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The Image of Daffodil in Art and Botanical Illustration: Clues to the History of Domestication and Selection of *Narcissus* subgenus *Ajax* (Amaryllidaceae)

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ABSTRACT

The "Ajax Group" (i.e. *Pseudonarcissus*) is one of the most important ancestors of modern daffodils cultivars. The manner in which these plants were introduced into the English, French and Dutch gardens appears relatively obscure since most are endemic to the Iberian Peninsula. This chapter compares data from Arab texts of agriculture, European Renaissance, and Prelinnaean texts and illustrations, with the morphological characteristics of primitive cultivars of trumpet daffodils and the related wild taxa from of Spain and Portugal. The relationships among wild plants, domesticated plants, and primitive cultivars were investigated through a cluster analysis of the characters available from figures or botanical illustrations. The tree resulting from the Complete linkage analysis and UPGMA analysis distinguished 26 different groups including wild; cultivated and wild; and cultivated daffodils. A comparison of early descriptions, localities, and illustrations with currently wild species confirmed that several Iberian Peninsula endemics were cultivated in Central European gardens between the 16th and 18th centuries. Examples are: *Narcissus abscissus* Pugsley, *N. jacetanus* Fernández Casas, *N. asturiensis* Hénon, *N. hispanicus* Gouan, *N. nobilis* (Haw.) Schult. var. *leonensis* (Pugsley) A. Fernandes, *N. pallidiflorus* Pugsley and *N. pseudonarcissus* L. The characters involved in flower pigmentation evolved independently from other morphological characters. It obviously occurred in different places and at different times. Thus any colour flower group, even whites, is polyphyletic.

1. INTRODUCTION

The "Ajax Group" (i.e. *Pseudonarcissus*) is one of the most important ancestors of modern daffodil cultivars. It has been estimated to be the parent of 99% of the yellow trumpet cultivars (Coats 1956). In fact, its is also involved in the origin of most of the daffodil cultivars groups included in the old class *Mediocoronati,* e.g., 'Incomparabilis', 'Barrii', 'Backhousei', 'Nelsonii', 'Humei', 'Leedsii' and 'Odorus' (Bahnert 1992). In the modern classification system (RHS 2000 2005a 2005b, Kington 2002), it is involved in the origin of Divisions 1, 2, 4, 6, and 11. The Iberian Peninsula is the center of diversity for *Narcissus* subgenus *Ajax* Spach with 30-40 taxa (Fernandes 1957, Andersen 1988 1990, Ríos et al. 1999). Fernandes (1951) proposed *N. nevadensis* Pugsley as the ancestral species of subgenus *Ajax*. The relationships among wild plants, domesticated plants, and primitive cultivars were investigated through a cluster analysis of the characters available from figures or botanical illustrations (Rivera *et al*. 2003). The more primitive European herbals represented trumpet daffodils in an unrealistic and naive manner and are not suitable for analysis (Arber 1988), however illustrations with a minimum level of accuracy exist since the 16th century.

There appears to have been little attention given to daffodils in England until the 16th century (Coats 1956). Turner identified the Pliny's daffodil as the English common daffodil, without mentioning any other related taxon (Britten, Daydon-Jackson and Stearn 1965). The "yealowe daffodil" of Turner (1548) is presumably the common *N. pseudonarcissus* of the English meadows and forests (Stace 1991). It seems that few daffodil species, presumably only the wild one, were available in England up to 1548.

Parkinson (1629) cited notices concerning the introduction of daffodils to the British Isles. Loudon (1841) subsequently referred to Parkinson as the earliest citations of most of the flowers of this group grown in England. Hereman (1868), Haworth (1831) and Pugsley (1933) increased the list of taxa. There are more recent reports by Cullen (1986), Webb (1980), and The International Daffodil Register (Kington 2002). Barkham

(1980a 1980b 1992) and Barkham and Hance (1982) studied the population dynamics of the wild daffodil in England. The recent discovery (1980s) of many new wild taxa in the Iberian Peninsula, mainly by J. Fernández Casas and co-workers, raised the question of describing their relationship to plants currently in cultivation.

2. MATERIALS AND METHODS

The study of Rivera *et al*. (2003) primarily utilized the comparison of data from ancient texts and illustrations with the morphological characteristics of the currently known wild taxa and primitive cultivars. The earliest iconography available (16th and 17th centuries) illustrates a relatively high degree of accuracy. The plant images in these illustrations are accurate enough to make a comparison with data obtained from the study of wild and cultivated populations. The illustrations by Weiditz (Blunt and Stearn 1994), Brunfels (1530), Clusius (1601 1605), Parkinson (1629), Gerarde (1597 1633), Besler (1613), Barrelier (1714) and Tabernaemontanus (1731) have been analysed for 13 vegetative and floral characters and were compared with wild taxa and modern daffodil cultivars (**Fig. 1**).

The selected set of characters was restricted to these that were easily detectable in high quality illustrations (**Table 1**). The comparisons were made using a data matrix involving 101 OTUs and 13 characters. Cluster analyses used agglomerative clustering by distance optimization (NCLAS) from the Sintax 5.0 package (Podani 1991). Hierarchical classification was generated using combinatorial agglomerative methods characterized by the recurrence formula as follows: $d_{h,ij} = \alpha_i d_{hi} + \alpha_j d_{hj} + \beta d_{ij} + \gamma \left| d_{hi} d_{hj} \right|$; where $d_{h,ij}$ was the new distance value between cluster C_h and cluster C_{ij} obtained from the fusion of C_i and C_j (Podani 1991). As recommended by Podani (1991), the data set was analyzed using two options. Complete linkage (farthest neighbour, euclidean distance) (CL) (**Fig. 1**) and unweighted group averages (average, euclidean distance) (UPGMA) were calculated. Similarities above 90%, as calculated using complete linkage, were interpreted in terms of close relationship and were used for interpreting the possible origin of cultivated daffodils.

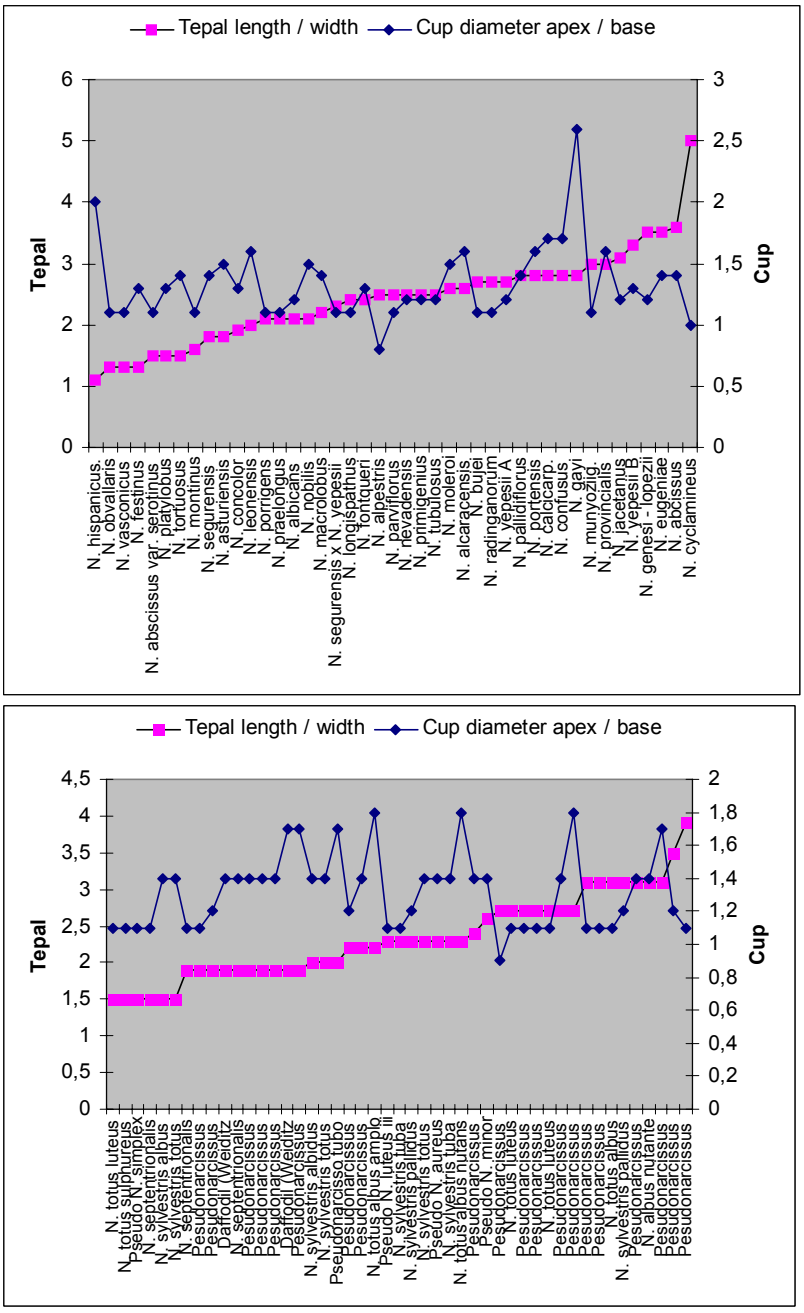

Fig. 1 Variation of the Quotient tepal length / width; and Quotient apical-diameter / basal-diameter of the Cup (**above**). In wild species and cultivars. **Below**. In old images.

3. RESULTS

The tree resulting from the Complete linkage analysis (**Fig. 2;** Rivera *et al.* 2003) and UPGMA analysis distinguished 26 different groups including wild; cultivated and wild; and cultivated daffodils. These groups are illustrated in **Figs. 3-6**. The cluster analysis supported in part the interpretations of Pugsley (1933) for the illustrations of Gerarde (1597 1633), Parkinson (1629), Besler (1613) or Barrelier (1714). It also showed that *N. nevadensis* Pugsley and *N. longispathus* Pugsley, are closely related (Group 11), in addition, they were clearly distinct from the other *Narcissus*. They do not appear to have been in cultivation before the publication of their descriptions in the 20th century. These species were not illustrated in the primitive illustrations of cultivated daffodils, and were not cited in early literature.

4. DISCUSSION

4.1. Relationships between wild populations and primitive cultivars

It seems that the Greek and Latin herbals of Dioscorides, Theophrastus, or Pliny did not mention any "bastard daffodil", which were unknown (at least as a garden plant) to the Greeks and Romans. López (1990) in his study of the anonymous *Kitab fi Tartib Awqat* (10th to 12th Centuries AD) recognised, three types of daffodils: *N. papyraceus* Ker. Gawler (the *naryis abyad* or white daffodil), *N. jonquilla* L. (the *nisrin* or *ward barri*), and *N. pseudonarcissus* L. (*sensu lato*) (the *naryis asfar* or *arar* or yellow daffodil). The Arab writer Ibn Bassal (11th C. AD) recommended growing these flowers in beds, from bulbs gathered in the meadows (their natural habitats), alternatively suggested to collect in May seeds from wild and cultivated plants to be sown in June (Millás and Azimán 1955, García and Hernández-Bermejo 1995).

At the Cathedral of Zamora, Spain, several Flemish carpets woven in the second half of the 15th century include in the floral background of mythological and biblical scenes illustrations of two types of trumpet daffodils. The English name for the species of *Narcissus* included within subgenus *Ajax* Spach is "bastard daffodil". In Spanish, these received the names of "embuillos", "quitapanes" or "narcisos de lechuguilla" (De los Ríos 1620, Parkinson 1629, Boutelou and Boutelou 1804).

The first printed illustration of a "bastard daffodil" is a print woodcut by Hans Weiditz (Brunfels 1530) and it was copied by Mattioli in 1554. A water colour drawing by Hans Weiditz, dated 1529, was presumably used as a model for the woodcut, which is at the Botanical Institute, Bern. It displays two single flowered species, one with a pale yellow flower (left and centre) with whitish tepals and a yellow Cup (cf. Blunt and Stearn 1994). These illustrations are similar to the wild Spanish species *N. nobilis* (Haw.) Schultes f. (= *N. pseudonarcissus* L. sensu stricto). Jan Brueghel the Elder, represented several daffodils belonging to this group in paintings between 1599 and 1607 (Schneider 1992).

Several Iberian Peninsula endemics were cultivated in Central European gardens between the 16th and 18th centuries. Examples are: *Narcissus abscissus* Pugsley, *N. jacetanus* Fernández Casas, *N. asturiensis* Hénon, *N. hispanicus* Gouan, *N. nobilis* (Haw.) Schult. var. *leonensis* (Pugsley) A. Fernandes, *N. pallidiflorus* Pugsley and *N. pseudonarcissus* L. (Rivera *et al.* 2003).

The similarities of part of the Gerarde (1633), Barrelier (1714) and Tabernaemontanus (1731) illustrations with *N. hispanicus* var. *bujei* (Fernández Casas) Fernández Casas, an Andalusian montane endemic species, indicate the presence of this species, or other closely related, in gardens of Central Europe. Presumably, these plants were later lost in cultivation in Central Europe and the British Isles.

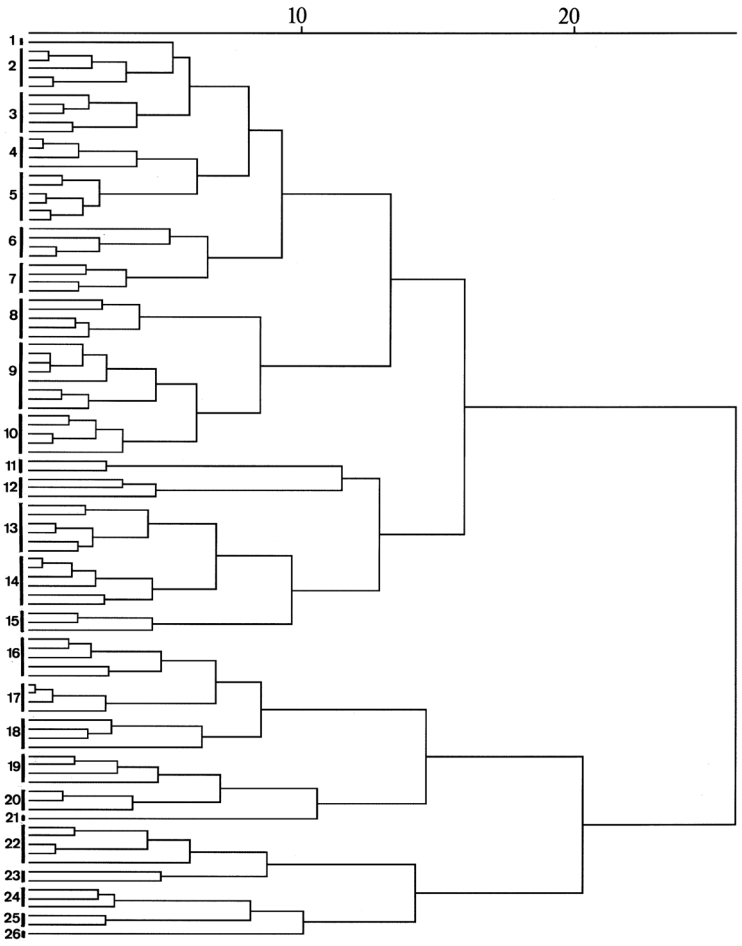

Fig. 2 Dendrogram resulting of the UPGMA analysis. From **Rivera *et al.*** (2003) *Scientia Horticulturae* **98**, 307-330, ©2003, with kind permission by Elsevier Science SV.

According to Miller (1754) and Parkinson (1629), the wild Spanish and Pyrenean "bastard daffodils" grown in the English gardens were produced from bulbs imported from their original countries. Most of the illustrations by Parkinson (1629) are very similar to Spanish wild species (Groups 2, 10, 12, 22 and 25 in **Figs. 3-6**).

Pritzel (1872) credited the son of the French gardener John Robin as the individual who introduced many Spanish plants into the French gardens by the end of the 16th century. Also, he was involved in the distribution of double forms of daffodils (Parkinson 1629, Gerarde 1633).

The famous Dutch botanist Charles de l'Ecluse (known as Clusius), who introduced the cultivation of tulips and potatoes to The Netherlands, was also involved into the development of daffodil cultivation. He received bulbs, originally collected in the Pyrenees, from different correspondents in Italy, France and Belgium (Clusius 1601 1605, Rivera *et al*. 2003). It seems that during his travel in Spain he did not collected daffodils himself (Clusius 1576).

The case of *N. minor* L. is noteworthy. The analysis showed a close resemblance with Barrelier's illustration (*N. sylvestris* 975) and with two endemic taxa of the Sierra de Alcaraz and Sierra de Segura (*N. alcaracensis* Ríos et aliis and *N. segurensis* Ríos et aliis) (Group 9). Rivera (1984) documented the travels of Barrelier in Alcaraz mountains, based on the localities cited by Barrelier (1714) for his collection of "*Rubeola montana*" and "*Polium montanum*". Very likely, this visit occurred during Spring based in the blossom period of the cited species. Hence, Barrelier may have been the collector of daffodils that subsequently through hybridization and selection led to the cultivated daffodil named by Linnaeus, *N. minor*. Unfortunately, the daffodils illustrated by Barrelier did not designate the collection locality (Barrelier 1714).

4.2. Relationships between white and bicolor flowered forms and wild populations

One of the daffodils in the Weiditz's 1529 water-color picture (n. 4 of **Table 1**, group 4) is a bicolored (tepals pale yellow or whitish, Cup deep golden yellow) form of *N. nobilis* (Group 4). Since Barra and López (1984) lectotypified *N. pseudonarcissus* L. (*sensu stricto*) in the sense of *N. nobilis*, this bicolored type probably belongs to the type species of the subgenus.

The plants named *N. bicolor* L. appear related to the yellow flowered natural hexaploid *N. nobilis* (Haw.) Schult. var. *leonensis* (Pugsley) A. Fernandes and to the bicolored cultivar 'Empress' (Group 15). Other bicolored forms were shown to be less related to yellow flowered taxa like *N. confusus* Pugsley or *N. asturiensis* (Group 6, **Fig. 3**) (cf. **Tables 1-2,** ns. 27, *Pseudonarcissus simplex belga* and 58, *Pseudonarcissus albo calyce* which are included in group 7, **Fig. 4**).

The primitive white flowered types, (**Tables 1-2,** ns. 33, *N. sylvestris albus* and 45, *N. sylvestris totus albicans* in **Table 1**), were included in the same cluster (Group 16, **Figs. 2, 5**). This cluster is closely related to groups 17 (**Fig. 6**) and 18 (**Fig. 4**) and includes taxa like *N. moschatus* L. and *N. alpestris* Pugsley. This cluster (Group 16, **Figs. 2, 5**) also contains pale yellow or bicolored forms (**Tables 1-2,** ns. 17, *N. sylvestris albidus*, 34, *N. sylvestris totus albus*, and 70, *N. sylvestris pallidus*). Thus it appears that white, pale yellow, and bicolor forms are closely related and

Fig. 3 (above) Illustrations of Clusters 3, 4, 6 and 8. Images from Besler (1613). With kind permission by Taschen (©).

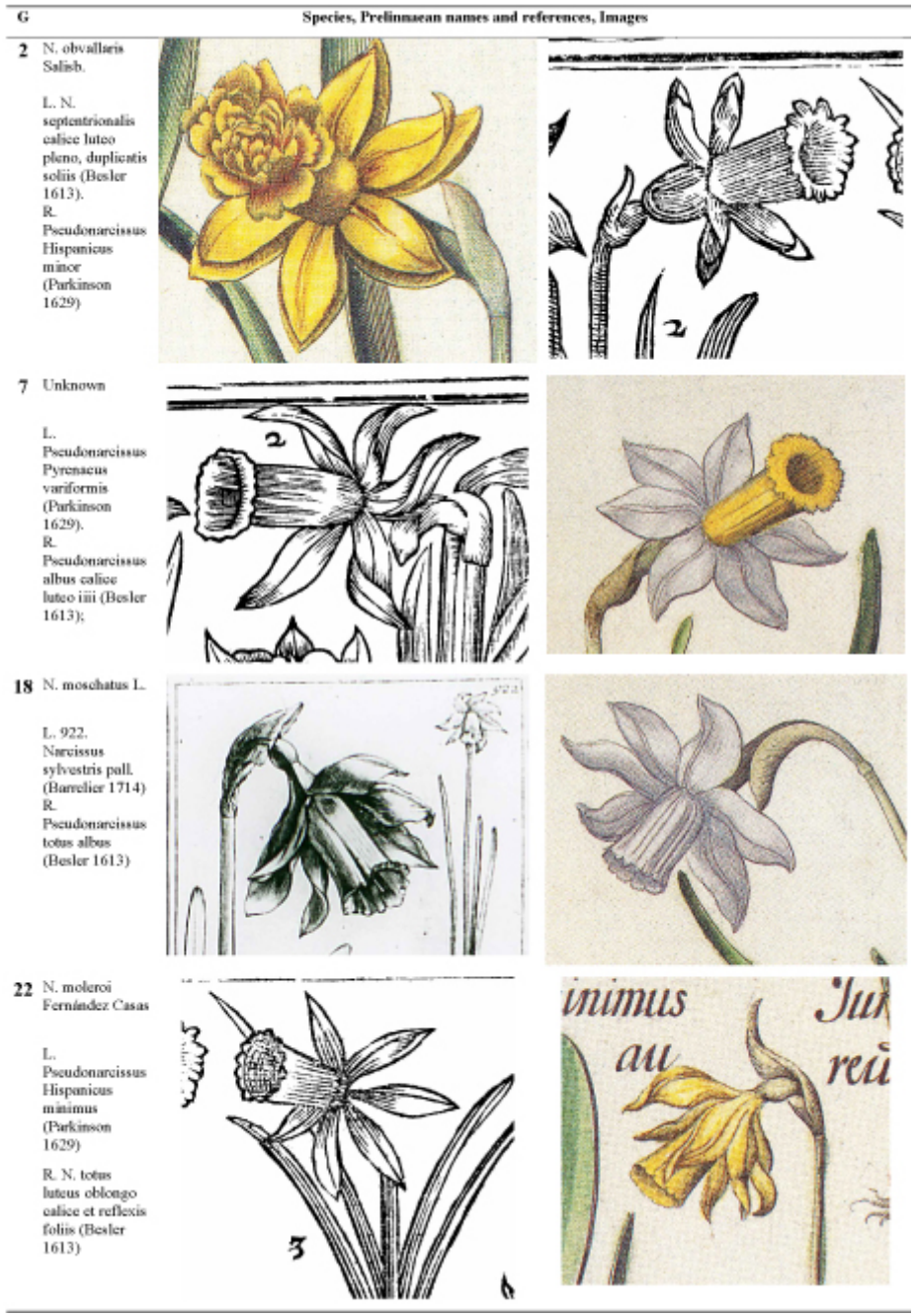

Fig. 4 (right) Illustrations of Clusters 2, 7, 18 and 22. Images from Besler (1613), Parkinson (1629) and Barrelier (1714). With kind permission by Taschen (©), and IDC (©).

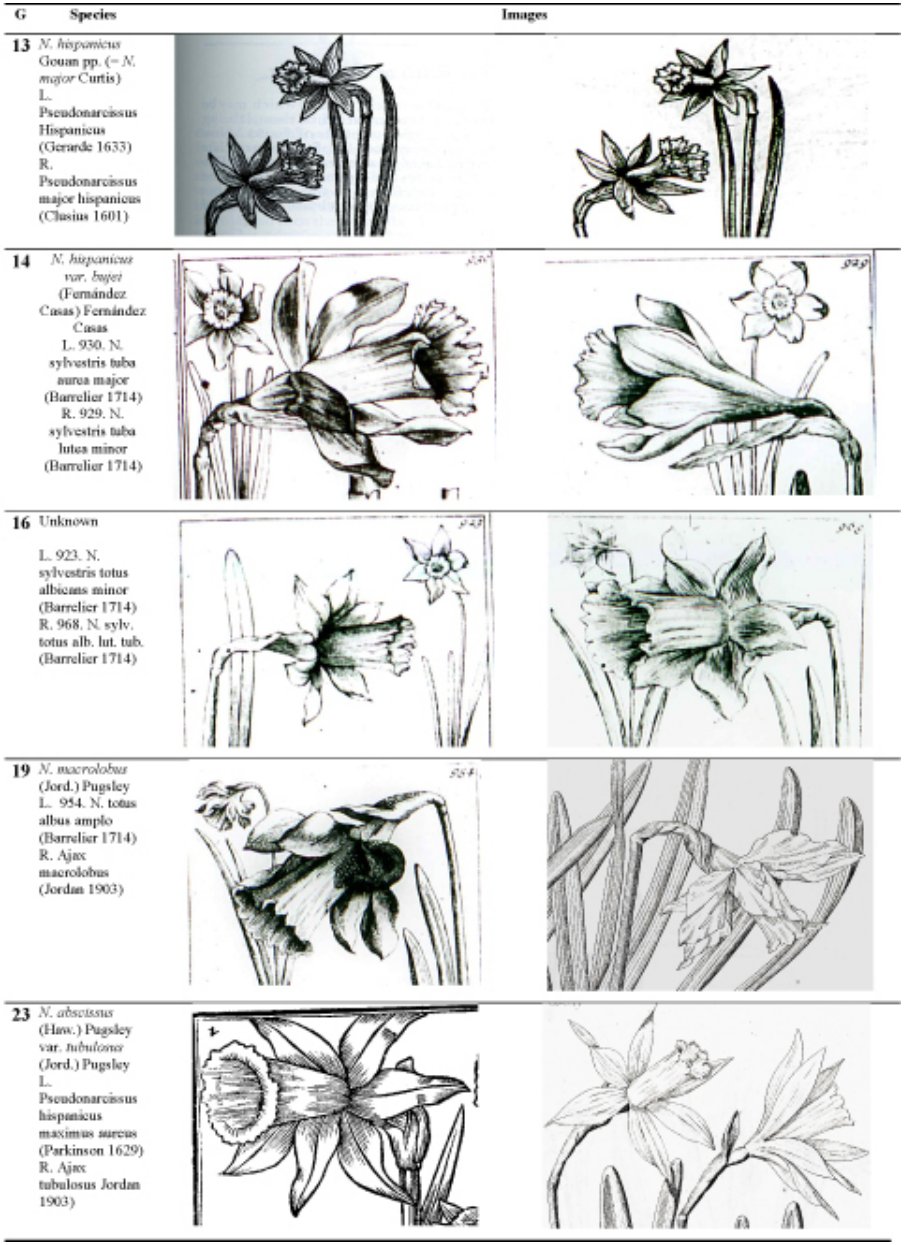

Fig. 5 Illustrations of Clusters 13, 14, 16 and 23. Images from Clusius (1601), Gerarde (1633), Barrelier (1714) and Jordan (1903). With kind permission by IDC (©).

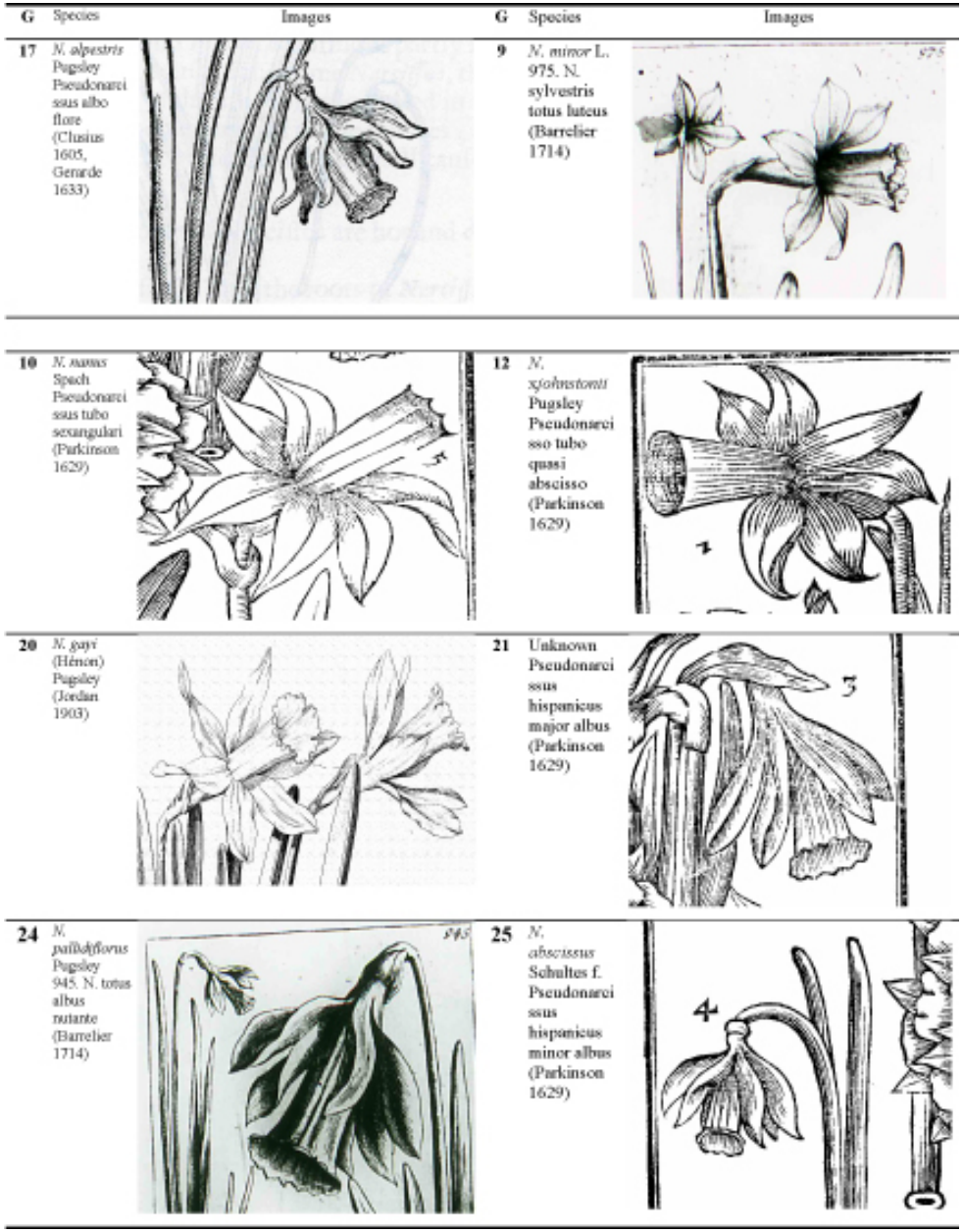

Fig. 6 Illustrations of Clusters 9, 10, 12, 17, 20, 21, 24 and 25. Images from Clusius (1601), Parkinson (1629), Barrelier (1714) and Jordan (1903). With kind permission by IDC (©).

Table 1 Characters available from the early iconography (Brunfels 1530, Clusius, 1601 1605, Besler 1613, Parkinson 1629, Gerarde 1633, Barrelier 1714, Tabernaemontanus 1731, Blunt and Stearn 1994). From **Rivera *et al.*** 2003 *Scientia Horticulturae* **98**, 307-330, ©2003, with kind permission from Elsevier Science SV.

N.	Icones	Lf.	Sc.	Sp.	Fl.	Pos.	Tp.	Tr.	T. l/w	Cl. / Tl.	A. / B.	Me.	Ms.	Fc.
3	Daffodil (Weiditz painting of 1529)	3 (1)	Md. (3)	Sh. (6)	1 (6)	Se. (0)	Pat. (2)	Tw. (2)	1,7-2,1 (2)	0,8-1,1 (0)	1,3-1,6 (2)	+ (4)	Lo. (0)	Py. (2)
4	Daffodil (Weiditz painting of 1529)	3 (1)	Md. (3)	Sh. (6)	1 (6)	Se. (0)	Pat. (2)	Tw. (2)	1,7-2,1 (2)	0,8-1,1 (0)	1,6-1,9 (3)	+ (4)	Lo. (0)	Bi. (4)
80	*N. albus nutante* (Barrelier 1714) 946.	3 (1)	Dw (6)	Sh. (6)	1 (6)	Pen. (6)	Se. (0)	Tw. (2)	2,9-3,3 (5)	2,0-2,3 (4)	1,3-1,6 (2)	+/- (2)	To. (2)	W. (6)
31	*N. septentrionalis calice luteo pleno, duplicatis soliis* (*) (Besler 1613)	3-5 (3)	Md. (3)	Sh. (6)	1 (6)	Hor. (3)	Pat. (2)	Not. (0)	1,3-1,7 (1)	1,4-1,7 (2)	1,0-1,3 (1)	+ (4)	Lo. (0)	Y. (0)
39	*N. septentrionalis calice pleno luteo oris incisis* (*) (Besler 1613)	4 (3)	Dw. (6)	Sh. (6)	1 (6)	Se. (0)	Pat. (2)	Tw. (2)	1,7-2,1 (2)	1,4-1,7 (2)	1,0-1,3 (1)	+ (4)	Lo. (0)	Y. (0)
73	*N. septentrionalis flore pleno luteo* (*) (Besler 1613)	2-4 (2)	Md. (3)	Sh. (6)	1 (6)	Se. (0)	Pat. (2)	Not. (0)	1,7-2,1 (2)	1,7-2,1 (2)	1,3-1,6 (2)	+/- (2)	Lo. (0)	Y. (0)
17	*N. sylvestris albidus tubo luteo minor* 924. (Barrelier 1714)	1-2 (0)	Dw. (6)	Sh. (6)	1 (6)	Hor. (3)	Pat. (2)	Not. (0)	1,7-2,1 (2)	1,1-1,4 (1)	1,3-1,6 (2)	+/- (2)	To. (2)	Bi. (4)
33	*N. sylvestris albus* 921. (Barrelier 1714)	2-3 (1)	Dw. (6)	Md. (3)	1 (6)	Pen. (6)	Pat. (2)	Not. (0)	1,3-1,7 (1)	1,4-1,7 (2)	1,3-1,6 (2)	+/- (2)	Cre. (4)	W. (6)
77	*N. sylvestris pallidus* 922. (Barrelier 1714)	2-3 (1)	Md. (3)	Sh. (6)	1 (6)	Pen. (6)	Se. (0)	Tw. (2)	2,1-2,5 (3)	2,0-2,3 (4)	1,0-1,3 (1)	+ (4)	To. (2)	Py. (2)
70	*N. sylvestris pallidus tuba aurea* 976. (Barrelier 1714)	2 (0)	Dw. (6)	Sh. (6)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	2,9-3,3 (5)	1,7-2,0 (3)	1,0-1,3 (1)	+/- (2)	Lo. (2)	Bi. (4)
45	*N. sylvestris totus albicans minor* 923. (Barrelier 1714)	1-3 (1)	Dw. (6)	Sh. (6)	1 (6)	Hor. (3)	Pat. (2)	Not. (0)	2,1-2,5 (3)	1,4-1,7 (2)	1,3-1,6 (2)	- (0)	Cre. (4)	W. (6)
34	*N. sylvestris totus albus luteo tubo* 968. (Barrelier 1714)	3-4 (3)	Md. (3)	Md. (3)	1 (6)	Hor. (3)	Pat. (2)	Not. (0)	1,3-1,7 (1)	1,4-1,7 (2)	1,3-1,6 (2)	+/- (2)	To. (2)	Bi. (4)
18	*N. sylvestris totus luteus* 975. (Barrelier 1714)	2 (0)	Dw. (6)	Md. (3)	1 (6)	Hor. (3)	Pat. (2)	Not. (0)	1,7-2,1 (2)	1,1-1,4 (1)	1,3-1,6 (2)	+/- (2)	Lo. (2)	Y. (0)
67	*N. sylvestris tuba aurea major* 930. (Barrelier 1714)	2-3 (1)	Md. (3)	Long (0)	1 (6)	Hor. (3)	Se. (0)	Tw. (2)	2,1-2,5 (3)	1,7-2,0 (3)	1,0-1,3 (1)	+ (4)	Lo. (2)	Py. (2)
83	*N. sylvestris tuba lutea minor* 929. (Barrelier 1714)	1-3 (1)	Dw. (6)	Long (0)	1 (6)	Hor. (3)	Se. (0)	Not. (0)	2,1-2,5 (3)	2,3-2,6 (5)	1,3-1,6 (2)	+ (4)	To. (2)	Py. (2)
66	*N. totus albus amplo* 954. (Barrelier 1714)	2-3 (1)	Md. (3)	Md. (3)	1 (6)	Pen. (6)	Se. (0)	Tw. (2)	2,1-2,5 (3)	1,7-2,0 (3)	1,6-1,9 (3)	+/- (2)	To. (2)	W. (6)
44	*N. totus albus nutans* 953. (Barrelier 1714)	2-3 (1)	Md. (3)	Md. (3)	1 (6)	Pen. (6)	Pat. (2)	Not. (0)	2,1-2,5 (3)	1,4-1,7 (2)	1,6-1,9 (3)	+ (4)	Lo. (0)	W. (6)
96	*N. totus albus nutante* 945. (Barrelier 1714)	3 (1)	Md. (3)	Sh. (6)	1 (6)	Pen. (6)	Se. (0)	Tw. (2)	2,9-3,3 (5)	3,2-3,5 (8)	1,0-1,3 (1)	+/- (2)	Cre. (4)	W. (6)
2	*N. totus luteus montanus maior i* (Besler 1613).	5 (4)	Md. (3)	Md. (3)	1 (6)	Se. (0)	Pat. (2)	Not (0)	1,3-1,7 (1)	0,8-1,1 (0)	1,0-1,3 (1)	+ (4)	Lo. (0)	Py. (2)
10	*N. totus luteus montanus, minimus ii* (Besler 1613)	5 (4)	Dw. (6)	Md. (3)	1 (6)	Hor. (3)	Pat. (2)	Not (0)	2,5-2,9 (4)	0,8-1,1 (0)	1,0-1,3 (1)	+ (4)	Lo. (0)	Py. (2)
99	*N. totus luteus oblongo calice et reflexis foliis* (Besler 1613)	7 (6)	Dw. (6)	Md. (3)	1 (6)	Pen. (6)	Se. (0)	Tw. (2)	2,5-2,9 (4)	4,7-5,3 (9)	1,0-1,3 (1)	- (0)	To. (2)	Py. (2)
14	*N. totus sulphureus* 967. (Barrelier 1714)	3 (1)	Md. (3)	Md. (3)	1 (6)	Se. (0)	Pat. (2)	Not. (0)	1,3-1,7 (1)	1,1-1,4 (1)	1,0-1,3 (1)	+/- (2)	Cre. (4)	Y. (0)
41	*Pseudo N. aureus praecox* (Besler 1613)	6 (6)	Md. (3)	Sh. (6)	1 (6)	Se. (0)	Se. (0)	Tw. (2)	2,1-2,5 (3)	1,4-1,7 (2)	1,3-1,6 (2)	+/- (2)	Lo. (0)	Y. (0)
19	*Pseudo N. luteus iii* (Besler 1613)	4 (3)	Md. (3)	Sh. (6)	1 (6)	Se. (0)	Se. (0)	Tw. (2)	2,1-2,5 (3)	1,1-1,4 (1)	1,0-1,3 (1)	+ (4)	Lo. (0)	Py. (2)
23	*Pseudo N. minor luteus repens iv* (Besler 1613)	2 (0)	Dw. (6)	Long (0)	1 (6)	Se. (0)	Pat. (2)	Tw. (2)	2,5-2,9 (4)	1,1-1,4 (1)	1,3-1,6 (2)	+ (4)	Lo. (0)	Py. (2)
27	*Pseudo N. simplex Belga* (Besler 1613)	7 (6)	Md. (3)	Sh. (6)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	1,3-1,7 (1)	1,4-1,7 (2)	1,0-1,3 (1)	+/- (2)	Lo. (0)	Py. (0)
40	*Pseudo N.tubo quasi abscisso* (Parkinson 1629)	3-4 (3)	Md. (3)	Sh. (6)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	1,7-2,1 (2)	1,4-1,7 (2)	1,6-1,9 (3)	- (0)	Ab. (6)	Y. (0)
81	*Pseudo N. albo flore* (Clusius 1605)	3 (1)	Dw. (6)	Sh. (6)	1 (6)	Pen. (6)	Se. (0)	Tw. (2)	2,9-3,3 (5)	2,0-2,3 (4)	1,0-1,3 (1)	+/- (2)	Cre. (4)	W. (6)
78	*Pseudo N. albo flore* (Gerarde 1633)	3 (1)	Dw. (6)	Sh. (6)	1 (6)	Pen. (6)	Se. (0)	Tw. (2)	2,5-2,9 (4)	2,0-2,3 (4)	0,7-1,0 (0)	+/- (2)	Cre. (4)	W. (6)
58	*Pseudo N. albus calice luteo iii* (Besler 1613)	5-7 (6)	Md. (3)	Sh. (6)	1 (6)	Se. (0)	Pat. (2)	Tw. (2)	1,7-2,1 (2)	1,7-2,0 (3)	1,0-1,3 (1)	+ (4)	To. (2)	Bi. (4)
16	*Pseudo N. anglicus* (Gerarde 1633)	5 (4)	Md. (3)	Sh. (6)	1 (6)	Hor. (3)	Pat. (2)	Not (0)	1,7-2,1 (2)	1,1-1,4 (1)	2,7 (6)	+ (4)	Lo. (0)	Y. (0)
69	*Pseudo N. hispanicus* (Gerarde 1633)	2 (0)	Md. (3)	Long (0)	1 (6)	Hor. (3)	Pat. (2)	Not (0)	2,5-2,9 (4)	1,7-2,0 (3)	1,6-1,9 (3)	+ (4)	Lo. (0)	Y. (0)
72	*Pseudo N. hispanicus major albus* (Parkinson 1629)	6 (6)	Lg. (0)	Long (0)	1 (6)	Pen. (6)	Se. (0)	Not (0)	3,3-3,7 (6)	1,7-2,0 (3)	1,0-1,3 (1)	+/- (2)	To. (2)	W. (6)
94	*Pseudo N. hispanicus maximus aureus* (Parkinson, 1629)	6-7 (6)	Lg. (0)	Sh. (6)	1 (6)	Hor. (3)	Pat. (2)	Not (0)	2,1-2,5 (3)	3,2-3,5 (8)	1,3-1,6 (2)	+/- (2)	To. (0)	Y. (0)
84	*Pseudo N. hispanicus minimus* (Parkinson 1629)	4 (3)	Dw. (6)	Sh. (6)	1 (6)	Hor. (3)	Pat. (2)	Not (0)	2,9-3,3 (5)	2,3-2,6 (5)	1,0-1,3 (1)	+/- (2)	To. (2)	Y. (0)
48	*Pseudo N. hispanicus minor* (Parkinson 1629)	3 (1)	Dw. (6)	Sh. (6)	1 (6)	Se. (0)	Pat. (2)	Tw. (2)	2,5-2,9 (4)	1,4-1,7 (2)	1,3-1,6 (2)	+ (4)	Lo. (0)	Y. (0)
97	*Pseudo N. hispanicus minor albus* (Parkinson 1629)	2 (0)	Dw. (6)	Sh. (6)	1 (6)	Pen. (6)	Se. (0)	Tw. (2)	3,7-4,1 (7)	3,2-3,5 (8)	1,0-1,3 (1)	+/- (2)	To. (0)	W. (6)
75	*Pseudo N. luteus* (Tabernaemontanus 1731)	3-5 (3)	Md. (3)	Long (0)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	1,7-2,1 (2)	2,0-2,3 (4)	1,3-1,6 (2)	+ (4)	Cre. (4)	Y. (0)
7	*Pseudo N. luteus gemino flore* (Tabernaemontanus 1731)	2 (0)	Dw.? (6)	Long (0)	2 (3)	Se. (0)	Se. (0)	Not (0)	2,1-2,5 (3)	0,8-1,1 (0)	1,3-1,6 (2)	+/- (2)	Lo. (0)	Y. (0)
46	*Pseudo N. luteus simplici flore* (Tabernaemontanus 1731)	2 (0)	Md. (3)	Md. (3)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	2,5-2,9 (4)	1,4-1,7 (2)	1,0-1,3 (1)	+ (4)	Lo. (0)	Y. (0)
71	*Pseudo N. major hispanicus* (Clusius 1601)	2 (0)	Lg. (0)	Long. (0)	1 (6)	Hor. (3)	Pat. (2)	Not. (0)	2,9-3,3 (5)	1,7-2,0 (3)	1,6-1,9 (3)	+ (4)	Lo. (0)	Y. (0)
93	*Pseudo N. minor Hispanicus* (Clusius 1601)	7 (6)	Dw. (6)	Sh. (6)	1 (6)	Pen. (6)	Pat. (2)	Not. (0)	1,7-2,1 (2)	2,9-3,2 (7)	1,3-1,6 (2)	+ (4)	To. (2)	Y. (0)
92	*Pseudo N. minor Hispanicus* (Gerarde, 1633)	7 (6)	Md. (3)	Sh. (6)	1 (6)	Pen. (6)	Pat. (2)	Not (0)	1,7-2,1 (2)	2,9-3,2 (7)	1,0-1,3 (1)	+ (4)	To. (2)	Y. (0)
21	*Pseudo N. Pyrenaeus variformis* (Parkinson 1629)	6 (6)	Md. (3)	Sh. (6)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	2,5-2,9 (4)	1,1-1,4 (1)	1,0-1,3 (1)	+/- (2)	To. (2)	Bi. (4)
59	*Pseudo N. totus albus* (Besler 1613)	6 (6)	Md. (3)	Sh. (6)	1 (6)	Pen. (6)	Pat. (2)	Tw. (2)	1,7-2,1 (2)	1,7-2,0 (3)	1,3-1,6 (2)	- (0)	To. (2)	W. (6)
24	*Pseudo N. triplici tubo* (*) (Clusius 1605)	4 (3)	Dw. (6)	Sh. (6)	1 (6)	Pen. (6)	Pat. (2)	Tw. (2)	2,9-3,3 (5)	1,1-1,4 (1)	1,3-1,6 (2)	+ (4)	To. (2)	Py. (2)
63	*Pseudo N. tubo sexangulari* (Parkinson 1629)	2-3 (1)	Md. (3)	Md. (3)	1 (6)	Se. (0)	Pat. (2)	Tw. (2)	2,1-2,5 (3)	1,7-2,0 (3)	1,0-1,3 (1)	- (0)	To. (2)	Y. (0)

Note: Lf. Leaves per bulb; Sc. Scape length; Fl. Flowers per bulb; Sp. Dimensions of the spatha; Pos. Position of flowers; Tp. Tepals position; Tr. Tepals rotation; T. l/w: Quotient tepal length / width; Cl./Tl. Quotient Cup length / tube length; A/ B. Quotient apical diameter / basal diameter of the Cup; Me. Degree of margin expansion at the Cup apex; Ms. Cup apex margin shape; Fc. Flower colour. Pat. Patent; Se. Suberect; To. Toothed; Lo. Lobed; Cre. Crenulate; Y. Yellow; Py. Pale yellow; W. White; Bi. Bicolour. Lg. Lg.; Md. Medium; Dw. Dwarf; Sh. Short; Hor. Horizontal; Pen. Pendent; Tw. Twisted; Not. Not twisted. Between brackets are shown the values used for the matrix. Double flowered forms are represented by an asterisk (*) after the icon name.

presumably are derived by single mutations.

The well characterized cluster, around *N. alpestris* Pugsley (Group 17, **Fig. 6**) includes several types with white pendent flowers (**Tables 1-2**, ns. 78, *Pseudonarcissus albo flore,* 80, *N. albus nutante* and 81, *Pseudonarcissus albo flore*). Presumably, these are different interpretations by different artists of the same taxon or cultivar.

A third group of white flowered types (**Tables 1-2**, ns. 96, *N. totus albus* and 97, *Pseudonarcissus hispanicus* Table 1) is related to pale yellow or bicolor flowered species, e.g., *N. pallidiflorus* Pugsley or *N. abscissus* (Haw.) Schultes f. included in groups 24 and 25 (**Fig. 6**), respectively.

After the agglomerative analysis of similarities between the 101 illustrations and taxa, it appears that the characters involved in flower pigmentation evolved independently from other morphological characters. It obviously occurred in different places and at different times (Rivera *et al*. 2003). Thus all flower group based in color, even whites, is polyphyletic. This may be relevant for taxonomic purposes, since flower color was used by Haworth (1831) and Pugsley (1933) in the systematics of subgenus *Ajax.*

4.3. Relationships between Double forms and wild populations

Double types may have been produced by the duplication of the number of tepals, by changes involving the Cup, or by changes in the whole

flower. They are extremely rare in Spain and Portugal; whereas, in Italy (Lugano), Turkey (Belgrat forest), and Britain (Tenby), doubles are frequently found. The prevalence of doubles in a district was interpreted by Pugsley (1933) as an introduction or relict of former cultivation and not indigenous. A summary of the origin of primitive doubles is presented in **Table 3**.

Double yellow trumpet daffodils were grown in gardens as early as in 1597 and Parkinson indicated several doubles (Parkinson 1629, Coats 1956). From the 16th to the 19th centuries the doubles were primarily imported to the British Isles from France and the Netherlands. They were obtained as seeds in these countries (Miller 1754). Many of them were sterile, presumably due to their hybrid origin. This supposed hybrid origin is sometimes not properly referred to in English by adding "bastard" to the common name.

The 'Van Sion' daffodil, known also as *Ajax telamonius* β *grandiplenus* Haw., first flowered in England in 1620. It is now naturalised in many places in Britain and on the Continent (Coats 1956). A double daffodil is also naturalised near Istanbul in the Belgrat forest, and is presumed to have escaped from cultivation of Spanish daffodils (Baytop and Mathew 1984).

Several primitive double forms were included in the analysis by Rivera *et al*. (2003). The *Pseudonarcissus triplici tubo* described by Clusius (1605) appear to be related to *N. moschatus* L (Group 18, **Fig. 4**). The different double types described by Besler (1613) and Barrelier (1714) (**Tables 1-2,** ns. 31, *N. septentrionalis calyce luteo*, 39, *N. septentrionalis calyce pleno* and 77, *N. sylvestris pallidus*) are related to *N. obvallaris* Salisb (Group 2, **Table 2, Fig. 2**). 'Van Sion' is very similar to the *N. totus sulphureus* illustrated by Barrelier (1714). In addition, it appears related to *N. hispanicus* Gouan, and showing some resemblance to 'King Alfred' (Group 3 in **Fig. 2, Table 2**).

4.4. Polyploids

Practically almost all wild taxa are diploid, with 14 chromosomes. Amongst the cultivated forms, *N. hispanicus* Gouan and *N. tortuosus* Haw. are triploid and those under *N. bicolor* are tetraploid. Polyploidy is extremely rare in wild populations, an exception is *N. leonensis,* a natural hexaploid. In contrast, polyploidy is relatively frequent in cultivated forms (Kington 2002).

The complete linkage analysis showed a high correlation (over 95%) between the wild hexaploid *N. leonensis* and 'Empress' (Group 5, **Fig. 2, Table 2**).

A hexaploid examined by Wylie (1952) was shown to have smaller flowers than its tetraploid parents. Thus it appears that the optimum level of ploidy in subgenus *Ajax* for landscape usage is the tetraploid. A primary example is the tetraploid 'King Alfred', which was obtained by John Kendall in 1899 (Bahnert, 1992). This cultivar is closely related and presumably derived from *N. hispanicus* Gouan, displaying a close resemblance in the analysis (over 95%) (Group 3, **Fig. 2, Table 2**).

4.5. Hybrids

Hybridization has played a relevant role in development of cultivated daffodils since the second half of the 19th century. It is not clear, however, that this occurred in early utilization of daffodils in the British Isles and Continental Europe. Most of these bulbs were imported from Spain and collected from wild populations (Clusius 1601, Parkinson 1629, Miller 1754). According to Pugsley (1933), the old types were not artificially created hybrids. It appears likely that the primitive horticultural hybrid forms were originally imported wild plants. The repertory of species employed for obtaining the first commercial hybrid cultivars (19th century) was low: Species such as *N. hispanicus* Gouan (including *N. major* Curtis), *N. moschatus* L. and *N. alpestris* Pugsley were the more widely used.

Intersubgeneric hybrids involving subgenera *Ajax* and *Narcissi* are relatively frequent in the wild and can be also obtained artificially. *N.* x*bernardii* DC is a fertile diploid hybrid species which occurs in the Pyrenees in zones of overlapping distribution areas of *N. hispanicus* Gouan and *N. poeticus* L. These pink flowers come from the red pigment in *N. poeticus* (Wylie 1952, Bahnert 1992). *N.* x*incomparabilis* Miller of garden origin has been described as being very similar to the former hybrid. It is considered to be a hybrid between *N. major* Curtis and *N. poeticus* L. Many pale yellow flowered types were obtained by Edward Leeds, in the 1840s, by crossing *N.* x *incomparabilis* with white flowered wild species of subgenus *Ajax* Spach. *N.* x*boutignyanus* Philippe from the Pyrenees is a hybrid between *N. moschatus* L. and *N. poeticus* L. (Bahnert 1992).

Hybrids between species of subgenus *Ajax* and section *Jonquilla* are not common and not as fertile as the former group. *N.* x*odorus* L. is a completely sterile diploid and unknown in the wild. Presumably, it originated in cultivation. It is intermediate between *N. pseudonarcissus* aggr. and *N. jonquilla* (Wylie 1952).

Hybridization between species of subgenus *Ajax* and the section *Ganymedes* is relatively frequent. *N.* x *johnstonii* Pugsley, a triploid, was discovered in 1885 in Portugal and later in Spain. Morphologically, the species was considered to be a natural cross of *N. triandrus* L. and *N. pseudonarcissus* L. Engleheart (1890) obtained similar forms by crossing the triploid trumpet daffodil 'Emperor' with *N. triandrus*. In the 1890s, thousands of bulbs of this species were imported in England by Peter Barr. These were collected from the wild populations in Northern Spain and Portugal, transported through Portugal and subsequently, sold under the name of 'Queen of Spain' (Wylie 1952, Bahnert 1992).

The complete linkage analysis (Rivera *et al*. 2003) showed similarities of the nothospecies *N.* x *johnstonii* Pugsley (*N. pseudonarcissus* x *N. triandrus* ssp. *pallidulus*) with *N.* x *susannae* Fernández Casas (*N. cantabricus* x *N. triandrus* ssp. *pallidulus*) and with the illustration of Parkinson (1629) under the name of *Pseudonarcisso tubo quasi absciso* (Group 12 in **Table 2, Fig. 6**). Thus, similar hybridizations may have occurred in different localities and at different times. Hybridization between Sect. *Bulbocodium* or Subgenus *Ajax* with sect. *Ganymedes* produces similarities in the hybrid descent.

Generally, hybrids of section *Cyclaminopsis* Pugsley are characterized by the reflexed tepals. By crossing *N. cyclamineus* DC. with the diploid *N. asturiensis* (Henon) Pugsley, it was obtained the diploid 'Minicycla'. 'February Gold' and 'Bartley' are triploids and were obtained from the crossing of *N. cyclamineus* with tetraploid yellow trumpet daffodils. This species has been also crossed with *N. tazetta* or *N. poeticus* groups (Wylie 1952). We did not have material of this group when we carried out our analyses.

4.6. Trumpet daffodils

Division 1 of cultivated *Narcissus*, the Trumpet (RHS 2000 2005), comprises daffodils with one flower per stem, with a cup (Cup) that is long as or longer than the perianth segments. These are derived from members of subgenus *Ajax* Spach. By the 1860s, triploid clones appeared independently among the seedlings of three English breeders (Backhouse, Leeds, and Horsefield). Their introduction into extensive cultivation

Table 2 Relationships between wild and cultivated daffodils of *Narcissus* subgenus *Ajax* Spach., as demonstrated by the comparative study of characters available from the illustrations of the 16th, 17th and 18th centuries and herbarium specimens. Results from the CL and UPGMA analysis from **Rivera *et al.*** 2003 *Scientia Horticulturae* **98**, 307-330, ©2003, with kind permission from Elsevier Science SV.

Group	Key Species	Prelinnaean names and references	Related species and cultivars	Origin
1	*N. jacetanus* Fernández Casas ssp. *vasconicus* (Fernández Casas) Fernández Casas	-	-	N Spain
2	*N. obvallaris* Salisb.	*N. septentrionalis calice luteo pleno, duplicatis soliis* (Besler 1613), *N. septentrionalis flore pleno luteo* (Besler 1613), *N. septentrionalis calice pleno luteo oris incisis* (Besler 1613), *Pseudonarcissus hispanicus minor* (Parkinson 1629)	-	Britain, Spain
3	*N. hispanicus* Gouan	*N. totus luteus montanus maior i* (Besler 1613), 967. *N. totus sulphureus* (Barrelier 1714)	'King Alfred' and 'Van Sion' (Bahnert 1992)	Pyrenees, S France
4	*N. nobilis* (Haw.) Schultes fil.	Daffodils (Weiditz painting of 1529), *Pseudo N. luteus iii* (Besler 1613)	-	NW Spain, Pyrenees
5	N. *albescens* (Haw.) Pugsley	-	*N. pseudonarcissus* L. var. *platylobus* (Jord.) Pugsley, *N. pseudonarcissus* L. var. *porrigens* (Jord.) Pugsley, *N. pseudonarcissus* L. var. *festinus* (Jord.) Pugsley; *N. pseudonarcissus* L. var. *montinus* (Jord.) Pugsley, *N. tortuosus* Haw.	-
6	*N. confusus* Pugsley	*Pseudonarcissus Anglicus* (Gerarde 1633), *N. totus luteus montanus*, *minimus ii* (Besler 1613)	*N. asturiensis* (Jord.) Pugsley	Central and N Iberian Peninsula
7	-	*Pseudonarcissus Pyrenaeus variformis* (Parkinson 1629), *Pseudonarcissus albus calice luteo iii* (Besler 1613), *Pseudo N. simplex Belga* (Besler 1613), *Pseudo N. aureus praecox* (Besler 1613)	-	?
8	*N. provincialis* Pugsley	*Pseudonarcissus luteus gemino flore* (Tabernaemontanus 1731), *Pseudo N. minor luteus repens iv* (Besler 1613)	*N. jacetanus* Fernández Casas; *N. genesi-lopezii* Fernández Casas	Pyrenees
9	*N. minor* L.	975. *N. sylvestris totus luteus* (Barrelier 1714)	*N. fontqueri* Fernández Casas and Rivas Ponce; *N. segurensis* Ríos and aliis, *N. alcaracensis* Ríos and aliis, *N. primigenius* (Fernández Suarez ex Laínz) Fernández Casas and Laínz, *N. eugeniae* Fernández Casas, *N. portensis* Pugsley	SE, Central and W Iberian Peninsula
10	*N. nanus* Spach	*Pseudonarcissus tubo sexangulari* (Parkinson 1629)	*N. radinganorum* Fernández Casas, *N. calcicarpetanus* Fernández Casas, *N. segurensis* x *N. yepesii*	Central and E Spain
11	*N. nevadensis* Pugsley	-	*N. longispathus* Pugsley	SE Spain
12	*N.* x*johnstonii* Pugsley	*Pseudonarcisso tubo quasi abscisso* (Parkinson 1629)	*N.* x*munyozii-garmendiae* Fernández Casas	W Spain, Portugal
13	*N. hispanicus* Gouan pp. (= *N. major* Curtis)	*Pseudonarcissus Hispanicus* (Gerarde 1633), *Pseudonarcissus major hispanicus* (Clusius 1601)	'Emperor' (Burbridge 1875)	Not known
14	*N. hispanicus var. bujei* (Fernández Casas) Fernández Casas	*Pseudonarcissus luteus simplici flore* (Tabernaemontanus 1731), 930. *N. sylvestris tuba aurea major* (Barrelier 1714), *Pseudonarcissus luteus* (Tabernaemontanus 1731), 929. *N. sylvestris tuba lutea minor* (Barrelier 1714)	*N. pumilus* Salisb; *N. hispanicus* Gouan var. *concolor*(Jord.) Pugsley, *N. yepesii* Ríos *et al.*	S and SW Iberian Peninsula
15	*N. nobilis* (Haw.) Schult. f. var. *leonensis* (Pugsley) A. Fernandes	-	'Empress' (Burbridge 1875); *N. bicolor* L.	N Spain, Pyrenees
16	-	924. *N. sylvestris alb. tub. lut. minor* (Barrelier 1714), 923. *N. sylvestris totus albicans minor* (Barrelier 1714), 976. *N. sylvestris pallidus tuba aurea* (Barrelier 1714), 921. *N. sylvestris albus* (Barrelier 1714), 968. *N. sylv. totus alb. lut. tub.* (Barrelier 1714)	-	-
17	*N. alpestris* Pugsley	946. *N. albus nutante* (Barrelier 1714), *Pseudonarcissus albo flore* (Gerarde 1633), *Pseudonarcissus albo flore* (Clusius 1605)	-	Pyrenees
18	*N. moschatus* L. (Burbridge, 1875)	*Pseudonarcissus triplici tubo* (Clusius 1605), 922. *Narcissus sylvestris pall.* (Barrelier 1714), *Pseudonarcissus totus albus* (Besler 1613)	-	Pyrenees
19	*N. macrolobus* (Jord.) Pugsley	953. *N. totus albus nutans* (Barrelier 1714), 954. *N. totus albus amplo* (Barrelier 1714)	*N. yepesii* Ríos et aliis	Pyrenees, SE Spain
20	*N. gayi* (Hénon) Pugsley	-	*N. gayi (Henon) Pugsley var. praelongus* (Jord.) Pugsley, *N. abscissus* (Haw.) Pugsley var. *serotinus* (Jord.) Pugsley;	Pyrenees?
21	-	*Pseudonarcissus hispanicus major albus* (Parkinson 1629)	-	Pyrenees?
22	*N. moleroi* Fernández Casas	*Pseudonarcissus Hispanicus minimus* (Parkinson 1629), *Pseudonarcissus minor Hispanicus* (Gerarde 1633), *Pseudonarcissus minor Hispanicus* (Clusius 1601), *N. totus luteus oblongo calice et reflexis foliis* (Besler 1613)	-	Pyrenees
23	*N. abscissus* (Haw.) Pugsley var. *tubulosus* (Jord.) Pugsley	*Pseudonarcissus hispanicus maximus aureus* (Parkinson 1629)	-	Pyrenees
24	*N. pallidiflorus* Pugsley	945. *N. totus albus nutante* (Barrelier 1714)	*N. parviflorus* (Jord.) Pugsley	Pyrenees
25	*N. abscissus* Schultes f.	*Pseudonarcissus hispanicus minor albus* (Parkinson 1629)	-	Pyrenees
26	*N. cyclamineus* DC.	-	-	NW Iberian Peninsula

was delayed until 1875, when Peter Barr bought these collections for commercial utilization.

Wylie (1952) suggested that in the origin of the Backhouse's trumpet varieties, e. g., 'Emperor' and 'Empress' an almost sterile triploid clone of the common tetraploid *N. bicolor* L was involved. The similarity analysis showed a very close relationship of 'Empress' with *N. nobilis* (Haw.) Schult. var. *leonensis* (Pugsley) A. Fernandes (a wild hexaploid) (Group 15). 'Emperor' is very similar to the Clusius' (1601) *Pseudonarcissus major hispanicus* and at a longer distance appears related to cultivated species like *N. hispanicus* Gouan pp. (= *N. major* Curtis) and wild Spanish endemics such as *N. yepesii* Ríos *et al*. or *N. hispanicus* var. *bujei* (Fernández Casas) Fernández Casas (Group 13 in **Table 2, Fig. 5**).

By the 1890s, several tetraploid clones had emerged. One of the first was 'King Alfred', which may have been obtained from a cross of 'Empress' (a triploid) with *Narcissus hispanicus* Gouan (also triploid) (Wylie 1952). The influence of *N. hispanicus* in 'King Alfred' is clearly supported by the analysis (Group 3 in **Table 2, Figs. 2, 3**), but 'Empress' appear grouped at a relatively long distance from this cluster (only a similarity of 85%) (Group 15 in **Table 2, Fig. 2**).

Table 3 Primitive names, illustrations and descriptions of double forms of *Narcissus* subgenus *Ajax* Spach. From **Rivera *et al.*** 2003 *Scientia Horticulturae* **98**, 307-330, ©2003, with kind permission from Elsevier Science SV.

English name	Prelinnaean names	Literature	Origin
Greatest double yellow bastard daffodil	*Pseudonarcissus maximus aureus flore pleno* (= *N. septentrionalis flore pleno luteo*)	Lobel 1570 1576, Clusius 1601, Besler 1613, Parkinson 1629	John Tradescant's collections, presumbaly from continental Europe
Mr. Wilmer's great double Daffodil = 'Van Sion'	*Pseudonarcissus aureus Anglicus maximus*	Parkinson 1629	Vincent Sion obtained flowering plants in 1620, seeds or bulbs provenient from J. de Franqueville's collection
Parkinsons daffodil	*Pseudonarcissus aureus Hispanicus flore pleno*	Parkinson 1629	John Parkinson obtained in 1618 this form from seeds from the common Spanish daffodil
Greater double French	*Pseudonarcissus Gallicus maior flore pleno*	Clusius 1605, Besler 1613, Parkinson 1629	Presumably from France or from Germany
Greater double German	*N. septentrionalis calice luteo pleno, duplicatis soliis*	Besler 1613	Germany?
Gerards double daffodil	*Pseudonarcissus Anglicus flore pleno*	Parkinson 1629	Gardens of West of England, Isle of Wight
Lesser French double bastard daffodil	*Pseudonarcissus Gallicus minor flore pleno*	Parkinson 1629, Gerarde 1633	From Orleans (France), it was distributed by J. Robin

4.7. Influence of cultivation on the conservation of wild populations

The introduction of bulbs from Spain into British, French, and Flemish (now Dutch and Belgian) gardens has been significant since the 16th century. Presumably, this commerce caused the extinction of many wild populations, especially those bulbs that were easily accessible to collectors. With a reduction of natural populations over the years, the commercial market declined. This reduction of imported bulbs was reflected in a decrease of taxonomic diversity in gardens. In addition, the lack of commercial bulb production contributed to this decline. In fact, this led to the extinction, as cultivated plants, of some taxa discovered and introduced during the 16th and 17th centuries by explorers and botanists (*N. cyclamineus, N.* x *johnstonii*). Many, however, were rediscovered during the revival of daffodil cultivation in the second half of the 19th century (Rivera *et al*. 2003).

Portugal (the Douro region, including Oporto) and France appear to have been the most important routes to introduce Spanish daffodils to Britain and the Netherlands in the 16th and 17th centuries and, again, in the 19th century (Parkinson 1629, Pugsley 1933, Bahnert 1992). By the 1890s, Peter Barr was involved in the annual massive importation of thousands of bulbs, collected from wild populations from Spain and Portugal (Bahnert 1992).

In addition, it appears that some taxa currently found exclusively in cultivation (viz. *N. abscissus* (Haw.) Schultes f. var. *tubulosus* (Jord.) Pugsley*, N. hispanicus* Gouan var. *concolor* (Jord.) Pugsley) are of an ancient origin. They may be interpreted as hybrids resulting by growing together compatible species, or as vegetatively propagated species which became extinct in their natural habitats. Other taxa only known in cultivation (*N. minor* L.*, N. nanus,* etc.) have wild relatives (*N. asturiensis, N. fontqueri, N. segurensis*). They may have originated through selection or hybridization, or both.

4.8. Chronology for Daffodil domestication

Daffodils of subgenus *Ajax* were domesticated during three different periods (Rivera *et al*. 2003). They are separated by a gap characterized by the loss of diversity in cultivation. The first period was the Middle Ages, the second was the 16th and 17th centuries and, the third was the second half of the 19th century. Several types of *N. pseudonarcissus* L.*, N. hispanicus* Gouan, and *N. pallidiflorus* Pugsley were grown in Central Europe at the beginning of the 16th Century. These may have evolved from the Spanish cultivated forms cited by the Arab writers and from wild European taxa (Medieval group of domesticated). Hence, the cultivation of primitive trumpet daffodils in British and Central European gardens, mainly those species which were not wild in Central Europe (*N. hispanicus* Gouan, *N. pallidiflorus* Pugsley), is connected with the early introduction of plants grown in medieval Spanish and Provençal gardens. This does not appear to be the case for cultivars related to *N. hispanicus* var. *bujei* (Fernández Casas) Fernández Casas.

Between 1590 and 1620 a large number of Spanish species were introduced into cultivation by Venerio, Tradescant, Clusius, Robin and associated plant collectors. From the descriptions, localities, and illustrations by Parkinson (1629), Tabernaemontanus (1731), Barrelier (1714), Clusius (1601 1605) and Besler (1613) we have identified Iberian Peninsula endemics as *N. abscissus, N. jacetanus, N. asturiensis, N. hispanicus, N. leonensis, N. pallidiflorus, N. nobilis* amongst the primitively cultivated plants.

Plants raised from seed, which occurred in the Netherlands and France, led to a substitution of wild forms by selected hybrid types. This occurred mainly during the second half of the 18th and 19th centuries.

A third important period for daffodil domestication in Europe was the last quarter of the 19th century. At this time, general introduction of recently described wild taxa was equal to the raising of new hybrid cultivars.

The early hybrid trumpet daffodil cultivars are related to well known taxa that had been in cultivation for a long time. They presumably were derived from *N. hispanicus* Gouan, and *N. major* Curtis. Alternatively, these are also similar to natural hexaploids like *N. leonensis,* whose similarity may be interpreted as derived from the higher level of ploidy of both species.

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