# CHROMOSOME NUMBERS IN NARCISSUS CULTIVARS AND THEIR SIGNIFICANCE TO THE PLANT BREEDER 

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OF ALL THE STORIES of the development of modern ornamental cultivars, that of the genus Narcissus is one of great success, or maybe excess. This is because from the relatively few species and cultivars that were in our gardens 150 years ago many thousands of named cultivars have arisen, of which large numbers are now available to the horticultural trade and to specialist growers and breeders.

One of the main factors responsible for the establishment of so many Narcissus cultivars is their habit of growth and the way in which they are propagated. Deliberate or accidental cross-pollinations between species or cultivars differing in appearance gave (and continue to give) seeds which germinated to produce fine new forms. These forms are all of hybrid constitution, each carrying an individual combination of homozygous and heterozygous genes which determines its appearance and growth characteristics. Their hybridity prevents the obtaining of uniform offspring through self-pollination or the crossing of similar plants, because the heterozygous genes and gene combinations carried by the parents) are re-assorted during gamete formation to give further variation in the progeny. Vegetative propagation is thus the only way to perpetuate each entity in an unchanged state. This is easily achieved in bulbous perennials such as Narcissus through division of the bulb using traditional or more modern methods (micropropagation, etc). Consequently, any hybrid of sufficient merit can be described as a new cultivar very soon after its first flowering, without the necessity for the time-consuming processes of breeding and selection which delay the introduction of cultivars of annual species, sometimes by many years.

The best of these Narcissus hybrids have been introduced into cultivation as new cultivars. These have increased almost explosively in numbers since the mid-nineteenth century (Brandham, 1986), such that well over 22,000 cultivar names now exist in the genus (Kington, 1989). Many of these cultivars were inevitably short-lived and are now extinct, but there is a large and growing pool of named plants that narcissophiles can draw upon to introduce desirable characteristics into their breeding programmes.

Very important in the breeding of Narcissus is knowledge of the chromosome numbers of cultivars and the consequences of attempting to use plants with particular chromosome complements as parents, in terms of the viability of their gametes and the potential vigour and variability of their progeny. The chromosome numbers of Narcissus cultivars vary greatly, with 23 different ones being known, ranging from $2 n=14$ to $2 n=46$. Some of them confer high fertility on the plant and others almost total sterility. They are products of some or all of the following factors:
a. meiosis, which may be regular, irregular or disastrousiy unbalanced, depending on the chromosomal constitution of the plant in which it is taking place. It results in the eventual production of normal or aneuploid gametes, or in sterility if unbalanced;
b. polyploidy, where three or more basic sets of chromosomes are present in a plant instead of the usual two sets found in a diploid;
c. the presence of three basic chromosome numbers ( $x=7,10,11$ ) in the genus, combined with hybridization between plants with the same or different basic numbers at the same or different levels of polyploidy;
d. the production of viable non-reduced gametes via the by-passing of meiosis in fertile and in otherwise non-fertile plants.

Details of these four factors are as follows:

## Meiosis in diploid species and hybrids

In every cell of a normal diploid plant the chromosomes are present as two almost identical sets (of seven in most Narcissus species), one of which is inherited from each of the plant's parents. During the first phase of meiosis (a key feature of ovule and pollen development), each member of one set pairs throughout its length with the corresponding chromosome from the other set to form a bivalent. In the bivalent the paired chromosomes exchange segments (together with the genes situated on them) and later separate again to give the haploid chromosome complement found in the gametes. The diploid number is restored when gametes fuse.

The pairing process in meiosis is crucial for high fertility. Fertility is often reduced in hybrid diploids because their two chromosome sets (inherited from the two dissimilar parental taxa) differ from each other in structure to a greater or lesser extent, even if the number of chromosomes in each set is the same. In the more extreme cases, in which the parents of a diploid hybrid are genetically and chromosomally very dissimilar, the chromosomes will not pair properly during meiosis in the hybrid. Consequently they will not separate properly, resulting in the production of at least some gametes with unbalanced chromosome complements which are non-viable, leading to a certain amount of sterility in the hybrid. In the most extreme cases of wide hybridity the only viable gametes that can be produced by the plant are those which are non-reduced (see below).

Polyploidy
Many Narcissus cultivars and some of the species are polyploid, having three, four or more basic sets of chromosomes instead of the two that are found in diploids. Tetraploids have four sets, and where each set comprises seven chromosomes (the most frequent number in Narcissus) they tend to form seven associations of four chromosomes (quadrivalents) during meiosis. Quadrivalents often separate 2-2 after their formation, and if this occurs in every quadrivalent in a meiotic cell the resulting gametes are diploid and viable, each with two sets of seven chromosomes. Sometimes the separation of a quadrivalent is an irregular 3-1, and if this occurs in one quadrivalent in a cell the resulting gametes have 15 or 13 chromosomes (two sets of seven plus or minus one). This genetic imbalance is often viable, since the deleterious effect of the lack of, for instance, one chromosome of a set of seven in a 13 chromosome gamete is buffered by the presence of another complete set in the gamete. The imbalance is nevertheless sometimes expressed as an irregularity in the appearance of the progeny, which would have 27 or 29 chromosomes if the defective ( $\mathrm{n}=13$ or 15 ) gametes fuse with normal ones. If the irregular 3-1 chromosome separation occurs in two of the seven quadrivalents in a cell the gametes could contain 12 or 16 chromosomes, a greater genetic imbalance which is more likely to be expressed in the 26 - or 30 -chromosome progeny as a defect in growth or appearance. For instance, the statement that 'Weedy little... 'Falaise'...cannot be said to be outstandingly robust' (JeffersonBrown, 1969: 115, 31) indicates that the loss of two chromosomes in the production of this aneuploid tetraploid ( $2 \mathrm{n}=4 \mathrm{x}-2=26$ ) is a major degree of aneuploidy which has a severe adverse effect on the morphology and vigour of the plant.
Triploids and pentaploids have three or five sets of chromosomes and the trivalents and pentavalents produced during their meiosis cannot separate into equal groups. The resulting gametes are thus mostly unbalanced in their chromosomal constitution, and a low level of fertility would be expected in these plants. In autotriploids, where the three sets of chromosomes are very similar, regular trivalent formation occurs. Every trivalent segregrates $2-1$ as meiosis progresses, and when all seven trivalents in a cell separate in this way in the same direction viable haploid and diploid gametes are formed by that cell (Brandham, 1982), although this would be expected to occur at a low frequency in the whole anther or ovary. In pentaploids the chromosomes tend to form fives (pentavalents) during meiosis; otherwise threes and twos (trivalents and bivalents). Either way, the result is usually a 2-3 separation of each group of five. Consequently, the gametes produced by a pentaploid range in chromosome number between diploid and triploid. Most are unbalanced, but the adverse effect of the imbalance is cushioned by the presence of two full sets of chromosomes in them and some viability is retained. Hexaploids are
somewhat more fertile. Their six sets of chromosomes can segregate quite regularly during meiosis to form viable triploid gametes, although many aneuploid gametes can also be produced.

## Basic number variation and hybridity

The genus Narcissus is divided into a number of sections among which there is variation in the basic number of chromosomes ( x , which is the number in a normal gamete produced by a diploid). In Section Aurelia ( $N$. broussonetii only) the basic number is $\mathrm{x}=11$; in Section Serotini ( $N$. serotinus only) it is $\mathrm{x}=10$; in Section Hermione it is $\mathrm{x}=10$ and 11 in different species, and in the remainder, which constitute the majority (Sections Narcissus, Jonquilla, Apodanthe, Ganymedes, Bulbocodium and Pseudonarcissus), it is $x=7$. Hybrids can be made between members of different sections, and in many cases diploid hybrids can thus contain two chromosome sets differing in number, such as $7+10=17,7+11=18$ or $10+11=21$. In most of such plants the chromosome sets are so dissimilar that pairing fails almost completely during meiosis, as shown by Fernandes (1950) in the 17-chromosome cultivar 'Alsace'. Separation of chromosomes is chaotic and the developing gametes are grossly unbalanced genetically, resulting in sterility. The same applies in polyploid hybrids of this type, such as the allotriploids with $2 \mathrm{n}=7+7+10=24$ chromosomes, although an exception occurs in allotetraploids with, for instance, $2 \mathrm{n}=7+7+10+10=34$ chromosomes. These are fertile, because each chromosome has one and only one other with which to pair during meiosis. Meiosis is therefore regular, producing diploid gametes with $n=7+10=17$ chromosomes. In this way, allotetraploids behave as diploids and thus are known as amphidiploids.

## Non-reduction in gamete production

Because of many of the factors described above, irregularities of meiotic pairing and separation often result in the production of genetically unbalanced aneuploid gametes. In many cases these are of reduced viability or are totally non-viable, but all plants, whether hybrid, polyploid or not, can sometimes by-pass meiosis to produce non-reduced gametes which contain the same chromosome number as that of the plant which bears them. These are viable, and in some otherwise sterile cultivars they are the only viable gametes that the plant can produce. Fusion of a non-reduced gamete with a normal one in a diploid population can thus give rise to triploids, both in the wild (Brandham, 1982), and in cultivation, a process by which the old triploid Narcissus cultivars 'Emperor' and 'Empress' almost certainly arose from diploid parents. Similarly, a triploid $\times$ diploid cross can give rise to tetraploid progeny through the fusion of an unreduced triploid gamete with a normal haploid one from the diploid parent. The earliest tetraploid Narcissus cultivars probably arose in this way (Brandham, 1986).

The reduced fertility or almost complete sterility which occurs in a number of cultivars of Narcissus is a problem which has faced many breeders, the majority of whom were not familiar with the genetic or chromosomal principles involved. Some of the causes have been outlined above, but the main object of this article is to identify sterility etc. and patterns of potential variability by bringing together all the information on the chromosomal constitution of Narcissus cultivars that could be found in the literature and to supplement it with the results of an extensive survey of chromosome numbers carried out in the Jodrell Laboratory, Royal Botanic Gardens, Kew. Comment will be made on every chromosome number, which will be interpreted in terms of the origin of the cultivars, their expected degree of fertility and the probable chromosome numbers to be found in their gametes. This information will have a direct bearing on the probability of success or failure of crossing attempts and on the constitution and vigour of the progeny of such crosses. It is hoped that it will be used by breeders to distinguish more easily between plants of high potential and those of less use in their breeding programmes.

## Material and Methods

For the survey carried out at Kew large numbers of cultivars were obtained as bulbs from a wide range of commercial and private sources (see Acknowledgements) and were cultivated in open frames in pots of compost. Vouchers were prepared from those that flowered and were deposited in the Kew Herbarium. The names of those which did not flower were given by the suppliers. Clearly there was a risk of misidentification in these cases, but this was minimised through collaboration only with the most reliable sources of supply.
Root tips were collected in mild spells between October and March, pretreated in saturated aqueous alpha-bromonaphthalene for 20 hours at $4^{\circ} \mathrm{C}$ and fixed in $1: 3$ acetic ethanol. They were stained in Feulgen after hydrolysis in 1 M HCl for 7 minutes at $60^{\circ} \mathrm{C}$. Meristems were squashed on slides which were made permanent by freezing with liquid $\mathrm{CO}_{2}$, separating slide and coverslip, dehydrating in absolute ethanol and mounting in Euparal. Permanent slides are retained in the collection of the Jodrell Laboratory, Royal Botanic Gardens, Kew. Chromosomes were counted in at least five well-spread cells for each cultivar.

## Results

The chromosome counts are listed in Table 1. In the Kew survey 731 records were obtained, of which 61 agreed and 14 disagreed with those of at least one previous author. Also included are 301 more counts extracted from the literature, making a total of 1032 counts in 1005 cultivars, with 25 of the counts representing two or more different findings in a single cultivar, and two being records of somatic doubling of chromosome number. In the Kew survey 96 additional counts were
made of duplicate material which confirmed the first finding, but there were five cultivars in which different chromosome numbers were found in duplicate accessions (in 'Barrett Browning', 'Great Warley', 'Lilac Charm', 'Queen of Bicolors' and 'Rip Van Winkle'). Since clonal propagation is only rarely a source of variation in chromosome number (except in cases of somatic chromosome doubling) at least one of the two identifications in each case must be in error. Both counts of each are included in Table 1, as it is not possible to say which of the alternative cytotypes was named correctly and which incorrectly. Similarly, different records for the same cultivar by different authors have been included in the table. Most of these are also probably due to misnaming rather than to inaccurate work, and it is again not possible to say which number is right and which is wrong for these cultivars, so the alternatives are given without comment. There is nevertheless a high level of agreement in cultivars examined by two or more authors, even when the number is an aneuploid or a complex polyploid, which suggests that the great majority of the counts in the table are accurate and can be relied upon.
Important features of cultivars listed in Table 1 are their classification and dates of origin. Narcissus cultivars are classified into twelve divisions (Kington, 1989) which can be summarised as follows:

Division 1. Trumpet daffodils of garden origin. Flowers solitary, corona length equalling or exceeding that of the perianth segments.

Division 2. Large-cupped daffodils of garden origin. Flowers solitary, corona shorter than perianth segments but more than one third of their length.

Division 3. Small-cupped daffodils of garden origin. Flowers solitary, corona one third the length of the perianth segments or less.

Division 4. Double daffodils of garden origin and of any affinity. Flowers solitary or multiple, with doubling of perianth, corona or both.
Division 5. Triandrus daffodils of garden origin. Characteristics of $N$. triandrus evident; 2 or more pendent flowers per stem, perianth reflexed.

Division 6. Cyclamineus daffodils of garden origin. Characteristics of N. cyclamineus evident; flowers usually solitary, perianth reflexed, flower at acute angle to stem, pedicel short.

Division 7. Jonquilla daffodils of garden origin. Characteristics of $N$. jonquilla present; flowers fragrant, 1-3 on terete stem, perianth spreading, leaves narrow, dark green.

Division 8. Tazetta daffodils of garden origin. Characteristics of $N$. tazetta or its allies present; flowers fragrant, 3-20 on stout stem, perianth spreading, leaves broad.

Division 9. Poeticus daffodils of garden origin. Characteristics of $N$. poeticus dominating, with no evidence of hybridization with members of any other division. Flowers usually solitary, fragrant, corona very short, perianth white, spreading.

Division 10. Species, wild variants and wild hybrids, including double-flowered forms. (Only hybrids are included in Table 1, as the cytology of Narcissus species is a very large subject outside the chosen scope of this article).
Division 11. Split-corona daffodils of garden origin. Hybrids of any affinity, but with the corona split into lobes for at least half of its length.
Division 12. Miscellaneous daffodils, not falling into Divisions 1-11.
In addition to the division to which each cultivar belongs, the colour of its perianth, followed after a hyphen by that of the corona, is also given in Table 1, the codes for the colours being the initial letters of White, Green, Yellow, Pink, Orange and Red. Two or more letters, used frequently for the corona and very occasionally for the perianth, indicate a gradation in colour. This reads from the centre or base to the rim in the case of the corona, and from the outer zone to the base in that of the perianth. In Table 1 the classifications and colour codes follow those given by Kington (1989). In a very few cases these differ slightly from those in American Daffodil Society (1981).
The dates refer to the date of registration of the name of each cultivar, or the date when the name was first used, if earlier. They give only a rough approximation of each plant's actual date of origin, but are satisfactory guides for people interested in the ages of the material with which they are working.
Some of the original counts in Table 1 were published earlier (Brandham and Kirton, 1987), and in a very few cases they differ from those given here. The changes follow the re-checking of the identity or the chromosome preparations of the material, and the present version should be taken to be the correct one.

## $B$ chromosomes

In Table 1 are listed several cultivars containing a single B chromosome in addition to the quoted number, with 'Ultimus' having four. These chromosomes are clearly distinguishable from normal ones, usually being smaller. They are composed largely of non-coding or 'junk' DNA, and carry very few functional genes. Apart from delaying flowering by a short period in some plants and reducing fertility to some extent in others and a few other minor factors, 'effects due to B chromosomes on the growth and development of the external phenotype are slight and difficult to detect' (Jones and Rees, 1982; 69), and no study has yet been made of their effects in Narcissus, as far as I am aware. For practical purposes their presence or absence in Narcissus cultivars can therefore be ignored by breeders, although in some cases they can be used as interesting markers when pedigrees are being traced, since a plant carrying a B chromosome will transmit it via some of its gametes to some of its progeny.

## Discussion

There follows an analysis of the probable fertility of each chromosome number, together with comments on its probable genetic origin and on the gamete types that will be produced by it. Where particular counts are said to be slightly or very fertile these are the highest degrees of fertility that can be forecast from the particular chromosomal constitution of each. Other factors such as wide hybridity, where very dissimilar species are involved in the ancestry of a plant, can lower fertility in cytotypes which might otherwise be expected to be fertile. This lowering is the result of irregular chromosome pairing during meiosis. Modifications of the floral parts of double flowers can result in partial or complete male sterility if anthers are modified in structure or absent, and even the female parts of double flowers (ovary, style, stigma) are sometimes altered to non-functioning structures.
$2 n=14$ ( 111 records). These are diploids derived directly or indirectly from diploid species with the same basic number ( $\mathrm{x}=7$ ). They would normally be expected to produce bivalents during meiosis, which dissociate regularly to produce haploid gametes with $\mathrm{n}=7$ chromosomes. Fertility should be high, except where wide hybridity is involved.
$2 n=17$ ( 21 records). These are diploid hybrids between $N$. tazetta or one of its allies with $2 \mathrm{n}=20(\mathrm{x}=10)$ and a Narcissus species with $2 \mathrm{n}=$ $14(\mathrm{x}=7)$. Most of these plants are $N$. poeticus/tazetta or $N$. cyclamineus/tazetta hybrids ( $=$ poetaz, cyclataz) in Division 8, or are double-flowered forms of them in Division 4 (e.g. 'Abba' and 'Sir Winston Churchill', which are double-flowered selections derived vegetatively from 'Cragford' and 'Geranium' respectively). One plant, $N . \times$ bifloris is a similar hybrid occurring in the wild and classified into Division 10. In these plants the $10+7$ chromosomes are so dissimilar that they cannot pair during meiosis (Fernandes, 1950), which therefore fails to produce any fertile gametes. The only viable gametes that can be formed by these $2 \mathrm{n}=17$ plants are non-reduced, also with $\mathrm{n}=17$ chromosomes.
$2 n=18$ ( 2 records). 'Hiawassee', 'Minnow'. As above, but derived from a $2 n=14(n=7)$ Narcissus crossed with a $2 n=22(n=11)$ plant of the $N$. tazetta alliance. In the case of 'Hiawassee' this parentage is known to be 'Cassandra', a presumably diploid poeticus hybrid, crossed with 'Paper White' (from $N$. papyraceus, $2 \mathrm{n}=22$ ). These $2 \mathrm{n}=$ $7+11=18$ plants are also sterile except in cases of non-reduction.
$2 n=19$ 1 record). 'Bethany'. This plant is a triploid based on $\mathrm{x}=7$, but lacking 2 chromosomes, i.e. $2 \mathrm{n}=(3 \times 7)-2=19$. One of its parents is known to be a tetraploid and the other is probably triploid, as tetraploid grand-parentage is known for the latter. 'Bethany' probably arose from the fusion of a) a gamete from the tetraploid lacking 2 chromosomes as a result of its meiotic irregularity, and b) a viable haploid gamete from the triploid parent. 'Bethany' is probably largely
sterile because of its triploid nature compounded by its loss of two chromosomes, but it might produce a few viable haploid gametes ( $\mathrm{n}=$ 7 ), or non-reduced ones ( $\mathrm{n}=19$ ).
$2 n=20$ ( 7 records). 'Franklin', 'Gloriosus', 'Grand Soleil d'Or', 'Late Israeli Sol', 'Soleil d'Or' (Division 8) and 'Queen of Spain' (= $N . \times$ johnstonii, Division 10) are diploids based on $\mathrm{x}=10$. They should all be bivalent-formers and quite fertile. 'Piper's Barn' is an autotriploid ( $\mathrm{x}=7$ ) jonquil (Division 7) formed probably from diploid ancestors with non-reduction in one of them. In this plant there is a Robertsonian fusion, in which two chromosomes fuse to give a larger one, with loss of a segment, resulting in reduction of the chromosome number by one. Robertsonian fusion has been noted previously in Narcissus bulbocodium, in which the process reduced the chromosome number of a $\mathrm{x}=7$ pentaploid from $2 \mathrm{n}=35$ to 34 , with the formation of a single enlarged chromosome (Brandham and Kirton, 1987; Fig. 3D). It is unlikely that 'Piper's Barn' would be fertile, but it might produce some viable $\mathrm{n}=7$ or non-reduced $\mathrm{n}=20$ gametes.
$2 n=21$ (116 records). One of these, 'Sicily White' (Division 8), is a diploid hybrid between members of the $N$. tazetta alliance having $2 \mathrm{n}=$ 20 and $2 \mathrm{n}=22$ respectively (Kurita, 1954), i.e., its chromosomal constitution is $2 \mathrm{n}=10+11=21$. Fertility should be moderate to low in this plant due to difficulties of meiotic pairing between its dissimilar chromosome sets.

The remaining 115 plants are triploids based on $x=7$. They could have been produced by either of two routes: a) from diploid parents with non-reduction in one of them, the very old mid-nineteenth century triploids such as 'Emperor' and 'Empress' almost certainly originating in this way; b) from hybridization between a diploid and a tetraploid parent with regular meiosis in each, which is the route by which the more recent triploids probably arose. Either way, these triploids have $2 \mathrm{n}=7+(7+7)=21$ chromosomes. When their three sets of chromosomes are very similar the plants are autotriploid, forming trivalents at meiosis. Their fertility is generally low, because of the inherent meiotic problems associated with the segregation of the three chromosomes in each trivalent, but small quantities of haploid and diploid gametes are produced, together with some non-reduced ones, as has been shown to occur in autotriploid Aloe jucunda (Brandham, 1982). Allotriploids have one set of seven chromosomes differing from the other two. Similar chromosomes pair during meiosis, but the third set remains unpaired and the seven univalents cause great disruption to the meiotic division, resulting in almost complete sterility. The non-reduced gametes produced occasionally by triploid Narcissus hybrids can give rise to tetraploid offspring when the plants are crossed with diploids. The oldest known tetraploid Narcissus cultivars, appearing at the end of the nineteenth century, probably arose in this manner.
$2 n=22$ ( 13 records). 'Paper White', 'Paper White Grandiflorus' and 'White Pearl' (Division 8) are diploids based on $x=11$ chromosomes and should be as fertile as the diploids having $x=7(2 n=14)$ and $\mathrm{x}=10(2 \mathrm{n}=20)$. The remainder ('Bobbysoxer', 'Bunting', 'Buttonhole', 'Grandee', 'Grandis', 'Horsfieldii', 'Ice Chimes', 'Silver Bells', 'Skylon' and 'Victoria') are aneuploid triploids based on $x=7$ ( $2 \mathrm{n}=7$ $+7+7+1=22$ ). Because they are aneuploid they are unlikely to have arisen from diploid/diploid crosses with non-reduction in one parent, because these crosses involve only euploid gametes ( $n=7,14$ ). It is more probable that most of the $2 \mathrm{n}=22$ plants arose from diploid/tetraploid crosses with meiotic irregularities in the tetraploid parent of each, resulting in the production of aneuploid gametes with $n$ $=15$ chromosomes. These fused with the $\mathrm{n}=7$ gametes from the diploid parents. In the formation of 'Ice Chimes' the $n=15$ gamete came from its aneuploid ( $2 \mathrm{n}=22$ ) triploid parent, 'Silver Bells' ( F . Galyon, pers. comm.)
Because of the probable origin of most $2 \mathrm{n}=22$ plants from diploid/ tetraploid crosses, some doubt should be cast on the counts of $2 n=22$ in 'Horsfieldii'. They were made by both Philp (1934) and Janaki Ammal and Wylie (1949) and are thus probably correct, but as the plant arose in 1845 (Kington, 1989), well before the earliest known tetraploid (Brandham, 1986) it is unlikely to have come from a diploid/ tetraploid cross. It is more probable that it is a triploid plant originating from a diploid/diploid cross. It would not be expected to be aneuploid with this parentage (see above), so it is probably a triploid with $2 \mathrm{n}=$ 21, but carrying also an unusually large $B$ chromosome that is so similar to one of the normal chromosomes that it was not identified as such by the people who examined the chromosomes of the plant.

Not included among the counts of $2 \mathrm{n}=22$ are those made of 'Empress' by Nagao (1929, 1933) and Philp (1934). These have been clearly shown by other workers to be $2 \mathrm{n}=21+1 \mathrm{~B}$.

It is known that 'Buttonhole' is a split-corona sport of 'Victoria' derived from it by vegetative rather than sexual means (American Daffodil Society, 1981). The uncommon chromosome count of $2 \mathrm{n}=22$ in both confirms their close relationship.

Aneuploid triploids with $2 \mathrm{n}=22$ will have fertilities as low as those with 20 or 21 chromosomes, with a small incidence of viable haploid and diploid gametes, and some which are non-reduced.
$2 n=24$ ( 19 records). Most of these plants are in Division 8, or are double-flowered forms derived from them (Division 4). One is a Division 10 wild hybrid ( $\times$ biflorus) and three are in Division 6 ('Jumblie', 'Quince' and 'Tête-a-Tête'). All are allotriploids with two basic numbers $(2 n=7+7+10=24)$. They have arisen in two ways, both of which can be traced through their known pedigrees (American Daffodil Society, 1981).

The pedigrees of eleven of the plants are not known, but from one of
these ('Elvira', originating in 1904) a vegetatively produced sport with double flowers was named 'White Cheerfulness' (1923), which in turn gave rise to 'Yellow Cheerfulness' (1938) through mutations of one or more of the genes for flower colour.

Two of the remaining six plants with $2 \mathrm{n}=24, \times$ biflorus and $\times$ poetaz are $\mathrm{F}_{1}$ hybrids between $N$. tazetta and $N$. poeticus. They are products of a $n=10$ gamete from $N$. tazetta fusing with a $n=14$ gamete from $N$. poeticus. Interestingly, two different counts have been obtained for 'Biflorus', $2 \mathrm{n}=17$ (American Daffodil Society, 1981) and $2 \mathrm{n}=24$ (Stomps, 1919 and the present investigation). It is thus evident that this hybrid has arisen more than once, with the $\mathrm{n}=10$ gametes from $N$. tazetta fusing with either haploid or diploid gametes ( $n=7,14$ ) from $N$. poeticus.
Three of the last four plants with $2 \mathrm{n}=24$ arose from non-reduced gametes (the only viable ones), produced by a $2 \mathrm{n}=17$-chromosome parent, fusing with a $\mathrm{n}=7$ gamete from a $2 \mathrm{n}=14$ diploid. These three, 'Jumblie', 'Quince' and 'Tête-a-Tête', were produced by a single breeder, Alec Gray, from an open-pollinated cyclataz hybrid having $2 \mathrm{n}=17$ (two of them were stated wrongly to be from selfpollinated cyclataz in American Daffodil Society, 1981).
The last $2 \mathrm{n}=24$ plant, 'Golden Dawn', is derived from openpollinated 'Admiration' (Division 8). 'Admiration's chromosome number is unknown, but is probably $2 \mathrm{n}=17$ (see also below, under 2 n $=34$, the ancestry of 'Matador'), so 'Golden Dawn' arose from a nonreduced $\mathrm{n}=17$ gamete from 'Admiration' fused with $\mathrm{n}=7$ from an unknown $2 \mathrm{n}=14$ diploid.
Despite their vegetative vigour, ease of propagation and widespread popularity, especially of 'Cheerfulness' and 'Tête-a-Tête', all of the $2 n$ $=24$ plants are sterile unbalanced allotriploids. Their two sets of seven chromosomes can form bivalents during meiosis but the set of ten will not pair with them. Irregular segregation of the ten univalents will result in gross meiotic irregularity and almost total sterility. The plants can theoretically produce viable non-reduced gametes with $\mathrm{n}=24$ chromosomes, but these are too large to be of any practical value to the breeder.
$2 n=26$ ( 5 records). 'Charles I', 'Falaise', 'Orange Glow', 'Pink Glory' and 'Swansdown'. These are tetraploids based on $x=7$, but lacking two chromosomes. Through meiotic irregularities in one or both of the tetraploid parents producing aneuploid gametes with $n=$ 13 or 12 instead of 14 , these plants could have arisen either from $13+13$ or $14+12$ gamete fusions.

As stated in the Introduction, 'Falaise' is not very sturdy, which is perhaps symptomatic of its chromosomal imbalance, and the other four cultivars could be similarly affected. Despite their weakness, these plants could produce viable gametes with $n=14$, but also a larger number with $\mathrm{n}=13$ or 12 , which are unbalanced and not so vigorous, so the plants' overall fertility should be only moderate or less. ' F alaise'
and 'Swansdown' are double-flowered and possibly totally malesterile, although it might be possible to use them as female parents.
$2 n=27$ ( 48 records). Tetraploids ( $\mathrm{x}=7$ ) lacking one chromosome, these are products of tetraploid/tetraploid hybridization with one parent contributing 14 chromosomes and the other 13 through meiotic irregularities. As a result of their own meiotic irregularity compounded by aneuploidy, the $2 \mathrm{n}=27$ plants should be only moderately fertile. Approximately half of their gametes will contain 13 chromosomes and half 14 , although small numbers with 12 or 15 will also occur. In consequence, large numbers of aneuploids lacking chromosomes from the tetraploid complement will occur in the progeny of any two of these $2 n$ $=27$ plants crossed with each other. Although some might be vigorous others will be less so and a great deal of progeny variability will ensue.
$2 n=28$ ( 601 records). The great majority of these plants are autotetraploids based on $x=7$. Their quadrivalent frequency during meiosis is normally high, with regular 2-2 segregation, so many of their gametes are balanced with two sets of seven chromosomes ( $\mathrm{n}=14$ ), although some less vigorous gametes with $\mathrm{n}=12,13,15$ or 16 might also arise. Fertility in these plants should therefore range from moderate to high, with low fertility in some resulting from doubleness. Other $2 \mathrm{n}=28$ cultivars are allotetraploids with two similar sets of seven and two other sets of seven which are also similar to each other (i.e. the four sets are derived from the chromosomes of two quite dissimilar diploid species). During meiosis these plants form bivalents which segregate regularly to form gametes with $\mathrm{n}=14$, resulting in high fertility. Still further tetraploids are auto-allotetraploids with three similar sets of seven and a fourth set of seven which differs in genetic structure from the other three. These plants form trivalents and univalents during meiosis, which is thus very disturbed, resulting in a high level of sterility.
The oldest tetraploids probably arose at the end of the nineteenth century from triploid/diploid crosses, in each case through the fusion of a non-reduced triploid gamete with a normal haploid one from the diploid parent. Later tetraploids almost certainly arose from tetraploid /tetraploid crosses.
Another route to tetraploid formation is via the doubling of the chromosome number of individual somatic cells of a diploid through mitotic misdivision. If the tetraploid cells are formed in a stem meristem they can continue to divide and grow normally to form a tetraploid sector. This has a chance of becoming a purely tetraploid offset that can be detached and propagated to make a new tetraploid cultivar. I have not yet found pedigree evidence of this process giving rise to new Narcissus cultivars, although its early stages (tetraploid sector production) were reported in the cultivars 'Fusilier' and 'Lucifer' by de Mol (1925).

Only one plant known to have $2 \mathrm{n}=28(+1 \mathrm{~B})$ is classified in Division 8. This is 'Silver Chimes', a tribasic allotriploid with three
different sets of chromosomes, $x=10$ and 11 from 'Grand Monarque' (Division 8) and $x=7$ from Narcissus triandrus loiseleurii. It probably arose from a rare $\mathrm{n}=11+10$ gamete from the allotripioid 'Grand Monarque' $(2 \mathrm{n}=11+10+10=31)$ and a normal gamete from N.t. loiseleurii. The B chromosome was inherited from 'Grand Monarque'.

Because the three sets of chromosomes in 'Silver Chimes' are all different $(2 \mathrm{n}=11+10+7=28)$ its meiosis is expected to be very disturbed with a high incidence of univalent formation, leading to almost total sterility.
$2 n=29$ ( 44 records). These plants are tetraploids based on $\mathrm{x}=7$ with one additional chromosome. Their most probable origin is from tetraploid/tetraploid crosses with meiotic errors in one parent of each contributing 15 chromosomes to the gamete instead of 14 . They are basically similar to tetraploids having $2 \mathrm{n}=28$ as far as their fertility is concerned. Approximately half of their gametes will contain 14 chromosomes and half 15 . The genetic unbalancing effect of the extra chromosome in the $\mathrm{n}=15$ gametes is minimised by the presence of two full sets of chromosomes. As in other tetraploids some of the gametes will contain $n=12,13$ or 16 chromosomes, which will contribute to further progeny variation if they are viable.
$2 n=30$ ( 15 records). Eleven of these are Division 8 autotriploids derived from members of the tazetta alliance having $x=10$ chromosomes ('Chastity', 'Chinese Sacred Lily', 'Cypri', 'Grand Emperor of China', 'Grand Primo Citroniere' (also recorded as $2 \mathrm{n}=32$ ), 'Grand Soleil d'Or', 'Kashmir Local', 'McKenzie Tazetta', 'Soleil d'Or', 'Suisen' and 'Yellow Prize'). They should form trivalents at meiosis, with some bivalents and univalents. Meiosis is thus quite irregular, resulting in low fertility, although a few viable haploid ( $\mathrm{n}=10$ ) and diploid ( $\mathrm{n}=20$ ) gametes would be produced, as in the autotriploids based on $\mathrm{x}=7(2 \mathrm{n}=21)$. The triploid 'Soleil d'Or' ( $=$ 'Grand Soleil d'Or') is the true 'Sol' grown very widely, especially in the Scilly Isles. The diploid form $(2 \mathrm{n}=20)$ is probably an Israeli-grown relative similar to the old diploid cultivar 'Newton' (B. Welch, pers. comm.).

The four cultivars 'Gervo', 'Golden Spur' (also recorded to have 2 n $=14$ and 21), 'Modesta' and 'Pacific' are based on $x=7$ chromosomes, being tetraploids with two additional chromosomes. They will have irregular meiosis, producing gametes with $n=13-17$ chromosomes, with the extremes being of reduced viability. If crossed with normal tetraploids much variation in chromosome number will be found in the progeny, with corresponding variability in their appearance. Some of them will be genetically very unbalanced weak plants not worthy of selection.
$2 n=31$ ( 9 records). Seven of these are Division 8 plants ('Albany', 'Avalanche', 'Compressa', 'Chinita', 'Grand Monarque', 'Highfield Beauty' and 'Martha Washington'). Some (e.g. 'Albany', 'Chinita', 'Highfield Beauty' and 'Martha Washington') are auto-allotetraploids'
with three sets of seven chromosomes and one of ten, the latter from $N$. tazetta. Their origin is from a non-reduced $\mathrm{n}=17$ gamete from a $2 \mathrm{n}=$ 17 Division 8 hybrid fusing with a $\mathrm{n}=14$ gamete derived from a tetraploid with $2 \mathrm{n}=28$. Thus in these plants $2 \mathrm{n}=(10+7)+(7+7)=$ 31. One of them, 'Chinita', has documented evidence for this ancestry, (American Daffodil Society, 1981), being derived from 'Chaucer' (presumably $2 \mathrm{n}=28$ ) crossed with 'Jaune a Merveille' ( $2 \mathrm{n}=17$, see Table 1). All of these $10+7+7+7$ plants would be highly sterile, with triploid meiosis made more irregular by the presence of ten more univalents.
'Grand Monarque' is an allotriploid derived entirely from members of the tazetta alliance, as is 'Compressa' also, noted by F. Galyon (pers. comm.) to be almost entirely tazetta-like. They have $2 \mathrm{n}=10+10+11$ $=31$. The plants would not be expected to be very fertile, since their chromosomes would tend to form ten bivalents and 11 univalents during meiosis, the latter causing disruption and lowering fertility. Nevertheless, 'Grand Monarque' has contributed a non-reduced $\mathrm{n}=$ 31 gamete to the production of 'Killara' (see below) and an $n=10+11$ $=21$ gamete to 'Silver Chimes' (see above).
'Avalanche' is a selection from 'Grand Monarque', derived vegetatively and differing from it by a gene mutation only, rather than by a re-assortment of the entire genome through hybridization. The chromosome count of $2 \mathrm{n}=31$ and more particularly the single $B$ chromosome in each confirms their close relationship.

Another cultivar with $2 \mathrm{n}=31$ is 'Madame de Graaff'. This is a tetraploid based on $x=7$ with three additional chromosomes derived from irregular meiosis in one or both of its parents. It is one of the earliest known tetraploids, dating from before 1887, so it is unlikely to have tetraploid parentage. It probably arose from a triploid/triploid cross with non-reduction in one parent ( $N$. pseudonarcissus albescens) giving a $\mathrm{n}=21$ gamete, and irregular meiosis in the other ('Empress') giving an unusually viable $\mathrm{n}=10$ gamete, i.e. about midway between the viable $\mathrm{n}=7$ and $\mathrm{n}=14$ gameres that 'Empress' would be expected to produce. As in tetraploids with two additional chromosomes, 'Madame de Graaff' would have a very high incidence of gametes with more than 14 chromosomes, some of which would be non-viable. It should therefore have low fertility, but those of its progeny which survive should show considerable viability.
'Golden Perfection', listed as a jonquil (Division 7) by both the American Daffodil Society (1981) and Kington (1989), is also listed as such in Table 1. If this were so it would be thought to have arisen in a way similar to 'Madame de Graaff', and to have a similar chromosome constitution and behaviour, but it has been pointed out that it has no jonquil affinities (B. Welch, pers. comm.), so like 'Highfield Beauty', 'Martha Washington' and relations its chromosome complement is most probably $2 \mathrm{n}=(7+7)+(7+10)=31$, and its fertility would be
similar to theirs.
$2 n=32$ ( 7 records). These are Division 8 plants, or their doubleflowered derivatives in Division 4 ('Earlicheer', 'Early Pearl', 'Grand Primo Citroniere' (also recorded probably wrongly as $2 \mathrm{n}=30$-see below), 'Luna', 'New Zealand Tazetta', 'Polly's Pearl' and 'Scilly White'). They are allotriploids with $2 \mathrm{n}=10+11+11$. Each is possibly derived from a non-reduced $n=22$ gamete from one of the tazetta alliance with $2 \mathrm{n}=22$ (perhaps $N$. papyraceus or similar) fusing with a normal $\mathrm{n}=10$ gamete from another of the same alliance but with $2 \mathrm{n}=20$. An equally possible origin for these plants is with the involvement of a non-reduced gamete with $\mathrm{n}=21$ (from a $2 \mathrm{n}=21$-chromosome hybrid between species with $2 \mathrm{n}=20$ and 22 ) and a normal $\mathrm{n}=11$ gamete from a $2 \mathrm{n}=22$ tazetta ally.
'Earlicheer' is a double-flowered form of 'Grand Primo Citroniere', derived vegetatively, their relationship being confirmed by their identical chromosome complements (two of the three recorded counts of the latter are $2 \mathrm{n}=32$, the other of $2 \mathrm{n}=30$ probably being a case of mis-identification). 'Earlicheer' is not derived from 'White Pearl', as widely believed, since the latter has $2 \mathrm{n}=22$ (B. Welch, pers. comm. see Table 1).

Meiosis in these $2 \mathrm{n}=32$ plants will be irregular. The two sets of eleven will form eleven bivalents, but the products of meiosis will be contaminated by univalents from the set of ten. The great majority of gametes will be unbalanced and non-viable, but a very few will be viable with $\mathrm{n}=11$ or $\mathrm{n}=11+10$ chromosomes.
$2 n=33$ (1 record). 'Rijnveld's Early Sensation' (Division 1). This plant is based on $x=7$ and could be termed as a tetraploid plus five chromosomes or a pentaploid minus two. It is unlikely to have arisen from entirely tetraploid parents as its degree of aneuploidy is too high. It is more likely to have arisen via a non-reduced triploid gamete ( $\mathrm{n}=$ 21) from a triploid plant $(2 n=21)$ fusing with an aneuploid gamete ( $n$ $=12$ ) from a triploid or a tetraploid. This plant would be expected to produce some viable gametes with $\mathrm{n}=14$ chromosomes but many more with up to five extra ones, with a lowering of the viability of the more unbalanced gametes. The plant's fertility should be low, but not impossibly so for breeding purposes, and the high frequency of aneuploidy in the progeny should confer extra variability.
$2 n=34$ (3 records). 'Matador', 'Spangles' and 'Yellow Butterfly' (Division 8). These are allotetraploids with $7+7+10+10$ chromosomes. B. Welch (pers. comm.) has suggested that 'Matador' and 'Yellow Butterfly' arose directly from two $2 \mathrm{n}=17$ hybrids crossed with each other, with the involvement of non-reduced gametes on both the male and female sides. This is very probable, since non-reduced gametes are the only viable ones that these plants can produce (see above), and fusion of two of them is a distinct possibility when intercrossing is attempted. This origin is supported by pedigree evidence
(American Daffodil Society, 1981) that 'Matador' was produced by open pollination ( $=$ self-pollination in this case?) of 'Admiration', a Division 8 plant presumably with $2 \mathrm{n}=17$.
These allotetraploids are remarkably fertile. Because they have two of each of two different chromosome sets each chromosome has one other similar one with which to pair during meiosis. Seventeen bivalents are usually formed, which dissociate regularly to produce a majority of $\mathrm{n}=17$ gametes which are viable, giving a moderate to high level of fertility to the plant. I have observed the expected number of 2 n $=31$ in an unnamed hybrid obtained by B. Welch from crossing 'Matador' with a tetraploid ( $2 \mathrm{n}=28$ ) Division 3 hybrid. It appears that 'Matador' is self-fertile, because 'Spangles', a new variety named by S . Du Bose, is a self-pollination product of it with the same chromosome number.
These allotetraploids represent a new departure in the breeding of Division 8 plants, and should form the starting points to a new range of interesting fertile tazetta hybrids.
$2 n=35$ (2 records). 'February Silver' (Division 6) and 'White Owl' (Division 5). 'February Silver' is a pentaploid with five sets of seven chromosomes. Its probable origin is from the fusion of an unreduced gamete ( $\mathrm{n}=21$ ) from a triploid ( $2 \mathrm{n}=3 \mathrm{x}=21$ ) and a normal gamete ( $\mathrm{n}=14$ ) from a tetraploid ( $2 \mathrm{n}=4 \mathrm{x}=28$ ). In this plant the chromosomes will tend to form trivalents and bivalents during meiosis, less commonly quadrivalents and pentavalents. Gametes will be formed ranging mostly between diploid and triploid ( $\mathrm{n}=14-21$ ) with a high incidence of aneuploidy which will tend to lower the fertility of the plant quite considerably. There should nevertheless be a sufficient level of fertility to make the plant of use to the breeder, and the variation brought about by the aneuploidy of some of its gametes could be exploited.
The count of $2 \mathrm{n}=35 \mathrm{in}$ 'White Owl' is more interesting, since although it is placed in Division 5 it has clear affinities with N. tazetta and should more probably be in Division 8. Its chromosome complement confirms this suggestion, since it closely resembles that of 'Matador' ( $2 \mathrm{n}=34$ ). Furthermore, F. Galyon (pers. comm.) has reported success in crossing it with a seedling from a selfed 'Matador'. It is thus very probable that 'White Owl' is a complex allotetraploid with $2 \mathrm{n}=11+10+7+7$ chromosomes. Its claimed origin ('Scilly White' $\times$ 'Minnie Hume'), given by the American Daffodil Society (1981) can be interpreted as a normal $\mathrm{n}=14$ gamete from presumably tetraploid 'Minnie Hume' ( $2 \mathrm{n}=$ ? 28) fusing with a non-reduced gamete ( $\mathrm{n}=21$ ) from the tazetta ally 'Scilly White'. The latter is recorded as having $2 \mathrm{n}=32$ chromosomes (Fernandes \& de Almeida, 1971), but the one used as a parent of 'White Owl' could have been the 'Sicily White' ( $2 \mathrm{n}=21$ ) counted by Kurita (1954), because it is quite possible that Kurita's 'Sicily White' represents a misprint or a misunder-
standing of the name 'Scilly White' in the original reference. This confusion over names is confirmed by the absence of 'Sicily White' from the International Daffodil Checklist (Kington, 1989).
In crosses, 'White Owl' should behave similarly to the $2 \mathrm{n}=34$ allotetraploids but it will not be nearly so fertile. Its $7+7$ chromosomes will form seven bivalents during meiosis, but the $10+11$ chromosomes will not pair or separate so well. Some univalents will be formed which will give rise to unbalanced gametes and reduce fertility to a moderate or low level.
$2 \mathrm{n}=36$ ( 2 records). 'Great Warley' (Division 2) and 'Larkelly' (Division 6). These are pentaploids based on $\mathrm{x}=7$, with origins, chromosome behaviour and fertility similar to 'February Silver' ( $2 \mathrm{n}=$ 35), but with an extra chromosome. In the case of 'Great Warley' this would have been derived from the aneuploid triploid parent 'Horsfieldii' ( $2 \mathrm{n}=22$ ) via non-reduction. In that of 'Larkelly' the extra chromosome probably arose via an aneuploid gamete with $\mathrm{n}=15$ inherited from its tetraploid parent.
$2 n=37$ ( 1 record). 'Roger' (Division 6). Again as 'February Silver' ( $2 \mathrm{n}=35$ ), but with two additional chromosomes. The parents of 'Roger' are 'Beryl' and 'Nor-Nor' (American Daffodil Society, 1981). 'Beryl' is triploid, contributing a non-reduced triploid gamete ( $\mathrm{n}=$ 21). The other parent is probably tetraploid, contributing an aneuploid gamete ( $\mathrm{n}=14+2$ ) through an irregular meiotic division.
$2 n=43$ (l record). 'Queen of Bicolors' (Division 1). This is an aneuploid hexaploid with six sets of seven chromosomes plus one extra. It probably arose from tetraploid parents with a non-reduced gamete from one ( $\mathrm{n}=28$ ) fusing with an aneuploid gamete from the other ( $\mathrm{n}=$ $14+1)$. This plant should have irregular meiosis because of the presence of so many sets of chromosomes, but at least some gametes should be approximately triploid ( $\mathrm{n}=21$ or 22 ) and viable, conferring some viability to the plant.
$2 n=45$ (2 records). 'Killara' (Division 8) and 'Sanda' (Division 1). The pedigree of 'Killara' is given by the American Daffodil Society (1981) as 'Grand Monarque' $\times$ 'Empress'. These are known to have 2 n $=31+1 \mathrm{~B}$ and $21+1 \mathrm{~B}$ chromosomes respectively (Table 1). It is pointed out above that 'Grand Monarque' has irregular meiosis and low fertility, but similarly to all other Narcissus hybrids it can produce viable non-reduced gametes. 'Empress' is not totally sterile, but in common with other triploids it can produce a low frequency of viable haploid and diploid gametes. 'Killara' thus has the chromosomal constitution $2 \mathrm{n}=10+10+11+1 \mathrm{~B}$ from non-reduced 'Grand Monarque' added to a diploid $7+7$ gamete from 'Empress'. It is thus a complex allopentaploid ( $2 \mathrm{n}=7+7+10+10+11+1 \mathrm{~B}$ ). Its two sets of seven and two of ten should produce 17 bivalents during meiosis, but the single set of eleven will disrupt the meiosis, partly by pairing with some members of the sets of ten and partly by forming
univalents. The plant would thus be expected to form $\mathrm{n}=17$-chromosome gametes contaminated with various numbers of chromosomes from the set of eleven, of which the more unbalanced ones will not be viable. Fertility would be very low in this plant, but it would be worth attempting to cross it with the $2 \mathrm{n}=34$ allotetraploids, or with 'White Owl' $(2 \mathrm{n}=35)$. As the latter also have viable gametes with $\mathrm{n}=7+10$ $=17$ chromosomes the progeny should include some highly fertile 2 n $=34$ allotetraploids.
'Sanda' is chromosomally indistinguishable from 'Killara', even containing the same B chromosome. The two plants are also alike and there is now good evidence for the opinion of F. Galyon (pers. comm.) that 'Sanda' as is widely available is the same clone as 'Killara' that has been mis-named.
$2 n=46$ (1 record). 'Jamage' (Division 8). This plant, bred by George Tarry (B. Welch, pers. comm.) is known to be derived from a tetraploid Division 3 cultivar crossed with 'Grand Primo Citroniere' ( $2 \mathrm{n}=32$ ). The latter is of very low fertility (see under $2 \mathrm{n}=32$ above), but can produce some viable non-reduced gametes in common with many Narcissus cultivars that are otherwise sterile. The chromosome constitution of 'Jamage' is thus $2 \mathrm{n}=7+7$ from the tetraploid, united with $10+11+11$ from 'Grand Primo Citroniere'. The plant is a complex allopentaploid, and its two sets of seven and two sets of eleven will produce 18 bivalents during meiosis, but the last set will form ten univalents which will disrupt meiosis somewhat. Fertility will be low at best, with gametes carrying $\mathrm{n}=7+11=18$ chromosomes plus a variable number from the set of ten, the latter causing non-viability if too many are present.

## Future Developments

In those Narcissus cultivars having $\mathrm{x}=7$ as the only basic chromosome number this study has shown an increase in chromosome number which started in the middle of the nineteenth century with the origin of triploid cultivars from the diploid species and cultivars grown at the time, with formation of non-reduced gametes being instrumental in triploid formation. Typically of triploids these were larger, more vigorous and more showy than the diploids and were naturally seized upon by breeders, but initially there was little success in obtaining further progeny from them. Their triploid meiosis was irregular, their fertility was low, and when attempts were made to cross them with each other the problem was exacerbated because of low fertility in both parents. Indeed the only extant cultivars that can be reasonably confidently assigned to a triploid/triploid origin are 'Madame de Graaff' ( $2 \mathrm{n}=31$ ) and perhaps also 'Rijnveld's Early Sensation' ( $2 \mathrm{n}=$ 33).

It was not until triploids were crossed with diploids at the end of the nineteenth century that tetraploids ( $2 \mathrm{n}=28$ ) arose in any numbers,
again through meiotic non-reduction on the triploid side ( $\mathrm{n}=21$ ). Their origin constituted a major break-through in Narcissus breeding, since they are mostly vigorous, their fertility is adequately high for breeding purposes, and their progeny show considerable variability. They have been so successful that they now comprise the great majority of cultivars, with nearly 700 of the about 1000 chromosomally-known ones being tetraploid or approximately so.

An obvious question which must now be addressed is whether meiotic non-reduction can also occur in the tetraploids to give rise to a new race of hexaploid cultivars ( $2 n=6 x=42$ ) that are even larger and more vigorous. The answer to this is most certainly no. Tetraploids have existed for nearly 100 years and have been widely interbred, but the number of plants exceeding the tetraploid level of polyploidy is very low indeed, with only one ('Queen of Bicolors', $2 n=43$ ) probably arising from a tetraploid/tetraploid cross with meiotic non-reduction in one parent.

The process of non-reduction in tetraploids leading to the formation of hexaploid progeny certainly does occur, since in addition to the origin of 'Queen of Bicolors' it has also been noted by Wylie (1952), who found a spontaneously-produced hexaploid seedling growing among tetraploid cultivars, but the hexaploids so formed are not normally selected by breeders. It is clear that they exceed the level of polyploidy (and the amount of DNA per nucleus) that is optimal for plant size and vigour. They are evidently less vigorous than tetraploids and hence will not normally be selected from the progeny of a tetraploid/tetraploid cross. It is thus unlikely that such high polyploids will ever appear widely among newly-described $\mathrm{x}=7$ Narcissus cultivars.

The probability that high polyploids would be horticulturally successful is even lower in the tazetta alliance ( $x=10,11$ ), since not even the tetraploid derived solely from these basic numbers has yet been detected. It seems probable that vigorous plants exceeding the triploid level do not occur. The group is nevertheless fascinating as far as the breeder is concerned, since when tazettas are crossed with $\mathrm{x}=7$ plants their multiple-flowered habit is added to the normally larger flowers of the $\mathbf{x}=7$ group to give very desirable products. The lack of fertility in these hybrids, particularly in the ones with $2 \mathrm{n}=17,18,24$ etc., makes them difficult to breed further, but use can be made of meiotic non-reduction in them to produce a few viable gametes. Ideally this process should be utilised on the male side of a cross, because many more meiotic cells are present on the male (pollen) side of a plant than on the female (ovule) side, and if the frequency of non-reduced meiosis is constant there is thus a higher incidence of fertile non-reduced pollen than of fertile non-reduced ovules per flower in these otherwise sterile plants. In some cases, however, non-reduction can also be involved on the female side, as in the ancestry of 'Jumblie', 'Quince', 'Tête-a-

Tête', 'Matador' and 'Yellow Butterfly' (see above under $2 \mathrm{n}=24$ and 34).

As with the tetraploids in the $\mathrm{x}=7$ group, the break-through in the breeding of the genetically complex plants with mixtures of $x=7$ and 10 has now occurred. Allotetraploids with $2 \mathrm{n}=7+7+10+10=34$ have recently arisen ('Matador', 'Spangles' and 'Yellow Butterfly') which are bivalent-formers and should be adequately fertile for further breeding with each other and possibly with 'White Owl', which is genetically similar and has already been shown to be compatible with them. It is also quite feasible to use colchicine to double the chromosome numbers of sterile plants with $2 \mathrm{n}=7+10=17$ to restore fertility and produce new races of allotetraploids combining the best features of the $x=7$ complex and the tazetta alliance. These allotetraploids, together with those already known, should form the basis for a fascinating new series of 'multiflorus grandiflorus' cultivars in Narcissus, a genus which will surely continue to be one of the most successful of the decorative bulbous plants.

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## References

Those appearing in Table 1 are numbered in brackets.
american daffodil society, 1981. Daffodil Data Bank. Iowa Methodist Center, Des Moines, Iowa.(1)
BRANDHAM, P.E. 1982. Inter-embryo competition in the progeny of autotriploid Aloineae (Liliaceae). Genetica, Vol. 59, pp. 29-42.
brandham, P.e.1986. Evolution of polyploidy in cultivated Narcissus subgenus Narcissus. Genetica, Vol. 68, pp 161-167.
bRANDHAM. P.E. and KIRTON, P. 1987. The chromosomes of species, hybrids and cultivars of Narcissus L. Kew Bulletin, Vol. 42 pp. 65-102.
DE MOL, w.E. 1922. The disappearance of the diploid and triploid Magnicoronatae Narcissi from the larger cultures and the appearance in their place of tetraploid forms. Proceedings of the section of Sciences, Koninklijke Nederlandse Akademie van Wetenschappen, Vol. 25, pp.216-220 (2):
DE MOL. W.E. 1925. Het celkundig-erfelijk onderzoek in dienst gesteld van de veredeling der hyacinten, narcissen en tulpen. Genetica, Vol. 7, pp.111-118. (3). FERNANDES. A. 1950. La meiose chez Narcissus poetaz 'Alsace'. Génética Ibérica, Vol.2, pp. 149-174. (4).

FERNANDES, A.and DE almeida, M.t. 1971. Sur les nombres chromosomiques de quelques formes horticoles du genre Narcissus L. Boletim da Sociedad Broteriana, Vol. 45, pp.227-252. (5).
JANAKI AMMAL, E.K. and wylie, a.1949. Chromosome numbers of cultivated Narcissus. Royal Horticultural Society Daffodil and Tulip Year Book, Vol. 15, pp.33-40. (6).
JEFFERSON-BROWN, M.J. 1969. Daffodils and Narcissi, a complete guide to the Narcissus family. Faber and Faber, London.
jones, R.N. and rees, H. 1982. B Chromosomes. Academic Press, London, New York.
KARHALLOO, J.L. 1987. Variation in the karyotype of three cultivars of Narcissus tazetta L. (Amaryllidaceae). Genetica, Vol. 73, pp. 217-221. (7).
Karihaloo, J.l. and koul, a.K. 1985a. Cytogenetic studies in the genus Narcissus L. IV. Cytology of a naturalised variety of N. tazetta L. from Kashmir. Cytologia, Vol. 50, pp. 265-274. (8).
Karihaloo, J.L. and koul, a.K. 1985b. Cytogenetic studies in the genus Narcissus L. V. Cytology of a N. pseudonarcissus $\times N$. poeticus cultivar 'Whitewell'. Cytologia, Vol. 50, pp. 275-281. (9).
karihaloo, J.L. and Koul, a.K. 1989. Cytogenetic studies in the genus Narcissus L. VII. Karyotype and nucleolar condition in some $N$. pseudonarcissus L. cultivars. Cytologia, Vol. 54, pp. 589-595. (10).
kington, s. 1989. The International Daffodil Checklist. The Royal Horticultural Society, London.
kURITA, m. 1954. Cytological studies in Narcissus. 1. Karyotypes of some varieties and cultivated forms of N. tazetta L. Memoirs of Ehime University, Section II (Science), Series B, Vol. 2, pp. 23-31. (11).
NAGAO, s. 1929. Kariological studies of the Narcissus plant. 1. Somatic chromosome numbers of some garden varieties and some meiotic phases of a triploid variety. Memoirs of the College of Science of Kyoto Imperial University, Series B, Vol. 4, pp. 175-198 (12).
NAGAO, S. 1933. Number and behaviour of chromosomes in the genus Narcissus. Memoirs of the College of Science of Kyoto Imperial University, Series B, Vol. 8, pp. 81-200. (13).
PHILP, J. 1934. Narcissus chromosome numbers. Royal Horticultural Society Daffodil Year Book, Vol. 5, pp. 52-53. (14).
Sharma, a.k. and Sharma, a. 1961. Chromosome studies of some varieties of Narcissus tazetta L. Caryologia, Vol. 14, pp. 97-106. (15).
sTomps, T.J. 1919. Gigas-Mutation mit und ohne Verdoppelung der chromosomenzahl. Zeitschrift für Induktive Abstammungs und Vererbungslehre (Berlin), Vol. 21, pp. 10-15. (16).
wYLIE, A.P. 1952. The history of the garden Narcissi. Heredity, Vol. 6, pp. 137-156. (17).
$\overline{\text { a }}$ Table 1. Chromosome numbers in Narcissus cultivars. Those referred to as 0 are original results obtained in the author's laboratory.

| Cultivar | Classification and date of origin | 2 n | Ref. | Cultivar | Classification and date of origin | 2n | Ref. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Ababa | 2W-O, 1929 | 27 | 0 | Arcadia | 2W-O, 1910 | 28 | 6 |
| Abba | 4W-WOO, 1984 | 17 | 0 | Arctic Gold | 1Y-Y, 1951 | 28 | 0 |
| Abel Tasman | IIW-WYO, 1970 | 28 | 0 | Ardelinis | 1W-W, 1934 | 28 | 6 |
| Accolade | 3W-R, 1956 | 28 | 1 | Ardour | 3Y-R, 1952 | 28 | 0 |
| Ace of Diamonds | 9W-O, 1923 | 14 | 1 | Ard Righ | IY-Y, 1885 | 14 | 0 |
| Acropolis | 4W-R, 1955 | 28 | 0 | Arish Mell | 5W-W, 1961 | 21 | 0 |
| Actata | 9W-GWO, 1927 | 28 | 0, 5, 6 | Armada | 2Y-O, 1938 | 28 | 0 |
| Aflame | 3W-YOO, 1938 | 28 | 0 | Array | 9W-GYR, 1982 | 14 | 0 |
| Agnes Montefiore | 2W-WWY, 1928 | 28 | 6 | Ascot | 4Y-YOO, 1962 | 28 | 0 |
| Agora | 2W-O, 1959 | 28 | 0 | Aspasia | 8W-Y, 1908 | 24 | 0 |
| thoy | $11 \mathrm{~W}-\mathrm{Y}, 1960$ | 28 | 5 | Auburn | $5 \mathrm{Y}-\mathrm{Y}, 1951$ | 21 | 0 |
| Air Marshal | 2Y-O, 1953 | 28 | 0 | Aurelia | $7 \mathrm{Y}-\mathrm{Y}, 1913$ | 21 | 6 |
| Alabaster | 4W-W, 1972 | 14 | 0 | Avalanche | 8W-Y, 1906 | $31+1 B$ | 0 |
| Alayne | 2W-YYO, 1947 | 28 | 0 | Avenger | 2W-O, 1957 | 28 | 0 |
| Albany | 8W-YOO, 1931 | 31 | 0 | Baby Moon | $7 \mathrm{Y}-\mathrm{Y}, 1958$ | 14 | 0 |
| Albatross | 3W-YYO, 1891 | 28 | 0,17 | Baby Star | 7Y-Y, 1949 | 14 | 1 |
| Albicans | IW-W, 1884 | 14 | 12,13 | Baccarat | IIY-Y, 1950 | 28 | 5 |
| Albion | 3W-Y, 1877 | c. 14 | 16 | Bahram | $2 \mathrm{Y}-\mathrm{O}, 1935$ | 28 | 6 |
| Albus Plenus Odoratus | 4W-W, 1629 | 14 | 0 | Balamara | 2Y-Y, 1973 | 28 | 0 |
| Aldergrove | 2W-Y, 1953 | 28 | 0 | Balvenie | 2W-GPP, 1976 | 28 | 0 |
| Aleppo | 3W-R, 1928 | 28 | 0 | Bambi | 1W-Y, 1948 | 14 | 0 |
| Alison Johnstone | 2W-W, $19+1$ | 28 | 6 | Bantam | 2Y-OOR, 1950 | 27 | 0 |
| Allurement | 2W-P, 1959 | 28 | 0 | Barnby Moor | 3W-Y, 1979 | 28 | 0 |
| Alsace | 8W-YYO, 1907 | 17 | 4 | Barrett Browning | 3W-O, 1945 | 27 | 0 |
| Amber Castle | 2YW-WPP, 1976 | 28 | 0 | Barrett Browning | 3W-O, 1945 | 28 | 0 |
| Ambulle | 2Y-YYO, 1921 | 28 | 6 | Barrii Conspicuus | 3Y-Y, 1869 | 21 | 0 |
| Amor | 3W-YYO, 1971 | 28 | 0 | Bartley | 6Y-Y, 1934 | 21 | 0, 6, 17 |
| Anacapri | 3W-YYR, 1960 | 28 | 0 | Bath's Flame | $3 \mathrm{Y}-\mathrm{O}, 1914$ | 21 | 0 |
| Angel | 3W-W, 1960 | 28 | 0 | Bawnboy | IY-Y, 1960 | 28 | 0 |
| Ann Abbott | 2W-P, 1947 | 28 | 0 | Beacon | 3W-YOR, 1897 | 28 | 6 |
| Anzio | 2W-O, 1945 | 28 | 6 | Bealita | $3 \mathrm{Y}-\mathrm{O}, 1968$ | 28 | 0 |
| Apricot | 1W.Y, 1897 | 14 | 0 | Beersheba | 1W.W. 1923 | 28 | 0, 5, 6, 17 |
| April Tears | 5Y-Y, 1939 | 14 | 0 | Beersheba | 1W-W, 1923 | 29 | 10 |
| Aranjuez | 2Y-YYO, 1933 | 28 | 5 | Beirut | 2W-YYR, 1944 | 28 | 6 |


| Cultivar | Classification and <br> date of origin | 2n | Ref. |  | Cultivar | Classification and <br> date of origin | 2n |
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| Cultivar | Classification and date of origin | 2 n | Ref. | Cultivar | Classification and date of origin | 2n | Ref. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Caramel | 9W-O, 1913 | 28 | 0 | Colley Gate | 3W-YOR, 1972 | 28 | 0 |
| Caravelle | 1Y-Y, 1959 | 27 | 0 | Colorange | 11Y-O, 1950 | 28 | 0 |
| Carbineer | 2Y-O, 1927 | 28 | 0, 5, 6 | Coloratura | 3W-WWO, 1956 | 27 | 0 |
| Carlion | 2Y-Y, 1927 | 28 | 5 | Como | 9W-GYR, 1973 | 14 | 0 |
| Carnmoon | 3W-WWY, 1953 | 28 | 0 | Compressa | 8W-Y, ? | 31 | 0 |
| Cassata | 11W-W, 1963 | 28 | 0 | Concolor | 5Y-Y, 1877 | 14 | 0 |
| Catawba | 9W-GYO, 1948 | 28 | 0 | Conspicuous | 3Y-YYO, 1869 | 21 | 12 |
| Cathay | 2Y-R, 1962 | 29 | 0 | Constantine | IY-Y, 1930 | 28 | 0 |
| Cavssand | 2W-Y, 1978 | 28 | 0 | Content | IW-WWY, 1927 | 28 | 0 |
| Celestial | 5Y-Y, 1950 | 21 | 0 | Contrapunt | 2Y-O, 1962 | 27 | 0 |
| Ceylon | 2Y-O, 1943 | 27 | 0 | Convair | 1Y-Y, 1938 | 27 | 0 |
| Ceylon | 2Y-O, 1943 | 28 | 1 | Cora Ann | 7WW-Y, 1939 | 21 | 0 |
| Chania | 1W-W, 1984 | 28 | 0 | Coral Ribbon | 2W-WWP, 1964 | 28 | 0 |
| Chantain | 2W-Y, 1963 | 28 | 0 | Cornet | $6 \mathrm{Y}-\mathrm{Y}, 1953$ | 21 | 0 |
| Charity May | $6 \mathrm{Y}-\mathrm{Y}, 1948$ | 21 | 0 | Cotopaxi | 2Y-O, 1943 | 28 | 6 |
| Charles First | $1 \mathrm{Y}-\mathrm{Y} 1908$ | 26 | 6 | Court Martial | $2 \mathrm{Y}-\mathrm{O}, 1956$ | 28 | 0 |
| Charter | 2Y-W, 1964 | 28 | 0 | Cove | 2Y-Y, 1939 | 28 | 0 |
| Chastity | 8W-W,? | 30 | 15 | Coverack Glory | 2Y-Y, 1927 | 28 | 6 |
| Chatsworth | IW-Y, 1939 | 28 | 6 | Coylum | 3W-GWW, 1967 | 14 | 0 |
| Cheerfinlness | +W-WYY, 1923 | 24 | 0,6,15 | Cragford | 8W-O, 1930 | 17 | 1 |
| Cheerio | 2Y-O, 1932 | 28 | 6 | Craigdun | 2W-OOY, 1979 | 28 | 0 |
| Chelsho | 1Y-Y, 1929 | 28 | 6 | Cramer | ? ? | 21 | 5 |
| Cherie | 7W-P, 1935 | 21 | 6 | Crepello | 3W-GWY, 1957 | 28 | 0 |
| Chesterton | 9W-GYR, 1979 | 14 | 0 | Crescendo | 2Y-YYO, 1945 | 28 | 0 |
| Chevalier | IY-Y, 1956 | 28 | 0 | Crocus | 2Y-Y, 1927 | 28 | 0,6 |
| Chinese Sacred Lily | 8.? ? | 30 | 7,13 | Croesus | 2Y-YYO, 1912 | 21 | 0 |
| Chinese White | 3W-W, 1937 | 28 | 0 | Cromarty | 1Y-Y, 1933 | 28 | 6 |
| Chinita | 8Y-YRR, 1922 | 31 | 0 | Culmination | 2W-P, 1982 | 28 | 0 |
| Chinook | 2W-Y, 1952 | 28 | 0 | Curly | 2Y-Y, 1968 | 28 | 0 |
| Cibola | 2Y-Y, 1952 | 28 | 0 | Cushendall | 3W-GWW, 1931 | 14 | 0 |
| Cicely | 2W-W, 1927 | 28 | 0,6 | Cushendun | 3W-Y, 1980 | 14 | 0 |
| Citrix | IY-Y, 1953 | 28 | 5 | Cushlake | 3W-W, 1934 | 14 | 6 |
| C. J. Backhouse | 2Y-YOO, 1869 | 14 | 0 | Cyclataz | $8 \mathrm{Y}-\mathrm{O}, 1922$ | 17 | 17 |
| Cleena | 2W-OOY, 1939 | 28 | 6 | Cyclone | 6Y-Y, 1960 | 28 | 0 |
| Cloncarrig | 1Y-Y, 1952 | 28 | 0 | Cyclops | 1Y-Y, 1974 | 28 | 0 |
| Clumber | 3W-Y, 1975 | 28 | 0 | Cypri | 8-? ? | 30 | 7 |
| Codlings and Cream | 4W-Y, 1820 | 14 | 0 | Dactyl | 9W-GYR, 1923 | 14 | 0 |


| Cultivar | Classification and | 2 n | Ref. | Cultivar | Classification and | 2n |
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| Cultivar | Classification and date of origin | 2 n | Ref. | Cultivar | Classification and date of origin | 2 n | Ref. | 哭 |
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| Fair Lady | 9W-YYR, 1923 | 14 | 6 | Frou-frou | 4W-W, 1984 | 14 | 0 | 0 |
| Fairmaid | 3W-GYY, 1970 | 28 | 0 | Fuego | 2Y-R, 1976 | 29 | 0 | L |
| Fairy Circle | 3W-WWP, 1913 | 14 | 6 | Furbelow | $4 \mathrm{Y}-\mathrm{O}, 1961$ | 27 | 0 | Z |
| Fairy Footsteps | 3W-GWW, 1982 | 14 | 0 | Fusilier | $3 \mathrm{Y}-$ ?, 1907 | 14 | 3 | - |
| Fairy Wings | 6W-Y, 1938 | 14 | 6 | Fusilier | 3Y-?, 1907 | 28 | 3 | 3 |
| Falaise | 4W-O, 19.45 | 26 | 0 | Galway | 2Y-Y, 1942 | 28 | 0 | 2 |
| Farewell | 2W-Y, 1938 | 28 | 6 | Gamay | 1W-Y, 1984 | 28 | 0 | Z |
| Favell Lee | 2W-Y, 1944 | 28 | 6 | Garden Princess | $6 \mathrm{Y}-\mathrm{Y}, 1938$ | 28 | 5 |  |
| February Gold | 6Y-Y,'1923 | 21 | 0,17 | Garibaldi | $2 \mathrm{Y}-\mathrm{O}, 1933$ | 28 | 6 |  |
| February Silver | 6W-W, 1949 | 35 | 0 | Garron | 1Y-Y, 1934 | 28 | 0,6 |  |
| Felindre | 9W-GYR, 1930 | 14 | 1 | Gaucho | $2 \mathrm{Y}-\mathrm{O}, 1953$ | 29 | 0 |  |
| Fermoy | 2W-YOO, 1938 | 28 | 0 | Gaylord | 2Y.YOO, 1979 | 28 | 0 |  |
| Feu de Joie | 4W-O, 1927 | 21 | 6 | Gay Record | 4W-O, 1964 | 28 | 0 |  |
| Filly | 2W-W, 1984 | 28 | 0 | Gay Song | 4W-W, 1968 | 28 | 0 |  |
| Film Queen | 2Y-YYO, 1955 | 27 | 0 | Gay Symphony | $4 \mathrm{~W}-\mathrm{Y}, 1973$ | 28 | 0 |  |
| Finland | 2W.Y, 1940 | 28 | 0 | Gay Time | 4W-R, 1952 | 28 | 0 |  |
| Fiorella | 3W-YYO, 1963 | 28 | 0 | Gem of Antrim | 2W-P, 1964 | 28 | 0 |  |
| Firebrand | 3WY-R, 1903 | 14 | 0,6 | Gem of Ulster | 2W-P, 1964 | 28 | 0 |  |
| Fire Chief | 2Y-R, 1954 | 28 | 0 | George Leak | 2W-O, 1960 | 28 | 0 |  |
| Firemal | 3W-O, 1910 | 21 | 5 | Geranium | 8W-O, 1930 | 17 | 0,6,17 |  |
| Flamenco | 2W-O, 1935 | 28 | 0,6 | Gervo | 2W-W, 1944 | 30 | 5 |  |
| Flaneur | $11 \mathrm{Y}-\mathrm{Y}, 1948$ | 28 | 5 | Gimi | 6W-P, 1981 | 27 | 0 |  |
| Floore | 9W-WWO, 1939 | 28 | 6 | Gin and Lime | 1Y-GWW, 1973 | 28 | 0 |  |
| Flower Drift | 4W-OYO, 1966 | 28 | 0 | Gipsy Moth | 2W.W. 1967 | 29 | 0 |  |
| Flower Record | 2W-WWO, 1943 | 28 | 0, 5 | Glenravel | 1W-Y, 1934 | 28 | 6 |  |
| Flowersong | 2Y-YYO, 1960 | 28 | 0 | Gloria Mundi | 2Y-YOR, 1869 | 21 | 12, 13 |  |
| Folly | 2W-O, 1926 | 28 | 6 | Gloriosus | 8W-Y, 1850 | 20 | 0 |  |
| Foresight | 1W-Y, $19+4$ | 28 | 0 | Glorious | 8W-O, 1923 | 24 | 0,6 |  |
| Forte | 2W-P, 1986 | 28 | 0 | Glory of Lisse | 9W-YYR, 1901 | 14 | 0 |  |
| Fortune | 2Y.O, 1917 | 28 | 5,6,17 | Glowing Red | 4W-R, 1968 | 28 | 0 |  |
| Fortwilliam | IY-Y, 1960 | 28 | 0 | Glynver | 3W-O, 1921 | 28 | 0 |  |
| Foundling | 6W-P, 1969 | 27 | 0 | Godolphin | IY-Y, 1925 | 28 | 6 |  |
| Foxfire | 2W-GWP, 1968 | 28 | 0 | Gold Collar | 11Y-Y, 1956 | 28 | 5 |  |
| Fragrant Rose | 2W-GPP, 1978 | 28 | 0 | Golden Amber | 2Y-ORR, 1975 | 28 | 0 |  |
| Franklin | 8?, ? | 20 | 13 | Golden Aura | 2Y-Y, 1964 | 28 | 0 |  |
| Frigid | 3W-W, 1935 | 14 | 0 | Golden Cycle | 6Y-Y, 1916 | 21 | 0 |  |
| Frost in May | 9W-GGY, 1981 | 14 | 0 | Golden Dawn | 8Y-O, 1958 | 24 | 0 |  |


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$\left.\begin{array}{llll|lll}\text { Cultivar } & \begin{array}{lllll}\text { Classification and } \\ \text { date of origin }\end{array} & 2 n & \text { Ref. } & \text { Cultivar } & \text { Classification and } & \text { 2n } \\ & & & & \text { date of origin }\end{array}\right]$
$\left.\begin{array}{llll|llll}\text { Cultivar } & \begin{array}{lllll}\text { Classification and } \\ \text { date of origin }\end{array} & 2 \mathrm{n} & \text { Ref. } & \text { Ref. } \\ & & & \text { Cultivar } & \text { Classification and } \\ \text { date of origin }\end{array}\right]$

| Cultivar | Classification and <br> date of origin | $2 n$ | Ref. | Cultivar | Classification and <br> date of origin | 2n |
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| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Princeps Maximus | IW-Y, 1884 | 14 | 13 | Rip Van Winkle | 4Y-Y, 1885 | 21 | 0 |
| Principal | 1Y-Y, 1931 | 28 | 6 | Roberta | 1W-?, 1954 | 28 | 0 |
| Professor Einstein | 2W-R, 1946 | 28 | 0 | Roberta Watrous | 7Y-GYP, 1979 | 21 | 0 |
| Profile | 2W-Y, 1970 | 28 | 0 | Robey | IY-Y, 1937 | 28 | 0 |
| Prologue | IW-Y, 1952 | 28 | 0 | Rockery Beauty | IW-Y, 1925 | 14 | 6 |
| Queen of Bicolors | IW-Y, 1925 | 28 | 0 | Roger | $6 \mathrm{Y}-\mathrm{O}, 1952$ | 37 | 0 |
| Queen of Bicolors | IW-Y, 1925 | 43 | 0 | Romantica | 2O-O, 1960 | 29 | 5 |
| Queen of Narcissi | 3W-YYR, 1939 | 14 | 5 | Romeo | 8Y-O, 1946 | 17 | 0 |
| Queen of Spain | $10 \mathrm{Y}-\mathrm{Y}, 1888$ | 20 | 2,12 | Rosaline Murphy | 2Y-Y, 1958 | 14 | 1 |
| Queen of Spain | 10Y-Y, 1888 | 21 | 14 | Roselene | 2W-P, 1949 | 28 | 6 |
| Queen of the North | 3W-Y, 1908 | 21 | 0 | Rose of Tralee | 2W-P, 1937 | 27 | 0,6 |
| Quick Step | 7W-Y, 1955 | 28 | 0 | Rose Royale | 2W-P, 1958 | 28 | 0 |
| Quiet Day | 2W-GPP, 1983 | 28 | 0 | Rossini | 2W-O, 1968 | 28 | 0 |
| Quince | $6 \mathrm{Y}-\mathrm{Y}, 1953$ | 24 | 0 | Rosy Trumpet | 1W-P, 1928 | 14 | 0 |
| Quirinus | 2Y-O, 1939 | 28 | 0 | Rowallane | IY-Y, 1960 | 28 | 0 |
| Raeburn | 9W-GYR, 1913 | 14 | 1 | Roxane | IW-W, 1927 | 28 | 6 |
| Rainbow | 2W-WWP , 1961 | 28 | 0 | Royal Armour | 1Y-Y, 1967 | 28 | 0 |
| Rameses | 2W-R, 1960 | 28 | 0 | Royal Charm | 2Y-ORR, 1964 | 28 | 0 |
| Rashee | IW-W, 1952 | 28 | 0 | Royal Coachman | 2W-GYO, 1969 | 28 | 0 |
| Rathkenny | 1W-Y, 1938 | $28+1 \mathrm{~B}$ | 0 | Royal Gold | 1Y-Y, 1956 | 29 | 0 |
| Red Cottage | 2W-YYR, 1967 | 28 | 0 | Royal Mail | 2Y.O, 1937 | 28 | 6 |
| Red Defiance | $2 \mathrm{Y}-\mathrm{O}, 1932$ | 28 | 6 | Royal Orange | 2W-O, 1953 | 28 | 0 |
| Red Devon | 2Y-O, 1943 | 28 | 0 | Royal Regiment | 2W-O, 1961 | 28 | 0 |
| Red Goblet | 2Y-O, 1937 | 28 | 0 | Royal Revel | 2Y-O, 1967 | 28 | 0 |
| Redhill | 2W-R, 1978 | 28 | 0 | Royal Wedding | 2W-GWY, 1982 | 29 | 0 |
| Red Rascal | 2Y-R, 1950 | 28 | 0 | Rushlight | 2Y-O, 1957 | 28 | 0 |
| Red Rim | 9W-YYR, 1923 | 14 | 5 | Rustom Pasha | 2Y-O, 1930 | 28 | 0,6,17 |
| Rembrandt | 1Y-Y, 1926 | 28 | 0 | Sacajawea | 2Y-YYO, 1954 | 28 | 0 |
| Replete | 4W-P, 1975 | 28 | 0 | Sacramento | 3W-W, 1949 | 28 | 0 |
| Reprieve | 3W-GWY, 1947 | 28 | 0 | Safrano | ?, ? | 28 | 0 |
| Reynoldstown | $2 \mathrm{Y}-\mathrm{O}, 1937$ | 28 | 6 | Saint Agnes | 8W-O, 1926 | 17 | 0 |
| Rijnveld's Early Sensation | 1Y-Y, 1943 | 33 | 0 | Saint Ives Saint Keverne | 2Y-Y, 1927 2Y-Y, 1934 | 28 28 | 6 1 |
| Rima | IW-P, 1954 | 28 | 0 | Saint Keyne | 8W-O, 1927 | 24 | 0 |
| Riotous | $4 \mathrm{Y}-\mathrm{Y}, 1946$ | 28 | 0 | Saint Olaf | 3W-W, 1913 | 28 | 0 |
| Rippling Waters | SW-W, 1932 | 21 | 0,6 | Saint Patrick's Day | $2 \mathrm{Y}-\mathrm{Y}, 1964$ | 28 | 0 |
| Rip Van Winkle | 4Y-Y, 1885 | 14 | 0 | Salerno | 2W-O, 1944 | 27 | 6 |


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| Salmon Trout | 2W-P, 1948 | 27 | 0 | Silver Circle | 3W-W, 1941 | 28 | 6 |
| Salome | 2W-PPY, 1958 | 28 | 0 | Silver Convention | 1W-W, 1978 | 28 | 0 |
| Samba | SY-O, 1952 | 21 | 0 | Silver Leopard | 3W-WWY, 1972 | 28 | 0 |
| Sanda | 1W-W, 1954 | $45+1 B$ | 0 | Silver Moon | 2W-W, 1959 | 28 | 0 |
| Sandringham | 3W.Y, 1933 | 21 | ${ }^{6}$ | Silver Sand | 2W-GWW, 1963 | 14 | 0 |
| Sarchedon | 9W-GYR, 1913 | 14 | 6,17 | Silver Spell | 3W-WW, $194+$ | 28 | 0 |
| Sateen | 2W.YYP, 1968 | 27 28 | 6 | Silver Surf | 2W-W, 1978 | 28 | 0 |
| Scarlet Gem | $8 \mathrm{Y} .0,1910$ | 17 | 0,6 | Silvretta | 1Y-Y, 1949 | 29 | 5 |
| Scarlet Leader | $2 \mathrm{Y}-\mathrm{O}, 1921$ | 28 | 5 | Sioux | 2Y-O, 1966 | 28 | 0 |
| Scarlet Periection | $2 \mathrm{Y}-\mathrm{O}, 1921$ | 28 | 1 | Sir Samuel | 2W-P, 1973 | 28 | 0 0, 17 |
| Scarlett O'Hara | 2Y-R, 1950 | 28 | 0 | Sir Watkin | $2 \mathrm{Y}-\mathrm{Y}, 1884$ | 21 | 0,6,12, 17 |
| Scilly W'hite | $8 \mathrm{~W}-\mathrm{Y}, 1885$ | 32 | 5 | Sir Winston Churchill | 4W-O, 1966 | 17 | 0 |
| Scorcher | $2 \mathrm{Y}-\mathrm{O}, 1952$ | 28 | 0 | Skylon | 7Y-YRR, 1951 | 22 | 0 |
| Scotch Rose | 2W.P, 1942 | 28 | 6 | Sligo | 2Y-Y, 1943 | 28 | 6 |
| Sea Green | 9W-GWR, 1930 | 14 | 0 | Sneeuwprinses | 3W-YYO, 1944 | 27 | 1 |
| Seaiing W'ax | 2Y-R, 1957 | 28 | 0 | Snoople | ${ }_{7 W} \mathbf{6 W - G P P}$-1935 | 28 | 0 |
| Sea Shell | 2W-Y, 1908 | 28 | 6 | Snow Bunting | 3W-GWW, 1972 | 28 | O |
| Sea Urchin | 2W.Y, 1935 | 28 29 | 0 | Snowdean | $2 \mathrm{~W}-\mathrm{W}, 1950$ | 28 | 0 |
| Sedate | 2W-P, 1967 | 28 | 0 | Snow Gem | 3W-O, 1957 | 28 | 0 |
| Sempre Avanti | 2W.O, 1938 | 28 | 5 | Snow Gleam | 1W-GWW, 1977 | 28 | 0 |
| Sentinel | 2W-P, 1972 | 28 | 0 | Snow Princess | 2W-W, 1949 | 27 | 5 |
| Sextant | 6W-GWW, 1981 | 28 | 0 | Snow Queen | 2W-W, 1931 | 28 | 6 |
| Shah | $7 \mathrm{Y}-\mathrm{Y}, 1949{ }^{\text {a }}$ | 28 | 0 | Snowshill | 2W-W, 1949 | 28 | 0 |
| Shandon | 2W-GOO, 1979 | 28 | 0 | Solario | 2W-Y, 1927 | 28 | 6 |
| Shantallow | 3W-GGY, 1956 | 14 | 0 | Soleil d'Or | $8 \mathrm{Y}-\mathrm{O}, 1807$ | 20 |  |
| Shor Silk | 5W-W, 1933 | 21 | 0 | Soleil d'Or | ${ }^{8 Y} \mathrm{Y}-\mathrm{O}, 1807$ | 30 | 5, 6, 13, 17 |
| Show Countess | 2W-W, 1946 | 28 | 0 | Solferino | 1Y-Y, 1930 | 29 |  |
| Shriner | 2W-Y, 1972 | 28 | 0 | Sonata | 9W-GYR, 1910 | 14 | 0 |
| Shy Face | 2W-GWP, 1965 | 29 | I | Sonia Sloan | 2W.OOY, 1971 | 29 | 0 |
| Sicily White | 8W-Y, | 21 | 11 | Sorbet | 11W-YYO, 1966 | 28 | 0 |
| Sidney Torch | 2Y-YOO, 1951 | 28 | 0 | Southern Gem | 2W-W, 1913 | 21 | 0 |
| Silent Morn | 3W-YYO, 1964 | 28 | 0 | Spangles | 8Y-O, ? 1931 | 34 17 | 0 |
| Silent Valley | IW-W, 1964 | 28 | 0 | Sparkling Eye | 8W-GOO, 1931 | 17 | 5 |
| Silver Bells | SW-W, <br> 8W-W, <br> S | ${ }_{28}^{22}$ +1B | 0 0,17 | Spellibinder Spellbinder | IY-W, 1944 | 29 | 0 |


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| Spitzbergen | IW.Y, 1943 | 28 | 0 | Tebourba |  |  |  |
| Spring Glory | IW-Y, 1914 | 29 | 5 | Tecoma | 3W-R, 1944 | 28 | 6 |
| Squire | 1Y-Y, 1969 | 28 | 0 | Telamonius Plenus | 4Y-Y', | 28 14 |  |
| Stadium | 2W-Y, 1948 | 28 | 6 | Telamonius Plenus | 4Y-Y, ? | 14 | 2,6,10 |
| Stainless | 2W-W, 1960 | 28 | 0 | Telamonius Plenus | 4Y-Y, ? | 28 | 10 |
| Standard Value Standfast | $1 \mathrm{Y}-\mathrm{Y}, 1949$ | 28 | 0 | Tête-a-Tête | 6Y-Y, 1949 | $24+1$ B | 10 |
| Standrast | 1YW-YY'1982 1909 | ${ }_{28}^{29}+1 \mathrm{~B}$ | 0 | Texas | $4 \mathrm{Y}-\mathrm{O}, 1921$ | 21 | 5 |
| Stocken | 3W-?, 1950 | 28 | 0 | Thalia | ${ }_{5}^{5} \mathrm{~W}-\mathrm{W}, 1916$ | 21 | 5 |
| Straight | IW.Y. 1938 | 28 | 0 | Thoughtful | $5 \mathrm{Y}-\mathrm{Y}, 1951$ | 21 | 0 |
| Strines | 2Y-Y, 1965 | 28 | 0 | Tibet | 2W-W, 1942 | 28 | 0 |
| Stromboli | 2W-O, 1959 | 28 | 0 | Tinker | 2Y-O, 1937 | 28 | 0 |
| Sudan | 2Y-R, 1938 | 28 | 6 | Tittle Tattle | TY-Y, 1946 | 29 | 0 |
| Sugarbush | 7W-YYW, 1954 | 21 |  | Toorak Gold | 7Y-O, 1953 | 21 | 0 |
| Suisen | 8-?, ? | 30 | 11 | Topolino | 1Y-Y, 1965 | 28 14 | 0 |
| Sulphur Crown | $4 \mathrm{Y}-\mathrm{Y}, 1821$ | 14 | 5 | Toreador | 3W-R, 1961 | 28 | 0 |
| Sulphur Phoenix | $4 \mathrm{Y}-\mathrm{Y}, 1820$ | 14 | 0 | Tranquil Morn | 3W-W, 1962 | 28 | 0 |
| Sunburst | 1Y-Y, 1931 $4 \mathrm{Y}-\mathrm{Y}, 1955$ | 28 | 6 | Tredore | 3Y-O, 1927 | 28 | 6 |
| Sundial | 7Y-O, 1955 | 28 14 | 0 | Trena | 6W-Y, 1971 | 21 | 0 |
| Sun Fire | 3Y-R, 1962 | 28 | 0 | Trenithon | 1Y-Y, 1950 | 28 | 0 |
| Sunproof Orange | 2Y-O, 1935 | 28 | 6 | Tresamble | SW-W, 1930 | 21 | 0, 5 |
| Sunrise | 3W-YYO, 1901 | 14 | 0 | Trevithian | $7 \mathrm{Y}-\mathrm{Y}, 1927$ | 21 | 0, 5, 6, 17 |
| Sunstar | 3 3W-R, 1921 | 28 | 6 | Tricollet | TY-Y, 1949 | 28 | 0 |
| Suzy | $7 \mathrm{Y}-\mathrm{O}, 1954$ | 21 | 0 | Trifine | 2Y-O, 1970 | 28 | 0 |
| Swansdown | +W.W. 1939 | 26 | 0 | Tristram | 2Y-Y, 1976 | 29 | 0 |
| Sweet Memory Sweeiness | 2W-P, 1963 | 27 | 0 | Trostan | IW-Y, 1938 | 28 | 6 |
|  | $7 \mathrm{Y}-\mathrm{Y}, 1939$ | 21 | 0 | Trousseau | IW-Y, 1934 | 28 | 6 |
| Sydling | SW.GWWW 1977 | 21 | 0 | Trumpeter | 1Y-Y, 1975 | 28 | 0 |
| Taffeta | 12W-W, 1952 | 28 | 0 | Trumpet Major | IY-Y, | 14 | 14 |
| Tahiti | +Y-R, 1956 | 28 | 1 | Tuesday's Child | SW-Y, 1964 | 21 | 0 |
| Takoradi | 4W-W, 1963 | 28 | 0 | Tullyroe | 2W-R, 1960 | 28 | 0 |
| Talland | $2 \mathrm{Y}-$ ? 1965 | 28 | 0 | Turin | 2W-WWY, 1927 | 28 | 6 |
| Tamar Fire | 4Y-R, 1976 | 28 | 0 | Tutankhamun | 3W-GOO, 1927 | 28 | 6 |
| Tarlatan | 12W-W, 1952 | 28 | 1 | Twink | 4W-O, 1927 | 28 | 0 |
| $\underline{\text { Tawny Lad }}$ | 2Y-0, 1976 | 28 | 0 | Ucluluet Gem | 5-子, 19+9 | 21 | 6 |


| Cultivar | Classification and date of origin | 2 n | Ref. | Cultivar | Classification and date of origin | 2 n | Ref. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | 0 | White Lady | $\text { 3W-Y, } 1898$ | 21 | $0$ |
| Ulimus | 2Y-O, 1947 | ${ }_{28}^{28}+4 \mathrm{~B}$ | 0 | Whiteley Gem | $2 \mathrm{Y}-\mathrm{O}, 1928$ | 28 | $6,17$ |
| Unique | IW.Y, 1961 IY.Y. 1923 | $27+1 B$ | 0,5 | White Lion | 4W-WYY, 19.49 | 28 | 0 |
| Unsurpassable | 6W-P, 1981 | 28 | 0 | White Majesty | IW-W, 1970 | 28 | 0 |
| Valiant Spark | 2Y-O, 1959 | 28 | 0 | White Marvel | 4W-W, 1950 | 21 | 0 |
| Valinore | 2W-P, 1978 | 28 | 0 | White Nile | 2W-W, 1922 IIW-O,? | 29 28 | 0 |
| Van Sion | 4Y-Y, 1620 | 14 | ${ }_{2}^{0}$, 6, 17 | White Orange | 5W-W, 1950 | 35 | 0 |
| Van Waveren's Giant | IY-Y, 1900 | 28 | $\frac{2}{5}, 6,17$ | White Owl White Pearl | 8W-Y, 1861 | 22 | 11 |
| Van Wereld's Favourite | IW-Y, 1936 | 28 21 | 0 | White Pink | 11W-P,? | 28 | 0 |
| Verdin | 7Y-W, 3 W-R, 1930 | 28 28 | 0 | White Sail | 4W-W, 1946 | 14 | 0 |
| Verger | 3W-W, 1958 | 28 | 0 | White Sentinel | 2W-Y, 1926 | 28 | 6 |
| Vicoria | IW-Y, 1897 | 14 | 12, 13 | White's Hybrid | 8-? 2 W-W 1958 | 28 | 0 |
| Victoria | IW-Y, 1897 | 22 | 0, 2, 6, 14 | White Spire | 1W-W, 1970 | 28 | 0 |
| Victoria | IW-Y, 1897 | 28 | 5 | White Triumphator | IW-W, 1938 | 28 | 6 |
| Victorious | 2W-Y, 1954 +W-P, 1976 | 28 29 | 0 | Whitewell | 2W-Y, 1910 | 21 | 0,9 |
| Viennese Rose Vigil | +W-W, IW-W, 1947 | 28 | 0 | White Yellopink | 11W-YPP, ? | 28 | 0 |
| Vigilante | I $\mathrm{W}^{\prime}$-W, 1977 | 28 | 0 | Wild Rose | 2W-P, 1939 | 28 | 0 |
| Viking | ! Y- $\mathrm{Y}^{\prime}, 1956$ | 28 | 0 | William Farmer William the Silent | IY-Y, 1978 | 28 | 5 |
| Violetta | 2W-GPP, 1975 | 28 | 6 | Will Scarlet | 2W-O, 1898 | 14 | 0 |
| Volturno | ${ }_{2}^{2 W} \mathrm{~W} \cdot \mathrm{YYO}, 19.45$ | 28 | 6 | Winchester | 2Y-YOO, 1954 | 28 | 0 |
| Vulcan | 2Y-O, 1956 | 28 28 | () | Windblown | 4W-Y, 1946 | 29 | 0 |
| Wahkeena | 2W-YYO,1927 | 28 | 6,17 | Wingadee | 2W-OOY, 1967 | 28 | 0 |
| Waterperry | 7W-Y, 1953 | 21 | 0 | Winifred Van Graven | 3W-YYR, 1954 | 28 | 0 |
| Weicome Inn | ?,1979 | 28 | 0 | Woodcock | 6Y-Y, 19.49 | +29 | 0 |
| Wetherby | 3W-YYR, 1983 | 28 | 0 | Woodgreen | 2W-Y, 1956 | 28 | 0 |
| White Apricot | 11W-P, ? | 28 | 0 | Woodiand Prince | 3W-R, 1962 | 28 | 0 |
| White Chief | IW-W, 1975 | 28 | 0 | Woodiand Star | IY-Y, 1930 | 28 | 6 |
| White Diamond | 1W'W, 1982 | 28 | 0 | W.P. Milner | IW-W, 1869 | 14 | 6 |
| White Emperor | IW-W, 1913 | 28 | 0 | Wrestler | IY.Y, 1930 | 28 | 6 |
| White Empress | 1W-W, 1970 | 14 | 0 | Wybalena | 4W-W, 1968 | 27 | 0 |
| White Fairy | 9W-O, 1927 $2 \mathrm{~W}-\mathrm{Y}, 1973$ | 14 28 | 0 | Yankee Clipper | 2Y-YYO, 1939 | 28 | 0 |
| White Gold | 2W-Y, 1973 | 28 | 0 | Yellow Beauty | IY-Y, 1929 | 28 | 6 |
| Whitehead White Knight | 1W-W, 1907 | 14 | 1 | Yellow Butterfly | 8Y-O, 1981 | 34 | 0 |


| Cultivar | Classification and <br> date of origin | 2n | Ref. |
| :--- | :--- | :--- | :--- |
| Yellow Cheerfulness | 4Y-Y, 1937 | 24 | 0 |
| Yellow Dazzler | IY-Y,1958 | 28 | 0 |
| Yellow Poppy | 2Y-YYO, 1914 | 21 | 6 |
| Yellow Prince | $8 \mathrm{Y}-\mathrm{O}, 1872$ | 30 | 13 |
| Yellow Prize | 7Y-Y, 1931 | 28 | 6,17 |
| Yornup | 2Y-Y,1939 | 27 | 0 |
| Ypsilante | 9W-YYO, 1927 | 14 | 6 |
| Zeeland | 2W-Y,1930 | 28 | 6 |

