The Biogeographical Patterns of Floral Form in Wild Daffodils and Their Contribution to the Cultivar Groups of *Narcissus* L. Subgenus *Ajax* Spach (Amaryllidaceae)

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ABSTRACT

The purpose of this chapter is to analyze the biogeographical characteristics of *Narcissus* L. subgenus *Ajax* in which a wide range of floral morphological variability is shown. This variability has been interpreted in terms of genetic drift leading towards the emergence of species confined to small areas (micro endemics) in SW Europe. In this chapter, biogeographical comparison of the species and taxonomic assemblages, as well as the models of evolution is presented. The distribution is discussed. The more relevant habitat types colonized by species of subgenus *Ajax* are deciduous forests, thickets and wet grasslands. Most taxa of this group grow in supra-Mediterranean and montane bioclimatic belts, at altitudes between 600 and 1,800 m above sea level and under subhumid and humid precipitation regimes. Almost 90% of taxa are diploid, but triploids, tetraploids and hexaploids also occur. The center of diversity of this subgenus is the region lying between the Sierra Nevada in Southern Spain and the Northern Slopes of the Cantabric and Pyrenean mountains.

1. INTRODUCTION

The genus *Narcissus* L. comprises more than 180 species, subspecies and varieties from Central Europe, the Mediterranean Region and West Asia, including intrasectional hybrids (Willis 1988, RHS 2000 2005a 2005b). Subgenus *Ajax* (= Section *Pseudonarcissus* DC) comprises c. 65 taxa, thus 30% of the species, subspecies and varieties are included within the genus *Narcissus.* The Iberian Peninsula is the center of diversity for *Narcissus* L. subgenus *Ajax* (Fernandes 1957). Between 30 and 40 taxa have been described from this area. Fernandes (1957) proposed *N. nevadensis* Pugsley as the ancestral species of this group. This species inhabits the western slopes of the Sierra Nevada (Granada; **Fig. 1**). Thus it is the SE of the Iberian Peninsula that is the center of origin for this group but not the major center of diversity. Fernández-Casas and co-workers have described a high number of new taxa circumscribed to this subgenus viz. Dorda and Fernández-Casas (1984a 1984b 1990
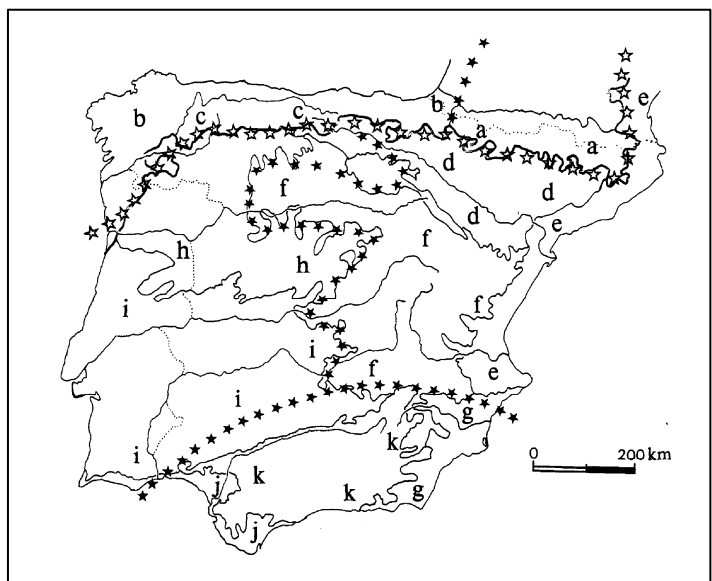

Fig. 1 Main biogeographical zones for the area of subgenus *Ajax*. Biogeographical provinces: (**a**) Cevennean-Pyrenean; (**b**) Atlantic-Cantabrian; (**c**) Orocantabrian; (**d**) Aragonian; (**e**) Valencian-Catalonian-Provenzal; (**f**) Castillian-Maestracean-Manchegan; (**g**) Murciane-Almerian; (**h**) Carpetan-Leonesian; (**i**) Luso-Extremadurenian; (**j**) Gaditane-Onubo-Algarvian, and (**k**) Baetic. North of the white stars line is the Eurosiberian region and South the Mediterranean region. Black stars are used for delimitation of the five large zones Baetic; Iberian Atlantic; Iberian Mediterranean; Cantabrian; Cevennean-Pyrenean. The Sub-Atlantic province extends from northeastern France northwards to the Baltic sea: it is off the map.

Table 1 Systematic Scheme of Subgenus *Ajax* Spach, cultivar groups and biogeographical zones in which are represented the different sections and series. CTT = Cup length x Tepal width / Tube length x Tepal length. All wild taxa within Section *Pseudonarcissus* and *Minores* fall automatically within Division 13 (Species, Wild Variants, and Wild Hybrids). Cf. for related cultivars see Rivera *et al*. 2003.

SECTIONS AND SERIES	WILD TAXA	RELATED DAFFODIL DIVISIONS	RELATED CULTIVARS	AREA
1. Section Pseudonarcissus. Bulb > 20 mm. Scape > 30 cm long. Tepals usually > 30 mm, never deflexed. Cup > 20 mm long, with margin expanded. CTT 0,5-1,5.				
1.1. Series Pseudonarcissus. Leaves short, 1 or 2 per bulb. Cup very long, up to 35mm. CTT 0,5 - 1,2. Stamens dorsifixed, inserted more than 3 mm above the base of the tube (except for *N. gayi* var. *praelongus* in which are basifixed).	*N. pseudonarcissus, N. abscissus* var. *abscissus, N. nobilis, N. macrolobus, N. bujei, N. gayi* var. *praelongus, N. leonensis*	1 Trumpet, 2 Long-Cupped, 4 Double	'Empress'	Eurosiberian region (Subatlantic, Orocantabrian, Cevennean-Pyrenean)
1.2. Series Nevadensis. Leaves equaling the scape. Scape very strout, c. 8 mm wide, parenchyma fistulose or lax - lacunose. 2 - 4 flowers per scape, with long pedicels. Ratio Cup length / tube length 0,9, the smallest of the subgenus. CTT < 1. Anthers dorsifixed, stamens inserted 4 mm above the base of the tube.	*N. nevadensis*	13 Wild	None?	Mediterranean region (Baetic).
1.3. Series Longispathi. Leaves usually shorter than scape. Scape up to 1,5 m, parenchyma fistulose or dense to dense - lacunose. Usually 1 - 3 flowers per scape. Pedicel usually > 4 cm. Spathe 4-10 cm. Cup length / tube length 1.4 - 2.2. Tepals 2,5 - 3 longer than wide. CTT 0,5 - 1,2. Anthers basifixed, stamens inserted 0 - 3 mm above the base of the tube.	*N. longispathus, N. yepesii, N. alcaracensis*	13 Wild	None?	Mediterranean region (Baetic).
1.4. Series Lutei. Approximately 1 - 6 leaves per bulb (clump). Cup usually less than 35 mm long with margin generally very expanded. CTT > 1. Anthers usually dorsifixed, stamens inserted 3 - 4 mm above the base of the tube.	*N. abscissus* var. *serotinus, N. abscissus* var. *tubulosus, N. albescens, N. calcicarpetanus, N. gayi, N. hispanicus* var. *hispanicus, N. hispanicus* var. *concolor, N. obvallaris, N. pallidiflorus, N. portensis, N. pseudonarcissus* var. *porrigens, N. pseudonarcissus* var. *platylobus, N. pseudonarcissus* var. *festinus, N. pseudonarcissus* var. *montinus, N. tortuosus*	1 Trumpet, 2 Long-Cupped, 4 Double	'King Alfred', 'Van Sion', 'Emperor'	Eurosiberian (Subatlantic, Cevennean-Pyrenean, Atlantic-Cantabrian) and Mediterranean region (Luso-Extremadurenian, Catalonian-Valencian-Provençal, Castilian-Maestracense-Manchegan)
2. Section Minores. Bulb < 20 mm. Scape < 30 cm. Generally more than 2 leaves per bulb. Flowers solitary. Tepals < 25 mm, erect to erecto-patent, never patent or deflexed. CTT 0,3-1.				
2.1. Series Minores. Flowers with very short pedicels (< 10 (13) mm). Cup < 20 (25) mm long. Perianth tube < 20 mm. Scape short and narrow (diameter < 4 mm), parenchyma dense.	*N. minor, N. jacetanus, N. vaconicus, N. asturiensis, N. parviflorus, N. provincialis, N. genesii-lopezii, N. radinganorum.*	1 Trumpet, 2 Long-Cupped, 4 Double, 13 Wild	'Minor', 'Rip Van Winkle'?	Eurosiberian (Subatlantic, Cevennean-Pyrenean, Orocantabrian, Atlantic-Cantabrian) and Mediterranean (Catalonian-Valencian-Provençal, Castilian-Maestracense-Manchegan)
2.2. Series Alpestris. Flowers with short pedicels (10 - 25 mm). Scape fistulose, usually 3.5 - 5.5 wide.	*N. alpestris, N. eugeniae, N. fontqueri, N. moleroi, N. munyozii-garmendiae, N. primigenius, N. segurensis*	13 Wild	None?	Eurosiberian (Subatlantic, Cevennean-Pyrenean, Orocantabrian) and Mediterranean (Aragonese, Castilian-Maestracense-Manchegan, Carpetan-Leonesian, Baetic, Luso-Extremadurenian)
3. Section Cyclaminopsis. Scape < 30 cm; with 2 - 3 leaves. Perianth tube < 3 mm long; ratio Cup / tube > 7. Tepals completely deflexed, approximately 4 times longer as wide. CTT > 1,5.				
3.1. Series Cyclaminopsis.	*N. cyclamineus*	6 Cyclamineus	'February Gold'?, 'Jenny', 'Jack Snipe'?, 'Mini Cycla', 'Jetfire'?, 'Peeping Tom', Quince', 'Téte á Téte'?	Eurosiberian (Atlantic-Cantabrian)

1994), Dorda *et al*. (1991), Fernández-Casas (1982a 1982b 1983a 1983b 1984a 1984b 1986 1987a 1987b 1996), Fernández-Casas and Rivas-Ponce (1988), Ríos *et al*. (1999) described three new endemic species of SE Spain.

The subgenus *Ajax* is more or less closely related to the subgenera *Narcissus* and *Bulbocodium*. From the former it differs in the longer coronas and from the latter in the wider leaves, longer tepals and shorter cups. The presence of two or more flowers for each spathe in some taxa of the subgenus *Ajax* suggests a relationship with multi-flowered taxa of subgenus *Narcissus*. The basic chromosome number for the three subgenera is x = 7, polyploids being relatively scarce. Intersubgeneric hybrids are frequent, both wild and as cultivars (Webb 1980).

Several of these species, endemic to the Iberian Peninsula (**Fig. 1**), were taken into cultivation to the English, French and Dutch gardens. According to Miller (1754) and Parkinson (1629) the wild Spanish and Pyrenean "bastard" or "trumpet daffodils" grown in the English gardens were raised from bulbs imported from their original countries. These former introductions were often lost. According to Miller (1754) plants died because of a lack of adaptation to the peculiarities of the climate of England. In other words these were lost most often because of the lack of technical knowledge for growing them, because the particular requirements of each species were unknown. After several reintroductions these were successfully grown and originated in the trumpet daffodils cultivars now included within Divisions 1 (Trumpet), 2 (Long Cup) and 11 (Split-Cupped) of the Horticultural Classification (RHS 2000, The American Daffodil Society 2004). These were also involved in the origin of some double daffodil cultivars in Division 4. The remaining are included under the Latin name within Section *Narcissus* in Division 13.

Systematics of wild daffodils (subgenus *Ajax*) was set on floral characters (dimensions and color pattern of the perianth segments (sepals and petals) (**Tables 1, 2, 3**). These characters are closely related with natural variability within this subgenus as well as dependant of selective pressures or unintentional crossing occurring in gardens. Botanic gardens are the "loci classici" for most of the Linnaean daffodil taxa.

Table 2 Analysis of characters concerning general morphology of the reproductive organs and details of the perianth tube. conc. concolor; disc. discolor; dro. dropping; hor. horizontal; pend. pendent; sha. shallowlly; tw. twisted; y. yellow; w. white.

Taxa	Code	Spate (mm)	Nº of flowers	Colour of flower	Colour tepals / corolla	Pedicel (mm)	Position of the flower	Perianth tube (mm)	Ratio antherae/ filament (mm)	Filament adnate (mm)
N. abscissus	1	10 - 30	1	y.	disc.	15 - 35	hor.	8 - 15	-	2 - 4
N. abscissus var. serotinus	40	35 - 45	1	y.	conc. to disc.	8 - 12	hor.	12 - 20	-	3 - 4
N. abscissus var. tubulosus	42	35 - 45	1	y.	conc.	20 - 25	suberect	18 - 20	0,9	0
N. albescens	2	35 - 40	1	pale y. to w.	conc. to disc.	14 - 18	hor.	13 - 15	0,7	0
N. alcaracensis	3	43 - 60	1 - 2	y.	conc.	15 - 46	hor.	9 - 11	-	2 - 3
N. alpestris	4	30 - 40	1	w.	conc.	10 - 12	dro.	5 - 9	-	0 - 2
N. asturiensis	5	15 - 28	1	pale y.	conc.	3 - 10	hor.	12 - 13	0,5	5
N. bujei	6	40 - 60	1	y.	conc.	8 - 35	hor.	16 - 18	0,6	6 - 8
N. calcicarpetanus	7	30	1	y.	conc.	3 - 5	erect to hor.	12 - 16	0,7	1 - 2
N. confusus	9	30 - 53	1	y.	conc.	2 - 16	hor.	10 - 20	-	3 - 4
N. cyclamineus	10	18 - 20	1	y.	conc.	6 - 10	dro. to pend.	2 - 3		0 - 2
N. eugeniae	11	27 - 32	1	y.	conc.	0 - 3	erect to suberect	14 - 18	0,8	0
N. fontqueri	13	28	1	y.	conc.	0 - 1	hor.	14 - 16	0,6	1 - 3
N. gayi	14	30 - 35	1	y.	conc. to disc.	10 - 15	hor.	27	-	-
N. gayi var. praelongus	34	30 - 45	1	y.	conc. to disc.	12 - 15	hor.	14 - 17	0,5	0
N. genesi - lopezii	15	30 - 40	1	y.	conc.	3 - 4	erect to suberect	12	1	1 - 2
N. hispanicus	16	38	1	y.	conc.	15	suberect	14 - 15	0,8	3 - 6
N. hispanicus var. concolor	8	35 - 45	1	y.	conc.	14 - 17	hor.	20	-	3 - 4
N. jacetanus	19	40 - 50	1	y.	conc.	2 - 5	erect	20 - 25	-	7
N. leonensis	20	60 - 100	1	y.	disc.	20 - 25	suberect	10 - 15	0,6	2 - 3
N. longispathus	21	60 - 100	1 - 2(3)	y.	conc.	40 - 90	hor.	0 - 5	-	3 - 4
N. macrolobus	22	30 - 45	1	y.	disc.	5 - 10	hor.	10	-	-
N. moleroi	23	22 - 30	1	y.	conc.	5 - 8	dropping	14 - 16	0,7	0 - 2
N. munyoziigarmendiae	25	25 - 30	1(2)	y.	conc.	10 - 22	suberect to hor.	9 - 12	-	-
N. nevadensis	26	20 - 60	2 - 4	y.	conc. to disc.	20 - 30	hor.	15 - 25	-	4 - 5
N. nobilis	27	20 - 30	1	y.	conc. to disc.	5 - 15	hor. or suberect	20 - 30	-	4 - 5
N. obvallaris	28	25 - 35	1	y.	conc.	10 - 15	hor. or suberect	12 - 15	-	3
N. pallidiflorus	29	15 - 20	1	pale y.	conc.	2 - 10	dro.t to patent	8 - 12	-	3 - 4
N. parviflorus	30	20 - 25	1	y.	conc. to disc.	8 - 10	suberect to dro.	6 - 8	1,0	4 - 7
N. portensis	33	30	1	y.	conc.	5 - 15	suberect	15 - 20	0,6	0
N. primigenius	35	15 - 20	1	y.	conc.	0 - 2	erect	13 - 15	0,8	0 - 1
N. provincialis	36	20 - 40	1	y.	conc.	7 - 13	suberect	12 - 17	-	4 - 5
N. pseudonarcissus var. festinus	12	23 - 35	1	y.	disc.	0 - 5	hor.	12 - 14	0,5	0 - 1
N. pseudonarcissus var. montinus	24	35 - 40	1	y.	conc. to disc.	6 - 8	hor.	15 - 20	-	-
N. pseudonarcissus var. platylobus	31	25 - 30	1	y.	conc. to disc.	2 - 5	hor.	11 - 18	-	-
N. pseudonarcissus var. porrigens	32	20 - 25	1	y.	cocolorous to disc.	6 - 10	hor.	16	0,6	3
N. radinganorum	37	30	1	y.	conc. -	5	suberect	10 - 12	1,1	2 - 3
N. segurensis	38	40 - 42	1	y.	conc.	14 - 25	hor.	10 - 12	0,7	0 (1)
N. segurensis x N. yepesii	39	37 - 45	1 (2)	y.	conc.	15 - 28	hor. or suberect	8 - 10	0,9	0 - 2
N. tortuosus	41	35 - 35	1	pale y.	conc. to disc.	10 - 15	suberect to dro.	3 - 4	0,4	0
N. vasconicus	43	17 - 19	1	y.	conc.	0 - 2	erect, suberect or hor.	9 - 10	0,5	1 - 2
N. yepesii A	17	40 - 75	1 (2)	y.	conc.	18 - 48	hor. or suberect	13 - 16	0,8	0
N. yepesii B	18	40 - 90	1 (2)	y.	conc. to disc.	20 - 55	hor. or suberect	12 - 17	0,7	0

Parkinson (1629) made a first attempt of definition for this group:

"I will first divide them into two principal or primary kinds: that is, into *Narcissos*, true daffodils and *Pseudonarcissos*, bastard daffodils. It consists only in the flower (when as in all other parts they cannot be distinguished) and chiefly in the middle cup or chalice [corona]; for that we doe in a manner, only account those to be *Pseudonarcissos* bastard Daffodils, whose middle cup is altogether as long, as sometime a little longer than the outer leaves [perianth] that do surround it so that it seems rather like a trunk or long nose, although the cup of some of the true Daffodils be great, yet it is wider open at the brim or edge, and not so long and narrow all alike as the bastard kinds are".

Parkinson (1629) organized the cultivated forms into such groups as: *latifolii*, *angustifolii*, *juncifolii*, and *marini*. The dimensions of the whole plant were adopted for distinguishing species. Parkinson often applied distinction between "greater" and "lesser", "greatest" and "least" to the distinction at specific rank.

Haworth (1819) produced the first post-Linnaean systematic approach for trumpet daffodils, dividing *Narcissus* into two genera: *Oileus* with short coronas and other, *Ajax,* with longer coronas. The genus *Ajax* is divided into four sections according to dimensions and flower color. Pugsley (1933) proposed some amendments to Haworth's systematics. He abandoned the genus *Oileus*, and created the section *Cyclaminopsis* on the base of a more or less bent (deflexed) perianth. This section comprises *N. cyclamineus* and *N. johnstonii,* which were not treated by Haworth. Parts of Haworth's groups were conserved with minor amendments, changes of level and transferal of taxa (*Minores*, *Albiflorae*, *Pallidiflores*). Section *Lutei* was included in the section *Pseudonarcissus* and divided into three different series: *Lutei*, *Vulgares* and *Nobiles*.

2. MATERIALS AND METHODS

For the analysis a set of 31 characters was measured and scored for 43 Operational Taxonomic Units (OTUs) (Sokal and Sneath 1963). The SynTax package, version 5.0, was employed (Podani 1991) for comparison, and UPGMA average linkage and complete linkage were calculated.

Table 3 Analysis of the reproductive organs in wild daffodil species: tepals and corona. conc. concave; conv. convexe; cre. crenulate; dent. dentate; ere. erect; exp. expanded; lob. lobed; pt. patent; sere. suberect; sli. slightly; tw. twisted; y. yellow; w. white.

Taxa	Code	Tepals length (mm)	Tepal direction	Tepal curvature	Tepal length / width	Corona. length (mm)	Cup Apex / base	Cup Profile	Cup apex	Cup margin
N. abcissus	1	40 - 50	pt.	tw.	3,6	35 - 45	1,4	flat or conc.	sli. exp.	dent. to lob.
N. abscissus var. serotinus	40	28 - 30	pt.	tw.	1,5	25 - 30	1,1	flat	sli. exp.	dent. to lob.
N. abscissus var. tubulosus	42	35 - 38	ere. - pt.	tw. or not tw.	2,5	25 - 30	1,2	flat	sli. exp.	lob.
N. albescens	2	34 - 36	ere. - pt.	tw.	2,1	35 - 40	1,2	flat	very exp.	lob.
N. alcaracensis	3	14 - 22	pt.	not tw. or tw.	2,6	15 - 23	1,6	flat or conc.	sli. exp.	dent.
N. alpestris	4	18 - 22	ere.	tw.	2,5	25 - 30	0,8	flat	not exp.	cre.
N. asturiensis	5	7 - 14	ere. - pt.	not tw.	1,8	8 - 16	1,5	conc.	sli. exp.	lob.
N. bujei	6	15 - 28	ere. - pt.	tw.	2,7	16 - 30	1,1	flat or conc.	very exp.	lob.
N. calcicarpetanus	7	20 - 23	ere.	not tw.	2,8	25 - 28	1,7	flat or conc.	not exp.	cre.
N. confusus	9	6 - 19	pt.	not tw. or tw.	2,8	17 - 35	1,7	flat or canc.	very exp.	lob.
N. cyclamineus	10	18 - 20	deflexed	not tw.	5,0	18 - 20	1,0	flat	not exp.	cre.
N. eugeniae	11	19 - 21	ere. - pt.	tw. or not tw.	3,5	21 - 22	1,4	flat or conc.	not exp.	cre.
N. fontqueri	13	18	ere. to sere.	tw.	2,4	18	1,3	flat or conc.	sli. exp.	cre. - dent.
N. gayi	14	40 - 45	pt.	tw.	2,8	40 - 45	2,6	flat	sli. exp.	lob.
N. gayi var. praelongus	34	35 - 38	pt.	tw.	2,1	30 - 35	1,1	conc.	very exp.	dent. to lob.
N. genesi - lopezii	15	15 - 16	sere.	tw.	3,5	18 - 19	1,2	flat	not exp.	lob. or dent.
N. hispanicus	16	25 - 30	pt.	not tw.	1,1	26	2,0	conc.	very exp.	lob. or dent.
N. hispanicus var. concolor	8	34 - 36	ere. - pt.	tw.	1,9	38 - 42	1,3	flat	very exp.	lob.
N. jacetanus	19	12 - 13	ere.	not tw.	3,1	14 - 15	1,2	conc.	sli. exp.	cre. - dent.
N. leonensis	20	40 - 50	ere. to ere. - pt.	not tw.	2,0	30 - 40	1,6	flat to conc.	very exp.	cre.
N. longispathus	21	25 - 32	ere. - pt. to pt.	tw. or not tw.	2,4	25 - 30	1,1	flat to conc.	sli. exp.	cre.
N. macrolobus	22	25 - 30	ere. to ere. - pt.	not tw.	2,2	30 - 35	1,4	flat to conc.	sli. exp.	dent. to lob.
N. moleroi	23	24 - 30	ere. - pt.	not tw.	2,6	24 - 30	1,5	flat	sli. exp.	cre. - dent.
N. munyoziigarmendiae	25	9 - 14	ere.	not tw.	3,0	10 - 14	1,1	flat or conc.	not exp.	cre.
N. nevadensis	26	15 - 20	pt. to ere. - pt.	tw. or not tw.	2,5	15 - 20	1,2	flat	sli. exp.	cre. - dent.
N. nobilis	27	30 - 55	ere. - pt.	tw. or not tw.	2,1	30 - 45	1,5	conc.	not exp.	cre. to lob.
N. obvallaris	28	35 - 45	ere.	not tw.	1,3	25 - 30	1,1	flat to conc.	very exp.	lob.
N. pallidiflorus	29	30 - 40	sere.	tw.	2,8	30 - 40	1,4	conc.	not exp.	cre.
N. parviflorus	30	20 - 25	ercto - pt.	tw.	2,5	18 - 22	1,1	flat	not exp.	cre.
N. portensis	33	20 - 30	ere. - pt.	tw. or not tw.	2,8	25 - 35	1,6	conc.	sli. exp.	cre.
N. primigenius	35	10 - 14	sere.	not tw.	2,5	15 - 20	1,2	conc.	not exp.	cre.
N. provincialis	36	14 - 25	sere. to ere. - pt.	not tw.	3,0	20 - 25	1,6	flat to conc.	very exp.	lob. or dent.
N. pseudonarc. var. festinus	12	24 - 26	pt. to ere. - pt.	tw.	1,3	20 - 25	1,3	flat	very exp.	lob. or dent.
N. pseudonarc. var. montinus	24	26 - 30	pt.	tw.	1,6	25 - 30	1,1	flat	very exp.	dent. to lob.
N. pseudonarc. var. platylobus	31	30 - 35	ercto - pt.	tw.	1,5	25 - 35	1,3	conc.	very exp.	dent. to lob.
N. pseudonarc. var. porrigens	32	24 - 26	ercto - pt.	tw.	2,1	25 - 30	1,1	flat	very exp.	dent. to lob.
N. radinganorum	37	17 - 19	ere.	not tw.	2,7	19	1,1	conv.	not exp.	dent.
N. segurensis	38	14 - 16	ere.	not tw.	1,8	15 - 17	1,4	conv.	not exp.	cre. - dent.
N. segurensis x N. yepesii	39	15 - 19	ere. - pt.	not tw.	2,3	19 - 24	1,1	conv. to flat	sli. exp.	lob. or dent.
N. tortuosus	41	25 - 35	ere. - pt. to deflexed	tw.	1,5	30 - 40	1,4	conc. to flat	sli. exp.	dent. to lob.
N. vasconicus	43	13 - 14	ere. to ere. - pt.	not tw.	1,3	10 - 11	1,1	conc.	not exp.	cre. - dent.
N. yepesii A	17	19 - 25	pt. to ere. - pt.	tw.	2,7	20 - 28	1,2	conc.	very exp.	lob. or dent.
N. yepesii B	18	13 - 28	pt. to ere. - pt.	tw.	3,3	15 - 30	1,3	conc.	very exp.	lob.

Hierarchical classification is generated using combinatorial agglomerative methods characterized by the recurrence formula as follows:

$dh,ij = ai\, dhi + aj\, dhj + b\, dij + g\, ½dhi\, dhj½$, where dh,ij is the new distance value between cluster Ch and cluster Cij just obtained from the fusion of Ci and Cj (Podani 1991). As recommended by Podani (1991) the data set was analized using two options. Complete linkage (farthest neighbor, Euclidean distance) (CL) and unweighed group average (average, Euclidean distance) (UPGMA) were calculated.

As was recognized by Pugsley (1933) among daffodils most of the organs of the plant are of some importance for furnishing taxonomic characters. The size of the bulbs is relatively variable depending on genetic information, but also on the special features of the substrates. Larger bulbs are typical of softener soils, associated to forest environments whereas more compacted, meadow-land soils led to a reduction in the bulb diameter. Foliage is significant not only in the number and dimensions of leaves, but also in anatomic features available through microscopic examination.

The scape is more or less taller, but it also displays a sort of lateral compression and some microscopic features concerning surface and parenchyma that are useful for recognizing species and cultivar groups. General shape and flower characters are summarized in **Tables 2** and **3**. The spathe dimensions are relevant, also its consistency, ranging from membranous to sub-herbaceous (but this latter character is difficult to detect in dried herbarium specimens). Although normally only one flower is produced in each scape, some taxa display two, three or even four large flowers per scape, which makes them more interesting for ornamental purposes. Dimensions and curvature of the pedicel are relevant. Large bent down daffodils look less attractive in garden displays. Pedicel diversity reflects early radiation of this group from a wild ancestor provided with long and erect pedicels. The absolute and relative dimensions of the perianth, flower tube and corona are important for differentiating species and thus cultivars (**Tables 2, 3**). The shape, curvature and direction of the sepals are also characteristic. However, Pugsley (1933) detected narrower and straighter perianth-segment forms in plants grown under adverse conditions. The shape of the corona, including marginal expansion and division of the margin are useful in distinguishing species.

Flower color varies from snow-white (cultivar Peggy White) to lemon-yellow (cultivars Rapture, Temple Gold) and deeper yellowish-orange (cultivar Cutting Edge). Differences in shade and hue are found between the colors of corona and perianth segments. These differences were

Figs. 2-13 (**2**) Calcicolous beech forests (*Carici-Fagetum; Buxo-Fagetum*). Habitat for *Narcissus hispanicus*; *N. jacetanus*; *N. moleroi*; *N. vasconicus*. (**3**) Deciduous oak forests (*Quercion pyrenaicae*). Habitat for *Narcissus confusus*; *N. eugeniae*; *N. munyoziigarmendiae*; *N. pallidiflorus*; *N. perezchiscanoi, N. segurensis*. (**4**) Pine forests. *Pinus uncinata* forests (*Pinion uncinatae*). Habitat for *Narcissus abscissus, N. alpestris*; *N. bicolor*. (**5**) *Xerobromion*. Habitat for *Narcissus moleroi*. (**6**) Calcicolous wet grasslands (*Holoschoenion*). Habitat for *Narcissus bujei*; *N. calcicarpetanus*; *N. eugeniae*; *N. genesilopezii*; *N. nevadensis*; *N. radinganorum*; *N. yepesii*. (**7**) Large sedge communities (*Magnocaricion elatae*). Habitat for *Narcissus alcaracensis*. (**8**) Silicicolous grasslands (*Nardetalia*). Habitat for *Narcissus abscissus*; *N. alpestris*; *N. asturiensis*; *N. confusus*; *N. fontqueri*; *N. leonensis*. (**9**) Heaths. (**10**) Wet grasslands (*Molinio-Arrhenatheretea*). Habitat for *Narcissus abscissus* var. *serotinus*; *N. abscissus* var. *tubulosus*; *N. albescens, N. nobilis*; *N. parviflorus*; *N. pallidiflorus*; *N. primigenius*; *N. pseudonarcissus*; *N. pseudonarcissus* var. *festinus*; *N. tortuosus*. (**11**) Riparian communities (*Salicetalia purpureae* and related). Habitat for *Narcissus longispathus*. (**12**) *Alnus glutinosa* riparian woods and thickets (*Alnion incanae*). Habitat for *Narcissus cyclamineus*; *N. pallidiflorus*; *N. tortuosus*. (**13**) Calcicolous *Echinospartum horridum* scrubs (*Echinospartion horridi*). Habitat for *Narcissus alpestris*; .*N. jacetanus*.

exploited while trying to obtain cultivars 'Corbiere 1', 'Colorama 11', 'Empress', 'Saint Louie Louie', 'Silver Minx', 'Smooth Trumpet'. Taxonomists use distance from the base of the perianth tube to the zone of stamen insertion (mm of adnate filament in **Table 2**). Pugsley (1933) interpreted this character in terms of partial attachment of staminal filaments to the perianth tube. The ripe capsules differ greatly in shape, mainly among wild plants (Pugsley 1933). There are few samples preserved in herbaria of capsulated fruiting specimens. Moreover these lack completely for several species recently described. This difficulty was considered and characters pertinent to the capsules and seeds were disregarded for the analysis. However it could be useful for systematic purposes.

We have visited the natural habitats and localities for most of the taxa here discussed (**Figs. 2-13**). Information about the plant communities was collected. Daffodil populations are well recognized only at flowering time, which sometimes is extremely short and varies from one year to another, thus we compared our data with the available references for the different species, subspecies and varieties. Also ecological data in the labels of the herbaria consulted (MA, MAF, MUB, BM, K) were used. Regional and local vegetation studies were reviewed. Attribution to particular vegetation types is made according to the above sources. Climatic data were drawn from Capel (1981). Rivas-Martínez (1981 1991) was followed in naming the different climates and bioclimatic belts. Main biogeographical units were named according to Braun-Blanquet (1952), Molinier (1959), Rivas-Martínez (1979 1987 1991). Syntaxonomical checklist by Rivas-Martínez *et al.* (2001) was followed in naming vascular plant communities.

3. RESULTS

Determining the specific rank in this group is a difficult matter. Linnaeus (1753) condensed the whole subgenus *Ajax* into one single species: *N. pseudonarcissus*. Haworth (1831) and Jordan (1903), who displayed a splitting tendency, furnished a contrasting counterpart by making a new species of every daffodil with noteworthy features.

Pugsley (1933) proposed as a better method to determine the specific rank in daffodils to look at, both resemblances as well as differences, and making an attempt to estimate the relative importance of the different characters. This author opted for a somewhat analytic approach.

The resemblance is calculated in this paper using average linkage (UPGMA) (**Fig. 14**) and complete linkage (**Fig. 15**). A preliminary view of the trees resulting from the analysis furnishes some interesting points for discussion. The "Jordanian" taxa (**Tables 3, 4**) appear grouped mainly forming pairs of closely resembling OTUs (viz. *N. pseudonarcissus* L. var. *festinus* (Jord.) Pugsley/*N. pseudonarcissus* L. var. *montinus* (Jord.) Pugsley; *N. pseudonarcissus* L. var. *platylobus* (Jord.) Pugsley / *N. abscissus* (Haw.) Pugsley var. *serotinus* (Jord.) Pugsley. etc.). These pairs appear more or less closely related to other taxa, described by Jordan or by other authors or even appear independent. A similar situation is found when looking at other authors' taxa, like Fernández Casas, Haworth or Pugsley (**Tables 3, 4; Figs. 14, 15**).

When considering the whole trees it appears clear that local variability amongst populations sampled belonging to a single species (viz. *Narcissus yepesii* A and B in **Tables 2, 3**) is reflected in terms of the closest resemblance (**Figs. 8, 9**; dissimilarity values below 0.1). In the remaining cases differences are somewhat higher. For pairs like *N. vasconicus / N. asturiensis, N. munyoziigarmendiae / N. eugeniae* or *N. calcicarpetanus / N. portensis* the difference may be interpreted in the sense of infraspecific variability (viz. subspecies) or as a mere local variability devoid of taxonomic relevance. Several amongst these pairs should merit the conservation as separate entities on account of the ecological and geographical distances existing between both members of the pair.

When situating the limits for specific rank at a higher level (dissimilarity between 0.1-0.2) in the trees the number of species will become dramatically reduced but accordingly the infraspecific heterogeneity will rise to a degree in which the species concept will be ambiguous and the resulting taxa unmanageable.
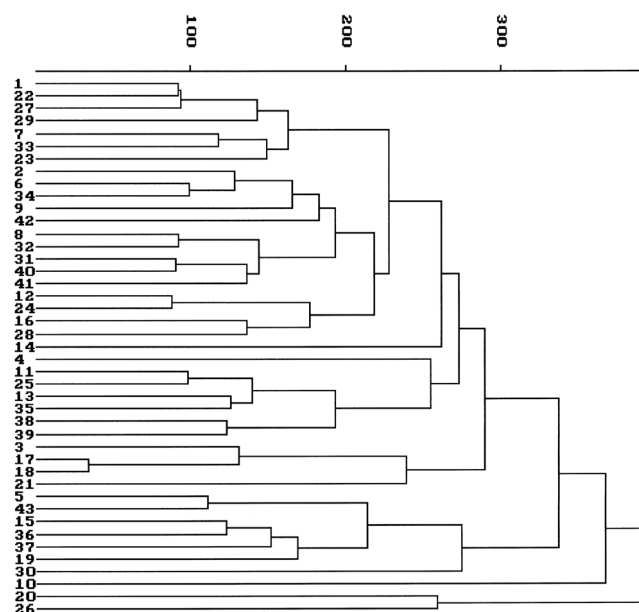

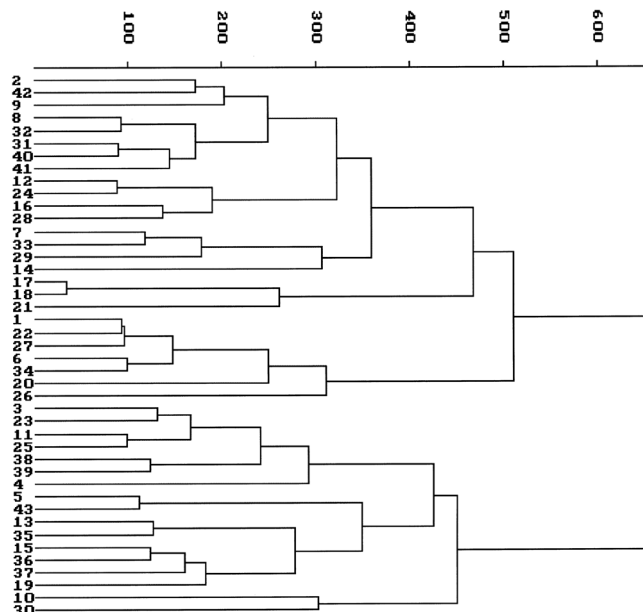**Fig. 14** Tree resulting from the UPGMA (Average Linkage). Codes as in **Tables 1** and **2**.

Fig. 15 Tree resulting from the Complete Linkage. Codes as in **Tables 1** and **2**.

3.1. Analysis of floral characters

The allometric relationships between corona and perianth tube (allometric CT, **Table 3**) show a noteworthy variation pattern starting from the ancestor species (*N. nevadensis*), in the sense of Fernandes (1951), leading to the more evolved species *N. cyclamineus*. The rapport CTT

(Corona length x Tepal width / Tube length x Tepal length) obtained from dividing the allometric CT by Twl is used as an index for separating the Section Cyclaminopsis and Series Lutei (both with values surpassing 1) from the Section Minores, Series Nevadensis, Series Longispathis and Series Pseudonarcisis all with values below 1.

Spathe length, when compared with pedicel length, may give some information about possible evolutionary patterns. The longer spathes are characteristic of *N. longispathus, N. leonensis* and *N. yepesii.* In the case of *N. leonensis,* a hexaploid, the longer spathe is associated with a short pedicel (c. 20 mm) while *N. longispathus* and *N. yepesii* show longer pedicels (exceeding 50 mm). The coincidence of a long spathe and long pedicel points to a primitive syndrome connecting this group with the subgenus *Narcissus.* A longer spathe and pedicel are both associated to the presence of two, three or four flowers per scape. A shorter spathe seems derivate and associated to single flowered stems, and short pedicels. These latter forms may have originated far from the ancestral center in SE Spain.

Table 4 Distribution by biogeographical provinces of the different wild taxa. (M) Mediterranean region, (T) Eurosiberian region. (C) Only known as cultivated, (W) Wild populations known. Names of biogeographical units (provinces and sectors) after Rivas-Martínez (1987 1991) and Rivas-Martínez and Loidi (1999). Limits of each province are given in **Fig 1**.

Taxa and status	Biogeography (Provinces)
Narcissus abscissus (Haw.) Schultes fil. (W)	(T) Cevennen-Pyrenean and (T) Orocantabrian
Narcissus abscissus (Haw.) Schultes fil. var. *serotinus* (Jord.) Pugsley (W)	(T) Cevennen-Pyrenean
Narcissus abscissus (Haw.) Schultes fil. var. *tubulosus* (Jord.) Pugsley (W)	(T) Cevennen-Pyrenean
Narcissus albescens (Haw.) Pugsley (W)	(T) Atlantic-Cantabrian
Narcissus alcaracensis Ríos *et al.* (W)	(M) Baetic
Narcissus alpestris Pugsley. (W)	(T) Pyreanean and (M) Aragonian
Narcissus asturiensis (Jord.) Pugsley. (W)	(T) Orocantabrian
Narcissus asturiensis (Jord.) Pugsley. subsp. *villarvildensis* (T.E. Díaz & T. Prieto) Rivas-Martínez *et al.* (W)	(T) Orocantabrian and (M) Carpetan-Leonesian
Narcissus bicolor L. (W)	(T) Cevennen-Pyrenean
Narcissus bujei (Fernández Casas) Fernández Casas. (W)	(M) Baetic
Narcissus calcicarpetanus Fernández Casas. (W)	(M) Castillian-Maestracean-Manchegan
Narcissus confusus Pugsley. (W)	(M) Carpetan-Leonesian
Narcissus cyclamineus DC. (W)	(T) Atlantic-Cantabrian
Narcissus eugeniae Fernández Casas (W)	(M) Castillian-Maestracean-Manchegan and (M) Carpetan-Leonesian
Narcissus fontqueri Fernández Casas & Rivas Ponce (W)	(M) Carpetan-Leonesian
Narcissus gayi (Henon) Pugsley (C)	(T) Subatlantic
Narcissus gayi (Henon) Pugsley var. *praelongus* (Jord.) Pugsley (C)	(T) Subatlantic
Narcissus genesi-lopezii Fernández Casas (W)	(M) Castillian-Maestracean-Manchegan
Narcissus hispanicus Gouan (W)	(T) Subatlantic
Narcissus hispanicus Gouan var *concolor* (Jord.) Pugsley (W)	(M) Valencian-Catalonian-Provenzal
Narcissus jacetanus Fernández Casas (W)	(T) Cevennen-Pyrenean
Narcissus x *johnstonii* Pugsley (W?)	(T) Atlantic-Cantabrian
Narcissus leonensis Pugsley (W)	(T) Orocantabrian
Narcissus longispathus Pugsley (W)	(M) Baetic
Narcissus macrolobus (Jord.) Pugsley (W)	(T) Cevennen-Pyrenean
Narcissus minor L. (C)	(T) Gardens of Europe (Subatlantic, Britanian, etc.)
Narcissus moleroi Fernández Casas (W)	(T) Subatlantic
Narcissus moschatus L. (W)	(T) Subatlantic
Narcissus munyozii-garmendiae Fernández Casas (W)	(M) Luso-Extremadurenian
Narcissus nevadensis Pugsley (W)	(M) Baetic
Narcissus nobilis (Haw.) Schultes fil. (W)	(T) Orocantabrian
Narcissus obvallaris Salisb. (W)	(M) Luso-Extremadurenian
Narcissus pallidiflorus Pugsley (W)	(T) Atlantic-Cantabrian
Narcissus parviflorus (Jord.) Pugsley (W)	(T) Cevennen-Pyrenean
Narcissus perez-chiscanoi Fernández Casas (W)	(M) Luso-Extremadurenian
Narcissus portensis Pugsley (W)	(T) Cantabrian -Atlantic
Narcissus primigenius (Fernández Suarez ex Laínz) Fernández Casas & Laínz (W)	(T) Orocantabrian
Narcissus provincialis Pugsley (W)	(M) Valencian-Catalonian-Provenzal
Narcissus pseudonarcissus L. (British auct)	(T) Subatlantic
Narcissus pseudonarcissus L. var. *festinus* (Jord.) Pugsley (W)	(T) Subatlantic
Narcissus pseudonarcissus L. var. *montinus* (Jord.) Pugsley (W)	(T) Subatlantic
Narcissus pseudonarcissus L. var. *platylobus* (Jord.) Pugsley (C)	(T) Subatlantic
Narcissus pseudonarcissus L. var. *porrigens* (Jord.) Pugsley (W)	(T) Subatlantic
Narcissus radinganorum Fernández Casas (W)	(M) Valencian-Catalonian-Provenzal
Narcissus segurensis Ríos *et al.* (W)	(M) Baetic
Narcissus tortuosus Haworth (W)	(T) Atlantic-Cantabrian
Narcissus vasconicus (Fernández Casas) Fernández Casas (W)	(T) Atlantic-Cantabrian and (T) Cevennen-Pyrenean
Narcissus yepesii Ríos *et al.* (W)	(M) Baetic

3.2. Systematics

Taxa above the species level and below the subgenus may be distinguished according to the trees (**Figs. 14, 15**) but these are not so clear-cut as presented by Pugsley (1933). The systematic scheme is presented in **Table 1**. The subgenus is divided in 3 sections and 7 series. It differs mainly from the systematics proposed by Pugsley (1933) in recovering the rank of section, previously adopted by Haworth (1831) for the series Minores and by proposing two new series: Nevadensis and Longispathis for primitive isolated taxa endemic to SE Spain.

3.3. Arial of sections and series

Almost all sections and series (**Table 1**) extend over the whole area of the subgenus *Ajax*. Exceptions are represented by the section *Cyclaminopsis,* which is endemic to the NW Iberian Peninsula, in the Atlantic-Cantabrian province of the EuroSiberian region (**Fig. 1**; see *N. cyclamineus* in **Tables 2, 3**). Also series *Nevadensis* (*N. nevadensis* in **Table 1**) and series *Longispathis* (*N. longispathus*, **Tables 2, 3**) are endemic, both being restricted to SE Spain, within the Baetic province of the Mediterranean region (**Fig. 1**).

Table 5 Relative abundance of wild taxa of subgenus Ajax, organized by main biogeographical zones and provinces. Names of biogeographical units (provinces and sectors) after Rivas-Martínez (1987 1991). Limits of each province are given in **Fig. 1** Left: Total number of taxa living in the zone; Right: Total number of taxa which are endemic exclusive to the zone. In zone V are found other five species but these are only known in cultivation. Species comprise also infraspecific taxa.

	Zone I		Zone II		Zone III		Zone IV		Zone V	
Sections	2	0	2	0	2	0	3	1	2	0
Series	4	2	2	0	2	0	4	0	4	0
Species	6	6	7	6	7	6	13	10	19	12

Provinces	EUROSIBERIAN REGION	
Cevennean-Pyrenean		9
Orocantabrian		6
Atlantic-Cantabrian		7
Subatlantic		9
Provinces	**MEDITERRANEAN REGION**	
Baetic		7
Aragonian		1
Carpetanic-Iberian		4
Valencian-Catalonian-Provenzal		3
Luso-Extremadurenian		3

3.4. Distribution areas and biogeographical zones

A high percentage of subgenus *Ajax* taxa grow in the EuroSiberian region. Most of these are endemic to the Iberian Peninsula. There are only two taxa whose areas cross the limits between the Mediterranean and Eurosiberian regions (*N. alpestris* and *N. asturiensis* subsp. *villarvildensis*; **Table 4**) the rest is either exclusive to one or the other region (29 EuroSiberian and 17 Mediterranean). Seemingly EuroSiberian taxa outnumbered those from the Mediterranean. However, five of the EuroSiberian taxa are only known as "cultons", thus not found in the wild. These are presumably cultigens of hybrid origin. A further group of six strictly EuroSiberian taxa is recognized in recent studies only to merit treatment at infraspecific level, thus varietal. Therefore the number of "true" EuroSiberian taxa is reduced drastically to only six species.

When considering the biogeographical provinces as recognized by Rivas-Martínez (1987), there are five relevant zones accounting for 6 or more taxa (**Table 4**). The sub-Atlantic province seems to be the richest in numbers of taxa, but it must be discarded as a relevant center of primary genetic diversity because part of these eleven taxa are found only in gardens (presumably cultigens). These sub-Atlantic cultivars, interpreted by botanists in terms of subspecies or species, have presumably originated under cultivation by selection and breeding starting mainly from introduced species. In contrast in the Cevennean-Pyrenean province, the populations of Daffodils are nearly exclusive of natural habitats and this area may be taken as the major center of genetic diversity for this subgenus, because here two of the three sections and four of the seven series in which the genus is divided are found. The presence of six endemic exclusive taxa to the Baetic province (Mediterranean Region) is also notable (**Tables 4, 5**). The relevance of the Baetic province becomes clearer after considering the presence of two endemic exclusive series: series *Nevadensis* and *Longispathis* (**Table 1**).

3.5. Major habitat types

Amongst the 48 taxa analyzed, 28 are restricted to a single habitat type. The remaining 20 taxa grow in two or more different types of habitats. Up to 12 taxa are able to grow in 2 different habitat types, 6 in 3 types and 2 in 4 types (**Tables 6, 7**). The widest ecological plasticity is shown by *N. alpestris*, a species that is able to colonize a high number of diverse habitat types (deciduous forests, pine forests, grasslands and thickets) and *N. pallidiflorus* (deciduous forests, grasslands, wet grasslands and riparian communities; **Table 6**). These are potential material for obtaining cultivars able to grow in a wider range of garden conditions.

Both deciduous forest (18 taxa) and wet grasslands (including large sedge formations) (26 taxa) are the most common environments for species of subgenus *Ajax* (**Table 7**). Thickets with 11 taxa and grasslands with 9 taxa are also habitats favorable for daffodils. Riparian communities (5 taxa) and pine forests (4 taxa) are less common habitat types for wild daffodils. The prevalence of wet grasslands over the forests and other habitat types is more markedly found in the Mediterranean region (**Table 7**). The southwestern EuroSiberian region (Pyrenees, Southern France) now offers favorable conditions for daffodils, in which there is a wide range of habitats available for these species: bogs, thickets, pine forests, together with the aforementioned deciduous forests and wet grasslands (**Tables 6, 7**). However some particularly interesting daffodil habitats are far north found in deciduous oak woods of Cumbria in the British Isles (Lemmey 2005).

Last, but not least, gardens became a relevant habitat for daffodil evolution. Unconscious selection brought about by the fact that the plants concerned were transported from their original wild environments into new (and usually very different) human-made environments (Zohary 1997).

3.6. Altitudinal ranges and bioclimatic belts

Wild relatives of trumpet daffodils grow in the Iberian Peninsula within an altitudinal range from 100 m in the Portuguese coast to above 2,400 m in the Pyrenees. Most taxa grow in intermediate environments at 600-1,800 m altitude, under subhumid or humid climates, in supra Mediterranean or montane belts. There the high humidity is associated to relatively mild spring temperatures (**Tables 6, 7**).

The major concentration of taxa within the Mediterranean region is in the supra Mediterranean vegetation belt. The summits of the mountains do not offer favorable conditions for the development of daffodils belonging to the subgenus *Ajax.* At altitudes above 2,000 m, corresponding to the crioro Mediterranean and Alpine bioclimatic belts daffodils of this group are very rare (**Tables 6, 7**).

The favorable distribution of rainfall and/or relative air humidity in the Coline and Montane circles of the EuroSiberian region, which is associated with moderate temperatures at flowering time for daffodils, could explain the higher abundance of plants of this group at lower altitudes when compared with the Mediterranean region (**Tables 8, 9**).

3.7. Climates

Persistent drought is harmful for bulbs, leaves and flowers of daffodils of the subgenus *Ajax.* These plants are not found in arid and semiarid

zones of the Iberian Peninsula, being rare in dry zones with precipitation below 500 mm. Thus the minimal average precipitation for normal development of natural populations is approximately 550-650 mm. Most taxa grow in zones with an average rainfall comprising between 800-1,400 mm (subhumid, humid or perhumid; **Table 9**), both in the EuroSiberian and Mediterranean regions.

Winter precipitation may occur in the form of snow in the natural habitats of most of these plants. The persistence of the snow layer varies from a few days a year, even none in the case of *N. obvallaris,* or *N. perezchiscanoi,* to several months as it occurs for the upper limit of the area of *N. moleroi.*

Table 6 Plant communities and habitat types for taxa of *Narcissus* subgenus *Ajax*. (List of the plant communities and groups: *Aceri granatensis-Quercion fagineae* (Rivas Goday, Rigual & Rivas-Martínez in Rivas Goday, et al. 1960) Rivas-Martínez 1987, *Agrostion castellanae* Rivas Goday 1958 corr. Rivas Goday & Rivas-Martínez 1963, *Alnion incanae* Pawlowski in Pawlowski, Sokolowski & Wallisch 1928, *Blechno-Fagetum sylvaticae* (Tüxen & Oberdorfer 1958) Rivas-Martínez 1963, *Blechno spicanti-Quercetum roboris* Tüxen & Oberdorfer 1958, *Brizo-Holoschoenion* Rivas Goday 1964, *Buxo sempervirentis-Fagetum sylvaticae* Br.-Bl. ex Br.-Bl. & Susplugas 1937, *Calluno-Uliceta* Br.-Bl. & Tüxen ex Klika & Hadac 1944, *Caricetalia curvulae* Br.-Bl. in Br.-Bl. & Jenny 1926, *Carici sylvaticae-Fagetum sylvaticae* (Rivas-Martínez 1965) C. Navarro 1982, *Echinospartion horridi* Rivas-Martínez, T.E. Díaz, F. Prieto, Loidi & Penas 1991, *Ericion tetralicis* Schwickerath 1933, *Festucion eskiae* Br.-Bl. 1948, *Festuco-Brometea* Br.-Bl. & Tüxen ex Br.-Bl. 1949, *Genistion polygaliphyllae* Rivas-Martínez, T.E. Díaz, F. Prieto, Loidi & Penas 1984, *Geo urbani-Coryletum avellanae* F. Valle, Mota & Gómez-Mercado 1986, *Holoschoenion* Br.-Bl. 1931, *Juncion acutiflori* Br.-Bl. in Br.-Bl. & Tüxen 1952, *Magnocaricion elatae* Koch 1926, *Molinio-Arrhenatheretea* Tüxen 1937, *Nardetalia strictae* Oberdorfer ex Preising 1949, Nardion strictae Br.-Bl. in Br.-Bl. & Jenny 1926, *Pinion uncinatae* Rivas-Martínez & Costa 1998, *Quercetalia pubescentis* Klika 1933, *Quercion pyrenaicae* Rivas Goday ex Rivas-Martínez 1965, *Querco-Fagetea* Br.-Bl. & Vlieger in Vlieger 1937, *Salicetalia purpureae* Moor 1958, *Seslerietalia coeruleae* Br.-Bl. in Br.-Bl. & Jenny 1926, *Violion caninae* Schwickerath 1944).

Plant communities	Taxa
DECIDUOUS FORESTS	
Siliceous Beech forests (*Blechno-Fagetum*)	*Narcissus asturiensis*; *N. asturiensis* subsp. *villarvildensis*; *N. leonensis*; *N. nobilis*; *N. pallidiflorus*; *N. provincialis*
Calcicolous beech forests (*Carici-Fagetum*; *Buxo -Fagetum*).	*Narcissus hispanicus*; *N. jacetanus*; *N. moleroi*; *N. vasconicus*
Deciduous hazelnut and mountain elm forests (*Geo-Coryletum avellanae*)	*Narcissus segurensis*
Deciduous oak forests (*Blechno-Quercetum roboris*)	*Narcissus asturiensis*; *N. asturiensis* subsp. *villarvildensis*; *N. nobilis*
Deciduous oak forests (*Quercion pyrenaicae*)	*Narcissus confusus*; *N. eugeniae*; *N. muyozii-garmendiae*; *N. pallidiflorus*; *N. perez-chiscanoi*
Calcicolous deciduous oak forests (*Quercus pubescens*) (*Querco-Fagetea*)	*Narcissus hispanicus* var *concolor*
Quercus faginea woods (*Aceri-Quercion fagineae*)	*Narcissus alpestris*; *N. jacetanus*; *N. longispathus*
PINE FORESTS	
Pinus pinea and *Pinus pinaster* woods (siliceous sandy soils)	*Narcissus portensis*
Pinus sylvestris forests	*Narcissus alpestris*
Pinus uncinata forests (Pinion uncinatae)	*Narcissus abscissus*, *N. alpestris*; *N. bicolor*
GRASSLANDS	
Calcicolous grasslands	*Narcissus vasconicus*
Grasslands (*Festuco-Brometea*)	*Narcissus asturiensis*; *N. pallidiflorus*
Grasslands (*Seslerietalia*)	*Narcissus asturiensis*
Silicicolous grasslands (*Nardetalia*)	*Narcissus abscissus*; *N. alpestris*; *N. asturiensis*; *N. confusus*; *N. fontqueri*; *N. leonensis*
Xerobromion	*Narcissus moleroi*
WET GRASSLANDS	
Large sedge communities (*Magnocaricion elatae*)	*Narcissus alcaracensis*
Calcicolous wet grasslands (*Holoschoenion*)	*Narcissus bujei*; *N. calcicarpetanus*; *N. eugeniae*; *N. genesi-lopezii*; *N. nevadensis*; *N. radinganorum*; *N. yepesii.*
Silicicolous wet grasslands (*Juncion acutiflori*)	*Narcissus confusus*; *N. cyclamineus*; *N.* x *johnstonii*; *N. munyozii-garmendiae*; *N. nevadensis*
Silicicolous wet grasslands (*Violion caninae*)	*Narcissus eugeniae*
Silicicolous wet grasslands (*Agrostion castellanae*)	*Narcissus obvallaris*
Silicicolous wet grasslands (*Brizo-Holoschoenion*)	*Narcissus perez-chiscanoi*
Silicicolous wet grasslands (*Caricetalia curvulae*: *Festucion eskiae*)	*Narcissus moleroi*
Silicicolous wet grasslands (*Caricetalia curvulae*: *Nardion strictae*)	*Narcissus macrolobus*
Wet grasslands (*Molinio-Arrhenatheretea*)	*Narcissus abscissus* var. *serotinus*; *N. abscissus* var. *tubulosus*; *N. albescens, N. nobilis*; *N. parviflorus*; *N. pallidiflorus*; *N. primigenius*; *N. pseudonarcissus*; *N. pseudonarcissus* var. *festinus*; *N. tortuosus*
Bog borders *Caricetalia fuscae* (*Ericion tetralicis*)	*Narcissus obvallaris*; *N. pallidiflorus*; *N. primigenius*
RIPARIAN COMMUNITIES	
Alnus glutinosa riparian woods and thickets (*Alnion incanae*)	*Narcissus cyclamineus*; *N. pallidiflorus*; *N. tortuosus*
Calluno-Ulicetea; riparian communities	*Narcissus nobilis*
Riparian communities (*Salicetalia purpureae* and related)	*Narcissus longispathus*
THICKETS AND SCRUBS	
Arctostaphylos uvaursi scrublands	*Narcissus alpestris*
Broom fields (*Genistion polygaliphyllae*)	*Narcissus asturiensis*; *N. asturiensis.* subsp. *villarvildensis*
Buxus sempervirens thickets	*Narcissus abscissus*, *N. alpestris*
Calcicolous *Echinospartum horridum* scrubs (*Echinospartion horridi*)	*Narcissus alpestris*; *.N. jacetanus*
Heaths and Hedgehog heaths (*Calluno-Ulicetea*)	*Narcissus albescens*; *N. fontqueri*; *N. primigenius*; *N. pseudonarcissus* var. *montinus*; *Narcissus pseudonarcissus* var. *porrigens*
Juniper and bog myrtle scrubs	*Narcissus leonensis*
Rhododendron ferrugineum scrublands	*Narcissus alpestris*
GARDENS	
Gardens (unknown in the wild)	*Narcissus gayi*; *N. gayi* var. *praelongus*; *Narcissus minor*; *Narcissus moschatus*; *Narcissus pseudonarcissus* var. *platylobus*

Table 7 Relative abundance of wild taxa in the different habitat types in the Eurosiberian and Mediterranean regions. Between brackets appear the numbers of wild taxa, which are exclusive to this particular group of habitats.

	Deciduous forests	Pine forests	Thickets	Large-sedge formations	Wet grasslands	Dry grasslands	Only known in cultivation
Mediterranean	9 (4)	1 (0)	1 (0)	1 (1)	11 (6)	3 (0)	0
Eurosiberian	12 (1)	5 (2)	10 (3)	0	8 (4)	7 (1)	5 (0)

Table 8 Relative abundance of wild taxa by altitudinal range and average precipitation. The total number of studied taxa is 48 but several amongst these have a relatively large altitudinal and precipitation - temperature range, thus overlapping in several categories.

EuroSiberian Region					
Altitude			**Climate**		**Totals**
	Dry-subhumid	**Subhumid**	**Humid**	**Perhumid**	
above 2400 m	0	0	0	0	0
1800-2400 m	0	1	2	0	3
1200-1800 m	0	3	11	3	17
600-1200 m	0	1	10	2	13
0-600 m	0	8	6	4	18
Totals	0	13	29	9	51
Mediterranean Region					
above 2400 m	0	0	0	0	0
1800-2400 m	0	0	0	0	0
1200-1800 m	0	8	8	0	16
600-1200 m	1	9	4	0	14
0-600 m	0	2	0	0	2
Totals	1	19	12	0	32

Table 9 Distribution of taxa in the different vegetation belts. Numbers represent total of taxa present in each belt.

	Meso	**Supra**	**Oro**	**Crioro**
Mediterranean	4	14	4	0
	Coline	**Montane**	**Subalpine**	**Alpine**
Eurosiberian	7	16	9	0

4. DISCUSSION

4.1. Reproduction and matting patterns in wild habitats and gardens

Trumpet daffodils, as many other wild geophytes reproduce and get disseminated in the wild mostly by seed (Zohary 1997). Sexual reproduction is the rule and outcrossing is usually assured by self-incompatibility or by other devices that prevent selfing. However there is a strong tendency in this group to form clumps in which vegetative propagation is equally relevant. The *Narcissus* that grows in the bogs of Cabañeros National park (Spain) form bulbs, above soil level, in summer that are disseminated by occasional flooding of the Alcobillas river. Daffodil growers use vegetative propagation to "fix" attractive types, and to maintain them as vegetative clones under cultivation. Cultivars are, thus, not true races. They represent only clones derived from "exceptional individuals" picked up by the grower from the original wild populations or from among segregating products of artificial crosses between types (Zohary 1997).

Population dynamics of wild trumpet daffodil was modeled in the seminal works of Barkham (1980a 1980b 1992) and Barkham and Hance (1982), analyzing the relative contribution of clonal growth and sexual reproduction to the clumps. Barkham (1992) experimentally demonstrated in ancient English deciduous woodlands that daffodil clonal growth rate was density-dependent but establishment of plants from seed was not. Mortality was density-independent, except at high density in open ground, and clonal growth was twice as fast in open ground as in shaded sites.

Narcissus species display a late-acting self-sterility system associated with stylar polymorphisms, with self-sterility expressed in the ovary. Self-pollinations result in little seed set, cross-pollinations produce variable quantities of seed, and prior self-pollination causes significant reductions in outcrossed seed set (Barrett *et al.* 2000). Stigma-height dimorphism is distributed in numerous species of the sections *Apodanthae*, *Jonquilla* and *Tazettae*, however heterostyly is only reliably reported in a few species (Barret *et al.* 2000, Arroyo 2002, Pérez *et al.* 2003). Most *Narcissus* species with stylar polymorphisms produce multi-flowered inflorescences whereas the majority of those with stylar monoporphism are solitary flowered. Perhaps because floral designs that reduce levels of self-interference should be selectively advantageous in the genus (Barrett *et al.* 2000). The multiflowered spathae in some taxa of the subgenus *Ajax* points in favor of a relationship with the multiflowered subgenus *Narcissus,* or, simply, suggest a similar stylar polymorphism (not yet described in this subgenus). The origin of stylar polymorphisms in *Narcissus* may have been initially stimulated by the spread of short-styled variants in ancestral long-styled populations because their morphology reduced levels of self-interference. However Arroyo (2002) reported for the whole subgenus *Ajax* stylar monomorphism associated with hercogamy.

Flowers in subgenus *Ajax* are with large funnel-like coronas and short, wide or highly funnel-form floral tubes. These are pollinated by a wide range of small- and large-bodied bees that generally forage for pollen from anthers enclosed within the corona (Graham and Barrett 2004).

Within *Narcissus,* subgenus *Ajax* is closely related to sections *Narcissus* and *Bulbocodium*. Section *Narcissus* differs from subgenus *Ajax* in the longer coronas. Subgenus *Ajax* mainly differs from section *Bulbocodium* in the wider leaves and sepals. The basic chromosome number for the three groups is x = 7.

Spontaneous intersectional hybridization of members of subgenus *Ajax* is frequent. Up to 24 different hybrids of this type are recorded (RHS 2000 2005a). Amongst these hybrids six are with each one of sections *Narcissus, Jonquilla* and *Bulbocodium*, five with section *Ganymedes* and only one with section *Tazettae*. Recent molecular phylogeny studies (Graham and Barrett 2004) show close relationships of subgenus *Ajax* with section *Jonquilla* (*N. assoanus, N. gaditanus*), section *Tapeinanthus* (*N. cavanillesii*), section *Narcissus* (*N. poeticus*) and section *Ganymedes* (*N. triandrus*).

4.2. Chromosome numbers and relationships with habitat diversity

Brandham (1986) and Brandham and Kirton (1987) reviewed chromosome numbers and ploidy levels in *Narcissus*. Further counts are recorded in TROPICOS (2006). However only chromosome number counts for 29 wild taxa of subgenus *Ajax* out of the 43 studied (**Table 10**) are available. Diploids are predominant (24 taxa), 4 taxa are triploid, 6 are tetraploid and 3 hexaploid. The miniature or dwarf trumpet daffodils grown in gardens are usually diploid (those of Divisions 6 and some of Divisions 4 and 13).

Polyploids are relatively rare in the subgenus *Ajax* (**Table 10**). Amongst the rare polyploids, the majority live in the Eurosiberian zone, and are much more rare in the Mediterranean region. Polyploids are able to grow in an extremely diverse number of habitats, being found amongst these the more recently colonized by this subgenus (thickets, mountain grasslands and forest borders). Only *N. alpestris* and *N. pallidiflorus* are able to colonize up to four different habitat types. The former is a diploid, but from the latter both diploid and tetraploid populations are known. Among the six taxa with known chromosome number, that are able to colonize up to three different habitat types only one is exclusively diploid (*N. abscissus*) while the five are diploid to tetraploid or hexaploid (*N. asturiensis, N. confusus, N. leonensis, N. pallidiflorus, N. nobilis*). Most of the diploid taxa are only able to colonize one single type of habitat.

Diploid taxa are dominant in the Mediterranean Region (**Tables 4, 10**), and only two cases of tetraploidy are reported from there. These tetraploid taxa live in the borderline of the Mediterranean and EuroSiberian regions in the Iberian Peninsula. There is a considerable increase in ploidy level in the latter region. Diploidy has been reported in twenty-four taxa, triploidy in four taxa, tetraploidy in six taxa and hexaploidy in three taxa (**Table 10**). Polyploids might have originated through the functioning of 2n (unreduced) gametes, thus are sexual polyploids (Harlan and De Wet 1975, Ramana and Jacobsen 2003). Occurrence of 2n-gametes in ornamental *Narcissus* has been reported (Brandham 1986, Tuyl and Lim 2003).

Sexual polyploids are a major resource for obtaining taller daffodils. Breeders also occasionally induce polyploid conversion of daffodils with Orzyalin and other chemicals. However diploid large-flowered tall daffodil species are common in the section *Pseudonarcissus*. Induced polyploidy starting from these materials might be a shortcut for improvement of extra-large flowered daffodil cultivars.

Intersubgeneric hybrids are frequent both in nature and under cultivation (Webb 1980). Triploids are relatively rare in nature, but a good example of this level is documented for *N. x johnstonii*, which according to Fernandes (1946) is a hybrid of *N. pseudonarcissus* sl. (tetraploid) and *N. triandrus* L. (diploid) with a double set of chromosomes from the former and a single set from the latter. Brandham and Kirton (1987) reported examples of fertile allotriploids among *Narcissus* species.

Table 10 Chromosome numbers. Data from Brandham and Kirton (1987), Pugsley (1933); Sañudo (1984), Webb (1980), TROPICOS (2006). **A**. Relative abundance of each ploidy level expressed in number of wild taxa. **B**. Taxa with known chromosome numbers.

A

	Diploid	Triploid	Tetraploid	Hexaploid
Nº Taxa	24	4	6	3

B

	n	2n
Narcissus abscissus (Haw.) Schultes fil.	-	14
Narcissus alpestris Pugsley.	-	14
Narcissus asturiensis (Jord.) Pugsley.	7, 14?	14, 28?
Narcissus asturiensis (Jord.) Pugsley. subsp. *villarvildensis* (T.E. Díaz & T. Prieto) Rivas-Martínez et al..	-	28
Narcissus bicolor L.	-	14
Narcissus bujei (Fernández Casas) Fernández Casas.	7	14
Narcissus calcicarpetanus Fernández Casas.	-	14
Narcissus confusus Pugsley.	-	14, 28
Narcissus cyclamineus DC.	-	14
Narcissus eugeniae Fernández Casas	-	14
Narcissus genesi-lopezii Fernández Casas	-	14
Narcissus hispanicus Gouan	-	14, 21
Narcissus jacetanus Fernández Casas	7	14
Narcissus x *johnstonii* Pugsley	-	21
Narcissus leonensis Pugsley	21	24?, 42
Narcissus longispathus Pugsley	-	14
Narcissus macrolobus (Jord.) Pugsley	-	14
Narcissus minor L.	-	14
Narcissus moleroi Fernández Casas	-	14
Narcissus moschatus L.	-	14
Narcissus muyozii-garmendiae Fernández Casas	7	14
Narcissus nevadensis Pugsley	-	14
Narcissus nobilis (Haw.) Schultes fil.	-	28, 42?
Narcissus obvallaris Salisb.	-	14
Narcissus pallidiflorus Pugsley	14	14, 28
Narcissus primigenius (Fernández Suarez ex Laínz) Fernández Casas & Laínz	-	14
Narcissus provincialis Pugsley	-	14
Narcissus pseudonarcissus s.l.	-	14, 21, 43
Narcissus tortuosus Haworth,	-	21, 28

4.3. Habitat specialization and adaptive features

The diploid ancestral species *N. nevadensis* (Fernandes 1951) habits wet grasslands (sedge formations) in the Mediterranean Region. The more closely related species (*N. longispathus, N. bujei, N. alcaracensis*), which are diploid as far as their chromosome numbers are known (**Table 10**), grow in similar habitats (**Table 6**).

Permanently inundated areas are not favorable habitats for daffodils of subgenus *Ajax*. Nevertheless there are three hygrophilous species that colonize this type of habitat. One diploid and tetraploid species (*N. pallidiflorus*) inhabit bogs of the EuroSiberian zone (**Fig. 10**). Other diploid species (*N. obvallaris*) grow in similar environments but within the Mediterranean Region. A third diploid species (*N. primigenius*) is able to grow in bogs both within EuroSiberian and Mediterranean Regions (**Table 6**). Only *N. alcaracensis* is exclusive of *Carex* formations included in the Alliance *Magnocaricion elatae* (fen sedge beds and basiphilous bogs with rushes, inundated most of the year but occasionally dry; **Fig. 7**).

Pine forests (**Fig. 4**), thickets (**Fig. 13**) and mountain grasslands (**Fig. 8**) seem to have been colonized from the primary wet grasslands, a long time after the first diversification process occurred in SE Spain. This expansion of habitat types may have been associated with the dispersal of this group in the EuroSiberian Region after the Last Glacial Maximum (c. 18,000 BC).

The sedge formations (wet grasslands) (**Fig. 10**) inhabiting wet substrates are the most common plant community and habitat type for this subgenus (21% of the taxa are exclusive to those communities and habitats). The fidelity of daffodils of subgenus *Ajax* is less pronounced in the case of deciduous forests and woodlands (**Figs. 2, 3**; 43% of the taxa grow in this habitat but only 10% are exclusive). The southern limit for daffodils living within forests and woodlands is in the Sierra de Segura (Jaén) with *N. segurensis* that grows under the canopy of *Quercus pyrenaica* trees.

Small flowered daffodil taxa are prevalent in climax forests or their substitution formations (thickets and dry grasslands; **Fig. 5**). The larger flowers are typical of open habitats with a shallow water table (wet grasslands, sedge communities, etc.; **Figs. 6, 7, 10**). Although pollinators prefer large flowers, experimental reduction in flower diameter did not affect seed production (Worley *et al*. 2000), therefore pollinators are not the major factor leading to selection for large flowers.

The daffodils of subgenus *Ajax* show staggered flowering from February to July. This period ends a bit earlier, in June, at altitudes below 1,500 m.a.s.l. Daffodils start to blossom a bit later, in March at altitudes above 1,500 m. *Narcissus confusus, N. cyclamineus, N. hispanicus, N. pallidiflorus, N. portensis, N. munyoziigarmendiae,* and *N. vasconicus* are the earliest, thus starting blossom in February. *Narcissus abscissus, N. albescens, N. alpestris, N. asturiensis* and *N. jacetanus* are the latest, but long-lasting, still in blossom in July. All taxa overlap their flowering period in April, thus temporal barriers for intercrossing are lacking. *Narcissus alcaracensis, N. leonensis* and *N. longispathus* are the latest in blossom at altitudes below 1,500 m. These grow in riparian communities (**Fig. 11**) or wet grasslands (**Fig. 10**), at c. 1,000 m.a.s.l.

Several features show a gradual reduction from South to North, such as smaller number of flowers per stem and shortening of pedicel and spathe. Conversely there is an increase in corolla size, number of leaves and bulb size. The albino forms and the presence of deflexed perianth segments are exclusive to the Northern part of the distribution area of subgenus *Ajax.*

Worley *et al*. (2000) showed that flower number varied negatively with flower diameter among 45 *Narcissus* species, which supports a trade-off between these traits. However, in contrast, an intrapopulational positive relation between flower number and diameter could be found.

4.4. Biogeographical comparison of the taxonomical assemblages

From the three sections into which subgenus *Ajax* has been divided (**Table 1**) only the section *Cyclaminopsis* is concentrated in the NW part of the Iberian Peninsula. The two remaining sections are widespread within the subgenus area (both in Eurosiberian and Mediterranean regions), thus overlapping their areas. The Baetic province (included in zone I, **Fig. 1**) is likely the glacial refuge area and actual center of origin and diversity of the subgenus. However it is not the largest in number of species (**Tables 4, 5**). Sections *Pseudonarcissus* and *Minores* are represented within the Baetic province. Series *Lutei,* with the exception of *N. obvallaris*, is endemic exclusive to the EuroSiberian region (Zones IV and V, **Fig. 1**). Series *Minores,* though not reaching the Southern part of the Iberian Peninsula (Zone I, **Fig. 1**), extends to the Southern slopes of the Iberian Mountain range (Sistema Ibérico) in Central Spain. The bridge between series *Longispathis* (section *Pseudonarcissus*) and series *Minores* (section *Minores*) has recently been found. The transitional species filling this gap is *Narcissus alcaracensis*, an endemic to the NE Baetic sierras (Ríos *et al*. 1999).

Series *Nevadensis* and *Longispathis* are endemic to the Baetic province (included in Zone I, **Fig. 1**). These are more directly related to the subgenus *Narcissus* (on account of the floral morphology and the number of flowers per stem). Plants of the aforementioned series are among the taller and stouter of the subgenus, being only analogous to the wild hexaploid *N. leonensis* or to different vigorous taxa obtained in cultivation.

4.5. Cultivation

Under cultivation the shift in ecology leads to shifts in selection pressures. Numerous adaptations for survival in the wild lose their fitness advantages under the new set of conditions (Zohary 1997).

The relatively high air humidity in late winter and spring could explain the extraordinary relevance of trumpet daffodils as ornamental plants in gardens of Central Europe and the British Isles as opposed to the scarce representation of these taxa in Spanish Mediterranean gardens. In spite the center of origin and diversity for trumpet daffodils being in the mountain ranges of Spain, there are few suitable habitats for successful cultivation of trumpet daffodils in Mediterranean Region, outside of these mountains, in the inhabited zones. Climatic constraints such as low air humidity at flowering time may be invoked for this scarce impact of *Narcissus* subg. *Ajax* in Mediterranean gardens. However the experiences of daffodil cultivation in Murcia (SE Spain, with 280 mm of yearly precipitations) have shown successful use of autumn and winter flowering daffodil cultivars as excellent ornamental plants, even for gardens in dry areas. This led us to suppose that cultural factors were more relevant for the low interest in Spain for daffodils.

5. CONCLUSION

The pattern of ecological and geographical isolation detected may explain the high inter-populational variability which has been translated into taxonomic diversity, and has been interpreted in terms of genetic drift leading towards the emergence of species confined to small areas, microendemics associated to biogeographical criteria (isolated areas and ecological factors). The center of diversity of this subgenus is the region lying between Sierra Nevada in Southern Spain and the Northern Slopes of the Cantabric and Pyrenean mountains. Most taxa of this group grow in supra-Mediterranean and montane belts, at altitudes between 600 and 1,800 m above the sea level and under subhumid and humid precipitation regimes. The more relevant habitat types colonized by species of subgenus *Ajax* are deciduous forests (secondarily), and wet grasslands (primarily). Almost 90% of taxa are diploid, but triploid, tetraploid and hexaploid taxa may occur. Polyploids are rare in the southern part of the area.

Many aspects are open for new research specially concerning ecological comparisons of daffodils included in Division 13 of the Horticultural Classification (RHS 2000) and their wild populations. Phylogenetic studies may help in the understanding of the relationships among the different daffodil species and their patterns of evolution.

Taxonomy of this group of daffodils is mainly eclectic and relatively open to the acceptance of microspecies. This analytical approach needs further revision in order to determine synonyms that are to be expected more frequent on account of the high variability detected within some

populations. A modern general taxonomic study is much needed since those available are becoming obsolete.

The repertory of Trumpet Daffodil cultivars is based in a short number of wild relatives, most being diploid. The use of natural polyploids, and of large wild species (single or multiflowered) in the breeding experiences open promising opportunities to the development of a wide range of completely new cultivars and cultivar groups, hitherto unexpected.

ACKNOWLEDGEMENTS

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Appendix I. Wild taxa and references

Narcissus abscissus (Haw.) Schultes f. Pugsley (1933); Dorda, Rivas Ponce & Fernández Casas (1991); Villar (1980); Moreno & Sáinz (1992)

Narcissus abscissus (Haw.) Schultes f. var. ***serotinus*** (Jord.) Pugsley. Jordan (1903)

Narcissus abscissus (Haw.) Schultes f. var. ***tubulosus*** (Jord.) Pugsley. Jordan (1903)

Narcissus albescens (Haw.) Pugsley. Jordan (1903); Díaz *et aliis* (1994)

Narcissus alcaracensis Ríos *et. al.* Ríos *et al.* (1999)

Narcissus alpestris Pugsley. Pugsley (1933); Fernández Casas (1982b, 1986, 1996); Dorda & Fernández Casas (1990, 1994). Montserrat, J.M. (1987); Montserrat, G. (1987), Villar (1980); Moreno & Sáinz (1992)

Narcissus asturiensis (Jord.) Pugsley. Pugsley (1933); Jordan (1903); Moreno & Sáinz (1992); Rivas-Martínez, S. *et aliis* (1984); Nava (1995); Aseguinolaza *et aliis* (1984); Puente (1988)

Narcissus asturiensis (Jord.) Pugsley. subsp. ***villarvildensis*** (T.E. Díaz & T. Prieto) Rivas-Martínez *et aliis.* Rivas-Martínez, S. *et aliis* (1984); Puente (1988); Laínz (1982).

Narcissus bicolor L. Pugsley (1933)

Narcissus bujei (Fernández Casas) Fernández Casas. Valdés (1987); Fernández Casas (1982b); Dorda & Fernández Casas (1990 and 1994); Moreno & Sáinz (1992); Stocken (1969)

Narcissus calcicarpetanus Fernández Casas. Fernández Casas. 1982b, Dorda & Fernández Casas. 1990, 1994; Moreno & Sáinz (1992); Romero & Rico (1989)

Narcissus confusus Pugsley. Pugsley (1933: 59-60); Barra & López González (1983); Fernández Casas. (1982b); Dorda & Fernández Casas. (1990 and 1994); Moreno & Sáinz (1992); Romero & Rico (1989)

Narcissus cyclamineus DC. Fernández-Casas (1996); Merino (1909: 116-117); Pugsley (1933: 36-37); Rozeira (1946)

Narcissus eugeniae Fernández Casas. Fernández Casas (1982a and 1982b); Dorda & Fernández Casas (1990, 1994); Moreno & Sáinz (1992); Mendiola (1983); Rivas-Goday & Borja (1962)

Narcissus fontqueri Fernández Casas & Rivas Ponce. Castroviejo (1977); Fernández Casas & Rivas Ponce (1988); Nieto (1985)

Narcissus gayi (Henon) Pugsley. Pugsley (1933). Jordan (1903)

Narcissus gayi (Henon) Pugsley var. ***praelongus* (Jord.)** Pugsley. Jordan (1903)

Narcissus genesi-lopezii Fernández Casas. Fernández Casas (1987a); Dorda & Fernández Casas (1990 and 1994); Moreno & Sáinz (1992) Jordan (1903)

Narcissus hispanicus Gouan. Pugsley (1933). Specimen from Grasse (MA 299989); Gouan (1773)

Narcissus hispanicus var. ***concolor*** (Jord.) Pugsley. Jordan (1903)

Narcissus jacetanus Fernández Casas. Dorda & Fernández Casas (1994); Fernández Casas (1984b, 1986); Moreno & Sáinz (1992)

Narcissus leonensis Pugsley. Pugsley (1933); Dorda & Fernández Casas (1994); Nava (1995); Rivas-Martínez *et aliis.* (1984); Díaz *et aliis* (1994); Laínz (1982)

Narcissus longispathus Pugsley. Pugsley (1933). Webb *in* Tutin *et al.* 1980. Fernández Casas (1982b; 1996), Dorda & Fernández Casas (1994); Moreno & Sáinz (1992)

Narcissus macrolobus (Jord.) Pugsley. Pugsley (1933). Jordan (1903); Dorda, Rivas Ponce & Fernández Casas (1991); Carreras *et aliis* (1993)

***Narcissus minor* L. Pugsley** (1933)

Narcissus moleroi Fernández Casas. Dorda & Fernández Casas (1994). Typus: Herb. MA 29998. Fernández-Casas (1996); Vigo (1983); Moreno & Sáinz (1992); Romo (1989); Braun-Blanquet (1948)

Narcissus munyozii-garmendiae Fernández Casas. Fernández Casas (1982b; 1996); Dorda & Fernández Casas (1990 and 1994); Moreno & Sáinz (1992); Peinado (1980)

Narcissus nevadensis Pugsley. Pugsley (1933). Webb *in* Tutin *et al.* (1980); Fernández Casas (1982b; 1996), Dorda & Fernández Casas. (1990 and 1994); Moreno & Sáinz (1992); Molero & Pérez-Raya (1987); Stocken (1969)

Narcissus nobilis (Haw.) Schultes fil. Pugsley (1933); Webb *in* Tutin *et al.* (1980); Fernández Casas (1983), Aseguinolaza *et aliis* (1984)

Narcissus obvallaris Salisb. Pugsley (1933); Peinado (1980)

Narcissus pallidiflorus Pugsley. Pugsley (1933); Fernández Casas (1983); Dorda & Fernández Casas (1990); Aseguinolaza *et aliis* (1984); Díaz *et aliis* (1994); García, Bascones & Medrano (1985)

Narcissus parviflorus (Jord.) Pugsley. Pugsley (1933); Jordan (1903)

Narcissus perez-chiscanoi Fernández Casas. Moreno & Sáinz (1992); Peinado (1980)

Narcissus portensis Pugsley. Pugsley (1933); Webb *in* Tutin *et aliis* (1980); Dorda & Fernández Casas (1994); Fernández-Casas (1996)

Narcissus primigenius (Fernández Suarez ex Laínz) Fernández Casas & Laínz. Fernández Casas (1982b); Fernández Casas (1983b); Dorda & Fernández Casas (1994); Díaz *et aliis* (1994); Laínz (1982)

Narcissus provincialis Pugsley. Dorda & Fernández Casas (1994); Specimen from Gourdon (MA 192293)

Narcissus pseudonarcissus L. Pugsley (1933)

Narcissus pseudonarcissus L. var. ***festinus*** Pugsley. Jordan (1903)

Narcissus pseudonarcissus L. var. ***montinus*** Pugsley. Jordan (1903)

Narcissus pseudonarcissus L. var. ***platylobus*** Pugsley. Jordan (1903)

Narcissus pseudonarcissus L. var. ***porrigens*** Pugsley. Jordan (1903)

Narcissus radinganorum Fernández Casas. Fernández Casas (1984b); Dorda & Fernández Casas (1994); Peris (1983)

Narcissus segurensis Ríos *et al.* Ríos *et al.* (1999)

Narcissus tortuosus Haworth. Pugsley (1933); Dorda & Fernández Casas (1990); Díaz *et aliis* (1994)

Narcissus vasconicus (Fernández Casas) Fernández Casas. Dorda & Fernández Casas (1994); Fernández Casas (1984b and 1986); Moreno & Sáinz (1992)

Narcissus yepesii Ríos *et al.* Ríos *et al.* (1999)