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Timing imbalance in the meiosis of the F_1 hybrid *Oryza sativa* × *O. australiensis*

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The F_1 hybrid *Oryza sativa* ($2n = 24$) × *O. australiensis* ($2n = 24$) was secured and studied by Gopalakrishnan (1959). The study of meiosis in this hybrid assumed special significance in view of the controversy regarding the taxonomic position of *O. australiensis*. The observation of Shah (1955) that *O. australiensis* and *O. perennis* ($2n = 24$) are similar in having perennial rhizomatous stems and large spikelets and anthers was responsible for the inclusion of both these species in the section Sativa (Ghose, Ghatge & Subrahmanyan, 1956). Gopalakrishnan (1959) re-examined the morphology of *O. australiensis* and considered that this species is intermediate between the sections Sativa and Officinalis since whorling of panicle branches characteristic of *O. officinalis* is present in the former species. Further, while a maximum of four bivalents were recorded by him in the F_1 hybrid *O. sativa* × *O. officinalis*, a maximum of eight bivalents were recorded in the F_1 hybrid *O. sativa* × *O. australiensis*. Richharia (1960), in his treatise on inter-specific relations in the genus *Oryza*, supported Gopalakrishnan's view and suggested that *O. australiensis* might have originated by hybridization between the members of the sections Sativa and Officinalis in Australia.

Korah (1961) and Sampath (personal communication) observed that the chromosomes of *O. australiensis* were larger than those of *O. sativa* at somatic metaphase. Gopalakrishnan (1959) and Shastry & Rao (1961) reported that the bivalents of *O. australiensis* appeared to be larger than those of *O. sativa*. The comparison of total chromatin lengths at pachytene (Shastry, Rao & Misra, 1960; Shastry & Rao, 1961), however, revealed that the species *O. sativa* and *O. australiensis* have comparable lengths (*ca.* 400 μ) at this stage. Further, the pachytene bivalents of *O. australiensis* were highly heterochromatic. Shastry & Rao (1961) concluded that apparent largeness of the bivalents of *O. australiensis* is due to their undergoing less condensation (because of greater amount of heterochromatin) from pachytene to metaphase I stages.

The observation of a maximum number of eight bivalents in the F_1 hybrid *O. sativa* × *O. australiensis* (Gopalakrishnan, 1959) and the inference of hybrid origin of *O. australiensis* (Richharia, 1960) were considered unlikely by the present authors for the following reasons:

1. *O. australiensis* is endemic to Australia. No other species of *Oryza* belonging to either of the sections Sativa or Officinalis is reported from Australia.

2. There is no evidence of human introduction of rice into Australia except in very recent times.
3. The karyotype of *O. australiensis* is highly symmetric and the pachytene bivalents of this species are highly heterochromatic, a situation not yet discovered in any other species of the genus (Shastry & Rao, 1961).

A reinvestigation of the meiosis of the F_1 hybrid *O. sativa* × *O. australiensis* was therefore considered necessary. Since the parents differed in the sizes of their chromosomes at metaphase I, it was hoped that it would be possible to distinguish between auto- and allosyndesis, an aspect not studied by Gopalakrishnan (1959). To avoid the discrepancies in pairing due to varietal differences in parents, the F_1 hybrid obtained and studied by Gopalakrishnan (1959) was secured by the courtesy of Dr R. H. Richharia, Director, Central Rice Research Institute, Cuttack, and was used in the present investigation.

Spikes of suitable stage were fixed in acetic-alcohol (1:3 by volume) to which traces of ferric chloride were added. After fixation for 24 hours at low temperature (10–14° C.), the material was transferred to 70% ethyl alcohol in which it was stored. Simple aceto-carmine smears were employed for the study of meiosis. Temporary slides were used for photomicrography.

OBSERVATIONS

The meiotic data of this hybrid were based upon the examination of 223 PMCs at meta-anaphase I, 44 at diakinesis and 10 at diplotene. The chromosomes of *O. australiensis* are so distinctly larger and darker stained than those of *O. sativa* that, at all stages of meiosis, they could be distinguished (Plate I, Figs. 2, 5; Plate II, Figs. 8, 12, 13). The meiotic stages from pro-metaphase to late anaphase I were indistinguishable because of the high frequency of univalents, and consequently what is described as meta-anaphase I represents a heterogeneous group of PMCs.

1. *Pairing at prophase*

Several PMCs at pachytene stage were analysed in the F_1 hybrid, in which the univalent nature of the chromosomes was clear. In the ten PMCs analysed at diplotene stage, only twelve configurations were visible, all of which were univalents. It was inferred that they corresponded to the complement of *O. australiensis*, for reasons to be discussed later. In all the forty-four PMCs of early and late diakinesis that were analysed, the chromosomes of *O. australiensis* were distinct by their darker staining and larger size (Plate II, Fig. 8). No true allosyndetic bivalents were noted in any of these PMCs. In fifteen PMCs at diakinesis, two autosyndetic bivalents of *sativa* were recorded. The most significant feature of this stage was the variable number of visible univalents. While in every one of these forty-four PMCs the full complement of *australiensis* chromosomes was recognizable as univalents, the number of *sativa* chromosomes that were visible (those which have been sufficiently condensed) was variable. A variable number of non-chiasmatic associations have been noted at this stage (Plate II, Fig. 8).

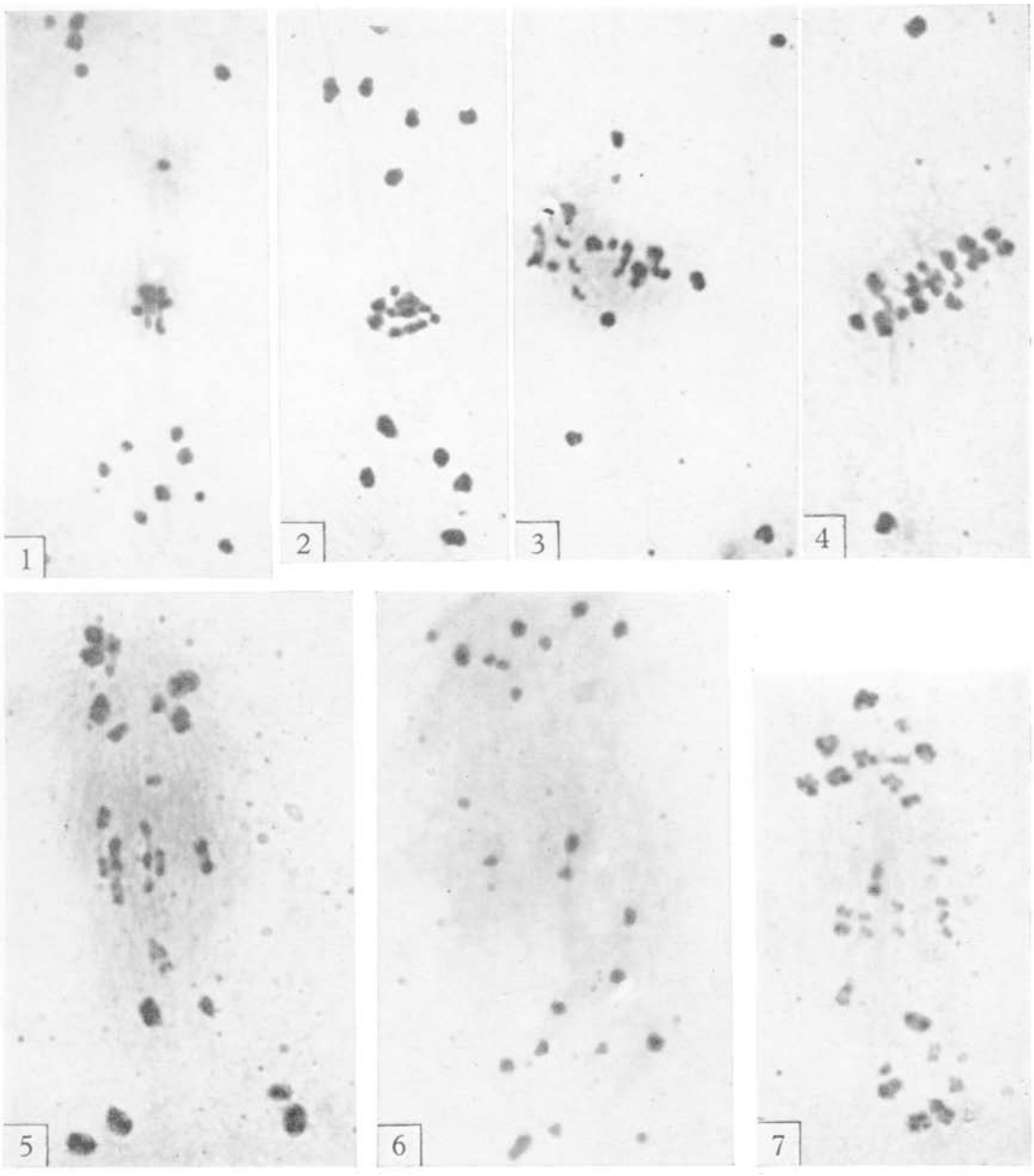

Fig. 1. Meta-anaphase I. Two autosyndetic bivalents, one e-e allo-association and two *sativa* univalents at equator. × 1100.

Fig. 2. Meta-anaphase I. Full complement of *O. sativa* and two univalents of *O. australiensis* at equator. × 1100.

Fig. 3. Meta-anaphase I. Note the congression on the equatorial plate with four e-e allo-associations. Four *australiensis* univalents migrated to poles. × 1100.

Fig. 4. Meta-anaphase I. Four e-e allo-associations. Two *australiensis* univalents at the poles. × 1100.

Fig. 5. Meta-anaphase I. Ten *australiensis* and four *sativa* chromosomes at poles. *Sativa* univalents at equator dividing. × 1500.

Fig. 6. Meta-anaphase I. One lagging e-e allo-association. × 1400.

Fig. 7. Meta-anaphase I. Full complement of *O. australiensis* at poles. *Sativa* univalents at equator dividing. × 1100.

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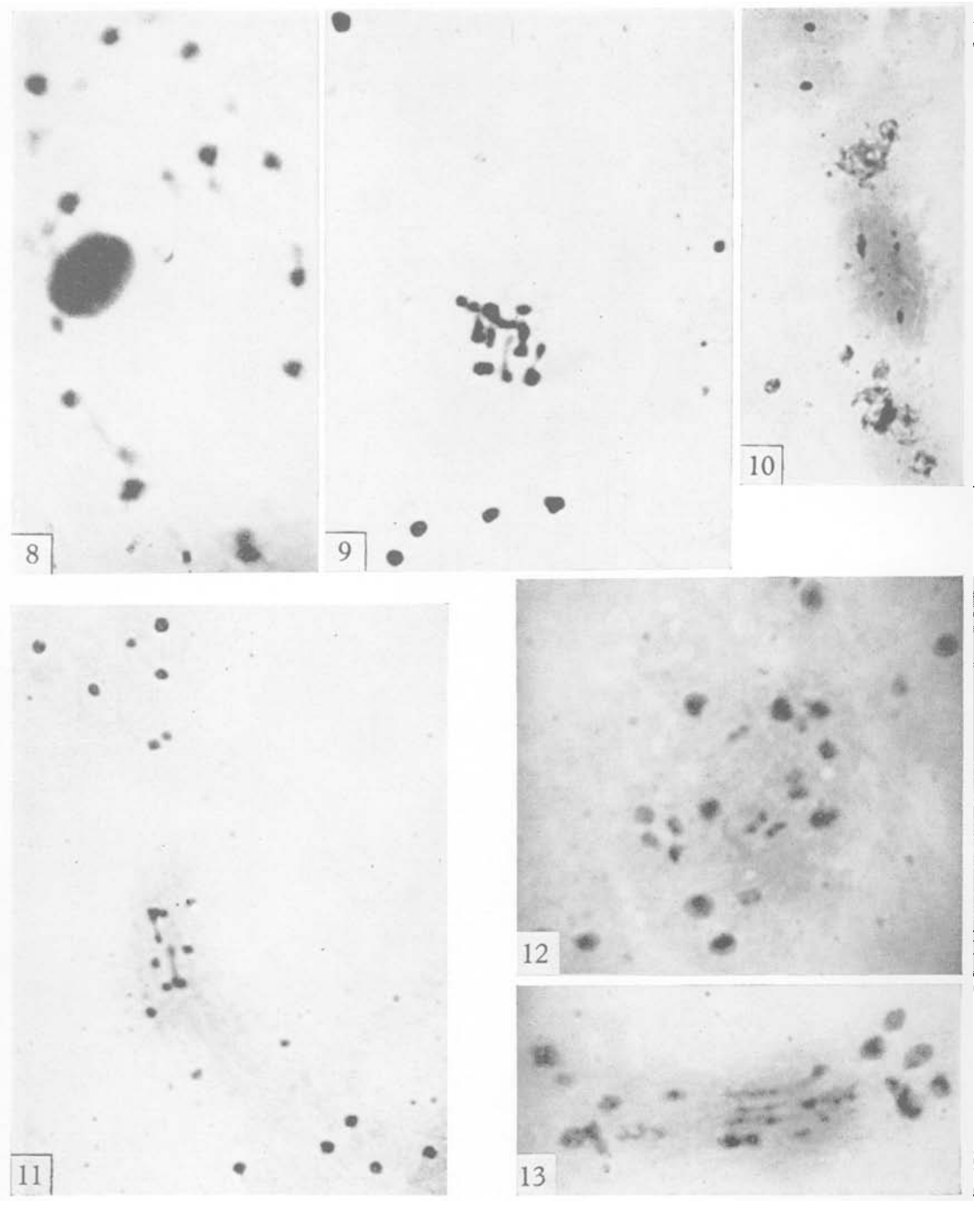

Fig. 8. Diakinesis. Note the chromosomes of *O. australiensis* which are stained darker and larger. Five univalent pairs secondarily associated. × 1200.

Fig. 9. Meta-anaphase I. Five e-e allo-associations at equator. Five *australiensis* univalents at poles. × 1400.

Fig. 10. Anaphase I. Note the wide differences in the condensation between the univalents. × 1400.

Fig. 11. Meta-anaphase I. Two e-e allo-associations at equator. Ten *australiensis* univalents at poles. × 1800.

Fig. 12. Metaphase I. Polar view. Twelve large *australiensis* univalents. Four divided and eight undivided *sativa* univalents. × 1500.

Fig. 13. Meta-anaphase I. Full complement of *O. australiensis* at poles. Three pairs of univalents of *O. sativa* formed false bridges. × 1500.

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The number of univalents visible in different PMCs at this stage and the number which were secondarily associated are presented in Table 4. It could be clearly seen that the chromosomes of *sativa* were not all condensed at the same time while those of *australiensis* were more uniform in this respect. Further, the residual homology between the genomes seemed to permit a high degree of secondary association.

2. *Meta-anaphase I*

Out of 223 PMCs studied at this stage, 194 had twenty-four univalents each (Plate I, Fig. 3). In the remaining 29 PMCs, 1, 2 and 3 autosyndetic bivalents involving the chromosomes of *O. sativa* were recorded in 24, 4 and 1 PMCs respectively (Table 1, and Plate I, Fig. 1). In a single PMC, what appeared to be an

Table 1. *Frequency distribution of PMCs with autosyndetic bivalents and univalents at meta-anaphase I of the F_1 hybrid* O. sativa × O. australiensis

	Number of autosyndetic bivalents				
	O. sativa			*O. australiensis*	
Twenty-four univalents	1	2	3	1	Total
194	23	4	1	1	223

autosyndetic bivalent involving the chromosomes of *O. australiensis* was recorded. All the autosyndetic bivalents were rod-shaped with a single chiasma each. No true bivalent involving the chromosomes of the two species (allosyndetic) was recorded in any one of the PMCs scored. While in a majority of the PMCs no regular equatorial plate was formed, in twenty (8·6%) PMCs all the univalents were congressed on an equatorial plate (Plate I, Figs. 3, 4). In fifteen (6·4%) PMCs, while the entire complement of *O. australiensis* were at the poles, univalents and autosyndetic bivalents of *O. sativa* were aligned on the equatorial plate (Plate I, Figs. 5, 7; Plate II, Fig. 13).

The most frequent associations met with during meiosis in the hybrid appeared to be non-chiasmatic and they were arranged on the equatorial plate. The frequency of these pseudobivalents varied from 0 to 7, the modal value being 2 per PMC. The frequency distribution of the PMCs with varying numbers of pseudobivalents is given in Table 2. Autosyndetic pseudobivalents were not observed in any one of the PMCs. The pseudobivalents were all end-to-end associations (Plate I, Figs. 3, 4, 6; Plate II, Figs. 9, 11).

Table 2. *Frequency distribution of PMCs with various number of allosyndetic end-to-end pseudobivalents in the F_1 hybrid* O. sativa × O. australiensis

Number of allosyndetic, end-to-end pseudobivalents								
0	1	2	3	4	5	6	7	Total
122	21	40	23	12	3	1	1	223

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3. *Distribution of univalents*

Of the 223 PMCs studied at meta-anaphase I, 142 could be clearly classified for the contribution of univalents at the poles. In all these PMCs, with the exception of five, univalents were arranged in three groups, one each at the two poles and a group of laggards at the equator (Plate I, Figs. 1, 2). The total number of *sativa* and *australiensis* chromosomes at the two poles is presented in a two-way table (Table 3). The frequency in each cell refers to the number of PMCs with the

Table 3. *Frequency distribution of* sativa *and* australiensis *chromosomes at both the poles of the meta-anaphase I PMCs in the* F_1 *hybrid* O. sativa × O. australiensis

Number of *sativa* chromosomes at both the poles	Number of *australiensis* chromosomes at both the poles													
	0	1	2	3	4	5	6	7	8	9	10	11	12	Total
0		1	2	—	5	4	7	7	7	7	10	2	5	57
1					1	5	5	2	3	2	3	2	1	24
2						3	1	2	3	2	1	1	1	14
3				1	—	2	1	—	2	4	3	1	1	15
4				1	—	—	—	1	3	4	2	2	1	14
5							1	—	3	1	1	3	1	10
6								2	2	—	—	—	—	4
7												1	—	1
8								1						1
9											1			1
10												1		1
Total		1	2	2	6	14	15	15	23	20	21	13	10	142

corresponding number of *sativa* and *australiensis* chromosomes. It will be seen from this table that while there were several PMCs (fifty-seven) with 1–12 chromosomes of *O. australiensis* at the poles, but no chromosomes of *sativa*, the reverse situation where one or more *sativa* chromosomes were present to the exclusion of *australiensis* chromosomes was not met with. In view of the large sample that has been employed, this could not be due to chance. Evidently, the chromosomes of *australiensis* either migrate to the poles earlier than those of *sativa* or fail to congress more frequently on the equatorial plate. The full congression on the equatorial plate in 8·6% PMCs can be accounted for by either of the causes.

In nine PMCs, 1–4 *australiensis* chromosomes migrated to poles with 0 or 1 chromosomes of *sativa*. These PMCs might represent early stages of meta-anaphase. In eighteen PMCs, 6–12 chromosomes of *australiensis* were observed along with 6–12 chromosomes of *sativa* and these PMCs might correspond to the late stage of meta-anaphase I. With the exception of these twenty-seven (19·0%) PMCs (Table 3), the two-way table clearly reveals the asymmetry in distribution of the chromosomes indicating either early migration to the poles or failure of congression at the equator of *australiensis* chromosomes (Plate I, Figs. 2, 5, 7; Plate II, Fig. 13). Further, the *sativa* univalents were dividing in some PMCs

(Plate I, Fig. 7) and exhibited stickiness in others (Plate II, Fig. 13). Wide differences in condensation of the univalents were observed in some cells (Plate II, Fig. 10).

Table 4. *Frequency distribution of univalents of* O. sativa *visible at diakinesis and attached to those of* O. australiensis *in the* F_1 *hybrid* O. sativa × O. australiensis

Number of *sativa* chromosomes secondarily associated with those of *australiensis*	Number of *sativa* chromosomes visible in addition to the full complement of *australiensis* chromosomes											
	2	3	4	5	6	7	8	9	10	11	12	Total
0											6	6
1											1	1
2	1											1
3					1							1
4						1					3	4
5					1		2		4		2	9
6						1	2		2		5	10
7						1	2				3	6
8							1				4	5
9												—
10											1	1
Total	1	—	—	—	2	3	7	—	6	—	25	44

DISCUSSION

1. *Nature and extent of pairing*

Gopalakrishnan (1959) recorded a maximum of eight bivalents (3·49% PMCs) and a maximum of twenty-four univalents (6·99% PMCs) with a mean pairing of $0{\cdot}06_{IV} + 0{\cdot}1_{III} + 3{\cdot}83_{II} + 15{\cdot}80_{I}$ per PMC in the hybrid *O. sativa* × *O. australiensis*. This suggests considerable lack of homology between the genomes, though more than between the genomes of *O. sativa* and *O. officinalis*. The cytological analysis done in the present investigation, on the other hand, gave no evidence of pairing leading to chiasma formation between the genomes of *O. sativa* and *O. australiensis*, the mean autosyndetic bivalent frequency being 0·15 per PMC and that of non-chiasmatic pseudobivalents, 1·06 per PMC. This discrepancy cannot be accounted for by the varietal differences since the same hybrid as was studied by Gopalakrishnan (1959) was employed in the present study. Although environmental factors do modify chiasma (thereby bivalent) frequency, such a wide discrepancy in observations cannot be attributed to this cause alone. It is, therefore, most likely that many of the pseudobivalents were scored as bivalents by Gopalakrishnan. In support of such a view, two points seem significant:

(i) While the present authors recorded 1–7 pseudobivalents per PMC in 43·3% of the cells, Gopalakrishnan made no mention of their occurrence.

(ii) Many of the drawings of PMCs with 'bivalents' are quite unconvincing as regards the chiasmatic connexion between the chromosomes and are comparable to allosyndetic pseudobivalents scored by the present authors.

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2. *Autosyndetic pairing and its significance*

The occurrence of two bivalents in haploid variants of *O. sativa* (Morinaga & Fukushima, 1934; Hu, 1958) and *O. glaberrima* has been hitherto explained on the basis of the hypothetical secondarily balanced allotetraploid origin (Nandi, 1936) of the diploid species of *Oryza*. If the basic chromosome number for the tribe as postulated was 5, the haploids of the species with $2n = 24$ are expected to form two bivalents. Since it is established that no pairing occurs between the genomes of *O. sativa* and *O. australiensis*, the interspecific hybrid between these species offers an opportunity to test the expectations of autosyndetic pairing on the basis of alteration of the basic number from 5 to 7.

With the exception of the occurrence of a single PMC each (0·043 %) with three autosyndetic *sativa* and one autosyndetic *australiensis* bivalents, most commonly one (9·87 % PMCs) or two (1·7 % PMCs) autosyndetic bivalents involving *sativa* chromosomes were found in the F_1 hybrid *O. sativa* × *O. australiensis*. Consequently, the occurrence of autosyndetic bivalents in *O. sativa* and their non-occurrence in *O. australiensis* raised severe doubts regarding their being valid indicators of basic chromosome number in *Oryza*. This observation might mean either that (1) chromosome structural changes subsequent to alteration of the basic number from 5 to 7 have destroyed the homology between the chromosomes originally identical in *O. australiensis*, or (2) the bivalents in haploid *O. sativa* and the autosyndetic bivalents in the hybrid under study are the result of structural changes and do not point to the secondarily balanced allotetraploid nature of these species. If the former alternative is considered to be true, it is most surprising that the homology between duplicated chromosomes could be preserved in a species with a high variability and exposure to natural and human selection (*O. sativa*) and is lost in a species which is more primitive, with very limited geographic distribution (endemic to Australia), and is highly uniform (*O. australiensis*). On the other hand, it is more likely that the autosyndetic bivalents are the result of structural differences in *O. sativa* which is highly evolved. This interpretation, however, does not contradict the allopolyploid origin of the diploid species of *Oryza*, but it only emphasizes their functional diploid nature. Non-complementation for viability of the gametes in the desynaptic interspecific hybrid (*O. sativa* × *O. officinalis*) with a high degree of numerical regularities at anaphase I (Shastry, Sharma & Rao, 1960) likewise points to the same conclusion.

3. *Timing imbalance in the condensation of chromosomes*

Several cases exist in the literature (Darlington, 1937) where one or more chromosomes of a species are either retarded or advanced in condensation with reference to others at metaphase I. These differences in timing of condensation of chromosomes, referred to as timing imbalance, are often used as indications of allopolyploid origin of the species. Implicit in such an argument is that either the genomes of the related species differ in the duration of meiosis or that the different genomes interact in a hybrid so as to produce such an imbalance. Meiosis

of the F_1 hybrid *O. sativa* × *O. australiensis* offers an excellent example of such a situation.

The occurrence of twelve chromosomes of *O. australiensis* alone at the onset of diplotene, followed by a varying number of *sativa* univalents at diakinesis and probable early migration of *australiensis* univalents to the poles, clearly indicates the timing imbalance for condensation and mobility of the chromosomes of these two genomes. This is so striking that in 97·85 % of the PMCs at meta-anaphase I, laggards remain at the equator, the composition of laggards being predominantly *sativa* chromosomes and a few *australiensis* chromosomes. These observations indicate one of the following possibilities:

1. The meiotic cycle of *O. australiensis* is much shorter than that of *O. sativa*.
2. The presence of *australiensis* chromosomes delays the condensation of *sativa* chromosomes; or
3. The presence of *sativa* chromosomes hastens the condensation of *australiensis* chromosomes.

It is not possible to distinguish between these alternatives, nor is it possible to decide whether these differences are intrinsic to genomes or the result of their interaction.

4. *Significance of pseudobivalents*

The use of the terms 'pseudobivalents' (Håkansson, 1940; Walters, 1954), 'quasi-bivalents' (Östergren & Vigfusson, 1953), 'associations not due to chiasmata' (Shastry, Sharma & Rao, 1961) and 'secondary pairing' (Darlington, 1928; Lawrence, 1929), and their classification into 'end-to-end', 'side-by-side' and 'end-to-side' types (Person, 1955), was made necessary because of the limited sense in which the term 'bivalent' was applied, and because of the concept that bivalent formation is indicative of homologous pairing at prophase followed by persistent chiasma formation at the stage of analysis (diakinesis or metaphase I). Several hypotheses have been advanced to explain the occurrence of pseudobivalents—(i) breakage and reunion of chromosomes originally brought into contact by chance, with no dependence on homology (Walters, 1950); (ii) matrical connexions between univalents (Walters, 1954); (iii) suspected pairing at early prophase followed by failure of chiasma formation (s-s associations; Person, 1955), and (iv) heterochromatic fusion, stickiness and non-specific attractions (Riley & Chapman, 1957; Natarajan & Swaminathan, 1958). Secondary pairing or secondary association, in its strict sense, pertains to inter-bivalent attraction which is apparent in the post-synaptic phase, not accompanied by actual visible connexions, and is related to residual homology in higher polyploids (Darlington, 1937), although similar attractions between univalents can be visualized. Person (1955) attached special significance to the sites of attachment between univalents of pseudobivalents. He observed a negative correlation between the number of s-s associations and true bivalents, indicating a competition between them. No such correlation was observed of e-s and e-e associations with true bivalents,

indicating that the latter two forms of pseudobivalents do not depend upon homology.

Although the pseudobivalents reported in the present study of the F_1 hybrid *O. sativa* × *O. australiensis* resemble the e-e associations of Person (1955) and pseudobivalents of Walters (1954), they are yet distinctive in the following respects from all the previously reported cases: (i) allosyndetic pairing is exclusively in the form of pseudobivalents and consequently it is not possible either to study the correlation between the true bivalents and pseudobivalents (Person, 1955) or estimate the 'potential bivalents' (Gaul, 1959); (ii) all pseudobivalents are allosyndetic, which indicates that whatever might be the cause of their origin, they are not random associations; (iii) all pseudobivalents conform to the end-to-end arrangement of Person (1955); (iv) the parental species are distinctive in their karyotypes, one (*O. australiensis*) being exceedingly heterochromatic; and (v) their occurrence is coupled with a distinct timing imbalance in condensation and possibly in migration between the chromosome complements of the parental species.

It is hazardous to consider that any one of the views expressed (Walters, 1954; Person, 1955; Riley & Chapman, 1957) on the origin of pseudobivalents are conclusive and of universal applicability. The interpretation of the pseudobivalents of the F_1 hybrid *O. sativa* × *O. australiensis* is further complicated by the five special features accompanying their detection enumerated above. The strongest points in favour of their reflecting homology between the genomes are that all of these associations are allosyndetic and that timing imbalance does not provide the necessary conditions for the formation of true bivalents. The weakest points of their being indicators of homology are that all of them are end-to-end associations and that the karyotype of one of the species (*O. australiensis*) has extensive heterochromatic segments, which can exhibit stickiness. The present evidence does not make it possible to choose between these two alternatives.

5. *Genetic differentiation and hybrid sterility in* Oryza

Absence of true allosyndetic bivalents in the F_1 hybrid *O. sativa* × *O. australiensis*, in the light of the suggested timing imbalance, can be interpreted to mean either that no homology exists between the chromosome complements of the constituent species or that the necessary conditions for pairing and persistence of chiasmata are not provided by the superimposition of the timing imbalance during meiosis. Preference for either of these alternatives is not justified by the present evidence.

Complete sterility is reported in the F_1 hybrids *O. sativa* × *O. officinalis* and *O. sativa* × *O. australiensis* (Gopalakrishnan, 1959). In the former hybrid, pairing at pachytene was complete followed by desynapsis in later stages of meiosis (Shastry, Sharma & Rao, 1960). In the latter hybrid, reported here, the timing imbalance followed by infrequency of complete separation of the full complement of the parental species to the poles at anaphase I is the possible reason for sterility. High sterility in inter-subspecific hybrids of *O. sativa* have already been demon-

strated by pachytene analysis to be due to chromosomal differentiation (Yao, Henderson & Jodon, 1958; Shastry & Misra, 1961). Other interspecific hybrids of the genus have thus far not been subjected to critical analysis. It is interesting to note that different mechanisms control hybrid sterility in the genus *Oryza*.

6. *Taxonomic position of* O. australiensis

The controversy regarding the taxonomic status of *O. australiensis* is largely due to its resemblance to *O. perennis* in having a perennial branched rhizomatous stem, bold grains and long anthers, and to *O. officinalis* with regard to the whorling of the branches in the panicle and the size of the chromosomes. This intermediate morphological appearance could be attributed to two causes:

1. *O. australiensis* could have been the progenitor of members belonging to both the sections Sativa and Officinalis, which have been subject to divergent evolution with regard to the distinguishing characters. If this hypothesis is true, the species *O. australiensis* might represent one branch in the evolution and isolation of the pre-Sativa and pre-Officinalis members of *Oryza*.
2. *O. australiensis* is of more recent origin, as a result of hybridization between the well-differentiated members of the sections Sativa and Officinalis. Richharia (1960) and Gopalakrishnan (1959) favoured the latter view, while the present authors are inclined to support the former view for the following reasons:

   (i) The karyotype of *O. australiensis* is highly symmetric, being classed in 2b of Stebbins' (1958) classification in contrast to *O. sativa* classifiable in 3c (Shastry & Rao, 1961). Such a high degree of symmetry is least expected in a highly evolved species.

   (ii) Shastry & Rao (1961) observed that pachytene bivalents of *O. australiensis* are unmistakably distinct from those of *O. sativa* and *O. officinalis* in their 'differentiated' appearance (Hyde, 1953). Primitive taxa of several other genera (cf. Stebbins, 1950, and Venkateswarlu, 1961) are characterized by excessive heterochromatic segments in their karyotype.

   (iii) The occurrence of a higher frequency of bivalents in *O. sativa* × *O. australiensis* than in *O. sativa* × *O. officinalis* (Gopalakrishnan, 1959) is not substantiated in the present study.

SUMMARY

The meiosis in the F_1 hybrid *Oryza sativa* × *O. australiensis* was studied. Contrary to the observations of Gopalakrishnan (1959), true allosyndetic bivalents were not found at metaphase I. The most frequent associations were non-chiasmatic, end-to-end pseudobivalents. Autosyndetic bivalents were recorded mostly in the complement belonging to *O. sativa*, which are distinguishable by their smallness and lighter staining. The meiotic cycle exhibits timing imbalance with

earlier condensation, and possibly migration, of the univalents belonging to *O. australiensis*. The data on meiotic pairing in the F_1 hybrid and the comparative morphology of *O. sativa*, *O. officinalis* and *O. australiensis* inicate that the last species is the most primitive member, having originated from the pre-Sativa and pre-Officinalis complex.

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