

SUMMARY

1. Cytological investigations have been made on 116 species belonging to 59 genera and 11 tribes of the Compositae. Chromosome determinations made in 35 species are fresh reports, and those in eight others are new counts. Detailed karyotype analysis was done in 50 species.

2. An array of basic numbers ($x=4, 5, 7, 8, 9, 10, 11, 12, 13, 15, 16, 17, 18, 20$) have been found to occur among the members of the family reported here. Of these, $x=9$ was found to be the most frequent.

3. Six of the species exhibited irregular meiosis. In spite of very high pollen sterility, four of them (Eupatorium glandulosum, E. odoratum, Erigeron karvinskianus and Blumea belangeriana) showed appreciable seed set. The other two species (Solidago virga-aurea and Chrysanthemum frutescens) showed high pollen inviability and low seed set.

4. Polyploidy was induced in a diploid ornamental species, Tagetes erecta using colchicine. Detailed cytomorphological studies of the diploid and induced tetraploids were made. The tetraploid plants showed varying numbers of univalents, bivalents, trivalents and quadrivalents at meiosis. Complete bivalent formation was noticed in about 10 per cent of the PMCs of the tetraploid plants. Colchiploids showed about 50 per cent pollen fertility.

5. The induced tetraploids showed increased size of capitulum and decreased plant height both of these being desirable from the

horticultural point of view.

6. Of the 116 species reported here, 44 were polyploids at various levels, tetraploidy being the most frequent. Most of the polyploid species showed normal meiosis and high pollen fertility suggesting allopolyploidy.

7. Two of the tetraploid species (Erigeron karvinskianus and Blumea belangeriana) and one triploid species (Eupatorium glandulosum) showed notable meiotic abnormalities. The latter two showed lack of synaptic pairing suggestive of hybrid origin. In the former one, varying frequencies of univalents, bivalents, trivalents and quadrivalents were seen, suggestive of autopolyploidy or segmental allopolyploidy. One of the hexaploid species (Eupatorium odoratum) showed some degree of meiotic abnormalities consequent on the formation of univalents and trivalents. This taxon could be an auto-allohexaploid.

8. Intraspecific polyploidy was detected in Siegesbeckia orientalis, which occurs in diploid ($n=15$) and tetraploid ($n=30$) cytotypes. Intraspecific aneuploidy was noticed in Coreopsis grandiflora.

9. Accessory chromosomes in PMCs and/or root tip cells were observed in eight species belonging to five genera such as Solidago, Conyza, Chrysanthemum and Launaea (one species each) and Blumea (four species). The Bs in four of them were clearly

smaller in size than the normal chromosomes, and in the others (species of Blumea) they were comparable to the smaller chromosomes of the complement. The Bs of seven of the species were euchromatic, and in the other species (Chrysanthemum frutescens), the Bs were heterochromatic.

10. Cell to cell variation in the number of Bs were noticed in three species. In species of Blumea, the Bs were mostly confined to the shoot tissue.

11. None of the plants with Bs reported here seemed to show any visible unfavourable effects.

12. Basic chromosome constitutions and their evolution in the various tribes represented in the study are briefly considered.

(a) Vernonieae

Of the various basic numbers existing in the tribe ($x=7, 8, 9, 10, 11, 15, 16$ and 17), $x=10$ and 9 show greater preponderance. In this tribe, the $x=10$ constitution is considered to be the earlier evolved condition from which $x=9$ arose by aneuploid reduction. The present karyomorphological data on species of Vernonia support this possibility. The higher basic chromosome constitutions in the tribe, namely $x=17, 16, 15$ etc. are considered to have arisen secondarily, by polyploidy on $x=9$ followed by aneuploidy.

(b) Eupatorieae

Ten basic numbers are known for the tribe ($x=4, 5, 9, 10, 11, 12, 15, 17, 18$ and 19), of which $x=10$ and 17 are more frequent. Various suggestions regarding the original basic constitution of the tribe are considered. The contention postulating $x=10$ and 17 as parallel ancestral lines, evolved from a prototype with $x=5$, appear to be more probable.

(c) Astereae

Basic numbers of this tribe range from $x=2-9$, of which $x=9$ is very predominant. It seems that $x=9$ could have arisen from an ancestral $x=5$ constitution.

(d) Inuleae

A wide array of basic numbers, ranging from $x=3-14$, exist in the tribe, of which $x=10, 9$ and 7 are more frequent. $x=10$ could be the earlier evolved constitution in the tribe, which in turn may have arisen from $x=5$. Other lower constitutions such as $x=9, 8$ etc. must be aneuploid derivations from $x=10$. The occurrence of accessory chromosomes in some of the $x=9$ species of Blumea reported here is shown to support this possibility. Here, the aneuploid reduction from $x=10$ could have been through formation of Bs followed by their elimination.

(e) Heliantheae

This tribe displays a very complex cytological situation

with a wide array of base numbers. Many of the genera are polybasic. It is postulated that the ancestral basic number in the tribe could have been rapidly altered in both directions in the course of evolution.

(f) Anthemideae

There are only fewer basic numbers in the tribe, of which $x=9$ show overwhelming preponderance. It is suggested that $x=9$ could be a derivation from $x=10$.

(g) Senecioneae

In this tribe, $x=10$ is the most predominant basic number. Considering the occurrence of $x=5$ constitution in a few genera like Emilia and the absence of intermediate numbers between $x=5$ and 10, it is suggested that $x=5$ could be the original basic number of the tribe.

(h) Cynareae

A large array of basic numbers occur in the tribe, ranging from $x=8-19$, with concentration around $x=10$.

(i) Cichorieae

Basic numbers in this tribe vary from $x=3-9$, of which $x=9$ is most predominant. The suggestion postulating $x=9$ as the original type, (which in turn originated by polyploidy from $x=5$, followed by aneuploid reduction) seems to be the possibility.

13. Regarding the ancestral basic chromosome constitutions of the entire family, there are mainly two postulations, namely $x=9$ and $x=5$. The contention postulating $x=5$ as the ancestral basic number from which the $x=9$ arose by polyploidy followed by aneuploid reduction is favoured. Karyological situations in a few genera reported in this study, especially Vernonia and Blumea are shown to support this possibility.

14. The role of polyploidy and aneuploidy in speciation and evolution of the family is discussed in the light of available cytological data.

(a) Among the species studied, highest incidence of polyploidy occurs in herbaceous perennials and annuals. Polyploidy is strikingly low in woody plants. Highest frequency of polyploids occurs on $x=10$ and 9.

(b) The great bulk of polyploid species showed meiotic behaviour suggestive of allopolyploid origin. A few others showed evidences suggestive of autopolyploidy or segmental allopolyploidy.

(c) Aneuploid alterations are widespread in the family. Available chromosome data indicate that 26 out of the 59 genera represented in the present study have aneuploid chromosome numbers occurring at diploid and/or polyploid levels.

Descending aneuploidy has been noticed in two of the genera reported here, namely Vernonia and Artemisia ($10 \rightarrow 9$),

whereas both ascending and descending aneuploidy occur in Blumea (8←9←10→11) and Eupatorium (9←10→12) at the diploid level.

(d) Chromosome data indicate that both polyploidy and aneuploidy have been widely operative in the evolution of the family.

15. Data of karyomorphology of species reported here show that karyotypes of moderate asymmetry (2A and 2B) predominate. Karyotype specialization in them has been mostly through shift of centromere positions rather than through factors affecting relative size of chromosomes within the complement.

16. Association of morphological and karyotype advancements has been recognised in the genus Emilia, while the reverse trend has been noticed in a few other genera like Sphaeranthus and Sonchus.

17. In Vernonia, karyotype advancement is seen to be associated with herbaceous perennial growth habit. Association of karyotype specialization with decreasing basic chromosome number also has been noticed in this genus. Further, karyotype specialization in the genus appeared to show a trend in the direction of polyploidy.

18. In the genus Blumea, species under the $x=8$ series had less specialized karyotypes than those with $x=9$. It is conjunctured

that karyotypes of species of this genus were relatively symmetrical before the numerical change from the $x=9$ to 8 had occurred, and that structural changes resulting in karyotype specialization have been more active in the $x=9$ group of species.

19. Out of the seven species of Blumea coming under the $x=9$ series, karyotypes of five species showed recognisable bimodality. Loss of segments of chromosomes, in addition to unequal translocations, has been considered to be responsible for the occurrence of bimodality in the genus. An apparent association between morphological advancement and specialization of the karyotype (bimodality) is recognisable in this genus.

20. Although there is remarkable similarity of systematic treatment of the family by various taxonomists, there are certain notable difference of opinion as regards the origin, systematic position and interrelationships of various tribes. These aspects are briefly considered, and the intrafamilial relationships discussed in the light of chromosome data. On account of the very complex cytological situation present in most of the tribes, it is felt that the scope of chromosome data in dealing with tribal relationships of the family is very limited.

21. Regarding the phyletic relationships and affinities of the family also there exists some controversy. Families such as the Campanulaceae, Rubiaceae, Valerianaceae, Dipsacaceae, Calyceraceae, Brunoniaceae, Umbelliferae are the extant families

with which the Compositae are postulated to have affinities based on various criteria. These relationships are considered in the light of cytological data. It is seen that a few of these families, especially the Rubiaceae exhibit a very unrelated chromosome number $x=11$ which is almost nonexistent in the Compositae, whereas most of the other families show chromosome situation comparable with the Compositae (frequent occurrence of $x=9$ and/or 10, 8, 7) so much so it is rather difficult to point out any reasonable affinity between these families and the Compositae.