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 Baam to Delft after the appointment of Albert Jan Kuyper 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 Kuyper 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 heterobasidionymycetous 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), Woltomyces (Yamada & Nakase 1985; now included in...
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, 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 Assesosporon 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).

Fig. 1. Asci with ascospores of Kluyveromyces polysporus (Vanderwaltozyma polyspora) After Barnett et al. (2000). A. YM agar, 16 d. B. McCary acetate agar, 2 weeks. Bar = 5 μm.

Fig. 2. Three famous yeast taxonomists (left to right): Herman J. Pfaff, 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.
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 grass, 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 ascii with more ascospores than the normal 1–4 ascospores which he described as Klyuvomyces multispores (now Vanderwaltozyma polyspora; Fig. 2). One of his new species, Saccharomyces insitus, 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 basionsyms 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 basionsyms of other yeast taxonomist and presently recognized, are listed below:

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

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

| Year | Genus               | Author(s)               | Present generic status¹ (year of description of the genus) |
|------|---------------------|-------------------------|---------------------------------------------------------------|
| 1964 | Dekkera             | Van der Walt            | Recognized                                                   |
| 1970 | Aessepsorron        | Van der Walt            | Not recognized (ex-type culture mates with Spondobolus salmonicolor) |
| 1971 | Klyuvomyces         | Van der Walt            | Recognized                                                   |
|      | Lodderomyces        | Van der Walt            | Recognized                                                   |
|      | Cynicolomyces       | Van der Walt & D.B. Scott| Recognized                                                   |
|      | Wingea              | Van der Walt            | Not recognized (type species belongs to the genus Debaryomyces) |
| 1972 | Ambrosiozyma        | Van der Walt            | Recognized                                                   |
| 1973 | Wickerhamiella      | Van der Walt            | Recognized                                                   |
| 1976 | Hyphopicha          | Arx & van der Walt      | Recognized                                                   |
|      | Stephanoascus       | M.T. Sm., Van der Walt & Johannsen | = Trichomonascus (1947)                                     |
| 1978 | Pachytichospora     | Van der Walt            | = Kazachstania (1971)                                        |
|      | Debaryomyza         | Van der Walt & Johannsen| Not recognized (the genus name Debaryomyces is conserved)    |
| 1980 | Yarrowia            | Van der Walt & Arx      | Recognized                                                   |
| 1981 | Myxozyma            | Van der Walt, Weijman & Arx | Recognized                                                   |
|      | Arxiozyma           | Van der Walt & Yarrow   | = Kazachstania (1971)                                        |
| 1987 | Zygozyma            | Van der Walt & Arx      | = Lipomyces (1952)                                           |
| 1990 | Arxula              | Van der Walt, M.T. Sm. & Y. Yamada | = Blastobotrys (1961)                                        |
| 1995 | Babjevia            | Van der Walt & M.T. Sm. | = Dipodascopsis (1978)                                       |
|      | Smithiozyma         | Kock, Van der Walt & Y. Yamada | = Lipomyces (1952)                                           |

¹ Present status in Kurtzman et al. (2011)

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 |
|------|-------------------------------------|-----------------------------|--------------------------------------|--------------------------------|----------------------------------|
| 1956 | *Kluyveromyces africana*            | Van der Walt                | Soil                                 |                                | = *Kazachstania africana*        |
|      | *Saccharomyces transvaalensis*      | Van der Walt                | Soil                                 |                                | = *Kazachstania transvaalensis*  |
|      | *Saccharomyces delphensis*          | Van der Walt & Tscheuschner | Dried figs                           |                                | = *Nakaseomyces delphensis*      |
|      | *Saccharomyces capensis*            | Van der Walt & Tscheuschner | Soil                                 |                                | = *Saccharomyces cerevisiae*     |
|      | *Pichia vanrijii* (= *P. vanrijiae*)| Van der Walt & Tscheuschner | Soil                                 |                                | = *Schwanniomyces vanrijiae var. Vanrijiae* |
|      | *Saccharomyces preotoriensis*       | Van der Walt & Tscheuschner | Soil                                 |                                | = *Torulaspora preotoriensis*    |
|      | *Kluyveromyces polysporus*          | Van der Walt                | Soil                                 |                                | = *Vandenwaltozyma polyspora*     |
| 1957 | *Hanseniaspora vineae*              | Van der Walt & Tscheuschner | Soil                                 | Recognized                     |                                  |
|      | *Saccharomyces telluris*            | Van der Walt                | Soil                                 | = *Kazachstania telluris*       |                                  |
|      | *Hansenula beijerinckii*            | Van der Walt                | Soil                                 | = *Lindnera saturnus*           |                                  |
|      | *Saccharomyces lodderae*            | Van der Walt & Tscheuschner | Soil                                 | = *Kazachstania lodderae*       |                                  |
|      | *Pichia temicola*                   | Van der Walt                | Soil                                 | Recognized                     |                                  |
|      | *Pichia pijperi*                    | Van der Walt & Tscheuschner | Buttermilk                           | = *Wickerhamomyces pijperi*     |                                  |
|      | *Candida natalensis*                | Van der Walt & Tscheuschner | Soil                                 | Recognized                     |                                  |
| 1959 | *Endomycopsis wickerhamii*          | Van der Walt                | Insect frass                         | = *Barnettozyma wickerhamii*    |                                  |
|      | *Pichia robertsi* (= *Probertysi*)  | Van der Walt                | Insect                               | = *Debaryomyces robertsi*       |                                  |
|      | *Endomyces reessii*                 | Van der Walt                |                                        | = *Galactomyces reessii*        |                                  |
| 1960 | *Torulopsis domercqii* (= *T. domerqiae*) | Van der Walt & Kerken       | Wine vat                             | = *Wickerhamiella domericqiae*  |                                  |
| 1961 | *Brettanomyces custersonii*         | Van der Walt                | Brewery                              | Recognized                     |                                  |
|      | *Torulopsis vanzyllii*              | Van der Walt & Kerken       | Equipment of wine making             | = *C. norvegica*                |                                  |
|      | *Candida ingens*                    | Van der Walt & Kerken       | Wine cellar                          | = *Saprochaeta ingens*          |                                  |
|      | *Torulopsis cantarelli*             | Van der Walt & Kerken       | Industrial grape must                | = *Trigonopsis cantarelli*      |                                  |
|      | *Torulopsis capsuligena*            | Van der Walt & Kerken       | Wine cellar                          | = *Filobasidium capsuligenum*   |                                  |
| 1962 | *Schwanniomyces persoonii*          | Van der Walt                | Soil                                 | = *S. occidentalis var. persoonii* |                                  |
| 1963 | *Saccharomyces vanudenii*           | Van der Walt & E.E. Nel     |                                     | = *Kluyveromyces lactis var. drosophilum* |                                  |
|      | *Fabospora phaffii*                 | Van der Walt                | Winery equipment                     | = *Tetrapispora phaffii*        |                                  |
| 1964 | *Dekkera bruxellensis*              | Van der Walt                | From Belgian stout, Belgium          | Recognized                     |                                  |
|      | *Dekkera intermedia*                | Van der Walt                | Tea-beer                             | = *Dekkera bruxellensis*        |                                  |
| 1965 | *Saccharomyces vafer*               | Van der Walt                | Unknown                              | = *Torulaspora delbrueckii*     |                                  |
|      | *Saccharomyces inconspicuus*        | Van der Walt                | Grapes, France                       | = *Torulaspora delbrueckii*     |                                  |
Table 2. (Continued)

| Year | Species name            | Authors                                      | Type strains of South African source | Type strains from other source | Present status of the type strain¹ |
|------|-------------------------|----------------------------------------------|-------------------------------------|--------------------------------|-----------------------------------|
| 1966 | Kluyveromyces cicerisporus | Van der Walt, E.E. Nel & Kerker             | Beer                                | Unknown                        | = K. marxianus                     |
|      | Kluyveromyces wikenii    | Van der Walt, E.E. Nel & Kerker             | Bantu beer                          |                                | = K. marxianus                     |
|      | Pichia acaciae          | Van der Walt                                 | Insect frass                        |                                | = Millerzyma acaciae              |
| 1968 | Candida edax            | Van der Walt                                 | Insect frass                        |                                | = Sugiyamaella smithiae           |
|      | Torulopsis humilis      | E.E. Nel & Van der Walt                     | Bantu beer                          |                                | = C. humilis                      |
| 1970 | Saccharomyces amurcae   | Van der Walt                                 | “Alpechin”, Malaga, Spain           |                                | = Lachancea fermentati            |
|      | Saccharomyces saitoanus | Van der Walt                                 | Sour milk, Japan                    |                                | = Torulopsis delbruecki           |
|      | Hansenula philodendri   | Van der Walt & D.B. Scott                   | Insect frass                        |                                | = Ogataea philodendri             |
|      | Hansenula sydowiorum    | D.B. Scott & Van der Walt                   | Insect frass                        |                                | = Wickerhamomyces sydowiorum      |
|      | Syringospora stellatoidea | Van der Walt                             | Sputum                              |                                | = C. albicans                     |
|      | Syringospora clauseni   | Van der Walt                                 | Unknown                             |                                | = C. albicans                     |
|      | Aessosporon salmonicolor | Van der Walt                               | Curious dentine of man              |                                | Synonym of Sporidiobolus salmonicolor |
|      | Bullera dendrophi       | Van der Walt & D.B. Scott                   | Insect frass                        |                                | Recognizec                       |
|      | Sterigmatomyces polybonus | D.B. Scott & Van der Walt             | Insect tunnels                       |                                | = Fellomyces polybonus            |
|      | Trichosporon melibiosaceum | D.B. Scott & Van der Walt             | Insect frass                        |                                | = C. fennica                      |
| 1971 | Pichia ambrosiae        | Van der Walt & D.B. Scott                   | Insect frass                        |                                | = Ambrosiozyma ambrosiae          |
|      | Pichia cicatricosa      | D.B. Scott & Van der Walt                   | Insect frass                        |                                | = Ambrosiozyma cicatricosa        |
|      | Saccharomyces symaedendra | D.B. Scott & Van der Walt             | Insect frass                        |                                | Recognized                       |
|      | Hansenula dryadoides    | D.B. Scott & Van der Walt                   | Insect frass                        |                                | = Starmera dryadoides             |
|      | Torulopsis dendrica     | Van der Walt, Klift & D.B. Scott            | Insect frass                        |                                | = C. dendrica                    |
|      | Candida silvanorum      | Van der Walt, Klift & D.B. Scott            | Insect frass                        |                                | Recognized                       |
|      | Candida dendronema      | Van der Walt, Klift & D.B. Scott            | Insect frass                        |                                | Recognized                       |
|      | Candida entomophila     | D.B. Scott, Van der Walt & Klift            | Insect frass                        |                                | Recognized                       |
|      | Torulopsis insectalens  | D.B. Scott, Van der Walt & Klift            | Insect frass                        |                                | = C. insectalens                 |
|      | Torulopsis nemodendra   | Van der Walt, Klift & D.B. Scott            | Insect frass                        |                                | = C. nemodendra                  |
|      | Torulopsis silvatica    | Van der Walt, Klift & D.B. Scott            | Insect frass                        |                                | = C. silvatica                   |
|      | Candida hyophila        | Van der Walt, Klift & D.B. Scott            | Insect frass                        |                                | = Rhodotorula hyophila           |
| Year | Species name                        | Authors                                      | Type strains of South African source | Type strains from other source | Present status of the type strain |
|------|-------------------------------------|----------------------------------------------|-------------------------------------|-------------------------------|-----------------------------------|
| 1972 | Torulopsis phylia                   | Van der Walt, Kliff & D.B. Scott             | Insect tunnels                      |                               | = Rhodotorula phylia             |
|      | Ambrosiozyma philentoma             | Van der Walt, D.B. Scott & Kliff             | Insect tunnels                      |                               | Recognized                       |
|      | Pichia melissophila                 | Van der Walt & Kliff                         | Gut honey bee                       |                               | = Piceomyces melissophillus      |
|      | Candida nitrativorans               | Van der Walt, D.B. Scott & Kliff             | Insect tunnels                      |                               | = Wickerhamomyces sydowiorum     |
|      | Candida entomaeae                   | Van der Walt, D.B. Scott & Kliff             | Insect tunnels                      |                               | = Yamadazyma mexicana            |
|      | Candida insectamans                 | D.B. Scott, Van der Walt & Kliff             | Insect frass                        |                               | Recognized                       |
|      | Candida insectorum                  | D.B. Scott, Van der Walt & Kliff             | Insect frass                        |                               | Recognized                       |
|      | Candida siliquicola                 | Van der Walt, D.B. Scott & Kliff             | Insect frass                        |                               | Recognized                       |
|      | Candida amylolenta                  | Van der Walt, D.B. Scott & Kliff             | Insect frass                        |                               | = Cryptococcus amylolentus       |
| 1973 | Wickerhamiella domerciae            | Van der Walt                                 | Wine vat                            |                               | Recognized                       |
|      | Candida homilenta                   | Van der Walt & Nakase                        | Insect frass                        |                               | Recognizec                       |
|      | Candida naedendra                   | Van der Walt, Johannsen & Nakase             | Insect frass                        |                               | Recognizec                       |
|      | Entelexis magnolia                  | Van der Walt & Johannsen                     | Flower                              |                               | = C. magnolia                    |
|      | Aessosporon dendrophilum            | Van der Walt                                 | Frass of larvae in galleries        |                               | = Bullera dendrophila            |
|      | Hansenula lynferdi                  | Van der Walt & Johannsen                     | Soil                                |                               | = Wickerhamomyces lynferdi      |
|      | Pichia philogaea                    | Van der Walt & Johannsen                     | Soil                                |                               | = Yamadazyma philogae            |
|      | Trichosporon terrestrae             | Van der Walt & Johannsen                     | Soil                                |                               | = Blastobotrys terrestris        |
| 1976 | Stephanosascus ciferri              | M.T. Sm., Van der Walt & Johannsen           | Mating type a from soil            |                               | = Trichomonascus ciferri         |
| 1978 | Pachydiscospora transvalensis       | Van der Walt                                 | Soil                                |                               | = Kazachstania transvalensis     |
|      | Torulopsis azyma                    | Van der Walt, Johannsen & Yarrow             | Licher                              |                               | = C. azyma                       |
|      | Torulopsis geochares                | Van der Walt, Johannsen & Yarrow             | Soil                                |                               | = C. geochares                   |
|      | Candida fermenticorens              | Van der Walt                                 | Licher                              |                               | Recognized                       |
| 1980 | Debaryomyza yamadae                 | Van der Walt & Johannsen                     | Soil                                |                               | = Schwanniomyces yamadae         |
| 1982 | Hansenula euphorbiaphila            | Van der Walt                                 | Flower                              |                               | = Cyberlindnera euphorbiaphila   |
|      | Pichia meyerae                      | Van der Walt                                 | Flower                              |                               | = Cyberlindnera meyerae          |
|      | Pichia kodamae                      | Van der Walt & Yarrow                        | Insect infestations                |                               | = Ogataea kodamae                |
| 1983 | Pichia euphorbiiae                  | Van der Walt & Opperman                      | Flower                              |                               | = Cyberlindnera euphorbiiae      |
| 1986 | Kuyveromyces yarrowii               | Van der Walt, Johannsen, Opperman & Hallanc  | Stable mutant of crossing auxothrophic subcultures of CBS 2684 and CBS 6070, both isolated from tanning liquors of bark tree, France | = Vanderwaltdzyma yarrowii       |
| Year | Species name                        | Authors                                                                 | Type strains of South African source | Type strains from other source | Present status of the type strain |
|------|------------------------------------|-------------------------------------------------------------------------|--------------------------------------|---------------------------------|----------------------------------|
| 1987 | Zygozyma oligophaga                | Van der Walt & Arx                                                      | Insect frass                         |                                 | = Lipomyces oligophaga           |
| 1988 | Candida lyxosophila                | Van der Walt, N.P. Ferreira & Steyn                                    | Soi                                  |                                 | Recognized                       |
| 1989 | Myxozyma geophila                  | Van der Walt, Y. Yamada & Nakase                                       | Soi                                  |                                 | Recognized                       |
| 1990 | Myxozyma lipomycoïdes              | Van der Walt, Y. Yamada & Nakase                                       | Lichen                               |                                 | Recognized                       |
| 1992 | Sterigmatomyces wingfieldii         | Van der Walt, Y. Yamada & N.P. Ferreira                                | Insect frass                         |                                 | = Cryptococcus amyloleitus       |
| 1988 | Sporobolomyces phyllophorus        | Van der Walt & Y. Yamada                                                | Leaf                                 |                                 | Recognized                       |
| 1988 | Debaryomyces arxii                 | Van der Walt, M.T. Sm. & Y. Yamada                                     | Soil, Ontario, Canada                 |                                 | = Debaryomyces arxii             |
| 1988 | Lipomyces japonicus                | Van der Walt, M.T. Sm., Y. Yamada                                     | Garden soil, Japan                   |                                 | Recognized                       |
| 1990 | Zygozyma suomiensis                | M.T. Sm., Van der Walt & Y. Yamada                                     | Skin lesion of a cow, Finland        |                                 | = Lipomyces suomiensis           |
| 1990 | Myxozyma kluven                    | Van der Walt, Spencer-Martins & Y. Yamada                              | Soil                                 |                                 | Recognized                       |
| 1992 | Sporobolomyces phyllophorus        | Van der Walt & Y. Yamada                                                | Leaf                                 |                                 | = Benstonia phyllophora          |
| 1992 | Zygozyma smithiae                 | Van der Walt, Wingfield & Y. Yamada                                    | Insect frass                         |                                 | = Lipomyces smithiae             |
| 1997 | Myxozyma udenii                    | Spaaij, Weber, Oberwinkler & van der Walt                              | Soil around Magnifera indica, Florida, USA |                                 | Recognized                       |
| 1997 | Zygozyma picaeae                   | Weber, Spaaij & Van der Walt                                           | Rhizosphere of Picea abies, Germany  |                                 | = Kazachstania picaeae           |
| 1998 | Sporobolomyces phyllophorus        | Van der Walt & Y. Yamada                                                | Leaf                                 |                                 | Recognized                       |
| 1999 | Myxozyma neglecta                  | Spaaij, Van der Walt & Weber-Spaaij                                    | Cactus                               |                                 | Recognized                       |
| 1999 | Lipomyces doorenjorgii             | Van der Walt & M.T. Sm.                                                | Soil                                 |                                 | Recognized                       |
| 1999 | Lipomyces kockii                   | M.T. Sm. & Van der Walt                                                | Soil                                 |                                 | Recognized                       |
| 1999 | Lipomyces mesembrius               | Van der Walt & M.T. Sm.                                                | Soil                                 |                                 | Recognized                       |
| 1999 | Lipomyces yarrowii                 | Van der Walt & M.T. Sm.                                                | Soil                                 |                                 | Recognized                       |
| 1999 | Lipomyces yarrowii                 | 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, unpublish.). 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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