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Cytogenetics of Garden Gladiolus. IV. Origin and Evolution of Ornamental Taxa

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Hybridization and polyploidy have played a major role in the origin of garden gladiolus because of lack of crossability barriers and reasonably high hybrid fertility among eight elemental species (both diploid and polyploid). Repeated cycles of hybridization involving recombination between multiple sets of genomes and tetrasomic inheritance have led to intense genic interaction resulting in the breakage of size barriers and other floral and vegetative characters hitherto unknown in the elemental species. The major change appeared in the shape of flower which was zygomorphic in the elemental species but became nearly actinomorphic in large-flowered types with simultaneous thickening of floral parts. Concomitantly great variation in colour was possible due to recombination between colour genes proper (often of multigenic type) and their intensifiers, inhibitors, etc. Novel recombinants thus emanating have been easily fixed through vegetative propagation.

On the basis of growth period, garden gladioli can be divided into two groups viz., early-flowering and summer-flowering types. The early-flowering gladioli have been primarily raised from diploid (2n = 30) winter-flowering species. The first important hybrid *G.* × *colvillei* Sweet was raised in 1823 from the cross *G. tristis* var. *concolor* × *G. cardinalis*. Another hybrid *G.* × *insignis* was the result of a cross between *G. carneus* and *G. cardinalis*. The third important hybrid *G.* × *ramosus* Paxt. was raised in early 1930's from a cross between *G. carneus* and *G. oppositiflorus*. These three constituted a group of hybrids which were extensively cultivated during mid-nineteenth century and were generally referred to as *G.* × *nanus*. These comprised of diploids (2n=30), triploids (2n=45) as well as tetraploids (2n=60).

The most crucial event in gladiolus culture, however, took place in 1837 when the first summer-flowering gladiolus *G.* × *gandavensis* was synthesized by crossing *G. natalensis* and *G, oppositiflorus*. This hybrid combined in one step, the gene pools of a hexaploid and diploid species at tetraploid level which later turned out to be the optimum level of ploidy among garden cultivars. *G.* × *gandavensis* was crossed with *G. papilio* to produce *G.* × *lemoinei* which in turn was crossed with *G. saundersii* to give rise to *G.* × *nanceianus*.

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G. × *nanceianus* was further crossed with *G.* × *gandavensis* to produce *G.* × *kelwayi*. *G.* × *gandavensis* was again crossed with *G. saundersii* resulting in *G.* × *leichtlinii* in 1877, which was later known as *G.* × *childsii*. The last species to be introduced was *G. primulinus* in 1890 and it was crossed with all the existing races to form 'Primulinus hybrids in 1915. In the later period, further improvement by intercrossing all the races of Summer-flowering gladioli was carried out to such an extent that it is now impossible to distinguish one from the other so they are collectively known as *G.* × *hybridus* Hort.

It is, therefore, evident that the speed of evolution during first 90 years (1823-1910 AD) when elemental species from South Africa were introduced and hybridized to produce various hybrid groups, was rather rapid and was governed by following principles of selection: increase in hardiness, increase in spike length; form and colour of leaves, time of blooming, constitution of spike; flower form and shape; colour diversity; scent; vegetative multiplication; disease resistance, etc.

Key Words: Garden gladiolus, Origin and evolution, Principles of selection, Cytogenetic mechanism

Introduction

While the foregoing papers of this series deal with breeding system, patterns of chromosomal evolution and hybridization (Ohri & Khoshoo 1981 a, b, 1983), the present paper summarizes the mode of origin and evolution of the garden taxa. Like most ornamental plants (Crane & Lawrence 1952, Horn 1968, Mukherjee & Khoshoo 1969, Darlington 1973, Khoshoo & Pal 1973, Khoshoo & Guha 1975, Zadoo et al. 1976, Narain & Khoshoo 1977, Khoshoo 1979), garden gladioli also have a short history of domestication. Although some Eurasian species were cultivated in European gardens previously, the real impetus to gladiolus culture was provided after the introduction of South African species in the early 19th century. Based on the available literature and also the present work, it has been possible to produce a coherent picture of the various steps involved in the transformation of wild *Gladiolus* to a cultivated one. Such a study has not only revealed the nature and extent of genetic-evolutionary processes accompanying domestication, but also help to chalk out steps for further improvement.

Ancestors

Out of a total of about 180 species of *Gladiolus* in the world, only 8 are believed to have been involved in the origin of the garden gladioli. In this connection it is important to note that not even one of the Eurasian species has been used in developing modern gladioli. All the elemental species (figure 1, Ohri & Khoshoo 1981b) are native of South Africa, although *G. natalensis* (Eckl.) Reinw. ex Hook. f. (*G. psittacinus* Hook.f.) and *G. primulinus* Baker extend to tropical East Africa. Of these elemental species, *G. tristis* L. and *G. carneus* Delaroche (*G. blandus* Ait.) are winter-flowering and others are summer-flowering in their natural habitat.

Evidently, these were introduced into Europe, starting with *G. tristis* [Curtis's bot. Mag. t. 1098 (1808)] in 1739, which was brought to flowering by Philip Miller in 1745 (Beal 1916). This was followed by *G. carneus* Delaroche (*G. blandus* Ait.) [Curtis's bot. Mag. t. 625 (1803)] which was sent to Kew from South Africa in 1774 by Francis Masson (Beal 1916, Greaves 1930). In 1789, *G. cardinalis* Curt. [Curtis's bot. Mag. t. 135 (1790)] reached Europe and *G. oppositiflorus* Herb. [Curtis's bot. Mag. t. 7292 (1893)] was first collected by John Forbes in 1822 (Bernard 1972). It was named by Herbert in 1837. *G. natalensis* (Eckl.) Reinw. ex Hook.f. (*G. psittacinus* Hook.f. Curtis's bot. Mag. t. 3084 (1831) was imported into Europe in 1827 (Bernard 1972) from Port Natal. *G. papilio* Hook.f. [*G. purpureo-auratus* Hook.f. (Curtis's bot. Mag. t. 5565 (1866)] was introduced in 1870 by William Bull. *G. saundersii* Hook.f. [Curtis's bot. Mag. t. 5873 (1870)] also came in the same year. Last species to reach Europe was *G.primulinus* Baker [Curtis's bot. Mag. t. 8080 (1906)] which according to Ingram (1931) is actually a closely related species *G. nebulicola* Ingram, having been discovered by JT Last in 1887 and it first flowered in Kew in 1890 (Beal 1916, Greaves 1930).

Hybrids

Out of about 15 Eurasian species, *G.segetum* Ker.-Gawl, *G. communis* and latter *G. byzantinus* were cultivated in Europe for several centuries (Beal 1916, Jeffers 1932). However, these species lost their importance soon after the advent of African species, although their potential as source of frost resistance is now being increasingly realized and *G. byzantinus* is becoming popular again (Hamilton A P 1976).

The earliest attempt to hybridize African species was made by Dean Herbert in the early 19th century (Herbert 1822a,b) and he used *G. carneus* (*G. blandus*), *G. cardinalis*, *G. tristis*, *G. angustus*, *G. caryophyllaceous*, *G. carinatus*, *G. liliaceus*, etc., all from Cape region, now known to be diploid (2n = 30). The ease with which he could cross and backcross these species shows that these species are interfertile (Herbert 1847). It is reported that none of these hybrids survived and could be utilized later on (Jeffers 1932, Tamberg 1972). However, his work induced many nurserymen all over Europe to start hybridizing African species resulting in the origin of the present-day garden gladioli, which may be divided into two groups based on their time of flowering. These are: Early-flowering and Summer-flowering types; and origin and evolution is discussed separately and illustrated in figure 1.

Early-flowering gladioli These gladioli have been primarily raised from winter-flowering Cape species. The first important hybrid, *G.* × *colvillei* Sweet, was raised in 1823 at Colville's nursery Chelsea, by crossing *G. tristis* var. *concolor* × *G. cardinalis* (Hottes 1915, Beal 1916, Greaves 1930, Jeffers 1932, Emsweller et al. 1937, Tamberg 1972, Hamilton A 1976). The flowers were fragrant, and bright scarlet with lanceolate blotches of white on the three lower perianth segments. A plate of this hybrid [t. 1993 in Flores des Serres ed. 2 (1873)] clearly shows its hybrids vigour and dominance of *G. cardinalis*. Later, it gave rise to *G.* × *colvillei albus*, a white sport with coloured anthers, which was subsequently supplemented by another white sport with white anthers, *G. colvillei* 'The Bride' (Beal 1916, Jeffers 1932). These forms are still popular today and are known to be diploid (2n=30) (Ohri & Khoshoo 1981b).

Another development occurred at the sale of Colville's nursery in 1835; Messers Lucombe and Prince purchased a stock of a hybrid of *G. carneus* (*G. blandus*) and *G. cardinalis*, named it as *G.* × *insignis* (Jeffers 1932, Bernard 1972). It was far more richly coloured than Colvillei types; the flowers were rich reddish crimson, with a dash of bluish purple, in the centre of lower perianth segments. It is illustrated in Paxton's Mag. Bot. (VII, 223, 1840).

The third important hybrid of this group *G.* × *ramosus* Paxt. was raised in early 1830's by Schneevogt at Haarlem and was cultivated in England in 1835 (Beal 1916, Jeffers 1932). Its ancestry is little doubtful but its cultural requirements show that it was a hybrid between a summer and a winter-flowering species, and is thought to have originated from *G. carneus* (*G. blandus*) × *G. oppositiflorus* cross (Hottes 1915, Beal 1916, Bernard 1972). This hybrid was illustrated in Paxton's Mag. Bot. (6,99,100, 1839). The plant was tall with broad leaves, the flower was openly funnel-shaped, bright red with deep blotches at the base of three lower perianth segments. This hybrid was certainly an important step in gladiolus culture and the fact that it bloomed later than the existing varieties (because of *G. oppositiflorus* being one of the parents) accounted for its popularity in the next two decades. Among its forms were such noteworthy kinds as 'Formossissimus', 'Neplus Ultra' 'Queen Victoria', 'Rosamundi', and Floribundus' (Greeves 1930), *G.* × *ramosus* is known to be triploid (Ohri & Khoshoo 1981b).

These three group hybrids viz. *G.* × *colvillei*, *G.* × *insignis*, and *G.* × *ramosus* gave rise to yet another set of hybrids which were extensively cultivated during mid-ninteenth century and were generally referred to as *G.* × *nanus*. These types comprise of diploids (2n = 30), triploids (2n = 45) as well as tetraploids (2n = 60) (Ohri & Khoshoo 1981b). Although the importance of this group declined after the appearance of summer-flowering large-flowered group, they are still available in Europe and interest in them, as well as in Cape winter-flowering basal species, is being revived due to their specific horticultural attributes (Hamilton A 1976, Adamovic 1978).

In early-twentieth century, attempts were made to further improve the winter-flowering group. In 1893 Damman and Co. of Naples produced *G.* × *victorialis*, an hybrid of *G. byzantinus* × *G. cardinalis* (Beal 1916, Tamberg 1972). If the parentage is true, this can be taken as a first attempt of a cross between a Eurasian and an African species. The time of flowering was the same as that of other early-flowering types, the flowers were pink or dark red, and this hybrid was supposed to combine the beauty of African species with hardiness of Eurasian species. Five varieties were offered, i.e. 'Amathusia', 'Amphitrite', 'Andromeda', 'Penelope' and 'Eris', but they did not become popular (Beal 1916).

T M Hoog in Haarlem, developed *G.* × *haarlemensis*, a miniature from *G.* × *colvillei* in 1935. The varieties of this group, i.e., 'Ambition', 'Blue Gem', 'Delight', 'Magnet', etc., flower earlier than all the other varieties (Schauenberg 1965, Tamberg 1972).

In 1914, Van Tubergen of Haarlem crossed some varieties of *G.* × *nanus* with those of *G.* × *childsii* (summer-flowering) resulting in 'Herald Gladioli' (Greaves 1930, Jeffers 1931) which include triploid (2n=45) and tetraploid (2n = 60) forms (Ohri & Khoshoo 1981b). Later, in 1924, Van Tubergen crossed

'Heralds' with *G. tristis* var. *concolor*, and obtained *G.* × *tubergenii*. These forms, besides having open flowers as those of *G. tristis*, flowered earlier than 'Heralds' (Greaves 1930), and are known to be triploids (2n=45) (Ohri & Khoshoo 1981b). In recent years, Unwins of Cambridge have crossed *G.* × *nanus* with 'Primulinus' types to develop Peacock hybrids. Similarly, Konijenburg and Mark of Holland have evolved 'Caronodo' gladioli (small-flowered with conspicuous blotches or other throat markings) by crossing *G.* × *nanus* with butterfly types (Hamilton A 1976).

Summer-flowering gladioli: The most crucial event in gladiolus culture took place in 1837, when M Bedinghaus gardener to the Duc d'Armberg at Enghien crossed *G. natalensis* (*G. psittacinus*) with *G. oppositiflorus*. One of the seedlings was bought by Messers V Houtte of Ghent who introduced it as *G.* × *gandavensis*. Its parentage was later disputed by Hottes (1915) who thought it to be a cross between *G. natalensis* (*G. psittacinus*) and *G. cardinalis* or *G.* × *ramosus*. But the presence of distichous spike in earlier hybrids of *G.* × *gandavensis* (a character also exhibited by *G. oppositiflorus*) goes strongly in favour of *G. oppositiflorus* being one of the parents (Beal 1916). According to Lewis and Obermeyer (1972) it was *G. oppositiflorus* spp. *oppositiflorus* (having distichous spike) which was used. Had breeders used spp. *salmoneus* (having secund spike) lot of labour would have been saved in eliminating undesirable distichous flower arrangement. This hybrid proved to be a turning point in the evolution of garden gladiolus as is evident from the way Van Houtte described it (Beal 1916): "In stateliness and colour it exceeds all others we have seen among gladioli. Its dimensions surpass 'ramosus', its majestic flowers to the number of 18-20 are of the most charming vermilion, their inferior petal, adorned with chrome, amaranth, and brown, are relieved by anthers of an azure blue, which descends to the centre of the flower". Such was the impact of this hybrid that its further segregates and selections resulted in 2000 named varieties by 1880. Being hybrids between hexaploid *G. natalensis* (2n=90) and diploid *G. oppositiflorus* (2n=30), these are, as expected, tetraploid (2n=60) (Ohri & Khoshoo 1981b).

G. × *gandavensis* began to be increasingly used by many nurserymen in crosses with some other species introduced from South Africa. Victor Lemoine of Nancy procured some of the best varieties of *G.* × *gandavensis* and used them as male parent in crosses with *G. papilio* (*G. purpureo-auratus*). The result was another race called *G.* × *lemoinei*, developed in 1880 from two original seedlings obtained by V Lemoine in 1875 (Beal 1916, Tamberg 1972, Bernard 1972). This race was characterised by bell-shaped flowers with rich colours and the presence of velvet dark blotches on the flower perianth segments. In due course, many new varieties were obtained by further segregation and selection: noteworthy among them were those with blue and violet tendencies, the best being 'Baron Josef Hulet' which was raised by Lemoine in 1896 (Jeffers 1932). The earlier blue and violet forms are the progenitors of modern varieties of these shades (Greaves 1930). *G.* × *lemoinei* hybrids are known to be tetraploid (2n = 60) (Ohri & Khoshoo 1981b). However, *G. papilio* is known to be pentaploid (2n=75) (Ohri & Khoshoo 1981b), and if this cytotype

was used, the earlier crosses must have given rise to aneuploids which, as shown by the present study, must have 'stabilized' to tetraploid level (2n=60) on further crossing with existing tetraploid hybrids (Ohri & Khoshoo 1983).

In 1883, V Lemoine crossed *G.* × *lemoinei* varieties with *G. saundersii*, using the latter as female parent. But of the four resulting seedlings, he selected two, viz., 'Present Carnot' and 'Mauricede Vilmorin', from which originated a new race *G.* × *nanceianus* (Beal 1916, Greaves 1930, Jeffers 1932, Bernard 1972, Hamilton A 1976). The plants were upright and vigorous, but the most remarkable feature of this race was the wide open and richly coloured flowers. *G. saundersii* is triploid (2n=45) (Bamford 1935) and as triploid is known to contribute diploid gemetes in crosses (Jones & Bamford 1942), resulting in a tetraploid (2n=60) *G.* × *nanceianus* race (Ohri & Khoshoo 1981b).

In 1885, James Kelway produced *G.* × *kelwayi* by inter-crossing *G.* × *nanceianus* and *G.* × *gandavensis*. *G.* × *kelwayi* hybrids had strong growth and shorter spike, they achieved widespread popularity, one of the most outstanding varieties was 'Golden Measure' (Jeffers 1932). These hybrids also were presumably tetraploid (2n = 60) being a cross between two tetraploid parents.

G. × *gandavensis* was used again when Max Leichtlin crossed its varieties with *G. saundersii* using the latter as female parent (Greaves 1930, Jeffers 1932), the hybrids first flowered in 1877 and were named as *G.* × *leichtlinii*. These hybrids were also presumably tetraploid (2n = 60) resulting from diploid gametes contributed by *G. saundersii* (2n = 45). Later, *G.* × *leichtlinii* hybrids went into the hands of John Lewis Childs of New York, who developed and named them as *G.* × *childsii* (Beal 1916, Jeffers 1932, Emsweller et al. 1937, Bernard 1972). This race was tall erect and more robust than *G.* × *nanceianus*, the flowers were large and well open as those of *G.* × *gandavensis* but without blotches. Further breeding and selection resulted in more delicate colours. *G.* × *childsii* proved to be well adapted to North American drier and cold climate, therefore, it was used by many breeders, and has given rise to many of the modern American gladioli (Beal 1916, Jeffers 1932).

As has already been mentioned, the last elemental species to be introduced was *G. primulinus*. It was used by breeders all over Europe and United States, and was crossed with all the existing races of summer-flowering group. In 1908 Cayeux et Le Clerc used *G. primulinus*, both as male and female parent, in crosses with different varieties of *G.* × *lemoinei*, *G.* × *nanceianus* and *G.* × *grandavensis* (Beal 1916). In the same year V. Lemoine et Fils produced hybrids involving *G. primulinus* (Lemoine et Fils 1923, Beal 1916). Some years later Messers. Vilmorin Andreieux and Co. crossed this species with some varieties of *G.* × *gandavensis* and *G.* × *nanceianus* (Mottet 1916). In 1910, Kelway crossed *G. primulinus* with *G.* × *kelwayi* and *G.* × *gandavensis*. He named these hybrids as 'Langprim gladioli' (Beal 1916). In United States A.E. Kunderd took to hybridizing *G. primulinus* and introduced his first named hybrid in 1915 (Jeffers 1932). The result of all these crosses and intercrosses was the evolution of a new race, popularly known as 'Primulinus Hybrids'. The diversity in these hybrids is to be expected due to their multiple parentage. Two

groups are recognised amongst them. One group resembles *G. primulinus* in most of the characters while the other is intermediate between it and the large flowered types and this is known as *G. primulinus grandiflorus*. The two groups, however, do not have any sharp distinction and merge into each other by intermediate forms. Some of the unique features of 'Primulinus Hybrids' are their slender form (as compared to *G.* × *gandavensis* and *G.* × *nanceianus* hybrids), which made them useful as cut flowers, hooded upper perianth segment, and soft pleasing colours (because of subduing of brilliant hues of previous forms by pure yellow of *G. primulinus*). In addition to this the florets are placed one above the other alternately instead of forming two rows as in *G.* × *gandavensis* types. The three lower perianth segments are much shorter than the three upper ones and are much reflexed. Besides, the 'Primulinus Hybrids' proved to be more disease resistant and more prolific in producing cormlets. These hybrids as expected are all tetraploid (2n = 60), as these resulted from crossing *G. primulinus* (2n = 60) with existing tetraploid races (Ohri & Khoshoo 1981b).

In later years, further improvement by intercrossing these races, *i.e.*, *G.* × *gandavensis*, *G.* × *lemoinei*, *G.* × *nanceianus*, *G.* × *childsii*, *G.* × *kelwayi* and 'Primulinus hybrids' has been carried out to such an extent, that it is now impossible to distinguish one from the other, and they are collectively known as 'Large-flowered Summer-flowering' Group (*G.* × *hybridus* Hort.). The cultivars of this group are all tetraploid (2n= 60) (Ohri & Khoshoo 1981b).

Other hybrids: Apart from above described principal hybrid groups, several other hybrids were also developed. Many of them, though did not produce any new race, they deserve brief mention.

A cross involving *G. psittacinus* and *G.* × *gandavensis* was named *G.* × *massiliensis* by Krelage in 1892. The hybrid had all the undesirable characters of *G. psittacinus* (Beal 1916).

G. × *princeps* was produced by Van Fleet in 1885 by crossing *G. cruentus* with a variety of *G.* × *childsii* (Beal 1916, Jeffers 1932).

G. × *turicensis* was raised by M. Froebal of Zurich in 1889, by crossing *G. saundersii* with *G.* × *gandavensis* (Beal 1916).

A group of hybrids known as *G.* × *praecox* was obtained by crossing the earliest varieties of *G.* × *gandavensis*, *G.* × *lemoinei*, *G.* × *childsii* and *G.* × *nanceianus* (Beal 1916).

In 1889, Jackson described hybrids between *G. dracocephalus* and *G.* × *gandavensis*. Lemoine also produced *G. dracocephalus* × *G.* × *lemoinei* hybrids in 1900.

Several effrots have been made to cross early and summer-flowering forms to get types which would have intermediate blooming period. Although, change in blooming period was apparent, such hybrids did not become popular perhaps, because of the smaller size of flowers. Moreover, these could not be improved further, as they were presumably triploid and consequently sterile to various degrees as has been noticed in the present study (Ohri & Khoshoo 1983).

G. × *colvillioides* was raised by Lemoine in 1905 by crossing some variety of *G.* × *lemoinei* with *G. angustus* (Beal 1916).

M Porcher-Dionnean crossed *G.* × *colvillei* with *G.* × *nanceianus*, and in 1916 introduced some selected strains which

flowered earlier while having larger flowers than *G.* × *colvillei* (Beal 1916.

Around 1926, Mrs H Prins produced *G.* × *prinsianus* by crossing *G.* × *colvillei* with *G. primulinus*, these hybrids bloomed slightly in advance of *G. primulinus* but did not become popular (Jeffers 1930).

Principles of Selection

The present-day garden gladiolus is the result of breeding and selection of approximately 150 years, which took place in Europe and North America, far away from South Africa, the original home of the elemental species. The major development of course took place during the first 90 years (1823-1910 AD) when elemental species from South Africa were introduced and hybridized to produce various hybrid groups, as described above. In the later period, the varieties of these hybrid groups were intensively intercrossed (this process is continuing even today) and the selections from these hybrid-segregates resulted in the modern gladioli. The selective processes underlying evolution under domestication can now be discussed.

Increase in hardiness: The elemental species are inhabitants of sub-tropical and tropical Africa. From such a stock there has been selection for cold resistance to make the cultivars adaptible to the temperate conditions of Europe. The cultivars of *G.* × *childsii* proved to be more adapted to the North American drier and cold climate and, hence, are the progenitors or many present-day American gladioli. Similarly, *G.* × *lemoinei* was hardy even in New York city.

Increase in spike length: The *G.* × *nanus* group did not show much improvement over the elemental species in this respect. Spectacular increase in spike length and number of flowers/spike was achieved in *G.* × *gandavensis* and still larger size in subsequent hybrids such as *G.* × *nanceianus*.

Form and colour of leaves: *Gladiolus* is essentially a cut flower, so the leaves have not been considered of much importance. The *G.* × *nanus* group had narrow and thin leaves on wiry stems. In summer-flowering types such as *G.* × *gandavensis* which were also grown in borders, an equitant arrangement of thick leaves which just touched each other to completely hide the stem was preferred.

Time of blooming: Before 1837, only early-flowering cultivars (*G.* × *nanus*) were evolved which were planted in fall and flowered in spring, so they were prone to frost. The change in blooming period was achieved when summer-flowering species were introduced and the first summer-flowering type i.e. *G.* × *gandavensis* was evolved. To bridge the gap in blooming period and also to extend the flowering season crosses were made between these two groups with desired results.

Constitution of spike: The *G.* × *nanus* group had dwarf stature and wiry slender stems with flowers loosely arranged on the spike. This undesirable character was removed in the first summer-flowering type i.e. *G.* × *gandavensis* which had tall erect, stiff and heavy spikes. The flowers were however, arranged distichously and this character was eliminated in the later selections and subsequent hybrids such as *G.* × *lemoinei*, *G.* × *nanceianus*, *G.* × *childsii*, etc. Many of the cultivars of these groups had heavy spikes with many flowers opening at a time which made them top heavy and unwieldy for indoor decoration. This character was later rectified by the introduction of *G.*

primulinus which resulted in lax and graceful spikes with ten to twenty flowers arranged alternately having spaces in between them. This enhanced the value of gladiolus as a cut flower. For the same purpose there has been a resurgence of interest in miniature forms among summer-flowering group as also in the dainty *G.* × *nanus* group, in the recent years.

Flower form and shape: The *G.* × *nanus* group did not show much improvement over elemental species in this regard. The increase in thickness of floral parts and bigger size of flower were achieved in the summer flowering group due to combined effect of heterosis and polyploidy which increased the value of gladiolus as a cut flower. Consequently, this also resulted in selection and preference for tetraploids, which turned out to be the optimum level of polyploidy among garden cultivars.

Due to luxuriance and hybrid vigour, flower shape underwent a major change *vis-a-vis* elemental species, in which three upper perianth segments are larger than the three lower ones which have blotches or markings on them. The zygomorphic form among *Gladiolus* species is considered to be derived from more simple regular actinomorphic form. But, due to luxuriance and hybrid vigour, the large-flowered groups such as *G.* × *gandavensis*, *G.* × *lemoinei*, *G.* × *nanceianus*, etc. showed a tendency to become nearly actinomorphic with perianth segments becoming almost of equal size and spreading laterally. This character is present in most of the cultivars of 'Grandiflorus' class even today. This trend was, however, offset by the introduction of *G. primulinus* which resulted in the evolution of highly zygomorphic 'Primulinus' types with hooded upper perianth segment of inner whorl. Later selections and segregants among these groups have resulted in some forms such as ruffled, Butterfly, Face-up, Laciniated, Dragon, etc., hitherto unknown in elemental species.

Colour diversity: Present-day gladioli possess practically all the colours except pure black and all the intermediate combinations with different blotches, streaks, etc. This has been brought about by the expression of cryptic variation among elemental species due to recombination between colour genes proper (often of multigenic type) and their intensifiers inhibitors, etc. The first instance of intensification of colour appears to be the expression of blue colour in *G.* × *lemoinei* cultivars derived from greenish yellow of *G. purpureo-auratus*. The colour in large flowered forms e.g. *G.* × *gandavensis*, *G.* × *lemoinei*, *G.* × *nanceianus* etc. was very intense. The introduction of pure-yellow *G. primulinus* set in the trend for lesser colour tones as 'Primulinus' hybrids have pastel shades.

Scent: This is rather a recent line of development. Besides, selecting for scent within the available gladiolus cultivars like 'Acacia', 'Perfume', 'Angel's Breath', 'Fragrant Beauty', 'Yellow Rose', etc. (Adamovic 1974, Buell 1976), variously scented South African species and *Acidanthera* have been crossed with garden cultivars (Wright 1971, Buell 1976, Ohri & Khoshoo 1983) with promising results. In crosses involving *Acidanthera bicolor* with 'La Paloma' nearly 25% of the progeny inherited slight to moderates cent (Ohri & Khoshoo 1983). However, a desirable scented gladiolus is still to be produced.

Prolific vegetative multiplication: Most of the cultivars reproduce well by means

of cormlets under suitable conditions as this character has been selected over the years. 'Primulinus' hybrids, however, are the most prolific in vegetative propagation (a character derived from *G. primulinus*) which may have accounted for their immediate popularity.

Disease resistance: This character has not been taken care of in persuit of novelty. Present day garden cultivars are susceptible to large number of diseases like Botrytis blight, Curvularia blight, Bacterial leaf spot, Stromatinia dry rot, Botrytis neck rot, Bacterial corm rot, Fusarium corm rot, etc. (Magie & Poe 1972). However, now there is much awareness to select diseases resistant cultivars and also to introduce this character from some species (Mc Clellan & Pryor 1957, Palmer et al. 1965, Jenkins 1971, Jones & Jenkins 1975).

Future Aims of Breeding

Today, there are roughly 30,000 cultivars of garden gladiolus mainly belonging to summer-flowering group. As a result of breeding and selection of existing cultivars about 100–200 new cultivars are evolved every year and the same number is dropped. Such extent of great variation in gladioli has been derived from barely eight elemental species. Considering the number of species in *Gladiolus* (about 180), which are crossable at the same and at different ploidy levels (Bamford 1941, Ohri & Khoshoo 1983) and even with different genera (Ingram 1967, Wright 1971, Ohri & Khoshoo 1983) there is considerable scope for further improvement of gladiolus. For this purpose our insight into the genetic variability of the genus *Gladiolus*, the related genera and the already existing garden cultivars is essential.

As hybridization is possible irrespective of ploidy level and species designation (Bamford 1941, Jones & Bamford 1942, Ohri & Khoshoo 1983), the gene pools of various species at different ploidy levels can be merged and brought to tetraploid level, which is the optimum ploidy level.

Species growing in Cape winter-rainfall area are particularly suitable for the regions of the world with mild winters (Plessis 1974). Moreover, they possess many remarkable characters like scent, short stature and different flower shapes (Lewis & Obermeryer 1972), which can be transferred to tetraploid cultivars by inducing tetraploidy in diploid Cape species, as it has been shown that in crosses between a diploid and a tetraploid, the hybrid resembles more closely the tetraploid parent, because the latter is polyploid. This has been observed in crosses with *Acidanthera* ($2n = 30$) (Seidle 1973, Ohri & Khoshoo 1983).

It is worth mentioning here, that earlier improvement work was carried out by the European nurserymen who inadvertently selected only those ecotypes of the elemental species which were suitable for the European conditions. Now as gladiolus is cultivated almost throughout the world, the species and ecotypes suitable for different parts of the world can be selected. This is the principle followed by gladiolus breeders in Israel who have been able to produce cultivars with short day requirement by crossing the existing cultivars requiring long day with the short day species brought from South Africa (Anonymous 1978). Further impetus to work on such lines in different parts of the world is required.

Another important character which has to be taken care of in future is the disease resistance. Besides, selecting for disease resistant cultivars, many species showing more resistance to diseases than

the garden cultivars may be used (Jenkins 1971).

Gladiolus genotype can also be drastically altered by crossing it with its close allies like, *Acidanthera*, *Iris*, *Homoglossum*, *Watsonia*, *Freesia*, *Crocus*, *Belamcanda*, etc. Such crosses are, however, difficult but studies have shown (Ingram 1967, Wright 1971, Present work) that they may be accomplished.

In short, it may be stated that gladiolus breeding has tremendous future and by widening the germ plasm base disirable changes are possible in blooming period, constitution of spike, shape and colour of flowers, keeping quality and most importantly disease resistance.

Cytogenetic Mechanisms underlying Evolution

The main events which transformed *Gladiolus* from a wild to cultivated plant took nearly 90 years. It is possible to review the underlying genetic factors accompanying domestication which have generated amazing diversity in garden gladioli.

Breeding System

The genus *Gladiolus* is essentially an outbreeder, as revealed by positional barrier between stigma and anthers, protandry and self-incompatibility, described earlier. Self-incompatibility is present in diploi d species as well as in some tetraploid garden cultivars (Ohri & Khoshoo 1981a). The cultivars, despite, their 150 years of domestication have uniform breeding system, which resembles that of elemental species. The anthers are held below the stigma uniformly in all the cultivars (present study) and also in the South African species (Lewis & Obsermeyer 1972), therefore there is total failure of seed set after bagging in the former. The garden cultivars, however, have a low frequency of natural cross pollination which may be due to the absence of original insect vector

Outbreeding coupled with a highly developed mode of vegetative propagation has of course been an important factor in the evolution of polyploid series ranging from 2x to 12x in the genus. Since any new genotype arising through hybridization and/or polyploidy would be fixed by vegetative propagation provided it has some adaptive value (Stebbins 1950). The consequences of such a reproductive system (outcrossing along with vegetative propagation) are quite evident under garden conditions also and nurserymen have been able to fix tremendous variability among garden gladioli by vegetative propagation as cultivars, being highly heterozygous, do not breed true on selfing.

Bud Mutations

Spontaneous mutations, an important source of variation in vegetatively propagated plants have been observed from time to time in garden gladioli (Hottes 1916, Anonymous 1972, Durst 1975). These mutants have often been lighter in colour than the varieties from which they mutated. The first report of such a mutation is *G.* × *covillei albus* and 'The Bride' both of which are white coloured and mutated from bright scarlet *G.* X *covillei*. One of the most commonly grown varieties 'Picardy' has produced several white mutants (Anonymous 1972). Many such sports must have been ignored due to the difficulty in recognizing them. To be propagated, they must occur in corms or cormlets, in which case they may be due to the expression of recessive mutants as has occurred in case of

recessive mutation for extended blooming period and pelargonidin in roses (Wylie 1955, Darlington 1973). *G.* × *colvillei albus* and 'The Bride' might have arisen similarly (Hottes 1916).

It is worth mentioning that the highly heterozygous nature of garden gladioli per se may be conducive to bud mutations, as hybrid genotypes are more responsive to induced mutations (Sparrow et al. 1965, Mukherjee & Khoshoo 1970). This is corroborated by the fact that mutations can be easily induced by radiation in garden gladioli (Buiatti & Tesi 1968, Buiatti et al. 1965, 1967, Dryagina 1964, Dryagina & Kazarinov 1966, Dryagina et al. 1967, Grabowska & Mynett 1970, Grabowska 1972, Moes 1966, 1969, Sheehan & Sagawa 1959).

Hybridization and Polyploidy

Now, it is evident that hybridization and polyploidy have been greatly responsible for the evolution of *Gladiolus* species as such. Natural hybridization among the species is quite frequent in the areas where they meet, in nature only geographical and ecological separation and difference in the time of blooming serve as barriers to prevent free gene exchange. (Lewis & Obermeyer 1972, Hamilton A 1976). However, under cultivation, these barriers were eliminated, except to some extent the time of blooming. Besides, possibility of hybridization irrespective of ploidy level and species designation (Bamford 1941, Jones & Bamford 1942, Ohri & Khoshoo 1983), self-incompatibility further increased possibilities of production of hybrids under garden conditions.

Before 1840, only diploid South African species were used as is evident from the experiments of Herbert (1822a, b). This resulted in the formation of winter-growing gladioli which possessed triploid and tetraploid types in addition to diploid types (Ohri & Khoshoo 1981b). This must have resulted from the formation of unreduced gametes as has occurred in *Primula malacoides* (Skiebe 1958), sugar beet (Ellerton & Hendriksen 1959), *Festulolium* (Dijkstra & De Vos 1975), potatoes (Mok & Peloquin 1975) and tulips (Karoon & Van Eijk 1977). In gladioli this process might have been aided by the presence of self-incompatibility barrier. In *Tulipa*, *Pyrus*, *Hyacinthus*, *Lolium* and *Tradescantia* unreduced gametes are selected in self-fertilization in preference to reduced ones (Lewis 1943).

But, the real breakthrough in gladiolus culture was achieved after the introduction of summer-flowering species ranging in ploidy from 2x to 6x. The first cross between hexaploid *G. natalensis* (2n=90) and diploid *G. oppositiflorus* (2n = 30) combined the gene pools of these species at tetraploid level. (*G.* × *gandavensis* 2n = 60) (figure 1), which incidently turned out to be the optimum level of ploidy, as all the modern garden gladioli are tetraploid. This was followed by repeated cycles of hybridization involving other diploid and polyploid species over a period of about 50 years (figure 1) followed by further selection and indiscriminate selfing and crossing under garden conditions. All these processes have resulted in the release of tremendous genetic variability due to recombination between multiple sets of genomes and tetrasomic inheritance (Stebbins 1971, Jackson 1976) super imposed on a multigenic type of inheritance (as is clear from the experiments of Tamberg 1976). As polysomy coupled with allogamy provides intense genic interaction possible in polyploidy, the whole range of alleles depending upon the number of

ORIGIN OF GARDEN GLADIOLUS

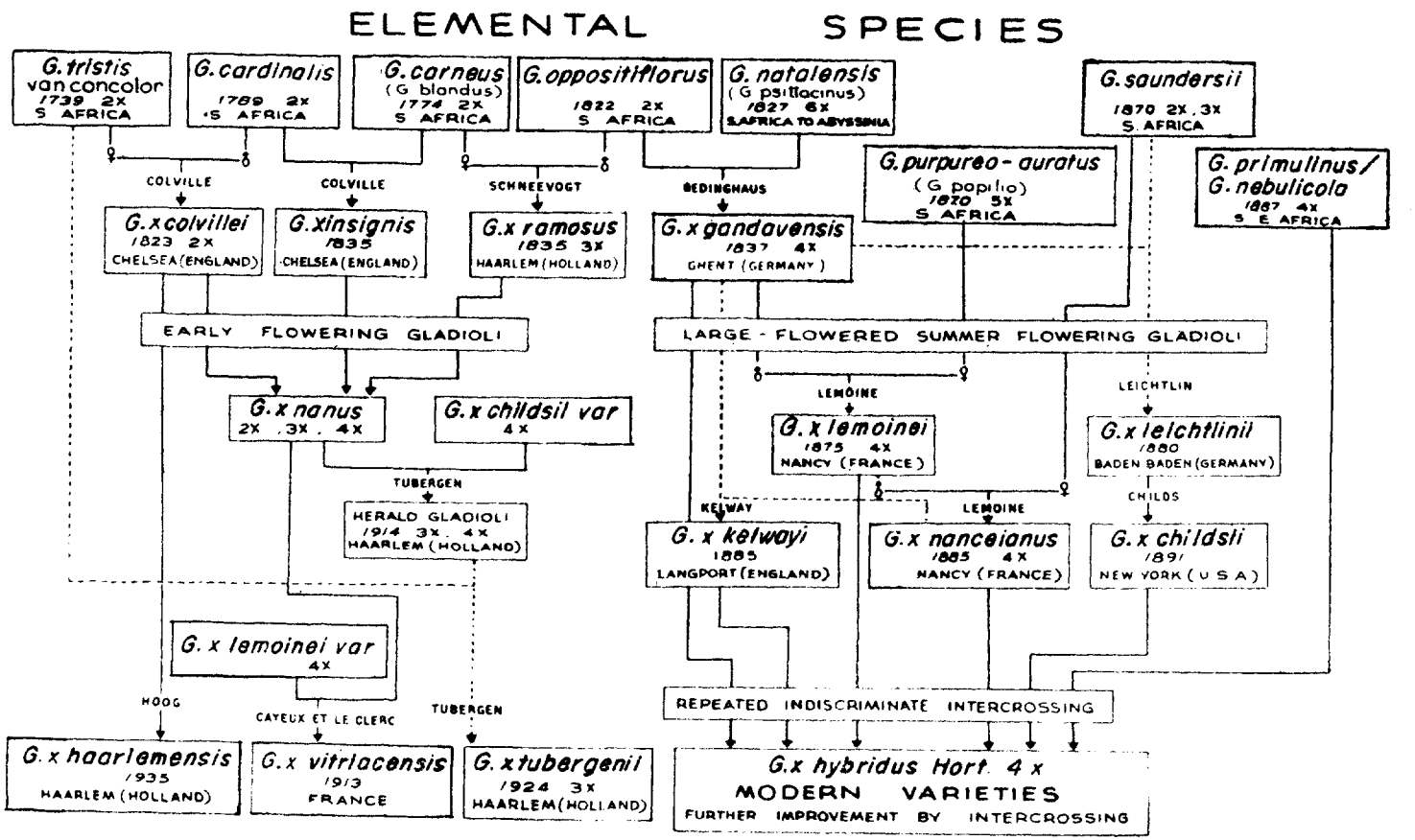

FIGURE : 1

homoeologous loci can be utilized in creating a range of heterotic combinations (Mac Key 1970, 1974). This is borne out by the fact that present day tetraploid garden gladioli show different types of heterosis, with regard to size of flowers, colour, ruffling and various other flower and spike shapes. This is also reported in octoploid varieties of garden strawberry, resulting from random distribution of parental chromosomes into different varieties (Bauer 1974). Such heterotic recombinants, as showing luxuriance in plant parts, or any other novel character have been easily fixed in gladioli through vegetative propagation.

References

Adamovic A A 1978 Species hybrids of *Gladiolus*; North *Amer. Gladiolus Coun. Bull.* **134** 54–56

Adamovic I I 1974 First step on the way to fragrance; *North Amer. Gladiolus coun. Bull.* **117** 71–73

Anonymous 1972 in *Gladiolus Breeding Splash*; 45-47

——, 1978 New developments in Israel; *North Amer. Gladiolus Coun. Bull.* **134** 145

Bamford R 1935 The chromosome number in *Gladiolus*; *J. agric. Res.* **51** 945–950

——, 1941 Chromosome number and hybridization in *Gladiolus*; *J. Hered.* **32** 419–422

Bauer R 1974 New patterns of heterosis in *Fragaria* hybrids in heterosis in plant breeding; *Proc. 7th Cong. Eucarpia* eds A Janossy and F G J Luptoh (Amsterdam, Oxford, New York: Elsevier Scientific Publishing Company)

Beal A C 1916 Gladiolus studies. I. Botany, history and evolution of the *Gladiolus*: *New York State Coll. Agric. (Cornell) Ext. Bull.* **9** 93–188.

Bernard T T 1972 On hybrids and hybridization; in A revision of the South African Species of *Gladiolus* by G J Lewis and A A Obermeyer *Jl. S. Afr. Bot. Suppl.* **Vol. 10** (Purnell, Cape Town, Johannesburg, London, New York)

Buell C 1976 Fragrance headachs and accomplishments; *North Amer. Gladiolus Coun. Bull.* **127** 52-53

Buiatti M and Tesi R 1968 *Gladiolus* improvement through radiation-induced somatic mutations; Publ. No 1 Laboratorio di Mutagenesis e differenziaments del C.N.R. Pisa 1–6

——, Ragazzini R and Tognoni F 1965 Effects of gamma irradiation on *Gladiolus*; *Radiat. Bot.* **5** 97–98

——, Molino M and Tesi R 1967 Prove di miglioraments genetico mediante radiazioni ionizzanti in una pianta da fisre a propogazione vegetative (gladiolo); *Riv. Ortoflorofruttia Ital.* **51** 616–627

Crane M B and Lawrence W J C 1952 in *Genetics of Garden Plants* (London: MacMillan and Co. Ltd.)

Darlington C D 1973 in *Chromosoma Botany and the Origins of Cultivated Plants* 3rd edn (London: G Allen and Unwin Ltd.)

Dijkstra J and DeVos A L F 1975 Meiotic doubling of chromosome number in *Festulolium*; *Euphytica* **24** 743–749

Dryagina I V 1964 On the effects of ionizing radiation on *Gladiolus*; *Nucl. Sci. Abstr.* **19** No. 38430

——, and Kazarinow G E 1966 Effects of ionizing radiation on gladiolus tubers and seeds; *Nucl. Sci. Abstr.* **20** No 35290

——, —— and Kalinichenko I M 1967 Mutations in fruit and ornamental plants induced by the action of neutrons and γ-rays Co 60; in *Symp. Mutation and Induction Factors*, G Mendel Memorial Symp., Prague 1965, pp 131–135

Durst J 1975 Glads in Hungary and my work with them; *North Amer. Gladiolus Coun. Bull.* **121** 66–68

Ellerton S and Hendriksen A J Th 1959 Note on the probable cause of the occurrence of tetraploid plants in commercial triploid varieties of sugarbeet; *Euphytica* **8** 99–103

Emsewller SL, Brierley P, Lumsden DV and Mulford F L 1937 *Improvement of Flowers by Breeding*; (Year Book: US Deptt. Agric.) 890–998

Goldblatt P 1971 Cytological and morphological studies in the southern African Iridaceae; *J. S. Afr. Bot.* **37** 317–460

Grabowska B 1972 Attempts to induce mutations in gladiolus (*Gladiolus hybr.* hort.) by 60 Co gamma rays; *Biul. Inst. Hodowli Aklim, Rosl.* **5-6** 267–268 (in Polish with English Summary

——and Mynett K 1970 Induction of changes in garden gladiolus (*Gladiolus hybr.* Hort.) under the influence of 60 Co; *Biul. Inst. Hodowle Aklim. Rosl.* **1-2** 85-88 (in Polish with English summary)

Greaves H 1930 The evolution of modern gladioli; *Gdnrs' Chron.* April 5 **272**, April 12, **290**

Hamilton A 1976 A history of garden gladiolus; *The Garden* **101** 424-428

Hamilton A P 1976 The European gladioli; *North Amer. Gladiolus Coun. Bull.* **125** 73-77, 85

Herbert W 1822a On the production of hybrid vegetables, etc; *Trans. Hort. Soc. Lond.* **4** 15-50

——1822b On the culture of African gladioli and other Cape bulbs in the open borders; *Trans. Hort. Soc. Lond.* **4** 153–155

——1847 On hybridization amongst vegetables; *Jl. hort. Soc. Lond.* **2** 81–107

Horn W 1968 Genetische Ursachen der variation bei zierpflanzen; *Die Gartenbauwissens Chaft* **33** 317-333

Hottes A C 1915 Garden gladioli; *J. Hered.* **6** 499-504

——1916 Gladiolus studies. II. Culture and hybridization of the gladiolus; *New York State Coll. Agric. Cornell Ext. Bull.* **10** 191-271

Ingram C 1932 *Gladiolus nebulicola* Ingram; *Gdnrs' Chron* Jan. 31 87

——1967 A so called bigeneric hybrid; *J. Roy. Hort. Soc.* **92** 309-311

Jackson R C 1976 Evolution and systematic significance of polyploidy; *Ann. Rev. Ecol. Syst.* **7** 209-234

Jeffers R H 1930 The evolution of modern gladioli; *Gdnrs' Chron.* May 10 366–367

——Jeffers R H 1931 The herald race of gladioli; *Gdnrs' Chron.* July 25 72–73

——1932 Gladiolus hybrids; *Gdnrs' Chron* July 2 11-12; July 16, 45-46; July 23 64

Jenkins J M Jr. 1971 Breeding for disease resistance. *North*; *Amer. Gladiolus Coun. Bull.* **108** 88-89

Jones R E and Bamford R 1942 Chromosome number in the progeny of triploid *Gladiolus* with special reference to the contribution of the triploid; *Amer. J. Bot.* **29** 807–813

Jones R K and Jenkins J M Jr. 1975 Evaluation of resistance in *Gladiolus* sp. to *Fusarium oxysporum* sp. *gladioli*; *Phytopathology* **65** 481–484

Khoshoo T N 1979 Cytogenetics in relation to plant evolution and improvement; in *Progress in Plant Research* pp 2 1-74 eds T N Khoshoo and P K K Nair (New Delhi: Today & Tomorrow Printers)

——and Guha I 1975 Origin and evolution of cultivated cannas; *Glimpses Pl. Res.* **3** 1–81

——and Pal M 1973 Probable origin and relationships of garden cockscomb; *J. Linn. Soc. Bot.* **66** 127–141

Kroon G H and Van Eijk J P 1977 Polyploidy in tulips (*Tulipa* L.). The occurrence of diploid gametes; *Euphytica* **26** 63-66

Lemoine V and Fils1923 Earliest hybrids of *Gladiolus primulinus*; *Gdners Chron.* Jan. 6 10

Lewis D 1943 The incompatibility sieve for producing polyploids; *J. genet.* **45** 261-264

Lewis G J and Obasermeyer A A 1972 A revision of the South African species of *Gladiolus*; *Jl. S. Afr. Bot. Suppl.* Vol. **10** (*Purneli Cape Town, Johannesburg London New York*)

Mac Key J 1970 Significance of mating systems for chromosomes and gametes in polyploids; *Hereditas* **66** 165-176

——, 1974 Genetic and evolutionary principles of heterosis; in *Heterosis in Plant Breeding Proc. Seventh Cong. Eucarpia* eds A Janossy and F G H Lupton (Amsterdam, Oxford, New York: Elsevier Scientific Publishing Company)

Magie R O and Poe S L 1972 Disease and pest associates of bulb and plant; in *The World of Gladiolus.* (Edgewood Press, Edgewood, Maryland)

Mc Clellan W D and Pryor R L 1957 Susceptibility of gladiolus varieties to *Fusarium, Botrytis* and *Curvularia*; *Plant. Dis. Rep.* **41** 47–50

Moes A 1966 Mutations induites chez le glaieul (*Gladiolus*); *Bull. Rech. Agron. Gembloux* 1 976-95

——, 1969 *Mutation Breeding in Tetraploid Gladiolus* (*Gladiolus gandavensis* V.H.); in eds G C Chisa and G Haussman Fifth Eucarpia Cong. Milan 1968; *Genet. Agrar* **23** 176–179

Mok D W S and Peloquin S J 1975 Three mechanisms of 2n pollen formation in diploid potatoes; *Can. J. Genet. Cytol.* **17** 217–225

Mottet S 1916 The hybrids of *Gladiolus primulinus*; *Gdnrs Chron. April* **22** 219–220

Mukherjee I and Khoshoo T N 1969 Origin and evolution of gardenspansy; *Nucleus* **12** 78–186

——, ——, 1970 Genetic-evolutionary studies in cultivated Cannas. IV. Parallelism between natural and induced mutations; *Rad. Bot.* **10** 351-364

Narain P and Khoshoo T N 1977 Origin and evolution of garden amaryllis; *Indian J. Hort.* **34** 80-85

Ohri D and Khoshoo T N 1981a Cytogenetics of garden gladiolus. I. Pollination mechanism and breeding system; *Proc. Ind. natn. Sci. Acad.* B47 510-515

——, ——, 1981b Cytogenetics of garden gladiolus. II. Variation in chromosome complement and meiotic system; *Cytologia* (in press)

——, ——, 1983 Cytogeneties of garden gladiolus. III. Hybridization; *Z. Pflanzenzuchtg.* 90

Palmer J G, Pryor RL and Steward R N 1965 Resistance of gladious to Fusarium yellows; *Proc. Am. Soc. Hortic. Sci.* 86 656-661

Plessis N M Du 1974 The Cape gladioli; *North Amer. Gladiolus Coun Bull. No.* **118** 75–77

Schauenberg P 1965 in *The Bulb Book* (London, New York: Frederick Warne and Co. Ltd)

Seidle W J 1973 Hybridizing with *Gladanthera* Lucky Star; *North Amer. Gladiolus Coun. Bill. No.* **114** 75–77

Sheehan T J and Sagawa Y 1959 The effects of gamma radiation on *Chrysanthemum* and *Gladiolus*: *Proc. Fl. State Hortc. Soc.* **72** 388–391

Skiebe K 1958 Die Bedeutung von unreduzierten Gameten fur die Polyploidie-Zuchtung beider Fliederprimel (*Primula malacoides* Franchet); *Zuchter* **28** 353–359

Sparrow A H, Sparrow R C, Thompson K H and Schairer L A 1965 The use of nuclear and chromosomal variables in determining and predicting radiosensitivities; *Suppl. Rad. Bot.* **5** 101-132

Stebbins G L 1950 in *Variation and Evolution in Plants* (New York: Columbia University Press)

——1971 in *Chromosome Evolution in Higher Plants* (London: Edward Arnold (Publishers) Ltd.)

Tamberg T G 1972 The provance and selection of the cultivated gladioli; *Trudy po Prikladnoi Botanike, Genetike i Selektsi* **46** 243–269

——1976 Inherited traits in intervarietal hybrids of gladioli; *North Amer. Gladiolus Coun. Bull.* No. 127 21-20 30