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STRUCTURE AND BEHAVIOR OF CHROMOSOMES IN DIFFERENT VARIETIES OF *ASTER AMELLUS* L. AND THEIR MODE OF ORIGIN

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INTRODUCTION

The species of the genus *Aster* L. occur both in the tropic and temperate parts of the world. Many of them are cultivated as ornamentals, specially for their attractive flowers. *A. amellus* L. is cultivated in the plains of India during the winter season.

An analysis of the literature on their cytology shows that the species of *Aster* can be classed into three distinct categories with $x = 5$, 8 and 9 chromosomes respectively (*vide* DARLINGTON and WYLIE 1955). Majority of the species studied so far belong to the class showing $x = 9$ chromosomes. One species, viz. *A. adscendens* (J. CLAUSEN *et al.* 1940) has upto now been found to have $x = 8$ chromosomes, whereas the rest are characterized by chromosome number $x = 5$. Both polyploid and aneuploid forms have been found in the species of *Aster* as well. It is apparent from the literature, therefore, that numerical differences of chromosomes have played at least some role in the differentiation of broad taxonomic unit under this genus.

A. amellus, which is cultivated as garden plants in the plains of India, is characterized by $2n = 18$ chromosomes. Garden forms having high aneuploid numbers such as 66, 76 have been reported in *A. amellus* (ANNEN 1945). In spite of the fact that a large number of garden forms of *A. amellus* are in existence only two such high aneuploids, other than diploids, has so far been reported. It is therefore evident that numerical differences have played no significant role in the evolution of garden forms of this species.

In recent years, considerable works have been done indicating the importance of structural alterations of chromosomes in the evolution of the strains of the same species (BOSE 1956, BHADURI and GHOSH 1954, SHARMA 1956, and *vide* SHARMA and SHARMA 1959). Several cases have been reported where each strain can be identified on the basis of its chromosome characteristics. The importance of structural alterations can be studied specially in cases where the varieties are characterized by a common chromosome number. In view of this, varieties of *A. amellus* provide good material for such study. In addition to having common chromosome number in all its varieties, an added advantage is the low number

and long size of chromosomes. Taking all these facts into account, the present work on six varieties of *A. amellus* has been under-taken to work out the role of structural alteration, if any, of chromosomes in the evolution of its garden forms.

MATERIALS AND METHODS

Materials. — Six different horticultural varieties of *Aster* were studied during the present investigation. The varieties differ from each other in the coloration of flowers. They are:

- i) *Aster amellus* L. var. with white flowers.
- ii) *A. amellus* L. var. with dark blue flowers.
- iii) *A. amellus* L. var. with mauve flowers.
- iv) *A. amellus* L. var. with blue flowers.
- v) *A. amellus* L. var. with lavender flowers.
- vi) *A. amellus* L. var. with pink flowers.

The seeds of all the varieties were obtained from Sutton and Sons, Calcutta.

For root tips, the seeds were sown in earthenware pots in a mixture of loose sand, manure and clay, and for flowers a duplicate set was planted in the experimental plot. The plants flowered in winter.

Methods. — Somatic chromosomal studies were made from temporary squashes as greater clarification of karyotype was noted than with permanent preparations. Of the different pretreating chemicals tried, saturated solution of Aesculin for two hours at temperature of 14°-16° C gave the best result (SHARMA and SARKAR 1955). The root tips were then heated in a mixture of 2% aceto-orcein and (N)HCl (9:1) for a few seconds and kept in the stain for an hour. They were then squashed in 1% aceto-orcein solution. The slides were sealed and observed under the microscope.

For the study of meiotic chromosomes, flower buds were both smeared in 1% aceto-carmin for temporary preparations and fixed in Navaschin's fluid A and B (1:1) after treatment in Carnoy's fluid. Sections were cut at a thickness of 14 μ and stained following the normal schedule of Newton's crystal violet.

Figures were drawn at a table magnification of approximately \times 1900 using compensating eye-piece of \times 12,5 and a 1.3 apochromatic objective with a condenser of 1.3 N.A.

The chromosomes with secondary constrictions have been drawn in outline in the drawings.

OBSERVATIONS

All the six different varieties cytologically examined reveal constant chromosome number, being $2n = 18$. In general, the chromosomes are medium to short in size. There is a good deal of similarity in the morphology of the chromo-

somes between the different varieties although they may differ in their minute details of the karyotype. Somatic chromosomes have been studied in all the varieties excepting the « mauve » one, where the number has been determined only from the meiotic counts. Meiosis has also been studied in three other varieties. The number of chromosomes with secondary constrictions varies from two to four. The largest pair of chromosomes are always characterized by secondary constrictions, confirming HUZIWARA'S (1957) observation on Japanese Asters. Nuclei showing variant chromosome numbers have not been observed.

The description of the principal morphologically distinguished types is given below:

Type A - Comparatively long chromosomes, longest in the set, each provided with two constrictions, primary and secondary. One is nearly median to median in position and the other subterminal on the distal end of one arm.

Type B - Comparatively long to medium sized chromosomes having median to nearly median primary constrictions.

Type C - Comparatively long chromosomes, each having a nearly subterminal primary constriction and a satellite at the distal end of the long arm.

Type D - Medium-sized chromosomes with nearly submedian to submedian primary constrictions.

Type E - Comparatively medium-sized chromosomes each having two constrictions, primary and secondary, one median in position and the other subterminal at the distal end of one arm.

Type F - Comparatively short chromosomes with submedian to nearly submedian primary constrictions.

Type G - Short chromosomes with median to nearly median primary constrictions.

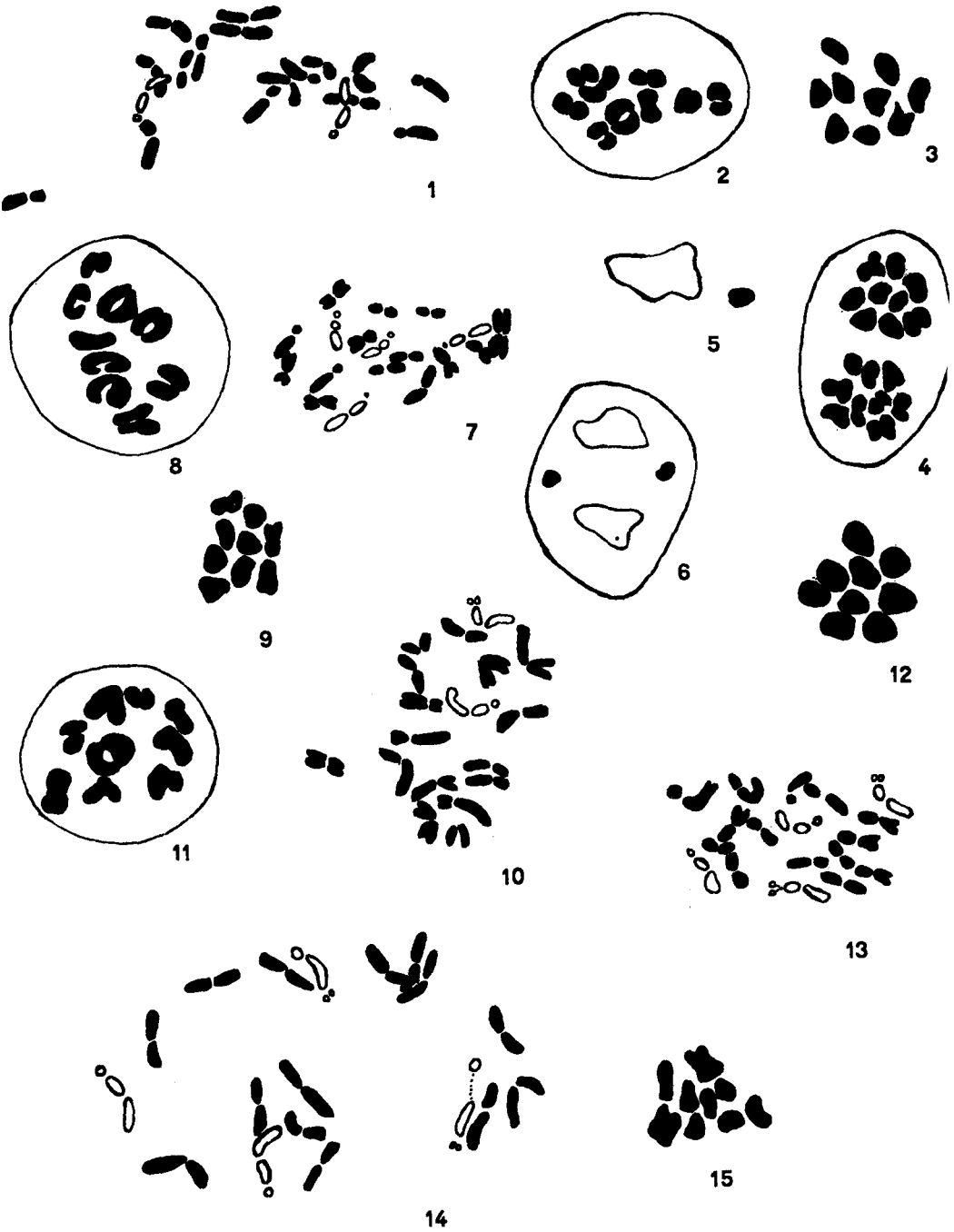
1. « *Aster amellus* » var. with white flowers

$$(2n = 18 = A_2 + B_6 + D_2 + F_6 + G_2)$$

The normal somatic set of the variety shows eighteen chromosomes (Fig. 1). Size difference is seen within the complement, ranging from 2.5 μ to 4.8 μ . The chromosomes are graded in size, one type merging into the other. The largest pair is satellited.

The karyotype includes one pair of A, three pairs of B, one pair of D, three pairs of F and a pair of G chromosomes (Fig. 1a).

During meiosis, nine clear bivalents are found both in diakinesis and metaphase I (Figs. 2, 3) respectively. Metaphase II also shows nine chromosomes in each pole (Fig. 4). Irregularities in division, including early separation and lagging (Figs. 5, 6), are also observed.



2. « *Aster amellus* » var. with dark blue flowers

$$(2n = 18 = A_2 + B_2 + E_2 + F_8 + G_4)$$

Eighteen chromosomes are present in the normal somatic cells of this variety (Fig. 7).

Size difference is present, but not very marked. The chromosomes form a graded series, ranging from $1,8 \mu$ to $4,5 \mu$. Secondary constrictions are present on two pairs of chromosomes.

The complement consists of one pair of A, a pair of B, one pair of E, four pairs of F and two pairs of G chromosomes (Fig. 7a).

3. « *Aster amellus* » var. with mauve flowers

$$(n = 9)$$

The somatic studies in this variety could not be done, as the seeds brought from nursery did not germinate.

Meiotic studies reveal nine clear bivalents in both diakinesis and metaphase I (Figs. 8, 9).

4. « *Aster amellus* » var. with blue flowers

$$(2n = 18 = A_2 + B_6 + D_2 + F_6 + G_2)$$

Eighteen chromosomes are found in the normal somatic cells (Fig. 10). Size difference though present is not very marked. The size varies from $2,8 \mu$ to $4,8 \mu$. Only the largest pair of chromosomes bears secondary constrictions.

The detailed morphological studies show that there are one pair of A, three pairs of B, one pair of D, three pairs of F and a pair of G chromosomes (Fig. 10a).

In meiotic studies, nine clear bivalents are found both in diakinesis and metaphase I (Figs. 11, 12).

5. « *Aster amellus* » var. with lavender flowers

$$(2n = 18 = A_2 + B_4 + D_2 + E_2 + F_2 + G_6)$$

The normal somatic cells contain eighteen chromosomes (Fig. 13). The size

Figs. 1-6. — *Aster amellus* var. "white", showing $2n=18$ chromosomes (Fig. 1), diakinesis and metaphase I with 9 bivalents (Figs. 2, 3), metaphase II with 9 chromosomes (Fig. 4), early separation and lagging (Figs. 5, 6).

Fig. 7. — *A. amellus* var. "dark blue", showing $2n=18$ chromosomes.

Figs. 8, 9. — *A. amellus* var. "mauve", showing 9 bivalents in diakinesis and metaphase I respectively.

Figs. 10-12. — *A. amellus* var. "blue", showing $2n=18$ chromosomes (Fig. 10), diakinesis and metaphase I with 9 bivalents (Figs. 11, 12).

Fig. 13. — *A. amellus* var. "lavender", showing $2n=18$ chromosomes.

Figs. 14, 15. — *A. amellus* var. "pink", showing $2n=18$ chromosomes (Fig. 14), and 9 bivalents in metaphase I (Fig. 15).

of the chromosomes varies from 2.0μ to 4.3μ . Two pairs of chromosomes are characterized by secondary constrictions.

The complement consists of a pair of A, two pairs of B, a pair of D, a pair of E, one pair of F and three pairs of G chromosomes (Fig. 13a).

6. « *Aster amellus* » var. with pink flowers
 $(2n = 18 = A_2 + B_{1,4} + C_2)$

The normal somatic cells show $2n = 18$ chromosomes (Fig. 14). The chromosomes of this variety are in general larger than those of the others. The size ranges from 4.0μ to 5.3μ . The chromosomes form a uniformly graded series.

The karyotype includes one pair of A, seven pairs of B and one pair of C chromosomes. The C-type chromosomes observed here are not present in any other variety during the present report (Fig. 14a).

In meiosis nine clear bivalents are found in metaphase I (Fig. 15).

DISCUSSION

Importance of polyploidy and aneuploidy in the evolution of the species of « Aster ».

In the introductory part it has been pointed out that in the genus *Aster*, species having multiples of three different chromosome numbers, viz. five, eight and nine, have been reported. It is clear therefore that aneuploidy has been effective at least in delimiting to certain extent the species of the genus *Aster*. In spite of the fact that a number of aneuploid biotypes have been reported in several species, there is a distinct line of demarcation between species representing multiples of the three chromosome numbers. For example, in *A. frikartii* ($2n = 54$) individuals have been found with $2n = 52$ chromosomes (ANNEN 1945). But in none of the individuals either the multiples of eight or of five has been observed. This fact clearly indicates that though aneuploidy is in existence even at an intra-specific level, the demarcation between the three broad aneuploid series is rigid.

In addition to aneuploidy, significance of polyploidy in evolution can not at all be ignored. Clear polyploid species with $2n = 54$ chromosomes, etc. has been observed. However, as a large number of species have been found with the same polyploid chromosome number, the importance of this process in evolution is not very significant. But even then their minor role too, can not be totally set aside, as the very fact that the species exist with polyploid number along with diploid ones is an evidence of its association with evolution.

The role of structural alteration of chromosomes in speciation.

The predominant factor controlling the process of speciation in *Aster* seems to be the structural alterations of chromosomes. In spite of the existence of polyploidy and aneuploidy a large number of species show a common chromo-



Fig. 16. — Idiograms of the different varieties of *Aster amellus* L. - 1a. var. "white"; 7a. var. "dark blue"; 10a. var. "blue"; 13a. var. "lavender"; 14a. var. "pink".
 Fig. 17 (On the right). — Histogram showing the chromatid length in the haploid complement of the different varieties of *Aster amellus* L.

some number. Their affinities with each other in having karyotype similarity in gross morphology are undeniable. But a study of the idiogram shows that in *A. amellus* alone, out of the six varieties studied so far, at least three can be identified on the basis of their karyotype (vide Idiogram in Fig. 16). In the varieties, blue and white the chromosomes could not be distinguished from each other, and both are found to possess one pair of long chromosomes with more than one constriction. Presence of this pair is universal for all species of *Aster* so far studied (HUZIWARA 1957). In the variety pink, in addition to this A pair of chromosomes with slight modification, another chromosome type is present, i.e. C-type, in which two constrictions are present at two ends of the chromosome. The lavender and dark blue varieties, however, show identical chromosome morphology with two pairs of chromosomes, one long and one short, with more than one constrictions. The presence of at least three distin-

guishable karyotype within the five varieties of *A. amellus* shows the great extent to which the karyotype alteration has affected the origin of new forms in this genus. In cases where two varieties look identical in chromosome morphology, the importance of minute imperceptible genic changes in evolution becomes obvious.

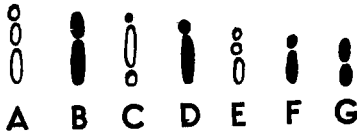


Fig. 18. — Common chromosome types in different vars. *Aster amellus* L.

TABLE I
Chromosome analysis in « Aster amellus » L.

Varieties	2n	No. of chromosomes with sec. constrictions	Total amount of chromatin length in haploid complement	Difference in the types of chromosomes
<i>A. amellus</i> var. white	18	2	37.5 μ	$A_2 + B_6 + D_2 + F_6 + G_2$
<i>A. amellus</i> var. dark blue	18	4	29.0 μ	$A_2 + B_2 + E_2 + F_8 + G_4$
<i>A. amellus</i> var. blue	18	2	39.0 μ	$A_2 + B_6 + D_2 + F_6 + G_2$
<i>A. amellus</i> var. lavender	18	4	32.4 μ	$A_2 + B_4 + D_2 + E_2 + F_2 + G_6$
<i>A. amellus</i> var. pink	18	4	45.5 μ	$A_2 + B_{14} + C_2$

Meiotic behaviour and its significance.

Out of the six varieties investigated, meiotic analysis could be performed in four of them. Regular formation of nine bivalents is characteristic for all the varieties. Apparently this seems striking as structural alteration has been visualized to have affected their evolution, which in turn brings about irregularities in chromosome behaviour. But this regular behaviour can easily be explained on the basis of homozygosity for changes attained by these varieties. Such preservation of homozygosity is quite expected in view of the wide cultivation of *Aster amellus*, whereby by judicial selection heterozygous forms have been elimi-

nated. Crossing between different varieties may lead to significant chromosome behaviour in meiosis, making possible the identification of chromosome ends which had undergone segmental interchanges.

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SUMMARY

Detailed cytological study has been performed on six different horticultural varieties of *Aster amellus*, L. All the individuals have been found to contain $2n=18$ chromosomes.

Karyotype analysis has been done in five varieties, while in one variety, « mauve », the number has been determined from the meiotic count only. On the basis of the minute karyological differences between the different varieties, the role of structural alterations of chromosomes in the origin of the different garden forms has been suggested.

From the present and the previous records, the importance of aneuploidy in the evolution of the different species of *Aster* has also been emphasized.

Meiosis has been studied in four varieties. Regular bivalent formation has been noted in all of them, inspite of the occurrence of structurally altered chromosomes. It has been explained by the fact that these varieties have attained homozygosity for changes during cultivation with the possible elimination of heterozygous forms.

RIASSUNTO

Sono state esaminate citologicamente sei differenti varietà coltivate di *Aster amellus* L. È risultato che tutti gli individui erano caratterizzati da $2n=18$.

Su cinque varietà è stata fatta anche l'analisi del cariotipo, mentre in una varietà,

(“mauve”) il numero dei cromosomi è stato determinato solo su piastre meiotiche. Sulla base delle differenze cariologiche tra le varietà, è stato supposto il probabile ruolo delle alterazioni strutturali dei cromosomi nell'origine delle diverse forme da giardino.

In base ai presenti e a precedenti risultati, viene messa in luce l'importanza dell'aneuploidia nell'evoluzione delle differenti specie di *Aster*.

La meiosi è stata studiata in quattro varietà. In tutte la formazione dei bivalenti è apparsa regolare, nonostante la presenza di cromosomi strutturalmente alterati.