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

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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 important to allow for growth of specific fungi

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 alloclferrii* (≡ *Candida alloclferrii*), *B. fungorum* (≡ *Sporothrix fungorum*), *B. mucifer* (≡

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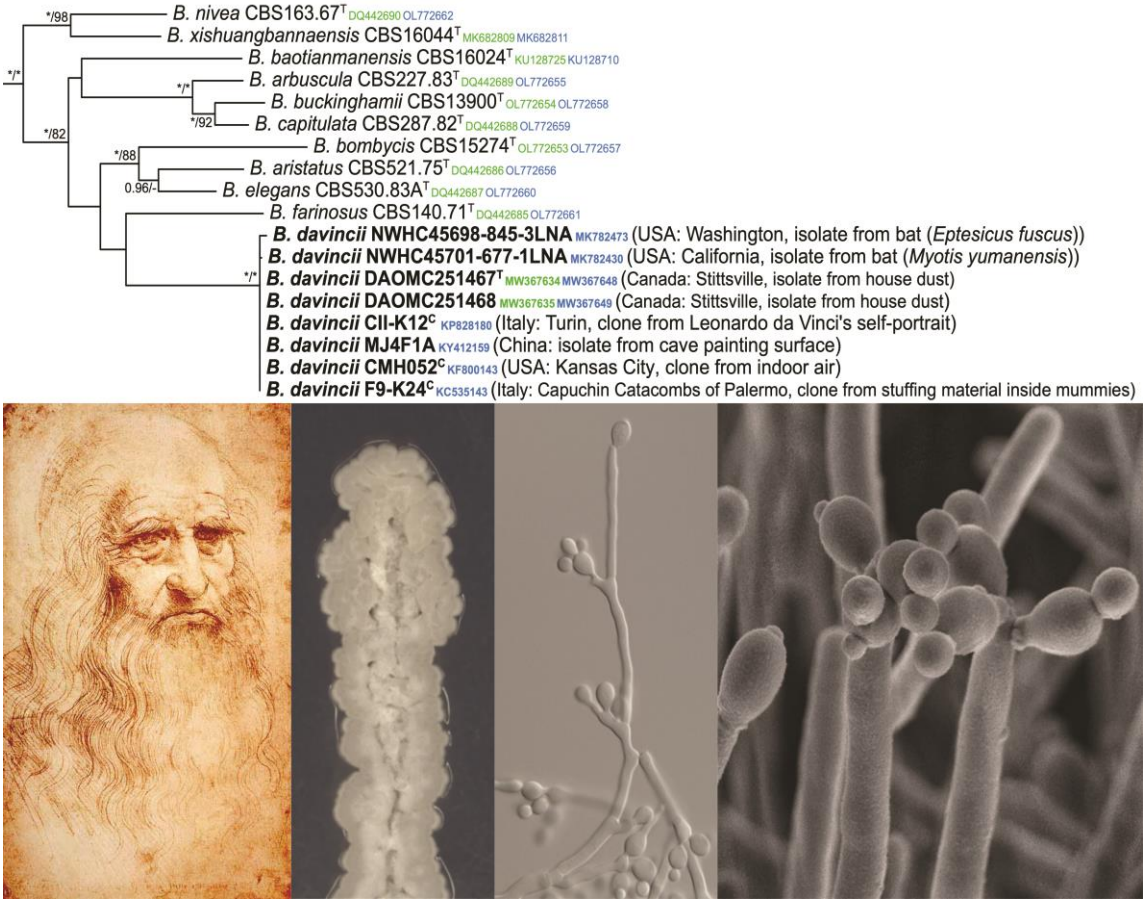
Candida mucifera) and *Blastobotrys vanleenenianus* (≡ *Trichomonascus vanleenenianus*). We provide a nomenclatural review and an accepted species list for the 37 accepted species in the *Blastobotrys/Trichomonascus* clade. Finally, we discuss the identity of the DNA clones detected on the da Vinci portrait, and the importance of using appropriate media to isolate xerophilic or halophilic fungi.

Graphical Abstract



Several surveys from around the world reported the same yeast species from a wide range of substrates, most notably from the iconic self-portrait of Leonardo da Vinci. None of these identified their strains, clones or OTUs as *Blastobotrys*. Here we describe this as a new species and name it *Blastobotrys davincii*.

Keywords: *Arxula*, nomenclature, phylogeny, *Sporothrix*, taxonomy, xerophilic fungi.

Taxonomic novelties: New species: *Blastobotrys davincii* Visagie, Boekhout, Theelen, Yilmaz & Seifert; **New combinations:** *Blastobotrys allociferrii* (Ueda-Nishimura & Mikata) Visagie & Boekhout; *Blastobotrys ciferrii* (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.

INTRODUCTION

Humans spend ±90% of their time in the built environment (Höppe & Martinac, 1998). We share 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 non-recalcitrant carbon sources (e.g., building materials, textiles, food and dust). When fungi grow, they typically release billions of airborne spores and fragments that can 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; Kauserud et al., 2007; Ljaljevic-Grbic et al., 2013; Piñar et al., 2013; Piñar et al., 2020; Piñar et al., 2015; 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 etc.), labour 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; Weikl et al., 2016). However, it is difficult to distinguish which species in HTS surveys are non-viable, 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; Kõljalg et al., 2013; Nilsson et al., 2018; Nilsson et al., 2015; Schoch et al., 2014). Also, the large number of undescribed fungi (Boekhout et al., 2021; Hawksworth & Lucking, 2017; Lucking 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*, etc. (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 (Bensch et al., 2018; Hirooka et al., 2016; Nguyen, Jancic, 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 (Fig. 1), 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*, *Spencermartinsiella*, *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.

MATERIALS AND METHODS

Sampling & Isolations

House dust samples were collected from various homes across Canada and Hawai'i, 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).

DNA extraction, sequencing and phylogenetic analysis

DNA was extracted from 7 d old colonies grown on MEA using the Ultraclean™ Microbial DNA isolation Kit (MoBio Laboratories Inc., Solana Beach, USA). The internal transcribed spacer (ITS1-5.8S-ITS2) rDNA region (ITS) and large subunit (LSU) were amplified with primer pairs V9G & LS266 (de Hoog & Gerrits van den Ende, 1998; Masclaux et al., 1995) and LR5 & LROR (Vilgalys & Hester, 1990). 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, Waltham, USA) 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, New Zealand) and newly generated sequences submitted to GenBank (https://www.ncbi.nlm.nih.gov/genbank/).

A reference sequence dataset was compiled using previously deposited sequences obtained from the NCBI nucleotide database (https://www.ncbi.nlm.nih.gov/nuccore), mainly based on a core set of DNA reference sequences recommended by Smith, de Hoog, Malloch, et al. (2011) and Smith, de Hoog, 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, Schmidt, 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, Nottingham, UK). 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.

Morphology and physiology

Strains were characterised from growth on malt extract agar (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, Kharkiv, Ukraine). Low-temperature scanning electron microscopy (SEM) was performed by cutting out 5 x 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, Duiven, the Netherlands) mixed with one-part colloidal graphite (Agar Scientific, Stanstead, UK). 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, Tokyo, Japan) equipped with 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 one week.

RESULTS

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, A. pullulans, Candida parapsilosis, Cystobasidium slooffiae, Debaryomyces hansenii, Exophiala dermatitidis, E. xenobiotica, Rhizosphaera pini, Rhodotorula* cf. *toruloides, R. diobovata, R. mucilaginosa, Sterigmatomyces halophilus, Sydowia polyspora* and *Vishniacozyma carnescens* with *Aureobasidium melanogenum* and *Hortaea werneckii* isolated from Hawaii (see Suppl. Table 1).

In Amend et al. (2010) an OTU identified as *Sterigmatomyces halophilus* was found to be one of the most common species, however, it was not recovered during isolations from the same house dust when malt extract agar (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.

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* (Fig. 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 *B. aristatus*, *B. bombycis* and *B. elegans*, with *B. farinosus* and *B. fungorum* more distantly related. Generally, the *Blastobotrys* clade had poor backbone support. Similarities between *B. davincii* (DAOMC 251468^{T}) and its closest relatives were low with LSU sequences that 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 (Fig. 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) and Piñar et al. (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 (Kõljalg 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 (Suppl. Fig. 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 *Blastobotrys davincii*.

TAXONOMY

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

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.

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.

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.

Barcode sequences: ITS = MW367648, MW367649. LSU = MW367634, MW367635.

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

Description: Growth in 5 % glucose in yeast nitrogen broth: After two 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 x 6–12 µm. Growth on yeast morphology agar: After two 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 x 5–11 µm. Dalmau plate on yeast morphology agar: Extensive hyphae and yeast cells present. Growth on GYPA and MEA: After two 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) x 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 x 1.5–3 µm, form on short denticles, 1.5–3.5 x 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.

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

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 adeninivorans: see under ***Blastobotrys adeninivorans***.

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

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

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

Blastobotrys allociferrii (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 allociferrii* 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, Fell & Boekhout 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 mokoenaii (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 mokoenaii* 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. Sequence identification markers: ITS OK623478; LSU OK623486.

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

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 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-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 strain: 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. Sequence identification markers: 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 allociferrii: see under ***Blastobotrys allociferii***.

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

Candida mokoenaii: see under ***Blastobotrys mokoenaii***.

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

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

Sporothrix catenata: see under ***Blastobotrys ciferrii***

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

Stephanoascus ciferrii: see under ***Trichomonascus ciferrii***.

Stephanoascus farinosus: see under ***Trichomonascus 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] ≡ *Anthracocystis flocculosa* (Traquair, L.A. Shaw & Jarvis) M. Lutz & Piątek, Mycological Progress 14 (10/88): 9 (2015) [MB 813438].

*Note: The recombination as *Anthracocystis 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. & Dlauchy, 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 ciferrii (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 ciferrii* 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. Sequence identification markers: 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 adeninivorans: see under ***Blastobotrys adeninivorans***.

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

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 re-identify 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 2.2–3.8 (Hawksworth & Lucking, 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 (Lucking et al., 2021). At the current annual rate of about 2000 new species descriptions (Lucking 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 Lucking 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 (Kõljalg et al., 2005; Kõljalg 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 26 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 (Suppl. Fig. 1)

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FIGURE LEGENDS

Fig. 1. Self-portrait of Leonardi 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.

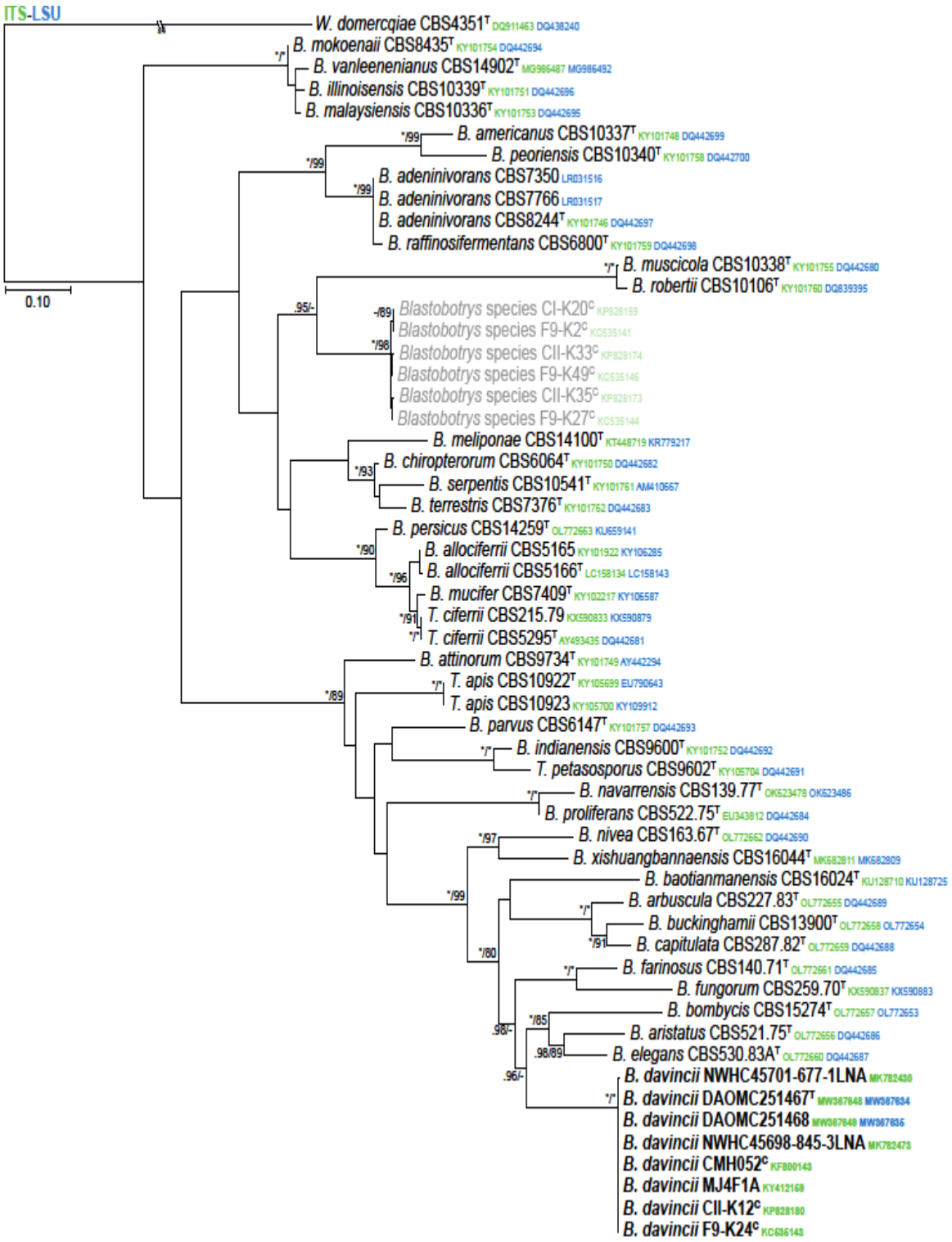

Fig. 2. Combined phylogenetic tree of described *Blastobotrys* and *Trichomonascus* species based on ITS and LSU. The tree is rooted to *Wickerhamiella domercqiae* CBS3451^{T}. Posterior probabilities (≥ 0.95) and Bootstrap support values (≥ 80 %) are given above branches. The new species is indicated in **bold** text, uncultured 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).

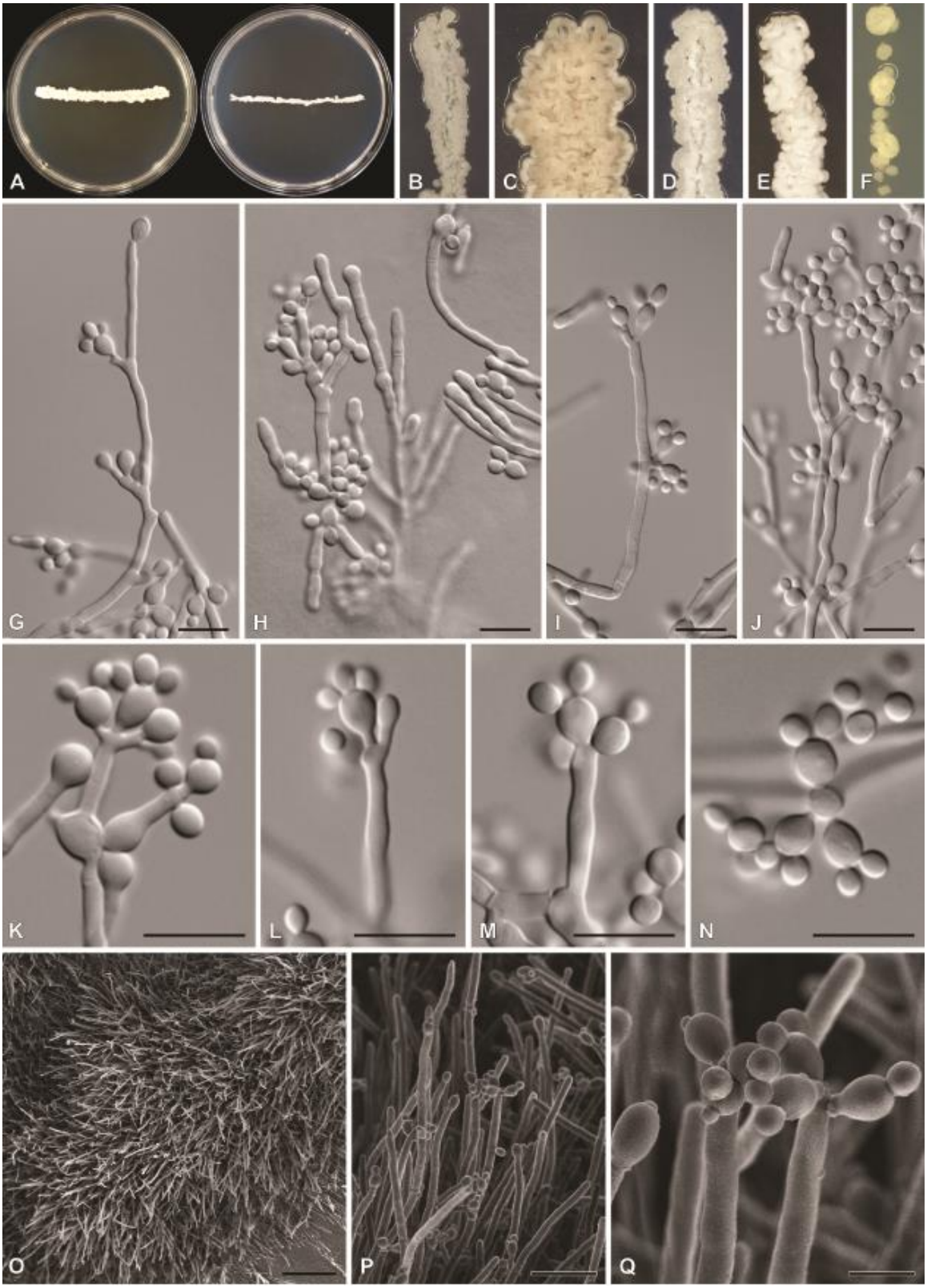

Fig. 3. *Blastobotrys davincii* (DAOMC 251467^{T}). A. Colonies on, from left to right, MEA and YPGA. B–F. Colony close-ups on: (B) MEA, (C) YPGA, (D) PDA, (E) DG18 & (F) YMA. G–N. Fertile conidiophores and conidia observed under a light microscope. O–Q. Hyphae and fertile conidiophores observed using cryo-SEM. Scale bars: G–N = 10 µm, O = 100 µm, P = 20 µm & Q = 5 µm.

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Table 1: Strains used for phylogenetic analyses

Taxon name	Strain	Location	Source	GenBank: ITS	GenBank: LSU
Blastobotrys adeninivorans	CBS 7350	Netherlands	Maize	n.a.	LR031516
Blastobotrys adeninivorans	CBS 7766	Sweden	Liver and intestines of a Gila monster (*Heloderma suspectum*)	n.a.	LR031517
Blastobotrys adeninivorans	CBS 8244 = NRRL Y-17692 IFO 10858 = IGC 4638 = PYCC 4638 (ex-type)	The Netherlands: Wageningen	Soil	KY101746	DQ442697
Blastobotrys allociferrii	CBS 5165 =	Netherlands	Fence post	KY101922	KY106285

	IFO 10193				
Blastobotrys allociferrii	CBS 5166 = NBRC 10194 = IFO 10194 (ex-type)	Germany	Human	LC158134	LC158143
Blastobotrys americanus	CBS 10337 = NRRL Y-6844 = LRB 70B3 (ex-type)	USA: Kansas	Unknown	KY101748	DQ442699
Blastobotrys arbuscula	CBS 227.83 = NRRL Y-17585 (ex-type)	Finland	Indoor air	OL772655	DQ442689
Blastobotrys aristatus	CBS 521.75 = NRRL Y-17579 = ATCC 34215 = CCM F-410 = HFM 2672 = UAMH 4665 (ex-type)	Czech Republic	Moldy plaster	OL772656	DQ442686
Blastobotrys attinorum	CBS 9734 = NRRL Y-27639 = UNESP-S156 (ex-type)	Brazil: Sao Paulo	Fungal garden of nests of the leaf-cutting ant (*Atta sexdens*)	KY101749	AY442294
Blastobotrys baotianmanensis	CBS 16024 = CICC 33083 (ex-type)	China: Henan Province, Baotianman Nature Reserve	Gut of ground beetle (*Pterostichus gebleri*)	KU128710	KU128725
Blastobotrys bombycis	CBS 15274 (ex-type)	India: Dharwad	Silkworm (*Bombyx mori*)	OL772657	OL772653
Blastobotrys buckinghamii	CBS 13900 = NRRL Y-63727 = yHAB 196 (ex-type)	USA: Michigan, Tahquamenon Falls State Park	Mushroom associated with American beech (*Fagus grandfolia*)	OL772658	OL772654
Blastobotrys capitulata	CBS 287.82 = NRRL Y-17573 (ex-type)	South Africa	Flower, decaying tissue of candelabra tree (*Euphorbia ingens*)	OL772659	DQ442688
Blastobotrys chiropterorum	CBS 6064 = NRRL Y-17071 (ex-	Columbia	Liver of bat (*Mormoops*	KY101750	DQ442682

	type)		*megalophylla*)		
Blastobotrys ciferrii	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
Blastobotrys davincii	CBS 16861 = DAOMC 251467 = CMW 56638 = CN 002G3 = KAS 5710 (ex-type)	Canada: Ontario, Stittsville	House dust	MW367648	MW367634
Blastobotrys davincii	CBS 16862 = DAOMC 251468 = CMW 56639 = CN 002G4 = KAS 5711	Canada: Ontario, Stittsville	House dust	MW367649	MW367635
Blastobotrys davincii	clone CII-K12	Italy: Turin	Leonardo da Vinci's self-portrait	KP828180	n.a.
Blastobotrys davincii	clone CMH052	USA: Missouri, Kansas City	Indoor air	KF800143	n.a.
Blastobotrys davincii	clone F9-K24	Italy: Capuchin Catacombs of Palermo	Stuffing material from mummies	KC535143	n.a.
Blastobotrys davincii	MJ4F-1A	China	Cave painting surface	KY412159	n.a.
Blastobotrys davincii	NWHC 45698-845_3LNA	USA: Washington	Bat (*Eptesicus fuscus*)	MK782473	n.a.
Blastobotrys davincii	NWHC 45701-677_1LNA	USA: California	Bat (*Myotis yumanensis*)	MK782430	n.a.
Blastobotrys elegans	CBS 530.83A = NRRL Y-17572 (ex-type)	Finland	Indoor air	OL772660	DQ442687

Blastobotrys farinosus	CBS 140.71 = NRRL Y-17593 = IGC 4592 = JCM 2935 (ex-type)	The Netherlands	*Hirneola auricula-judae*	OL772661	DQ442685
Blastobotrys fungorum	CBS 259.70 = CMW 17165 = UAMH 3678 (ex-type)	Germany	Old *Fomes fomentarius* basidiome	KX590837	KX590883
Blastobotrys illinoisensis	CBS 10339 = NRRL YB-1343 (ex-type)	USA: Illinois, Marion, Wohlwend farm	Tree	KY101751	DQ442696
Blastobotrys indianensis	CBS 9600 = NRRL YB-1950 (ex-type)	USA: Indiana, Spencer, McCormick' s Creek State Park	White fungus associated with pine	KY101752	DQ442692
Blastobotrys malaysiensis	CBS 10336 = NRRL Y-6417 = EMMONS S3,539A (ex-type)	Malaysia	Cave soil	KY101753	DQ442695
Blastobotrys meliponae	CBS 14100 = URM7224 (ex-type)	Brazil: Pernambuco, Recife	Honey	KT448719	KR779217
Blastobotrys mokoenaii	CBS 8435 = NRRL Y-27120 (ex-type)	South Africa	Soil	KY101754	DQ442694
Blastobotrys mucifer	CBS 7409 = CCY 29-170-1 = IFO 10918 (ex-type)	Brazil: Manaus	Liver of toad (*Rhinella granulosa*)	KY102217	KY106587
Blastobotrys muscicola	CBS 10338 = NRRL Y-7993 (ex-type)	USA: Louisiana, near New Orleans	Moss on fallen log	KY101755	DQ442680
Blastobotrys navarrensis	CBS 139.77 = ATCC 36955 = IJFM 2642 = UAMH 4664 (ex-type)	Spain: Pampelona	Black pepper (*Piper nigrum*)	OK623478	OK623486

Blastobotrys nivea	CBS 163.67 = NRRL Y-17581 = ATCC 18420 = HFM 26 = UAMH 4663 = MUCL 6078 (ex-type)	Germany	Municipal compost	OL772662	DQ442690
Blastobotrys parvus	CBS 6147 = NRRL Y-10004 (ex-type)	Antarctic Ocean	Seawater	KY101757	DQ442693
Blastobotrys peoriensis	CBS 10340 = NRRL YB-2290 (ex-type)	USA: Illinois, Peoria	Unknown	KY101758	DQ442700
Blastobotrys persicus	CBS 14259 = IBRC-M30238 (ex-type)	Iran: Ilam	Soil	OL772663	KU659141
Blastobotrys proliferans	CBS 522.75 = NRRL Y-17577 = ATCC 34216 = CCM F-493 = HFM 2673 = UAMH 4666 (ex-type)	Brazil	Mite-infested nut (*Bertholletia excelsa*)	EU343812	DQ442684
Blastobotrys raffinosifermentans	CBS 6800 = NRRL Y-27150 (ex-type)	Unknown	Unknown	KY101759	DQ442698
Blastobotrys robertii	CBS 10106 = NRRL Y-27775 (ex-type)	The Netherlands: Wageningen forest	Rotten pine wood (*Pinus sylvestris*)	KY101760	DQ839395
Blastobotrys serpentis	CBS 10541 = NRRL Y-48249 = MTCC 8332 = W113A = YS W113A (ex-type)	India: Hyderabad City	Trinket snake gut	KY101761	AM410667
Blastobotrys sp.	clone CI-K20	Italy: Turin	Leonardo da Vinci's self-portrait	KP828159	n.a.
Blastobotrys sp.	clone CII-K33	Italy: Turin	Leonardo da Vinci's self-portrait	KP828174	n.a.

Blastobotrys sp.	clone CII-K35	Italy: Turin	Leonardo da Vinci's self-portrait	KP828173	n.a.
Blastobotrys sp.	clone F9-K2	Italy: Capuchin Catacombs of Palermo	Stuffing material from mummies	KC535141	n.a.
Blastobotrys sp.	clone F9-K27	Italy: Capuchin Catacombs of Palermo	Stuffing material from mummies	KC535144	n.a.
Blastobotrys sp.	clone F9-K49	Italy: Capuchin Catacombs of Palermo	Stuffing material from mummies	KC535146	n.a.
Blastobotrys sp.	NCAIMY.01950	Unknown	Unknown	n.a.	GU195655
Blastobotrys sp.	UFMG-CM-Y6482	Brazil: Caxiuanã National Forest	Gut from fruit fly (*Hirtodrosophila* sp.)	n.a.	MK130971
Blastobotrys sp.	BG98-12-9-2-1	Unknown	Gut of ciid beetle	n.a.	AY242297
Blastobotrys sp.	BG00-7-5-1-2-1	Unknown	Gut of tenebrionid beetle	n.a.	AY242247
Blastobotrys sp.	BG01-7-21-005C-1-4	Unknown	Gut of scarabaeid beetle	n.a.	AY242291
Blastobotrys sp.	BG01-7-21-001A-1-1	Unknown	Gut of anthribid beetle	n.a.	AY242321
Blastobotrys sp.	BG01-7-24-002F-2-1	Unknown	Gut of endomychid beetle	n.a.	AY242286
Blastobotrys sp.	BG01-7-22-001B-1-1	Unknown	Gut of erotylid beetle	n.a.	AY242276
Blastobotrys sp.	BG01-7-22-018A-1-1	Unknown	Gut of endomychid beetle	n.a.	AY242285
Blastobotrys sp.	BG01-7-24-002C-Egg-1-1	Unknown	Gut of erotylid beetle	n.a.	AY242272

Blastobotrys sp.	BG99-11-14-1-4-1	Unknown	Gut of mycetophagid beetle	n.a.	AY242316
Blastobotrys sp.	BG01-7-26-005A-2-1	Unknown	Gut of nitidulid beetle	n.a.	AY242313
Blastobotrys sp.	BG01-7-21-010A-4-1	Unknown	Gut of tenebrionid beetle	n.a.	AY242251
Blastobotrys sp.	BG00-6-26-2-2-1	Unknown	Gut of tenebrionid beetle	n.a.	AY242248
Blastobotrys sp.	BG01-7-23-021A-4-1	Unknown	Gut of tenebrionid beetle	n.a.	AY242250
Blastobotrys sp.	KBP-Y6879	Russia	Tunnels under the bark of oak tree		ON887274
Blastobotrys terrestris	CBS 7376 = NRRL Y-17704 = CSIR Y914 = IFO 10859 = IGC 5133 = PYCC 5133 (ex-type)	South Africa: Barberton	Soil	KY101762	DQ442683
Blastobotrys vanleenenianus	CBS 14902 (ex-type)	The Netherlands	Soil	MG986487	MG986492
Blastobotrys xishuangbannaensis	CBS 16044 = CICC 33360 (ex-type)	China: Yunnan Province, Jinghong	Rotting wood	MK682811	MK682809
Trichomonascus apis	CBS 10922 = NRRL Y-48475 = NCAIM Y.01848 (ex-type)	Hungary	Mouldy honeycomb	KY105699	EU790643
Trichomonascus apis	CBS 10923 = NRRL Y-48476 = NCAIM Y.01849	Hungary	Mouldy honeycomb	KY105700	KY109912
Trichomonascus ciferrii	CBS 215.79 = CMW 17161 (ex-type of *Sporothrix*	Romania	Calf skin	KX590833	KX590879

	catenata)				
Trichomonascus petasosporus	CBS 9602 = NRRL Y-B2092 (ex-type)	USA: Missouri, Salem	White Oak (*Quercus sp*)	KY105704	DQ442691
Wickerhamiella domercqiae	CBS 4351 = NRRL Y-6692 (ex-type)	South Africa	Wine vat	DQ911463	DQ438240

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	-	-
methanol	-	+
ethanol	-	-
propane 1,2 diol	dw	+
butane 2,3 diol	-	v
quinic acid	-	-
saccharate	dw	dw
galactonic acid	dw	dw

Table 3: Physiological characters of *Blastobotrys* and *Trichomonascus* species (colors indicate clades from the phylogeny in Fig. 1; + = growth; - = no growth; w = weak; v = variable; n = not done)

	B. davisii	*B. elegans*	*B. aristatus*	*B. bombycis*	*B. farinosus*	*B. fungorum*	*B. arbusculi*	*B. buckinghamii*	*B. capitulata*	*B. baotianmenensis*	*B. nivea*	*B. xishuangbannaensis*	*B. navarrensis*	*B. proliferans*	*B. indianensis*	*T. petasosporus*	*B. parvus*	*T. apis*	*B. attinorum*	*B. chiropterorum*	*B. meliponae*	*B. serpentis*	*B. terrestris*	*T. cifernii*	*B. allociferni*	*B. mucifer*	*B. persicus*	*B. americanus*	*B. peoriensis*	*B. adeninivorans*	*B. raffinosifermentans*	*B. muscicola*	*B. roberti*	*B. illinoisensis*	*B. malaysiensis*	*B. mokoenaii*	*B. vanleenenianus*
	TYTS5th	TYTS5th	TYTS5th	10.1099/ijsem.0.002890	TYTS5th	10.1007/BF00444231	TYTS5th	10.1093/femsyr/foy002	TYTS5th	10.1099/ijsem.0.004275	TYTS5th	10.1099/ijsem.0.004275	doi.org/10.1007/BF00473158	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	10.3767/003158516x692185	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	10.1007/s10482-017-0972-x	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	TYTS5th	10.1093/femsyr/foy076
F glucose	+	-	+	+	+	n	+	+	+	-	+	+	+	+	+	+	-	+	+	-	+	-	-	-	-	-	-	+	+	+	+	-	-	+	+	+	+
F galactose	w	-	v	+	v	n	+	+	+	-	+	+	+	+	+	+	-	+	-	-	+	-	-	-	-	-	-	-	+	+	+	-	-	+	+	+	n
F sucrose	w	-	-	-	-	n	-	-	-	-	-	+	+	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-	+	+	-	n
F maltose	w	-	+	-	v	n	+	w	v	-	+	-	-	+	+	+	-	-	v	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	+	-	n
F lactose	w	-	-	-	v	n	-	-	-	-	-	+	-	-	-	-	-	-	-	-	n	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	n
F raffinose	w	-	-	-	-	n	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	n

F trehalose	w	-	+	+	v	n	+		v	-	+	+	+	v	+	+	-	-	-	-	n	-	-	-	-	-	-	+	+	+	+	-	-	+	+	+	n
G glucose	+	+	+	+	+	n	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
G galactose	+	+	+	+	+	n	+	n	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
G L-sorbose	+	v	+	+	v	n	+	w	+	-	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	n	+	+	+	+	-	-	+	+	+	+
G D-glucosamine	- / w	+	+	-	v	n	+	n	+	+	+	+	n	+	+	+	+	+	n	+	-	+	-	-	-	w	n	+	+	+	+	+	-	+	+	+	+
G D-ribose	+	+	+	+	v	n	+	w	+	-	+	+	-	v	-	-	v	+	+	+	n	+	+	v	v	+	-	+	+	+	+	-	-	-	-	-	+
G D-xylose	+	+	+	+	v	n	+	w	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	+	+	+	+
G L-arabinose	+	v	+	+	v	n	+	n	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	+	+	+	+
G D-arabinose	+	-	+	-	v	n	-	w	v	-	+	+	-	+	+	+	v	+	+	+	n	+	+	+	+	+	-	+	+	+	+	-	-	+	-	-	n
G L-rhamnose	v	-	v	-	-	n	-	n	+	-	-	+	+	v	-	-	+	+	+	+	+	+	+	+	+	+	-	-	+	-	-	-	+	+	+	+	+
G sucrose	+	-	+	-	-	n	-	n	v	+	v	+	+	+	-	-	+	+	-	+	n	+	+	+	+	-	+	-	+	+	+	+	+	+	+	+	+
G maltose	+	+	+	+	v	n	+	+	v	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+
G trehalose	+	+	+	+	+	n	+	n	+	+	+	+	+	+	+	+	+	+	-	+	n	+	+	+	+	+	+	-	+	-	v	+	-	+	+	+	+
G methyl-a-D-glucoside	+	-	v	n	v	n	v	n	-	-	v	+	+	v	+	+	-	+	+	+	n	n	+	v	v	-	n	+	+	+	+	v	v	+	+	+	+
G cellobiose	+	+	+	+	+	n	+	+	+	+	+	+	+	+	+	+	+	+	+	+	n	+	+	v	v	-	+	+	+	+	+	+	+	+	+	+	+
G salicin	+	v	+	-	v	n	-	n	+	+	+	+	+	+	-	+	-	+	+	+	n	+	+	v	v	-	w	+	+	+	+	v	+	+	+	-	n
G arbutin	+	n	n	n	v	n	n	n	n	+	n	+	n	n	n	n	n	v	n	+	n	n	n	v	v	n	+	n	n	n	n	n	n	n	n	-	n
G melibiose	+	-	v	+	v	n	-	n	-	-	+	+	+	+	+	+	-	+	-	-	-	+	-	v	v	-	w	+	+	+	+	v	+	-	-	-	-
G lactose	+	+	+	-	v	n	-	n	v	+	+	+	-	+	-	-	-	v	-	-	+	-	-	-	-	-	-	-	+	+	-	+	+	-	+	-	-
G raffinose	+	-	v	-	v	n	-	n	v	-	-	+	+	+	+	+	-	v	-	+	-	+	+	+	+	-	+	+	+	+	+	v	+	-	-	-	-
G melezitose	+	-	-	-	-	n	-	n	-	-	-	+	+	v	-	-	-	v	-	+	n	-	-	-	-	-	w	-	+	+	+	+	-	-	+	-	-
G inulin	+	v	v	-	-	n	v	n	v	+	v	+	-	v	-	-	-	-	-	-	n	-	-	-	w	-	n	-	-	-	+	-	-	-	-	+	n
G soluble starch	+	v	+	-	v	n	+	n	+	-	+	+	-	v	+	+	-	+	+	+	n	-	+	v	v	-	-	-	+	+	+	+	+	+	+	+	n
G glycerol	+	+	+	+	+	n	+	+	+	-	+	+	w	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	-
G erythritol	+	+	+	+	v	n	+	n	+	+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+	+	n	+	+	+	+	+	-	+	+	+	+
G ribitol	+	+	+	v	+	n	+	n	+	+	+	+	+	+	+	+	+	+	+	+	n	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	n
G xylitol	+	n	n	n	n	n	n	n	n	-	n	+	+	n	n	n	n	n	n	-	n	+	+	n	+	+	n	n	n	n	n	n	n	n	+	n	
G L-arabinitol	+	n	n	n	n	n	n	n	n	-	n	+	n	n	n	n	n	n	n	-	n	n	n	n	n	n	n	n	n	n	n	n	n	n	+	n	
G D-glucitol	+	+	+	-	+	n	+	n	+	-	+	+	+	+	+	+	+	+	+	n	+	+	+	+	+	-	n	+	+	+	+	+	-	+	+	+	+
G D-mannitol	+	+	+	+	+	n	+	n	+	-	+	+	+	+	+	+	+	+	+	n	n	+	+	+	-	-	+	+	+	+	+	+	+	+	+	+	+
G galactitol	+	v	+	+	v	n	+	n	+	-	+	+	+	+	-	-	-	+	+	n	+	+	+	+	+	n	+	+	-	+	+	-	+	-	+	n	
G myo-inositol	+	-	v	+	-	n	-	-	+	-	+	+	n	+	+	+	+	+	+	n	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	
G 2-keto-D-gluconate	n	n	n	n	n	n	n	n	n	-	n	+	n	n	+	n	n	v	-	+	n	-	-	+	+	+	n	-	+	+	+	-	n	+	+	+	+
G 5-keto-D-gluconate	n	n	n	n	n	n	n	n	n	+	n	-	n	n	+	n	n	n	n	+	n	n	n	+	+	n	n	+	+	n	+	-	n	+	+	n	n
G D-gluconate	v	+	n	+	-	n	n	n	n	-	n	+	v	n	-	v	-	+	+	+	n	+	+	+	+	+	n	+	+	+	+	n	v	+	-	+	+
G DL-lactate	v	-	-	-	-	n	v	n	-	-	-	+	v	v	-	-	-	+	+	+	n	+	+	+	+	-	w	+	-	-	+	-	-	-	+	-	+
G succinate	-	+	+	+	v	n	+	n	+	-	+	+	n	+	+	+	-	+	-	-	n	+	+	v	v	w	-	+	+	+	+	+	+	+	+	+	n

G citrate	-	+	v	+	v	n	-	w	v	-	+	+	v	+	+	+	-	+	-	+	-	+	+	v	-	-	-	-	-	+	+	+	+	+	+	+	n
G methanol	v	n	n	n	n	n	n	n	n	-	n	-	n	n	-	-	-	-	-	-	n	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	n
G ethanol	-	+	-	-	v	n	-	+	+	-	+	-	-	+	+	v	-	+	-	-	n	-	+	v	v	w	w	+	+	+	+	+	-	+	+	+	n
G propane 1,2 diol	-/w	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	-	n	n	n	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	n	n	n	n	n	n	-	n	n	n	n	n	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	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	n	+	+	+	+	+	+	n	n	n	n	n	+	n	+	+	n	+	n	+	+	+	n	+
G hexadecane	n	n	n	-	n	n	n	n	n	n	n	n	n	n	+	+	-	v	-	-	n	n	n	n	n	+	w	+	+	n	+	-	+	+	-	n	n
G nitrate	+	-	-	-	-	n	-	-	-	-	-	+	n	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	+	+	-	-	-	-	-	-
G nitrite	+	n	n	n	n	n	n	-	n	-	n	+	n	n	n	n	n	n	n	n	n	n	n	n	v	-	-	n	n	n	n	n	n	n	n	-	
G ethylamine	+	n	n	n	n	n	n	n	n	-	n	-	n	n	n	n	n	n	n	+	n	n	n	n	+	+	+	n	n	n	n	n	n	n	+	+	
G L-lysine	+	n	n	n	n	n	n	+	n	+	n	+	n	n	n	n	n	n	n	+	n	n	n	n	+	+	+	n	n	n	n	n	n	n	+	+	
G cadaverine	+	n	n	n	n	n	n	n	n	+	n	-	n	n	n	n	n	n	n	+	n	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	n	n	n	n	n	n	n	n	n	n	w	n	n	n	n	n	n	n	n	n	
G vitamin free	n	-	-	-	-	n	-	n	-	+	-	+	n	-	-	-	-	-	-	-	n	-	-	-	-	-	n	-	-	-	-	v	-	+	+	+	n
G 50% glucose	-	n	n	n	n	n	n	-	n	n	n	n	+	n	n	n	-	n	+	+	n	n	+	n	+	w	+	n	n	+	n	n	n	n	n	-	n
G 10% NaCl / 5% glucose	n	n	n	+	n	n	n	n	n	-	n	+	n	n	+	+	-	+	n	+	n	n	n	+	n	+	n	+	+	n	+	-	n	+	+	+	n
Starch formation	-	n	n	n	n	n	n	n	n	-	n	-	n	n	-	n	-	-	-	n	n	-	-	-	-	-	-	-	-	-	-	n	-	-	n	n	
Urease	-	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	-	n	n	n	+	n	n	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	n	-	n	-	n	n	n	n	n	n	-	n	-	n	-	-	n	-	+	n	+	+	n	n
G cycloheximide 0.01%	-	n	n	+	n	n	n	n	+	+	n	+	+	n	+	+	n	+	+	+	n	+	+	n	+	+	-	+	+	+	+	+	n	+	+	+	+
G cycloheximide 0.1%	-	n	n	+	n	n	n	n	+	n	n	n	+	n	n	+	n	+	+	+	n	+	+	n	+	+	-	n	n	+	n	n	n	n	n	+	n
G 19°C	n	+	+	n	+	n	+	n	+	n	+	n	n	+	+	+	+	+	+	+	n	+	+	+	+	n	+	+	+	+	+	+	+	+	+	+	n
G 25°C	+	+	+	n	+	n	+	n	+	n	+	n	n	+	+	+	+	+	+	+	n	+	+	+	+	n	+	+	+	+	+	+	+	+	+	+	n
G 30°C	+	+	+	+	+	n	+	+	+	n	+	n	n	+	+	+	-	v	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	n
G 35°C	-	n	n	n	+	n	n	+	+	+	+	n	n	+	n	+	-	-	+	+	+	-	+	+	+	n	+	n	n	+	+	+	-	+	+	+	n
G 37°C	-	-	-	-	n	n	-	+	+	-	+	+	n	+	-	+	-	-	+	+	+	-	+	+	+	-	+	-	-	+	+	+	-	+	+	+	n
G 40°C	-	-	-	n	-	n	-	n	n	n	n	-	v	n	-	n	-	-	n	n	n	-	+	n	n	n	+	-	-	+	n	n	-	n	n	+	+
G 45°C	-	-	-	n	-	n	-	n	n	n	n	n	n	n	-	n	-	-	n	n	n	-	n	n	n	n	-	-	-	n	n	n	-	n	n	+	-
CoQ	n	n	n	n	94	n	n	n	n	n	n	n	n	n	n	n	94	n	n	9	n	9	9	94	n	n	n	n	n	9	n	n	n	n	n	n	n
Mol% G+C	n	n	n	n	49.2	n	n	n	n	n	n	n	n	n	n	n	46.3	b	n	48	n	5-,2	n	46.6	n	n	n	n	n	n	n	n	n	n	n	47.8	n
DBB	-	-	-	n	-	n	-	n	-	n	-	n	n	-	-	-	-	-	-	-	n	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	n