CYTOGENETICAL STUDIES OF *ORYZA SATIVA* L. AND ITS RELATED SPECIES

2. A Preliminary Note on the Interspecific Hybrids within the Section *Sativa* Roschev.[1]

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Roschevcz (1931) divided the genus *Oryza* into 4 sections, *viz.*, *Sativa*, *Granulata*, *Coarctata* and *Rhynchoryza*. Of these, the section *Sativa* Roschev. is the largest one, consisting of 12 species, *viz.*, *O. australiensis*, *O. breviligulata*, *O. glaberrima*, *O. grandiglumis*, *O. latifolia*, *O. longistaminata*, *O. minuta*, *O. officinalis* *O. punctata*, *O. sativa*, *O. schweinfurthiana* and *O. stapfii*. Since Roschevcz's classification was based merely on the external morphology, it may not be a natural one, though it has been adopted by many rice workers.

Based on this type of classification to start with, the phylogenetical relationships between species may be more directly ascertained by cytological study of interspecific hybrids. This was followed by Ghose *et al.* (1956). They divided the genus *Oryza* into 3 sections, *Sativa*, *Officinalis* and *Granulata*. The section *Sativa* consisted of *O. sativa*, *O. glaberrima*, *O. breviligulata*, *O. perennis* and *O. australiensis;* the section *Officinalis*, of *O. officinalis*, *O. minuta*, *O. eichingeri*, *O. latifolia* and *O. alta;* and the section *Granulata*, of the other species such as *O. granulata*, *O. ridleyi*, *O. coarctata* and *O. brachyantha*, the interrelationships of which were mostly unknown. This classification was further supported by Richharia (1960) who made a comparative study of the morphology, cytology and geographical distribution of some of the *Oryza* species.

From statistic-taxonomical studies of 16 species, Morishima and Oka (1960) also reached at quite the same conclusion as that of Ghose *et al.* (1956) and Richharia(1960). Morishima and Oka divided the genus *Oryza* into 3 groups, namely *Sativa*, *Officinalis* and the *miscellaneous* group, and subdivided the *Sativa* group into 2 minor groups, one consisting of *O. sativa*, *O. sativa* var. *spontanea* and

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Table 1. Interspecific crosses in the genus *Oryza*.

Section	♀ \ ♂		*sativa*	*sat.* var. *spontanea*	*perennis*	*cubensis*	*longistaminata*	*glaberrima*	*breviligulata*	*australiensis*	*officinalis*	*latifolia*	*alta*	*paraguaiensis*	*minuta*	*eichingeri*	*brachyantha*
Sativa	*sativa*	24		+ *	+ *	+	+	+	+ *	+	+ *	+ *	+	+ *	+ *	+	
	sativa var. *spontanea*	24			+ *			+		+		*	*	*		*	
	perennis	24										*	*				
	cubensis	24			+												
	longistaminata	24															
	glaberrima	24	+		+				+						+	+	
	breviligulata	24		*	*												
	australiensis	24											+				
Officinalis	*officinalis*	24										+		+	+		
	latifolia	48												+	+		
	alta	48															
	paraguaiensis	48		*						+	*	*			*		*
	minuta	48									*	+		+			
	eichingeri	48									*				+		
Granulata	*brachyantha*	24															

*Hybrids obtained by the present authors. +Hpbrids reported by other workers.

and the other, of *O. glaberrima* and *O. breviligulata.* The *miscellaneous* group of Morishima and Oka can be regarded as corresponding to the section *Granulata* of the classification of Ghose *et al.* In this paper, classification of Ghose *et al.* is followed strictly.

In the genus *Oryza,* the genome of *O. sativa, O. minuta* and *O. latifolia* was first investigated by Morinaga (1943). Recently, many more interspecific hybrids were obtained and the genomes of some more species were identified and designated by different workers (Kihara and Nezu, 1960; Richharia, 1960; Morinaga and Kuriyama, 1960; Yeh and Henderson, 1960; Li *et al.,* 1961). Their results are given in Table 1 and Table 2.

With a view to re-examining the taxonomical relationships and genomic constitutions of the more closely related species in the genus *Oryza,* the authors made a number of interspecific crosses within the section *Sativa* Roschev. in 1960. This is a brief report on the cytological study of these hybrids.

Table 2. Genomic constitutions of the genus *Oryza.*

Sepecies	Morinaga *et al.*	Richharia	Yeh & Henderson	Li *et al.*
O. sativa	AA	P^2P^2	A_1A_1	
O. sativa var. *fatua*			A_1A_1	
O. sativa var. *formosana*			A_1A_1	
O. sativa var. *spontanea*	AA			
O. balunga			A_1A_1	
O. perennis	AA	P^1P^1		
O. perennis var. *cubensis*	AA		A_2A_2	
O. perennis var. *barthii*			A_2A_2	
O. glaberrima	AA	P^3P^3	EE	
O. breviligulata	AA	P^1P^1	EE	
O. stapfii		P^3P^3	EE	
O. australiensis	Not AA			
O. officinalis	CC			
O. latifolia	CCDD	$O^1O^1O^2O^2$		
O. paraguaiensis	CCDD			
O. alta		$O^1O^1O^2O^2$		
O. minuta	BBCC	$O^1O^1M^1M^1$		
O. eichingeri	BBCC			
O. malampuzhiensis		$O^1O^1O^3O^3$		
O. brachyantha				FF

Material and Methods

Nine species in all were used as parents in the hybridization (Table 3). The cultivated species *O. sativa* var. Pai-mi-fen was provided locally. All other species were kindly fur-

nished by Dr. H. I. Oka of the National Institute of Genetics, Japan, to whom the authors are grateful.

Table 3. Some remarks on the parent species used in the hybridization.

Acc. No.	Oka's No.	Species	2n	Source
2	—	*O. sativa* L. var. Pai-mi-fen	24	Taiwan
4	W106	*O. sativa* var. *spontanea* Roschev.	24	India
11	W208	*O. perennis* Moench.	24	India
12	W042	*O. breviligulata* Chev. *et* Roehr.	24	W. Africa
16	W012	*O. officinalis* Wall	24	India
18	W045	*O. minuta* Presl.	48	P. I.
21	W020	*O. latifolia* Desv.	48	Guatemala
25	W054	*O. paraguaiensis* Wedd.	48	Paraguay
19	W043	*O. eichingeri* Peter	48	Africa

Hybridization was made in the same way as in the previous work done by the same authors (Li *et al.*, 1961).

Aceto-carmine squashes were used exclusively throughout the experiment.

Cytology of the Hybrids

Cytological observations were made exclusively from the metaphase plates of PMC's. The numbers of various chromosome associations in the hybrids, together with their percentage of pollen fertility, are summarized in Table 4. It should be noted here that physiological barriers causing hybrid inviability or weak grouth did exist and they prevented the normal growth or reproduction of some of the hybrids. In the present study, the hybrid *O. minuta*×*officinalis* appeared to be semi-lethal and the hybrid *O. sativa*×*officinalis* could never reach the flowering stage. Still in some others, the PMC's usually degenerated even prior to meiosis, thus making it impossible to obtain enough PMC's for sufficient observation.

1. Relationships of species in section *Sativa*:

All species belonging to this section are diploid with $2n=24$. According to Morinaga and Kuriyama (1960), the genomes of these species were AA. Richharia (1960) also stated that they carried identical or similar genomes. However, in contrast to the A genome, E was designated for three African species (see Table 2) by Yeh and Henderson (1960). In the present study, it was found that hybrids *O. sativa*×*sativa* var. *spontanea*, *O. sativa*×*perennis* and *O. sativa* var. *spontanea*×*perennis* showed normal chromosome pairing as well as normal pollen fertility, whereas *O. sativa*×*breviligulata*, *O. breviligulata*×*sativa* var. *spontanea* and *O. breviligulata*×*perennis* showed slight irregularity in chromosome behavior

Table 4. Chromosome pairing at MI and pollen fertility in the interspecific hybrids of the genus *Oryza*.

Hybrids	Plant no.	No. of cells observed	IV Range (Mean)	III Range (Mean)	II Range (Mean)	I Range (Mean)	% Pollen fertility
Hybrids within the section *Sativa*:							
O. sativa × *sativa* var. *spontanea*	38-2	46	0	0	12(12.00)	0	73.60
O. sativa × *sativa* var. *spontanea*	64-1	80	0	0	12(12.00)	0	67.45
O. sativa × *perennis*	42-1	100	0	0	12(12.00)	0	24.30
O. sativa var. *spontanea* × *perennis*	63-4	50	0	0	6-12(10.38)	0-12(3.24)	53.00
O. sativa var. *spontanea* × *perennis*	65-1	90	0	0	12(12.00)	0	53.50
O. sativa × *breviligulata*	34-5	30	0	0	0-12(10.34)	0-24(3.33)	0
O. breviligulata × *sativa* var. *spontanea*	68-1	90	0	0	11-12(11.98)	0-2 (0.04)	3.55
O. breviligulata × *perennis*	67-2	70	0	0	7-12(10.74)	0-10(2.51)	0
Hybrids within the section *Officinalis*:							
O. minuta × *officinalis*	31	—	—	—	—	—	—
O. paraguaiensis × *officinalis*	49-8	56	0	0-1 (0.01)	5-14(10.64)	7-26(14.66)	0
O. paraguaiensis × *latifolia*	43-1	16	0-1 (0.31)	0	21-24(23.31)	0-2 (0.13)	3.20
O. paraguaiensis × *minuta*	32-23	27	0	0-2 (0.33)	5-14(10.59)	20-30(25.11)	0
O. minuta × *latifolia*	33-7	20	0	0-1 (0.05)	8-13(11.30)	22-32(25.25)	0
Hybrids between sections *Sativa* and *Officialis*:							
O. sativa × *officinalis*	35	—	—	—	—	—	—
O. sativa × *paraguaieusis*	37-2	50	0	0	0-4 (0.96)	28-36(34.10)	0
O. sativa × *latifolia*	46-2	68	0-1 (0.06)	0-1 (0.18)	0-11(6.26)	11-36(22.75)	0
O. sativa × *latifolia*	47-1	36	0-1 (0.03)	0-2 (0.11)	1-8 (4.64)	20-34(26.00)	0
O. sativa var. *spontanea* × *paraguaiensis*	57-1	43	0		0-5 (0.56)	26-36(34.70)	0
O. paraguaiensis × *sativa* var. *spontanea*	62-1	200	0-1 (0.01)	0-1 (0.03)	0-8 (3.55)	20-36(28.78)	0
O. sativa var. *spontanea* × *latifolia*	41-2	32	0	0	0-7 (0.96)	22-62(28.56)	0
O. sativa var. *spontanea* × *alta*	72-1	—	—	—	—	—	0
O. sativa × *minuta*	44-1	8	0	0	1-5 (3.00)	26-34(30.00)	0
O. sativa var. *spontanea* × *eichingeri*	70-2	103	0	6	0-2 (0.14)	32-36(35.18)	0

Notes: IV, III, II and I stand for tetravalent, trivalent, bivalent and univalent, respectively.

and almost complete sterility of pollen (Table 4). However, since the frequency of univalents at MI was very low it might be hard to assert that they had different genomes as far as the materials used in this studies were concerned.

In the hybrid *O. sativa*×*breviligulata*, almost all of the PMC's showed normal chromosome pairing (Fig. 1), though a certain number of cells were found to have two univalents. In some extreme cases, however, univalents were present in higher frequency than were the bivalents. In one PMC, for instance, all 24 chromosomes were left as univalents and less condensed (Fig. 2). The same was also found in the hybrid *O. sativa* var. *spontanea*×*latifolia* by the present authors and in *O. sativa*×*latifolia* by Hu (unpubl.). The reduced condensation of chromosomes and the failure of chromosome pairing might have resulted from chance variation within the cells, insofar as the majority of cells from the same anther showed normal chromosome pairing and normal condensation.

Two sister crosses of *O. sativa* var. *spontanea*×*perennis* were studied which had the same parent species but differed in the individuals used as parents in hybridization. One had 12 bivalents in the PMC's, while the other had a mean number of 3.24 univalents per PMC. Since no difference in pollen fertility was found in these two hybrids (Table 4), the presence of univalents in one of them might be ascribed to genotypic difference between the individuals within the species, thus causing the early separation of some bivalents.

2. Relationships of species in section *Officinalis*:

As previously cited, *O. officinalis* had 24 chromosomes (Nandi, 1936), and *O. latifolia, O, paraguaiensis, O. minuta* and *O. eichingeri* had 48 chromosomes (Gotoh and Okura, 1933; Morinaga and Kuriyama, 1960; Moringa, 1934; Pathak, 1940). According to Morinaga and Kuriyama (1960), the genomes of *O. officinalis* were CC; those of *O. latifolia* and *O. paraguaiensis*, CCDD; and those of *O. minuta* and *O. eichingeri*, BBCC (Table 2).

In the present case of interspecific hybrids within the section *Officinalis*, only *O. paraguaiensis*×*officinalis, O. paraguaiensis*×*latifolia, O. paraguaiensis*×*minuta* and *O. minuta*×*latifolia* were studied cytologically. In the hybrid *O. paraguaiensis*×*officinalis*, 56 PMC's were observed at MI. The mean number of bivalents per PMC was 10.64, which was close to the haploid chromosome number of *O. officinalis*. It was apparent that *O. paraguaiensis*, being a tetraploid, had one *officinalis* genome in its constitution.

In the hybrid *O. paraguaiensis*×*latifolia*, most of the microsporocytes had 24 bivalents. This result was in agreement with that of Morinaga and Kuriyama (1960), that is, *O. paraguaiensis* and *O. latifolia* had genomes CCDD in common.

The mean numbers of bivalents per PMC at MI were 10.59 in *O. paraguaiensis*×*minuta* and 11.30 in *O. minuta*×*latifolia*, respectively. This indicated that one

of the *minuta* genomes was in common with that of *O. latifolia* and *O. paragnaiensis* (in this case, genome C), insofar as these two species had the same genomes.

3. Relationships between species of section *Sativa* and those of section *Officinlis*:

Morinaga and Kuriyama (1960) obtained F_1 plant of *O. sativa* and *O. paraguaiensis* but no cytological results thereof were reported in their article. In the same type of hybrid obtained by the present authors, there was an almost entire absence of chromosome pairing, which fact indicated that the genomes of *O. paraguaiensis* were different from those of *O. sativa*. This was also the case with *O. minuta* and *O. sativa*. The same might be also true of the relationships between *O. sativa* var. *spontanea* and the three tetraploid species of the section *Officinalis*, namely, *O. paraguaiensis*, *O. latifolia* and *O. eichingeri*. It was formerly known that *O. sativa* var. *spontanea* had the same genomes as *O. sativa*, *i.e.*, A. In two hybrids of *O. sativa* and *O. latifolia*, however, the mean numbers of bivalents per PMC were found to be 6.26 and 4.64, respectively, and in some of their PMC's, the number of bivalents even went up to a maximum of eleven, of which some were found to be of closed type (see discussion).

In the hybrid *O. spontanea*×*alta*, chromosomes were found to be unpaired at diakinesis and MI. In some PMC's many nucleolar-like droplets were detected at diakinesis (Fig. 12), each being usually attached to one or more chromosomes. The presence of those stainable droplets had been already suggested by Chen (1961) to be due to an excessive production of nucleolar substances.

Discussion

As previously pointed out by Ghose *et al.* (1956), Richharia (1960), and Morishima and Oka (1960), the section *Sativa* Roschev. was by no means a homogeneous one, and it could be further divided into two distinct sections, *Sativa* and *Officinalis*. From cytogenetical studies of the interspecific hybrids, the present authors reached at the same conclusion as that of Ghose *et al.*, because almost no chromosome pairing was found in the hybrids between the section *Sativa* and the section *Officialis*.

However, in the hybrid of *O. sativa*×*latifolia*, as many as eleven bivalents are found at meiosis. Although intragenome association was found to exist in the haploids of *O. sativa* and *O. glaberrima* (Hu, 1957, 1960), and autosyndesis was offerred to explain the occassional formation of bivalents in some *Oryza* hybrids (Morinaga, 1943; Shama Rao and Seetharaman, 1757), some of the bivalents observed in the hybrid *O. Sativa*×*latifolia* seem to arise from allosyndesis, *i.e.*, pairing between chromoses of *O. sativa* and *O. latifolia*. This type

of chromosome paring seems to be rather predominant in this hybrid. It is speculated, therefore, that chromosomes of *O. sativa* are partially homologous to those of *O. latifolia.* Based on the same assumption, Kihara and Nezu (1960) have also suggested that *O. minuta* has one modified *sativa* genome.

According to Kihara and Nezu (1960), Morishima and Kuriyama (1960) and Richharia (1960), there is no irregularity in chromosome pairing in the interspecific hybrids within the section *Sativa.* They concluded that species within this section had normal homologous genomes. On the other hand, Yeh and Henderson (1960) have reported that irregularities in chromosome behavior are consistently found in *glaberrima-sativa* hybrid at various stages of meiosis, and therefore E has been suggested to designate the genome of *O. glaberrima, O. breviligulata* and *O. stapfii.* In the present study, the authors agree with Morishima and Oka (1960) that the section *Sativa* can be subdivided into two minor groups; since the hybrids within the respective minor groups have normal chromosome pairing and pollen fertility, while in hybrids between these minor groups chromosome behavior is slightly irregular and pollens are almost completely sterile.

Summary

During 1960–61, the authors obtained 20 interspecific hybrids within the section *Sativa* Roschevcz. From cytogenetical studies of these hybrids the following conclusions were drawn:

1. In regard to genomic constitution of the genus *Oryza,* results from the present study agreed quite well with those reported by Morinaga *et al.* (1960).

2. The section *Sativa* Roschev. seemed to be not a homogeneous one, and it could be divided into two distinct sections, *Sativa* and *Officinalis.* The former was represented by those species having genome A. The latter consisted of *O. officicinalis* and its related tetraploid species having genomes C, BC or CD.

3. Concerning the absence or presence of univalents at MI and the pollen fertility of the hybrids, the aforementioned section *Sativa* could be subdivided into two minor groups, one consisting of *O. sativa, O. sativa* var. *spontanea* and *O. perennis,* the other of *O. glaberrima* and *O. breviligulata.*

4. In *O. sativa*×*latifolia,* bivalents occurred in rather high frequency. Possibly, the *latifolia* parent used in this experiment might have a modified *sativa* genome.

Oryza sativa L. 及其近緣種之細胞遺傳學研究

2. Section *Sativa* Roschev. 內的種間雜種之初步研究報告

李先聞 翁登山 陳其昌 王文浩

作者等於1960～61年間舉行 Section *Sativa* Roschev. 內之種間雜交，先後獲得二十個種間雜種，茲將此等種間雜種之細胞遺傳學研究結果撮要報告如後：

1. 就本研究初步所得的結果觀之，稻屬染色體組結構似與 Morinaga *et al.* (1960) 所報告者大致相若。

2. Section *Sativa* Roschev. 似應再分爲兩個 Sections, 即 Section *Sativa* 及 Section *Officinalis*。前者包括具有A染色體組之各個種；後者則包括 *O. officinalis* 及其近緣之四元體種，其染色體組爲C，BC 或 CD。

3. 就各種間雜種在減數分裂第一中期有單價染色體與否及其有效花粉百分率之高低而論，上述的 Section *Sativa* 似可再分爲兩個 Groups，其一 以 *O. Sativa, O. Sativa* var. *spontanea* 及 *O. perennis* 爲代表，另一 則以 *O. glaberrima* 及 *O. breviligulata* 爲代表。

4. *O. sativa*×*latifolia* 的雜種在減數分裂第一中期具有相當高頻度的二價染色體，可見本試驗中所用的 *O. latifolia* 似乎含有一個蛻變的A染色體組。

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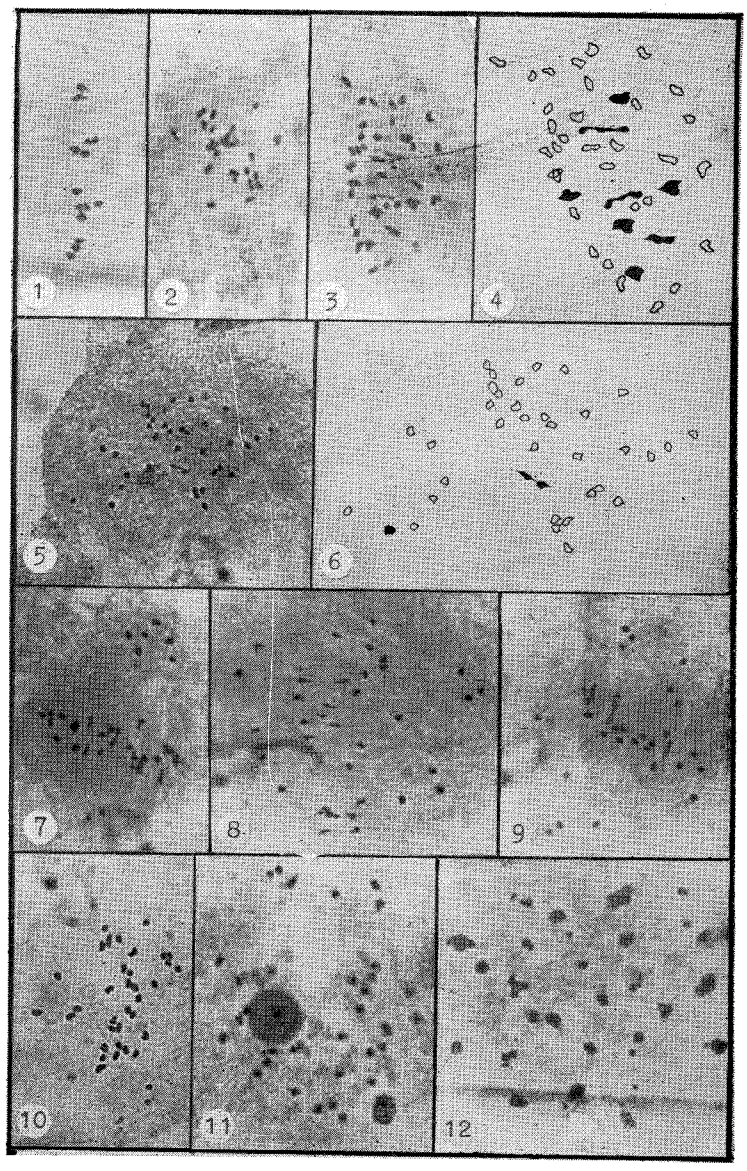

Meiosis of the Hybrids

Fig. 1. *O. sativa* × *breviligulata.* MI, showing 12 II.

Fig. 2. *O. sativa* × *breviligulata.* MI, showing 24 I.

Fig. 3. *O. minuta* × *latifolia.* MI, showing 8 II+20 I.

Fig. 4. Same as Fig. 3. Camera lucida drawing.

Fig. 5. *O. sativa* × *paraguaiensis.* MI, showing 1 II+34 I.

Fig. 6. Same as Fig. 5. Camera lucida drawing.

Fig. 7. *O. sativa* × *latifolia.* MI, showing 10 II+16 I.

Fig. 8. *O. sativa* × *latifolia.* Early AI ,showing 8 II+20 I.

Fig. 9. *O. paraguaiensis* × *sativa* var. *spontanea.* MI, showing 1 IV+1 III+2 II+25 I.

Fig. 10. *O. sativa* var. *spontanea* × *eichingeri.* MI, showing 36 I.

Fig. 11. *O. sativa* var. *spontanea* × *alta.* Diakinesis, showing one nucleolus.

Fig. 12. *O. sativa* var. *spontaea* × *alta.* Diakinesis, showing many nucleolar-like droplets, most of them are attached to one or more chromosomes.