Cytogenetic Studies in Some Ornamentals

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CERTIFICATE

This is to certify that the thesis entitled "Cytogenetic studies in some ornamentals" submitted by Shri M.A. Nazeer for the award of the degree of Doctor of Philosophy in Botany is a record of bonafide research work carried out by him under my supervision.

(T.N. Khoshoo)

Lucknow
March 25, 1982.

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DECLARATION

I hereby declare that the thesis entitled "Cytogenetic studies in some ornamentals" submitted by me for the Degree of Doctor of Philosophy in Botany, of the University of Kerala incorporates the work done by me at the National Botanical Research Institute, Lucknow. I further declare that this thesis has not previously formed the basis for award of any degree, diploma, associateship, fellowship or other similar title or recognition.

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I. INTRODUCTION

The genus Chrysanthemum, comprising nearly 160 species, is of wide spread occurrence in the temperate and many other regions, mostly of the old world. The two main centres of distribution are, the Mediterranean region, particularly Algeria and Canary Islands, and the China and Japan. The genus constitutes a large polyploid complex ranging from 2x to 22x, besides a number of aneuploids. The garden chrysanthemum (C. morifolium Ramat.), also known as the "Queen of the East" is a highly versatile accommodating ornamental and is one of the most important flower crops of the world. Although garden chrysanthemums were cultivated more than 3000 years ago in China, these were actually improved in Japan over 1000 years ago, and it was not until the seventeeth century that they reached Britain and other countries. Nearly 150 years after they were introduced into North America. C. morifolium is supposed to have arisen from a complex of Chinese species, chiefly C. indicum Linn. and C. morifolium Ramat. (C. sinense Sabine) through repeated cycles of hybridization followed by selection over a period

of 2500 years. The process of transformation from wild to cultivated condition took place in historic time in the gardens of Japan, Europe and China. Though new forms originated as hybrid seedlings, several cultivars have also arisen as spontaneous bud mutations. The purpose of the present study is to bring out a coherent picture of the various mechanisms underlying the origin and evolution of garden chrysanthemums. The study deals with morphological variation, breeding system, variation in chromosome complement and meiotic system in C. morifolium complex.

The genus Sansevieria (Family Agavaceae) is the other plant included in the present study. It is commonly known as "Bowstring Hemp" and contains nearly 60 species which are chiefly confined to Tropical Africa, Arabia and Madagascar. Three species are found in India. The individual species of Sansevieria show an extremely wide variation in growth, form and habitat. Some species are highly prized as a source of fibre crop which is used to make coarse fabrics, fish nets and bowstring. In addition to this, few species are ornamentals, cultivated for their beautifully variegated leaves

either as pot plants for indoor purpose or as border plants in rock gardens. The present study deals with an analysis of mitotic complement and meiotic system which may throw some light regarding speciation process in this important group of plants.

II. MATERIAL AND METHODS

The present investigation is based on 13 species of Chrysanthemum, approximately 183 cultivars of garden chrysanthemum (C. morifolium Ramat.) and 15 species of Sansevieria. Seeds of Chrysanthemum species were obtained from various botanic gardens. Nearly 400 cultivars of garden chrysanthemum are maintained at National Botanical Research Institute, Lucknow. Majority of these cultivars are of exotic origin and initially introduced by the late Mr. S. Percy Lancaster, former Senior Technical Assistant. The collection was further enriched with material obtained from Japan around 1972 by Mr. M.A. Kher, Scientist, Floriculture Laboratory. In 1978 several American cultivars were also introduced. Many promising hybrids were evolved by Mr. M.A. Kher, which have been included in the present study. Similarly the Sansevieria species, (nearly 20) were obtained from South Africa by the effort of the late Mr. S. Percy Lancaster. Most of the chrysanthemum cultivars are unregistered and wherever the name is absent, the cultivars are numbered. A

A consolidated account of all the taxa together with their source, is given in Table 1.

Table 1

Sources of Chrysanthemum species/cultivars and Sansevieria species under investigation

Taxon	Source
CHRYSANTHEMUM	
C. carinatum Schousb.	Gradina Botanica CLUJ-Napoca, Republica Socialista, Romania, NBRI, Lucknow.
C. cinerariaefolium Vis.	Gradina Botanica CLUJ
C. coronarium L. C. coronarium cv. Plenum	Napoca, Republica-Socialista, Romania.
C. corymbosum L.	
C. frutescens L.	NBRI, Lucknow.
C. macrophyllum Waldst. et Kit.	Gradina Botanica CLUJ Napoca, Republica Socialista, Romania.
C. multicaule Desf.	T. Sakata and Co., 2. Kiribataka Kanguaku, Yokahama, Japan.
C. myconis L.	Simee S.P.A. 25088 Toscolano (Brescia) -via Rellglone.
C. nipponicum Matsum.	Botanical Garden Tohoku University Sendai, Japan.

Taxon	Source
C. peludosum cv. White	T. Sakata and Co., 2, Kiribateke, Kanguaku, Yokehama, Japan.
C. parthenium (L.) Benth.	Botanischer Garten der Universitat Halle/S Sektion Biowissenschaften.
C. parthenium cv. Aureum	Gradina Botanica CLUJ Napoca, Republica Socialista, Romania
C. parthenium cv. Gold Ball	
C. sagatum L.	NBRI, Lucknow.
C. morifolium cultivars	NBRI, Lucknow.

'Adra Shoesmith', 'Ajina Purple', 'Alfred Durham', 'Alfred Simpson', 'Alfred Wilson', 'Alba', 'Anamika', 'Apsara', 'Badger', 'Basanti', 'Bharat Ratna', 'Birbal Sahni', 'Bob Pulling', 'Bosstau', 'Bronze Turner', 'Bullen Hall size', 'Cleopatra', 'Connie Mayhew', 'Dainty Maid', 'Dipti', 'Donald', 'Evening Star', 'Fish Tail', 'Flirt', 'Florence Shoesmith', 'Freedom', 'Ghenghiskhan', 'Golden Anniversary', 'Golden News', 'Grape Bowl', 'Harvest Home', 'Heloisa', 'Hopa, 'Improved Louis Pocket', ''Innocence', 'Jessie', 'John Bull', 'John Reid', 'John Webber', 'J.H. Salisbury', 'Kanchen', 'Kasturba Gandhi', 'Kasturi', 'Kikubiyouri', 'Knox', 'Lalquila', 'Laura', 'Lilith', 'Liliput', 'Linda', 'Lohengrin', 'Lord Roberts', 'Maharaja of Sikkim', 'Mahatma Gandhi', 'Magami', 'Mercury', cv. Miniature, 'Mohini', 'Morris White', 'Mrs. C. Totty', 'Mrs. G. Lloyd Wigg', 'Nanako', 'Nigeria', 'Northern Lights', 'Otome Zakura', 'Phil Houghton', 'Phyllis', 'Pink Cloud', 'Potomac', 'President Viger', 'Pride of Madford', 'Red Star', 'Roger Thompson', 'Rosa', 'Rupasa Bangla', 'Salmon Shoesmith', 'Sharad Bahar' 'Sharad Mala', 'Sharad Mukta', 'Sharad Shobha', 'Sharad Prabha', 'Shinfuji', 'Silver Cloud', 'Snow White', 'Sonar Bangla', 'Spoon', 'Summer Gem', 'Svata', 'Valiant', 'W.A. Etherington', cv. White (Kerala), White Cloud', cv. Yellow (Bombay) cvs. A5, A16, AA4, AA6, C1, C6, C7, C8, C9, D5, E10, L11, E14, F10, G2, J4, K1, K2, M4, M7, M16, M27, M30, M31, M45, M52, M56, N10, N14, N15, N18, NO1, NN9, NN10 — NBRI, Lucknow

Taxon	Source
NN12, NN14, ON1, ON3, ON10, OO2, OO8, OO10, O4, O6, P1, P3, P5, P8, Q8, R10, R18, S_1, S3, S_4, S5, S_7, S_8, S_9, SO_2, SO_4, SS_1, T_1, T2, T5, T6, T7, T8 (Small), T8 (Large), T9, T10, T17, T19, T35, T38, U2, U1, U4, U9, U14, U20, U23, U25, X1, X2, X_5, Y_1, Y_{15}, Y_{21}, cv. No.5.	
SANSEVIERIA	
S. canaliculata Carr.	NBRI, Lucknow
S. caulescens N.E. Brown	"
S. cylindrica Bojer	"
S. deserti N.E. Brown	"
S. ehrenbergii Schweinf.	"
S. gracilis N.E. Brown	"
S. intermedia N.E. Brown	"
S. metallica Cur. et Labr.	"
S. pearsonii N.E. Brown	"
S. powellii N.E. Brown	"
S. senegambica Baker	"
S. subspicata Baker	
S. suffruticosa N.E. Brown	"
S. trifasciata Prain	"
S. zeylanica Willd.	"

METHODS

For mitotic studies actively dividing root tips were pretreated with saturated solution of para-dichlorobenzene for 1.5 to 2 hours at 15°C. The root tips were then washed, fixed in acetic alcohol (1:3) mixture for 24 hours, hydrolysed in 1N Hcl at 60°C for 15 minutes and stained in feulgen and finally squashed in iron-acetocarmine.

Karyotypes were analysed from root tips from a minimum of 5 cells for arm ratio and other morphological details. Photoidiograms were prepared by cutting out individual chromosomes, arranging them in descending order of their length and matching on the basis of morphology. The classification of Levan et al. (1964), metacentric 'M' (r index 1.0), metacentric 'm' (r index 1.0 to 1.7) submetacentric 'sm' (r index 1.7 to 3.0), subtelocentric 'st' (r index 3.0 to 7.0) and telocentric 'T' (7 to ∞) was used to determine the exact position of the centromere. Stebbins' (1958) method was used for assessing the degree of asymmetry.

For meiotic studies, young flower buds were fixed in Carnoy's fluid (1 acetic acid : 3 chloroform : 6 alcohol) in which the acetic acid component was

saturated with ferric acetate. Material was fixed between 9 A.M. to 10.30 A.M. After a week, the material was squashed in 1 per cent aceto carmine.

Analysis of mitotic and meiotic chromosomes was made from temporary slides from which suitable cells were photographed using Olympus ECTr microscope in combination with PM6 photomicrographic attachment. Initial magnification obtained was either x350 or x500 which has been enlarged x1500.

DNA Estimation

Root tips were fixed in 1:3 acetic alcohol and then hydrolysed in 1N Hcl at 60°C for 15 minutes, stained in leuco-basic fuchsin at pH 3.6 for 2 hours. Then they were given three 10 - minutes washes in So_2 water, followed by a washing in distilled water, and finally squashed in a drop of glycerol. Four slides of each material were prepared, and each slide was prepared using a single root tip from a different plant. The relative absorption at 570 nm of individual Feulgen stained nuclei were measured using Vickers M 86 Scanning Microdensitometer. Measurements of at least 10 early telophase nuclei per replicate of each cultivar were made. As a check, 10 large presumably 4C nuclei were also

measured to make sure that transitional, i.e. 2C-4C values were not included. The absolute values were calculated using standard *Allium cepa*, whose nuclear DNA value is 33.55 picograms. (Van't Hof, 1965).

III. CHRYSANTHEMUM

1. SYSTEMATIC POSITION AND DISTRIBUTION

The Chrysanthemum is a member of the family Compositae, which have composite flowers each consisting of a large number of florets arranged very closely. The name 'chrysanthemum' owes its origin to Linnaeus (1753) who composed a Greek composite word 'Chryse' meaning gold and 'anthemon' meaning flower, thus signifying "golden flower". The colour of earliest chrysanthemums were yellow and Linnaeus might have applied this term to the small yellow flowers of C. indicum Linn.

Chrysanthemums are among the earliest flowers to be cultivated and was known since the time of Confucious (551-478 B.C.). Early botanists classified Chrysanthemum by giving various synonyms like Matricaria (Breyne, 1688; Pativer, 1703; Plunket, 1705; Kaempfer, 1712; Miller, 1768; Rametuelle, 1792), Anthemis (Willdenow, 1800; Moench, 1802) and Pyrethrum (De Candolle, 1837; Phono zoufou, 1828; Maximowicz, 1872). For the first time Linnaeus in his 'Species Plantarum' (ed. 1753) gave the generic name to this plant as Chrysanthemum. Since then the name has been referred to by many authors

like Thunberg (1784), Ramatuelle (1792), Curtis (1796) and Eduard (1815, 1820, 1821).

The genus Chrysanthemum has been placed under the tribe Anthemideae of the family Compositae. Based on differences in the seed morphology, Bentham and Hooker made 22 sub-groups of which about 6 groups include garden forms (Bailey, 1953). Engler and Prantl (1924) divided the genus into eight sections, four containing annual and four perennial species (cf. Dowrick, 1953). The annual species are included under Pinardia, Coleostephus, Ismelia and Ammanthus, while the perennial species in Argyranthemum, Pyrethrum, Gymnocline and Tanacetum. C. indicum which is responsible for the development of garden chrysanthemums falls under the section Pyrethrum. Hutchinson (1917) considered 5 species endemic to South Africa under the genus Chrysanthemum. However, Nordenstam (1976) has shown that there are infact 7 species and these species are categorised under four genera such as Adanenthema, Cymbopappus, Leucoptera and Adenoglossa. These classifications were based on carpological and other morphological studies.

The generic concept in the tribe Anthemideae have been changed by Heywood and Humphries (1977) in

a recent review. According to these authors, similarity of floral forms exhibited by many species of Anthemideae has obscured the recognition of evolutionary groups in some cases like Chrysanthemum complex. By adopting criteria based upon carpological studies, embryo sac data and phytochemical data they have recognised five principal genera in the Chrysanthemum complex. These five genera are Argyranthemum, Chrysanthemum, Leucanthemum, Tanacetum and Dendranthema. The genus Chrysanthemum L. (sensu stricto) applies to a group of three distinct annual species, C. carinatum, C. coronarium and C. segetum. However, the autumn flowering cultivars of garden chrysanthemum have been placed in the genus Dendranthema (DC). Desmoul, which contains nearly 30 species. Dendranthema includes perennial herbs and/or shrubs. The cultivars of Dendranthema (D. morifolium) exceeds 7000 and are derived from Asian species of D. indica and D. morifolium (Heywood and Humphries, 1977).

The taxonomic history of florist's chrysanthemum, D. morifolium as reviewed by Ackerson (1957) is summarized below:

Ramatuelle (1792) described a fully double incurved flower as Anthemis grandiflora, which he later

classified as Matricaria morifolium. However, botanists considered it as C. indicum. In 1823 Joseph Sabine called this as C. sinense. Hemsley (1889) attempted to correct the nomenclature proposing C. morifolium as was suggested by Ramatuelle. He further states that though Ramatuelle described the garden forms as Anthemis grandiflora and Matricaria morifolium, he had suggested that if the plant is refered to Chrysanthemum, then it might be called C. morifolium. Bailey (1953) proposed a new name C. hortorum, but later he used the valid name C. morifolium.

Key to the species

The genus Chrysanthemum contains annual as well as perennial species. The classification of important ornamental taxa following Bailey (1953) is as given below.

4. Plant annual

1. Glabrous annual, 60 cm to 90 cm high, stem much branched, leaves rather fleshy, pinnatifid, flowers in solitary heads which are nearly 5 cm across with typically white rays and yellow ring at the base. Involucral bracts keeled.

... C. carinatum Schousb.

2. Annual, 90 cm to 120 cm, leaves bipinnately parted, somewhat clasping or eared at the base, glabrous, the segments closer together than in C. carinatum. Involucral scales broad, rays lemon coloured or nearly white.

... C. coronarium Linn.

3. Annual, 30 cm to 45 cm high, leaves sparse, clasping, oblong or oblanceolate, variable. Flower petioled and upper clasping, incisions coarse or fine, deep or shallow, but usually only coarsely serrate, with a few and distant teeth, the lower ones less cut, bracts of involucre broad, obtuse, rays obovate and emarginated, golden yellow.

... C. segetum Linn.

AA. Plant perennial

1. C. indicum Linn. Perennial, one of the sources of the florist's chrysanthemums. Much like C. morifolium leaves thin and flaccid, pinnately parted, with acute or mucronate teeth: outer involucral bracts broad and scarious except the herbaceous mid nerve, rays yellow, shorter than diameter of the disc.

2. C. morifolium Ramat. (C. sinense Sabine) Perennial, one of the sources (alongwith C. indicum) of the large florist's chrysanthemum. Wild plant shrubby,

erect and rigid, 60 cm to 90 cm, branching, few leaved: leaves thick and stiff, 5 cm long densely white tomentose beneath, variable in shape from ovate to lanceolate, cuneate at base, margin entire or coarsely toothed: outer bracts of involucre thick, linear, acute, white-tomentose, flower heads small, with yellow disc and white rays somewhat exceeding the disc.

There is much controversy regarding the number of species belonging to the genus Chrysanthemum. Bailey (1953) estimated 150 species, while Cumming (1964) reported 160 species and Pizzetti and Cocker (1975) recorded more than 200 species. According to Haywood and Humphries (1977) the Chrysanthemum complex contains nearly 170 species, which is very near the general belief that the genus contains nearly 160 species.

Although the original home of Chrysanthemum is China, the species are of wide spread occurrence in temperate regions and in many parts of the globe, mostly in the old world (Hemsley, 1889; Bailey, 1953). According to Dowrick (1952b) there are two main centres of distribution, one is the Mediterranean area, particularly in the Algeria and Canary Islands and the other in China and Japan. The genus has spread throughout Europe and Asia.

According to Haywood and Humphries (1977), the genera of Chrysanthemum complex show an interesting geographical pattern. In the genus Chrysanthemum, C. carinatum is endemic to Atlantic coast of Morocco. C. coronarium and C. segetum are two Mediterranean annuals which are now wide spread weeds occurring in many temperate areas. Dendranthema is centred in the Far East and according to Hu (1965) most species are confined to Sikang, Yunnan, Szechuan, Shansi, Mongolia and Sinkiang provinces of China. Kitamura (1940) reported about 18 species from Japan. According to Tzalev et al. (1961) 12 species are wide ranging with D. borealo in Japan, Korea and China and D. zawadskii extending right throughout from Asia to Europe as far as Carpathian and Urals. D. arcticum occure in coastal regions throughout the northern hemisphere particularly in Japan, China, Russia and just reaches along the Scandinavian coast line (cf. Haywood and Humphries, 1977).

Hooker (1897) records two species of Chrysanthemum in India, C. indicum, cultivated in gardens and C. coronarium found in the wild state. He also reported C. atkinsoni from Sikkim Himalayas. Dourick (1952) states that 12 species are endemic to Himalayas. Hemsley (1889) reports that Rheede in his

Hortus malabaricus recorded the cultivation of double variety of chrysanthemum in South India as early as 1690. Recently, Kitamura (1968) reported a new species, C. dolicophyllum from Himalayas.

One of the speculations most widely accepted by many as a fact, is that our present day florist's and garden chrysanthemums were derived from C. indicum and C. morifolium (C. sinense). The large flowered cultivars are supposed to have originated from C. morifolium and the small flowered ones from C. indicum (Emsweller, 1947).

C. indicum (Fig. 1) is short, while C. morifolium (C. sinense) (Figs. 2 and 3) is slightly taller, robust with single or double flowers. However, the present day garden chrysanthemums are considered as C. morifolium and are the product of intensive cross breeding and selection by many over the years.

2. MORPHOLOGICAL FEATURES

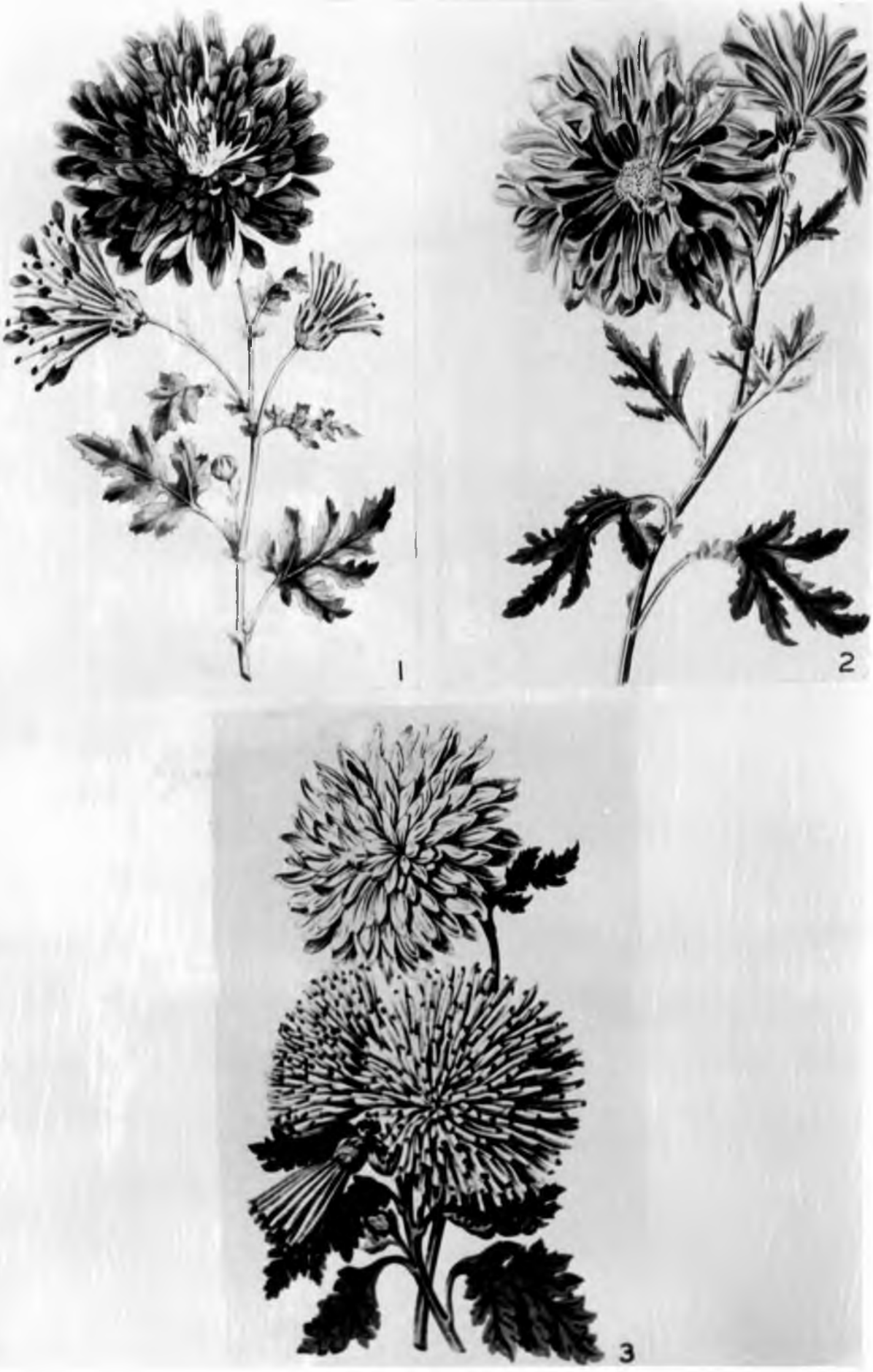
About 100 representative cultivars of C. morifolium growing at the National Botanical Research Institute, Lucknow were studied for morphological characteristics, which were recorded at the time of

Figs. 1-3: Elemental species involved in the origin of garden chrysanthemum

Fig. 1: C. indicum Linn. (From Curtis' Botanical Magazine vol. 9, p.327).

Fig. 2: C. sinense Sabine (From Curtis' Botanical Magazine vol. 52, p.2556).

Fig. 3: Chrysanthemum x hortorum (From Botanical Register, 1815, plate 4).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full blooming i.e. in the month of December-January, so that it remained uniform for all the cultivars analysed. It was observed that not much variability exists in the general morphology except the size, shape and colour of the flower heads. The size of the capitula may be influenced by the cultural practices. Morphological variation has been recorded in Table II.

Observations

Stem

The garden forms of C. morifolium are perennial herbs, perennating with the help of underground stem. The aerial stem is herbaceous at the young stage and becomes stiff and woody at maturity. The stem is generally unbranched, but small flowered cultivars produce a number of branches. C. morifolium is propagated vegetatively by means of division of clumps, suckers or through stem cuttings. Propagation through stem cutting is mainly employed for large flowered chrysanthemum. The suckers originate from the underground portion of the stem which run first horizontally under the soil giving rise to shoots and roots from the node. These suckers are separated and planted from which new branches arise. Maximum suckering is

seen when the blooming is over and aerial stem starts perishing. The shoots from the suckers grow upwards, ultimately forming an independent plant.

Plant height

Height in the garden cultivars varies from 29 cm to 127 cm (Table II). The cultivars can be arranged into two groups, based on height. The large flowered cultivars (incurved, reflexed, etc.) are the tallest, with height ranging from 32 cm (cv. 'Chenghis-khan') to 127 cm (cv. H51). The second group comprises of small flowered cultivars whose height ranges from 29 cm (cv. NN4) to 67 cm (cv. K3). Plant height is influenced by the soil and cultural practices like the type of bloom desired, therefore, it may not be possible to correlate plant height with most other characteristics including ploidy level.

Leaf

Leaves in cultivars of C. morifolium are simple, usually exstipulate and alternate in arrangement. Sometimes foliaceous stipules are seen, which may encircle the stem and form an outgrowth. These stipules usually show sharp dentation. Leaves are usually

Figs. 4–15: Variability in leaf of *C. morifolium* cultivars.

Fig. 4: cv. ON_1

Fig. 5: 'Nanako'

Fig. 6: cv. NN_{10}

Fig. 7: cv. P_4

Fig. 8: cv. N_4

Fig. 9: cv. P_1

Fig.10: cv. G_2

Fig.11: cv. M_{42}

Fig.12: cv. M_3

Fig.13: 'Kasturba Gandhi'

Fig.14: 'Snow White'

Fig.15: cv. M_{50}


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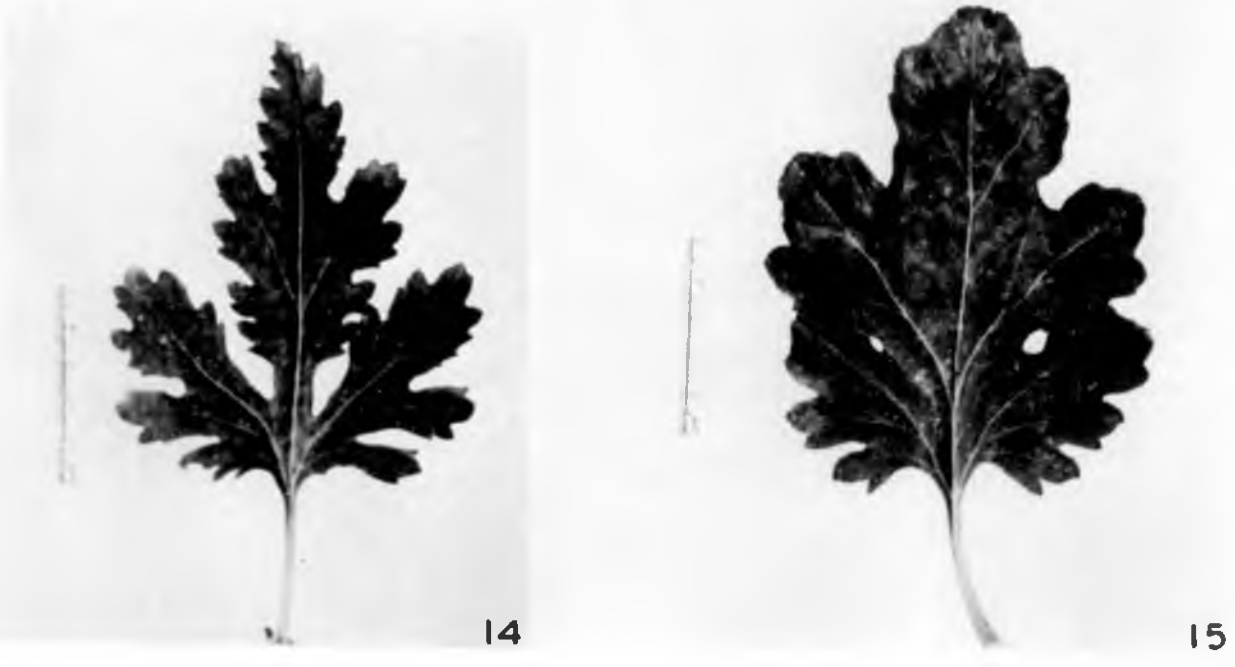
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petiolated, or even sessile (cv. M42). The leaves are variable in shape and size (Figs. 4-15). The margin of the leaf is variously dissected in different cultivars (Table II). Sometimes the leaf blade is cut to such an extent that it almost touches the midrib (Fig. 10).

Among large flowered cultivars, the size of the leaf varies from 10.0 cm x 5.6 cm (cv. M21) to 17.7 x 7.3 cm (cv. M39). In small flowered cultivars, it ranges from 3.5 x 2.0 cm (cv. DN1) to 8.1 x 4.3 cm (cv. 'Birbal Sahni'). The tetraploid 'Liliput' has a leaf size 5.8 x 3.6 cm, whereas in octoploid 'Chenghiakhan', it is only 8.5 x 4.5 cm. The leaves of octoploid 'Chenghiakhan' are thicker and darker green in colour, in comparison to the tetraploid 'Liliput' and other hexaploid cultivars.

Capitula and florets

Under Lucknow conditions, available cultivars of garden chrysanthemums bloom from November to December. Both small and large flowered cultivars require 6 to 12 weeks to come in full bloom, after the initiation of flower buds.

A great deal of variation exists in the floral heads of chrysanthemums with regard to their size and shape of the florets. The number, form, size and arrangement of florets show variation which give different shapes to the flower heads (Figs.16-36). The capitula are primarily single, double or decorative, and form globular to flat or bell shaped heads.

The capitulum consists of many individual flowers or 'florets' arranged on a common axis called thallamus. Two types of florets are distinguishable in a capitulum. They are the 'ray florets' which occupy the periphery of the thallamus and the centrally placed ones, 'disc florets'. Ray florets are female and disc bisexual. The strap-like corolla of a ray floret shows teeth-like projections towards its tip which indicates the number of petals that have united to form it. Disc florets have got a tubular corolla. In some cultivars, disc may be completely hidden by the rays, or it may be absent. Disc florets are occasionally found scattered singly or in groups among the ray florets. The basal type of cultivars have single row of ray florets and the derived ones have semidouble or double heads with more than five rows.

Figs. 16–24: Variability in the flower heads of *C. morifolium* cultivars (small flowered types)

Fig. 16: cv. AA_{10} (Anemone)

Fig. 17: 'Liliput' (Button)

Fig. 18: cv. F_4 (Korean)

Fig. 19: cv. E_9 (Pompon)

Fig. 20: 'Harvest Home' (Stellate)

Fig. 21: 'Kasturi' (Cineraria)

Fig. 22: cv. T_1 (Quilled)

Fig. 23: cv. T_3 (Spoon)

Fig. 24: cv. S_6 (Striped)

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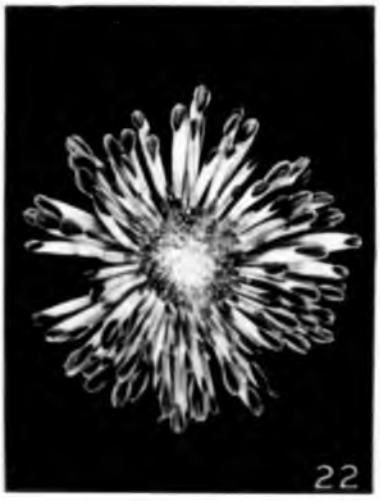

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Figs. 25-30: Variability in flower heads of *C. morifolium* cultivars (Large flowered types)

Fig. 25: cv. M_{13} (Incurved)

Fig. 26: 'Chenghiekhan' (Incurving)

Fig. 27: 'Dae' (Reflex)

Fig. 28: 'Pink Cloud' (Intermediate)

Fig. 29: 'Grape Soul' (Irregular)

Fig. 30: 'S.L. Andre' (Ball)


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Figs. 31-36: Variability in flower heads of *C. morifolium* cultivars (Large flowered types)

Fig. 31: cv. W_{24} (Quilled)

Fig. 32: cv. W_{14} (Spider)

Fig. 33: cv. W_9 (Thread)

Fig. 34: 'Fred Yule' (Pompon)

Fig. 35: 'Mahathma Gandhi' (Tubular)

Fig. 36: cv. R_{23} (Semidouble/spoon)


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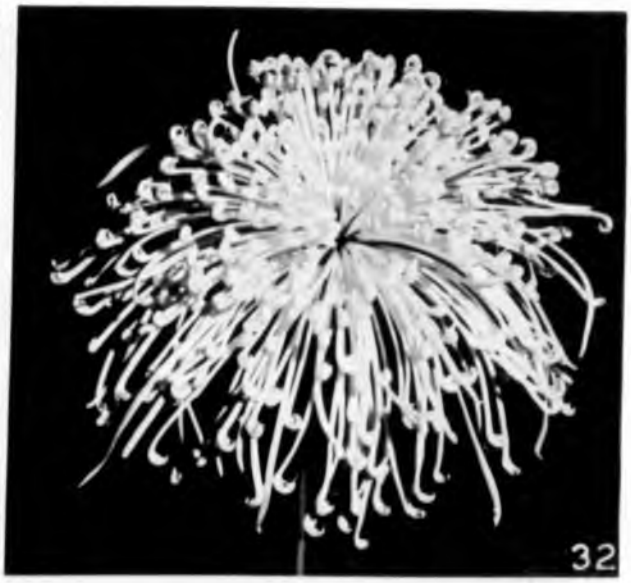
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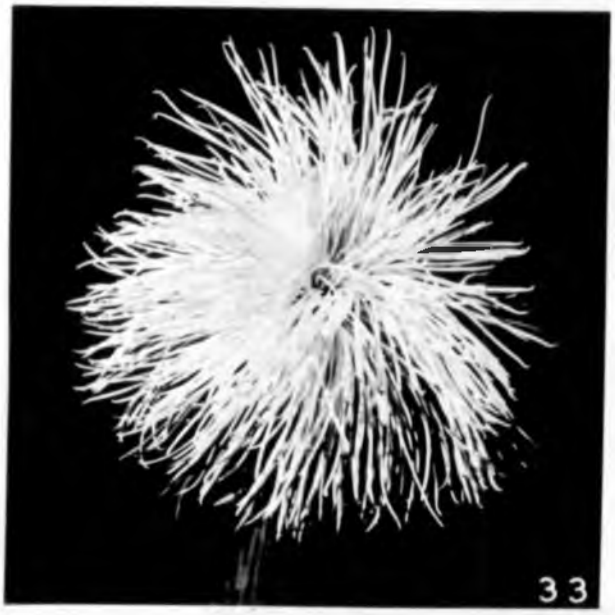
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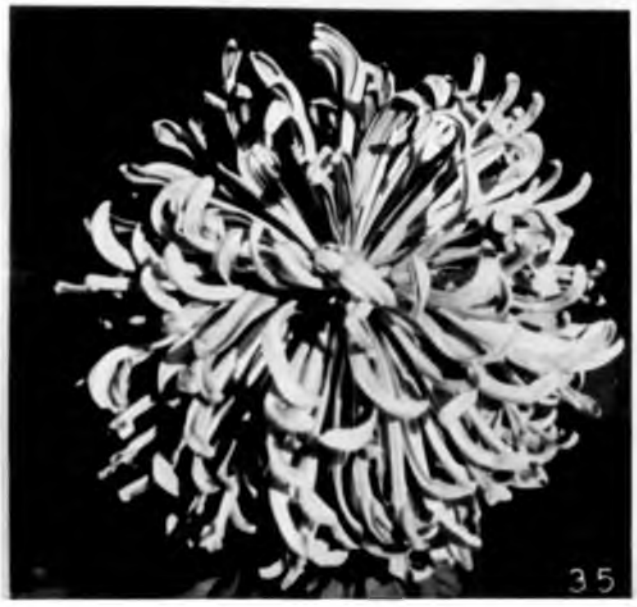
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The straps are arranged on the heads in single row (stellate, coronate and anemone types), 1 to 5 flat rows (charm or cineraria and single korean). The strap shaped ray florets have both the sides compressed downwards and they are usually twisted in stellate type, while the outermost disc florets are converted into buckle in coronate type. Twisted straps are also observed in some of the anemone flowered cultivars (cvs. 'Gem' and AA16). The straps are provided with perfect striations or streaks of different colours in striped types.

The straps are found in more than 5 rows and are flat in double korean and semidoubles. In small flowered pompons and decoratives the ray florets are short, broad and regularly arranged. In pompons the straps are diverging and straight giving the bloom a compact hemispherical shape. Straps are larger in large flowered semidoubles.

In large flowered cultivars the ray florets assume various shapes (Figs. 37-48) which are mainly responsible for the different categories of blooms. In incurved types the ray florets are stiff broad and curve upwards and inward towards the centre to give the bloom a globular shape (cvs. 'Snow Ball', 'Kikubiyouri').

Figs. 37–48: Variability in ray florets of *C. morifolium* cultivars

Fig. 37: 'John Wabber'

Fig. 38: cv. W_{36}

Fig. 39: cv. M_{26}

Fig. 40: cv. W_{13}

Fig. 41: cv. W_{23}

Fig. 42: 'Mahathma Gandhi'

Fig. 43: 'Chenghiskhan'

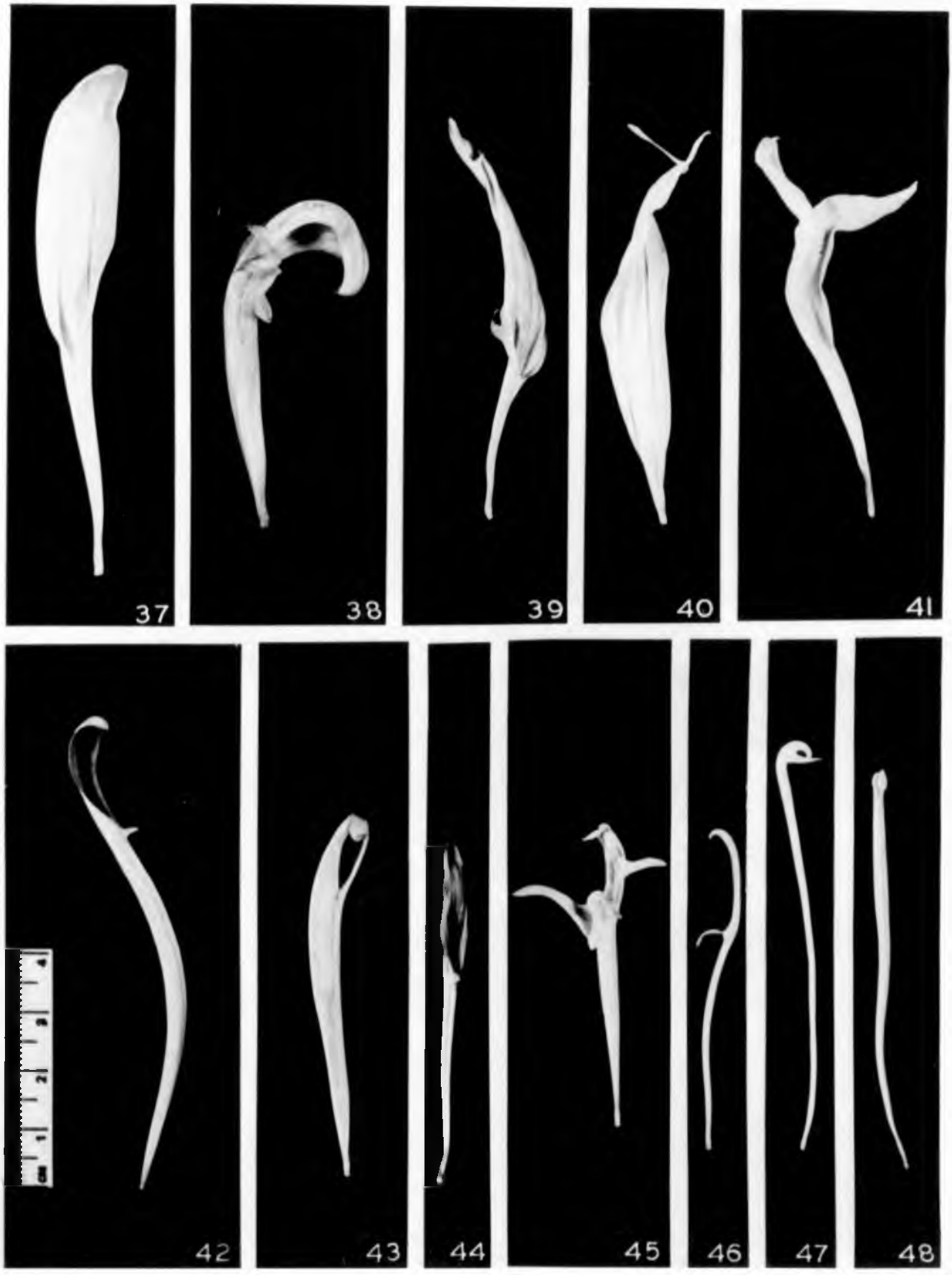
Fig. 44: cv. M_{23}

Fig. 45: cv. M_{52}

Fig. 46: cv. W_{14}

Fig. 47: cv. W_{14}

Fig. 48: cv. W_{2}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The ray floret in its basal portion is tubular and narrow and the rest of the portion remains open to assume a boat-shaped structure. In some cultivars the outer florets open towards the end in the form of a hook (Fig. 38). In other instances the florets are twisted and turning in disorderly manner.

In reflexed types, the straps are spreading, curved outward and downward away from the centre so that their upper surface is seen. In the early stages, the inner florets remain incurved. Sometimes the bloom becomes irregular due to irregular shape of the straps caused by twisting and turning in a haphazard manner. In some cases the basal portion of the straps remain tubular but the upper portion is opened, forming a prominent spoon.

In ball or rayonants, the ray florets are usually channelled and closely packed and radiate in all directions giving the bloom the shape of a ball (cvs. 'Pride of Madford' and U23).

The tubular florets assuming the shape of a quill and elongating with their tips open or closed results in quilled flowers (Fig. 48). The tubes may be thick, medium or thin. In various cultivars the

quills may be arranged from one (cv. 'Donald') to many rows (cvs. 'Golden quill' and W_2). Quills are sometimes pressed flat and open at the tip. Quilled ray florets are also observed in some anemone types (cvs. 'Mercury', 'Rosa').

In spider types (cvs. W14 and Y15) the ray florets are tubular and arranged at right angles to the stem. The opening of the tubular strap is bilipped. In some thread type the central portion of the capitulum is occupied by a column of rays which form an outgrouth or corona. In laceniate types the mouth of the tubular ray floret is variously dissected and the ray florets are compactly arranged.

Size of the ray florets

The size of the ray florets varies according to their different shape (Table II). In small flowered singles (single korean, stellate, cineraria, striped, coronate and anemone) and doubles (button, pompon and double korean) it ranges from 0.7 x 0.2 cm to 3.0 x 1.0 cm. In large flowered incurves the size of the ray florets ranges from 5.8 x 0.9 cm to 9.7 x 1.2 cm. In large flowered reflexes and in some irregular types the size of the strap ranges from 5.7 x 0.4 cm to 8.2 x 0.6 cm. In large flowered rayonante/ball, the size of the ray

florets varies from 4.4 x 0.3 cm to 6.7 x 0.5 cm. The size of the ray florets in small and large flowered tubular/quilled types ranges from 3.3 x 0.2 cm to 10.8 x 2.4 cm. In thread types the size of the ray florets varies from 4.7 x 0.2 cm to 10.6 x 0.3 cm.

Disc is very conspicuous in all singles and majority of the semidoubles. However, it is concealed or is almost inconspicuous in pompon, ball, incurves and reflexes. The disc florets in anemone is prominently developed and is usually hemispherical in form. In cv. 'Maneko' the ray florets are absent and the entire capitulum is represented by disc florets which are well developed. The stamens are rudimentary in this case.

Flower colour

The basic colour in chrysanthemum cultivars is yellow but there is an array of colours in different shades. True blue colour is absent in chrysanthemums. In the present study, the colours were matched with the horticultural colour charts of the Royal Horticultural Society, London. Garden cultivars fall in four different colour groups like yellow, white, mauve and terracotta/red and their different shades

(Table II). With regard to yellow, it ranges from sulphur yellow 1/3 (cvs. Y21 and Y23) to lemon yellow 4 (cv. 'Nanako') and orange shades as in cv. 'Fred Yule' (cadmium orange 8/1). In striped yellows (cv. S2) the base colour is canary yellow 2/1 and the streaks oxblood red 823/2. In mauve coloured cultivars there is a range from rose pink 427/3 (cv. M14) to pastel mauve 433/3 (cv. M16). Red and/or teracotta colours show a greater gradation from saffron yellow 7/3 (cv. T13) to cardinal red 822 (cv. 'Alfred Simpson') and simple red 23/2 (cv. R1).

The flowers may show a single colour or may be biocloured when the upper and lower surfaces of the florets are in different colours. The florets may be streaked or blotched in different shades.

Capitula size

The size of the capitula is influenced by the size and number of ray florets present. The size of the bloom is taken as the diameter of the flower head and in chrysanthemum cultivars the size varies from 1.9 cm (cv. NN3) to 23.0 cm (cv. M30). Based on the capitula size, the cultivars may be grouped into two, small flowered and large flowered ones. In small

flowered singles the size varies from 2.3 cm to 7.5 cm. The diameter of the capitula in tetraploid button (cv. 'Liliput') is 2.1 cm and in the pentaploid cultivars like P_1, P_5, 'Kasturi' etc. it ranges from 3.4 cm to 3.8 cm. The smallest flower head was found in cv. NN3 (1.9 cm). The diameter of large flowered incurves varies from 12.7 cm to 16.0 cm. The diameter in bell or rayonante varies from 9.7 cm to 12.9 cm, however, in threads and spiders, the range was from 10.7 cm to 19.5 cm. The largest flower head was found to be of cv. M30 with a diameter of 23.0 cm. The capitula diameter in octoploid 'Chenghiakhan' was 14.7 cm.

Conclusions

From the foregoing account of morphological analysis, a few general conclusions emerge. With regard to plant height, large flowered cultivars were found to be taller, with height ranging from 32 cm to 127 cm, while small flowered cultivars are from 29 cm to 67 cm.

Leaves are simple and variously dissected in all the cultivars and analysis of length: breadth ratio hardly revealed any relationship between the leaf size and flower type. However, tetraploid cultivar had smaller leaves when compared to heptaploid and octoploid

cultivars. In heptaploid and octoploid cultivars the leaves were broader, dark green and thick. It is worth recalling that Dourick (1953) observed variation in morphological characteristics accompanied by a change in chromosome number in a sporting cultivar 'Favourite'. Sports of 'Favourite' showed varying chromosome number like 2n = 54, 55, 56 and 57. One sport 'Shuffil's Favourite' had a chromosome number 2n = 47. This plant was very weak morphologically and the leaf was distorted in shape. Thus Dourick (1953) concluded that the loss of chromosomes have deleterious effects on the phenotype. Similar results were also obtained by Iwasa *et al.* (1972) who studied sporting cultivars of 'Amagahara family' (2n = 56). In the five plants with different chromosome numbers, four had either 2n = 54 or 55, one plant with 2n = 52 chromosomes was distinguished by its weakness and smaller leaves. One sport of the cultivar 'Kiamagahara' having 2n = 57 showed vigorous growth and increased plant height (Iwasa *et al.*, 1972). In the present study, no strict correlation between morphology and cytological status was discernable.

Table II

Distinguishing morphological characters of *C. morifolium* cultivars (Flower colour as per Horticultural Colour Chart of RHS, London)

Taxon	Plant height (cm)	Leaf		Capitulum		Ray florets			Disc florets
		Size (L/B ratio)	Shape	Diameter (cm)	Shape	Shape	Size (L x B) (cm)	Colour	
1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
'Snow Ball'	97.5	2.01	Ovate, sinuate, apex obtuse	13.7	Incurved	Tubular, upper half open and boat shaped	6.2x0.2	White	Absent
'Elsie Phillipe'	67.0	1.66	Elongate, lacerate, apex acute	16.0	Incurved	Tubular, opened at the tip	9.7x0.8	Sulphur yellow 1/3	Absent
'Super Giant'	47.0	1.71	Elongate, sinuate, apex acute	11.0	Incurved	Channeled, boat-shaped	5.8x1.2	Canary yellow 2/3	Absent
'Mrs.R. E.Pulling'	94.0	1.76	Elongate, sinuate, apex acute	14.7	Intermediate	Strape flat and twisted	6.7x0.5	White	Interspersed with rays
'Pink cloud'	56.0	1.40	Elongate, sinuate, apex acute	15.7	Incurving	Strape flat and boat shaped	7.2x1.3	Pastel mauve 433/3	Absent

Table II contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
cv.M27	90.6	1.66	Elongate, lacerate, apex acute	15.2	Incurving	Strape channelled tips curved inwards	6.7x0.6	Inside, amaranth rose 530/2, outside peetel mauve 433/1	Concealed
cv.M33	59.5	1.55	Ovate, lacerate, apex acute	12.0	Incurving	Outer tubular inner channelled	6.0x0.5	Purple 632/3	Prominent
'Imperial'	54.0	1.67	Elongate, sinuate, apex acute	15.2	Reflexed	Lower half of the ray tubular, upper flat	6.2x1.0	White	Prominent
'Dee'	53.0	1.58	Elongate, incised, apex obtuse	14.7	Reflexed	Strape flat and sword shaped	7.7x0.8	White	Prominent
'President Viger'	63.5	1.14	Ovate, sinuate, apex obtuse	17.2	Reflexed	Flat strape, upper end dissected	8.7x0.6	Inside orchid purple 31/1 outer orchid purple 31/3	Absent
'Miss Maud Jeffries'	50.0	1.78	Elongate, sinuate, apex acute	16.2	Reflexed	Flat, twisted strape with spine-like appendages at the upper end	8.2x1.4	White	Absent

Table II contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
'Otome Zakura'	50.5	1.25	Ovate, sinuate, apex obtuse	9.7	Pompon	Flat straps	4.4x0.8	Rose pink 28/3	Absent
'Fred Yule'	29.0	1.92	Ovate, sinuate, apex obtuse	8.2	Pompon	Flat straps	3.1x0.9	Cadmium orange 8/1 inside. Lemon yellow 4/1 on back side.	Absent
'Chen-ghiskhen'	32.5	1.88	Ovate, sinuate, apex obtuse	14.7	Irregu-lar	Tubular with dissected ends	8.5x0.9	Inside meri- gold orange 11/3 outer Egyptian buff 407/2	Prominent
'Grape Soul'	40.0	1.64	Ovate, sinuate, apex acute	12.0	Irregu-lar	Outer tubular inner flat	6.5x0.6	Inside orchid purple 31/3 outside Mauvette 537/3	Concealed
'Undaun-ted"	79.0	1.78	Elongate, parted, apex acute	13.2	Irregu-lar	Flat straps with dissected ends	6.2x1.0	Inside petunia purple 32/2 outside orchid purple 31/3	Absent
'Melo-dy lane'	90.0	1.82	Elongate, lacerate, apex acute	15.0	Spider	Tubular with dissected end	7.3x0.5	Sulphur yellow 1/3	Reduced

Table II contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
cv.U14	87.5	1.45	Nearly ovate, sinuate, apex obtuse	17.7	Spider	Tubular,mouth of which is bilipped	8.6x0.2	White	Absent
cv.Y15	30.0	1.62	Elongate, lacerate, apex acute	15.0	Spider	Tubular with bilipped mouth	7.8x0.1	Aureoline 3/2	Prominent
cv.U2	61.5	1.66	Ovate, lacerate, apex acute	14.2	Quilled	Tubular, tipe opened	6.7x0.4	White	Prominent
cv.U1	57.5	1.56	Nearly ovate, lacerate, apex acute	15.5	Quilled	Tubular, tipe opened	5.4x0.5	White	Prominent
'Fish Tail'	45.0	1.97	Elongate, lacerate, apex acute	12.2	Lacini-niated	Tubular florete with apex variously dissected	5.7x0.5	Amaranth Rose 530/3	Absent
'Pink Casket'	62.5	1.66	Elongate, sinuate, apex obtuse	13.5	Spoon	Tubular, spetulate	6.4x0.3	Pastel mauve 433/3	Prominent

Table II contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
Small flowered cultivars									
'Paragon'	68.0	1.36	Ovate, lacerate, apex acute	6.8	Anemone	Flat straps	3.8x0.6	Ray chrysanthemum crimson 824, Disc Erythrite Red 0024/1	Prominent
'Dainty Maid'	44.0	1.95	Elongate, sinuate, apex obtuse	6.0	Anemone	Flat straps	3.0x1.0	Orange buff 507/2	Prominent
'Liliput'	32.0	1.61	Elongate, sinuate, apex acute	1.9	Button	Flat straps	0.7x0.2	Canary yellow 2/1	Concealed
'Phyllis'	38.0	1.82	Elongate, sinuate, apex acute	3.2	Cineraria	Flat straps	1.6x0.5	Canary yellow 2/25	Prominent
'Jessie'	40.0	2.19	Elongate, sinuate, apex acute	3.0	Cineraria	Flat straps	1.2x0.4	Chrysanthemum crimson 824 petal margins aureolin 3 Disc Nasturtium red 14/21	Prominent
'Freedom'	50.0	1.60	Ovate, sinuate, apex, obtuse	4.2	Decorative	Flat, incurved	1.8x0.4	Dresden 64/2 yellow	Prominent

Table II contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
'Himani'	55.0	2.34	Elongate, sinuate, apex acute	3.5	Double korean	Outer flat, inner tubular	1.8x0.6	Tip lemon yellow 4/2	Prominent
'Candle Light'	45.5	1.65	Ovate, sinuate, apex obtuse	6.5	Double korean	Outer flat, strape, upper quilled	2.1x0.3	Magnolia purple 30/1	Reduced
'Chara'	35.0	1.65	Elongate, sinuate, apex obtuse	4.2	Decora-tive	Twisted strape	1.6x0.3	Mauve 633/3	Small
F_3	41.0	1.37	Ovate, sinuate, apex obtuse	4.0	Stellate	Flat strape	2.1x0.6	Cardinal red 822 base, top chrome yellow 605	Prominent
'Laura'	51.0	1.90	Elongate, lacerate, apex acute	5.8	Stellate	Flat strape, and twisted	3.0x0.7	Sulphur yellow 1/1	Prominent
'Molly'	45.0	1.60	Ovate, sinuate, apex acute	3.0	Incurving	Flat strape	1.5x0.5	Chrysanthe-mum crimson 824/1	Prominent

Table II contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
'Fanny'	43.0	1.51	Ovate, sinuate, apex obtuse	4.10	Incurving	Flat straps	2.2x0.6	Erythrite Red 27/1	Prominent
'Dolore'	48.0	1.57	Ovate, sinuate, apex obtuse	6.5	Korean (single)	Flat straps	3.1x0.6	Empire yellow 603	Prominent with ray like out grouth
cv.N9	51.0	1.64	Elongate incised apex acute	4.6	Korean (single)	Flat straps	1.7x0.6	Blood red 823/3	Prominent
'Fair Tuck'	50.5	2.27	Elongate, lacerate apex acute	4.6	Quilled	Tubular	3.1x0.2	Salmon 412/3	Prominent
'Donald'	50.0	2.37	Elongate, lacerate apex acute	6.5	Quilled	Tubular	2.7x0.2	Egyptian buff 407/2 signal red 791/2 at the mouth of tube	Prominent
cv.S6	40.0	1.57	Ovate lacerate, apex acute	5.8	Single (striped)	Single row of flat straps	2.5x0.7	Streake- Erythrite Red base Canary yellow 2/2	Prominent

Table II contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
cv.58	38.0	1.35	Ovate, sinuate apex obtuse	6.0	Single (Striped)	Flat straps	2.9x0.7	Aureolin base 3/1 streaks Chrysanthemum crimson 824	Prominent
'Jean'	46.0	1.88	Elongate lacerate, apex obtuse	6.5	Semi-quilled	Spatulate	3.0x0.3	Chrysanthemum crimson 824/2	Prominent

Dowrick (1953) and Simpson *et al.* (1956) found a correlation between capitule size and the chromosome number i.e. an increase in capitula diameter with an increase in chromosome number. Again no such correlation was found from the result of the present study. While the capitulum size can be increased or decreased with cultural practices, under identical conditions in the garden, the diameter of the flower head was smallest (1.9 cm) in a hexaploid (cv. NN3), while the largest flower head (23.0 cm) was found in cv. R30 (2n = 8x + 2 = 56). However, tetraploid 'Liliput' had a diameter of 2.1 cm and octoploid 'Chenghiekhen', only 14.7 cm. In general, the small flowered cultivars tend to have lower chromosome numbers ranging from 2n = 36 to 55 and large flowered cultivars showed higher chromosome numbers, the range being 2n = 53 to 72.

It is apparent that in the strict sense garden chrysanthemums (4x-8x), there is no correlation between the morphological diversity and chromosome number. The present day forms have originated from daisy-like primitive types and during domestication, highly floriferous types have been evolved.

3. POLLINATION MECHANISM AND BREEDING SYSTEM

An understanding of the breeding system of a species helps in standardising breeding methodology for genetic upgrading on the one hand, and in unravelling its evolutionary mechanisms on the other side. The type of breeding system e.g. type of pollination and reproduction determines the extent and nature of genetic recombination and adaptive changes possible in the face of changing environmental conditions. Obviously, the breeding system of a species exerts an influence on its evolutionary potentialities. With the help of available literature and present observations an attempt has been made to understand the pollination and reproductive systems in the garden chrysanthemums.

Among other features the type of pollination in most cases is correlated to morphology and colour of flower, relative length of the style and stamens, time of anther dehiscence, receptivity of the stigma and incompatibility system.

Observations

Each Chrysanthemum capitulum consists of many individual flowers called 'florets', the outer showy ones - 'ray florets' which are mostly female

with well developed bifid stigma and the inner tubular ones - 'disc florets' which are bisexual. The disc florets usually carry five adnate stamens around the style.

In chrysanthemums the capitulum matures centripetally and flowers open one by one from early morning till late hours of afternoon. This is followed by the dehiscence of anthers and the receptivity of stigma. The style lengthens until the stigma at the top pushes the anthers causing its dehiscence. The stigmatic arms carry some quantity of pollen on its end. When the pollen is completely shed, the two stigmatic arms curve outwards exposing their sticky receptive surface. The flower opening, dehiscence of anthers and receptivity of stigma are subjected to temperature changes, being earlier on warm dry days and a little later on cooler days.

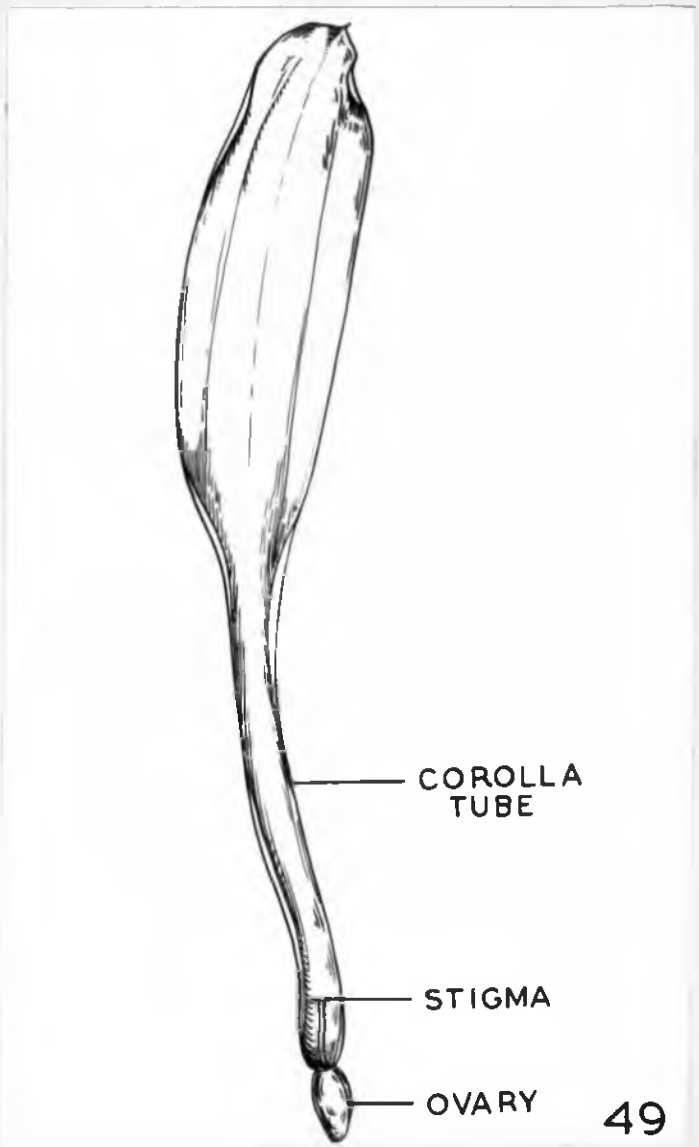
The cultivars of garden chrysanthemum show a wide range of floral morphology. The conspicuousness of capitula and florets, presence of a large quantity of pollen and fragrance attract a large number of insect pollinators. Under Lucknow condition, honey bees are the predominant visitors and small insects, wasps, moths,

bumble bees and butterflies were also found to visit often. While collecting pollen and honey, they carry considerable amount of pollen on their body which is transferred from one plant to another. However, large flowered cultivars were seldom visited by these pollinators. The concealed disc florets and the mechanical barrier caused by the enormous length of corolla tube of the ray florets and very small size of the style prevent the insects from reaching the stigma (Fig. 49). However, if the long corolla tube of the ray florets is trimmed off and hand pollinated, there is sufficient seed setting.

Conclusions

From the foregoing description of pollination mechanism, it is clear that chrysanthemum capitula are adapted for cross-pollination as is the case with most of the members of Compositae. In Chrysanthemum there is a wide range of floral morphology which is associated with out-breeding. The capitulum of Chrysanthemum has centripetal development. The close association of many florets render the capitulum more conspicuous and the conspicuousness is further increased by the colour polymorphism exhibited by the ray florets. The disc

Fig. 49: Ray floret - showing the position of pistil inside corolla tube



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florets are numerous in types with single and semi-double capitula and there is free accessibility for all insect visitors. Outbreeding is further maintained by protandry and the centripetal maturation of the capitulum. The adnate anthers forming a cylinder around the style, dehisce introrsely and the pollen is carried out by the growing style which is made available to the pollinators. Thus the floral organization in garden chrysanthemum ensures high degree of cross-fertilization, which according to Grant (1955) and Stebbins (1957) ensures greater genetic variability through recombination in hetero-zygotic individuals.

Another widespread genetic device favouring outbreeding is self-incompatibility. The Chrysanthemum species are usually self-incompatible which has been recorded for species such as C. cinerariaefolium, C. makinoi, C. wakasaense (Fryxell, 1957) and C. carinatum (Jain and Gupta, 1960). Tanaka (1952) observed self sterility in pollination studies within diploid and tetraploid species of chrysanthemums which was attributed to self-incompatibility. Fryxell (1957) found some degree of self-compatibility in C. japonense, C. ornatum, C. pacificum, C. shiwogiku and one of the

elemental species of modern chrysanthemums, C. indicum. Fryxell (1957) reported complete self-incompatibility in tetraploid forms of C. indicum, while the hexaploids showed slight self-compatibility. Mulford (1937) and Tanaka (1952) observed self-compatibility in cultivars of C. morifolium, however, there is no explanation offered regarding the nature of incompatibility. Jain and Gupta (1960) and Brewer (1974) established four intra compatible groups in C. carinatum and proposed a sporophytic incompatibility system involving 2 loci. Similarly Brewer and Parlevliet (1969) suggested a sporophytic system for C. cinerariaefolium.

Dreulou et al. (1973) studied in detail the nature of self-incompatibility in hexaploid cultivars of C. morifolium and concluded that it is sporophytically controlled and there are more than one locus. Here, self-incompatibility is stable even at polyploid level and sterility is no problem as the cultivars of C. morifolium are perennial and propagation is through vegetative means.

Fryxell (1957), though unable to offer an explanation, observed that there is slight self-compatibility in garden chrysanthemums. This is further supported by recent study of Ronald and Ascher (1975)

who reported that there is some degree of self-compatibility in C. morifolium. They offered the explanation that the breakdown of self-incompatibility is caused by mutations of major genes (switch genes) controlling 'S' alleles.

4. CYTOLOGY

Upto 1981, out of nearly 160 species of the genus Chrysanthemum, 103 species have been cytologically worked out (Table III). The chromosome numbers in different cultivars of C. morifolium complex including the present study have been summarised separately in Table IV.

Table III

CHROMOSOME NUMBER IN CHRYSANTHEMUM SPECIES

Taxon	2n	Reference
C. alpinum L.	18	Skalinska et al. 1959; Favarger, 1964c; Polatschek 1966a.
	18,36	Contandriopoulos, Favarger, 1959 (L.1961); Favarger, 1962c; Titz, 1965.
	36	Chiarugi 1927a,b; Shimotomai, 1937b; Polatschek, 1966b.

Taxon	2n	Reference
C. anethifolium Hook et Harth.	18	Harling 1951a; Larsen, 1958b, 1960b; Linder, Lambert, 1965; Powell et al., 1974.
C. aphrodite Kitam.	54	Aijma (Shimotomai, 1938).
C. arcticum L.	64	Troy, Wimber, 1968; Dowrick, 1952b; Natarajan, 1964.
	90	Tahara, 1915a,c; 1921.
C. argentium	18	Dowrick, 1952b.
	18,27	Dowrick, El-Bayoumi, 1969.
C. arisanense Hayata	18	Mehra, P.N., Ramanandan, 1974; Ching-I-Peng, 1977.
C. atratum Jacq.	18	Shimotomai, 1937b, 1938.
	18,36	Dowrick, 1952b.
	18,54	Favarger, Villard, 1965a, b, 1966.
C. balsamita L.	18	Koul, M.L., 1964b. Dowrick, El-Bayoumi, 1969.
	18,54	Harling, 1951a; Dowrick, 1952b.
	54	Shimotomai, 1937b, 1938.
C. bipinnatum L.	72	Packer, McPherson, 1974.
C. boreale Makino	18	Dowrick, 1952b; Arano, 1965; Dowrick, El-Bayoumi, 1969; Scrugli, 1972; Terasaka, Tanaka, 1974; Watanabe, 1977a,b.
	18,19	Tanaka, 1959a.
	18,36	Kaneko, 1957.

Taxon	2n	Reference
C. broussonettii Sch. Bip.	18	Larsen, 1958b, 1960a,b.
C. brunatii Brig et cav.	18	Guinochet, Logeais, 1962.
C. callichryaum Svent	18	Borgen, 1974.
C. camphoratum (Less.) Voss.	54	Harling, 1951a.
C. canariense (Sch.Bip.) Christ.	18	Larsen, 1960b.
C. carinatum Schousb.	18	Tahara, 1914a, 1915a,c, 1921; Harling, 1951a; Vilmorin, Chopinet, 1954; Jain, Gupta, 1960; Sudha, Bhatnagar, 1963; Kapoor, Tandon, 1964a-d; Khamankar, Jain, 1965; Rana, 1964a, 1965b; Rana, Jain, 1965; Blixt (in Lamprecht, 1966); Kumari et al. 1967; Choukssnova et al. 1968a; Dourick, El-Bayoumi, 1969; Paria, Pradhan, 1971; Mehra, P.N., Ramanandan, 1974; Chaudhuri et al. 1976; Present study.
C. cassium	18	Dourick, 1952b.
C. catananche	18	Dourick, 1952b.
C. caucasium Pers.	36	Choukssnova et al. 1968b.
C. ceratophylloides All.	54	Shimotomai, 1937b, 1938.
C. cinerariaefolium Vis.	18	Tahara, 1915c, 1921; Shimotomai, 1947b (L. 1961); Dourick, 1952b; Fujiwara, 1954; Kawatani et al., 1956; Corsi, 1962; Koul, M.L., 1964a; Tominaga, 1968, 1969.
	18,27,36	Tominaga, 1959, 1967.
	36,36+18	Present study.

Taxon	2n	Reference
C. coccineum Willd.	18	Dourick, 1952b; Fujiwara, 1954; Tominaga, 1968, 1969.
C. coronarium L.	18	Tahara, 1914, 1915, C, 1921; Shimotomai, Takemoto, 1936, 1939; Glotov, 1939; Martinoli, 1943; Blixt (in Lamprecht, 1966); Dourick, El-Gayoumi, 1969; Granvall et al., 1971; Paria, Pradhan, 1971, 1976; Nordenstam, 1972; Queiroz, 1973; Scrugli, 1973; Mehra, P.N., Remanandan, 1974; Vanloon, 1974; Bhattacharya, 1977; Present study.
	18, 36	Shimotomai, Mara, 1935b (O., 1955); Dourick, 1952b.
	36	Scrugli, 1972.
C. coronopifolium Sch. Bip.	18	Larsen, 1960a,b.
C. corsicum	36	Contandriopoulos, 1964b.
C. corymbosum L.	18	Troy, Wimber, 1968; Majovsky et al., 1974.
	18, 18+8, 36	Dourick, 1952b.
C. crassum Kitamura	89	Watanabe, 1981c.
	36	Shimotomai, 1937b, 1938; Bijok, 1955, 1960; Murin, Vacheva (I. Slov. Fl. I, 1967); Dourick, El-Gayoumi, 1969; Present study.
C. cuneifolium	36	Shimotomai (Kitamura, 1957).
C. decaisneanum (Maxim.) Matsum.	72	Tahara, 1915a, 1921; Shimotomai, 1930, 1932, 1933, 1938.

Taxon	2n	Reference
C. erubescens	54	Dourick, 1952b.
C. filifolium Christ.	18	Shimotomai, 1937a,b; 1938.
C. flavifolium (Haffg. and Link) P. Lout	18	Mueiroe, 1973
C. flosculosum	18	Martinoli, 1942 (D.1955)
C. foeniculaceum Steud.	18	Harling 1951b; Lareen, 1958b, 1960b.
C. frutescens L.	18	Shimotomai, 1938; Harling, 1951a; Lareen, 1958b, 1960a,b; Dourick, El-Bayoumi, 1969; Bhattacharya, 1977.
	27	Tahara, 1915d; Dourick, 1952b.
	36	Present study
C. graminifolium L.	18	Favarger, 1962c.
C. hakusanense Makino	18	Tahara (Ishikawa, 1916)
	42	Tahara, 1921
	54	Shimotomai, 1933
C. heterophyllum Willd.	72	Favarger, 1959b; Favarger, Villard, 1965a,b; 1966.
	74,74+1-3B	Favarger, 1963b.
C. indicum L.	20	Hern, Lee, 1968
	36	Tahara, 1915a, 1921; Shimotomai, 1933, 1938; Shimotomai, Hara, 1935 (L.1961); Shimotomai, Takamoto, 1936, 1939; Takamoto, 1939; Tanaka, 1957; Watanabe, 1977.
	36,54	Dourick, 1952b; Tanaka, 1952 (L. 1961), 1955; Shimotomai et al., 1957; Shimotomai, Yoshinari, 1960.

Taxon	2n	Reference
	54	Dourick, 1953; Tanaka, 1955; Dourick, El-Bayoumi, 1969.
C. integrifolium Richards	18	Knaben, 1968; Mulligan, Cody, 1973.
C. ircutinsum Turez.	36	Shimotomai, 1930, 1937b, 1938; Gocher, Larsen, 1957a; Favarger, 1959b; Favager, Villard, 1965a,b; Larsen, 1965b; Bostick, 1965.
	36, 36+18	Favarger, 1963b.
	36+2-38, 38	Dorvard, Malloch, 1967.
C. japonense Nakai	54	Tahara, 1915a; Shimotomai, 1933, 1938; Dourick, 1952b; Watanabe, 1972, 1977a,b.
	72	Watanabe, 1977a,b, 1981a.
	54,72,90	Shimotomai et al. 1956, 1958.
	89	Watanabe, 1977a,b.
	54,90	Kaneko, 1961.
C. japonicum Makino	18	Tahara, 1914, 1915a,c, 1921; Shimotomai, 1932.
C. koreanum	54	Dourick, El-Bayoumi, 1969.
C. lacustre	198	Dourick, 1952b; Natarajan, 1964; Troy, Wimber, 1968.
C. latifolium (Max.) Kitagawa	36	Lee, 1967
C. lavandulaefolium Makino	16	Harn, Lee, 1968
	18	Tahara, 1914, 1915a,c, 1921; Tahara, Shimotomai, 1927, 1933, 1937b, 1938; Shimotomai, Takamoto, 1936, 1939; Tanaka, 1954, 1955.

Taxon	2n	Reference
C. leucanthemum L.	18	Tahara, 1921; Polya, 1950; Martin, Smith, 1955; Bakeay, 1956, 1960; Hostick, 1965; Duckert, Favarger, 1956; Favarger, Villard, 1965a,b; Larsen (C.n.IV.1965); Hindakova Uhrikova (I.Slov. fl. I. 1967); Jones S.B. 1968b) Pryzwara, Schmager, 1968, Taylor, Mulligan, 1968; Mehra, P.N., Ramanandan, 1974.
	25,26,27	Dourick, El-Bayoumi, 1969
	18+38	Doruard, Malloch, 1967
	18,36	Mehra, P.N. et al. 1965; Gadella, Kliphuis, 1966; Vasshaug (Knaben, 1966a); Mulligan, 1968b.
	18,36,54	Dourick, 1952b; Bocher, Larsen, 1957a; Mulligan, 1958, 1959; Skalinska et al., 1961; Czapik (Skalinska et al 1964); Gacek (Skalinska et al. 1964).
	18,36	Favarger, 1963b.
	54,54+1-3B 72	Favarger, 1963b.
	36	Tahara, 1915a,b,c,d, 1921; Uhrt D.C., Mahony, 1935; Negodi, 1937b (T. 1930); Rheuader, 1937; Shimotomai, 1937b, Love-A, Love. D., 1956b; Gadella, Kliphuis, 1963; Dourick, El-Bayoumi, 1969; Bhattacharya, 1977.
	90	Favarger, 1962a.

Taxon	2n	Reference
C. linearе Matsum.	18	Tahara, 1921; Shimotomai, 1933; 1938; Shimotomai, Takemoto, 1936, 1939; Tanaka, Shimotomai, 1961; Lee, 1972; Tanaka, 1966.
C. macrophyllum Waldst et Kit.	18	Shimotomai, 1937b, 1938; Dowrick, 1952b; Reese, 1953; Present study.
	36	Brosse-Sz 1970
C. macrotum Ball	18	Harling, 1951a; Dowrick, 1952b.
C. makino Matsum. et Nakai	18	Tahara, 1915a, 1921; Shimotomai, 1933, 1938; Shimotomai, Takemoto, 1936, 1939; Dowrick, 1953; Shimizu, 1962a; Watanabe, 1977b.
	18,19, 27	Tanaka, 1959b.
	36	Tahara, 1915a,c,d; Muziuara, 1958c; Shimizu, 1962.
C. marchallii Aschers	18	Choukeanova et al. 1968a.
C. marginatum Miq.	90	Tahara (Ishikawa, 1916), 1921; Tahara, Shimotomai, 1927; Shimotomai, 1931, 1932.
C. mauii	18	Dowrick, 1952b.
C. maximum Ramond	54	Bakaŝay, 1956, 1957a.
	≈72	Shimotomai, 1938.
	72	Favarger, Villard, 1966.
	85,90,126, 148,154,160, 171	Dowrick, 1952b.

Taxon	2n	Reference
	≃90	Harling, 1951a.
	108	Favarger, Villard, 1965a,b.
C. millefoliatum	18,18+8	Dourick, 1952b.
C. monspeliense L.	35,36	Favarger, Villard, 1965b.
C. montanum Allioni	54	Favarger, 1959b; Favarger, Villard, 1965a,b.
	54,54+1-38	Favarger, 1963b.
C. morifolium	42	Tahara
	54	Tahara, 1915c; Shimotomai, 1931,1932, 1933; Dourick, 1953.
	54,56	Tahara, 1915a.
C. multicaule Desf.	18	Harling, 1951a; Bhattacharya, 1977; Present study.
C. myconis L.	18	Tahara (Ishikawa, 1916), 1921; Harling, 1951a; Dourick, 1952b; Dourick, El-Bayoumi, 1969; Present study.
C. nipponicum Matsum.	18	Tahara, 1914, 1915a,c, 1921; Shimotomai, 1933, 1938; Shimotomai, Takamoto, 1936, 1939; Dourick, 1952b, Tanaka, Shimotomai, 1961; Nataraja, 1964; Tanaka, 1966; Watanabe, 1972; Present study.

Taxon	2n	Reference
C. nivellei Braun Blanquet et Maire	18	Harling, 1951a; Dowrick, 1952b.
C. oraeticum Herd.	18	Bhattacharya, 1977
C. ochroleucum Sch. Bip.	18	Larsen, 1958b, 1960a,b; Bhattacharya, 1977.
C. okiense	36	Shimotomai et al. 1957; Shimotomai, Yoshinari, 1960.
C. oreades	36	Dowrick, 1952b.
C. ornatum Hemsley	54	Dowrick, 1953.
	72	Shimotomai, 1933, 1938; Kaneko, 1961; Watanabe, 1972, 1977a,b, 1981b.
	90	Shimotomai, 1956 (Kitamura, 1958).
C. pacificum Nakai	90	Tahara, 1921; Shimotomai, 1933, 1938; Kaneko, 1957, 1961; Watanabe, 1977a.
C. pallens J.Gay	54	Bocher, Larsen, 1957a; Favarger, Villard, 1965a,b.
C. paludosum	18	Present study.
C. parthenium (L.) Benth.	18	Shimotomai, 1938; Harling, 1951a; Dowrick, 1952b; Turner et al., 1962; Dowrick, El-Bayoumi, 1969; Queiros, 1973; Present study.
	18,27	Gupta, P.K., Agarwal, 1972.
C. praelatum	36	Dowrick, 1952b.

Taxon	2n	Reference
C. praeteritum	18	Dourick, El-Bayoumi, 1969.
C. ptarmicaefolium (Vell. et Barth.) Brenan	36	Larsen, 1960a,b.
C. pyrenaicum	72	Ehrt (T. 1927).
C. roseum (Web. et Morris) Sch. Bip.	18	Tahara, 1914, 1921.
C. rotundifolium Waldst. et Kit.	18	Shimotomai, 1937b, 1938; Welelo (Skalinska et al. 1989a).
C. rubellum Sealy	54	Dourick, El-Bayoumi, 1969.
	63	Dourick, 1952b.
	70-80	Harling, 1951a.
C. rupestre Matsum et Koidz.	18	Sugiura, 1936a, 1937a; Nagami, 1957 (I. 1957); Tanaka, Shimotomai, 1961.
	19	Kitagawa, Nagami, 1960.
C. segetum L.	18	Tahara, 1921; Tischler, 1934; Rhoweder, 1937; Shimotomai, 1938; Delay, 1947; Harling (T. 1950); Bijok, 1960; Cadella, Kliphuis, 1968c; Strother, 1972; Muhra, P.N., Ramanandan, 1974; Bhattacharya, 1977; Present study.
	18,36	Dourick, 1952b; Dourick, El-Bayoumi, 1969.
C. serotinum L.	18	Dourick, 1952b, Bakaev, 1958; Hindakova (I.Solov fl. I. 1967).

Taxon	2n	Reference
C. shimotomai, Makino	54	Shimotomai, 1933, 1938.
	49.53, 54,55	Iwasa et al., 1972
	90	Dourick, 1952b.
C. shiuogiku Kitam.	72	Hara, Mori, 1935; Kanaka, 1961, 1962; Watanabe, 1972.
	72,90	Shimotomai, et al. 1968.
	71-76,76-80 86-92, 94	Shimotomai et al. 1968.
	90	Watanabe, 1977b.
C. sibiricum Fisch.	18,54	Shimizu, 1958a; Shimotomai, Hara, 1935 (D. 1955); Shimotomai, 1938.
C. silvaticum	54	Dourick, 1952b.
C. sonara	80	Dourick, 1952b.
C. subcorymbosum (Schur.) Beck.	18	Bijok, 1955, 1960.
C. togakuahiense	54	Kitagawa, Nagami, 1960.
C. tomentosum	18	Contandriopoulos, Favarger, 1959,(I.1959); Contandriopoulos,1962.
C. trifurcatum Desf.	18	Reese, 1957
C. uliginosum	18	Dourick, 1952b.

Taxon	2n	Reference
C. vikutsamus	36	Natarajan, 1964
C. viscidi-hirtum (Schott) Thell.	18	Harling, 1951a; Dowrick, 1952b.
C. viscosum L.	18	Battaglia, 1951.
	18,34, 36,37	Dowrick, El-Bayoumi, 1969.
C. vulgare Bemh.	18	Rosenberg, 1905; Shimotomai, 1937b, 1938; Sokolovskaja et. S. 1941; Vaarama, 1943; Harling, 1951a; Suzuka, 1953 (I.1956. Suppl.); Tanaka, Shimotomai, 1961; Soresa, 1962; Virrankoski et al. 1969.
C. wakasaense Shimotomai	27,34 36,72	Tanaka, 1959c.
	36	Shimotomai, 1938; Dowrick, 1952b; Tanaka, 1957.
C. webbii Nasf.	18	Harling, 1951a.
C. weyrichii Miyabe et Miyake	54	Shimotomai, 1933, 1938.
C. yezoense Maekawa	90	Shimotomai, 1933, 1938; Dowrick, 1952b.
C. yoshinoanthum Makino ex Kitam.	36	Natarajan, 1964; Shimotomai (Kitamura, 1957); Tanaka, 1957, 1960.

Taxon	2n	Reference
C. zawadskii Herbich.	18	Shiganaga (Shimizu, 1961).
	36	Harn, Lee, 1967b; Majovsky et al., 1974.
	54	Shiganaga (Kitamura, 1957); Shimizu, 1958a, b, 1961; Yamanaka, Moriehita, 1958; Pietrowicz (Skalinska et al. 1959); Shimizu, 1961; Lee, 1967; Watanabe, 1972.
	45-67	Shimotomai, 1938; Douriok, 1952b.
	72	Shimotomai, 1937b, 1938.

Table IV

CHROMOSOME NUMBER IN GARDEN CULTIVARS OF *CHRYSANTHEMUM MORIFOLIUM*

Taxon	2n	Reference
Amagahara Family	52, 54, 55, 56, 57, 58	Iwata *et al.* 1972
Bulkely Family		
'Bronze'	54	Sampson *et al.* 1958.
'Dark Pink'	55	" "
Brenda Talbot Family		
'Brenda Talbot'	55	Dowrick, El-Bayoumi, 1966a.
'Bronze'	53, 54	" "
'Incurving'	52, 53	" "
'Incurved Rose'	54, 55	" "
Favourite Family		
'Shuffle'	46, 47	Dowrick, 1953.
'Golden'	53, 54, 55, 56, 57	" "
'Deep Pink', 'Golden'	54, 55	Dowrick, El-Bayoumi, 1966a.
'White'	54, 56	Dowrick, 1953.
'Deep Pink', 'Favourite Supreme'	55	" "
'Bronze', 'Red Bronze'	56	" "
'Primrose'	57	" "
Fred Shoesmith Family		
'Fred Shoesmith'	54, 56, 57, 58	Dowrick, El-Bayoumi, 1966a.
'Apricot'	56, 57, 58	" "

Taxon	2n	Reference
'Florence'	54,57,58	Dowrick, El-Bayoumi, 1966a.
'Yellow'	52,58	" "
'Golden'	56,57,58,60	" "
Indianapolis Family		
'Golden Bronze'	54	Sampson et al. 1958
'Dark Yellow', 'Gold'	56	" " "
'Apricot', 'Bronze', 'Dark Bronze', 'Improved white', 'Pink', 'White', 'Yellow', 'Yellow C.C.F.'	57	" " "
Lace Family		
'Gold'	54	Sampson et al. 1958
'Hooked Yellow', 'Queen's Lace'	55	" " "
'Yellow'	55,56	" " "
Loveliness Family		
'Bronze'	52,54	Dowrick, 1953
'Lilac'	54,57	" "
'Amber', 'Apricot', 'Loveliness', 'Primrose', 'Purple', 'Salmon', 'Salmon Bronze'	56	" "
'White'	56,57	" "
Majestic Family		
'Red'	57	Dowrick, 1953
'Florence Reede', 'Yellow'	60,61	" "

Taxon	2n	Reference
Masterpiece Family		
'Bronze', 'Dark Bronze', 'Masterpiece', 'Rose', 'Salmon'	57	Sampson et al. 1958
My Lady Family		
'Red'	54	Dowrick, El-Bayoumi, 1966a.
'My Lady'	53,54	" "
'Apricot'	54,55	" "
News Family		
'Detroit News', 'Good News'	56	Sampson et al. 1958
Pocket Family		
'Louise', 'Yellow',	61	Sampson et al. 1958
'Thomas W. Pocket'	58,60	" " "
Princess Anne Family		
'Cream'	53+f	Dowrick, El-Bayoum, 1966a.
'Apricot'	53+1-2f, 54+f	" "
'Princess Anne'	51,54,55	" "
'Yellow'	53,55	" "
Queen Family		
'Jean Elizabeth'	57	Sampson et al. 1958
'Orchid Queen'	56,57,58	" " "
'Bronze Orchid'	57,59	" " "
'Crystal', 'Dark Orchid'	58	" " "
'Lavander'	58,59	" " "

Taxon	2n	Reference
Rayonnante Family		
'Amber', 'Yellow'	53, 54	Dowrick, El-Bayoumi, 1966a.
'White'	53, 54, 55	" "
'Bronze'	55	" "
'Rayonnante'	51, 54, 55, 57	" "
Shastha Family		
'Cream'	55	Sampson et al. 1958
'Shastha', 'Yellow Shastha'	56	" " "
Sweet Heart Family		
'Orange'	51, 54, 55, 56, 59	Dowrick, 1953
'Salmon'	53, 54, 56	" "
'Bronze', 'Sweet Heart'	54, 55	" "
'Apricot', 'Egerton', 'Peach', 'Pearl', 'Red'	55	" "
'Golden'	56	" "
Turner Family		
'Bronze'	59, 60	Sampson et al. 1958
'Yellow'	60	" " "
'William Turner'	60, 61, 62	" " "
'Eva Turner'	63, 64, 65	" " "
Valencia Family		
'Yellow'	56	Sampson et al. 1958
'Apricot', 'Crimson', 'Dark' 'Dubbonnet', 'Orchid', 'Salmon', 'Valencia', 'White'	57	" " "

Taxon	2n	Reference
Individual Cultivars		
'Janet Wills', 'Red Planet'	53	Dourick, 1953
'Wendy'	51,53,54	" "
'Irene Torrence', 'Mayford Red', 'Zenith'	53,54	" "
'Anastasia, 'Apollo' 'Autumn Gold', 'Bronze Freda', 'Cascade', 'Charm','Conqueror', 'Finale', 'Harvester','Honey Dew', 'Ivory', 'Mayland Flame','Salmon Freda', 'Snowfall', 'Youth'.	54	" "
'Harmony'	54,55,57	Dourick, El-Bayoumi, 1966a.
'Ronald'	54,56	" "
'Golden Coralie','Market Gold'	55	Dourick, 1953.
'Friendly Rival'	55,57	Dourick, El-Bayoumi, 1966a.
'Mrs. R.C. Pulling'	56,58	Dourick, 1953.
'Ballone'	57,58	Dourick, El-Bayoumi, 1966a.
'Louis Barthou'	58	Dourick, 1953
'Mrs. H. Wells'	59	" "
'Rise of Day'	60,61	
'Canada', 'Goliath', 'James', 'Bryant'	61	
'Duchess of Kent'	63	
'Birmingham'	63,64	

Taxon	2n	Reference
(ii) Japanese Cultivars		
cv. YS	36	Endo, 1969b.
cv. WS	51	" "
'Kôen-no-tsuki', 'Oriflame', 'Primavera', cv. RSE, 'Unalaga'.	52	Endo, 1969a,b.
'Nisshoki', 'Saga-no-tukasa', 'Saiko', 'Rose Star'.	52+1B	Endo, 1969a,b.
'Bibeni', 'Fuji-Botan', 'Fuji-Otome', 'Genkai', 'Hachinoche-jiku', 'Haku-ryuza', 'Hana-no-Sugata', 'Kan-Kobai, 'Kinpai', 'Kiryuzan', 'Kodama', 'Matsu-no-yuki', 'Mino-Kogane', 'Miyako-Ume', 'Myôjô', 'Natsu-botan', 'Natsu-remon', 'Oken-F1' 'Setsuciso', 'Tiptop', 'Touch Down', 'Utagaki', 'White Blush', 'White Tiptop', 'Yae-goromo', 'Yellow Iceberg', 'Yellow No.24, cvs. PL,RL,VL.	53	Endo, 1969a,b.
'Everest', 'Gold Arrow', 'Indian Summer', 'Miss-America', 'Nisshoki', 'Shin-Kogane', 'Tsuki-ga-se', 'Vanguard', 'Yuk-gesho'	53+1B	Endo, 1969a,b.
	53+2B	" "
'Abôkyu', 'Aka-Kogiku', 'Aka-Kogiku'-S_1, 'Aka-Kogiku-'S2, 'Appare', 'Ariyoshi-F_1, 'Asahi-no-hikari', 'Asa-no-yuki', 'Asayume', 'Beni-Otome-Zakura',	54	Endo, 1969a,b.

Taxon	2n	Reference
'Blazing Gold', 'Bogai-no-Kan', 'Daikan-Kinsei', 'Doseji', 'Fuji-hime', 'Fuji-no-mine', 'Ginzan', 'Hagorome-no-Kyoku', 'Haru-no-tsuki', 'Hatsuchinode', 'Hatsushi', 'Hatsushimo', 'Hi-no-maru', 'Hirakata-no-Sato', 'Hiroshima-haiua', 'Hokizuka', 'Iceberg', 'Kagayaki', 'Kan-botan', 'Ki-ari', 'Kingetsu', 'Ki-rihon-bara', 'Kinkanshoku', 'Kin-matsuba', 'Kinsei', 'Ki-Otome-Zakura', 'Kishi-no-gyokuo', 'Kishi-no-namikaze', 'Kiyomasa', 'Kogane-maru', 'Komachi Zakura', 'Ma', 'Midori-no-Koromo', 'Minami-taiheiyo', 'Mino-no-Konami', 'Miou-hiroshima-haiua', 'Mokuren-Ki', 'Mokuren-Shiro', 'Momo-no-Sato', 'Mura-musume', 'Nakamura', 'Namikoshi-no-Sakura', 'Natsu-giku', 'Nihon-bare', cvs.No.6, No.17, 'Ogonhiroshima-haiua, 'OM', 'Oranji', 'Oranji-ki', 'Otome-Zakura', 'Ouchiyama', 'Pink No.6', 'Red Skin', 'Rusruck', 'Saga-no-akatsuki', 'Saga-no-Sugata', 'Saga-no-yokobue', 'Seiko-bizan', 'Seiko-no-todoroki', 'Seiza', 'Shin-Kishi-no-gyokuo', 'Shin-Kori-Komachi', 'Shin-megami', 'Shin-Otome-Zakura', 'Shirayuki', 'Shiro-ari', 'Shiro-tome-Zakura', 'Tagoto-no-tsuki', 'Tokiwayuja', 'Tsuki-no-miyako', WE, White No.2, 'White Star', cv.Y. 'Yaguruma', 'Zao-giku' (Niga-giku).		
'Fred Yule', 'Furo' 'Gyokusui-no-nen', 'Kasai-Jin'.	54+18	Endo, 1969a,b.

Taxon	2n	Reference
'Saiko-no-sugata', 'Shin-Saiko-no-Sugata'	54+2B	Fukushima et al. 1955; Endo, 1969.
'Shin-oka-no-Sugata'	54+2B	Fukushima et al. 1965
'Aka-otome-Zakura', 'Alzuki', 'Ama-Otome', 'Ava-botan', 'Bronze Crou', 'Chikubu-jima', 'Delware', 'Elizabeth', 'Explorer', 'Ginkaku', 'Ginpo', 'Gimpo-zan', 'Gintaki', 'Gyokko-no-todoroki', 'Hagani-no-yuki', 'Hanazono-no-asa', 'Hanazono-no-hikari', 'Hyakka-Kincho', 'Ikuchiyo', 'Imizu', 'Jet Fire', 'Koyo-no-Sakura', 'Kincha-nishiki', 'Kin-byobu', 'Ki-tairin', 'Kiyomizu', 'Kôgetsu', 'Kogen-no-haru', 'Kori-komachi', 'Kusamakura', 'Mine-no-matsu', 'Miau-yamato, 'Miyo-no-takara, 'Mura-no-takara', cv. MT. 'Ogon-Okina-no-tomo', 'Okayamahaiwa', 'Pinocchio', 'Red Boise', 'Red Zam', 'Saga-no-iori', 'Saidai-no-toku', 'Saiko onootakara', 'Shimizu-no-ike', 'Statesman', 'Tachibana', 'Takasago', 'Tokyô-no-hana', 'Tokyô-no-kagayaki', 'Tokyô-no-yuki', 'Vedova', 'White Boie', 'Yachigo', 'Yellow Boie', 'Yellow Delware', 'Yellow Vedova'.	55	Endo, 1969a,b.
'Everest', 'Ito-Zakura'.	55+1B	Endo, 1969a,b.
'Adeka', 'Ama-ga-hara', 'Genkai', 'Good News', 'Hakuogo', 'Hamanaka-Fukuro-ogiku', 'Kasugahima', 'Ki-ama-ga-hara', 'Kinkazan', 'Konao', 'Matsukaze', 'Misono', 'Saiko-fuji', 'Shin-Kagura', 'Shirotsubaki', 'Shoua-no-kagayaki', 'Tenkai'.	56	Endo, 1969a,b.

Taxon	2n	References
'Ume-goton', 'Yoshida-giku', 'Okano-hatsuyuki', Shin-Okano-hatsuyuki.	56	Endo, 1969a,b.
	56+1B	Fukushima et al.1965
'Gyokko-no-nami', 'Konjiki-yasha'	56+1B	Endo, 1969a,b.
'Jackstrau', 'Mono-asobi'	57	Endo, 1969a,b.
'Okano-hatsuyuki'	57+1B	Fukushima et al. 1965
'Bansei-arupusu', 'Dai-manzetsu', 'Fred Shoesmith', 'Goko-no-aki', 'Kogen-no-izumi', 'Kogen-no-kumo', 'Lemon Fredshoesmith', 'Shin-taiho bizan', Taiho-bizan'.	58	Endo, 1969a,b.
'Fuzan-no-kumo', 'Iyasaka', Saiko-no-hana'.	59	Endo, 1969a,b.
'Taiho-no-Sakae'	59+1B	" "
'Manazuru'	61	" "
'Beni-tengu', 'Kago-no-taki', 'Sennyo-goromo', 'Shinroku-Kikuo', 'Shinrokuen'.	62	" "
'Enmei-raku', 'Miyako-no-tsuki'.	63	Endo, 1969a.
'Aka-tairin', 'Sanyo-nishiki', 'Uji-meguri'.	64	Endo, 1969a.
'Kurama-tengu', 'Motte-no-hoka', 'Taiho-yamabuki'.	65+1B	" "
'Aikoku-den', 'Kasumi-ga-ura, Kirin-Zakura'.	66	" "
'Kinkonshiki', 'Shin-kasumi-ga-ura'.	67	" "

Taxon	2n	Reference
'Ora-no-aki'	68	Endo, 1969a.
'Haisu-zakura', 'Nobi-no-otome'	69	" "
'Tokiwa-no-matsu'	70	" "
'Hakusan-goten'	70+1B	" "
'Dando-no-hana', 'Mino-no-Shirabe', 'Wako-den'	71	" "
'Shuko-den'	71+1B	" "
'Chiyo-giku', 'Gyokko-no-akatsuki', 'Iorihime-kii' 'Mino-no-sakae', 'Ogon-den'	72	" "
'Gingetsu', 'Gyokusui-no-kobai,' 'Hana-katami', 'Oke-no-sakae'.	73	" "
'Fuki-den'	73+1B	" "
'Mino-no-homare', 'Oku-goten'.	74	" "
'Momoyama-goten'	75+1B	" "

(iii) Indian Cultivars

'Liliput'	36	Present study
'Kasturi', 'Phyllis', cvs. P1, P5	45	" "
'Anamika', 'Rosa', 'Sharad Mala', cvs. AA6, C8, G2, OO5, SO2, SS_1, T_2, T_5, X_2, Y_{15}.	63	" "
'Alba', 'Adra Shoesmith', 'Ajina Purple', 'Alfred Durham', 'Apsara', 'Badger', 'Bharat Ratna', 'Basanti', 'Boustau',	54	" "

Taxon	2n	Reference
'Bullan Hall size', 'Cleopatra' 'Dipti', 'Fish Tail', 'Freedom', 'Heloise', 'Hope', 'Jessie', John Reid', 'Kanchen', 'Lalquila', 'Laura', 'Lilith', 'Linda', 'Lord Roberts', cv. Maharaja of Sikkim', 'Mercury', cv. Miniature, 'Mohini', 'Mrs. C. Totty', 'Mrs. G. Llyod Wigg', 'Nanako', 'Northern Lights', 'Otome Zakura', 'Pride of Madford', 'Red Star', 'Roger Thompson', 'Sharad Mukta', 'Sharad Prabha', 'Sharad Shobha', 'Shinfuji', 'Silver Cloud', 'Snow White', 'Spoon', 'Summer Gem', 'Sveta', 'W.A. Etherington', 'White Cloud', cv. Yellow (Bombay), cvs. A5, A16, AA4, C6, C7, C9, D5, E10, E11, E14, J4, K1, K2, M4, M45, M52, MS2, N10, N14, N15, N18, NN12, NN14, ON1, ON3, ON10, O4, P6, Q6, QQ2, QQ10, P8, Q8, R18, S1, S3, S4, S7, S8, S9, s04, T1, T6, T7, T8(S), T8(L), T9, T19, T38, W9, W20, W23, X1, X5, Y21, cv. No.5.	54	Present study
'Nigeria', 'Red Princess Anne' cv. U1	54+1B	Present study
'Birbal Sahni', 'Bob Pulling', 'Dainty Maid', 'Donald', 'Flirt', 'Lohengrin', 'Megami', 'Pink Cloud', 'Sharad Bahar', 'Valiant', cvs. C1, F10, M16, M56, NO1, NN9, NN10, P3, S5, T10, T19, U2, U4, U14, cv. White (Kerala), X2.	55	Present study
'Evening Star', 'Golden News' 'Kikubiyouri', cv. M27, M30.	56	Present study
'Innocence'	56+1B	Present study

Taxon	2n	Reference
'Connie Maynew', cv. M_{31} 'Bronze Turner', 'J.H. Salisbury', 'Knox'	57	Present study
'Salmon Shoesmith' cvs. M_7, R10	58	" "
'R.M. Quittenton', cv. T17	59	" "
'Rupasa Bangla'	60	" "
'Kasturba Gandhi' 'Mahathma Gandhi'	62	" "
'Grape Soul', 'Improved Louie Pocket', 'John Webber', 'Morris White', 'President Viger'	63	" "
'Alfred Simpson', 'Alfred Wilson', 'Florence Shoesmith'	64	" "
'Harvest Home', 'John Bull' 'Golden Anniversary'	65	" "
'Sonar Bangla' cv. W25	67	" "
'Phil Houghton'	68	" "
'Ghenghiskhan', 'Potomac'	72	" "

The above reports of chromosome number in the genus Chrysanthemum are clearly indicative of a common basic number of 9 which forms a polyploid series ranging from 2x to approximately 22x. Apart from this, several aneuploid chromosome numbers such as 2n = 19, 20, 25, 26, 29, 34, 37, 42, 47, 53, 55, 56, 57, 58, 59, 71, 80, 85 etc. have also been reported in the genus. The cytological work on this genus has been confined mostly to chromosome counts and cytotaxonomic studies. The present investigation deals with cytological analysis of 13 species and 183 cultivars of C. morifolium. Out of 183 cultivars, one was tetraploid, 4 pentaploids, 98 hexaploids, 5 heptaploids, 2 octoploids and 69 were aneuploids. Four cultivars showed one B-chromosome each in their somatic cells (Fig. 50).

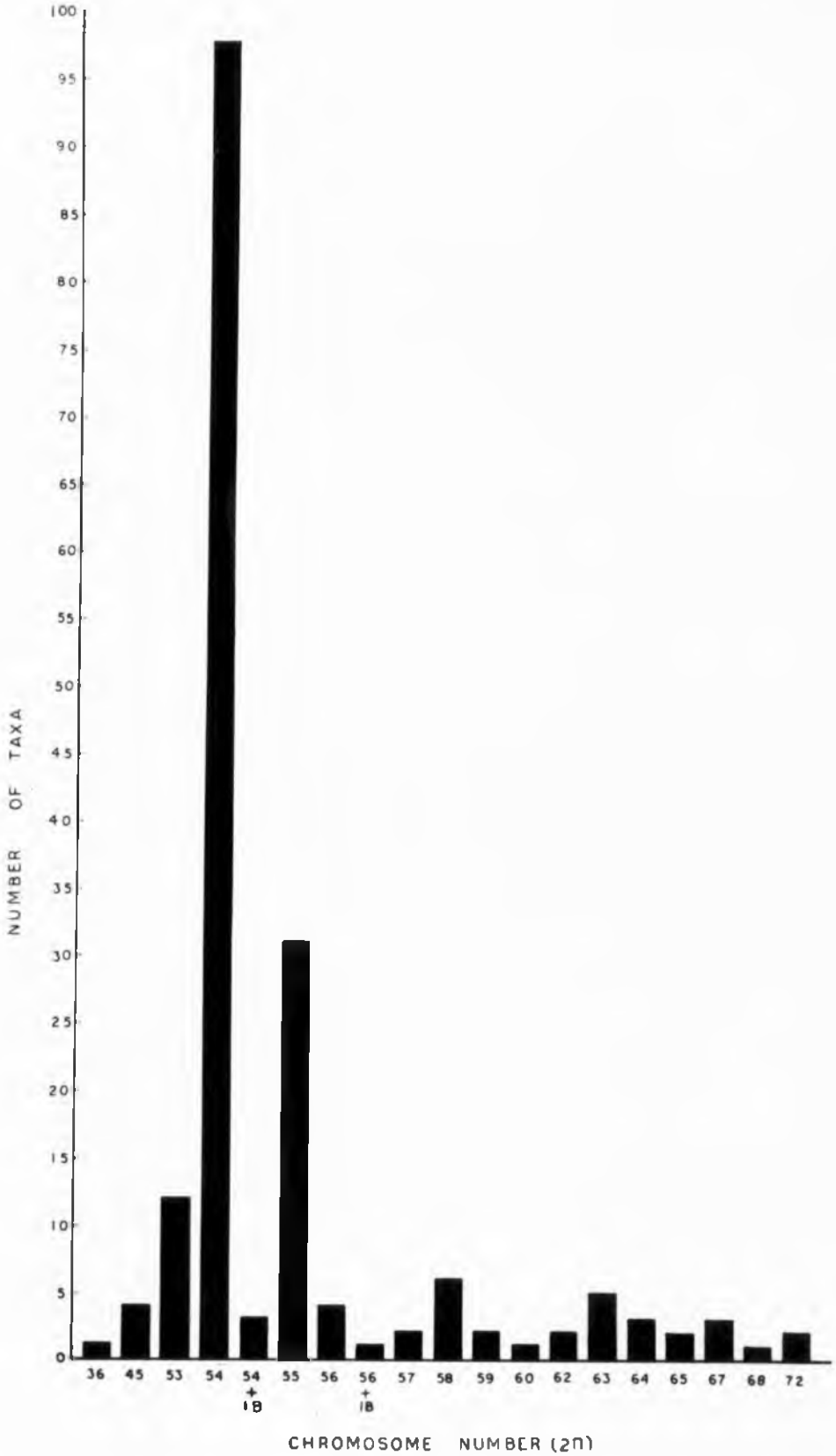
Observations

TETRAPLOID

Karyotype

One and the only cultivar ('Liliput') belonging to the Button group was found to be tetraploid. Thirtysix chromosomes were counted in the root tip mitosis (Fig.51). These chromosomes could be resolved into 9 more or less homomorphic sets containing 4 chromosomes each (Fig.52).

Fig. 50: Histogram showing various chromosome numbers in *C. morifolium* cultivars


NUMBER OF TAXA
100
95
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
36
45
53
54
54 + 1B
55
56
56 + 1B
57
58
59
60
62
63
64
65
67
68
72
CHROMOSOME NUMBER (2n)

One chromosome belonging to the 9th set showed heteromorphicity due to its greater length and a submedian centromere. This resulted in a change of arm ratio (Table V). To a lesser extent such heteromorphicity is seen in the 6th and 7th sets of chromosomes (Fig. 52). In the complement, four chromosomes with satellite was observed, two of which have primary constrictions in median position (1st set) and two others in submedian position (8th set).

Meiosis

Meiosis in the tetraploid cultivar was characterised by the presence of quadrivalents and bivalents (Figs. 53-55). The data on chromosomal associations at metaphase I is summarised in Table VI. The number of quadrivalents per cell ranged from 0 to 3 with mean at 1.08 ± 0.25, and bivalents from 12 to 18 with mean at 15.84 ± 0.31. At diakinesis 2 bivalents were found to be attached to the nucleolus (Fig. 53). Anaphase I segregation was predominantly normal (Fig.55) but in some cells lagging chromosomes were also observed. Pollen stainability was 81.20% and there was moderate seed setting.

PENTAPLOIDS

Karyotype

Four cultivars were found to be pentaploids with 45 chromosomes in their root tip cells (Figs.56-58), out of which cvs. P_1, P_5 and 'Kasturi' have been studied in detail. The karyotypic data of these cultivars are summarised in Table V. In all the cultivars, 45 chromosomes formed 9 sets with varying number in each set (Table V and Figs. 59 and 60). Cultivar 'Kasturi' had 9 chromosomes with strictly median centromere (M, r index=1). Chromosomes of other cultivars possessed median to subterminal centromeres. Heteromorphic sets were seen in 'Kasturi' and cv. P_1 and in both the cases heteromorphicity was due to variation in length of the short arm. In 'Kasturi' such heteromorphic chromosomes were seen in the 1st, 2nd and 8th sets (Fig. 59). In cv. P_1 the 3rd set was heteromorphic (Fig. 60), however, one chromosome belonging to the subterminal group (9th) in cv. P_5 showed a larger long arm. One small odd chromosome with a median centromere was seen in the 8th set of 'Kasturi' and 7th set of cv. P_1. Five satellitic chromosomes were observed in 'Kasturi' which formed the 2nd set. Only one such chromosome (submedian centromere) was seen in the 8th set in cv. P_1. In cv. P_5 four

satellited chromosomes could be seen in the 1st set. Nucleolar chromosomes of 'Kasturi' exhibited small but consistent variation in their relative length.

Meiosis

Meiotic analysis of the pentaploid cultivars revealed the presence of pentavalents, quadrivalents, trivalents, bivalents and univalents at diakinesis and metaphase I (Figs. 61-65). The data regarding chromosomal associations and pollen stainability etc. are summarised in Table VII. In 'Kasturi' the number of pentavalents ranged from 0 to 2 with a mean number of 0.22 ± 0.50 while cvs. P_1 and P_5 showed a range of 0 to 1 and mean at 0.24 ± 0.14 and 0.38 ± 0.21 respectively. The number of quadrivalents in all the cases range from 0 to 1 with mean 0.13 ± 0.38, 0.13 ± 0.09 and 0.56 ± 0.28 respectively. However, the trivalents showed a range from 0 to 5 in 'Kasturi' with mean at 2.09 ± 0.12, in cv. P_1 the range was 1 to 3 with mean at 1.60 ± 0.44 and cv. P_5 showed a range of 1 to 4 with mean at 2.24 ± 0.89. At diakinesis, in cv. P_1, one pentavalent was found attached to the nucleolus (Fig. 62). The number of bivalents varied in different cultivars and the highest mean number of bivalents (16.52 ± 0.42) was observed in 'Kasturi' (see Table VII). The mean number of univalents varied from 4.08 ± 0.59 ('Kasturi', cv. P_5) to 6.20 ± 0.13 (cv. P_1).

As expected, anaphase I segregation in all the cultivars was highly irregular with unequal segregations like 19:26, 21:24, 20:25 etc. (Fig. 66). Lagging chromosomes, precocious division of univalents etc. were encountered (Fig. 67). Subsequent division was also abnormal, which resulted in the formation of micronuclei (Fig. 68) leading to the formation of aneuploid gametes. The pollen stainability in 'Kesturi' was very low (15.60%) and highest pollen stainability (84.75%) was observed in cv. P_5. However, only cv. P_1 set seed and other cultivars were totally seed sterile.

HEXAPLOIDS

Karyotype

Out of 98 hexaploid cultivars studied, 27 were karyotypically analysed, the data of which is summarised in Table V. These cultivars uniformly showed 54 chromosomes in their root tip cells (Figs. 69-76), and include both small flowered as well as large flowered types. The karyotypic data show considerable heterogenity in the karyotypes ranging from the presence of strictly median (M, r index 1.0) to those with subterminal and in one case even a pair of terminal chromosomes (Table V and Figs. 77-90).

There are five cultivars viz. cvs. 59, 'Dipti', M_{52}, 'White Cloud' and 'Red Star' with 4-7 strictly median chromosomes in the karyotype (Figs. 77 and 78). In fourteen cultivars viz. cvs. K_1, 'Snow White', 'Laura', 'Summer Gem', 'Nagami', 'Silver Cloud', 'Lilith', 'Linda', cv. T_1, 'Badger', 'Rosetsu', 'Basanti', cv. NN_{12}, and 'Hope', there is preponderance of either median (m) or submedian (sm) chromosomes (Figs. 79-85). While seven cultivars viz. X_1, M_{45}, K_2, 'Spoon' NN_{14}, 'Nanako' and P_8 have invariably shown the presence of subterminal (st) chromosomes in the complement (Figs. 86-89). One cultivar ('Mohini') possess two chromosomes with terminal centromere (Fig. 90).

The number of each set are seldom homomorphic and shows more or less small differences with regard to the total length of the chromosomes and the exact location of centromere which changes the long/short arm ratios. This is clearly seen in cultivars 'Rosetsu', 'Summer Gem', 'Spoon', 'Hope', cv. M_{52}, NN_{14}, P_8, 'Linda', 'Badger', 'White Cloud', X_1 etc. One odd chromosome each with a median and submedian centromeres respectively was found in cultivars like NN_{12} and NN_{14} (Figs. 85 and 88).

The number of nucleolar organizers varies from one (cvs. K_1, 'Silver Cloud' and 'Nanako') to 5 ('Red Star'). These are located in different sets of chromosomes. The variation in number of nucleolar chromosomes is perhaps the result of varying condensation of chromosomes, as also the satellite themselves.

Meiosis

Seventeen representative taxa were subjected to meiotic analysis. At diakinesis and metaphase I various chromosomal configurations ranging from hexavalents to univalents were observed in the PMCs (Figs. 91-96). The details of chromosomal associations, pollen stainability etc. are recorded in Table VIII. In majority of the cultivars analysed, meiosis was characterised by the presence of a large number of bivalents and a few multivalents. Cultivars 'Sharad Shobha', 'Sharad Prabha', cv. Y_{21} and cv. No.5 have revealed the presence of large number of bivalents and a few univalents in nearly 90 per cent of the PMCs. No pentavalent association was found in any of the cultivar studied.

Hexavalents are generally absent, but one (Fig. 94) or at the most two (Table VIII) may be found.

Their mean number varies from 0.04 ± 0.11 ('Lalquila') to 0.42 ± 0.22 (cv. U 18) per cell. The number of quadrivalents ranged from 0 to 4 and the mean was from 0.56 ± 0.20 ('Lalquila') to 1.60 ± 0.07 (cv. No.5). The number of trivalents in various cultivars ranged from 0 to 3, however, cv. ONI was an exception, where no trivalent was found. The range in mean number of trivalents was from 0.04 ± 0.12 in cv. T_7 to 0.64 ± 0.66 in 'White Cloud'. In all, the cultivars a large number of bivalents were seen, which ranged from 14 to 27 with mean 22.75 ± 0.45 (cv. T_6) to 25.53 ± 0.32 (cv. Y_{21}). Only few univalents could be seen, the mean number was as low as 0.07 ± 0.50 ('Lilith') or as high as 0.88 ± 0.41 ('Lalquila') per cell. In most cases univalents appear to have originated as a result of precocious separation of bivalents. In 'Mohini' the two telocentric chromosomes often paired to form a bivalent.

Anaphase I was quite normal with a segregation of 27:27 in most of the cultivars. Occasionally, some cultivars showed unequal segregation, such as 25:29, 24:30, 26:28 etc. (Fig. 97). Sometimes the univalents lag at anaphase I or divide precociously. The second division, in general, was irregular with formation of

laggards, micronuclei etc. (Fig. 98). Irrespective of abnormalities in the second division, there was high percentage of pollen stainability and good seed setting.

HEPTAPLOIDS

Karyotype

Three cultivars with a somatic chromosome number of 2n = 63 in the root tip cells (Figs. 99 and 100) were karyotypically analysed. The karyotypic details are shown in Figs. 101-103 and summarised in Table V. The over all nature of the karyotype resembles the hexaploid cultivars in as much as the chromosomes may be submedian or subterminal, and members of different sets of chromosomes differ in over all length and arm ratios (Figs. 101-103). One ('Grape Bowl') or two ('John Webber') chromosomes were indeed small and rather odd and could not be assigned to any of the sets. In the former the odd chromosome was with a more or less median constriction, while in the latter, one such chromosomes each was with submedian or subterminal centromeres. The maximum number of nucleolar chromosomes seen, was five in 'Grape Bowl'. All these were located in the second set of chromosomes (Fig. 102).

Meiosis could not be studied for want of sufficient material at the right stage.

OCTOPLOIDS

Karyotype

Out of two octoploid cultivars showing 72 chromosomes in the root tip cells (Fig. 104), cv. 'Chenghiakhan' was analysed karyotypically. The karyotype resolved into 9 more or less homomorphic sets (Fig. 105). The details of karyomorphology, arm ratio, etc. have been recorded in Table V. Two chromosomes, belonging to the 6th set, had slightly smaller short arms and could be differentiated from the other chromosomes. Due to over condensation of the chromosomes, the nucleolar chromosomes were not clear. Majority of the chromosomes were either metacentric or submetacentric. Only 6 chromosomes of the 9th set showed subterminal primary constrictions of which one was odd in the complement and showed a very small short arm (Fig. 105).

Meiosis

Meiosis in 'Chenghiakhan' was characterised by the presence of octevalents, hexavalents, bivalents, etc. (Figs. 106-110). A detailed analysis of chromosomal associations at metaphase I was carried out and the data is summarised in Table IX. The octavalents ranged from 0 to 1 per cell with a mean of 0.08 ± 0.05; heptevalents

were not seen. The number of hexavalents and pentavalents showed a range of 0 to 1 with mean 0.17 ± 0.30 and 0.02 ± 0.12 respectively. The mean number of quadrivalents per cell was 1.17 ± 0.44 and trivalents 1.08 ± 0.98. Bivalents ranged from 25 to 34 and the mean number was 30.41 ± 0.65. Univalents were seen in very low frequency and the average number per cell was 1.50 ± 0.12. Anaphase I segregation was irregular with unequal segregation of chromosomes, presence of laggards, etc. Sometimes chromatid bridges were also seen to persist even in the late stages of anaphase I (Fig. 111). Subsequent division was also irregular with formation of laggards, micronuclei etc. (Fig. 112).

It is interesting to note that in 44% of the PMCs one B-chromosome was consistently seen which was very small in size when compared to other A-chromosomes (Figs. 109 and 110). The B-chromosomes showed a tendency to remain unpaired and away from the A-chromosomes. During anaphase, the B-chromosome either divided or got included in one of the poles without undergoing division. However, in root tip cells, it was completely eliminated. Though pollen stainability was 93.5%, there was no seed setting.

ANEUPLOIDS

2n = 53 (6x - 1)

Karyotype

Nine cultivars having a chromosome number of 2n = 53 (Figs. 113-116) have been karyotypically analysed and the data is summarised in Table V. The chromosomes formed more or less homomorphic sets in all the cultivars (Figs. 117-121). In none of the cultivars, the deficient chromosome could be identified with certainity. The different cultivars under this group differ in details of karyotype like composition of chromosome sets, length of chromosomes, arm ratio and the number and nature of satellites. This effect the morphology of the chromosomes. Minor heteromorphicity was noted in the complement of various cultivars like 'Sharad Mala', cvs. 005, G_2, SS_1 and T_5. The number of SAT chromosomes varies from one (cvs. SS_1 and G_2) to seven (cv. T_2). Some of these variations have been depicted in Figs. 117 to 121.

Meiosis

Four aneuploid cultivars of the above category have been meiotically analysed and the data is summarised in Table X. There was predominant bivalent formation in

all these cultivars. The number of multivalents, though few, was variable. The various chromosomal configurations in representative cultivars are depicted in Figs. 131 and 132. The number of hexavalents ranged from 0 to 1 with mean ranging from 0.04 ± 0.06 ('Rose') to 0.08 ± 0.60 (cv. AA6). Quadrivalents ranged from 0 to 3 with mean ranging from 0.23 ± 0.45 ('Sharad Mala') to 1.05 ± 0.04 ('Anamika'). Trivalents showed a range of 0 to 2 with mean from 0.10 ± 0.28 ('Sharad Mala', 'Anamika') to 0.33 ± 0.60 (cv. AA6), and bivalents 20 to 26 with mean from 23.75 ± 0.30 ('Anamika') to 25.43 ± 0.63 ('Sharad Mala'). In cells forming a maximum number of 26 bivalents, one univalent was always observed (Fig. 131), however, in some cells these univalents associated with bivalents to form trivalents (Fig. 132). Unequal distribution of chromosomes such as 26:27, 25:28 etc. was observed at anaphase I and subsequent division also showed anomalies. Often, the univalents were found to disjoin precociously and go to either poles.

The pollen stainability was appreciably high and there was good seed setting.

2n = 55 (6x + 1)

Karyotype

Twelve cultivars having somatic number 2n = 55 (Figs. 122-125) have been karyotypically analysed and the details of karyomorphology is summarised in Table V and Figs. 126 to 130. It was not possible to identify the extra chromosome through karyotype analysis. The individual cultivars differed in the composition of the karyotypic details like morphology of chromosomes and the number of satellites and such other details (Figs. 126-130). As is the case with other cultivars, heteromorphic sets of chromosomes were seen in cultivars like X_2, U_2, C_1, NN_8, 'Flirt' and 'Valiant'. One small odd chromosome was located in the complement of cv. NN_8. The number of SAT chromosomes varied from one (cv. NN_{10}) to five (cv. NN_9).

Meiosis

The data on meiotic analysis of four cultivars is given in Table X. Metaphase I in PMCs was characterised by predominant bivalent formation and occasional appearance of multivalents (Figs. 133-134). In cells where multivalents are formed, the number of hexavalents ranged from 0 to 2 with mean ranging from 0.08 ± 0.60

(cvs. P_3, T_{19}) to 0.16 ± 0.95 ('Dainty Maid'). In 'Sharad Bahar' no hexavalents were found. The number of quadrivalents in different cultivars ranged from 0 to 3 with mean from 0.45 ± 0.05 ('Sharad Bahar') to 0.87 ± 0.18 ('Dainty Maid'). The trivalents showed a range of 0 to 1 with mean ranging from 0.05 ± 0.43 ('Sharad Bahar') to 0.36 ± 0.50 (cv. T_{19}). Seventeen to 27 bivalents were seen and the range in mean was 24.37 ± 0.58 ('Dainty Maid') to 25.97 ± 0.70 ('Sharad Bahar'). Few univalents were observed and the maximum number per cell was 1.11 ± 0.15. One chromosome generally remained as a univalent (Fig. 133), however, occasionally it was found to pair with bivalents to give rise to trivalent configurations (Fig. 134). Whether this was the extra chromosome, can not be said with certainity. Other univalents were mostly the result of precocious separation of bivalents.

As expected of an aneuploid, anaphase I segregation was unequal with varying number of chromosomes going to either poles (Fig. 135). One chromosome was often seen to divide precociously (Fig. 135) and reached opposite poles towards the end of anaphase I. Unequal segregation of chromosomes resulted in further errors

in the second division leading to the formation of aneuploid gametes. Though meiosis was irregular, there was reasonable pollen stainability (72.4% to 89.2%) and moderate seed setting.

$\underline{2n = 56}$ (6x + 2)

Karyotype

Two cultivars having a chromosome number of 2n = 56 in the root tip cells (Fig. 136) have been karyotypically analysed and the data is summarised in Table V. Varying number of chromosomes appeared in different sets and the karyotype resolved into 9 more or less homomorphic sets. Cultivar N_{27} had completely homomorphic sets while 'Golden Wave' showed the presence of two heteromorphic chromosomes with smaller short arms in the first set and one of the chromosomes carried a satellite on its short arm (Fig. 144). Another small chromosome was detected in the 8th set of 'Golden Wave'. In cv. N_{27}, 3 SAT chromosomes were observed, one in the second set and one each in the sixth and ninth sets.

Meiosis

Meiotic data of one cultivar i.e. cv. N_{30} is available and at metaphase I bivalents and multivalents

were detected (Fig. 156). The details of chromosomal association are shown in Table X. The average number of hexavalents per cell was 0.06 ± 0.51, quadrivalents 0.51 ± 0.03, trivalents 0.35 ± 0.18 bivalents 25.87 ± 0.12 and univalents 0.71 ± 0.35. Anaphase I was predominantly normal, however, abnormal segregation and formation of laggards etc. were also found in few PMCs. Though the pollen stainability was high (81%) no seed formation was seen.

$$\underline{2n = 57}\ (6x + 3)$$

Karyotype

Cultivar 'Lennie Mayhew' showed 57 chromosomes in its root tip cells. Karyotypic analysis revealed the presence of more or less homomorphic sets (Fig.148). The number of chromosomes belonging to individual sets varied (Table V). The cultivar possessed metacentric, sub-metacentric and subtelocentric chromosomes. Owing to extreme condensation of the chromosomes, nucleolar pairs were not seen in the complement.

Meiosis

Like other aneuploid cultivars, predominant bivalent formation and a few multivalents were seen

at diakinesis and metaphase I in the pollen mother cells (Fig. 157 and Table X). The mean number of hexavalents and pentavalents was 0.03 ± 0.18 per cell, quadrivalents 0.58 ± 0.06 and trivalents 0.68 ± 0.63. The average number of bivalents was 25.27 ± 0.37 and univalents showed a mean of 1.67 ± 0.45. Anaphase segregation was highly irregular. Pollen stainability was very low (37.5%) and there was no seed setting.

2n = 58 (6x + 4)

Karyotype

Out of 5 cultivars having a chromosome number of 2n = 58 in their root tip cells (Fig. 137) two have been karyotypically analysed. The karyomorphology is shown in Fig. 146 and arm ratio etc. is summarised in Table V. Cultivar 'R1D' had metacentric (M, r index 1.0) to submetacentric chromosomes in the complement and the chromosomes in general, resolved into homomorphic sets. The exception was with regard to few chromosomes in 2nd and 8th set. The 8th set had a pair of heteromorphic chromosomes, one of them having a smaller short arm and the other one had longer long arm. In 'Bronze Turner' the 9th set contained one pair of heteromorphic chromosomes. Nucleolar pairs were not seen in either of the two cultivars.

Meiosis

Cultivar 'J.H. Salisbury' was meiotically analysed, the metaphase I data is depicted in Table X. Univalents, bivalents, multivalents etc. were seen at diakinesis and metaphase I (Fig. 158). The mean number of hexavalents per cell was 0.08 ± 0.36, that of quadrivalents 0.69 ± 0.27, trivalents 0.43 ± 0.50, bivalents 26.21 ± 0.52 and univalents 0.57 ± 0.19. Anaphase I in most of the cells showed normal segregation, however, irregular segregation was also observed in some PMCs. Pollen stainability was 53.2% and there was no seed setting.

$2n = 59$ (6x + 5)

Karyotype

The somatic chromosomes of cv. T17 resolved into 9 sets with varying number of chromosomes in the individual sets (Fig. 147 and Table V). The first set was heteromorphic and one of its chromosomes was with a median centromere (M, r index 1.0) while in others the short arm length varied considerably. The 7th and 9th sets had subtelocentric chromosomes. The rest of the sets had more or less homomorphic chromosomes.

Meiosis

Cultivar 'R.M. Quittenton' was studied for meiosis and metaphase I in PMCs showed various chromosomal associations such as hexavalents, pentavalents, etc. (Fig. 159). The data on chromosomal associations is given in Table X. The mean number of hexavalents per cell was 0.18 ± 0.62; pentavalents 0.09 ± 0.12; quadrivalents 0.84 ± 0.15 and trivalents 1.24 ± 0.20. The bivalents showed a mean of 23.72 ± 0.48 and univalents of 1.95 ± 0.25. Anaphase I showed abnormal segregation, lagging chromosomes etc. (Fig. 165). Subsequent division was also irregular. Pollen stainability was 48.2% and there was no seed setting.

$2n = 60$ (6x + 6)

Karyotype

Cultivar 'Rupasa Bangla' showed 60 chromosomes in the root tip cells. An analysis of karyotype showed pronounced heteromorphicity in different sets of chromosomes (Fig. 148 and Table V). Four heteromorphic sets were seen in the complement. In all these groups heteromorphicity was due to an abrupt variation in the length of short arms within a set. One chromosome

of the 5th set had a submedian centromere and carried a satellite on its short arm. The 9th set contained submetacentric chromosomes. Chromosomes with subterminal centromeres were not seen in the complement.

Meiosis

Analysis of PMCs at metaphase I showed multivalents and bivalents (Fig. 160). The details of chromosomal association is depicted in Table X. The mean number of hexavalents was 0.07 ± 0.37. An average number of 1.14 ± 0.40 quadrivalents was also noted. The mean number of trivalents per cell was 0.88 ± 0.12, whereas, the bivalents showed a mean of 25.62 ± 0.01. Average number of univalents per cell was 1.04 ± 0.56. Anaphase I was quite normal, however, anaphase II showed irregular segregation (Fig. 167), and pollen stainability was 95.6%. This cultivar showed good seed setting.

2n = 62 (6x + 8 or 7x - 1)

Karyotype

'Mahatma Gandhi' and 'Kasturba Gandhi' are two cultivars which showed 62 chromosomes in their root tip cells (Figs. 138 and 139), the karyomorphology

of which is given in Table V. In 'Mahathma Gandhi' 2nd, 4th and 8th sets were heteromorphic. In the 2nd set, 3 chromosomes with larger short arms could be distinguished (Fig. 149). In 'Kasturba Gandhi', the 1st set was highly heteromorphic due to variation in the length of short arms. One long chromosome with a submedian centromere appeared in the 1st set (Fig. 150). Heteromorphicity was seen in the 7th (2 chromosomes) and 9th (3 chromosomes) sets also. The chromosomes of 7th set had smaller short arms, whereas the 9th set showed increased length of long arms. One small telocentric chromosome was found in the complement of both the cultivars which did not match with any set.

Meiosis

Metaphase I in PMCs of 'Mahathma Gandhi' and 'Kasturba Gandhi' revealed the presence of bivalents, univalents, multivalents etc. (Figs. 161 and 162). The data regarding chromosomal association in depicted in Table X. Majority of the PMCs in 'Mahathma Gandhi' showed bivalent formation and the mean number of hexavalents was 0.19 ± 0.76, quadrivalents 0.83 ± 0.12, trivalents 0.64 ± 0.55, bivalents 26.54 ± 0.18 and univalents 2.44 ± 0.34 (Table X). In 'Kasturba Gandhi'

the average association per P/C was as follows: hexavalents and pentavalents 0.06 ± 0.98 each, quadrivalents 0.70 ± 0.25, trivalents 1.26 ± 0.22, bivalents 25.56 ± 0.42 and univalents 3.64 ± 0.18. The telocentric chromosome frequently remained as a univalent. Anaphase segregation in both the cultivars was irregular. Unequal distribution of chromosomes, laggards, precocious separation of univalents etc. was also encountered (Fig. 166). The pollen stainability in 'Mahathma Gandhi' was very low (20.3%), however, it was high (65.9%) in 'Kasturba Gandhi'. Both the taxa did not set seed.

$\underline{2n = 64}$ (7x + 1)

Karyotype

Cultivar 'Alfred Wilson' and 'Alfred Simpson' had 64 chromosomes in the root tip cells. Karyotypic analysis of the former showed that all the sets contain nearly homomorphic chromosomes. One long chromosome with a submedian centromere was seen in the first set (Fig. 151). The number of chromosomes in different sets was variable (Table V). Satellitic chromosomes were 4 and the satellites were seen on 3 submetacentric

chromosomes (2 in the 1st set and one in the 6th set). The 4th SAT chromosome had a subterminal centromere which belonged to the 7th set.

$$\underline{2n = 65} \ (7x + 2)$$

Karyotype

Three cultivars having a somatic chromosome number of 2n = 65 in the root tip cells (Fig. 140) have been karyotypically analysed, the data of which is summarised in Table V. The karyomorphology of one of these cultivars is depicted in Fig. 152. In 'Harvest Home' the 1st, 2nd and 7th sets were heteromorphic as a result of variable length of short arms within the sets. However, consistent differences in the length of long arm were apparent in the 7th set. Cultivar 'John Bull' had more or less homomorphic sets and 16 subtelocentric chromosomes falling in the 3rd, 7th and 9th sets were characteristic of this cultivar (Fig.152). All the five chromosomes of the 5th set in 'John Bull' contain SAT chromosomes which depict variation in length of long and/or short arms. Cultivar T_{35} possessed high degree of heteromorphicity in varying sets. In all cases heteromorphicity was the result of variable length of short arms. Three satellited chromosomes were seen in the complement of cv. T_{35}, which appeared on submetacentric chromosomes of the 5th and 8th sets. One metacentric chromosome of the 9th set also possessed a satellite.

The satellites in this cultivar was very small in size. Ten SAT chromosomes appeared in 'John Bull', 2 of these in the first set, 3 in the 2nd and 5 in the 5th set (Fig. 152).

$\underline{2n = 67}$ (7x + 4)

Karyotype

Two cultivars with a chromosome number of 2n = 67 were karyotypically analysed. The details of karyotype is shown in Fig. 153 and Table V. Cultivar 'Sonar Bangla' showed varying number of heteromorphic sets of chromosomes (Fig. 153). The 1st set contained a very long chromosome with an arm ratio 2.5 (Table V), which could be separated from the other chromosomes. Similar variation was found in the 2nd and 7th sets also. One small chromosome with a median centromere (M_1 r index 1.0) appeared in the 9th set. In the 8th set one chromosome was odd. The exceptionally long chromosome as well as short chromosome in the complement possibly shows structural alterations. Similarly the 7th set contained three chromosomes with smaller short arms. In cv. W_{25} the karyotype resolved into more or less homomorphic sets. In cv. W_{25} five satellited chromosomes were found in the karyotype, one in the

1st set and the rest in the 2nd. SAT chromosomes of the 2nd set showed slight variation in length of short arms.

Meiosis

Cultivar 'Sonar Bangla' was meiotically analysed and metaphase I in PMCs revealed the presence of univalents, bivalents and multivalents (Fig. 163 and Table X). The mean number of hexavalents per cell was 0.20 ± 0.01; pentavalents 0.04 ± 0.35 and quadrivalents 1.16 ± 0.66. The trivalents showed a mean of 1.0 ± 0.44 and bivalents 27.88 ± 0.18. Univalents showed a mean of 2.20 ± 0.28. Anaphase segregation was irregular and pollen stainability was 32.5%. No seed formation was seen.

B-CHROMOSOMES

Karyotype

Out of four cultivars with one B-chromosome in their root tip cells (Figs. 141-143), two have been karyotypically analysed. Cultivar W_1 had a somatic chromosome number 2n = 54 and 'Innocence' 56 chromosomes (Fig. 141). In both the cultivars the size of the B-chromosome was small. In cv. W_1 the centromere in

B-chromosome was in submedian, while in 'Innocence' it was in terminal position. In cv. V_1 1st, 7th and 8th sets were heteromorphic. In 'Innocence' heteromorphicity was observed in the 1st, 2nd and 3rd sets. One odd chromosome with a submedian primary constriction and a smaller short arm was detected in the 1st set. The length of short arms varied considerably between the 9 chromosomes of the 2nd set; such variation was seen in the 3rd set also. Cultivar V_1 showed two SAT chromosomes in the 3rd set. No satellitic chromosome was seen in 'Innocence'.

Meiosis

Cultivar 'Innocence' was meiotically analysed. As is the case with other aneuploid cultivars, here also multivalents, bivalents etc. were seen (Table X). In 90% of the PMCs analysed, one B-chromosome was consistently present (Fig. 16A). The B-chromosome did not pair with A-chromosomes. In most of the PMCs there was predominant bivalent formation. Univalents were mostly the result of early disjunction of bivalents. Anaphase I was normal and the B-chromosome was either found to divide or pass to one of the poles without undergoing division. The pollen stainability was moderately high while the cultivar was totally seed sterile.

DNA values

Twelve cultivars with a ploidy range from 4x to 8x were analysed. DNA content among cultivars varied from 12.64 to 25.33 pg. (Table XI) and shows a ratio of approximately 1:1, 2:1, 5:2 among tetraploid, pentaploid, hexaploid and octoploid respectivaly. There is a positive correlation between DNA content and ploidy level and the regression is significant ($p < 0.01$) (Fig. 16B).

Figs. 51-55: Tetraploid Taxon ('Liliput')

Fig. 51: Somatic chromosomes (2n = 36)

Fig. 52: Photo-idiogram (Heteromorphic set marked)

Fig. 53: Diakinesis. 3 IV + 12 II, 2 II attached to the nucleolus.

Fig. 54: Metaphase I. 1 IV + 16 II.

Fig. 55: Anaphase I. 18:18.

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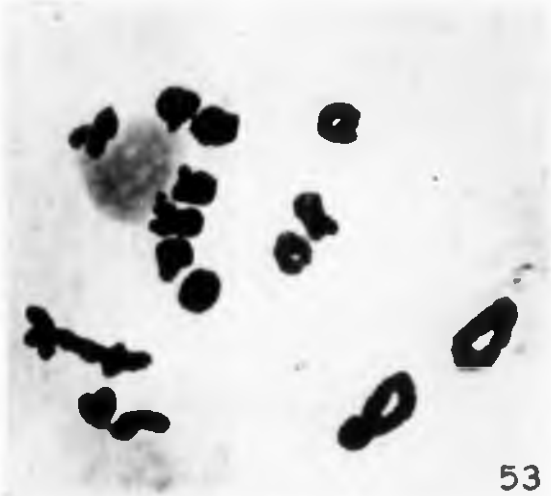

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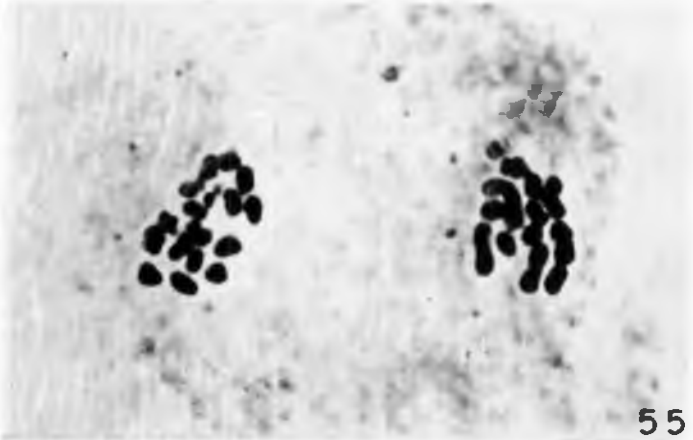

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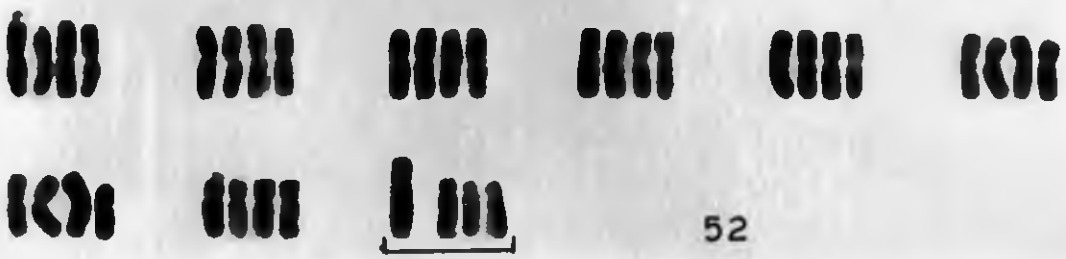

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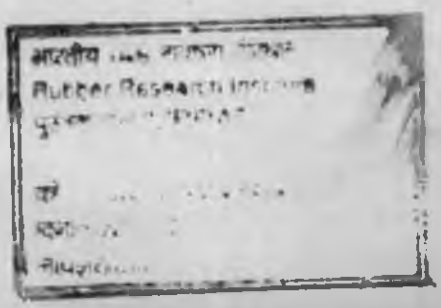


Figs. 56-60: Pentaploid Taxa: Somatic chromosomes (2n = 45)

Fig. 56: cv. P_1

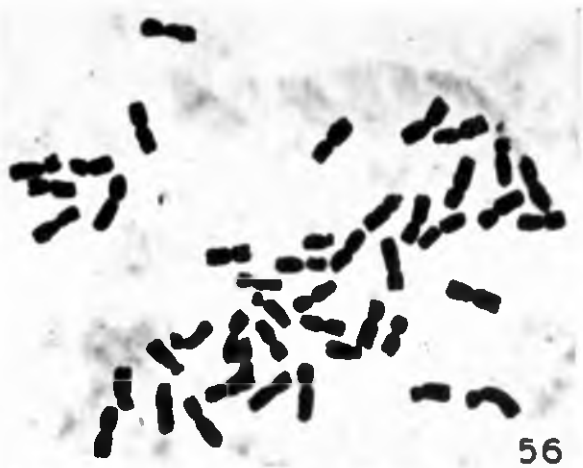
Fig. 57: cv. P_5

Fig. 58: 'Kasturi'

Fig. 59: Photo-idiogram of 'Kasturi'

Fig. 60: Photo-idiogram of cv. P_1

Heteromorphic sets marked



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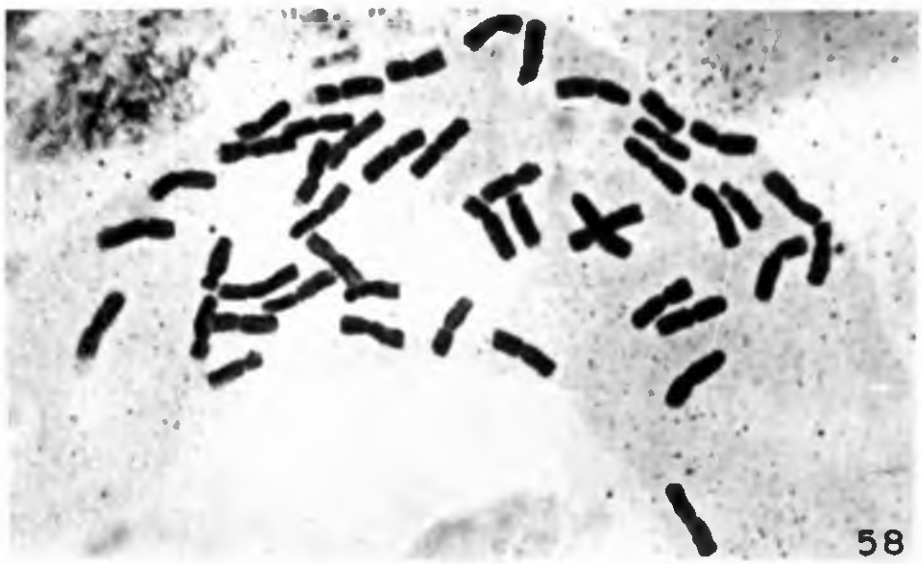

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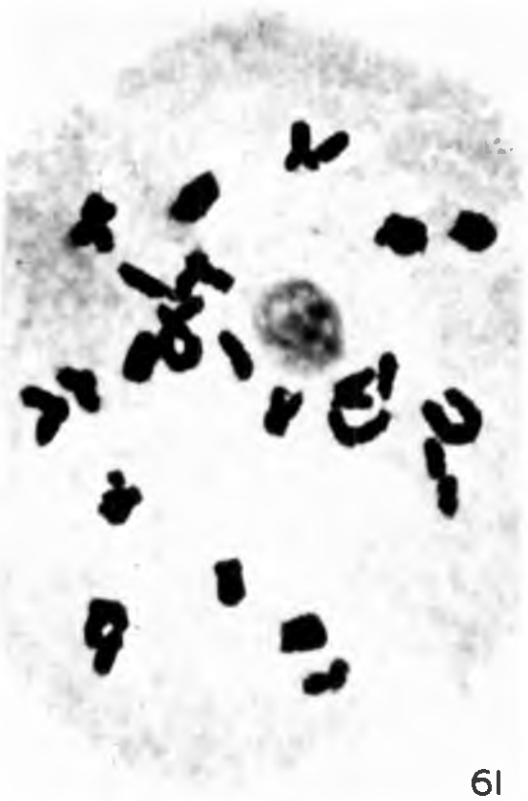
Figs. 61-64: Meiosis in Pentaploid Taxa

Fig. 61: Diakinesis in cv. P_5.
3 III + 16 II + 4 I.

Fig. 62: Diakinesis in cv. P_1.
1 IV + 1 III + 16 II + 5 I.

Fig. 63: Metaphase I in 'Kasturi'.
2 V + 1 IV + 2 III + 11 II + 3 I.

Fig. 64: Metaphase I in 'Kasturi.
5 III + 12 II + 6 I.



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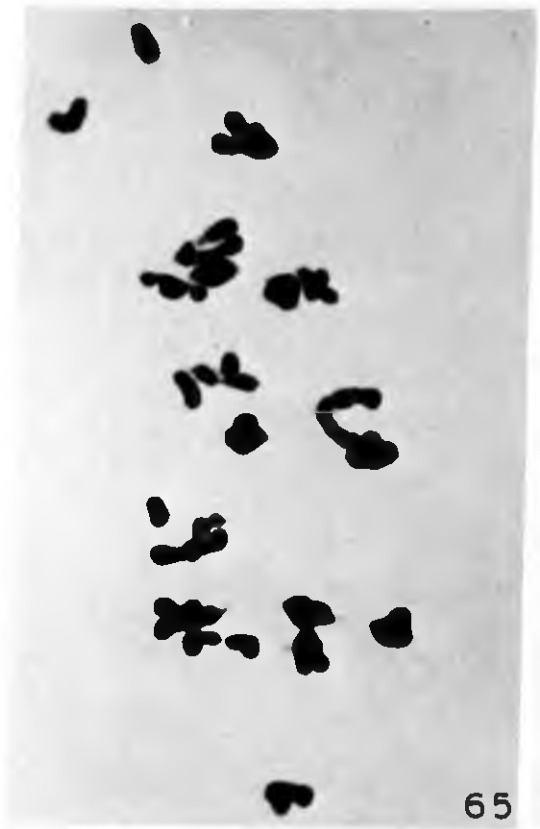
Figs. 65-68: Meiosis in Pentaploid Taxa

Fig. 65: Metaphase I in 'Kasturi'
1 IV + 4 III + 12 II + 5 I.

Fig. 66: Anaphase I in cv. P_5. 21:25.

Fig. 67: Anaphase I in 'Kasturi' showing lagging chromosomes.

Fig. 68: Telophase II in cv. P_1.
Micronuclei and fragments.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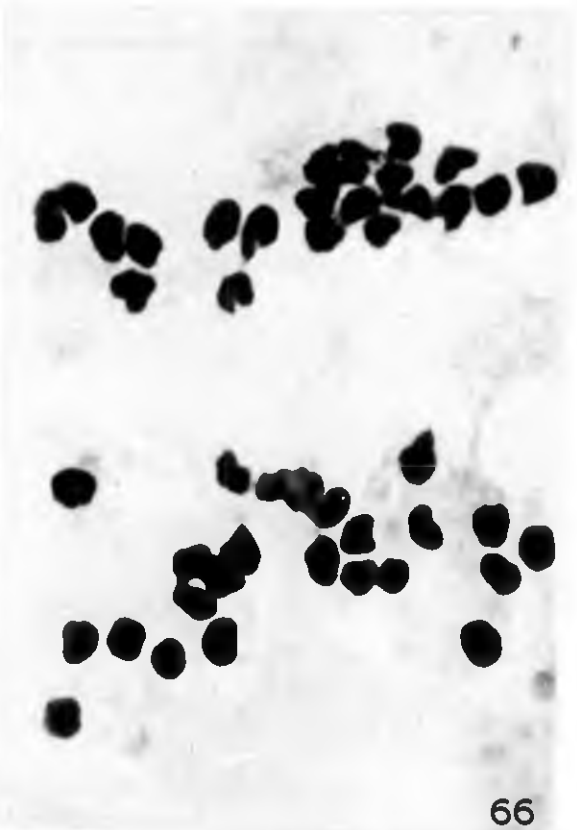
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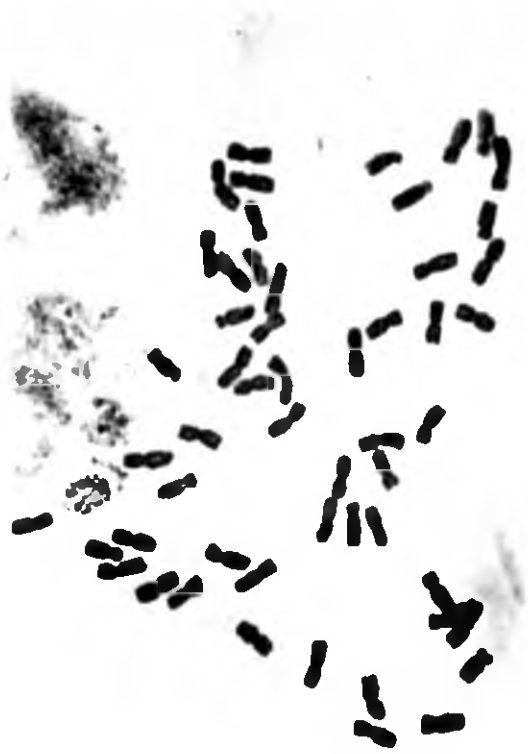
Figs. 69–72: Somatic chromosomes of Hexaploid Taxa (2n = 54)

Fig. 69: 'Snow White'

Fig. 70: 'Spoon'

Fig. 71: 'Laura'

Fig. 72: cv. P_8



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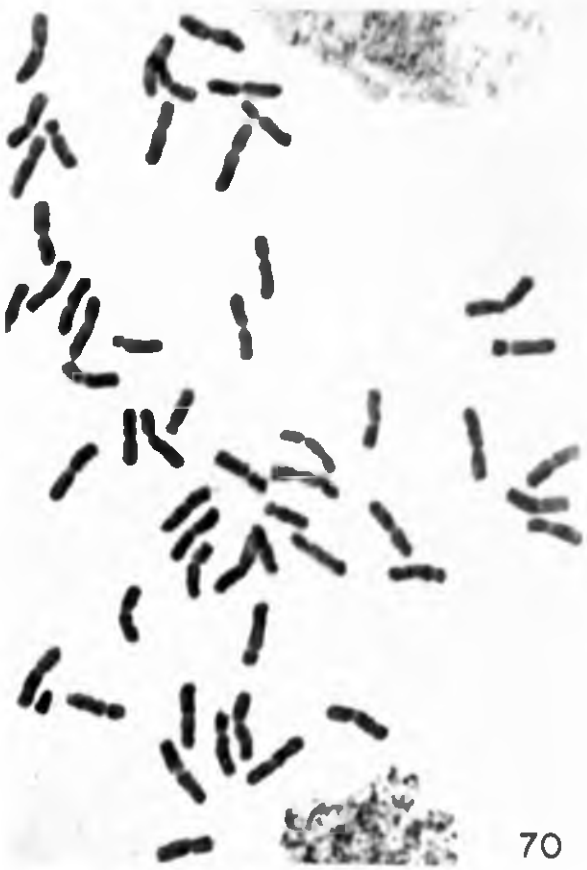

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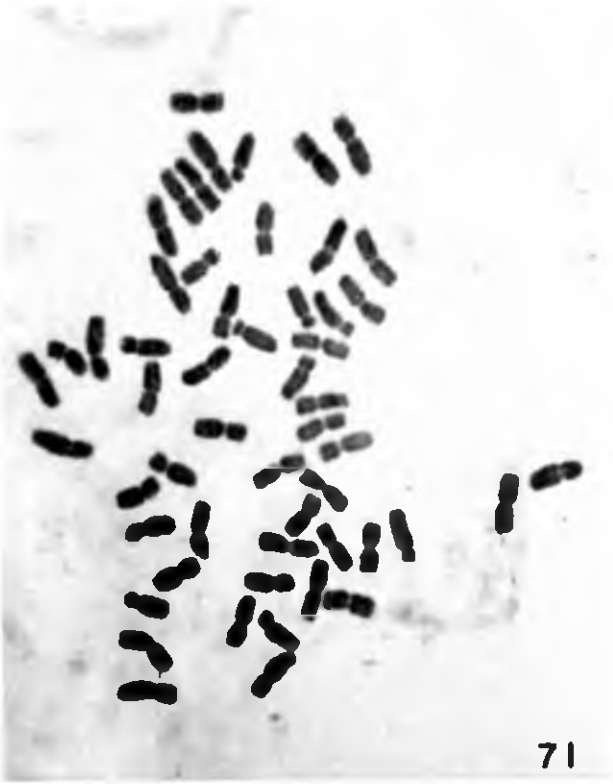

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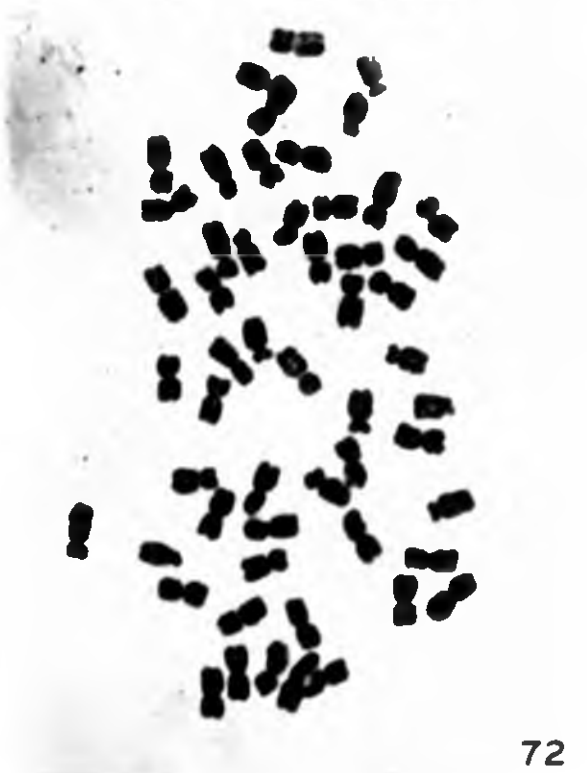

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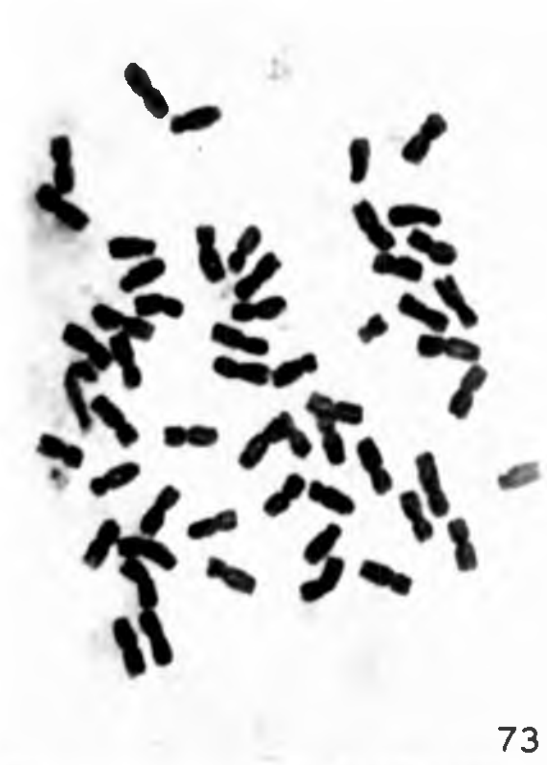
Figs. 73-76: Somatic chromosomes of Hexaploid Taxa (2n = 54)

Fig. 73: cv. NN_{14}

Fig. 74: 'Summer Gem'

Fig. 75: 'Roseteu'

Fig. 76: 'Mohini' (2n = 52 + 2T)



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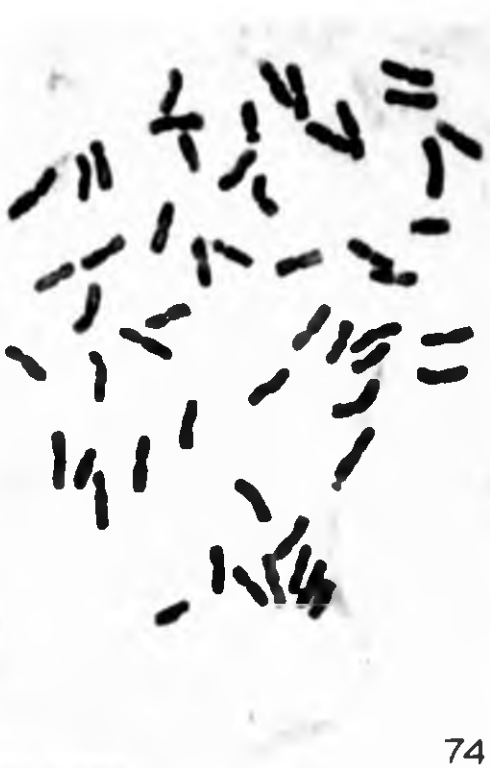

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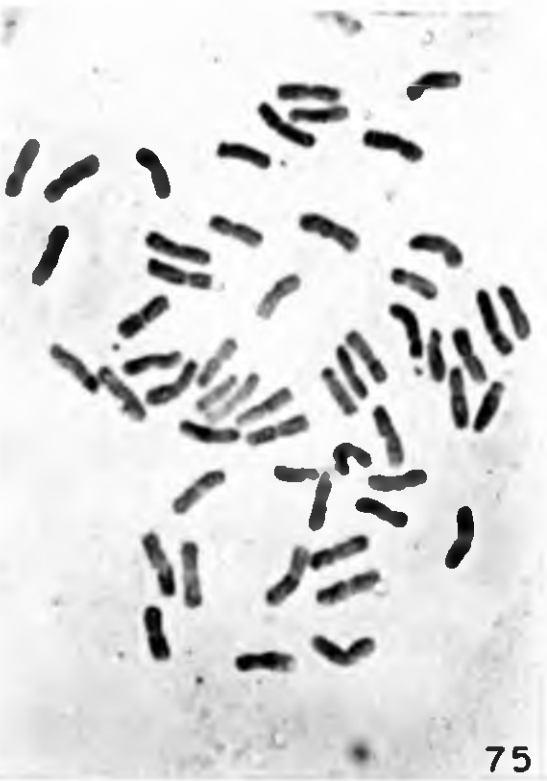

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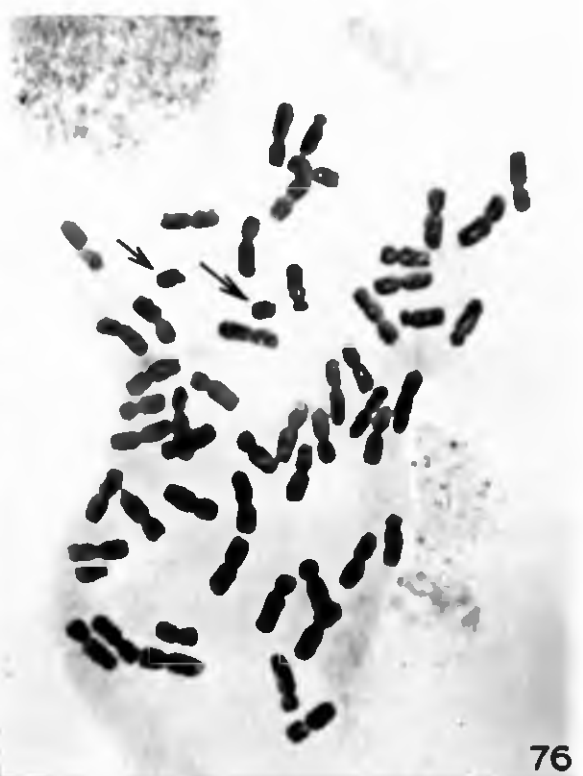

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Figs. 77-83: Photo-idiograms of Hexaploid Taxa

Fig. 77: cv. S_g

Fig. 78: 'Dipti'

Fig. 79: 'Laura'

Fig. 80: 'Summer Gem'

Fig. 81: 'Lilith'

Fig. 82: 'Nagama'

Fig. 83: 'Linda'

Heteromorphic sats marked

Figs. 84-90: Photo-idiogram of Hexaploid Taxa

Fig. 84: 'Basanti'

Fig. 85: cv. NN_{12}

Fig. 86: cv. K_2

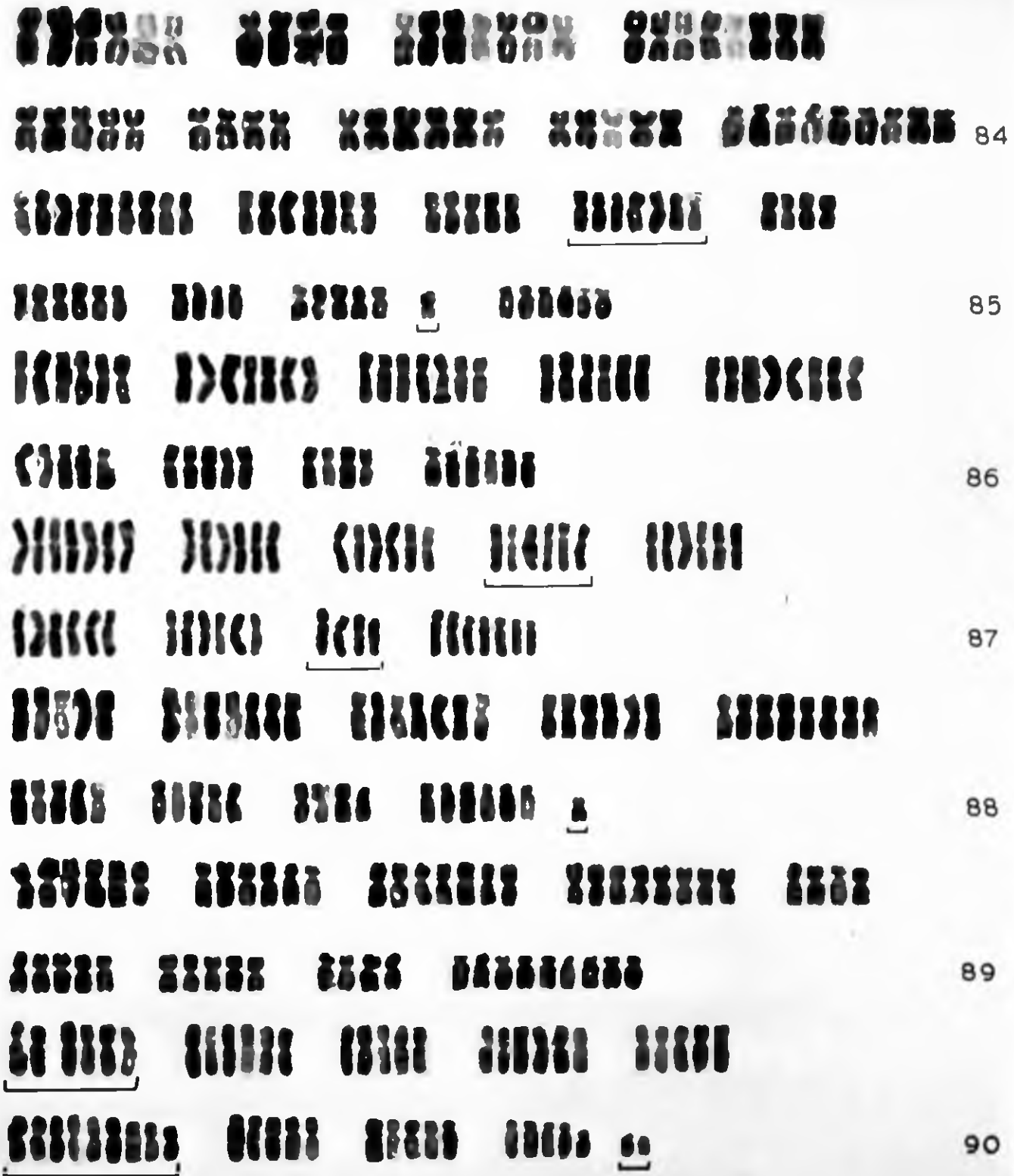
Fig. 87: 'Spoon'

Fig. 88: cv. NN_{14}

Fig. 89: cv. P_8

Fig. 90: 'Mohini' (2n = 52 + 2T)

Heteromorphic sets marked



Figs. 91-94: Meiosis in Hexaploid Taxa

Fig. 91: Diakinesis in 'Sharad Shobha'
1 III + 25 II + 1 I.

Fig. 92: Metaphase I in 'Lilith'
2 IV + 1 III + 22 II + 1 I.

Fig. 93: Metaphase I in 'Laiquila'
1 IV + 25 II.

Fig. 94: Metaphase I in cv. T_6
1 VI + 1 IV + 22 II.

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Figs. 95-98: Meiosis in Hexaploid Taxa

Fig. 95: Metaphase I in cv. D_5. 27 II.

Fig. 96: Metaphase I in cv. Y_{21}. 27 II.

Fig. 97: Anaphase I in cv. A_{16}. 24:30.

Fig. 98: Anaphase II in cv. 'Linda'. Laggards and irregular segregation.

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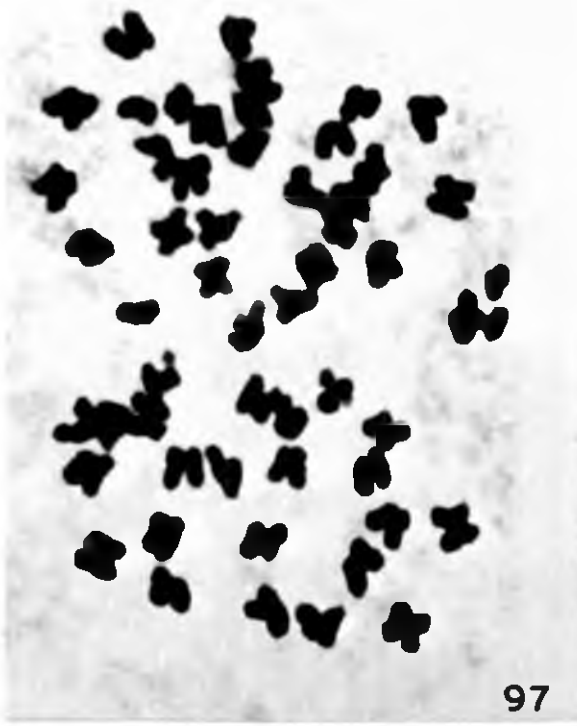

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Figs. 99-103: Heptaploid Taxa
(2n = 7x = 63)

Figs.99 & 100: Somatic chromosomes

Fig. 99 : 'John Webber'

Fig.100 : 'President Viger'

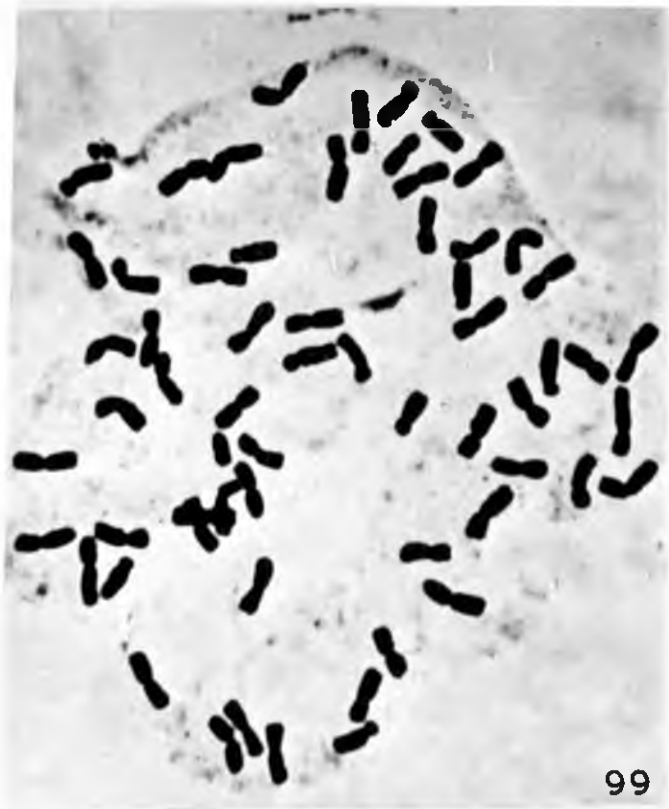
Figs.101-103: Photo-idiogram of heptaploid taxa

Fig. 101 : 'President Viger'

Fig. 102: 'Grape Bowl'

Fig. 103: 'John Webber'

Heteromorphic sats marked



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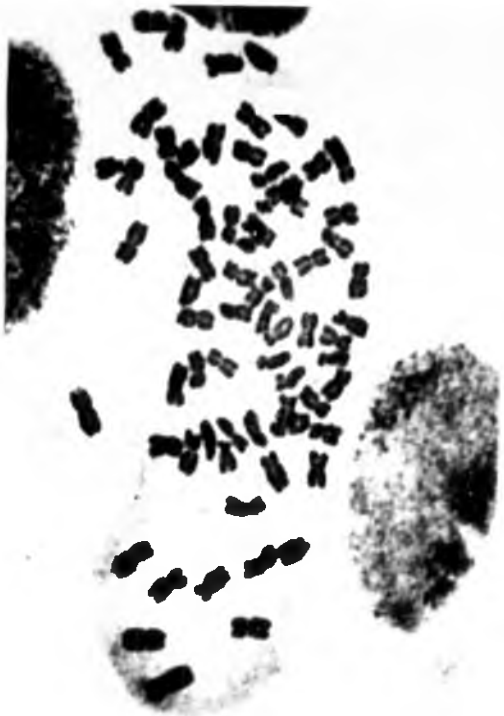

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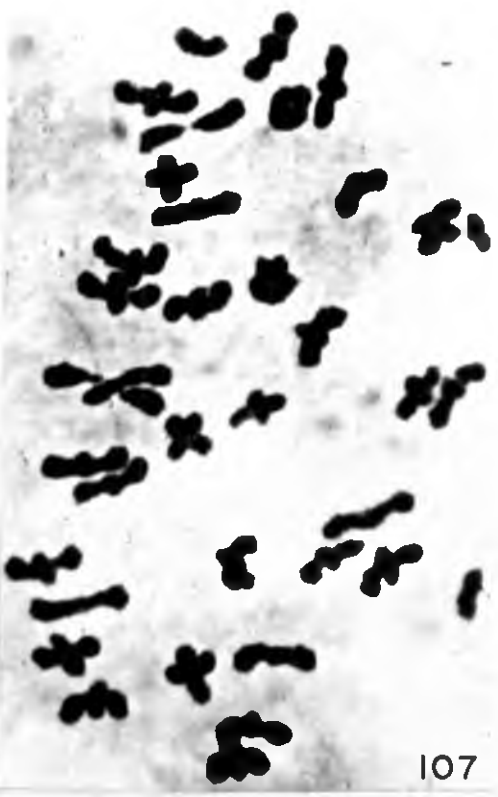

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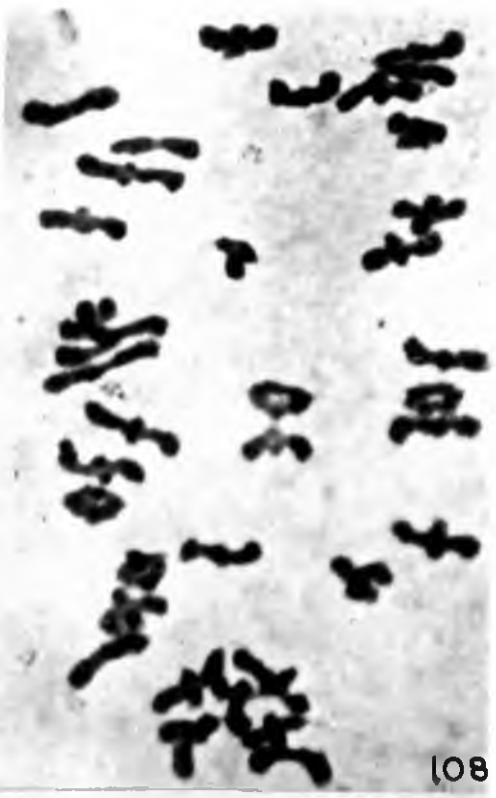

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Figs. 109-112 : Meiosis in Octoploid Taxon

Fig. 109 : Metaphase I

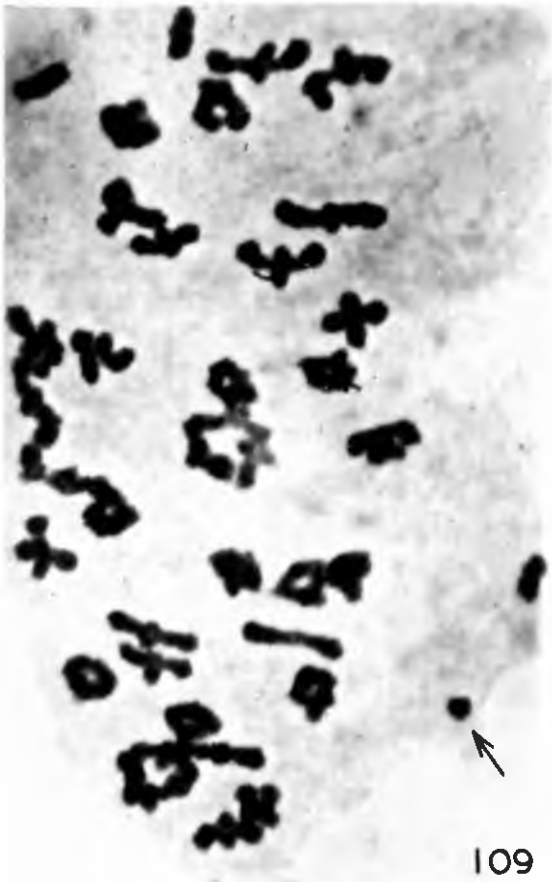
1 VIII + 1 VI + 1 V + 25 II + 3 I + 18

Fig. 110 : Metaphase I

1 IV + 33 II + 2 I + 18

Fig. 111 : Anaphase I showing chromatid bridge

Fig. 112 : Anaphase II showing laggards



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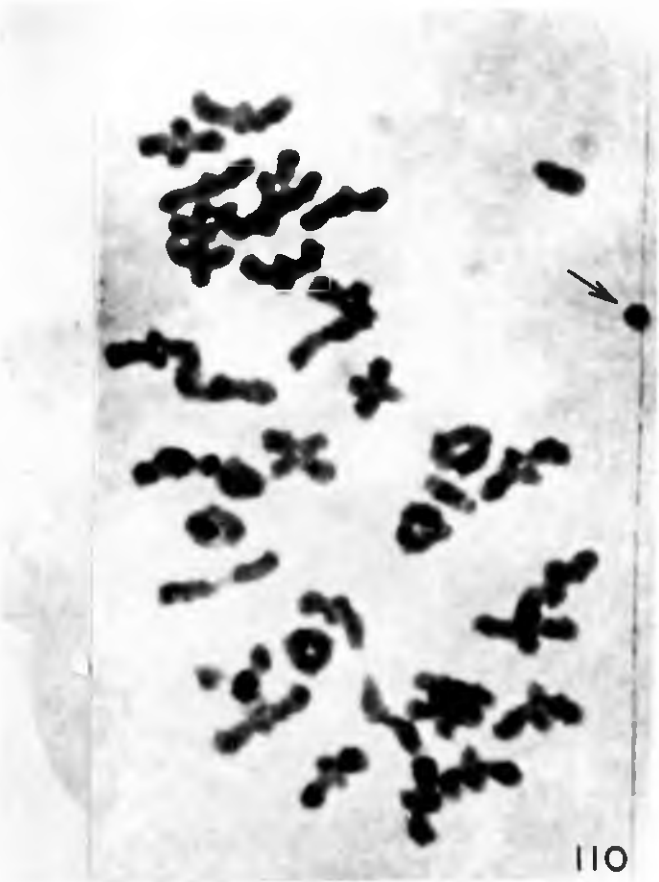
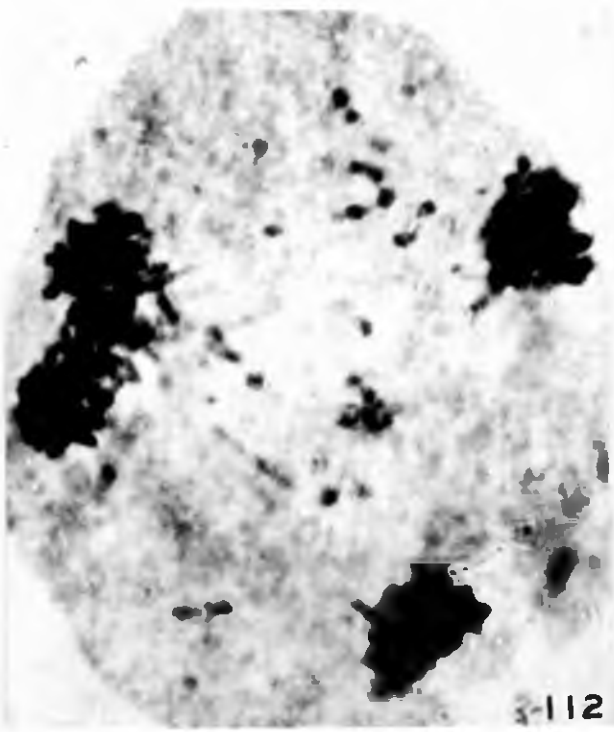


110



112

111

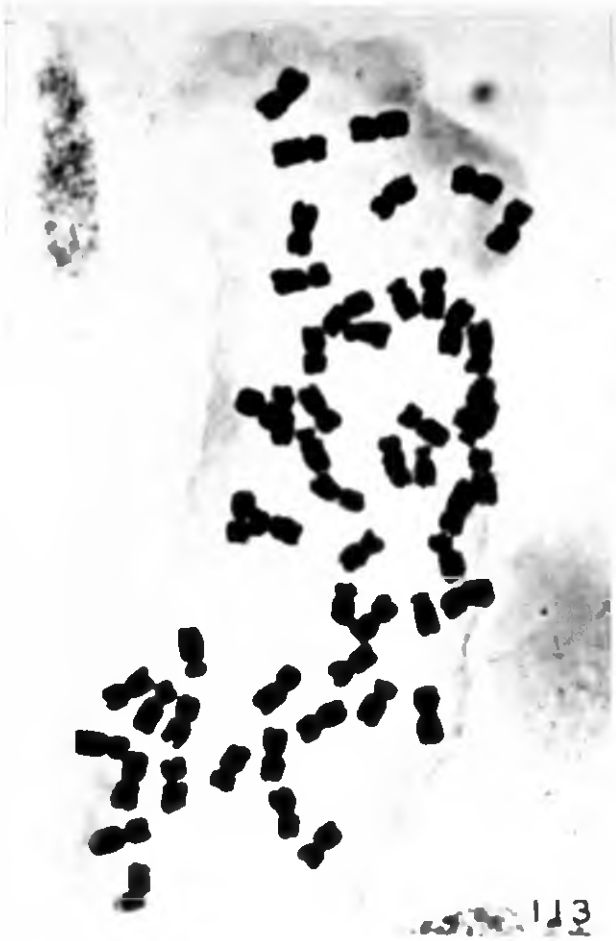
Figs. 113-116 : Somatic chromosomes of Aneuploid Taxa (2n = 53)

Fig. 113 : cv. G_2

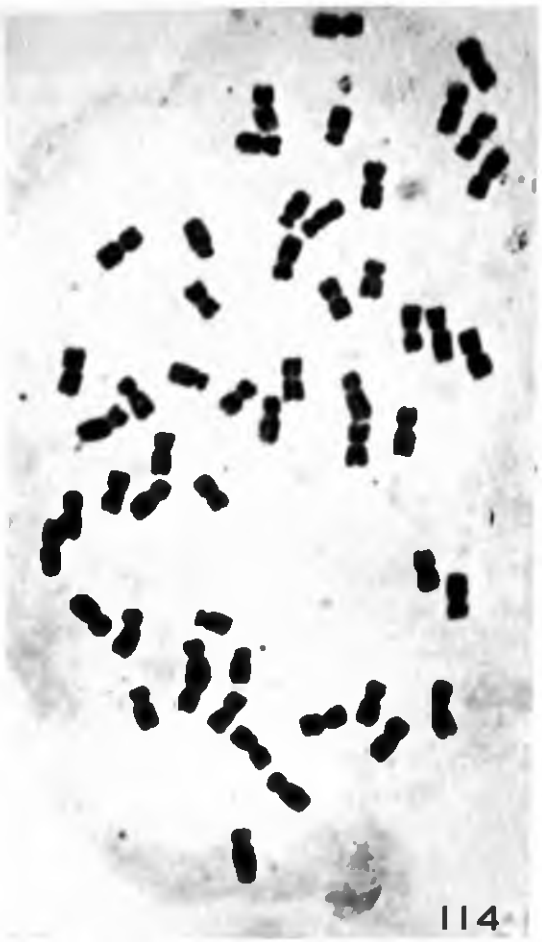
Fig. 114 : cv. E_{10}

Fig. 115 : cv. AA_6

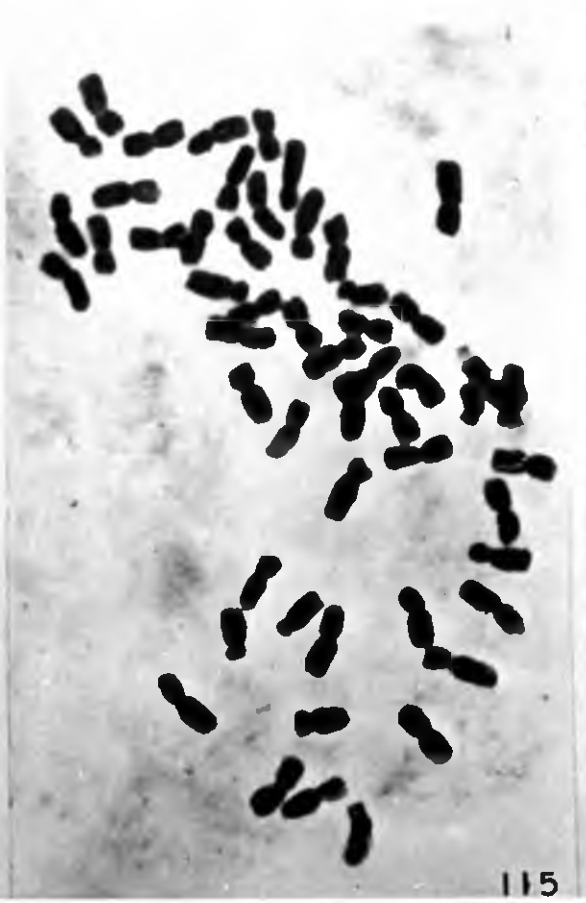
Fig. 116 : 'Sharad Mala'



113



114



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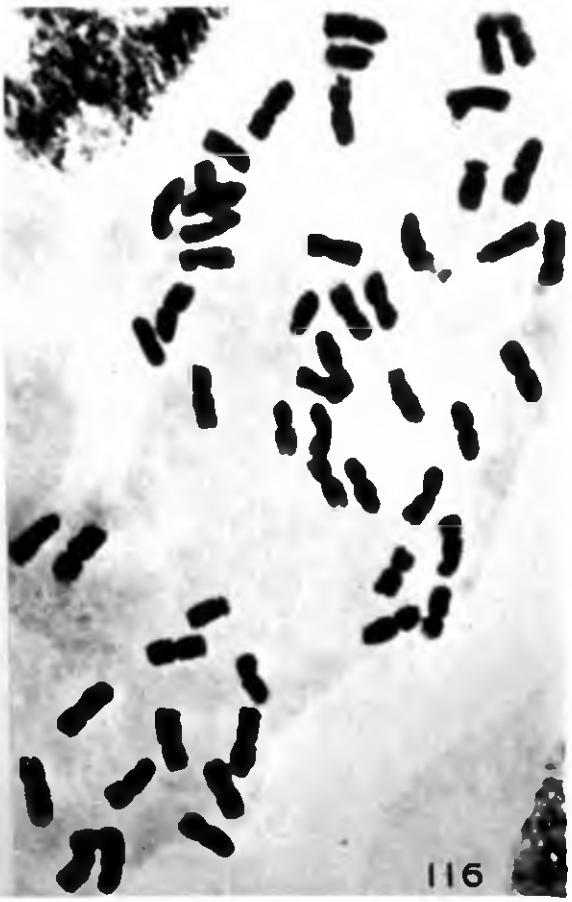


116

Figs. 117-121 : Photo-idiogram of
Aneuploid Taxa (2n = 53)

Fig. 117 : cv. OO_5

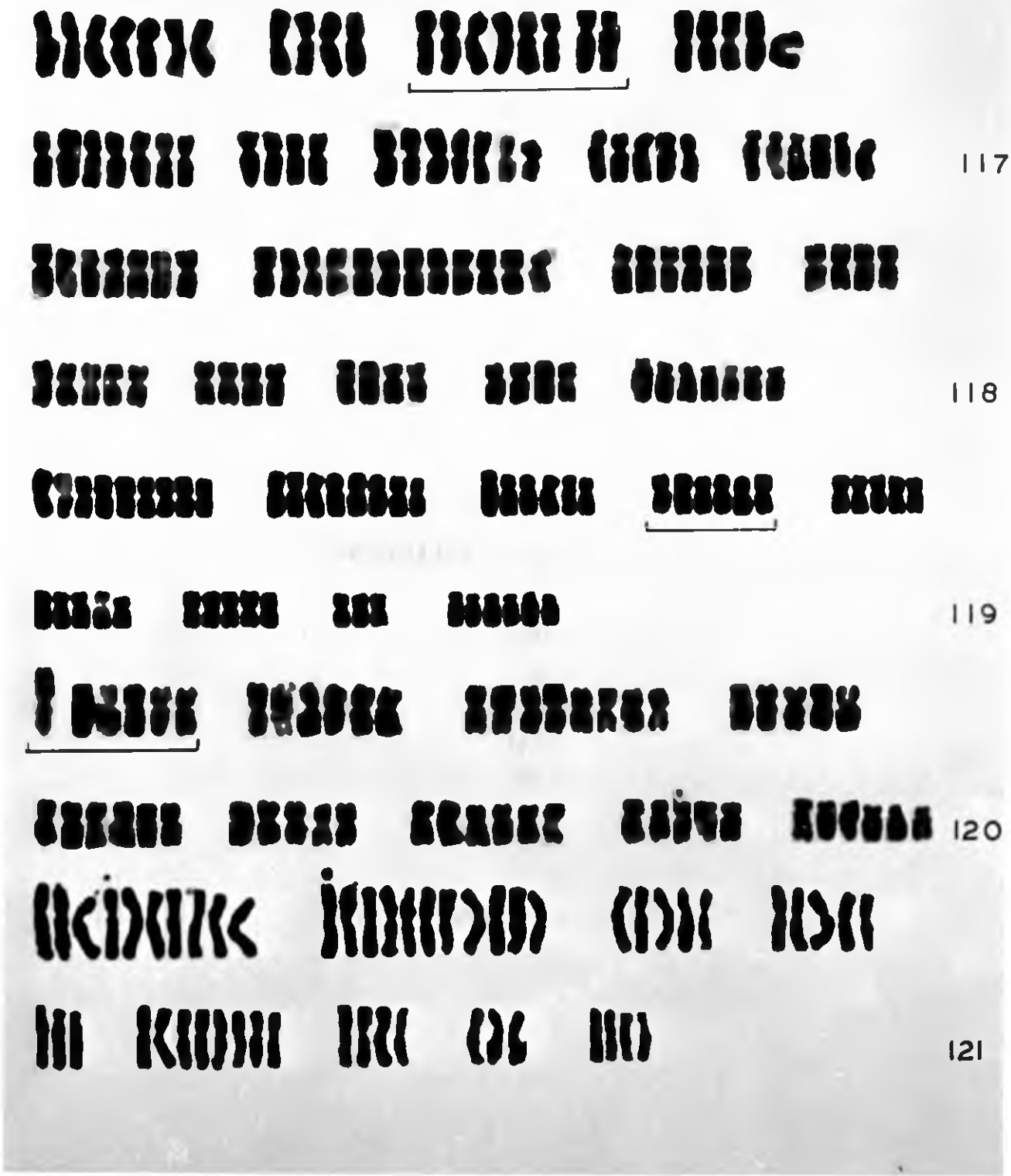
Fig. 118 : cv. G_2

Fig. 119 : cv. L_{10}

Fig. 120 : cv. SS_1

Fig. 121 : cv. T_2

Heteromorphic sets marked


117
118
119
120
121

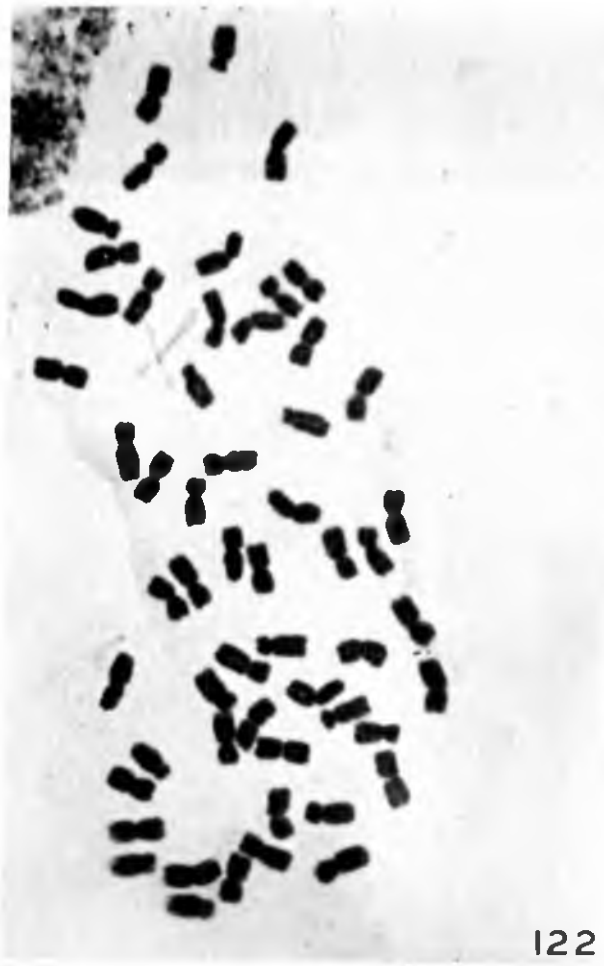
Figs. 122–125 : Somatic chromosomes of Aneuploid Taxa (2n = 55)

Fig. 122 : 'Dainty Maid'

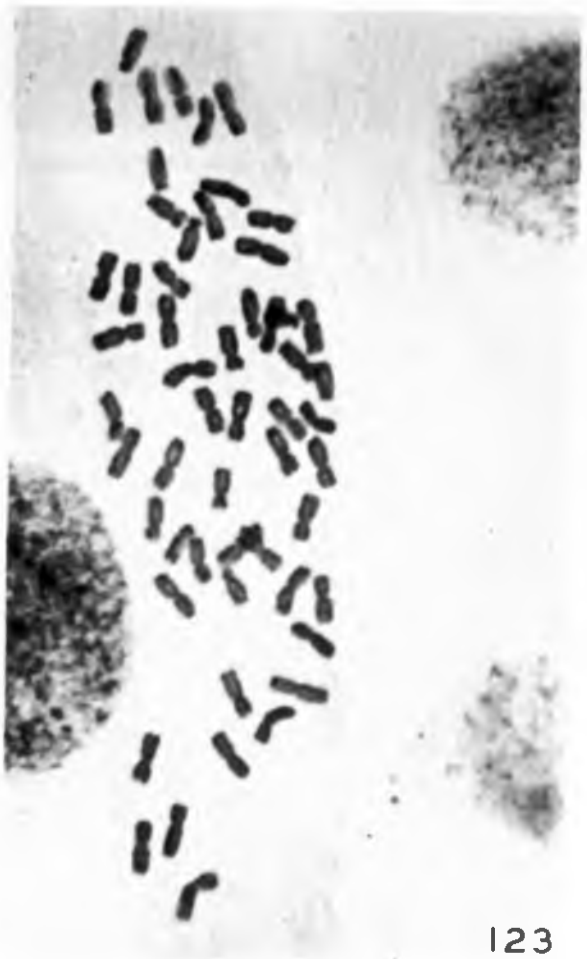
Fig. 123 : cv. S_5

Fig. 124 : 'Flirt'

Fig. 125 : cv. U_2



122



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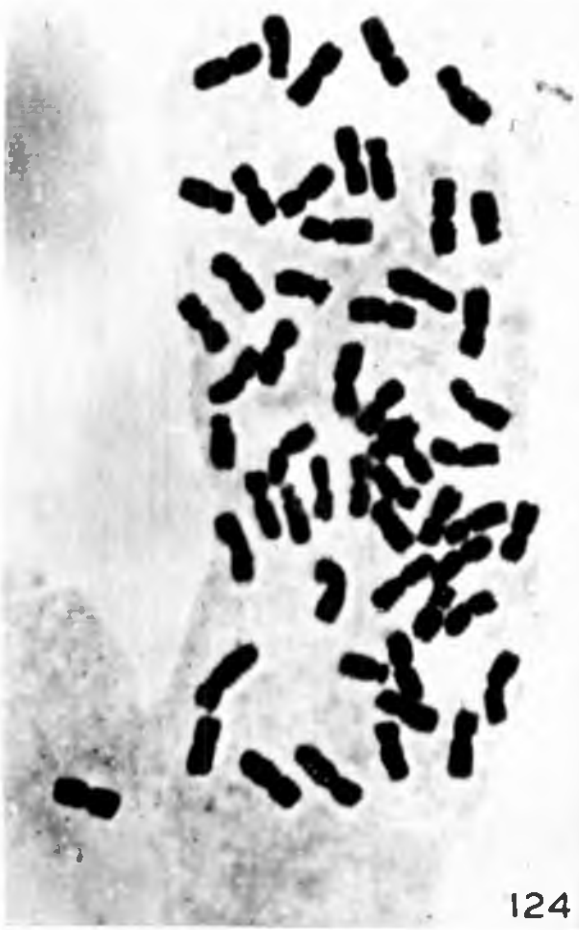
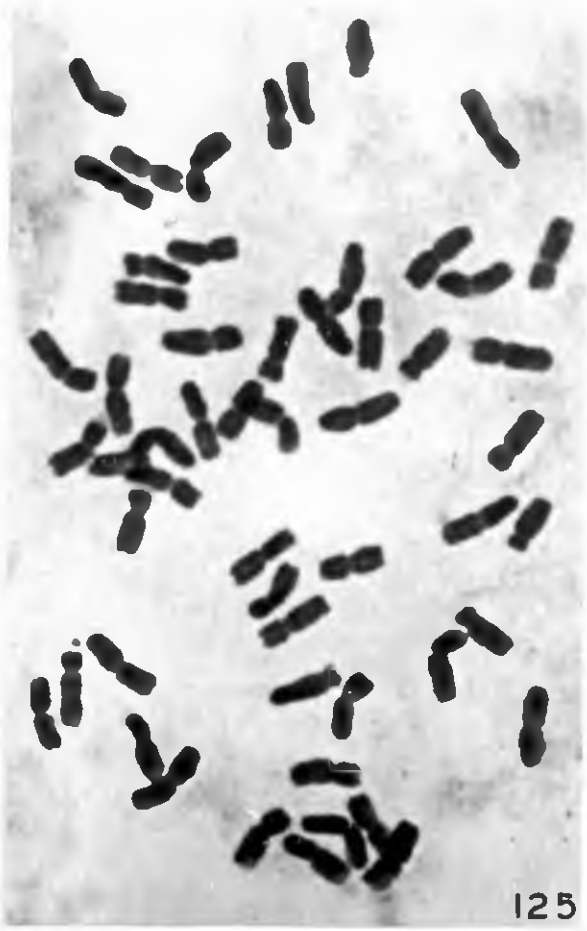


124



125

Figs. 126-130 : Photo-idiogram of
Aneuploid Taxa (2n = 55)

Fig. 126 : 'Donald'

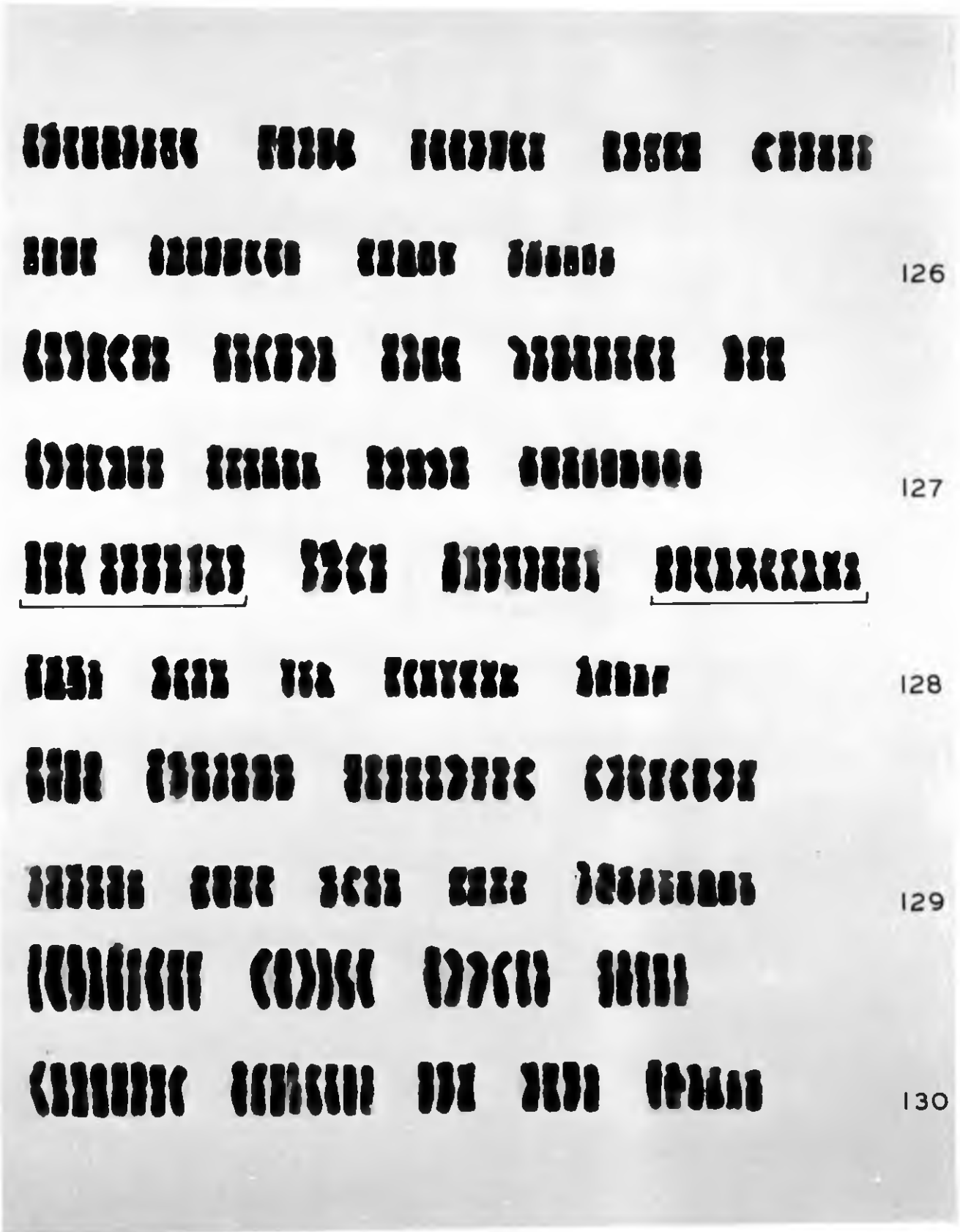
Fig. 127 : 'Dainty Maid'

Fig. 128 : cv. X_2

Fig. 129 : cv. C_1

Fig. 130 : cv. NN_{10}

Heteromorphic sets marked



Figs. 131-135 : Meiosis in Aneuploid Taxa

Figs. 131-132 : 2n = 53

Fig. 131 : Metaphase I in 'Sharad Mala'

26 II + 1 I

Fig. 132 : Metaphase I in 'Anamika'

1 IV + 1 III + 22 II + 2 I

Figs. 133-135 : 2n = 55

Fig. 133 : Metaphase I in cv. P_3

27 II + 1 I

Fig. 134 : Metaphase in cv. P_3

1 III + 26 II

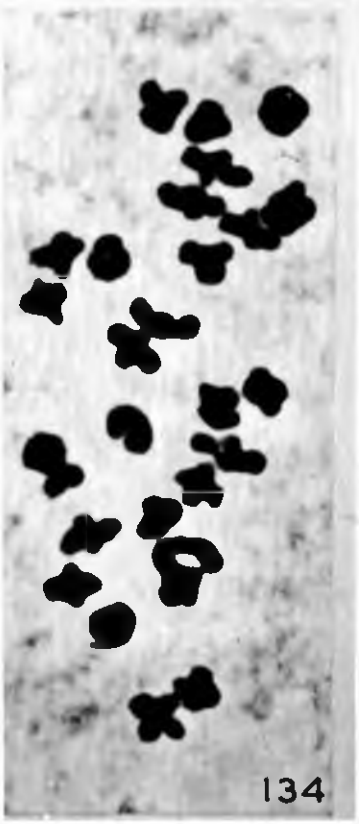
Fig. 135 : Anaphase I in 'Dainty Maid'

27:1/1:27

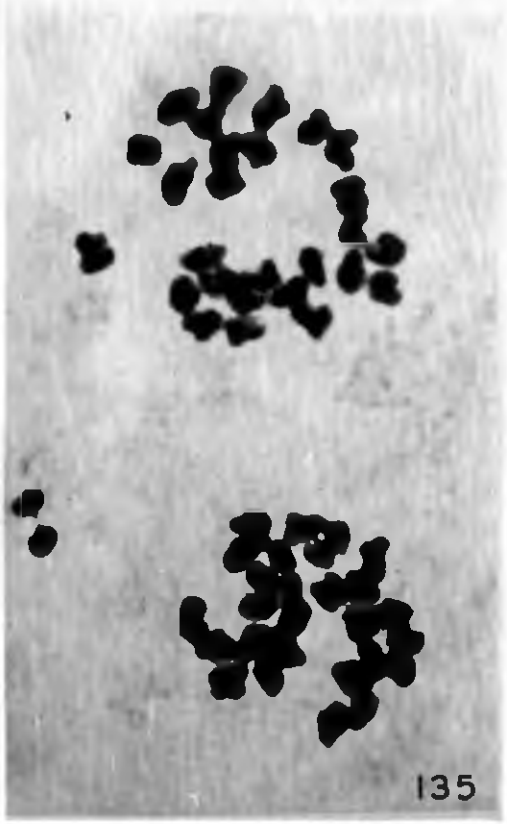
131

132

133



134



135

Figs. 136-139 : Somatic chromosomes of Aneuploid Taxa

Fig. 136 : 'Golden News' (2n = 56)

Fig. 137 : 'Bronze Turner' (2n = 58)

Fig. 138 : 'Mahathma Gandhi' (2n = 61 + 1T)
Telocentric chromosome marked

Fig. 139 : 'Kasturba Gandhi' (2n = 61 + 1T)
Telocentric chromosome marked

136

137

138

139

Figs. 140–143 : Somatic chromosomes of Aneuploid Taxa

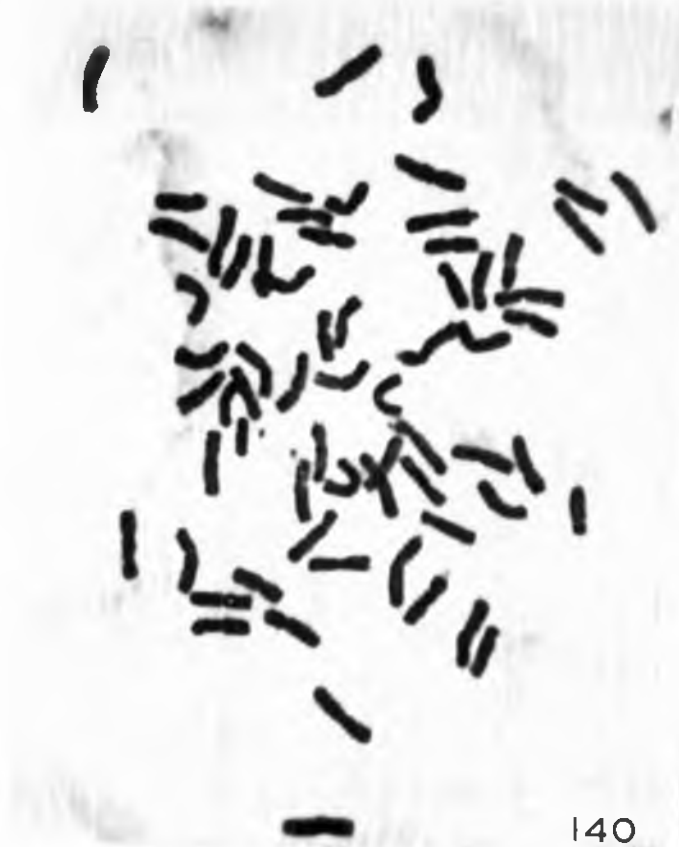
Fig. 140 : 'John Bull' (2n = 65)

Fig. 141 : 'Innocence' (2n = 56 + 1B)

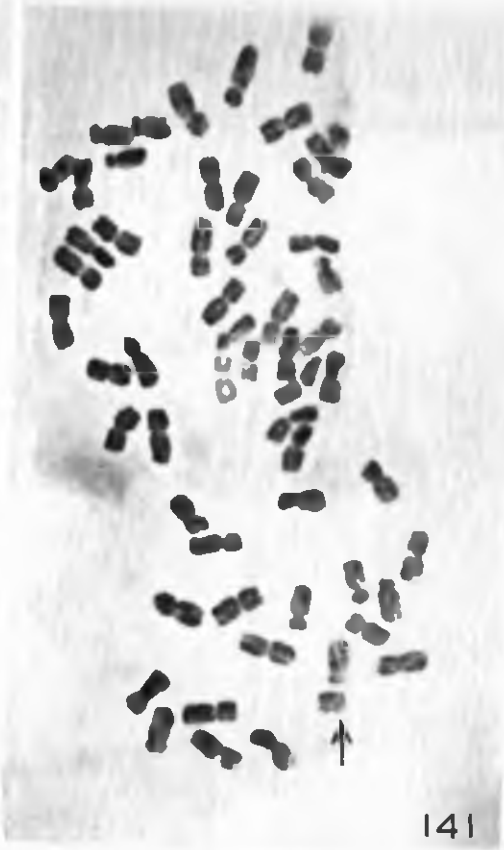
Fig. 142 : 'Red Princess Anne' (2n = 54 + 1B)

Fig. 143 : 'Nigeria' (2n = 54 + 1B)

B-chromosomes marked

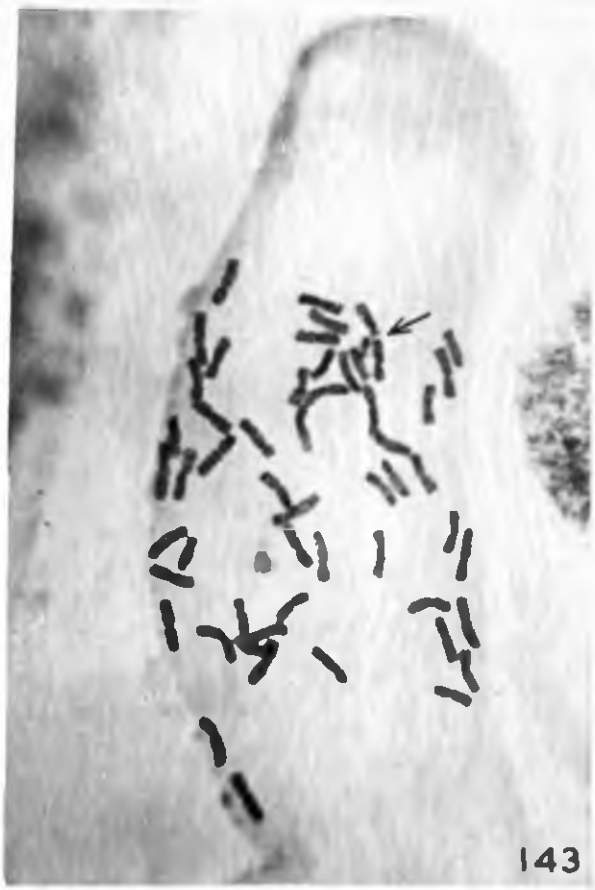


140



141

142



143

Figs. 144-149 : Photo-idiogram of Aneuploid Taxa

Fig. 144 : 'Golden Nugget' (2n = 56)

Fig. 145 : 'Connie Mayhew' (2n = 57)

Fig. 146 : 'Bronze Turner' (2n = 58)

Fig. 147 : cv. T_{17} (2n = 59)

Fig. 148 : 'Rupees Bangle' (2n = 60)

Fig. 149 : 'Mahatma Gandhi' (2n = 61 + 1T)

Heteromorphic sats, odd chromosome and telocentric are marked

[illegible]

[illegible] 144

[illegible]

[illegible] 145

[illegible]

[illegible] 146

[illegible]

[illegible] 147

[illegible]

[illegible] 148

[illegible]

[illegible] 149

Figs. 150-155 : Photo-idiogram of

Aneuploid Taxa

Fig. 150 : 'Kasturba Gandhi' (2n = 61 + 1T)

Fig. 151 : 'Alfred Wilson' (2n = 64)

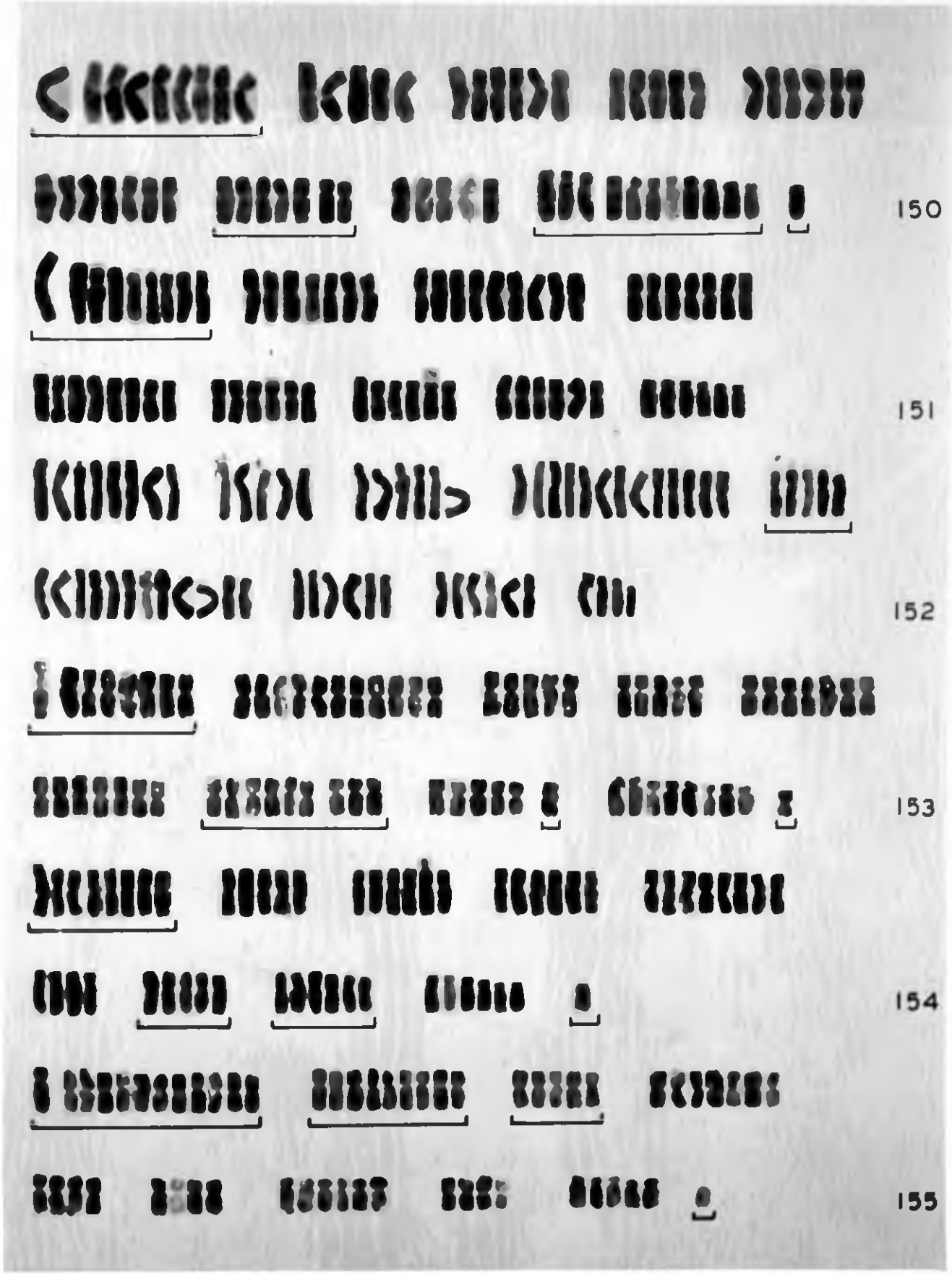
Fig. 152 : 'John Bull' (2n = 65)

Fig. 153 : 'Sonar Bangla' (2n = 67)

Fig. 154 : cv. W_1 (2n = 54 + 1B)

Fig. 155 : 'Innocence' (2n = 56 + 1B)

Heteromorphic sats, odd and B-chromosomes and telocentrics are marked



Figs. 156–159 : Meiosis in Aneuploid Taxa

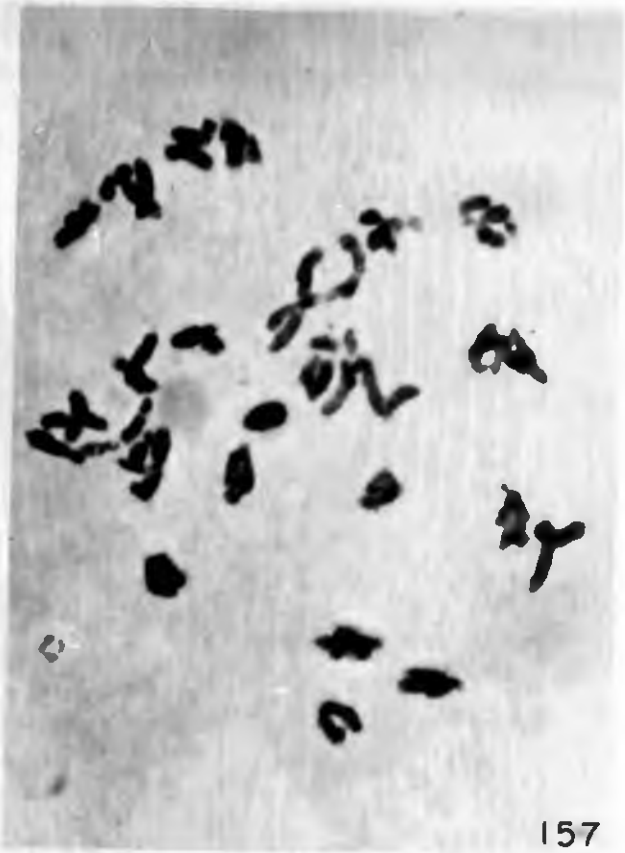
Fig. 156 : Metaphase I in cv. M_{30} (2n = 56)
1 III + 25 II + 3 I
see the precociously dividing
univalents.

Fig. 157 : Diakinesis in 'Connie Mayhew'
(2n = 57). 3 III + 23 II + 2 I.

Fig. 158 : Diakinesis in 'J.H. Salisbury'
(2n = 58). 1 III + 27 II + 1 I.

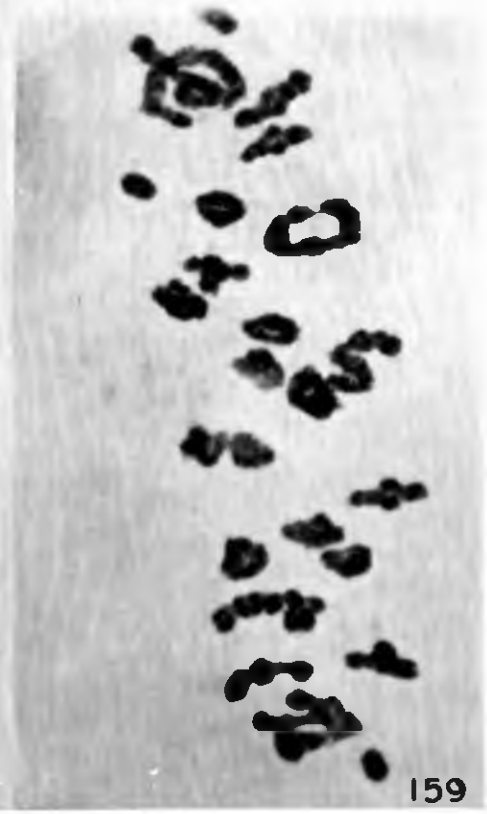
Fig. 159 : Metaphase I in 'R.M. Quitteunton'
(2n = 59). 3 IV + 2 III + 19 II + 3 I.

156



157

158



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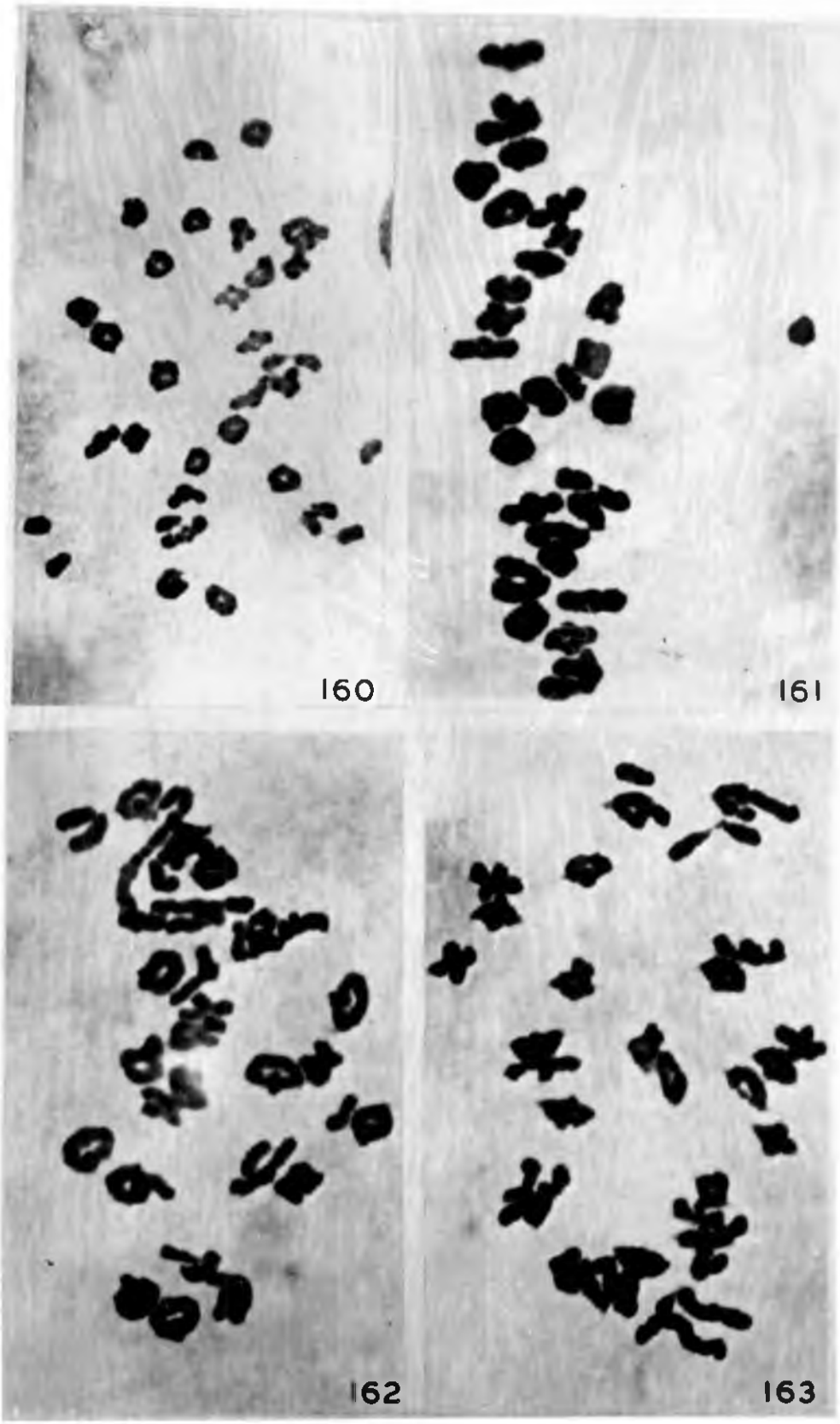
Figs. 160–163 : Meiosis in Aneuploid Taxa

Fig. 160 : Metaphase I in 'Rupasa Bangla' (2n = 60). 1 III + 25 II + 7 I.

Fig. 161 : Metaphase I in 'Mahatma Gandhi' (2n = 61 + 1T). 1 IV + 2 III + 25 II + 2 I.

Fig. 162 : Metaphase I in 'Kasturba Gandhi' (2n = 61 + 1T). 1 VI + 1 III + 25 II + 3 I.

Fig. 163 : Metaphase I in 'Sonar Bangla' (2n = 67). 1 IV + 4 III + 25 II + 1 I.


160
161
162
163

Figs. 164–167 : Meiosis in Aneuploid Taxa

Fig. 164 : Metaphase I in 'Innocence' (2n = 56 + 1B). 1 III + 24 II + 5 I + 1 B (B-chromosome marked).

Fig. 165 : Anaphase I in R.M. Quittenton showing laggards.

Fig. 166 : Late anaphase I in 'Kasturba Gandhi'. Note the precocious disjunction of lagging univalents.

Fig. 167 : Anaphase II in 'Rupasa Bangla' showing unequal segregation and laggards.

164

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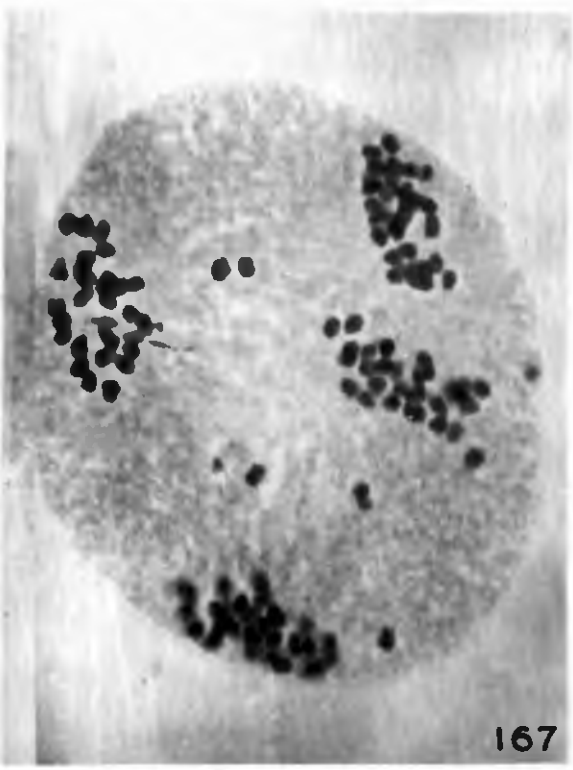
166



167

Fig. 168 : 2 C DNA content plotted against chromosome number of *Chrysanthemum* cultivars.

1. 'Liliput', 2. 'Phyllis',
3. 'Kasturi', 4. cv. P_5,
5. cv. P_1, 6. cv. U_{20},
7. 'Nanako', 8. 'Summer Gem',
9. 'Nagami', 10. cv. F_3,
11. cv. U_2, 12. 'Potomac'.

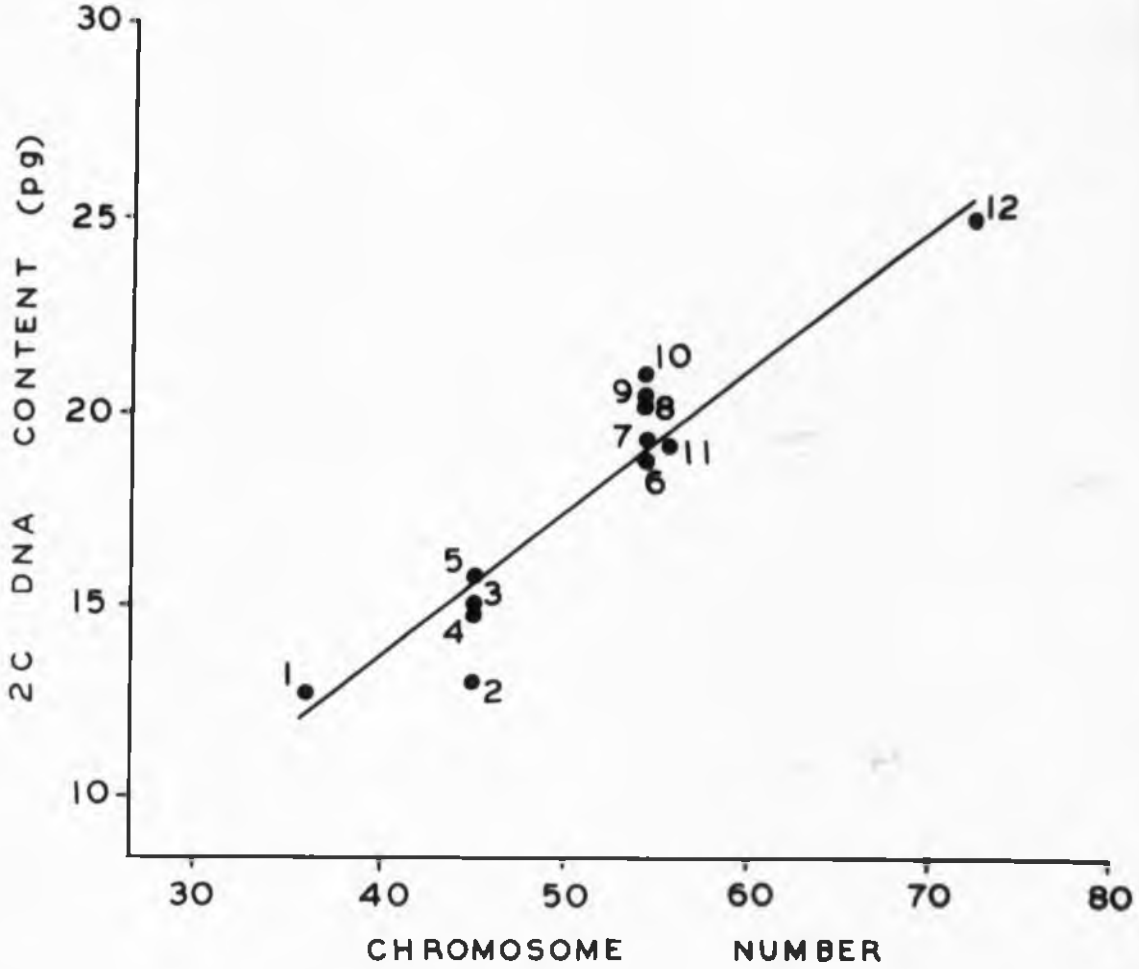

30
25
20
15
10
2C DNA CONTENT (pg)
30
40
50
60
70
80
CHROMOSOME NUMBER
1
2
3
4
5
6
7
8
9
10
11
12

Table V

Arm ratio and karyomorphology in *Chrysanthemum morifolium* cultivars

Taxon	Chromosome No.(2n)	L/S Ratio I	II	III	IV	V	VI	VII	VIII	IX	Karyotype formulae
1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
Tetraploid											
'Liliput'	36	1.1 (4)	1.2 (4)	1.1 (4)	1.4 (4)	1.1 (4)	1.3 (4)	1.2 (4)	1.8 (4)	2.9(1) 3.3(3)	28m + 5sm + 3st
Pentaploid											
'Kasturi'	45	1.6 (5)	1.1 (5)	1.0 (5)	1.3 (5)	1.0 (4)	1.2 (4)	1.7 (5)	1.2 (5)	3.0 (7)	9M + 29m + 7sm
cv. P_1	45	1.5 (5)	1.2 (6)	2.4 (5)	1.3 (6)	1.4 (5)	1.3 (5)	1.3 (5)	2.0 (4)	3.3 (4)	32m + 9sm + 4st
cv. P_5	45	1.2 (5)	1.5 (5)	1.5 (5)	1.5 (5)	1.1 (5)	1.5 (5)	1.1 (5)	1.5 (4)	3.1 (6)	39m + 6st
Hexaploid											
cv. S_9	54	1.1 (7)	1.3 (7)	1.0 (7)	1.5 (6)	1.2 (5)	2.1 (6)	1.2 (5)	1.1 (5)	2.7 (6)	7M + 35m + 12sm
'Dipti'	54	1.6 (7)	1.1 (7)	1.4 (5)	1.7 (5)	1.0 (6)	1.8 (5)	1.3 (5)	1.4 (6)	2.5 (8)	6M + 35m + 13sm
cv. P_{52}	54	2.0 (7)	1.3 (8)	1.0 (5)	1.6 (8)	1.1 (5)	1.2 (5)	1.6 (5)	1.3 (5)	2.8 (6)	5M + 36m + 13sm
'White Cloud'	54	1.8 (5)	1.1 (7)	1.2 (7)	1.0 (5)	1.7 (6)	1.5 (6)	1.1 (6)	1.1 (4)	2.7 (8)	5M + 36m + 13sm

Table V contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
'Red Star'	54	1.4 (6)	1.9 (7)	1.0 (4)	1.3 (9)	1.4 (7)	1.6 (5)	1.1 (5)	1.3 (4)	3.3 (7)	4M + 36m + 7sm + 7st
cv. K_1	54	1.3 (8)	1.7 (8)	1.1 (4)	1.1 (4)	1.2 (5)	1.4 (4)	1.3 (7)	1.7 (6)	2.9 (8)	46m + 8sm
'Snow White'	54	1.4 (6)	1.1 (5)	1.6 (9)	1.1 (8)	2.5 (5)	1.3 (5)	1.2 (6)	1.6 (6)	2.4 (4)	45m + 9sm
'Laura'	54	1.5 (6)	1.1 (9)	1.2 (5)	1.2 (7)	1.4 (7)	2.2 (6)	1.1 (5)	1.1 (4)	2.5 (5)	43m + 11sm
'Summer Gem'	54	1.5 (8)	1.1 (6)	1.4 (7)	1.9 (4)	1.1 (7)	1.3 (4)	1.3 (5)	1.2 (5)	3.0 (8)	42m + 12sm
'Megami'	54	1.5 (4)	1.1 (9)	1.4 (8)	1.9 (5)	1.1 (6)	1.3 (4)	1.4 (6)	1.1 (5)	2.7 (7)	42m + 12sm
'Silver Cloud'	54	1.7 (5)	1.6 (6)	1.1 (6)	2.3 (4)	1.5 (6)	1.1 (5)	1.5 (10)	1.2 (4)	2.7 (8)	42m + 12sm
'Lilith'	54	1.5 (10)	1.2 (6)	1.1 (6)	1.5 (8)	1.1 (5)	2.5 (4)	1.3 (4)	1.2 (3)	2.6 (8)	42m + 12sm
'Linda'	54	1.8 (6)	1.2 (5)	1.1 (8)	1.4 (8)	1.5 (6)	1.1 (5)	1.1 (5)	1.7 (3)	2.5 (8)	40m + 14sm
cv. T_1	54	1.3 (4)	1.3 (6)	1.6 (8)	1.2 (6)	1.4 (4)	1.3 (4)	1.8 (8)	1.4 (8)	2.7 (6)	40m + 14sm
'Badger'	54	1.5 (6)	1.8 (5)	1.1 (8)	1.6 (4)	1.5 (9)	1.1 (5)	1.5 (5)	1.2 (4)	2.4 (9)	40m + 14sm

Table V contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
'Bosetsu'	54	1.3 (6)	1.8 (7)	1.1 (7)	1.5 (5)	1.7 (5)	1.2 (4)	1.1 (4)	1.1 (7)	3.0 (7)	40m + 14sm
'Basanti'	54	1.2 (6)	1.8 (4)	1.4 (7)	1.1 (8)	1.4 (5)	2.0 (4)	1.1 (6)	1.1 (5)	2.3 (9)	37m + 17sm
cv. NN_{12}	54	1.5 (9)	1.2 (7)	1.3 (5)	1.8 (7)	1.2 (4)	1.5 (6)	2.5 (4)	1.1 (6)	3.0 (6)	37m + 17sm
'Hope'	54	1.4 (7)	2.1 (7)	1.7 (5)	1.1 (6)	1.1 (7)	1.8 (6)	1.9 (6)	1.2 (5)	2.7 (5)	36m + 18sm
cv. X_1	54	1.3 (10)	1.1 (7)	2.1 (8)	1.1 (5)	1.6 (4)	1.2 (5)	1.1 (6)	2.0 (4)	3.2 (5)	37m + 12sm + 5st
cv. M_{45}	54	1.2 (7)	1.9 (5)	1.1 (6)	1.8 (6)	1.2 (5)	1.9 (7)	1.1 (6)	1.5 (6)	3.9 (6)	30m + 18sm + 6st
cv. K_2	54	1.4 (6)	1.1 (7)	1.8 (7)	1.5 (6)	1.1 (8)	2.5 (5)	1.3 (5)	1.4 (4)	3.3 (6)	36m + 12sm + 6st
'Spoon'	54	1.2 (7)	1.2 (6)	1.6 (6)	2.2 (6)	1.2 (6)	1.1 (6)	1.5 (6)	1.3 (4)	3.3 (7)	41m + 6sm + 7st
cv. NN_{14}	54	1.6 (5)	1.2 (7)	1.3 (7)	1.5 (6)	1.1 (8)	2.3 (5)	1.5 (5)	1.1 (4)	3.1(6) 1.5(1)	43m + 5sm + 6st
'Nanako'	54	1.6 (8)	1.3 (7)	1.3 (4)	1.1 (6)	1.5 (6)	1.9 (5)	1.6 (5)	1.1 (5)	3.1 (8)	41m + 5sm + 8st
cv. P_8	54	1.4 (6)	2.1 (6)	1.3 (7)	1.2 (8)	1.5 (4)	1.4 (5)	1.1 (5)	1.4 (4)	3.1 (9)	39m + 6sm + 9st

Table V contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
'Mohini'	54	1.4 (6)	1.2 (6)	1.4 (5)	1.5 (6)	1.8 (5)	2.3 (9)	1.2 (5)	1.6 (5)	3.3(5) (2) ∞	33m + 14sm + 5st + 21
Heptaploid											
'Grape Bowl'	63	1.5 (8)	1.9 (7)	1.1 (8)	1.4 (10)	1.1 (8)	2.2 (6)	1.2 (5)	1.1 (4)	2.9 (7)	43m + 20sm
'John Webber'	63	1.4 (6)	1.1 (7)	1.6 (6)	1.1 (12)	1.4 (5)	1.4 (6)	2.6 (6)	1.7 (8)	3.6 (7)	50m + 6sm + 7st
'President Viger'	63	2.3 (5)	1.2 (11)	1.4 (6)	1.6 (6)	1.3 (7)	2.2 (5)	1.5 (7)	1.2 (8)	3.8 (8)	45m + 10sm + 8st
Octoploid											
'Chenghiskhan'	72	1.1 (10)	1.5 (11)	2.4 (9)	1.2 (7)	1.2 (8)	1.7 (7)	1.8 (7)	1.1 (7)	3.5(5) 1.4(1)	51m + 16sm + 5st
Aneuploid											
'Sherad Mala'	53	1.0 (6)	1.8 (6)	1.5 (7)	1.9 (6)	1.0 (6)	1.6 (6)	1.4 (6)	1.2 (5)	3.6 (5)	12M + 24m + 12sm + 5st
cv. 00_5	53	1.4 (7)	1.2 (4)	1.7 (8)	1.0 (5)	1.3 (7)	1.7 (4)	1.0 (7)	2.0 (5)	3.5 (6)	12M + 30m + 5sm + 6st
cv. G_2	53	1.6 (7)	1.0 (12)	1.7 (6)	1.4 (4)	1.2 (5)	1.4 (4)	2.1 (4)	1.4 (4)	3.3 (7)	12M + 30m + 4sm + 7st
cv. E_{10}	53	1.1 (9)	1.4 (8)	2.1 (6)	1.4 (6)	1.3 (5)	1.8 (5)	1.0 (5)	1.2 (3)	2.9 (6)	5M + 31m + 17sm
cv. SS_1	53	1.6 (6)	1.1 (6)	1.1 (8)	1.6 (5)	1.4 (6)	1.2 (5)	1.4 (6)	1.9 (5)	2.8 (6)	42m + 11sm

Table V contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
cv. C_8	53	1.4 (7)	1.1 (4)	1.7 (4)	1.3 (6)	1.8 (4)	1.1 (4)	1.2 (8)	1.5 (5)	2.7 (11)	38m + 15am
cv. T_2	53	1.6 (10)	1.1 (11)	2.0 (5)	1.2 (5)	5.4 (3)	1.4 (8)	1.3 (4)	1.9 (3)	2.9 (4)	38m + 12am + 3at
cv. AA6	53	1.7 (6)	1.2 (5)	1.4 (7)	1.1 (6)	1.3 (5)	2.6 (4)	1.6 (8)	1.2 (6)	3.1 (6)	43m + 4am + 6at
cv. Y_{15}	53	1.5 (6)	1.1 (9)	1.6 (7)	1.4 (6)	2.2 (4)	1.2 (5)	1.8 (4)	1.2 (5)	3.1 (7)	38m + 8am + 7at
'Donald'	55	1.6 (9)	1.0 (5)	1.8 (7)	1.1 (5)	1.3 (6)	1.1 (4)	1.6 (8)	1.2 (5)	3.0 (6)	5M + 37m + 13am
'Dainty Maid'	55	1.8 (8)	1.5 (6)	1.1 (3)	1.4 (8)	1.0 (3)	1.2 (7)	1.7 (6)	1.1 (5)	2.9 (9)	3M + 35m + 17am
cv. X_2	55	1.3 (10)	1.0 (4)	1.6 (8)	1.1 (10)	1.3 (4)	1.4 (4)	1.5 (3)	1.1 (7)	3.7 (5)	4M + 46m + 5at
cv. U_2	55	1.5 (7)	1.1 (8)	1.3 (7)	1.8 (8)	1.0 (3)	1.4 (5)	2.5 (7)	1.2 (4)	3.0 (5)	3M + 32m + 20am
cv. C_1	55	1.2 (4)	1.3 (7)	1.1 (9)	1.2 (8)	1.7 (6)	1.3 (4)	1.5 (4)	1.1 (4)	2.6 (9)	46m + 9am
'Flirt'	55	1.4 (8)	1.1 (7)	1.1 (4)	1.5 (7)	1.3 (4)	1.1 (5)	1.6 (7)	1.1 (4)	2.5 (9)	46m + 9am

Table V contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
cv. S_9	55	1.5 (8)	1.1 (10)	1.4 (7)	1.2 (4)	1.1 (4)	1.4 (6)	1.2 (4)	2.1 (4)	2.6 (8)	43m + 12sm
cv. T_{10}	55	1.2 (8)	1.1 (7)	1.9 (5)	1.3 (7)	1.1 (5)	1.3 (6)	1.5 (5)	1.3 (5)	2.8 (7)	43m + 12sm
cv. NN_{10}	55	1.5 (9)	1.1 (6)	1.6 (8)	1.4 (5)	1.4 (8)	1.7 (8)	1.5 (3)	1.3 (4)	3.4 (6)	49m + 6st
'Lohengrin'	55	1.2 (4)	1.7 (9)	1.1 (6)	1.1 (7)	2.0 (7)	1.2 (6)	1.5 (7)	1.1 (2)	3.1 (7)	41m + 7sm + 7st
cv. NN_9	55	2.0 (6)	1.1 (4)	1.2 (8)	1.3 (6)	1.6 (5)	1.4 (7)	2.2 (5)	1.2 (6)	3.6 (8)	36m + 11sm + 8st
'Valiant'	55	1.5 (8)	1.0 (8)	1.5 (6)	2.6 (6)	1.3 (6)	1.1 (5)	1.2 (5)	1.7 (5)	4.2 (6)	8M + 35m + 6sm + 6st
cv. R_{27}	56	2.1 (7)	1.4 (11)	1.2 (6)	1.5 (6)	1.2 (4)	2.0 (6)	2.8 (6)	1.4 (4)	3.6 (6)	31m + 19sm + 6st
'Golden Wave'	56	1.9 (7)	1.2 (6)	1.0 (6)	1.7 (6)	1.3 (6)	1.2 (6)	1.6 (6)	1.4 (6)	2.7 (7)	6M + 36m + 14sm
'Connie Mayhew'	57	1.6 (8)	1.2 (11)	1.1 (5)	2.0 (7)	1.5 (7)	1.2 (8)	1.4 (6)	2.1 (3)	3.7 (5)	42m + 10sm + 5st
cv. R_{10}	58	1.1 (5)	1.5 (8)	1.5 (7)	1.1 (5)	2.7 (5)	1.0 (7)	1.3 (6)	1.7 (7)	3.3 (8)	7M + 38m + 5sm + 8st

Table V contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
'Bronze Turner'	58	1.2 (8)	1.4 (6)	1.6 (7)	2.0 (7)	1.5 (6)	1.1 (5)	1.9 (5)	1.6 (6)	3.4 (8)	38m + 12sm + 8st
cv. T_{17}	59	1.6 (5)	1.1 (10)	1.5 (9)	1.8 (5)	1.2 (7)	1.5 (6)	3.1 (4)	1.3 (5)	3.1 (8)	42m + 5sm + 12st
'Rupasa Bangla'	60	1.3 (7)	1.7 (6)	1.2 (7)	1.5 (8)	2.2 (6)	1.0 (4)	1.2 (7)	1.6 (7)	2.7 (8)	4M + 42m + 14sm
'Mahathma Gandhi'	62	1.2 (7)	1.9(5) 2.8(3)	1.1 (9)	1.2 (10)	2.2 (4)	1.5 (5)	1.1 (7)	1.8 (5)	3.4(6) ∝(1)	38m + 17sm + 6st + 1T
'Kasturba Gandhi'	62	1.4(1) 1.9(8)	1.1 (8)	1.5 (6)	1.2 (5)	1.2 (6)	1.5 (7)	1.7 (7)	1.2 (5)	3.5(11) ∝(1)	42m + 8sm + 11st + 1T
'Alfred Wilson'	64	2.2 (9)	1.5 (7)	1.2 (9)	1.3 (7)	1.4 (8)	1.5 (6)	3.2 (6)	1.2 (6)	3.7 (6)	43m + 9sm + 12st
'Harvest Home'	65	1.7 (7)	1.7 (13)	1.2 (8)	1.3 (6)	1.1 (9)	1.4 (7)	1.8 (5)	1.1 (4)	2.9 (8)	52m + 13sm
'John Bull'	65	1.4 (8)	2.1 (5)	4.1 (6)	1.2 (13)	2.2 (5)	1.5 (12)	4.3 (6)	1.3 (6)	3.2 (4)	39m + 10sm + 16st
cv. T_{35}	65	2.2 (5)	1.1 (6)	1.4 (10)	1.2 (6)	1.7 (9)	1.3 (7)	1.2 (5)	1.6 (7)	3.3 (10)	50m + 5sm + 10st
'Sonar Bangla'	67	2.5(1) 1.6(7)	1.1 (11)	1.4 (5)	1.5 (5)	1.4 (7)	1.1 (7)	1.4(6) 2.[illegible](3)	1.0(1) 1.3(5)	1.0(1) 3.1(8)	2M + 53m + 4sm + 8st

Table V contd.

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
cv. U_{25}	67	1.4 (7)	1.4 (10)	1.6 (8)	1.1 (11)	1.1 (7)	1.7 (6)	2.1 (7)	1.4 (4)	3.5 (7)	53m + 7em + 7at
cv. U_1	54+18	1.4(7) 2.3(1)	1.1 (8)	1.8 (6)	1.4 (6)	1.3 (8)	3.2 (4)	1.5 (5)	1.4 (6)	2.7(6) +18	37m + 13em + 4at + 18
'Innocence'	56+18	1.2 (12)	1.9 (9)	1.3 (5)	1.1 (7)	1.4 (4)	1.4 (4)	2.1 (6)	1.1 (4)	3.7(5) +18	36m + 15em + 5at + 18

Table VI

Chromosome Associations at metaphase I in Tetraploid *C. scrifolium* cultivar (2n = 36)

Taxon	Number of cells analysed	CHROMOSOME ASSOCIATION IV Range	IV Mean	III Range	III Mean	II Range	II Mean	I Range	I Mean	Pollen stainability (%)
'Liliput'	25	0-3	1.08± 0.25	-	-	12-18	15.84 ± 0.31	-	-	81.20

Table VII

Chromosome Associations at metaphase I in Pentaploid *C. morifolium* cultivars (2n = 45)

Taxon	No. of cells analysed	CHROMOSOME ASSOCIATION V Range	V Mean	IV Range	IV Mean	III Range	III Mean	II Range	II Mean	I Range	I Mean	Pollen stainability (%)
'Kasturi'	25	0–2	0.22 ±0.50	0–1	0.13 ±0.38	0–5	2.09 ±0.12	12–21	16.52 ± 0.42	1–5	4.08 ±0.59	15.6
cv. P_1	25	0–1	0.24 ±0.14	0–1	0.13 ±0.90	1–3	1.60 ±0.44	15–17	16.14 ± 0.23	5–8	6.20 ±0.31	75.9
cv. P_5	25	0–1	0.36 ±0.21	0–1	0.56 ±0.28	1–4	2.24 ±0.89	12–18	15.08 ± 0.41	3–6	4.08 ±0.22	84.7

Table VIII

Chromosome Associations at metaphaseIin Hexaploid *C. morifolium* cultivars (2n = 54)

Taxon	No. of cells analysed	CHROMOSOME ASSOCIATION										Pollen stainability (%)
		VI		IV		III		II		I		
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
'Lalquila'	25	0-1	0.04 ±0.11	0-2	0.56 ±0.20	0-2	0.32 ±0.58	21-27	24.84 ± 0.16	0-2	0.88 ±0.41	88.0
'Lilith'	25	0-1	0.08 ±0.82	0-2	0.88 ±0.24	0-2	0.08 ±0.13	20-27	24.84 ± 0.33	0-2	0.07 ±0.50	80.7
'Sharad Mukta'	25	0-1	0.12 ±0.50	0-2	0.64 ±0.48	0-2	0.32 ±0.64	21-27	24.68 ± 0.42	0-3	0.40 ±0.37	75.6
'Sharad Prabha'	25	-	-	0-3	0.70 ±0.15	0-1	0.08 ±0.41	21-27	25.37 ±0.75	0-2	0.22 ±0.18	85.6
'Sharad Shobha'	25	-	-	0-2	0.68 ±0.56	0-1	0.12 ±0.32	23-27	25.40 ± 0.84	0-1	0.12 ±0.60	94.4
cv. A_{16}	25	0-1	0.08 ±0.23	0-4	0.20 ±0.11	0-1	0.08 ±0.41	18-27	24.12 ± 0.50	0-2	0.24 ±0.32	72.0
cv. D_5	25	0-1	0.12 ±0.30	0-3	0.92 ±0.85	0-2	0.08 ±0.72	19-27	24.08 ± 0.25	0-2	0.20 ±0.45	86.4
cv. DN_1	25	0-1	0.15 ±0.29	0-4	1.30 ±0.24	-	-	19-27	23.69 ± 0.13	0-2	0.52 ±0.15	70.3
'Linda'	25	0-2	0.24 ±0.18	0-3	1.20 ±0.56	0-1	0.12 ±0.70	17-27	23.64 ±0.18	0-1	0.12 ±0.07	66.5

Table VIII contd.

Taxon	No. of cells analysed	CHROMOSOME ASSOCIATION VI Range	VI Mean	IV Range	IV Mean	III Range	III Mean	II Range	II Mean	I Range	I Mean	Pollen stainability (%)
cv. S_3	25	0-1	0.16 ±0.55	0-3	1.00 ±0.16	0-2	0.20 ±0.98	19-27	24.16 ± 0.34	0-1	0.12 ±0.37	88.5
'Mohini'	25	0-2	0.33 ±0.85	0-2	0.77 ±0.50	0-2	0.38 ±0.55	19-27	23.66 ± 0.22	0-2	0.48 ±0.41	82.5
cv. T_6	25	0-1	0.35 ±0.32	0-4	1.25 ±0.39	0-1	0.35 ±0.50	20-27	22.75 ± 0.45	0-1	0.35 ±0.16	95.1
cv. T_7	25	0-1	0.28 ±0.56	0-2	0.72 ±0.38	0-1	0.04 ±0.12	22-27	24.52 ± 0.40	0-2	0.28 ±0.55	68.0
'White Cloud'	25	0-1	0.42 ±0.22	0-3	0.78 ±0.10	0-3	0.64 ±0.66	18-27	22.85 ± 0.23	0-4	0.74 ±0.14	93.6
cv. Y_1	25	0-1	0.20 ±0.87	0-4	1.20 ±0.95	0-2	0.16 ±0.50	14-27	23.60 ±0.84	0-2	0.32 ±0.66	81.5
cv. Y_{21}	25	-	-	0-2	0.69 ±0.45	-	-	23-27	25.53 ± 0.32	0-2	0.18 ±0.11	82.2
cv. No_5	25	-	-	0-4	1.60 ±0.07	0-1	0.08 ±0.15	19-26	23.28 ± 0.28	0-4	0.80 ±0.10	70.5

Table IX

Chromosome Associations at metaphase in Octoploid *C. morifolium* cultivars (2n = 72)

Taxon	No. of cells analysed	CHROMOSOME ASSOCIATION																Pollen stainability (%)
		VIII		VII		VI		V		IV		III		II		I		
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
'Chenghis-khan'	25	0-1	0.08 ±0.05	-	-	0-1	0.17 ±0.30	0-1	0.02 ±0.12	0-3	1.17 ±0.44	0-3	1.08 ±0.98	25-34	30.41 ± 0.65	0-5	1.50 ±0.12	93.5

Table X

Chromosome Associations at metaphase I in Aneuploid *C. morifolium* cultivars

Taxon	Chromosome No. (2n)	No. of cells analysed	CHROMOSOME ASSOCIATION VI Range	VI Mean	V Range	V Mean	IV Range	IV Mean	III Range	III Mean	II Range	II Mean	I Range	I Mean	Pollen stainability (%)
cv.$4A_6$	53	25	0-1	0.08 ±0.10	-	-	0-3	0.33 ±0.07	0-2	0.33 ±0.50	20-26	24.58 ± 0.35	0-2	1.03 ±0.30	79.6
'Anamika'	53	25	-	-	-	-	0-3	1.05 ±0.04	0-2	0.10 ±0.32	20-26	23.75 ± 0.30	0-1	1.00 ±0.25	68.3
'Sharad Mala'	53	25	-	-	-	-	0-2	0.23 ±0.45	0-1	0.10 ±0.28	22-26	25.43 ± 0.63	0-1	0.92 ±0.38	70.4
'Rosa'	53	25	0-1	0.04 ±0.06	-	-	0-2	0.29	0-1	0.12 ±0.47	21-26	25.12 ± 0.47	0-3	0.95 ±0.83	83.5
'Dainty Maid'	55	25	0-2	0.16 ±0.95	-	-	0-2	0.87 ±0.18	0-2	0.33 ±0.60	17-27	24.37 ± 0.58	0-3	0.83 ±0.30	80.0
'Sharad Bahar'	55	25	-	-	-	-	0-3	0.45 ±0.05	0-1	0.05 ±0.43	21-28	25.97 ± 0.70	0-3	1.11 ±0.15	72.4
cv. P_3	55	25	0-1	0.08 ±0.60	-	-	0-2	0.79 ±0.38	0-1	0.12 ±0.43	20-27	25.04 ± 0.25	0-1	0.92 ±0.05	89.2
cv. T_{19}	55	25	0-1	0.08 ±0.02	-	-	0-3	0.76 ±0.14	0-1	0.36 ±0.50	21-27	24.76 ± 0.20	0-3	0.88 ±0.19	76.1
cv. M30	56	25	0-1	0.06 ±0.51	-	-	0-2	0.51 ±0.03	0-2	0.35 ±0.18	21-28	25.87 ±0.12	0-3	0.71 ±0.35	81.0

Table X contd.

Taxon	Chromosome No. (2n)	No. of cells analysed	CHROMOSOME ASSOCIATION VI Range	VI Mean	V Range	V Mean	IV Range	IV Mean	III Range	III Mean	II Range	II Mean	I Range	I Mean	Pollen stainability (%)
'Connie Mayhew'	57	25	0-1	0.03 ±0.18	0-1	0.03 ±0.01	0-3	0.58 ±0.06	0-3	0.68 ±0.63	20-28	25.27 ±0.37	0-4	1.67 ±0.45	37.5
'J.H.Salisbury'	58	25	0-1	0.08 ±0.36	-	-	0-2	0.69 ±0.27	0-2	0.43 ±0.50	21-29	26.21 ±0.52	0-3	0.57 ±0.19	53.2
'R.M.Quittenton'	59	25	0-1	0.18 ±0.62	0-2	0.09 ±0.12	0-3	0.84 ±0.15	0-3	1.24 ±0.20	18-28	23.72 ±0.48	0-6	1.95 ±0.25	48.2
'Rupasa Bangla'	60	25	0-1	0.07 ±0.37	-	-	0-3	1.14 ±0.40	0-2	0.88 ±0.12	22-30	25.62 ±0.01	0-4	1.04 ±0.56	95.6
'Mahathma Gandhi'	62	25	0-2	0.19 ±0.76	-	-	0-3	0.83 ±0.12	0-2	0.64 ±0.55	21-30	26.54 ±0.18	0-6	2.44 ±0.34	20.3
'Kasturba Gandhi'	62	25	0-1	0.06 ±0.98	0-1	0.06 ±0.50	0-3	0.70 ±0.25	0-3	1.26 ±0.22	23-29	25.56 ±0.42	0-7	3.64 ±0.18	65.9
'Sonar Bangla'	67	25	0-1	0.20 ±0.01	0-1	0.04 ±0.35	0-3	1.16 ±0.66	0-4	1.0 ±0.44	21-31	27.88 ±0.18	0-6	2.20 ±0.28	32.5
'Innocence'	56+18	25	0-1	0.09 ±0.09	-	-	0-3	1.27 ±0.17	0-1	0.27 ±0.12	22-28	24.36 ±0.57	0-1	0.85 ±0.65	65.3

Table XI

2C nuclear DNA contents in pg DNA using *Allium cepa* as standard

Taxon	2N =	X DNA (pg)
Chrysanthemum morifolium		
cv. 'Liliput'	4x = 36	12.64
cv. 'Phyllis'	5x = 45	13.47
cv. 'Kasturi'	5x = 45	15.12
cv. 'P5'	5x = 45	14.80
cv. 'P1'	5x = 45	15.57
cv. 'Nenako'	6x = 54	19.41
cv. '020'	6x = 54	19.17
cv. 'Megami'	6x = 54	20.67
cv. 'Summer Gem'	6x = 54	20.42
cv. 'F5'	6x = 54	20.98
cv. 'U2'	6x+1 = 55	19.34
cv. 'Potomac'	8x = 72	25.33

5. DISCUSSION

Basic Number

A perusal of Table III shows that the most common basic number in the genus Chrysanthemum is 9, however, polyploids do not necessarily show an exact multiple of the basic number; instead there is a wide range of aneuploid numbers (see Table III and IV). Hern and Lee (1968) found new aneuploid numbers in Chrysanthemum species such as C. lavandulaefolium (2n = 16) and C. indicum (2n = 20) (Table III). It is worth mentioning that there is much controversy regarding the basic number in the family Compositae as such. In Asteraceae there are a large number of species with n = 4 and n = 5 and Turner et al. (1961) proposed a hypothesis that species with 2x = 9 are polyploid derivatives. However, in the tribe Anthemideae, to which Chrysanthemum belongs, there is an overwhelming constancy of x = 9. Powell et al. (1974) are of opinion that this number would be established as the ancestral base number, rather than x = 5, 8, etc. Numerous examples are available to show the aneuploid reduction in basic number.

Thus, Huziwara (1959) using chromosome number, morphology, etc. concluded that in Aster ageratoides polyploid complex species with x = 5 and x = 8 are aneuploid derivatives of species with x = 9. Similar aneuploid reduction is common in species of Crepis where a reduction in chromosome number is followed by increasing morphological specialisation (Stebbins, 1971). Occurrence of aneuploid reduction in Chrysanthemum, as stated above, could be substantiated with the findings of Rana (1965a,b, 1967). In Chrysanthemum carinatum he found spontaneous interchanges occurring in many geographically isolated populations. Further, he could discover monosomic interchange heterozygotes and nullisomics among progenies of cross between interchange heterozygotes from different localities. In an intervarietal hybrid of the above species, he found PMCs with two different chromosome numbers in the same anther. In nature, Chrysanthemum indicum exists in tetraploid and hexaploid forms. The occurrence of 2n = 20 in C. indicum shows that it might have come through polyploid reduction. The conclusion drawn by Solbrig (1977) seems to be most widely accepted and according to him polyploid-aneuploid reduction and chromosome loss are believed to be the basic mechanism of chromosome number change within the family Compositae, as in other angiosperms.

Range in Somatic numbers

Table III depicts the chromosome number in species and in Table IV, chromosome number for cultivars of C. morifolium is given. A perusal of Table III shows that the chromosome number in Chrysanthemum species ranges from 2n = 18 (2x) to 2n = 198 (22x). In cultivars of C. morifolium the somatic number ranges from 2n = 36 (4x) to 2n = 75 (8x + 3) with various aneuploid numbers in between. In the present analysis of 183 cultivars, the various chromosome numbers encountered are 2n = 36, 45, 53, 54, 55, 56, 57, 58, 59, 60, 62, 63, 64, 65, 67, 68 and 72. Figure 50 depicts the number of cultivars showing different chromosome numbers, with the most common number being 2n = 54. Most of the cultivars had 2n = 53 to 55 chromosomes.

Previous reports of chromosome numbers in C. morifolium also show a poly-aneuploid series. Thus Shimotomai (1933) found the chromosome number in 60 Japanese cultivars to vary between 53 to 67, however, the most common number being 2n = 54. Similarly, Dowrick (1953) found that 68 English cultivars varied between 47 to 63, and most cultivars showed 54 to 56 chromosomes with a peak at 2n = 54. Similar variation was reported by Walker (1955) and Sampson et al. (1958)

who found that the American cultivars varied between 45 to 64. The most frequent number in American cultivars was 2n = 57. Dowrick and El-Bayoumi (1966a) studied an additional 27 English cultivars, the chromosomes number of which ranged from 2n = 51 to 60 with a peak at 2n = 54. An extensive chromosome survey of nearly 284 Japanese cultivars consisting of all the representative horticultural types by Endo (1969a,b) had shown that the chromosome number ranges from 2n = 36 to 75+8. It was quite remarkable that the cultivars having large single capitula showed unusually a much higher chromosome number, ranging from 2n = 70 to 75+8. He has encountered the lowest chromosome number 2n = 36 for the first time with a certain small flowered cultivar used as cut flower in commerce.

The above authors attempted a correlation between the chromosome number and the inflorescence size. In all the above cases large flowered cultivars tended to have higher chromosome number. Thus in Japanese cultivars, plants with large inflorescence showed higher chromosome numbers ranging from 2n = 56 to 67, while those with smaller inflorescence have lower numbers ranging from 2n = 53 to 55. Shimotomai (1933), Walker (1955) and Sampson et al. (1958) found

similar correlation in American cultivars. Dowrick (1953), and Dowrick and El-Beyoumi (1966a) confirmed such correlation in English cultivars. Endo (1969a,b) could recognize an appreciable intimate relationship between flower size and chromosome number, only in certain limited forms of the large flowered chrysanthemums. Most of the giant flowered cultivars were almost exclusively confined to forms with 2n = 60 (Endo, 1969a,b).

In the present study also an attempt was made for a similar correlation as mentioned above. (see section 2). Present data is in confirmity with the previous reports in the sense that cultivars with small and medium-sized capitula exhibited lower chromosome numbers (2n = 36 to 55) and the large flowered cultivars showed a range of somatic numbers from 53 to 72. However, as Sampson et al. (1958) pointed out, it is difficult to draw a correlation that the inflorescence diameter increases with increase in chromosome number, since the capitula diameter is prone to changes depending upon the cultural practices.

Variation in chromosome size and morphology

The chromosome size varies with environmental influence and/or different experimental conditions

(Swanson, 1957; Rothfels and Simnovitch, 1958; Bennett and Rees, 1969). Bennett and Rees (1969) have shown that in Secale cereale and Allium cepa there is a positive effect of age and nutrition on the chromosome size in root meristems and the variation is entirely due to protein content. Lighty and Pleisted (1960) stressed the idea that critical estimate can be obtained only after environment is controlled and statistical methods are employed. Chromosome size is subjected to genotypic control as well; its extent can therefore be altered by changes at the genic level following either mutation or recombination (John and Lewis, 1968). Such genotypic control can even influence tissue-specific variation within an organism (Jackson, 1971). Although differences in chromosome size in various cultivars of Chrysanthemum have not been studied critically, in the present investigation, in general, there was no sharp size difference within the complement, so that no different size classes such as long, medium and short could be recognized. The longest chromosome differed in length only by 1.3 to 1.5 times from the shortest. In diploid species of Chrysanthemum, the chromosome size ranges from 6 to 8 µm and there is gradual size diminution throughout polyploid series to C. lacustre (2n = 198) whose average chromosome

size is under 3 µm (Dourick, 1952). In tetraploid cultivar analysed in the present case, the size of the chromosomes ranged from 3.8 to 5.0 µm whereas in various hexaploid cultivars the size range was 3.2 to 4.8 µm. However, the octoploid cultivar 'Chenghiakhan' showed a decrease in chromosome size which ranged from 2.1[illegible] to 3.4[illegible] µm. Thus decrease in the size of the chromosome with an increase in the level of ploidy is apparent in C. morifolium. Such decrease in chromosome size in polyploid taxa is found in several genera like Allium (Ved Brat, 1965a), Crinum and Zephyranthes (Raina and Khoshoo, 1971a,a), Hemerocallis (Zadoo et al., 1976), Amaryllis (Narain, 1977) and Chrysanthemum (Watanabe, 1981a,b,c). According to Darlington (1973) this property is an adaptation of polyploids to resolve the nuclear cytoplasm balance near the diploid level. This can also be due to a decrease in the level of polyploidy (Darlington, 1958) or by losing small portions of duplicated genetic material.

Following Stebbins' (1958) classification, karyotype of all cultivars fall in 2A category. This implies that karyotypes are reasonably symmetrical. A lack of appreciable size difference between the shortest and longest sets is one of the reasons for overall stability of the degree of asymmetry.

Throughout the genus there is uniformity in the form and size between the chromosomes of the basic complement and in many cases centromeres are all median or nearly so (Dowrick, 1952). While the basic chromosome number is 9 in the genus and karyotype of garden cultivars could be resolved into 9 sets, the details regarding the basikaryotype are not clear from a comparison of 76 taxa ranging from 4x to 6x.

The exact ancestry of many of the garden chrysanthemums is more or less unknown. There is a speculation that species like C. indicum and C. morifolium (C. sinense) have been involved in the development of garden chrysanthemums. According to Darlington (1973), they are derived entirely from hybrids within a hexaploid complex of chinese species loosely known as C. indicum. Nohara (1927) considers that the Japanese ornamental chrysanthemum are derivatives from wild C. sinense var. spontaneum. Stapf (1933) is of view that species such as C. erubescens (6x), C. ornatum (6x, 8x and 10x), C. japonense (6x, 8x, 10x, 10-1) and C. makinoi (2x, 3x and 4x) were also involved in the origin of garden chrysanthemums. The similarity of chromosome size and morphology both between and within species and a lack of information regarding the basikaryotype of

elemental species removes one important lead for the establishment of a basikaryotype in garden cultivars. Cultivation and selection for a long time resulted in plants bearing little resemblance to their ancestral species.

Diploid species of Chrysanthemum such as C. boreale, C. lineare, C. vulgare, C. rupestre and C. nipponicum were reported to have chromosomes with median, submedian and subterminal centromeres (Tanaka and Shimotomai, 1961; Watanabe, 1981a). Virpi and Bores (1968) found metacentric and submetacentric chromosomes in diploid species C. vulgare, Tominaga (1969) found submedian and subterminal centromeres in the compliment of diploid species like C. cinerai-aefolium and C. coccineum. Tanaka (1960) studied the karyotype of tetraploid form of C. indicum, one of the elemental species of present day garden chrysanthemum. He had shown that the karyotype consists of metacentric, submetacentric and subtelocentric chromosomes and the karyotype formula from his data could be resolved as 8M + 12m + 8sm + 8st. Though Dowrick and El-Gayoumi (1966a) stated that the basic complement in C. morifolium cultivars have only median to submedian centromeres, the karyotype pattern of elemental species

is recognizable in the complement of cultivars analysed. In addition to this, three cultivars possessed telocentric chromosomes. However, various polyaneuploid taxa did not represent the modal karyotype of elemental species and there was no constancy of the basic pattern.

The variation in types of chromosomes (M, m, sm and st) in different polyploid and aneuploid taxa is readily apparent from Table V. In almost all the cultivars the longest chromosome in a complement (1st set) contained metacentric (m) chromosomes. Only exception was cv. 'Sharad Mala' where the 1st set showed an arm ratio of 1.0 (M chromosomes). In all the cultivars the last set (9th) invariably contained either submetacentric (sm) or sub-telocentric (st) chromosomes. In tetraploid 'Liliput' M type chromosomes were not seen (Fig. 52). Among pentaploid taxa cv. 'Kasturi', possessed 9 M chromosomes (Fig. 59) and there was no chromosome with subterminal constriction. The hexaploid cultivars contain 3 categories: the first category is represented by cultivars showing varying number of M chromosomes (Table V). The second category is comprised of cultivars having metacentric (m) and submetacentric (sm) chromosomes only could be recognized. The third category is composed of all types of chromosomes

including telocentrics. The heptaploid cultivars had either median to submedian or rarely subterminal centromeres, while octoploid cultivar contained m, sm and st chromosomes.

Variation in the complement of aneuploid taxa was not regular. At lower aneuploid level, the number of M chromosomes increase in some cultivars. Thus, three cultivars, 'Sharad Mala', 005 and G_2 (all 2n = 53) had 12 such chromosomes. Cultivars with a somatic number 2n = 55 depicted a range of 0 to 8 M chromosomes. Other cultivars with somatic numbers like 2n = 56, 57, 58, 59, 60 and 67 had the same range as in 2n = 55 cytotype. However, cvs. 'Connie Mayhew' (2n = 57) and 'Bronze Turner' (2n = 58) did not possess any M chromosomes. Cultivars with 2n = 62, 64 and 65 contained appreciably high number of subtelocentric (st) chromosomes, when compared to other polyploid and/or aneuploid taxa (see Table V). The number of st chromosomes ranged from 10 to 16, however, 'Harvest Home' (2n = 65) did not show such type of chromosomes. In conclusion, all the cultivars analysed in the present study tended to have higher number of m chromosomes and there is no selective accumulation of any other chromosome type with respect to a particular polyploid/aneuploid grade.

Sources of chromosomal variation

In addition to the above mentioned variation in karyotype, the present analysis revealed another type of heterozygosity. There was a remarkable inconstancy of the number of chromosomes appearing in a particular set (see Table V). Only the tetraploid cultivar showed a constancy of chromosome number within a set, however, at higher levels of ploidy the pattern of variation is different from cultivar to cultivar. Thus in 'Lohengrin' (2n = 55) the seventh set showed the lowest number i.e. 2 metacentric (m) chromosomes. The highest number of chromosomes within a set was 13 median chromosomes (m) which appeared in the 4th set of 'John Bull' (2n = 65) (Fig. 152). Failure to recognise discrete sets with identical chromosomes in a set, may be the result of ancestors differing in chromosome morphology followed by recombination between them. This leads to tremendous reshuffling of chromosomes resulting in chromosomally unbalanced gametes which are viable due to buffering effect of polyploidy. Union of such gametes results in entirely new chromosome combinations, which are tolerated as there is some interchromosome balance and the degree of differentiation of the 9 chromosomes

of the basic set is very little (Darlington, 1973). According to Jones (1978) if the chromosome sets of a polyploid are homologous or even partly so, the general duplication of gene loci of whole chromosomes provides a balance which allows deleterious mutations in one or more chromosomes to persist in development and heredity under the cover of homologues, hence polyploidy can be said to buffer the effect of chromosome changes which would have little chance of survival in the diploids.

New chromosome combinations resulting from reshuffling of genomes are being continually formed under garden conditions due to intensive and indiscriminate intervarietal hybridization by nurserymen. This view is corroborated by the present study involving a cross between 6x (cv. 'Nanako') and 8x (cv. 'Chenghiskhan') cultivars. Cultivar 'Nanako' is a pompon type and 'Chenghiskhan' irregular type. In the progeny of above cross, as expected, 7x taxon was obtained, and in addition, aneuploid variants like 2n = 60, 61, 62 64, 65, and 66 were also obtained. Karyotype of heptaploid and other aneuploid variants were analysed. From Table XII it is clear that the pattern of variation of the number of chromosomes in a particular set of a

complement is random, as was the case in various cultivars. Moreover, these aneuploid variants gave rise to different flower types such as cineraria, double, pompon, etc. Thus aneuploidy resulting from hybridization has brought about chromosomal repatterning and subsequent origin of new cultivars.

In the above context, it would be interesting to look into the way in which various polyploid and aneuploid taxa ranging from 4x to 8x, might have originated. As stated elsewhere, present day garden chrysanthemums originated from a complex of polyploid species, of which C. indicum is one of the important elemental species. The majority of Chrysanthemum cultivars had arisen from seedlings or in other words through hybridization, both natural as well as deliberate, followed by selection by nurserymen. C. indicum exists in two different forms i.e. tetraploid and hexaploid (see Table III). In the present studies on C. morifolium one tetraploid and two octoploid cultivars have been recorded. From the available data, it can be presumed that the tetraploid taxon might have originated as a result of a cross between a hexaploid garden cultivar and tetraploid forms of C. indicum which could give rise

Figs. 104–108 : Octoploid Taxon
('Chenghiskhan', 2n = 72)

Fig. 104 : Somatic chromosomes

Fig. 105 : Photo-idiogram
(Heteromorphic set marked)

Fig. 106–108: Meiosis

Fig. 106 : Metaphase I
(1 VIII + 1 VI + 2 III + 26 II

Fig. 107 : Metaphase I
1 III + 33 II + 3 I

Fig. 108 : Metaphase I
(2 III + 33 II

Table XII

Variation in chromosome number per set of a cross 'Chenghiakhan' (2n = 72) x 'Nanako' (2n = 54).

Taxon	Chromosome Number	Number of chromosomes per set								
		I	II	III	IV	V	VI	VII	VIII	IX
Seedling										
No. I	60	7	7	5	8	5	7	5	7	9
No. II	63	6	9	5	5	8	9	4	7	10
No. III	63	5	5	8	11	5	7	6	6	10
No. IV	65	8	6	9	6	8	7	5	6	10
No. V	65	6	11	8	8	5	6	5	9	7
No. VI	66	9	8	6	5	5	9	7	8	9

to pentaploid forms. Repeated back cross of this 5x hybrid with 4x C. indicum could produce a 4x cultivar. Since this 4x type is highly vigorous, as is the case in cv. 'Liliput' (2n = 36), unconcious selection might have resulted in the establishment of such a cultivar. According to Darlington (1973) some of the variations in chromosome number have arisen from irregular meiosis and germ cell formation in 6x parents and a seedling with 60 chromosomes may originate from parent with 5A or crossed by 6O or indeed any other known types. Such a mechanism may be operative in the origin of higher aneuploids and the octoploid form. Any sort of chromosome unbalance is tolerated because of duplicated genetic material and low degree of differentiation between the basic sets in a complement.

According to Stebbins (1950) in high polyploids when extensive duplication of chromosome material exists, regular behaviour of chromosomes at meiosis is not essential to the production of viable gametes, since different combinations of various number of chromosomes can function. Love and Suneson (1945) found that F_1 hybrid between Triticum macha and Agropyron trichophorum, both of which have 2n = 42, gave rise to F_2 plant with 70 chromosomes which is

best explained as due to the union of an unreduced gamete with 2n = 42 chromosomes with a partially reduced one having 2n = 28. Plants with 2n = 84 and other numbers might be expected to arise from this same F_1 so that it is potentially the progenitor of a number of different lines each with a different chromosome number and capable of becoming a different species (cf. Stebbins, 1950). In the genus Saccharum Bremer (1928) and Grassl (1946) have found at high polyploid levels a great variety of different chromosome numbers, ranging from 2n = 60 to 2n = 120. Many of these numbers are found in the recently produced "Noble Canes" and are therefore the result of plant breeding in recent times. Most of the forms, whether euploid or aneuploid, are reasonably fertile. A similar mechanism as described above, seems to be operative in C. morifolium complex.

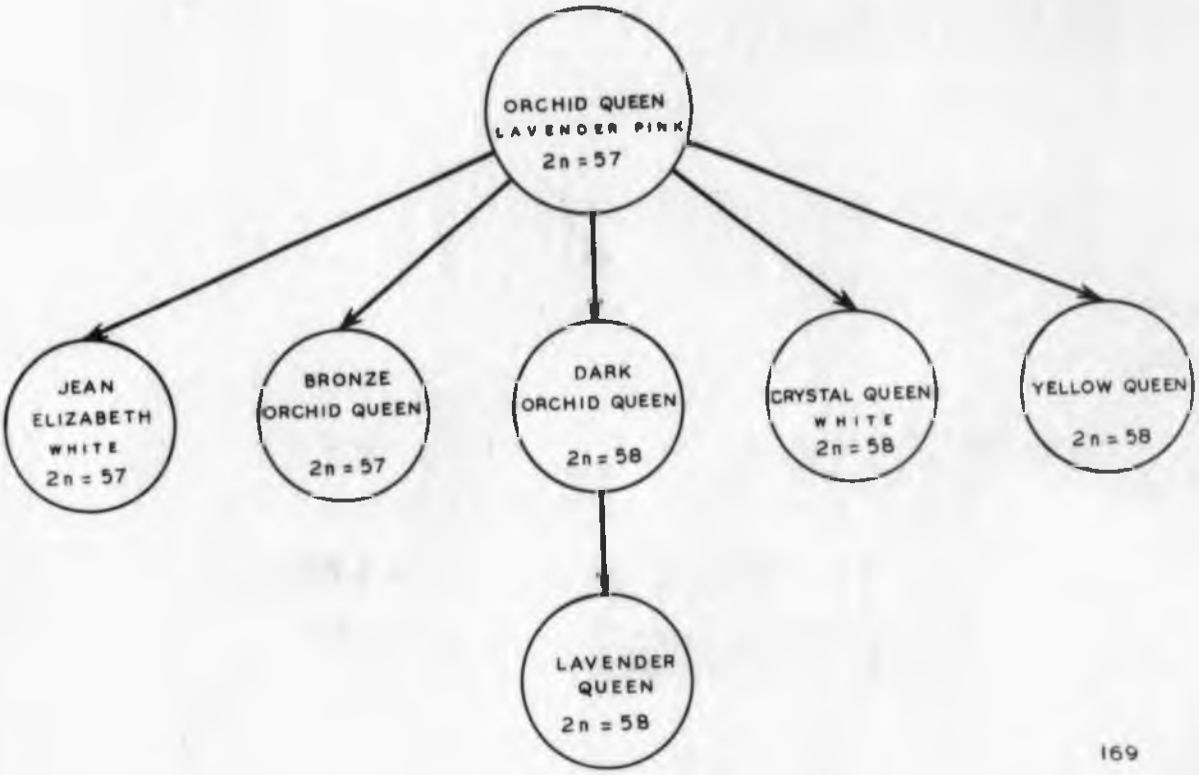
Such disregard for chromosome unbalance as has been observed in garden chrysanthemums has been reported in many plant genera like Hyacinthus (Darlington et al., 1951; Ved Brat, 1967, 1969), Cyrtanthus (Ising, 1962, 1969), Hibiscus (Singh and Khoshoo, 1970; Khoshoo, 1979), Hymenocallis and Zephyranthes (Raina and Khoshoo, 1971d,e; Khoshoo and Raina, 1971, 1976), Narcissus bulbocodium (Darlington, 1973) and Gladiolus (Ghri,1979).

Other examples of sexual species having polyaneuploid cytotypes in nature are Erophela verna (Winge, 1940), Claytonia virginica (Lewis, 1962), Mimulus (Mc Arthur et al., 1972), Stellaria longipes (Chinnappa and Morton, 1974) etc. Besides, several plant genera at polyploid level are reported to have high degree of tolerance to chromosome unbalance, examples are wheat (Kihara, 1924), Nicotiana tabacum (East, 1933), Pyrus and Populus (Levan, 1942), Anthoxanthum (Borril and Carrol, 1965), Gossypium (Brown, 1966) Avena sativa (Khush, 1973) and Hordeum vulgare (Sandfaer, 1979). It can be concluded that certain kinds of unbalance are hardly inferior to the normal state so that changes in number by gain or loss appear to have little effect. According to John and Lewis (1968) such plant species are of remote polyploid or hybrid origin. The principal differentiation which operates between the members of a chromosome complement, and which is co-existent with concept of balance implies that different chromosomes have specific developmental qualities (John and Lewis, 1968). In this context, another point worth mentioning is that in Chrysanthemum cultivars analysed in the present study, it is uncertain whether chromosomes of different sets in the complement are genetically alike.

Bud sports

Another source of chromosomal variation is due to sporting, and a large number of cultivars owe their origin to this (Fig. 169). These arise spontaneously and several cultivars sport continuously to give rise to bud sport families. It has been estimated that one third of the commercial chrysanthemums originated in this way (Baeacher, 1956). From a study of various sporting families, Dowrick (1953) and Sampson et al. (1958) concluded that often sporting is accompanied by change in chromosome number. Chromosomes are lost or gained at mitosis in meristems in the ordinary course of growth and layers of tissue must arise with changed chromosome numbers. The cultivars become chimeral and eventually may form a wholly new type (Darlington, 1973). The new type survives as new garden cultivar. Dowrick and El-Seyoumi (1966a) have shown that the sporting occurs as a result of three kinds of mitotic abnormalities. These are non-disjunction, lagging and stickiness of chromosomes at anaphase. The first two may result in change in chromosome number resulting in change of genetic material. Stickiness of chromosomes and presence of chromatin bridges at anaphase may lead to the formation of fragment chromosomes. Such fragment

Fig. 169 : Pedigree of the 'Queen' family of chrysanthemum bud sport showing the chromosome number. (After Sampson *et al.*, 1958)


ORCHID QUEEN
LAVENDER PINK
2n = 57
JEAN ELIZABETH
WHITE
2n = 57
BRONZE ORCHID QUEEN
2n = 57
DARK ORCHID QUEEN
2n = 58
CRYSTAL QUEEN
WHITE
2n = 58
YELLOW QUEEN
2n = 58
LAVENDER QUEEN
2n = 58

chromosomes were noted in various Japanese, English and American cultivars (see Table IV).

Iwasa *et al.* (1972) noticed different chromosome numbers within and between individual plants of *C. morifolium*. They found abnormal mitotic division in the sporting cultivars of 'Amagahara' family (2n = 56) and in sporting species of *C. shimotomai* (2n = 54). The abnormal mitotic division in 'Amagahara' family was 2.12 per cent and *C. shimotomai* it was 1.05 per cent. The highest rate of mitotic abnormalities (5.5%) was found in a cultivar 'Ki-amagahara', which was placed in a high temperature condition in the day time. From this study Iwasa *et al.* (1972) concluded that it is probable that mitotic abnormalities are common in hexaploid chrysanthemums and the frequency of abnormalities is affected by the environmental factors, especially temperature.

Chimeras

It has been suggested that *Chrysanthemum* cultivars are periclinal chimeras. By rearrangement of chimeral tissue, sports could originate without changes in chromosome number within a plant.

The eversporting nature of some cultivars like 'Anne' had been explained on the basis of such a structure (Anderson, 1935). Popham and Chan (1950) distinguished five zones in the shoot apex of the cultivated chrysanthemums. The outer zone, the tunica, consists of 2 to 5 cell layers of which the outermost layer divides anticlinally and periclinally. An error in cell division is most likely to result in a mericlinal chimera. A lateral branch with a periclinal constitution can arise from a mericlinal tissue depending upon the type of cell division and indeed most chrysanthemum cultivars are of periclinal constitution. However, only those changes which involve the second layer of meristem will affect the flower colour. As new roots arise endogenously, it does not represent all cell layers, the chromosome number obtained from roots cannot be expected to show the complete chimeral make-up of the cultivar.

Aneuploidy

Aneuploidic variation contributes some degree of karyotypic heterozygosity in Chrysanthemum cultivars. Dowrick (1953), Sampson et al. (1958), Dowrick and El-Sayoumi (1966a,b) and Iwasa et al. (1972) observed different chromosome numbers within

root tips of sporting cultivars. The aneuploidy number reported by these authors is represented in Table IV. In chrysanthemum sports, in majority of the cases, chromosomal variation is followed by change in flower colour. However, few sports with changed flower colour were reported to have same chromosome number (Sampson et al., 1958; Dowrick and El-Bayoumi, 1966a). The extreme case of aneuploidy reduction reported by Dowrick (1953) was in the 'Favourite' family. A loss of 7 chromosomes in 'Golden Favourite' (2n = 54) resulted in the origin of 'Shuffils Favourite' (2n = 47). However, reduction in chromosome number was followed by weakness and morphological deformation. Aneuploidy has also been reported in various plant genera like Arabidopsis (Bouharmount, 1969), Claytonia (Lewis, 1962), Allium (Khoshoo et al., 1966), Hordeum (Rajhathy, 1963) etc. Unlike Chrysanthemum, aneuploidic changes in ornamental taxa like Amaryllis (Khoshoo and Narain, 1967), Crinum, Hymenocallis and Zephyranthes (Raina and Khoshoo, 1971b), have not played any significant role in the origin of new taxa. In Crinum, Hymenocallis and Zephyranthes, aneuploidy is attributed to hybridity and polyploidy (Khoshoo and Raina, 1971). According to these authors, polyploidy per se could disturb the nuclear-cell volume

ratio and aneusomatic changes are an indication of the restoration of original ratio. Hybridity involving genic and/or cytoplasmic combination could upset the genetic control of chromosome and spindle behaviour. However, in chrysanthemum sports the aneusomatic variations have resulted from mitotic abnormalities like non-disjunction, lagging of chromosomes, persistence of chromatin bridges etc. (Dowrick, 1953; Dowrick and El-Sayoumi, 1966a,b).

Karyotypic Heteromorphicity

One of the significant markers in chromosomes is the position of centromere. Based on this, arm ratios are calculated for each chromosome and zygotic complements are resolved on the basis of the length of chromosomes and the arm ratio. From the karyotype of various polyploid and aneuploid taxa of C. morifolium it is apparent that heteromorphic sets of chromosomes appear in the complement irrespective of the level of ploidy. The 1st set in almost all the cultivars showed small but consistant variation in the position of centromeres. However, as it was difficult to record the variable arm ratio of all the chromosomes in a set, average value was established for each set (Table V).

In majority of the cases, karyotypic heteromorphicity was due to either a change in the total length of the morphological homologues or variation in arm length and a shift in centromeric position. Such changes in centromeric position and an altered arm ratio might have been brought about by pericentric inversions. Paracentric inversions may not be recognized by standard karyotype analysis unless they involve one of the major chromosome markers such as a secondary constriction or obvious heterochromatic segments (John and Lewis, 1968). Structural alterations are also seen to be operative in Chrysanthemum cultivars. In some cultivars like 'Kasturba Gandhi' (2n = 62) 'Alfred Wilson' (2n = 64), 'Sonar Bangla' (2n = 67), etc. one very long chromosome appeared in the first set (Figs. 151, 152 and 153). In 'Sonar Bangla' one small chromosome with a median centromere was seen in the complement. From Fig. 153 it is apparent that perhaps a reciprocal translocation has occurred in 'Sonar Bangla'. Similar structural changes might have played an important role in the origin of karyotypic heteromorphicity in other cultivars also. Such heteromorphicity could also arise due to hybridity, therefore, an indication of the difference between

parental taxa, or may have arisen subsequent to the origin of the cultivars. Karyotypic heteromorphicity in garden chrysanthemum can be maintained through vegetative multiplication as is the case with many plant genera like Allium (Singh et al., 1967), Amaryllis (Narain and Khoshoo, 1967a, Narain, 1977), Crinum, Hymenocallis and Zephyranthes (Raina and Khoshoo, 1971a,d,e) and Hemerocallis (Zadoo et al., 1976).

B-chromosomes

Small odd chromosomes were found in the complement of few cultivars. Thus in 'Kasturi' (2n = 45), cvs. NN14, 'Mohini' (both 2n = 54) and cv. NN9 (2n = 55), the odd chromosome had submedian constriction. In 'Grape Soul' (2n = 63) and 'Changiskhan' (2n = 72), the small chromosome was subtelocentric type, in addition, 'John Webber' contained another small metacentric chromosome. 'Sonar Bangla' (2n = 67) also showed a metacentric odd chromosome. Apparently, they may look like B-chromosomes, but they are feulgen positive and their number is constant and appear to be regular members of the complement. Chromosome fragments

and small chromosomes have been reported for different species of the genus, and cultivars of C. morifolium. Thus Shimotomai (1932) observed 1 fragment in a large flowered cultivar 'Kikusen' (2n = 59) and in a small flowered cultivar 'Tenshin' (2n = 54). The exact nature of these fragment chromosomes was not clear. Dowrick (1953) observed 64+f constitution in a large flowered English cultivar 'Turbulent' and Dowrick and El-Bayoumi (1966) observed 1 fragment in 'Cream Princess Anne' (2n = 53). The possibility of these fragments being B-chromosome can not be over ruled. Dowrick (1952) observed 2 small fragments in C. lacustre (2n = 198) which were in fact euchromatic with sub-terminal centromeres, and in C. corymbosum var. poterifolium and C. millefoliatum (2n = 18) one iso-B was located in the karyotype as well as in meiosis. Favarger (1963) observed 0 to 1 supernumerary fragment in C. ircutianum (2n = 36) and 0 to 3 in C. heterophyllum (2n = 72) and C. montanum (2n = 54). Fukushima et al. (1965) reported two types of B-chromosomes (F_1 and F_2) in garden cultivars of C. morifolium. The F_1 had a median centromere and F_2 a submedian centromere. The number of Bs ranged from 1 to 2 (see Table IV). Endo (1969a,b) conducted an extensive chromosome survey of nearly 285 cultivars of garden chrysanthemums grown

in Japan. Out of the total taxa studied, 8.4% were found to have 18-chromosome in their somatic cells. The cultivars often showed 2B-chromosomes.

In the present study, B-chromosomes were located in root tip cells of 4 cultivars, such as cv. M_1 (2n = 54 + 1B), 'Nigeria' (2n = 54 + 1B), 'Red Princes Anne' (2n = 54 + 1B) and 'Innocence' (2n = 56 + 1B). The meiotic behaviour of B in 'Innocence' was also studied. In cv. M_1, the B-chromosome had a submedian constriction whereas, the other cultivars contained subtelocentric Bs. However, the B-chromosome in 'Innocence' was telocentric type. Cultivar 'Changhiskhan' (2n = 72) showed the presence of 1B in some PMCs analysed, however, it was completely eliminated from the root tip cells. B-chromosomes observed in the present study were smaller to A chromosomes, which could be readily recognized from the latter. Their exact nature of origin and mode of transmission is not known, however, they are maintained in cultivars through vegetative propagation.

Telocentrics

Another source of variation in the karyotype is the occurrence of telocentric chromosomes. Two

telocentric chromosomes were observed in 'Mohini' (2n = 52 + 2T) and one each in 'Kasturba Gandhi' and 'Mahathma Gandhi' (2n = 51 + 1T). One telocentric B-chromosome was noted in cv. Innocence (2n = 36 + 1B). Telocentrics are usually regarded as ephemeral products of centromere misdivisions whose future is limited by the centric inefficiency or by conversion to short lived isochromosomes (Darlington, 1939, 1940; cf. Jones, 1978). However, recently true and stable telocentrics have been shown to exist in different plant genera like Nothoscordum (Levan and Emsweller, 1938), Veluitechia (Khoshoo and Ahuja, 1963), Cycads (Marchant, 1968) Crinum (Jones and Smith, 1967), Tradescantia micrantha (Jones and Golden, 1968), Nigella doerfleri (Strid, 1968), Hymenocallis (Raina and Khoshoo, 1971a), Hemerocallis (Sadoo et al., 1976), Crocus (Brighton, 1978), etc. In Chrysanthemum cultivars the telocentrics appear to be normal and stable members of the complement. Their behaviour at meiosis is not very clear, however, in cultivar 'Mohini' the two telocentrics formed a bivalent and in 'Kasturba Gandhi and 'Mahathma Gandhi' one telocentric remained as a univalent in most of the PMCs. In Chrysanthemum species such as C. corymbosum var. Poterifolium and C. millefoliatum (both 2n = 18)

an accessory iso-B chromosome was found to misdivide and give rise to two telocentrics (Dourick, 1952). Unlike Zephyranthes (Raina, 1969; Raina and Khoshoo, 1971a) in which the telocentrics encountered in the cultivars seem to have been inherited from the elemental species, in Chrysanthemum cultivars they appear to be of recent origin. There is no increase in the number of telocentrics with the grade of ploidy as was observed in Hemerocallis (Zadoo et al., 1976).

Telocentrics may originate spontaneously by breakage of biarmed chromosomes. John and Hewit (1966) and John and Lewis (1968) have discussed the light microscopic evidence for telocentric chromosomes in animals, and Todd (1970) has advocated centric fission as a major factor in canid phylogeny. Sometimes telocentrics originate as a result of deletion of short arm in a highly acrocentric chromosome. Thus in chrysanthemum cultivar, 'Mohini' (2n = 52 + 2T), it is plausible to suggest a similar mechanism as that of Oxalis dispar in which the long arms are selected in comparison to short arms which contained deleterious genes and a deletion of smaller arm resulted in telocentrics (Marks, 1957a).

Seedling data suggested the detrimental nature of the short arms and a positive selection for telocentrics resulting in 6 to 10 telocentrics in the progeny (Marks, 1957b; John and Lewis, 1968). Another possibility is that a deletion in the centromere of a pair of sub-metacentric chromosomes and loss of the long arms could result in two small telocentrics. The origin of one telocentric in 'Kasturba Gandhi' and 'Mahathma Gandhi' could be due to misdivisions in a metacentric chromosome resulting in two telocentrics with subsequent loss of one of them or it may be due to the loss of short arm in a highly acrocentric chromosome.

Nucleolar chromosomes

Nucleolar chromosomes were present in almost all the cultivars studied, but owing to small size of the satellites and over-condensation of chromosomes, most cultivars did not show any SAT-chromosomes. The nucleolar organizers appeared on the short arm of chromosomes in all the cultivars analysed. Usually, satellites were seen on chromosomes with median and submedian constriction; often subtelocentric chromosomes were also found to have satellites. There was no constancy of number, which ranged from

0 to 10 in various polyaneuploid taxa. 'Liliput' (4x) showed 4 SAT chromosomes, pentaploids 4 to 5 and hexaploid cultivars 0 to 5. One aneuploid cultivar 'John Bull' (2n = 65) contained 10 SAT chromosomes. Distribution of SAT chromosomes in different sets was at random (see section 4). Some cultivars exhibited heteromorphicity in nucleolar pairs, resulting from variation in length of chromosomes in a set or due to a shift in centromeric position and altered arm ratio. As stated earlier, such heteromorphicity was observed in non-nucleolar chromosomes as well, which is attributed to para or pericentric inversions, translocation etc.

Diploid species of Chrysanthemum, C.nipponicum, was found to have only 2 SAT chromosomes, whereas C. rupestre, C. vulgare, C. lineare, C. makinoi, C. boreale etc. showed 4 to 6 SAT chromosomes (Tanaka and Shimotomai, 1961, 1968; Watanabe, 1981a). Tanaka (1959a) found a decrease in SAT chromosomes in C. boreale. Tanaka (1960) reported 8 nucleolar chromosomes in C. indicum (2n = 36) and 8 to 10 in various hybrid forms of tetraploid C. yoshinaganthum. Watanabe (1981a,b) reported intraspecific variation

in the number of SAT chromosomes in high polyploid strains of native Chrysanthemum species such as C. japonense (2n = 6x = 54), and C. ornatum (2n = 8x = 72) obtained from different geographical ranges. Tanaka and Shimotomai (1961) concluded that a decrease in number of nucleolar chromosomes may be responsible for the evolution of diploid species such as C. nipponicum and C. rupestre. However, no such correlation is possible in garden chrysanthemums. Dowrick and El-Nayoumi (1966a) observed 1 to 2 SAT chromosomes in various sporting cultivars 'Harmony', 'Ronald', 'Fred Shoesmith', 'Apricot My Lady', etc. In the present investigation an increase in the number of SAT chromosomes with an increase in the grade of ploidy was not observed, which may even be indicative of hybridity between taxa involved in the origin of these polyploids. In such hybrid taxa the stronger nucleolar organisers suppress the weaker ones, a phenomenon known as amphiplasty (Navashin, 1934). Similar non-confirmity has been observed in several other plant genera like Allium (Khoshoo et al., 1960; Singh et al., 1967; Ved Brat, 1965a; Dyer, 1963), Crinum (Jones and Smith, 1967; Raina and Khoshoo, 1971a), Hemerocallis (Zadoo et al., 1976) and Amaryllis (Narain, 1977). The appearance of

varying number of SAT chromosomes in cultivars may also be due to a random segregation of chromosomes which will lead to accumulation or loss of such chromosomes. The appearance of 10 SAT chromosomes in cv. 'John Bull' (2n = 65) might have resulted in a similar fashion.

Meiosis

The only report of meiotic study in garden cultivars of C. morifolium is that of Dowrick (1953), otherwise there is paucity of information of the meiotic system in this poly-aneuploid complex. The only tetraploid cultivar found in the present analysis is 'Liliput', a button form; the probable origin of which is discussed elsewhere by the present author. In this tetraploid taxon, metaphase I showed few quadrivalents and in most of the cells bivalent formation was seen. No trivalents and univalents were observed. Anaphase segregation was quite regular resulting in high pollen stainability and good seed setting. The presence of few quadrivalents is indicative of segmental alloploid nature, where some heterogenetic pairing occurs resulting in small number of multivalents. Other chromosomes of the complement form only bivalents due to preferential pairing.

In the pentaploid taxa, multivalents, bivalents and univalents were seen. Among the multivalents encountered, pentavalents and quadrivalents were few while trivalents were rather more (Table VII). Univalents were observed in all the taxa studied. Presence of pentavalents indicates similarity between all the genomes, however, it is difficult to define the nature and extent of pairing in large number of bivalents and trivalents. The reasonably good number of trivalents and univalents may be due to potential quadrivalent formation restricted by competition in pairing. As expected of an odd numbered polyploid, anaphase segregation showed high degree of irregularities resulting in lagging of chromosomes, formation of micronuclei etc. However, there was good pollen stainability in all the taxa except in cv. 'Kasturi'. Low pollen stainability in 'Kasturi' may be due to the presence of high number of trivalents which segregate irregularly resulting in the production of unbalanced gametes. Only cv. P_1 set seed and other cultivars did not form seeds.

Meiosis in hexaploid cultivars were characterised by the presence of lower number of

multivalents and predominant bivalent formation. Hexavalents were occasionally found, while quadrivalents were the most common type of multivalent. Pentavalents and trivalents were rather rare. Univalents originated as a result of precocious separation of multivalents or bivalents. Anaphase I was generally normal whereas anaphase II was highly irregular. Inspite of segregational irregularities there was good deal of pollen stainability and moderate seed setting. According to Stebbins (1950) most of the polyploid taxa of Chrysanthemum studied by Shimotomai (1933) are probably of autoalloploid origin. Autoalloploids are usually found at hexaploids and higher levels in which two or more genomes are derived from one of the parental species and only one genome from the other (Stebbins, 1947a, 1950). The duplicated genome from one parent may pair to form multivalents, while preferential pairing of the genomes from the other parent will give rise to bivalents. In this case a higher number of multivalents are expected, however, in C. morifolium cultivars there is a reduction in the frequency of multivalents (Table VIII). From this it can be inferred that the first formed cultivars may be autoalloploid in nature, however,

the structural mutations and recombination have led to modification of the genomes under garden conditions. The secondary modification of genomes will lead to reduced pairing or homeologous associations, resulting in lower number of multivalents. The structural heteromorphicity of the genomes is apparent from the karyotypic analysis of the cultivars. In this context mention may be made of Dowrick's studies on hexaploid cultivars of C. morifolium, where he found lower number of multivalents. The maximum association observed by him was quadrivalent which are explained as association of four homologous chromosomes or interchange complex (Dowrick, 1953). Incidence of interchange heterozygosity is clear from the karyotypic analysis and in an aneuploid cultivar 'Sener Bangla' (2n = 67) the complement shows a possible reciprocal translocation involving two chromosomes. However, it has not been possible to detect such interchanges meiotically. The quadrivalents and other multivalents may include interchange complexes which will be mistaken as homeologous associations. In addition to this, the abnormal meiosis in cultivars results in random segregation of chromosomes during germ cell formation and in the resulting hybrid progenies there may be predominant bivalent formation.

In the present study, few hexaploid cultivars showed diploid-like meiotic behaviour characterized by predominant bivalent formation. According to Darlington and Mather (1932) the larger chromosomes are expected to form more multivalents, however, though the size of the chromosomes in C. morifolium is medium to large, multivalent formation is restricted. Later, Morrison and Rajhathy (1960) have shown that multivalents are formed irrespective of chromosome size. So the regularity of bivalent formation observed in hexaploid garden cultivars may be accounted for some sort of genetic control of diploidisation, a mechanism reported in Triticum (Riley and Chapman, 1958) and in cotton (Kimber, 1961). Similar mechanism has been encountered in various plant genera such as hexaploid oats (Rajhathy and Thomas, 1972), Verbena (Khosheo and Arora, 1969), Celosia (Khosheo and Pal, 1973), Festuca arundinaceae (Jauhar, 1975), polyploid Chrysanthemum species (Watanabe, 1977a), Gladiolus (Dhri, 1979). In a recent study by Watanabe (1981a,b,c), the genetic control system of diploid-like meiosis has been clarified in various polyploid Chrysanthemum species like C. japonense Nakai (2n = 6x = 54), C. ornatum

Hemsley (2n = 8x = 72) and C. crassum Kitamura (2n = 10x - 1 = 89). This has been verified by the cytogenetic analysis of interspecific hybrids obtained between polyploid and diploid taxa, their back cross progenies etc. In all the F_1 hybrids, homoeologous chromosome pairing from different base sets derived from parental species was extensively observed. The genetic control theory of diploid-like meiosis may be compatible with slight modification of the zygomere localizing model proposed by several authors (John and Henderson, 1962; Sved, 1966 and Sybenga, 1966a). The diploid-like meiosis in polyploid taxa of Chrysanthemum must be ensured by the following genetic system although all of the constituent genomes of these polyploids are sufficiently homologous to pair with each other: (i) Chromosome pairing is initiated at two sites, A and B (the zygomeres localize in two loci of the chromosome), and they are under independent and fundamentally different control, respectively, (ii) At either site pairing is always two-by-two, with the pairing initiated at the A site being independent of that initiated at the B site; (iii) The initiation of pairing at the A site always precedes that at the B site, and (iv) The initiation of pairing at B

sits is usually suppressed by multiple or polygenic control (Watanabe, 1981a,b,c). These conclusions are tentative as detailed meiotic studies both of the elemental species and cultivars and experimental hybrids need to be undertaken. It might also be possible that in the perennial taxa of L. morifolium gradual divergence of homeologues by selective accumulation of many small changes of chromosome structure, leads to the establishment of diploid-like meiosis.

The meiotic behaviour of octoploid cultivar 'Chenghiakhan' was more or less similar to other polyploid taxa. The highest association encountered was octavalent which assumed chain or ring shape. Most of the PMCs showed lower multivalent frequency (Table IX) which is again an indication of segmental alloploid nature. In 44 per cent of the PMCs, one B-chromosome was observed. The inconsistent occurrence of B-chromosome may be due to the elimination, through anaphase lagging, and mitotic non-disjunction during flower initiation or premeiotic divisions leading to the formation of PMCs (Jones, R.N., 1975). At anaphase I, bridges without fragments were observed. This may be the result of non-terminalisation

of bivalents and can lead to random breakage of chromosomes at one or two points. Obviously, it results in deficiencies and duplication of some segments. Anaphase II was highly irregular, while pollen stainability was very high. The cultivar did not set seed.

Meiosis in aneuploid cultivars was characterised by the presence of a large number of bivalents and few multivalents and univalents. In odd numbered aneuploids the extra chromosome remained as a univalent, occasionally it associated with bivalents to form trivalent. However, Gouriok (1953) did not find any trivalent association in aneuploid cultivars with 2n = 53 and 55. Though anaphase segregation was highly irregular in all aneuploid taxa, the pollen stainability was appreciably high and few cultivars set seed.

In all the polyploid aneuploid taxa studied, the pollen stainability was reasonably high irrespective of high degree of meiotic abnormalities. This may be due to the high polyploid nature of the taxa, with the result that gain and/or loss of chromosome(s) arising from meiosis with segregational errors can be tolerated well. This is in accordance

with the observations in polyaneuploid Hibiscus rosasinensis complex (Singh, 1971; Khoshoo, 1979), Lathe paulestris (Kostin and Woodell, 1971), Zephyranthes (Raina, 1969, Raina and Khoshoo, 1972a), Gladiolus (Dhri, 1979), etc. No correlation could be obtained between pollen stainability and seed formation as all the cultivars form seed, if artificially pollinated. Lack of seed set in large flowered cultivars may be due to the absence of insect visit, as the ray florets are enormously long and the insects have no access to the pistil. However, where the disc is conspicuous the pollinators visit the capitulum and effective pollination takes place, reasonable amount of seed production results.

DNA content

During the past 20 years, the relation between DNA content of nuclei and the evolution of karyotype has been a major field of investigation. Correlations have been recorded between changes in DNA content, both increase and decrease, and various morphological, physiological and bio-chemical characteristics. These show that quantitative changes in the amount of DNA per nucleus may play a

considerable role in determining some kind of evolutionary change, including those that affect regulations as well as the amount of genetic information present (Stebbins, 1976). Coming to Chrysanthemum, Dourick and El-Bayoumi (1969) noted significant differences in the nuclear DNA content in various diploid species. There are similar variations in the triploid and tetraploid species. The nuclei of three hexaploid species studied, contained identical DNA contents. It has been argued that the phenotypically similar diploid species may contain similar number of genes, however, the wide variation in total DNA content must mean that some of the nuclear DNA is genetically inactive and that some species contain relatively large quantities of this inactive DNA (Dourick and El-Bayoumi, 1969). In the present study involving various polyploid/aneuploid taxa of C. morifolium, there is a direct correlation between DNA content and the grade of ploidy (Fig. 16B). The slight discrepancy in DNA values with respect to ploidy level (Table XI) may be due to chromosomal reshuffling and/or rearrangements which these cultivars have undergone during evolution (see previous chapters for details).

6. ORIGIN AND EVOLUTION OF ORNAMENTAL TAXA

Unlike most ornamental plants (Crane and Laurence, 1952; Horn, 1968; Mukherjee and Khoshoo, 1969; Darlington, 1973; Khoshoo and Pal, 1973; Khoshoo and Guha, 1975; Zadoo et al., 1976; Narain and Khoshoo, 1977; Khoshoo, 1979; Dhri, 1979) garden chrysanthemums have almost well recorded history of domestication. The Chinese were growing improved forms centuries back, and the first written report of the cultivated chrysanthemums dates back to 500 B.C. The original garden chrysanthemum was probably a single, many-flowered cultivar and cultivation has resulted in the transformation of the corolla of individual florets in one of following directions: the small five toothed disc florets gave rise to either broad ray florets or alternately, elongated without splitting and resulted in quilled or tasselled forms; increase in the disc florets produced anemone types. These changes have been accompanied by gradual disappearance of stamens. Sometimes the size of the anther may be reduced, and only stalk may be present, while in others the stamens totally disappeared (Dowrick, 1953). Though garden chrysanthemums have been cultivated in China

longback, actual improvement has been affected in Japan over 1000 years ago, and later in Europe and America. Based on the available literature as also the present work, an attempt has been made to recapitulate the various steps which transformed chrysanthemums from a wild to a cultivated plant. Such a study helps to unravel the nature of genetic evolutionary processes accompanying domestication as also helps to devise methodology for further improvement.

Ancestors

Like all the cultivated plants, present day garden chrysanthemums have been developed by conscious and unconscious selection by man over the years from wild species of the genus. The widely accepted theory is that the modern chrysanthemums are the result of hybridization between two basal species C. indicum and C. morifolium (C. sinense) (Hemsley, 1889; Henslow, 1897; Bailey, 1953; Emsweller, 1947; Flory, 1952; Dowrick, 1953; Ackerson, 1957; Woolman, 1957; Li, 1959; Cumming, 1964; Gorer, 1970; Darlington, 1973; Pizzetti and Cocker, 1975; Heywood and Humphries, 1977).

C. indicum is native to China, it is dwarfer in habit and bears small primitive daisy-like flowers almost yellow in colour. The delicate stem bears thin and small foliage, especially near the base. Leaves are green on both sides, flower heads are small and numerous and the dwarf habit of this species distinguishes it from C. morifolium. The small flowered garden chrysanthemums are supposed to have originated from C. indicum.

C. morifolium (C. sinense) was first identified by Maximowicz, the wild form of which is a robust plant, very variable in foliage and always more or less tomentose and the ray florets are different in colour from that of the disc (Hemsley, 1889). The flowers are 3 cm across with rays considerably larger than the diameter of the disc. As a rule, the colour is rosy lilac to lilac-pink, rarely white with contrasting yellow disc tones. C. morifolium (C.sinense) is supposed to be forerunner of large flowered chrysanthemums.

Many authors believe that species other than C. indicum and C. morifolium (C. sinense) have also been involved in the origin of the present day garden chrysanthemums. Thus, Stapf (1933) considers

that C. arubescens, a very distinct species with somewhat succulent leaves and pink flowered heads together with C. ornatum. C. japonense and C. makinoi have been involved in the origin of garden chrysanthemums. He considers that oriental gardners would not ignore the naturally occurring species and that C. morifolium has resulted from their hybridization. Bailey (1953) says that C. ornatum is a form of C. indicum. Nohara (1927) believes that Japanese ornamental chrysanthemums are derivatives from wild C. sinense var. spontaneum. Huggins (1946) includes C. coronarium as an elemental species. According to Dr. Makino, Japanese species C. morifolium Ramat. var. spontaneum Makino (C. japonense Nakai) should be considered the original species of our cultivated chrysanthemums (Anonymous, 1967). Other Japanese scientists believe that C. zawadskii var. latilobum Kitam. and C. rubellum Seely, are the original basal species, which are found in Korea, Mongolia and China with few plants in some districts of Kyushu, Japan. Prof. Shiro Kitamura founded the theory that horticultural chrysanthemums resulted from crossing of diploid C. zawadskii x tetraploid C. indicum and subsequent doubling of the chromosome number in the F_1 hybrids or through a cross of octoploid form of the former with tetraploid

C. indicum (Anonymous, 1967). According to Darlington (1973) the garden forms are derived entirely from hybrids within a hexaploid complex of Chinese species loosely known as C. indicum, and from this complex, new wild types of different geographical races have been continually crossed with the main group of ornamentals.

The foregoing views are only tentative. In recent times many species, such as C. zawadskii, C. rubellum, C. nipponicum, etc. have been extensively employed in the improvement of garden forms (Flory, 1952; Cumming, 1964; Jackson, A.A., 1971). Nothing less than centuries of development could have changed the wild growing species of Eastern Asia, into colourful chrysanthemums first seen in the western world. The evolutionary changes in a span of over 2500 years could make it difficult to prove these speculations.

Historical

The history of garden chrysanthemum is scarcely recorded from its ancient origin to the scientific breeding of 20th century. The primary centre of origin is China and the secondary centres of development are Japan, Holland, France, England

and U.S.A. The garden chrysanthemums reached various places from its centre of origin as importations in the form of seedlings and/or seeds. The hybrid seedlings imported in most of the countries were 'miniature' (single) and 'Chusan' (double) with small flowers which were grouped under 'Chusan Daisy'. This has played an important role in the origin of present day garden chrysanthemums. A brief account of the important events and developments of garden chrysanthemum in various countries is given below. New cultivars have arisen both as hybrid seedlings and from bud sports, or in other words as recombinants and mutants (Dowrick, 1953; Sampson et al., 1958; Darlington, 1973).

The garden chrysanthemum is exclusively of Chinese origin. According to Chinese writers it was being grown in China as early as 1000 B.C. (Emeuller, 1947). Confucious (550 B.C.) wrote of chrysanthemum's "yellow glory". Liue-Chieh-Yuan of Peking, a modern authority famous for the knowledge of chrysanthemum history states that the flower became popular between 355 and 417 A.D. Tao-Yuen-Ming (365-427 A.D.), an influential grower named his city as 'Chu-heien' or chrysanthemum city. Tao-Hung-Ching raised the first

known white, between 452-532 A.D., in his life time. The oldest preserved book on chrysanthemum culture prepared in China between 960 and 1127 A.D. mention 30 recognized forms (Woolman, 1937; Cumming, 1964). The name of famous Chinese cultivars translated to English are, 'The white wave of autum', 'The purple pheasant tail', etc. Quickly spanning to the year 1961, we find the chrysanthemum honoured by portrayals on a series of chinese postage stamps (Cumming, 1964).

In A.D. 386 chrysanthemum reached Japan via Korea from China, where it was selected and improved to give a great deal of variation in form and colour. The first chrysanthemum reaching Japan was named 'Kiku' and contained many colours like red, yellow, white, violet and even blue. At first they were grown in the garden of Imperial palace. The Japanese hailed it as their National flower in A.D. 797 and the flower became the crest of Mikado and its great design was added to all important state documents (Woolman, 1957). According to Ryozo Miyamura, who was in-charge of Shinjuku National gardens Tokyo, there have been two great chrysanthemum eras in Japan. The first one, Heian period, occurred roughly from 800 to 1200 A.D.

In 910 Emperor Uda instituted the Imperial Chrysanthemum Show. The second great era, known as Genroku, commenced in 1736 when the first known illustrated catalogue was published which depicted 100 cultivars. World War II called an end to chrysanthemum shows and again in 1949 shows were resumed and in 1960 about 427 cultivars were represented at Shinjuku. Japanese taste was for irregular types (Cumming, 1964).

Evidently, Holland was the first European country to have access to the Far East and imported chrysanthemums for the first time. In 1689 Jacob Breynius, a Dutch merchant and botanist, writing in his prodromus told of six chrysanthemum cultivars being grown in Holland. He named it as Matricaria japonica (Hemsley, 1889). In the same year several cultivars were reported as being grown in Netherlands, but soon passed out of cultivation. In 1690 H. Van Rheede described a Holland grown type from India called 'Cool-dasoodi' and according to Roxburgh everywhere in India, it bears the hindi name 'Cool-dasoodi', 'Cool' signifying rose (Hemsley, 1889; Cumming, 1964).

During chrysanthemum's early days in Europe, no nation accomplished more in initiating new forms than France. French people consider it as cemetry flower to honour All Saints' Day on November 1 (Cumming, 1964). The earliest specimen in existence in Europe are two small flowered chrysanthemums preserved in British museum. This was brought by James Cunninghams, a surgeon to the honourable East India company from 1698 to 1703. Kaempfer visited China and Japan in 1712 wherein he described 9 cultivars of chrysanthemum and speak of their high ornamental character. In 1764, Philip Miller evidently received the first chrysanthemum in England for the Chelsea Physic Garden, from Ningpo China, which he called Matricaria indica (Emsweller, 1947; Cumming, 1964). Successful culture began only by 1790. According to Dourick (1953) the first chrysanthemum was introduced into England in 1754 where it had been cultivated as Matricaria japonica which was subsequently lost.

Reintroduction into England was due to Mr. Blancard, a merchant of Marseilles, who brought home three cultivars from China in 1789, one white, one violet and one purple, but he succeeded in saving

the last only. This was named 'Old Purple', the inflorescence and general habit of which was similar to many present day cultivars (Hemsley, 1889; Dourick, 1953; Cumming, 1964). The 'Old Purple' sported to 'Changeable White', a form whose rays were streaked crimson, later it sported to 'Changeable Buff' (Cumming, 1964). The first English man to raise seedlings by cross-fertilization was Mr. Wheeler of Oxford. In 1827 new forms were first produced by hybridization and from these have arisen the incurved forms of today. The first vegetative sport was noticed in 1832 (Dourick, 1953; Woolman, 1957; Darlington, 1973). In 1838 Mr. John Salter raised a greatly improved incurved which was larger and of finer quality than existing imported ones and thus the first large exhibition incurved was accomplished. The cultivar was named 'Queen of England'. In due course it gave a primrose sport which was named 'Empress of India' (Woolman, 1957). In 1846 Robert Fortune introduced the small flowered chrysanthemum, the 'Chusan Daisy', the first pompon from which numerous modern forms have been raised (Emsweller, 1947; Cumming, 1964). He returned in 1861 with 7 Japanese types or "Japs". He raised seedlings which were not only incurved types but

those with reflexed petals. The first early blooming cultivars were selected from existing stocks in about 1850. Since then there have been introductions, such as Korean and Midget types. In 1930 McGregor sent from China a plant similar to C. indicum from the progeny of which were selected Sutton's charm and cascade (Dowrick, 1953). English preference is mostly for incurves and reflexes.

Except Thomas Pockett (1854-1932) Australia has figured little in the chrysanthemum world. His cultivars like 'Nellie Pockett', 'Turners', 'Lloyds' etc. are famous. Unfortunately the early history of chrysanthemums in United States is very obscure. According to 1828 catalogue of William Prince, the first chrysanthemum known in United States is 'Dark Purple', imported by John Stevens of Hoboken, New Jersey and for a number of years chrysanthemum had come from China (Emsweller, 1947); Dumming, 1964). In 1826 the Prince Nursery listed 26 cultivars and by 1835 fifty distinct forms were available in U.S.A., however, no record is available concerning their origin. One of the earliest chrysanthemum breeders in U.S.A. was Robert Kilvington of Philadelphia. In 1841 he exhibited a new seedling named 'William Penn' which bore a large white double flower almost globular in shape.

Dr. H.P. Walcott (1879) of Cambridge Massachusetts is apparently the first American to raise his own seedlings (Cumming, 1964). Among the famous chrysanthemum breeders of U.S.A. are Elmer D. Smith, Lloyd Mulford, Alex Cumming, Baur, Totty, De Petris, Yoder Brothers and Bristol nurseries. Alex Cumming (1945) in the first man to use a wild species in the improvement of garden chrysanthemums. He made a cross between 'Ruth Hatton' x C. sibiricum, the first seedling of which were a poor lot, and as breeding continued, new tints and shades began to appear. By 1932 some promising seedlings such as 'Mercury', 'Apollo', 'Daphne' etc. were released. The popular term 'Korean hybrids' was given to these seedlings since Korea was the source of the species.

7. PRINCIPLES OF SELECTION

As is obvious from the historical account, garden chrysanthemums are essentially plants of China and Japan where it is in cultivation since 500 B.C. However, the major developments in chrysanthemum improvement took place in Japan over 1000 years ago (from A.D. 386), when seedlings were imported from China, hybridized and selected for great variation in

form and colour of blooms. From their native habitat, introductions were made to temperate conditions of European gardens by early part of seventeenth century and a hundred years later to America. Thus intensive interbreeding and conscious or unconscious selection from the hybrid segregates, coupled with selection of spontaneous mutants over a span of 2500 years resulted in modern chrysanthemums. The principles of selection underlying evolution can now be examined.

Increase in Hardiness

The elemental species are inhabitants of South East Asia and from such a stock there has been selection for hardy characters imparting greater cold resistance in European gardens. The 'Korean hybrids' are particularly adaptable and survive in open in relatively severe European and American conditions. In recent years hybrids have been evolved using hardy wild species and there is a great demand for such cultivars.

Reduction in Height

C. morifolium (C. sinense), one of the elemental species of modern chrysanthemums has got

tall habit, when compared to C. indicum, which is dwarf. Selection for dwarf habit has resulted in the production of cultivars with accommodating characters like compact growth habit, larger leaves, strong and thick stem etc. This habit is especially utilized for pot-mum culture.

floral characters

Ancestral species and early cultivars bore single daisy-like blooms and selection has resulted in transformation of the small five toothed corolla of the disc florets to broad ray florets. Subsequent to this, various types such as button, pompon, decorative, incurved, reflexed, spider, quilled, etc. originated. An enlargement of disc florets resulted in anemone types. In various countries selection of cultivars is based on emphasis on different aspects, ranging from perfection of the bloom for exhibition and qualitative aspects, to those for use in commercial trade. Large flowered forms are mostly preferred for exhibition and in trade especially as cut flowers, while small flowered forms are grown as pot plants for decoration or used for landscaping.

Early flowering

Ancestral species and early hybrids were late blooming. Early flowering cultivars were noted in European gardens by 18th century. Such early blooming cultivars were introduced into different chrysanthemum growing regions, hybridized with local cultivars and subsequent selection has resulted in innumerable number of early blooming cultivars.

Colour diversity

The colour of the ancestral species like C. indicum and most other species are yellow, while earlier cultivars of C. morifolium exhibited colours like pink, white, lilac, purple, etc. Mutations and hybridization, followed by selection, resulted in rich colour diversity. Though green coloured chrysanthemum cultivars are known, there is a conspicuous absence of blue. The only colour nearing blue is deep mauve. Certain cultivars retain their colour for a quite long time while others fade even before complete opening of the flower heads. There has been selection for the former types.

Increase in thickness of floral parts

This character is important when the flowers are used mainly for commercial purposes. Increase in

thickness of floral parts can intensify the colour as well as extend the vase life of cut flowers. This character also enabled the growers to raise bloom even under relatively severe agroclimatic conditions.

Fragrance

Few small flowered cultivars are known for their fragrance. This character may be useful to evolve more scented cultivars in large flowered types also.

8. FUTURE AIMS OF BREEDING

The florist's chrysanthemum (*C. morifolium* Ramat.) is one of the most important international flower crops (Tija and Kawete, 1971) which display a wide range of variability in colour and form. Usually under natural conditions, chrysanthemum cultivars bloom for a period of six weeks, however, application of modern scientific methods helped in reducing the unusually long vegetative period of over 10 months, and now it has been possible to stretch the flowering period to about six months from mid-October to March end. In India so far not much attention was paid in this regard, but lately, at NBRI, Lucknow, several

early blooming Japanese cultivars were introduced, hybridized with local cultivars and new early flowering forms were selected (Kher, 1975, 1977). In addition to this, by manipulation of photoperiod it has been possible to delay flowering and thus extend the flowering period towards summer season. In western countries year round production of chrysanthemum flowers have been achieved since mid-1940 in a programmed manner for commercial purposes (Machin and Scopes, 1978). In India attention is also being paid for such year round production of chrysanthemums as it has great scope in cut flower trade.

Langton and Lockshull (1976) have proposed, following trial using a wide range of cultivars, an ideotype for summer-flowering in year round programmes. They considered the following characters for the ideotype:

i) Strong apical dominance during vegetative growth.

ii) Immediate and rapid flower bud initiation in short days in both apical and axillary meristems.

iii) A very high leaf number for delaying bud initiation in long days (this helps to prevent budding on stock plants).

iv) A very high leaf initiation rate in long days.

v) Long internodes and rapid internode extension in short days.

vi) Extremely rapid flower development in short days.

vii) Moderate peduncle extension in short days.

viii) A 'thermozero' temperature response showing little or no delay in flowering at temperatures above and below 15.6°C.

ix) Easily rooted cuttings which can withstand at least 10 days cold storage.

x) Strong peduncles and stems which take up water adequately.

xi) Large, horizontally displayed leaves.

xii) Pink flowers (which give rise to all other colour by mutations).

xiii) Low competitive ability in flowering area.

In a recent report on year-round chrysanthemum breeding programme, attempts were made to incorporate rapid flower bud development character and longer vegetative growth phase into various cultivars by crossing early x late flowering types (Langton, 1981). In his experiment, significant positive phenotypic correlation between flower bud development time and

vegetative duration was observed. It was concluded that the clones showing rapid flower bud development in long days have relatively short durations of vegetative growth while clones showing slow bud development can have any duration (Langton, 1981).

To the foregoing characteristics of the ideotype, must be added the flower characters like colour, form and size required by the consumer.

A large number of colours appear in pure and mixed forms in garden cultivars, whereas blue is conspicuously absent. The absence of blue may be because of its recessive, nature. There is a record that blue coloured cultivars were there among first introductions reaching Japan, but later it was lost and did not reappear anywhere (Cumming, 1964). The nearest colour to blue is deep mauve. It would be interesting if the rare blue colour can be obtained through either mutation breeding, or hybridization so that it can be maintained as the propagation is mainly through vegetative means.

Some small flowered chrysanthemums are odoriferous and this character may be suitable in evolving scented cultivars of large flowered types.

9. CYTOGENETIC MECHANISMS UNDERLYING EVOLUTION

The origin of present day garden chrysanthemums (*C. morifolium* complex), mainly from two ancestral species viz. *C. indicum* and *C. morifolium* (*C. sinense*) took approximately 2500 years. During this span of time the early hybrids have undergone great transformation in the hands of man, and from daisy-like small flowered type have arisen innumerable forms with great colour diversity. The changes in the genetic system accompanying the transformation from wild to cultivated condition may now be examined. Such a study will help in unravelling the evolutionary steps involved in the modification of breeding system and structural and numerical alterations in the chromosome complement.

Breeding system

The genus *Chrysanthemum* contains annual as well as perennial taxa with showy flowers which are predominantly cross-pollinated. The ancestral species often bore single heads with conspicuous disc which is adapted for cross-fertilization. The garden cultivars of *C. morifolium* show a wide range of floral morphology and the conspicuous

capitula with a large quantity of pollen where the disc is prominant, and in some instances even fragrance, all ensure cross-pollination. The details of breeding system are discussed in section 3. Most of the Chrysanthemum species at the diploid level are self-incompatible, while in polyploid species, as also the garden chrysanthemums, there is some degree of self-compatibility. However, protandry and centripetal opening of the florets ensures cross-pollination. In large flowered cultivars, the enormous length of the ray florets and small size of the pistil creates mechanical barrier and no pollination takes place. Such cultivars do not set seed and there is almost a dead end for natural evolutionary process. However, variability is created under garden conditions in the hands of nurserymen who effect artificial pollination by trimming off the floral tubes and hand pollinating. Outbreeding creates tremendous genetic variability among the progenies, and new genotypes, arising through hybridization and/or polyploidy, are fixed by vegetative multiplication, provided that they have some adaptive value (Stebbins, 1950). This process occurs both under natural as well as garden conditions.

Bud mutations

A large number of chrysanthemum cultivars now grown in garden have arisen as spontaneous mutations. Many of the cultivars sport continually to give rise to families of sports (Dowrick, 1953; Sampson et al., 1958; Dowrick and El-Bayoum, 1968a). It has been estimated that one third of commercial chrysanthemums have originated as bud mutations (Wassecher, 1956). The sports of well-known cultivars like 'Sweet Heart', 'Favourite', 'Rayonante', 'Indianapolis', 'Loveliness', 'Shoesmiths', 'Long Island Lady', 'Shuffle', 'Meneing', etc. are very popular among commercial growers. The first bud sport was noticed in England in the year 1832 (Bemsley, 1889; Dowrick, 1953; Woolman, 1957; Darlington, 1973). The famous cultivar 'Old Purple', which was introduced into Europe during early days of chrysanthemum growing later gave rise to sports like 'Changeable White' and 'Changeable Buff'. Even green sports are also on record (Henslow, 1897-98).

It has been widely accepted that chrysanthemum cultivars are periclinal chimeras and somatic mutation arise by rearrangement of

unstable chimeral tissues (Popham and Chan, 1950). The abnormal cell division may either replace one layer by other or that solid mutants, consisting of cells from either LI or LII layer, is formed. The flower colour is determined by the LI and LII layers as anthocyanin and other colour pigments are present in these layers. However, the sex cells are produced only from LII. Thus a cultivar in which LI is white and LII is pink will have a white flower, but transmits pink colour to the progeny. This is further corroborated by the studies on carotenoid inheritance and the breeding behaviour of some yellow sports and their white progenitors (Langton, 1980).

From study of various sporting families, Dourick (1953) and Sampson *et al.* (1958) reached the conclusion that sporting can occur due to irregular mitosis in the meristem resulting in gain or loss of chromosomes. Dourick and El-Sayoumi (1966a) have shown that sporting occurs as a result of three kinds of mitotic abnormalities like non-disjunction and lagging, and stickiness of chromosomes leading to chromosome fragmentation at anaphase. Later, Stewart and Dermen (1970)

have proved that sporting in 'Indianapolis' cultivars (from white to variegated forms with yellow blotches) is due to loss in mitosis of a chromosome carrying a suppressor for the formation of yellow chromoplast giving yellow sector. The chromosome loss theory is strengthened by the finding that yellow plants grown from LI of 'Yellow Snowdown' were agronomically very different from either 'Yellow Snowdown' or 'Snowdown' itself (Langton, 1980). All colours give rise to white sports and pink is more prone to mutations while yellow colour does not sport freely. The pink colour was never found to mutate directly to yellow, since it requires both suppression of pink colour by mutation and de-repression of yellow by chromosome loss (Stewart and Dermen, 1970).

As is clear from the foregoing account, mutations have played an important role in the evolution of garden cultivars. The mutants have been selected, propagated and fixed for their novel characters under garden conditions. It is interesting to note that the highly heterozygous nature of garden chrysanthemums itself may be conducive to bud mutations. This is corroborated with the fact that hybrid genotypes are more responsive to induced mutations (Sparrow et al., 1965; Mukherjee and Khoshoo, 1970). In recent years,

several mutant varieties were obtained by various workers using *in vivo* and *in vitro* techniques of induced mutations using physical as well as chemical mutagens (Sheenan and Sagawa, 1959; Fuji and Nabuchi, 1961; Matsumura *et al*., 1961; Nybom, 1961; Ruprecht, 1961; Bowen *et al*., 1962; Fuji, 1962; Shimotomai and Sakurai, 1962; Van Hoeck, 1962; Weaver, 1963; Cawse, 1965, 1966; Scherbakov, 1965; Broertjes, 1966; Broertjes *et al*., 1966b, 1980; Chan, 1966; Dourick and El-Sayoumi, 1966b; Gupta, 1966; Nakajima and Kawase, 1967; Yamaguchi and Takato, 1970; Dreulou and Widmer, 1971; Gupta and Shukla, 1971; Satory,1975; Broertjes and Van Harten, 1978). The physical mutagens were found to be more effective than the chemical mutagens and repeated cycles of irradiation has been experimented with great success (Broertjes *et al*., 1980). A large number of promising induced mutants have been selected and introduced into commercial cultivation as new cultivars. Somatic mutations have been a source of variability in several vegetatively propagated ornamentals like *Dahlia*, *Bougainvillea*, *Sansevieria trifasciata Laurentii*, *Kalanchoe*, *Poinsettia*, *Canna*, *Gladiolus* etc. (Boescher, 1956; Zadoo *et al*., 1976b; Khoshoo, 1979; Bhri, 1979).

Chromosomal Repatterning

The present cytological data indicate that majority of the taxa within C. morifolium complex are hexaploids and the rest range from tetraploid to octoploids with a number of aneuploids in between. Karyotypic analysis of representative cultivars showed high degree of chromosomal repatterning. Though the karyotypes resolved into 9 sets, there was no consistency of the number of chromosomes appearing within a set and it was not possible to locate the exact morphological homologue of each chromosome in a complement. This sort of variation is due to abnormal meiosis resulting in random segregation of chromosomes. Even the basikaryotype also could not be drawn. The karyotype exhibited high degree of heteromorphicity both in nucleolar and non-nucleolar chromosomes which appeared in the form of centric shifts resulting from pericentric inversions and/or unequal translocations. However, owing to high polyploid nature of the taxa, it is difficult to locate interchanges meiotically. The karyotypic heteromorphicity can also be accumulated through hybridization between karyotypically dissimilar taxa so that in the hybrids there is accumulation of

such differences. In the progeny of such types, fresh heterozygosity arises due to recombination between different karyotypes as has also been noted in Allium (Emsweller and Jones, 1938), Lycoris (Ising, 1962), Zephyranthus (Raina and Khoshoo, 1971) Hemerocallis (Zadoo et al., 1976) etc. Another type of chromosomal repatterning is the occurrence of telocentrics. From a critical comparison of karyotypes it has been inferred that the telocentrics are the result of either deletion of short arms in a highly acrocentric chromosome or the centric fission of chromosomes in which one of the telocentric armsis lost in course of time. In either case, karyotypic heterozygosity is prepetuated by efficient vegetative multiplication.

Hybridization

The garden chrysanthemums have arisen mainly from two basal species viz., C. indicum and C. morifolium (C. sinense). Both the natural and artificial hybridization have been reported in the genus. This has been greatly aided by the presence of self-incompatibility and cross pollination by insects and lack of hybrid sterility in most cases. Artificial hybrids have been raised at inter-specific level to study the cytogenetic relationships. Intra-specific hybridization is most common in C. morifolium

complex to increase variability in flower forms, colour diversity, etc. several hybridization studies involving basal species and other polyploid-diploid species have been on record. Thus Shimotomai (1930, 1931, 1932, 1933) made crosses between different species like C. decaisneanum x C. indicum, C. ornatum x C. indicum, C. marginatum x C. morifolium, C. marginatum x C. indicum, C. japonicum x C. morifolium, C. japonicum x C. decaisneanum, C. japonicum x C. marginatum, etc. In all the above crosses the F_1 hybrids were reasonably fertile. Takamoto (1939) obtained fertile hybrids from a cross of C. indicum var. procumbens x C. lavendulaefolium. Tanaka (1958) has reported the production of polyhaploids from a cross of C. indicum var. hexaploid x diploid C. lavendulaefolium. However, Watanabe (1977a,b) reported failure of crosses involving high polyploid and diploid species, due to collapse of embryo development. Later, this barrier has been overcome by ovary culture on an artificial medium and in this way successful fertile hybrids, back cross progenies etc. have been established in species crosses like C. japonense (2n = 6x = 54) x C. boreale (2n = 2x = 18), C. ornatum (2n = 8x = 72) X C. boreale and C. crassum (2n = 10x = 90) x C. boreale (Watanabe, 1981a,b,c). In recent times many wild species have

been involved in the improvement of garden chrysanthemums so that the ancestry of the cultivars have become more complex.

From the foregoing account it is clear that the garden cultivars also have undergone rampant hybridization. New recombinants could originate in various ways like transgressive segregation, release of latent mutations with an increased mutation rate in hybrids, perhaps due to elimination through recombination of mutation suppressors. Evolution through hybridization is fast in garden cultivars as there is no prolonged vegetative growth resulting in delayed flowering. The seedlings produce flowers in the same season. In this way promising recombinants are immediately available for selection and the fixation of such variants is possible through vegetative propagation.

Polyploidy

The present study together with previous reports indicate that about 61.4% of the taxa in the genus are polyploids and polyploidy is both at intra and interspecific levels ranging from 2x to 22x (Table III). The range of polyploidy in *C. morifolium*

complex is from 4x to 8x and 8x + 3, with a number of aneuploids ranging in between the lowest and highest numbers (Table IV). Polyploidy coupled with vegetative propagation has played an important role in the evolution of garden chrysanthemums. A detailed karyotypic analysis revealed a good deal of heteromorphicity both in nucleolar and non-nucleolar chromosomes which could have been the result of hybridization between different taxa. The most common feature is the non-conformity between the number of nucleolar chromosomes and the grade of ploidy.

The meiosis in polyploids is characterised by a low frequency of univalents and multivalents and predominant bivalent formation, characteristic of segmental alloploidy or autoalloploidy. Though the meiosis is irregular, there is good pollen fertility due to the presence of duplicated genetic material which can withstand a good deal of cytological aberrations. The chromosome heterozygosity is preserved through efficient vegetative multiplication.

10. HORTICULTURAL CLASSIFICATION

The common garden chrysanthemums are the result of hybridization between C. indicum and C. morifolium (C. sinense) native to Japan and China. Chrysanthemum cultivars show good deal of variability in flower colour, shape, size etc. which have been brought about by extensive interbreeding and selection. The bloom assumes different shape because of difference in number, size, form and arrangement of florets. National Chrysanthemum Societies in different countries have variously classified the bloom types occurring in their countries. These classifications are based on over all shape and size of the bloom as well as number, form and arrangement of florets. The horticultural sections are wholly arbitrarty, being chiefly for the convenience of competitors at exhibitions.

There are nearly 400 cultivars of chrysanthemum growing at NBRI, Lucknow. Most of them are unregistered and their ancestry is unknown. In recent years several Japanese and American cultivars have been introduced to enrich the germplasm. Several promising seedling selections have been released as new cultivars. The Indian cultivars have been

classified by Khar (1975), based on NCS classification. According to this classification, blooms are broadly classified into two, large flowered and small flowered groups.

A) Large flowered

1. Incurved: The ray florets in this class are broad and curve upward and inward towards the centre to give the bloom a globular shape. Disc is not visible. This class is further subdivided into:

i) Regular incurves, if florets are incurved neatly in orderly manners e.g. 'Snow Ball', 'Super Giant'.

ii) Irregular incurve, if the florets are twisted and turning in disorderly manner e.g. cv. W_{10}.

iii) Skirted incurve, if the lower florets hang down like a skirt e.g. Nil.

2. Incurving: The ray florets curve inward and upward in a loose manner so as not to form a compact globe, but give an airy appearance to the bloom e.g. 'Pink Cloud', 'Beauty'.

3. Reflexed: The ray florets curve outwards and downward away from the centre so that only their upper surface is seen. In the early stages, the inner florets remain incurved. Disc is not visible. This class is further subdivided into:

i) Regular reflex: florets reflex in orderly manner. e.g. 'Evening Star'.

ii) Irregular reflex: florets twist and turn in disorderly manner e.g. 'Roger Thompson', 'Goldie'.

iii) Aster flowered reflex, syn. Reflexing: blooms are flat e.g. 'John Webber'.

4. Intermediate: In this class while the outer ray florets curve outward and downward showing upper surface, the inner ones continue to remain incurved. e.g. 'General Petain', 'Mrs. R.C. Pulling'.

5. Irregular: This is similar to Class 4. Outer florets are reflexed and inner incurved. The distinguishing feature is that, unlike Class 4, the ray florets are twisted and irregularly overlapping e.g. 'Grape Soul', 'Alfred Simpson'.

6. Ball or Pompons: The ray florets which are usually channelled and closely packed radiate in all directions, thus giving the bloom the shape of a ball e.g. 'Pride of Madford', cv. W_{23}.

7. Quilled: The ray florets are tubular like a quill and elongate with tips open or closed e.g. 'Golden Quills', 'Red Quills'.

8. Spider: This class has also tubular, elongated ray florets like Class 7. The distinguishing feature is

that the tubes are thin and usually curved and the tips are coiled or hooked e.g. 'Valiant', 'Diamond Jubilee'.

9. Spoon: Ray florets are tubular with spatula-like open tips. The florets remain at right angles to the stem. Disc is visible e.g. 'Pink Casket', 'Knox'.

10. Anemone: The disc florets are prominently developed and is usually hemispherical in form and raised. The ray florets may be ligulate e.g. Nil.

11. Single: Strap like ray florets in not more than five rows. The disc is conspicuously visible e.g. 'Golden Anniversary', 'Potomac'.

12. Semidouble: Strap shaped ray florets in more than five rows. The disc is conspicuous e.g. Nil.

B) Small Flowered

1. Anemone: Disc florets are well developed and make a raised disc. Ray florets may be flat, twisted or quilled. e.g. 'Paragon', 'Lohengrin'.

2. Button: Blooms are very small (2-3 cm in diameter) and compact with short rayonants like florets. e.g. 'Liliput'.

3. Korean (Single): Strap shaped ray florets. Blooms are flat and the number of whorls of ray florets five or less than five. Disc conspicuously visible. e.g. 'Sunset', 'Pat'.

4. Korean (Double): Like Class 3 except that the whorl of ray florets is more than five. Disc visible. e.g. 'Sharad Bahar', 'Flirt'.

5. Decorative: Like double Korean except that the disc is not visible due to developed ray florets.e.g. 'Shinfuji', 'Hosteau'.

6. Pompon: Ray florets short, broad and regularly arranged to give the bloom a compact, hemispherical shape. The disc is concealed or absent. e.g. 'Nanako', 'Apsara'.

7. Stellate: Like single Korean except that the ray florets have both sides compressed downwards and they are usually twisted. e.g. 'Laura', 'Heloise'.

8. Charm or Cineraria: Like Korean except that the size of the bloom is not more than 3 cm in diameter. The plants are usually dwarfer than Korean. e.g. 'Phyllis', 'Jessie'.

9. Quilled: The ray florets are tubular like a quill. The tips of the florets may be open but not developed. e.g. 'Fair Tuck', 'Donald'.

10. Semiquilled (spoon): The ray florets are tubular upto some length and then open. Open portion may be flat, reflexed or incurved. e.g. 'Gumti', 'Jean'.

IV. SANSEVIERIA

Sansevieria is a succulent member of the family Agavaceae and is known variously as Bow-String Hemp, Snake Plant, Zebra Lily, etc. (Graf, 1973). The genus contains perennial herbs with erect, stiff leaves and short, thick stoloniferous rhizomes. The individual species of Sansevieria show an extremely wide variation in growth, form and habit. Some have flat or nearly flat leaves, others possess concave leaves and still others have cylindrical leaves. Some species are important as a source of useful fibre, and their potentiality as fibre crops has been recognized since early times. The plant was harvested in the wild by Africans and the fibre used for making coarse fabrics, fish nets and bowstring (Gangstad et al., 1951). Besides, some species are ornamentals, cultivated for their variegated or mottled decorative leaves. According to Graf (1973) they are among the most resistant house plants capable of growing in difficult locations. They are tough and can tolerate poor light, as also drought.

Nearly 20 species of Sansevieria have been introduced in NBRI by the late Mr. S. Percy Lancaster, out of which 15 species were available

for the present study (Table I). Like most of the allied genera, the species of the genus Sansevieria flower twice in the year, one during the onset of monsoon and then during the winter. Some species like S. powellii have not flowered under Lucknow conditions. The present studies were mainly based on meiotic analysis and it was difficult to study the karyotype due to small size of the chromosomes.

SYSTEMATIC POSITION AND DISTRIBUTION

Systematic position: The name 'Sansevieria' commemorates Raimond de Sangrio born at Naples (1710-1771), who was Prince of Sansevieria (Bailey, 1953; Marshall Cavendish, 1969; Graf, 1973). The genus Sansevieria was established by Thunberg in 1794 in his Prodromus Flora Capensis and seven years later two species viz. S. thyrsiflora and S. aethiopica have been described.

The genus has been variously placed with regard to its taxonomic position. Bentham and Hooker (1862-1883) placed the genus in Haemodoraceae preceding Iridaceae. Later, Engler and Prantl (1924) included it under Liliaceae together with Ophiopogon.

Dracaena, Yucca and other genera. However, Hutchinson(1959) placed the genus in the family Agavaceae. Based on cytological studies of 2 species of Sansevieria, Roy (1956) argues that the genus should be included in a seperate family co-ordinate in rank with Liliaceae and Agavaceae. The cytotaxonomical evidence obtained by Sharma and Chaudhuri (1964) does not justify the inclusion of the genus under Agavaceae. According to these authors, the cytological affinity of genera like Sansevieria, Dracaena and Ophiopogon is reasonable enough to suggest the inclusion of these three genera into one tribe under Liliaceae, provided the external morphological considerations permits such inclusion. Recently embryological studies in a species of Sansevieria showed that the genus differs from other members of Agavaceae and its inclusion in the family by Hutchinson is not justified (Lakshmi, 1979).

Distribution: Brown (1915) considered 54 species in the genus, mostly African, in his monograph of the genus and Greenway (1941) noted at least 8 additional species. Many authors have reported the existence of nearly 60 species (Biswas, 1936; Anonymous, 1959, 1976; Pate et al., 1960; Pureeglove, 1972). Most of the

species are confined to tropical Africa, Madagascar and the islands near its coast and Arabia. Five species occur in South Africa and one is found in extratropical region (Brown, 1915; Marshall Cavendish, 1969). Only 4 species are definitely known to inhabit any other regions, and these are natives of Ceylon, India, Burma, and perhaps China (Brown, 1915). Certain species have become widely distributed in tropical and sub-tropical regions of the world, where they have frequently escaped from cultivation (Byrom, 1950-51). Very little information is available as to the geographical ranges and ecological requirements of many of the species. The various species differ greatly in size, growth-habit and leaf form and occupy a wide range of climatic and geographical niches. Greenway (1941) points out that some species are adapted to extremely dry conditions, others to tropical rain forests, and some are found growing on coral rocks. All have strongly developed means of vegetative persistence and reproduction and are readily propagated in cultivation by leaf or rhizome cuttings or both.

Three species of Sansevieria are recorded in India which grow up to an elevation of 600 metres extending from the foothills of Himalayas to

Cape Comorin (Anonymous, 1959, 1976). Biswas (1936) reported 4 species, indigenous to India. They are S. zeylanica Willd., S. languinosa Willd., S. roxburghiana Schult., and S. burmanica N.E. Brown. S. languinosa grows wild in sandy places in Malabar coast. S. zeylanica is common in the drier rocky and sandy regions. S. roxburghiana is the most common species, which is widely distributed along the coast of Coromandel, Lower Bengal, Orissa and Chotta Nagpur (Biswas, 1936).

For convenience, Bailey (1953) has recognized three categories within the genus: Species with flat leaves or nearly so, e.g. S. thyrsiflora; Species with concave leaves, e.g. S. zeylanica; and Species with cylindrical leaves, e.g. S. cylindrica.

CYTOLOGY

Out of 60 species belonging to the genus, only 25 are known cytologically (Table XIII). Nearly 20 species of exotic sansevierias are growing at NBRI, Lucknow, of which the cytology of 15 species has been reported in the present study (Table XIII).

The chromosome number of 4 species have been reported for the first time together with intraspecific polyploidy in one species. Based on the grade of ploidy, the 15 species can be divided into four groups: diploids, tetraploids, hexaploids and aneuploids. The studies were mainly based on meiosis, but karyotype of 3 species was also studied.

Observations

The karyotype of three species, viz. S. ehrenbergii (2n = 40), S. cylindrica (2n = 112) and S. powellii (2n = 120) was studied from root tip cells. All the species had chromosomes with approximately same range of size and type (figs. 176 and 177). Analysis of karyotype was not possible because of the very small size of the chromosomes. The chromosomes in the complement of all the taxa possessed median to submedian primary constrictions (figs. 176 and 177). There was an abrupt size difference within a complement and in general the small chromosomes outnumbered the larger ones. The longer chromosomes usually had submedian constrictions while the short chromosomes mostly had median constrictions. Nucleolar chromosomes were not clear in any of the taxa studied.

Figs. 170–173 : Meiosis in *Sansevieria* species

Fig. 170 : Metaphase I in *S. trifaciata* (2n = 40). 20 II. Heteromorphic bivalent marked.

Fig. 171 : Metaphase I in *S. pearsonii* (2n = 40). 20 II. See the precocious seperation of bivalent.

Fig. 172 : Metaphase I in triploid *S. gracilis* Clone I (2n = 60). 13 III + 7 II + 7 I.

Fig. 173 : Anaphase I in *S. gracilis* Clone I showing lagging chromosomes.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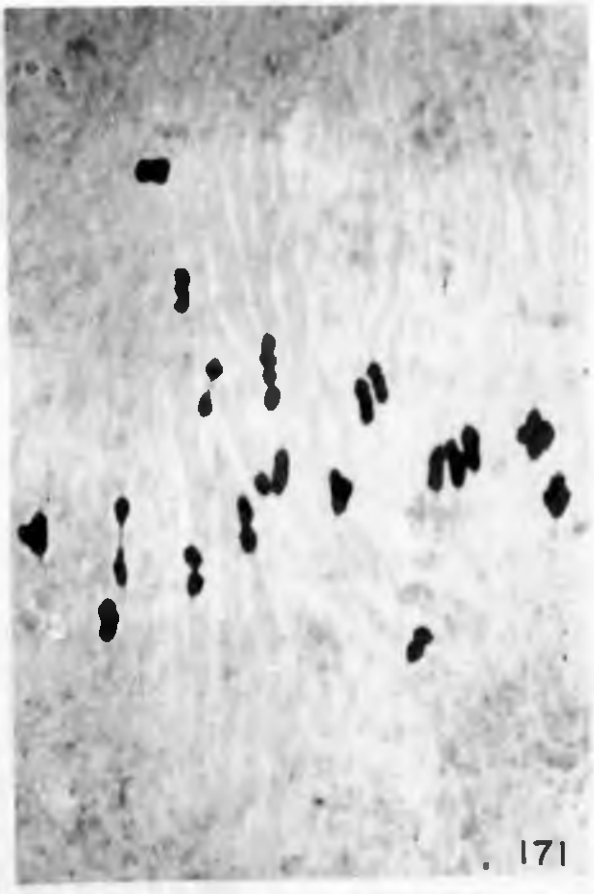
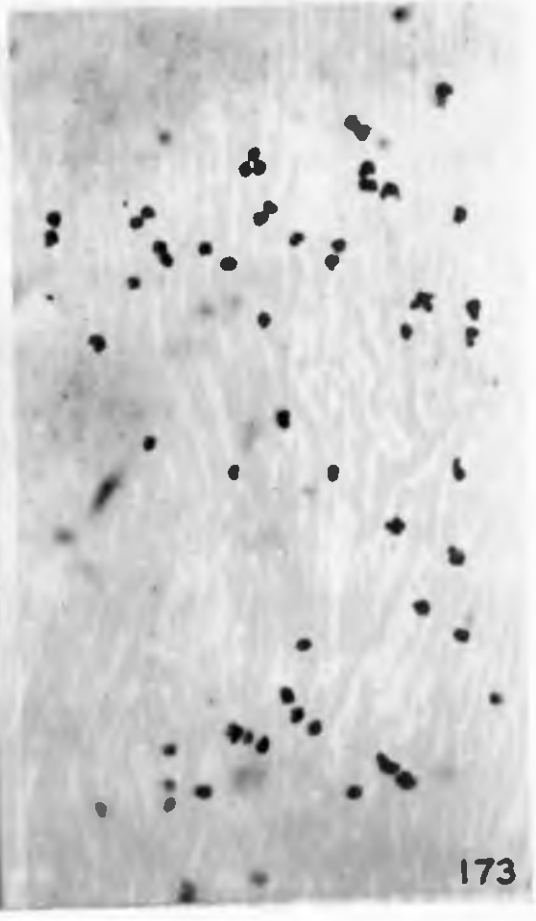

171


172


173

Figs. 174-177 : Meiosis and karyotype in polyploid Sansevieria species.

Fig. 174 : Metaphase I in S. canaliculata (2n = 80). 4 III + 33 II + 2 I.

Fig. 175 : Anaphase I in S. canaliculata showing lagging chromosomes.

Fig. 176 : Somatic chromosomes of S. cylindrica (2n = 112).

Fig. 177 : Somatic chromosomes of S. powellii (2n = 120).

174

175

176

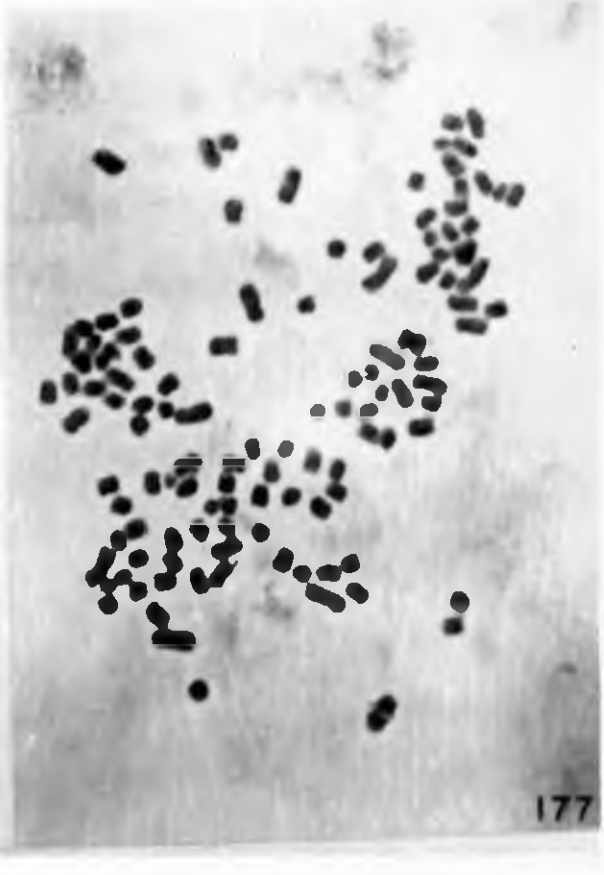


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Table XIII

CHROMOSOME NUMBER IN SANSEVIERIA SPECIES

Taxon	2n	Reference
aethiopica Thunb.	14	de Wet, 1957
	40	Menzel, Pate, 1960.
anquistiflora Lindb.	40	Menzel, Pate, 1960.
arboreecens Hort.	76	Sharma, Chaudhuri, 1964
canaliculata Carr.	42	Sharma, Chaudhuri, 1964
	80	Menzel, Pate, 1960
		Present study.
caulescens N.E. Brown	40	Present study.
concinna N.E. Brown	120	Menzel, Pate, 1960
cylindrica Bojer	18	Sarkar et al., 1977
	40	Roy, M., 1956
	84	Roy, R.P., Misra, 1961.
	92	Sharma, Chaudhuri, 1964
	102-104	Heitz, 1926
	112	Present study
	120±1	Menzel, Pate, 1960
daruei Staff.	≈ 120	Menzel, Pate, 1960
deserti N.E. Brown	28	de Wet, 1957
	40	Menzel, Pate, 1960
		Present study

Table XIII contd.

Taxon	2n	Reference
ehrenbergii Schweinf.	40	Sharma, Chaudhuri, 1964
		Menzel, Pate, 1960
		Present study
gracilis N.E. Brown	42	Parker, 1955 (Menzel, Pate, 1960).
	40	Present study
Clone I	60	Present study
grandis Hook.f.	44	de Wet, 1957
	40	Menzel, Pate, 1960
	100	Satô, D., 1942
intermedia N.E. Brown	40	Present study
laurentii Willd.	40	Sharma, Chaudhuri, 1964
liberica Ger. et Labr.	79-80	
	80	Menzel, Pate, 1960
	80±2	
longiflora Sims.	40	Parker, 1955 (Menzel, Pate, 1960)
		Menzel, Pate, 1960
metallica Ger. et Labr.	40	Satô, D., 1942
		Menzel, Pate, 1960
		Present study
nilotica Baker	36,40	Roy, M. 1936
parva N.E. Brown	40	Menzel, Pate, 1960

Table XIII contd.

Taxon	2n	Reference
pearsonii N.E. Brown	40	Present study
powellii N.E. Brown	120	Present study
roxburghiana Schult.f.	40	Patel, Narayana, 1937
		Satô, D., 1942
		Roy, R.P., Misra, 1961
		Sharma, Chaudhuri, 1964
senegambica Baker	40	Harvey (cn. VII. 1966)
		Miege, 1962
		Sharma, Chaudhuri, 1964
		Present study
stuckyi Godef. Lab.	79-80	Menzel, Pate, 1960
	116	Sharma, Chaudhuri, 1964
subspiceata Baker	120	Menzel, Pate, 1960
	120	Present study
suffruticosa N.E. Brown	40	Menzel, Pate, 1960
		Present study
thyrsiflora Thunb.	40	Menzel, Pate, 1960
trifasciata Prain	36	Sharma, Chaudhuri, 1964
	40	Menzel, Pate, 1960
		Present study
	42	Parker, 1955
zeylanica Willd.	40	Takagi, 1938, Satô D.1942
		Present study
	40, 42	Matsura, Satô, 1935
	42	Janaki Ammal (D. 1945)

Meiosis of 13 species was studied of which 11 were diploids with somatic number 2n = 40. All the diploid taxa invariably formed 20 bivalents at metaphase I (Figs. 170 and 171). The bivalents were mostly rod shaped with one terminal chiasma. The ring bivalents were mostly found to have interstitial chiasmata, often 2 in one or both arms at metaphase I. Two bivalents were larger than the rest and contained interstitial chiasmata. One heteromorphic bivalent was regularly seen in most of the diploid species (Fig. 169). In most species few bivalents were seen to disjoin at metaphase I (Fig. 171). Anaphase I and subsequent division was quite normal. Pollen stainability was very high (80%) in all the taxa and most of them set seed.

Natural triploidy has been located for the first time in the genus by the present author. A clone of S. gracilis was found to have 2n = 60 chromosomes. A detailed analysis of metaphase I in PMCs revealed the presence of trivalents, bivalents and univalents (Fig. 172). The number of trivalents ranged from 11 to 20 with an average of of 14.26 ± 0.25. The trivalents showed a tendency to disjoin early at metaphase I resulting in bivalents

and univalents. The number of bivalents and univalents ranged from 0 to 11 and 0 to 9 with a mean of 6.63 ± 0.56 and 3.96 ± 0.42 respectively. Anaphase I exhibited high degree of irregularities with unequal distributions, formation of laggards, micronuclei, precocious division of univalent etc. leading to the production of aneuploid gametes (Fig. 173). Though the taxon had 31.25% pollen stainability, there was no seed setting.

Meiotic studies in higher polyploids was rather difficult, due to extreme stickiness and small size of the chromosomes. In hexaploids and aneuploids such as S. subepicata (2n = 120) and S. cylindrica (2n = 112) it was difficult to study the nature of multivalent associations. Only one tetraploid species, S. canaliculata showed clear metaphase plate, where trivalents, bivalents and univalents were seen (Fig.174). Anaphase I was characterised by unequal separation, presence of laggards etc. (Fig. 175). Pollen stainability in polyploids was rather low (40-45 per cent) with no seed set.

Conclusions

A perusal of Table XIIIshows that lower chromosome numbers like 2n = 14, 18, 36 etc. have been

recorded by various authors. However, the most common diploid number is 2n = 40. The cytological screening of 11 diploid species by the present author did not show any gametic number less than 20. This finding together with the previous report of several authors shows that there is preponderance of n = 20 in diploids. Hence the basic number in the genus may be considered as x = 20. Similar conclusion was drawn by Menzel and Pate (1960) who suggested the same basic number.

The chromosome morphology and size are very similar in all the diploids and polyploids. Earlier workers like Roy, M. (1956), Roy, R.P. and Misra (1961) and Sharma and Choudhuri (1964) observed 8 to 10 nucleolar chromosomes in diploid taxa and upto 22 SAT chromosomes in species like S. stuckyi (2n = 116). Due to rather small size of the chromosomes, it was difficult to locate structural changes in the karyotype.

Meiosis in diploids was characterised by complete bivalent formation. In diploid taxa, one heteromorphic bivalent was seen regularly. This may indicate a possible structural alteration involving

the two homologues. Similar unequal associations were noticed by Menzel and Pate (1960) in polyploid species and they felt that the unequal multivalents were the result of structural alterations. At metaphase I, there was a tendency for precocious separation of bivalents in most of the taxa. The bivalents involved in the early disjunction were of rod type with a single terminal chiasma.

The existence of natural triploidy has been reported for the first time by the present author. The triploid clone of S. gracilis showed the presence of a maximum of 20 trivalents which indicates its autoploid origin, obviously it may have arisen through the fusion of reduced and unreduced gametes.

Meiotic studies in polyploid taxa were rather difficult due to extreme stickiness of the chromosomes. However, the tetraploid species, S. canaliculata showed clear metaphase in which trivalents, bivalents and univalents were seen. Higher polyploids and aneuploids like S. subspicata (2n = 120) and S. cylindrica (2n = 112) contain multivalents, bivalents and univalents. The frequency of multivalents was low in all the cases. This may be an indication of segmental alloploid nature of the taxa.

The role of hybridization and polyploidy in the evolution of Sansevieria has been discussed by Menzel and Pate (1960) and Sharma and Chaudhuri (1964). Menzel and Pate (1960) obtained fertile hybrids in interspecific crosses involving diploid species and also between diploid and tetraploid species. Interspecific hybridization has also been reported by various workers like Pate et al. (1954, 1960), Wilson et al. (1962), etc. Crossability of different species indicates their close cytogenetic relationship. Irrespective of wide morphological variation among species, the chromosomes have little genetic differentiation. The speciation at diploid level has occurred principally through mutations and hybridization accompanied by incomplete barriers to crossability (Menzel and Pate, 1960). The polyploids have arisen principally through segmental alloploidy which has been successful despite the low level of chromosome differentiation in the genus, because the various diploid genomes, though similar, are sufficiently differentiated to exhibit preferential pairing in polyploids. Aneuploidy has also played some role in the evolution of species like S. cylindrica, where different aneuploid cytotypes are reported.

Aneuploids might have originated as a result of hybridization involving polyploid taxa in which irregular meiosis results in the production of unbalanced gametes. Once an aneuploid individual arises, it is perpetuated and preserved in nature through efficient vegetative reproduction, particularly by rhizome or stolon.

V. SUMMARY

Chrysanthemum is a member of the family Compositae, and the tribe Anthemideae. In a recent review, Haywood and Humphries (1977) have revised the genus and split it into *Argyranthemum*, *Chrysanthemum*, *Leucanthemum*, *Tanacetum* and *Dendranthema*. The garden chrysanthemums have been placed under *Dendranthema*. The genus contains nearly 160 species which are of wide spread occurrence in temperate regions and in many parts of the world, mostly old world. The two main centres of distribution are the Mediterranean area, particularly Algeria and Canary Islands and China and Japan. *Dendranthema* is centred in the Far East, mainly in China.

The genus *Chrysanthemum* constitutes a large polyploid complex ranging from 2x to 22x, with a large number of aneuploids in between. The garden chrysanthemum (*C. morifolium* Ramat.), one of the most important flower crops of the world, originated more than 3000 years ago in China, mainly from two elemental species, *C. indicum* L. and *C. morifolium* Ramat. (*C. sinense* Sabine).

The present investigation is based on 13 species of the genus and approximately 183 cultivars of garden chrysanthemums, and deals with morphological variation, breeding system and variation in the chromosome complement and meiotic system in C. morifolium complex.

About 100 representative cultivars from different horticultural groups were studied morphologically. C. morifolium is a perennial herb, perennating with the help of underground stem. With regard to plant height, large flowered cultivars were found to be taller, with height ranging from 32 to 127 cm while small flowered cultivars show a range from 29 to 67 cm. Leaves are simple, usually exstipulate and alternate. The variation in leaf shape etc. was uniform throughout the polyploid/ aneuploid taxa ranging from 4x to 8x.

Considerable variation exists in number, form, size and arrangement of the florets which ultimately effects the shape of the flower heads. The size of the ray florets varies according to the type of the bloom. In small flowered types, the size ranges from 0.7 x 0.2 cm to 3.0 x 1.0 cm and in large flowered forms the range is 5.8 x 0.9 cm to

9.7 x 1.2 cm. The disc is very conspicuous in all singles and most of the semidoubles. However, it is almost concealed in other types. The basic colour in Chrysanthemum is yellow, but the cultivars of C. morifolium exhibits an array of colours in different shades except true blue. The capitula diameter varies from 1.9 to 23.0 cm, while the capitulum size can be increased or decreased with cultural practices, under identical conditions in the garden, no correlation was found between capitula size and chromosome number. In general, the small flowered cultivars have lower chromosome numbers, ranging from 2n = 36 to 55, while large-flowered cultivars tend to have higher chromosome numbers, the range being 2n = 53 to 72.

The capitula are adapted to cross-pollination as is the case with most of the members of Compositae. In Chrysanthemum, floral morphology, colour polymorphism, protandry, fragrance etc. are associated with out-breeding. Self-incompatibility is operative in chrysanthemum species, which enhances cross-pollination. The self-incompatibility in C. morifolium is sporophytically controlled. Quite often, there is break down of incompatibility system which results in some degree of self-compatibility.

Out of 183 cultivars of C. morifolium, one was tetraploid, 4 pentaploids, 98 hexaploids, 5 heptaploids, 2 octoploids and 69 were aneuploids. Besides, four cultivars showed the presence of one B-chromosome each in the somatic cells. The polyploid series in the genus as well as cultivars is based on x = 9, which is the most common basic number in the species. However, high polyploids are not necessarily exact multiples of the basic number. In cultivars of garden chrysanthemums the somatic number ranges from 2n = 36 to 75 with various aneuploid numbers in between. The karyotype and meiosis of most of the cytotypes have been studied in detail.

There was no significant size difference within a complement, and the longest chromosome was 1.3 to 1.5 times longer than the shortest chromosome. The size of the chromosomes varied from 3.8 to 5.0 µm. Decrease in size of the chromosomes with an increase in the level of ploidy was noted in C. morifolium complex. The karyotypes are reasonably symmetrical (2A category) and could be resolved into 9 sets. However, different cultivars could not be distinguished on the basis of karyotypic comparisons. There is considerable heterogenity in the karyotype ranging

from the presence of strictly median (M, r index 1.0) to those with subterminal and even terminal chromosomes. In all the cultivars analysed in the present study, the number of metacentric (m) chromosomes were high, and there is no selective accumulation of any other type with respect to a particular polyploid/aneuploid cytotype.

There was considerable inconstancy in the number of chromosomes in a set. Failure to recognize discrete sets with identical chromosomes in a set, may be the result of ancestors differing in chromosome morphology followed by recombination between them. This leads to reshuffling of chromosomes resulting in chromosomally unbalanced gametes which are viable due to buffering effect of polyploidy. Union of such gametes results in entirely new chromosome combinations, which are tolerated as there is some interchromosomal balance and the degree of differentiation of the 9 chromosomes of the basic set is very little. New chromosome combinations resulting from reshuffling of genomes are being continually formed under garden conditions due to intensive indiscriminate hybridization by nurserymen.

Another source of karyotypic variation is due to sporting. Sporting is often accompanied by gain or loss of chromosomes during mitosis in the meristem, resulting from mitotic abnormalities like non-disjunction, lagging, stickiness of chromosomes at anaphases etc. Such anuusomatic variation contributes some degree of karyotypic variation in Chrysanthemum cultivars.

Karyotypic heteromorphicity was observed in the complement of almost all the taxa studied. In majority of the cases, heteromorphicity was due to a change in total length of the chromosomes and a shift in centromeric position. Such changes might have been brought about by pericentric inversion. The presence of small odd chromosomes and abnormally long ones in various cultivars show the role of structural alteration in the origin of karyotypic heteromorphicity.

Four cultivars had one B-chromosomes each in their complement. The Bs in all the cases were smaller than A-chromosomes and in one cultivar the B-chromosome had a terminal centromere. In cultivar 'Chenghiakhan' one B-chromosome was found in the PMCs, and not in the root tip cells. The exact nature of their origin and mode of transmission is not known.

Telocentric chromosomes were observed in cultivars like 'Mohini' (2n = 52 + 2T), 'Kasturba Gandhi' and 'Mahathma Gandhi' (2n = 61 + 1T). They are stable members of the complement and appears to be of recent origin. It is probable that they might have originated due to centric fission or deletion of short arms in highly acrocentric chromosomes.

Nucleolar chromosomes were present in almost all the taxa studied, but owing to rather small size of the satellites and over-condensation of chromosomes, a few cultivars did not show any satellites. The satellites appeared on the short arm of the chromosomes in all the taxa. Their number varied from 1 to 10 in various polyploid/aneuploid taxa. In the present study, it was not possible to find a correlation between chromosome number and the number of SAT chromosomes, which may be indicative of hybridity between different taxa involved in the origin of the cultivars.

The only report of meiotic studies in C. aorifolium is that of Dourick (1953), otherwise there is a paucity of data on the meiotic system of this poly-aneuploid complex. In the present study, the tetraploid taxon showed few quadrivalents and a

large number of bivalents in the PMCs, which indicates its segmental alloploid origin. In pentaploid cultivars, pentavalents and quadrivalents were few, whereas trivalents were rather more. Univalents were also observed. Presence of pentavalents indicates similarity between all the genomes, however, it is difficult to define the nature and extent of pairing in large number of bivalents and trivalents. The reasonably high number of trivalents and univalents may be due to potential quadrivalent formation restricted by competition in pairing. In hexaploid cultivars also the number of multivalents was low and there was predominant bivalent formation. Quadrivalents were the most common type of multivalents. A few cultivars exhibited diploid-like meiotic behaviour, characterised by predominant bivalent formation in 90 per cent of the PMCs. The regularity of bivalent formation observed in these cultivars may be attributed to some sort of genetic control for diploidisation. The meiotic behaviour in octoploid taxon was more or less similar to other polyploid taxa. Here again, the highest association encountered was octovalents which assumed chain or ring shape. Most of the PMCs exhibited lower multivalent frequency which again indicates segmental alloploid nature.

Meiosis in aneuploid cultivars was characterised by the presence of a large number of bivalents and few multivalents and univalents. In odd numbered aneuploids the extra chromosome remained mostly as a univalent; however, occasionally it associated with bivalents to form a trivalent.

In all the taxa studied, irrespective of the grade of ploidy, anaphase I segregation was apparently normal. However, anaphase II showed high degrees of irregularities with lagging chromosomes, formation of micronuclei, etc. Inspite of all these anomalies, there was good deal of pollen stainability and seed set. The high degree of pollen stainability may be due to the high polyploid nature of the taxa, with the result gain and/or loss of chromosome(s) arising from segregational irregularities can well be tolerated.

DNA content

In the present study involving various polyploid/aneuploid taxa of C. morifolium, there is a direct correlation between DNA content and the grade of ploidy. The slight discrepancy in DNA values with respect to ploidy level may be due to chromosomal reshuffling and/or rearrangements which these cultivars have undergone during evolution.

Origin and evolution of ornamental taxa

Unlike most of the ornamental plants, garden chrysanthemums have an ancient history of domestication. The primary centre of origin is China and Chinese have been growing improved forms since 2,500 years. The garden forms have arisen mainly from two elemental species, C. indicum and C. morifolium (C. sinense). The original forms were probably single, many flowered, and cultivation for a long time has resulted in the transformation of the corolla of individual florets into numerous forms seen today.

The actual improvement of garden cultivars has been accomplished in the gardens of Japan, Europe and America. In A.D. 386 chrysanthemums reached Japan via Korea, from China. Holland was the first European country to import chrysanthemums. From Holland it reached France and later to England by about 1754. Americans obtained chrysanthemums from China still later. In USA attempts have been made to hybridize garden cultivars with wild species and promising hybrids like 'Korean Hybrids' have been evolved. In all the above cases, garden chrysanthemums have reached various countries in the form of seedlings or seeds. From these stocks new cultivars have arisen both as hybrid seedlings and from bud sports.

The chief factor underlying evolution has been indiscrimate inter-varietal hybridization by nurserymen and enthusiasts, followed by selection. Further diversity has been brought about by crossing with wild species. Selection of spontaneous mutations and fixing the useful ones through vegetative propagation also resulted in the origin of many cultivars.

During a span of 2500 years the primitive hybrids have undergone great transformation in the hands of man, and innumerable forms with great colour diversity have resulted. This has been accomplished by various factors like outbreeding, spontaneous and intentional hybridization, bud mutations, chromosomal differentiation, repatterning and polyploidy.

Principles of selection

From the native regions of China and Japan, garden chrysanthemums were introduced into European and American gardens where different criteria were used for selection of cultivars. These involved increased hardiness, dwarf habits, perfection of blooms for exhibition purposes, qualitative aspects

in commercial trade, early blooming, colour diversity, increased thickness of floral parts to enhance the vase life as cut flower, and introduction of fragrance. Usually, the chrysanthemum cultivars bloom for a period of six weeks only. In recent years, more attention has been paid for year round production of chrysanthemum blooms. Selection of various cultivars for this purpose has been done in India and other chrysanthemum growing countries.

Horticultural classification

Chrysanthemum cultivars show a great deal of variability in flower colour, shape etc. Based on different shapes of the bloom, horticultural classification has been employed, mainly for the purpose of competition in exhibitions. The blooms are broadly classified into large flowered and small flowered forms. The large flowered group contains different sub-groups like Incurved, Incurving, Reflexed, Intermediate, Irregular, Ball or Rayonante, Quilled, Spider, Spoon, Anemone, Single and Semidouble. The small flowered group contains Anemone, Button, Korean (single and double), Decorative, Pompon, Stellate, Charm or Cineraria, Quilled and Semiquilled or Spoon.

SANSEVIERIA

The genus Sansevieria belongs to the family Agavaceae. Some species are highly prized as a source of fibre crop to make coarse fabrics, fish nets etc., while others are cultivated for their ornamental, variegated leaves. The purpose of the present study is to understand the evolution process in this important group of plants.

Benthem and Hooker (1862-1883) placed the genus in the order Haemodoraceae. Later, Engler and Prantl (1929) included this under Liliaceae together with Ophiopogon, Dracaena, Yucca and other genera. However, Hutchinson (1959) placed the genus in the family Agavaceae. Recent studies on embryology as well as cytology by various authors did not justify the placement of this genus in Agavaceae.

Nearly 60 species have been reported in the genus, most of these are confined to tropical Africa, Madagascar and the islands near its coast and Arabia. Three species are recorded from India.

Out of 60 species belonging to the genus, only 25 are known cytologically. In the present study,

15 species have been cytologically analysed, of which the chromosome number of 4 species has been reported for the first time. Out of the 15 species, 11 are diploids, 1 tetraploid, 2 hexaploids and one aneuploid.

The karyotype of the species is characterised by the presence of very small chromosomes, which outnumber the larger ones. The chromosomes of all the taxa possess median to submedian primary constrictions. Nucleolar chromosomes were not clear in any of the taxa studied.

Meiosis of 13 taxa were studied. Diploids regularly formed 20 bivalents at metaphase I. Two bivalents were larger than the rest. One heteromorphic bivalent was observed in most of the species. Anaphase I segregation was regular. Pollen stainability was very high and seed formation was seen in some species. A natural triploid has been found for the first time in a clone of the diploid species, S. gracilis N.E. Brown. It showed a high number of trivalents in the PMCs indicating its autoploid origin. Meiosis in high polyploids was rather difficult due to extreme stickiness of the chromosomes. However, predominant bivalent formation was observed in these taxa.

The most common number in diploid species is 2n = 40 hence the genus is based on x = 20. Hybridization and polyploidy seems to have played an important role in the evolution of the genus. Irrespective of the wide morphological variation among species, the chromosomes have little genetic differentiation. The polyploids have arisen through segmental alloploidy.

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