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1.3 A Contribution of Antarctic Ecology to Yeast Systematics

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Summary: The McMurdo Dry Valleys (informally known as the Ross Desert) of Antarctica has provided a unique opportunity to observe the selctive effects of aridity on yeast evolution and, consequently, to assess the systematic value of phenotypic characters. The yeasts of the arid highlands differ from some yeasts of melt streams and lakes in failure to produce mycelium and/or pseudomycelium, a characteristic formerly given generic importance. Although the presence of liquid water has complex consequences and the causal relationship of aridity with negative selection for this trait is incompletely understood, these findings indicate that filamentous growth habits are negatively selected in cold deserts and therefore may be considered to be presently undervalued in yeast taxonomy.

Zusammenfassung: Die McMurdo Dry Valleys (auch Ross Desert genannt) bieten eine einzigartige Gelegenheit, die selektiven Effekte von Aridität auf die Evolution der Hefen zu beobachten und daraus folgend den systematischen Wert von Phänotypen festzustellen. Die Hefen der trockenen und hochgelegenen Gebiete unterscheiden sich von einigen Hefen der Schmelzwasserströme und Seen dadurch, daß sie kein Mycel und/oder Pseudomycel bilden, was bisher als entwicklungsgeschichtlich bedeutend galt. Obwohl die Verfügbarkeit von Wasser komplexe Wirkungen hat und der kausale Zusammenhang zwischen Aridität und negativer Selektrion sich in diesem Fall noch nicht vollständig nachvollziehen läßt, zeigen die Untersuchungen, daß filamentöse Wuchsformen in Kältewüsten eine negative Auslese bilden und deshalb in Kältewüsten eine negative Auslese bilden und deshalb noch in der Taxonomie der Hefen unterschätzt werden.

1. INTRODUCTION

The Antarctic has provided a unique opportunity to correlate controversial generic characters in yeast systematics with selective forces in a natural habitat. Yeast species are now considered to be most reliably delimited by DNA homology, while rRNA-DNA homology holds promise for the definition of genera (KREGER-VAN RIJ 1984a). Since the nucleic acid homologies of yeasts are at present incompletely known, many yeasts are now both identified and classified on the basis of empirically chosen phenotypic characters whose selctive advantages are incompletely understood. The most obvious ecologic variable within the McMurdo Dry Valleys (informally known as the Ross Desert, southern Victoria Land, Antarctica) is the presence or absence of water. It has been claimed that water is the limiting factor in microbial growth in the dry valleys (HOROWITZ et al 1972). We have compared the characteristics of yeasts isolated from sites in or near liquid with those of yeasts isolated from arid upland soils. In contrast with other soils, no yeasts isolated from arid upland soils produced mycelium or pseudomycelium, suggesting that this characteristic has greater systematic value than it is presently accorded.

2. MATERIALS AND METHODS

594 yeast isolates from 23 fertile Dry Valley soil samples were characterized as 58 biotypes differing in one or more of the standard tests for yeast identification (VAN DER WALT & YARROW 1984). The areas from which soil samples were taken are indicated in Figure 1. The population density of yeasts in these soil samples was too low to allow counts to be made by plating aliquots of soil suspensions. Counting was done either by sprinkling a known mass of soil on a plate of appropriate solid medium or (for extremely sparse populations) by adding a dilute, non-selective, medium to 5 g or more of soil and incubating under simulated in situ conditions before sprinkling (VISHNIAC 1983, 1985b). Population density in soil samples is therefore expressed below as microcolonies per gram of soil. It was assumed that each colony which appeared on an individual soil grain sprinkled directly was enate from a microcolony (1 to several yeast cells), but that only each biovar (rather than colony) appearing from nutritionally-enriched soil represented an original microcolony.

Characterization was performed as previously described (VISHNIAC 1985a), except that cells for nitrogen utilization tests were nitrogen-starved by growth for 3—6 days at 10° C in a thin liquid layer on Y-2 agar prepared without nitrogen sources. Compounds tested as sole substrates (at 0.2% in appropriately supplemented Y-2 mineral

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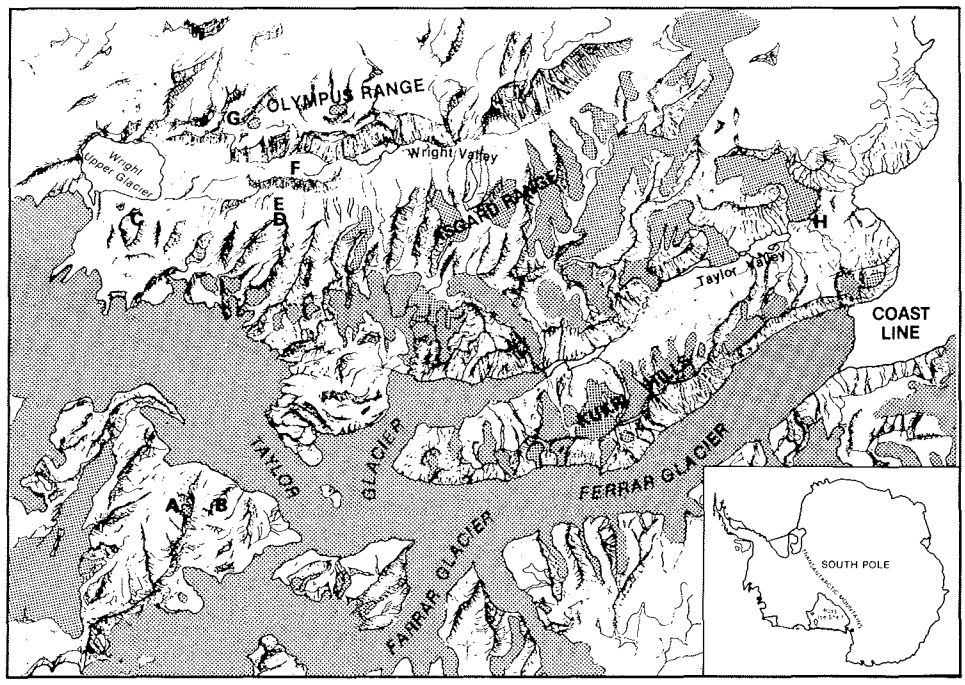

Fig. 1: The McMurdo Dry Valleys. The relationship of this area to the continent of Antarctica is indicated by the black dot opposite the tip of the Ross Ice Shelf on the inset outline map. The features mentioned in this paper are identifiable as follows: A, University Valley (note the glaciated area, indicated by half-tone shading, at the head of this hanging valley); B, Arena Valley; C, Tyrol Valley; D, Mount Oliver; E, Linnaeus Terrace, a high plateau below Mt. Oliver, above Wright Valley; F, The Dais, a high plateau in Wright Valley; G, Mount Dido; and H, a glacial melt stream in Taylor Valley.

base agar) were: L-arabinitol, D-arabinose, L-arabinose (AR), cellobiose (CE), citrate (pHh6.0) (CI), erythritol, ethanol (ET), galactitol (= dulcitol), D-galactose, D-glucitol (= sorbitol) (GS), D-gluconate (pH 6.0) (GN), D-glucosamine, glucuronate (pH 5.5) (GR), glycerol (GY), myo-inositol, 2-ketogluconate (ehmicalcium salt) (KB), DL-lactate, lactose (LA), maltose (MA), D-mannitol (ML), melezitose (MZ), melibiose, α-methyl glucoside (MG), raffinose (RA), L-rhamnose (RH), ribitol (= adonitol) (RL), salicin (SA), soluble starch (ST), L-sorbose, succinate (pH 6.0) (SI), sucrose (SR), trehalose (TR), xylitol (XL), and xylose (XY). Any substrate not mentioned further may be assumed not to have been utilized by previously undescribed biotypes. The abbreviation TA, below and in the tables, indicates growth at 25° C.

3. RESULTS

The 52 biotypes which were psychrophilic or psychrotrophic and considered probably indigenous were characterized as follows:

3.1 *Isolates from arid and unglaciated upland sites* containig ≤ 1
microcolony per gram of air-dry soil: All isolates failed to produce mycelium or pseudomycelium.

1. Biotype 65 ("SLO") isolated from samples taken from arid, upland sites on Linnaeus Terrace and in Arena Valley, did not produce mycelium or pseudomycelium but was otherwise uncharacterizable, failing to grow after isolation except on yeast-malt agar.
2. Undescribed ascomycete: biotype 69 (psychrophilic, nitrate negative and assimilating only CI, GY, SR) isolated from a Linnaeus Terrace sample
3. *Cryptococcus albidus* var. *albidus*: biotype 70 (psychrotrophic), from Linnaeus Terrace: Differences between

this isolate and psychrophilic biotypes isolated from University Valley soils (below) are shown in Table 1.

4. *Cr. consortionis*, a nitrate negative psychrophilic species isolated from a Linnaeus Terrace soil sample (VISHNIAC 1985a).

biotype	*TA	AR	CI	GN	GS	LA	RA	XL	XY
/52	—	+	—	—	+	—	+	—	+
/61	—	+	—	—	—	—	—	—	—
/64	—	—	+	+	+	—	+	—	+
/67	—	—	+	+	+	—	—	—	+
/70	+	+	+	+	+	+	—	+	+

Tab. 1: Differences among biotypes resembling *Cr. albidus* var. *albidus*.

*TA, growth at 25°C. Assimilation of AR, L-arabinose; CI, citrate; GN, gluconate; GS, glucitol; LA, DL-lactate; RA, raffinose; XL, xylitol; XY, xylose

5. *Cr. lupi* (resembling the *Cr vishniacii* complex (below) except for failure to assimilate 2-ketogluconate): isolated from Tyrol Valley soil samples (BAHARAEEN & VISHNIAC 1982).

6. cf. *Cr. lupi*: biotypes 30, 36 39A, 39B, 40, 42, 45, and 59, isolated from sites on The Dais, Wright Valley. Differences between these biotypes and the type of *Cr. lupi* are shown in Table 2.

biotype:	*AR	CE	CI	MG	RA	RH	SA	SI
Cr. lupi	+	+	+	+	+	—	+	—
30	+	+	+	—	—	w	+	+
36	+	+	—	+	—	+	+	+
39A	+	+	+	w	+	—	+	+
39B	+	+	—	w	+	—	+	+
40	+	+	+	—	+	—	+	+
42	—	+	w	+	+	—	—	w
45	+	—	+	—	+	+	+	+
59	+	+	+	+	—	—	w	—

Tab. 2: Differences between *Cr. lupi* and similar undescribed biotypes.

*Assimilation of AR, L-arabinose; CE, cellobiose; CI, citrate; MG, α-methyl glucoside; RA, raffinose; RH, rhamnose; SA, salicin; SI, succinate.

7. *Cr. socialis*, a nitrate negative psychrophilic species isolated from a Linnaeus Terrace soil sample (VISHNIAC 1985a).

8. cf. *Cr. socialis*: biotype 31 (differed in CI, SA, XY), isolated from a sample from The Dais, Wright Valley.

9. *Cr. vishniacii* complex: *Cr. vishniacii* var. *vishniacii*, Cr. v. var. *wolfii*,*Cr. v.* var. *vladimirii*, *Cr. v.* var. *asocialis*, *Dr. asgardensis*, *Cr. baldrensis*, *Cr. hempflingii*, *Cr. tyrolensis*, *Cr. wrightensis* (VISHNIAC & BAHARAEEN 1982), are psychrophiles which are similar in utilizing nitrate, assimilating 2-ketogluconate, glucose, glucuronate, maltose, melezitose, trehalose, and xylose, as well as in the characters common to *Cr.* species with significant 25S rRNA homology (p. e. monopolar budding, neither mycelium nor pseudomycelium formed, amylose produced) (BAHARAEEN & VISHNIAC 1984). Isolated from Tyrol Valley soil samples (VISHNIAC & HEMPFLING 1979). *Cr. vishniacii* var. *asocialis* was subsequently isolated from an additional Tyrol Valley soil sample. *Cr. tyrolensis* was also isolated from an Arena Valley soil sample.

10. cf. *Cr. vishniacii* complex: biotype 25 (SI negative, similar to *Cr. baldrensis* except in CE and RH assimilation; to *Cr. hempflingii* except in AR and CI assimilation; to *Cr. tyrolensis* except in CI and RH assimilation) isolated from an Arena Valley soil sample, and biotype 45 (SI positive, most similar to *Cr. wrightensis* and *Cr. asgardensis* but differing in AR from *Cr. wrightensis* and in SA from *Cr. asgardensis*), isolated from The Dais, Wright Valley.

11. Undescribed *?Cr. spp.* (psychrophilic, nitrate utilizing): biotypes with monopolar budding and amylose production, lacking either the GR or XY common assimilation character of the *Cr. vishniacii* complex: 19 (Linnaeus Terrace); 23 (Tyrol Valley); 26, 29, and 34 (Arena Valley); 60 and 71 (Linnaeus Terrace). All assimilated (besides glucose) maltose, melezitose, sucrose, and trehalose. Differences between these biotypes are shown in Table 3.

12. Biotype 24, from an Arena Valley soil sample, was not considered with the preceding group because of its failure to produce amylose, a character which is common to the species we consider assignable on other grounds to the genus *Cryptococcus*. Biotype 24 was similar to the preceding yeast biotypes in psychrophily, monopolar budding, and nitrate utilization, but assimilated (in addition to glucose) only AR, GN, KB, MG, RA, SA, SI, and XY.

biotype	*AR	CE	GN	GR	KB	MG	RA	SA	SI	XY
19	—	+	—	—	—	+	+	w	—	w
23	+	+	—	—	—	w	—	—	—	+
26	—	—	+	—	+	+	+	—	+	+
29	+	+	—	—	—	+	—	+	—	+
34	—	—	+	—	+	+	+	—	—	+
60	w	w	—	+	—	—	—	—	—	—
71	+	+	—	+	+	+	w	w	—	—

Tab. 3: Differences between undescribed nitrate-utilizing? *Cryptococcus* biotypes.

*Assimilation of AR, L-arabinose; CE, cellobiose; GN, gluconate; GR, gluconate; KB, α-ketogluconate; MG, α-methyl glucoside; RA, raffinose; SA, salicin; SI, succinate; xy, xylose.

biotype:	*AR	CE	GN	KB	MZ	SI	SR	XY
35	+	+	+	+	—	+	+	—
51	+	w	—	—	—	—/w	—/w	—
57	—	w	—	+	—	—	+	—
62	+	+	w	—	—	—	+	—
63	—	—	—	—	+	—	—	—
68	—	+	+	—	w	—	—	+

Tab. 4: Differences between undescribed nitrate negative? *Cryptococcus* biotypes.

*Assimilation of AR, L-arabinose; CE, cellobiose; GN, gluconate; KB, 2-ketogluconate; MZ, melezitose; SI, succinate: SR, sucrose; XY, xylose.

13. Undescribed *?Cr. spp.* (psychrophilic, nitrate negative): biotypes with monopolar budding, no mycelium or pseudomycelium, producing amylose, growing without vitamins, assimilating glucuronate and trehalose: 35 (valley west of Oliver Peak, Asgard Range), 51 and 57 (east slope of Mt. Dido, Olympus range), and 62, 63, 68 (Linnaeus Terrace). The differences among these biotypes are shown in Table 4.
14. cf. *Leucosporidium scottii*: biotype 28, bipolarly budding cells not forming mycelium or pseudomycelium, differed from recorded assimilation patterns for *L. scottii* in Cl, ET, GS, ML, SI, and XY; isolated from an Arena Valley soil sample.
15. *Sterigmatomyces* sp., lacking mycelium or pseudomycelium, isolated from The Dais, Wright Valley.

3.2 *Isolates from arid sites in University Valley*
(glaciated at head, containing ≤ 1 mc g^{-1} soil): All isolates failed to produce mycelium or pseudomycelium.
cf. *Cr. albidus* var. *albidus* psychrophilic biotypes 52, 61, 64, 67, isolated from University Valley sites. These biotypes resembled the standard description of the variety given by RODRIGUES DE MIRANDA (1984), though biotypes failing to grow at 25° C and/or not assimilating L-arabinose would not be ascribed to this species if the short list of BARNETT et al. (1983) were used for identification. Atlas et al. (1978) have previously reported the isolation of Antarctic *Cr. albidus* strains with low maximal growth temperatures. Differences between these biotypes are shown in Table 1.

3.3 *Isolates from glacial melt stream sediment, Taylor Valley,*
containing ca. 70 colony-forming units of yeast cells mL^{-1} and ca. 32 mc g^{-1} of drained sediment: Mycelium and/or pseudomycelium was produced by 5 of 7 biotypes.
1. *Dioszegia hungarica* (*Cr. hungaricus* in RODRIGUES DE MIRANDA, 1984, BARNETT et al. 1983): biotype 46 (psychrotrophic) differed from strains of this species described by RODRIGUES DE MIRANDA (1984) and BARNETT et al. (1983) in forming both pseudohyphae and clamped mycelium and in bipolar budding. The type culture (NRRL-Y-6667) also exhibited bipolar budding. This species might be better assigned to the genus *Rhodotorula,* since *Cryptococcus* typically exhibits monopolar budding (BAHARAEEN & VISHNIAC 1981). The validity of budding behaviour as a generic descriptor is supported by 25S rRNA homology (BAHARAEEN & VISHNIAC 1984).
2. *?Leucosporidium antarcticum* biotypes: 47A, 47NM, 47B, 47NX, 48, isolated from Taylor Valley glacial melt stream sediment. This psychrophilic, bipolarly budding, and nitrate positive species has been described by FELL & TALLMAN (1984a) as having no unvarying positive assimilation characters. Since characters of the type culture have not been determined in this laboratory, these biotypes have been assigned to *L. antarcticum* by exclusion, on the basis of assimilation of very few of the standard substrates. All assimilated ethanol. Only biotype

47NM failed to form pseudomycelium and unclamped filaments. This biotype might more properly be considered a species of *Vanrija*. Biotype 47A produced spherical teliospores. Differences in assimilation are schown in Table 5.

biotype:	*CE	GS	GR	GY	KB	ML	MG	RL	SR
47A	—	w	—	w	+	—	—	—	—
47NM	—	—	—	+	+	—	—	—	—
47B	—	+	+	+	+	—	—	—	—
47NX	—	—	—	—	—	—	+	—	+
48	+/w	+	—	—	—	+	—	+	—

Tab. 5: Assimilation differences between *L. antarcticum* biotypes.

*Assimilation of CE, cellobiose; GS, glucitol; GR, glucuronate; GY, glycerol; KB, 2-ketogluconate; ML, mannitol; MG, α-methyl glucoside; RL, ribitol; SR, sucrose.

3. *Vanrija* sp: Biotype 50 was characterized by bipolar budding, production of pseudomycelium and mycelium, failure to utilize nitrate, rapid assimilation of GS; ML, and RL, and failure to produce amylose. Biotype 50 differed from the *Vanrija* anamorphs of all described *Leucosporidium* species in failure to utilize nitrate; it might otherwise be assignable to *L. antarcticum*. Nitrate utilization may not be a valid specific or generic descriptor. *Dekkera bruxelensis* and *D. intermedia* (VAN DER WALT 1984) and *Sterigmatomyces halophilus* (FELL et al. 1984b) are variable in this respect; nitrate utilization does not distinguish the genera *Hansenula* and *Pichia* (KURTZMAN 1984).
4. The isolation of *Candida curiosa* and *C. foliorum* from this soil sample, reported in 'Yeasts in the Antarctic deserts' (VISHNIAC & KLINGLER 1988) is now considered to have been based on premature identifications.

4. DISCUSSION

Before the possible causes of the correlation between water and myceliation or the importance of mycelium production in yeast systematics, one must ask whether this correlation is real or artifactual. We have examined a single well-watered site in the McMurdo Dry Valleys, though many sites from the arid uplands. Previous investigators have, however, isolated yeasts most frequently from more or less well-watered sites, as is evident from the list of continental Antarctic yeasts reported by others in Table 6.
These records are pertinent to this discussion only when a myceliating isolate with appropriate temperature responses (i. e. ability to colonize a cold habitat) was reported from an arid upland site. Since previous investigators were not specifically concerned with the correlation we have found, it is uncertain whether pertinent observations have always been reported. The following listed species (but not necessarily the Antarctic isolates ascribed to them) have been described as producing mycelium and/or pseudomycelium: *Aureobasidim pullulans, Candida albicans, C. antarctica, C. sake, Cryptococcus laurentii, Cr. macerans, Leucosporidium frigidum, L. gelidum, L. nivale, L. scottii, L. stokesii, Rhodotorula glutinis, Rh. graminis, Rh. minuta, Rh. rubra, Sporobolomyces salmonicolor, Trichosporon cutaneum, Tr. pullulans, Vanrija diffluens,* and *V. humicola*. The production of mycelium or pseudomycelium was not mentioned in connection with Antarctic isolates of *Cryptococcus, Rhodotorula,* or *Sporobolomyces*. Mycelia are unusual in isolates of *Cr. laurentii* (discussed below); pseudohyphae are rare in *Cr. macerans* (PHAFF & FELL 1970). Mycelium and pseudomycelium formation are variable in *Rh.* spp ("some strains produce extensive, well developed pseudo- or true mycelium", FELL et al. 1984a), and *Sp. salmonicolor* ("pseudomycelium and mycelium may occur with considerable strain variation", FELL & TALLMAN 1984b). *Sporobolomyces holsaticus* was also described as myceliated by FELL & TALLMAN (1984), but the *Sp.* strains isolated by VISHNIAC & HEMPFLING (1979) did not myceliate (unpublished data) and grew poorly at 4° C. A single isolate of *Tilletiopsis washingtonensis* recorded by VISHNIAC & HEMPFLING (1979) did myceliate but was also mesophilic.
The literature does not always indicate whether a mesophilic species known primarily from other climates is also psychrotrophic, making it difficult to judge whether the species was in fact established in the Antarctic. Of the yeasts mentined above, only the *Leucosporidium* spp and some strains of *Cr. laurentii* were psychrophilic. Although no minimum growth temperature has apparently been reported for *C. albicans,* a number of strains of this well-known human symbiont have failed to grow at 5° C in our laboratory (unpublished data); we therefore assume that isolation of this species was the result of recent human presence. The isolation of other mesophilic

Taxon	Habitat	Reference
Aureobasidium pullulans	Antarctic soils	Cameron et al., 1976; Atlas et al., 1978
Candida albicans	Antarctic soils	Cameron et al., 1976
*Candida antarctica**	Lake Vanda	Goto et al., 1969
*Candida famata**	Antarctic soils	Soneda, 1961; Tubaki, 1961
	soil near glacier	di Menna, 1966
*Candida psychrophila**	penguin dung	Goto et al., 1969
	Arena Valley soil	Atlas et al., 1978
*Candida sake**	Penguin dung; fresh water	Goto et al., 1969
*Cryptococcus albidus**	Antarctic soils	Atlas et al., 1978; Cameron, 1971; di Menna, 1960,1966
	Lake Vanda	Goto et al., 1969
Cryptococcus laurentii	Antarctic continent	Soneda, 1961
	by Lake Vanda; McMurdo Sta	Atlas et al., 1978
	Wright Valley	di Menna, 1960
	soil near glaciers; Ross Island	di Menna, 1966
Cryptococcus luteolus	poolside, near Lake Vanda	di Menna, 1960
	soil near glaciers; Ross Island	di Menna 1966
	Antarctic soils	Cameron et al., 1976
	The Strand Moraines	Atlas et al., 1978
*Cryptococcus macerans**	soil near glaciers	di Menna, 1966
*Debaryomyces hansenii**	soil near Koettlitz glacier	di Menna, 1966
*Leucosporidium frigidum**	Ross Island	di Menna, 1966
*Leucosporidium gelidum**	soil near glaciers; Ross Island	di Menna, 1966
*Leucosporidium nivale**	soil near glaciers; Ross Island	di Menna, 1966
*Leucosporidium scottii**	Wright Valley soils	di Menna, 1960
	soil near glaciers; Ross Island	di Menna, 1966
	Lake Fryxell; Lake Vanda	Goto et al., 1969
	Heald Is, Valley; McMurdo Sta.	Atlas et al., 1978
Leucosporidium stokesii	Antarctic soils	Sinclair and Stokes, 1965
Rhodotorula graminis	Poolside, near Lake Vanda	di Menna, 1960
	soil near glacier	di Menna, 1966
	Antarctic soils	Cameron et al., 1976
	Asgard Range	Atlas et al., 1978
Rhodotorula glutinis	Lake Vanda	Goto et al., 1969
*Rhodotorula minuta**	Wright Valley soil	di Menna, 1960
	soil near glaciers, Ross Island	di Menna, 1966
	Lake Vanda; Lake Miers	Goto et al., 1969
	Antarctic soils	Cameron et al., 1976
	Asgard Range; McMurdo Sta.	Atlas et al., 1978
*Rhodotorula rubra**	soil near glaciers; Ross Island	di Menna, 1966
	Lake Vanda; Lake Miers	Goto et al., 1969
	Victoria Valley	Atlas et al., 1978
*Sporobolomyces salmonicolor**	Wright Valley soil	di Menna, 1960
	Antarctic soils	Cameron et al., 1976
	Marble Pt., Brown Peninsula	Atlas et al., 1978
Trichosporon cutaneum	Antarctic soil	Soneda, 1961; tubaki, 1961
	Lake Vanda	Goto et al., 1969
Trichosporon pullulans	Ross Island	di Menna, 1966
*Vanrija diffluens**	Lake Vanda, Lake Miers	Goto et al., 1969
*Vanrija humicola**	Lake Vanda	Goto et al., 1969

Tab. 6: Yeats of the Antarctic Continent reported by other investigators. *With the exception of species of *Vanrija* Moore, taxa are given in accordance with the usage of Kreger-van Rij (1984c); epithets used in references cited differed from this usage as follows: *Candida antarctica* = *Sporobolomyces antarcticus* (Goto et al., 1969; *Candida famata* = *Torulopsis famata* (di Menna, 1966b; Soneda, 1961; Tubaki, 1961), anamorph of *Debaryomyces hansenii* (Kreger-van Rij, 1984b); *Candida psychrophila* = *Torulopsis psychrophilia* (Atlas et al., 1978); *T. psychrophila* (Goto et al., 1969); *Candida sake* = *Candida australis* (Goto et al., 1969); *Cryptococcus albidus* = *Cr. diffluens* (di Menna, 1966); *Cryptococcus macerans* = *Rhodotorula macerans* (di Menna, 1966b); *Debaryomyces hansenii* = *Deb. kloeckeri* (di Menna, 1966); *Leucosporidium* spp = *Candida* spp (di Menna, 1960, 1966; Goto et al., 1969; Atlas et al., 1978); *Rhodotorula minuta* = *Rhodotorula texensis* (Goto et al., 1969; di Menna, 1960) and *Rh. pallida*, *Rh. marina* (di Menna, 1966); *Rhodotorula rubra* = *Rh. mucilaginosa* (Soneda, 1961; di Menna; 1966; Atlas et al., 1978); *Sporoblomyces salmonicolor* = *Sp. odorus* (di Menna, 1960); *Vanrija diffluens* = *Candida diffluens* (Goto et al., 1969); *Vanrija humicola* = *Candida humicola* (Goto et al., 1969).

yeasts might have resulted from environmental contamination by clothing or equipment, the process to which we ascribe our own isolation from certain soil samples of cellulolytic *Chaetomium* sp. which freezing would certainly have killed before fruiting could be completed in situ. The possibility of deposition from the airspora of common mesophilic yeast (*Tr. cutaneum*, for example) reported only rarely or as minor components of the Antarctic yeast microbiota must also be considered. The only mesophile reported as common in Antarctic sites (including the Asgard Range), *Aureobasidium pullulans*, was reprorted by only one expeditionary force. We have felt justified, therefore, in considering further only reports of psychrophilic isolates.

The psychrophilic strains of *Cr. laurentii* (the ability of which to produce mycelium is unknown) were isolated by DI MENNA (1966) from soil near glaciers and from coastal areas sufficiently moist to support cryptogamic

plants, with only a single isolate of unspecified temperature responses from Dry Valley soil. A single *Cr. laurentii* isolate reported by VISHNIAC & HEMPFLING (1979) from Dry Valley (Tyrol Valley) soil was amyceliate (unpublished data) and mesophilic. DI MENNAs (1960, 1966) isolates of *Leucosporidium* spp were made from sites similar to those which yielded the psychrophilic *Cr. laurentii* and from poolside or damp organic sand in the Dry Valleys. The location of SINCLAIR & STOKES (1965) Antarctic collections was not specified; the *Leucosporidium* isolates of GOTO et al. (1969) were made from lake water and sediment. Our observations therefore appear to be corroborated by the experience of other investigators.

It is easy to rationalize the hypothesis that the aridity of the Dry Valley highlands selects against yeasts which produce mycelium. Yeasts which are capable of doing so produce mycelium when growth is slowed by the exhastion of readily assimilable substrates. The directions for inducing both myceliation by anamorphic yeasts and sexual reproduction specify 'lean' media (VAN DER WALT & YARROW 1984). (Sexual reproduction in basidiomycetous yeasts involves mycelium formation.) Switched to the mycelial morph, yeasts lose the ability (unusual among eucaryotic vegetative cells) to survive freezing. While there is little quantitative information on the ability of fungal filaments (devoid of spores or yeast cells) to survive freezing, the lethal effects of freezing and of freeze-drying (lyophilization) are common knowledge (MAZUR 1966; CENTRAALBUREAU VOOR SCHIMMELCULTURES 1987). The survival of spores and yeast cells has been attributed to their lower water content.

One of the consequences of the aridity of the highland soils is a depauperate community in which primary production is apparently absent. In any case, energy resources can be as limiting as water in these soils (VISHNIAC & KLINGLER 1988). In contrast, the glacial melt streams and lakes of the McMurdo Dry Valleys are quite productive (HEYWOOD 1984, HOWARD-WILLIAMS et al. 1986), containing a complex community supported by the primary production of cyanobacteria, algae (see PARKER et al. 1981, WHARTON et al. 1983) and the southernmost moss, *Bryum* cf. *algens* (KASPAR et al. 1982). The yeast population of the Taylor Valley glacial melt stream was correspondingly larger and presumably grew sufficiently rapidly that some yeast cells and/or sexual spores were always present at the onset of freezes. In lakes, the ability to survive freezing may not be required. While melt streams and damp soil minimally undergo daily freezing, some lake depths are sufficiently warmed by geothermal heat as to remain permanently unfrozen. Biothermal effects have been implicated in the growth of sunken glacial communities (cryoconite holes), in which primary production also occurs (WHARTON et al. 1985).

But it is conceivable that other factors have selected the yeasts of arid soils. The effects of water are clearly complex; our hypothesis has not been tested experimentally. GOLUBEV et al. (1984) have suggested that capsulated yeasts survive desiccation better than acapsulate species. However, the dominant *Cryptococcus* biotypes of the arid highlands (unlike more widely known *Cryptococcus* species) have capsules which are no thicker than those of *l. scottii* (BAHARAEEN & VISHNIAC 1981).

In the absence of any rationale connecting other morphological differences between these yeasts with effects of aridity, we have compared (faute de mieux) the physiological characters used in identification of all of the psychrophilic species recorded from the three habitat types (arid unglaciated valleys and plateaus, arid glaciated valleys, glaciers and their melt streams and lakes). Such comparisons do not encompass the full potential of yeast physiology; characteristics which are not included in the standard descriptions have been shown to be of major signifcance in other habitats (see PHAFF & STARMER 1987).

The availability of appropriate nitrogen resources should not prevent *Leucosporidium* species from colonizing the arid highlands, since all described *Leucosporidium* species utilize nitrate, relatively abundant in Dry Valley soils (WADA et al. 1981, CLARIDGE & CAMPBELL 1977, CAMERON 1974, VISHNIAC & KLINGLER 1988). Microbes unable to utilize nitrate must depend upon biogenic N-resources in Dry Valley soils; such yeasts have been referred to as 'social' (VISHNIAC 1985a). In fact, 'social' yeasts, unable to utilize nitrate-N (and in one case with a growth factor requirement), are included in the list of our highland isolates above, though the number of such biotypes was insufficient to distinguish it statistically from the number of isolates of exogenous yeasts (VISHNIAC & KLINGLER 1988).

The carbon resources of Antarctic soil and water have not been analysed. The combined substrate assimilation profiles of communities can, however, be a useful indicator of habitat characteristics (see PHAFF & STARMER 1987). In arid highland soils, the dominant heterotrophs were psychrophilic yeasts characterized above as assimilating (besides glucose) 1—13 carbon sources, an average of 8.54 ± 2.89, from among L-arabinose, cellobiose, citrate, D-gluconate, glucuronate, glycerol, 2-ketgluconate, maltose, melezitose, α-methyl glucoside, raffinose, rhamnose, salicin, soluble starch, succinate, sucrose, trehalose, and xylose. One is hampered in comparing well-watered sites by uncertainty as to biotype characteristics, since most yeast isolates have been

identified only as species in which some assimilation characters are variable. We have accordingly used for our calculations only the invariable (i. e., minimal) assimilations for psychrophilic isolates described by others, combining these with our data (above). Yeasts of well-watered sites used 1—22 carbon sources, an average (minimally) of 11.25 ± 8.39. The high standard deviation indicates that two populations of yeast species are described: the *L. antarcticum*-like biotypes with a very restricted range of substrate utilization (3.67 ± 1.75) and a group, including all other yeasts, which is much more versatile (minimally 18.83 ± 3.71 substrates assimilated). It is probably significant in terms of habitat description that both groups assimilate substrates of a class, polyols, which are not utilized by the yeasts of the arid highlands. All other species of *Cryptococcus* assimilate at least D-glucitol, D-mannitol, and *myo*-inositol (sometimes variably), as did most of the psychrophilic *Cr. albidus* strains which we isolated from the soil of glaciated University Valley. The described species of *Leucosporidium* (with the exception of 2 which do not assimilate *myo*-inositol) also assimilate these polyols, though sometimes slowly or variably, but the *L. scottii*-like isolate from the arid highlands did not. One or another of the psychrophilic yeasts of well-watered sites is capable of assimilating each of the 35 substrates we have used (BARNETT et al. 1983, KREGER-VAN RIJ 1984c). The psychrotrophic/mesophilic yeasts of these sites need not be considered, since they add nothing to the substrate utilization spectrum. (This would not be true for the psychrotrophic *Cr. albidus* isolate from arid Linnaeus Terrace; the radically different substrate profile of this single isolate, taken with its higher maximal growth temperature, has led us to suspect that it was exogenous.) It appears, then, that the carbon resources of the arid highlands should be assimilable by all of the yeasts of well-watered sites except some biotypes of *L. antarcticum*. We are left with no alternative hypothesis for the restriction of myceliating yeast to well-watered sites.

A character which is subject to selection pressure may reasonably be expected to have systematic value. The ability to form pseudo- and true mycelium has been a controversial character in yeast systematics. The production of mycelium and pseudomycelium was used, on an empirical basis, to distinguish the genus *Candida* Berkhout from the genus *Torulopsis* Berlese and as part of the constellation of characters defining the genus *Cryptococcus* Kützing emend Phaff et Spencer. The contradictions resulting from this use (VAN UDEN & BUCKLEY 1970) led YARROW & MEYER (1978) to transfer the species classified in *Torulopsis* to *Candida*. The genus *Candida* thus constituted (see MEYER et al. 1984) is a vast assemblage of species so unrelated as to belong to two classes of fungi. Since the utility of a characteristic may vary from taxon to taxon, it ist more pertinent here to discuss the genus *Cryptococcus*. Earlier descriptions of *Cryptococcus* as lacking more than rudimentary pseudomycelium were confirmed by RODRIGUES DE MIRANDA (1984). However, GOLUBEV, having induced pseudomycelium formation in several species of *Cryptococcus* (1980), transferred several pseudomycelium and/or mycelium producing *Vanrija* or basidiomycetous *Candida* species to *Cryptococcus* (GOLUBEV 1981). Pseudomycelium production as a result of mutagen-induced failure of buds to separate does not appear immediately relevant to the definition of this genus. But while we consider these transfers inappropriate for other reasons, some generally accepted species of *Cryptococcus* have been described as producing mycelium and/or pseudomycelium on occasions which did not appear to involve sexual reproduction.

In the case of *Cryptococcus laurentii*, it is possible that more than one taxon has been included in the species (KURTZMAN 1973). *Candida podzolica* (a basidiomycetous yeast assignable to *Vanrija*) differs from *Cr. laurentii* only in variable assimilation characters, leading MEYER et al. (1984) (but neither RODRIGUES DE MIRANDA 1984, nor BAHARAEEN & VISHNIAC 1984) to consider these species synonymous. In our opinion, the figures of *Cryptococcus laurentii* exhibiting clampless mycelium and pseudomycelium published by BOIDIN et al. (1963) resemble the type of *C. podzolica* rather than that of *Cr. laurentii*. The same objection cannot be made to the figure of GOLUBEV et al. (1977), of clampless mycelium and yeast cells, Myceliating strains ascribed to *Cr. laurentii* will conjugate (KURTZMAN 1973, RODRIGUES DE MIRANDA 1974), but not with the type strain of this genus. Since these conjugants fail to complete the process of sexual reproduction, the teliomorph has yet to be described. Further investigations are obiously desirable.

Further investigations might also clarify the nuclear status of apparently anamorphic myceliating strains. the only myceliating anamorph related to *Cryptococcus* species which is indubitably capable of mating and completing basidiospre production is the type strain of mating type a of *Filobasidium capsuligenum*, which regularly produced branched, septate mycelium (see KWON-CHUNG % FELL 1984). The anamorphs of this species have never been attributed to the genus *Cryptococcus*, though related at the generic level to *Cr. uniguttulatus* (anamorph of *F. uniguttulatum*) (BAHARAEEN & VISHNIAC 1984, KWON-CHUNG & FELL 1984). Early reports of myceliating strains of *Cryptococcus neoformans*, strains later shown to be genuine members of this species (ERKE & SCHNEIDAU 1973), were clarified when SHADOMY (1970) pointed out that the clamped hyphae belonged to "another growth phase ot the organism", i. e. abortive sexual reproduction. Completed sexual reproduction was

described only in 1975 (KWON-CHUNG 1975), in the teliomorph *Filobasidiella neoformans*. The pseudohyphae of this species figured by FREED et al. (1971) were arguably teratologies, since they could only be found in spinal fluid. The ability of *Cr. neoformans* to produce pseudohyphae was much better established by the elegant experiments of NEILSON et al. (1978), demonstrating the selective pressure exerted against the yeast morph by predation. A pathogenic pseudohyphal strain reverted in the mouse, but the nature of selective pressures favoring the yeast morph was unknown. These strains did not produce true mycelium, but did exhibit occasional clamp connections, suggesting anomalies in nuclear condition. Such strains are not known to occur in nature.

It is at this point uncertain whether haploid, monokaryotic *Cryptococcus* strains rarely or never produce pseudo- or true mycelium, though the instance of *F. capsuligenum* suggests that this might occur in some species. This uncertainty need not prevent the use of mycelium or pseudomycelium production in identification. For purposes of identification, rare or rarely expressed characters can be accomodated in the probalistic computer programs now available. For the purpose of understanding the evolution of yeasts, understanding of the selective pressures affecting phenotypic characters is as valuable as molecular measures of evolutionary distance. The cold aridity of the McMurdo Dry Valleys has provided an environment which favors the yeast morph over the mycelial morph in basidiomycetous yeasts. This evidence of selective pressure suggests that mycelium production is presently an undervalued character with potential usefulness in a systematics which is consistent with phylogenetic relationships. Temporary cold and arid conditions in other ecosystems may have been among the factors responsible for the development (or retention) of yeast morphs in unrelated fungal taxa. Only in the Antarctic can an environment be found which clearly favors free-living yeast morphs.

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