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

Diego Rivera1* • Segundo Ríos2 • Concepción Obón3 • Francisco Alcaraz1

1 Departamento de Biología Vegetal, Facultad de Biología, Universidad de Murcia, 30100 Murcia, Spain
2 Departamento de Biología Animal, Vegetal y Ecosistemas. Universidad de Alicante, San Vicente del Raspeig, Alicante, Spain
3 Departamento de Biología Aplicada, Universidad Miguel Hernández, EPSO, 03312 Orihuela, Alicante, Spain

Corresponding author: *drivera@um.es

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ABSTRACT

The "Ajax Group" (i.e. *Pseudonarcissus*) is one of the most important ancestors of modern daffodil 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 abscessus* Pugsley, *N. jacetanus* Fernández Casas, *N. asturiensis* Hénon, *N. hispanicus* Gouan, *N. nobilis* (Haw.) Schult. var. *leonenis* (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., 'Incomparabiliis', '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 herbaria 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

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 those 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: \( d_{i,j} = \alpha d_{i} + \gamma + \beta d_{i} + \gamma \mid d_{i} \mid \); where \( d_{i,j} \) was the new distance value between cluster \( C_{i} \) and cluster \( C_{j} \) 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.

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 \( N. longispathus \) Pugsley, are closely related (Group 1), 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 Tarib Awat (10th to 12th Centuries AD) recognised, three types of daffodils: \( N. papyraceus \) Ker. Gawler (the naryis abyad or white daffodil), \( N. jonquilla \) L. (the nisin or ward barn), 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, Garcia 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.) Schultz 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).


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.

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* Rios et alii and *N. segurensis* Rios et alii) (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 bicolor (tepals pale yellow or whitish, Cup deep golden yellow) form of *N. nobilis* (Group 4). Since Barra and López (1984) lectotypified *Pseudonarcissus* L. (*sensu stricto* in the sense of *N. nobilis*, this bicolor 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 bicolor cultivar ‘Empress’ (Group 15). Other bicolor 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 albicaya* 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 bicolor 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), Gerard (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 (©).
presumably are derived by single mutations.

... (Table 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. 78, N. totus albiflorus and 79, Pseudonarcissus hispanicus) is related to pale yellow or bicolor flowered species, e.g., N. pallidiflorus Pugsley or N. assimilis (Haw.) Schultes I. included in groups 24 and 25 (Table 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 within the different 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 Hathorn (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 relic 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 mainly 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 telamoniensis (Parkinson 1629, 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. cylindrical pallidus) are related to N. obvallaris Salisb (Group 2, Table 2, Fig. 2). ‘Van Sion’ is very similar to the N. tos 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. turgosus 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. xbernardii 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. xincomparabilis 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.

Hybrids between species of subgenus Ajax and section Jonquilla are not common and not as fertile as the former group. N. xodorus L is a completely sterile diploid and unknown in the wild. Presumably, it originated in cultivation. It is intermediate between N. pseudonariccus 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. pseudonariccus 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. pseudonariccus 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 Pseudonarccisco tubo quasi absisco (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 Scienza Horticulturae 98, 307-330, 2003, with kind permission from Elsevier Science BV.

<table>
<thead>
<tr>
<th>Group</th>
<th>Key Species</th>
<th>Prelinnae names and references</th>
<th>Related species and cultivars</th>
<th>Origin</th>
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<tbody>
<tr>
<td>1</td>
<td>N. jaculanus Fernández - Casas sp. var. asconicus (Fernández Casas)</td>
<td>-</td>
<td>N Spain</td>
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<td>2</td>
<td>N. obvallarius Salisb.</td>
<td>N. septentrionalis calla luteo pleno, duplicata solia (Besler 1613), N. septentrionalis calla luteo oris incisa (Parkinson 1629), Pseudonarcissus hispanicus minor (Parkinson 1629)</td>
<td>Britain, Spain</td>
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<td>3</td>
<td>N. hispanicus Gouan</td>
<td>N. totus luteus montanus maior i (Besler 1613), 987, N. totus sulphureus (Barreler 1714)</td>
<td>Pyrenees, S France</td>
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<td>4</td>
<td>N. nobilis Schultes f. (Haw.)</td>
<td>Daffodils (Weidt painting of 1529), Pseudo N. luteus ii (Besler 1613)</td>
<td>NW Spain, Pyrenees</td>
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<td>N. albenscens (Haw.) - Pugsley</td>
<td>Pseudonarcissus l. var. platybus (Jord.) - Pugsley, N. pseudonarcissus l. var. pomponis (Jord.) Pugsley, N. pseudonarcissus L. var. fistulosus (Jord.) Pugsley, N. pseudonarcissus L. var. montinis (Jord.) Pugsley, N. tortuosus Haw.</td>
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<td>6</td>
<td>N. confusus Pugsley</td>
<td>Pseudonarcissus Anglicus (Gerarde 1633), N. totus luteus montanus, minus ii (Besler 1613)</td>
<td>Central and N Iberian Peninsula</td>
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<td>7</td>
<td>-</td>
<td>Pseudonarcissus Pyrenaicus variformis (Parkinson 1629), - Pseudonarcissus albus calla luteo ii (Besler 1613), Pseudo N. simplex Belga (Besler 1613), Pseudo N. aureus precox (Besler 1613)</td>
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<td>N. minor L.</td>
<td>975, N. sylvestris totus luteus (Barreler 1714)</td>
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<td>N. nanus Spach</td>
<td>Pseudonarcissus tubo sexangulari (Parkinson 1629)</td>
<td>N. radianorganorum Fernández Casas, N. Central and E Spain calcicarpatus N. nanus Casas, N. luteus minor x N. peyeasal</td>
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<td>‘Emperor’ (Burbridge 1875) Not known</td>
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<td>'Empress’ (Burbridge 1875); N. bicolor L.</td>
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<td>-</td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>N. mordic Fernandez Casas</td>
<td>Pseudonarcissus Hispanicus minor minimus (Parkinson 1629), - Pseudonarcissus minor Hispanicus (Gerarde 1633), Pseudonarcissus minor Hispanskus (Clausius 1601), N. totus luteus oblono calce et reflexo folii (Besler 1613)</td>
<td>Pyrenees</td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>N. abscissus (Haw.) Pugsley var. tubulosus (Jord.) Pugsley</td>
<td>Pseudonarcissus hispanicus maximus aureus (Parkinson 1629)</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>N. paeifolius Pugsley</td>
<td>945. N. totus albus nutantes (Barreler 1714)</td>
<td>Pyrenees</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>N. abscissus Schultes f.</td>
<td>Pseudonarcissus hispanicus minor albus (Parkinson 1629)</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>26</td>
<td>N. cyclamineus DC.</td>
<td>-</td>
<td>NW Iberian Peninsula</td>
<td>-</td>
</tr>
</tbody>
</table>

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. yepeisal Rios et al. or N. hispanicus var. bujie (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.

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

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 1833, 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. abscessus* (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 *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. abscessus*, *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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REFERENCES

Alton W, Alton WT (1854) Hortus Kewensis (ed 2, vol 2), London
Besler E (1613) Hortus Eystettensis, Nuremberg, Germany (Facsimile edition by Taschen)
Boutelou C, Boutelou E (1804) Tratado de las Flores, Villalpando, Madrid
Brunfels O (1530) Herbarium vivae exornae, John Schot, Antwerp, Belgium
Clusius C (1576) Rariorum plantarum Historia. Plantinus, Antwerp
Clusius C (1601) Plantarum historia, Plantinus, Antwerp
Fernandes A (1951) Contribution to the knowledge of the biosystematics of some species of Genus Narcissus L. V. Simposio de Flora Europea, Trabajos y Comunicaciones 1, 245-284
Haworth AH (1819) Narcissorum revisio. London
Lobel M (1750) Stritum Adversaria Nova. London
Lobel M (1756) Plantanum seu Stritum Historia, Plantinus, Antwerp
Parkinson J (1629) Paradisi in Sole, Paradisus Terrestris. Lowens and Young, London
Pritzel GA (1872) Thesaurus Literaturae Botanicae, Brockhaus, Leipzig
Pugsley HW (1933) A monograph of Narcissus sub-genus Aja. Journal of the Royal Horticultural Society 58, 17-93
Schneider N (1992) Naturaleza Muerta, Taschen, Köln
Tabernaemontanus J (1731) Krauterbuch, J. Ludwig Konigs, Offenbach
Wylie AP (1952) The History of the Garden Narcissi. Heredity 6, 137-156