	-	v	-	-	+	+	-	-	-	-
G raffinose	+	+	+	-	v	-	+	+	+	+	+	+	-
G melezitose	v	-	-	-	v	-	+	n	-	-	-	-	-
G inulin	v	-	-	-	-	-	-	n	-	-	-	w	-
G soluble starch	v	+	+	-	+	+	+	n	-	+	v	v	-
G glycerol	+	+	+	+	+	+	+	-	+	+	+	+	+
G erythritol	+	-	-	+	+	+	+	+	+	+	+	+	+
G ribitol	+	+	+	+	+	+	+	n	+	+	+	+	+
G xylitol	n	u	u	u	n	u	-	u	+	+	n	+	+
G L-arabinitol	n	u	n	u	n	u	-	u	+	+	n	n	n
G D-glucitol	+	+	+	+	+	+	+	u	+	+	+	+	-
G D-mannitol	+	+	+	+	+	+	+	u	+	+	+	+	-
G galactitol	+	-	-	-	+	+	+	u	+	+	+	+	+
G myo-inositol	+	+	+	+	+	+	+	n	+	+	+	+	+
G 2-keto-D-gluconate	n	+	n	n	v	-	+	n	-	-	+	+	+
G 5-keto-D-gluconate	n	+	n	u	n	n	+	u	n	n	+	+	u
G D-gluconate	n	-	v	-	+	+	+	u	+	+	+	+	+
G DL-lactate	v	-	-	-	+	+	+	u	+	+	+	+	-
G succinate	+	+	+	-	+	-	-	u	+	+	v	v	w
G citrate	+	+	+	-	+	-	+	-	+	+	v	-	-
G methanol	n	-	-	-	-	-	-	u	-	-	-	-	-
G ethanol	+	+	v	-	+	-	-	u	-	+	v	v	w
G propane 1,2 diol	n	u	n	u	n	n	-	u	u	u	n	n	u
G butane 2,3 diol	n	u	n	u	n	n	-	u	u	u	n	n	n
G saccharate	n	-	u	-	-	u	-	u	-	-	-	-	u
G N-acetyl-D-glucosamine	n	+	+	+	+	+	+	u	u	u	n	n	+

TABLE 3 (Continued)

	<i>B. proliferans</i>	<i>B. indianensis</i>	<i>T. petasosporus</i>	<i>B. parvus</i>	<i>T. apis</i>	<i>B. attinorum</i>	<i>B. chiropterorum</i>	<i>B. melliponae</i> 10.3767/ 003158516x692185	<i>B. serpentis</i>	<i>B. terrestris</i>	<i>T. ciferrii</i>	<i>B. allociferii</i>	<i>B. mucifer</i>
	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th
G hexadecane	n	+	+	-	v	-	-	n	n	n	n	n	+
G nitrate	-	-	-	-	-	-	-	-	-	+	-	-	-
G nitrite	n	n	n	n	n	n	n	n	n	n	n	v	-
G ethylamine	n	n	n	n	n	n	+	n	n	n	n	+	+
G L-lysine	n	n	n	n	n	n	+	n	n	n	n	+	+
G cadaverine	n	n	n	n	n	n	+	n	n	n	n	+	+
G creatinine	n	n	n	n	n	n	n	n	n	n	n	n	n
G vitamin free	-	-	-	-	-	-	-	n	-	-	-	-	-
G 50% glucose	n	n	n	-	n	+	+	n	n	+	n	+	w
G 10% NaCl/5% glucose	n	+	+	-	+	n	+	n	n	n	+	n	+
Starch formation	n	-	n	-	-	-	n	n	-	-	-	-	-
Urease	n	n	n	-	n	n	n	+	n	n	n	n	n
Gelatin	n	-	n	-	n	n	n	n	n	n	-	n	-
liquefaction													
G cycloheximide	n	+	+	n	+	+	+	n	+	+	n	+	+
0.01%													
G cycloheximide	n	n	+	n	+	+	+	n	+	+	n	+	+
0.1%													
G 19°C	+	+	+	+	+	+	+	n	+	+	+	+	n
G 25°C	+	+	+	+	+	+	+	+	+	+	+	+	n
G 30°C	+	+	+	+	v	+	+	+	+	+	+	+	+
G 35°C	+	n	+	-	-	+	+	+	-	+	+	+	n
G 37°C	+	-	+	-	-	+	+	+	+	+	+	+	-
G 40°C	n	-	n	-	-	n	n	n	-	+	n	n	n
G 45°C	n	-	n	-	-	n	n	n	-	n	n	n	n
CoQ	n	n	n	9	n	n	9	n	9	9	9	n	n
Mol% G+C	n	n	n	46,3	b	n	48	n	5-,2	n	46,6	n	n
DBB	-	-	-	-	-	-	-	n	-	-	-	-	-
	<i>B. persicus</i> 10.1007/s10482- 017-0972-x	<i>B. americanus</i>	<i>B. peoriensis</i>	<i>B. adeninivorans</i>	<i>B. raffinosofermentans</i>	<i>B. muscicola</i>	<i>B. robertii</i>	<i>B. illinoisensis</i>	<i>B. malaysiensis</i>	<i>B. makoensis</i>	<i>B. vanleenenianus</i> 10.1093/femsyr/ foy076		
	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th		
F glucose	-	+	+	+	+	-	-	+	+	+	+		
F galactose	-	-	+	+	+	-	-	+	+	+	n		
F sucrose	-	-	-	+	+	-	-	+	+	-	n		
F maltose	-	-	-	+	+	-	-	+	+	-	n		
F lactose	-	-	-	-	+	-	-	-	-	-	n		
F raffinose	-	-	-	+	+	-	-	-	-	-	n		
F trehalose	-	+	+	+	+	-	-	+	+	+	n		
G glucose	+	+	+	+	+	+	+	+	+	+	+		
G galactose	+	+	+	+	+	-	-	+	+	+	+		
G L-sorbose	n	+	+	+	+	+	+	+	+	+	+		
G D-glucosamine	n	+	+	+	+	+	+	+	+	+	+		
G D-ribose	-	+	+	+	+	-	-	+	+	+	+		
G D-xylose	+	+	+	+	+	-	-	+	+	+	+		
G L-arabinose	+	+	+	+	+	-	-	+	+	+	+		
G D-arabinose	-	+	+	+	+	-	-	+	+	-	n		
G L-rhamnose	+	-	-	+	+	-	-	+	+	+	+		
G sucrose	+	-	+	+	+	+	+	+	+	+	+		

(Continues)

TABLE 3 (Continued)

	<i>B. persicus</i> 10.1007/s10482- 017-0972-x	<i>B. americanus</i>	<i>B. peioratus</i>	<i>B. adeninivorans</i>	<i>B. raffinosofermentans</i>	<i>B. muscicola</i>	<i>B. robertii</i>	<i>B. illinoisensis</i>	<i>B. malaysiensis</i>	<i>B. mokoensis</i>	<i>B. vanleenenianus</i> 10.1093/femsyr/ foy076
G maltose	+	-	+	+	+	+	+	+	+	+	+
G trehalose	+	+	-	+	-	v	+	-	+	+	+
G methyl- α -D- glucoside	n	+	+	+	+	v	v	+	+	+	+
G cellobiose	+	+	+	+	+	+	+	+	+	+	+
G salicin	w	+	+	+	+	v	+	+	+	-	n
G arbutin	+	n	n	n	n	n	n	n	n	-	n
G melibiose	w	+	+	+	+	v	+	-	-	-	-
G lactose	-	-	+	+	-	+	+	-	+	-	-
G raffinose	+	+	+	+	+	v	+	-	+	-	-
G melezitose	w	-	+	+	+	+	+	-	+	-	-
G inulin	n	-	-	-	+	-	-	-	+	+	n
G soluble starch	-	-	+	+	+	+	+	+	+	+	n
G glycerol	+	+	+	+	+	+	-	+	+	+	-
G erythritol	n	+	+	+	+	+	-	+	+	+	+
G ribitol	+	+	+	+	+	+	-	+	+	+	n
G xylitol	n	n	n	n	n	n	n	n	n	+	n
G L-arabinitol	n	n	n	n	n	n	n	n	n	+	n
G D-glucitol	n	+	+	+	+	+	-	+	+	+	+
G D-mannitol	-	+	+	+	+	+	+	+	+	+	+
G galactitol	n	+	+	-	+	+	-	+	-	+	n
G myo-inositol	+	+	+	+	+	+	-	+	+	+	+
G 2-keto-D- gluconate	n	-	+	+	+	-	n	+	+	+	+
G 5-keto-D- gluconate	n	+	+	n	+	-	n	+	+	n	n
G D-gluconate	n	+	+	+	+	u	v	+	-	+	+
G DL-lactate	w	+	-	-	+	+	+	-	+	-	u
G succinate	-	+	+	+	+	+	+	+	+	+	u
G citrate	-	-	-	+	+	+	+	+	+	+	u
G methanol	-	-	-	-	-	-	-	-	-	-	u
G ethanol	w	+	+	+	+	+	-	+	+	+	u
G propane 1,2 diol	n	n	n	n	n	n	n	n	n	-	n
G butane 2,3 diol	n	n	n	n	n	u	n	n	n	n	n
G saccharate	n	-	-	-	-	-	n	-	-	n	n
G N-acetyl-D- glucosamine	n	+	+	n	+	u	+	+	+	n	+
G hexadecane	w	+	+	u	+	-	+	+	-	n	n
G nitrate	-	-	+	+	+	-	-	-	-	-	-
G nitrite	-	u	u	u	u	u	u	u	u	+	+
G ethylamine	+	u	u	u	u	u	u	u	u	+	+
G L-lysine	+	u	u	u	u	u	u	u	u	+	+
G cadaverine	+	u	u	u	u	u	u	u	u	+	+
G creatinine	w	u	u	u	u	u	u	u	u	u	u
G vitamin free	n	-	-	-	-	v	-	+	+	+	u
G 50% glucose	+	u	+	+	u	u	u	u	u	-	u
G 10% NaCl/5% glucose	n	+	+	n	+	-	u	+	+	+	u

TABLE 3 (Continued)

	<i>B. persicus</i> 10.1007/s10482- 017-0972-x	<i>B. americanus</i>	<i>B. peoriensis</i>	<i>B. adeninivorans</i>	<i>B. raffinosifermentans</i>	<i>B. muscicola</i>	<i>B. robertii</i>	<i>B. illinoisensis</i>	<i>B. malaysiensis</i>	<i>B. mokoensis</i>	<i>B. vanleenenianus</i> 10.1093/femsyr/ foy076
Starch formation	-	-	-	-	-	-	-	-	-	-	-
Urease	-	-	-	-	-	-	-	-	-	-	-
Gelatin	-	-	-	-	-	-	-	-	-	-	-
Liquefaction	-	-	-	-	-	-	-	-	-	-	-
G cycloheximide	-	-	-	-	-	-	-	-	-	-	-
0.01%	-	-	-	-	-	-	-	-	-	-	-
G cycloheximide	-	-	-	-	-	-	-	-	-	-	-
0.1%	-	-	-	-	-	-	-	-	-	-	-
G 19°C	+	+	+	+	+	+	+	+	+	+	+
G 25°C	+	+	+	+	+	+	+	+	+	+	+
G 30°C	+	+	+	+	+	+	+	+	+	+	+
G 35°C	+	+	+	+	+	+	+	+	+	+	+
G 37°C	+	+	+	+	+	+	+	+	+	+	+
G 40°C	+	+	+	+	+	+	+	+	+	+	+
G 45°C	+	+	+	+	+	+	+	+	+	+	+
CoQ	-	-	-	-	-	-	-	-	-	-	-
Mol% G+C	-	-	-	-	-	-	-	-	-	-	-
DBB	-	-	-	-	-	-	-	-	-	-	-

Blastobotrys nivea Klopotek, Archiv für Mikrobiologie 58: 92 (1967) [MB 327003]. Holotype CBS163.67. Ex-type strains CBS 163.67 = NRRL Y-17581 = ATCC 18420 = HFM 26 = UAMH 4663. Barcode sequences: ITS OL772662; LSU DQ442690.

Blastobotrys parvus (Fell & Statzell) Kurtzman & Robnett, FEMS Yeast Research 7 (1): 149 (2007) [MB 530157]. Holotype CBS 6147. Ex-type strains CBS 6147 = NRRL Y-10004. Barcode sequences: ITS KY101757; LSU DQ442693.

Basionym: *Sympodiomyces parvus* Fell & Statzell, Antonie van Leeuwenhoek 37 (3): 362 (1971) [MB 324368].

Blastobotrys peoriensis Kurtzman, International Journal of Systematic and Evolutionary Microbiology 57 (5): 1161 (2007) [MB 505839]. Holotype NRRL YB-2290. Ex-type strains CBS 10340 = NRRL YB-2290. Barcode sequences: ITS KY101758; LSU DQ442700.

Blastobotrys persicus H. Nouri, S. Nasr & Moghimi, Antonie van Leeuwenhoek <https://doi.org/10.1007/s10482-017-0972-x>: 6 (2017) [MB 819148]. Holotype IBRC-M 30238. Ex-type strains CBS 14259 = IBRC-M30238. Barcode sequences: ITS OL772663; LSU KU659141.

Blastobotrys proliferans Marvanová, Transactions of the British Mycological Society 66 (2): 217 (1976) [MB 309586]. Holotype BRNU 445 809. Ex-type strains CBS 522.75 = NRRL Y-17577 = ATCC 34216 = CCM F-493 = HFM 2673 = UAMH 4666. Barcode sequences: ITS EU343812; LSU DQ442684.

Blastobotrys raffinosifermentans Kurtzman, International Journal of Systematic and Evolutionary Microbiology 57 (5): 1161 (2007) [MB 505840]. Holotype NRRL Y-27150. Ex-type strains CBS 6800 = NRRL Y-27150. Barcode sequences: ITS KY101759; LSU DQ442698.

Blastobotrys robertii Middelhoven & Kurtzman, Antonie van Leeuwenhoek 92 (2): 234 (2007) [MB 510429]. Holotype CBS 10106. Ex-type strains CBS 10106 = NRRL Y-27775. Barcode sequences: ITS KY101760; LSU DQ839395.

Blastobotrys serpentis Bhadra, Rao & Shivaji, FEMS Yeast Research 8 (3): 495 (2008) [MB 533888]. Holotype MTCC 8332. Ex-type strains CBS 10541 = NRRL Y-48249 = MTCC 8332 = W113A = YS W113A. Barcode sequences: ITS KY101761; LSU AM410667.

Blastobotrys terrestris (Van der Walt & Johannsen) Kurtzman & Robnett, FEMS Yeast Research 7 (1): 149 (2007) [MB 530158]. Holotype CBS 278.86. Ex-type strains CBS 7376 = NRRL Y-17704 = CSIR Y914 = IFO 10859 = IGC 5133 = PYCC 5133. Barcode sequences: ITS KY101762; LSU DQ442683.

Basionym: *Trichosporon terrestre* Van der Walt & Johannsen, Antonie van Leeuwenhoek 41 (3): 361 (1975) [MB 324996].

≡ *Geotrichum terrestre* (Van der Walt & Johannsen) Weijman, Antonie van Leeuwenhoek 45 (1): 126 (1979) [MB 314425].

≡ *Arxula terrestris* (Van der Walt & Johannsen) Van der Walt, M.T. Sm. & Y. Yamada, Antonie van Leeuwenhoek 57: 60 (1990) [MB 126539].

Blastobotrys vanleenenianus (M. Groenew. & M.T. Sm.) Visagie & Boekhout, *comb. nov.* [MB 843370]. Holotype CBS 14902. Ex-type strain CBS 14902. Barcode sequences: ITS MG986487; LSU MG986492.

Basionym: *Trichomonascus vanleenenianus* M. Groenew. & M.T. Sm., *FEMS Yeast Research* 18 (7): foy076, 9 (2018) [MB 824963].

*Note: *Trichomonascus vanleenenianus* is only known from its asexual state (Groenewald et al., 2018).

Blastobotrys xishuangbannaensis F.L. Hui & Huang, *International Journal of Systematic and Evolutionary Microbiology* 70 (7): 4222 (2020) [MB 834578]. Holotype NYNU 181030. Ex-type strain CBS 16044 = CICC 33360. Barcode sequences: ITS MK682811; LSU MK682809.

Candida allociferii: see under **Blastobotrys allociferii**.

Candida chiropterorum: see under **Blastobotrys chiropterorum**.

Candida mokoenaai: see under **Blastobotrys mokoenaai**.

Candida mucifera: see under **Blastobotrys mucifer**.

Geotrichum terrestre: see under **Blastobotrys terrestris**.

Sporothrix catenata: see under **Trichomonascus ciferii**.

Sporothrix fungorum: see under **Blastobotrys fungorum**.

Stephanoascus ciferii: see under **Trichomonascus ciferii**.

Stephanoascus farinosus: see under **Blastobotrys farinosus**.

Stephanoascus flocculosus Traquair, L.A. Shaw & Jarvis, *Canadian Journal of Botany* 66 (5): 927 (1988) [MB 133759] = *Pseudozyma flocculosa* (Traquair, L.A. Shaw & Jarvis) Boekhout & Traquair, *Journal of General and Applied Microbiology Tokyo* 41 (4): 364 (1995) [MB 415207] = *Anthracoecystis flocculosa* (Traquair, L.A. Shaw & Jarvis) M. Lutz & Piątek, *Mycological Progress* 14 (10/88): 9 (2015) [MB 813438].

*Note: The recombination as *A. flocculosa* (Piątek et al., 2015) is considered to be erroneous with this species thought to belong to *Thecaphora* [MB 16347] (Yurkov & Boekhout, unpublished observation).

Stephanoascus rugulosus Traquair, L.A. Shaw & Jarvis, *Canadian Journal of Botany* 66 (5): 929 (1988) [MB 133760] = *Pseudozyma rugulosa* (Traquair, L.A. Shaw & Jarvis) Boekhout & Traquair, *Journal of General and Applied Microbiology Tokyo* 41 (4): 364 (1995) [MB 434595].

Stephanoascus smithiae Gim.-Jurado, *Systematic and Applied Microbiology* 17: 240 (1994) [MB 362705] = *Sugiyamaella smithiae* (Gim.-Jurado) Kurtzman & Robnett, *FEMS Yeast Research* 7 (1): 141–151 (2007) [MB 528979].

Sympodiomyces attinorum: see under **Blastobotrys attinorum**.

Sympodiomyces indianensis: see under **Blastobotrys indianensis**.

Sympodiomyces parvus: see under **Blastobotrys parvus**.

Trichomonascus apis G. Péter, Tornai-Leh. & Dlačny, *International Journal of Systematic and Evolutionary Microbiology* 59 (6): 1551 (2009) [MB 514356]. Holotype NCAIM Y.01848. Ex-type strains CBS 10922 = NRRL Y-48475 = NCAIM Y.01848. Barcode sequences: ITS KY105699; LSU EU790643.

Trichomonascus ciferii (M.T. Sm., Van der Walt & Johannsen) Kurtzman & Robnett, *FEMS Yeast Research* 7 (1): 149 (2007) [MB 530083]. Holotype mixed specimen of isotypes CBS 6699 and CBS 5295. Ex-type strains CBS 5295 = NRRL Y-10943 = ATCC 58443 = CCRC 21427 = Goto TH-26 = IFO 1854 = IGC 4164 = IMI 344641 = JCM 7621. Barcode sequences: ITS AY493435; LSU DQ442681.

Basionym: *Stephanoascus ciferii* M.T. Sm., Van der Walt & Johannsen, *Antonie van Leeuwenhoek* 42 (1-2): 125 (1976) [MB 324077].

= *Sporothrix catenata* de Hoog & Constant., *Antonie van Leeuwenhoek* 47 (4): 367 (1981) [MB 111942].

Trichomonascus farinosus: see under **Blastobotrys farinosus**.

Trichomonascus mycophagus H.S. Jacks., *Mycologia* 39 (6): 712 (1947) [MB 291581]. Holotype TRT 21820. Ex-type strain unknown.

*Note: Taxonomic position uncertain due to a lack of DNA sequence data and access to ex-type material.

Trichomonascus petasosporus Kurtzman, *Antonie van Leeuwenhoek* 85 (4): 300 (2004) [MB 530085]. Holotype NRRL YB-2092. Ex-type strains CBS 9602 = NRRL YB-2092. Barcode sequences: ITS KY105704; LSU DQ442691.

Trichomonascus rutilus Hauerslev, *Friesia* 11 (5): 281 (1987) [MB 132945]. Type strain unknown.

*Note: Taxonomic position uncertain due to a lack of DNA sequence data or reference material.

Trichomonascus vanleenenianus: see under **Blastobotrys vanleenenianus**.

Trichosporon adenivorans: see under **Blastobotrys adenivorans**.

Trichosporon terrestre: see under **Blastobotrys terrestris**.

5 | DISCUSSION

The challenge of linking DNA barcode data, classical specimen-based taxonomy, culture studies, and environmental HTS or other DNA-based surveys is well-illustrated by the fungi detected on Leonardo da Vinci's self-portrait. The study by Piñar et al. (2015) was part of a decades-long effort to understand the chemical and biological fading and discoloration, or foxing (i.e., a deterioration that results in brown spots), of this delicate artwork during its centuries of storage in the Royal Library in Turin, Italy. Destructive sampling of any part of the work is forbidden, and only the gentlest contact with its surface is allowed. In an earlier study, Valenti (2005) failed to isolate cultures from cotton swabs touched to visibly mouldy areas; however, they did not use media that would yield xerophiles, the most likely fungi to grow on such a substrate. Piñar et al. (2015) examined isolated fibres from the front and the back of the paper using SEM and used DNA methods based on cloning and ITS sequencing of representative bands on DGGE gels to detect other fungi and actinomycetes

harvested with cotton swabs or nylon membranes. With SEM, they observed ascospores and conidia typical of *Aspergillus halophilicus*, a well-known xerophilic fungus growing on cellulosic substrates in libraries and archives (Samson et al., 2019; Sklenář et al., 2017). Despite being the only visible fungus, and the inclusion of this species as a positive control in their DGGE gels, they could not clone sequences from the bands that putatively represented *A. halophilicus* in their samples. However, their cloning survey did recover several other species of *Aspergillus*, including sequences that with improved reference data (Houbraken et al., 2020; Samson et al., 2014), we can now reidentify as *Aspergillus atacamensis* (KP828162, 2.6% of the fungi detected from the back of the drawing by DGGE), *A. kalimae* (KP82188, KP828189, 17.2%, back), *A. whitfieldii* (KP828177, 8.6%, front) and an unidentified species belonging to *Aspergillus* section *Polypaecilum* (KP828179, KP828193, 11%, back and pooled samples). Coincidentally, these xerophilic species were also detected, but remained unidentified, during a survey of mummies inside the Capuchin catacombs in Palermo, Italy (Piñar et al., 2013). All of these *Aspergillus* species are at least moderate xerophiles, with a simplified morphology (formerly designated by the generic name *Phialosimplex*; Tanney et al., 2017) in which the conidiophores lack vesicles.

One of the ITS clones from the Piñar et al. (2015) study represents *B. davincii*, the new species described here. We chose the name for this species to acknowledge its occurrence on this most iconic of substrates, where it represented ca 5.7% of the fungal DNA detected on the front of the portrait. *Blastobotrys davincii* seems to have an interesting ecology, and has been detected on a wide range of substrates (bats, air, cave paintings, stuffing material in catacombs) across the northern hemisphere (Canada, China, Italy, USA) (Piñar et al., 2013; Piñar et al., 2015; Rittenour et al., 2014). The species can ferment glucose, and, hence, is able to grow under anoxic conditions. In addition, it can utilize a broad diversity of carbon—and nitrogen sources, suggesting that it may be an ecological generalist rather than a specialist. Few of the strains, OTUs or DNA clones in these previous studies were identified even to genus level. For example, Piñar et al. (2013) and Duan et al. (2017) submitted KC535143 and KY412159 as "*Pichia*", Rittenour et al. (2014) and Piñar et al. (2015) KF800143 and KP828180 as "fungus," and Vanderwolf MK782430 as "*Saccharomycetales*" and MK782473 as "*Dothideales*". Another clone (KP828159) was designated as an unidentified *Stephanoascus* species (Piñar et al., 2015), a genus now considered a synonym of *Blastobotrys* (fide Kurtzman and Robnett 2007, see above). This is not surprising considering the low similarity of the *B. davincii* ITS sequence to other available *Blastobotrys* sequences at the time (*B. proliferans*; EU343812, 82%). The description and release of reference data associated with *B. davincii* to some degree alleviates this problem. However, before this study, several *Blastobotrys* species lacked publicly available ITS sequences. We addressed this by reviving ex-type strains preserved in the CBS collection and generating ITS sequences for them.

One problem experienced by public sequence repositories like NCBI, is the high number of misidentified or incompletely named sequences in the database. These often results in subsequent

incorrect identifications. An excellent initiative to overcome this is the NCBI ITS RefSeq Targeted Loci project (Schoch et al., 2014) which provides a curated ITS reference database of sequences generated from species' type material. These provide an anchor point for correctly identified sequences and thus more reliable determinations, which should have a snowball effect on public sequence databases expanding with reliable reference sequences, as we tried to do with our IM-BOL project (Amend et al., 2010 and subsequent papers). For yeasts, a digital platform on yeast diversity (<https://theyeasts.org>) is currently under development.

The gap between cultured and uncultured fungi remains daunting. Current global estimates predict between 2.2 and 3.8 (Hawksworth & Lücking, 2017) to 5.1 million (Blackwell, 2011) fungal species. These figures are significantly higher than the previously widely quoted estimate of 1.5 million species (Hawksworth, 1991; Hawksworth, 2001). Whatever the correct number, only ±150,000 species are currently accepted (Lücking et al., 2021). At the current annual rate of about 2000 new species descriptions (Lücking et al., 2021), it would take nearly 1000 years to find and describe the missing fungi. More concerning though, is that the National Center for Biotechnology Information (<https://www.ncbi.nlm.nih.gov>) currently archives just less than 50,000 named species represented by sequence data (Sayers et al., 2019; Schoch et al., 2020). About two-thirds of described species thus cannot be identified using DNA sequences. Failure to name so-called "dark taxa," or environmental nucleic acid sequences (ENAS), often even to genus level, has resulted in "unidentified fungi" becoming one of the most frequently reported OTU's in HTS studies. This is far from an ideal situation because information about imprecisely named organisms cannot be communicated effectively. This situation also adds pressure on mycologists to adapt the International Code of Nomenclature for algae, fungi, and plants (ICNafp) to allow DNA sequences to serve as type material and thus formalise naming of ENAS (De Beer et al., 2016; Hibbett & Taylor, 2013; Zamora et al., 2018). This is currently not formally endorsed, but Lücking et al. (2021) argued for the need to work towards a standardised approach for provisional naming of ENAS. One such option for informal naming suggested adopting UNITE's (<https://unite.ut.ee/>) Species Hypotheses (SH), where an SH is represented by clustered ITS sequences linked to a DOI number (Köljalg et al., 2005; Köljalg et al., 2013; Nilsson et al., 2015). Based on this approach, Piñar et al. (2015) would then have identified their clone as *Blastobotrys* SH2279294.08FU, until a culture was isolated and formally named as we have done in this paper.

In our work on the built environment, we followed what we imagined would be a standard approach to bridging the taxonomic gap between classical and molecular taxonomic studies: We (1) isolated strains from house dust; (2) identified them using modern taxonomic approaches (morphology and DNA sequences); (3) described new species; (4) generated reference sequences for existing species that lacked this data; (5) completed taxonomic/nomenclatural revisions where needed, and (6) deposited all relevant data in publicly available databases. To this, we later added the use of media favouring the growth of xerophilic and halophilic fungi,

reasoning that the arid indoor environments would welcome such microbes. An example of this approach was the study by Hirooka et al. (2016) of *Spiromastigaceae* (Onygenales), another group with a significant number of ENAS records in GenBank, which doubled the number of species in the family based on strains isolated using xerophilic media. It is ironic that the da Vinci portrait was colonized by at least five xerophilic fungi that were unknown to science at the time of the 2015 survey; *B. davincii* and the four recently named *Aspergillus* spp. noted above. The common occurrence of xerophiles both in house dust and on cellulosic materials was noted in the rediscovery of the hyphomycete *Diploöspora rosea* in house-dust by Tanney et al. (2015), a century after the discovery of that species on salt-saturated cardboard.

A decision on whether to use the generic name *Blastobotrys* (originally for the asexual or anamorphic state) or *Trichomonascus* (sexual or teleomorphic state) to represent this clade has not been made after the adoption of the "One Fungus = One Name" in 2012. Even though *Trichomonascus* is the older name, it is our opinion that *Blastobotrys* should be used over the latter as previously suggested without explanation by Wijayawardene et al. (2017). The asexual state is much more commonly observed, as indicated by the current 34 accepted *Blastobotrys* names compared to the seven *Trichomonascus* names, and thus adopting *Blastobotrys* will result in fewer new combinations. We also consider *Blastobotrys* to be the more stable generic name because no culture is available for the generic type of *Trichomonascus*, *T. mycophagus*, rendering its taxonomic position uncertain. Finally, *Blastobotrys* is the more frequently used name, revealed by searches on Google Scholar (<https://scholar.google.com/>; 1080 vs. 352 results) and Scopus (<https://www.scopus.com/>; 385 vs. 155 results). In the taxonomy section above, we include an 'accepted species list' for *Blastobotrys* and introduce a new combination for *Trichomonascus vanleenenianus*, a species for which only the asexual state is known. New combinations for *T. apis*, *T. ciferri*, and *T. petasosporus* will be proposed after a formal decision on the generic name for the clade is made. A timely resolution on this would be ideal considering the large number of new species that remain to be described in the clade (Supporting Information: Figure 1).

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ORCID

Cobus M. Visagie  <http://orcid.org/0000-0003-2367-5353>

Teun Boekhout  <http://orcid.org/0000-0002-0476-3609>

Bart Theelen  <https://orcid.org/0000-0003-1333-2058>

Neriman Yilmaz  <https://orcid.org/0000-0002-4396-4630>

Keith A. Seifert  <https://orcid.org/0000-0001-8877-4796>

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