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Evolution and Improvement of Cultivated Amaranths

VII. Cytogenetic Relationships in Vegetable Amaranths

MOHINDER PAL and T. N. KHOSHOO

National Botanic Gardens, Lucknow (India)

Summary. Of the four interspecific hybrids, three (*A. graecizans* var. *graecizans* × *A. tricolor* cv. 'Purple leaf', *A. lividus* var. *lividus* × *A. tricolor* var. *viridis* and *A. gracilis* × *A. tricolor* cv. 'Purple leaf') were studied cytologically. In all the three, differentiation between the parents is chiefly a result of interchanges and paracentric inversions. The interchange complexes may involve from four (*A. gracilis* × *A. tricolor* cv. 'Purple leaf') to fourteen (*A. lividus* var. *lividus* × *A. tricolor* var. *viridis*) chromosomes, indicating that the parents differ from each other in 1 to 6 interchanges. Because of the small size of the chromosomes, it is possible that crossing-over in interchange for small segments is restricted. The particular parental species representing the ancestral condition from which others were derived or compounded is difficult to pin-point. With preferential pairing and the restoration of fertility in the amphidiploid *A. lividus-tricolor*, it became clear that it is very likely that the interchanged segments are small and sterility in the hybrid is entirely chromosomal.

This situation is in strong contrast to that in Sect. *Amaranthus*, where the single male flower per glomerule and huge showy inflorescences lead to more cross-pollination; coupled with this are strong morphological divergences between taxa and less genetic differentiation. In the Sect. *Blitopsis*, there are a number of male flowers per glomerule and small non-showy axillary inflorescences, leading to self-pollination, and less morphological but strong genetic differentiation by interchanges and inversions.

Introduction

The vegetable amaranths belong to the Section *Blitopsis* and although eight naturally occurring interspecific hybrids have been reported from time to time in this Section (Table 1), none has been studied cytologically so far. In the present study, four interspecific hybrids emanating from 5 taxa belonging to four species were investigated for this purpose: *A. graecizans* var. *graecizans* × *A. tricolor* cv. 'Purple leaf', *A. lividus* var. *lividus* × *A. tricolor* var. *viridis*, *A. graecizans* var. *graecizans* × *A. lividus* var. *lividus*, and *A. gracilis* × *A. tricolor* cv. 'Purple leaf'.

Observations

Parents

In all the parents 17 bivalents were found at diakinesis and metaphase I (Figs. 1–4). At diakinesis in *A. lividus* var. *lividus*, one bivalent was usually associated with the nucleolus (Fig. 1). In *A. lividus* var. *lividus* (Fig. 2) and *A. tricolor* cv. 'Purple leaf' one of the bivalents was seen to disjunct early, a feature common to many species of the genus. One or two randomly distributed chiasmata per bivalent were found, but some bivalents in *A. graecizans* var. *graecizans* (Fig. 3) and *A. lividus* var. *lividus* were seen to have even three chiasmata. Anaphase I was perfectly regular (Fig. 4) in all the taxa except for a few cases of late disjunction noted in bivalents with three chiasmata in some cells of *A. graecizans* var. *graecizans*. Subsequent stages of meiosis in all four taxa were regular, resulting in normal pollen and seed fertility.

Interspecific Hybrids

A. graecizans var. *graecizans* × *A. lividus* var. *lividus*: The two species do not seem to be very compatible, as only three hybrids were obtained from a very heavy pollen dusting on the female parent. Morphologically, the hybrid was intermediate in branching pattern, leaf shape and colour, though there appeared to be overall dominance by the female parent *A. graecizans*, except in the small terminal inflorescence (2–4 cms) which is absent in *A. graecizans* but present in *A. lividus*. The most peculiar feature of the hybrid was that the inflorescences were composed almost exclusively of very poorly developed female flowers, and only a few stamens were found in the entire plant. Meiotic studies could not be made on this hybrid because of lack of sufficient anthers.

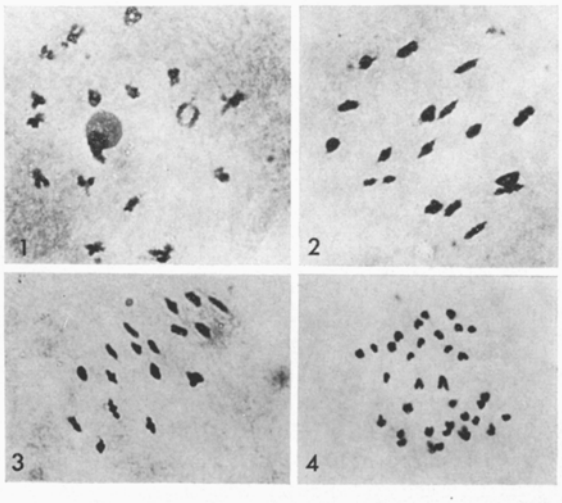
A. gracilis × *A. tricolor* cv. 'Purple leaf': A solitary plant of the hybrid was detected in a sympatric population of the two species in the experimental plot. Morphologically the hybrid was intermediate between the parents.

Detailed studies of meiosis could not be made because a large number of analyzable cells were not available. In the few cells which were studied, a ring of four chromosomes was always present at diakinesis (Fig. 5) and metaphase I (Fig. 6). Heteromorphic bivalents were also observed. The hybrid was com-

Table 1. *Interspecific hybrids reported in Sect. Blitopsis*

Species involved	Known under the specific name	Fertility
A. albus × *A. blitoides*	*A.* × *budensis*	Very small seed production
A. angustifolius? var. *graecizans* × *A. gracilis*	—	Seeds unknown
A. crispus × *A. deflexus* var. *rufescens*	*A. thevenaei* Degen et Thell.	Seeds badly formed
A. crispus × *A. deflexus* var. *deflexus*	*A.* × *polygarianus* Priszter et Karpati	Seeds badly formed
A. deflexus var. *deflexus* × *A. muricatus*	*A. tarraconensis* Sennen et Pau	Seed formation sparse
A. deflexus var. *rufescens* × *A. gracilis*	*A. mauritii*	—
A. deflexus? var. *rufescens* × *A. vulgatissimus*	*A.* × *jansen-wachterianus* Thell.	Fruit and seed not formed
A. gracilis × *A. muricatus*	*A.* × *parodii* Thell.	Seeds formed
**A. graecizans* var. *graecizans* × *A. lividus* var. *lividus*	—	Fruit and seed not formed
**A. gracilis* × *A. tricolor* var. 'Purple Leaf'	—	Sterile
**A. graecizans* var. *graecizans* × *A. tricolor* cv. 'Purple Leaf'	—	Sterile
**A. lividus* var. *lividus* × *A. tricolor* var. *viridis*	—	Sterile

The last four hybrids are (*) based on the present work, while the data on remaining eight cases has been taken from Aellen 1961).

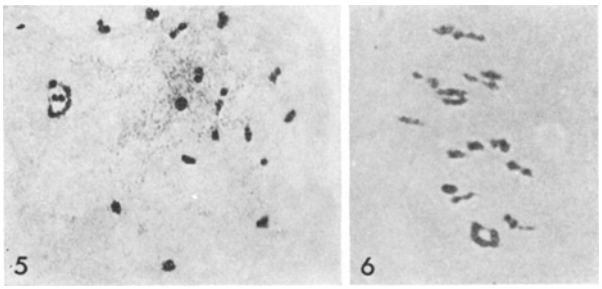


Figs. 1 and 2. *A. lividus* var. *lividus*. Diakinesis and Metaphase I, 17 II with precocious disjunction in one bivalent in the latter

Figs. 3 and 4. *A. graecizans*. Metaphase I, 17 II and anaphase I, 17:17 respectively

pletely pollen and seed sterile. A limited amount of natural hybridization between *A. gracilis* and *A. tricolor* var. *viridis* has also been observed near the drains where the two parents often grow together.

A. graecizans var. *graecizans* × *A. tricolor* cv. 'Purple leaf': The two species are not very compatible. Extensive dusting of pollen on to *A. graecizans* var. *graecizans* gave only two hybrids out of a population of nearly 40 plants raised from the maternal parent. The reciprocal cross was not tried. However,



Figs. 5 and 6. F_1 *A. gracilis* × *A. tricolor*. Diakinesis, R_4 + 14 II + 2 I and Metaphase I, R_4 + 15 II respectively

the hybrid was vigorous. In most of the morphological characters, such as leaf shape and floral parts, the hybrid was intermediate between the two parents but there was clear dominance by the male parent in colour and the presence of a terminal inflorescence. In general habit and branching pattern, the hybrid was nearer the female parent.

An analysis of 21 cells at metaphase I is given in Table 2. 20 cells (95%) contained 1 to 3 interchange complexes with 4 to 6 chromosomes in each, while the remaining one cell contained 14 II + 6 I. The most common arrangement, seen in 47.6% cells, was an interchange complex of 4 chromosomes, mostly in the form of a ring (Fig. 7) but, failing that, in the form of a chain. A chain of 5 chromosomes was seen in 9.52% cells. Eight chromosomes were involved either as 2 chains of 4 chromosomes (Fig. 8), or as one ring and one chain of four chromosomes, in 19.04% cells. Ten chromosomes were found involved

in one ring of four and one chain of six chromosomes (Fig. 9) in 14.28% cells, and in 4.76% cells 12 chromosomes were in the form of 2 chains and one ring of 4 chromosomes each.

It is clear from this that the parental chromosomes differ by not more than 3 exchanges, which involve in all not more than 12 chromosomes, but by far the most common situation is one exchange giving rise to an interchange complex of 4 chromosomes. In any one complex there are never more than 6 chromosomes. Furthermore, while rings are composed of 4 chromosomes, the chains contain 4 to 6 chromosomes. The full potential of three interchanges involving the 12 chromosomes is generally not realized, perhaps due to the small chromosomal segments involved in the interchanges. The orientation of most rings was adjacent, while the chains were mostly alternate. Again, such orientations may be due to the small size of the chromosomes involved in the interchanges (John and Lewis, 1965; Khoshoo and Mukherjee 1966; Sybenga, 1968; Khoshoo and Raina, 1967; Zadoo and Khoshoo, 1968).

Table 2. *Associations at metaphase I in F_1 A. graecizans var. graecizans × A. tricolor cv. 'Purple Leaf'*
R = Ring; C = Chain

No. of cells	Chromosome associations						Orientation
	VI	V	IV	III	II	I	
3	—	—	IR	—	13	4	Adjacent
1	—	—	IC	—	14	2	Adjacent
1	—	—	IR	—	14	2	Adjacent
2	—	—	IR	—	15	—	Adjacent
1	—	—	IR	—	15	—	Alternate
2	—	—	IC	—	15	—	Alternate
2	—	—	IR + IC	—	11	4	C alternate; R adjacent
2	—	—	2C	—	13	—	IC each alternate and adjacent
1	—	—	—	—	14	6	—
2	—	IC	—	—	14	1	Alternate + adjacent
1	—	—	IR + 2C	—	9	4	C alternate; R adjacent
1	IC	—	IR	—	11	2	Alternate and adjacent
2	IC	—	IR	—	12	—	Alternate and adjacent

The remaining chromosomes formed 9 to 15 bivalents with one or two chiasmata per bivalent, which indicates a reasonable degree of homology. The number of univalents varied from 0—6 and may lag and undergo precocious division at anaphase I (Fig. 10). One bridge-fragment configuration was seen in about 60% of cells at anaphase I (Fig. 11), indicating inversion heterozygosity for at least one segment. In one cell, two fragments were present with one bridge. Nearly 50% of the cells (Table 3) at anaphase I showed 17:17 while the rest had 16:18 (Fig. 12) distribution. Some cells at anaphase II also showed a bridge-fragment configuration, which might mean nondisjunction at anaphase I in the bivalent heterozygous for inversion. The pollen was completely sterile and there was no seed formation.

Table 3. *Chromosome distribution at anaphase I in A. graecizans var. graecizans × A. tricolor cv. 'Purple Leaf'*

Distribution	No. of cells	No. of bridge and fragments
17:17	3	—
17:17	1	1 bridge + 1 fragment
16:18	2	1 bridge + 1 fragment
16:18	1	1 bridge + 2 fragments

A. lividus var. *lividus* × *A. tricolor* var. *viridis*

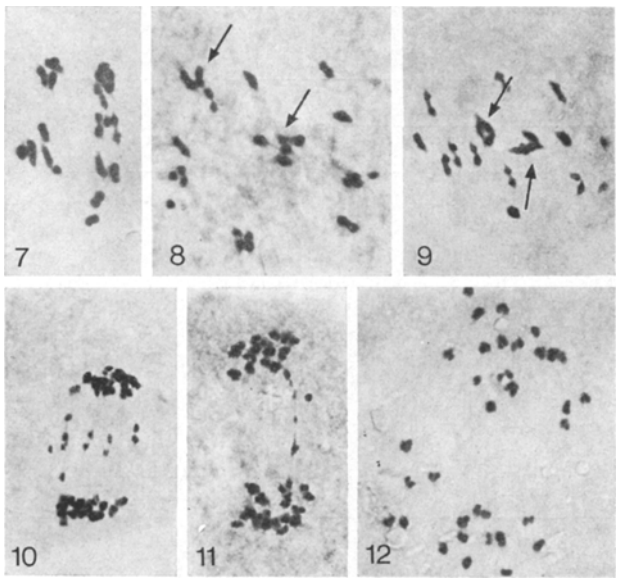
The two species cross readily and hand pollinations, without any emasculation, with *A. lividus* as the seed parent yielded progeny in which nearly 33% were hybrids. Because of the high proportion of male flowers in the glomerules in *A. tricolor*, the reciprocal hybrid was not attempted.

Morphologically the hybrids showed overall dominance by *A. tricolor* in habit and floral characters, but, in leaf shape and colour, the hybrids were intermediate and both these characters were used to spot them while young.

Table 4. *Different associations at metaphase I in F_1 A. lividus var. lividus × A. tricolor var. viridis*

Associations	No. of cells
C10 + C4 + 9II + 2I	1
C11 + 11II + 1I	1
C10 + 12II	3
C10 + 11II + 2I	1
C9 + 12II + 1I	1
C8 C4 + 10II + 2I	2
C8 + 13II	5
R8 + 11II + 4I	1
C6 + C4 + 12II	4
R6 + 14II	1
C5 + 14II + 1I	2
C4 + C4 + C4 + 11II	1
C4 + C4 + 13II	1
C4 + 15II	1
Total:	25

In contrast to the previous hybrid, there was no cell among the 25 scored at metaphase I (Table 4; Figs. 13—17) without interchanges. In 20% of cells C8 + 13 II (Figs. 13—14) were formed; there were 16% cells with C6 + C4 + 12 II, 12% with C10 + 12 II and 8% each with C8 + C4 + 10 II + 2 I



Figs. 7–12. F_1 *A. graecizans* × *A. tricolor* cv. 'Purple leaf'. Metaphase I, R_4 + 14 II + 2 I (Fig. 7), C_4 + C_4 + 12 II + 2 I (Fig. 8), R_4 + C_6 + 11 II + 2 I (Fig. 9) and Anaphase I with lagging univalents undergoing precocious division (Fig. 10), dicentric bridge and a fragment (Fig. 11) and 16:18 distribution (Fig. 12)

(Fig. 15) and C5 + 14 II + 1 I. The remaining 36% cells contained 9 different arrangements. There were 1 to 5 interchanges with 4 to 11 (12?) chromosomes in each complex. In all, a maximum of 14 chromosomes in a cell might be involved in 2 complexes, followed by 12 chromosomes in 2 or 3 complexes, and 11 or 10 chromosomes in 1 or 2 complexes. The chain of 11 chromosomes plus one univalent might actually be a complex of 12 chromosomes. The minimum number of chromosomes involved in a cell was four (4% cells), but most of the cells contained more than 4 chromosomes in a complex. The maximum number of chromosomes involved was 14. Whether all the 15 chromosomes involved form a single and continuous series of 6 interchanges or two series of 4 and 1 interchanges giving rise to C10 + C4 + 9 II + 2 I is not certain. The cells containing chains of 11 or 10 chromosomes would point to the former possibility, because of the unusual length some chiasmata either having failed or slipped off in the chain containing 14 chromosomes. The occurrence of rings of 6 or 8 chromosomes (Fig. 16), found in 8% of cells, can not be explained on this basis. The remaining 92% cells contained chains.

The orientation of any one interchange complex was more often both adjacent and alternate (Figs. 14, 15), particularly of the longer complexes. The number of bivalents varied from 9 to 15, some of which were distinctly heteromorphic (Fig. 17). About 45% of cells contained 1 to 2 univalents. Four univalents were found in one cell.

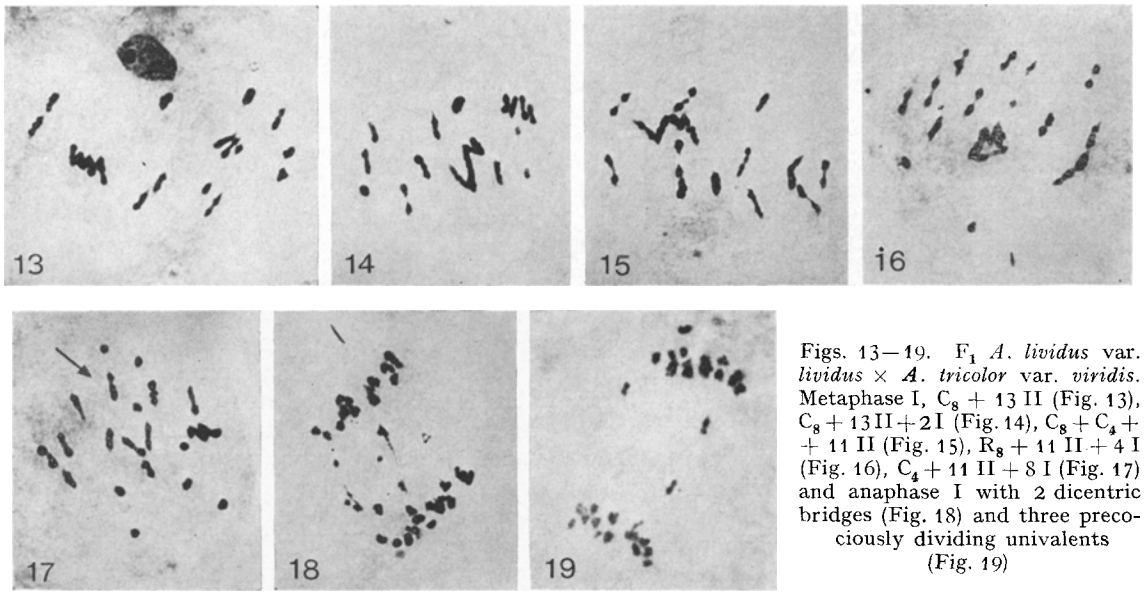
Of the 35 cells at anaphase I (Table 5), nearly 45.7% showed a normal 17:17 distribution, while the rest were characterized by unequal distribution ranging from 16:18 (25.7%) to 19:15 (11.4%). The other cases of unequal distribution were due to lag-

Table 5. *Summary of anaphase I data in F_1 A. lividus var. lividus × A. tricolor var. viridus (B = bridge; f = fragment)*

Anaphase I segregation	No. of cells	No. of cells with		No. of cells with lagging			No. of cells (Normal)
		1B + 1f	2B + 2f	One Bivalent	Univalents 1	Univalents 2	
17:17	16	3	1	—	—	—	12
16:18	9	2	2	—	—	—	5
15:19	4	3	—	—	—	—	1
16:17	2	—	—	—	2	—	—
16:16	1	—	—	—	—	1	—
14:18	2	—	—	1	—	1	—
15:17	1	—	—	1	—	—	—
Total:	35	8	3	2	2	2	18

Table 6. *Chromosoue associations in C_0 and C_1 amphidiploids of A. lividus-tricolor*

Generation	Chromosome association IV	III	II	I	Pollen fertility %	No. of cells
C_0 Mean	0.8	0.1	32.0	0.5	63.7	10
Range	0–2	0–1	30–34	0–2		
C_1 Mean	1.3	0.133	30–33	1.733	44–64.2	30 (10 each from 3 plants)
Range	0–3	0–1	27–33	1–4		



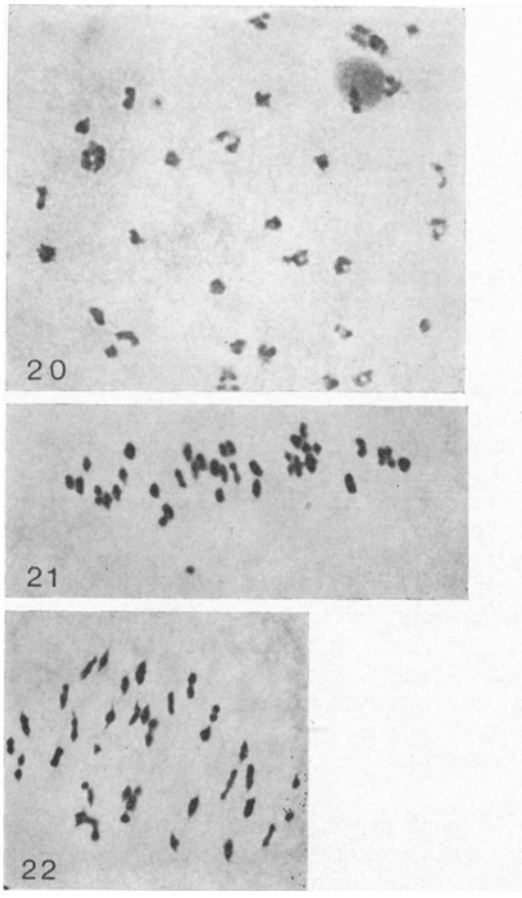
Figs. 13—19. F_1 *A. lividus* var. *lividus* × *A. tricolor* var. *viridis*. Metaphase I, $C_8 + 13$ II (Fig. 13), $C_8 + 13$ II $+ 2$ I (Fig. 14), $C_8 + C_4 +$ $+ 11$ II (Fig. 15), $R_8 + 11$ II $+ 4$ I (Fig. 16), $C_4 + 11$ II $+ 8$ I (Fig. 17) and anaphase I with 2 dicentric bridges (Fig. 18) and three precociously dividing univalents (Fig. 19)

ging of chromosomes. Besides unequal distribution at anaphase I, nearly 25.7% of cells contained a bridge-fragment configuration, which, from the uniform size of the fragments appeared to be due to inversion heterozygosity. In 8.5% of cells, two bridges with a fragment each (Fig. 18) were seen, indicating that there are at least two bivalents heterozygous for inversions. The small percentage of cells with bridge-fragment configuration may be a result of the restriction imposed on pairing by translocation, or the small size of the inverted segment and consequent failure of chiasma formation. A few cells contained lagging bivalents and univalents, the latter undergoing precocious division (Fig. 19). The hybrid was completely pollen and seed sterile.

Amphidiploid A. lividus var. *lividus–tricolor* var. *viridis*. The amphidiploid was raised by colchicine treatment of the F_1 hybrid seedlings. Studied in the second generation, the plants were vigorous and uniform. The leaves were larger than those of the parents and had less emargination at the tip than *A. lividus* or the F_1 hybrid. The floral characters showed the usual gigantism.

In a study of 40 cells from 4 plants (one of C_0 and three of C_1) of the amphidiploid, 27 to 34 bivalents were noted (Table 6). The remaining associations were in the form of loose quadrivalents and some trivalents and univalents. There was a small, but perceptible, increase in quadrivalent, trivalent and univalent number in C_1 plants compared with the C_0 (Figs. 20—22). The most noteworthy feature was the total absence of the interchange complexes so characteristic of the F_1 hybrid.

Anaphase I was regular with 34:34 distribution at each pole. Some cells had the unequal distribution 36:32. By and large, pollen fertility was restored (63.7%) and there was profuse seed production.



Figs. 20—22. Amphidiploid *A. lividus-tricolor* ($2n = 68$). Diakinesis, 1 IV + 32 II (Fig. 20) and metaphase I with 1 IV + 31 II + 2 I (Fig. 21) and 1 IV + 30 II + 4 I (Fig. 22)

Discussion

From the foregoing meiotic analysis of the three interspecific hybrids belonging to the Section *Bli-*

topsis, it is apparent that the cytogenetic differentiation is chiefly due to interchanges and paracentric inversions. This is in strong contrast to the prevailing situation in Section *Amaranthus* (Khoshoo and Pal, 1972; Pal and Khoshoo, 1973). Interchange complexes containing up to 14 chromosomes have been noted. In simpler cases, such as *A. gracilis* × *A. tricolor* cv. 'Purple Leaf', there is R4 + 15 II, indicating that the two species differ by one interchange. In the other two combinations, *A. graecizans* var. *graecizans* × *A. tricolor* 'Purple Leaf' and *A. lividus* var. *lividus* × *A. tricolor* var. *viridis*, particularly the latter, the differentiation is rather more complex. The former combination differs by a maximum of 3, but the latter by 5 or 6 interchanges which may form one, or at the most, two series. Furthermore, one or two paracentric inversions were encountered during anaphase. Because of the small size of the chromosomes, it is possible that crossing over in interchanges for small segments may be restricted. Thus, because of the failure of chiasmata and/or the small size of interchanges, all the potential interchanges may not be discernible.

In three hybrids the pollen parent is *A. tricolor* and there are no data to show the nature of differentiation between the two components of this species involved in the three interspecific hybrids. Since all the taxa involved in the present hybridization are at diploid level, it is not easy to decide which of them represents the ancestral condition from which the remaining rearrangements have been derived or compounded. Some of the morphological features of the species offer the only pointers in this direction. If, as it appears reasonable to assume, the terminal inflorescence represents the ancestral condition in the genus compared with the axillary glomerules, then *A. tricolor* as a whole, and *A. tricolor* var. *viridis* in particular, is very generalized morphologically. In hybrids (*A. graecizans* × *A. lividus*) involving parents with axillary and terminal inflorescences, the latter is dominant which may indicate that it is the original or ancestral condition. It is of interest to note that *A. tricolor* var. *viridis* shows the maximum differentiation of about 6 interchanges from *A. lividus* var. *lividus*, but *A. tricolor* 'Purple Leaf' differs at the most by 3 interchanges from *A. graecizans* var. *graecizans*. This may mean that *A. tricolor* var. *viridis* represents a more ancestral condition than *A. tricolor* 'Purple Leaf'.

Although morphological evidence gives some indication of the probable direction of chromosomal evolution, systematic analysis of intra- and interspecific hybrids for crossability, interfertility and translocation patterns within the Section *Blitopsis* is likely to give a clearer picture, even though the chromosomes are small and not individually identifiable.

It is clear that in the interspecific hybrids in the Section *Amaranthus* there are bivalents coupled with reasonable fertility (Khoshoo and Pal, 1972; Pal and Khoshoo, 1973), but in the Section *Blitopsis* there are interchanges, inversions and sterility. The almost total sterility in all the 8 natural, cytogenetically uninvestigated, interspecific hybrids of this section reported so far (Table 1) is akin to the situation in four hybrids investigated in the present study. If the situation revealed by the analysis of 6 interspecific hybrids of the Section *Amaranthus* and 3 of the Section *Blitopsis* is representative of the two Sections of the genus *Amaranthus*, then such differences in the mechanism of cytogenetic differentiation between the two Sections have important cytotaxonomic implications. Correlated with this is the difference in the breeding system. The members of the Section *Blitopsis* are predominantly self-pollinated because of the presence of a number of male flowers per glomerule, a small non-showy terminal inflorescence (when present), greater development of the axillary glomerules and strong and exclusive ecological preferences; members of the Section *Amaranthus*, with a single male flower per glomerule and huge showy inflorescences, are predominantly cross-pollinated. Thus the Section *Amaranthus* lacking interchanges, is relatively more cross-pollinated. A correlation between inbreeding and chromosomal repatterning is understandable in as much as such a breeding system helps not only in the accumulation of interchanges and inversions but also rendering them homozygous. Thus, inbreeding is likely to help in the establishment and maintenance of homozygotes. Very likely such rearrangementsare associated with linkage of some adaptive gene combinations and, with continued inbreeding, sterility barriers appear. As seen in the present hybrids, total sterility results from the recombination of such repatterning. With continued isolation and differential selection, the possibility of gene exchange is almost totally restricted and evolutionary divergence from the ancestral type is to be expected. A close parallel with the situation in the two Sections of the genus *Amaranthus* is seen in the genus *Oenothera*, in which there is a high incidence of structural heterozygotes in inbred species compared with the outbred species of California (Cleland, 1949; Rees, 1961). A high frequency of interchange heterozygotes is also associated with inbreeding in *Clarkia* (Lewis and Raven, 1958) and cockroach (Lewis and John, 1957). Although the occurrence of interchange heterozygotes intraspecifically (within different populations of a species) is well known in a number of plant species (see Burnham, 1956), the evidence for such a mechanism as a means of cytogenetic differentiation at interspecific level has been found in *Datura* (Avery, Satina and Rietsema, 1959), *Clarkia* (Lewis, 1953; Raven and Lewis, 1959; Vasek, 1960; Snow, 1960), *Gossypium* (Gerstel, 1953), *Secale* (Riley, 1955; Khush, 1962), *Gilia* (Grant, 1956), *Collinsia* (Garber, 1960; Garber and Dhillon, 1962), *Avena* (Holden, 1966), *Linum*

(Gill and Yermanos, 1967a, b), *Epilobium* (Mosquin, 1968), etc. Studies on all these genera have shown that chromosomal reorganisation is a frequent mode of speciation and often morphologically similar taxa differ in chromosomal arrangements which can be detected only through hybridization. Lewis (1966) calls it 'saltational' speciation.

An important aspect of this study has been to investigate, as far as possible, the extent and innate nature of the interchange complexes and whether total sterility in the hybrids is the result of irregular segregation of the interchanges and inversions or has genic causes. To clarify some of these points, amphidiploids of the F_1 hybrid *A. lividus* var. *lividus* × *A. tricolor* var. *viridis*, showing the maximum chromosomal differentiation, were raised. In strong contrast to the interchange complexes of 4 to 14 chromosomes in the F_1 hybrid, in its amphidiploid bivalent pairing was predominant with an occasional, loosely-joined quadrivalent, which is not the translocation type but is similar to the quadrivalents met with in autotetraploids. This may be a result of the overall small size of the chromosomes giving a smaller number of quadrivalents, because fewer chiasmata can be formed along the short length of the chromosomes; this has been postulated by Darlington (1965). The institution of complete preferential pairing may indicate the very small size of interchanges which, though enough to bring about pairing in the terminal segments in the absence of competition for pairing in the F_1 hybrid, are probably not enough to maintain the *status quo* in pairing in the presence of the completely homologous mates available in the amphidiploids.

Polyploids of intra- and interspecific interchange and inversion heterozygotes behave differently. While complete preferential pairing is induced in tetraploids of the *Zea-Teosinte* hybrid (Shaver, 1962), interspecific hybrids within *Collinsia* (Garber and Dhillon, 1962), *Zebrina pendula* (Venkateswarlu and Rao, 1963), *Drosophila* (Grell, 1961) and interchange and inversion heterozygotes in maize (Shaver, 1963; Doyle, 1963), such was not the case in rye (Sybenga, 1966; Ahloowalia, 1963), *Oenothera* (Linnert, 1962) and *Rhoeo discolor* (Walters and Gerstel, 1948; Braungart, 1949). Analysis of all these cases indicates that although the size of the interchange may be a factor, in as much as it may be small in the former group showing preferential pairing in the tetraploids but large in the latter with non-preferential pairing, a more plausible explanation for such differential behaviour has been suggested by Walters and Gerstel (1948) and Sybenga (1966). According to them, the chiasmata are localized, perhaps to a single point at or very near the distal end of the chromosomes, in *Secale*, *Oenothera* and *Rhoeo*. Naturally, pairing starts at these points and is delayed considerably in the interstitial regions, perhaps because of the heavy concentration of heterochromatin in some cases. Thus, small terminal homologous regions in otherwise dissimilar chromosomes and the presence of central differential regions of heterochromatin block interstitial pairing in the diploids. In spite of the homologous chromosomes in the tetraploid, the property of what has been called "terminally initiated and time limited pairing" in the diploids restricts preferential pairing in the tetraploids, which remains unaffected by the complete homology of the interstitial region. The result is that random pairing between all homologous end segments occurs in these three taxa and large configurations continue to appear in the tetraploids.

The restoration of fertility in the amphidiploid shows that sterility in the F_1 is entirely chromosomal, being segregational in character, and not due to genic causes. This is also the case in amphidiploids in *Collinsia* (Garber and Dhillon, 1962) in which, as in Section *Blitopsis*, interspecific sterility barriers are due to chromosomal rearrangements such as interchanges and inversions.

It is generally assumed that in the diploid progenitors of alloploids there is a total lack of pairing accompanied by sterility (Stebbins, 1947, 1950; Clausen, Keck and Hiesey, 1945), but in the ensuing allotetraploids there is homogenetic pairing and fertility is restored. However, in the present case a good deal of pairing due to interchange and inversion hybridity and also some homology is accompanied by sterility. The tetraploid has alloploid or segmental alloploid characteristics such as predominantly bivalent pairing and good fertility rather than the autoploid properties of quadrivalent pairing and reduced fertility as seen in the amphidiploids from hybrids between grain amaranths and also in their autotetraploids. It appears that, in contrast to the Section *Amaranthus*, the species in the Section *Blitopsis* are sufficiently differentiated for successful alloploidy to be instituted. Why this has so far not happened in nature is not known, although in a genus such as *Clarkia* (Lewis and Lewis, 1955), with similar interspecific genetic differentiation, natural polyploids do exist.

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Dr. M. Pal
Dr. T. N. Khoshoo
National Botanic Gardens
Lucknow (India)