

The treasure trove of yeast genera and species described by Johannes van der Walt (1925–2011)

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Abstract: Yeast taxonomy and systematics have in recent years been dealt with intensively primarily by a small group of individual researchers with particular expertise. Amongst these was Johannes P. van der Walt, who had a major role in shaping our current understanding of yeast biodiversity and taxonomy. Van der Walt based his taxonomic studies not only on available cultures, but also by going into the field to isolate yeasts from various substrates. This pioneering work led to the discovery of many new genera and species, which were deposited in the Centraalbureau voor Schimmelcultures (CBS) collections for future studies in taxonomy, genomics, and industrial uses. These treasures collected during more than 60 years provide an outstanding legacy to the yeast community and will continue to exist in his absence. This contribution provides a comprehensive overview of the current nomenclatural and taxonomic status of the yeast genera and species introduced by van der Walt during his career.

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INTRODUCTION

Johannes van der Walt passed away after a short illness on 13 November 2011. He will be remembered as a person very much interested in the biodiversity of yeasts, a passion which is apparent from the many yeast strains representing novel taxa that he isolated from various, mainly South African, sources.

The first yeast species that was isolated in South Africa was from an infected human nail and was described as *Hanseniaspora guilliermondii* by Adrianus Pijper (Pijper 1928), a pathologist practicing in Pretoria. The type strain of this species was deposited by Pijper in the yeast collection of the Centraalbureau voor Schimmelcultures (CBS), at that time located in Delft. The yeast collection had been transferred from Baarn to Delft after the appointment of Albert Jan Kluver as Professor of Microbiology of the Technical University in Delft in 1921 (Samson *et al.* 2004), and came back together with the CBS filamentous fungal collection in Utrecht in 2000.

As a result of Pijper's mediation, Johannes van der Walt started to study for his PhD in Delft under the guidance of Kluver in 1949, obtaining his degree in 1952 for a thesis entitled "On the yeast *Candida pulcherrima* and its pigment pulcherrimine" (van der Walt 1952). It was also in Delft that van der Walt was instructed in the use of specific enrichment techniques for the isolation of soil-borne microorganisms. After his return to South Africa in 1952, van der Walt started to search for novel yeast species. Applying a wide range

of enrichment methods, van der Walt and his collaborators spent almost 50 years hunting intermittently for new taxa associated not only with natural sources such as uncultivated grassland soils, arboricolous beetle infestations and other similar niches, but also manufactured products such as wine and beer. This broad-based survey led to the discovery of many novel sexual and asexual ascomycetous taxa and some of heterobasidiomycetous affinity. Some of these species are still only known from South African isolates.

Although originally trained in chemistry, van der Walt developed a great interest in the systematics, ecology, and genetics of yeasts. His interest in yeast systematics was a consequence having the CBS yeast collection close to his work-place in Delft, facilitating his study of these organisms. From that time, van der Walt maintained strong connections with the CBS, consulting their yeast taxonomists on taxonomic problems, and by depositing 492 strains in the collection. These strains formed the basis for 20 new genera and 109 new species. Because of his broad knowledge of enrichment techniques, but also of yeast systematics, van der Walt was invited to contribute several chapters to the second and third editions of *The Yeasts: a taxonomic study* (Lodder 1970, Kreger-van Rij 1984).

Van der Walt's broad knowledge of yeasts and his discovery of previously unrecognized genera and species was much respected by other yeast taxonomists, who named four genera and four species in his honour: *Vanderwaltia* (Novak & Zsolt 1961; now included in *Hanseniaspora*), *Waltomyces* (Yamada & Nakase 1985; now included in

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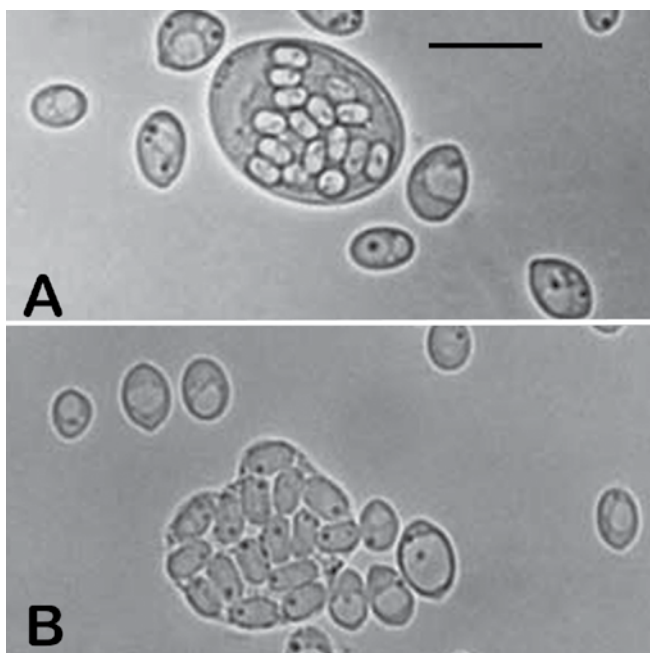


Fig. 1. Asci with ascospores of *Kluveromyces polysporus* (*Vanderwaltozyma polyspora*) After Barnett *et al.* (2000). **A.** YM agar, 16 d. **B.** McClary acetate agar, 2 weeks. Bar = 5 μ m.



Fig. 2. Three famous yeast taxonomists (left to right): Herman J. Phaff, Nico van Uden, and Johannes P. van der Walt. Photograph taken in 1987 at the international symposium "The expanding realm of yeast-like fungi", Amersfoort, The Netherlands.

Lipomyces), *Waltiozyma* (Muller & Kock 1986; now included in *Wickerhamomyces*), *Vanderwaltozyma* by Kurtzman (2003), *Torulopsis vanderwaltii* (Vidal-Leira 1966; reclassified by Yarrow & Meyer 1978, as *Candida vanderwaltii*), *Kluveromyces waltii* (Kodama 1974; reclassified by Kurtzman 2003, as *Lachancea waltii*), *Myxozyma vanderwaltii* (Spaaij *et al.* 1993), and *Bullera waltii* (Sugita *et al.* 1999; reclassified by Wang & Bai 2008, as *Dexomyces waltii*).

In the early years of taxonomy, a group of scientist that included Johannes van der Walt, Nico van Uden and Herman J. Phaff (Fig. 1), as well as Lynford J. Wickerham, made a huge contribution by using phenotypic characteristics of morphology and physiology for the description of novel

genera and species. At that time, these features were considered as important for generic assignment and species distinction. One relevant practical contribution for species characterization was the introduction of the Diazonium Blue B (DBB) test by van der Walt & Hopsu-Havu (1976). In cases where the sexual cycle of a yeast was unknown, this DBB test could be used by yeast taxonomists to determine whether the yeast had an ascomycetous or basidiomycetous affinity. Basidiomycetous yeasts gave a dark red colour reaction when the DBB solution was applied, while this reaction was absent in ascomycetous yeasts.

Since the 1970s, following the trends set for bacterial taxonomy, molecular criteria such as mol% G+C and DNA-DNA hetero-duplex formations, and later gene sequencing, were introduced for the yeasts. Today, the introduction of novel species is predominantly based on molecular information obtained by sequencing one or several genes. This evolution in yeast taxonomy can be reconstructed from the five monographs on yeasts that have been published over the years (Lodder & Kreger-van Rij 1952, Lodder 1970, Kreger-van Rij 1984, Kurtzman & Fell 1998, Kurtzman *et al.* 2011).

YEAST GENERA

Between 1964 and 1995, twenty novel yeast genera were introduced by van der Walt (Table 1). The first of these genera was *Dekkera*. Species of this genus are known as spoilage organisms of soft drinks and alcoholic beverages (Dequin *et al.* 2003, Dufour *et al.* 2003, Stratford & James 2003). Besides *Dekkera*, seven more genera were introduced by van der Walt as single author. Of the remaining genera, eight were published in collaboration with researchers at CBS and four with other authors.

As a consequence of the application of DNA sequence comparisons, eight of these genera were not accepted in the most recent edition of *The Yeasts* (Kurtzman *et al.* 2011), but were reduced to synonymy (Table 1). The generic name *Debaryozyma* (van der Walt & Johannsen 1978) was not accepted because the proposal of Lodder & Kreger-van Rij (1978) to conserve the name *Debaryomyces* was approved (Greuter *et al.* 1988) The monospecific genus *Wingea* is not now retained because the type species of this genus was phylogenetically shown to belong in *Debaryomyces* (Suzuki *et al.* 2012). Further, since the ex-type culture *Aessosporon* was found to mate with strains of *Sporidiobolus salmonicolor* (Sampaio 2011, unpubl.), this generic name can be considered a synonym of the earlier *Sporidiobolus*. The status of the genus *Entelexis* is uncertain; Lachance *et al.* (2011) commented on this in a discussion of *Candida magnolia* (previously *Torulopsis magnoliae*), since that species was indicated as the type species of *Entelexis* by van der Walt & Johannsen (1973).

YEAST SPECIES

Van der Walt was (co-)responsible for the introduction of 109 novel yeast species during the period 1956 to 1999 (Table 2).

Table 1. Genera introduced by van der Walt and co-authors.

Year	Genus	Author(s)	Present generic status ¹ (year of description of the genus)
1964	<i>Dekkera</i>	Van der Walt	Recognized
1970	<i>Aessosporon</i>	Van der Walt	Not recognized (ex-type culture mates with <i>Sporidiobolus salmonicolor</i>)
1971	<i>Kluyveromyces</i>	Van der Walt	Recognized
	<i>Lodderomyces</i>	Van der Walt	Recognized
	<i>Cyniclomyces</i>	Van der Walt & D.B. Scott	Recognized
	<i>Wingea</i>	Van der Walt	Not recognized (type species belongs to the genus <i>Debaryomyces</i>)
1972	<i>Ambrosiozyma</i>	Van der Walt	Recognized
1973	<i>Wickerhamiella</i>	Van der Walt	Recognized
	<i>Entelexis</i>	Van der Walt & Johannsen	Not recognized (status of the genus uncertain)
1976	<i>Hyphopichia</i>	Arx & van der Walt	Recognized
	<i>Stephanoascus</i>	M.T. Sm., Van der Walt & Johannsen	= <i>Trichomonascus</i> (1947)
1978	<i>Pachytichospora</i>	Van der Walt	= <i>Kazachstania</i> (1971)
	<i>Debaryozyma</i>	Van der Walt & Johannsen	Not recognized (the genus name <i>Debaryomyces</i> is conserved)
1980	<i>Yarrowia</i>	Van der Walt & Arx	Recognized
1981	<i>Myxozyma</i>	Van der Walt, Weijman & Arx	Recognized
	<i>Arxiozyma</i>	Van der Walt & Yarrow	= <i>Kazachstania</i> (1971)
1987	<i>Zygozyma</i>	Van der Walt & Arx	= <i>Lipomyces</i> (1952)
1990	<i>Arxula</i>	Van der Walt, M.T. Sm. & Y. Yamada	= <i>Blastobotrys</i> (1967)
1995	<i>Babjevia</i>	Van der Walt & M.T. Sm.	= <i>Dipodascopsis</i> (1978)
	<i>Smithiozyma</i>	Kock, Van der Walt & Y. Yamada	= <i>Lipomyces</i> (1952)

¹ Present status in Kurtzman *et al.* (2011)

Of the taxa compiled in Table 2, 30 species were described by van der Walt alone, 15 in collaboration with co-authors at the CBS, and the remaining species with mycologists in other countries. Most of the type strains of these species are isolates from South African sources, and only 20 are from elsewhere. Thirty types were isolated from soil in different localities of South Africa; eight came from vegetable material; 35 from insect-related sources such as frass, tunnels or insect guts; ten are from processed food products such as beer, wine, and buttermilk; and three are from lichens.

One of the highlights of his career was the isolation of a strain that produced asci with more ascospores than the normal 1–4 ascospores which he described as *Kluyveromyces multisporus* (now *Vanderwaltozyma polyspora*; Fig. 2). One of his new species, *Saccharomyces inusitatus*, is now considered to have a hybrid genome on the basis of DNA/DNA reassociation experiments by A. Vaughan and A. Martini (Kurtzman *et al.* 2011) with high levels of similarity to both *S. bayanus* (94 %) and *S. pastorianus* (91 %).

Van der Walt introduced 16 new combinations of species of which the basionyms were described previously by other yeast taxonomists. As these species are not seen as species first introduced by van der Walt we have not included them in Table 2. These species names, introduced by van der Walt on basis of basionyms of other yeast taxonomist and presently recognized, are listed below:

Ambrosiozyma monospora (Saito) Van der Walt 1972
Ambrosiozyma platypodis (J.M. Baker & Kreger) Van der Walt 1972

Cyniclomyces guttulatus (C.P. Robin) Van der Walt & D.B. Scott 1971
Hyphopichia burtonii (Boidin *et al.*) Arx & Van der Walt 1976
Kluyveromyces aestuarii (Fell) Van der Walt 1971
Kluyveromyces dobzhanskii (Shehataet *al.*) Van der Walt 1971
Kluyveromyces lactis (Dombrowski) Van der Walt 1986
Kluyveromyces marxianus (E.C. Hansen) Van der Walt 1971
Kluyveromyces wickerhamii (Phaff *et al.*) Van der Walt 1971
Lodderomyces elongisporus (Recca & Mrak) Van der Walt 1971
Myxozyma melibiosi (Shifrine & Phaff) Van der Walt *et al.* 1981
Myxozyma mucilagina (Phaff *et al.*) Van der Walt *et al.* 1981
Saccharomycopsis vini (Kreger-van Rij) Van der Walt & D.B. Scott 1971
Torulaspota globosa (Klöcker) Van der Walt & Johannsen 1975
Torulaspota microellipsodes (Osterwalder) Van der Walt & E. Johannsen 1975
Yarrowia lipolytica (Wickerham *et al.*) Van der Walt & Arx 1980

CONCLUSIONS

Most of the species described early in his career by van der Walt were based on phenotypic features, and, as with genera, molecular data have led to the revision of the status of species described in the “pre-molecular era”. This is

Table 2. Species introduced by van der Walt and co-authors.

Year	Species name	Authors	Type strains of South African source	Type strains from other source	Present status of the type strain ¹
1956	<i>Kluyveromyces africanus</i>	Van der Walt	Soil		= <i>Kazachstania africana</i>
	<i>Saccharomyces transvaalensis</i>	Van der Walt	Soil		= <i>Kazachstania transvaalensis</i>
	<i>Saccharomyces delphensis</i>	Van der Walt & Tschuschner	Dried figs		= <i>Nakaseomyces delphensis</i>
	<i>Saccharomyces capensis</i>	Van der Walt & Tschuschner	Soil		= <i>Saccharomyces cerevisiae</i>
	<i>Pichia vanriji</i> (= <i>P. vanriji</i>)	Van der Walt & Tschuschner	Soil		= <i>Schwanniomyces vanriji</i> var. <i>vanriji</i>
	<i>Saccharomyces pretoriensis</i>	Van der Walt & Tschuschner	Soil		= <i>Torulopsis pretoriensis</i>
1957	<i>Kluyveromyces polysporus</i>	Van der Walt	Soil		= <i>Vanderwaltozyma polyspora</i>
	<i>Hanseniaspora vineae</i>	Van der Walt & Tschuschner	Soil		Recognized
	<i>Saccharomyces telluris</i>	Van der Walt	Soil		= <i>Kazachstania telluris</i>
	<i>Hansenula beijeirnickii</i>	Van der Walt	Soil		= <i>Lindnera saturnus</i>
	<i>Saccharomyces lodderae</i>	Van der Walt & Tschuschner	Soil		= <i>Kazachstania lodderae</i>
	<i>Pichia terricola</i>	Van der Walt	Soil		Recognized
	<i>Pichia pipperi</i>	Van der Walt & Tschuschner	Buttermilk		= <i>Wickerhamomyces pipperi</i>
	<i>Candida natalensis</i>	Van der Walt & Tschuschner	Soil		Recognized
1959	<i>Endomyces wickerhamii</i>	Van der Walt	Insect frass		= <i>Barnettozyma wickerhamii</i>
	<i>Pichia robertsii</i> (= <i>P. robertsii</i>)	Van der Walt	Insect		= <i>Debaryomyces robertsii</i>
	<i>Endomyces reessii</i>	Van der Walt		water-rotted <i>Hibiscus cannab</i> is, Indonesia	= <i>Galactomyces reessii</i>
1960	<i>Torulopsis domercqii</i> (= <i>T. domercqiae</i>)	Van der Walt & Kerken	Wine vat		= <i>Wickerhamiella domercqiae</i>
1961	<i>Brettanomyces custerianus</i>	Van der Walt	Brewery		Recognized
	<i>Torulopsis vanzylii</i>	Van der Walt & Kerken	Equipment of wine making		= <i>C. norvegica</i>
	<i>Candida ingens</i>	Van der Walt & Kerken	Wine cellar		= <i>Saprochaete ingens</i>
	<i>Torulopsis cantarellii</i>	Van der Walt & Kerken	Industrial grape must		= <i>Trigonopsis cantarellii</i>
	<i>Torulopsis capsuligena</i>	Van der Walt & Kerken	Wine cellar		= <i>Filobasidium capsuligenum</i>
1962	<i>Schwanniomyces persoonii</i>	Van der Walt	Soil		= <i>S. occidentalis</i> var. <i>persoonii</i>
1963	<i>Saccharomyces vanudenii</i>	Van der Walt & E.E. Nel	Soil		= <i>Kluyveromyces lactis</i> var. <i>drosophilae</i>
	<i>Fabospora phaffii</i>	Van der Walt	Winery equipment		= <i>Tetrapisispora phaffii</i>
1964	<i>Dekkera bruxellensis</i>	Van der Walt		From Belgian stout, Belgium	Recognized
	<i>Dekkera intermedia</i>	Van der Walt		Tea-beer	= <i>Dekkera bruxellensis</i>
1965	<i>Saccharomyces vafer</i>	Van der Walt		Unknown	= <i>Torulopsis delbrueckii</i>
	<i>Saccharomyces inconspicuus</i>	Van der Walt		Grapes, France	= <i>Torulopsis delbrueckii</i>

Table 2. (Continued)

Year	Species name	Authors	Type strains of South African source	Type strains from other source	Present status of the type strain ¹
	<i>Saccharomyces inusitatus</i>	Van der Walt		Beer	Possible hybrid between <i>S. pastorianus</i> and <i>S. bayanus</i> ¹
1966	<i>Kluyveromyces cicerisporus</i>	Van der Walt, E.E. Nel & Kerken		Bantu beer	= <i>Saccharomyces bayanus</i> 2
	<i>Kluyveromyces wikenii</i>	Van der Walt, E.E. Nel & Kerken			= <i>K. marxianus</i>
	<i>Pichia acaciae</i>	Van der Walt	Insect frass		= <i>K. marxianus</i>
1968	<i>Candida edax</i>	Van der Walt	Insect tunnels		= <i>Milleromyza acaciae</i>
	<i>Torulopsis humilis</i>	E.E. Nel & Van der Walt	Bantu beer		= <i>Sugiyamaella smithiae</i>
1970	<i>Saccharomyces amurcae</i>	Van der Walt		"Alpechin", Malaga, Spain	= <i>C. humilis</i>
	<i>Saccharomyces saitoanus</i>	Van der Walt		Sour milk, Japan	= <i>Lachancea fermentati</i>
	<i>Hansenula philodendri</i>	Van der Walt & D.B. Scott	Insect frass		= <i>Torulopora delbrueckii</i>
	<i>Hansenula sydowiorum</i>	D.B. Scott & Van der Walt	Insect frass		= <i>Ogataea philodendri</i>
	<i>Syringospora stellatoidea</i>	Van der Walt		Sputum	= <i>Wickerhamomyces sydowiorum</i>
	<i>Syringospora clausenii</i>	Van der Walt		Unknown	= <i>C. albicans</i>
	<i>Aessosporon salmonicolor</i>	Van der Walt	Carious dentine of man		= <i>C. albicans</i>
	<i>Bullera dendrophila</i>	Van der Walt & D.B. Scott	Insect frass		Synonym of <i>Sporidiobolus salmonicolor</i>
	<i>Sterigmatomyces polyborus</i>	D.B. Scott & Van der Walt	Insect tunnels		Recognized
	<i>Trichosporon melibiosaceum</i>	D.B. Scott & Van der Walt	Insect frass		= <i>Fellomyces polyborus</i>
1971	<i>Pichia ambrosiae</i>	Van der Walt & D.B. Scott	Insect tunnels		= <i>C. fennica</i>
	<i>Pichia cicatricosa</i>	D.B. Scott & Van der Walt	Insect tunnels		= <i>Ambrosiozyma ambrosiae</i>
	<i>Saccharomyopsis synnaedendra</i>	D.B. Scott & Van der Walt	Insect tunnels		= <i>Ambrosiozyma cicatricosa</i>
	<i>Hansenula dryadoides</i>	D.B. Scott & Van der Walt	Insect tunnels		Recognized
	<i>Torulopsis dendrica</i>	Van der Walt, Kliff & D.B. Scott	Insect frass		= <i>Starmera dryadoides</i>
	<i>Candida silvanorum</i>	Van der Walt, Kliff & D.B. Scott	Insect frass		= <i>C. dendrica</i>
	<i>Candida dendronema</i>	Van der Walt, Kliff & D.B. Scott	Insect frass		Recognized
	<i>Candida entomophila</i>	D.B. Scott, Van der Walt & Kliff	Insect tunnels		Recognized
	<i>Torulopsis insectalens</i>	D.B. Scott, Van der Walt & Kliff	Insect tunnels		Recognized
	<i>Torulopsis nemodendra</i>	Van der Walt, Kliff & D.B. Scott	Insect tunnels		= <i>C. insectalens</i>
	<i>Torulopsis silvatica</i>	Van der Walt, Kliff & D.B. Scott	Insect tunnels		= <i>C. nemodendra</i>
	<i>Candida hylophila</i>	Van der Walt, Kliff & D.B. Scott	Insect tunnels		= <i>C. silvatica</i>
					= <i>Rhodotorula hylophila</i>

Table 2. (Continued)

Year	Species name	Authors	Type strains of South African source	Type strains from other source	Present status of the type strain ¹
	<i>Torulopsis phillyla</i>	Van der Walt, Klift & D.B. Scott	Insect tunnels		= <i>Rhodotorula phillyla</i>
1972	<i>Ambrosiomyces philentoma</i>	Van der Walt, D.B. Scott & Klift	Insect tunnels		Recognized
	<i>Pichia melissophilus</i>	Van der Walt & Klift	Gut honey bee		= <i>Priceomyces melissophilus</i>
	<i>Candida nitrivorans</i>	Van der Walt, D.B. Scott & Klift	Insect tunnels		= <i>Wickerhamomyces sydowiorum</i>
	<i>Candida entomaea</i>	Van der Walt, D.B. Scott & Klift	Insect tunnels		= <i>Yamadazyma mexicana</i>
	<i>Candida insectamans</i>	D.B. Scott, Van der Walt & Klift	Insect frass		Recognized
	<i>Candida insectorum</i>	D.B. Scott, Van der Walt & Klift	Insect frass		Recognized
	<i>Candida silvicultrix</i>	Van der Walt, D.B. Scott & Klift	Insect frass		Recognized
	<i>Candida amylolepta</i>	Van der Walt, D.B. Scott & Klift	Insect frass		= <i>Cryptococcus amyloleptus</i>
1973	<i>Wickerhamiella domercqiae</i>	Van der Walt	Wine vat		Recognized
	<i>Candida homilentoma</i>	Van der Walt & Nakase	Insect frass		Recognized
	<i>Candida naeodendria</i>	Van der Walt, Johannsen & Nakase	Insect frass		Recognized
	<i>Entelexis magnoliae</i>	Van der Walt & Johannsen		Flower	= <i>C. magnoliae</i>
	<i>Aessosporon dendrophilum</i>	Van der Walt	Frass of larvae in galleries of <i>Dichrostachys cinerea</i>		= <i>Bullera dendrophila</i>
1975	<i>Hansenula lynferdii</i>	Van der Walt & Johannsen	Soil		= <i>Wickerhamomyces lynferdii</i>
	<i>Pichia philogaea</i>	Van der Walt & Johannsen	Soil		= <i>Yamadazyma philogaea</i>
	<i>Trichosporon terrestre</i>	Van der Walt & Johannsen	Soil		= <i>Blastobotrys terrestris</i>
1976	<i>Stephanosascus ciferrii</i>	M.T. Sm., Van der Walt & Johannsen	Mating type a from soil		= <i>Trichomonascus ciferrii</i>
1978	<i>Pachytichospora transvaalensis</i>	Van der Walt	Soil		= <i>Kazachstania transvaalensis</i>
	<i>Torulopsis azyma</i>	Van der Walt, Johannsen & Yarrow	Lichen		= <i>C. azyma</i>
	<i>Torulopsis geochares</i>	Van der Walt, Johannsen & Yarrow	Soil		= <i>C. geochares</i>
	<i>Candida fermenticarens</i>	Van der Walt	Lichen		Recognized
1980	<i>Debaryozyma yamadadae</i>	Van der Walt & Johannsen	Soil		= <i>Schwanniomyces yamadadae</i>
1982	<i>Hansenula euphorbiaphila</i>	Van der Walt	Flower		= <i>Cyberlindnera euphorbiaphila</i>
	<i>Pichia meyeriae</i>	Van der Walt	Flower		= <i>Cyberlindnera meyeriae</i>
	<i>Pichia kodamae</i>	Van der Walt & Yarrow	Insect infestations		= <i>Ogataea kodamae</i>
1983	<i>Pichia euphorbiae</i>	Van der Walt & Opperman	Flower		= <i>Cyberlindnera euphorbiae</i>
1986	<i>Kluveromyces yarrowii</i>	Van der Walt, Johannsen, Opperman & Halland		Stable mutant of crossing auxothrophic subcultures of CBS 2684 and CBS 6070, both isolated from tanning liquors of bark tree, France	= <i>Vanderwaltozyma yarrowii</i>

Table 2. (Continued)

Year	Species name	Authors	Type strains of South African source	Type strains from other source	Present status of the type strain ¹
1987	<i>Sporobolomyces kluyveri-niellii</i>	Van der Walt	Leaf		Recognized
	<i>Zygozoma oligophaga</i>	Van der Walt & Arx	Insect frass		= <i>Lipomyces oligophaga</i>
	<i>Candida lyxosophila</i>	Van der Walt, N.P. Ferreira & Steyn	Soil		Recognized
	<i>Myxozyma geophila</i>	Van der Walt, Y. Yamada & Nakase	Soil		Recognized
	<i>Myxozyma lipomycooides</i>	Van der Walt, Y. Yamada & Nakase	Lichen		Recognized
	<i>Sterigmatomyces wingfieldii</i>	Van der Walt, Y. Yamada & N.P. Ferreira	Insect frass		= <i>Cryptococcus amylolentus</i>
1988	<i>Sporobolomyces phyllomatis</i>	Van der Walt & Y. Yamada	Leaf		Recognized
1989	<i>Debaryomyces udenii</i>	Van der Walt, M.T. Sm. & Y. Yamada		Soil, Ontario, Canada	Recognized
	<i>Zygozoma arxii</i>	Van der Walt, M.T. Sm. & Y. Yamada	Soil		= <i>Lipomyces arxii</i>
	<i>Lipomyces japonicus</i>	Van der Walt, M.T. Sm., Y. Yamada & Nakase		Garden soil, Japan	Recognized
	<i>Zygozoma suomiensis</i>	M.T. Sm., Van der Walt & Y. Yamada		Skin lesion of a cow, Finland	= <i>Lipomyces suomiensis</i>
	<i>Myxozyma kluyveri</i>	Van der Walt, Spencer-Martins & Y. Yamada	Soil		Recognized
1990	<i>Sporobolomyces phylladus</i>	Van der Walt & Y. Yamada	Leaf		= <i>Bensingtonia phyllada</i>
	<i>Zygozoma smithiae</i>	Van der Walt, Wingfield & Y. Yamada	Insect frass		= <i>Lipomyces smithiae</i>
	<i>Myxozyma udenii</i>	Spaaij, Weber, Oberwinkler & van der Walt		Soil around <i>Magnifera indica</i> , Florida, USA	Recognized
1992	<i>Kluyveromyces piceae</i>	Weber, Spaaij & Van der Walt		Rhizosphere of <i>Picea abies</i> , Germany	= <i>Kazachstania piceae</i>
1997	<i>Lipomyces spencer-martinsiae</i>	(Van der Walt & M.T. Sm.) van der Walt & M.T. Sm.		Soil, Nigeria	Recognized
1998	<i>Myxozyma neglecta</i>	Spaaij, Van der Walt & Weber-Spaaij	Cactus		Recognized
1999	<i>Lipomyces doorenjongii</i>	Van der Walt & M.T. Sm.	Soil		Recognized
	<i>Lipomyces kockii</i>	M.T. Sm. & Van der Walt	Soil		Recognized
	<i>Lipomyces mesembrius</i>	Van der Walt & M.T. Sm.	Soil		Recognized
	<i>Lipomyces yamadadae</i>	Van der Walt & M.T. Sm.	Soil		Recognized
	<i>Lipomyces yarrowii</i>	M.T. Sm. & Van der Walt		Soil, Mauritius	Recognized

¹ Present status in Kurtzman et al. (2011)

evident by comparing the initial status of the species with that in the present classification. From Table 2, it can be seen that 20 species were placed in synonymy with existing taxa, while 54 species were reassigned to different genera and are still recognized as well defined species. However, even after the addition of DNA sequence data, 34 species have retained their original status and stand as tribute to a great yeast taxonomist.

Even after his official retirement, van der Walt did not lose his passion for isolating interesting yeasts. For example, in 2010, over 20 years later, in collaboration with Teresa Coutinho, mating types of the presumed asexual species *Candida deformans* were isolated from lichens and soil (Groenewald & Smith, unpubl.). The last manuscript that he was actively involved with, resolving species within the *Geotrichum/Galactomyces* group (Groenewald *et al.* 2012), was possible because South African strains he isolated in 2009 had been sent to CBS.

The yeast community is indebted to van der Walt for his contribution to the yeast biodiversity and taxonomy over 63 years. It is also likely that further novel taxa remain to be discovered among the strains that he has deposited over the years, supporting the quotation of Pliny (23–79 AD) “Ex Africa semper aliquid novi”, a quotation that Johannes van der Walt was fond of citing.

On a personal note, one of us, M. T. S., who collaborated with van der Walt for many years adds: “Those who may have had the privilege to meet Johannes van der Walt or to collaborate with him, as I have, will definitely remember him not only from his taxonomic work, but will also remember him as an amiable person full with stories to tell while enjoying a fine dinner with a good glass of wine.”

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