

NINTH SILVER JUBILEE COMMEMORATION LECTURE

EXPERIMENTAL TAXONOMY AND ITS APPLICATION TO
HORTICULTURAL BOTANY

T. N. KHOSHOO

National Botanical Research Institute, Lucknow-226 001, India

I AM indeed very grateful to the management of the Birbal Sahni Institute of Palaeobotany, Lucknow, for inviting me to deliver the Ninth Silver Jubilee Commemoration Lecture. Although I have never had the privilege of knowing personally the founder, the late Prof. Birbal Sahni, I have read a large number of his valuable papers while I was working on the cytogenetics of gymnosperms which was my first love in research. This helped me to widen my knowledge regarding variation and evolution of the gymnosperms in space and time and to produce a reasonable account of underlying cytogenetic mechanisms. I, therefore, feel privileged to be here. Having worked on living plants, at first I was at a loss to decide about the topic on which I should talk to this august gathering. However, it came to my mind that as botanists, the common denominator that binds all of us is taxonomy which is indeed the mother science, whose relevance has in fact increased over the years although molecular, ultrastructural and genetical botany have become fashionable pursuits. Never before there has been such a realization as at present that the future of man on this planet depends on plants and plant cover. Thus inventories of plant wealth for purposes of conservation and survey and screening for their uses have assumed considerable importance. Obviously, there is an urgent need to update the taxonomy of the plants, a subject which for some time had fallen out of grace.

Taxonomy is the oldest discipline of botany and in fact at one time botany meant only taxonomy. However, with time, it widened considerably and data from other disciplines like morphology, anatomy, cytology, palynology, embryology, chemistry and

biochemistry, physiology, ecology, geography, history, palaeobotany, phylogeny, evolution, genetics, biometry and, last but not the least, computer science have enriched taxonomy. Out of these, the impact of genetics on taxonomy has been indeed most profound, because if two taxa hybridize freely and exchange genes without impairment of fertility and vigour in F_1 and subsequent generations, they are considered to belong to the same breeding group, biological unit or species, and taxonomic status of one of the entities is in doubt in as much as one of the taxa is conspecific with the other. Such data when collated with those emanating from other disciplines, resulted in a synthetic approach which is known as experimental taxonomy or biosystematics. This is one of the most important tenets of experimental taxonomy. This approach overshadowed all others, because it was broad based and genetical data gave an estimate of the direct phylogenetic relationship, and came to be regarded as perhaps the nearest to the ideal approach. Indubitably, it is time-consuming and laborious and cannot be applied for all types of plants (viz., arborescent species with a long generation) as also in the preparation of floras of countries with rich plant-wealth where, of necessity, the approach has to be descriptive. For such encyclopaedic purposes morphological discontinuity is very important so that species can be identified by ordinary means.

Broadly speaking the aim of experimental taxonomy is twofold, namely descriptive and experimental. The former includes studies on morphology, geographic distribution, ecological preferences, chromosome numbers and their morphology, while the latter includes possibilities for hybridization (including natural), pairing

of parental chromosomes in the F_1 , segregation and vigour of hybrid and physiological and other studies (Clausen, 1963). Experimental taxonomy aims at unravelling total relationship and is, therefore, not only observational and descriptive but also important in experimental, analytical and synthetic studies in herbarium, library, garden, laboratory and computer sciences. Judicious use of experimental taxonomy can give an estimate of direct phylogenetic relationship.

It is now a well known fact that there are stages in the evolution of species (Clausen, 1951). On the one side of the spectrum are the ecological races with only ecological separation, and on the other are full-fledged species with three descriptive properties: morphological differentiation, genetical discontinuity, and eco-geographical preferences. An analysis of evolutionary entities based on these characters is given below (Clausen, 1963):

point with interesting results. From the taxo-genetic angle, these plants may be divided into two broad groups. Those that have evolved from a *single, taxonomic species*, and those in which *two or more than two species* have been involved in origin. In the former, the ancestral species may be diploid or polyploid, while the latter may involve all diploid, some diploid and other polyploid, or all polyploid species. An example of each category may be considered, before some general conclusions are drawn.

MONOSPECIFIC ORIGIN

A. DIPLOID ANCESTOR

Under this category the case of snapdragon (*Antirrhinum majus* Linn.) may be considered. The species as a whole is

MORPHOLOGY	ECOLOGY AND AREA	GENETIC RELATIONSHIPS: HYBRIDS			
		Fertile, F_2 vigorous	Partially sterile, F_2 weak	Sterile	None
Distinct	Distinct	Distinct subspecies	Distinct species (ecospecies)	Distinct species complexes (ceno-species)	Distinct genera (comparia)
	The same	Local variations biotypes	Species, overlapping in common areas		
Similar	Distinct	Distinct ecotypes (ecological races)	Genetic species only		
	The same	The same entity	(Examples: autopolyploidy; certain kinds of chromosomal repatterning)		

In essence, over the years, experimental approach to taxonomy emerged from the detailed studies on the cultivated plants, such as wheat, maize, barley, rice, cotton, brassicas, potato, tobacco, banana, tomato, sugarcane, etc. and was then extended to wild plant genera such as *Crepis*, *Layia*, *Madia*, *Clarkia*, *Datura*, *Epilobium*, *Oenothera*, *Geum*, *Gillia*, *Achillea*, and many other genera and species-complexes within genera. Several polytypic species (eg. *Sisymbrium irio* Linn. complex) were also analysed utilising the same principles (Khoshoo, 1960). At the NBRI, Lucknow, decorative plants have been studied from this view-

diploid ($2n = 16$) and the ancestral/elemental type still grows wild in Europe. There are 5 subspecies recognizable in this species, out of which only two are important in the origin of the cultivated snapdragon. These are ssp. *majus* and ssp. *tortuosum*. The former was domesticated in the middle ages of Europe and is self-sterile but self-fertility has been restored through mutation of an overriding self-fertility gene. The ssp. *tortuosum* is self fertile and was domesticated by Romans. The two subspecies cross through insects. The wild types have small and loosely arranged flowers in only pink colour in comparison

to the large, closely set and many coloured flowers in the cultivated types. As expected the characters of the wild type are dominant and in fact looks as if it is one of the primitive cultivars of the cultigen. Over the years, genotypes have been selected which show a high rate of mutation. In essence the origin and evolution of the cultivated types has been the result of extraordinary high number of mutations. Up to 1966, the mutation spectrum has involved 389 mutations (Stubbe, 1966), of which 353 were recessive and the remaining 36 dominant. According to Bauer (vide Stubbe, 1966), nearly 50 mutational steps have been responsible for the origin of the cultivated types from the wild one and 20 of these were concerned with flower colour alone.

Mutations have been both phylogenetic and commercially useful. One of the phylogenetic mutation has converted the flower into peloric form with symmetrical corolla. A commercially useful mutation changed flower form from the bilipped personate type to open type which resembles the allied genus *Penstemon*. The latter is a very recent 2-gene mutation which has gone into the nursery trade. Another commercially useful mutation rendered the flower double and when hybridized with penstemon-type, the result was an open and double type of flower.

An idea about the extent of the latent variation can be obtained when the wild and the cultivated types are crossed. There is normal fertility and vigour in F_2 and the subsequent generation. However, wide variation arises which over-shoots even the taxonomic boundaries and is termed as explosive variation. Such macro-recombinations are of considerable interest to the florists because of their novelty.

Obviously, in cultigens with diploid monospecific origin, evolution has taken place at diploid level within the confines of a single taxonomic species.

B. POLYPLOID ANCESTOR

Celosia — The only cultivated species in this genus is *C. cristata* Linn. (= *C. argentea* var. *cristata* (Linn.) Kuntze) which has a grotesque inflorescence with excessive fascina-

tion for which the species breeds true. This species is tetraploid and exists only in cultivation. There is another species, a pantropical weed, *C. argentea* Linn., which has a primitive simple inflorescence and has been regarded, both by taxonomists and horticulturists, as the ancestor of *C. cristata*. However, the pantropical weedy species is octoploid (36 II) while the cultigen (*C. cristata*) is a tetraploid (18 II) and Grant (1954) found in the hexaploid hybrid between the two taxa, $18 \text{ II} + 18 \text{ I}$ and concluded that the cultivated taxon is one of the parents of the wild one. This may be understandable from purely genetical point of view, but not on the basis of comparative morphology as also the fact that a taxon existing exclusively in cultivation could not be an ancestor of a pantropical and widely distributed weed. Accordingly, no taxonomist or a horticulturist accepted Grant's (1954) suggestion. Furthermore, van Steenis (1958) came to the conclusion that with more search, a wild tetraploid race would be found which, instead of *C. cristata*, may have been the parent of the octoploid *C. argentea*. During the course of investigation, Khoshoo and Pal (1973) found such taxon in Central India, as predicted by van Steenis. This taxon fits beautifully in the scheme and is taxonomically referable to *C. argentea* with the difference that its leaves are broader than long and abruptly pointed at the top, while in the octoploid form leaf is ovate-lanceolate. The tetraploid *C. argentea* forms fertile (over 50%) hybrids (F_1 and subsequent generations) with *C. cristata*. The hybrids show dominance of the wild tetraploid parent. The differentiation between the two taxa is at the ecospecific level and the wild tetraploid could have been the ancestor of *C. cristata*. The former even shows incipient fasciation. Obviously, the cultigen arose as a result of Mendelian variation, recombination and selection. South east Asia is regarded as the centre of domestication of cockscomb and it is possible that the tetraploid wild form accompanied early Indian migration to South-east Asia. The primitive man cultivated it for magical, superstitious and religious properties associated with this plant and in fact there are traces of its cultivation even in India in the Rajmahal

Hills. In its new home in south east Asia, it underwent a new and a bigger cycle of selection resulting in its bizarre morphology — an over-evolved type that cannot exist in nature all by itself. Mutations resulting in widening of the growing point, soon after normal seedling growth, have been selected, affecting the length of the main floral axis, which becomes fan-shaped, truncate and ribbed. At genic level it involves many genes and with complex control.

The whole complex is phylogenetically one, in which, genetically speaking, the wild tetraploid *C. argentea* and the cultivated *C. cristata* are one species, while the wild 8X *C. argentea* and 12X cultivated *C. whiteii* have a reproductive barrier between them as also with the 2 tetraploids. Therefore, the 8X *C. argentea* and 12X *C. whiteii* are also 2 distinct species from genetical viewpoint. If morphological discontinuity is given due consideration, the complex as a whole is referable to one species, *C. argentea*, with varietal rank for different polyplotypes, namely *C. argentea* var. *argentea* for 8X, var. *cristata* for cultivated tetraploid (cockscomb), var. *orbiculata* (?) for the wild tetraploid and var. *whiteii* for the 12X synthetic fasciated type. It may be pointed out that most taxonomists have regarded cultivated tetraploid as *C. argentea* var. *cristata* (Khoshoo & Pal, 1973).

Obviously, both the cultigens (snapdragon & cockscomb) have a monospecific origin where evolution, within the confines of a single taxonomic species, has been through Mendelian variation, recombination and selection.

C. VARIEGATED PLANTS

Variation is essentially duality of colour in leaves arising as a result of gene or cytoplasmic mutation affecting chlorophyll formation. Such plants are generally monospecific in origin. Variations, therefore, leads to non-uniform development of chlorophyll or related pigments in plastids, cells or tissues of the plant organs, especially leaves, under normal conditions of nutrition temperature, and light. The chimeras may be periclinal (internal normal tissue surrounded by 1 or more layers of mutated

cells), sectorial (mutated tissue forms a complete sector extending from epidermis to pith), mericlinal (mutated tissue forms a discrete layer in one sector only), and in some cases the mutated and normal cells may be randomly mixed in all layers. The last is an unstable condition and leads to one of the three stable conditions enumerated above. Another category is mosaic and striped variegations in which variegated areas follow cell lineages, but in which the mutations do not appear to affect the growing point initials or germ cells (Kirk & Tilney-Bassett, 1967).

In general, variegated plants, being pollen and seed sterile are, therefore, vegetatively propagated. An experimental analysis of such horticultural taxa is indeed difficult. However, conclusions can be drawn on the basis of the involvement of various layers of the shoot apex. In this connection, Satina *et al.* (1940) recognized three germinal layers L_1 , L_2 and L_3 in a dicotyledonous shoot-apex which was also confirmed by Derman (1960) from his study of cytochimeras. L_1 divides anticlinally, while L_2 and L_3 divide both anti-and periclinal. L_1 gives rise to epidermis, L_2 produces a portion of the tissue under the epidermis in leaf, stem and fruit, while L_3 gives rise to the central (including vascular) tissue. Furthermore, according to Derman (1960) in dicotyledons in general, L_2 is the layer from which sexual tissue (pollen grains and egg cells) in anthers and ovaries is derived, although there may occur exceptional cases also. In monocotyledons, sexual tissue in an anther is developed regularly from L_1 and partly also from L_2 . Obviously, chances of inheritance are only if the mutations occur in L_1 and/or L_2 depending on whether the plant is dicotyledonous or monocotyledonous. The normal pattern, enumerated above, is modified by cell displacement which results in incursions into or replacement by cells of adjacent germinal layers, thereby disturbing the normal pattern.

To begin with, a mutated shoot is selected and is multiplied clonally, which becomes the source of a new cultivar and is given a fancy name. More often during the process of tissue recombination, there may be reversion to the parental type as also new types may arise.

MULTISPECIFIC ORIGIN

A. DIPLOID ANCESTORS

Bougainvillea — It is a South American tropical genus of about 10 species, only 3 species of which are ornamental, which are, *B. spectabilis* Willd., *B. glabra* Choisy and *B. peruviana* Humb. and constitute the basal/ancestral species and each is represented by a few cultivars only. However, most of the garden cultivars fall under three hybrid groups, *B. × glabra-peruviana* (= *× buttiana*), *B. × specto-peruviana* and *B. × specto-glabra*. There are some cultivars which do not conform to any of these groups and are more complex and represent hybrids between the hybrid-groups. Over the years, varieties with high rate of somatic mutations have been selected and bud-sports have added to the diversity within the hybrid-groups. These affect colour and form (single or double) of bracts, leaf variegation and flower tube (perfect or imperfect).

The flowers are nectariferous and are regularly visited by humming birds in the natural habitats in South America, but by sun birds in India. Apart from this, some butterflies are also successful pollinators. The species as also the cultivars are self incompatible with obligate cross-pollination, which is retained even after polyploidy. This system has been a boon to bougainvillea breeders, because any seed set spontaneously is necessarily of hybrid origin. Once new seedlings are selected, clonal propagation helped in fixation and perpetuation of the types under garden and/or natural conditions irrespective of the extent and nature of sexual sterility.

The species and most of the cultivars are diploid ($n = 17$), some are triploid having arisen through fertilization between reduced and unreduced gametes. Many of the primary hybrids have been synthesized and compared with those existing in cultivation. The genomes of the three basal species may be referred to as AA for *B. glabra*, A_1A_1 for *B. spectabilis* and BB for *B. peruviana* (Zadoo *et al.*, 1975). The sterility barrier caused by indiscriminate hybridization involving the BB genome has been broken by colchiploidy, and a new cycle of variability has been introduced into culti-

vation because absence of pollen and ovule fertility restricted the origin of new types of bougainvilleas (Khoshoo & Zadoo, 1969).

Extensive cross-compatibility studies among cultivars have shown that bud-sport families share the same incompatibility alleles and are, therefore, unable to cross. The unidirectional incompatibility involving interploidal cultivars is perhaps the result of alteration of embryo-endosperm-maternal tissue chromosome balance.

While the origin (at least the female parent) of all the cultivars is reasonably well documented, it has been possible to re-synthesize some cultivars from the putative parents. In some cases biochemical analysis of the betalains in bracts using electrophoresis has been used to trace their origin and affinities. Cultivars of each of the basal species shows a uniform band pattern. *B. spectabilis* is characterized by a maximum of 3 betacyanin and one betaxanthin band, however, the latter is absent in its cultivar 'Splendens'. *B. glabra* has a maximum of one band each of betacyanin and betaxanthin, whereas in its white cultivars the former is absent. *B. peruviana* has 2 bands each of betacyanins and betaxanthins. *B. × specto-peruviana* has 3 betacyanins and 2 betaxanthins; *B. × specto-glabra* has a peculiar constitution in as much as 8 of its cultivars do not have any betaxanthin, although all other cultivars in this group have 1 to 3 bands of betacyanins and one betaxanthin. In F_1 *B. × glabra-peruviana* shows 2 bands of betacyanins and 3 of betaxanthins. Interspecific hybridization has resulted in a large variation in colour, from relatively simple pigment constitution and limited colour range of basal species to comparatively complex pigment constitution and broad spectrum of colours in hybrids. Furthermore, from a study of the bud sport families it has been found that the mutation occurs in the direction of complete or partial loss of betacyanin with concurrent qualitative and/or quantitative gain of betaxanthins, which may be the precursors of betacyanins. It may be surmised that the genetic blockage to betacyanin production occurs at post-betaxanthin stage. Furthermore, it was also found that pigments of bracts under normal sunlight resolve into the usual

pattern of betacyanins and betaxanthin, but when grown in diffuse light they show faint development of betacyanins, and totally absent in bracts that grow in dark. It is not unusual to find development of betacyanins in white cultivars such as 'Shubra' during summer when light intensity is the maximum (Ohri, unpublished data).

The band patterns have been used to diagnose the affinities of a cultivar of unknown origin. This technique is particularly helpful in deciphering synonymy in cultivars because nurserymen, in order to boost their sales, often give different fancy names to the same cultivars and there are even cases where same names have been given to different cultivars.

Canna — Based on a systematic experimental analysis of the garden cannas, it was shown by Khoshoo and Mukherjee (1970) that they have arisen from five elemental diploid species, native to tropical Americas and West Indies. These were *C. glauca* Linn., *C. indica* Linn., *C. irridiflora* Ruiz and Pav., *C. warszewiczii* A. Dietr. and *C. flaccida* Salib. From their original habitats, the species were introduced in Europe in 16th century and most of these botanical species were cultivated to give a tropical effect to the European gardens. Then began a phase of intensive and indiscriminate hybridization and from middle nineteenth century onwards, the emphasis changed from tall, leafy, long-jointed and small flowered species to summer-flowering cultivars with medium to dwarf habit with close compact growth and prominently held inflorescences of very large, highly colourful, circular flowers. This was accomplished in nearly 44 years (AD 1848-1892) in which hybridization has played a dominant and a decisive role in the origin of cultivated types. Four species *C. glauca*, *C. indica*, *C. irridiflora* and *C. warszewiczii* lack any serious genetic barriers and there ensues considerable recombination with good deal of fertility. Obviously, these species show ecospecific differentiation and thus represent a homogamic and clonal hybrid complex (sensu Grant, 1953) in which different components are diploid, meiotically normal and often retain sexual mode of reproduction but are also vegetatively reproduced. From the recombination, in interspecific hybrids of a wide range

of genes, segregating simultaneously and involving complex segregation, arise a wide variety of heterozygous genotypes, with new colours and colour combinations, releasing much genetic variability including that which is transgressive in character. Repeated cycles of hybridization have led to destruction of barriers to increase in size and variability in colour of flowers. Associated with this are other useful characters like number of flowers per inflorescence, extended blooming period, cold resistance, etc. All such gains were fixed by vegetative propagation. By 1868, a group of cannas known as Crozy Cannas was evolved. These were included under a synthetic or horticultural species *C. × generalis* Bailey. This species was then hybridized to another botanical species *C. flaccida* Salib. The two have a cenospecific level of genetic differentiation. By 1892, this led to development of Italian Cannas referred to as *C. × orchiodes* Bailey.

In essence, cultivars within the two synthetic species are 'macro-recombinants' and the entire complex, the five elemental and the two synthetic species, constitutes a phylogenetic reticulum or a 'syngameon' (sensu Grant, 1957). However, the synthetic species are distinguishable from the elemental species on the basis of habit and, in particular, the floral characters, although there is no intersterility between the botanical and the synthetic species. Any variation pattern that is unravelled experimentally as far as is possible, needs to be expressed in traditional taxonomic units even though there may be some inter-grading types. From this view point, the recognition of two synthetic species is essentially sound in as much as they take into account their mode of ancestry and is, at the same time, utilitarian. Furthermore, while cultivars within *C. generalis* are diploid, interchange heterozygotes and autotriploids, those in *C. × orchiodes* are asynaptic non-seeded diploids, and allo- or segmental allo-triploids.

The two species show the following morphological differences in flower:

More or less similar genetic events underline the origin of garden verbena, *V. × hybrida* ($n = 5$) from four diploid ($n = 5$) botanical species namely *V. peruviana* Linn., *V. phlogiflora* Cham., *V. incisa* Hook,

CHARACTER	<i>C. × generalis</i> Bailey	<i>C. × orchiodes</i> Bailey
Diameter	Medium to large, always less than 12.5 cm	Very large 12.5-21 cm
Colour	Varied	Bright yellow to deep red, striped, splashed, never pink or clear white
Petals	Narrow, erect or ascending	Reflexed after about the first day
Tube	About 1.25 cm long, not longer than sepals	About 2.5 cm or more, much longer than sepals
Staminodia	Narrow to broad, mostly erect or strongly upright, well separated in outline	Broad and soft with flowing outline, lip funnel form at the base
Cultivars	Crozy, Gladiolus or French Dwarf Cannas	Italian, Iris, Orchid, or Giant flowered cannas

and *V. platensis* Spreng., and also garden petunia, *P. × hybrida* Vilm. ($n = 7$) from two diploid ($n = 7$) botanical species, *P. axillaris* BSP. and *P. violacea* Lindl. In both cases, the cultivated synthetic species are a vast improvement over the elemental botanical species and garden types show considerable diversity in flower form, colour and size. The elemental species in both cases are weekly differentiated genetically thereby permitting genetic recombination.

B. DIPLOID AND POLYPLOID ANCESTORS

Amaryllis — This ornamental has arisen from a very wide germ plasm base comprising at least 10 botanical species namely *A. belladonna* Linn., *A. reginae* Linn., *A. striata* Lamarck, *A. reticulata* L' Herit., *A. vittata* L' Herit., *A. aulica* Ker. Gawl., *A. pardina* Hook., *A. leopoldii* T. Moore, *A. espiritensis* Traub. and *A. psittacina* Ker-Gawl. Between these species there has been considerable hybridization which in fact has been single important factor involved in the origin of the garden cultivars.

Normally all the elemental species are isolated, but ever since these were brought in cultivation, there were opportunities for hybridization, under garden conditions both by natural agents and by man. The barriers broke between the taxa and due to their being genetically compatible, there ensued considerable gene-exchange between the elemental species. The segregating progenies were subjected to rigorous selection, and types possessing characteristics of interest to man, were selected, preserved and multiplied by vegetative means. The process

of recombination and segregation also helped in transgression as also in unmasking genes for novel characters which may not have any adaptive value under natural conditions. Next in importance has been polyploidy and majority of the large flowered types are tetraploid. Of particular interest are the triploids which are outstanding and often surpass the diploids and tetraploids.

The most important types are grouped under *A. × johnsonii*, *A. × acramanii*, and group-hybrids like *A. × gh. reginaeoides*, *A. gh. leopoldaeoides*, etc. The first hybrid was *A. × johnsonii* raised in 1799 and the last in the series are *A. henryae* and *A. gladwaynensis* both released in 1951 involving the former and two botanical species (Narain & Khoshoo, 1977).

C. POLYPLOID ANCESTORS

Zephyranthes — The garden types are a mixture of complex hybrids raised by Mr S. Percy Lancaster and his father involving *Z. brazosensis* Traub., *Z. drummondi* D. Don, *Z. grandiflora* Lindl., *Z. citrina* Baker, etc. The first two species were previously included under the genus *Cooperia* which has now been merged in *Zephyranthes*. The complex of cultivars supports and maintains efficiently an astonishing array of chromosome numbers ranging from $2n = 18$, to 22, 24, 25, 28, 38, 40-50, 54, 58-61, 66, 72, 73 and 96. This series perhaps began with $X = 6$ and owes its origin to chromosomal repatterning due to peri- and paracentric inversions, interchange heterozygosity and misdivision. This is coupled with self compatibility/

incompatibility and sexual/apomictic reproduction together with hybridization and polyploidy. The interchange polyploids because of their abnormal meiosis produce together with hybridization and polyploidy. The interchange polyploids because of their abnormal meiosis produce sex cells with a wide range of numbers, which are well tolerated because of the inherent polyploid constitution. This results in a cycle of aneuploid variability. The genetic system has the potentialities to conserve and preserve all heterozygosity through agamospermy and in particular through vegetative multiplication. With such a pattern, morphologically diverse and taxonomically complex nature of the genus is quite natural (Raina & Khoshoo, 1972).

Viola × *wittrockiana* Gams — The origin and evolution of garden pansy has been traced to elemental species like *V. tricolor* Linn. ($n = 13$) and *V. lutea* Hudson ($n = 24$), through hybridization followed by selection from 1813 onwards (Horn, 1956). The greater part of the development took place in Britain in the 19th Century. The two species hybridized when grown together, the seedling progenies were variable in growth and shape, size and colour of flowers. The work of gardeners from 1813 to 1841 resulted in 'Show Pansies'. On the European continent development of pansy did not conform to the rigid rules prevailing in Britain and there began another cycle of development which resulted in the origin of 'Fancy Pansies'.

Cytogenetically due to reshuffling of chromosomes and loss of suppressors for flower colour and size has been rendered possible because of the weak genetic differentiation between the two parents, *V. tricolor* ($n = 13$) and *V. lutea* ($n = 24$). Altogether new recombinations arose and there was release of new variability. During this process, the chromosome number in garden pansy (*V.* × *wittrockiana*) stabilized at $n = 24$ (8X), although the range of variation is from $2n = 44$ to 55. This could also happen through repeated backcrossing to *V. lutea* ($n = 24$). The garden pansy in a sense is, therefore, modified *V. lutea*. The few *tricolor* characters in the former are due to their introduction from *V. tricolor* as a result of past hybridization.

The plants with $2n = 48$ have superior selective value because of vigour and larger flowers with greater colour diversity. Whether the first hybrids between *V. tricolor* and *V. lutea* were spontaneous or were planned is not known but from 1862 *V. lutea* was systematically crossed with *V. tricolor*. The behaviour of hybrids between garden pansy and *V. lutea* is in agreement with such an origin of the former. Very likely the nature of ploidy in garden pansy is segmental-allopolyploidy (Mukherjee & Khoshoo, 1969).

Hibiscus rosasinensis complex — There has been rampant hybridization between *H. rosasinensis* Linn. (sensu stricto), probably a native of Asia, and 8-9 species from two disjunct areas like South Indian Ocean and Pacific Ocean Islands. These are: *H. schizopetalus* Hook. f., *H. liliiflorus* Cav., *H. fragilis* DC. and *H. boryanus* DC. (all from South Indian Ocean Islands), and *H. kokio* Hilleb. ex Wawra, *H. arnottianus* A. Gray (*H. waimeae* A. A. Heller), *H. densonii* Hort. ex Flor. and *H. storckii* Seem. (all from Pacific Ocean Islands). Repeated cycles of hybridization followed by selection have played a major role in the evolution of garden *H. rosasinensis*. Recombination between these species has been possible because of their intercompatibility. New variants were selected from the variability thus produced. Hybridization may have also helped to produce transgressive segregation and unlocking of useful recessives responsible for increased size and colour variation in flower, and extension of the blooming period. Coupled with hybridization, there seems to be total disregard for chromosome number because of the high polyploid nature of the taxa involved, with the result gain and/or loss of chromosome(s) emanating from the irregular meiosis with segregational errors can be well tolerated. The role of mutation is not clear although some data show that somatic mutations arise. Fixation of useful variants that arise from the above processes is no problem because of the rampant vegetative reproduction. The total range in chromosome number is from $2n = 36$ to 46, 54, 56, 60, 63, 68, 70, 72, 77, 84, 90, 92, 96, 98, 112, 132, 140, 144, 147, 150, 160, 164, 165, 168, 180 and 255. This is an unique man-made phylogenetic reticulum (unpublished data).

EXTENT OF MORPHOLOGICAL AND GENETICAL DIVERGENCE UNDER DOMESTICATION

The most ideal taxonomic treatment combines morphological variation with phylogenetic relationships and needs to be presented in a practical or a utilitarian form based on morphological discontinuities. It is often difficult to balance these aspects properly. In horticultural plants (for that matter cultivated plants in general) there is a high speed of evolution under domestication for morphological, physiological or chemical characters of interest to man. The high speed is the result of a 'directed' evolution. A study of morphological discontinuity in relation to genetical divergence is interesting and the most ideal situation is where both are at the same level. This is seen in cultivated taxa like *Amaranthus caudatus* Linn. and *A. edulis* Speg. used for their ornamental inflorescences and the nutritive grain respectively.

The two types are closely related having probably arisen from a wild ancestor *A. quitensis* (Sauer, 1967). *A. caudatus* Linn. (sensu stricto), originally a native of Andean region, has long drooping maroon soft velvety inflorescences with large globular glomerules, and ivory coloured seeds with translucent centre, flushed red round the rim. *A. edulis* Speg. (often included under *A. caudatus* Linn.), is a native of North western Argentina and has erect greenish brown inflorescences which are determinate in character because the main inflorescence together with the branches end in a 7-9-merous male flower which ordinarily is only 5-merous. *A. edulis* is most distinctive in the whole genus on account of this character. Though the seeds are ivory coloured with translucent centre, they have a white margin. The floral parts in the two taxa are similar. It is clear that the two taxa can be distinguished due to morphological discontinuity but they cross most readily in both directions as shown by Khoshoo and Pal (1970) and, what is most important, contrary to many other species which apparently resemble one another, there is no developmental malformation of any kind in F_1 hybrids. However, in F_2 there is considerable seedling mortality and nearly 18% plants are unthrifty. The F_1 shows complete dominance of *A. caudatus* as also heterotic vigour. The red colour

and drooping inflorescence are both monogenic dominants. Polymerous male flower, which is a digenic character, of *A. edulis* is recessive. Except for some unpaired segments and a possible terminal deletion in one bivalent, pairing during male meiosis is otherwise normal in F_1 with 16 II. Pollen fertility is only 25% and threshable percentage of seed is 68 in F_1 , but the corresponding figures in F_2 are higher being 40-85% and 60-80% respectively.

A. edulis due to unattractive inflorescence is essentially used for its nutritive grain and has arisen from *A. caudatus* during the course of domestication on the South American continent. Both taxa are found only in cultivation and never in wild condition. However, on account of the seedling mortality and unthrifty plants in F_2 , sterility in F_1 and F_2 and a measure of chromosomal difference, the two taxa are genetically reasonably well differentiated. This is commensurate with the strong morphological differentiation between the two taxa. From a critical and painstaking taxonomic analysis of grain types and their weedy relatives made by Sauer (1976), it is clear that the presence of a large erect determinate inflorescence and the polymerous male flower in *A. edulis* is more than the required level of differentiation used for species delimitations in the genus. From this point of view, *A. caudatus* and *A. edulis* are good species and need to be treated separately although there are valid reasons for regarding *A. edulis* as a recessive grain derivative that has arisen during domestication from *A. caudatus*, a species which is essentially an ornamental type and contains dominant genes for most characters of the former and, therefore, represents the ancestral condition. This is a very ideal condition in as much as the morphological differentiation resulting from the altered use, from ornamental to grain type, is associated with commensurate genetical differentiation.

A. caudatus-*A. edulis* complex has very likely arisen from *A. quitensis*. The two cross in both directions and except for a mild form of virus-like syndrome in the hybrids there are no barriers. The hybrids are semifertile. *A. quitensis* has perhaps arisen from *A. hybridus*. The hybrids between the two are morphologically intermediate with normal meiosis but with genic

male sterility. The domesticates like *A. caudatus* and *A. edulis* while showing semi-sterility with *A. quitensis*, are indeed strongly isolated from *A. hybridus* which produce total seedling mortality (Khoshoo & Pal, 1970; Pal unpublished). While the case of *A. caudatus-A. edulis* complex represents a near-ideal situation where morphological differentiation and genetical divergence have progressed at reasonably equal rates, the extreme situations may now be considered.

One such situation is encountered in *Portulaca grandiflora* Hook. This species, originally a native of Brazil, is widely cultivated summer ornamental. Among the single flowered types there is a cultivar 'Jewel' which has significantly large flowers (diameter 5.3 ± 0.7 cm) and broad petals (2.1 ± 0.028 cm) in comparison to the usual cultivars of *P. grandiflora* in which corresponding dimensions are 4.5 ± 0.07 and 1.7 ± 0.034 cm respectively. Furthermore, in 'Jewel' branching starts from the base of the main stem and the branches are closely set, leaves are somewhat larger and flower buds are thicker and shorter, in comparison to the cultivars of *P. grandiflora* in which branches are lax, leaves are smaller and buds are thinner and longer. Under Lucknow conditions, while *P. grandiflora* is strictly annual, its cultivar 'Jewel' tends to be perennial. In contrast to the presence of $n = 9$ in *P. grandiflora*, 'Jewel' is unquestionably $n = 5$ and the two types are totally cross incompatible. Furthermore, 'Jewel' contains homozygotes with 5 II as also heterozygotes with 1 or 2 interchange complexes of four chromosomes (Rizvi *et al.*, 1972). The homozygote recovered from the selfed progeny showed segregational irregularities while the heterozygotes were with directed segregation resulting in high fertility. Obviously, the interchanges seem to have been incorporated in the genetic system. If the basic number $n = 9$ is of amphiploid origin, it is possible the 'Jewel' ($n = 5$) could very well be one of the parents of *P. grandiflora* proper with $n = 9$. The other parent may be any of the species with $n = 4$ (Syakudo *et al.*, 1960; Rizvi *et al.*, 1972).

Between the two cytotypes, the 9-chromosome type exhibits much diversity, like single or double flowers in a variety of brilliant colours, while the 5-chromosome type has only single flowers which are magenta

coloured. This colour along with yellow represent the ancestral colours in the genus. Furthermore, former is cytologically uniform but morphologically heterogeneous, while the latter is cytologically polymorphic but morphologically uniform. Existence of genetically isolated cytotypes within the limits of a single taxonomic species may indicate cryptic or genetic speciation where phenotypic differentiation has not proceeded to a scale commensurate with the presence of a complete genetic barrier.

There may not be many examples of such cryptic speciation under domestication because man evolves cultivars for morphological, physiological or chemical attributes which arise at a great speed. The short time during domestication is hardly sufficient for attaining genetic incompatibility except perhaps in situations where the cultigen is a polyploid and due to interploidal barrier cannot cross with the parental diploid.

The reverse of the situation found in *Portulaca grandiflora* is encountered in *Antirrhinum majus*. Stubbe's (1966) monograph is replete with such examples and, among others, a noteworthy case is the cultivar 'Bright Butterfly' evolved by Knapp (1967) in which instead of the tubular flower with bilipped personate mouth (distinctive character of the genus), this cultivar has a funnel-shaped tube with widely open and spread out mouth. It is actually a two-gene mutant (Div/Div; hem^{rad}/hem^{rad}) arisen by hybridization between *Divaricata* (Div/Div) and *Hemiradialis* (hem^{rad}/hem^{rad}). *Divaricata* is partially dominant mutant which also lacks the characteristic bend of the normal snapdragon flower, but the upper and lower lips are close together. *Hemiradialis* is a monogenic recessive mutant with partially radial flower with the 3 petals of lower lip showing radial arrangement so that the typical bend is not revealed; while the shape of the 2 petals in the upper lip is normal and zygomorphic. The 'Bright Butterflies' when crossed with normal snapdragon mutant shows typical dihybrid ratio. Thus it differs from the normal in 2 genes, but has a flower form that transgresses the limits of the genus *Antirrhinum*. In case genetic history of the new type is overlooked, taxonomically though referable to subfamily Antirrhinoideae, it has characteristics of tribe *Cheloneae* (to which belongs genus *Pentstemon*) and

not the tribe Antirrhineae to which *Antirrhinum* belongs.

Another such mutant in *A. majus* is the Radialis with actinomorphic flower (like the genus *Verbascum*) which also transgresses the taxonomic limits of the genus (Stubbe, 1966). There are several such examples of evolution in morphological characters making the cultigens significantly different. One of the classical cases is *Brassica oleracea* Linn. with its several distinctive cultivars. Obviously, in all such cases, gene mutations result in significant changes which often approach species or even genera. More often such mutations are recessive and do not have any selective value in nature. For instance, Pentstemon-type of *A. majus* left to itself, does not seed because of the alteration in the position of the reproductive parts and the flower is no longer of interest to bumble bees (Knapp, 1967).

From the foregoing it is clear that the experimental taxonomic methods are very important for proper taxogenetic evaluation of horticultural taxa.

DOCUMENTATION OF VARIATION PATTERN

As indicated earlier, any experimental taxonomic study using a synthetic approach remains incomplete if the variation pattern so unravelled is not documented in the traditional taxonomic units using gross morphological characters so as to make it useful to the end users who, in the case of horticultural plants, are gardeners, horticulturists, agronomists, geneticists, etc. It may, however, be pointed out that these plants have not received the deserved attention from this aspect. In fact, taxonomic treatment of cultivated plants has never been attempted by persons who are trained in taxonomy, and even Darwin (1868) nearly 111 years ago has remarked that "Botanists generally neglected cultivated varieties, as beneath their notice". The situation has hardly improved since then. It is now realised that taxonomic treatment of cultivated plants can best be attempted only after genetic evolutionary history as also mechanisms underlying the change from wild to the domesticated condition are thoroughly understood. It is also to be realised that the spectrum of variation in horticultural plants is constantly changing

depending on man's interest, his needs, fancies and fads, resulting in continuous replacement and loss of cultivars that are no longer of interest to man. Due to the fact that evolution in cultivated plants is more or less directed by man, there is greater speed of evolution, resulting in morphological evolution being far ahead of the commensurate genetic discontinuity. Obviously, there are situations when a cultigen may morphologically transgress specific or even generic limits, but genetically the level of differentiation, may not be more than that of a biotype. Therefore, for utilitarian purposes the taxonomic treatment in cultivated plants is to be based primarily on genetic and secondarily on morphological considerations, although reverse may be true of taxonomy of wild plants particularly in the case of floras of tropics-subtropics which are not well worked out. Even in the cultivated plants, while main outlines of taxonomy of the temperate components are reasonably well-known, the tropical cultivated plants are still unknown from this aspect (Khoshoo, 1980).

From time to time, several systems have been suggested. However, the basic taxonomic unit for cultivated plants is the *cultivar* which is not to be confused with a botanical variety. The different systems of classification of cultivated plants have been recently reviewed by Parker (1978) and starting with the basic unit as *cultivar*, he suggests the following levels: *provar* (identical with a race) which is a group of related cultivars with enough characteristics in common to permit their recognition as a group; *convar*, a group of related provars; *multivar*, a group of related convars; *subspeciod*, the equivalent of subspecies in the case of wild plants; and finally a species.

Each cultivar needs to be registered and typified with an authentic specimen, description and photograph/painting, year and place of origin and introduction, exact ancestry, etc.

CONCLUDING REMARKS

In comparison to wild plants, the cultivated plants in general have a relatively short history of evolution. This is particularly true for the horticultural plants which, more often, have been domesticated in historical time. Among the latter, in

the decorative plants the evolutionary history is still shorter and sequence of events leading to the transformation from wild to the cultivated condition is often documented and intervening stages still preserved. Like all cultivated plants and domesticated animals, the horticultural plants also have, in the ultimate analysis, arisen from the wild parents. During domestication, their genetic systems have been modified and such a process starts as soon as a wild species is brought, from its particular native habitat, under cultivation in the garden (Khoshoo, 1979). Sometimes such a change in habitat may be rather drastic, e.g. from tropical to temperate conditions as has happened in the case of cannas (Khoshoo & Mukherjee, 1970). By and large the selection is both conscious (for characters of interests to man), and unconscious or accidental. Among the latter is the modification of the genetic system with its characteristic future consequences in the case of obligate outbreeders and inbreeders as also apomicts. The other parameters are population size, nature and extent of isolation, with reference to the role of hybridization and disruptive selection.

Decrease in the size of the breeding group accompanies all change, which by itself has considerable genetic implications, in as much as due to increased inbreeding, chances of expression of latent variation (often recessive) increase considerably under garden conditions. The chances of hybridization (natural or by man) between taxa ordinarily isolated in nature, but brought together by man under cultivation increase. Both these increase chances of release of variability, either latent or recombinational. Often breeding system undergoes considerable changes as a result of hybridization. In *Ruellia*, hybridization has resulted in change from facultative cross pollinated chasmogamous flowers in parents to obligate self pollination and cleistogamy in hybrids (Khoshoo *et al.*, 1969). The chances of selection of newer variation increase under domestication on account of the fact that unusually large progenies are raised and novel individuals of interest to man are selected which may not otherwise have any selective value in nature. Another important aspect is that under domestication evolution is very fast because of the directive influence of man. There thus results

considerable change in both morphology and genetic constitution of the cultigens in comparison to the wild taxa, with their attendant taxonomic implications.

In the cultivated plants, therefore, there is a situation that they exist in very large communities over extensive areas under conditions favourable to them. Their spectrum of variation changes depending upon the interest, need, fancies and fads of man. Accordingly, there is a continuous replacement and loss of cultivars leading to disappearance of land races and cultigens. Thus the importance of experimental taxonomy with reference to cultivated plants cannot be under estimated. Although the chief purpose is to document variation on phylogenetic basis, the advantages are that such work helps in an understanding of:

1. Genetic evolutionary race-histories of the taxa concerned enabling knowledge regarding genetic mechanisms underlying evolution as also particular patterns and pathways of evolution under natural and/or domesticated states.

2. The nature of genetic system which controls heredity and variation. Obviously, information on the breeding system (extent and nature of pollination and compatibility system and mode of reproduction, sexual/apomictic/vegetative) and the meiotic system. The information is of vital importance and helps in chalking out a breeding methodology suiting the particular traits of the genetic system.

3. Circumscription of the gene pools which helps in building up knowledge regarding the limits of the gene pools on one side and the nature and extent to which the genes can be exchanged on the other. Such knowledge helps in breeding programmes.

4. Location of centres of diversity where ancestral species and/or primitive cultivars and land races are still available. It is well known that in such centres important genes for adaptation to stress condition, disease resistance, etc. are usually available.

5. Documentation of variation would help in identification of elemental and other related species, primitive cultivars/land races as also registration of cultivars for ensuring plant breeders' rights under 'International Convention for the Protection of new varieties of Plants'. This is important

because there is a general tendency among nursery men to name the same cultivar under different names for boosting their sales. Retrieval of such information for purposes of what exactly constitutes a particular gene pool for utilization of plant breeders as also for purposes of conservation, is very important so that morphological, physiological, geographical, chemical, genetical and other attributes of the members of the gene pool as also total spectrum of ensuing cultivars are readily available for purposes of plant breeding. In turn, such information is most vital for designing new cultivars to fulfil new needs or demands. The genes conferring the particular attributes which need to be incorporated in the new cultivars have to be located in the gene pool covering also centres of diversity and/or origin.

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