

The systematic value of nuclear DNA content for all species of *Narcissus* L. (Amaryllidaceae)

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Abstract The taxonomy of all species of *Narcissus* (Amaryllidaceae), an important horticultural crop, has not been investigated recently. As a new approach, genome size was determined by flow cytometry with propidium iodide from 375 accessions. The somatic nuclear DNA contents (2C) were shown to range from 14 to 38 pg for the diploids. *Narcissus assoanus* and *N. gaditanus* are, based on their nuclear DNA content, removed from section *Apodanthi* and placed in a new section *Juncifolii*. The different ploidy levels and species involved were entangled for *N. "fernandesii"* s.l. and a new allotetraploid form is named here. Section *Pseudonarcissus* was much more heterogeneous in nuclear DNA content than expected. Sixty-five accessions of *N. pseudonarcissus* possessed, with 23.7 pg, similar amounts of DNA. However, several species from this section were clearly distinctive in nuclear DNA content. It runs from the diploid *N. primigenius* with 21.7 pg to the also diploid *N. nevadensis* with 38.2 pg. Also *N. abscissus* and *N. moleroi* are with about 26 pg clearly different from *N. pseudonarcissus*. For the first time, in 11 accessions, hexaploidy was found in *N. pseudonarcissus* ssp. *bicolor*. A new section *Nevadensis* with 30–39 pg of nuclear DNA was split off from the section *Pseudonarcissus* with now 21–27 pg. A nonoploid *N. dubius* with 96.3 pg has by far the highest amount of nuclear DNA and can be calculated to have the highest ploidy ever reported in *Narcissus*. The total number of *Narcissus* species was determined as 36, nine more than in Flora Europaea and they were divided up in two subgenera and

11 sections. Flow cytometry is shown to produce easily obtainable and original systematic data that lead to new insights. Genome size or C-value turns out to be one of the most salient features to define the status of the species in the genus *Narcissus*.

Keywords *Narcissus* · Taxonomy · DNA content · Flow cytometry

Introduction

Since the articles of Fernandes (1966a, b; 1968a, b; 1975), based strongly on cytological investigations, no complete account of all species based on new data has appeared. This seems the more amazing as *Narcissus* is a horticultural and pharmaceutical important genus. It exhibits the taxonomic difficulties which arise from narrow endemism in the Mediterranean flora and weak reproductive barriers often lead to solitary hybrid specimens (Blanchard 1990; Thompson 2005). Polyploidy contributes significantly to speciation (Fernandes 1968a, b). After doubling chromosome numbers some of these original sterile hybrids occupy large areas and are now recognized as species. Moreover, a high morphological variability makes it doubtful if any *Narcissus* species can be identified from comparative measurements (Smythies 1973; Blanchard 1990). Also long-established cultivation, hybridization and selection and subsequent escape and naturalization (Webb 1980) have contributed to the taxonomic problems.

The important cytological work of Fernandes (1951; 1968a, b; 1975) has helped greatly to delineate the species, showing the nature of ancient hybrids and in establishing the hybrid nature of taxa formerly regarded as independent species. Fernandes (1951), accepting 22 species, formed

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the basis of the 27 species of Webb in Flora Europaea (1980). Later Fernandes (1968a, b) accepted 63 species. Based on Fernandes (1968), even 87 species are accepted in “Botanical names in the genus *Narcissus*” from the International Daffodil Register, updated September (2006). Here, the opinion of Webb is followed (see for a comparison Table 4), but recently described species and new data resulted in 36 accepted species here.

Graham and Barrett (2004) constructed a phylogenetic tree, based on the sequence data of the *ndhF* and the *trnL-F* region of the chloroplast genome. Our results are compared to the results of Graham and Barrett, although their investigations were restricted to 36 of the 65 species as recognized by Blanchard (1990). Consequently, several species and subspecies measured here were not included. Moreover, citing Graham and Barrett (2004): “If taxa of hybrid origin are not removed from analysis this can seriously mislead phylogenetic inference”. They removed therefore *N. × tortifolius* Fern. Casas and *N. dubius* Gouan from analysis but they were not aware of other ancient hybrids like *N. fernandesii* Pedro s.l., *N. hedraeanthus* (Webb & Heldr.) Colmeiro, *N. serotinus* L. s.l. and may be *N. cavanillesii* Barra & G. Lopez).

Nuclear DNA content has not often been exploited for taxonomic purposes. It can conveniently be measured by flow cytometry using propidium iodide, a stoichiometric DNA stain that intercalates in the double helix. Where many species in a genus have the same chromosome numbers, differences in nuclear DNA content are often present and have proven to be very effective in delimiting infrageneric divisions in a number of taxa (Ohri 1998). Genome size has been demonstrated to often vary a factor 1.5–3 between taxa with identical chromosome numbers (Ohri 1998; Yokoya et al. 2000; Zonneveld 2001; Zonneveld and van Iren 2001; Ellul et al. 2002; Zonneveld et al. 2003a, b; Hirsch et al. 2004; Albach and Greilhuber 2004; Zonneveld and Duncan 2006). Moreover, Greilhuber (1998, 2005) has clearly shown that intraspecific variation of genome size is much less than assumed. The evolution of genome size (Cx-value, Greilhuber 1979) has received increased attention during recent years (Bennett and Leitch 2005). Primitive angiosperms are now supposed to have had small genomes; increases up to a factor 1,000 have occurred independently in various modern taxa (Leitch et al. 1998). The low intraspecific variation in most *Narcissus* species shows that genome size can be used as one of the basic factors demarcating infrageneric taxa.

Repetitive DNA elements, including retro-transposons, are major components of eukaryotic genomes and such elements have a tendency towards amplification (Bennetzen and Kellogg 1997; Kalender et al. 2000). Major decreases in genome size occur less frequently and such decreases have been observed especially following a

doubling of the total genome by polyploidization (Ohri 1998), or the change from perennial to annual habit (Bennett 1972).

A complete review of the genus *Narcissus* is long overdue knowing its importance as a horticultural crop. So far genome size was determined in only three species: *N. hedraeanthus*, *N. cantabricus* DC. and *N. poeticus* L. with respectively, 13.1, 14.5 and 27.5 pg (Gonzalez et al. 1990). The relationship between its species is the more important as *Narcissus* has attracted attention as a source of potentially valuable pharmaceuticals like galanthamine that might have application in the treatment of Alzheimer disease (Colina 2002). In this study, nuclear DNA content was introduced as a novel approach for the study of *Narcissus* taxonomy. A total of 375 different accessions representing nearly all known species and representatives of 43 natural hybrids were investigated.

Materials and methods

Plant material

Plant material was mainly obtained from the collections of J. Blanchard (UK) and D. Donnison-Morgan (UK), but specimens were also obtained from The Netherlands (C.P. Breed, C. van de Veek, W. Lemmers, Hortus Bulborum Limmen and S. de Groot), from the UK (J.M. Grimshaw, M. Salmon and I. Young), from France (L. de Jager) and from the USA (N. Wilson and H. Koopowitz). Where possible, material of known wild origin was used, and care was taken to ensure correct identification of all material, relying also on the expert opinions of J. Blanchard, D. Donnison-Morgan and S. de Groot. Leaves were used from live plants from the wild or available in the different collections.

Determination of nuclear DNA content

For the isolation of nuclei, about 0.5 cm² of a fresh full-grown leaf was chopped together with a piece of *Agave americana* L. or *Agave stricta* Salm-Dyk as internal standard. The nuclear DNA content (2C-value) of *A. americana* was measured as 15.9 pg per nucleus with human leukocytes (2C = 7 pg, Tiersch et al. 1989) as the standard. *A. stricta* with 7.8 pg was used for those sections with DNA values below 20 pg. The chopping was done with a new razor blade in a Petri dish in 0.25 ml nuclei-isolation buffer, with 0.01% RNase added, as described by Zonneveld and van Iren (2001). After adding 1.8 ml propidium iodide solution (50 mg/l in isolation buffer) the suspension with nuclei was filtered through a 30 µm nylon filter. The fluorescence of the nuclei was measured, 30 and

60 min after addition of propidium iodide, using a PAR-TEC CA-II flow cytometer. The more DNA is present in a nucleus, the higher is the intensity of the fluorescence. The 2C DNA content of the sample was calculated as the sample peak mean, divided by the Agave peak mean, and multiplied with the amount of DNA of the Agave standard. From chopping of a leaf piece of 0.5 cm² about 50,000 nuclei could be isolated. For each clone, two to six different runs (determinations) with at least 3,000–5,000 nuclei were measured with two runs from a single nuclear isolation.

Pollen vitality staining

To obtain pollen from plants of section *Nevadensis* and *N. hedraeanthus*, anthers were removed just before opening of the flower. Vitality of pollen was determined by suspending and staining the dry pollen into a drop of Cotton Blue Lactophenol (BDH). Empty pollen stays colourless. The percentage of blue pollen grains was considered as an upper value for viability. At least 300 grains were assayed microscopically and in each case three determinations were done.

Results

Based on the work of four consecutive years, nuclear DNA contents of 375 accessions of *Narcissus* attributed to 36 species in 11 sections are listed in Table 1. Fernandes (1977) remarks: Il serait donc d'intérêt de mesurer la quantité d'acide désoxyribonucléique existant dans les deux groupes (i.e. section *Pseudonarcissus* and section *Ganymedes*). This suggestion of the eminent expert on the genus is followed here and extended to all sections. Fernandes (1951) divides *Narcissus* into two subgenera, subgenus *Hermione* with the basal chromosome number of $n = 5$ (11) and subgenus *Narcissus* with basal chromosome number $n = 7$ (13). This is followed here, although these two subgenera overlap in nuclear DNA content with for the diploids in subgenus *Hermione* 20.9–37.4 pg and in subgenus *Narcissus* 14.2–38.7 pg. This is also in accordance with the phylogeny of Graham and Barrett (2004) based on the sequences of two chloroplast genes. The division here in species and sections, based on DNA amounts, largely follows Webb (1978, 1980), (but not in his treatment of section *Jonquillae* s.l.) and also takes into account the results of Graham and Barrett (2004). Also a new section *Nevadensis* is added here. A low intraspecific variation is found in most cases. The interspecific variation shows that genome size in diploid *Narcissus* varies between 14 pg in the section *Bulbocodium* to 38 pg in *Nevadensis*. The difference between the highest and lowest

DNA contents is about 24 pg, equivalent to nearly 3×10^{10} bp. This must be the result of a vast number of genomic changes. Even a single picogram difference equates to a difference of 1,000,000,000 bp. Increases in ploidy are accompanied by increases in amount of nuclear DNA. The discussion of species and sections follows the classification presented in Table 1. The allocation to synonymy by Fernandes (1951) and Webb (1978) is largely followed here for the more obscure names. To prevent repeating the same sentence, the picograms used in the discussion below are the average amounts of nuclear DNA for the number of accessions of a certain species as can be found in Table 1. For determination of the standard deviation all relevant measurements were used. Recent hybrids found as solitary plants (in contrast to ancient hybrids that are here treated as species) are presented in Table 2. A resume of the main results compared with those of Webb (1978, 1980) is given in Table 4.

From the data presented it cannot be concluded where or when there was an increase or a decrease or both in the amount of nuclear DNA. The results are compared and discussed in the respective sections. I refrain in most cases to express an opinion on ecological adaptation or geographical distribution in relation to nuclear DNA content as that needs an additional set of data.

Discussion

Genus *Narcissus*

Subgenus Hermione (Haw.) Spach

Section *Serotini* Parl.: *N. serotinus* L., *N. miniatus* Koop., Donnison-Morgan, Zonn. The rare *N. serotinus* with $2n = 10$ and 20.9 pg is now separated from *N. miniatus*, widespread along the Mediterranean coasts, with $2n = 30$, but with 51.3 pg. This amount of nuclear DNA does not fit a hexaploid *N. serotinus*, suggested by its chromosome number, as that would have $3 \times 20.9 \text{ pg} = 62.7 \text{ pg}$ (Donnison-Morgan et al. 2006). The intermediate nature of the morphology of the ancient hybrid *N. miniatus* and the amount of nuclear DNA shows that it is actually a doubled form of the hybrid *N. serotinus* ($2n = 10$; 20.9 pg) \times *N. elegans* (Haw.) Steud. ($2n = 20$; 30.2 pg). Knowing the amounts of nuclear DNA this was easy to spot, especially so, as these are all three autumn flowering species. Lifante and Camacho (2007) did extensive morphological measurements on these taxa and concluded that, apart from the two parents a third form, a hybrid, was involved. They did not refer to the earlier work of Donnison-Morgan et al. (2006). *Narcissus obsoletus* (Haw.) Steud., used

Table 1 All species of *Narcissus* with their 2C amount of DNA, average, standard deviation, place of origin and the names under which the clones were received

Coll. #	Species	2C DNA in pg	Aver.	SD	Chrom. #	Origin	Received as: (deviating names only)
Genus Narcissus							
<u>Subgenus Hermione (Haw.) Spach.</u>							
Section Serotini Parlatore							
D608	<i>N. serotinus</i> L.	20.8	20.8	0.4	$2n = 10$	Rabat, Morocco	
D614	<i>N. serotinus</i> L.	20.9				Amareleja, Portugal	
D623	<i>N. serotinus</i> L.	20.9				Castro Marim, Portugal	
D194	<i>N. serotinus</i> L.	20.9				Bouznika, Morocco	
A8921	<i>N. serotinus</i> L.	21.0				Zaian Mountains, Morocco	
	<i>N. serotinus</i> L.	20.4				ex G. Knoche	
W14	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	49.3	51.3	2.2	$2n = 6x = 30$	ex Nancy Wilson	<i>N. serotinus</i>
D884	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	49.9				Crete, Ravdooha	<i>N. serotinus</i>
D885	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	49.8				Crete, Marathi	<i>N. serotinus</i>
D111	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	50.0				Cadiz, Spain	<i>N. serotinus</i>
D173	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	50.2				Alicante, Spain	<i>N. serotinus</i>
D883	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	50.6				Crete, Afrata	<i>N. serotinus</i>
H4	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	50.9				Cyprus	<i>N. serotinus</i>
D881	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	51.0				Crete, Mohos	<i>N. serotinus</i>
D862	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	51.1				Crete, Elounda	<i>N. serotinus</i>
	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	51.1				ex H. Koopowitz	<i>N. serotinus</i>
D880	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	51.4				Crete, Amigdalolakos	<i>N. serotinus</i>
D616	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	51.5				Cordoba, Medina Arzahara	<i>N. serotinus</i>
D622	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	51.5				Sevilla, La Lantejula	<i>N. serotinus</i>
D619	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	51.6				Cordoba, Polygano	<i>N. serotinus</i>
D882	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	51.6				Crete, Laloumas	<i>N. serotinus</i>
D631	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	51.8				Almeria, Cortijo Grande	<i>N. serotinus</i>
D607	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	51.9				Valencia, Simat/Barxeta	<i>N. serotinus</i>
G13	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	52.4				Greece	<i>N. serotinus</i>
D606	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	52.7				Valencia, Carcaixent	<i>N. serotinus</i>
D605	<i>N. miniatus</i> Koop., Donnison-Morgan, Zonn.	52.9				Cadiz, Jerez/Medina	<i>N. serotinus</i>
Section Tazettae DC.							
A8823	<i>N. elegans</i> (Haw.) Spach	29.7	30.2	0.5	$2n = 4x = 20$	Tanger, Morocco	
D190	<i>N. elegans</i> (Haw.) Spach	30.5				Tanger, Morocco	
A8822	<i>N. elegans</i> (Haw.) Spach	30.5				Tanger, Morocco	
S1	<i>N. tazetta</i> ssp. <i>tazetta</i> L.	30.0	30.3	1.2	$2n = 4x = 20$	ex M. Salmon, L/SA 174	
S3	<i>N. tazetta</i> ssp. <i>tazetta</i> L.	30.0				Sardinia, L/SA 243,	
W1	<i>N. tazetta</i> ssp. <i>tazetta</i> L.	30.8				ex Nancy Wilson	<i>N. cypri</i>
W4	<i>N. tazetta</i> ssp. <i>aureus</i> (Loisel.) Baker	29.5				ex Nancy Wilson	<i>N. tazetta</i> var. <i>discolor</i>
A...	<i>N. tazetta</i> ssp. <i>aureus</i> (Loisel.) Baker	29.8				Akfadou forest, Algeria	<i>N. tazetta</i> var. <i>discolor</i>
Z13	<i>N. tazetta</i> ssp. <i>aureus</i> (Loisel.) Baker	30.1				ex P. Christian	<i>N. tazetta</i> var. <i>cupularis</i>
J6	<i>N. tazetta</i> ssp. <i>aureus</i> (Loisel.) Baker	30.1				Arles, Camarque	
B29	<i>N. tazetta</i> ssp. <i>aureus</i> (Loisel.) Baker	30.1				ex C. Breed	<i>N. bertolonii</i>
A45	<i>N. tazetta</i> ssp. <i>aureus</i> (Loisel.) Baker	30.3				ex commerce	
S4	<i>N. tazetta</i> ssp. <i>aureus</i> (Loisel.) Baker	30.7				Italy, BS 369	
S6	<i>N. tazetta</i> ssp. <i>aureus</i> (Loisel.) Baker	30.7				ex M. Salmon, L/SA 157	<i>N. tazetta</i> <i>cupularis</i>
A64	<i>N. tazetta</i> ssp. <i>aureus</i> (Loisel.) Baker	31.6				Monte Limbara, Sardinia	<i>N. tazetta</i> <i>cupularis</i>
B33	<i>N. tazetta</i> "Caniculatus"	45.2	45.0	0.6	$2n = 6x = 30$	ex C. Breed	

Table 1 continued

Coll. #	Species	2C DNA in pg	Aver.	SD	Chrom. #	Origin	Received as: (deviating names only)
B13	<i>N. tazetta</i> "Odoratus"	44.5				ex C. Breed	
J2	<i>N. tazetta</i> "Chinese Sacred Lily"	45.0				ex Agrexco, Israel	
S2	<i>N. tazetta</i> "Flore Plenus"	44.6				Cyprus, PB 184	
G01	<i>N. tazetta</i> "Grand Soleil d'Or"	45.6				ex J. Grimshaw/Zonn.	
A8808	<i>N. papyraceus</i> ssp. <i>papyraceus</i> Ker Gawl.	33.5	33.7	1.4	$2n = 4x = 22$	Taza, Morocco	
S9	<i>N. papyraceus</i> ssp. <i>papyraceus</i> Ker Gawl.	33.8				ex M. Salmon, SL 390	
J3	<i>N. papyraceus</i> ssp. <i>papyraceus</i> Ker Gawl.	34.1				Antibes, Cote d'Azur	
D001	<i>N. papyraceus</i> ssp. <i>papyraceus</i> Ker Gawl.	33.9				ex Donnison-Morgan	
D0298/7	<i>N. papyraceus</i> ssp. <i>panizzianus</i> (Parl.) Arcang.	32.9				Malaga, Los Navzos	
H.Taylor	<i>N. papyraceus</i> ssp. <i>panizzianus</i> (Parl.) Arcang.	32.9				Cliff Encinas Borrachas	
A53	<i>N. papyraceus</i> ssp. <i>panizzianus</i> (Parl.) Arcang.	33.1				Grazalema, Spain	
Z14	<i>N. papyraceus</i> ssp. <i>panizzianus</i> (Parl.) Arcang.	35.2				ex S. de Groot, MCB 2867	
S8	<i>N. papyraceus</i> ssp. <i>polyanthos</i> (Loisel.) Asch. & Graebn.	33.9				ex M. Salmon	
D004	<i>N. papyraceus</i> ssp. <i>pachybolbus</i> (Durand) Webb	34.1				ex Chelsea Physic Garden	<i>N. canariensis</i>
Z16	<i>N. papyraceus</i> ssp. <i>pachybolbus</i> (Durand) Webb	33.1				ex S. de Groot	<i>N. pachybolbus</i>
S7	<i>N. papyraceus</i> ssp. <i>pachybolbus</i> (Durand) Webb	34.1				ex M. Salmon	<i>N. pachybolbus</i>
A48	<i>N. papyraceus</i> ssp. <i>pachybolbus</i> (Durand) Webb	34.3				ex J. Blanchard	<i>N. canariensis</i>
D002	<i>N. papyraceus</i> "Cyprì"	34.6				ex D. Donnison-Morgan	<i>N. papyr.</i> var. <i>cyprì</i>
	<i>N. papyraceus</i> "Paperwhite"	32.7				ex commerce	
	<i>N. papyraceus</i> "Ziva"	33.8				ex commerce	
B1	<i>N. broussonetii</i> Lag. y Segura	36.8	37.4	0.9	$2n = 22, 44$	Morocco	
S10	<i>N. broussonetii</i> Lag. y Segura	37.1				Morocco	
A9130	<i>N. broussonetii</i> Lag. y Segura	37.5				Et Tnine, Atlas, Morocco	
Z12	<i>N. broussonetii</i> Lag. y Segura	37.4				Morocco	
D003	<i>N. broussonetii</i> Lag. y Segura	38.3				Morocco	
W13	<i>N. broussonetii</i> Lag. y Segura	37.6				ex Nancy Wilson	<i>N. brouss. grandiflora</i>
A9801	<i>N. dubius</i> Gouan	64.8	66.3	3.0	$2n = 6x = 50$	Villena, Spain	
D555	<i>N. dubius</i> Gouan	67.3				Valencia, Alzira	
D556	<i>N. dubius</i> Gouan	66.0				Alicante, Santa Eulalia	
D533	<i>N. dubius</i> Gouan	66.1				Cast. Alto de Montmayor	
D035	<i>N. dubius</i> Gouan	66.4				Castelleon Altura	
D009	<i>N. dubius</i> Gouan	65.4				ex Donnison-Morgan	as <i>N. × pujolii?</i>
W11	<i>N. dubius</i> Gouan	68.3				ex Nancy Wilson	
D345	<i>N. dubius</i> Gouan	96.3	96.3	2.7	$(2n = 9x = 75)$	Valencia, Alzira	
Subgenus Narcissus							
Section Bulbocodii DC.							
A9021	<i>N. bulbocodium</i> ssp. <i>nivalis</i> (Graells) Baker	14.5	14.2	0.1	$2n = 14$	Serra de Estrella, Portugal	
D358	<i>N. bulbocodium</i> ssp. <i>nivalis</i> (Graells) Baker	13.8				S. de Guadarama, Spain	
B10	<i>N. bulbocodium</i> ssp. <i>bulbocodium</i> L.	28.2	28.7	0.8	$2n = 4x = 28$	ex C. Breed	<i>N. bulb. filifolius</i>
D101	<i>N. bulbocodium</i> ssp. <i>bulbocodium</i> L.	28.7				N. Africa	<i>N. bulb. genuinus</i>
D374	<i>N. bulbocodium</i> ssp. <i>bulbocodium</i> L.	27.9				S. de Guadarama, Spain	<i>N. bulb. graellsii</i>
D691	<i>N. bulbocodium</i> ssp. <i>bulbocodium</i> L.	29.6				Cuenca, Las Majadas	<i>N. bulb. ectandrus</i>
D707	<i>N. bulbocodium</i> ssp. <i>bulbocodium</i> L.	29.8				Punto de el Cubillo, Teruel	<i>N. bulb. ectandrus</i>
Z17	<i>N. bulbocodium</i> ssp. <i>praecox</i> Gatt. & Weiller	27.9				ex S. de Groot	<i>N. bulb. paucinervis</i>
D666	<i>N. bulbocodium</i> L.	34.1	34.1	0.1	$(2n = 5x = 35)$	Cuidad Real, Agudo	
J10	<i>N. bulbocodium</i> ssp. <i>quintanilhae</i> A. Fern.	42.2	42.2	1.5	$(2n = 6x = 42)$	ex van Eden	<i>N. bulb. conspicuus</i>

Table 1 continued

Coll. #	Species	2C DNA in pg	Aver.	SD	Chrom. #	Origin	Received as: (deviating names only)
B19	<i>N. bulbocodium</i> "Golden Bells"(Grex)	47.3	47.3		($2n = 7x = 49$)	ex C. Breed	
A50	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	14.5	15.0	0.6	$2n = 14$	Cazorla, Spain	
Z09	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	14.5				ex Potterton & Martin	
G05	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	14.9				ex J. Grimshaw	
D090	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	14.8				Albacete, P. Crucetillas	
D685	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	14.9				Jaen, Cazorla	
D698	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	14.9				Villamanrique, Spain	
D697	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	15.0				Las Correderas, Spain	
W03	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	15.2				ex Nancy Wilson	
D535	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	15.3				C. Real, N Hertzuelas	
D688	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	15.4				Albacete, Pilas Verdes	
D687	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	15.5				Jaen, Cazorla	
D544	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	15.6				C. Real, Aldeaquemada	
D526	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	14.9				Albacete, Penascosa	
D700	<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	15.0				Albacete, Pilas Verdes	
A9805	<i>N. cantabricus</i> ssp. <i>cantabricus</i> DC.	14.4	14.5	0.2	$2n = 14$	Almaden, Spain	
D536	<i>N. cantabricus</i> ssp. <i>cantabricus</i> DC.	14.4				C. Real, Cast. Calatrava	
D30	<i>N. cantabricus</i> ssp. <i>monophyllus</i> (Durand) A. Fern.	14.8				Almeria, S.E. Spain	
A.SF284	<i>N. cantabricus</i> ssp. <i>cantabricus</i> DC.	29.4	29.0	1.2	$2n = 4x = 28$	Mahomedia, Morocco	<i>N. cant. foliosus</i>
	<i>N. cantabricus</i> ssp. <i>cantabricus</i> DC.	29.4				Col de Kerdons Anti-Atlas	<i>N. cant. kesticus</i>
W12	<i>N. cantabricus</i> ssp. <i>cantabricus</i> DC.	29.0				ex Nancy Wilson	<i>N. cant. kesticus</i>
A9127	<i>N. cantabricus</i> ssp. <i>tananicus</i> (Maire) A. Fern.	28.1				Immouzer, Morocco	
A8912	<i>N. romieuxii</i> ssp. <i>romieuxii</i> Braun Blanq. & Maire	27.0	28.8	1.0	$2n = 4x = 28$	Middle Atlas, Morocco	
J11	<i>N. romieuxii</i> ssp. <i>romieuxii</i> Braun Blanq. & Maire	28.5				ex Coll. Southampton	
B9	<i>N. romieuxii</i> ssp. <i>romieuxii</i> Braun Blanq. & Maire	28.1				ex C. Breed	<i>N. rom. mesatlanticus</i>
	<i>N. romieuxii</i> ssp. <i>romieuxii</i> Braun Blanq. & Maire	29.8				ex seed from AGS	<i>N. rom. mesatlanticus</i>
	<i>N. romieuxii</i> ssp. <i>romieuxii</i> Braun Blanq. & Maire	29.2				ex seed from AGS	<i>N. rom. rifanus</i>
A9608	<i>N. romieuxii</i> ssp. <i>jacquemoudii</i> (F. Casas) Zonn.	28.9	28.9			Amizmiz, Morocco	<i>N. jacquemoudii</i>
B4	<i>N. romieuxii</i> ssp. <i>albidus</i> (Emb. & Maire) A. Fern.	28.8	29.3			ex C. Breed	
	<i>N. romieuxii</i> ssp. <i>albidus</i> (Emb. & Maire) A. Fern.	29.8				ex seed from AGS	<i>N. rom. zaianicus</i>
D007	<i>N. romieuxii</i> ssp. <i>albidus</i> (Emb. & Maire) A. Fern.	29.3				ex Donnison-Morgan	<i>N. rom. zaianicus</i>
A9003	<i>N. obesus</i> Salisbury	26.0	26.5	0.3	$2n = 4x = 26!$	Arrabida, Portugal	
D239	<i>N. obesus</i> Salisbury	26.6				Setubal, Portugal	
G14	<i>N. obesus</i> Salisbury	26.9				Cape St Vincent, Portugal	
Section Ganymedes Schultes & Schultes							
D792	<i>N. lusitanicus</i> Dorda & Fern. Casas	16.2	16.9	0.9	$2n = 14$	Monte Gordo, Portugal	
D559	<i>N. lusitanicus</i> Dorda & Fern. Casas	16.9				Aguas Belas, Portugal	
D558	<i>N. lusitanicus</i> Dorda & Fern. Casas	17.2				S. de Sao, Mamede, Port.	
W5	<i>N. lusitanicus</i> Dorda & Fern. Casas	17.2				Portugal	
D368	<i>N. lusitanicus</i> Dorda & Fern. Casas	16.9				S. de Guadarama, Spain	
D230	<i>N. lusitanicus</i> Dorda & Fern. Casas	17.1				Mede do Mouros, Port.	
A.SB206	<i>N. lusitanicus</i> Dorda & Fern. Casas	17.2				N. Portugal	
D545	<i>N. pallidulus</i> Graells	17.6	18.1	0.8		C. Real, Aldeaquemada	
D541	<i>N. pallidulus</i> Graells	18.2				C. Real, Huertezuelas	
D672	<i>N. pallidulus</i> Graells	18.0				Cuidad Real, Almaden	
D675	<i>N. pallidulus</i> Graells	18.5				C. Real, Puerto Rehoyos	

Table 1 continued

Coll. #	Species	2C DNA in pg	Aver.	SD	Chrom. #	Origin	Received as: (deviating names only)
	<i>N. triandrus</i> L.	18.3	19.0	0.6	$2n = 14$	ex commerce	<i>N. triandrus</i> "Alba"
A0006	<i>N. triandrus</i> L.	18.5				Riano, Spain	
D699	<i>N. triandrus</i> L.	18.7				Albacete, Pilas Verdes	
D388	<i>N. triandrus</i> L.	19.3				Palencia, C. de Pisuegra	
D389	<i>N. triandrus</i> L.	19.5				Cantabria, Fuente De	
	<i>N. triandrus</i> "Capax"	19.9				ex D. Karnstedt	<i>N. triandrus loiselurei</i>
Section Juncifolii (A. Fern.) Zonn. stat. nov.							
B7	<i>N. assoanus</i> Dufour	18.2	18.8	0.6	$2n = 14$	ex C. Breed	
D333	<i>N. assoanus</i> Dufour	18.4				Alicante, Mont'go	
B8	<i>N. assoanus</i> Dufour	18.5				ex C. Breed	
A42	<i>N. assoanus</i> Dufour	18.6				Grazalema, Spain	
D143	<i>N. assoanus</i> Dufour	18.9				Alicante, Mont'go	
D402	<i>N. assoanus</i> Dufour	19.0				Huesca, Toria	
HTaylor	<i>N. assoanus</i> Dufour	19.5				Above Grazalema	
Z08	<i>N. assoanus</i> Dufour	18.1				ex M. Salmon, M.S 852	<i>N. baeticus</i>
A8715	<i>N. assoanus</i> Dufour	19.8				Teruel, Spain	<i>N. ass. praelongus</i>
A9704	<i>N. gaditanus</i> Boiss. & Reuter	19.6	19.3	0.7	$2n = 14$	Algarve, Portugal	
A9017	<i>N. gaditanus</i> Boiss. & Reuter	19.1				Soides, Algarve	
D712	<i>N. gaditanus</i> Boiss. & Reuter	18.9				Teruel, Punto Majalinos	
G03	<i>N. gaditanus</i> Boiss. & Reuter	19.8				ex J. Grimshaw	
Section Tapeinanthus Traub							
D517	<i>N. cavanillesii</i> Barra & G. Lopez	34.3	33.3	1.0	$2n = 4x = 28$	Cadiz, Spain	
D460	<i>N. cavanillesii</i> Barra & G. Lopez	34.4				460–86 Chelsea Physics G,	
A.SF260	<i>N. cavanillesii</i> Barra & G. Lopez	31.0				W. High Atlas, Morocco	
D524	<i>N. cavanillesii</i> Barra & G. Lopez	32.3				Cadiz, Las Palomas	
D516	<i>N. cavanillesii</i> Barra & G. Lopez	32.8				Sevilla, Cazalla	
D223	<i>N. cavanillesii</i> Barra & G. Lopez	33.1				Tangier, Morocco	
	<i>N. cavanillesii</i> Barra & G. Lopez	34.7					
D'11/11	<i>N. cavanillesii</i> Barra & G. Lopez	17.7	17.7	0.1	$2n = 14?$	Spain, ex Chelsea Ph. G.	<i>N. cavanillesii</i> ??
Section Apodanthi Fernandes							
A8502	<i>N. calcicola</i> Mendonça	26.9	26.6	0.2	$2n = 14$	Porto de Mos, Portugal	
D229	<i>N. calcicola</i> Mendonça	26.9				Travainho, Portugal	
D805	<i>N. calcicola</i> Mendonça	26.0				ex D. Donnison-Morgan	
A9123	<i>N. scaberulus</i> Henriques	25.6	26.3	0.3	$2n = 14$	Mordego Valley, Portugal	
D823	<i>N. scaberulus</i> Henriques	26.9				Oliveria do Hospital, Port.	
D812	<i>N. scaberulus</i> Henriques	26.8				Ribamondego, Portugal	
D821	<i>N. scaberulus</i> Henriques	26.1				Corregas du Sal, Portugal	
G04	<i>N. rupicola</i> ssp. <i>rupicola</i> Dufour	26.2	26.6	0.5	$2n = 14$	ex J. Grimshaw	
B20	<i>N. rupicola</i> ssp. <i>rupicola</i> Dufour	25.2				ex C. Breed	
	<i>N. rupicola</i> ssp. <i>rupicola</i> Dufour	26.3				ex seed from AGS	
A9119	<i>N. rupicola</i> ssp. <i>rupicola</i> Dufour	26.7				La Crolina, Spain	
D543	<i>N. rupicola</i> ssp. <i>rupicola</i> Dufour	27.3				Cuidad Real, Hertzuelas	
D674	<i>N. rupicola</i> ssp. <i>rupicola</i> Dufour	27.4				C.Real, Puerto Rehoyos	
A68	<i>N. rupicola</i> ssp. <i>watieri</i> (Maire) Maire & Weiller	26.0				Tizi-n-Tichka ABS4514	
B12	<i>N. rupicola</i> ssp. <i>watieri</i> (Maire) Maire & Weiller	26.5			$2n = 14$	ex C. Breed	
G22	<i>N. rupicola</i> ssp. <i>watieri</i> (Maire) Maire & Weiller	26.7				ex J. Grimshaw	

Table 1 continued

Coll. #	Species	2C DNA in pg	Aver.	SD	Chrom. #	Origin	Received as: (deviating names only)
A.ABS441	<i>N. rupicola</i> ssp. <i>marvieri</i> (Jah. & Maire) Maire & Weiller	27.2				Middle Atlas, Morocco	
A44	<i>N. rupicola</i> ssp. <i>marvieri</i> (Jah. & Maire) Maire & Weiller	26.8				Amizmiz Morocco:E.Balls	<i>N. atlanticus</i>
Section jonquillae DC.							
L10	<i>N. jonquilla</i> ssp. <i>jonquilla</i> L.	32.3	32.9	1.1	$2n = 14$	H. Bulborum, Limmen	
B14	<i>N. jonquilla</i> ssp. <i>jonquilla</i> L.	33.0				ex C. Breed	
D006	<i>N. jonquilla</i> ssp. <i>jonquilla</i> L.	33.2				ex D. Donnison-Morgan	
D819	<i>N. jonquilla</i> ssp. <i>jonquilla</i> L.	33.0				Alcacovas, Portugal	
D527	<i>N. jonquilla</i> ssp. <i>jonquilla</i> L.	32.4				Jaen, Sierra Morena	<i>N. jonquilla</i> var. <i>minor</i>
D657	<i>N. jonquilla</i> ssp. <i>jonquilla</i> L.	32.6				C. Real, N. Puerto Rayo	<i>N. jonquilla</i> var. <i>minor</i>
D669	<i>N. jonquilla</i> ssp. <i>jonquilla</i> L.	31.7				C. Real, Inter Mestanza	<i>N. jonquilla</i> var. <i>minor</i>
B17	<i>N. jonquilla</i> ssp. <i>jonquilla</i> L.	32.7				ex C. Breed	<i>N. jonq.</i> var. <i>henriquesii</i>
S11	<i>N. jonquilla</i> ssp. <i>jonquilla</i> L.	33.0				ex M. Salmon, BS410	<i>N. jonq.</i> var. <i>henriquesii</i>
A55	<i>N. jonquilla</i> ssp. <i>willkommii</i> (A. Fern.) Zonn.	32.9			$2n = 14$	ex J. Blanchard	<i>N. willkommii</i>
Z09	<i>N. jonquilla</i> ssp. <i>willkommii</i> (A. Fern.) Zonn.	33.6				ex S. de Groot	<i>N. willkommii</i>
D010	<i>N. jonquilla</i> ssp. <i>fernandesii</i> (Pedro) Zonn.	32.6			$2n = 14$	ex D. Donnison-Morgan	<i>N. fernandesii</i>
D537	<i>N. jonquilla</i> ssp. <i>fernandesii</i> (Pedro) Zonn.	34.0				Jaen, Las Correderas	<i>N. fernandesii</i>
A.TN	<i>N. jonquilla</i> ssp. <i>fernandesii</i> (Pedro) Zonn.	32.1				Almaden, Spain	<i>N. fernandesii</i>
D370	<i>N. jonquilla</i> ssp. <i>fernandesii</i> (Pedro) Zonn.	33.2				C. Real, Sierra Madrona	<i>N. fernandesii</i>
D065	<i>N. jonquilla</i> ssp. <i>fernandesii</i> (Pedro) Zonn.	33.1				Jaen, S. Virgen Cabeza	<i>N. fernandesii</i>
H Taylor	<i>N. jonquilla</i> ssp. <i>fernandesii</i> (Pedro) Zonn.	32.9				Puerto del Rayo	<i>N. fernandesii</i>
A9802	<i>N. jonquilla</i> ssp. <i>cordubensis</i> (Fern. Casas) Zonn.	33.7				Montecorto, Spain	<i>N. cordubensis</i>
B11	<i>N. jonquilla</i> ssp. <i>cordubensis</i> (Fern. Casas) Zonn.	32.8				ex C. Breed	<i>N. cordubensis</i>
S13	<i>N. jonquilla</i> ssp. <i>cordubensis</i> (Fern. Casas) Zonn.	33.0				ex M. Salmon 434	<i>N. cordubensis</i>
J12	<i>N. jonquilla</i> ssp. <i>cordubensis</i> (Fern. Casas) Zonn.	33.6				ex Coll. Southampton	<i>N. cordubensis</i>
D027	<i>N. jonquilla</i> ssp. <i>cordubensis</i> (Fern. Casas) Zonn.	32.8				Cadiz, Grazalema	<i>N. cordubensis</i>
B2	<i>N. viridiflorus</i> Schousboe	63.7	63.4	1.0	$2n = 4x = 28$	ex C. Breed	
D518	<i>N. viridiflorus</i> Schousboe	63.2				Cadiz, Spain	
D530	<i>N. cuatrecasasii</i> Fern. Casas	32.0	31.7	0.8	$2n = 14$	Jaen, El Almaden	
A.JCA	<i>N. cuatrecasasii</i> Fern. Casas	30.9				Cazorla, Spain	
B31	<i>N. cuatrecasasii</i> Fern. Casas	32.6				ex C. Breed	
D694	<i>N. cuatrecasasii</i> Fern. Casas	31.3				Jaen, El Almaden	
B8	<i>N. blanchardii</i> Zonn. stat. nov.	50.8	51.2	1.4	$2n = 4x = 28$	ex C. Breed	<i>N. fernandesii</i>
G02	<i>N. blanchardii</i> Zonn. stat. nov.	52.1				ex J. Grimshaw	<i>N. fernandesii</i>
D696	<i>N. blanchardii</i> Zonn. stat. nov.	50.8				Pto de Los Jardines	<i>N. fernandesii</i>
Section Pseudonarcissi DC.							
D356	<i>N. pseudonarcissus</i> ssp. <i>pseudonarcissus</i> L.	23.0	23.8	0.4	$2n = 14$	S. M. Alameda, Madrid	Concolored
D255	<i>N. pseudonarcissus</i> ssp. <i>pseudonarcissus</i> L.	22.7				S. M. Alameda, Madrid	Bicolored
L03	<i>N. pseudonarcissus</i> ssp. <i>pseudonarcissus</i> L.	23.8				H. Bulborum, Limmen	
L08	<i>N. pseudonarcissus</i> ssp. <i>pseudonarcissus</i> L.	24.4				H. Bulborum, Limmen	<i>N. gayi</i>
B30	<i>N. pseudonarcissus</i> ssp. <i>pseudonarcissus</i> L.	24.2				ex C. Breed	<i>N. gayi</i>
A9905	<i>N. pseudonarcissus</i> ssp. <i>pseudonarcissus</i> L.	23.5				Almaden, Spain	<i>N. perez-chiscanoi</i>
D337	<i>N. pseudonarcissus</i> ssp. <i>pseudonarcissus</i> L.	24.2				Cuidad Real, Fuente	<i>N. perez-chiscanoi</i>
G11	<i>N. pseudonarcissus</i> ssp. <i>pseudonarcissus</i> L.	24.3				ex J. Grimshaw	<i>N. perez-chiscanoi</i>
L04	<i>N. pseudonarcissus</i> ssp. <i>major</i> (Curtis) Baker	23.8	23.9	0.6		H. Bulborum, Limmen	<i>N. obvallaris</i>
A.CMS	<i>N. pseudonarcissus</i> ssp. <i>major</i> (Curtis) Baker	24.3				Frostrasol, Wales	<i>N. obvallaris</i>

Table 1 continued

Coll. #	Species	2C DNA in pg	Aver.	SD	Chrom. #	Origin	Received as: (deviating names only)
H6	<i>N. pseudonarcissus</i> ssp. <i>major</i> (Curtis) Baker	23.8				ex Bot. G. Leiden	<i>N. obvallaris</i>
B26	<i>N. pseudonarcissus</i> ssp. <i>major</i> (Curtis) Baker	23.5				ex C. Breed	<i>N. obvallaris</i>
A9026	<i>N. pseudonarcissus</i> ssp. <i>major</i> (Curtis) Baker	23.8				Zezeze, Portugal	<i>N. lusitanicus</i>
A59	<i>N. pseudonarcissus</i> ssp. <i>major</i> (Curtis) Baker	23.3				Sierra de Gredos, Spain	<i>N. confusus</i>
A...	<i>N. pseudonarcissus</i> ssp. <i>major</i> (Curtis) Baker	23.8				Sierra de Higuera, Spain	<i>N. hispanicus</i>
D647	<i>N. pseudonarcissus</i> ssp. <i>major</i> (Curtis) Baker	24.3				C. Real, E. T.de Abraham	<i>N. hispanicus</i>
L16	<i>N. pseudonarcissus</i> ssp. <i>major</i> (Curtis) Baker	36.5			$2n = 3x = 21$	H. Bulborum, Limmen	<i>N. hispanicus</i>
B35	<i>N. pseudonarcissus</i> ssp. <i>major</i> (Curtis) Baker	36.1			$2n = 3x = 21$	ex C. Breed	<i>N. hispanicus</i>
GO9	<i>N. pseudonarcissus</i> ssp. <i>pallidiflorus</i> (Pugsley) A. Fern.	24.0	23.9	0.7		ex J. Grimshaw	<i>N. pallidif.</i> "Nutt Clone"
D593	<i>N. pseudonarcissus</i> ssp. <i>pallidiflorus</i> (Pugsley) A. Fern.	23.8				Vall d'Incles, Andorra	
A8714	<i>N. pseudonarcissus</i> ssp. <i>eugeniae</i> Fern. Casas	23.8	23.4	0.5	$2n = 14$	Valdelinares, Teruel	type locality
Z05	<i>N. pseudonarcissus</i> ssp. <i>eugeniae</i> Fern. Casas	23.3				ex P. Christian	<i>N. eugeniae</i>
D350	<i>N. pseudonarcissus</i> ssp. <i>eugeniae</i> Fern. Casas	23.5				Cuenca, S Garaballa	<i>N. eugeniae</i>
D713	<i>N. pseudonarcissus</i> ssp. <i>eugeniae</i> Fern. Casas	23.1				Allepuz, Teruel	<i>N. eugeniae</i>
A36	<i>N. pseudonarcissus</i> ssp. <i>eugeniae</i> Fern. Casas	23.0				Albacete, Spain	<i>N. radinganorum</i>
S15	<i>N. pseudonarcissus</i> ssp. <i>eugeniae</i> Fern. Casas	24.0				ex M. Salmon, BS 434	<i>N. radinganorum</i>
D547	<i>N. pseudonarcissus</i> ssp. <i>eugeniae</i> Fern. Casas	23.2				Valencia, La Hunde	<i>N. radinganorum</i>
L13	<i>N. pseudonarcissus</i> ssp. <i>moschatus</i> (L.) Baker	24.3	23.6	0.4	$2n = 14$	H. Bulborum, Limmen	<i>N. moschatus</i>
B28	<i>N. pseudonarcissus</i> ssp. <i>moschatus</i> (L.) Baker	23.5				ex C. Breed	<i>N. cernuus</i>
B23	<i>N. pseudonarcissus</i> ssp. <i>moschatus</i> (L.) Baker	23.8				ex C. Breed	<i>N. cernuus</i> "Double"
D720	<i>N. pseudonarcissus</i> ssp. <i>moschatus</i> (L.) Baker	23.5				Huasca, Cerler-Benasque	<i>N. alpestris</i>
D721	<i>N. pseudonarcissus</i> ssp. <i>moschatus</i> (L.) Baker	23.0				Huasca, Cerler-Benasque	<i>N. alpestris</i>
D722	<i>N. pseudonarcissus</i> ssp. <i>moschatus</i> (L.) Baker	23.3				Huasca, Cerler-Benasque	<i>N. alpestris</i>
A0217	<i>N. pseudonarcissus</i> ssp. <i>moschatus</i> (L.) Baker	23.6				Huasca, Cerler-Benasque	<i>N. alpestris</i>
A0222	<i>N. pseudonarcissus</i> ssp. <i>moschatus</i> (L.) Baker	23.6				Col de Crueta, Barcelona	<i>N. moleroi</i>
H12	<i>N. pseudonarcissus</i> ssp. <i>minor</i> (L.) Baker	23.4	23.8	0.4	$2n = 14$	ex Bot. G. Leiden	<i>N. minor</i>
L14	<i>N. pseudonarcissus</i> ssp. <i>minor</i> (L.) Baker	23.4				H. Bulborum, Limmen	<i>N. nanus</i>
L06	<i>N. pseudonarcissus</i> ssp. <i>minor</i> (L.) Baker	23.4				H. Bulborum, Limmen	<i>N. pumilus</i>
G07	<i>N. pseudonarcissus</i> ssp. <i>minor</i> (L.) Baker	23.5				ex J. Grimshaw	<i>N. provincialis</i>
WL3	<i>N. pseudonarcissus</i> ssp. <i>minor</i> (L.) Baker	23.6				ex W. Lemmers	<i>N.</i> "Little" Gem/ "WeeBee"
G19	<i>N. pseudonarcissus</i> ssp. <i>minor</i> (L.) Baker	24.2				ex J. Grimshaw	<i>N.</i> "Douglasbanks"
L12	<i>N. pseudonarcissus</i> ssp. <i>minor</i> (L.) Baker	24.1				H. Bulborum, Limmen	<i>N. lobularis</i>
H11	<i>N. pseudonarcissus</i> ssp. <i>minor</i> (L.) Baker	24.0				ex Bot. G. Leiden	<i>N. lobularis</i>
G08	<i>N. pseudonarcissus</i> ssp. <i>minor</i> (L.) Baker	24.5				ex J. Grimshaw	<i>N. lobularis</i>
D790	<i>N. pseudonarcissus</i> ssp. <i>nobilis</i> (Haw.) A. Fern.	45.9	45.9	0.1	$2n = 4x = 28$	Pinheiro, Portugal	<i>N. nobilis</i> ?
L15	<i>N. pseu.</i> ssp. <i>leonensis</i> (Pugsley) Fern. Casas & Lainz	65.8	66.1	2.1	$2n = 6x = 42$	H. Bulborum, Limmen	<i>N. leonensis</i>
A0002	<i>N. pseu.</i> ssp. <i>leonensis</i> (Pugsley) Fern. Casas & Lainz	66.5				Riano, Spain	<i>N. leonensis</i>
A8715	<i>N. pseu.</i> ssp. <i>leonensis</i> (Pugsley) Fern. Casas & Lainz	63.6				Picos de Europa, Spain	<i>N. leonensis</i>
B15	<i>N. pseu.</i> ssp. <i>leonensis</i> (Pugsley) Fern. Casas & Lainz	66.1				ex C. Breed	<i>N. leonensis</i>
A5930	<i>N. pseu.</i> ssp. <i>leonensis</i> (Pugsley) Fern. Casas & Lainz	65.8				Vittoria, Spain	<i>N. varduliensis</i>
A0601	<i>N. pseu.</i> ssp. <i>leonensis</i> (Pugsley) Fern. Casas & Lainz	68.6				Vittoria, Spain	<i>N. varduliensis</i>
Z023	<i>N. pseu.</i> ssp. <i>leonensis</i> (Pugsley) Fern. Casas & Lainz	66.0				ex S. de Groot	<i>N. leonensis</i>
D601	<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Baker	68.5	67.7	2.0	$2n = 6x = 42$	Col du Pradel, France	<i>N. abscissus</i>
D739	<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Baker	68.5				Col du Pradel, France	<i>N. abscissus</i>

Table 1 continued

Coll. #	Species	2C DNA in pg	Aver.	SD	Chrom. #	Origin	Received as: (deviating names only)
D601A	<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Baker	67.0				Col du Pradel, France	<i>N. sp.</i>
D601B	<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Baker	67.0				Col du Pradel, France	<i>N. sp.</i>
A0218	<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Baker	66.9				Superbagneres, Pyrenees	<i>N. bicolor</i>
D725	<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Baker	69.3				Superbagneres, Pyrenees	<i>N. bicolor</i>
A. '06	<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Baker	68.7				Pyrenees, Spain	<i>N. bicolor</i>
A9401	<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Baker	68.8				Auvergne, France	<i>N. pseudonarcissus</i>
A0603	<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Baker	68.3				Auvergne, France	<i>N. pseudonarcissus</i>
L07	<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Baker	67.2				H. Bulborum, Limmen	<i>N. pseudonarcissus</i>
G12	<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Baker	65.0				ex J. Grimshaw	<i>N. radiganorum</i>
A0010	<i>N. primigenius</i> Fern. Casas	21.4	21.5	0.4	$2n = 14$	Riano, Picos de Europa	
A0004	<i>N. primigenius</i> Fern. Casas	21.6				Riano, Picos de Europa	
Z15	<i>N. jacetanus</i> Fern. Casas	22.3	22.3	0.4	$2n = 14$	ex S. de Groot	
B25	<i>N. jacetanus</i> Fern. Casas	22.6				ex C. Breed	<i>N. minor</i>
V007	<i>N. jacetanus</i> Fern. Casas	22.6				ex C. Van de Veek	<i>N. minor</i>
Y001	<i>N. jacetanus</i> Fern. Casas	21.8				ex I. Young	
A602	<i>N. jacetanus</i> Fern. Casas	22.0				Pyrenees, Spain	
Z11	<i>N. asturiensis</i> ssp. <i>asturiensis</i> Pugsley	24.0	24.1	0.6	$2n = 14$	ex S. de Groot	
G06	<i>N. asturiensis</i> ssp. <i>asturiensis</i> Pugsley	24.2				ex J. Grimshaw	
D797	<i>N. asturiensis</i> ssp. <i>asturiensis</i> Pugsley	24.8				S. do Estrela, Portugal	
D237	<i>N. asturiensis</i> ssp. <i>asturiensis</i> Pugsley	24.4				S. do Estrela, Portugal	
D794	<i>N. asturiensis</i> ssp. <i>asturiensis</i> Pugsley	24.2				S. do Estrela, Portugal	
B27	<i>N. asturiensis</i> ssp. <i>asturiensis</i> Pugsley	23.5				ex C. Breed	<i>N.</i> "Wavertree"/"Giant"
A0303	<i>N. asturiensis</i> ssp. <i>asturiensis</i> Pugsley	24.0				Xiabre, Spain	
A43	<i>N. asturiensis</i> ssp. <i>villarvildensis</i> Barra & G. Lopez	47.4	48.3	1.0		Villablino, Spain	
A0301	<i>N. asturiensis</i> ssp. <i>villarvildensis</i> Barra & G. Lopez	49.5				West of Lugo, Spain	<i>N. lagoi</i>
G21/B6	<i>N. asturiensis</i> ssp. <i>villarvildensis</i> Barra & G. Lopez	48.0				ex J. Waddick from C. Morris	<i>N. minor</i> "Cedric Morris"
A0201	<i>N. cyclamineus</i> DC.	26.1	26.2	0.5	$2n = 14$	Santiago de Compostella	
Z06	<i>N. cyclamineus</i> DC.	26.2				ex Van Tubergen	
D598	<i>N. abscissus</i> (Haw.) Schult. f.	26.9	26.4	0.8		Lleida, Val d' Aran	
A9206	<i>N. abscissus</i> (Haw.) Schult. f.	25.6				Val d' Aran, France	
A221	<i>N. abscissus</i> (Haw.) Schult. f.	26.6				Pyrenees, France	
D599	<i>N. abscissus</i> (Haw.) Schult. f.	26.2				Cires, France	
D727A	<i>N. abscissus</i> (Haw.) Schult. f.	25.8				Cires, France	
D727B	<i>N. abscissus</i> (Haw.) Schult. f.	26.6				Cires, France	
Z024	<i>N. abscissus</i> (Haw.) Schult. f.	27.2				ex S. de Groot	
D597	<i>N. moloroi</i> Fern. Casas	26.0	26.1	0.4		Barcelona, Col de Crueta	
D746	<i>N. moloroi</i> Fern. Casas	26.6				Barcelona, Col de Crueta	
D741	<i>N. moloroi</i> Fern. Casas	25.8				Gerona, La Molina	
Section Nevadensis Zonn. sect. nov.							
A8715	<i>N. bujei</i> Fern. Casas	29.3	30.0	0.5	$2n = 14$	Cabra, Spain	
D678	<i>N. bujei</i> Fern. Casas	30.5				Albacete, Alcaraz	
D701	<i>N. bujei</i> Fern. Casas	30.0				Fuente de la Piteta	<i>N. sp.</i>
D008	<i>N. bujei</i> Fern. Casas	30.1				ex M. Salmon SF137	<i>N. longispatus?</i>
A0110	<i>N. nevadensis</i> Pugsley	38.3	38.2	1.1	$2n = 14$	Sierra Nevada, Spain	
B37	<i>N. nevadensis</i> Pugsley	38.2				Sierra Nevada, Spain	
G20	<i>N. nevadensis</i> Pugsley	39.4				Sierra Nevada, Spain	

Table 1 continued

Coll. #	Species	2C DNA in pg	Aver. SD	Chrom. #	Origin	Received as: (deviating names only)
D692	<i>N. nevadensis</i> Pugsley	36.9			Sierra Nevada, Spain	
Z020	<i>N. nevadensis</i> Pugsley	38.0			ex S. de Groot	
A8616	<i>N. longispathus</i> ssp. <i>longispathus</i> Pugsley	36.1	36.0 0.7	$2n = 14$	Cazorla, Spain	<i>N. longispathus</i>
D549	<i>N. longispathus</i> ssp. <i>alcaracensis</i> (Rios et al.) Zonn.	35.9			Albacete, Penascosa	<i>N. alcarensis</i>
A0107	<i>N. longispathus</i> ssp. <i>alcaracensis</i> (Rios et al.) Zonn.	35.8			S. de Alcaraz, Spain	<i>N. alcarensis</i>
D3+	<i>N. longispathus</i> ssp. <i>alcaracensis</i> (Rios et al.) Zonn.	35.1			Albacete, S. de Alcaraz	<i>N. alcarensis</i>
A0105	<i>N. longispathus</i> ssp. <i>segurensis</i> (Rios et al.) Zonn.	36.1			S. de Segura, Spain	<i>N. segurensis</i>
D690	<i>N. longispathus</i> ssp. <i>segurensis</i> (Rios et al.) Zonn.	35.1			S. de Segura, Spain	<i>N. segurensis</i>
Z022	<i>N. longispathus</i> ssp. <i>segurensis</i> (Rios et al.) Zonn.	36.8			ex S. de Groot	<i>N. segurensis</i>
A0103	<i>N. longispathus</i> ssp. <i>yepesii</i> (Rios et al.) Zonn.	35.8			Hornos, S.de Segura	<i>N. yepesii</i>
D662	<i>N. longispathus</i> ssp. <i>yepesii</i> (S. Rios et al.) Zonn.	36.3			Hornos, S.de Segura	<i>N. yepesii</i>
Z021	<i>N. longispathus</i> ssp. <i>yepesii</i> (S. Rios et al.) Zonn.	36.9			ex S. de Groot	<i>N. yepesii</i>
Section <i>Narcissus</i> L.						
D592	<i>N. poeticus</i> ssp. <i>poeticus</i> L.	25.5	26.0 0.5	$2n = 14$	Vall d'Incles, Andorra	
D596	<i>N. poeticus</i> ssp. <i>poeticus</i> L.	25.8			Huesca, Cerler-Benasque	
D731	<i>N. poeticus</i> ssp. <i>poeticus</i> L.	25.9			Girona, Arties	
B22	<i>N. poeticus</i> ssp. <i>poeticus</i> L.	26.0			ex C. Breed	<i>N. poeticus physaloides</i>
D724	<i>N. poeticus</i> ssp. <i>poeticus</i> L.	26.0			Huesca, Cerler-Benasque	
H8	<i>N. poeticus</i> ssp. <i>poeticus</i> L.	26.1			ex Hortus Bot. Leiden	<i>N. albus plenus odoratus</i>
Z01	<i>N. poeticus</i> ssp. <i>poeticus</i> L.	26.5			Broadleigh gardens	<i>N. poeticus praecox</i>
L17	<i>N. poeticus</i> ssp. <i>poeticus</i> L.	26.6			H. Bulborum. Limmen,NL	<i>N. poeticus physaloides</i>
W17	<i>N. poeticus</i> ssp. <i>radiiflorus</i> (Salisb.) Baker	25.8	26.1 0.9	$2n = 14$	ex Nancy Wilson	
	<i>N. poeticus</i> ssp. <i>radiiflorus</i> (Salisb.) Baker	25.8			ex W. Snoeijer	
Z02	<i>N. poeticus</i> ssp. <i>radiiflorus</i> (Salisb.) Baker	25.8			ex S. de Groot	<i>N. poeticus ornatus</i>
	<i>N. poeticus</i> ssp. <i>radiiflorus</i> (Salisb.) Baker	25.9			ex commerce	<i>N. poeticus ornatus</i>
L02	<i>N. poeticus</i> ssp. <i>radiiflorus</i> (Salisb.) Baker	26.0			H. Bulborum. Limmen	<i>N. poeticus ornatus</i>
	<i>N. poeticus</i> ssp. <i>radiiflorus</i> (Salisb.) Baker	26.0			ex commerce	<i>N. poeticus ornatus</i>
Z03	<i>N. poeticus</i> ssp. <i>radiiflorus</i> (Salisb.) Baker	26.5			ex S. de Groot	<i>N. poeticus poetarum</i>
B16	<i>N. poeticus</i> ssp. <i>radiiflorus</i> (Salisb.) Baker	27.1			ex C. Breed	<i>N. poeticus radiiflorus</i>
A65	<i>N. poeticus</i> "Hellenicus"	39.1	38.7 0.6	$2n = 3x = 21$	ex J. Blanchard	
Z04	<i>N. poeticus</i> "Hellenicus"	38.8			ex S. de Groot	
L01	<i>N. poeticus</i> "Recurvus"	38.6			H. Bulborum. Limmen	
B32	<i>N. poeticus</i> "Recurvus"	38.3			ex C. Breed	
38	<i>N. poeticus</i> "Pheasant Eye"	38.6			ex commerce	
L23	<i>N. poeticus</i> "Actaea"	52.7	52.7 1.7	$2n = 4x = 28$	H. Bulborum. Limmen	

Chromosome counts were taken from literature (de Mol 1923; Fernandes 1968a, b; Sanudo 1984) (when estimated, it is between brackets).

A = J. Blanchard; B = C. Breed; D = D. Donnison-Morgan; G = J. Grimshaw; H = Hortus Leiden; J = L. de Jager; L = Limmen, Hortus Bulborum; S = M. Salmon; V = C. Van de Veek; W = N. Wilson; WL = W. Lemmers; Y = I. Young; Z = S. de Groot, de Zilk; ex = obtained from

subsequently for different taxa by various authors, was equated with this hybrid (Lifante and Camacho 2007). However this application is doubtful as they do not make a distinction between the diploid hybrid *N. × obsoletus* (*N. elegans* × *N. serotinus*) (Table 2) found as solitary specimen amidst its parents in Morocco (Maire 1959)

and its widespread tetraploid form *N. miniatus* (Table 1). Therefore, *N. obsoletus* is better considered as a *nomen confusum* or should be confined to the diploid hybrid. Chloroplast DNA data of Graham and Barrett (2004) did not allow them to discriminate between *N. serotinus* (20.9 pg), *N. elegans* (30.2 pg) and *N. tazetta* (30.3 pg).

Table 2 Species hybrids of *Narcissus* with their amount of nuclear DNA, standard deviation, origin and suggested parents

Coll. #	Species hybrids	2C DNA in pg	SD	Chrom. #	Origin	Suggested parents
B3	<i>N. romieuxii</i> × <i>N. bulbocodium</i>	30.1	0.3		ex C. Breed	<i>N. albidus</i> × <i>bulb</i> genuin.
d28	<i>N. × alleniae</i> Donnison-Morgan	56.2	0.9		Cadiz, Spain	<i>N. serotinus</i> × <i>viridiflorus</i>
S14	<i>N. × aloysii-villarii</i> Fern. Casas	22.5	0.1		ex M. Salmon	<i>N. alpestris</i> × <i>jacetanus</i>
D654	<i>N. bulbocodium</i> × <i>N. assoanus?</i>	17.0	0.5		Cuidad Real, Mestanza	<i>N. bulboc.</i> × <i>cantabricum</i>
HB	<i>N. bulbocodium</i> × <i>N. assoanus?</i>	17.1	0.6		Andalusia Mazagon,	as <i>N. bulbocodium</i>
D728	<i>N. × boutingianus</i> Philippe	25.4	0.4		Cires, France	<i>N. poeticus</i> × <i>molerio</i>
D735	<i>N. × boutingianus</i> Philippe	25.1	0.5		Girona, Tredos	<i>N. poeticus</i> × <i>molerio</i>
D359	<i>N. × carpetanus</i> Fern. Casas	20.4	0.2		Sierra de Guadarrama	<i>N. bulb. niv.</i> × <i>b. graelsii</i>
D534	<i>N. × cazorlanus</i> Fern. Casas	15.8	0.2		Cuidad Real, Hertezuclas	<i>N. hedraeanthus</i> × <i>triandrus</i>
D272	<i>N. × cazorlanus</i> Fern. Casas	15.6	0.5		Albacete, P. Crucetillas	<i>N. hedraeanthus</i> × <i>triandrus</i>
D270	<i>N. × cazorlanus</i> Fern. Casas	15.5	0.4		Jaen, Sierra de Segura	<i>N. hedraeanthus</i> × <i>triandrus</i>
D531	<i>N. × consolationis</i> Fern. Casas	15.5	0.5		Cuidad Real, Fuente	<i>N. bulb. niv</i> × <i>triandrus</i>
B18	<i>N. × gracilis</i> Sabine	28.8	0.3		ex C. Breed	<i>N. jonquilla</i> × <i>poeticus</i>
L25	<i>N. × gracilis</i> Sabine	26.3	0.3		H. Bulborum, Limmen	<i>N. jonquilla</i> × <i>poeticus</i>
	<i>N. × incurvicervicus</i> Barra & G. Lopez	33.7	0.5		ex commerce	<i>N. fernand.</i> × (<i>triandrus</i> 2X)
B21	<i>N. × intermedius</i> Loisel. & Deslong.	31.4	0.3		ex C. Breed	<i>N. jonquilla</i> × <i>tazetta</i>
L21	<i>N. × intermedius</i> Loisel. & Deslong.	31.9	0.4	2x = 17	H. Bulborum, Limmen	<i>N. jonquilla</i> × <i>tazetta</i>
Taylor	<i>N. × koshinomurae</i> (christopheri) Fern. Casas	26.7	0.9		Cliff Encinas Borachas	<i>N. assoanus</i> × <i>panizzianus</i>
D542	<i>N. × maginae</i> Fern. Casas	24.6	0.4		Jaen. El Almaden	<i>N. cuatrecasasii</i> × <i>triandrus</i>
B36	<i>N. × medioluteus</i> = <i>biflorus</i> Miller	40.4	0.8	2x = 24	ex C. Breed	<i>N. poeticus</i> 4X × <i>tazetta</i>
J8	<i>N. × medioluteus</i> = <i>biflorus</i> Miller	40.7	0.9		Arles, France	<i>N. poeticus</i> 4X × <i>tazetta</i>
D729	<i>N. × monseratii</i> Fern. Casas	26.4	0.1		Cires, France	<i>N. poeticus</i> × <i>abscissus</i>
D187	<i>N. × obsoletus</i> (Haworth) Steud.	26.1	0.2		Rabat, Morocco	<i>N. serotinus</i> × <i>elegans</i>
Koop	<i>N. × obsoletus</i> (Haworth) Steud.	25.6	0.5		ex H. Koopowitz	<i>N. serotinus</i> × <i>elegans</i>
	<i>N. × odorus</i> L. "Campernelle"	28.3	0.3		double flowers	<i>N. jonquilla</i> × <i>pseudon.</i>
L26	<i>N. × odorus</i> L. "Campernelle"	27.4	0.4		H. Bulborum, Limmen	<i>N. jonquilla</i> × <i>pseudon.</i>
L11	<i>N. × odorus</i> L. "Campernelle"	27.8	0.6		Single flowers	<i>N. jonquilla</i> × <i>pseudon.</i>
D513	<i>N. × perezlarae</i> Fontquer	42.2	0.4		Sevilla, Spain	<i>N. miniatus</i> × <i>cavanillesii</i>
	<i>N. hybr. novus?</i>	28.0				<i>N. serotinus</i> × <i>cavanillesii</i>
S18	<i>N. × pugsleyi</i> Fern. Casas	22.0	0.3		BS 480	<i>N. assoanus</i> × <i>alpestris</i>
D653	<i>N. × susannae</i> Fern. Casas	16.0	1		C. Real, Puerto Rehoyos	<i>N. bulbocodium</i> × <i>triandrus</i>
	<i>N. × tortifolius</i> Fern. Casas	37.4	0.7	(3x = 25)	Sorbas, Spain	<i>N. gadit.</i> 2X × <i>panizzianus</i>
D342	<i>N. × tortifolius</i> Fern. Casas	46.5	1.1	4x = 36	Almeria, Los Molinos	(<i>N. gaditanus</i> × <i>panizz.</i>) 2X
D737	<i>N. pseudonarcissus</i> × <i>poeticus?</i> L.	24.9			Vall d'Incles, Andorra	received as : <i>N. gayi</i>
S12	<i>N. jonquilla</i> ssp. <i>fernandesii</i> 2X × <i>N. gaditanus</i>	42.8	1.7	(2n = 3x = 21)	ex M. Salmon 414	received as <i>N. fernandesii</i>
Z07	<i>N. jonquilla</i> ssp. <i>fernandesii</i> 2X × <i>N. gaditanus</i>	41.6			ex S. de Groot	received as <i>N. gaditanus</i>
W15	<i>N. jonquilla</i> ssp. <i>fernandesii</i> 2X × <i>N. gaditanus</i>	43.2			ex Nancy Wilson	received as <i>N. fernandesii</i>

May be the widespread *N. miniatus* (51.3 pg) was masquerading for *N. serotinus*.

Section *Tazettae* DC.: *N. broussonetii* Lag. y Seg., *N. elegans* (Haw.) Spach, *N. papyraceus* Ker Gawl.,

N. tazetta L. The values for the species of this section vary from 30.2 to 37.4 pg. *Narcissus tazetta* including the ssp. *aureus* Baker, range from 30.0 to 31.8 pg with an average of 30.3 pg. Although the chromosome numbers $2n = 20$ point to ancient tetraploidy (*N. serotinus* has $2n = 10$),

Fernandes (1966a, b; 1968a, b) has shown they behave now as diploids forming only bivalents in meiosis. If *N. tazetta* is considered as a diploid, five accessions must then be considered as being triploid. They have a 50% higher amount of DNA and include the so-called *N. “Chinese Sacred Lily”* ($2n = 30$) that centuries ago must have naturalized in China and Japan. The 16 values for *N. papyraceus* including the ssp. *panizzianus* (Parl.) Arcang., ssp. *polyanthus* (Loisel.) Asch. & Graebn. and ssp. *pachybolbus* (Durand) Webb have an average of 33.7 pg. The more than 3 pg difference in DNA content between *N. tazetta* and *N. papyraceus* supports the separation of these two taxa. It seems likely that authentic *N. tazetta* has $2n = 20$ and *N. papyraceus* $2n = 22$. Reports on plants with $2n = 21$ are then likely based on sterile hybrids (Fernandes 1966b). The three accessions of *N. elegans* from Morocco have on average 30.2 pg as stated above.

Based on published chromosome numbers ($2n = 22, 44$), tetraploids (*N. broussonetii* f. *grandiflorus* Maire) are found as solitary plants among the diploids (Maire 1959). Only plants with on average 37.6 pg were measured here in six accessions. In flower, in karyotype, in chromosome number and in the amount of nuclear DNA (assuming that the measured plants are all diploids) it resembles *N. papyraceus* with which it is easy to cross (Maire 1959), so section *Aurelia*, containing only *N. broussonetii*, is placed here in section *Tazettae*. This is also in accordance with the phylogeny of Graham and Barrett (2004).

Subgenus *Narcissus*

Section *Bulbocodii* DC.: *N. bulbocodium* L., *N. cantabricus* DC., *N. hedraeanthus* (Webb & Heldr.) Colmeiro, *N. obesus* Salisb., *N. romieuxii* Braun-Blanq. & Maire. Amounts of nuclear DNA in this section range from 14.2 to 15 pg for the diploids and 28.7–47.3 pg for the polyploids. *Narcissus bulbocodium* has the most numerous and the most different types of polyploids of all *Narcissus* species (Fernandes 1963). He showed that some populations had triploids and hexaploids but not tetraploid plants. This suggests an origin of the hexaploids from non-reduced gametes. Moreover, the higher the ploidy, the wetter the localities were they were found (Fernandes 1963). For the plants here measured two diploids, six tetraploids, one pentaploid, one hexaploid and one heptaploid was found, the latter two from commerce. Fernandes (1963) reports also on an occasional octoploid that would have $4 \times 14.2 = 56.8$ pg. *Narcissus cantabricus* seems the white counterpart of the yellow flowering *N. bulbocodium*. Contrary to *N. bulbocodium*, only diploids and tetraploid forms, each with four accessions, were measured. Although the amounts of nuclear DNA are very similar, Fernandes (1959) found that the hybrid between two diploid forms of

these species was nearly fully sterile and their karyograms were different. It seems that *N. cantabricus* originated from *N. bulbocodium* through structural chromosome changes (Fernandes 1959). *Narcissus romieuxii* from Morocco was considered by Fernandes (1963) to be the ancient allotetraploid of *N. bulbocodium* and *N. cantabricus*. The amount of nuclear DNA of 28.8 pg for all subspecies of *N. romieuxii* does not counter this. *Narcissus bulbocodium*, with a nuclear DNA-content of only 14 pg, has by far the lowest amount of DNA of any *Narcissus* species. This might indicate a plesiomorphic position within the genus, but this is not reflected in the phylogeny based on plastid data by Graham and Barrett (2004). There the *Bulbocodium* section together with the *Pseudonarcissus* section formed a well supported clade. With scarcely developed perianth segments, *N. bulbocodium* s.l. is morphologically the opposite of the other supposed “primitive” species *N. cavanillesii* with a diminutive corona. Both may be adaptations to a dryer, southerly climate.

Narcissus hedraeanthus, although sometimes included in *N. bulbocodium* as *N. bulbocodium* ssp. *hedraeanthus* (Webb & Heldr.) Voss, is clearly different from *N. bulbocodium* and *N. cantabricus* with its 15.0 pg measured in 14 accessions.

The flower shape and the small plant size of *N. hedraeanthus* reminds of a *N. bulbocodium* \times *N. triandrus* hybrid. Blanchard (1990) remarks that *N. hedraeanthus* can be grown from seed but that it carries very small capsules containing far fewer seeds than is usual with the species of this section (apomixis?). Moreover, I measured only 80 and 90% good pollen in two accessions of *N. hedraeanthus*. As the amount of nuclear DNA is intermediate between the supposed parents, an ancient hybrid origin for *N. hedraeanthus* cannot be excluded.

Narcissus obesus is a tetraploid but with $2n = 4x = 26$ chromosomes instead of the regular 28. As the amount of nuclear DNA is, with 26.5 pg in three accessions, also 2 pg lower than those of a tetraploid *N. bulbocodium*, it can be calculated that it has lost 7% of its nuclear DNA content. Fernandes (1963) shows that *N. obesus* is homozygous for a single Robertsonian fusion with loss of the short arms which reduces the chromosome number from 28 to 26.

Section *Ganymedes* (Haw.) Schult.f.: *N. pallidulus* Graells, *N. lusitanicus* Dorda & Fern. Casas, *N. triandrus* L. Nuclear DNA content in this section varies from 16.9 to 19.0 pg. For the mainly yellow flowering *N. lusitanicus* from Portugal 16.9 pg is found. The pale yellow *N. pallidulus* with four accessions from below and around Madrid have a nuclear DNA content of 18.1 pg. The robust, whitish flowering *N. triandrus* with six accessions from above Madrid up to the Cantabrian Mountains has on average 19.0 pg. The latter includes the isolated

N. triandrus “Loiseleurii” or “Capax” from the Iles Glenans, France, considered by Webb (1980) as a separate subspecies. Apart from a different nuclear DNA content they can be separated in plants with a leaf width of about 2 mm for *N. pallidulus* and *N. lusitanicus* and more than 4 mm for *N. triandrus* (Blanchard 1990). *Narcissus triandrus* is usually divided in three varieties or subspecies (Webb 1980; Barra Lazaro 2000). However Dorda and Fernandez Casas (1989) considered them to be separate species and also Perez-Barrales et al. (2006) did so, based on chloroplast DNA data. Our data support three species, although it cannot be excluded that the presence of B-chromosomes might influence this difference. Blanchard (1990) did find all three colours in single populations. However, it cannot be excluded that each species occasionally can show all three colours or that they occasionally form hybrid swarms.

Section *Juncifolii* (A. Fern.) Zonn. sect nov. Typus *N. assoanus* Dufour Other species: *N. gaditanus* Boiss. & Reuter).

Based on subsection *Juncifolii* A. Fern. Bol. Soc. Brot.II, 40: 207–261 (1966).

The rare *N. gaditanus* Boiss. & Reuter confined to southern Spain and Portugal, has smaller but more numerous flowers to a scape compared to the widespread *N. assoanus* from northern Spain and southern France. *Narcissus gaditanus* and *N. assoanus* are closely related with 18.8 and 19.3 pg, respectively, and are here separated from section *Jonquillae* with about 33 pg for the diploid forms. This corroborates with the plastid DNA data of Graham and Barrett (2004) where they are also placed separately from the *Jonquillae* clade. A strong cytological difference was already observed by Fernandes (1975) who placed them in a subsection *Juncifolii* of section *Jonquillae*. Their unique amount of nuclear DNA is otherwise only found in the unrelated *N. triandrus*. Because there is only a small difference in morphology and genome size, *N. gaditanus* is here doubtfully maintained as a species separate from *N. assoanus*.

Section *Tapeinanthus* (Herb.) Traub: *N. cavanillesii* Barra & G. Lopez). Six accessions of *N. cavanillesii* were measured, from Spain as well as from Morocco with an average value of 33.3 pg. Hardly any difference was found between these localities. Chromosome numbers are reported as $2n = 4x = 28$ (Fernandes and Fernandes 1951). The species most similar, excluding *N. bulbocodium* and *N. triandrus* s.l. on morphological grounds, is *N. assoanus/gaditanus* of section *Juncifolii* with about 19 pg. Fernandes (1975) remarks on the analogy between the karyotypes of *N. cavanillesii* and *N. assoanus*. If *N. cavanillesii* is an ancient allotetraploid, the amount of nuclear DNA suggests that

N. assoanus (including *N. gaditanus*) and *N. bulbocodium* could be the parents. Graham and Barrett (2004) placed them all three in the same section with *N. pseudonarcissus* in their phylogenetic tree. However, the nearly absent corona in *N. cavanillesii* seems to contradict this. A single plant from the Chelsea Physics Garden, England had 17.7 pg. So if properly diagnosed it could be a diploid form of *N. cavanillesii*. This species is considered to be a primitive narcissus with hardly a corona and was until recently even placed in a separate genus, *Tapeinanthus* Herb.

Section *Apodanthi* A. Fern.: *N. calcicola* Mendonsa, *N. rupicola* Dufour ex Schult.f., *N. scaberulus* Henriq. The species of section *Apodanthi* with about 26 pg are very similar in this respect and have very similar karyotypes (Fernandes 1975). They differ from section *Jonquillae* also by their karyotypes and the presence of strophioles. *Narcissus scaberulus* with scabrid leaves and an incurved corona is considered here as a distinct species despite a similar amount of DNA as was found in *N. calcicola*. The results of Graham and Barrett (2004) also show a well supported split between *N. calcicola* on one side and *N. albimarginatus* D. & U. Mull.-Doblies, *N. atlanticus* Stern, *N. cuatreacasii* Fern. Casas, Lainz & Ruiz Rejon, *N. rupicola* and *N. scaberulus*, on the other side. *Narcissus wattieri* Maire and *N. marvieri* Jahand. & Maire both from Morocco are considered here as subspecies of the Spanish *N. rupicola*. This is in accordance with the results of Perez-Barrales et al. (2006) based on chloroplast DNA sequences. The similarity in average DNA content may infer close phylogenetic relationships between these members of section *Apodanthi*. They are all morphologically very similar but differ in that *N. rupicola* s.l. has only a single flower per stem and *N. calcicola* and *N. scaberulus* have several. *Narcissus cuatreacasii* was removed from section *Apodanthi* to section *Jonquillae* (see below).

Section *Jonquillae* DC.: *N. blanchardii* Zonn., *N. cuatreacasii* Fern. Casas, Lainz & Ruiz Rejon, *N. jonquilla* L., *N. viridiflorus* Schousb. Webb (1980) included subsection *Juncifolii* and section *Apodanthi* here. These are here treated as separate sections based on their vastly different amounts of nuclear DNA. The diploid species in this section have similar amounts of nuclear DNA with 31.7 and 32.9 pg. However all kinds of polyploids are found in this section too. To start with the easy one: *N. viridiflorus* is an autumn flowering narcissus with unique green flowers. It is a tetraploid ($2n = 4x = 28$) and has an average of 63.5 pg DNA. It clearly fits this section as a *N. jonquilla* type with a doubled nuclear DNA content. *Narcissus jonquilla* ssp. *jonquilla* has 32.8 pg for seven accessions. *Narcissus cordubensis* Fern. Casas with 33.2 pg is here treated as a subspecies of *N. jonquilla*.

Analyses of morphological characters (Webb 1978) and plastid DNA sequences (Graham and Barrett 2004) place *N. cuatrecasasii* in section *Apodanthi*. The amount of nuclear DNA however, 31.7 pg, based on four accessions, is clearly different from the about 26 pg of DNA of the remaining species in that section. Fernandes (1968a) also states that the karyotype of *N. cuatrecasasii* is different from the other species of section *Apodanthi* there. It is provisionally placed in section *Jonquillae* here and may be it is even only a form of wet mountains and should be named *N. jonquilla* ssp. *cuatrecasasii*.

The difficult part was *N. fernandesii* where opinions differ and results were at first difficult to interpret. Webb (1978) leaves the species as *incertae sedis* and remarks that it is in most characters intermediate between *N. (jonquilla* ssp.) *willkommii* (Samp.) A. Fern. and *N. gaditanus*. Fernandez Casas (1996) considers them all, from diploids up to hexaploids, as forms of the ancient hybrid *N. jonquilla* × *N. assoanus* and that is not far away from what is proposed here. He places all these forms under *N. fernandesii*. When more accessions were measured, the following solution presented itself. Five diploid accessions of *N. "fernandesii"* were found with 33.0 pg. These are here considered as *N. jonquilla* ssp. *fernandesii*, as was already suggested by Fernandes (1966a). Fernandes (1968a) remarks that the diploid *N. fernandesii* could not be found anymore in the *locus classicus* in Portugal, but later several populations were located in Spain. However the bulbs he obtained from Gomos Pedro, the author of this species, had $2n = 14$. The most common in nature (Fernandes 1966a) were the *N. "fernandesii"* with $2n = 28$, that are found here to have 51.2 pg DNA. Fernandes remarks that it has two different sets of chromosomes that form bivalents only and are fully fertile. However, he considers it despite these results as autotetraploids and named it as *N. fernandesii* var. *major*. Based on nuclear DNA amounts, these cannot be autotetraploids of *N. (jonquilla* ssp.) *fernandesii*. The amount of nuclear DNA clearly points to the fact that it must be an allotetraploid as is shown below.

Narcissus blanchardii Zonn. stat. nov.

Ancient allotetraploid form of *N. jonquilla* (ssp. *fernandesii*) × *N. gaditanus*

Based on *N. fernandesii* var. *major* A. Fern. in: Bol. Soc. Brot. II, 40: 239(1966). Named after John Blanchard who wrote an eminent book on *Narcissus*.

The most difficult to interpret at first were the three samples of *N. "fernandesii"* (Table 2) with 42.5 pg that cannot be triploid forms of *N. jonquilla* ssp. *fernandesii* as these would have $1.5 \times 32.8 = 49.2$ pg. Fernandes (1966a) describes diploids of *N. willkommii* with $2n = 14$

and considers the plant with $2n = 21$ as an allotriploid. The diploid *N. willkommii* is considered by Fernandes (1966a) to be derived from *N. jonquilla*. It has a fitting 33.3 pg of nuclear DNA and is here considered as *N. jonquilla* ssp. *willkommii* (A. Fern) Zonn. It was already placed under *N. jonquilla* by Coutinho (1939). The triploid form of *N. "fernandesii"* that was measured gave a fitting DNA value for the hybrid *N. jonquilla* ssp. *fernandesii* (Pedro) Zonn. (two sets of chromosomes) and *N. gaditanus* (one set of chromosomes): $33.8 + 9.4 = 43.2$ pg. It seems related to the triploid described by Fernandes (1966a) as *N. willkommii* (non-reduced) × *N. gaditanus*. Montserrat and Vives (1991) even found a hexaploid form of *N. fernandesii* and this could be the doubled form of the allotriploid mentioned here.

If it is supposed that all *N. fernandesii* s.l. (excluding the diploids that are forms of *N. jonquilla*) are hybrids of *N. jonquilla* × *N. gaditanus* it must be remarked that we did not encounter the diploid, or the pentaploid or the hexaploid hybrid forms. A plant from the same locality from where the hexaploid hybrid was reported (Santuario de la Virgen de la Cabeza) had a diploid amount of DNA and is considered to be *N. jonquilla* ssp. *fernandesii*.

Section *Pseudonarcissus* DC.: *N. abscissus* (Haw.) Roem. & Schult., *N. asturiensis* (Jord.) Pugsley, *N. cyclamineus* DC., *N. moleroi* Fern. Casas, *N. primigenius* (Fern. Suarez ex Lainz) Fern. Casas & Lainz, *N. pseudonarcissus* L. This section is characterized, apart from its large corona, by its uniseriate anthers, biseriate in the other sections (Blanchard 1990). A large number of species has been described in this section. This has surely to do with the fact that these species are the most popular spring flowers. Numerous hybrids are found and named in the wild and thousands of cultivars are raised and do occasionally escape. Some authors considered that there is just a single variable species in this section, like Burbridge and Baker (1875) or Rouy (1912), others like Pugsley (1933) came up with 27 species, eight of which are accepted here. Since 1933 16 more species were described in this same section of which only three are accepted here (Table 1). Webb (1980) is mainly followed here. Those species that have very similar amounts of DNA, are here all considered to be at most subspecies if not synonyms. *Narcissus alpestris* Pugsley, *N. cernuus* Salisb., *N. confusus* Pugsley, *N. lobularis* Schult. f., *N. nanus* (Haw.) Spach, *N. perez-chiscanoi* Fern. Casas, *N. provincialis* Pugsley, *N. pumilus* Salisb. and *N. radiganorum* Fern. Casas are here all considered synonyms of *N. pseudonarcissus*, for details see Table 1. Eight subspecies are recognized here. Compared with Webb (1980), *N. nevadensis* is here reinstated as a distinct species and placed in a different section, *N. portensis* Pugsley as *incertae sedis* and *N. pseudonarcissus* ssp. *bicolor* (L.)

Baker, ssp. *eugeniae* (Fern. Casas) Fern. Casas, and ssp. *minor* (L.) Baker are added here. *Narcissus pseudonarcissus* ssp. *pseudonarcissus* (with six accessions), ssp. *major* (16), ssp. *pallidiflorus* (2), ssp. *eugeniae* (4), ssp. *moschatatus* (8) and ssp. *minor* (8) have on average about 23.7 pg of DNA.

Two accessions of *N. primigenius* (Fernandez Suarez ex Lainz) Fern. Casas & Lainz ($2n = 14$, Fernandes 1991) from Riano, northern Spain, had only 21.7 pg. This value is the lowest found in section *Pseudonarcissus*. This could be indicative of a primitive position, but there are no other arguments. The plant is only half the size of the tetraploid *N. pseudonarcissus* ssp. *nobilis* (Haw.) A. Fern and is suggested to be the diploid form of it (Sanudo 1984). Although they are similarly bicoloured, the nuclear DNA content points to independent species. *N. asturiensis* (eight accessions) and its tetraploid form ssp. *villarvildensis* (T. E. Diaz & Fern. Prieto) Rivas Mart., T. E. Diaz, Fern. Prieto, Loidi & Penas have an amount of nuclear DNA of 24.2 and 48.2 pg, respectively. They differ from *N. pseudonarcissus* in their small size and this small difference in amount of DNA. Fernandez and Fernandez Casado (1991) report that *N. (pseudonarcissus* ssp.) *pallidiflorus* \times *N. asturiensis* has only 6% good pollen and this might further indicate that they are separate species.

Barra and Lopez (1995) have two subspecies under *N. minor* L.: ssp. *minor* (with *N. jacetanus* Fern. Casas as a synonym and with var. *brevicoronatus* (Pugsley) Barra & G. Lopez with *N. vasconius* (Fern. Casas) Fern. Casas as synonym) and ssp. *asturiensis* (with the vars. *villarvildensis* T. S. Diaz & Fern. Prieto and *cuneiflorus* Willk. & Lange). On the other hand, Uribe-Echebarria Diaz (1998) divided *N. asturiensis* in three subspecies: ssp. *asturiensis* (with ssp. *villarvildensis* as synonym), ssp. *brevicoronatus* (Pugsley) Uribe-Ech. and ssp. *jacetanus* (Fern. Casas) Uribe-Ech. (with *N. vasconius* as a synonym). *Narcissus jacetanus* is growing on limestone whereas *N. asturiensis* grows on acid soils. It is considered to be a separate species here as with only 22.3 pg it seems to differ in this respect also. Moreover, the hybrid *N. jacetanus* \times *N. alpestris* (= *N. pseudonarcissus* ssp. *moschatatus* (L.) Baker) has only 5% good pollen (Fernandez Casas 1986b).

Four (sub)species are accepted here for these small flowered daffodils: *N. pseudonarcissus* ssp. *minor* (23.6 pg), *N. primigenius* (21.5 pg), *N. asturiensis* (24.2 and 48.2 pg) and *N. jacetanus* (22.3 pg). It cannot be excluded that the *N. pseudonarcissus* ssp. *minor* measured here), as they all came from cultivated material, including the plant from Linnaeus, are just small forms of *N. pseudonarcissus*. Based on the difference in nuclear DNA content, *N. minor* cannot be equated with *N. jacetanus* as did Barra and Lopez (1995).

There are a few more notable exceptions with respect to nuclear DNA content in the section *Pseudonarcissus*. *Narcissus cyclamineus*, long recognized as being morphological different because of its reflexed perianth segments, has 26.0 pg. Graham and Barrett (2004) could not find a difference in plastid DNA sequence between *N. cyclamineus* and *N. asturiensis*.

A similar high amount, 26.2 pg, is found for *N. abscessus* (Haw.) Schult.f. from the Pyrenees. A comparable amount, 26.0 pg, is found in *N. poeticus* L. *Narcissus abscessus* is morphologically very similar and has even been equated (Webb 1980) with *N. bicolor* L., the latter described from a cultivated plant. The close relationship between *N. bicolor* and *N. abscessus* suggested by Webb (1980) and others is not confirmed here, as there are clearly differences in ploidy and basic amounts of DNA between these species. Apart from its wild provenance, the main morphological characteristics of *N. abscessus*, compared to *N. bicolor*, are a much smaller bulb size, leaves nearly half the width and a cylindrical, seemingly cut-off corona. The corona is sometimes coloured an almost orange yellow (Meadows 1972). However, there is a difference in opinion on the shape of the corona. Whereas Blanchard (1998), Meadows (1972) and Mathew (2002) consistently describe *N. abscessus* with a truncated corona, Fernandez Casas (1991) and Susanna and Garnatje (2005) describe and figure it as having an expanded one. The latter even writes: "A distinctive trait of *N. abscessus*... is the intense yellow corona with the margin strongly curved outwards in contrast with the straight pale yellow corona of, e.g. *N. pallidiflorus*". The English opinion is followed here as already Haworth (1831) placed *N. abscessus* and four other species, based on its "clipt-trunke" corona, in a separate genus *Oileus* (Haw.) (Pugsley 1933).

Another question is whether *N. abscessus* is a species or a hybrid. It could be speculated that *N. abscessus* is an (ancient) hybrid, derived from *N. poeticus* \times *N. pseudonarcissus*. All three taxa can still be found together in de Val d'Aran, Pyrenees (Meadows 1972) and many other places. The F1 hybrid shows a shorter, but also truncated corona. Repeated (back) crosses could have selected the truncated corona and nuclear amount of DNA from *N. poeticus*, but the length of the corona and its overall appearance from *N. pseudonarcissus*. Also the almost white to medium yellow tepals, the long pedicels and late flowering might be due to the influence of *N. poeticus*. Already Engleheart (1894) reported that among the selfed progeny of *N. \times bernardii* DC. ex Henon (*N. poeticus* \times *N. pseudonarcissus*), forms were found that covered the whole range of variation from *N. pseudonarcissus*, via *N. abscessus* to *N. \times bernardii* and *N. poeticus* (Wylie 1952). I am inclined to consider *N. abscessus* an ancient hybrid.

A third plant, with 26.1 pg also deviating in the amount of nuclear DNA from *N. pseudonarcissus* is *N. moleroi* Fern. Casas from N.E. Spain (Gerona, Barcelona). It is usual considered to be a pale yellow form of the icy-white *N. alpestris*, but the *N. alpestris* measured from Cerler-Benasque had only 23.4 pg of nuclear DNA. *Narcissus alpestris* is a synonym of *N. moschatus* L., now *N. pseudonarcissus* ssp. *moschatus* (L.) Baker. *Narcissus moleroi* too has a drooping flower, but with a straight pale yellow corona and nearly white petals. Maybe it is a colour form of *N. abscissus* with a similar amount of DNA. Peculiar is that from the same two places, Col de la Crueta and Cerler, Blanchard reported white flowering narcissi whereas Norman and Norman (2003) report oxlip yellow narcissi. Maybe there is a difference in flowering time (and amount of nuclear DNA!) between the white flowering *N. alpestris* and the yellowish flowering *N. moleroi*.

Section *Nevadensis* Zonn. sect. nov.: *N. nevadensis* Pugsley. J. Roy. Hort. Soc. 58:17–93 (1933) Scapus multiflores, corona and spatha longissima, DNA contentus nucleorum 30–39 pg a sectione *Pseudonarcissus* differt. Species: *N. bujei* Fern. Casas, *N. nevadensis*, *N. longispathus* ssp. *longispathus*, *N. longispathus* ssp. *alcarensis*, *N. longispathus* ssp. *segurensis* and *N. longispathus* ssp. *yepesii*.

Very surprising is the result for the species from just northeast of the Sierra Nevada, *N. longispathus*, *N. alcarensis* Rios et al. *N. segurensis* Rios et al. and *N. yepesii* Rios et al. (Rios-Ruiz et al. 1998) as these have all 36–38 pg of DNA. These species often have more than one flower to a scape, not found elsewhere in section *Pseudonarcissus*. The high amount of nuclear DNA seems at first glance easily explained as all four being triploid forms of *N. pseudonarcissus* (23.7 pg). Although only the chromosome number for *N. nevadensis* and *N. longispathus* with similar amounts of DNA is known ($2n = 2x = 14$, Fernandes 1968; Sanudo 1984), it makes it feasible that the same number will be found in the other three taxa. This means that they have the highest amount of DNA of all diploid *Narcissi*. For further assurance, the fertility of the pollen was also tested. Having found more than 95% good pollen in *N. alcarensis*, *N. segurensis* and *N. yepesii*, it is highly unlikely that they are triploids. The latter three are here treated therefore as subspecies of *N. longispathus*. *Narcissus nevadensis* from the same area has consistently a 2 pg higher amount of nuclear DNA. Also Graham and Barrett (2004) could separate *N. longispathus* and *N. nevadensis* with a bootstrap value of 76% and both were well separated from *N. pseudonarcissus*. Fernandes (1951) considers *N. nevadensis* to be the most primitive of the section *Pseudonarcissus* and the Sierra Nevada as the centre of origin of the section. Webb (1980) and others consider it a subspecies of *N. pseudonarcissus* but with a

12 pg difference that is highly unlikely. With its high amount of nuclear DNA it would then suggest that the other species of this section have lost 50% or so of their DNA without a change in chromosome number, an unlikely event. Graham and Barrett (2004) place *N. assoanus* and *N. gaditanus* with 18–19 pg in the same clade as *N. longispathus* and *N. nevadensis* with 36–38 pg, although with a low bootstrap value of 56. It seems attractive to suggest an ancient tetraploidy for *N. longispathus/nevadensis* from *N. assoanus/gaditanus*. This would fit the amounts of nuclear DNA but would suggest that *N. longispathus/nevadensis* retained the full amount of DNA and yet at the same time reduced the number of chromosomes again from $2n = 28$ to $2n = 14$, an unlikely event. Both *N. nevadensis* and *N. longispathus* are here kept separate.

Clearly separate from *N. pseudonarcissus* in nuclear DNA content but hardly morphologically is the plain yellow *N. bujei* with 30.0 pg, described from the Serrania de Ronda, southern Spain. This value more or less fits *N. longispathus* (36 pg) \times *N. spec.* with 26 pg. Several populations of section *Pseudonarcissus* are now found with about 26 pg of DNA. So it comes as no surprise that were they meet plants of section *Nevadensis*, hybrids like *N. bujei* are found. This (ancient) hybridisation seems not too far fetched as *N. bujei* was first described as a variety of *N. longispathus* (*N. longispathus* var. *bujei* Fern. Casas), later as a variety of *N. hispanicus* and then as a subspecies of it and finally as a species, all by the same author. Fernandez Casas (1986a) reports on seeds in *N. bujei* having a black strophiole, so it seems to produce seed and its fertility is confirmed by Blanchard (personal communication).

Despite the fact that a large number of accessions of *N. pseudonarcissus* had similar amounts of DNA of approximately 23.7 pg, several species from this section, as shown above, are clearly distinctive in nuclear DNA content. It runs from the diploid *N. primigenius* with 21.7 pg to the also diploid *N. nevadensis* with 38.2 pg. This is contrary to what is found in other sections where most species have a similar amount of DNA. The evidence presented here indicates that comparisons may be based on superficial characters. There are only small differences in the amount of nuclear DNA of the species in the other sections. Therefore, to stay in line with this, the section *Pseudonarcissus* is divided in two separate sections *Pseudonarcissus* s.s. with 21–27 pg for the plants from mainly France, northern Spain and Portugal, and *Nevadensis* with 30–39 pg for the plants from southern Spain.

Section *Narcissus*: *N. poeticus* L. Hardly a difference in DNA content was found between *N. poeticus* and *N. radiiflorus*, with 26.0 and 26.1 pg. These data strengthen the viewpoint (Webb 1980) based on morphological evidence, that *N. radiiflorus* cannot be upheld as a separate species.

So the latter is indeed best treated as a subspecies: *N. poeticus* ssp. *radiiflorus* (Salisb.) Baker. Apart from the 16 diploid accessions, five plants with a triploid amount of DNA and one plant with a tetraploid amount of DNA was found, the latter from cultivated plants. It seems possible that the triploids *N. poeticus* “Hellenicus” and *N. poeticus* “Recurvus” described from Greece and Switzerland are actually garden escapes or alternatively were selected from nature for their triploid vigor. Fernandes (1968a) remarks on the similarity of the karyotypes of this section and section *Pseudonarcissus*. Also Graham and Barrett (2004) place *N. poeticus* in the *Pseudonarcissus* clade. As the hybrid between these two seems to be the only fertile intersectional hybrid it is mainly the deviating morphology of the flower, with a very short and orange coloured corona, that has prevented so far to unite these two sections.

Polyplids in Section *Pseudonarcissus*

The polyplids in this section are here treated separately. Fernandes (1991) found several populations in Spain and Portugal with tetraploid [as *N. c.f. nobilis* (Haw.) Schult. f.] or hexaploid (as *N. leonensis* Pugsley) chromosome numbers. Sanudo (1984) reported on tetraploid and hexaploid *N. nobilis* (the latter = *N. leonensis*?). Based on amounts of nuclear DNA, *N. asturiensis* ssp. *villarvildensis*, including the very early flowering *N. “Cedric Morris”* from Ribalden, Costa Verde and a single accession of *N. pseudonarcissus* ssp. *nobilis* were found here to have a tetraploid amount of DNA. Although received under different names 11 hexaploid accessions from four different locations are arranged here under *N. pseudonarcissus* ssp. *bicolor*. As expected from its higher ploidy, it has larger bulbs and leaves compared to the often equated diploid *N. abscissus*. *N. pseudonarcissus* ssp. *bicolor* differs in turn by its smaller size and earlier flowering from the very large hexaploid *N. pseudonarcissus* ssp. *leonensis* (Fernandes 1991; Table 1). These wild hexaploids are interesting as hardly any are found among the cultivated forms investigated. This seems to exclude that they are escapes from cultivation. Moreover, Wylie (1952) remarked that the optimum level of ploidy in *Narcissus* cultivars seems to be the tetraploid one. Maybe the hexaploids are discarded in culture as too slow growing.

Sanudo (1984) found a diploid chromosome number for his “*N. bicolor*” but this could point to the often equated *N. abscissus*. On the other hand, the *N. pseudonarcissus* used by Graham and Barrett (2004) has the same accession number (Blanchard 9401) as the plant here determined as the hexaploid *N. bicolor*. Fernandes and Fernandes (1946) found triploid and tetraploid chromosome numbers for *N. bicolor*. These lower chromosome numbers are difficult

to reconcile with the hexaploid amount of nuclear DNA found in plants here ascribed to *N. bicolor*. No one so far has reported on hexaploid chromosome numbers in *N. bicolor* or in *N. radinganorum* for that matter. The single tetraploid *N. nobilis* reported here is of doubtful wild origin (Donnison-Morgan, personal communication). An alternative could be to combine all hexaploids (18 measured here) under *N. pseudonarcissus* ssp. *bicolor*.

In seven species of *Narcissus*, *N. asturiensis*, *N. bulbocodium*, *N. broussonetii*, *N. cantabricus*, *N. poeticus*, *N. pseudonarcissus* and *N. tazetta*, apart from the diploid forms, polyploids are found. Some are considered separate species, some are given separate subspecific names and in some cases there is not a separate name at all. It seems better to give them all a subspecific status when they form separate populations. So instead of the hexaploid *N. bicolor* and *N. leonensis* and the tetraploid *N. nobilis* it seems better to use *N. pseudonarcissus* ssp. *bicolor* (L.) Baker, *N. pseudonarcissus* ssp. *leonensis* Pugsley and *N. pseudonarcissus* ssp. *nobilis* (Haw.) A. Fern. If they are single plants or from cultivated origin like the triploid *N. tazetta* or the triploid and tetraploid *N. poeticus* it is better to give them a cultivar name.

Hybrids between species

Forty-three putative primary hybrids of wild origin were also investigated (Table 2). A distinction is made here between ancient hybrids growing over a larger area and therefore considered as species, included in Table 1 and more recent hybrids growing as solitary plants amidst their parents (Table 2). A suggested pairing can be confirmed as probable, when this is between species with distinct DNA values and the expected intermediate DNA value of putative hybrids is readily apparent. Of the 43 hybrids between species here measured, nearly all have an amount of nuclear DNA that is compatible with this calculation. Everywhere where two species of *Narcissus* meet it seems possible to find the hybrid and most of these have been given names. The occurrence of these hybrids in nature seems a major mechanism for the formation of new species and several instances are indicated above.

Narcissus portensis Pugsley is known from herbarium material only. It is said to be common (!) in central Spain and can be found in several floras, both as a species or as subspecies of *N. pseudonarcissus*. Unfortunately, not a single plant could be located for measurements. Based on its description, I suspect that it is a hybrid of *N. bulbocodium* × *N. pseudonarcissus*. It is clearly very rare in culture and nature. It has, according to the literature, narrow (6 mm) leaves, narrow perianth segments, shorter than the funnel shaped corona, biseriate? anthers and “the flowers give it something of the aspect of a *N. bulbocodium*” (Pugsley

Table 3 Ploidy in hybrids of *N. assoanus* Dufour and *N. papyraceus* ssp. *panizzianus* (Parl.) Arcang

Ploidy	Species	Parents	2C DNA in pg	Chromos. number
Diploid	<i>N. assoanus</i>	<i>N. assoanus</i>	18.7	$2n = 14$
Diploid	<i>N. p. panizzianus</i>	<i>N. papyraceus</i> ssp. <i>panizzianus</i>	33.7	$2n = 22$
Diploid	<i>N. × koshinomurae</i>	<i>N. p.</i> ssp. <i>panizzianus</i> × <i>N. assoanus</i>	26.7	($2n = 18$)
Triploid	<i>N. × tortifolius</i>	<i>N. p.</i> ssp. <i>panizzianus</i> × <i>N. assoanus</i> 2X	37.4	($2n = 25$)
Tetraploid	<i>N. × tortifolius</i>	(<i>N. p.</i> ssp. <i>panizzianus</i> × <i>N. assoanus</i>)*2	46.5	$2n = 36$
Tetraploid	<i>N. × pujolii</i>	(<i>N. p. panizzianus</i> × <i>assoanus</i> 2X) × <i>assoanus</i>	n.d.	$2n = 32$
Hexaploid	<i>N. dubius</i>	(<i>N. p. panizzianus</i> × <i>assoanus</i> 2X)*2	66.1	$2n = 50$
Nonoploid	<i>N. dubius</i>	[(<i>N. p. pan.</i> × <i>ass.</i> 2X)*2] × (<i>p. pan.</i> × <i>ass.</i> 2X)	96.3	($2n = 75$)

Chromosome numbers between brackets are calculated from their 2C amount of DNA. Parents: haploid gametes unless 2X = diploid (non-reduced) gamete; *2 = doubled chromosome number n.d. = not determined but predicted value is $16.8 + 18.8 + 9.4 = 45$ pg

1933; Gadeceau in Pugsley 1933). Moreover, Fernandez Casas (1986a) speaks of an intersectional hybrid *N. × portensis*, unfortunately without giving any further details. I suppose he means the same plant.

Interesting is also *N. dubius*, an allohexaploid plant with $2n = 6x = 50$ originating from a doubled hybrid of *N. papyraceus* × *N. assoanus* (non-reduced) (Table 3). Eight accessions were measured with an average of 66.1 pg. Most remarkable was the find of a plant with a nonoploid amount of DNA with 96.3 pg. It not only has by far the highest amount of nuclear DNA ever reported in *Narcissus*, but it can be calculated to have by far the highest ploidy.

In *N. × tortifolius* forms with a triploid and tetraploid ($2n = 36$) amount of DNA are found. Fernandez Casas (1977) reported $2n = 22$. This is probably a mistake and more likely should be $2n = 25$ for the triploid. The putative parents according to him are *N. gaditanus* and (*N. papyraceus* ssp.) *panizzianus*. The tetraploid ($2n = 36$, Romero et al. 1983) is then a doubled *N. gaditanus* × *N. panizzianus* and the triploid form is then *N. gaditanus* (non-reduced) × *N. panizzianus*. Leaving aside the subtle differences between *N. papyraceus* versus *N. panizzianus* and *N. gaditanus* versus *N. assoanus*, we then have the triploid *N. × tortifolius* which by doubling its DNA gives the hexaploid *N. dubius* and from this the nonoploid *N. dubius*. Furthermore, we have the tetraploid form *N. × tortifolius*, presumably from the diploid hybrid not encountered here. However, *N. koshinomurae* Fern. Casas is described (1996) as *N. fernandesii* × *N. panizzianus* (in description: Forma externa *Narcisso dubio* simile, et cum illo interdum confusus!). Blanchard (1998) however, found hybrids in the same population and considers them to be *N. assoanus* × *N. panizzianus*. The nuclear DNA content fits the parents suggested by Blanchard, not those by Fernandez Casas. Graham and Barrett (2004) place *N. × tortifolius* and *N. dubius* amidst their *Jonquillae* clade. This is

incongruent with the fact that the chloroplast DNA must be of one of the supposed parents either *N. panizzianus* or *N. assoanus*, both not in the *Jonquillae* clade. The data on this *N. dubius* complex are summarized in Table 3.

Allopolyploids like *N. dubius* or *N. miniatus* bring up the question when a hybrid must be considered as a species. In this article, if not found as single plants but forming one or more populations they are considered to be distinct species. It needs further investigation, e.g. sequencing of nuclear DNA, whether or not plants that are suggested here as possible of hybrid origin, i.e. *N. abscessus*, *N. blanchardii*, *N. bujei*, *N. hedraeanthus* and *N. portensis* are indeed (ancient) hybrids.

Two *N. bulbocodium* look-alike plants had a peculiar amount of DNA. From Mazagon, Andalucia, H. Berkhout did give me a leaf of a single plant with 17 pg and from Ciudad Real, Mestanza there is plant, received as *N × barrae* Fern. Casas, that is supposed to be *N. cantabricum* × *N. bulbocodium*, but has 17.1 pg. If not aneuploids, these two may be considered as *N. gaditanus* (19.2 pg) × *N. bulbocodium* (14 pg) as that would fit the amount of nuclear DNA. A *N. bulbocodium* look-alike plant was also reported by Graham and Barrett (2004) but ended up in their *Jonquifoliae* clade, suggesting it had a different hybrid origin.

B-chromosomes

Fernandes and Franca (1974) report on B-chromosomes in *N. assoanus*, *N. asturiensis*, *N. bulbocodium*, *N. gaditanus* and *N. hispanicus*. Brandham and Kirton (1985) found them in *N. assoanus*, *N. asturiensis*, *N. bicolor*, *N. calicicola*, *N. cyclamineus*, *N. eugeniae*, *N. minor*, *N. tazetta* and in *N. triandrus*. In *N. bulbocodium* Fernandes (1963) found 0–5 B-chromosomes. They are about two third of the length of the smallest chromosomes and may or may not be heterochromatic. They seem to be widespread and it cannot

Table 4 All species of *Narcissus* with their 2C amount of DNA and chromosome numbers, Chromosome numbers between brackets are calculated from their 2C amount of DNA.

Species	acc. WEBB (1980) –	2C DNA in pg	Corresponding chromosome #	Other chrom. #
Genus Narcissus				
Subgenus Hermione (Haw.) Spach.				
Section Serotini Parl.		Section Serotini Parl.		
<i>N. serotinus</i> L.	<i>N. serotinus</i>	20.8	2x = 10	
<i>N. miniatus</i> Koop., Donnison-Morgan & Zonn.	–	51.3	6x = 30	
Section Tazettae DC.		Section Tazettae DC.		
<i>N. elegans</i> (Haw.) Spach	<i>N. elegans</i>	30.2	2x = 20	
<i>N. tazetta</i> L.	<i>N. tazetta</i>	30.3	2x = 20	2n = 20; 30
<i>N. papyraceus</i> Ker Gawl.	<i>N. papyraceus</i>	33.7	2x = 22	
<i>N. broussonetii</i> Lag. y Segura	<i>N. broussonetii</i>	37.4	2x = 22	2n = 22; 44
<i>N. dubius</i> Gouan	<i>N. dubius</i>	66.3	6x = 50	2n = 50; 75
Subgenus Narcissus L.				
Section Bulbocodii DC.		Section Bulbocodii DC.		
<i>N. bulbocodium</i> L.	<i>N. bulbocodium</i>	14.2	2x = 14	2n = 14–56
<i>N. cantabricus</i> DC.	<i>N. cantabricus</i>	14.5	2x = 14	2n = 14; 28
<i>N. romieuxii</i> Braun-Blanq. & Maire	(<i>N. romieuxii</i>)	28.8	4x = 28	
<i>N. hedraeanthus</i> (Webb & Heldr.) Colmeiro	<i>N. hedraeanthus</i>	15.0	2x = 14	
<i>N. obesus</i> Salisbury	<i>N. bulbocodium</i> ssp. <i>obesus</i>	26.5	2x = 26	2n = 26; 39
Section Ganymedes Schult. & Schult.f.		S. Ganymedes Sch. & Sch.		
<i>N. lusitanicus</i> Dorda & Fern. Casas	<i>N. triandrus</i> ssp. <i>pallidulus</i>	16.9	2x = 14	
<i>N. pallidulus</i> Graells	<i>N. triandrus</i> ssp. <i>pallidulus</i>	18.0	2x = 14	
<i>N. triandrus</i> L.	<i>N. triandrus</i> ssp. <i>triandrus</i>	19.0	2x = 14	
<i>N. triandrus</i> L.	<i>N. triandrus</i> ssp. <i>capax</i>			
Section Tapeinanthus (Herbert) Traub		S. Tapeinanthus (Herb.) Traub		
<i>N. cavanillesii</i> Barra & G. Lopez	<i>N. humilis</i>	33.3	4x = 28	
Section Jonquillae DC.		Section Jonquillae DC.		
<i>N. jonquilla</i> L.	<i>N. jonquilla</i>	32.8	2x = 14	
<i>N. jonquilla</i> ssp. <i>wilkommii</i> (A. Fern.) Zonn.	<i>N. willkommii</i>	33.2	2x = 14	
<i>N. jonquilla</i> ssp. <i>fernandesii</i> (Pedro) Zonn.	–			
<i>N. jonquilla</i> ssp. <i>cordubensis</i> (Fern. Casas) Zonn.	–			
<i>N. cuatrecasatii</i> Fern. Casas, Lainz & Ruiz Rejon	<i>N. cuatrecasatii</i>	31.7	2x = 14	
<i>N. blanchardii</i> Zonn.	–	51.2	(4x = 28)	
<i>N. viridiflorus</i> Schousboe	<i>N. viridiflorus</i>	63.5	4x = 28	
Section Apodanthi A. Fern.		–		
<i>N. calcicola</i> Mendonca	<i>N. calcicola</i>	26.6	2x = 14	
<i>N. scaberulus</i> Henriq.	<i>N. scaberulus</i>	26.3	2x = 14	
<i>N. rupicola</i> Dufour	<i>N. rupicola</i>	26.6	2x = 14	
Section Juncifolii (A. Fern.) Zonn.		–		
<i>N. gaditanus</i> Boiss. & Reuter	<i>N. gaditanus</i>	19.3	2x = 14	
<i>N. assoanus</i> Dufour	<i>N. requienii</i>	18.8	2x = 14	
Section Pseudonarcissi DC.		Section Pseudonarcissi DC.		
<i>N. primigenius</i> Fern. Casas & Lainz	–	21.7	2x = 14	
<i>N. jacetanus</i> Fern. Casas	–	22.3	2x = 14	
<i>N. pseudonarcissus</i> L.	<i>N. pseudonarcissus</i>	23.5	2x = 14	
<i>N. pseudonarcissus</i> ssp. <i>minor</i> (L.) Baker	<i>N. minor</i>	23.6	2x = 14	
<i>N. pseudonarcissus</i> ssp. <i>bicolor</i> (L.) Willk. & Lange	<i>N. bicolor</i>	67.7	6x = 42	

Table 4 continued

Species	acc. WEBB (1980)	2C DNA in pg	Corresponding chromosome #	Other chrom. #
<i>N. asturiensis</i> (Jord.) Pugsley	<i>N. asturiensis</i>	24.2	2x = 14	
<i>N. cyclamineus</i> DC.	<i>N. cyclamineus</i>	26.0	2x = 14	
<i>N. abscissus</i> (Haw.) Schult. f.	<i>N. bicolor</i>	26.4	2x = 14	
<i>N. moloroi</i> Fern. Casas	–	26.1	2x = 14	
Section Nevadensis Zonn.	–			
<i>N. bujei</i> Fern. Casas	–	30.0	(2x = 14)	
<i>N. longispathus</i> Pugsley	<i>N. longispathus</i>	36.0	2x = 14	
<i>N. longispathus</i> ssp. <i>alcarensis</i> (S. Rios et al.) Zonn.	–			
<i>N. longispathus</i> ssp. <i>segurensis</i> (S. Rios et al.) Zonn.	–			
<i>N. longispathus</i> ssp. <i>yepesii</i> (S. Rios et al.) Zonn.	–			
<i>N. nevadensis</i> Pugsley	<i>N. pseudon.</i> ssp. <i>nevadensis</i>	38.2	2x = 14	
Section Narcissus L.	Section Narcissus L.			
<i>N. poeticus</i> L.	<i>N. poeticus</i>	26.0	2x = 14	2n = 14; 21

Compared with Webb (1980)

– Not mentioned

be excluded that they contribute a few percent to the total amount of DNA as measured here. At first sight they could explain the “anomalous” pseudonarcissi with 26 pg or the differences between the three species in section *Ganymedes*. However, Fernandez Casas (1996) did not find them in *N. cyclamineus* or *N. moloroi* with 26 pg, although he did report on two B-chromosomes in *N. eugeniae* with 23.2 pg. B-chromosomes might increase the amount of nuclear DNA and will consequently increase nuclear size, cell size and perhaps even plant size. This will lead to a later flowering according Fernandez (1968a). However, it cannot be excluded that B-chromosomes are leftovers from deletions of repeats in the regular chromosomes. In that case the total amount of nuclear DNA will not change at first. Also variation in constitutive heterochromatin can result in intraspecific genome size variation (Greilhuber and Speta 1978; Greilhuber 1995). It would be worthwhile to investigate the relationship between the total amount of nuclear DNA, the number of B-chromosomes and/or amount of heterochromatin present and their effect on any other character.

Conclusions

In Table 4 all *Narcissus* species have been arranged in two subgenera and 11 sections and compared to the work of Webb (1978, 1980). A strong correlation is found between genome size and the division into sections. Therefore, those few were the amount of nuclear DNA did not fit with other species in the section are here confidently placed in others. The number of 36 species

proposed here can be compared to the 26 (+1) species suggested in Flora Europaea by Webb (1980), the 28 species described in the R.H.S. Dictionary of Gardening (1992) or the 22 species of Fernandes (1951) but not with the number of the about 60 species suggested by Fernandes (1968a, b), Nutt (1993) or Blanchard (1990). Especially section *Pseudonarcissus* turns out to be heterogeneous. It runs from the diploid *N. primigenius* with 21.7 pg via *N. pseudonarcissus* with 23.7 pg and *N. abscissus* with 26 pg to the also diploid *N. nevadensis* with 38.2 pg. Therefore a new section *Nevadensis* is introduced. Based on the same arguments section *Jonquillae* (according to Webb 1978) is now divided in three sections: section *Jonquillae* s.str. with about 31 p., section *Apodanthi* with about 26 p. and section *Juncifolii* with about 19 p. The *N. fernandesii* complex is now entangled and this has led to a new taxon *N. blanchardii*.

Flow cytometry is shown here to be a useful tool to indicate or decide on the taxonomic status of different accessions of *Narcissus*. This is especially clear if one looks at the last column in Table 1 (“received as”). This method also indicates new and published chromosome counts through the amounts of nuclear DNA. Also several new instances of polyploidy were observed. At the same time the results point out taxonomic problems that need further investigation. *Narcissus dubius* and *N. fernandesii* show where even sequencing would not have given the detailed results obtained here with flow cytometry. The speed and cost effectiveness of measuring nuclear DNA content and its predicative accuracy makes it a useful tool for identifying species.

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Appendix: New combinations

N. jonquilla ssp. *cordubensis* (Fern. Casas) Zonn. comb. et stat. nov. Basionym: *N. cordubensis* Fern. Casas. (1982) Fontqueria 1: 10.

N. jonquilla ssp. *fernandesii* (Pedro) Zonn. comb. et stat. nov. Basionym: *N. fernandesii* Pedro (1947) Bol. Soc. Brot. II, 21: 60.

N. jonquilla ssp. *willkommii* (A. Fern.) Zonn. comb. et stat. nov. Basionym *N. willkommii* (Samp.) A. Fern. (1966) Bol. Soc. Brot. II, 40: 213.

N. longispathus ssp. *alcaracensis* (S. Rios, D. Rivera, Alcaraz & Obon) Zonn. comb. et stat. nov. Basionym: *N. alcaracensis* S. Rios, D. Rivera, Alcaraz & Obon. (1998) Bot. J. Linn. Soc 131: 153–165.

N. longispathus ssp. *segurensis* (S. Rios, D. Rivera, Alcaraz & Obon) Zonn. comb. et stat. nov. Basionym: *N. segurensis* S. Rios, D. Rivera, Alcaraz & Obon. (1998) Bot. J. Linn. Soc 131: 153–165.

N. longispathus ssp. *yepesii* (S. Rios, D. Rivera, Alcaraz & Obon) Zonn. comb. et stat. nov. Basionym: *N. yepesii* S. Rios, D. Rivera, Alcaraz & Obon. (1998) Bot. J. Linn. Soc 131: 153–165.

N. romieuxii ssp. *jacquemoudii* (Fern. Casas) Zonn. comb. et stat. nov. Basionym: *N. jacquemoudii* Fern. Casas (1986) Fontqueria 10: 11.

New taxa already mentioned in the text:

N. blanchardii Zonn. stat. nov.

Ancient allotetraploid form of *N. jonquilla* (ssp. *fernandesii*) × *N. gaditanus*

Based on *N. fernandesii* var. *major* A. Fern., Bol. Soc. Brot. II, 40: 239 (1966) Named after John Blanchard who wrote an eminent book on *Narcissus*.

Section *Juncifolii* (A. Fern.) Zonn. stat. nov. Typus *N. assoanus* Dufour ex Schult. & Schult.f in J. J. Roemer & J. A. Schultes, Syst. Veg. 7: 962 (1830). Based on subsection *Juncifolii* A. Fern. (1966). Bol. Soc. Brot. II, 40: 207–261. Species included: *N. assoanus* Dufour, *N. gaditanus* Boiss. & Reuter

Section *Nevadensis* Zonn. sect. nov. Typus: *N. nevadensis* Pugsley, J. R. Hort. Soc. 58: 62 (1933). Scapus

multiflores, corona and spatha longissima, DNA contentus nucleorum 30–39 pg a sectione *Pseudonarcissus* differt.

(Sub)species included: *N. bujei* Fern. Casas, *N. longispathus* ssp. *alcaracensis* (S. Rios, D. Rivera, Alcaraz & Obon) Zonn., *N. longispathus* ssp. *longispathus* Pugsley, *N. longispathus* ssp. *segurensis* (S. Rios, D. Rivera, Alcaraz & Obon) Zonn., *N. longispathus* ssp. *yepesii* (S. Rios, D. Rivera, Alcaraz & Obon) Zonn., *N. nevadensis* Pugsley.

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