Theoretical and Applied Genetics 43, 329–334 (1973)

The Genus *Argemone*

II. Cytogenetic Relationships of *A. ochroleuca* ssp. *ochroleuca* (2n = 56) and some Diploid (2n = 28) *Argemone* Species

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Summary. Crosses between three diploid (*A. mexicana*; *A. subfusiformis*; *A. albiflora*) and one tetraploid (*A. ochroleuca*) *Argemone* species were made. The F_1's were cytogenetically analysed. All the triploid hybrids were sterile and did not set any seed. In the species there was predominantly bivalent pairing (14_{II}; 28_{II}) and high pollen and seed fertility. The F_1's displayed different configurations, e.g. I, II and III, and pollen fertility was low; the capsules were shrunken and did not contain any seed.

In the two combinations *mexicana* × *ochroleuca* and *subfusiformis* × *ochroleuca*, pairing was identical and both auto- and allosyndesis were observed. The number of univalents, bivalents and trivalents varied in the three combinations but the number of associations did not differ significantly. In the *albiflora* × *ochroleuca* combination as many as 13 trivalents were observed.

In general a negative correlation was observed between univalents and chiasmata per cell. However, chiasma frequency and paired associations displayed a positive correlation.

It is deduced that sufficient similarities existed between one of the *ochroleuca* and the three diploid species genomes; the remainder of the *ochroleuca* genome had homologous chromosomes. Apparently *A. ochroleuca* carried enough cryptic intergenomal homologies which ordinarily remained unexposed. In the hemizygous state however, as in the F_1's, there was intergenomal pairing. In an attempt to resolve the conflict between homology and bivalent pairing in the species, a diploidizing genetic mechanism is envisaged. Alternatively an acute propensity to preferential pairing caused bivalent formation. Such a system or systems caused meiotic isolation of various genomes and instituted normal fertility. Furthermore, the segmental allotetraploid nature of *A. ochroleuca* is concluded. The cytogenetic relationship between *mexicana* and *ochroleuca* is appraised.

Bivalency in a polyploid species had always been attributed to amphiploidy until the genotypic suppression of multivalent formation in bread wheat was demonstrated by Riley and Chapman (1958). It came to be appreciated that bivalent formation could be encountered in any of the four types of polyploids even though the presence of multivalents indicated auto- or segmental allopolyploidy. Since then, bivalent forming polyploids have been interpreted with great caution. Tetraploid *A. ochroleuca*, like bread wheat, is bivalent forming; presumably their genetic architecture may be more complex than is suggested by the meiotic behaviour.

Several diploid species are known in the genus *Argemone*. Some will, presumably, have been key species in the evolution of the polyploid form. Ownbey (1958) suggested that *A. mexicana* had a role in the evolution of *A. ochroleuca* through autopolyploidy. Venkatesh (1960) assumed the alloploid nature of *A. ochroleuca*.

Our main objective is to verify these inferences. A series of triploid hybrids involving *ochroleuca* and some of the diploid species has been raised. A detailed analysis of the nature and extent of chromosome pairing in these inter-specific hybrids has been carried out with the aim of producing valuable evidence on the genome relationships of different taxa.

Material and Methods

Three diploid 2n = 28: *A. mexicana* L., *A. subfusiformis* ssp. *subfusiformis* Ownb., *A. albiflora* Hornem. subsp. *texana* Ownb. and one tetraploid, 2n = 56: *A. ochroleuca* ssp. *ochroleuca* Sweet species were used in the present studies. Flower buds were emasculated at a young stage and subsequently crosspollinated as desired. As many as 20 flowers per species were emasculated.

To study meiosis, anthers were fixed in Carnoy (1:3:6) and stained in 1% aceto-carmine.

Observations

The morphology and cytology in the 3 interspecific triploid hybrids are described briefly. Fig. 1 shows young floral buds in the species and their hybrids. Fig. 2 displays mature capsules in the different species while Fig. 3 shows capsules of the hybrids. Fig.3C is interesting because it was derived from the cross *ochroleuca* × *subfusiformis* (4x). The capsule is uniform, well inflated and apparently full of seeds.

1. *A. albiflora* × *A. ochroleuca*

Seeds obtained after using *ochroleuca* as male parent only germinated. The hybrids manifested heterosis and were intermediate type (Fig. 1).

Chromosome pairing at Metaphase I was analysed and detailed data are given in Table 1.

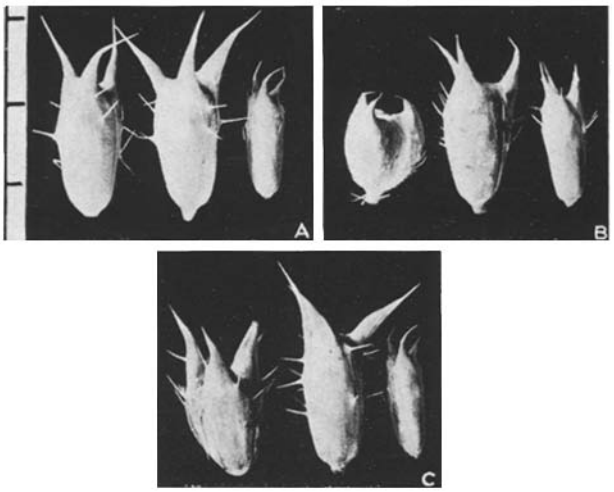

Fig. 1. A—C, Flower buds in *Argemone* species and hybrids. Left to right: A: *subfusiformis*; *Hybrid*; *ochroleuca*; B: *albiflora*; *Hybrid*; *ochroleuca*; C: *mexicana*; *Hybrid*; *ochroleuca*

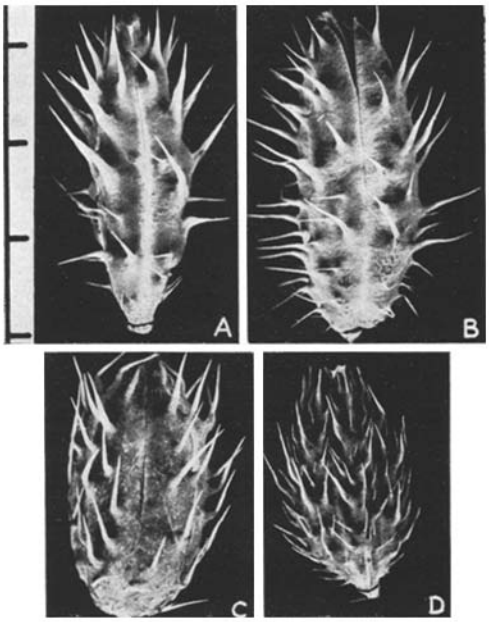

Fig. 2. A—D, Mature capsules in *Argemone* species. A: *subfusiformis*; B: *ochroleuca*; C: *mexicana*; D: *albiflora*

The mean chromosome pairing was 5.87_{III}, 8.71_{II}, 6.97_{I}.

On average 16.6% of chromosomes remained unpaired and the number of univalents ranged from 1—10. One cell had as many as 20 univalents. Total number of associations varied from 11 to 17 per cell. The mean number of bivalents per cell was 8.6 (range 1—15); of these, 33.7% had two and 66.3% had one chiasmata per bivalent. In addition heteromorphic bivalents (1—4 per cell) were also observed. Fig. 4A is a Metaphase I.

The mean number of multivalents per cell was 5.87 and 41.3% of chromosomes associated as multivalents (trivalents) (0—13) were observed. The majority of the trivalents (66.4%) were 'V' shaped. The recorded mean of chiasmata per cell was 23.6 and their number ranged from 13—28 (Table 1).

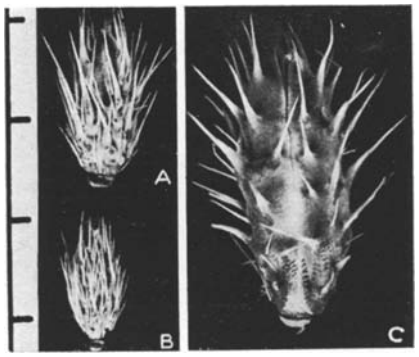

Fig. 3. A—C Mature capsules of *Argemone* triploid hybrids. A: *mexicana* × *ochroleuca*; B: *albiflora* × *ochroleuca*; C: *ochroleuca* × *subfusiformis* (4 x). Figs. 1—3. The scale on left side is in centimetres

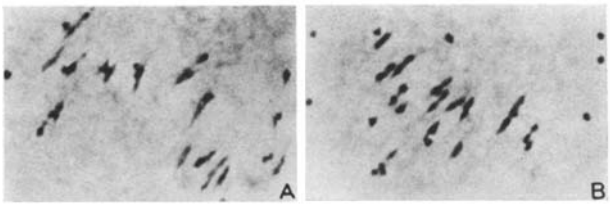

Fig. 4. A—B, Meiotic stages in some *Argemone* sp. hybrids × 1250.
A: *albiflora* × *ochroleuca*. Note trivalents, a few univalent and bivalents at Metaphase-I; B: *subfusiformis* × *ochroleuca*. $14_{II} + 14_{I}$ at Metaphase-I

The distribution of chromosomes at Anaphase I was irregular. An analysis of 30 cells is given in Table 2. The chromosome number at the poles varied from 18—24. Moreover, lagging chromosomes (0—6) and precociously dividing chromosomes were also observed at this stage. About 12% of cells showed 1—2 bridges with or without fragments. Sometimes chromosomes underwent precocious disjunction. It is of particular interest that micronuclei were not observed either at Telophase I or Telophase II.

2. *A. mexicana* × *A. ochroleuca*

Seeds were obtained in the reciprocal crosses. In the cross involving *ochroleuca* × *mexicana*, germination was very poor and the few seedlings obtained after germination did not survive flower. Only in the *mexicana* × *ochroleuca* cross was seed germination high and seedling mortality comparatively low. The hybrids reflected hybrid vigour (Fig. 1C). On the whole they were intermediate in almost all features. The colour of the petals was light yellow and the stigmatic lobes were spreading.

The chromosome pairing relationship was studied in the PMCs of natural as well as synthetic F_1 hybrids. Both had variable chromosome pairing, having con-

Table 1. *Cytological analysis (Metaphase I) of the species and hybrids*

Combination	n		I	II	Ring	Rod	III	IV	Xta/cell	cV
albiflora × *ochroleuca*	50	$\bar{X}$	6.97	8.71	3.05	5.66	5.87	—	23.6	14.7
		R	1—10	1—15	0—9	1—15	0—13		13—28	
		%	16.6	41.9	—	—	41.3	—	—	—
mexicana × *ochroleuca*	50	$\bar{X}$	9.75	11.97	7.3	4.67	2.6	.125	25.25	11.8
		R	6—14	8—15	3—11	0—11	0—5	0—2	16—31	
		%	23.3	57.02	—	—	18.6	1.08	—	—
subfusiformis × *ochroleuca*	50	$\bar{X}$	9.6	11.6	6.3	5.3	3.07	—	24.20	11.1
		R	7—15	9—14	2—10	2—8	1—5	—	—	
		%	22.8	55.2	—	—	—	—	—	—
ochroleuca × *subfusiformis*	50	$\bar{X}$	12	12.6	7.6	5.0	7.31	—	23.5	9.1
		R	8—18	9—15	5—10	2—8	0—5	—	—	—
		%	28.6	46.0	—	—	60	—	—	—
ochroleuca × *subfusiformis* (4 x)	50	$\bar{X}$	3.78	21.4	9.67	11.73	.32	2.13	38.7	7.3
		R	0—8	18—27	8—16	6—17	0—3	0—5	36—44	—
		%	6.8	76.4	—	—	1.6	15.2	—	—
albiflora	50	$\bar{X}$	—	14	7.5	6.5	—	—	21.5	10.01
		R	—	—	6.11	3—8	—	—	18—25	—
mexicana	50	$\bar{X}$	—	14	9.2	4.8	—	—	23.25	5.5
		R	—	—	6—12	2—8	—	—	20—26	—
subfusiformis	50	$\bar{X}$	—	14	10.9	3.08	—	—	24.08	6.7
		R	—	—	7—13	1—7	—	—	21—27	—
ochroleuca	50	$\bar{X}$	—	28	22.15	5.85	—	—	50.05	7.8
		R	—	—	13—28	0—12	—	—	38—56	—

n = number of analyzed cells

Table 2. *Anaphase I distribution in the hybrids*

Distribution	24 — 18	21 — 21	20 — 22	19 — 23
Number of cells	3	13	5	9 = 30

figurations ranging from univalents to quadrivalents in varying proportions. About 76.7% of the chromosomes were associated while the rest were unpaired. Univalents ranged from 6—14. In the pollen mother cells with high multivalent frequency, some exhibited secondary associations. The mean number of bivalents per cell was 11.97 (range 8—15) and 60.9% and 2 chiasmata. Occasionally 1—3 heteromorphic bivalents were also observed. Sometimes bivalents had one arm very small. On average 2.6 trivalents were observed and most of them were 'V' shaped.

The associations per cell varied from 12—27 though 35% cells had 15 associations. The mean chiasmata frequency per cell was recorded as 25.25 ± 2.98.

Normal anaphasic distribution was observed in 32 out of 60 analysed cells (=53%) but in the rest Anaphase I was typified by variable chromosome distribution with up to 18 chromosomes lagging between the two poles. Chromatid bridges were not observed.

Sometimes these laggards divided precociously and even exhibited pronounced neocentric activity. The chromosomes at the poles varied from 11—21. Telophase II was also studied and no laggards were observed.

The capsules were shrunken and devoid of seeds (Fig. 3). Out of 100 capsules 6 seeds were collected.

It is of particular interest that in the F_2 two plants were obtained, one with 2 n = 56 and the other with 2 n = 49. The two plants exhibited divergent cytological behaviour. In the plant with 2 n = 49, the mean chromosome pairing in 50 analysed cells was $22_{II} + 5_I$ and chiasmata frequency was 32.39 ± 3.34. The Anaphase I distribution was irregular.

In the plant with 2 n = 56, quadrivalents and occasionally trivalents were encountered. The mean chromosome pairing of 50 analysed cells was $0.428_{IV} + +1.043_{III} + 25.75_{II} + 2.75_I$. The Anaphase I distribution was irregular in some cells with as many as 5—8 chromosomes lagging on the equator.

3. *A. subfusiformis* × *A. ochroleuca*

Using *subfusiformis* as female the F_1 was fast-growing, tall and intermediate in almost every character (Fig. 1A). The data are presented in Table 3.

The meiotic behaviour was essentially similar to that described in the preceding hybrid. Data on chromosome pairing at Metaphase I in this hybrid are given in Table 1. Meiosis was irregular, univalents and multivalents as well as bivalents being observed (Fig. 4B). The mean chiasma frequency was recorded as 24.2.

About 55.2% of chromosomes formed bivalents. The number of bivalents per cell was 11.6 and they

Table 3. *Comparison of morphological characters of species and hybrids*

Characters		*subfusiformis*	F_1	*ochroleuca*
Number of spines/internode	$\bar{X}$	4	5	4
	R	0–6	4–6	3–5
Length × width of leaf	$\bar{X}$	17.5 × 5.9	13 × 14.5	16.6 × 5.8
Number of stomata/unit area (sq. mm)	$\bar{X}$	381	134	139
Length × width of floral bud (cms.)	$\bar{X}$	1.3 × 0.6	1.2 × 0.6	1.4 × 0.7
	R	1–1.4 × 5–8	1.3–1.7 × 0.7–0.8	1.2–1.5 × 0.6–0.8
Diameter of flower	$\bar{X}$	4.5	4.2	4
	R	4–5.5	3.5–4.0	3.0–4.5
Colour of petals		Light yellow (+++)	Light yellow (++++)	Light yellow (++)
Length × width of capsule (cm.)	$\bar{X}$	3.5 × 1.4	–	3.1 × 1.5
Number of spines		65	–	75

were of both ring and rod types. From one to four bivalents were heteromorphic. Nearly 22% of the chromosomes constituted trivalents, and a majority (71.6%) of the trivalents were 'V' shaped.

The number of associations per cell varied from 13–17 though only one cell had as few as 13. About 47% of cells had 15 associations per cell.

Anaphase I was irregular with 0–12 lagging chromosomes. Even then 29 out of 60 analysed cells (=50%) had normal disjunction of chromosomes.

4. *A. ochroleuca* × *A. subfusiformis* (*unreduced gamete*)

One plant in the cross involving *ochroleuca* × *subfusiformis* was vigorous with capsules full of seeds (Fig. 3C). Cytological examination of this individual revealed 2 n = 56. The mean chromosome pairing at Metaphase I was $2.13_{IV} + 0.32_{III} + 21.4_{II} + 3.78_{I}$. About 15% of the chromosomes formed quadrivalents and these ranged from 0–5. Most of the quadrivalents were N-shaped. The trivalent frequency was low and they never exceeded 3 per cell. As many as 76.4% of the chromosomes paired as bivalents. Nearly 28 out of 60 cells (= 47%) analysed at Anaphase I displayed irregular distribution or lagging.

All the diploid species formed 14 bivalents at Metaphase I (Table 1) while the tetraploid *ochroleuca* had 28 bivalents. The mean chiasma frequency and other meiotic data are given in Table 1.

The triploid hybrids belonging to three separate cross combinations were analysed statistically. Fig. 5 indicates the correlation between the various components in *albiflora* × *ochroleuca*. When chiasmata per cell and univalent frequency were plotted against each other a negative correlation was observed. When paired associations per cell were plotted against chiasmata per cell a positive correlation was obtained. Clearly the adjustment of chromosome association frequency is a result of change in chiasma frequency. It is now well accepted that chiasma frequency is genotypically controlled. These figures also provide additional evidence for the chromosomal differentiation between the three categories of hybrids. At the same time it is demonstrated that there is a greater degree of non-consistency within the hybrids.

Further inspection of the data for the three hybrids reveals that their pairing behaviour was almost identical as shown by the mean frequencies of univalents, bivalents and even trivalents. A similar inference could be made from chiasma frequency and ring bivalents. On comparing the latter two characters a meaningful conclusion may be drawn: the differences between *albiflora* and *ochroleuca* were significant while no statistically significant difference could be observed between *albiflora* × *ochroleuca* and *subfusiformis* × *ochroleuca* and *mexicana* × *ochroleuca*.

The number of univalents ranged from 1–18 in the three hybrids. An analysis of variance showed a highly significant P-ratio for the hybrid mean of *albiflora* × *ochroleuca* and *mexicana* × *ochroleuca* (F = 2.5**; P = 0.01), *subfusiformis* × *ochroleuca* (F = 3.5**). However, between *mexicana* × *ochroleuca* and *subfusiformis* × *ochroleuca* the F value was 1.2 i.e. non-significant.

A similar comparison for the mean value of bivalents revealed F = 4.1*** for *albiflora* × *ochroleuca*

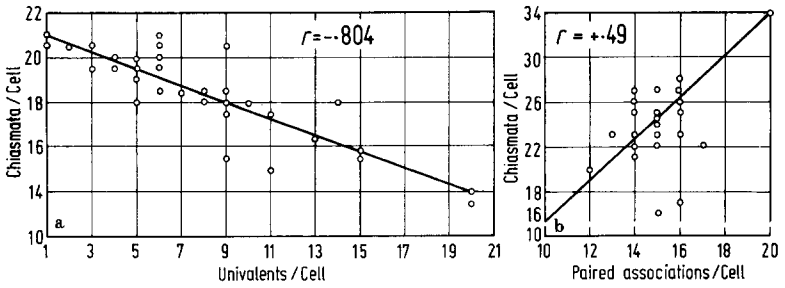

Fig. 5. a) Negative correlation between the mean chiasmata/cell and the number of univalents; b) Positive correlation between the chiasmata/cell and the number of paired associations, in *albiflora* × *ochroleuca*

versus *mexicana* × *ochroleuca*. The value of F was 3.2** for *albiflora* × *ochroleuca* versus *subfusiformis* × *ochroleuca*. However, *mexicana* × *ochroleuca* versus *subfusiformis* × *ochroleuca* had a non-significant value (F = 1.17).

It is interesting that the number of associated chromosomes in the 3 hybrids did not differ significantly.

The relationships between the hybrids with regard to the mean values of chiasma frequency and ring bivalent frequency indicated a low frequency of ring bivalents in *albiflora* × *ochroleuca* (3.05 per cell). However, there was an apparent correlation between the two meiotic metrics. Thus, there is some indication that genetic control for these two meiotic characters could not be differentiated independently.

The mean frequency of trivalents per cell was 5.87 in *albiflora* × *ochroleuca* and 2.6 and 3.7 in *mexicana* × × *ochroleuca* and *subfusiformis* × *ochroleuca* hybrids, respectively. The maximum number observed was 13, in *albiflora* × *ochroleuca*, and the lowest 0—1, in almost all the combinations. It is suggested that the trivalents represent a case of intergenomic pairing.

Discussion

Meiotic data for the two combinations (*mexicana* × *ochroleuca*; *subfusiformis* × *ochroleuca*) showed that their pairing behaviour was almost identical in mean frequencies of univalents, bivalents and trivalents.

a) *mexicana* × *ochroleuca*: only 23.3% of the chromosomes remained unpaired and about 57% formed bivalents which ranged from 8—15; of these, 7.3 were ring and 4.6 were rod bivalents. Fourteen chromosomes which formed ring bivalents could pair in both arms indicating a high degree of homology. The mean frequency of trivalents was 2.6 per cell and the maximum number observed was 5, while infrequently IV associations were also found. From these data one may conclude that the bivalents were formed by pairing of two genomes and the trivalents must have resulted from the pairing of the third genome chromosomes with the bivalents. Clearly, sufficient homology existed between some of the *mexicana* chromosomes on the one hand and the two *ochroleuca* genomes on the other. Since the maximum number of bivalents and trivalents observed was never a multiple of 7, there appears to be a strong case for partial homology of some of the chromosomes of the *mexicana* and *ochroleuca* genomes. In addition, if we suppose that the rest of the *ochroleuca* genome chromosomes were partially homologous among themselves, the origin of trivalents and quadrivalents could be explained. This would indicate the existence of complex basic number for the genus. Incidentally Suguira (1940) suggested 4 + 3 as the original basic number of the genus *Argemone*.

b) *subfusiformis* × *ochroleuca*: The mean chromosome pairing data for this hybrid revealed almost identical pairing with the previously discussed combinations. It is, therefore, tentatively suggested that the two species are probably structurally sufficiently identical.

c) *albiflora* × *ochroleuca*: Data on the pairing behaviour in this combination revealed that chromosome pairing was almost complete compared with the previous two combinations. Here, about 41% of the chromosomes were associated into trivalents with a maximum of 13 in some cells. In some cells as few as one univalent was present. Thus not only did the mean frequencies of configurations differ from those of the previous two combinations, but also pairing was complete.

From all these data we are tempted to suggest that *albiflora* is structurally different from the other two diploid species (*mexicana*, *subfusiformis*) and that it is more similar to the tetraploid *ochroleuca*. Alternatively, it may be that the *ochroleuca* genomes possess a genetic system or systems which exert a differential dominant influence on pairing behaviour between the three species. Possibly such a system or systems controlled the frequency of associations by regulating the probability of chiasmata formation between the necessary series of homologous segments. Malik and Grover (in press) have demonstrated structural differentiation between *albiflora* and *mexicana*.

The origin of the hexaploid hybrid may be explained by assuming the fusion of 2 n *subfusiformis* and reduced *ochroleuca* gametes. An unreduced gamete in *subfusiformis* must have been the causative factor. Indeed such gametes were observed in the off-season plants. Perhaps extreme climatic and ecological conditions, e.g. high summer temperature, among other factors exerted a strong influence upon the meiotic system. In fact, temperature variations have been shown to cause the breakdown of norms of meiosis (Malik and Grover, 1968).

The precise cytogenetic structure of *ochroleuca* can now be deduced on the basis of interspecific hybrids as well as its polyhaploid. It is pertinent to record that Malik and Mary (1973) came across one polyhaploid of *ochroleuca* (2 n = 28) which displayed the formation of 14 bivalents at Metaphase I. Most of the cells had 1—4 heteromorphic bivalents. The pollen fertility was low and there was no seed set. This situation is interesting when compared with that of the species where as many as 28 bivalents were observed and pollen fertility was high.

From the meiotic analysis of *albiflora* × *ochroleuca* hybrids one might interpret them as autotriploids since as many as 13 trivalents were observed in some of the cells. In fact, the situation compared with other instances of high numbers of trivalents in the autotriploids. From this, one would expect autoploid behaviour of *ochroleuca*, but this was not the case.

The incongruities in the cytogenetic behaviour of the *ochroleuca* species and 3x hybrids may be explained by the assumption that *ochroleuca* is a case of segmental allotetraploid and two genomes entering into *ochroleuca* had chromosomal structural similarities. It is also very probable that the *Argemone* species have had a monophyletic origin and many still retain considerable structural homologies. There is also a strong possibility that in *ochroleuca* there is genesis of bivalent pairing, and that this system only operated in the homozygous state. This is supported by our studies of the hexaploid (NH_5) and amphiploids.

A. mexicana and *A. ochroleuca* have always been considered closely related. In fact the latter was taken to be a white-flowered form of the former and this partly explains its exclusion from several Indian floras (Hooker, 1872; Duthie 1903, 1929). Ownbey (1958) confirmed *A. ochroleuca* as a distinct species on grounds of morphology, ecology, geography and chromosome number.

Ownbey (1958, p. 9) suggested that *mexicana, ochroleuca, aeana* and *superba* formed one alliance. Further, Ownbey (1958, p. 10) postulated that *A. ochroleuca* might have arisen as an autotetraploid of *mexicana*, because they were very similar in general characteristics and reproductive behaviour. Added to this, plants of both species were highly self-compatible and both species exhibited a high degree of crossability with other species.

From chromosome pairing in the pollen mother cells of the F_1 hybrids, it appears that *ochroleuca* genomes are similar to those of *mexicana*. The available data for the *ochroleuca* × *subfusiformis* and *ochroleuca* × *albiflora* hybrids permit some useful conclusions as to the parallel nature of the genomes in the 3 species, *subfusiformis, mexicana* and *albiflora*. Moreover, the polyhaploid of *A. ochroleuca* (Malik and Mary, 1973) provides sufficient evidence against the proposal of *mexicana* as one of the putative parents of *ochroleuca*. Furthermore, autotetraploids of *mexicana* were grossly different from the *ochroleuca* plants.

The collective evidence, based on comparative chromosome pairing, polyhaploid and induced ploidy, shows that it is unlikely that autopolyploidy was involved in the origin of the tetraploid *ochroleuca* form. Ownbey (1958) may, therefore, be wrong in supposing that *ochroleuca* represents an autopolyploid of *mexicana*. His evidence was based on morphological similarities, ease of crossability etc. The discovery of *A. subfusiformis* produces a new contender; *subfusiformis* is more like *ochroleuca* than *mexicana* though both the species (i.e. *subfusiformis, mexicana*) are highly interfertile. Regardless of the origin of the tetraploid *ochroleuca*, our conclusion concerning the inability of gene flow between *ochroleuca* and the other two species substantiates the findings of Ownbey (1958). The abnormal meiotic behaviour of the 3x hybrids makes further introgression impossible.

Subfusiformis and *ochroleuca* are very similar in the size and shape of the floral bud, size and shape of the stigma and length of style; the number of stamens and flower colour are also nearly the same. Incidentally, *subfusiformis* was included under *A. mexicana* variety *ochroleuca* until recently.

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Received September 27, 1972
Communicated by F. Mechelke

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