Numerical Analysis of *Hansenula*, *Pichia* and Related Yeast Genera

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SUMMARY

Numerical analysis of published standard descriptions of the eight species of *Debaryomyces*, 48 species of *Pichia* and the single species of *Wingea* failed to distinguish separate genera. It is proposed that they be combined as a single genus *Pichia* of 41 species, three of which were formerly allocated to the genus *Endomycopsis*. The genus *Hansenula*, of 20 species including *Pachysolen tannophilus* and three former species of *Endomycopsis*, is closely related to the genus *Pichia* and is distinguished only by the ability of *Hansenula* species to assimilate nitrate. In the genus *Schwanniomyces* the number of species is reduced from four to two, and in *Lipomyces*, from three to one.

INTRODUCTION

The taxonomy of the genus *Pichia* was examined by Poncet (1957) by factor analysis of single strains of each species. Kreger-van Rij (1969) criticized the representation of species by a single strain, since many species showed wide variations in properties. A similar study was undertaken of the genus *Hansenula* (Poncet, 1970), again by analysis of single strains of each species. The genera *Hansenula* and *Pichia* were re-examined, as in an earlier analysis of *Kluyveromyces* and *Saccharomyces* (Campbell, 1972), by analysis of the descriptions of species provided by Wickerham (1970a) and Kreger-van Rij (1970a), and by authors who have subsequently described new species of these genera. In this way, all known variations between strains were considered. Poncet's analyses were limited to the genera *Pichia* and *Hansenula*. In this present report, other genera known (Lodder, 1970; Campbell, 1971) or suspected to be similar to *Hansenula* and *Pichia* are also included: *Citeromyces*, *Debaryomyces*, *Dekkera*, *Endomycopsis*, *Lipomyces*, *Lodderomyces*, *Pachysolen*, *Schwanniomyces* and *Wingea*. Although it was initially intended to limit the analysis to sporing yeasts, the imperfect equivalent of *Dekkera*, the genus *Brettanomyces*, was easily included.

METHODS

Characters for numerical analysis. The system for analysis of the genus *Saccharomyces* (Campbell, 1972) was modified to deal with the different range of properties under examination: 58 characters described by Lodder (1970) were examined, as follows.

Morphology (18 characters). Pellicle (two characters) absent (—), thin and weak (+ —) or well developed (+ +); capsule or slime (one character); spores (five characters) 1 to 2 (+ —), ≥ 3 (— +) or 1 to ≥ 3 (+ +) per ascus, spherical/oval (+ —), hat (— + —) or Saturn (— —) shaped. Colony (two characters) and cell (five characters) morphology,

and formation of pseudomycelium (two characters) were as described previously (Campbell, 1972).

Physiology (40 characters). The number of tests was determined by those properties common to all standard descriptions, e.g. splitting of arbutin and resistance to cycloheximide were omitted from Wickerham's (1970a) standard descriptions of *Hansenula* species and were therefore not used in the analyses. Fermentation was assessed as six characters: glucose, galactose, sucrose, maltose, $\frac{1}{3}$ raffinose and $\frac{2}{3}$ /complete raffinose. Fermentation of melibiose was disregarded, being automatically included in complete fermentation of raffinose. Assimilation of carbon sources, other than glucose, provided 30 characters, and the data were completed by four additional tests: assimilation of nitrate, growth in vitamin-deficient media, in 10 % NaCl + 5 % glucose or in 50 % glucose (regarded for this analysis as equivalent tests of osmophily) and at 37 °C. The matching coefficients, S_s (Sneath, 1972), between strains was determined from both positive and negative matches (Campbell, 1970) by computer programs 1 and 2 (Campbell, 1970, 1973) and the results were expressed in dendrogram form at highest mutual similarity level expressed to the nearest 5 % (Campbell, 1970).

RESULTS

Because a single analysis of all genera involved an extremely large number of species, two separate groups of genera were tested in preliminary analyses. The resulting clusters were then compared.

Numerical analysis of standard descriptions of Ambrosiozyma, Debaryomyces, Endomycopsis, Pichia, Schwanniomyces and Wingea species

The standard descriptions analysed included eight species of *Debaryomyces* (Kreger-van Rij, 1970b), 36 of *Pichia* (Kreger-van Rij, 1970a), ten of *Endomycopsis* (Kreger-van Rij, 1970c), four of *Schwanniomyces* (Phaff, 1970) and one species of *Wingea* (van der Walt, 1970a). The following recently described species were also included: *Endomycopsis muscicola* Nakase & Komagata (1966), *Pichia ambrosiae* van der Walt & Scott (1971a), *P. besseyi* Kurtzman & Wickerham (1972), *P. cicatricosa* Scott & van der Walt (1971a), *P. crossotarsi* Batra (1971), *P. heimii* Pignal (1970), *P. melissophila* van der Walt & van der Klift (1972), *P. microspora* Batra (1971), *P. mucosa* Wickerham & Kurtzman (1971), *P. nonfermentans* Nakase (1971), *P. sargentensis* Wickerham & Kurtzman (1971), *P. spartinae* Ahearn, Yarrow & Meyers (1970) and *P. xylopsoci* van der Walt & Scott (1971b). *Ambrosiozyma philentoma* van der Walt *et al.* (van der Walt, 1972) was included because of its close association with species of *Endomycopsis* and *Pichia*. *Pichia faecalis* (Batista & Silveira) de Queiroz (1970) was regarded as synonymous with *P. etchellsii* (Kreger-van Rij, 1970a) and was therefore not examined.

Five main groups were distinguished, mutually related at 70 % matching coefficient (Fig. 1). Fifteen *Pichia* species and two *Endomycopsis* species related to *Pichia membranaefaciens* formed the first group; 17 species of *Pichia*, and possibly also *P. media* which was difficult to allocate to a taxonomic group, five of *Endomycopsis* and *Ambrosiozyma philentoma* formed a second group, of which the main species were *Endomycopsis fibuligera* and *P. guilliermondii*. Eight species of *Pichia* and four of *Endomycopsis* formed a poorly defined third group. Five species of *Pichia* were associated with *Wingea robertsii* and seven *Debaryomyces* species in the fourth main group. The genus *Schwanniomyces*, related at 70 % matching to the *Debaryomyces* group, was related at approx. 65 % matching to the other groups of *Pichia* and *Endomycopsis*. It is interesting that the *Debaryomyces* group is composed entirely of species which form spherical and usually warty spores (see Kreger-van Rij,

1970a, b); in other groups of the genus *Pichia* only *P. fluxuum*, *P. kudriavzevii* and *P. terricola*, and occasionally four other species of the *P. membranaefaciens* group, form such spores (Kreger-van Rij, 1970a).

Following the precedent of our analysis of the genus *Saccharomyces* (Campbell, 1972), species related at $S_s \geq 90\%$ were considered synonymous, and therefore the 68 species of *Ambrosiozyma*, *Debaryomyces*, *Endomycopsis*, *Pichia* and *Wingea* in this analysis were reduced to 50 valid species. The four species of *Schwanniomyces* (Phaff, 1970) were reduced to two.

Numerical analysis of standard descriptions of Brettanomyces, Citeromyces, Dekkera, Hansenula, Lipomyces, Lodderomyces and Pachysolen species

The standard descriptions of the 25 species of *Hansenula* described by Wickerham (1970a) were analysed, i.e. including the two species also classified as *Endomycopsis* (Kreger-van Rij, 1970c). To that group were added seven species of *Brettanomyces* (van der Walt, 1970b), two species of *Dekkera* (van der Walt, 1970c), three of *Lipomyces* (Slooff, 1970), *Citeromyces matritensis* (Wickerham, 1970b), *Lodderomyces elongisporus* (van der Walt, 1970d) and *Pachysolen tannophilus* (Wickerham, 1970c). The following recently described species were included in the analysis: *Brettanomyces abstinens* Yarrow & Ahearn (1971), *B. naardenensis* Kolfshoten & Yarrow (1970), *Hansenula dryadoides* Scott & van der Walt (1971b), *H. muscicola* (Nakase & Komagata) Yarrow (1972), *H. philodendra* Scott & van der Walt (1970a) and *H. sydowiorum* Scott & van der Walt (1970b). *Hansenula malanga* Dwidjoseputro & Wolf (1970) was not included since the standard description could not be fitted into the Lodder (1970) pattern.

The genera *Citeromyces*, *Hansenula* and *Pachysolen* were clearly related (Fig. 2), forming two main groups related at $S_s 70\%$. In a group of 20 species which contained *Citeromyces matritensis* and *Pachysolen tannophilus*, six species were closely related to *Hansenula polymorpha*, and four capsulate or slime-forming species formed a separate subgroup. The remaining *Hansenula* species formed a group of ten species at $S_s 80\%$ in which the major species were *H. anomala*, *H. saturnus* and *H. subpelliculosa*.

Species of *Brettanomyces* and *Dekkera* were arranged in two groups: the two species of *Dekkera* and six species of *Brettanomyces* formed a homogeneous group equivalent to a single species, *Brettanomyces abstinens* Yarrow & Ahearn, *B. custersianus* and *B. naardenensis* Kolfshoten & Yarrow formed a group at $S_s 75\%$, separated at 70% matching coefficient from the main group of *Brettanomyces*. *Lodderomyces elongisporus* was placed at $S_s 65\%$ with *Brettanomyces* and *Hansenula*.

The genus *Lipomyces* was unlike the other genera of this series of tests, being related at approx. 60 to 65% matching to the other groups. The three species of *Lipomyces* included a 20% variation, and overlapped so extensively as to be indistinguishable by numerical analysis.

Combined analysis

Having determined the main groups of clusters in the two groups of genera (Fig. 1, 2), the analysis was completed by a series of comparisons in which each species was compared with all others. The results were confirmed by comparison of the main groups detected and illustrated in Fig. 1 and 2. Fig. 3 shows these results in dendrogram form. A large cluster at $S_s 70$ to 75% included the genera *Citeromyces*, *Endomycopsis*, *Hansenula*, *Pachysolen* and *Pichia*. *Brettanomyces*, *Debaryomyces* and related *Pichia* species, *Dekkera*, *Lipomyces*, *Lodderomyces*, *Schwanniomyces* and *Wingea* (included in the *Debaryomyces hansenii* group) were related to the 70% cluster and to each other at 65% matching.

Fig. 1

Fig. 2

Fig. 3. Dendrogram of main taxonomic groups of the genera *Ambrosiozyma*, *Brettanomyces*, *Citeromyces*, *Debaryomyces*, *Dekkera* (included in *Brettanomyces* group), *Endomycopsis*, *Hansenula*, *Lipomyces*, *Pachysolen* (included in *H. polymorpha* group), *Pichia*, *Saccharomyces*, *Schwanniomyces* and *Wingea*.

Fig. 1. Taxonomic dendrogram of species of the genera *Ambrosiozyma*, *Debaryomyces*, *Endomycopsis*, *Pichia*, *Schwanniomyces* and *Wingea*, from analysis of standard descriptions of species.

Fig. 2. Taxonomic dendrogram of species of the genera *Brettanomyces*, *Citeromyces*, *Dekkera*, *Hansenula*, *Lipomyces*, *Lodderomyces* and *Pachysolen*, from analysis of standard descriptions of species.

Fig. 4. Comparison of taxonomic groups of the genus *Hansenula*. —, Groups by Poncet (1970); - - - -, groups by Fig. 2. Key to species: 1, *H. anomala*; 2, *H. beckii*; 3, *H. beijerinckii*; 4, *H. bimundalis*; 5, *H. californica*; 6, *H. canadensis*; 7, *H. capsulata*; 8, *H. ciferri*; 9, *H. dimennae*; 10, *H. fabianii*; 11, *H. glucozyma*; 12, *H. henricii*; 13, *H. holstii*; 14, *H. jadinii*; 15, *H. minuta*; 16, *H. mrakii*; 17, *H. petersonii*; 18, *H. platypodis*; 19, *H. polymorpha*; 20, *H. saturnus*; 21, *H. silvicola*; 22, *H. subpelliculosa*; 23, *H. wickerhamii*; 24, *H. wingei*.

Kluyveromyces lactis, *Saccharomyces cerevisiae*, *S. cidri*, *S. dairensis*, *S. delbrueckii*, *S. kluyveri* (formerly *Debaryomyces globosus* according to Lodder & Kreger-van Rij, 1952), *S. montanus* (*D. mandshuricus* Naganishi), *S. rosei* and *S. rouxii*, representing the *Saccharomyces* group, were compared with representatives of the main *Hansenula*, *Pichia*, *Brettanomyces*, *Debaryomyces* and *Endomycopsis* groups, and *Lipomyces* and *Lodderomyces* species. Three pairs were matched at 80 %: *S. dairensis* and *Pichia membranaefaciens*, *S. kluyveri* and *D. tamarii*, and *S. rouxii* and *D. coudertii*. Otherwise matches were at 70 % or less, and the three results at a higher level were regarded as exceptions. *Saccharomyces* was most closely associated with the genera *Debaryomyces* and *Schwannomyces*, at approx. 70 % matching (Fig. 3).

DISCUSSION

Very few of the species in the present analysis were represented by strains in our culture collection, and standard descriptions by the contributors to Lodder's (1970) book provided the information for comparison of species. The good correlation between numerical analyses of standard descriptions of *Kluyveromyces* and *Saccharomyces* species and of actual strains

(Campbell, 1972) suggested that standard descriptions alone would provide accurate information for the present series of analyses.

The genera Ambrosiozyma, Endomycopsis, Hansenula and Pichia

Our results of analyses of the genera *Hansenula* and *Pichia* confirmed Poncet's (1967, 1970) results in most respects. Fig. 1 suggests that Poncet's large groups A and C of the genus *Pichia* (Fig. 1 by Poncet, 1967) should be further subdivided. Poncet's (1970) and our analyses of the genus *Hansenula* also provided similar results, but the groups arranged by her factor analyses did not coincide exactly with clusters in our dendrogram, Fig. 2. Possibly the discrepancies, indicated in Fig. 4, are the result of Poncet's use of single strains, in contrast to our use of published standard descriptions, to represent large and variable species, but the two different forms of calculation must also account for some differences. It is interesting that Poncet's fig. 3 (1970) showed a difference between *Hansenula saturnus* and *H. suaveolens* (Klöcker) Dekker, now regarded as synonymous (Wickerham, 1970a), and between *H. polymorpha* and *H. angusta* Teunisson *et al.*, also synonyms at present.

The majority of species of *Endomycopsis*, *Hansenula* and *Pichia* formed an inseparable group (Fig. 3). *Endomycopsis bispore*, *E. muscicola* Nakase & Komagata and *E. platypodis*, which assimilate nitrate as sole source of nitrogen, have been allocated to the genus *Hansenula* (Wickerham, 1970a; Yarrow, 1972); in the case of *Hansenula beckii* and *H. platypodis* this is justified by their close association with true *Hansenula* species in Fig. 2 and 3, but *H. muscicola* is related to other *hansenulae* at only 70 % matching, and is equally closely related to nitrate-negative *Endomycopsis* and *Pichia* species. *Endomycopsis monospora* and the closely related species *E. platypodis*, *Pichia ambrosiae* and *P. cicatricosa* were transferred to the genus *Ambrosiozyma* by van der Walt (1972). While these species and *Ambrosiozyma philentoma* appeared as a distinct group at 80 % matching in Fig. 1, there is little justification for a separate genus since the species are equally closely related to other species not classified as *Ambrosiozyma*. Van der Walt's genus *Ambrosiozyma* is simply a subgroup of the species *E. fibuligera* (Fig. 1).

Several new genera were proposed by von Arx (1972), but were not confirmed by our series of numerical analyses. *Hormoascus platypodis* (Baker & Kreger-van Rij) von Arx (*Endomycopsis platypodis*) is related at 80 % matching to species of *Hansenula* and *Pichia*, therefore *Hormoascus platypodis* is as unacceptable, and for the same reasons, as *Ambrosiozyma platypodis* (Baker & Kreger-van Rij) van der Walt. *Arthroascus javanensis* (Klöcker) von Arx (*E. javanensis*) is related at 80 % to *E. ovetensis* and the *Pichia membranaefaciens* group, and is synonymous with *P. nonfermentans* Nakase. Nor was von Arx's suggestion of synonymy of *Ambrosiozyma monospora* (Saito) van der Walt (*E. monospora*) and *P. crossotarsi* Batra confirmed by numerical analysis of the standard descriptions provided by Kreger-van Rij (1970c) and Batra (1971) respectively. *Pichia crossotarsi* and *P. microspora* Batra, which are synonymous at 90 % matching, are shown in Fig. 1 as a distinct species from *E. monospora*. The status of a separate genus *Guilliermondella*, revived by von Arx (1972), is supported by numerical analysis; *Guilliermondella selenospora* Nadson & Krassilnikov is related at only 75 % matching to *E. capsularis* and could be a separate genus.

Current taxonomic practice favours the abolition of the generic name *Endomycopsis* (Wickerham, 1970a; Batra, 1971; van der Walt & Scott, 1971c; von Arx, 1972; Yarrow, 1972). There is no clear separation between filamentous genera and pseudomycelial yeasts of the genera *Hansenula* and *Pichia*. Suggested definitions of genera by von Arx (1972) which concern the present paper are: no assimilation of nitrate, septate hyphae – *Saccharomycopsis*; no assimilation of nitrate, septate hyphae – *Pichia*; assimilation of nitrate, septate

Table 1. *Comparison of published properties of Hansenula, Pichia and related genera*

	Pmr type ¹	GC proportion ^{2,3}	Serological type ⁴	Antigenic structure ^{2,5}
<i>Hansenula beijerinckii</i>	11d	42.7	—	1, 2, 14, 16, 17, 20, 21, 22
<i>H. fabianii</i>	10a	44.4–45.6	—	—
<i>H. jadinii</i>	11f	43.2	F	1, 2, 14, 16, 17
<i>H. anomala</i>	10a	35.6–36.6	F	1, 2, 14, 15, 16, 17, 20
<i>H. ciferrii</i>	10a	32.2	—	1, 2, 14, 15, 16, 20
<i>H. subpelliculosa</i>	10a	33.4–33.9	F	1, 2, 14, 15, 16, 20
<i>H. mrakii</i>	11d	42.0	F	1, 2, 14, 15, 16, 17, 20, 21, 22
<i>H. saturnus</i>	10e/11e	42.4–43.7	F	1, 2, 14, 15, 16, 17, 20, 21, 22
<i>H. californica</i>	11a	44.0	—	—
<i>H. dimennae</i>	11a	42.4–42.9	—	—
<i>H. canadensis</i>	11g	39.3–40.0	—	—
<i>H. wingei</i>	10a	39.0	—	—
<i>H. bimundalis</i>	10a	40.0–42.9	—	—
<i>H. beckii</i>	11g	36.3–36.9	—	—
<i>H. platypodis</i>	9d	31.5–36.8	—	—
<i>H. capsulata</i>	11h	46.8–47.1	—	—
<i>H. holstii</i>	11b	36.8–37.1	—	—
<i>H. silvicola</i>	10a	34.1–35.1	—	1, 2, 14, 15, 16, 20
<i>H. polymorpha</i>	9b	47.8–48.3	—	1, 2, 5, 11, 17
<i>H. wickerhamii</i>	9b	45.4	—	—
<i>H. glucozyma</i>	9b	45.1	—	—
<i>H. henricii</i>	9b	49.8–50.2	—	—
<i>H. minuta</i>	9b	46.8–47.3	—	—
<i>H. nonfermentans</i>	9b	45.6	—	—
<i>Pichia terricola</i>	9a	36.6–36.8	—	1, 2, 5, 11, 12, 14, 18, 31
<i>P. fluxuum</i>	9b	32.2	—	1, 2, 5, 11
<i>P. saitoi</i>	—	32.2	—	—
<i>P. dispora</i>	—	36.3–37.1	—	—
<i>P. membranaefaciens</i>	9a	41.5–42.4	F	1, 2, 5, 11
<i>P. kluyveri</i>	9b	28.3–28.5	—	—
<i>P. fermentans</i>	9c	42.2	F	1, 2, 5, 11
<i>P. kudriavzevii</i>	9c	38.5	—	—
<i>P. wickerhamii</i>	—	43.2	—	—
<i>P. rhodanensis</i>	12a	50.2	—	—
<i>P. toletana</i>	6a	39.3	D	—
<i>P. bovis</i>	10a	39.8	—	—
<i>P. polymorpha</i>	11c	33.2	—	—
<i>P. pseudopolymorpha</i>	5a	—	—	—
<i>P. vini</i>	16p	36.8–37.3	D	—
<i>P. etchellsii</i>	17k	38.5	—	—
<i>Wingea robertsii</i>	15a	—	D	—
<i>Debaryomyces cantarellii</i>	—	33.9	—	1, 2, 3, 5, 13, 14, 15
<i>D. vanrijii</i>	15a	32.4–32.7	—	—
<i>D. castellii</i>	16c	34.4	—	1, 2, 3, 5, 13, 14, 15
<i>D. hansenii</i>	16c	36.6–37.3	D	1, 2, 3, 4, 9, 14
<i>D. marama</i>	—	36.6	—	1, 2, 3, 4, 9, 14

References: ¹ Gorin & Spencer (1970); ² Meyer & Phaff (1969); ³ Nakase & Komagata (1970, 1971*a, b*); ⁴ Campbell (1971); ⁵ Tsuchiya *et al.* (1965).

hyphae present or absent – *Hansenula*. Those descriptions do not separate the genera adequately in terms of numerical analysis, although there is no suggestion of synonymy of the genera *Hansenula* and *Pichia*. Previous attempts to ignore the distinction between *Hansenula* and *Pichia* by assimilation of nitrate and to substitute other tests (reviewed by Wickerham, 1970a, p. 236) did not greatly affect classification. However, Fig. 3 shows that species of different genera are closely related but not closely enough to suggest synonymy: *Endomycopsis fibuligera* and the *Hansenula bimundalis*, *H. californica*, *Pichia ambrosiae*, *P. strasburgensis* and *P. toletana* groups are related at 80 % matching coefficient.

The majority of taxonomic deductions from numerical analyses (Fig. 1, 2) were confirmed by previously published data. Proton magnetic-resonance (pmr) spectra of wall mannans (Gorin & Spencer, 1970), GC proportion in DNA bases (Meyer & Phaff, 1969; Nakase & Komagata 1970, 1971a, b) and serological properties (Tsuchiya, Fukazawa & Kawakita, 1965; Campbell, 1971) of a selection of species are listed in Table 1 to support our classification. The few exceptions require comment: members of the *Pichia membranaefaciens* group, although related in pmr spectra and antigenic structure, vary over a wide range of GC proportions (28.3 to 42.2). *Pichia rhodanensis*, of GC proportion 50.2 %, is in a group of GC 39.3 to 43.2 %, and *Hansenula capsulata*, GC proportion 46.8 to 47.1 %, is associated with *H. holstii* and *H. silvicola*, GC proportion 34.1 to 37.1 %. Otherwise, the GC proportions of species in taxonomic groups fall within a range of ± 2 % of the mean value. It is generally true that species allocated by numerical analysis to the same taxonomic group were placed by Gorin & Spencer (1970) in the same pmr type or in types which showed peaks of the spectra at similar τ values thus indicating chemical similarity.

The genera Brettanomyces and Dekkera

Brettanomyces custersianus, *B. abstinens* Yarrow & Ahearn and *B. naardenensis* Kolf-schoten & Yarrow were clearly separated and are therefore valid species. The remaining seven species of *Brettanomyces* and the two of *Dekkera* overlapped so extensively that they were regarded as a single species. The 5 % difference between *B. bruxellensis* and *Dekkera bruxellensis*, and between *B. intermedius* and *D. intermedia*, was accounted for by properties of the spores of *Dekkera* species; this emphasizes earlier criticisms (Barnett, 1960, 1971; Campbell, 1971) of the use of spore properties in classification. The group is therefore defined as *B. bruxellensis*, of wider variation than at present. For computerized yeast identification (Campbell, 1973), two descriptions of invariable properties were required.

The genera Citeromyces and Pachysolen

Citeromyces matritensis and *Pachysolen tannophilus* are similar to *Hansenula* species (Wickerham, 1970b, c) but the 75 % matching coefficient between *C. matritensis* and the most closely related species of *Hansenula* distinctly separates the genera. Unfortunately the form of the spores is the only obvious difference from *Hansenula* species. Wickerham's (1970b) suggestion of a relationship between *C. matritensis*, *Debaryomyces hansenii* and *Schwanniomyces occidentalis* was not supported by our analyses (Fig. 3). Tsuchiya *et al.* (1965) demonstrated a close serological relationship (Table 2), but Gorin & Spencer (1970) allocated the species to different pmr groups, with peaks at different τ values.

Analysis of strains of *Pachysolen tannophilus*, *Hansenula capsulata*, *H. holstii* and *H. silvicola* (Campbell, 1971) showed 80 % matching coefficient, which suggested that *P. tannophilus* should be included in the genus *Hansenula*. Although Gorin & Spencer (1970) indicated a difference between *P. tannophilus* and *Hansenula* species, it was not confirmed by analysis of the whole range of published properties (Fig. 2). To include *P. tannophilus*,

the definition (Wickerham, 1970a) of the genus *Hansenula* should be amended thus: 'Asci have the shape of the vegetative cells or are rod-shaped', deleting the section '. . . and are not rod-shaped as in the nitrate-positive genus *Pachysolen*'.

The genera Debaryomyces and Wingea

The complete overlap of *Debaryomyces*, *Wingea* and five species of *Pichia* suggests that these five species were wrongly allocated to the genus *Pichia*, or that there is no justification for a separate genus *Debaryomyces*. Kreger-van Rij (1970a, b) described the difficulty of allocating species to the correct genus, and indeed the difficulty of defining each genus. A distinction was only possible by electron microscopy of sporing cultures, and even so, intermediate forms occurred which were arbitrarily placed in the genus *Pichia* as *Pichia fluxuum* and *P. terricola*. Although species in Fig. 1 which could be allocated to a separate genus *Debaryomyces* were distinct from the remaining species of *Pichia*, there were no properties which satisfactorily distinguished the two genera.

Available data on pmr spectra, GC proportions and serology (Table 1) confirm that the genera *Debaryomyces*, *Pichia* and *Wingea* form a homogeneous group. *Pichia pseudo-polymorpha*, of pmr group 5a, is not as anomalous as first appears, since the peaks of spectra 5a and 11c (*P. polymorpha*) are in the same τ positions (Gorin & Spencer, 1970). With the exception of *Debaryomyces tamarii*, which is taxonomically different in Fig. 1, all species of the *D. hansenii*/*P. polymorpha* group are of GC proportion 32.4 to 38.5.

There appears to be no convenient alternative to a single genus *Pichia*, to which the definition by Kreger-van Rij (1970a) is applicable on insertion of the words 'The spores have smooth or warty walls' and deleting 'The spores are generally smooth; they may have warts formed exclusively by the outer layer of the spore wall.' The definition should also state that 'The spores are spherical, hat- or Saturn-shaped or lentiform . . .' to include van der Walt's (1970c) genus *Wingea*, for which, according to our results, there is no justification as a separate genus. Its single species is described below as *Pichia robertsii* van der Walt.

The genera Lipomyces, Lodderomyces and Schwanniomyces

These genera are sufficiently different to remain separate from the other genera of this analysis. The three species of *Lipomyces* (Slooff, 1970) are mutually related at 90 % matching, but vary over approximately 20 % of properties. Therefore the three species may be described as a single species, *Lipomyces starkeyi*, of wider variation than at present described, and as two units for computerized identification (Table 1). In the genus *Schwanniomyces* there is insufficient difference between *Schwanniomyces alluvius* and *S. castellii* and between *S. occidentalis* and *S. personii* to justify separate species, and a reduction of the genus to two species is suggested. This is in accord with Gorin & Spencer's (1970) results; all were placed in group 15.

List of synonyms

The analyses of standard descriptions of species have indicated the following amendments to the classification by Lodder (1970) of the genera *Brettanomyces*, *Debaryomyces*, *Dekkera*, *Endomycopsis*, *Hansenula*, *Lipomyces*, *Pachysolen*, *Pichia*, *Schwanniomyces* and *Wingea*. The genera *Citeromyces* and *Lodderomyces*, also analysed in the present paper, are unchanged.

Genus *Brettanomyces* Kufferath & v. Laer.

The genus contains four species:

- (1) *Brettanomyces abstinens* Yarrow & Ahearn (1971)
- (2) *Brettanomyces bruxellensis* Kufferath & v. Laer

Synonyms: *B. anomalus* Custers, *B. clausenii* Custers, *B. custersii* Florenzano, *B. intermedius* (Krumbholz & Tauschanoff) v.d. Walt & v. Kerken, *B. lambicus* Kufferath & v. Laer and synonyms of *B. anomalus*, *B. bruxellensis*, *B. clausenii*, *B. intermedius* listed by van der Walt (1970).

- (3) *Brettanomyces custersianus* v. d. Walt
- (4) *Brettanomyces naardenensis* Kolschoten & Yarrow (1970)

Since it is customary to allocate sporing and non-sporing yeasts to separate genera, we reluctantly recognize the genus *Dekkera* v. d. Walt. The genus contains one species:

- (1) *Dekkera bruxellensis* v. d. Walt
- Synonym: *D. intermedia* v. d. Walt.

Genus *Hansenula* Sydow & Sydow

The genus contains 20 species, of which nine are as listed by Wickerham (1970a):

- (2) *Hansenula beckii* Wickerham
- (3) *Hansenula beijerinckii* v. d. Walt
- (6) *Hansenula capsulata* Wickerham
- (8) *Hansenula holstii* Wickerham
- (13) *Hansenula platypodis* de Moraes & Maia
- (14) *Hansenula polymorpha* de Moraes & Maia
- (16) *Hansenula silvicola* Wickerham
- (17) *Hansenula subpelliculosa* Bedford
- (20) *Hansenula wickerhamii* Capriotti

The following amendments are suggested to the list of species by Wickerham (1970a).

- (1) *Hansenula anomala* (Hansen) Sydow & Sydow

Synonyms: *H. ciferrii* Lodder and synonyms of *H. anomala* var. *anomala*, *H. anomala* var. *schneggii* (Weber) Wickerham and *H. ciferrii* listed by Wickerham (1970a).

- (4) *Hansenula californica* (Lodder) Wickerham

Synonyms: *H. bimundalis* Wickerham & Santa Maria var. *bimundalis*, *H. bimundalis* var. *americana* Wickerham, *H. wingei* Wickerham and synonyms of *H. bimundalis*, *H. californica* and *H. wingei* listed by Wickerham (1970a).

- (5) *Hansenula canadensis* Wickerham

Synonyms: *H. dimennae* Wickerham and *Azymohansenula canadensis* (Wickerham) Novak & Zsolt, *Acta bot. hung.* (1961), 7, 93.

- (7) *Hansenula dryadoides* Scott & v. d. Walt (1971b)

- (9) *Hansenula jadinii* (Sartory *et al.*) Wickerham

Synonyms: *H. fabianii* Wickerham, *H. petersonii* Wickerham and synonyms of *H. fabianii* and *H. jadinii* listed by Wickerham (1970a).

- (10) *Hansenula minuta* Wickerham

Synonyms: *H. glucozyma* Wickerham, *H. henricii* Wickerham and *H. nonfermentans* Wickerham.

- (11) *Hansenula muscicola* (Nakase & Komagata) Yarrow (1972)

- (12) *Hansenula philodendra* Scott & v. d. Walt (1970a)

- (15) *Hansenula saturnus* (Klöcker) Sydow & Sydow

Synonyms: *H. mrakii* Wickerham, *H. saturnus* var. *saturnus*, *H. saturnus* var. *subsufficiens* Wickerham and synonyms of *H. saturnus* listed by Wickerham (1970a).

(18) *Hansenula sydowiorum* Scott & v. d. Walt (1970b)

(19) *Hansenula tannophilus* (Boidin & Adzet) Campbell *nov.comb.*

Basionym: *Pachysolen tannophilus* Boidin & Adzet, *Bull. Soc. mycol. Fr.* (1957), **73**, 331.

Synonym: *P. pelliculatus* Boidin & Adzet, *Bull. Soc. mycol. Fr.* (1957), **73**, 331.

Genus *Lipomyces* Lodder & Kreger-v. Rij

The genus contains one species:

(1) *Lipomyces starkeyi* Lodder & Kreger-v. Rij

Synonyms: *L. kononenkoae* Nieuwdorp *et al.*, *L. lipofer* Lodder & Kreger-v. Rij and synonyms of *L. lipofer* listed by Slooff (1970).

Genus *Pichia* Hansen

The genus contains 41 species, of which 16 are as listed by Kreger-van Rij (1970a):

(1) *Pichia acaciae* v. d. Walt

(3) *Pichia angophorae* Miller & Barker

(7) *Pichia chambardii* (Ramirez & Boidin) Phaff

(11) *Pichia farinosa* (Lindner) Hansen

(15) *Pichia guilliermondii* Wickerham

(17) *Pichia haplophila* Shifrine & Phaff

(19) *Pichia kudriavzevii* Boidin *et al.*

(21) *Pichia media* Boidin *et al.*

(25) *Pichia ohmeri* (Etchells & Bell) Kreger-v. Rij

(27) *Pichia pastoris* (Guilliermond) Phaff

(28) *Pichia pijperi* v. d. Walt & Tscheuschner

(30) *Pichia pseudopolymorpha* Ramirez & Boidin

(33) *Pichia salictaria* Phaff *et al.*

(35) *Pichia scolyti* (Phaff & Yoneyama) Kreger-v. Rij

(37) *Pichia stipitis* Pignal

(40) *Pichia trehalophila* Phaff *et al.*

The following amendments are suggested to the list of species by Kreger-van Rij (1970a):

(2) *Pichia ambrosiae* v. d. Walt & Scott (1971a)

(4) *Pichia burtonii* Boidin *et al.*, *Bull. Soc. mycol. Fr.* (1964), **80**, 396

Synonyms: *Endomycopsis burtonii* (Boidin *et al.*) Kreger-v. Rij and synonyms of *E. burtonii* in Lodder, *The Yeasts* (1970), p. 174.

(5) *Pichia cantarellii* (Capriotti) Campbell *nov.comb.*

Basionym: *Debaryomyces cantarellii* Capriotti, *Arch. Mikrobiol.* 1961, **39**, 123.

Synonym: *D. phaffii* Capriotti, *J. Bact.* (1961), **82**, 326.

(6) *Pichia castellii* (Capriotti) Campbell *nov.comb.*

Basionym: *Debaryomyces castellii* Capriotti, *Arch. Mikrobiol.* (1958), **28**, 344.

Synonym: *Zymodebaryomyces castellii* (Capriotti) Novak & Zsolt, *Acta bot. hung.* (1961), **7**, 93.

(8) *Pichia coudertii* (Saëz) Campbell *nov.comb.*

Basionym: *Debaryomyces coudertii* Saëz, *Bull. mens. Soc. linn. Lyon* (1960), **29**, 288.

(9) *Pichia crossotarsi* Batra (1971)

Synonym: *P. microspora* Batra (1971).

- (10) *Pichia dispersa* (Dekker) Kreger-v. Rij.

Synonyms: *P. besseyi* Kurtzman & Wickerham, *P. delftensis* Beech, *P. saitoi* Kodama *et al.* and synonyms of *P. dispersa* listed by Kreger-van Rij (1970a).

- (12) *Pichia fasciculata* (Batra) Boidin *et al.*, *Bull. Soc. mycol. Fr.* (1965), **81**, 5

Synonyms: *Endomycopsis monospora* Saito, and synonyms of *E. monospora* in Lodder, *The Yeasts* (1970), p. 189.

- (13) *Pichia fibuligera* (Lindner) Boidin *et al.*, *Bull. Soc. mycol. Fr.* 1964, **80**, 396

Synonyms: *Endomycopsis fibuligera* (Lindner) Dekker, and synonyms of *E. fibuligera* in Lodder, *The Yeasts* (1970), p. 181.

- (14) *Pichia fluxuum* (Phaff & Knapp) Kreger-v. Rij

Synonyms: *P. terricola* v. d. Walt and synonyms of *P. fluxuum* and *P. terricola* listed by Kreger-van Rij (1970a).

- (16) *Pichia hansenii* (Zopf) Campbell *nov.comb.*

Basionym: *Saccharomyces hansenii* Zopf, *Ber. dt. bot. Ges.* (1889), **7**, 94.

Synonyms: *Debaryomyces hansenii* (Zopf) Lodder & Kreger-v. Rij in *The Yeasts* (1952), p. 270, and synonyms in Lodder, *The Yeasts* 1970, p. 140.

- (18) *Pichia heimii* Pignal (1970)

- (20) *Pichia marama* (di Menna) Phaff, *Antonie van Leeuwenhoek* (1956), **22**, 113.

Synonyms: *Debaryomyces marama* di Menna and *Zymodebaryomyces marama* (di Menna) Novak & Zsolt in Lodder, *The Yeasts* 1970, p. 146.

- (22) *Pichia melissophila* v. d. Walt & v. d. Klift (1972)

- (23) *Pichia membranaefaciens* Hansen

Synonyms: *P. fermentans* Lodder, *P. kluyveri* Bedford and synonyms of *P. fermentans*, *P. kluyveri* and *P. membranaefaciens* listed by Kreger-van Rij (1970a).

- (24) *Pichia mucosa* Wickerham & Kurtzman (1971)

- (26) *Pichia pastoris* (Guilliermond) Phaff

Synonyms: *P. quercuum* Phaff & Knapp and synonyms of *P. pastoris* and *P. quercuum* listed by Kreger-van Rij (1970a).

- (29) *Pichia polymorpha* Klöcker

Synonyms: *Debaryomyces vanrijii* (v. d. Walt & Tscheuschner) Abadie *et al.* and synonyms of *D. vanrijii* and *P. polymorpha* listed by Kreger-van Rij (1970a, b).

- (31) *Pichia rhodanensis* (Ramirez & Boidin) Phaff

Synonyms: *P. bovis* v. Uden & do Carmo-Sousa, *P. toletana* (Socias *et al.*) Kreger-v. Rij, *P. wickerhamii* (v. d. Walt) Kreger-v. Rij, *P. xylopsoci* v. d. Walt & Scott and synonyms of *P. bovis*, *P. rhodanensis*, *P. toletana* and *P. wickerhamii* listed by Kreger-van Rij (1970a).

- (32) *Pichia robertsii* v. d. Walt, *Antonie van Leeuwenhoek* (1959), **25**, 337

Synonym: *Wingea robertsii* (v. d. Walt) v. d. Walt, *Antonie van Leeuwenhoek* (1967), **33**, 97.

- (34) *Pichia sargentensis* Wickerham & Kurtzman (1971)

- (36) *Pichia spartinae* Ahearn *et al.* (1970)

- (38) *Pichia strasburgensis* (Ramirez & Boidin) Phaff

Synonyms: *P. onychis* Yarrow and synonyms of *P. strasburgensis* listed by Kreger-van Rij (1970a).

- (39) *Pichia tamaritii* (Ohara & Nonomura) Campbell *nov.comb.*

Basionym: *Debaryomyces tamaritii* Ohara & Nonomura, *J. agric. chem. Soc. Japan* (1954), **28**, 337.

- (41) *Pichia vini* (Zimmermann) Phaff

Synonyms: *P. etchellsii* Kreger-v. Rij, *P. vini* var. *vini*, *P. vini* var. *melibiosi* Santa Maria and synonyms of *P. etchellsii* and *P. vini* listed by Kreger-van Rij (1970a).

Genus *Schwanniomyces* Klöcker

The genus contains two species:

- (1) *Schwanniomyces castellii* Capriotti
Synonym: *S. alluvius* Phaff *et al.*
- (2) *Schwanniomyces occidentalis* Klöcker
Synonym: *S. persoonii* v. d. Walt.

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