equatorial view, oval $20 \cdot 8\mu \times 32 \cdot 0\mu$ (Fig. 4). exine thick with a thin cutin-like layer, exine further thickened at the poles, surface smooth; (Fig. 5) oval, the three oval translucent areas which appear along the equatorial line at a different focus, may be the germ pores. Brown in colour.

Type 4 (*Fig.* 6 *and Photo.* 4).—Equatorial view triangular, $44 \cdot 8\mu \times 38 \cdot 4\mu$, exine thick, granular with thin cuticle, pores three, one at each angle. Yellow in colour.

Type 5 (*Figs.* 7-8 *and Photo.* 5).—Tricolpate. Oblique polar view (Fig. 7) $28 \cdot 8\mu \times 32 \cdot 0\mu$; equatorial view (Fig. 8) $35 \cdot 2\mu \times 30 \cdot 4\mu$, the two median thickenings in Fig. 8 are perhaps the two ridges of the wall which are seen in the polar view. Exine thick, surface uneven, negatively reticulate. Brown in colour. The grain resembles in appearance but not in size the pollen grain of *Cornus amomum*.

Type 6 (*Figs.* 9-10 *and Photo.* 6)—Tetracolpate. Polar view (Fig. 9), $38 \cdot 4\mu \times 43 \cdot 2\mu$, colpæ diagonally placed, walls folded inwards, germinal slits thin and narrow along the colpæ (Fig. 10), exine thick, surface smooth. Brown in colour A pentacolpate grain whose oblique polar view is seen in Fig. 11 and Photo. 7, belongs perhaps to the same type although there is some difference in size. The grain resembles in appearance and to a certain extent in size also, the pollen of *Tilia americana*.[3]

Type 7 (*Fig.* 12 *and Photo.* 8).—Tricolpate. Polar view (Fig. 12,), $35 \cdot 5\mu \times 33 \cdot 6\mu$, three lobed, clefts deep, exine thick, granular surface reticulate and sculptured. Light brown in colour.

Type 8 (*Fig.* 13 *and Photo.* 9).—Probably equatorial view, elliptic, $25 \cdot 6\mu \times 44 \cdot 8\mu$, no furrow or germ pore seen. Photo. 9 shows the surface of the grain covered by dome-shaped structures which are responsible for the sscrobiculate sculpture of the exine. A comparison in appearance but not in size, can be made with the pollen grains of *Potamogeton natans*.[4] Wall dark brown in colour, body lighter.

Type 9 (*Figs.* 14, 15, 16 *and Photo* 10.)—Tricolpate, brachitrilistrium type. Oblique polar views (Figs. 14 and 15) at the higher and lower foci respectively, $57 \cdot 6\mu \times 56 \cdot 0\mu$, three flanged, flanges cleft upto the middle of the grain exine thick with reticulate thickenings. Equatorial view (Fig. 16), $56 \cdot 0\mu \times 38 \cdot 4\mu$. Dark brown in colour.

Type 10 (*Figs.* 17, 18, 19 *and Photos.* 11-12).—Tricolpate, brachitrilistrium type, polar view (Fig. 17 and Photo. 11), $28 \cdot 8\mu \times 33 \cdot 6\mu$, exine thick, surface with reticulate thickenings; equatorial view with the two flanges in focus (Fig 18 and Photo. 12) $33 \cdot 6\mu \times 32 \cdot 0\mu$; oblique equatorial view with one flange in focus (Fig. 19 $28 \cdot 0\mu \times 27 \cdot 2\mu$) Light brown in colour.

Cuticle (Photo. 13) with epidermal cells measuring about $44 \cdot 8\mu \times 24 \cdot 0\mu$, average thickness of wall $4 \cdot 0\mu$. Yellow in colour.

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1. Naumova, S. N., "Spores and pollen oft he coals of U.S.S.R.," *Rep.* XVII, *International Geological Congress*, 1, 353-64. 2. Erdtman, G., *An Introduction to Pollen Analysis*, 1943, 85, fig. 143. 3.—, G., *Loc. cit.*, 123, fig. 359. 4. Wodehouse, R. P., *Pollen Grains*, 1935, 221, fig 8.

IRREGUALR SEGREGATIONS IN YEAST HYBRIDS

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DEVIATIONS in tetrad segregation from the 2:2 Mendelian expectation in heterozygous *Saccharomyces* hybrids have recently been attributed (Winge and Roberts[1]) to a degeneration of four nuclei from an initially 8-nucleate complement A chance survival of any four nuclei from among the gametic products of two successive mitoses (following a reduction of the hybrid nucleus) has been considered an explanation for 2 : 2, 3 : 1. 1 : 3, 4 : 0 and 0 : 4 ascus types. This view is based on their analysis of four 5- and 6-spored heterozygous asci genetically marked for one character only—the fermentation of maltose—and is adopted as an alternative explanation to that held by Winkler[2], Lindegren[3], and Mundkur[4].

The following considerations, based on data presented earlier, will indicate the inadequacy of employing a single genetical marker in investigating non-Mendelian inheritance.

1. Five different crosses involving from five to ten genetical markers (Mundkur[1]) yielded asci in which segregations of loci determining the fermentation of various sugars and the syntheses of a purine and some B vitamins were markedly disturbed. In spite of the extensive non-Mendelian ratios for such markers, segregations of mating type specificity (a and α segregants) conformed to the expected 2 : 2 Mendelian ratio in all but three of twenty-four 4-spored asci. Clones from the three exceptional asci mated with neither a nor α standard

testers. No irregularities of mating type segregation were descernible in ten other 3-spored asci. Mating reactions of each segregant from these thirty-four asci were tested against both *a* and *α* standard haplophase clones. This behaviour is not consistent with the explanation advanced by Winge and Roberts since the *a*/*α* alleles would not be exempted from irregularities on their hypothesis.

2. Mundkur[4] found that among these same asci the adenine independent white haplophase parents AD* (W) when crossed to adenine deficient, pink haplophase parents *ad*(P) yielded tetrads of the constitutions AD(W) AD(W) AD(W) AD(W); AD(W) AD(W) *ad*(W) *ad*(W); *ad*(W) *ad*(W) *ad*(W) AD(W); and *ad*(P) *ad*(P) AD(W) AD(W). It had been demonstrated previously[5] that the pink clones are generally associated with adenine dependence.

3. Meiosis is completed in two successive divisions. No matter how many genes may be involved, a single reduction division can produce a maximum of four different genotypes and no more. Subsequent divisions of the nuclei derived from the tetrad do not increase the variety of genotypes. This fact has been amply confirmed by analyses of 8-spored asci of *Neurospora*. More than four kinds of clones from a single 8-spored ascus have never been reported, no matter how many genes have been heterozygous in the hybrid. A hybrid heterozygous for two pairs of genes can produce only four kinds of progeny. One heterozygous for three or more pairs is potentially capable of producing 8 or more genotypes. On Mendelian theory, however, each single tetrad can produce only 4 kinds of clones, irrespective of the heterozygosis of the hybrid. Winge and Roberts' explanation of irregular segregations is automatically excluded since it can be shown to require more than 4 genotypes in a single tetrad. For example, the tetrad listed below (Lindegren[3], page 25-2) produced three pink cultures and one white culture:

5919 *α G IN PN PY s TH AD*(W)
5920 *α g in pn py S th ad*(P)
5921 *α g IN pn PY s TH ad*(P)
5922 *a G in PN Py S th ad*(P)

The three pink cultures are genetically different at two loci, *e.g.*, *g in*, *g IN*, *G in*. The white culture is different from the three pinks being, G *IN*. If eight nuclei had been produced and four had died, it would be neccssary to account for one absent pink and three absent white clones without increasing the variety of genotypes beyond the maximum, namely, four. Inspection reveals that this cannot be done. For example, if culture *G IN* were white it would not increase the variety of genotypes, but two more white cultures must be accounted for. If the *g in* culture were white, the reduction would have produced five kinds of segregants and if the *g IN* culture were white, six kinds of clones would have resulted from the reduction: *G IN* (*White*), *g in* (*Pink*), g in (White), *g IN* (*Pink*), g IN (White), *G in* (*Pink*). The italics designate clones grown from the ascus; the roman letters indicate clones required by Winge and Roberts' hypothesis.

4. Mundkur[4] reported a mating (C1A × 3349) which yielded a tetrad of the following constitution. It is discussed as an example; many similar tetrads were found. (The cross was heterozygous for all the markers used).

M532 *α G ME MG MA ad*(W) *pn in*
M533 *a G ME MG ma ad*(W) *pn in*
M534 *a g ME MG MA AD*(W) *PN IN*
M535 *a g me MG MA AD*(W) *PN IN*

On the basis of Winge and Roberts' view, each of the ascospores would necessarily have an identical twin, since each one is different and the maximum of four genotypes has been attained. This would, however, mean a 6 : 2 ratio for *ME*/*me*, an 8 : 0 ratio for *MG*/*mg*, and a 6 : 2 ratio for *MA*/*ma*, since the hybrid was heterozygous for these loci. In addition, the anomalous *ad*(W) appeared in this ascus.

This analysis proves that the origin of non-Mendelian, mature 4-spored asci is not amenable to Winge and Roberts' view that a random destruction of four nuclei occurs in an initially Mendelian, 8-nucleate complement. It is evident, moreover, that use of one marker alone in evaluating irregular segregations is deceptive, and that the greater the number of diagnostic genetical markers employed the easier it is to detect inadequacies in the interpretation advanced by Winge and Roberts.

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1. Winge, O., and Roberts, C., *Nature*. 1950, **165**, 157. 2. Winkler, H., Die Konversion, *der Gene. Jena.*, 1930. 3. Lindegren, C. C., *The Yeast Cell. Educational Publishers, Inc., St. Louis*, 1949. 4. Mundkur, B. D., *Ann. Missouri bot. Gard.*, 1949, **36**, 259. 5. Lindegren, C. C., and Lindegren, G., *Proc. Nat. Acad. Sci.*, (*US*) 1947 **33**, 314.

* *Abbreviations:*

G/*g*, *ME*/*me*, *MG*/*mg*, *MA*/*ma* and *S*/*s* indicate galactose, melibiose, alpha methyl glucoside, maltose, and sucrose fermentations, respectively. *AD*/*ad*, *PY*/*py*, *TH*/*th*, *PN*/*pn*, and *IN*/*in* indicate abilities (or inabilities) to synthesize adenine, pyridoxine, thiamin, pantothenate and inositol, respectively. P and W indicate pink and white clones,