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MICROBIOLOGY

Antarctic-derived yeasts: taxonomic identification and resistance to adverse conditions

GABRIELE S. FARIAS, JULIANA A. SANTOS, PATRICIA GIOVANELLA & LARA D. SETTE

Abstract: Antarctic harsh conditions favor the development of microbial adaptations. In this study, a molecular approach was applied to identify/refine the taxonomy of five yeasts isolated from different Antarctic samples, which were tested against ranges of temperature, UV radiations, salinity, and pH. Based on sequencing and phylogenetic analysis, strain CRM 1839 was confirmed as *Naganishia* sp., and strains CRM 1874, CRM 1565, CRM 2571, and CRM 2576 were identified as *Goffeauzyma gilvescens*, *Goffeauzyma gastrica, Candida atlantica,* and *Camptobasidium* sp., respectively, being this last one possibly a new species. Growth at different temperatures indicates that these yeasts are psychrotolerant, with the exception of *Camptobasidium* sp., which presents psychrophilic characteristics. *G. gastrica* recovered from marine sediment showed the best results of resistance to UV radiation, being able to grow even after the exposure to UVB dose of 9144 J/m² and UVC dose of 6102 J/m². *C. atlantica* isolated from glacier soil showed high cellular growth from 3 to 10% NaCl. The majority of the strains produced higher biomass at pH 7; nevertheless, *G. gilvescens* showed higher biomass production at pH 9. The studied Antarctic-derived yeasts have adaptations to extreme conditions, which makes them useful for biotechnological applications and studies of extremophiles.

Key words: Antarctica, environmental stress, extremophiles, UV radiation.

INTRODUCTION

The Antarctic is a small and characteristically diverse continent divided into three regions: Continental, Maritime, and Periantarctic Islands. The Continental region is mostly ice-covered, with temperatures below 0 °C even in the warmest months; Maritime Antarctica is the region with the mildest characteristics, registering positive temperatures, but not higher than 15 °C, and with more precipitation compared with the rest of the continent; at last, the Periantarctic Islands are represented by the islands spread in the ocean around the continent, where the mean temperatures in the warmest periods can reach 6 °C (Bölter et al. 2002). Antarctica is isolated from all other landmasses by ocean currents and great distances and it is characterized by extremes in climate, habitats, and biogeography. The key features of the Antarctic ecosystems render the title of the most challenging place on Earth for the development of life. Dry air, shortage of nutrients, freeze and thaw cycles, high incidence of wind and ultraviolet radiation (0.1% - 1.5%), high salinity (35% - 150%), and very low temperatures (Turner et al. 2009, Orellana et al. 2018) are some of the harsh conditions found in Antarctica.

Despite the difficulties for thriving, according to Wauchope et al. (2019), over 2000 species can be found in the Antarctic continent, including vertebrates, invertebrates, plants and microorganisms, being the last ones, the major

components of life inhabiting the Antarctic soils (Vishniac & Hempfling 1979, Lysak et al. 2018, Rosa et al. 2020). These microorganisms can be classified, depending on the temperature at which they can grow, as psychrophilic, which have an optimum growth temperature ≤ 15 °C and the maximum at 20 °C; psychrotolerant, which have higher values for the maximum growth temperatures, and optimum between 15 and 25 ºC, but can also grow at a slower rate at low temperatures; and mesophilic-psychrotolerant, those that can grow at low temperatures, but with optimum growth temperature between 25 and 40 ºC (Pesciaroli et al. 2012). They can also be classified as acidophilic and alkaliphilic, which are those that can grow at pH ≤ 5 and pH ≥ 9, respectively, and based on their capacity to develop under highly saline conditions (60 to 300 g L^{-1} NaCl and higher) (halophilic), as well as on their resistance to prolonged exposure to UV radiation (radiotolerant) (Oren 2002, Hoover & Pikuta 2010, Orellana et al. 2018).

Antarctic-derived yeasts have been the focus of attention for polar scientists due to their great diversity and tolerance to Antarctica's extreme conditions (Onofri et al. 2004, Shivaji & Prasad 2009, Duarte et al. 2013, 2016, Wentzel et al. 2019). They have developed different mechanisms to endure the Antarctic harsh conditions, including protection against UV radiation, antifreeze molecules, new constituents of the plasma membrane, temperature-resistant enzymes, pigments, and photoreactivation (Robinson 2001, Onofri et al. 2004, Bölter 2011, Pulschen et al. 2015, Duarte et al. 2018). Considering that all those adaptations can lead to biotechnological advances and new biomolecules, the study of Antarctic fungi and their tolerance to extreme conditions has to be stimulated. In this sense, the aim of this study was to investigate the resistance of yeasts isolated from different Antarctic environments to UV radiation, salinity, different temperatures, and pH.

MATERIALS AND METHODS

Antarctic yeasts

The studied yeasts were isolated from different Antarctic samples collected at three sites in King George Island, Antarctic Peninsula, in January/February 2015 (XXXIII Brazilian Antarctic Operation, OPERANTAR) (Figure 1) and selected based on their different taxonomic classification and origin (Table I). Sampling at Yellow point (soil) and Punta Ulman (marine sediment) and yeast isolation were conducted as described by Wentzel at al. (2019). Glacier soil sampling and yeast isolation were performed as described by Santos et al. (2020). These yeast strains are deposited at the Central of Microbial Resources (CRM-UNESP) of the São Paulo State University (UNESP, Brazil), where they are being maintained by cryopreservation at -80 °C.

Taxonomic identification

Antarctic-derived yeast strains CRM 1839, CRM 1874, and CRM 1565 were identified at the genus level and reported by Wentzel et al. (2019). In the present study, the identification of these strains was refined. The yeast strains isolated from the Collins glacier soil (CRM 2571 and CRM 2576) were identified in the present study, using the molecular taxonomy as described below.

DNA extraction followed the method adapted from Sampaio et al. (2001) and De Almeida (2005). The LSU (D1/D2, 28S-rDNA) region was amplified and sequenced with the primers NL1 (5'-GCATATCAATAAGCGGAGGAAAAG-3') and NL4 (5'-GGTCCGTGTTTCAAGACGG-3') (Kurtzman & Robnett 1998). PCR for LSU was performed according to Duarte et al. (2013). Amplicons were purified using the enzymes Exonuclease I and Alkaline phosphatase (Thermo Scientific,

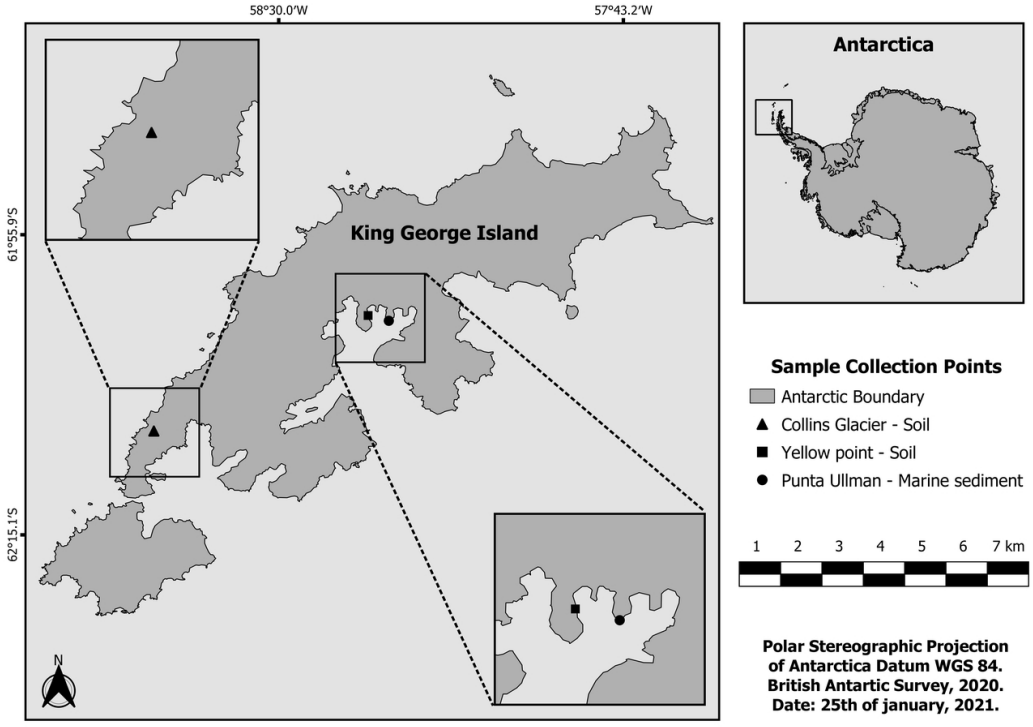

Figure 1. Sampling sites in King George Island (Admiralty Bay and Fildes Peninsula), Maritime Antarctica.

Massachusetts, USA) according to the manufacturer's protocol. The samples were quantified using NanoDrop® (Thermo Scientific) and sequenced using the BigDye Terminator® v.3.1 kit (Applied Biosystems, California, USA) according to the manufacturer's instructions in an ABI 3500 sequencer (Applied Biosystems). The sequencing conditions were 96 °C/3min followed by 35 cycles of 96 °C/30 s, 61 °C/45 s, 72 °C/1 min, 10 °C/∞. The generated sequences were assembled into contigs using BioEdit v.7.2.5 (Hall 1999) and compared to homologous sequences deposited in the NCBI-GenBank and CBS Fungal Biodiversity Centre databases using BLAST. The sequences were aligned using ClustalX (Thompson et al. 1997) and analyzed using MEGA v.7.1 (Kumar et al. 2016). Evolutionary distances were calculated using the maximum likelihood algorithm and Kimura-2p nucleotide substitution model (Kimura 1980). The robustness of the trees was calculated using the bootstrap method, with 1000 generations. The sequences are deposited in GenBank under the following accession numbers: MG736015 (CRM 1565), MW854309 (CRM 1874), MG735794 (CRM 1839), MW854303 (CRM 854303), and MW854308 (CRM 2576).

Resistance assays

Inoculum preparation

The yeasts were cultured in Petri dishes containing YMA (Yeast Malt Agar) medium (in g L^{-1}: 5 enzymatic digest of gelatin, 3 malt extract, 10 dextrose, 3 yeast extract, 15 agar) at 15 °C for 7 to 14 days. The yeast colonies were transferred to flasks containing 25 mL of YM broth (in g L^{-1}: 5 enzymatic digest of gelatin, 3 malt extract, 10 dextrose, 3 yeast extract). After 7 days of incubation at 15 °C and 120 rpm, the cells were counted using a Neubauer chamber, adjusted to a final concentration of 10^7 CFU mL^{-1} in a 0.9% w/v NaCl solution, and considered as yeast inoculum.

Table I. Data related to the sites, the samples of origin, and yeast isolation conditions and codes. Samplings were performed during OPERANTAR XXXIII (January/February 2015) at King George Island, Antarctic Peninsula.

Site	Geographic coordinates	Sample (temperature, deph, and pH)	Isolation condition	Yeast original code	Collection code
Yellow Point	62° 04.479'S 58° 23.726'W	Yellowish soil (3.6 ºC; 5 cm; 4.8)	MA2 at 5 ºC	7P-1.3I-5C	CRM 1839
Yellow Point	62° 04.479'S 58° 23.726'W	Yellowish soil (3.6 ºC; 5 cm; 4.8)	B&K at 5 ºC	7P-1.2IIII-5C	CRM 1874
Punta Ulman	62° 05.015'S 58° 20.987'W	Marine sediment (0.3 ºC; 20 m; 8)	PDA at 15 ºC	4A-3C315IIII	CRM 1565
Collins glacier	62° 09.821'S 58° 55.373'W	Soil at 0 m from the glacier (0.9 ºC; 5 cm; 6.1)	MA2 at 15 ºC	L40	CRM 2576
Collins glacier	62° 09.821'S 58° 55.373'W	Soil at 0 m from the glacier (0.9 ºC; 5 cm, 6.1)	MA2 at 15 ºC	L01	CRM 2571

MA2: malt extract 20 g.L^{-1}, agar 15 g.L^{-1}; B&K: glucose 10 g.L^{-1}, peptone 2 g.L^{-1}, yeast extract 1 g.L^{-1}, agar 20 g.L^{-1}, 4 mM guaiacol; PDA: 200 g.L^{-1} of potato, 20 g.L^{-1} of glucose, 15 g.L^{-1} agar (diluted in artificial seawater - ASW).

Temperature

The spread plate method was used to inoculate 0.1 mL of the yeast inoculum onto Petri dishes containing YMA medium. The Petri dishes were incubated at different temperatures: 5, 10, 15, 25 and 35 °C. All experiments were made in triplicates and evaluated after 14 days. Cell growth was visually evaluated and qualitatively classified according to Figure 2. The growth at 15 °C was considered as the control condition, in which cold-adapted microorganisms recovered from samples from the Antarctic Peninsula can grow well independently of their classification for temperature adaptation (Vishniac 1987, Buzzini et al. 2012, Rovati et al. 2013).

UVA, UVB and UVC

The spread plate method was used to inoculate 0.1 mL of the yeast inoculum onto Petri dishes containing YMA medium. Each Petri dish was then placed in a chamber containing at each time one of the three Hg-low pressure lamps used to obtain the desired UV type: UVA (15W, 352 nm, 1.6 W/m^2, F15W/350 BL-tb, Sylvania), UVB (15W, 305nm, 2.54 W/m^2, G15T8E, Ushio), and UVC (15W, 254 nm, 3.39 W/m^2, G13T8, Osram). All Petri dishes were placed 35 cm below the lamps. The irradiance for each of the lamps was measured using the photodiode UV-100 from OSI Optoeletronics. In the chamber, the samples received four different doses for each of the UV wavelengths: UVA (480, 1440, 2880, and 5760 J/m^2), UVB (762, 2286, 4572, and 9144 J/m^2), and UVC (1017, 3051, 6102, and 12204 J/m^2). After the period of exposure, all plates were incubated in the dark at 15 °C for 14 days. The experiments were made in triplicate and evaluated after 14 days. Cell growth was visually evaluated and qualitatively classified according to Figure 2. Triplicates of each yeast in the Petri dishes with YMA medium and not exposed to UV radiation (0 J/m^2) were used as control.

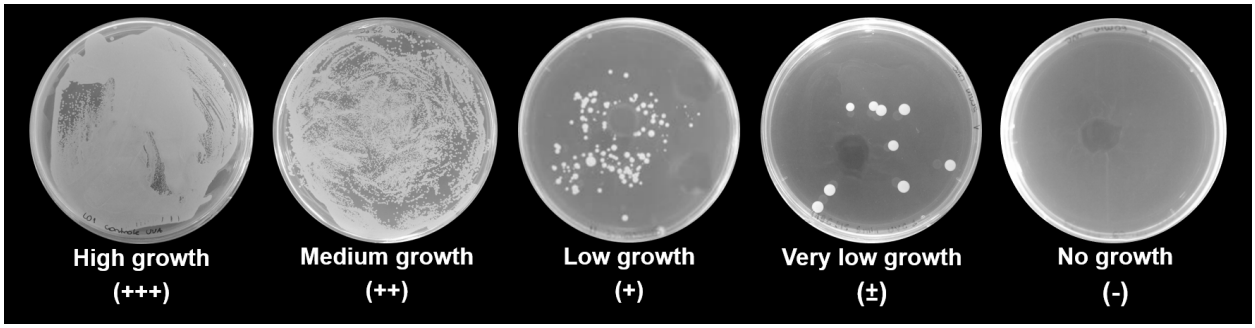

Figure 2. Visual evaluation and qualitative classification of the cell growth. High growth: a layer of colonies covering a relatively large area of the agar (+++), Medium growth: colonies too numerous for an accurate count (++), Low growth: total colonies count > 10 and < 100 (+), Very low growth: total colonies count ≤ 10 (±), No growth: no colonies formed (-).

Salinity

The spread plate method was used to inoculate 0.1 mL of the yeast inoculum onto Petri dishes containing YMA medium with different concentrations of NaCl (w/v): 3, 5, 7 and 10%. The plates were incubated for 14 days at 15 °C. All experiments were made in triplicate and evaluated after 14 days. Cell growth was visually evaluated and qualitatively classified according to Figure 2. As control, triplicates of the YMA medium with no addition of NaCl were used.

pH

A volume of 0.1 mL of the yeast inoculum was transferred to Erlenmeyer flasks containing 50 mL of YMB medium adjusted to different pH values: 3, 5, 7 and 9. The flasks were incubated for 7 days at 15 °C and 120 rpm. After the incubation period, the cell suspensions were centrifuged at 10,000 rpm for 15 minutes at 15 °C. The supernatant was separated, and the biomass produced was dried in a drying oven at 100 ºC for 24 h (until constant mass). The dry biomass was determined by discounting the previously measured mass of the flasks. All experiments were performed in triplicates.

RESULTS

Taxonomic identification

Amongst the Antarctic-derived yeasts used in this study, three had been identified at the genus level and reported by Wentzel et al. (2019) as *Naganishia* sp. CRM 1839 (isolated from yellowish soil), *Goffeauzyma* sp. CRM 1874 (isolated from yellowish soil), and *Cryptococcus* sp. CRM 1565 (isolated from marine sediment). In the present study, the refinement of the molecular analyses (new blast and phylogenetic analyses) allowed the identification of two of them at the species level.

The 28S-rDNA sequence of *Goffeauzyma* sp. CRM 1874 showed 100% of similarity with different sequences of *Cryptococcus gilvescens* (current *Goffeauzyma gilvescens*) and with *G. gilvescens* type strain (CBS 7525^T). In the phylogenetic tree, the sequence of the strain CRM 1874 (593 nt) grouped in a cluster composed only of sequences of *Goffeauzyma* (*Cryptococcus*) *gilvescens* isolates, with a bootstrap value of 78% (Figure 3). Based on these results, the yeast strain CRM 1874 was identified as *Goffeauzyma gilvescens*. In a similar way, the 28S-rDNA sequence of the Antarctic yeast CRM 1565 (548 nt) showed 98.69-98.52% of similarity with *Goffeauzyma gastrica* (former *Cryptococcus gastricus*) sequences (including the sequence of the type strain CBS 2288^T), forming a cluster isolated from the other

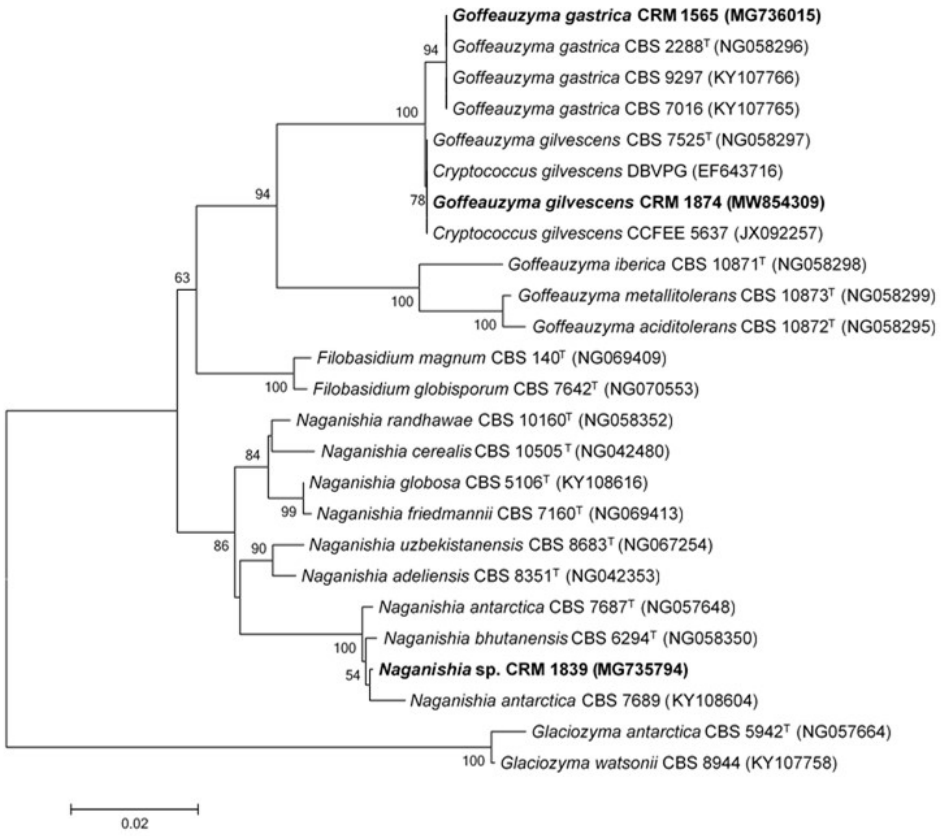

Figure 3. Phylogenetic analysis of partial 28S-rDNA gene sequences of the yeasts CRM 1839, CRM 1874 and CRM 1565 isolated from soil (Yellow point) and marine sediment (Punta Ulman) previously identified at the genus level and reported by Wentzel et al. (2019). Evolutionary distances were calculated using the Maximum Likelihood algorithm and Kimura-2p nucleotide substitution model. Bootstrap values (1000 replicate runs) >50% are listed.

species in the phylogenetic tree, supported by a bootstrap of 94% (Figure 3). These results allowed the identification of strain CRM 1565 as *Goffeauzyma gastrica*. On the other hand, it was not possible to identify *Naganishia* sp. CRM 1839 at the species level. The 28S-rDNA sequence of *Naganishia* sp. CRM 1839 (637 nt) showed 93.39-99.36-% of similarity with different species from this genus and, in the phylogenetic tree, the sequence of this Antarctic strain formed a cluster (100% bootstrap) together with sequences of *N. antarctica* and *N. buthanensis* isolates, including the type strains (CBS 7687^T and CBS 6294^T).

The two Antarctic-derived yeasts CRM 2571 and CRM 2576 isolated from the Collins glacier soil were identified as *Candida atlantica* and *Camptobasidium* sp., respectively. The 28S-rDNA sequence of the yeast CRM 2571 (530 nt) showed 100% of similarity with different isolates of *C. atlantica*. Additionally, based on the phylogenetic analysis, the sequence of the strain CRM 2571 clustered only with *C. atlantica* sequences with 100% of bootstrap (Figure 4), including the sequence of the type strain (NRRL Y-17759^T). For the yeast CRM 2576, the results from the 28S-rDNA sequence and phylogenetic analysis indicate that this strain can be a putative new species of the genus *Camptobasidium*. Sequence similarity with known species of this new yeast genus was low, ranging from 96.20 to 97.58%. In the phylogenetic tree, the sequence of strain CRM 2576 (634 nt) formed a group supported by 82% of bootstrap composed of the three species of the genus *Camptobasidium*, including the type strains (Figure 5): *C. gelus* CBS 8941^T, *C. hydrophylum* CBS 8060^T, and *Pucciniomycotina* sp. EXF-12713 (type strain of *C. arcticum*, according to Perini et al. 2021).

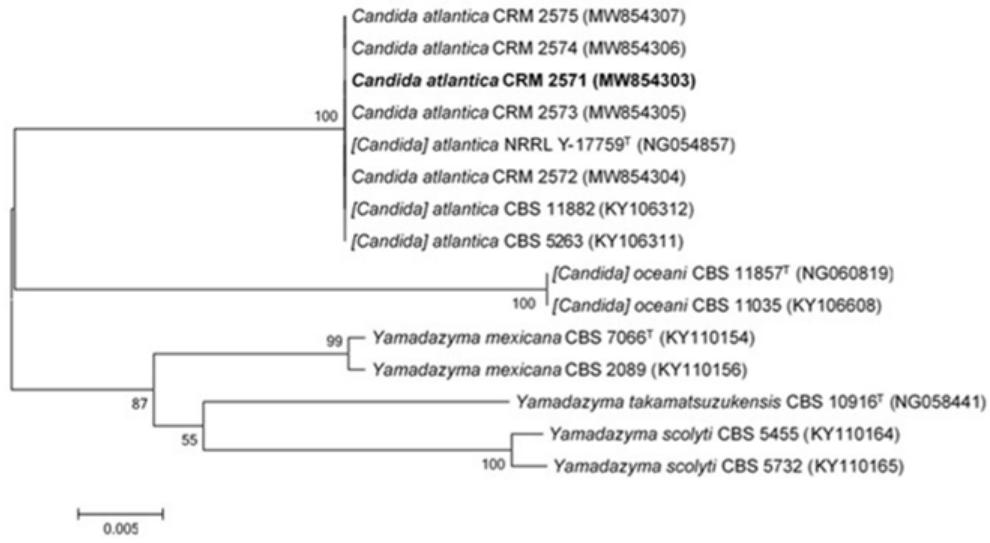

Figure 4. Phylogenetic analysis of partial 28S-rDNA gene sequences of the yeast CRM 2571 isolated from the Collins glacier soil. Evolutionary distances were calculated using the Maximum Likelihood algorithm and Kimura-2p nucleotide substitution model. Bootstrap values (1000 replicate runs) >50% are listed.

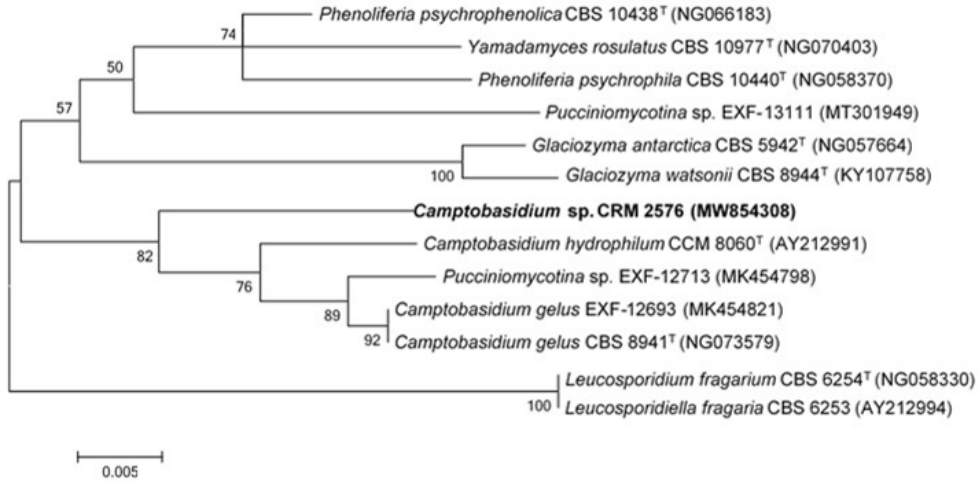

Figure 5. Phylogenetic analysis of partial 28S-rDNA gene sequences of the yeast CRM 2576 isolated from the Collins glacier soil. Evolutionary distances were calculated using the Maximum Likelihood algorithm and Kimura-2p nucleotide substitution model. Bootstrap values (1000 replicate runs) >50% are listed.

Resistance to adverse conditions

Six different stress conditions were applied to the Antarctic-derived yeasts: temperature, ultraviolet radiation (UVA, UVB and UVC), salinity, and pH. The results are shown in Table II.

None of the Antarctic yeast strains were able to grow at 35 ºC and only *C. atlantica* CRM 2571 did not grow at 5 ºC. Strains *G. gastrica* CRM 1565 and *Camptobasidium* sp. CRM 2576 were also not able to grow at 25 ºC. *Naganishia* sp. CRM 1839 showed high growth at 5, 10, and 15 ºC, while high cell growth was achieved by *Camptobasidium* sp. CRM 2576 at 5 and 10 ºC, *G. gastrica* CRM 1565 at 10 and 15 ºC, and *G. gilvescens* CRM 1874 and *C. atlantica* CRM 2571 at 10 and 25 ºC. These results suggest that the yeast strains *Naganishia* CRM 1839, *G. gilvescens* CRM 1874, *G. gastrica* CRM 1565, and *C. atlantica* CRM 2571 are psychrotolerant, due to their better growth (high growth) at temperatures of 15 and/or 25 ºC. For the yeast *Camptobasidium* sp. CRM 2576 the results indicate that it is a psychrophilic strain, considering its inability to grow at temperatures above 25 ºC and the better growth (high growth) at temperatures below 15 ºC. In general, there was no correlation between the results of cell growth at the different temperatures and the temperature of

Table II. Response of the Antarctic-derived yeast strains to different adverse conditions (stress factors).

Adverse conditions		Yeasts				
		Naganishia sp. **CRM 1839 (Yellowish soil)**	***Goffeauzyma gilvescens*** **CRM 1874 (Yellowish soil)**	***Goffeauzyma gastrica*** **CRM 1565 (Marine sediment)**	***Candida atlantica*** **CRM 2571 (Glacier soil)**	***Camptobasidium sp.*** **CRM 2576 (Glacier soil)**
Temperature (ºC)	5	+++	++	++	-	+++
	10	+++	+++	+++	+++	+++
	15	+++	+++	+++	+++	++
	25	++	+++	-	+++	-
	35	-	-	-	-	-
UVA (J/m²)	C	+++	+++	+++	+++	+++
	480	+++	+++	+++	+++	+++
	1440	+++	+++	+++	+++	+++
	2880	+++	+++	+++	+++	+++
	5760	+++	+++	+++	+++	+++
UVB (J/m²)	C	+++	+++	+++	+++	+++
	762	++	+++	+++	+++	+
	2286	++	++	+++	+	±
	4572	+	+	++	±	-
	9144	±	±	+	±	-
UVC (J/m²)	C	+++	+++	+++	+++	+++
	1017	±	±	+	±	+++
	3051	±	±	±	-	-
	6102	±	-	±	-	-
	12204	-	-	-	-	-
Salinity (%)	C	+++	+++	+++	+++	+++
	3	+++	++	++	+++	+++
	5	+++	++	++	+++	++
	7	++	+	+	+++	-
	10	-	-	-	+++	-
*pH	3	0.18 ± 0.04	1.85 ± 0.08	5.63 ± 0.2	2.41 ± 0.2	0.16 ± 0.05
	5	6.64 ± 0.3	2.21 ± 0.3	6.83 ± 0.8	6.24 ± 0.7	0.41 ± 0.05
	7	7.37 ± 0.5	2.82 ± 0.1	7.04 ± 0.3	17.48 ± 1.8	0.61 ± 0.18
	9	6.30 ± 0.05	3.04 ± 0.1	6.64 ± 0.5	9.61 ± 2.3	0.46 ± 0.02

High growth: a layer of colonies covering a relatively large area of the agar (+++), Medium growth: colonies too numerous for an accurate count (++), Low growth: total colonies count > 10 and < 100 (+), Very low growth: total colonies count ≤ 10 (±), No growth: no colonies formed (-). * The result of biomass refers to values in g L^{-1}.

the yellowish soil, marine sediment and glacier soil (Table I). The temperatures of the samples were low, two of them being very low (below 1 ºC), and only one of the yeast strains showed psychrophilic characteristics.

Concerning UV radiations, none of the yeasts showed signs of stress in any of the UVA doses applied, showing cell growth equivalent to the controls (0 J/m²). For the other two types of ultraviolet radiation (UVB and UVC) the resistance decreased as the dose of exposure increased for all yeasts. However, they showed differences in the tolerance after exposure to UVB and UVC radiations. With the exception of *Camptobasidium* sp. CRM 2576, all yeasts were able to grow at UVB doses ranging from 762 to 9144 J/m². The most resistant yeast was *G. gastrica* CRM 1565, which showed similar cell growth to the control (0 J/m²) until exposure to UVB dose of 2286 J/m², medium cellular growth after exposure to 4572 J/m² UVB, and low growth at 9144 J/m² UVB. The yeast *G. gilvescens* CRM 1874 showed the second-best result of UVB resistance, followed by *Naganishia* sp. CRM 1839, *C. atlantica* CRM 2571, and *Camptobasidium* sp. CRM 2576, which was able to grow until exposure to UVB dose of 2286 J/m². *G. gastrica* CRM 1565 also showed the best result of resistance to UVC radiation, being able to grow after being exposed to doses varying from 1017 to 6102 J/m², although cell growth was low after the exposure to 1017 J/m² UVC, and very low after the exposure to 3051 and 6102 J/m² UVC. Similar results were achieved by *Naganishia* sp. CRM 1839; nevertheless, for this strain cell growth was very low after the exposure to UVC doses of 1017 to 6102 J/m². The yeast *G. gilvescens* CRM 1874 was able to grow after the exposure to UVC doses of 1017 and 3051 J/m² (very low growth). Both *C. atlantica* CRM 2571 and *Camptobasidium* sp. CRM 2576 were able to grow only after the exposure to 1017 J/m² UVC (very low growth and high growth, respectively). The best resistance to UVB and UVC radiation in relation to the doses applied and cellular growth was verified in the yeast *G. gastrica* CRM 1565 isolated from marine sediment, followed by the yeasts *G. gilvescens* CRM 1874 and *Naganishia* CRM 1839 isolated from yellowish soil. The yeasts *C. atlantica* CRM 2571 and *Camptobasidium* sp. CRM 2576 from glacier soil showed less resistance to these radiations. However, *Camptobasidium* sp. CRM 2576 showed high growth capacity after exposure to a UVC dose of 1017 J/m².

Results of the growth at different saline concentrations revealed that *C. atlantica* CRM 2571 was the most resistant yeast, since it showed similar cell growth to the control (high growth) in all NaCl concentrations tested (3, 5, 7 and 10%). The second-best result of resistance was achieved by *Naganishia* sp. CRM 1839, which showed high growth up to 5% of NaCl and medium growth at 7%. The two species of the genus *Goffeauzyma* (*G. gilvescens* CRM 1874 and *G. gastrica* CRM 1565) showed the same results of saline resistance: medium growth at 3 and 5% and low growth at 7%. Additionally, *Camptobasidium* sp. CRM 2576 was able to grow at 3 (high growth) and 5% (medium growth) of NaCl.

Data from yeast growth (biomass) at different pH values revealed that the yeasts *Naganishia* CRM 1839, *G. gastrica* CRM 1565, *C. atlantica* CRM 2571, and *Camptobasidium* sp. CRM 2576 had a preference for neutral pH, since the amount of biomass produced was higher at pH 7. The yeast *G. gilvescens* CRM 1874 showed a higher amount of biomass at pH 9. Under the most acidic condition (pH 3), *Naganishia* sp. CRM 1839, *C. atlantica* CRM 2571, and *Camptobasidium* sp. CRM 2576 produced less than half of the biomass observed in the neutral media. Both *G. gilvescens* CRM 1874 and *G. gastrica* CRM 1565 had a low biomass variation in the studied pH

range. Considering the results at different pH values and the pH of the yellowish soil, marine sediment, and glacier soil (Table I), the pH of the best biomass production by *G. gastrica* CRM 1565, *C. atlantica* CRM 2571, and *Camptobasidium* sp. CRM 2576 was near the pH of the samples from which they were isolated (Table I). Nevertheless, for the strains isolated from yellowish soil (*Naganishia* sp. CRM 1839 and *G. gilvescens* CRM 1874), the best biomass production was quite different from that obtained at the pH of their samples of origin.

DISCUSSION

Results derived from molecular taxonomy (sequencing and phylogenetic analyses) confirmed the identification of strain CRM 1839 as *Naganishia* sp. and allowed the identification of the Antarctic-derived yeasts CRM 1874, CRM 1565, CRM 2571, and CRM 2576 as *G. gilvescens*, *G. gastrica*, *C. atlantica,* and *Camptobasidium* sp., respectively. It is important to highlight that strain CRM 2576 is possibly a new species of the genus *Camptobasidium*. However, further investigations will be necessary to confirm the hypothesis of new species.

The majority of the Antarctic-derived yeasts studied belong to the phylum Basidiomycota, which is the predominant phylum of yeasts reported in the Antarctic environment (Duarte et al. 2018) due to its better adaptation to the cold conditions (Vishniac 2006). Only the genus *Candida* (order Saccharomycetales and family Debaryomycetaceae) is representative of the phylum Ascomycota. The genera *Naganishia* and *Goffeauzyma* belong to the order Filobasidiales and family Filobasidiaceae, with their representatives previously identified as *Cryptococcus*. Representatives of *Camptobasidium* belong to the order Kriegeriales and family Camptobasidiaceae.

All studied yeasts have already been described as cold-adapted microorganisms and reported in Antarctic (Martorell et al. 2017), Artic (Pathan et al. 2010), and Alpine glacier (Turchetti et al. 2008) environments. *Goffeauzyma* (formerly *Cryptococcus*) is one of the most predominant genera found in Antarctica (Zhang et al. 2014) and, besides the cold tolerance, the success of inhabiting this kind of environment has been attributed to the polysaccharide capsules produced by them, resulting in an advantage against competing-bacteria (Białkowska et al. 2017). It is unsurprising that the majority of the studied Antarctic-derived yeasts are possibly psychrotolerant and not psychrophilic, since this is a well-known and widely described event related to microorganisms isolated from cold environments (Mohan et al. 2017, Białkowska et al. 2017). Most of the microorganisms recovered from samples in the Antarctic Maritime region (Antarctica Peninsula) are psychrotolerant (Ruisi et al. 2007) and this predominance can be explained by the fact that in some periods of the year the soil temperature can reach 15 ºC (Möller & Dreyfuss 1996). Additionally, although the air temperature in the Antarctica Peninsula may reach -13 °C in the cold winter, the soil creates a microhabitat that can maintain higher temperatures, ranging from 5 to 10 °C, providing a more suitable site not only for the growth of the psychrophilic microorganisms, but also for the psychrotolerant ones (Rakusa-Suszczewski 2002, Krishnan et al. 2011). The only yeast considered as psychrophilic, and possibly a new species, was *Camptobasidium* sp. CRM 2576. According to Perini et al. (2021), all species representative of this genus are classified as psychrophilic. The tolerance for very low temperatures derives from a series of factors, including synthesis of cryoprotective sugars that protect the cell from dehydration; glycerol and mannitol to maintain the turgor pressure; anti-freezing proteins to

prevent the formation of crystals in the cytosol; and enzymes capable of functioning at low temperatures (Robinson 2001).

In Antarctica, the hole in the ozone layer allows a greater incidence of radiation (Narayanan et al. 2010, Sivasakthivel & Reddy 2011). Amongst the three types of UV radiation, type A is the most common and abundantly present in the sunlight, justifying the high tolerance shown by all Antarctic-derived yeasts studied. In relation to type B, with the exception of *Camptobasidium* sp. CRM 2576, all yeast strains survived even after 60 min of exposure to UVB (total dose of 9144 J/m²). According to Chen et al. (2011), the maximum tolerance of *Saccharomyces cerevisiae* to UVB radiation is 35 min of exposure to this radiation. The results of tolerance to UVC radiation revealed the low tolerance of the Antarctic yeasts to this type of radiation, although *Naganishia* sp. CRM 1839 and *G. gastrica* CRM 1565 showed very low growth after UVC dose of 4572 J/m². All studied yeasts have non-pigmented colonies (white/creamy color), which corroborates the idea reported by Sinha & Häder (2002) and Schiave et al. (2009), who proposed that pigmentation is not the main protection factor against the damage to DNA caused by radiation. The possible mechanisms of UV resistance include the production of photoprotective molecules (e.g. mycosporine) (Libkind et al. 2009), antioxidant enzymes (Hoerter et al. 2005), and photoreactivation system (Zenoff et al. 2006). The fact that *G. gastrica* CRM 1565, isolated from marine sediment, was observed as the most resistant strain to UV radiations can be justified by the widespread presence of the genus in Antarctica, which makes it naturally adapted to harsh conditions (Zhang et al. 2014), and by the transparency of the waters, enabling the passage of UV radiation which can penetrate the water column at depths up to 95 m (Garcia-Pichel & Bebout 1996, Rakusa-Suszczewski 2002). The low UV resistance of the yeasts isolated from the Collins glacier retreating soil may be explained by the shorter exposure time to the natural UV radiation in comparison to the exposure of yeasts from yellowish soil and marine sediment, since the samples from their origin (0 m from the glacier) have recently been ice-uncovered.

The most halotolerant strain was *C. atlantica* CRM 2571, a marine endemic species (Burgaud et al. 2011), which showed high cell growth with up to 10% of NaCl. On the other hand, the yeast *G. gastrica* CRM 1565, isolated from marine sediment, showed medium growth with 3 and 5% of NaCl and low growth with 7% of NaCl. Nevertheless, the salinity in Admiralty Bay in January/February 2015 (month and year of the sampling) was about 3.4% (I.G.C. Ferreira, unpublished data). Considering that this species may vary its salt toleration from 4 to 15% of NaCl (Pathan et al. 2010, Białkowska et al. 2017), the results shown herein (tolerance up to 7% of salt concentration) are as expected. *Naganishia* sp. CRM 1839 also showed the ability to grow with up to 7% of NaCl. According to Schmidt et al. (2017), high salt tolerance (% NaCl) for this genus is not found in the Antarctic-isolated species. Osmotic stress occasioned by the salt concentration can be avoided by the accumulation of osmoregulatory compounds, glycerol, and arabitol, and the last two can be synthetized after the activation of specific genes that are triggered in the event of stress signals (Han & Prade 2002, Pascual et al. 2002, Ruisi et al. 2007).

Most microorganisms are classified as neutrophiles, with the optimum pH around the neutral point (pH 7); nonetheless, many of them may show tolerance for acidic and basic conditions, particularly in Antarctica, where the soil may vary from slightly acidic (pH 6) in the islands and high altitudes to extremely

alkaline (pH 9) on the coastal area (Aislabie et al. 1998, Battcock & Azam-Ali 2001, Tasseli et al. 2017, Fotedar et al. 2018). Representatives of the genus *Goffeauzyma, G. gilvescens* CRM 1874 and *G. gastrica* CRM 1565, were able to thrive even in the most acidic medium (considering their biomass in all pH values studied). In the description of the species *Cryptococcus ibericus* (current *G. iberica*), *C. aciditolerans* (current *G. aciditolerans*) and *C. metallitolerans* (current *G. metallitolerans*), isolated from extreme environmental conditions, all of them were reported as able to grow at very low pH (< 3) (Gadanho & Sampaio 2009). *G. gastrica* CRM 1565, *C. atlantica* CRM 2571, and *Camptobasidium* sp. CRM 2576 showed better biomass production at pH near the one from their sample of origin (marine sediment and glacier soil). On the other hand, *Naganishia* sp. CRM 1839 and *G. gilvescens* CRM 1874 produced better amounts of biomass at pH different from the one of the sample of origin (yellowish soil). Considering that microbial spores may be widespread on a global scale and some of the microorganisms found in the Antarctic soil may be dormant (Schmidt et al. 2017), the isolation of species in locations with different characteristics from the ones preferred under laboratory conditions could be justified. Nevertheless, to be viable after long aerial transportation from a location to another, the species must have adaptations to deal with long exposure to UV radiation and extreme temperatures, characteristics that have been reported in the genus *Naganishia* (Griffin et al. 2001, Pulschen et al. 2015, Schmidt et al. 2017).

Antarctic yeasts and their cold-adapted enzymes have been the aim of many kinds of research and turned out to be a source of biotechnological innovations that can be used in various environments or processes, such as dye decolorization (Rovati et al. 2013), biodegradation of petroleum hydrocarbons (Martorell et al. 2017), production of cryoprotectant compounds (Buzzini et al. 2012), among others. Apart from the biotechnological applications, extremophile yeasts can also be used as models for astrobiology researches (Onofri et al. 2008). In this sense, the results shown herein are promising and open new perspectives for further investigations in the field of extremophiles and their biotechnological applications.

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GABRIELE S. FARIAS[1]
https://orcid.org/0000-0003-2285-5651

JULIANA A. SANTOS[1]
https://orcid.org/0000-0003-4654-4698

PATRICIA GIOVANELLA[1,2]
https://orcid.org/0000-0002-1207-4459

LARA D. SETTE[1,2]
https://orcid.org/0000-0002-5980-3786

[1]Universidade Estadual Paulista Júlio de Mesquita Filho (UNESP), Instituto de Biociências, Departamento de Biologia Geral e Aplicada, Av. 24A, 1515, 13506-900 Rio Claro, SP, Brazil

[2]Universidade Estadual Paulista Júlio de Mesquita Filho (UNESP), Instituto de Biociências, Centro de Estudos Ambientais, Av. 24A, 1515, 13506-900 Rio Claro, SP, Brazil

Correspondence to: **Lara Durães Sette**
E-mail: lara.sette@unesp.br

Author contributions

GSF: experimental analyses and original draft preparation; JAS: yeast's isolation and co-supervision; PG: conceptualization, table editing and reviewing; LDS: conceptualization, supervision, reviewing, editing, figure editing and funding acquisition.