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Review

The origin of cultivation and wild ancestors of daffodils (*Narcissus* subgenus *Ajax*) (Amaryllidaceae) from an analysis of early illustrations

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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. Therefore, it was necessary to determine how their introduction into cultivation and domestication occurred. This study primarily utilised the comparison of data from Arab texts of agriculture, European Renaissance, and Prelinnaean ancient texts and illustrations, with the morphological characteristics of the currently known wild taxa from the territories of Spain and Portugal and primitive cultivars, which are the ancestors of the modern hybrid trumpet daffodils. 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 (CL) analysis and UPGMA analysis distinguished 26 different groups including wild; cultivated and wild; and cultivated daffodils. The cluster analysis demonstrated that *N. nevadensis* Pugsley and *N. longispathus* Pugsley, are closely related, and clearly distinct. They do not appear to have been in cultivation before the publication of their descriptions in the 20th century. 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.

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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. Thus any colour flower group, even whites, is polyphylethic.

Keywords: Narcissus; Daffodils; History; Domestication; Illustrations

1. Introduction

The "Ajax Group" (i.e. *Pseudonarcissus*) is one of the most important ancestors of modern daffodils cultivars. It has been estimated to be the parent of 99% of the yellow trumpet cultivars (Coats, 1956). In fact, it 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 (Kington, 2002), it is involved in the origin of Divisions 1, 2, 4, 6, and 11. The Iberian Peninsula is the centre of diversity for *Narcissus* subgenus *Ajax* Spach. Between 20 and 30 taxa have been described from this area, and belonging to this section (Andersen, 1988, 1990). Fernandes (1951) proposed *N. nevadensis* Pugsley as the ancestral species of subgenus *Ajax*, since the south-eastern Iberian Peninsula is the centre of origin for this group. After a detailed study of the systematics of *Narcissus* subgenus *Ajax* and the discovery of three new endemic species of daffodils (Rios et al., 1999) we felt it was necessary to determine how their introduction into cultivation and domestication occurred.

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.

The relationships among wild plants, domesticated plants, and primitive cultivars can be investigated through a cluster analysis of the characters available from figures or botanical illustrations. These exists with a minimum level of accuracy since the 16th century. The more primitive European herbals represented daffodils in an unrealistic and naive manner and are not suitable for analysis (Arber, 1988).

There appears to have been little attention given to daffodils in England until the 16th century (Coats, 1956). 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. Turner identified the Pliny's daffodil as the English common daffodil, without mentioning any other related taxon (Britten et al., 1965).

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) increased the lis of taxa, and detailed reviews were published by Haworth (1831) and Pugsley (1933). There are more recent reports by Cullen (1986), Webb (1980), and The International Daffodil Register (Kington, 2002). Barkham (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

This study primarily utilised the comparison of data from ancient texts and illustrations with the morphological characteristics of the currently known wild taxa and primitive cultivars. Initially we reviewed ancient Arab texts of agriculture, European Renaissance, and Prelinnaean herbals in order to obtain data on localities and dates of the early collections. These references provided illustrations of the plants and, although they were not detailed, they were accurate (Table 1). Wild materials from the territories of Spain and Portugal, which constitute the centre of origin and distribution of *Narcissus* subgenus *Ajax* Spach. were also examined. In addition, several primitive cultivars, which are the ancestors of the modern hybrid trumpet daffodils were analysed (Table 2).

The earliest iconography available (16th and 17th centuries) illustrates a relatively high degree of accuracy. The plants in these illustrations is accurate enough to make a comparison with data obtained from the study of wild and cultivated populations (Table 1). The illustrations by Weiditz (Blunt and Stearn, 1994; Brunfels, 1530; Clusius, 1601, 1605; Parkinson, 1629; Gerarde, 1633; Besler, 1613; Barrelier, 1714; Tabernaemontanus, 1731) have been analysed for 13 vegetative and floral characters and were compared with wild and actively cultivated taxa.

The selected set of characters was restricted to these that were easily detectable in high quality illustrations (Tables 1 and 2). The comparisons were made using a data matrix involving 101 OTUs and 13 characters (Tables 1 and 2). Cluster analyses used agglomerative clustering by distance optimisation (NCLAS) from the Sintax 5.0 package (Podani, 1991). Hierarchical classification was generated using combinatorial agglomerative methods characterised by the recurrence formula as follows: $d_{h,ij} = \alpha_i d_{hi} + \alpha_j d_{hj} + \beta d_{ij} + \gamma |d_{hi} d_{hj}|$; 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 analysed using two options. There were calculated complete linkage (CL) (farthest neighbour, euclidean distance) (Figs. 1 and 2) and unweighted group averages (average, euclidean distance) (UPGMA). Similarities above 90%, as calculated using CL, were interpreted in terms of close relationship and were used for interpreting the possible origin of cultivated daffodils.

3. Results

The tree resulting from the CL analysis (Fig. 1) and UPGMA analysis distinguished 26 different groups including wild; cultivated and wild; and cultivated daffodils (Table 3).

The cluster analysis supported in part the interpretations of Pugsley (1933) for the illustrations of Gerarde (1633); Parkinson (1629), Besler (1613) or Barrelier (1714) (cf. Tables 4 and 5 and compare with Table 3).

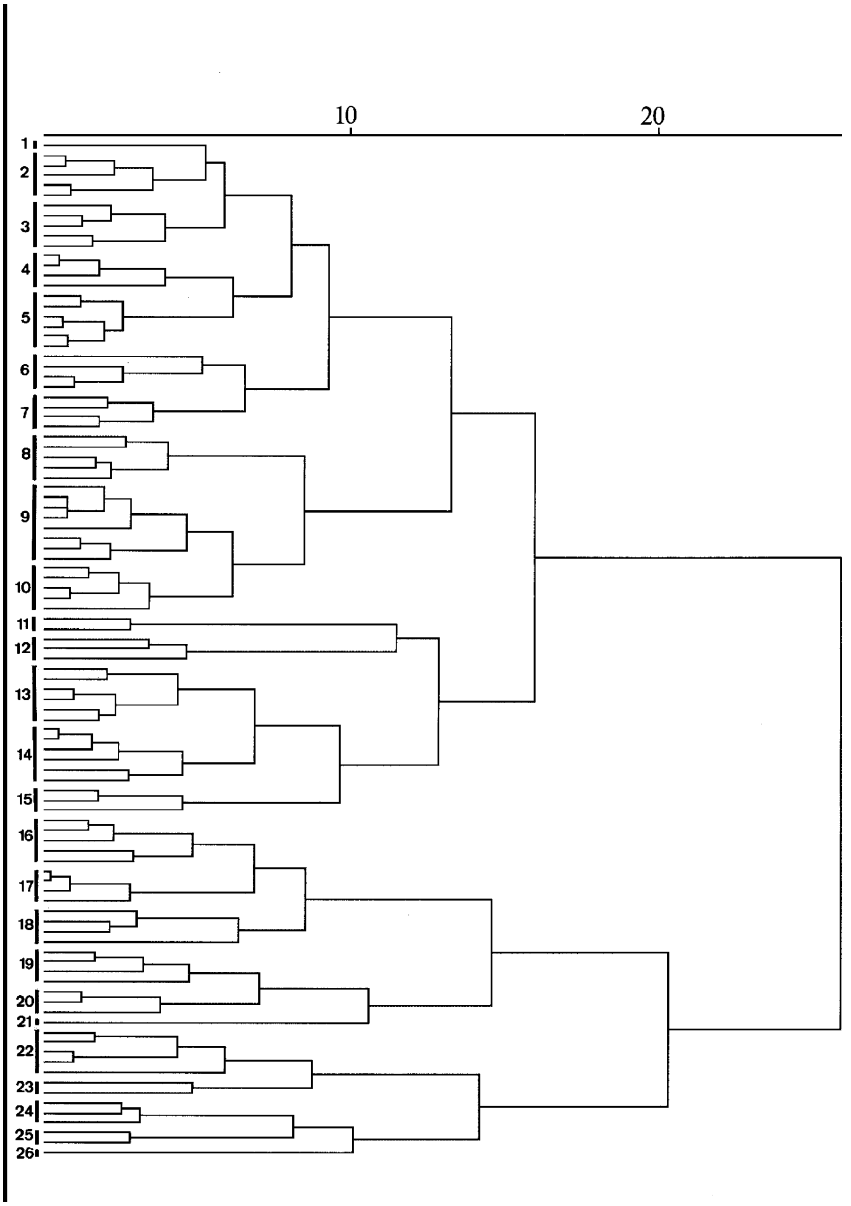

Fig. 1. Tree resulting from the CL (Euclidean distance) analysis of the 101 OTUs, icons and cultivars for the set of 13 characters described in Tables 1 and 2. There are 26 groups described in Table 3.

The cluster analysis of similarities showed that *N. nevadensis* Pugsley and *N. longispathus* Pugsley, are closely related (Group 11 in Fig. 1 and in Table 3), 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

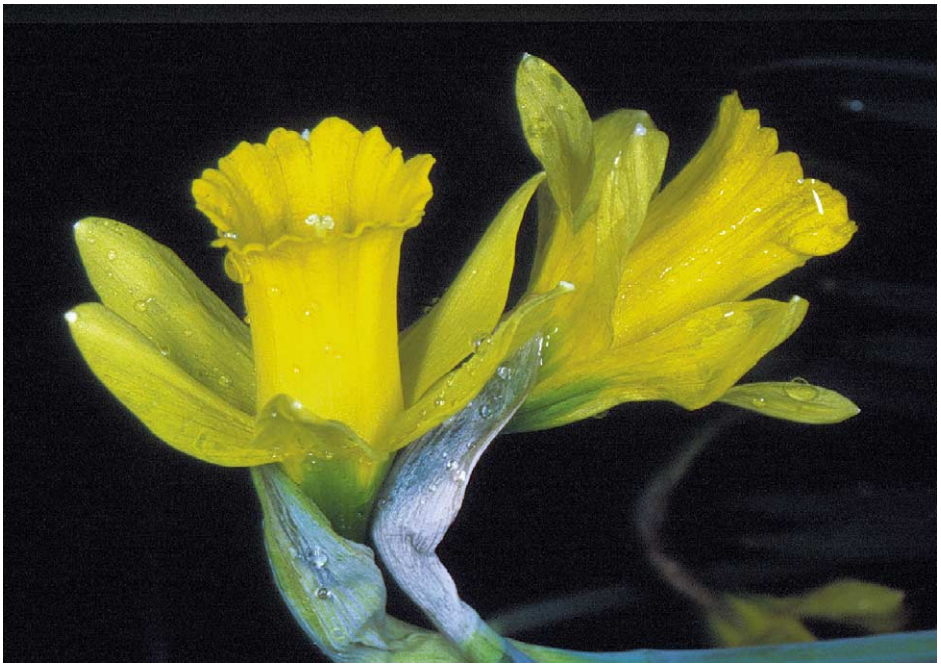

Fig. 2. *Narcissus segurensis* Rios et al. A recently discovered wild daffodil from southern Spain.

were not illustrated in the primitive illustrations of cultivated daffodils, and were not cited in early literature (cf. Tables 3 and 5).

4. Discussion

4.1. Relationships between wild and early cultivated forms

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'' (Boutelou and Boutelou, 1804; de los Ríos, 1620; Parkinson, 1629). 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.

The early records concerning cultivation of this group have been traced back to the Muslim times (10th to 12th Centuries). López (1990) in his study of the *Kitab fi Tartib Awqat*, in a review of the agronomic literature of this era, recognised, three types of daffodils: *N. papyraceus* Ker. Gawler (the *naryis abyad*), *N. jonquilla* L. (the *nisrin* or *ward barri*), and *N. pseudonarcissus* L. (sensu lato) (the *naryis asfar* or *arar*). The latter is described as a yellow flowered daffodil, but the recorded characters were inadequate for an accurate identification. Ibn Bassal recommended growing these flowers by collecting the

Table 1
Characters available from the early iconography (Blunt and Stearn, 1994; Barrelier, 1714; Clusius, 1601, 1605; Gerarde, 1633; Parkinson, 1629; Besler, 1613; Tabernaemontanus, 1731; Brunfels, 1530)[a]

No.	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* 946. (Barrelier, 1714)	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	*Pseudonarcisso 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	1.4–1.7 (2)	1.6–1.9 (3)	− (0)	Ab. (6)	Y. (0)
81	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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)

Table 1 (*Continued*)

No.	Icones	Lf.	Sc.	Sp.	Fl.	Pos.	Tp.	Tr.	T. l/w	Cl./Tl.	A./B.	Me.	Ms.	Fc.
97	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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	*Pesudonarcissus 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)

[a] 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 crown length/tube length; A./B., quotient apical diameter/basal diameter of the crown; Me., degree of margin expansion at the crown apex; Ms., crown 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., Long.; Md., medium; Dw., dwarf; Sh., short; Hor., horizontal. Between brackets are shown the values used for the matrix. Double flowered forms are represented by an asterisk (*) after the icon name. ? = doubtful.

Table 2
Characters available for the living wild taxa, double forms and relevant cultivars (Rios et al., 1999; Bahnert, 1992; Burbridge, 1875)[a]

No.	Taxa	Lf.	Sc.	Sp.	Fl.	Pos.	Tp.	Tr.	T. l/w	Cl./Tl.	A./B.	Me.	Ms.	Fc.
29	'Emperor' (Burbridge, 1875)	2 (0)	Lg. (0)	Long (0)	1 (6)	Se. (0)	Pat. (2)	Not. (0)	1.3–1.7 (1)	1.4–1.7 (2)	1.6–1.9 (3)	+ (4)	To. (2)	Y. (0)
30	'Empress' (Burbridge, 1875)	2 (0)	Lg. (0)	Md. (3)	1 (6)	Se. (0)	Pat. (2)	Not. (0)	1.3–1.7 (1)	1.4–1.7 (2)	1.3–1.6 (2)	+ (4)	To. (2)	Bi. (4)
32	'King Alfred' (Bahnert, 1992)	2–4 (2)	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)	+ (4)	Lo. (0)	Y. (0)
38	'Van Sion' (*) (Bahnert, 1992)	3–4 (3)	Md. (3)	Md. (3)	1 (6)	Hor. (3)	Pat. (2)	Not. (0)	1.7–2.1 (2)	1.4–1.7 (2)	1.3–1.6 (2)	± (2)	Cre. (4)	Y. (0)
98	*N. abscissus* Schultes f. var. *abscissus*	2 (0)	Md. (3)	Sh. (6)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	3.3–3.7 (6)	3.5–4.7 (9)	1.3–1.6 (2)	± (2)	Lo. (0)	Bi. (4)
91	*N. abscissus* Schultes f. var. *serotinus* (Jord.) Pugsley	1–6 (3)	Md. (3)	Md. (3)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	1.3–1.7 (1)	2.9–3.2 (7)	1.0–1.3 (1)	± (2)	Lo. (0)	Bi. (4)
100	*N. abscissus* Schultes f. var. *tubulosus* (Jord.) Pugsley	1–5 (2)	Md. (3)	Md. (3)	1 (6)	Se. (0)	Se. (0)	Not. (0)	2.1–2.5 (3)	5.3–6 (9)	1.0–1.3 (1)	± (2)	Lo. (0)	Y. (0)
56	*N. albescens* Pugsley	1–5 (2)	Md. (3)	Md. (3)	1 (6)	Hor. (3)	Se. (0)	Tw. (2)	1.7–2.1 (2)	1.7–2.0 (3)	1.0–1.3 (1)	+ (4)	Lo. (0)	Bi. (4)
20	*N. alcaracensis* Ríos & aliis	1–2 (0)	Dw. (6)	Md. (3)	1–2 (3)	Hor. (3)	Pat. (2)	Not. (0)	2.5–2.9 (4)	1.1–1.4 (1)	1.3–1.6 (2)	± (2)	To. (2)	Y. (0)
87	*N. alpestris* Pugsley	1–3 (1)	Dw. (6)	Md. (3)	1 (6)	Pen. (6)	Se. (0)	Tw. (2)	2.1–2.5 (3)	2.6–2.9 (6)	0.7–1.0 (0)	− (0)	Cre. (4)	W. (6)
37	*N. asturiensis* (Jord.) Pugsley	5 (4)	Dw. (6)	Sh. (6)	1 (6)	Hor. (3)	Se. (0)	Not. (0)	1.7–2.1 (2)	1.4–1.7 (2)	1.3–1.6 (2)	± (2)	Lo. (0)	Py. (2)
85	*N. bicolor* L.	2 (0)	Md. (3)	Md. (3)	1 (6)	Se. (0)	Pat. (2)	Not. (0)	0.9–1.3 (0)	2.6–2.9 (6)	1.3–1.6 (2)	± (2)	Cre. (4)	Bi. (4)
49	*N. calcicarpetanus* Fernández Casas	1–2 (0)	Md. (3)	Md. (3)	1 (6)	Se. (0)	Se. (0)	Not. (0)	2.5–2.9 (4)	1.4–1.7 (2)	1.3–1.6 (2)	− (0)	Cre. (4)	Y. (0)
50	*N. confusus* Pugsley	3–4 (3)	Dw. (6)	Md. (3)	1 (6)	Hor. (3)	Pat. (2)	Not. (0)	2.5–2.9 (4)	1.4–1.7 (2)	1.3–1.6 (2)	+ (4)	Lo. (0)	Y. (0)
101	*N. cyclamineus* DC.	2–3 (1)	Dw. (6)	Sh. (6)	1 (6)	Pen. (6)	Df. (4)	Not. (0)	4.9–5.3 (9)	6–8 (9)	0.7–1.0 (0)	− (0)	Cre. (4)	Y. (0)
6	*N. fontqueri* Fernández Casas & Rivas Ponce	1–2 (0)	Md. (6)	Sh. (6)	1 (6)	Hor. (3)	Se. (0)	Tw. (2)	2.1–2.5 (3)	0.8–1.1 (0)	1.0–1.3 (1)	± (2)	To. (2)	Y. (0)
90	*N. gayi* (Hénon) Pugsley	1–4 (1)	Md. (3)	Md. (3)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	2.5–2.9 (4)	2.6–2.9 (6)	2.5–2.8 (6)	± (2)	Lo. (0)	Bi. (4)
82	*N. gayi* (Hénon) Pugsley (=*N. praelongus* (Jord.) Pugsley)	1–3 (1)	Md. (3)	Md. (3)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	1.7–2.1 (2)	2.3–2.6 (5)	1.0–1.3 (1)	+ (4)	Lo. (0)	Bi. (4)
53	*N. genesi-lopezii* Fernández Casas	1–3 (1)	Dw. (6)	Md. (3)	1 (6)	Se. (0)	Se. (0)	Tw. (2)	3.3–3.7 (6)	1.4–1.7 (2)	1.0–1.3 (1)	− (0)	Lo. (0)	Y. (0)
13	*N. hispanicus* Gouan var. *hispanicus*	3 (1)	Md. (3)	Md. (3)	1 (6)	Se. (0)	Pat. (2)	Not. (0)	0.9–1.3 (0)	1.1–1.4 (1)	1.6–1.9 (3)	+ (4)	Lo. (0)	Y. (0)
68	*N. hispanicus* Gouan var. *bujei* (Fernández Casas) Fernández Casas	2 (0)	Md. (3)	Md. (3)	1 (6)	Hor. (3)	Se. (0)	Tw. (2)	2.5–2.9 (4)	1.7–2.0 (3)	1.0–1.3 (1)	+ (4)	Lo. (0)	Y. (0)
86	*N. hispanicus* Gouan var. *concolor* (Jord.) Pugsley	1–3 (1)	Md. (3)	Md. (3)	1 (6)	Hor. (3)	Se. (0)	Tw. (2)	1.7–2.1 (2)	2.6–2.9 (6)	1.0–1.3 (1)	+ (4)	Lo. (0)	Y. (0)
60	*N. hispanicus* Gouan (=*N. major* Curtis)	2 (0)	Lg. (0)	Long (0)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	1.7–2.1 (2)	1.7–2.0 (3)	1.3–1.6 (2)	+ (4)	Lo. (0)	Y. (0)

Table 2 (*Continued*)

No.	Taxa	Lf.	Sc.	Sp.	Fl.	Pos.	Tp.	Tr.	T. l/w	Cl./Tl.	A./B.	Me.	Ms.	Fc.
12	*N. jacetanus* Fernández Casas ssp. *jacetanus*	2–3 (1)	Dw. (6)	Md. (3)	1 (6)	Se. (0)	Pat. (2)	Not. (0)	2.9–3.3 (5)	0.8–1.1 (0)	1.0–1.3 (1)	± (2)	To. (2)	Y. (0)
1	*N. jacetanus* Fernández Casas ssp. *vasconicus* (Fernández Casas) Fernández Casas	3–4 (3)	Dw. (6)	Sh. (6)	1 (6)	Se. (0)	Se. (0)	Not. (0)	0.9–1.3 (0)	0.8–1.1 (0)	1.0–1.3 (1)	− (0)	To. (2)	Y. (0)
9	*N.* × *johnstonii* Pugsley	2–3 (1)	Md. (3)	Md. (3)	1 (6)	Pen. (6)	Pat. (2)	Tw. (2)	2.1–2.5 (3)	0.8–1.1 (0)	1.0–1.3 (1)	− (0)	Cre. (4)	Y. (0)
76	*N. longispathus* Pugsley	1–2 (0)	Lg. (0)	Long (0)	1–3 (0)	Hor. (3)	Se. (0)	Not. (0)	2.1–2.5 (3)	2.0–2.3 (4)	1.0–1.3 (1)	± (2)	Cre. (4)	Y. (0)
61	*N. macrolobus* (Jord.) Pugsley	1–2 (0)	Lg. (0)	Md. (3)	1 (6)	Hor. (3)	Se. (0)	Not. (0)	2.1–2.5 (3)	1.7–2.0 (3)	1.3–1.6 (2)	± (2)	Lo. (0)	Bi. (4)
42	*N. minor* L.	2–3 (1)	Dw. (6)	Md. (3)	1 (6)	Hor. (3)	Se. (0)	Not. (0)	2.1–2.5 (3)	1.4–1.7 (2)	1.0–1.3 (1)	± (2)	To. (2)	Y. (0)
89	*N. moleroi* Fernández Casas	2–4 (2)	Dw. (6)	Sh. (6)	1 (6)	Pen. (6)	Se. (0)	Not. (0)	2.5–2.9 (4)	2.6–2.9 (6)	1.3–1.6 (2)	± (2)	To. (2)	Y. (0)
43	*N. moschatus* Willk. & Lange (Burbridge, 1875)	2–4 (2)	Md. (3)	Md. (3)	1 (6)	Pen. (6)	Pat. (2)	Tw. (2)	2.1–2.5 (3)	1.4–1.7 (2)	1.0–1.3 (1)	+ (4)	Lo. (0)	Py. (2)
64	*N. nanus* Spach.	2–3 (1)	Md. (3)	Sh. (6)	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)
5	*N. nevadensis* Pugsley	1–2 (0)	Lg. (0)	Md. (3)	2–4 (0)	Hor. (3)	Se. (0)	Not. (0)	2.1–2.5 (3)	0.8–1.1 (0)	1.0–1.3 (1)	± (2)	To. (2)	Y. (0)
35	*N. nobilis* (Haw.) Schult. f. var. *nobilis*	1–2 (0)	Md. (3)	Sh. (6)	1 (6)	Se. (0)	Se. (0)	Not. (0)	1.7–2.1 (2)	1.4–1.7 (2)	1.3–1.6 (2)	− (0)	To. (2)	Bi. (4)
36	*N. nobilis* (Haw.) Schult. f. var. *leonensis* (Pugsley) A. Fernandes	1–2 (0)	Lg. (0)	Long (0)	1 (6)	Se. (0)	Se. (0)	Not. (0)	1.7–2.1 (2)	1.4–1.7 (2)	1.3–1.6 (2)	+ (4)	Cre. (4)	Bi. (4)
54	*N. obvallaris* Salisb. (The Tenby Daffodil)	1–2 (0)	Md. (3)	Sh. (6)	1 (6)	Se. (0)	Pat. (2)	Not. (0)	0.9–1.3 (0)	1.7–2.0 (3)	1.0–1.3 (1)	+ (4)	Lo. (0)	Y. (0)
95	*N. pallidiflorus* Pugsley	1–2 (0)	Lg. (0)	Sh. (6)	1 (6)	Pen. (6)	Se. (0)	Tw. (2)	2.5–2.9 (4)	3.2–3.5 (8)	1.3–1.6 (2)	− (0)	Cre. (4)	Py. (2)
88	*N. parviflorus* (Jord.) Pugsley	1–5 (2)	Md. (3)	Sh. (6)	1 (6)	Hor. (3)	Se. (0)	Tw. (2)	2.1–2.5 (3)	2.6–2.9 (6)	1.0–1.3 (1)	− (0)	Cre. (4)	Bi. (4)
79	*N. portensis* Pugsley	1–2 (0)	Dw. (6)	Sh. (6)	1 (6)	Se. (0)	Se. (0)	Not. (0)	2.5–2.9 (4)	2.0–2.3 (4)	1.3–1.6 (2)	± (2)	Cre. (4)	Y. (0)
8	*N. primigenius* (Fernández Suarez ex Lainz) Fernández Casas & Lainz	1–2 (0)	Dw. (6)	Sh. (6)	1 (6)	Se. (0)	Se. (0)	Not. (0)	2.1–2.5 (3)	0.8–1.1 (0)	1.0–1.3 (1)	− (0)	Cre. (4)	Y. (0)
52	*N. provincialis* Pugsley	2–3 (1)	Dw. (6)	Md. (3)	1 (6)	Se. (0)	Se. (0)	Not. (0)	2.9–3.3 (5)	1.4–1.7 (2)	1.3–1.6 (2)	+ (4)	Lo. (0)	Y. (0)

25	*N. pseudonarcissus* L. ssp. *eugeniae* (Fernández Casas) Fernández Casas	1–3 (1)	Dw. (6)	Sh. (6)	1 (6)	Se. (0)	Se. (0)	Not. (0)	3.3–3.7 (6)	1.1–1.4 (1)	1.3–1.6 (2)	− (0)	Cre. (4)	Y. (0)
26	*N. pseudonarcissus* L. var. *festinus* (Jord.) Pugsley	1–5 (2)	Dw. (6)	Md. (3)	1 (6)	Hor. (3)	Se. (0)	Tw. (2)	0.9–1.3 (0)	1.4–1.7 (2)	1.0–1.3 (1)	+ (4)	Lo. (0)	Bi. (4)
55	*N. pseudonarcissus* L. var. *montinus* (Jord.) Pugsley	1–5 (2)	Dw. (6)	Md. (3)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	1.3–1.7 (1)	1.7–2.0 (3)	1.0–1.3 (1)	+ (4)	Lo. (0)	Bi. (4)
28	*N. pseudonarcissus* L. var. *platylobus* (Jord.) Pugsley	1–4 (1)	Md. (3)	Sh. (6)	1 (6)	Hor. (3)	Se. (0)	Tw. (2)	1.3–1.7 (1)	1.4–1.7 (2)	1.0–1.3 (1)	+ (4)	Lo. (0)	Bi. (4)
57	*N. pseudonarcissus* L. var. *porrigens* (Jord.) Pugsley	1–5 (2)	Dw. (6)	Sh. (6)	1 (6)	Hor. (3)	Se. (0)	Tw. (2)	1.7–2.1 (2)	1.7–2.0 (3)	1.0–1.3 (1)	+ (4)	Lo. (0)	Bi. (4)
65	*N. pumilus* Salisb.	3 (1)	Dw. (6)	Md. (3)	1 (6)	Hor. (3)	Pat. (2)	Tw. (2)	2.1–2.5 (3)	1.7–2.0 (3)	1.3–1.6 (2)	+ (4)	Lo. (0)	Y. (0)
22	*N. radinganorum* Fernández Casas	2 (0)	Md. (3)	Sh. (6)	1 (6)	Se. (0)	Se. (0)	Not. (0)	2.5–2.9 (4)	1.1–1.4 (1)	1.0–1.3 (1)	− (0)	To. (2)	Y. (0)
62	*N. segurensis* Ríos & aliis × *N. yepesii* Ríos & aliis	1–2 (0)	Md. (3)	Md. (3)	1–2 (3)	Se. (0)	Se. (0)	Not. (0)	2.1–2.5 (3)	1.7–2.0 (3)	1.0–1.3 (1)	± (2)	Lo. (0)	Y. (0)
15	*N. segurensis* Ríos & aliis	1–2 (0)	Dw. (6)	Md. (3)	1 (6)	Hor. (3)	Se. (0)	Not. (0)	1.7–2.1 (2)	1.1–1.4 (1)	1.3–1.6 (2)	− (0)	To. (2)	Y. (0)
11	*N.* × *susannae* Fernández Casas (=*N.* × *munyozii-garmendiae* Fernández Casas	1–2 (0)	Md. (3)	Sh. (6)	1–2 (3)	Hor. (3)	Se. (0)	Not. (0)	2.9–3.3 (5)	0.8–1.1 (0)	1.0–1.3 (1)	− (0)	Cre. (4)	Y. (0)
74	*N. tortuosus* Haw.	1–5 (2)	Md. (3)	Md. (3)	1 (6)	Hor. (3)	Se. (0)	Tw. (2)	1.3–1.7 (1)	2.0–2.3 (4)	1.3–1.6 (2)	± (2)	Lo. (0)	Bi. (4)
47	*N. yepesii* Ríos & aliis (sample A)	2–3 (1)	Md. (3)	Long (0)	1–2 (3)	Hor. (3)	Se. (0)	Tw. (2)	2.5–2.9 (4)	1.4–1.7 (2)	1.0–1.3 (1)	+ (4)	Lo. (0)	Y. (0)
51	*N. yepesii* Ríos & aliis (sample B)	2–3 (1)	Md. (3)	Long (0)	1–2 (3)	Hor. (3)	Se. (0)	Tw. (2)	2.9–3.3 (5)	1.4–1.7 (2)	1.0–1.3 (1)	+ (4)	Lo. (0)	Bi. (4)

[a] 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 crown length/tube length; A./B., quotient apical diameter/basal diameter of the crown; Me., degree of margin expansion at the crown apex; Ms., crown 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., Long.; Md., medium; Dw., dwarf; Sh., short; Hor., horizontal. Between brackets are shown the values used for the matrix. Double flowered forms are represented by an asterisk (*) after the icon name. Nomenclature follows the International Daffodil Register (Kington, 2002).

Table 3
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[a]

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 and S. France
4	*N. nobilis* (Haw.) Schultes fil.	Daffodils (Weiditz painting of 1529); *Pseudo N. luteus* iii (Besler, 1613)	–	NW Spain and the 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	*P. 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 & Rivas Ponce; *N. segurensis* Ríos & aliis; *N. alcaracensis* Ríos & aliis; *N. primigenius* (Fernández Suarez ex Laínz) Fernández Casas & 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* × *N. yepesii*	Central and E. Spain
11	*N. nevadensis* Pugsley	–	*N. longispathus* Pugsley	SE Spain
12	*N.* × *johnstonii* Pugsley	*Pseudonarcisso tubo quasi abscisso* (Parkinson, 1629)	*N.* × *munyozii-garmendiae* Fernández Casas	W. Spain and 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	*P. luteus simplici flore* (Tabernaemontanus, 1731); 930. *N. sylvestris tuba aurea major* (Barrelier, 1714); *P. luteus* (Tabernaemontanus, 1731); 929. *N. sylvestris tuba lutea minor* (Barrelier, 1714)	*N. pumilus* Salisb.; *N. hispanicus* Gouan var. *concolor* (Jord.) Pugsley; *N. yepesii* Ríos & aliis	S. and SW Iberian Peninsula
15	*N. nobilis* (Haw.) Schult. f. var. *leonensis* (Pugsley) A. Fernandes	–	'Empress' (Burbridge, 1875); *N. bicolor* L.	N. Spain and the 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)	*P. 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 & aliis	Pyrenees and SE Spain

Table 3 (*Continued*)

Group	Key species	Prelinnaean names and references	Related species and cultivars	Origin
20	*N. gayi* (Hénon) Pugsley	–	*N. gayi* (Hénon) Pugsley var. *praelongus* (Jord.) Pugsley; *N. abscissus* (Haw.) Pugsley var. *serotinus* (Jord.) Pugsley	Pyrenees?
21	–	*P. 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	*P. 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.	*P. hispanicus minor albus* (Parkinson, 1629)	–	Pyrenees
26	*N. cyclamineus* DC.	–	–	NW Iberian Peninsula

? = doubtful.

[a] Results from the CL (Fig. 1) and UPGMA analysis. Group numbers corresponds with those in Fig. 1.

Table 4
Taxa traditionally recognised as naturally wild[a]

Species	Prelinnaean names	Literature	Origin
N. pseudonarcissus L.	*N. totus luteus montanus Teophr.*	Lobel (1570)	Europe
	Pseudo N. anglicus	Gerarde (1597)	
N. confusus Pugsley	*Pseudo N. major hispanicus*	Clusius (1576)	Central Spain
	Pseudo N. major hispanis	Clusius (1601)	
N. hispanicus Gouan	–	Lobel (1576)	SW France and Pyrenees
	Pseudo N. aureus praecox	Besler (1613)	
	P. aureus hispanicus maximus	Parkinson (1629)	
N. alpestris Pugsley	*Pseudo N. albo flore*	Clusius (1605)	The Pyrenees
	P. hispanicus flore albo minor	Parkinson (1629)	
N. cyclamineus DC.	*N. hispanicus minor luteus amplo calice foliis reflexis*	Vallet (1608)	NW Iberian Peninsula
N. asturiensis (Jord.) Pugsley	*Pseudo N. minor luteus repens*	Besler (1613)	NW Iberian Peninsula
	P. hisp. luteus minimus	Parkinson (1629)	
N. obvallaris Salisb.	*Pseudo N. major hispanicus*	de Bry (1612)	British Isles (perhaps)
	Pseudo N. luteus	Besler (1613)	
	N. totus luteus montanus major	Besler (1613)	
N. abscissus (Haw.) Schultes f.	*N. oblonga tuba rotunda quasi abscissa flavo flore*	Sweert (1612)	The Pyrenees
N. pumilus Salisb.	*N. totus luteus medius*	de Bry (1612)	Serra de Gerez (Portugal)
	P. hispanicus medius luteus	Parkinson (1629)	
N. johnstonii Pugsley	*N. subflavus tubo sexangulo*	Bauhin (1623)	NW Iberian Peninsula
N. tortuosus Haw.	*Pseudo N. hispanicus flore albo major*	Parkinson (1629)	N. Spain
N. pallidiflorus Pugsley	*Pseudo N. pallidus praecox*	Parkinson (1629)	N. Iberian Peninsula
N. macrolobus (Jord.) Pugsley	*Pseudo N. pyrenaeus hispanico* (pp.)	Parkinson (1629)	The Pyrenees
N. nobilis (Haw.) Schultes f.	*Pseudo N. pyrenaeus hispanico* (pp.)	Parkinson (1629)	N. Iberian Peninsula
N. moschatus L.	*Pseudo N. hispanicus flore albo medius*	Parkinson (1629)	The Pyrenees

[a] Identification of illustrations and prelinnaean names are according to Pugsley (1933), Loudon (1841) and Hereman (1868).

bulbs from the meadows (their natural habitats) and plant then in beds. At this time (May) seeds were also collected from wild and cultivated plants, and were sown in June (García and Hernández-Bermejo, 1995; Millás and Azimán, 1955).

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 first printed illustration of a ‘‘bastard daffodil’’ is a print woodcut by Hans Weiditz (Brunfels, 1530) and it was copied by Mattioli (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 corona (cf. Blunt and Stearn, 1994). These illustrations are similar to the *Pseudonarcissus luteus* iii (Besler, 1613) and is similar to the wild Spanish species *N. nobilis* (Haw.) Schultes f. According to Barra and

Table 5
Taxa only known under cultivation[a]

Species	Prelinnaean name	Literature	Origin
N. nanus Spach.	*Pseudo N. minor hispanicus latifolius*	Clusius (1601)	Unknown
N. albescens Pugsley	*Pseudo N. totus albus*	Besler (1613)	Spain (perhaps)
	P. maximus albidus	Parkinson (1629)	
N. bicolor L.	–	Lobel (1570)	Spain
	Pseudo N. albus calice luteo	Besler (1613)	
	N. albus calice flavo moscari odore	Bauhin (1623)	
N. minor L.	–	Lobel (1576)	Spain
	Pseudo N. minor hispanicus latifolius	Clusius (1601)	
	P. hispanicus minor luteus	Parkinson (1629)	
	N. totus luteus montanus minimus	Besler (1613)	

[a] Identification of illustrations and prelinnaean names according to Pugsley (1933) and Aiton and Aiton (1810–1813). Among these *N. minor*, and *N. bicolor* were reported by Loudon (1841) as introduced from Spain.

López (1984), it is exactly the same as *N. pseudonarcissus* L. sensu stricto. Jan Brueghel the Elder, represented several daffodils belonging to this group in paintings between 1599 and 1607 (Schneider, 1992).

A comparison of descriptions, localities, and illustrations of Parkinson (1629), Tabernaemontanus (1731), Barrelier (1714), Clusius (1601, 1605) and Besler (1613) (Table 1) with currently wild species (Table 2) 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. (Table 3).

No specific references were found that indicated the use of bulbs from the south of the Iberian Peninsula were used in European gardens. However, 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, and other closely related, in gardens of Central Europe. Presumably, these cultivated Andalusian plants disappeared during cultivation in Central Europe and the British Isles. These species tend to be less hardy than populations originating in Central and Northern Spain, and the Pyrenees.

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. They were, however, often lost after 1 or 2 years in cultivation because of a lack of adaptation to the English climate. Most of the illustrations by Parkinson (1629) are very similar to Spanish wild species (Groups 2, 10, 12, 22 and 25 in Fig. 1 and Table 3).

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. Clusius (1601) acknowledged the receipt of bulbs from John Moutono. They appear to be a Spanish dwarf daffodil. At that time this type was also grown by de Longatre, who sent some bulbs to the Leyden botanic garden. Clusius (1605) indicated that John Vincent Pinelli provided him some bulbs of *N.* cf. *moschatus* L. and other daffodil species, that were being grown in Italy by 1597. In 1600, a package with some daffodil bulbs was sent to Amsterdam from Brussels, presumably by van Ophem to Coonhart. Simon Parduyn sent an addit in a parcel to Clusius, which contained *Pseudonarcissi flore albo semine majus* (closely related to *N. alpestris* Pugsley, Group 17 in Table 3 and Fig. 1) which is very similar to the Italian grown species. Another related daffodil was sent by Theodor Coonhart from Amsterdam to Leyden. Mr. Venerio collected wild daffodil plants in the Pyrenees during 1603, and some were sent to Leyden (Clusius, 1605).

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 & aliis and *N. segurensis* Ríos & aliis) (Fig. 2, Group 9 in Table 3 and Fig. 1). 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 on the flowering of the cited species. Hence, Barrelier may have been the collector of daffodils that subsequently through hybridisation and selection have produced the cultivated daffodil named by Linnaeus, *N. minor*. Unfortunately, the daffodils illustrated by Barrelier did not designate the collection locality (Barrelier, 1714).

The mountains of Sierra Nevada and Sierra de Cazorla, which are centres of diversity and origin for this subgenus, have not contributed greatly to the group of trumpet daffodils now in cultivation. Thus, they may constitute an underexplored source of germplasm for new hybrid daffodil cultivars.

4.2. White and bicolour flowered forms

One of the daffodils in the Weiditz's 1529 water—colour picture (no. 4 of Table 1, Group 4 in Table 3 and Fig. 1) is a bicoloured type (tepals pale yellow or whitish, corona deep golden yellow) of *N. nobilis* (Group 4 of Fig. 1). Since Barra and López (1984) lectotypified *N. pseudonarcissus* L. (sensu stricto) in the sense of *N. nobilis*, this bicoloured type probably belongs to the species which gives name to the subgenus.

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

The primitive white flowered types (ns. 33, *N. sylvestris albus* and 45, *N. sylvestris totus albicans* in Table 1), were included in the same cluster (Group 16 of Table 3 and Fig. 1). This cluster is closely related to groups 17 and 18 of Fig. 1 and Table 3 and includes taxa

like *N. moschatus* L. and *N. alpestris* Pugsley. This cluster (group 16) also contains pale yellow or bicoloured forms (ns. 17, *N. sylvestris albidus*, 34, *N. sylvestris totus albus*, and 70, *N. sylvestris pallidus*). Thus it appears that white, pale yellow, and bicolour forms are closely related and presumably are derived by single mutations.

The well characterised cluster, around *N. alpestris* Pugsley (Group 17 of Fig. 1 and Table 3) includes several types with white pendent flowers (ns. 78, *P. albo flore*, 80, *N. albus nutante* and 81, *P. albo flore*). Presumably, these are different interpretations by different artists of the same taxon or cultivar.

A third group of white flowered types (ns. 96, *N. totus albus* and 97, *Pseudonarcissus hispanicus* Table 1) is related to pale yellow or bicolour flowered species, e.g., *N. pallidiflorus* Pugsley or *N. abscissus* (Haw.) Schultes f. which are included in Groups 24 and 25 of Table 3 and Fig. 1, 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. Thus any colour flower group, even whites, is polyphylethic. This may be relevant for taxonomic purposes, since flower colour was used by Haworth (1831) and Pugsley (1933) in the systematics of subgenus *Ajax*.

4.3. Double types

Double types may have been produced by the duplication of the number of tepals, by changes involving the corona, or 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 6.

A double yellow trumpet daffodil was in cultivation in 1597 and Parkinson indicated several doubles (Coats, 1956; Parkinson, 1629) (Table 6). 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 unproperly referred to in English by adding ''bastard'' to the common name (Table 6).

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 (cf. Baytop and Mathew, 1984).

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

Table 6
Primitive names, illustrations and descriptions of double forms of *Narcissus* subgenus *Ajax* Spach.

English name	Prelinnaean names	Literature	Origin
Greatest double yellow bastard daffodil	Pseudonarcissus maximus aureus flore pleno (=*N. septentrionalis flore pleno luteo*)	Lobel (1570), Clusius (1601), Besler (1613), Parkinson (1629)	John Tradescant's collections, presumably 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
Geater 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

? = doubtful.

related to *N. hispanicus* Gouan, and showing some resemblance to 'King Alfred' (Group 3 in Fig. 1 and Table 3).

4.4. Polyploids

Practically, all wild taxa are diploids, with 14 chromosomes. Amongst the cultivated forms, *N. hispanicus* Gouan and *N. tortuosus* Haw. are triploids and those under *N. bicolor* are tetraploids. 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 CL analysis showed a high correlation (over 95%) between the wild hexaploid *N. leonensis* and 'Empress' (Group 5 of Table 3 and Fig. 1).

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 of Table 3 and Fig. 1).

4.5. Hybrids of section pseudonarcissus

Hybridisation 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 utilisation of daffodils in the British Isles and Continental Europe. Most of these bulbs were imported from Spain and were 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 hybrid forms were originally imported wild plants and used in gardens. 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.* × *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 comes from the red pigment in *N. poeticus* (Wylie, 1952; Bahnert, 1992). *N.* × *incomparabilis* Miller of garden origin has been described as being very similar to the former hybrid. It is considered to a hybrid between *N. major* Curtis and *N. poeticus* L. Many pale yellow flowered types were obtained by Edward Leeds, in 1840s, by crossing *N.* × *incomparabilis* with white flowered wild species of subgenus *Ajax* Spach. *N.* × *boutignyanus* Philippe from the Pyrenees is an 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.* × *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).

Hybridisation between species of subgenus *Ajax* and the section *Ganymedes* is relatively frequent. *N.* × *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' (Bahnert, 1992; Wylie, 1952).

The CL analysis showed similarities of the nothospecies *N.* × *johnstonii* Pugsley (*N. pseudonarcissus* × *N. triandrus* ssp. *pallidulus*) with *N.* × *susannae* Fernández Casas (*N. cantabricus* × *N. triandrus* ssp. *pallidulus*) and with the illustration of Parkinson (1629) under the name of *Pseudonarcisso tubo quasi absciso* (Group 12 in Table 3 and Fig. 1). Thus, similar hybridisations may have occurred in different localities and at different times. Hybridisation between sect. *Bulbocodium* or subgenus *Ajax* with sect. *Ganymedes* produces similarities in the hybrid descent.

4.6. The trumpet daffodils

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

In has been suggested that in the origin of the Backhouse's trumpet varieties, e.g., 'Emperor' and 'Empress' (Table 2), involved an almost sterile triploid clone of the common tetraploid *N. bicolor* L. (Wylie, 1952). 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 in Table 3 and Fig. 1). '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 & aliis or *N. hispanicus* var. *bujei* (Fernández Casas) Fernández Casas (Group 13 in Table 3 and Fig. 1).

By the 1890s, several tetraploid clones had emerged. One of the first was 'King Alfred' (Table 2), 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 3 and Fig. 1), but 'Empress' appear grouped at a relatively long distance from this cluster (only a similarity of 85%) (Group 15 in Table 3 and Fig. 1).

4.7. Hybrids of section cyclaminopsis pugsley

Generally, these hybrids are characterised by the reflexing tepals. By crossing *N. cyclamineus* DC. with the diploid *N. asturiensis* (Hénon) 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.

4.8. Influence of cultivation on the conservation of wild populations

The import of bulbs from Spain to British, French, and Flemish (now Dutch and Belgian) 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.* × *johnstonii*). Many, however, were rediscovered during the revival of daffodil cultivation in the second half of the 19th century.

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 (Pugsley, 1933; Parkinson, 1629; 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). This was one of the darkest periods of plant exploitation.

Unfortunately, it is still a relatively common practice amongst Andalusian and Castillian farmers to collect wild daffodils for their gardens and to cut large numbers of flowers for local markets.

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 hybridisation, or both.

4.9. Chronology for daffodil domestication

Daffodils of subgenus *Ajax* were domesticated during three different periods. They are separated by a gap characterised 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, *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.

Our study reveals that excessive exploitation of natural populations of garden plants is not new to Spanish or Portuguese daffodils. They have experienced exploitation since, at least, the 11th century, not only for local uses but also for exportation as plants for Central European and British gardens.

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