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Studies on the crossability relationships of some spinous *Solanums*

S. V. Rao* and B. G. S. Rao
Department of Botany, Andhra University, Waltair-530 003, India

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Summary. Cytogenetic studies involving six species of spinous *Solanums* have been made using the parameters of crossability/fertility relationships and chromosome pairing in parental and derived hybrid genomes. These studies have made it possible to integrate hybrid reproductive performance with observed cytological phenomena and draw inferences on concerned intergenomic homeologies. It has been found that species' differences, as they exist, are ascribable to chromosome repatterning, in their divergence and maintenance as distinct taxa. In the light of these studies, the grouping of these species has to be reconsidered.

Key words: Spinous *Solanums* – Crossability relationships – Interspecific hybrids – Chromosome repatterning – *S. melongena*

Introduction

Spinous *Solanums,* which enjoy worldwide distribution, constitute an important group of plants of considerable economic value. They have been in usage both as vegetables and more particularly as plants of medicinal value (Kirtikar and Basu 1935; Chadha 1952). Although they are reported to constitute a distinct morphological group (Clarke 1883) separated by reproductive barriers from tuberous and non-tuberous, and non-spinous *Solanums* (Bhaduri 1951), the crossability relationships amongst them remain ill-defined. Earlier attempts at interspecific hybridization yielded variable results (Swaminathan 1949; Mittal 1950; Bhaduri 1951; Magoon et al. 1962; Narasimha Rao 1968; Rajasekaran 1969) so that the evolutionary trends in their divergence as distinct taxa need to be better understood. Such studies could also have the way for their better utilization as plants with useful alkaloids in the light of reports of genetic manipulation of their alkaloids through hybridization (Solomon and Crane 1969; Zutshi 1966), which has become possible only with an understanding of intergenomic relationships of different species In the light of the above considerations, interspecific hybridization was attempted involving six widely distributed and commonly used spinous *Solanums.* Results of their crossability relationships are presented in this paper.

Materials and methods

The six species used are *S. surattense* Burm. F. (=*S. xanthocarpum* Schrad. and Wendl), *S. melongena* L., *S. indicum* L., *S. indicum* var. 'multiflora' Whight (Fyson 1932), *S. trilobatum* L., and *S. torvum* Swartz. With the exception of *S. melongena,* all the others were derived from their natural wild habitats. The method used for interspecific crossing experiments was devised by the authors (Veerabhadra Rao and Rao 1977). Meiotic studies of pollen mother cells were done by customary technique of fixation in 3:1 isopropyl alcohol:propionic acid and squashing in 2% propionocarmine.

Results

Data on the attempts of interspecific hybridization are presented in Table 1. In 22 of 30 attempted cross combinations, some fruit was obtained. In five combinations there were complete maternal diploids indicating the apomictic nature of the pistillate parents. Even in these cases a large number of pollinations failed to yield hybrids. In all, ten interspecific hybrids were obtained for further studies. Many of these hybrids

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* Present address: Geneticist, C.T.R.I. Research Station, Hunsur-571 105, India

Table 1. Results of the attempted cross pollinations of different spinous Solanum species investigated

Parental species		No. of pollinations made	No. of fruits obtained	Maternal diploids (%)	Hybrid obtained (+) or not (–)	Frequency of hybrid seed[a]	Nature of hybrid[b] V/W/L
Pistillate	Staminate						
S. surattense	*S. melongena*	10	7	1	+	46.00	V
	S. indicum	78	60	–	+	22.40	L
	S. indicum var. 'multiflora'	102	31	30	+	3.00	W
	S. trilobatum	86	38	17	+	13.10	V–W
	S. torvum	26	4	100	–	–	–
S. melongena	*S. surattense*	16	–	–	–	–	–
	S. indicum	33	3	–	+	0.56	V
	S. indicum var. "multiflora'	24	4	–	–	–	–
	S. trilobatum	62	–	–	–	–	–
	S. torvum	13	3	–	–	–	–
S. indicum	*S. surattense*	63	–	–	–	–	–
	S. melongena	37	7	–	+	12.60	V
	S. indicum var. 'multiflora'	58	11	–	+	0.02	L
	S. trilobatum	24	–	–	–	–	–
	S. torvum	17	7	–	+	0.02	L
S. indicum var. 'multiflora'	*S. surattense*	89	19	–	+	0.03	L
	S. melongena	50	31	–	–	–	–
	S. indicum	46	32	–	–	–	–
	S. trilobatum	42	2	–	–	–	–
	S. torvum	79	26	–	–	–	–
S. trilobatum	*S. surattense*	109	49	90	+	0.08	W
	S. melongena	108	5	100	–	–	–
	S. indicum	38	2	–	–	–	–
	S. indicum var. 'multiflora'	126	8	–	+	0.70	V
	S. torvum	106	3	–	–	–	–
S. torvum	*S. surattense*	74	–	–	–	–	–
	S. melongena	34	–	–	–	–	–
	S. indicum	64	3	100	–	–	–
	S. indicum var. 'multiflora'	38	–	–	–	–	–
	S. trilobatum	68	–	–	–	–	–

[a] $\frac{\text{No. hybrids obtained}}{\text{No. ovules per flower} \times \text{No. crosses}} \times 100$

[b] *V*=vigours; *W*=weak; *L*=lethal

Table 2. Chromosome associations and chiasma frequencies in parental genomes

Parental species[a]	Stage and no. of PMCs analysed	Mean occurrence of Univalents	Mean occurrence of Bivalents		Chiasma frequency		Terminalization coefficient
			Rods	Rings	Mean	Range	
S. surattense	Diak. 50	–	8.44	3.56	15.56	14–17	0.668
	M-I 44	–	9.45	2.54	14.54	13–16	0.869
S. melongena	Diak. 80	–	1.75	10.25	22.37	21–24	0.978
	M-I 54	–	6.55	5.45	17.55	17–19	0.918
S. indicum	Diak. 64	–	2.06	9.94	21.93	19–23	0.720
	M-I 54	0.11	3.50	8.39	20.22	17–23	0.790
S. indicum var. 'multiflora'	Diak. 72	–	2.05	9.95	22.77	18–26	0.865
	M-I 48	–	2.00	10.00	22.47	20–24	0.937
S. trilobatum	Diak. 82	0.17	8.25	3.66	15.57	12–20	0.810
	M-I 80	0.30	9.97	1.87	15.25	15–18	0.816

[a] *S. torvum* was not represented since viable hybrids were not obtained involving it

Table 3. Cytological data on interspecific hybrids of spinous *Solanums*

Interspecific hybrid	Pollen fertil-ity (%)	Stage and no. of PMCs analysed	Mean occurrence of associations						Chiasma frequency		T.C.	Anaphase abnormalities[a]	
			Univa-lents	Bivalents			Triva-lents	Others	Mean	Range		A-I	A-II
				Rods	Rings	%							
S. surattense ×	0.75	Diak. 45	0.44	3.13	7.86	50.0	0.13	0.26	20.00	18–22	0.80	L/B	L/B
S. melongena		M-I 33	0.54	2.72	7.81		0.18	0.45	20.63	17–24	0.82	20%	23%
S. surattense ×	2.40	Diak. 82	2.08	8.08	2.28	20.5	0.19	0.13	13.51	9–17	0.69	L/B	L/B
S. trilobatum		M-I 25	0.92	7.88	2.92		0.28	0.16	14.14	12–21	0.79	22%	32%
S. trilobatum ×	0.50	Diak. 21	4.71	6.95	1.33	3.0	0.14	0.09	11.04	8–17	0.55	L/B	L/B
S. surattense		M-I 45	4.08	7.88	1.55		0.13	0.15	11.60	6–21	0.82	61%	58%
S. surattense ×	0.05	Diak. 32	1.43	8.48	2.06	56.0	0.31	0.15	13.40	12–21	0.79	L/B	L/B
S. indicum var. 'multiflora'		M-I 36	0.83	9.95	1.58		1.66	–	13.16	8–15	0.80	28%	38%
S. indicum var. 'multiflora' × *S. surattense*	0.05	Diak. 20	0.72	8.61	1.72	42.5	0.81	0.14	13.10	9–15	0.75	L/B 26%	L/B 28%
S. trilobatum ×	0.50	Diak. 49	0.48	5.98	5.02	45.5	0.12	0.28	17.24	13–20	0.56	L/B	L/B
S. indicum var. 'multiflora'		M-I 41	0.41	6.43	4.34		0.31	0.26	16.56	11–22	0.75	3%	9%
S. melongena ×	91.50	Diak. 85	0.11	2.76	9.02	99.5	–	–	21.11	13–23	0.56	I/B	L/B
S. indicum		M-I 65	0.33	4.16	7.41		0.10	–	19.00	14–23	0.75	3%	10%
S. indicum ×	95.00	Diak. 35	0.05	2.80	9.10	99.00	0.01	0.01	19.47	17–24	0.72	I/K/B	I/L/B
S. melongena		M-I 60	0.18	4.12	7.30		–	–	19.56	15–23	0.79	10%	9.5%

[a] *L* = laggards; *B* = bridge; *I* = inversion bridge and fragment
T. C. = terminalization coefficient

tended to resemble the maternal parents. However, erect habit, long branches, hairy brittle leaves, lengthy many (6–10) flowered inflorescences and red or orange coloured fruit showed dominance over pendant habit, short branches, glabrous and soft textured leaves, short and less (1–3) flowered inflorescence and white or yellow coloured fruit.

Data on the cytology of the parents (all $n = 12$) are given in Table 2. *S. surattense* and *S. trilobatum* formed fewer chiasma due to a larger number of rod bivalents compared to others, indicating a lower recombination index. All other cytological features were typical of normal chromosome behaviour. Data on the cytology of interspecific hybrids are given in Table 3. Hybrids between *S. indicum* and*S. melongena, S. surattense* and *S. melongena* and *S. trilobatum* and *S. indicum* var. 'multiflora' showed chiasma frequencies with a smaller range and mean chiasma frequencies intermediate between the concerned parents. In contrast, hybrids between *S. surattense* and *S. trilobatum* or *S. indicum* var. 'multiflora' showed a greater range of chiasma frequencies than those of the above-mentioned crosses and mean chiasma frequencies lower than both parents concerned.

Table 4. Occurrence of abnormal chromosome associations in interspecific hybrids of spinous *Solanums*

Details of associations	Interspecific hybrids[a]				
	1	2	3	4	5
Higher associations					
Maximum/cell	1	3	2	3	2
% cells	42.3	0.9	6.0	1.4	2.2
Most common no.	1	1	1	1	1
% cells	42.3	31.7	6.6	26.0	40.0
Trivalents (total)					
Chain	9	14	3	11	11
'Y' type	3	6	5	3	4
Spoon type	3	7	–	2	2
Quadrivalents (total)					
Chain	11	2	5	2	13
Ring	5	–	2	2	6
'Y' type	–	–	1	1	2
Fish type	1	1	–	–	1
Spoon type	–	3	–	–	2
'X' type	–	–	–	–	1
'8' type	1	3	1	–	–
Univalents					
Maximums/cell	3	6	12	6	4
% cells	3.8	2.8	1.5	2.8	4.4
Minimum/cell	0	0	0	0	0
% cells	73.0	30.0	9.0	57.0	71.0
No. of cells analysed	78	107	66	68	90

[a] 1 = *S. surattense* × *S. melongena;* 2 = *S. surattense* × *S. trilobatum;* 3 = *S. trilobatum* × *S. surattense;* 4 = *S. surattense* × *S. indicum* var. 'multiflora'; 5 = *S. trilobatum* × *S. indicum* var. 'multiflora'

Data on the different chromosome associations obtained in the hybrids are presented in Table 4. All hybrids studied showed the capability of forming 12 bivalents though to varying degrees depending on the parental combination. Chromosome pairing was less frequent in hybrids between *S. trilobatum* and *S. surattense.* Higher chromosome associations (Figs. 1–8) were most common in hybrids between *S. surattense* and *S. melongena* followed by *S. trilobatum* × *S. indicum* var. 'multiflora'. Among multivalents, chains of 3 or 4 are common, followed by rings, 'Y' and spoon type associations.

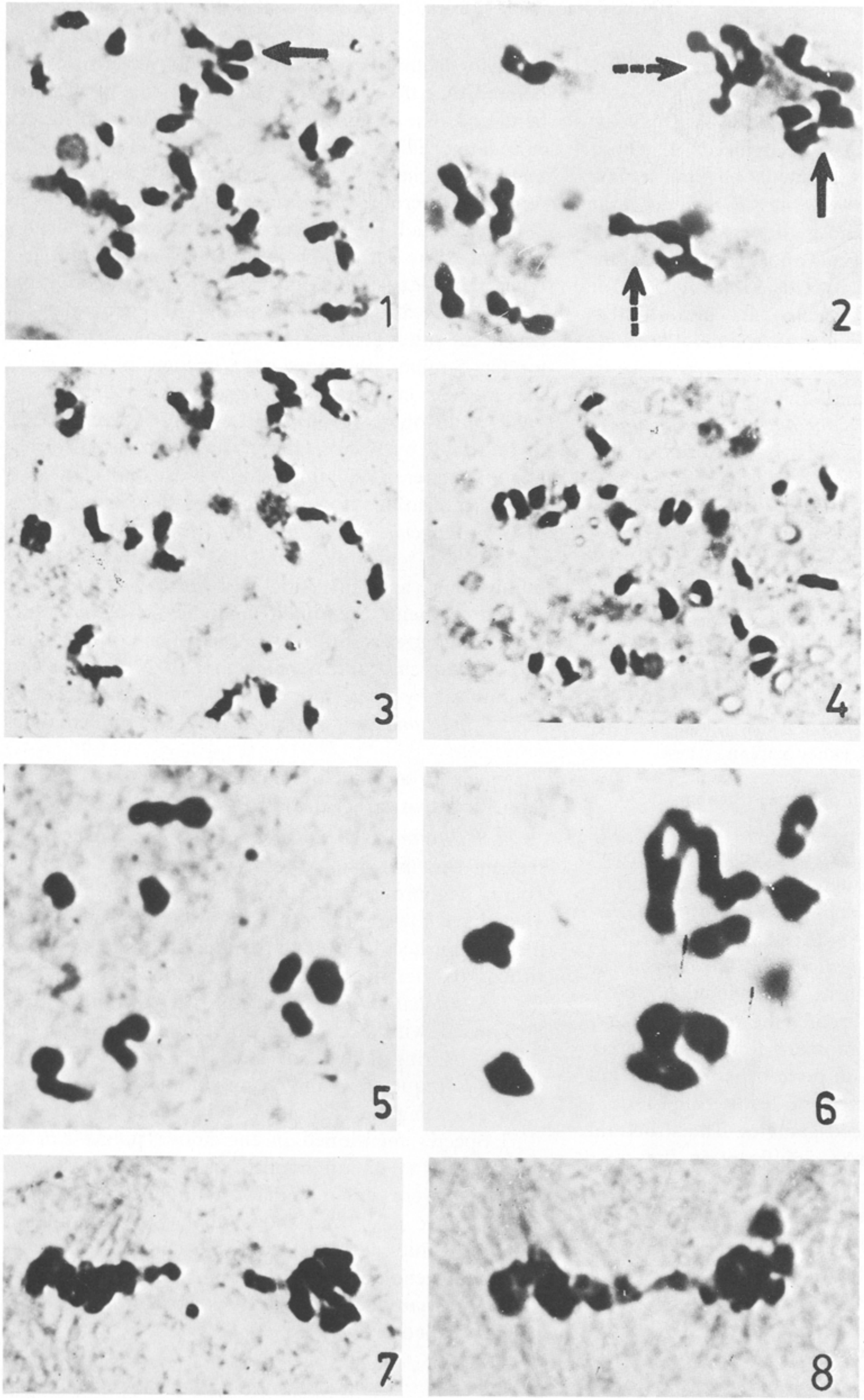
Discussion

The important criteria generally recognised for evaluating species relationships from a cytogenetic point of view relate to (a) the direction and ease with which two species can be crossed, (b) the nature and fate of hybrids and their derivatives, and (c) the behaviour of chromosomes at meiosis in the hybrids. While the former two parameters indicate genetic compatibilities, the latter reveals synaptic affinities and therefore intergenomic homeologies as well as differences in the structural organisation of chromosomes.

In the present study the degree of crossability varied with each combination. In some, crosses failed altogether, others produced fruit and seed set while still others produced hybrids. In the latter cases some crosses succeeded in only one direction.

The percentage of fruit set in relation to the total number of pollinations gives an estimate on the ease of crossing. Crosses such as *S. trilobatum* × *S. indicum* var. "multiflora' and *S. melongena* × *S. indicum,* where hybrids were obtained, the fruit set was not higher than 10%. In crosses *S. indicum* var. 'multiflora' × *S. indicum* or *S. torvum,* however, fruit set is higher than 30% although hybrids were not realised. Other crosses, however, show a relation between percentage of fruit set and success of the cross. In general, therefore, data on the higher percentage of fruit set indicate the absence of prezygotic incompatibilities, which is a one step advancement over total failure.

The frequency of hybrid seed produced in relation to actual number of ovules used as targets gives a reliable estimate on the ease of crossing in successful combinations. Crosses between *S. surattense* and *S. melongena* or *S. indicum,* or between *S. melongena* and *S. indicum* can be easily made; so also can the cross between *S. trilobatum* and *S. indicum* var. 'multiflora'. Hybrids involving other species require a larger



Figs. 1–8. Meiosis in interspecific hybrids. **1** Diakinesis in *S. surattense* × *S. melongena* – $1_{III} + 7_{II} + 7_{I}$ (Y-type trivalent with *arrow*); **2** Metaphase-I in *S. surattense* × *S. melongena* – $1_{IV} + 2_{III} + 7_{I}$ (Y-type quadrivalent with *arrow* and chain type trivalents with *broken arrows*); **3** Diakinesis in *S. surattense* × *S. trilobatum* – $1_{III} + 10_{II} + 1_{I}$ (chain type trivalent at *extreme right side; note* heteromorphic bivalents); **4** Diakinesis in *S. trilobatum* × *S. surattense* – $9_{II} + 6_{I}$; **5** Diakinesis – Metaphase-I in *S. trilobatum* × *S. indicum* var. 'multiflora' – $1_{IV} + 10_{II}$ (ring type quadrivalent at *extreme right*); **6** Diakinesis – Metaphase-I in *S. indicum* var. 'multiflora' $1_{IV} + 10_{II}$ (spoon type quadrivalent); **7** Metaphase-II in *S. indicum* × *S. melongena* bridge with fragment; **8** Metaphase-II in *S. indicum* × *S. melongena* with bridge. Fig. 2 ×1,200, others ×1,000

number of targets with no surity that the expected hybrid will be realised.

Considering the rates of survival of the hybrids, generally three classes can be recognised: 1. Those that are incapable of development beyond a few leaved stage: hybrids *S. surattense* × *S. indicum* and *S. indicum* × *S. torvum.* 2. Those that are capable of reaching maturity but are weak and therefore require more time for development: hybrids *S. indicum* × *S. indicum* var. 'multiflora', *S. indicum* var. 'multiflora' × *S. surattense* and its reciprocal, *S. trilobatum* × *S. surattense* and its reciprocal. 3. Those that are vigourous in growth and development and quick to reach maturity: hybrids *S. surattense* × *S. melongena, S. indicum* × *S. melongena* and its reciprocal, *S. trilobatum* × *S. indicum* var. 'multiflora'.

Hybrids *S. surattense* × *S. indicum* and *S. indicum* × *S. torvum* died in the seedling stage. Kirti and Rao (1981) obtained the latter hybrid only when reared under special conditions. Therefore, the intergenomic associations between these species may be regarded as lethal and comparable to the interspecific hybrids of *Crepis* (Hollingshed 1930), *Nicotiana* (East 1935), *Aegilops* (Sears 1944) and *Gossypium* (Gerstel 1954). Except for hybrids between *S. indicum* and *S. melongena,* all the others were more than 85% pollen sterile. However, hybrid derivatives were obtained in crosses *S. surattense* × *S. melongena* and *S. trilobatum* which are partly sterile and could not be crossed to either parents. These results clearly indicate how blockage or introgression can arise through recombination of certain genotypes (Stebbins 1958).

Comparative analysis of cytological data of the hybrids shows that haploid set of 12 chromosomes in heterozygotes synapse though to different extents. There is nearly 100% bivalency in *S. indicum* × *S. melongena* and its reciprocal, with nearly 95% fertility; this is followed by *S. surattense* × *S. melongena* or *S. indicum* with over 50% bivalency which, however, are completely sterile. Apparently the respective complements have segmental homologies to varying degrees and these are large enough to permit their pairing and crossing-over but at the same time leads to the formation of genetically unbalanced gametes. The structural divergence seems to be most significant in the cross *S. trilobatum* × *S. surattense* in which a maximum of only 3% of the PMCs analysed showed 12 bivalents. The occurrence of univalents, which approaches a maximum of 12 per cell in the above cross and with their percentage not exceeding 5 in the remainder of the crosses, may not be regarded as contributing significantly to gametic imbalance.

A comparative study of higher chromosome associations encountered in different crosses reveals that their range varies from a maximum of 3 per cell to a minimum of 1. In hybrids *S. surattense* × *S. melongena* at least one multivalent is observed in over 40% of the cells. These higher associations by themselves, irrespective of their orientation at Metaphase-I, may not be major factors for sterility. It should nevertheless be pointed that the occurrence of polyvalents on the one hand and that of univalents on the other could have a cumulative effect in bringing gametic lethalities. The higher associations, however, do indicate chromosomal repatterning in terms of interchanges. This is also supported by the occurrence of heteromorphic bivalents. The formations of 'Y', 'X', spoon and fish type higher associations provide evidence for multiple homeologies for a chromosome of one genome with two of the other genome involving the same arm of the former. Similar inferences have become obligatory in the meiotic configurations observed in *Clarkia* by Lewis and Roberts (1956) and Lewis and Raven (1958), in *Chenactis* by Kyhos (1965). On the basis of formation of higher associations and observations on anaphase segregations it can be inferred that the genomes of *S. melongena* and *S. indicum* differ by one interchange and one inversion. The low frequency of multivalents and inversion bridges reveal that the altered segments are small. Genomes of *S. surattense* and *S. melongena* differ by at least one interchange and *S. surattense* and *S. trilobatum* or *S. indicum* var. 'multiflora' by three interchanges, while *S. trilobatum* and *S. indicum* var. 'multiflora' by two interchanges only.

When an attempt is made to correlate all the inferences drawn earlier the following facts emerge:

1. *S. surattense, S. indicum* and *S. melongena* as a section can be crossed easily with each other to obtain vigourous and occasionally fertile hybrids. They have lower ranges of chiasma frequencies with means intermediate to both parents and there are fewer structural differences among the genomes involved.
2. *S. trilobatum* and *S. indicum* var. 'multiflora' can be crossed with each other to obtain vigourous but sterile offspring. They show an intermediate nature of chiasma frequencies and a maximum of two interchanges among their genomes.
3. Species mentioned in the above points can be intercrossed to obtain hybrids in some combinations but they were either lethal or highly sterile. The hybrids have also been shown to have lower recombination values, at least three structural differences among the genomes and high frequencies of univalents.
4. *S. torvum* was found to be isolated from all other species studied.

Aspects on causes of inconsistent results obtained by previous workers are worth investigating as they form the basis for speciation and evolutionary problems and also the grouping of these species Bhaduri (1951) and Rajasekaran (1969).

From the present study it is known that the breeding behaviour of *S. indicum* and *S. indicum* var. 'multiflora' are quite different. These differences are reflected in crosses involving these two species with others. This is also strengthened by the fact that hybrids obtained between these two species were weak and highly sterile. These observations together with morphological differences between *S. indicum* and *S. indicum* var. 'multiflora' support their recognition as separate species. Inter-racial differences exist in crossability and recombination values in hybrids involving different cultivars of *S. melongena* and races of *S. surattense* and *S. indicum* (Veerabhadra Rao 1977; Raju et al. 1981). Thus, differences observed in the results of previous workers using these species are attributable to the usage of different varieties of *S. indicum* – a species known to be highly polymorphic – and the existence of genotypic variability of different races of *S. surattense* and cultivars of *S. melongena.* Parallel situations by Sawant (1958) in *Lycopersicon* and in *Trifolium* by Morley et al. (1956) have been reported earlier.

Based on morphological aspects, crossability potentialities and fertility of obtained hybrids Bhaduri (1951) recognised two groups: *S. melongena, S. indicum* and *S. xanthocarpum* (= *S. surattense*) are brought together in the first group while the second group includes *S. torvum, S. ferox* and *S. hispidum.* The members of the two groups are cross-infertile. Rajasekaran (1969) obtained a hybrid between *S. surattense* and *S. trilobatum* (which was sterile) and included the latter in the first group of Bhaduri (1951).

The present study supports Bhaduri's (1951) placement of the three species already cited in group I. However, *S. indicum* var. 'multiflora' differs significantly from *S. indicum* in its crossability relationships as well as in cytology. These features, in addition to its morphological distinctness, clearly separate *S. indicum* var. 'multiflora' from *S. indicum.* Its relationship to *S. trilobatum* is quite different when compared with its relationship to other species of group I. It is therefore reasonable to bring together *S. trilobatum* and *S. indicum* var. 'multiflora' into a group of their own, *S. trilobatum* in itself is as different from the three others of group I. Therefore, the inclusion of *S. trilobatum* in group I as done by Rajasekaran (1969) is not supported by the present findings. It is therefore suggested that, while retaining group I of Bhaduri (1951) as it is, a second group consisting of *S. trilobatum* and *S. indicum* var. 'multiflora' can be recognised. The second group of Bhaduri (1951) may be treated as a third group. The validity for bringing together *S. torvum, S. ferox* and *S. hispidum,* however, needs verification from cytogenetic studies comparable to those made for group I and II. The present studies have shown that *S. torvum* stands quite apart from the five species investigated and therefore its separation from them is justified. From the cytological point of view also, members within each of the presently recognised group I and II show fewer structural differences in their genomes than those obtained between members of different groups.

In the light of the above overall conclusions, the cytogenetic incompatibilities among the species tested are attributable not only to the suspected cryptic structural hybridity suggested by Rajasekaran (1971) and Rangaswamy and Kadambavanasundaram (1974), but more importantly to major structural heterozygosity of the chromosomes. The prevalence of high bivalency coupled with higher chromosome associations in some of them is clear evidence that intergenomic homeologies are strong enough to permit a fair degree of pairing in the heterozygous state. The high degree of sterility in hybrids and their derivatives, hybrid inviability and weakness and hybrid breakdown acting as isolating mechanisms are, in addition to the blockage of introgression, obviously the chief factors in the maintenance of different species as distinct taxa.

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