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The yeast genus *Yarrowia* gen. nov.

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The ascigerous teleomorph of *Candida lipolytica* (Harrison) Diddens et Loder, previously classified as *Endomycopsis lipolytica* Wickerham et al. and as *Saccharomycopsis lipolytica* (Wickerham et al.) Yarrow, has been assigned to the new genus *Yarrowia*. *Yarrowia lipolytica* (Wickerham et al.) comb. nov. is the type species for the genus.

The remaining species of *Saccharomycopsis* are revised.

INTRODUCTION

Although the sexual stage of *Candida lipolytica* is well documented, its taxonomic position is still unsettled. Wickerham et al. (1970) first discovered that this saprobic, markedly lipolytic species, in fact constituted haploid mating types of a filamentous, heterothallic, ascigerous teleomorph. This teleomorph was reported to form solitary, lateral or terminal, ovoid, clavate, ellipsoidal, spheroidal, rarely cylindrical, sessile or pedunculate, one- to four-spored asci borne on branching, septate hyphae. Blastospores rarely produced asci. As there was no evidence for conjugation immediately preceding ascus formation, it was assumed that the ascigerous hyphae were diploid. Sporulating cultures were reported to become light pink or brown. The ascospores were described as varying in shape, ranging from spherical, spheroidal, angular, hemispheroidal, crateriform to hat-shaped (galeate) with a basal brim. Wickerham et al. (1970) published this teleomorph as *Endomycopsis lipolytica* Wickerham, Kurtzman et Herman.

As the generic name *Endomycopsis* Dekker was subsequently shown to be an obligate synonym of *Saccharomycopsis* Schiönnig (van der Walt and Scott, 1971; von Arx, 1972), Yarrow (1972) reclassified this teleomorph as *Saccharomycopsis lipolytica* (Wickerham et al.) Yarrow.

Redhead and Malloch (1977) revised the Endomycetaceae and included in it

the Ascoideaceae. They redescribed *Endomyces decipiens* Reess, the type species of the genus, a mycelial yeast growing on gills of *Armillaria mellea*, and restricted the family to taxa with galeate (hat- or helmet-shaped) ascospores. Some non-filamentous yeast genera, such as *Hansenula*, were also included in the Endomycetaceae. Excluded from the family were taxa with spherical, elongate, oblate or saturn-shaped ascospores.

According to this concept, the genus *Saccharomycopsis* Schiöningg *sensu* von Arx et al. (1977) appears to be heterogeneous. The type species, *S. capsularis* Schiöningg, has bivalvate, oblate or nearly spherical, smooth-walled, rather large ascospores with an indistinct equatorial rim (von Arx, 1974). Such ascospores are unknown in other yeast genera, but have been observed in *Narasimhella hyalinospora* (Küehn et al.) von Arx, an ascomycete classified in the Gymnoascaceae (von Arx, 1971).

Saccharomycopsis fibuligera (Lindner) Kloecker has galeate ascospores, similar in size and shape to those of *Endomyces decipiens*. In both species the asci develop on undifferentiated hyphae and are usually 4-spored. *S. fibuligera* therefore has to be treated as *Endomyces fibuliger* Lindner, as it was originally named.

Saccharomycopsis vini (Kreger-van Rij) van der Walt et Scott and *Saccharomycopsis crataegensis* Kurtzman et Wickerham, on the other hand, are both characterized by spiny, saturn-shaped ascospores which become markedly pigmented during maturation. In this respect and also on the basis of their formation of clavate conidia with a truncate base, these two species show close agreement with *Endomycopsella phaeospora* Boedijn (1960). Consequently, these two species have to be classified in *Endomycopsella* as ***Endomycopsella vini*** (Kreger-van Rij) von Arx comb. nov. (basionym *Endomycopsis vini* Kreger-van Rij, *Antonie van Leeuwenhoek* 30: 430, 1964) and ***Endomycopsella crataegensis*** (Kurtzman et Wickerham) von Arx comb. nov. (basionym *Saccharomycopsis crataegensis* Kurtzman et Wickerham, *Antonie van Leeuwenhoek* 39: 83, 1973). These two species show the same carbohydrate pattern of their cell walls as *S. fibuligera*, with mannose and glucose as the main constituents and small amounts of glucosamine (chitin) (A. C. M. Weijman, pers. comm.).

Saturn- or walnut-shaped, pitted or rugose ascospores are also known in non-filamentous yeast genera, e.g. *Schwanniomyces* Kloecker and *Williopsis* Zender containing soil-borne species. Also rather similar are the ascospores in the soil-borne filamentous yeast *Arthroascus javanensis* (Kloecker) von Arx (von Arx, 1972a, 1974). Saturn-shaped, often rugose or spiny ascospores with equatorial rims or rings are also typical for many Trichocomaceae (Eurotiaceae), especially for the teleomorphs of *Aspergillus* species (cf. Raper and Fennell, 1965; Samson, 1979). Redhead and Malloch (1977) therefore suggested a relationship with this group of cleistocarpous ascomycetes.

Saccharomycopsis lipolytica differs from all the above-mentioned genera in the structure of its ascospores which are variable in both size and shape. Free, mature ascospores are usually hemi-ellipsoidal, navicular in side view, with

apical, cap-like appendages (Fig. 1). Lateral projections may also be present. Other distinguishing characters are the cylindrical or ovate conidia with scars and the coenzyme Q9 system (Yamada et al., 1976). The coenzyme Q9 system is not characteristic for the Endomycetales, but appears to be widely distributed among the heterobasidiomycetous yeasts. Typical members of the Endomycetaceae and Saccharomycetaceae show the coenzyme Q systems 6, 7 or 8. Exceptions are mainly restricted to the genera *Debaryozyma* van der Walt et Johanssen (1978), which shows the coenzyme Q9 system, and *Schizosaccharomyces* Beijerinck, where some species show the coenzyme Q9 and others the coenzyme Q10 system.

Esser and Stahl (1976) studied this fungus cytologically and genetically. Its hyphal septa show a minute, ascomycete-type pore (Kreger-van Rij and Veenhuis, 1973).

The teleomorph of *Candida lipolytica* consequently takes an isolated position in the Endomycetales, with direct relatives not being known. The positive urease reaction and G + C values of 49.5–50.2% reported for DNA of this species (Nakase and Komagata, 1971), although high for an ascomycetous yeast, provide no clue to its possible filiation. In the carbohydrate composition of the whole cell, *C. lipolytica* differs from the other above-mentioned species by the presence of galactose. In this respect it corresponds with *Dipodascus* Lagerberg and its *Geotrichum* anamorphs (Weijman, 1977, 1979). As no generic name is available for the teleomorph, it is proposed that it be assigned to the new genus *Yarrowia*.

DESCRIPTION

Yarrowia van der Walt et von Arx gen. nov. (Endomycetales) (Fig. 1, a–d)

Cellulae zymoticae gemmiferae, pseudohyphae et hyphae septatae, ramosae. Hyphae 2–4 µm latae. Conidia ellipsoidea, pyriformia, clavata, cylindrica, sessilia in hyphis vel e cellulis conidiogenis denticulatis oriunda, cicatricibus fere distinctis praedita, 4–18 × 3–6 µm. Asci solitarii, laterales vel terminales, ovoidei, clavati, ellipsoidei vel sphaeroidales, raro cylindrici, sessiles vel pedunculati, raro liberi, persistentes, 1–2(–4) spori, 6–15 × 5–8 µm. Ascosporae globosae, sphaeroidales, ellipsoideae, juglandiformes, saturnoideae vel angulares, naviculares, crateriformes vel galeatae, margine angusto basilari circumdatae, torulosae, rugosae vel foveatae. 3.5–6 × 3–4 µm. Systema coenzymatis Q-9 adest.

Species typica: *Yarrowia lipolytica* (Wickerham, Kurtzman et Herman) van der Walt et von Arx comb. nov. (basionym: *Endomycopsis lipolytica* Wickerham, Kurtzman et Herman in Spectrum, Monogr. Ser. Arts Sci., Georgia State Univ. 1: 90. 1970). Anamorphosis *Candida lipolytica* (Harrison) Diddens et Lodder.

Budding cells, pseudohyphae and septate branching hyphae, 2–4 µm wide, present. Conidia ellipsoidal, pyriform, clavate or cylindrical, sessile on hyphae or

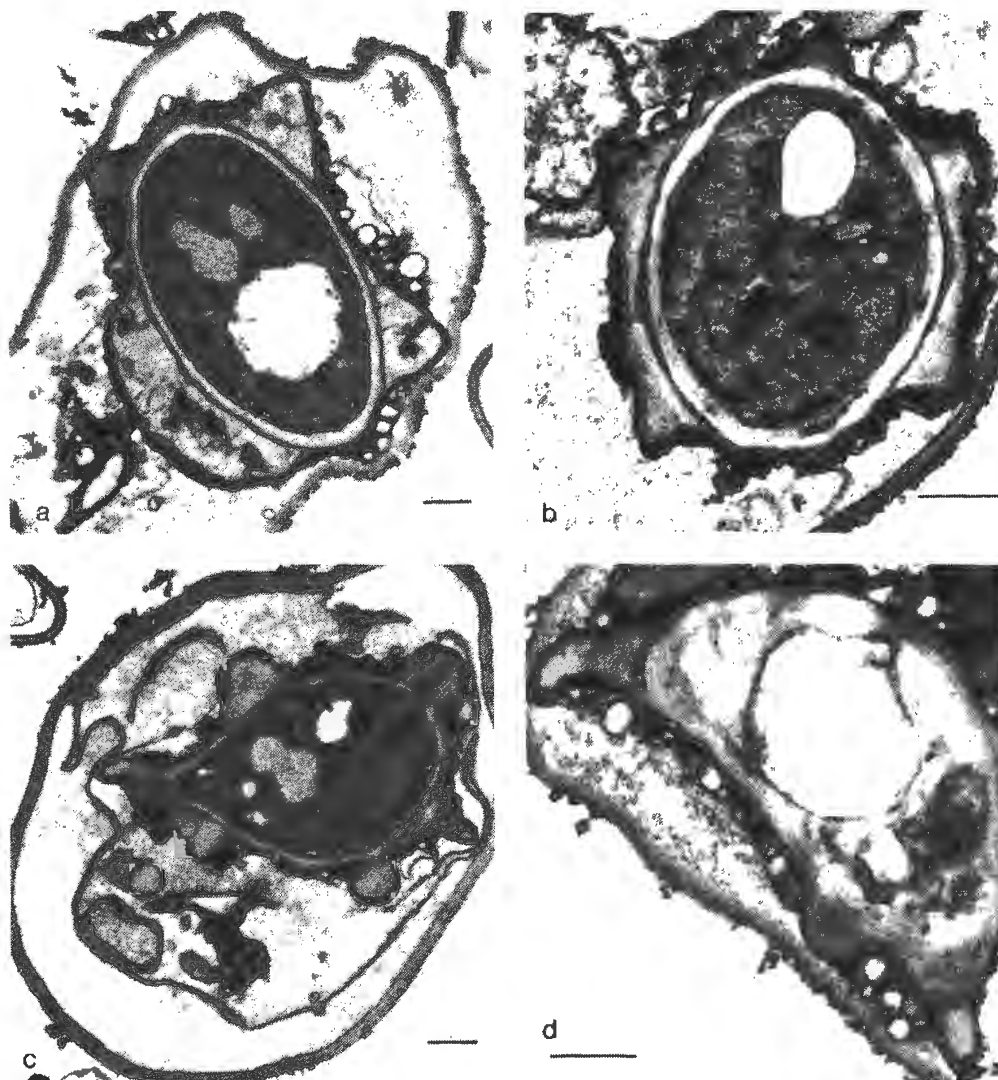


Fig. 1. *Yarrowia lipolytica*. TEM micrographs of ultra-thin sections of asci showing ellipsoidal (a, b), tapering (c), or navicular (d) ascospores, which are surrounded by an outer wall with irregular protrusions. The insert bar represents 0.5 μm . (Material fixed in 1.5% potassium permanganate and stained with uranyl acetate and Reynolds' lead citrate.)

formed on denticulate conidiogenous cells, with rather conspicuous scars, 4–18 $\times$ 3–6 μm . Asci solitary, lateral or terminal, ovoid, clavate, ellipsoidal or spheroidal, rarely cylindrical, sessile or pedunculate, rarely free, rather thick-walled and persistent, 1–2- (–4-) spored, 6–15 $\times$ 5–8 μm . Ascospores spherical, spheroidal to ellipsoidal, walnut-shaped, saturnoid to angular, navicular, crateriform or galeate with a narrow basal brim, torulose, rugose or pitted, 3.5–6 $\times$ 3–4 μm . Coenzyme Q-9 system present.

Etymology: The genus is named in honour of David Yarrow in recognition of his contributions to yeast systematics.

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