# The chromosomes of species, hybrids and cultivars of *Narcissus* L. (*Amaryllidaceae*)

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*Summary.* Chromosome counts are reported for 46 taxa, 8 F$_1$ hybrids and 230 cultivated varieties of *Narcissus* L. and the percentage pollen viability is given for most of them. B chromosomes were found in several species and cultivars. Chromosome numbers rise to the hexaploid level (2n = 42, 43) in species of the subgenus *Narcissus*, but the diploid (2n = 14) is the most commonly-occurring level of ploidy. In the subgenus *Hermione* diploid chromosome counts of 2n = 20 and 22 were obtained (x = 10, 11), in confirmation of reports by previous workers. In cultivars solely derived from the subgenus *Narcissus* eu- and aneu-tetraploids (2n = 28 ± 2) greatly exceed diploids in frequency. Cultivars with complex ancestry involving x = 7 and x = 10 or 11 plants display a wide range of chromosome numbers, and the probable derivation of the chromosome complements of these cultivars and of other real and apparent aneuploids, together with those of some of the more interesting euploids, are given in the light of current knowledge. The levels of ploidy extant in *Narcissus* cultivars are compared and contrasted with those of a range of other genera in which many ornamental cultivars have also been produced.

## INTRODUCTION

The genus *Narcissus* L. is native in western Asia and in Europe as far north as Britain and Scandinavia (Fernandes 1951) and has been the subject of a number of chromosomal investigations (Moore 1982), notably the many works by A. Fernandes (summarised by Jefferson-Brown 1969). The majority of the species (subgenus *Narcissus*) have chromosome numbers based on x = 7 and most of these are diploids (2n = 14), but polyploids ascending through all the possible euploid intermediates to octoploid (2n = 8x = 56) have been reported in *N. bulbocodium* (Fernandes 1967). Occasional triploids (2n = 21) and tetraploids (2n = 28) occur in other species (Fedorov 1969, Moore 1982).

Not closely related cytologically to the above, the subgenus *Hermione* (Haw.) Spach comprises a group of species with basic numbers other than seven, being x = 5, giving 2n = 2x = 10 and 2n = 6x = 30 in *N. serotinus* and perhaps 2n = 4x = 20 in *N. tazetta*, with a secondary alteration to 2n = 22 in some races of the same species and also in related species such as *N. papyraceus* (= *N.* 'Paper White'), *N. pachybolbus* and others (Maugini 1953, Fernandes 1966, Weitz & Feinbrun 1972). The changes to 2n = 20 and 22 are clearly very ancient, because these species behave strictly as diploids, forming only bivalents at meiosis (Fernandes 1950), and they will be referred to as diploids in this paper.

The genus is remarkable for the tremendous proliferation of cultivated varieties which has occurred, principally during the present century. These have been documented carefully by Dr T. Throckmorton of Des Moines, Iowa, U.S.A., and an abridged list has been published recently (Throckmorton 1980) which gives the name, breeder, year of introduction and coded entries summarising the size, flower morphology and colour, height and flowering

time of each cultivar. The work is based on a computerised data bank covering over 10,000 cultivars held by the American Daffodil Society. This is more comprehensive and gives in addition to the above the parentage of each cultivar, its breeder and its chromosome number, if known. As chromosome counts are not given in Throckmorton 1980) the printout of the data bank obtained from the Iowa Methodist Medical Center, 1200 Pleasant Street, Des Moines, Iowa 50309, U.S.A.) was taken as the source of some of the chromosome data used in this article, and will be referred to below as A.D.S. (1981).

Although so many thousands of cultivars of *Narcissus* have been described, chromosome numbers are known for relatively few of them, amounting to about 300 (A.D.S. 1981, Fernandes & de Almeida 1971). The origins of these cultivars are very diverse and must include hybridisations, not only between diploids, but also between individuals of similar or differing levels of polyploidy with the inevitable occurrence of aneuploid individuals among the progeny) and between individuals with differing basic chromosome numbers (x = 7, 10 or 11). Most of these hybridisations would have been made by breeders who had no idea of the chromosome complements of their plants, so the *Narcissus* cultivars constitute an ideal example of chromosome variation and evolution in a genus as influenced by the largely unknowing selection pressures exerted by Man.

In order to obtain more information on this variation the somatic chromosomes of over 200 cultivars were examined in the present study, the results of which will be presented below and analysed in conjunction with previous reports by other authors. While this work was under way the opportunity arose for us to examine a number of species (both in subgenus *Hermione* and in subgenus *Narcissus*) and $F_1$ hybrids between species of *Narcissus*, the chromosomes of some of which are unknown. These results are also included here.

The great majority of *Narcissus* cultivars are of hybrid origin and must therefore be propagated vegetatively in order that their identity can be retained. It follows that, assuming correct naming in every instance, any cultivar bearing the same name as one mentioned here which is used by anyone for further breeding will actually be the same clone as the one which we have studied and will consequently have the same chromosome constitution and behaviour. It was thus considered that it would be of considerable value to those intending to use particular cultivars in breeding programmes to report the pollen fertility of as many plants as possible, the pollen fertility being a good measure of the probable degree of success to be expected when a particular plant is used as a pollen parent in a trial cross. It will also give a similar measure of a plant's likelihood of success as a seed parent, except in those cultivars with double flowers (division 4, see below), many of which have no anthers and consequently zero pollen fertility. These can quite possibly possess a completely normal and fertile gynoecium and be fully seed-fertile.

This article will therefore present data on pollen fertility and chromosome number, the latter comprising 46 taxa, 8 $F_1$ hybrids and 230 cultivars, in order to increase the published knowledge of the cytology of the genus.

## MATERIAL AND METHODS

Bulbs were obtained from three of Britain's major *Narcissus* collections; the Royal Horticultural Society's Garden, Wisley, the Rosewarne Experimental Horticulture Station and the National Collection at the New University of

Ulster, Coleraine; $F_1$ hybrids, mostly between miniature species, were given by Mr J. Blanchard, and the living collection at RBG Kew was also sampled.

Plants were grown in pots placed in cold frames and root tips were collected for chromosome study during periods of maximum root growth, September to November and February to March. Root tips were pretreated for 24 hours at $4°C$ in saturated aqueous alpha-bromonaphthalene and fixed in 1:3 acetic alcohol. After hydrolysis in 1N HCl at 60°C for 7 min. they were stained in Feulgen. Squashes were made in 45% acetic acid, or if the Feulgen stain was too faint, in 1% aceto-orcein. Each slide was frozen with liquid $CO_2$ at $-75°C$ and the coverslip removed with a sharp blade. Both slide and coverslip were dehydrated in absolute ethanol and recombined with a drop of Euparal (B.D.H.). After a period of 2 weeks at 45°C for the mountant to harden the slides were screened with a Wild M20 microscope and suitable cells were photographed with a Zeiss photomicroscope. Slides are retained in the collection of the Cytology department of the Jodrell Laboratory.

For pollen fertility estimates mature dehisced anthers were tapped out on a slide in 1% cotton blue in lactophenol, the large debris removed and a coverslip applied. Stainable, presumed viable, pollen grains were expressed as a percentage of the total number of grains scored, the minimum being 500 for any single analysis.

Representative voucher specimens of leaves and flowers have been deposited in the Kew Herbarium.

## CLASSIFICATION OF Narcissus CULTIVARS

The 10,000 (approx.) cultivars of Narcissus have been grouped for convenience by the Royal Horticultural Society into twelve divisions (Throckmorton 1980). As these are referred to frequently in this article it is appropriate to summarise them here as follows:

Division 1, Trumpet daffodils. Solitary flowers with corona equal to or longer than the perianth segments.

Division 2, Long-cupped daffodils. Solitary flowers with corona one third to almost equal to the length of the perianth segments.

Division 3, Short-cupped daffodils. Solitary flowers with corona less than one third the length of the perianth segments.

Division 4, Double-flowered daffodils of any affinity among Divisions 1–3, 5–9 or 11–12.

Division 5, Triandrus daffodils. Characteristics of N. triandrus dominant in hybrid.

Division 6, Cyclamineus daffodils. Characteristics of N. cyclamineus dominant in hybrid.

Division 7, Jonquilla daffodils. Characteristics of N. jonquilla dominant in hybrid.

Division 8, Tazetta daffodils. Characteristics of N. tazetta dominant in hybrid.

Division 9, Poeticus daffodils. Characteristics of N. poeticus dominant in hybrid.

Division 10, Species, wild forms and wild hybrids, including double-flowered forms.

Division 11, Split-corona daffodils. Corona divided distally for at least one third of its length into segments.

Division 12, Miscellaneous daffodils not falling into Divisions 1–11.

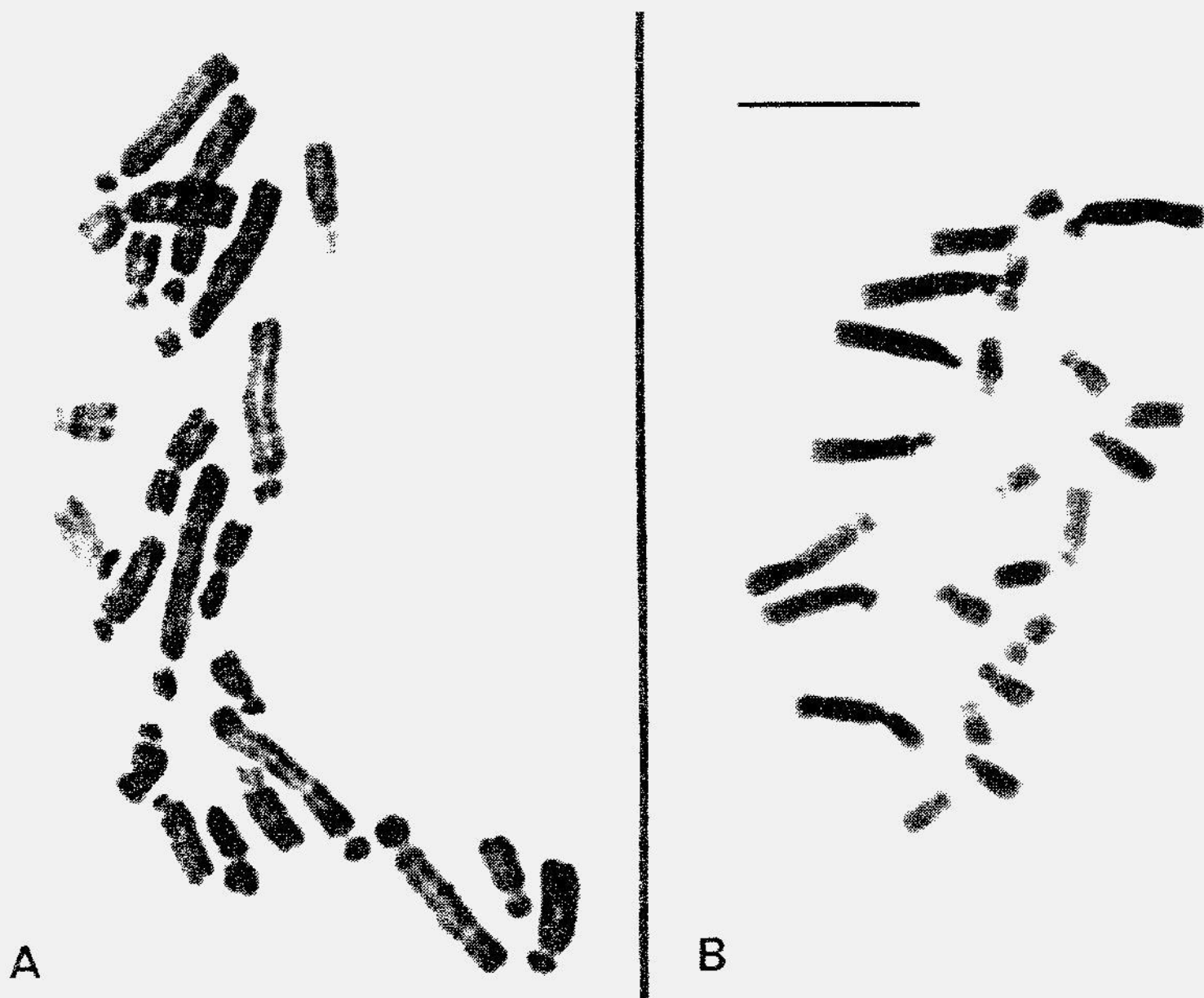All divisions are plants of garden origin except Division 10. Within each

FIG. 1. Somatic chromosomes of *Narcissus* subgenus *Hermione*. **A** *N.* aff. *tazetta*, 2n = 22; **B** *N. papyraceus*, 2n = 22. Scale = 10μm.

division flowers are colour-coded, firstly for the colour of the perianth and secondly for that of the corona, the latter being divided into two or three regions from the centre to the rim if two or more colour bands are present. Colour codes are W (white or nearly so), G (green), Y (yellow), P (pink), O (orange), and R (red). Under this system the cultivar 'Merlin', for example, is classified as 3W-YYR (Throckmorton 1980), which indicates that it has a solitary flower with a white perianth and a short yellow corona with a red rim. A second example 'Fermoy' (2W-YOO) has solitary flowers of which the corona has a yellow base but is predominantly orange and is not as long as the white perianth segments.

## SPECIES AND $F_1$ HYBRIDS

### Chromosome numbers

These are given in Table 1 and some of them are illustrated in Figs. 1–5. It is not intended here to describe in detail the karyotypes of every accession because this would largely duplicate the thorough work of Fernandes. Instead, description and comment will be restricted to features of particular interest.

Of the members of the subgenus *Hermione*, *N. pachybolbus*, *N. papyraceus* and *N.* aff. *tazetta* were found to have 2n = 22 chromosomes and *N. tazetta* to have 2n = 20, confirming earlier counts by Maugini (1953), Fernandes (1966) and Weitz & Feinbrun (1972). The karyotypes of these species tend towards bi-modality, with 8 very large acrocentrics and 14 smaller acro- or metacentrics in the 2n = 22 forms (Figs. 1A, 1B). It was not possible to analyse the karyotype of the 2n = 20 plant, but Fernandes (1966) illustrated a chromosome
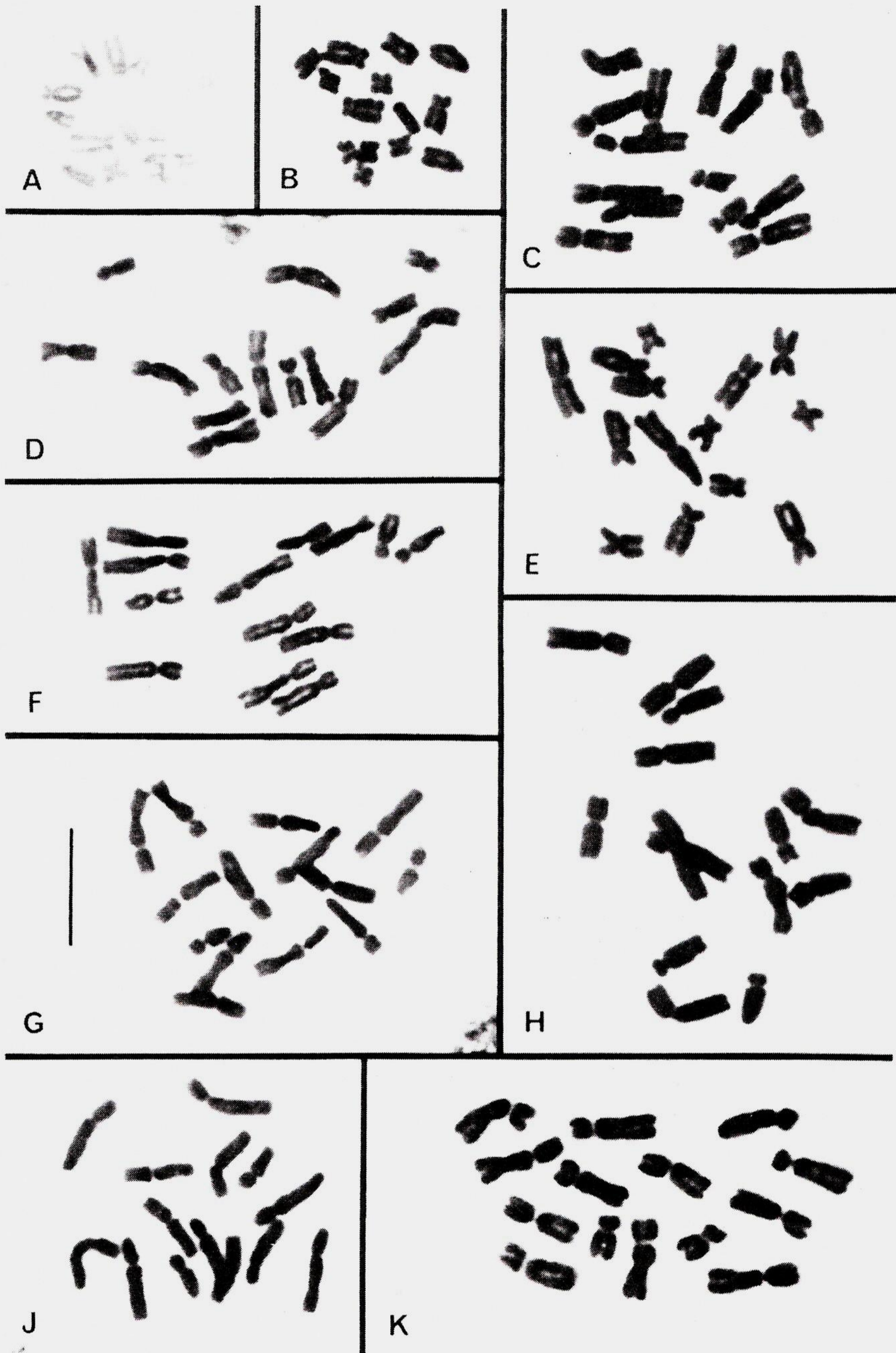
FIG. 2. Somatic chromosomes of diploid *Narcissus*, all 2n = 14. **A** *N. hedraeanthus;* **B** *N. bulbocodium* var. *conspicuus;* **C** *N. longispathus;* **D** *N. juncifolius;* **E** *N. calcicola;* **F** *N. cyclamineus;* **G** *N. nanus;* **H** *N. jonquilla;* **J** *N. hispanicus;* **K** *N. poeticus.* Scale = 10μm.

complement for *N. tazetta* (2n = 20) which was markedly different from the above, comprising 12 large acrocentrics and 8 smaller chromosomes.

The members of the subgenus *Hermione*, with x = 10 or 11 chromosomes are

TABLE 1. Chromosome numbers and pollen fertility in *Narcissus* species, varieties and interspecific F$_1$ hybrids.

| Taxon | Kew accession number | Origin | 2n | Pollen Fertility % |
|---|---|---|---|---|
| *N. bulbocodium* L. var. unknown | 295–82.03045 | Unknown | 14 | 97 |
| ,, ,, ,, ,, | 295–82.03047 | Unknown | 26 | 99 |
| ,, ,, ,, ,, | 232–78.02456 | Unknown | 42 | |
| ,, ,, var. *albidus* (Emb. & Maire) Maire | 341–82.03524 | *Blanchard* | 14 | |
| ,, ,, var. *citrinus* Baker | 341–82.03525 | *Blanchard* | 34 | 86 |
| ,, ,, ,, ,, | 400–82.04500 | Coleraine | 34 | 89 |
| ,, ,, var. *conspicuus* Baker | 341–82.03526 | *Blanchard* | 14 | 82 |
| ,, ,, ,, ,, ,, | 400–82.04501 | Coleraine | 14 | 87 |
| ,, ,, var. *filifolius* Hort. | 341–82.03527 | *Blanchard* | 26 | 99 |
| *N. calcicola* Mendonça | 295–82.03046 | Unknown | 14 | |
| *N. cantabricus* DC. var. *cantabricus* | CYT 82.1498 | *Walker* | 14 | |
| ,, ,, var. *foliosus* Maire | 400–82.04502 | Coleraine | 28 | |
| *N. compressa* Haw. | 257–83.03161 | Rosewarne | 31 | |
| *N. cyclamineus* DC. | 400–82.04503 | Coleraine | 14 + B | 86 |
| *N. fernandesii* G. Pedro | 326–79.02967 | *Mathew* | 21 | |
| ,, ,, | 341–82.03529 | *Blanchard* | 28 | 99 |
| ,, ,, | 400–82.04504 | Coleraine | 28 | 83 |
| *N. gayi* (Henon.) Pugsl. ( = *N. pseudonarcissus* L.) | 400–82.04528 | Coleraine | 14 | |
| *N. hedraeanthus* (Webb & Heldr.) Colmeiro | 341–82.03530 | *Blanchard* | 14 | 61 |
| *N. hispanicus* Gouan | 400–82.04505 | Coleraine | 14 | |
| *N. jonquilla* L. var. *jonquilla* | 400–82.04506 | Coleraine | 14 | 97 |
| ,, ,, var. *henriquesii* Samp. | 341–82.03531 | *Blanchard* | 14 | 41 |
| ,, ,, ,, ,, ,, | 400–82.04507 | Coleraine | 14 | |
| *N. juncifolius* Req. ex Lag. | 400–82.04508 | Coleraine | 14 | 65 |
| *N. lobularis* Schult. | 400–82.04509 | Coleraine | 42 | 30 |
| *N. longispathus* Pugsley | 400–82.04510 | Coleraine | 14 | 76 |

| Taxon | Kew accession number | Origin | 2n | Pollen Fertility % |
|---|---|---|---|---|
| *N. minimus* Kunth | 400–82.04511 | Coleraine | 14 + B | 96 |
| *N. nanus* Steudel | 400–82.04512 | Coleraine | 14 | |
| *N. ornatus* Haw. var. *ornatus* (= *N. poeticus* L.) | 400–82.04519 | Coleraine | 14 | |
| ”        ”        ”        ”        ” | 257–83.03187 | Rosewarne | 14 | |
| ”        ”        var. *maximus* Hort. | 400–82.04520 | Coleraine | 14 | 96 |
| ”        ”        ”        ”        ” | 399–82.04463 | Rosewarne | 14 | 99 |
| *N. pachybolbus* Durieu | 400–82.04515 | Coleraine | 22 | |
| *N. papyraceus* Ker-Gawl. | 400–82.04516 | Coleraine | 22 | 97 |
| *N. poeticus* L. var. *poeticus* | 011–81.00043 | *Sands* | 14 | 95 |
| ”        ”        var. *flore pleno* Hort. | 400–82.04517 | Coleraine | 14 | |
| ”        ”        ”        ”        ” | 399–82.04459 | Rosewarne | 14 | |
| ”        ”        subsp. *radiiflorus* (Salisb.) Baker | 400–82.04523 | Coleraine | 14 | |
| ”        ”        ”        ”        var. *poetarum* Burb. & Baker | 400–82.04521 | Coleraine | 14 | 94 |
| ”        ”        ”        ”        ”        ”        ”        ” | 257–83.03189 | Rosewarne | 14 | |
| *N. pseudonarcissus* L. subsp. *abscissus* (Schultes & Schultes fil.) A. Fernandes | 400–82.04527 | Coleraine | 14 | |
| ”        ”        subsp. *obvallaris* (Salisb.) A. Fernandes | 400–82.04530 | Coleraine | 21 | |
| ”        ”        subsp. *pallidiflorus* (Pugsl.) A. Fernandes | 232–78.02460 | Unknown | 14 | |
| ”        ”        subsp. *pseudonarcissus* | 232–78.02458 | *A. & M.H.* 7805 | 43 | |
| ”        ”        ”        ”        ” | 400–82.04526 | Coleraine | 14 | |
| *N. pumilus* Salisb. var. *plenus* Hort. (= 'Rip van Winkle') | 400–82.04531 | Coleraine | 21 | |
| *N. recurvus* Haw. (= *N. poeticus* L.) | 400–82.04524 | Coleraine | 21 | |
| ”        ”        ”        ” | 399–82.04498 | Rosewarne | 21 | 40 |
| *N. romieuxii* Braun-Blanquet & Maire var. *romieuxii* | 341–82.03532 | *Blanchard* | 28 | |
| ”        ”        ”        ”        ” | 400–82.04532 | Coleraine | 28 | |
| ”        ”        var. *mesantlanticus* Hort. | 341–82.03533 | *Blanchard* | 28 | 97 |

Table 1 *continued*. Chromosome numbers and pollen fertility in *Narcissus* species, varieties and interspecific $F_1$ hybrids.

| Taxon | Kew accession number | Origin | 2n | Pollen Fertility % |
|---|---|---|---|---|
| *N. romieuxii* Braun-Blanquet & Maire var. *mesatlanticus* Hort. | 400–82.04533 | Coleraine | 28 | 77 |
| „ „ var. *tananicus* Maire | 341–82.03534 | *Blanchard* | 14 | |
| *N. rupicola* Duf. | 356–78.03601 | Unknown | 14 | |
| *N. tazetta* L. | 135–79.01296 | *Chesterman* 103 | 20 | |
| *N.* aff. *tazetta* L. | 364–84.03754 | *Willis* | 22 | |
| *N. telamonius* Link var. *plenus* Hort. ( = *N. pseudonarcissus* L.) | 257–83.03194 | Rosewarne | 14 | |
| *N. triandrus* L. var. *albus* (Haw.) Baker | CYT.82.362 | *Blom* | 14 | |
| „ „ „ „ „ „ | CYT.83.935 | *Blanchard* | 14 + 0 − 3B | |
| „ „ var. *concolor* (Haw.) Baker | CYT.83.934 | *Blanchard* | 14 | |
| „ „ var. *pulchellus* (Salisb.) Baker | CYT.83.936 | *Blanchard* | 14 | |
| *N. willkommii* (Samp.) A. Fernandes | 341–82.03535 | *Blanchard* | 14 | 79 |
| „ „ | 400–82.04534 | Coleraine | 14 | |
| $F_1$ hybrids | | | | |
| *N. atlanticus* F. C. Stern × *N. asturiensis* (Jord.) Pugsley 'Navarre' | 341–82.03536 | *Blanchard* | 14 + B | 3 |
| *N. atlanticus* F. C. Stern × *N. cuatrecasasii* Casas, Lainz & Ruiz Rejon | 341–82.03537 | *Blanchard* | 14 | 69 |
| *N. jonquilla* L. × *N. watieri* Maire | 341–82.03538 | *Blanchard* | 14 | 0 |
| *N. poeticus* L. × *N. pseudonarcissus* L. ( = *N.* × *incomparabilis* Miller) | 232–78.02455 | *A. & M. H.* 7854 | 14 | |
| *N. pseudonarcissus* L. × *N. jonquilla* L. ( = *N.* × *odorus* L. var. *plenus* Hort.) | 400–82.04513 | Coleraine | 14 | |
| „ „ „ „ ( = *N.* × *odorus* L. var. *rugulosus* Hort.) | 291–82.02815 | Wisley | 14 | 2 |
| „ „ „ „ „ „ „ | 400–82.04514 | Coleraine | 21 | |
| *N. rupicola* Duf. × *N. asturiensis* (Jord.) Pugsley 'Navarre' | 341–82.03540 | *Blanchard* | 14 + B | 0 |
| *N. rupicola* Duf. × *N. gaditanus* Boiss. & Reut. | 341–82.03541-3 | *Blanchard* | 14 | 0 |
| *N. watieri* Maire × *N. calcicola* Mendonça | 341–82.03544 | *Blanchard* | 14 | |
| „ „ × *N. gaditanus* Boiss. & Reut. | 341–82.03545-6 | *Blanchard* | 14 | 0·5 |
| „ „ × *N. scaberulus* Henriq. | 341–82.03547 | *Blanchard* | 14 | |

at variance with the remainder of the genus (subgenus *Narcissus*), of which all species are based on x = 7. Subgenus *Hermione* was said by Maugini (1953) to be related to the x = 7 group through the stabilisation or 'diploidisation' of triploids with 2n = 3x = 21 chromosomes after aneuploid changes to 2n = 20 or 22. This seems to be an extremely unlikely explanation, particularly in the light of the discovery of 2n = 10 in *N. serotinus* (Fernandes 1975), which established a low basic number of x = 5 in the subgenus *Hermione* and consequently a tetraploid level in 2n = 20 races of *N. tazetta*, which is of ancient origin since the species is functionally a diploid. Fernandes (1975) further suggested that the x = 11 forms are derived from the hybridisation of a 2n = 2x = 10 plant with a 2n = 2x = 12 ancestral type followed by chromosome doubling to give an allotetraploid with 2n = 22.

The remainder of the genus, subgenus *Narcissus*, has x = 7 chromosomes, suggested by Fernandes (1975) also to have arisen from an x = 6 ancestral stock through aneuploid change. The species are not chromosomally uniform, however, unlike some other plant groups such as the *Liliaceae-Aloineae* (Brandham 1971), and representative diploids with 2n = 14 are illustrated in Fig. 2. There is a very wide variation in total chromosome size throughout these plants, with the smallest chromosomes in *N. bulbocodium* and *N. hedraeanthus* (Figs. 2A, 2B). The size increases through a range of intermediates to the longest, occurring in *N. longispathus* (Fig. 2C), *N. jonquilla* (Fig. 2H) and *N. poeticus*. *N. poeticus* has the most massive chromosomes of all, due largely to their increased thickness (Fig. 2K), the total chromosome length being little more than that of other species with large chromosomes.

Throughout most of the species in subgenus *Narcissus* the chromosomes display a range of chromosome length within a karyotype of about 2- or 2·5-fold between the longest and the shortest, although the chromosomes of *N. cyclamineus* vary less than this range (Fig. 2F) and those of *N. calcicola* a little more (Fig. 2E). The chromosomes are submetacentric in most cases, although all the short chromosomes of *N. bulbocodium* (Fig. 2B), *N. hedraeanthus* (Fig. 2A) and, unusually, one of the long pairs in each of *N. juncifolius* (Fig. 2D) and *N. calcicola* (Fig. 2E) are metacentric. In a few other species one or more of the shorter chromosome pairs are also metacentric (e.g. the second shortest pair in *N. cyclamineus*, Fig. 2F).

*Polyploids*

These occurred sporadically throughout the species studied, most polyploids being tetraploids with 2n = 28. The greatest range of ploidy was in *N. bulbocodium*, in which all the ploidy levels between diploid (2n = 14) and hexaploid (2n = 42) were found with the exception of the triploid (2n = 21). This reflects the finding by Fernandes (1967) that this species has the widest range of ploidy of any in the genus, ranging from diploid to octoploid (2n = 14–56). In the present study triploids were recorded in several species, e.g. *N. fernandesii*, *N. pseudonarcissus* subsp. *obvallaris*, *N. pumilus* var. *plenus* and *N. recurvus* (Table 1), but it is not known to what extent these are representative of vegetatively-reproducing triploid populations similar to those known to occur in *Haworthia* (Brandham & Cutler 1981), or whether they were selected by plant collectors as being more vigorous than the rest of the individuals in the presumably diploid populations in which they occurred. In *N. bulbocodium* the former alternative seems to apply because Fernandes (1967) found two entirely triploid populations in an extensive survey of this species in Portugal. Hexa-
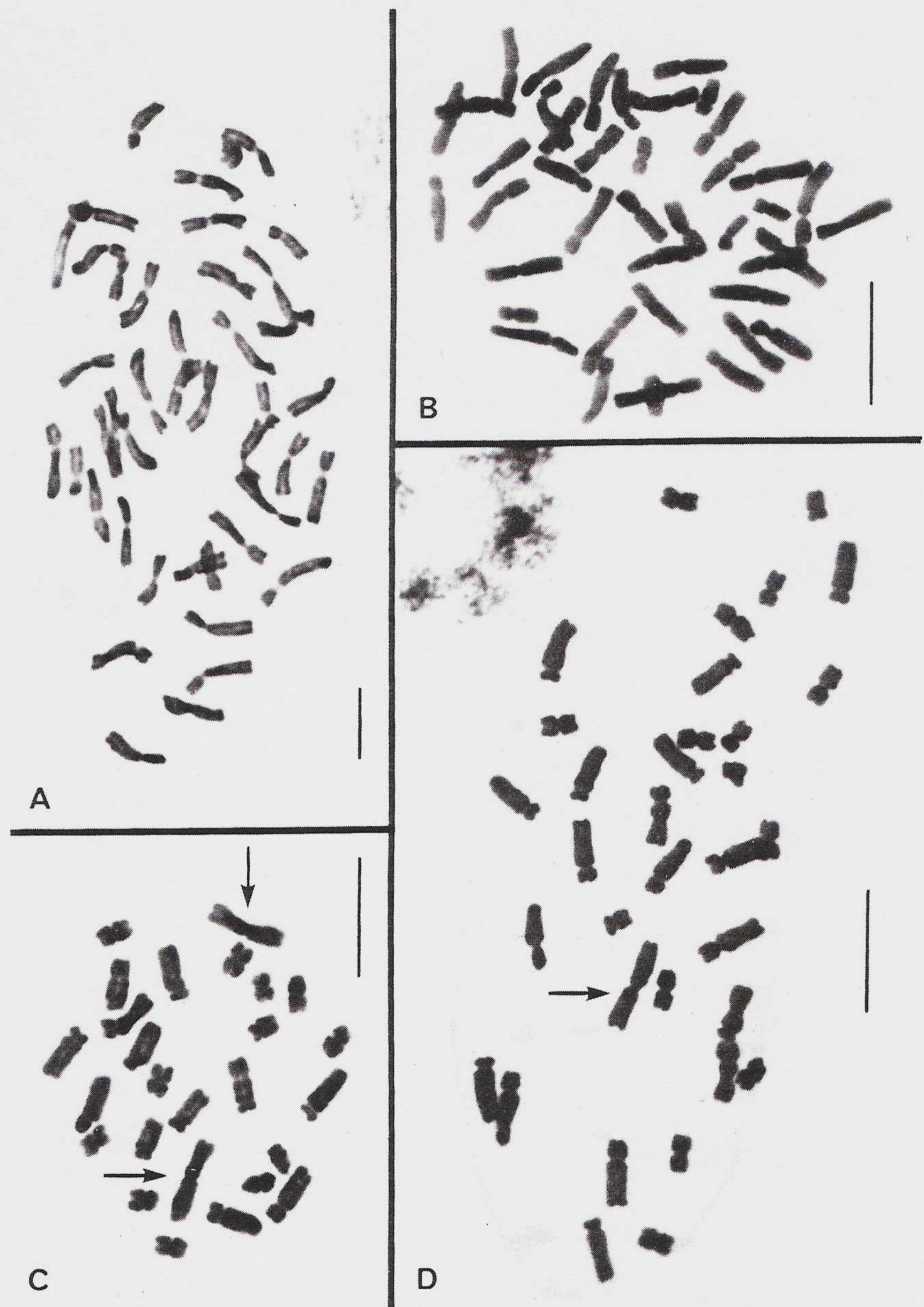
FIG. 3. Somatic chromosomes of polyploid *Narcissus*. **A** *N. pseudonarcissus*, 2n = 6x + 1 = 43; **B** *N. lobularis*, 2n = 6x = 42; **C** *N. bulbocodium*, 2n = 4x = 26, derived from 2n = 28 by homozygosity for a Robertsonian fusion producing 2 metacentrics (arrows) from 4 acrocentrics; **D** *N. bulbocodium* subsp. *bulbocodium* var. *citrinus*, a pentaploid with the chromosome number reduced from 2n = 35 to 2n = 34 by hybridity for the same same Robertsonian fusion as in **C** (metacentric arrowed). Scales = 10μm.

ploids or near-hexaploids were found in three species (Table 1), *N. bulbocodium*, *N. lobularis* (Fig. 3B) and *N. pseudonarcissus* subsp. *pseudonarcissus*.

*Aneuploidy*

This is uncommon in these wild-collected plants. A single instance occurred at the hexaploid level, with $2n = 6x + 1 = 43$ being found in *N. pseudonarcissus* subsp. *pseudonarcissus* (Fig. 3A). It is to be expected that aneuploidy should be more common in high polyploids. This is because the harmful effects, caused by the extra or missing chromosomes, on the aneuploid gametes that give rise to aneuploid individuals are extreme in haploid gametes but are progressively reduced in diploid and polyploid gametes because of the buffering effect of the presence of one or more extra intact sets of chromosomes. Thus in $x = 7$ plants aneu-haploid gametes with $n = x \pm 1 = 6$ or 8 chromosomes are less viable than aneu-diploid gametes with $n = 2x \pm 1 = 13$ or 15 chromosomes and these are less viable than aneu-triploid gametes with $n = 3x \pm 1 = 20$ or 22 chromosomes. The euploid and aneuploid gametes ($n = 21$ and 22 respectively) that gave rise to the $2n = 43$ aneu-hexaploid would have been almost equally viable, and populations of hexaploids such as the one from which our specimen came should therefore contain a significant number of aneuploids.

The apparent aneu-tetraploids reported in Table 1, $2n = 26$ (?4x − 2) in *N. bulbocodium* and $2n = 31$ (?4x + 3) in *N. compressa* and the apparent aneu-pentaploid $2n = 34$ (?5x − 1) in *N. bulbocodium* are the results of chromosomal events other than aneuploidy. Taking firstly the case of *N. compressa* with $2n = 31$ (Fig. 10A), this plant was described as a species and appears in Division 10 in Throckmorton (1980), so it has been included in Table 1. Nevertheless it is clearly allied morphologically to *N. tazetta* and is certainly of hybrid origin. It will be considered again below, together with the other hybrids and polyploids involving *N. tazetta*. Robertsonian fusion is the origin of the apparently aneuploid $2n = 26$ and 34 individuals of *N. bulbocodium*.

*Robertsonian fusion*

This is the process whereby two usually non-homologous acrocentric chromosomes each break at the centromere and the arms fuse in a new combination, the two short arms constituting a short metacentric and the long arms a long metacentric. Sexual reproduction following this change will result in the production of some viable gametes carrying the two metacentrics instead of the two original acrocentrics. Fusion of two such gametes produces a homozygote for the fusion in which four acrocentrics (two homologous pairs) are replaced by two long and two short metacentrics. Frequently Robertsonian fusion is accompanied by loss of the short arms, so the homozygote has a net loss of two chromosomes, four original acrocentrics being replaced by two larger metacentrics comprising the four long arms.

In tetraploids of *N. bulbocodium* homozygosity (or more accurately for tetraploids, duplex heterozygosity) for a single Robertsonian fusion, with loss of short arms, reduces the chromosome number from $2n = 28$ to $2n = 26$ including two metacentrics (Fig. 3C). The same event was reported over 50 years ago by Fernandes (1934) in the same species, and the present material is probably descended from plants brought into cultivation at that time. These $2n = 26$ plants are fully fertile and produce gametes with $n = 13$ chromosomes including one metacentric, and when they hybridise with a normal hexaploid of the same species ($2n = 42$) which produces gametes with $n = 21$ chromosomes (lacking the large metacentric) the resulting pentaploid plant contains
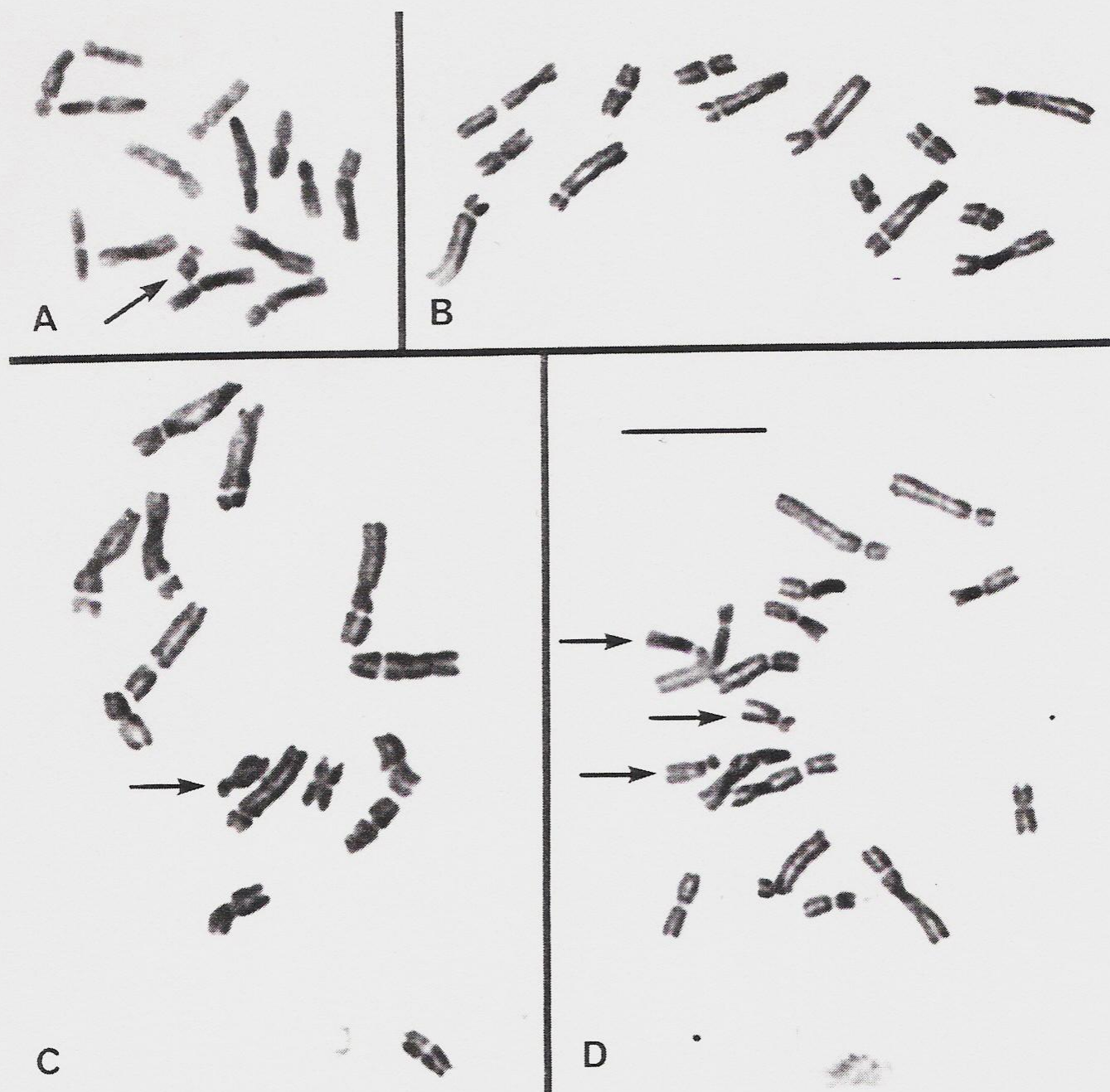
FIG. 4. Somatic chromosomes of diploid *Narcissus* (2n = 14) containing B chromosomes (arrows). **A** *N. minimus* (1B); **B, C, D** *N. triandrus* var. *albus* with (B), 0B, (C) 1B, (D) 3B. The Bs are constant within a plant but vary within the population. Scale = 10μm.

2n = 13 + 21 = 34 chromosomes including just one large metacentric. One such plant was located in the present study (Fig. 3D), the first time that this event has been recorded in pentaploid *N. bulbocodium*. It is probable that this individual arose through a chance hybridisation in cultivation between Fernandes' original Robertsonian fusion tetraploid homozygote and a normal hexaploid of unknown provenance.

## B chromosomes

These are additional to the normal or A chromosome complement of a species. They can be heterochromatic or euchromatic and are usually but not always smaller than the A chromosomes. They have few functional genes and often pair poorly during meiosis. They are consequently either absent or duplicated in the gametes of plants which carry them and thus vary in numbers from individual to individual within a population. Sometimes they will even vary in numbers from cell to cell within an individual because of mitotic irregularities, although this is very much less common than inter-individual variation.

In *Narcissus* they have been reported in several species and the numbers vary

from one to as many as five in *N. bulbocodium* (Wylie 1952, Jones & Rees 1982), with low numbers being the most common.

In the present study they were seen in three species: *N. cyclamineus* (2n = 14 + 1B), *N. minimus* (2n = 14 + 1B) and *N. triandrus* var. *albus* (2n = 14 + 0 − 3B). All of these are apparently euchromatic, staining identically to the A chromosomes. The single Bs found in *N. cyclamineus* and *N. minimus* resemble each other closely. They are acrocentric and are considerably shorter than the shortest A chromosomes (Fig. 4A). In *N. triandrus* var. *albus* the Bs are much larger acrocentrics, being longer than the shortest pair of A chromosomes, and varied in numbers from plant to plant. In a sample of eight bulbs that were examined, six had no Bs (Fig. 4B), one had a single B (Fig. 4C) and one had three (Fig. 4D). A short acrocentric B was also observed in Blanchard's F$_1$ hybrids between *N. atlanticus* and *N. asturiensis* 'Navarre' (Fig. 5A) and between *N. rupicola* and *N. asturiensis* 'Navarre' (Table 1), indicating that 'Navarre' also contains 2n = 14 + 1B chromosomes.

## F$_1$ hybrids

Most of the F$_1$ hybrids studied in this investigation were crosses between very dissimilar miniature species which were carried out by J. Blanchard. The hybrid *N. atlanticus* × *N. asturiensis* 'Navarre' is typical of the majority of them and shows a very high frequency of morphologically unique chromosomes (Fig. 5 A), and it is not possible to determine the homologies of these chromosomes simply from an examination of their length and centromere position, so it would be meaningless to attempt to construct a karyotype by pairing apparently similar chromosomes in this case.

Chromosome variation and heteromorphy is even more marked in another F$_1$ hybrid, *N. rupicola* × *N. gaditanus*, of which three accessions were studied, all with 2n = 14. Taking as an example just the easily-recognisable large metacentrics which occur in these plants, no.03541 has two similar ones (Fig. 5 C), 03542 has two dissimilar ones with one much longer than the other (Fig. 5 D) and 03543 has three similar ones (Fig. 5 E). It is evident that one or both of the parents of this hybrid contain heteromorphic homologous chromosomes which have segregated in various ways during gamete formation.

Another diploid F$_1$ hybrid between very dissimilar species, *N. pseudonarcissus* × *N. jonquilla* (=*N.* × *odorus* 'rugulosus') is also quite heteromorphic in its chromosome constitution, possessing several chromosomes having no closely-matching homologues. Indeed, the presence of one large and one small metacentric in this plant (Fig. 5 B) in a complement of chromosomes which is otherwise largely submetacentric-acrocentric suggests the presence of a Robertsonian fusion (see above), and it is possible that such a fusion played a part in the chromosomal differentiation of the two parental species from the original ancestral *Narcissus* stock. Nevertheless, it would be necessary to examine meiosis in this plant before Robertsonian fusion hybridity could be confirmed or discounted. If present, the fusion would lead to the pairing of the large and small metacentric with two of the acrocentrics to form a quadrivalent. It has not been possible to carry out this particular investigation because of shortage of material.

The extreme heteromorphy found in these examples of F$_1$ hybrids indicates clearly that a considerable amount of alteration has occurred in chromosome morphology (rather than number) during speciation in the x = 7 subgenus

*Narcissus* and confirms the obvious chromosomal differences between species that can be seen in Fig. 2.

### Pollen fertility

This is high in most of the species that were analysed, as might be expected in what are mostly the clonal descendants of wild-collected non-hybrid plants. Table 1 shows that the great majority of them were 80–99% pollen-fertile, even, surprisingly, the pentaploid Robertsonian fusion heterozygote *N. bulbocodium* subsp. *bulbocodium* var. *citrinus* which would be expected to be less fertile. The relatively low fertility of the diploid *N. jonquilla* var. *henriquesii* (03531) is also unexpected since no heteromorphy for any major structural change could be detected in its chromosome complement. It is therefore possible that the fertility of this plant is reduced by changes at the genic level or at the chromosome level, the latter necessarily being symmetrical and consequently irresolvable. The moderate fertility of the triploid *N. recurvus* is typical of autotriploids in which chromosome segregation is irregular, producing many aneuploid gametes, most of which are non-viable (Brandham 1982).

The remaining plant with low fertility, the hexaploid *N. lobularis*, is only one example of a wide range of fertilities that can exist among such high polyploids. A bivalent-forming allohexaploid would be expected to be very fertile, for instance the well-known example of bread wheat which has an AABBDD genotype (Darlington 1963) and forms mostly eu-triploid ABD gametes. A completely autohexaploid plant with six identical chromosome sets (i.e. an AAAAAA genotype) would form a large number of hexavalents at meiosis which, with the consequential irregularities of chromosome separation, would result in many widely aneuploid non-viable gametes and a considerable drop in fertility. Other hexaploids would display various amounts of homology between the chromosome sets and would present a range of fertilities between the two above extremes, and *N. lobularis* appears to be one such intermediate type. Again, a meiotic investigation, if sufficient material was available, would shed some light on the level of chromosome homology existing in this plant.

The pollen fertilities of the majority of the $F_1$ hybrids studied here are very low or zero (Table 1), reflecting the extreme dissimilarity of the chromosome sets donated by the two distantly-related parents of each hybrid as noted above. Only *N. atlanticus* × *N. cuatrecasasii* has a reasonably high pollen fertility, indicating the closer chromosomal relationship of this particular pair of species.

### The Cultivars

Chromosome counts were made of 230 *Narcissus* cultivars. These are plants of unknown or complex parentage (i.e. not simply $F_1$ hybrids between pairs of species) and were selected at random from the lists offered by the suppliers mentioned above in Material and Methods. They may thus be regarded as a representative random sample of the many thousands of cultivars extant in the genus, which is relevant to the discussions of the occurrence of aneuploidy and polyploidy below. The counts are given in Table 2, together with the RHS division/colour/morphology code of each cultivar and the pollen fertility of nearly every one.

Because these cultivars are all of complex origin they are to be expected to display a considerable degree of heteromorphy among homeologous pairs or
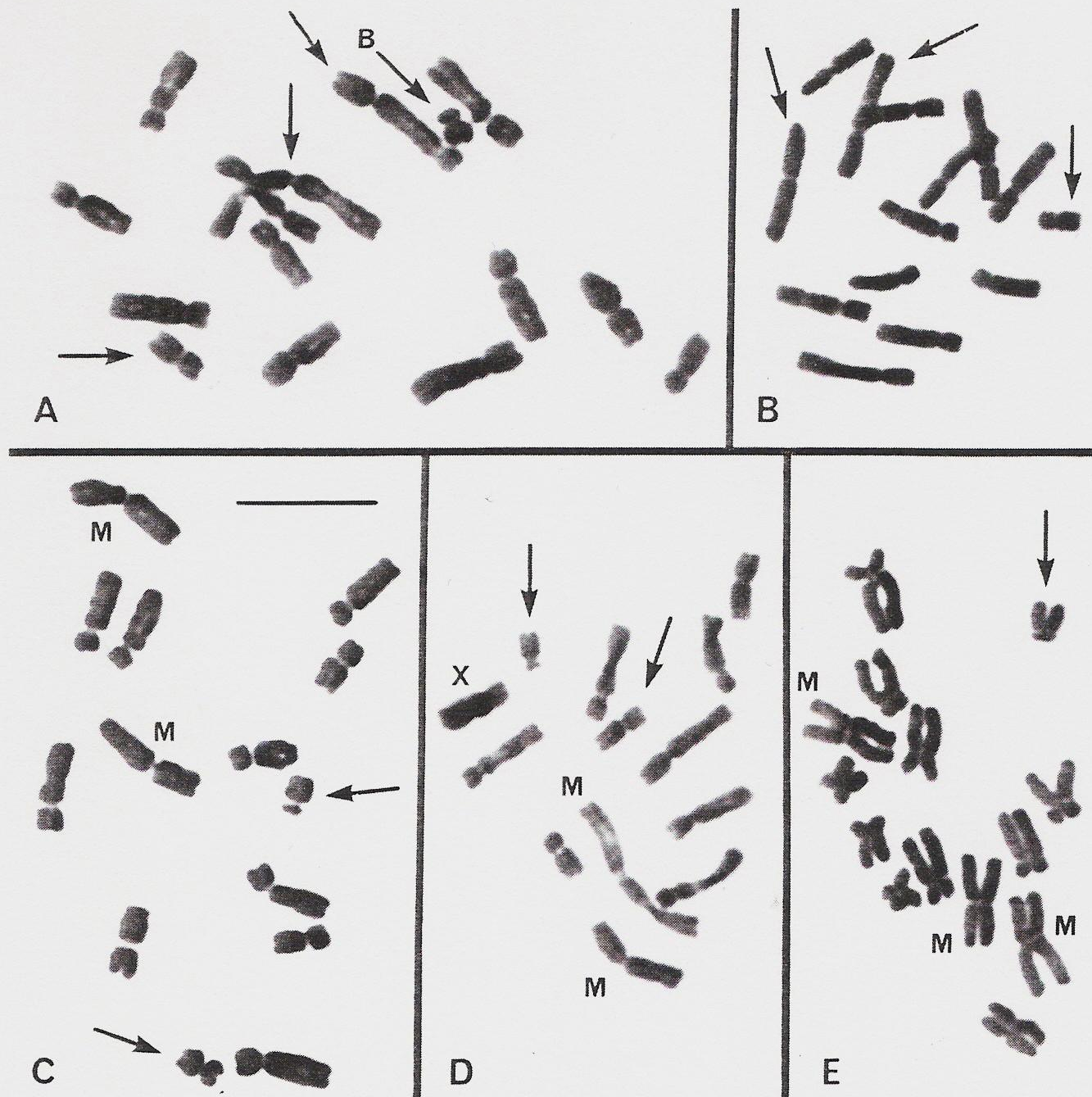
FIG. 5. Somatic chromosomes of sterile $F_1$ hybrid *Narcissus* diploids (2n = 14) showing hetero-morphy of genomes (morphologically unique and unpaired chromosomes arrowed.) **A** *N. atlanticus* × *N. asturiensis* 'Navarre' with 2n = 14 + 1B; **B** *N.* × *odorus* var. *rugulosus*; **C, D, E** *N. rupicola* × *N. gaditanus* showing variability in three sister hybrids, **C** with 2 similar metacentrics (M), **D** with 2 dissimilar metacentrics (M), **E** with 3 similar metacentrics (M). In **D** two chromosomes are completely overlapping at X. Scale = 10μm.

groups of chromosomes, so much so that it is difficult to construct karotypes showing chromosome homologies in these plants, since genetically similar homeologues might be very dissimilar morphologically. This part of the Results and Discussion section will therefore be devoted to the following matters only: the incidence of B chromosomes; the frequency of the various chromosome numbers; a summary, in the light of present knowledge, of the known parentage and the possible chromosomal derivation of a range of cultivars bearing the more uncommon chromosome numbers; pollen fertility; a comparison of ploidy levels in cultivation of *Narcissus* with those of some other popularly-cultivated decorative genera.

## B chromosomes

These are rather difficult to identify with accuracy in these cultivars because they are mostly euchromatic and mitotically quite stable, not varying from root to root nor from bulb to bulb of a particular cultivar (all of which are

TABLE 2. Chromosome numbers, R.H.S. division and pollen fertility in 230 *Narcissus* cultivars of mixed origin.

| Cultivar | Division/ colour | Kew accession number | Origin | 2n | Pollen Fertility % |
|---|---|---|---|---|---|
| 'Abel Tasman' | 11 W-WYO | 399–82.04378 | Rosewarne | 28 | 15 |
| 'Acropolis' | 4 W-R | 291–82.02813 | Wisley | 28 | 0 |
| 'Acropolis' | 4 W-R | 399–82.04379 | Rosewarne | 28 | 0 |
| 'Actaea' | 9 W-GYR | 291–82.02814 | Wisley | 28 | 94 |
| 'Alabaster' | 4 W-W | 399–82.04380 | Rosewarne | 14 | |
| 'Ann Abbott' | 2 W-YPP | 399–82.04381 | Rosewarne | 28 | 44 |
| 'Ardour' | 3 Y-R | 399–82.04382 | Rosewarne | 28 | 78 |
| 'Armada' | 2 Y-O | 291–82.02816 | Wisley | 28 | 84 |
| 'Aspasia' | 8 W-Y | 364–84.03755 | *Willis* | 24 | |
| 'Barrii Conspicuus' | 3 Y-YYR | 257–83.03154 | Rosewarne | 21 | |
| 'Bartley' | 6 Y-Y | 291–82.02818 | Wisley | 21 | 34 |
| 'Bath's Flame' | 3 Y-YYR | 257–83.03155 | Rosewarne | 21 | |
| 'Bawnboy' | 1 Y-Y | 291–82.02817 | Wisley | 28 | |
| 'Bealita' | 3 Y-O | 399–82.04384 | Rosewarne | 28 | 62 |
| 'Beersheba' | 1 W-W | 257–83.03156 | Rosewarne | 28 | |
| 'Benediction' | 3 W-GWW | 399–82.04385 | Rosewarne | 28 | 25 |
| 'Bernardino' | 2 W-YYO | 257–83.03157 | Rosewarne | 28 | |
| 'Big Wig' | 4 W-Y | 399–82.04386 | Rosewarne | 28 | 0 |
| 'Binkie' | 2 Y-W | 291–82.02819 | Wisley | 28 | 80 |
| 'Blaris' | 2 W-P | 291–82.02820 | Wisley | 28 | 83 |
| 'Brunswick' | 2 W-Y | 291–82.02821 | Wisley | 28 | 86 |
| 'Bryher' | 3 W-GWW | 399–82.04387 | Rosewarne | 28 | 56 |
| 'Camellia' | 4 Y-Y | 291–82.02822 | Wisley | 21 | 0 |
| 'Canasta' | 11 W-Y | 399–82.04388 | Rosewarne | 27 | 58 |
| 'Candida' | 4 W-Y | 399–82.04389 | Rosewarne | 27 | 0 |
| 'Cantatrice' | 1 W-W | 291–82.02823 | Wisley | 28 + B | 50 |
| 'Cape Kennedy' | 11 W-O | 399–82.04390 | Rosewarne | 27 | 79 |
| 'Capparoe' | 3 W-R | 399–82.04391 | Rosewarne | 27 | 74 |
| 'Caramel' | 9 W-O | 399–82.04392 | Rosewarne | 28 | 94 |
| 'Caravelle' | 1 Y-Y | 291–82.02824 | Wisley | 27 | 93 |
| 'Carbineer' | 2 Y-O | 291–82.02825 | Wisley | 28 | 81 |
| 'Cassata' | 11 W-W | 399–82.04393 | Rosewarne | 28 | 83 |
| 'Ceylon' | 2 Y-O | 291–82.02826 | Wisley | 27 | 77 |
| 'Charity May' | 6 Y-Y | 291–82.02827 | Wisley | 21 | 0 |
| 'Charter' | 2 Y-W | 291–82.02828 | Wisley | 28 | 55 |
| 'Chinese White' | 3 W-GWW | 257–83.03158 | Rosewarne | 28 | |
| 'Cicely' | 2 W-W | 291–82.02829 | Wisley | 28 | 86 |
| 'C. J. Backhouse' | 2 Y-YOO | 257–83.03159 | Rosewarne | 14 | |
| 'Codlins and Cream' | 4 W-Y | 257–83.03160 | Rosewarne | 14 | |
| 'Colorange' | 11 Y-O | 399–82.04394 | Rosewarne | 28 | 47 |
| 'Content' | 1 W-WWY | 257–83.03162 | Rosewarne | 24 | |
| 'Cornet' | 6 Y-Y | 399–82.04396 | Rosewarne | 21 | 15 |
| 'Court Martial' | 2 Y-R | 291–82.02832 | Wisley | 28 | 73 |
| 'Crepello' | 3 W-GWY | 291–82.02830 | Wisley | 28 | 86 |
| 'Crescendo' | 2 Y-YYO | 399–82.04395 | Rosewarne | 28 | 81 |
| 'Crocus' | 2 Y-Y | 291–82.02831 | Wisley | 28 | 72 |
| 'Croesus' | 2 Y-YOR | 257–83.03163 | Rosewarne | 21 | |
| 'Cyclone' | 6 Y-Y | 399–82.04397 | Rosewarne | 28 | 63 |
| 'Dactyl' | 9 W-YYR | 399–82.04458 | Rosewarne | 14 | 88 |
| 'Dalboyne' | 2 Y-O | 399–82.04403 | Rosewarne | 28 | 58 |
| 'Dallas' | 3 W-GWW | 399–82.04404 | Rosewarne | 14 | 79 |
| 'Double Eagle' | 4 | 399–82.04405 | Rosewarne | 27 | 0 |
| 'Double Event' | 4 W-Y | 399–82.04406 | Rosewarne | 29 | 0 |
| 'Doubledale' | 4 W-Y | 399–82.04407 | Rosewarne | 28 | 0 |
| 'Doublet' | 4 W-W | 399–82.04408 | Rosewarne | 14 | 0 |
| 'Dove Wings' | 6 W-Y | 291–82.02833 | Wisley | 21 | 3 |
| 'Downhill' | 3 W-W | 291–82.02834 | Wisley | 28 | |
| 'Dunkeld' | 2 Y-O | 257–83.03164 | Rosewarne | 28 | |
| 'Dunlewey' | 2 W-W | 291–82.02835 | Wisley | 28 | 30 |
| 'Early Splendour' | 8 W-O | 399–82.04479 | Rosewarne | 17 | 0 |
| 'Easter Moon' | 2 W-GWW | 291–82.02836 | Wisley | 28 | 25 |
| 'Eddy Canzony' | 2 W-YYO | 291–82.02837 | Wisley | 28 | 65 |

| Cultivar | Division/ colour | Kew accession number | Origin | 2n | Pollen Fertility % |
|---|---|---|---|---|---|
| 'Edward Buxton' | 3 Y-OOR | 399–82.04409 | Rosewarne | 28 | 85 |
| 'Elvira' | 8 W-Y | 257–83.03165 | Rosewarne | 24 | |
| 'Elvira' | 8 W-Y | 364–84.03756 | *Willis* | 24 | |
| 'Emperor' | 1 Y-Y | 257–83.03166 | Rosewarne | 21 | |
| 'Empress' | 1 W-Y | 257–83.03167 | Rosewarne | 21 + B | |
| 'Enterprise' | 4 Y-O | 399–82.04410 | Rosewarne | 28 | 0 |
| 'Entrancement' | 1 Y-W | 399–82.04411 | Rosewarne | 28 | 82 |
| 'Evening' | 2 W-W | 257–83.03168 | Rosewarne | 28 | |
| 'Extol' | 4 Y-R | 399–82.04412 | Rosewarne | 28 | 60 |
| 'Falaise' | 4 W-O | 257–83.03169 | Rosewarne | 26 | |
| 'February Gold' | 6 Y-Y | 291–82.02838 | Wisley | 21 | 39 |
| 'Fermoy' | 2 W-YOO | 399–82.04413 | Rosewarne | 28 | 6 |
| 'Firebrand' | 3 W-R | 257–83.03170 | Rosewarne | 14 | |
| 'Flamenco' | 2 W-O | 291–82.02839 | Wisley | 28 | 13 |
| 'Flower Drift' | 4 W-O | 291–82.02840 | Wisley | 28 | 87 |
| 'Fortwilliam' | 1 Y-Y | 399–82.04415 | Rosewarne | 28 | 80 |
| 'Furbelow' | 4 Y-O | 399–82.04416 | Rosewarne | 27 | 0 |
| 'Galway' | 2 Y-Y | 291–82.02841 | Wisley | 28 | |
| 'Garron' | 1 Y-Y | 399–82.04417 | Rosewarne | 28 | 84 |
| 'Gaucho' | 2 Y-R | 399–82.04418 | Rosewarne | 28 + B | 78 |
| 'Gay Record' | 4 W-O | 399–82.04419 | Rosewarne | 28 | 0 |
| 'Gay Time' | 4 W-R | 399–82.04420 | Rosewarne | 28 | 94 |
| 'Gem of Ulster' | 2 W-P | 399–82.04421 | Rosewarne | 28 | 63 |
| 'Geranium' | 8 W-O | 399–82.04480 | Rosewarne | 17 | 3 |
| 'Geranium' | 8 W-O | 364–84.03757 | *Willis* | 17 | |
| 'Glorious' | 8 W-R | 257–83.03171 | Rosewarne | 24 | |
| 'Glorious' | 8 W-R | 364–84.03758 | *Willis* | 24 | |
| 'Glory of Lisse' | 9 W-YYR | 399–82.04460 | Rosewarne | 14 | 90 |
| 'Glowing Red' | 4 W-R | 399–82.04432 | Rosewarne | 28 | 0 |
| 'Golden Dawn' | 8 Y-O | 399–82.04481 | Rosewarne | 24 | 0 |
| 'Golden Dawn' | 8 Y-O | 364–84.03759 | *Willis* | 24 | |
| 'Golden Ducat' | 4 Y-Y | 291–82.02843 | Wisley | 28 | 0 |
| 'Golden Harvest' | 1 Y-Y | 291–82.02844 | Wisley | 28 | 96 |
| 'Golden Incense' | 7 Y-Y | 399–82.04430 | Rosewarne | 21 | 0 |
| 'Golden Lacquer' | 6 Y-Y | 399–82.04398 | Rosewarne | 28 | 2 |
| 'Golden Sceptre' | 7 Y-Y | 291–82.02845 | Wisley | 21 | |
| 'Golden Spur' | 1 Y-Y | 257–83.03172 | Rosewarne | 14 | |
| 'Golden Torch' | 2 Y-Y | 291–82.02846 | Wisley | 27 | 90 |
| 'Great Leap' | 4 W-Y | 399–82.04425 | Rosewarne | 21 | 0 |
| 'Gulliver' | 3 Y-YYR | 257–83.03173 | Rosewarne | 28 | |
| 'Hannibal' | 11 Y-O | 399–82.04426 | Rosewarne | 28 | 72 |
| 'Hawaii' | 4 Y-R | 399–82.04427 | Rosewarne | 27 | 0 |
| 'Helios' | 2 Y-YOO | 257–83.03174 | Rosewarne | 21 | |
| 'Henry Irving' | 1 Y-Y | 257–83.03175 | Rosewarne | 14 | |
| 'Hiawassee' | 8 W-W | 399–82.04482 | Rosewarne | 18 | 0 |
| 'Hiawassee' | 8 W-W | 364–84.03760 | *Willis* | 18 | |
| 'Highfield Beauty' | 8 Y-GYO | 399–82.04483 | Rosewarne | 31 | 0 |
| 'Home Fires' | 2 Y-R | 291–82.02847 | Wisley | 28 | 98 |
| 'Horace' | 9 W-YOR | 399–82.04461 | Rosewarne | 14 | |
| 'Horn of Plenty' | 5 W-W | 291–82.02848 | Wisley | 21 | |
| 'Hospodar' | 2 Y-O | 257–83.03176 | Rosewarne | 29 | |
| 'Ideal' | 8 W-O | 364–84.03761 | *Willis* | 17 + B | |
| 'Inishkeen' | 1 W-Y | 291–82.02849 | Wisley | 28 | 89 |
| 'Irene Copeland' | 4 W-Y | 399–82.04428 | Rosewarne | 14 | 0 |
| 'Irish Luck' | 1 Y-Y | 399–82.04429 | Rosewarne | 28 | 90 |
| 'Irish Minstrel' | 2 W-Y | 291–82.02850 | Wisley | 28 | 88 |
| 'Jana' | 6 Y-Y | 399–82.04399 | Rosewarne | 21 | 39 |
| 'Jenny' | 6 W-W | 291–82.02851 | Wisley | 21 | 10 |
| 'Joseph Mcleod' | 1 Y-Y | 291–82.02852 | Wisley | 28 | 80 |
| 'Junco' | 1 W-W | 399–82.04437 | Rosewarne | 28 | 56 |
| 'Killara' | 8 W-Y | 399–82.04484 | Rosewarne | 45 + B | 0 |
| 'Killigrew' | 2 Y-R | 257–83.03177 | Rosewarne | 28 | |
| 'Kilmorack' | 2 Y-O | 291–82.02853 | Wisley | 28 | 73 |
| 'Kilmore' | 3 W-O | 399–82.04438 | Rosewarne | 28 | 48 |
| 'Kilrea' | 2 W-W | 399–82.04439 | Rosewarne | 28 + B | 3 |

TABLE 2 continued. Chromosome numbers, R.H.S. division and pollen fertility in 230 *Narcissus* cultivars of mixed origin.

| Cultivar | Division/colour | Kew accession number | Origin | 2n | Pollen Fertility % |
|---|---|---|---|---|---|
| 'King Alfred' | 1 Y-Y | 257–83.03178 | Rosewarne | 28 | |
| 'King Cardinal' | 2 W-R | 399–82.04440 | Rosewarne | 28 | 83 |
| 'Kingcraft' | 8 W-GOO | 364–84.03762 | *Willis* | 24 | |
| 'Kingscourt' | 1 Y-Y | 291–82.02854 | Wisley | 28 | 57 |
| 'Knowehead' | 2 W-W | 291–82.02855 | Wisley | 28 | 88 |
| 'Lady Margaret Boscawen' | 2 W-Y | 257–83.03179 | Rosewarne | 29 | |
| 'La Riante' | 3 W-YOO | 257–83.03180 | Rosewarne | 28 | |
| 'Larkelly' | 6 Y-O | 399–82.04401 | Rosewarne | 36 | 88 |
| 'Larkwhistle' | 6 Y-Y | 291–82.02856 | Wisley | 21 | 1 |
| 'Lawali' | 4 W-P | 399–82.04441 | Rosewarne | 28 | 80 |
| 'Lemon Doric' | 2 Y-W | 399–82.04442 | Rosewarne | 27 | 79 |
| 'Liberty Bells' | 5 Y-Y | 291–82.02857 | Wisley | 21 | 5 |
| 'Limelight' | 1 Y-Y | 291–82.02858 | Wisley | 28 | 74 |
| 'Lizard Light' | 3 Y-O | 399–82.04443 | Rosewarne | 27 | 60 |
| 'Love Song' | 2 W-O | 399–82.04444 | Rosewarne | 28 | 60 |
| 'Lucifer' | 2 W-GRR | 257–83.03181 | Rosewarne | 14 | |
| 'Lunar Spell' | 2 Y-W | 399–82.04445 | Rosewarne | 28 | 65 |
| 'March Sunshine' | 6 Y-Y | 291–82.02859 | Wisley | 21 | 28 |
| 'Matador' | 8 Y-R | 399–82.04485 | Rosewarne | 32 + B | 66 |
| 'Maximus Superbus' | 1 Y-Y | 257–83.03183 | Rosewarne | 21 | |
| 'Merlin' | 3 W-YYR | 291–82.02860 | Wisley | 28 | 55 |
| 'Milan' | 9 W-GYR | 399–82.04462 | Rosewarne | 14 | 96 |
| 'Mistral' | 11 W-Y | 399–82.04446 | Rosewarne | 28 | 72 |
| 'Mitylene' | 2 W-Y | 257–83.03184 | Rosewarne | 28 | |
| 'Monterrico' | 4 W-WOO | 399–82.04447 | Rosewarne | 28 | 0 |
| 'Mount Hood' | 1 W-W | 291–82.02861 | Wisley | 29 | 77 |
| 'Mr Jinks' | 3 W-O | 399–82.04449 | Rosewarne | 29 | 2 |
| 'Mrs Langtry' | 2 W-W | 257–83.03185 | Rosewarne | 14 | |
| 'Mystic' | 3 W-GWO | 257–83.03186 | Rosewarne | 14 | |
| 'Nampa' | 1 Y-W | 399–82.04450 | Rosewarne | 28 | 73 |
| 'Nelly' | 3 W-GYY | 257–83.03182 | Rosewarne | 28 | |
| 'Nemo' | 3 W-YYR | 291–82.02862 | Wisley | 28 | |
| 'Ninth Lancer' | 2 Y-O | 291–82.02863 | Wisley | 28 | 78 |
| 'Niveth' | 5 W-W | 399–82.04490 | Rosewarne | 21 | 3 |
| 'Olivet' | 2 W-W | 399–82.04451 | Rosewarne | 28 | 64 |
| 'Orangery' | 11 W-POY | 399–82.04452 | Rosewarne | 28 | 41 |
| 'Ormeau' | 2 Y-Y | 291–82.02864 | Wisley | 28 | |
| 'Papillon Blanc' | 11 W-W | 399–82.04453 | Rosewarne | 29 | 14 |
| 'Papua' | 4 Y-Y | 399–82.04454 | Rosewarne | 27 | 0 |
| 'Passionale' | 2 W-P | 291–82.02865 | Wisley | 28 | 60 |
| 'Patagonia' | 2 Y-R | 291–82.02866 | Wisley | 28 | 52 |
| 'Penpol' | 7 Y-Y | 399–82.04431 | Rosewarne | 21 | 2 |
| 'Penvose' | 2 W-Y | 291–82.02867 | Wisley | 28 | 36 |
| 'Pepper' | 2 Y-R | 291–82.02868 | Wisley | 14 | 53 |
| 'Pick Up' | 11 Y-O | 399–82.04455 | Rosewarne | 28 | 46 |
| 'Pink Chiffon' | 4 W-WPP | 399–82.04456 | Rosewarne | 27 | 6 |
| 'Pinza' | 2 Y-YOR | 291–82.02869 | Wisley | 28 | 91 |
| 'Planet' | 4 Y-Y | 399–82.04457 | Rosewarne | 28 | 78 |
| 'Polar Ice' | 3 W-W | 291–82.02870 | Wisley | 29 | 13 |
| 'Pontresina' | 2 W-Y | 291–82.02872 | Wisley | 28 | 80 |
| 'Portchapel' | 7 Y-Y | 399–82.04432 | Rosewarne | 21 | 21 |
| 'Primrose Beauty' | 4 Y-YOO | 399–82.04465 | Rosewarne | 24 | 0 |
| 'Princeps' | 1 W-Y | 257–83.03188 | Rosewarne | 14 | |
| 'Quick Step' | 7 W-P | 399–82.04433 | Rosewarne | 28 | 66 |
| 'Rathkenny' | 1 W-Y | 399–82.04466 | Rosewarne | 28 + B | 77 |
| 'Red Devon' | 2 Y-O | 291–82.02873 | Wisley | 28 | 82 |
| 'Red Goblet' | 2 Y-R | 291–82.02874 | Wisley | 28 | 87 |
| 'Rembrandt' | 1 Y-Y | 291–82.02875 | Wisley | 28 | 63 |
| 'Rijnveld's Early Sensation' | 1 Y-Y | 399–82.04469 | Rosewarne | 33 | 88 |
| 'Riotous' | 4 Y-Y | 399–82.04467 | Rosewarne | 28 | 24 |
| 'Rippling Waters' | 5 W-W | 291–82.02876 | Wisley | 21 | 19 |
| 'Roberta Watrous' | 7 Y-GYP | 399–82.04468 | Rosewarne | 28 | 63 |

| Cultivar | Division/ colour | Kew accession number | Origin | 2n | Pollen Fertility % |
|---|---|---|---|---|---|
| 'Romeo' | 8 Y-O | 399–82.04486 | Rosewarne | 17 | 0 |
| 'Rose of Tralee' | 2 W-P | 257–83.03190 | Rosewarne | 27 | |
| 'Rushlight' | 2 Y-W | 291–82.02877 | Wisley | 28 | 76 |
| 'Rustom Pasha' | 2 Y-R | 257–83.03191 | Rosewarne | 28 | |
| 'Salmon Trout' | 2 W-P | 291–82.02878 | Wisley | 27 | 54 |
| 'Salome' | 2 W-PPY | 291–82.02879 | Wisley | 28 | |
| 'Sateen' | 2 W-YPP | 291–82.02880 | Wisley | 28 | 40 |
| 'Scarlet Gem' | 8 Y-R | 364–84.03763 | *Willis* | 17 | |
| 'Sebastopol' | 2 W-Y | 399–82.04470 | Rosewarne | 29 | 45 |
| 'Shah' | 7 Y-Y | 399–82.04434 | Rosewarne | 28 | 54 |
| 'Sidney Torch' | 2 Y-YOO | 399–82.04471 | Rosewarne | 28 | 89 |
| 'Silent Morn' | 3 W-YYO | 399–82.04472 | Rosewarne | 28 | 30 |
| 'Silver Chimes' | 8 W-W | 291–82.02881 | Wisley | 28 + B | |
| 'Silver Chimes' | 8 W-W | 364–84.03764 | *Willis* | 28 + B | |
| 'Sir Watkin' | 2 Y-Y | 257–83.03192 | Rosewarne | 21 | |
| 'Sir Winston Churchill' | 4 W-O | 399–82.04473 | Rosewarne | 17 | 0 |
| 'Snowshill' | 2 W-GWW | 399–82.04474 | Rosewarne | 28 | 53 |
| 'Sonata' | 9 W-GYR | 399–82.04464 | Rosewarne | 14 | 87 |
| 'Sparkling Eye' | 8 W-GOO | 364–84.03765 | *Willis* | 17 | |
| 'Spellbinder' | 1 Y-W | 291–82.02882 | Wisley | 29 | 66 |
| 'Spitzbergen' | 1 W-Y | 399–82.04476 | Rosewarne | 28 | 27 |
| 'St Agnes' | 8 W-Y | 364–84.03766 | *Willis* | 17 | |
| 'St Keyne' | 8 Y-O | 399–82.04488 | Rosewarne | 24 | 3 |
| 'St Keyne' | 8 Y-O | 364–84.03767 | *Willis* | 24 | |
| 'Straight' | 1 W-Y | 291–82.02883 | Wisley | 28 | 31 |
| 'Sunburst' | 4 Y-Y | 399–82.04477 | Rosewarne | 28 | 21 |
| 'Sunrise' | 3 W-Y | 257–83.03193 | Rosewarne | 14 | |
| 'Sweetness' | 7 Y-Y | 291–82.02884 | Wisley | 21 | 0 |
| 'Takoradi' | 4 W-W | 399–82.04478 | Rosewarne | 28 | 0 |
| 'Tête-à-Tête' | 6 Y-O | 296–82.03048 | Rosewarne | 24 + B | 2 |
| 'Tibet' | 2 W-W | 291–82.02885 | Wisley | 28 | 51 |
| 'Tittle Tattle' | 7 Y-Y | 399–82.04436 | Rosewarne | 21 | 8 |
| 'Toreador' | 3 W-R | 291–82.02886 | Wisley | 28 | 50 |
| 'Trenithon' | 1 Y-Y | 399–82.04489 | Rosewarne | 28 | 78 |
| 'Tresamble' | 5 W-W | 291–82.02887 | Wisley | 21 | 16 |
| 'Verger' | 3 W-R | 291–82.02889 | Wisley | 28 | 95 |
| 'Verona' | 3 W-W | 291–82.02890 | Wisley | 28 | 23 |
| 'Victoria' | 1 W-Y | 257–83.03195 | Rosewarne | 21 + B | |
| 'White Emperor' | 1 W-W | 257–83.03197 | Rosewarne | 28 | |
| 'White Lady' | 3 W-Y | 257–83.03198 | Rosewarne | 21 | |
| 'White Lion' | 4 W-WYY | 291–82.02892 | Wisley | 28 | 30 |
| 'White Marvel' | 4 W-W | 291–82.02893 | Wisley | 21 | 0 |
| 'White Nile' | 2 W-W | 257–83.03199 | Rosewarne | 29 | |
| 'White Sail' | 4 W-W | 399–82.04494 | Rosewarne | 14 | 0 |
| 'White Spire' | 2 W-W | 399–82.04495 | Rosewarne | 28 | 86 |
| 'Will Scarlett' | 2 W-R | 257–83.03196 | Rosewarne | 14 | |
| 'Windblown' | 4 W-WYY | 399–82.04496 | Rosewarne | 29 | 0 |
| 'Yankee Clipper' | 2 Y-Y | 291–82.02894 | Wisley | 28 | 83 |
| 'Yellow Cheerfulness' | 4 Y-Y | 399–82.04497 | Rosewarne | 24 | 0 |

hybrid and necessarily propagated clonally). It is thus not easy to decide whether a B chromosome is present or not in a plant with, for example, $2n = 3x + 1 = 22$ chromosomes, even if the extra chromosome is small and morphologically different from the remainder. It could simply be a normal member of one of the parents' complements and the extra chromosome is actually one of the other larger A chromosomes present in excess, as is common in polyploids. The cases cited below are nevertheless plants in which we are reasonably confident that B chromosomes exist.

No more than a single B chromosome was found in any cultivar, with occurrences in 'Ideal' ($2n = 17 + B$), 'Empress' and 'Victoria' ($2n = 21 + B$),

'Tête-à-Tête' (2n = 24 + B), 'Cantatrice', 'Gaucho', 'Kilrea', 'Rathkenny' and 'Silver Chimes' (2n = 28 + B), 'Matador' (2n = 32 + B) and 'Killara' (2n = 45 + B). These B chromosomes are all smaller than the smallest A chromosome and vary in morphology. In 'Silver Chimes' and 'Killara' (Fig. 10B, 10C) the B is a minute metacentric (the B chromosome in 'Silver Chimes' was clearly illustrated in her Fig. 5A by Wylie, 1952, but was not recognised, since she reported 2n = 29 chromosomes in this cultivar rather than 28 + B). The B's in these two cultivars are apparently identical (see below) and hetero-chromatic, staining less intensely than the A chromosomes. In all other cases the B is euchromatic. In 'Ideal' and 'Matador' (Fig. 9B) it is slightly larger than that in 'Killara' (Fig. 10C), but it is still small and metacentric. In 'Tête-à-Tête' it is a submetacentric of similar size (Fig. 7C) and in the remain-ing cultivars they are larger acrocentrics, almost as large as the smallest A chromosome.

## Frequency of the various chromosome numbers

The chromosome numbers in our sample of 230 cultivars (ignoring the presence of B chromosomes in eleven of them) are summarised in Table 3. Also in Table 3 our results are combined with other published accounts of the chromosomes of *Narcissus* cultivars (de Mol 1923, Nagao 1929, Philp 1934, Fernandes 1950, Wylie 1952, Fernandes & de Almeida 1971, A.D.S. 1981) to give a total of 466 records which rises to 526 when those for the wild species and natural $F_1$ hybrids in division 10 are added. All records are classified in Table 3 according to the RHS division of the plants. In the first part of the following account all members of division 8 and some members of divisions 4, 6, 10 and 11 (identified by asterisks in Table 3) will be omitted. These plants are subgenus *Hermione*, *N. tazetta* and its allies (x = 10, 11) and cultivars having plants of this group in their ancestry. The combination, in various multiples and proportions, of x = 10 or 11 chromosomes of subgenus *Hermione* with x = 7 from subgenus *Narcissus* results in a series of complex aneuploids and apparent aneuploids which will be discussed in detail later.

The remainder of Table 3 is concerned with cultivated forms of species (division 10) or more complicated hybrid cultivars which are nevertheless derived solely from ancestors having x = 7 chromosomes. It shows that the species forms and natural hybrids of division 10 are largely diploid, in common with the majority of the species from which they have arisen (Fedorov 1969, Moore 1982), and only a relatively few of them are triploid (2n = 21) or tetraploid (2n = 28). To a lesser degree this pattern is repeated in division 9, the Poeticus group, which also has a majority of diploid records, with sixteen diploids against only six tetraploids and no triploids. In divisions 7 (Jonquilla hybrids), 6 (Cyclamineus hybrids) and 5 (Triandrus hybrids) there are indi-cations of an increase in the number of polyploids compared with that of diploids, with the triploid level being predominant (Fig. 6B) and the tetraploid level being roughly similar to that of the diploids with the exception of division 5 in which no tetraploid has been located so far. A single aneu-pentaploid has been recorded in division 6; 'Larkelly' (2n = 5x + 1 = 36), and its derivation will be discussed below.

Divisions 1 to 3 are principally derived from *N. pseudonarcissus* with some interbreeding with other species to reduce the length of the corona from very long in division 1 to quite short in division 3. Division 11 is of similar origin,

TABLE 3. Total of known chromosome numbers in *Narcissus* cultivars arranged in RHS divisions (466 records plus 60 in division 10). Present authors' findings on 230 cultivars in brackets. B chromosomes are omitted, also the authors' records of division 10 plants wnich are in Table 1.

| R.H.S. Division | 2n = | 14 | 17 | 18 | 19 | 20 | 21 | 22 | 24 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 36 | 45 | 50 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | No. of records of each chromosome number | | | | | | | | |
| 1 | | (3)6 | | | | | (4)5 | 2 | (1)1 | 1 | (1)3 | (21)58 | (2)4 | | 1 | | (1)1 | | | |
| 2 | | (5)10 | | | 1 | | (3)6 | | | 2 | (6)9 | (54)131 | (4)4 | 1 | | | | | | |
| 3 | | (4)9 | | | | | (3)7 | | | | (2)3 | (17)30 | (2)2 | | | | | | | |
| 4 | | (5)6 | (1)*1* | | | | (3)8 | | (2*)3* | (1)1 | (6)6 | (17)18 | (2)4 | | | | | | | |
| 5 | | 2 | | | | | (5)7 | | | | | | | | | | | | | |
| 6 | | 4 | | | | | (9)10 | | (1*)1* | | | (2)4 | | | | | | (1)1 | | |
| 7 | | 2 | | | | | (6)12 | | | | | (3)3 | | | 1 | | | | | |
| 8* | | | (7*)14* | (1*)1* | | 1* | | | (6*)6* | | | (1*)1* | | 4* | (1*)1* | (1*)2* | | | (1*)1* | |
| 9 | | (5)16 | | | | | | | | | | (2)6 | | | | | | | | |
| 10 | | 44 | 3* | | | | 5 | | | | | 5 | | 1* | 1* | | | | | 1* |
| 11 | | | | | | | 1 | | | | (1)1 | (6)12 | (1)1 | 1* | | | | | | |
| 12 | | | | | | | | | | | | 6 | | | | | | | | |

*Plants with subgenus *Hermione* partially or totally in ancestry.

TABLE 4. Frequency of chromosome numbers in *Narcissus* cultivars based solely on subgenus *Narcissus* (x = 7). The authors' records are taken separately and combined with earlier records. B chromosomes are omitted, also all records in division 10 (species and natural hybrids), division 8 and any other plant known to have *N. tazetta* or its allies in its ancestry (marked with asterisks in Table 3).

| | The authors' records | | | Authors' plus earlier records | |
|---|---|---|---|---|---|
| 2n = | No. of records | % | 2n = | No. of records | % |
| 14 | 22 | 10·58 | 14 | 55 | 12·82 |
| 19 | 0 | 0 | 19 | 1 | 0·23 |
| 21 | 33 | 15·87 | 21 | 56 | 13·05 |
| 22 | 0 | 0 | 22 | 2 | 0·47 |
| 24 | 1 | 0·48 | 24 | 1 | 0·23 |
| 26 | 1 | 0·48 | 26 | 4 | 0·93 |
| 27 | 16 | 7·69 | 27 | 22 | 5·13 |
| 28 | 122 | 58·65 | 28 | 268 | 62·47 |
| 29 | 11 | 5·29 | 29 | 15 | 3·49 |
| 30 | 0 | 0 | 30 | 1 | 0·23 |
| 31 | 0 | 0 | 31 | 2 | 0·47 |
| 33 | 1 | 0·48 | 33 | 1 | 0·23 |
| 36 | 1 | 0·48 | 36 | 1 | 0·23 |
| Total | 208 | | Total | 429 | |
| 26–31 | 150 | 72·11 | 26–31 | 312 | 72·73 |

except that the corona is partially or completely divided into segments. In these divisions (except division 11) there are some diploids (Fig. 6A) and triploids, but these are completely overshadowed by large numbers of cultivars at or near the tetraploid level (Figs. 6C, 6D, 6E), with $2n = 4x \pm 2 = 26 - 30$. There are also two records in division 1 of higher numbers, $2n = 31$ and 33 (Fig. 7A). Division 12 (Miscellaneous daffodils) contains only tetraploids, but numbers sampled are too low to be significant. Division 4 (Double-flowered cultivars) has a distribution of diploids, triploids, tetraploids and aneuploids similar to those of divisions 1–3.

The chromosome numbers of our plants taken alone and added to those of earlier workers' material are summarised in Table 4. In this table only hybrid cultivars based solely on x = 7 chromosomes are taken into account (i.e. division 10 is excluded, and also all plants with subgenus *Hermione* in their ancestry, comprising division 8 and a few other cultivars asterisked in Table 3).

The very low overall frequency of diploids (10·5–13%) and triploids (13–16%) is quite evident, also the very high frequency of tetraploids and near-tetraploids. The records at the tetraploid level are very similar, our findings being 58·65% and the total records being 62·47%, but these figures approach each other even more closely when records in the aneuploid/euploid/aneuploid range from $2n = 26$ to 31 are combined (Table 4), ours becoming 72·11% and the total records becoming 72·73%. Thus we found relatively slightly fewer eu-tetraploids ($2n = 28$) and relatively more aneu-tetraploids ($2n = 26, 27, 29$) than the previous workers did, indicating possibly that some aneuploids at this level were scored by early workers as eu-tetraploids, perhaps because they were working with poorly spread mitotic cells or with sections.

Notwithstanding the slight discrepancy over aneuploid frequency at the tetraploid level our data on the relative frequency of the various chromosome numbers in *Narcissus* cultivars match those of previous workers very closely. It therefore follows that our data are representative of the total data, and the latter, an overall sample of 429 cultivars based solely on $x = 7$ plants, may be taken confidently as being characteristic of all of the ten thousand cultivars, i.e. if every one of them was analysed chromosomally the relative frequencies of the various chromosome numbers should not differ markedly from those presented here.

Aneuploids have not been detected at the diploid level, showing either that meiosis is quite regular in diploids, producing only $n = 7$ gametes, or that any aneuploids produced are non-viable, or at best are too weak to be selected by breeders. At the tetraploid level they are more common, with many records (Tables 3 & 4) of plants having $4x \pm 1 = 27$ or 29 chromosomes (Figs. 6D, 6E), and a few having $4x \pm 2 = 26$ or 30 chromosomes. It is well-known that in autotetraploids having a high quadrivalent frequency at meiosis the production of aneuploid gametes is quite common. The aneuploid products of the fusion of these gametes with each other or with normal ones are viable, due to the presence of several sets of chromosomes which buffer the adverse effects of the chromosomal imbalance, and have been reported to survive even under the harshly competitive conditions of the wild environment (Brandham & Johnson 1977). These are clearly more likely to survive in the less competitive environment found in cultivation, and the aneuploidy could easily endow the individual with a morphological characteristic that appeals to the hybridist, provided that the aneuploids do not show too much loss of vigour.

At the triploid level aneuploidy is rare and the two records of $2n = 3x + 1 = 22$, 'Grandis' and 'Horsefieldii' were even suggested by Wylie (1952) actually to be $2n = 21 + B$ (i.e. similar to 'Empress' and 'Victoria' which are recorded above as triploids with one B chromosome). Because of its demonstrable irregularity, tetraploid meiosis produces many aneuploid gametes and it might thus be expected that aneuploidy would be more common in triploids if it is assumed that they normally result from diploid/tetraploid hybridisations. The almost complete absence of aneuploids at the triploid level therefore indicates that they are probably only rarely the products of diploid × tetraploid crosses and that the majority arise from diploids alone in another way. This is the process of non-reduction, in which a few gamete-mother cells of a diploid bypass normal meiosis and produce diploid gametes directly, which fuse with normal haploid gametes to produce triploid offspring (Brandham 1982). This process does not permit the formation of aneu-triploids, since the non-reduced gametes from a diploid can be only precisely diploid and not aneuploid. Non-reduction can occur at any level of polyploidy and also in wide hybrids. In fact in the latter the non-reduced gametes are often the only viable ones that the plant can produce (Wylie 1952). Non-reduction will be shown below to be an important and frequent source of many of the *Narcissus* cultivars at the triploid and higher levels of polyploidy.

Above the tetraploid level there are a few aneuploid cultivars which approach or slightly exceed the pentaploid level of $2n = 35$ (to be considered individually below), but no higher polyploids have been found. Wylie (1952) found an aneu-hexaploid ($2n = 6x - 1 = 41$) occurring spontaneously in a population of a presumably tetraploid cultivar, originating probably from the fusion of a non-reduced gamete ($n = 28$) with an aneuploid one ($n = 13$). This

FIG. 6. Somatic chromosomes of *Narcissus* cultivars. **A** Diploid 'Firebrand' (division 3), 2n = 14; **B** Triploid 'Jenny' (division 6), 2n = 21; **C** Tetraploid 'Nemo' (division 3), 2n = 28; **D** Aneu-tetraploid 'Salmon Trout' (division 2), 2n = 27; **E** Aneu-tetraploid 'Papillon Blanc' (division 11), 2n = 29. Scale = 10µm.

she reported to be viable but weak and it is very clear that the tetraploid is the optimal level for the cultivated forms of *Narcissus*. The allohexaploid *N. × dubius* (2n = 50) has been placed by A.D.S. (1981) in division 10 (Table 3) and

is a naturally occurring species of hybrid origin rather than a cultivar (see below).

### The derivation of apparent aneuploids and other uncommon chromosome numbers

The subgenus *Hermione* of *Narcissus* differs from subgenus *Narcissus* in having the basic chromosome numbers $x = 10$ or $11$ rather than $x = 7$, but despite this difference members of the two subgenera are often sexually compatible, at least as far as the $F_1$ hybrid stage. In these inter-subgeneric crosses breeders have mostly used the $x = 10$ forms of *N. tazetta* and its allies ($2n = 20$), giving hybrids with $2n = 17$ when crossing them with diploids having $2n = 14$ and hybrids with $2n = 24$ when crossing them with tetraploids having $2n = 28$. A wide range of true and apparent aneuploids also occurs within this particular group of hybrids (division 8), and their origin and probable chromosome constitution will now be considered individually, together with plants from other divisions which either have *N. tazetta* affinities, or are aneuploid or have uncommon or otherwise interesting euploid chromosome numbers. Data are taken from Nagao (1929), Philp (1934), Wylie (1952), Jefferson-Brown (1969) and A.D.S. (1981), supplemented by our own observations (Table 3).

In predicting the chromosomal origin of a cultivar several different types of chromosomal behaviour at meiosis are taken into account as possible mechanisms for the origin of particular gamete types:- a, non-reduction, in which a plant of any chromosome number can produce a gamete with the same chromosome number, or occasionally double that number, as in the extreme case of the *N. tazetta* hybrid 'Geranium' ($2n = 17$) in which the only viable gametes have $n = 17$ or $34$ chromosomes (Wylie 1952); b, the irregular nature of meiosis in autotriploids (in this case with $2n = 21$). Through the irregular 2:1 segregation of each of the potential maximum of seven trivalents at anaphase 1 the gametes of such triploids can contain any number of chromosomes between $n = 7$ and $n = 14$ with the numbers nearest to the extremes being the most viable (Brandham 1982); c, the irregular nature of meiosis in tetraploids ($2n = 28$). Although normally more regular than in triploids, meiosis in these plants can produce viable gametes with $n = 13$ or $15$ (less commonly 12 or 16) in addition to the expected $n = 14$ chromosomes.

Commonly-occurring aneuploids between $4x - 2$ ($2n = 26$) and $4x + 1$ ($2n = 29$) arise mostly as a result of meiotic irregularities in tetraploids and only two aneuploids between $2n = 26$ and $29$ will be considered in detail, together with the apparently eu-tetraploid 'Silver Chimes' ($2n = 28 + B$) which is actually a tribasic allotriploid of complex parentage (see below).

The analysis of the origin of selected cultivars follows, the account being arranged in R.H.S. division order and in order of increasing chromosome number within each division.

### Division 1.

'Maximus Superbus' ($2n = 21$). Selected from *N. pseudonarcissus* subsp. *major* Baker (= *N. hispanicus* Gouan), a diploid with $2n = 14$. The result of the fusion of a non-reduced gamete with a normal one.

'Magnificence' ($2n = 21$). A seedling from triploid 'Maximus'. *Narcissus* is not known to be self-fertile, so this cultivar is probably the result of a triploid × diploid cross or a triploid × tetraploid cross. Either of these crosses can

produce some triploid progeny, with a diploid gamete being produced by the autotriploid parent in the former case and a haploid gamete in the latter case (see Brandham 1982). The crosses can be written thus: $2n = 14$ (from 21) $+ 7$ (from 14) $= 21$ (the triploid $\times$ diploid cross) or $2n = 7$ (from 21) $+ 14$ (from 28) $= 21$ (the triploid $\times$ tetraploid cross). Other crosses or probable crosses will be expressed in the same way below.

'Victoria' ($2n = 21 + B$). Unknown origin; probably arose from a diploid ($2n = 14 + B$) through the fusion of a non-reduced gamete ($n = 14 + B$) with a normal gamete ($n = 7$) from another diploid ($2n = 14$). This plant has given rise vegetatively to the split-corona (division 11) cultivar 'Buttonhole', which also has $2n = 21 + B$.

'Emperor' ($2n = 21$) and 'Empress' ($2n = 21 + B$). Both are very old triploids introduced in 1865 from a cross between *N. pseudonarcissus* var. *pseudonarcissus* and *N. pseudonarcissus* var. *bicolor* Willk. The latter was reported to be tetraploid by A. & R. Fernandes (1946), but was suggested to be triploid by Wylie (1952) because of its very low fertility. Thus these triploids arose in one of two ways: $2n = 7$ (from 14) $+ 14$ (from 28) $= 21$, or $2n = 7$ (from 14) $+ 14$ (from 21) $= 21$, the former according to A. & R. Fernandes and the latter according to Wylie. The B chromosome in 'Empress' could have been inherited from var. *bicolor* (see below under 'Grandis').

'Grandis' ($2n = 22$, or $21 + B$ according to Wylie (1952)). Selected from *N. pseudonarcissus* var. *bicolor*, also most probably $2n = 21 + B$, after pollination by a diploid. Thus $2n = 14 + B$ (from $21 + B$) $+7$ (from 14) $= 21 + B$.

'Horsefieldii' ($2n = 22$, or $21 + B$ according to Wylie (1952)). From triploid 'Maximus' $\times$ probable triploid ($+ B$) *N. pseudonarcissus* var. *bicolor*. $2n = 7$ (from 21) $+ 14 + B$ (from $21 + B$) $= 21 + B$.

'Content' ($2n = 24$). No affinity with subgenus *Hermione*, unlike several division 8 cultivars with $2n = 24$ (see below). From 'Lord Antrim' $\times$ 'Beersheba'. The latter is known to have $2n = 28$ chromosomes, but the former is chromosomally unknown. As a cross between two tetraploids is unlikely to give progeny lacking four chromosomes ($2n = 24 = 4x - 4$) it is more probable that 'Lord Antrim' is a triploid, contributing $n = x + 3 = 10$ chromosomes to the hybrid as a result of irregular triploid meiosis. Thus in 'Content' $2n = 10$ (from 21) $+ 14$ (from 28) $= 24$.

'Charles' First' ($2n = 26$). Unknown origin; possibly from tetraploid $\times$ tetraploid or tetraploid $\times$ triploid cross with the involvement of aneuploid gametes, i.e. $2n = 13$ (from 28) $+ 13$ (from 28) $= 26$ or $2n = 13$ (from 28) $+ 13$ (from 21) $= 26$. It could also have arisen from a diploid $\times$ triploid cross through a combination of non-reduction and aneuploidy, thus $2n = 14$ (from 14) $+ 12$ (from 21) $= 26$.

'Madame de Graaff' ($2n = 31$, or more probably $30 + B$). No affinity with subgenus *Hermione*, unlike other plants with approximately this number (see below). From 'Empress' ($2n = 21 + B$) $\times$ *N. pseudonarcissus* var. *albescens*. The most probable origin assumes var. *albescens* also to be triploid. Thus with non-reduction in the female parent the plant is $2n = 21 + B$ (from $21 + B$) $+ 9$ (from 21) $= 30 + B$. Two less probable origins are as follows, assuming respectively that var. *albescens* is diploid or tetraploid; a, $2n = 16 + B$ (from $21 + B$) $+ 14$ (from 14 by non-reduction) $= 30 + B$, a very unlikely alterna-

FIG. 7. Somatic chromosomes of *Narcissus* cultivars. **A** Sub-pentaploid 'Rijnveld's Early Sensation' (division 1), 2n = 33; **B** Allotriploid 'Yellow Cheerfulness' (division 4), 2n = 24; **C** Allotriploid 'Tête-à-Tête' (division 6), 2n = 24 + B (arrow). Scale = 10μm.

tive because a triploid does not normally produce a gamete meiotically with more than the diploid number of chromosomes (in this case 14); b, 2n = 14 + B (the largest possible gamete from 21 + B) + 16 (from 28 through irregular meiosis) = 30 + B.

'Rijnveld's Early Sensation' (2n = 33). A sub-pentaploid of unknown origin; no evidence of *Hermione* ancestry unlike other plants with 2n = 33 (see below). As it is a 4x + 5 plant it is unlikely to have arisen from the hybridisation of two tetraploids because the degree of aneuploidy is too high. It can therefore have arisen in one of three ways; a, triploid × triploid with non-reduction in one parent and an aneuploid gamete from the other, i.e. 2n = 21 (from 21) + 12 (from 21) = 33; b, triploid × tetraploid, again with non-reduction and aneuploidy, i.e. 2n = 21 (from 21) + 12 (from 28) = 33; c, the least likely origin is the involvement of a hexaploid (2n = 42), of which very few are known to exist, i.e. 2n = 14 (from 21 or 28) + 19 (from 42) = 33 (Fig. 7A).

*Division 2.*

'Bethany' (2n = 19). From 'Binkie' (2n = 28) crossed with an unnamed seedling (which could only have been diploid) with the involvement of an aneuploid gamete from the former; thus 2n = 12 (from 28) + 7 (from 14) = 19.

'Gervo' (2n = 30). Unknown origin, but no *Hermione* ancestry. Probably 2n = 15 (from 28) + 15 (from 28) = 30.

*Division 4.*

'Sir Winston Churchill' (2n = 17). From *N. poeticus* × *N. tazetta* (2n = 20), i.e. 2n = 7 (from 14) + 10 (from 20) = 17.

'Cheerfulness' (2n = 24). Double-flowered form of 'Elvira' (division 8, see below) originating vegetatively.

'Yellow Cheerfulness' (2n = 24). A yellow-flowered mutation derived vegetatively from 'Cheerfulness' (Fig. 7B).

'Primrose Beauty' (2n = 24). Unknown origin, but clearly related to subgenus *Hermione*, so presumably derived from *N.* aff. *tazetta* crossed with an unknown tetraploid of subgenus *Narcissus*, i.e. 2n = 10 (from *taz.* 20) + 14 (from 28) = 24.

'Falaise' (2n = 26). From the double-flowered 'Mary Copeland' (2n = 21) × unknown (probably 2n = 28) with the involvement of an aneuploid gamete from the former; i.e. 2n = 12 (from 21) + 14 (from 28) = 26. Among plants of the *Aloineae* tribe (*Liliaceae*) crosses between triploids (2n = 21) and tetraploids (2n = 28) produce quite large numbers of 2n = 26 aneuploids, among others (Brandham 1982). "Weedy little…'Falaise'… cannot be said to be outstandingly robust" (Jefferson-Brown 1969: 115, 31), which is perhaps indicative of the fact that loss of two of the genetically more vital chromosomes from a tetraploid is quite a major degree of aneuploidy and can have extensive deleterious effects on the morphology and vigour of the plant.

*Division 6.*

'Tête-à-Tête' (2n = 24 + B). An allotriploid of complex parentage, including 'Soleil d'Or' (a diploid plant of subgenus *Hermione*) in its origin. The plants involved are: [(diploid *N. cyclamineus* × diploid 'Soleil d'Or') = 'Cyclataz'] × 'Op' (presumably also diploid). Chromosomally the origin is as follows: a. 2n = 7 (from 14) + 10 (from 20) = 17 'Cyclataz'; b. 2n = 17 (from 17 'Cyclataz' with non-reduction) + 7 (from 14) = 24 'Tête-à-Tête'. The B chromosome could have been inherited from any one of the three immediate ancestors (Fig. 7C).

'Larkelly' (2n = 36). This cultivar (5x + 1) is from an unnamed plant (presumably an aneu-tetraploid with 2n = 29) crossed with *N. cyclamineus*, of which forms with more than 14 chromosomes are unknown (A. & R. Fernandes 1946). Its probable origin is through a non-reduced gamete from the aneu-tetraploid, hence 2n = 29 (from 29) + 7 (from 14) = 36.

*Division 7.*

'Golden Perfection' (2n = 31). There are conflicting accounts of the origin of this cultivar, and without access to illustrations of its chromosomes we cannot say which is correct. Possibly there are two different cultivars with the same name in this case. Wylie (1952) proposed two types of *N. jonquilla-poeticus-tazetta* ancestry: a, tetraploid *N. poeticus* (2n = 28) crossed with diploid *N. tazetta* to give a 2n = 24 hybrid which produced a non-reduced gamete to fuse with a

haploid *N. jonquilla* gamete (n = 7) to result in a 2n = 31 allotetraploid with a genomic constitution Jo-Po-Po-Tz; b, diploid *N. poeticus* (2n = 14) crossed with diploid *N. tazetta* (2n = 20) to give a 2n = 17 hybrid which produced a non-reduced (n = 17) gamete to fuse with a non-reduced (n = 14) gamete from *N. jonquilla* to result in a 2n = 31 hybrid with the genomic constitution Jo-Jo-Po-Tz which is indistinguishable from the above.

The version of the origin of 'Golden Perfection' in A.D.S. (1981) is significantly different from Wylie's account, still with the involvement of *N. poeticus* and *N. jonquilla*, but with *N. pseudonarcissus* rather than *N. tazetta*. Details are as follows: The hybrid (2n = 31) is derived from the diploid (2n = 14) *N.* × *odorus* (from *N. pseudonarcissus* × *N. jonquilla*), which produced a non-reduced gamete to fuse with an aneuploid n = 17 gamete from the other parent 'Homespun' which has no *Hermione* ancestry. The chromosome constitution of 'Homespun' is unknown, but as the production of n = 2x + 3 = 17 gametes from tetraploids is very rare it is more likely that 'Homespun' is a pentaploid with 2n = 35, from which gametes with n = 17 would be more common. 'Homespun' is from diploid *N. poeticus* subsp. *ornatus* × 'Golden Spur' (? 2n = 4x = 28), a selection from *N. pseudonarcissus* subsp. *major*. Non-reduction in 'Golden Spur' would give a gamete with n = 28 chromosomes to fuse with a normal n = 7 gamete from *N. poeticus* subsp. *ornatus* to give 2n = 35 in 'Homespun'. There is also a possibility that 'Golden Spur' is triploid (2n = 21), and that 'Homespun' arose from non-reduction in both of its immediate parents i.e. 2n = 14 (from 14) + 21 (from 21) = 35.

*Division 8.*

'Cyclataz' (2n = 17). From *N. tazetta* 'Soleil d'Or' (2n = 20) × *N. cyclamineus* (2n = 14), i.e. 2n = 10 (from 20) + 7 (from 14) = 17.

'Early Splendour', 'Romeo', 'Sparkling Eye' (all 2n = 17), 'Ideal' (2n = 17 + B). All from unknown subgenus *Narcissus* diploids crossed with diploid *N. tazetta*, i.e. 2n = 7 (from 14) + 10 (from 20) = 17 (Fig. 8A). The B chromosome in 'Ideal' could have originated from either parent.

'Alsace', 'Cragford', 'Geranium', 'Irene', 'Jaune à Merveille', 'L'Innocence', 'Laurens Koster', 'Scarlet Gem', 'St. Agnes' (all 2n = 17). From *N. poeticus* (2n = 14) × *N. tazetta* (2n = 20), i.e. 2n = 7 (from 14) + 10 (from 20) = 17. These hybrids are sterile except for the production of some non-reduced or doubled gametes (Wylie 1952).

'Hiawassee' (2n = 18). From diploid 'Cassandra' (a hybrid between *N. poeticus* subsp. *poeticus* and *N. poeticus* subsp. *radiiflorus* var. *poetarum*) crossed with 'Paper White' (= *N. papyraceus*, 2n = 22), an ally of *N. tazetta*, i.e. 2n = 7 (from 14) + 11 (from 22) = 18 (Fig. 8B).

'Soleil d'Or' (2n = 20). A diploid selection from *N. tazetta* (2n = 20).

'Aspasia', 'Kingcraft', 'St. Keyne' (all 2n = 24). From unknown tetraploids of subgenus *Narcissus* (2n = 28) crossed with *N. tazetta* (2n = 20), i.e. 2n = 14 (from 28) + 10 (from 20) = 24.

'Elvira', 'Glorious' (both 2n = 24). From tetraploid *N. poeticus* crossed with diploid *N. tazetta*, i.e. 2n = 14 (from 28) + 10 (from 20) = 24 (Fig. 8C). All of these *N. tazetta* hybrids with 2n = 24 chromosomes are dibasic allotriploids
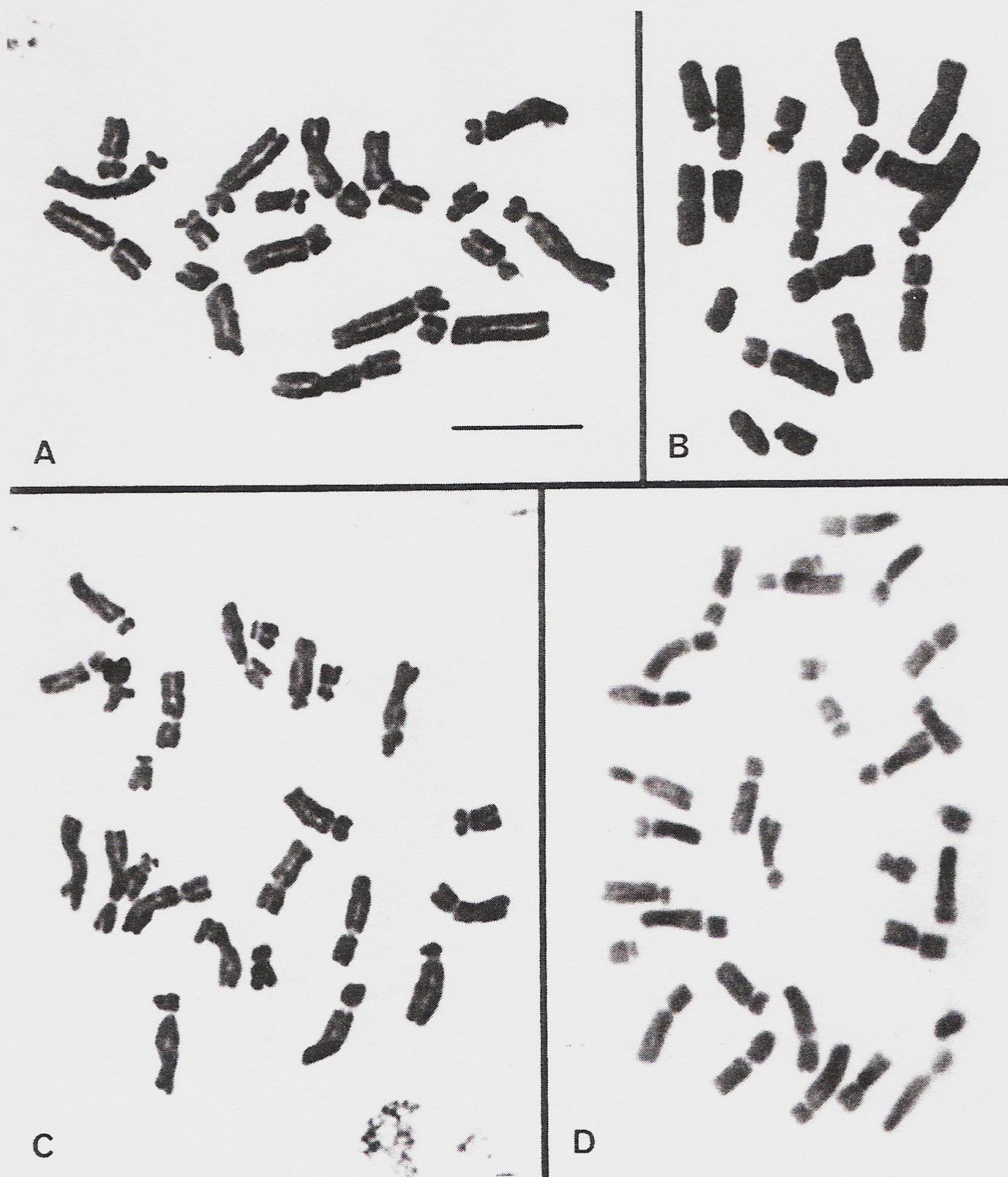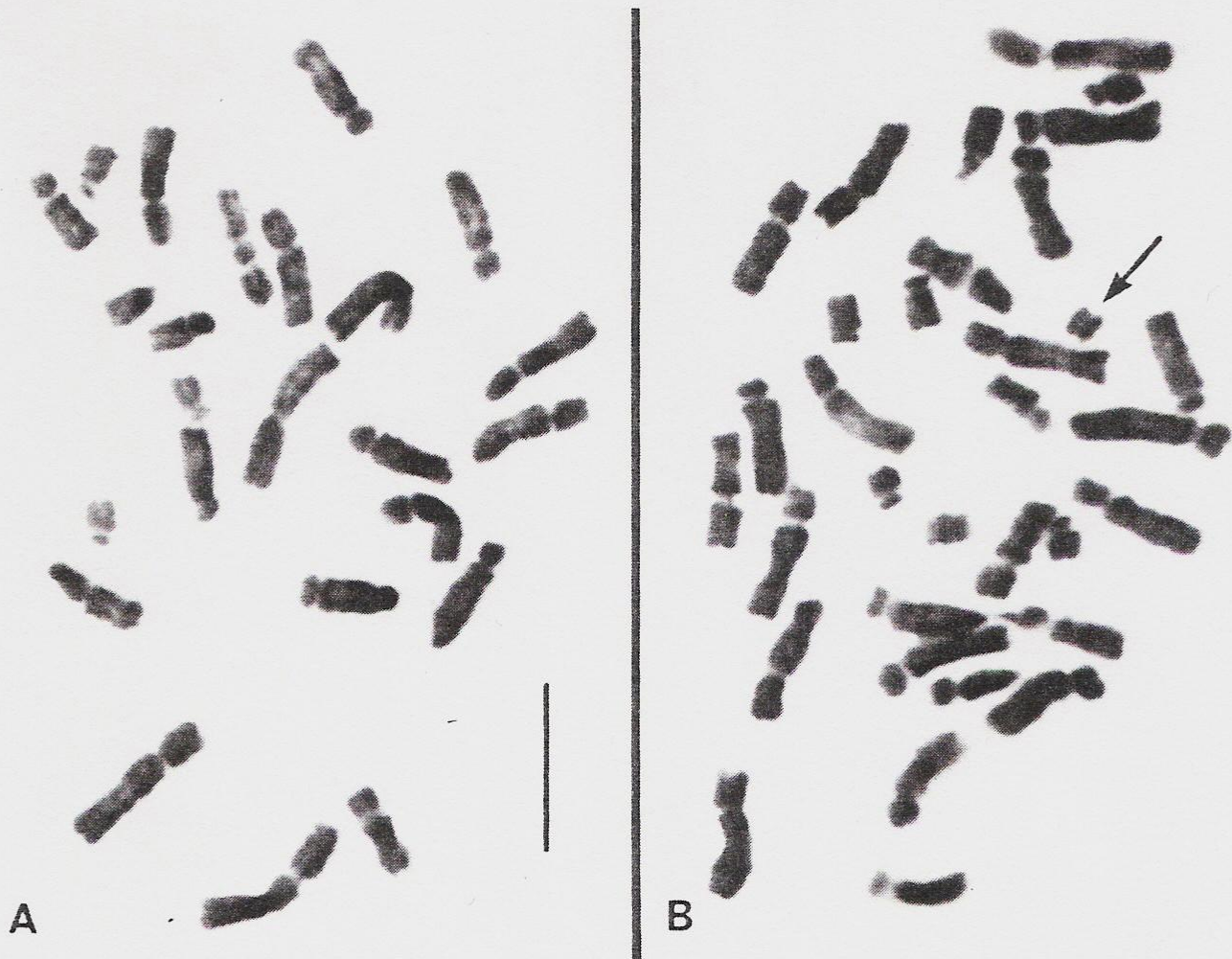
FIG. 8. Somatic chromosomes of *Narcissus* cultivars in division 8, the *N. tazetta* hybrids. **A** 'Sparkling Eye', 2n = 17; **B** 'Hiawassee', 2n = 18; **C** 'Elvira', 2n = 24; **D** 'Highfield Beauty', 2n = 31. Scale = 10μm.

which would be expected to be totally sterile except for the occasional production of non-reduced gametes (see discussion of 'Killara', below).

'Chinensis', 'Grand Emperor of China', 'Grand Primo Citronière', 'Grand Soleil d'Or' (all 2n = 30). All autotriploids selected from *N. tazetta* (2n = 20). 'Grand Soleil d'Or' is a triploid derivative of the diploid 'Soleil d'Or' (Wylie 1952).

'Highfield Beauty' (2n = 31). A cross between two plants of subgenus *Hermione* having 2n = 20 and 22 respectively, with non-reduction in the former. i.e. 2n = 20 (from 20) + 11 (from 22) = 31 (Fig. 8D).

'Scilly White' (2n = 32). Another cross between two plants of subgenus *Hermione* having 2n = 20 and 22 but with non-reduction in the latter, i.e. 2n = 10 (from 20) + 22 (from 22) = 32.

Fig. 9. Somatic chromosomes of *Narcissus* cultivars in division 8, the *N. tazetta* hybrids. **A** 'Golden Dawn', 2n = 24; **B** 'Matador', 2n = 32 + B (arrow). Scale = 10µm.

'Golden Dawn' (2n = 24) and 'Matador' (2n = 32 + B). Both were introduced by J. de Graaff of Oregon Bulb Farms in 1958 as hybrids between 'Admiration' and ?'Op' (A.D.S. 1981), so these two will be considered together. Their claimed common origin cannot be reconciled with the chromosome data now available. 'Op' is probably a diploid, as can be implied from the ancestry of 'Tête-à-Tête' (see above), but 'Admiration' is chromosomally unknown. It is clearly a *N. tazetta* form or hybrid (A.D.S. 1981), so could have 2n = 17, 20, 22 or 24 chromosomes. A significant fact relevant to this problem is that 'Matador' was said by Jefferson-Brown (1969) to set seeds occasionally, which is borne out by our finding quite a high pollen fertility (66%) in this cultivar (Table 2), which is unlike any other hybrid between subgenus *Hermione* and subgenus *Narcissus*. This would suggest that 'Matador' is chromosomally similar to 'Scilly White' (also 2n = 32), being an allotriploid between two closely related subgenus *Hermione* species or hybrids having 2n = 20 and 22 chromosomes with a B chromosome additionally present in one of them, the 2n = 20 plant being 'Admiration'. Thus 'Matador' is 2n = 10 (from 'Admiration', 20) + 22 + B (from 22 + B with non-reduction) = 32 + B (Fig. 9B).

Because of the close affinity of the x = 10 and x = 11 genomes of subgenus *Hermione*, 'Matador' (which has 2n = 10 + 11 + 11 + B) would behave as a cytological autotriploid and would be slightly fertile, as are other autotriploids (Brandham 1982). Clearly no subgenus *Narcissus* plant with x = 7 (e.g. 'Op') could have taken part in its parentage.

In the light of this suggested origin for 'Matador' the origin of the other plant produced by de Graaff, 'Golden Dawn' can be explained easily on the basis of the claimed cross, 'Admiration' (now probably 2n = 20) × 'Op' (2n = 14), with non-reduction in 'Op'. Chromosomally, 'Golden Dawn' is therefore 2n = 10 (from 'Admiration', 20) + 14 (from 'Op', 14) = 24 (Fig. 9A).

FIG. 10. Somatic chromosomes of *Narcissus* cultivars with *N. tazetta* in their ancestry. **A** N. ×
*compressa*, 2n = 31; **B** 'Silver Chimes', 2n = 28 + B (arrow); **C** 'Killara', 2n = 45 + B (arrow).
Scale = 10μm.

'Silver Chimes' (2n = 28 + B) and 'Killara' (2n = 45 + B). These two culti-
vars have one parent in common, the *N. tazetta* hybrid 'Grand Monarch'
(origin and chromosome number unknown), said to be crossed with diploid *N.
triandrus* to produce 'Silver Chimes' and with triploid 'Empress' to produce
'Killara' (A.D.S. 1981), but as will be shown below at least one of these crosses
cannot be as claimed. The affinity of these two hybrids is nevertheless demon-
strated by the fact that both carry what seems to be the same B chromosome,
presumably inherited from 'Grand Monarch'. This B is very small, sub-
metacentric, and is unusual in the genus *Narcissus* in being heterochromatic,
staining much less intensely than the A chromosomes (Figs. 10B, 10C).

Taking firstly 'Silver Chimes', its 2n = 28 + B chromosomes could have
been inherited as n = 7 from *N. triandrus*, which is known to be only diploid
(Fernandes 1967), leaving n = 21 + B as the chromosome constitution of the
gamete from 'Grand Monarch'. This could also be the somatic chromosome
number of this cultivar (assuming that non-reduction had taken place), since
the 2n = 20 and 22 forms of *N. tazetta* are known to hybridise to produce
2n = 21 plants (Fernandes 1966), this one containing a B chromosome also.
Thus 'Silver Chimes' is 2n = 21 + B (from *taz*. 20 + B × *taz*. 22 = 'Grand
Monarch', 21 + B) + 7 (from *N. triandrus*, 14) = 28 + B (Fig. 10B). Chromo-

somally it is a very unusual plant, being a tribasic allotriploid (2n = 3x = 11 + 10 + 7 in addition to the B).

If 'Grand Monarch' is indeed taken to be 2n = 21 + B two alternatives for the production of the 2n = 45 + B chromosomes of 'Killara' (Fig. 10C) can be suggested as follows, neither of which can possibly involve the known 2n = 21 + B chromosomes of 'Empress', either non-reduced or otherwise: either a, 'Killara', 2n = 10 + B (from 'Grand Monarch', 21 + B) + 35 (from an unknown subgenus *Narcissus* pentaploid with non-reduction) = 45 + B, or b, 'Killara', 2n = 21 + B (from 'Grand Monarch' 21 + B, with non-reduction) + 24 (a viable non-reduced gamete from an unknown allotriploid *N. tazetta* hybrid with 2n = 24, similar to 'Aspasia', 'Kingcraft' etc., as detailed above) = 45 + B.

Clearly a close investigation of 'Silver Chimes', 'Killara' and all of their putative parents is required before a definite answer to this particular problem can be reached.

*Division 10.*

*N.* × *biflorus* Curt. and *N.* × *medioluteus* Mill. (both 2n = 17). Natural hybrids between diploid *N. tazetta* (2n = 20) and *N. poeticus* (2n = 14).

*N.* × *intermedius* Lois. (2n = 17). Natural hybrid between diploid *N. tazetta* (2n = 20) and *N. jonquilla* (2n = 14).

*N. canaliculatus* Guss. (2n = 30). A synonym of *N. tazetta* subsp. *lacticolor* (Steud.) Baker, and presumably autotriploid (x = 10).

*N.* × *compressa* Haw. (2n = 31). Reported by Jefferson-Brown (1969) to be a hybrid between *N. tazetta* and *N. jonquilla*. Chromosomally 2n = 10 (from *taz.*, 20) + 21 (from triploid *N. jonquilla*, 21) = 31 (Fig. 10A).

*N.* × *dubius* Gouan (2n = 50). A well-known allohexaploid derived from *N. papyraceus* (2n = 22) and *N. juncifolius* (2n = 14). It arose from the fusion of a non-reduced *juncifolius* gamete (n = 14) with a normal *papyraceus* gamete (n = 11) to give a hybid with 2n = 25 which doubled its chromosome number to produce a plant with 2n = 50. The genomic constitution of this fertile allohexaploid is Ju-Ju-Ju-Ju-Pa-Pa. It is widespread in north-east Spain and southern France (Fernandes 1967). Chromosomally it is 2n = [11 (from 22) + 14 (from 14) = 25] × 2 = 50.

*Division 11.*

'Modesta' (2n = 30). Affinities and origin not known. Either an autotriploid form of *N. tazetta* (x = 10) or an aneu-tetraploid (2n = 4x + 2) of a subgenus *Narcissus* plant (x = 7).

*Pollen fertility*

Fertility levels in the cultivars range between zero and well over 90% (Table 2). Plants falling into the zero category are of two types. The first is hybrids between subgenus *Hermione* and subgenus *Narcissus* (i.e. most of division 8 and a few others). These hybrids, with 2n = 17, 18, 24, 31, 45 etc. (see above) display very little affinity between their component genomes and their resulting aberrant meiosis (Fernandes 1950) makes them almost completely

sterile. Only a few non-reduced or doubled gametes (e.g. n = 17 or 34 from a 2n = 17 plant) are viable in these plants (Wylie 1952).

The second type with zero pollen fertility is division 4, the double-flowered cultivars. Most of these plants have no anthers and are obviously totally pollen-sterile. It is nevertheless possible that they can possess a fully functional and fertile female reproductive system. Those plants of division 4 which do have some anthers in the flower (e.g. 'Riotous' and 'White Lion'), even if they are distorted or partially converted into corolla tissue, achieve a reasonable degree of pollen fertility. The total amount of pollen per flower may, however, be too small for the flower to be used easily by breeders as a pollen source.

Other cultivars with very low pollen fertilities are the triploids with 2n = 21 chromosomes. It has been established (Brandham 1982) that autotriploids can have a fairly efficient meiosis and can produce a reasonable number of viable haploid, near haploid, near diploid and diploid gametes (i.e. with n = 7, 8, 13, 14, less commonly 9 or 12 from a triploid with 2n = 3x = 21). Triploid cultivars of this type are 'Bartley' (34% pollen-fertile), 'Cornet' (15%) and 'Jana' (39%). These are evidently autotriploids derived from fusion of a normal gamete with a non-reduced one either within *N. cyclamineus* or between *N. cyclamineus* and a plant very closely related to it chromosomally.

Allotriploids have two similar genomes and a third which is genetically quite different, and usually arise from a tetraploid/diploid hybridisation involving distantly related entities. During meiosis many chromosomes do not pair in allotriploids and the resulting disruption of the division causes a high level of sterility. Examples of allotriploid *Narcissus* are 'St. Keyne' (one *N. tazetta* genome and two from subgenus *Narcissus*) which is only 3% pollen-fertile, also the cross between 'Mitylene' (division 2 tetraploid) and *N. cyclamineus* which has given rise to 'Charity May' (0% pollen-fertile), 'Dove Wings' (3%) and 'Jenny' (10%) and the cross between 'Gulliver' (division 3 tetraploid) and *N. jonquilla* which has produced 'Golden Incense' (0% pollen-fertile) and 'Tittle Tattle' (8%). These data are from Table 2 and A.D.S. (1981).

Other triploids of which the pollen fertility is known (Table 2) are of obscure origin, but in the light of the above examples it may be taken that those with well over 10% pollen-fertility are fundamentally autotriploid, having a fertility similar to the known autotriploids *Aloe jucunda* (15%, Brandham 1982) and *Tradescantia acaulis* (22%, Martinez, pers. comm.), while those with 10% pollen fertility or less are more probably allotriploids with a wider hybrid origin.

The remainder of the cultivars, diploids (2n = 14), tetraploids (2n = 28) and aneuploids (2n = 26, 27, 29 etc.) are remarkably fertile, with pollen fertilities well over 50% in most cases and very few that are below 30% (Table 2). Indeed the only members of this particular chromosome group that we have found to have pollen fertilities which are too low to be of any practical value to the breeder are 'Fermoy' (6%), 'Golden Lacquer' (2%), 'Kilrea' (3%) and 'Mr Jinks' (2%). All of these are tetraploid, with a B chromosome in 'Kilrea' and an extra A chromosome in 'Mr Jinks'. The precise cause of the sterility of these plants cannot be established at present in the absence of information on their meiotic behaviour.

In the majority of the tetraploids which have increasing levels of fertility, moderate fertility (i.e. ±50%) would be indicative of autotetraploidy (i.e. they have four very similar sets of chromosomes that can be expressed as AAAA). These plants form large numbers of quadrivalents during meiosis and consequently the later stages of meiosis display a high frequency of numerical

aberrations (i.e. gametes with a range of numbers which could be as wide as from $n = 10$ to $n = 18$). Abortion will result in those gametes that are excessively unbalanced chromosomally (i.e. with more than two more or fewer than the expected $n = 14$ chromosomes), with the result that overall pollen fertility is only moderate.

High fertility in tetraploids $(80\% +)$ is more indicative of allotetraploidy, in which the four genomes may be termed AABB. These tend to form bivalents at meiosis, with resultant more regular chromosome segregation and consequent high frequency of viable gametes with $n = 14$ chromosomes.

Not many diploid cultivars $(2n = 14)$ derived solely from the subgenus *Narcissus* are listed in Table 2, but those whose pollen fertilities were assessed are all at least 50% fertile, with most much higher, e.g. 'Dallas' (79%), 'Glory of Lisse' (90%), 'Milan' (96%), 'Pepper' (53%), 'Sonata' (87%), the only low fertilities occurring in double-flowered forms having no anthers, e.g. 'Doublet', 'Irene Copeland' and 'White Sail'. The diploid cultivars $(2n = 17)$ involving subgenus *Hermione* crossed with subgenus *Narcissus* are quite sterile apart from some non-reduced gametes that are viable.

### *Polyploid frequency in Narcissus cultivars compared with that in other ornamentals*

As can be seen from the information given in this article the optimum chromosome number for cultivated hybrid forms of *Narcissus* is clearly at or near the tetraploid level, a trend noted as early as 1923 by de Mol who was working on a relatively small amount of chromosomal information. This tendency towards the selection of polyploid forms of ornamental plants from diploid or lower polyploid wild ancestors is quite widespread, with the following being typical examples: *Dahlia*, cultivars octoploid $(2n = 64)$, from tetraploid wild ancestors; *Chrysanthemum*, all high polyploids, with large-flowered cultivars having more chromosomes, approximately 5x–7x with much aneuploidy; Roses, largely polyploid; bearded *Iris* (*Pogoniris* group), originally diploid but now almost entirely tetraploid (these examples from Darlington 1963); *Kalanchoe*, wild species diploid and tetraploid $(2n = 34, 68)$ in similar numbers but the great majority of cultivars circa-tetraploid or higher polyploids $(2n = 66, 67, 68, 69, 72, 75, 84, 85, 96)$ (van Voorst & Arends 1982).

The optimal level of polyploidy of cultivars of all of the above plants is tetraploid, as in *Narcissus*, or higher, but some cultivated ornamentals do not follow this pattern, with chromosome numbers below the tetraploid level being more common. Cultivars of *Canna* and *Bougainvillea*, for instance, are mostly diploid (Khoshoo & Zadoo 1969, Khoshoo & Mukherjee 1970), and also the sweet pea *Lathyrus odoratus*, in which tetraploid forms occur occasionally but are almost totally sterile and quite useless for breeding purposes (Darlington 1963). *Tulipa*, which might be regarded as a close equivalent to *Narcissus* with respect to its uses in cultivation and its many hundreds of named cultivars, is in fact very different from *Narcissus* as far as its optimum level of polyploidy in cultivation is concerned. In a major study of this genus Plavcova (1969) counted the chromosomes of 560 cultivars, finding 507 diploids $(2n = 24)$, 51 triploids $(2n = 36)$ and only two tetraploids $(2n = 48)$, the last being the cultivars 'Sunburst' and 'Mrs. John T. Scheepers'. Clearly tetraploids are not a great success in *Tulipa* and the triploid cultivars have arisen through non-reduced gametes from diploids as in many instances in *Narcissus* rather than through diploid-tetraploid hybridisation.

*Crocus* cultivars appear largely to be diploid selections from diploid parental species or hybrids, with polyploids being known but uncommon (Brighton *et al.* 1980). *Primula sinensis* is known as a series of diploid and tetraploid cultivars (Darlington 1963), as is *Pelargonium*, but in the latter the preferential selection of tetraploids seems to have occurred only in part of the genus. Daker (1969) showed that 91% of the *Pelargonium* cultivars based on x = 9 were diploids, a frequency identical to the percentage of diploids among his sample of *Pelargonium* species with x = 9, but in x = 11 forms of the same genus he found 62% diploids among the species, but only 22% diploids among the cultivars, the majority of the cultivars being tetraploid. In *Nerine*, wild species are diploid only (2n = 22), and most cultivars are also diploid, although a small number of tetraploids (2n = 44) and triploids or near-triploids have been selected (Roberts 1984).

*Hyacinthus* is unique as far as chromosome number distribution among its cultivars is concerned, and Darlington *et al.* (1951), in a survey of 106 cultivars, demonstrated a complete range, all chromosome numbers occurring between 2n = 2x = 16 and 2n = 4x = 32 with major peaks of frequency at the diploid and triploid levels (2n = circa 16 and circa 24 respectively). Early cultivars (dating from 1550 to 1850) were diploid only, but triploids arose from these through non-reduction (1700–1900). The autotriploids (2n = 24) are unusually fertile; indeed there is some unpublished suspicion based on their chromosome morphology that they are actually hexaploids, which would explain their high fertility. They could be crossed successfully with diploids to produce a range of hypotriploids (1800–1920) with 2n = 17 − 23, a result similar to that observed in triploid × diploid crosses in the *Liliaceae/Aloineae* (Brandham 1982). They were also crossed with each other to produce the lower hypertriploids (1850–1920), with perhaps 2n = 25 − 28, and the upper end of the 2n = 25 − 28 range could be intercrossed to give chromosome numbers approaching the tetraploid level of 2n = 32 (1900–1950) but so far only one plant has actually reached it, the cultivar 'Blue Giant' (Darlington 1963).

The reason why the selection of cultivars of *Narcissus* has evidently stabilised largely at the tetraploid level with very few higher polyploids is not completely clear. Presumably the larger size and greater vigour characteristic of most tetraploids applies in this genus also, resulting in their being selected preferentially over diploids, but it is quite evident that most of the higher polyploids that doubtless arise from the tetraploids show a reduction in size and/or vigour (Wylie 1952) and are not usually chosen for vegetative propagation by breeders when they appear in the progeny of their plants. In view of the comment by Darlington (1963: 107) that the only species of *Narcissus* to have autopolyploid races rising frequently above the tetraploid level (i.e. excluding the allohexaploid *N. dubius* and hexaploids occurring very rarely in other species) is *N. bulbocodium*, which has among the smallest chromosomes in the entire genus, it is possible that the generally large chromosomes in the rest of the genus constitute a nucleus that is too large for the efficiency and normal speed of DNA replication and/or mitosis to be maintained fully at levels above the tetraploid. The result of the loss of efficiency caused by exceeding this tetraploid nuclear volume is a slowing down of the mitotic system and growth rate and hence a smaller, weaker plant of little value to the breeder.

The chromosomes of *Narcissus* and *Tulipa* are of the same order of size, but the basic numbers of the two genera differ widely (x = 7 in most *Narcissus* species and x = 12 in *Tulipa*). It is therefore not surprising that the most

efficient nuclear size, found at the tetraploid level ($2n = 4x = 28$) in *Narcissus*, should be almost matched by a similarly critical size at the diploid level in *Tulipa* ($2n = 2x = 24$), since the chromosome numbers and nuclear volumes of tetraploid *Narcissus* and diploid *Tulipa* are comparable. It is therefore a tenable hypothesis that in these genera and in related monocotyledons there is a critical DNA level that cannot be exceeded without a severe impairment of mitotic efficiency, this level coming into operation at different ploidy levels depending on absolute chromosome size and basic number. Critical nuclear size could perhaps explain why no wild plants of *Narcissus* subgenus *Hermione* have been found at the tetraploid level ($2n = 40$ or $44$). These would greatly exceed the optimal DNA amount and would thus be too slow-growing to compete with diploids when they arise.

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