PACHYTENE ANALYSIS IN *ORYZA*

IV. Chromosome Morphology of *O. australiensis*, Domin., *O. glaberrima*, Steud. and *O. stapfii*, Rosch.

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Pachytene analysis in the genus *Oryza* was initiated by Yao, Henderson and Jodon (1958) for the analysis of cryptic structural hybridity in intervarietal crosses of *O. sativa*. Their study could not contribute any information regarding karyomorphology of the species, since they could not identify the centromeres with certainty. A detailed karyomorphological study based upon pachytene analysis was reported by Shastry, Rao and Misra (1960), where they pointed out the potentialities of this approach for various cytogenetical problems in the genus. Since the earlier data on karyomorphology in this genus were obtained by the analysis of metaphases in root-tips where the size variation of the chromosomes was limited (0·7–2·8 μ, Ramanujam, 1938), it was felt that a reinvestigation of the karyomorphology of the species by way of pachytene analysis was desirable. With this objective, the present study was undertaken on three species: *O. australiensis*, the wild rice of Australia, *O. glaberrima*, cultivated rice of West Africa, and *O. stapfii*, a presumed hybrid species between *O. perennis* and *O. glaberrima* (Richharia, 1960).

Material and Methods

Seeds of the species, *O. australiensis* and *O. stapfii* were made available by the Director, Central Rice Research Institute, Cuttack, while those of *O. glaberrima* were supplied by Mr. M. B. V. N. Rao of Andhra University, Waltair. The panicles of right stage were fixed at low temperature (14° C.) for 24 hours in acetic alcohol (1 : 3 by volume) to which traces of ferric chloride were added. Belling's aceto-carmine smear schedule was employed with 1% aceto-carmine as the stain. Slight warming and gentle tapping of the slide permitted excellent differentiation of the bivalents at pachytene.

While in all the PMCs analysed at pachytene, 5–6 bivalents were traceable end to end, in only 3–5 of the PMCs, the entire complement was

analysable. In addition to length, details of macrochromomeres, position of the centromere and attachment regions to nucleoli were used in the identification of bivalents. Temporary slides were used for drawings and photomicrography.

Results

All the three species investigated were diploids with $2n = 24$. Twelve pachytene bivalents in them were numbered in the descending order of their lengths. Salient features of each chromosome of the three species with regard to length, arm ratio and chromomere pattern are presented in Table I along with reference to corresponding idiograms of the karyotypes and photomicrographs of the PMCs.

Pachytene bivalents of *O. australiensis* are "differentiated" into darkly stained regions alternating with lightly stained ones. Detailed chromomeric analysis was not possible in this species for reasons of heterochromaticity of the bivalents. Centric constrictions are most pronounced in this species, since they are flanked by darkly stained regions of variable lengths.

The morphology of pachytene bivalents of *O. glaberrima* is distinct from that of *O. australiensis*. Each bivalent in the former species is differentiated into chromomeres of varying degrees of stainability and sizes. The aggregation of chromomeres into darkly stained regions is absent, permitting a detailed chromomere analysis. The centric constrictions are not as sharp as in *O. australiensis* but are, however, analyzable due to macrochromomeres flanking them.

Pachytene bivalents in *O. stapfii* are very similar to those of *O. glaberrima*. Most of the bivalents terminate in either darkly stained regions or in telochromomeres. The centric constrictions are as sharply defined as in *O. glaberrima*. In three bivalents, small unpaired segments, which are designated as differential segments were recorded. The significance of their occurrence is discussed later.

Discussion

(i) *Quality of preparations.*—As has been pointed out by Lima-de-Faria (1952), not all plant materials are equally suitable for pachytene analysis. The length of the bivalents offers the greatest handicap in proper spreading of the bivalents. The species, *O. australiensis*, which has total chromatin length 1/3 larger than the other two species and the karyotype of which, consists of 2 large ($> 50\,\mu$), 8 medium (20–50 μ) and 2 small ($< 25\,\mu$) chromosomes is much more difficult to be analysed at pachytene than the other two

TABLE I

Lengths, arm ratios and chromomeric pattern in the karyotypes of O. australiensis, O. glaberrima and O. stapfii

Name of the species	No. of the chromo-somes	Total length in microns	Arm ratio short arm/ long arm	Chromomeric pattern*
O. australiensis	1	62·0	·61	Darkly stained region in the middle of S.A. and distal end of L.A. centromere flanked by 3 μ long dark region (T.F. 1)
	2	52·3	·53	Centromere flanked by 5 μ and 8 μ long dark regions on S.A. and L.A. Another dark region 14 μ from distal end of L.A. (T.F. 1)
	3	43·0	·32	Uniformly lightly stained. Centromere not sharp.
	4	37·5	·31	S.A. uniformly lightly stained except for proximal region. L.A. has two distinct terminal and two interstitial macrochromomeres (T.F. 1 and P.F. 2)
	5	35·0	·79	Nucleolar bivalent with 2 μ long satellite. Centromere flanked by dark regions of equal length (T.F. 1)
	6	32·5	·35	S.A. uniform except for short proximal region. L.A. has an interstitial, 10 μ long dark region and two telochromomeres (T.F. 1)
	7	27·5	·57	Darkly stained throughout the length. S.A. has two telochromomeres. L.A. has 7 darkly stained regions (T.F. 1)
	8	25·0	·92	S.A. has 8 μ long distal dark region. L.A. has two distinct macrochromomeres (T.F. 1 and P.F. 4)
	9	25·0	·42	S.A. consists of 3 large chromomeres. L.A. uniformly stained with 4 distinct chromomeres (T.F. 1 and P.F. 4)
	10	25·0	·69	Centromere flanked by two small chromomeres. S.A. has 4 μ long dark region. L.A. has 3 pairs of dark chromomeres (T.F. 1 and P.F. 4)
	11	22·5	·55	S.A. terminates in dark region while L.A. has two distinct macrochromomeres 3 and 7 μ from its distal end (T.F. 1)
	12	19·0	·52	Both arms terminate in telochromomeres. Centromere flanked by distinct chromomeres. Two sub-terminal chromomeres are conspicuous in L.A. (T.F. 1)

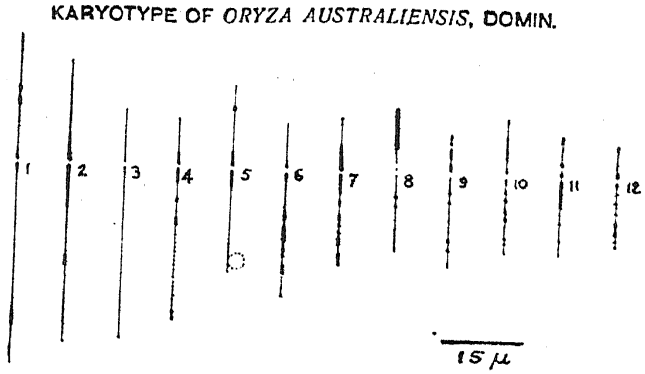
TABLE 1 (*Contd.*)

Name of the species	No. of the chromo-somes	Total length in microns	Arm ratio short arm/ long arm	Chromomeric pattern*
O. glabe-rrima	1	39·5	·34	S.A. uniformly stained. L.A. has 5 distinct chromomeres (T.F. 2 and P.F. 3)
	2	27·0	·54	S.A. has 7 distinct chromomeres in distal region and darkly stained proximal region. L.A. has 2 distinct chromomeres in sub-terminal region (T.F. 2)
	3	25·5	·45	S.A. has distal darkly stained (4 μ) region. L.A. has 3 μ long dark terminal region and 3 distinct chromomeres. Centromere flanked by chromomeres (T.F. 2 and P.F. 3 and 4)
	4	19·5	·34	Nucleolar bivalent. Centromere not very clear. S.A. terminates in 3 chromomeres. L.A. terminates in dark region (T.F. 2 and P.F. 3)
	5	19·0	·74	S.A. has two distinct chromomeres while L.A. is differentiated into 3 chromomeres close to centromere and a darkly stained terminal region (T.F. 2 and P.F. 3)
	6	19·0	·52	S.A. uniformly stained. L.A. has terminal dark region and 4 chromomeres in its middle (T.F. 2 and P.F. 3 and 4)
	7	17·0	·79	S.A. has 4 chromomeres in 3 μ of the sub-terminal region. L.A. uniformly stained (T.F. 2)
	8	16·0	·88	Nucleolar bivalent with 3 μ long satellite. S.A. uniformly stained. L.A. has a proximal darkly stained region (T.F. 2 and P.F. 3)
	9	14·0	·86	S.A. darkly stained except for 2 μ of proximal region. L.A. has 2 terminal and 1 proximal chromomeres (T.F. 2 and P.F. 3)
	10	14·0	·55	S.A. terminates in 4 chromomeres. L.A. has 4 interstitial chromomeres and a darkly stained 2 μ long terminal region (T.F. 2 and P.F. 3 and 4)
	11	12·0	·60	S.A. has 3 chromomeres in its proximal half. L.A. uniformly stained except for a 4 μ long dark region (T.F. 2 and P.F. 3 and 4)

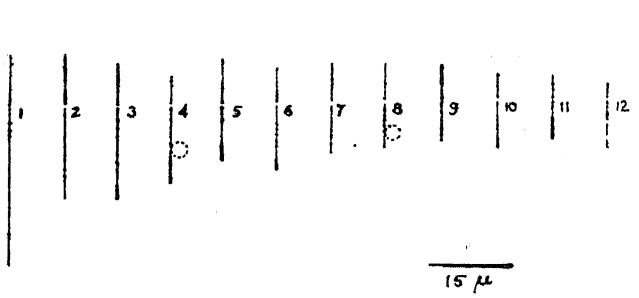
TABLE 1 (*Contd.*)

Name of the species	No. of the chromo-somes	Total length in microns	Arm ratio short arm/ long arm	Chromomeric pattern*
O.glabe-rrima	12	12·0	·33	S.A. terminates in 3 chromomeres. L.A. has 7 interstitial and 3 terminal chromomeres. (T.F. 2 and P.F. 3–4)
O. stapfii	1	43·6	·54	S.A. has a macrochromomere 3 μ from centromere and two sets of less distinct chromomeres in distal half. L.A. has two sets of 3 chromomeres each in its distal half (T.F. 3)
	2	38·0	·90	S.A. uniformly stained while L.A. has two proximal chromomeres (T.F. 3)
	3	35·5	·57	Two differential segments noted. Terminal regions of both the arms are darkly stained. S.A. has 3 chromomeres (T.F. 3 and P.F. 1)
	4	33·1	·63	S.A. darkly stained. L.A. for 4 μ long proximal region darkly stained (T.F. 3)
	5	30·1	·64	Both arms have telochromomeres. S.A. has 8 small proximal and 3 large distal chromomeres. L.A. has 4 interstitial and 3 telochromemeres (T.F. 3)
	6	28·0	·60	S.A. is differentiated into 8 chromomeres. L.A. uniformly stained except for 3 large proximal, 3 small distal and 1 small interstitial chromomeres (T.F. 3)
	7	27·1	·30	One differential segment noted on L.A. close to centromere. S.A. has 4 distal chromomeres. L.A. has 4 distal and 2 interstitial chromomeres (T.F. 3 and P.F. 1)
	8	24·5	·40	S.A. terminates in 3–4 chromomeres. L.A. has 3 interstitial and 3 distal chromomeres (T.F. 3 and P.F. 1)
	9	22·8	·70	Nucleolar bivalent with satellite of 5 μ length. L.A. terminates in 5 chromomeres (T.F. 3 and P.F. 3)
	10	19·1	·55	Nucleolar bivalent with satellite of 3 μ length. L.A. has 3 lightly stained interstitial and 3 darkly stained terminal chromomeres (T.F. 3)
	11	15·0	·50	Differential segment noted on the long arm. Entire chromosome darkly stained with several macro-chromomeres (T.F. 3 and P.F. 1)
	12	13·8	·22	Entire length differentiated into lightly stained chromomeres (T.F. 3 and P.F. 1)

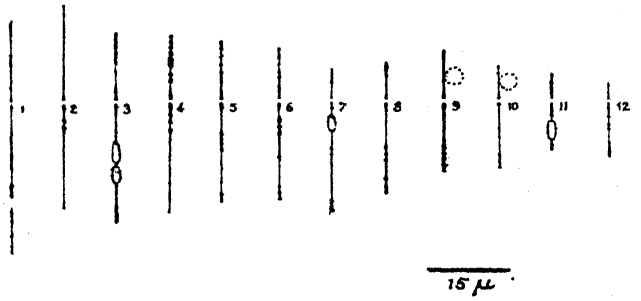
*L.A., Long arm; S.A., Short arm; T.F., Text Figure; P.F., Plate Figure.



TEXT-FIG. 1. Diagrammatic representation of the karyotype of *Oryza australiensis*. Note the heterochromatic regions on most of the chromosomes.



TEXT-FIG. 2. Diagrammatic representation of the karyotype of *O. glaberrima*. Note the chromomere pattern which is more clearly discernible than in *O. australiensis*. Chromosomes 4 and 8 are attached to nucleoli.



TEXT-FIG. 3. Diagrammatic representation of the karyotype of *O. stapfii*. Note the differential segments on the chromosomes 3, 7 and 11.

species where the karyotype consists of smaller chromosomes (*O. glaberrima*: 3 medium and 9 small; *O. stapfii*: 7 medium and 5 small).

The PMCs of *O. australiensis* are characterised by various degrees of non-homologous pairing between bivalents which offers an additional diffi-

culty in securing good preparations at pachytene. Such non-specific pairing has not been noticed in *O. sativa* (Shastry *et al.*, 1960; Misra, 1960) or in the species, *O. stapfii* and *O. glaberrima*, reported here. Randolph (1948) and Wellwood and Randolph (1957) reported that genetic differences between the stocks of maize were related to the quality of preparations they yield at pachytene. However, the interspecific differences in *Oryza* with regard to the quality of pachytene preparations might be traced more due to "heterochromaticity" of the bivalents rather than to genetic differences. The karyotypes which are more heterochromatic, *viz.*, of *O. australiensis*, exhibit greater degree of non-homologous pairing.

(ii) *Morphology of pachytene bivalents.*—The three species investigated in the present study exhibit significant differences in the appearance of pachytene bivalents. The bivalents in *O. australiensis* are on average more darkly stained and further, a detailed chromomeric analysis is not possible, since they are aggregated into darkly stained regions. Although the centric constrictions are flanked by darkly stained segments in a majority of the chromosomes in this species, they cannot be considered as "differentiated" in the sense of Hyde (1953), since such heterochromatic segments are limited in size and are not as localized as in *Lycopersicon* (Brown, 1949), *Plantago* (Hyde, 1953) and *Sorghum* (Venkateswarlu and Reddi, 1956).

The bivalents of *O. glaberrima and O. stapfii* are more suitable for detailed chromomere analysis and in this respect are similar to those of *O. sativa* (Shastry *et al.*, 1960) and *Zea mays* (Longley, 1941). Heterochromatic segments are much limited in these species in contrast to *O. australiensis.*

While all the varieties of *O. sativa* thus far investigated at pachytene (Misra, 1960), and *O. glaberrima* and *O. stapfii* in the present study, exhibit supernumerary nucleoli attached to the bivalents at pachytene, those of *O. australiensis* are distinct by their absence.

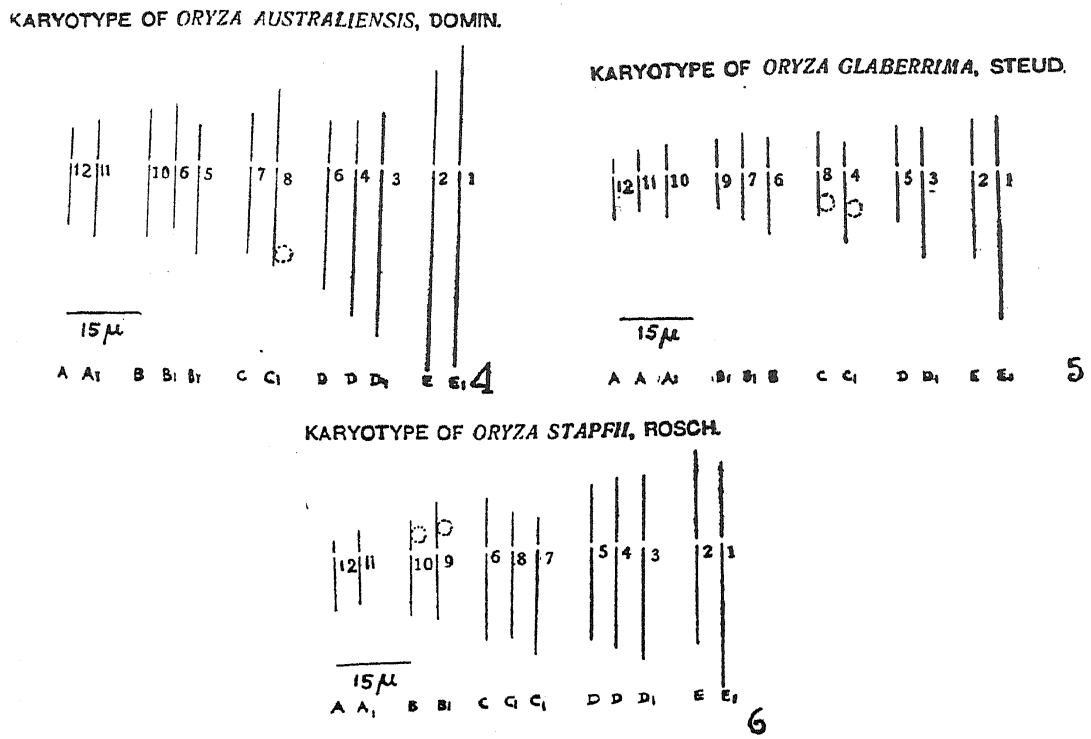
(iii) *Chromatin length.*—Karibasappa (1957) and Gopalakrishnan (1959), based upon the study of meiosis in *O. australiensis* and in the hybrid *O. sativa* × *O. australiensis*, concluded that the chromosomes of *O. australiensis* are distinctly larger than those of *O. sativa.* Data available on pachytene analysis up to date (Shastry *et al.*, 1960 and Misra, 1960) indicate that varieties of *O. sativa* differ in chromatin length between 300–400 μ. Similar variation may not exist in *O. australiensis* since much morphological variability has not been recorded in this species and the total chromatin length at pachytene is about 400 μ as revealed by the present study. It will, therefore, be obvious that some varieties of *O. sativa* have as large chromosomes

as those of *O. australiensis*. It is, therefore, likely that the chromosomes of *O. australiensis*, undergo less condensation from pachytene to metaphase I thus giving an impression of their being larger than those of *O. sativa*. The heterochromatin of the bivalents of *O. australiensis* might be responsible for this difference in condensation since it is known that the B-chromosomes in *Plantago*, which are more heterochromatic, undergo less condensation from pachytene to metaphase I (Palliwal, personal communication).

(iv) *Basic chromosome number*.—Nandi (1936), based upon his observations on karyomorphology in root-tips of *O. sativa* and secondary association (Sakai, 1931), concluded that the diploid species of *Oryza* are secondarily balanced allotetraploids and have originated from members with the basic chromosome number, $x = 5$. The most conclusive support to such a hypothesis is that 5 and 7 are the common basic numbers in the Graminæ (Stebbins, 1957) and that the genus *Zizania*, which is closely allied to *Oryza*, has $2n = 30$, which is more possibly derived from members with 5 as basic number (Ramanujam, 1938). This hypothesis of Nandi (1936) could not be either supported or contradicted in the past two decades mainly because the analysis was done in root tips, where the size variation between the extreme members of the karyotype is from 0·7 to 2·8 μ (Ramanujam, 1938). The present sudy made it possible to test this hypothesis.

The karyotypes of the three species was examined to find if any chromosome can be considered as duplicated and for this consideration a difference of 5 μ in total length and 0·1 in arm ratios was considered negligible. The chromosomes are renumbered by alphabets A–E and A_1–E_1 as per Nandi and the data are diagrammatically represented in Text-Figs. 4–6. It will be obvious that the karyotypes of all the three species can be visualized as having originated from the members with the basic number of 5. However, the chromosomes which are duplicated occupy different positions in the karyotype. If it is assumed that the alteration in the basic number from 5 to 12 was affected in the evolution of *Oryza*, this event might have taken place prior to the stage when the existing diploid species became sufficiently differentiated genetically. Consequently, spontaneous structural changes following such an alteration in the basic chromosome number might greatly modify the karyotype leading to non-detectability of the primary events.

(v) *Evolution of the karyotype in* Oryza.—The three species of *Oryza* investigated in the present study, and the published account on *O. sativa*-strain Norin 6 (Shastry *et al.*, 1960), permit some broad conclusions regarding the karyotypic evolution in this genus. However, in view of the limited



TEXT-FIGS. 4–6. Karyotypes of *O. australiensis*, *O. glaberrima* and *O. stapfii* redrawn as per Nandi's scheme (for explanation *see* text).

varietal diversity in one of the species, *O.australiensis*, and of limited studies on the other species, the conclusions will remain tentative.

The cultivated species, *O. sativa* and *O. glaberrima*, might be expected to be more evolved than the other species, *O. australiensis* and *O. stapfii*. The two criteria of asymmetry, *viz.*, the ratio of the longest to shortest chromosomes of the complements and the proportion of sub-median and sub-terminal chromosomes to the median members of the complement, are employed by Stebbins (1958) in the comparison of the karyotypes.

The ratio of the longest to the shortest chromosomes in *O. sativa*, (Norin. 6) is 4·4; in *O. glaberrima* 3·2; in *O. stapfii* 3·8; and in *O. australiensis* 3·2. All these species, except *O. sativa* which falls in the group (*c*), fall in the same broad group (*b*) of Stebbins (1958) where this ratio is 2: 4. The number of chromosomes whose long arms are at least twice as long as their short arms in these four species, *O. sativa*, *O. glaberrima*, *O. stapfii* and *O. australiensis*, are 7, 7, 4 and 5 respectively. According to Stebbin's classification, *O. sativa* falls in 3 *c*, *O. glaberrima* in 3 *b* and *O. stapfii* and *O. australiensis* in 2 *b*. It will therefore be obvious that the two wild species belong to different groups, as compared to the cultivated ones at least to the extent indicated by the present study.

The karyotypes of *O. australiensis* and *O. stapfii* are much more symmetrical than those of the cultivated species. Correlation between morphological specialization and asymmetry, and of domestication and asymmetry are too well known in several plant genera. The present concept regarding the taxonomic status of *O. stapfii* is that this is a hybrid species originated from a cross between *O. perennis* (African variety) and *O. glaberrima* (Richharia, 1960). Such an origin would have normally been accompanied by a high degree of asymmetry. This species having more symmetrical karyotype than *O. glaberrima* might indicate either that the latter species has undergone considerable kayrotypic differentiation subsequent to the origin of *O. stapfii* or that the other putative parent, *O. perennis* might, be characterised by highly symmetrical karyotype. The pachytene analysis of the African form of *O. perennis* would be expected to elucidate this problem.

O. glaberrima, which represents the cultivated varieties of West Africa, is one of the evolved species in this genus. According to Richharia (1960), *O. stapfii* might be considered as even more evolved than *O. glaberrima*. *O. australiensis* is more primitive in external morphology as well as by its being a wild species. The comparison of total chromatin lengths of these species reveals certain interesting features. The longest complement is that of *O. australiensis*, while the next in order is that of *O. stapfii* and the shortest is that of *O. glaberrima*. Diminution of the total chromatin length accompanying evolution has been a common experience in several plant genera. Delauney (1926) in *Muscari*, Ammal (1941) in *Saccharum*, Sharma and Ghosh (1956) in *Polyanthus*, Dowrick (1952, 1953 *a*, 1953 *b*) in *Chrysanthemum* and Sharma and Sarkar (1956) in the family Palmæ, indicated that the more evolved species have shorter chromosomes. However, this alone cannot serve as a conclusive evidence for the diminution in chromatin as an evolutionary tendency since genetic differences can modify the degree of condensation of chromosomes. Togby (1943) indicated such a situation in interspecific hybrids of *Crepis*.

(vi) *Differential segments and their significance*.—In one species, *O. stapfii*, three bivalents exhibited differential segments of 3–5 μ lengths. The nature of origin of these is as yet not clear, but based upon the chromomeric pattern in them, a tentative hypothesis can be attempted. In one of the bivalents (Chromosome 7), two distinct chromomeres were present on both the constituent chromosomal regions of this segment, but these were slightly displaced in their position. It is possible that such region might be an inverted segment in which the typical loop formation does not occur for mechanical reasons imposed upon them by their smallness. In the other two bivalents, the chromomeric pattern does not lend any evidence regarding

their origin. In any case, it is most probable that these differential segments represent structural hybridity. In some of the PMCs, however, the differential segments of the bivalents were not expressed as unpaired regions, presumably due to non-homologous pairing. In a single cell of *O. glaberrima*, one differential segment was recorded in just one of the bivalents of the complement. Further, within the region of differential segment, no chromomeric differences were noticed between the chromosome segments of the bivalent. Non-recurrence of this configuration in several PMCs and the identity of chromomeric details within this segment raise doubts regarding its validity. In *O. australiensis*, no such segments were recorded.

Consistent occurrence of differential segments at pachytene in *O. stapfii* and their non-occurrence in the other two species investigated at present, and in the species, *O. sativa* (Shastry *et al.*, 1960), might be of special significance. Richharia (1960) suggested a possible origin of *O. stapfii* by the introgression of an African variety of *O. perennis* (*barthii*) into *O. glaberrima* based upon the following observations:

(*a*) A sample of seeds of *O. stapfii* received at Cuttack from the Belgian Congo yield a heterogeneous progeny resulting in plants classifiable under *O. glaberrima* as well as *O. stapfii*;

(*b*) Gopalakrishnan (1959) recorded the occurrence of segregates resembling *O. stapfii* in the F_2 population of the cross between an Indian variety of *O. perennis* and *O. glaberrima*. These plants, however, were sterile, but they resembled *O. stapfii* very closely in their external morphology. A situation analogous to this has been pointed out earlier by Sampath and Rao (1951) for *O. spontanea*.

The hybrid origin of *O. stapfii*, which has been established by genetical studies, is supported by the occurrence of differential segments in this species. However, the most conclusive evidence regarding the origin of the species, *O. stapfii*, can come by a combined study of pachytene of the F_1 and later generations along with the genetic analysis of the cross between *O. perennis* var. *barthii* and *O. glaberrima* and by study of natural populations. Until the evidence from all these directions is corroborative, the conclusion regarding the hybrid origin of the species remains tentative.

SUMMARY

The karyomorphology of *Oryza australiensis*, *O. glaberrima* and *O. stapfii* was investigated at the pachytene stage. It was found that the twelve chromosomes of all the three species are identifiable by the lengths, arm

ratios and chromomeric pattern. A detailed description of each of the bivalents is given. The bivalents of *O. australiensis* are considered to be more heterochromatic than those of the other two species. The present study indicated that the karyotypes of wild species, *O. stapfii* and *O. australiensis*, are more symmetrical than those of the cultivated species, *O. glaberrima* and *O. sativa*. The present study lends support to Nandi's hypothesis that the basic chromosome number of the genus is 5. The karyotype of *O. australiensis* is distinct by aggregation of chromomeres and the absence of supernumerary nucleoli.

Acknowledgements

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EXPLANATION OF PLATE VI

FIG. 1. *O. stapfii.* Note the differential segments (→). 5 bivalents are traceable.

FIG. 2. *O. australiensis.* Note the distribution of heterochromatic regions. 4 bivalents are traceable.

FIG. 3. *O. glaberrima.* Note the uniform distribution of chromomeres. 10 bivalents are traceable.

FIG. 4. *O. glaberrima.* 5 bivalents are traceable.

FIG. 5. *O. stapfii.* Chromosomes attached to nucleolus.

FIG. 6. *O. australiensis.* Non-homologous pairing between bivalents.

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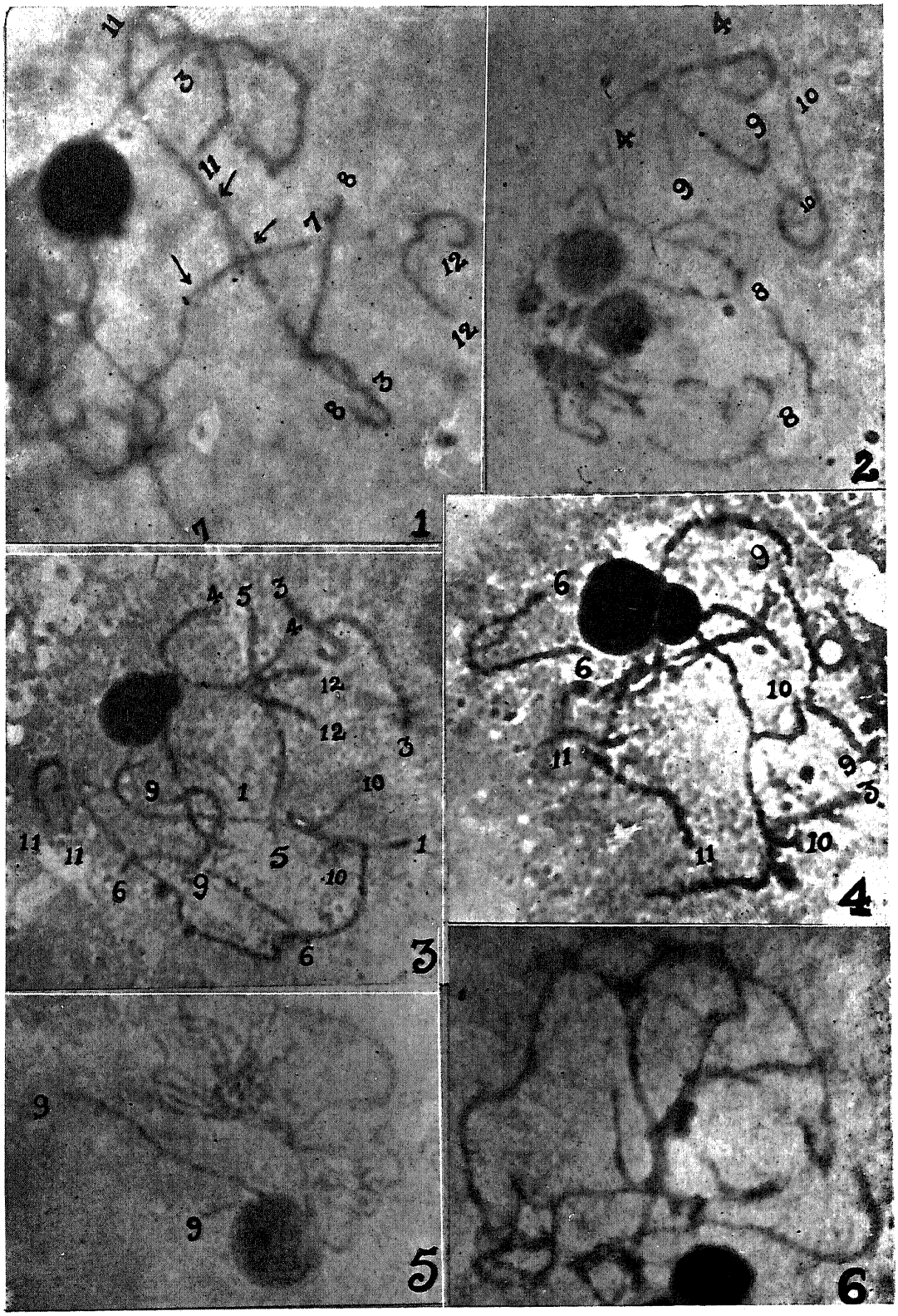

FIGS. 1–6