Morphological variation of *Narcissus serotinus* L. *s.l.* (Amaryllidaceae) in the Iberian Peninsula

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A morphological study of *Narcissus serotinus* L. *s.l.* was carried out in 40 populations, mainly located in the south-west Iberian Peninsula, by the application of ordination and classification analysis to 42 vegetative and flower characters. Wide morphological variability was found in the species. A total of 19 characters clearly differentiated two groups as distinct species, but intraspecific variation, associated with geographical distribution, was found. One of the species aligned with *N. serotinus* L. *s.s.*, having a six-lobed yellow corona and one flower per scape, with a distribution restricted to the south-west Iberian Peninsula and north-west Morocco. The other species, distributed widely throughout the circum-Mediterranean region, and characterized by a three-lobed, orange-brownish corona and one to three flowers per scape, matched the description of *N. obsoletus* (Haw.) Steud. The historical application of this pre-Linnean name, given to a Spanish plant by Parkinson in 1629, and used subsequently by various authors, is doubtful, and thus its typification was necessary. Two other populations identified as *N. elegans* (Haw.) Spach were included in this study as a reference, and allowed characters in *N. obsoletus*, intermediate between those of *N. serotinus* and *N. elegans*, to be found, suggesting a hybridization process occurring in its area of origin.   © 2007 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2007, **154**, 237–257.

ADDITIONAL KEYWORDS: hybridization – Mediterranean region – north Africa – speciation – taxonomy – typification – Wells' distance diagram.

INTRODUCTION

Some geographical regions are especially suitable for the occurrence of species differentiation. One such region is the Mediterranean Basin (Quézel, 1978, 1985, 1995), where the evolution of the species has been affected by the complex geological and climatic history and, more recently, by human activities (Thompson, 2005). Areas of the Mediterranean Basin recognized as hot spots of biodiversity include the southern Iberian Peninsula and northern Morocco (Médail & Quézel, 1997), where floristic links and a common flora have been found (Valdés, 1991). The differentiation patterns of some species are related to this area (Vargas, Morton & Jury, 1999; Lumaret *et al.*, 2002; Hampe *et al.*, 2003). In this context, the genus *Narcissus* constitutes an interesting case, with about 70–80 species, mostly restricted to the western Mediterranean area. The Iberian Peninsula is the main centre of diversity of the genus (Hanks, 2002; Blanchard, 1990), from where it radiates towards south-west France, north Africa, and eastwards to Israel. All sections of the genus [except section *Aurelia* (*N. broussonettii*)] are represented in the Iberian Peninsula.

The taxonomy of *Narcissus* is difficult because it is undergoing active evolution via various processes, including incomplete morpho-geographical speciation, polyploidization, and hybridization (Fernandes, 1975; Webb, 1978). This makes it difficult to establish a taxonomic rank for varying populations. In addition to its ancient incorporation into culture as an ornamental, breeding selection and after-naturalization make taxonomic delimitation difficult (Webb, 1978). Studies of variation patterns, species delimitation, and genome relationships of Spanish taxa are of importance, providing an understanding of *Narcissus* and its biogeographical patterns in north-west Africa and southern Spain, where maximum diversity occurs.

Narcissus serotinus L. belongs to the monotypic section *Serotini* Parl., and is distributed along the coastal

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band surrounding countries in the southern Mediterranean region: southern and eastern Spain, southern Portugal, Balearic Islands, Corsica, Sardinia, Sicily, western and eastern Italy, Croatia, southern Greece, Crete, Cyprus, Israel, north-west Morocco, Algeria, Tunisia, and Libya [Fig. 1A; based on Fernandes (1951), and corroborated by standard floras]. In the Iberian Peninsula, *N. serotinus* L. *s.l.* extends inwards to Alto Alentejo (Portugal), towards the Guadalquivir river valley and Badajoz (Spain), and towards Oulmès in Morocco (Blanchard, 1990).

According to recent literature (Valdés, 1987; Fernández Casas, 2002) *N. serotinus* does not appear to be a conflictive species. Standard Mediterranean floras describe it with scarcely any morphological variation. Only Pérez Lara (1886), Fernandes (1951), Valdés & Müller-Doblies (1984) and Blanchard (1990) made reference to any variability in the general size of plants, bulb size, number of flowers per inflorescence, and shape and colour of the corona. Moreover, all authors, with the exception of Fernandes (1951), referred to this variability only in populations from the Guadalquivir river valley. However, this species has a certain karyological complexity, with three ploidy levels [diploid ($2n = 10$), tetraploid ($2n = 20$), and hexaploid ($2n = 30$)] observed, and a hypothesis about their origin has been postulated (Fernandes, 1951, 1975).

Several hybrids have been found and named in relation to other autumnal species. Thus, *N. serotinus* hybridizes with *N. cavanillesi* Barra & G. López (*N. perez-larae* Font Quer), *N. bertolonii* Parl. (*N. chevassutii* Gorenflot, Guin. & Quézel), *N. viridiflorus* Schousb. (*N. georgemawii* Fern. Casas and *N. alleniae* Donn.-Morg.), and *N. elegans* (Haw.) Spach (*N. elegans* var. *intermedius* J. Gay). Another autumnal species, *N. obsoletus* (Haw.) Spach, has been indistinctly referred to as a hybrid between *N. serotinus* and *N. viridiflorus* (Maire, 1958; Fernández Casas, 1984; Blanchard, 1990) or between *N. serotinus* and *N. elegans* (Fernández Casas, 1997, 2002). The typification of this name therefore becomes essential.

In south-west Spain, a certain flower polymorphism has been detected in plants recognizable as *N. serotinus*. Two flower morphotypes can be differentiated at a glance using certain clear traits, such as flower size, number of flowers per inflorescence, and corona colour (yellow or orange to orange-brownish). The names by which the two morphotypes are referred to later in the paper (yellow morphotype and orange morphotype) are related to the latter character. Thus, this study was undertaken to distinguish between these morphotypes in order to clarify the patterns of variation of *N. serotinus* in south-west Spain. Field sampling of populations from this region was undertaken. Additional reference populations from other regions, and some populations of *N. elegans* resembling one of the morphotypes, were sampled.

The objectives of this study were as follows: (1) to group the specimens into discrete, biologically meaningful entities; (2) to establish the taxonomic rank for these entities; (3) to provide distinctive characters to distinguish between the taxa by means of appropriate, unambiguous numerical methods; and (4) to apply correct names to the taxa and discuss their relationships.

MATERIAL AND METHODS

SAMPLING

The collection of plants was concentrated in the lower part of the Guadalquivir river valley (named here as geographical region I; see Fig. 1B), in Sierra Morena and the Guadiana river valley (region II), and southeast Spain (region III), where floral variability was detected. As a reference, other populations from outside the region [north Morocco (region IV) and Greece (region V)], but within the area of distribution of *N. serotinus*, as shown in Figure 1A, were collected. Forty-two populations were sampled for the morphometric study: 40 were identified as *N. serotinus s.l.* and two as *N. elegans* (Haw.) Spach. Localities and voucher specimens (in herbarium SEV) are indicated in Table 1. The populations of *N. serotinus* were differentiated as belonging to the yellow or orange morphotype, mainly according to the colour of the corona exhibited in the field during collection. Only one morphotype was found in most populations, constituting an important factor for defining the limits. Nevertheless two flower morphotypes were found in populations 14 and 22. The 42 populations selected constitute the operational taxonomic units (OTUs) for this study. The study was completed by the observation of plants from certain herbaria (SEV, MUB, JAEN, MGC; according to Holmgren, Holmgren & Barnett, 1990).

Field sampling was carried out from 2001 to 2004 during the flowering period (October to November). For each locality, 5–30 bulbs were collected at regular distances along a linear transect which covered, where possible, almost the entire length of the population. Bulbs were grown in a glasshouse (University of Seville) for 3 years to examine the variability and stability of characters. In addition, 5–30 individuals of each population were pressed in the field, the flowers were fixed in formalin–alcohol–acetic acid (FAA) (Sass, 1940), and the bulbs were measured prior to pressing. The number of flowers per inflorescence and the coexistence of a scape and leaf in the same sheath per individual were recorded in the field, for which 100 counts were made along a linear transect in each population.
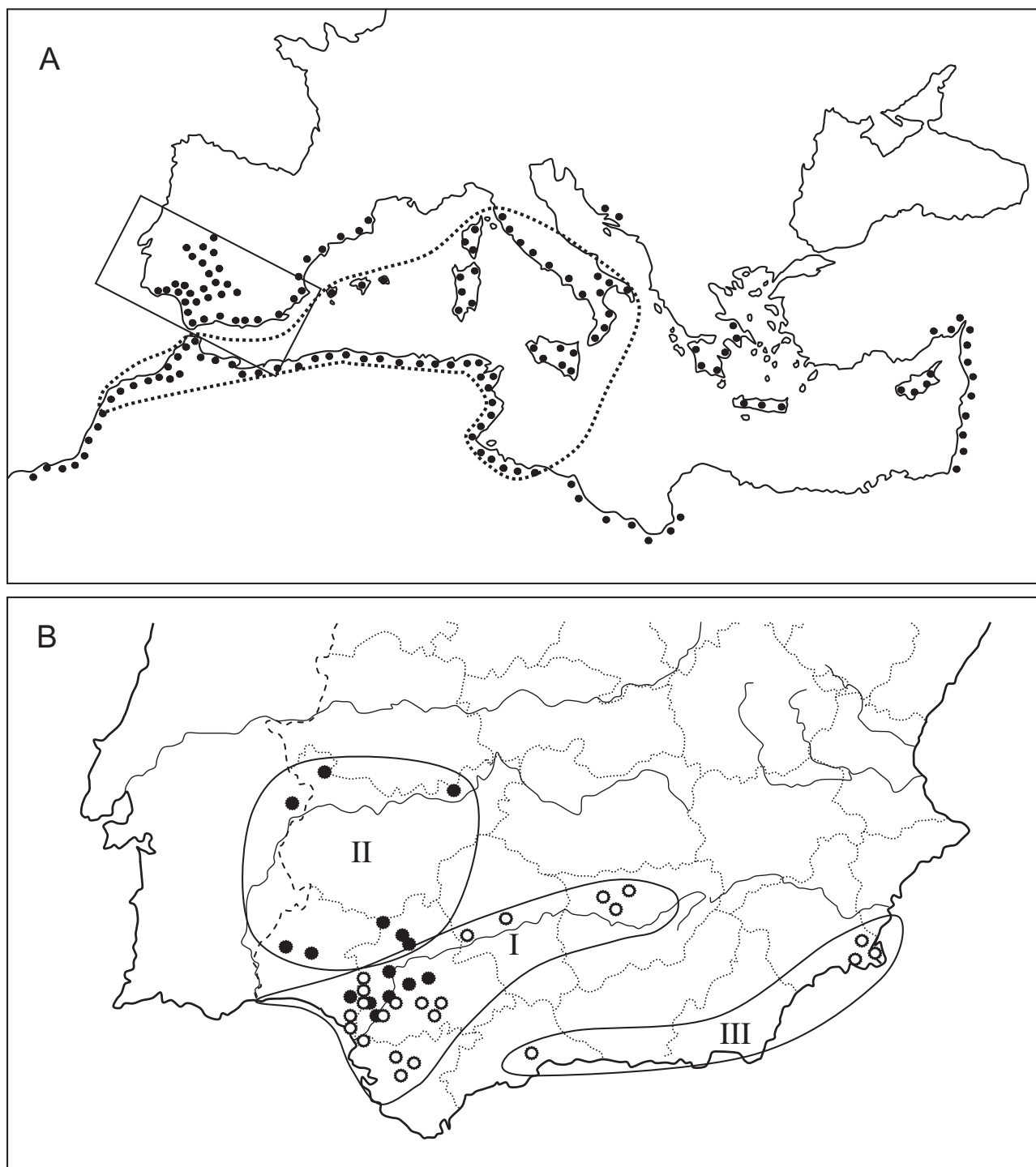
Figure 1. A, Geographical distribution of *Narcissus serotinus s.l.* (black circles) and *N. elegans* (Haw.) Spach (broken line), according to Fernandes (1951) and standard floras. The rectangular area is amplified in B. B, Localization of the populations studied in the Iberian Peninsula, with indication of the geographical regions I, II, and III (see 'Material and methods'). Black circles, *N. serotinus* yellow morph; white circles, *N. serotinus* orange morph.

Table 1. List of populations (operational taxonomic units, OTUs) sampled, arranged according to the flower morphotype shown in the field

Reference no.	Geographical region	Location and voucher (SEV)
Narcissus serotinus L. *s.l.*, yellow morph		
1	II	Portugal: Alto Alenteixo, Elvas, Ponte da Ajuda, 7.xi.2001, *DL & LL* (SEV 214098)
2	II	Spain: Badajoz, Orellana, 7.xi.2001, *DL & LL* (SEV 214113)
3	II	Spain: Badajoz, La Roca de la Sierra, 7.xi.2001, *DL & LL* (SEV 214112)
4	II	Spain: Sevilla, Almadén de la Plata, 30.x.2001, *DL & A. Rivero* (SEV 214105)
5	II	Spain: Sevilla, Cantillana, Hacienda de Los Melonares, 29.x.2001, *DL & LL* (SEV 214111)
6	II	Spain: Sevilla, between Cantillana and Castilblanco de los Arroyos, 30.x.2001, *DL & A. Rivero* (SEV 214110)
7	II	Spain: Huelva, between Zalamea la Real and Jabugo, 8.xi.2001, *AC & DL* (SEV 214100)
8	II	Spain: Huelva, Valdelamusa, salida a El Cerro del Andévalo, 8.xi.2001, *AC & DL* (SEV 214099)
9	I	Spain: Sevilla, Aznalcázar, 'Cañada Honda', 16.x.2001, *AC & DL* (SEV 214104)
10	I	Spain: Sevilla, Puebla del Río, 24.x.2001, *DL & C. Monteseirín* (SEV 214106)
11	I	Spain: Sevilla, Dos Hermanas, Universidad Pablo Olavide, 18.x.2001, *DL & C. Monteseirín* (SEV 214107)
12	I	Spain: Sevilla, Km 13 in road between Alcalá de Guadaira and Morón, 25.x. 2001, *AC & DL* (SEV 214103)
13	I	Spain: Sevilla, Utrera, Cortijo de Torre Abad, 27.x.2004, *AC & DL* (SEV 214078)
14	I	Spain: Sevilla: Bastero, La Corchuela, under *Pinus pinea*, 28.x.2004, *DL & LL* (SEV 214082)
15	I	Spain: Sevilla, between Bastero and Isla Menor, 28.x.2004, *DL & LL* (SEV 214080)
16	IV	Morocco: Casablanca, Mechra-Bennabbon, 5.xi.2003, *J. Arroyo et al.* (SEV 214114)
Narcissus serotinus L. *s.l.* orange morph		
17	I	Spain: Sevilla, Aznalcázar, road to Finca 'La Tiesa', 16.x.2001, *AC & DL* (SEV 214109)
18	I	Spain: Sevilla, Aznalcázar, road between 'Cañada Honda' and Venta del Cruce, 24.x.2001, *DL & C. Monteseirín* (SEV 214101)
19	I	Spain: Sevilla, Villafranco del Guadalquivir, 18.x.2002, *AC & DL* (SEV 214102)
20	I	Spain: Sevilla, Almensilla, 24.x.2001, *DL & C. Monteseirín* (SEV 214096)
21	I	Spain: Sevilla, Isla Menor, Rancho de Lila, 28.x.2004, *DL & LL* (SEV 214079)
22	I	Spain: Sevilla: Bastero, La Corchuela, roadsides, 28.x.2004, *DL & LL* (SEV 214081)
23	I	Spain: Cádiz, Trebujena, Cortijo El Ventu, 2.xi.2001, *AC & DL* (SEV 214091)
24	I	Spain: Cádiz, San José del Valle, 2.xi.2001, *AC & DL* (SEV 214090)
25	I	Spain: Cádiz, Arcos de la Frontera, 2.xi.2001, *AC & DL* (SEV214092)
26	I	Spain: Cádiz, El Algar, 2.xi.2001, *AC & DL* (SEV 214089)
27	I	Spain: Sevilla, Morón, 25.x.2001, *AC & DL* (SEV 214094)
28	I	Spain: Sevilla, Alcalá de Guadaira, 25.x.2001, *AC & DL* (SEV 214108)
29	I	Spain: Sevilla, between Marchena and Carmona, 25.x.2001, *AC & DL* (SEV 214097)
30	I	Spain: Sevilla, La Puebla de Cazalla, 26.x.2004, *DL & LL* (SEV 214077)
31	I	Spain: Córdoba, Hornachuelos, 29.x.2001, *DL & LL* (SEV 214088)
32	I	Spain: Córdoba, Medina-Azahara, 29.x.2001, *DL & LL* (SEV 214095)
33	I	Spain: Jaén, road between Linares and Fernandina, 17.x.2003, *DL & LL* (SEV 214076)
34	I	Spain: Jaén, Linares, 17.x.2003, *DL & LL* (SEV 214075)
35	I	Spain: Jaén, Vilches, Pantano del Guadalén, 16.xi.2001, *DL & LL* (SEV 214093)
36	III	Spain: Málaga, Churriana, 31.x.2002, *AC & DL* (SEV 214087)
37	III	Spain: Murcia, Atamaría, 18.x.2003, *DL, J. Díaz & ML. Díaz* (SEV 214086)
38	III	Spain: Murcia, Isla del Ciervo, 31.x.2003, *DL, J. Díaz & ML. Díaz* (SEV 214083)
39	III	Spain: Murcia, Los Nietos, 18.x.2003, *DL, J. Díaz & ML. Díaz* (SEV 214085)
40	V	Greece: Attiki, Cape Sounion, 10.x.2002, *DL* (SEV 214084)
Narcissus elegans (Haw.) Spach		
41	IV	Morocco: Tittaouen, Asilah, 23.x.2003, *B. Valdés* (SEV 214116)
42	IV	Morocco: Tittaouen, Cheznaia, 25.x.2003, *B. Valdés* (SEV 214115)

For simplicity, in the text and figures, each population is referred to by a number. Geographical regions (see Fig. 1B): I, Guadalquivir river valley; II, west Sierra Morena and Guadiana river valley; III, south-east Spain; IV, north-west Morocco; V, Greece. AC, Andrés Camacho; DL, Díaz Lifante; LL, Lifante Lozano.

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MEASUREMENTS

Nine hundred and sixteen individuals from 42 populations were collected in the field and analysed. The morphometric analyses were based on traits presented during the flowering period. The flower characters were measured in the preserved material. Where possible, in inflorescences with more than one flower, the first flower in the inflorescence was selected. Measurements were obtained with digital calipers and a ruler (0.1 mm) for small characters measured under the stereomicroscope. Vegetative characters were measured in the pressed plants, with the exception of the bulb size, which was measured before pressing. The flower and vegetative characters are listed in Table 2. The abbreviations for the characters, their quantitative or categorical nature, and the states for the categorical characters are specified. Some characters are illustrated in Figure 2A–E. 'Absolute' and 'relative' (i.e. ratio between absolute characters) characters have been selected. One of the two absolute characters used in the ratio was not considered in some cases, as width of bulb and tube, and length of inner tepals and lower stamen filaments. Some characters were completed using field records, and the constancy was determined in cultivated plants. The length and width of leaf characters were excluded because they were not regularly presented in all the natural populations during the flowering period, and were influenced strongly by the growth conditions in cultivated plants.

STATISTICAL ANALYSES

For multivariate analyses, a matrix was constructed from the individual's raw data matrix, using mean and mode population values for each quantitative and qualitative character, respectively. This data matrix comprised 42 populations and 42 characters, 28 of which were continuous quantitative and 14 of which were categorical, two-state and ordered multistate characters.

Ordination analyses were performed using SPSS 10.0.6 for Windows. Two types of ordination analysis were applied, according to the continuous quantitative or categorical nature of the characters, in order to find a relationship between them and to determine their influence in the OTU groupings. A distinction between the multivariate treatment of the two types of character has also been made in other recent systematic studies (Dawson, 2003; Meijaard & Groves, 2004). A principal component analysis (PCA) was applied to the 28 continuous quantitative characters. Normality was tested using the Shapiro–Wilk test (at a significance level of 0.05). The insertion of shorter filaments did not produce the normality condition at $P < 0.01$ for the total of 28 characters, and therefore a low influence

was assumed. The raw matrix for PCA was based on a correlation matrix. A categorical principal component analysis (CATPCA, version 1.0; Data Theory Scaling System Group (DTSS), 1999) was applied to the 14 categorical characters.

A classification analysis was carried out using the clustering method. In order to avoid too high a level of redundancy in the data sets, five quantitative characters (*spl*, *ssinw*, *tul*, *styl*, and *antupex*), showing high correlation coefficients ($R = 0.85$, $P < 0.05$), were removed from the raw matrix of 42 characters, resulting in a matrix with 37 characters for the final analysis (Sneath & Sokal, 1973). Similarities between populations were calculated using the coefficient of general similarity of Gower (1971), adequate for mixed matrices with qualitative and quantitative characters (Sneath & Sokal, 1973). When this coefficient is used, the Gower's ranging standardization method (values ranging from 0 to 1) is applied for quantitative variables (Sneath & Sokal, 1973). The similarity matrix was analysed using the unweighted arithmetic average clustering method (UPGMA, SAHN clustering program, NTSYS-pc 2.11Q, Exeter Software, New York, USA; Rohlf, 2000). The phenogram distortion was calculated from the cophenetic correlation coefficient (Rohlf & Sokal, 1981) between the similarity and cophenetic matrices. For this correlation, the moment-product Mantel test was applied using the MXCOMP program, NTSYS-pc.

The variation pattern was analysed using Wells' distance diagram (Wells, 1980), a useful multivariate analysis for testing morphological intermediacy. This analysis was also used by Seberg (1989), von Bothmer, Jacobsen & Seberg (1993), and Bartoli & Tortosa (1998) for the same purpose. As in UPGMA, this analysis was based on the Gower similarity matrix, which was transformed into the distance matrix by subtracting one from the similarity values. Quantitative and qualitative characters were taken into account. Reference points were calculated for the two more distant taxa (i.e. *N. serotinus* morphotype yellow and *N. elegans*), according to Wells (1980).

Univariate comparisons of quantitative characters between the two morphs found in *N. serotinus s.l.*, as corroborated by the multivariate analyses, were made, Student's *t*-tests were applied. When the variance was not homogeneous (Levene's test), a *t*-test with separate variance estimates was applied. The *t*-statistic was used to present the results of Student's *t*-test.

RESULTS

ORDINATION ANALYSIS

The entire set of 28 quantitative characters considered for PCA resulted in a value of 0.667 for the Kaiser–Meyer–Olkin measure of sampling adequacy

Table 2. List of characters studied and abbreviations used in the text. States for categorical characters are specified. Measurements of characters are expressed in millimetres (except for scape length in centimetres)

Code	Character
Quantitative continuous characters	
bul	Bulb length
bul/w	Ratio between bulb length and width
scl	Scape length, measured from base to bract insertion
scw	Scape width, measured above the leaf sheath
ssinl	Inner scape sheath length
ssinw	Inner scape sheath width
spl	Spathe length
spw	Spathe width
spl/spshl	Ratio between spathe length and spathe sheathing part length
pedl	Pedicel length
teoul	Outer tepal length
teoul/w	Ratio between outer tepal length and width
teoutip	Outer tepal tip length
teoul/inl	Ratio between outer tepal and inner tepal length
teoul/tul	Ratio between outer tepal length and hypanthial tube length
tul	Hypanthial tube length, measured from base to tepal's insertion point
tuw/tul	Ratio between width and length of hypanthial tube
corh	Corona height
cordia	Upper diameter of the corona contour
filupl	Upper stamen filament height, measured from tube base, including adnate and free parts
filupl/lol	Ratio between upper and lower stamen filament height, this measured as in *filupl*
filloadn	Lower stamen filament adnation point, measured from tube base (see Fig. 2A: 5)
antupl	Upper anther length
antupex	Exertion of upper anthers, measured from corona base up to upper part of anther
styl	Style length
styl/filupl	Ratio between style and upper stamen filament length
ovw	Ovary width
ovl/w	Ratio between ovary length and width
Categorical characters	
lsec	Leaf section (Fig. 2B):
	1, cylindrical to semicylindrical, narrow (i.e. usually < 2 mm in width) (Fig. 2B: 1–2)
	2, semicylindrical and caniculate, narrow (i.e. usually < 2 mm in width) (Fig. 2B: 3–6)
	3, flat and caniculate, wide (usually > 3 mm in width) (Fig. 2B: 7)
scsh	Number of leaf sheaths in base of scape:
	1, 1 leaf sheath
	2, 2 leaf sheaths
	3, > 2 leaf sheaths
l&sc	Coexistence of leaf and scape in the same sheath:
	1, never
	2, sometimes
	3, always
spcol	Spathe colour:
	1, whitish to pale brown
	2, brown to dark brown
sptr	Spathe transparency:
	1, yes
	2, no
n ºfl	Presence of 2 flowers/inflorescence in the population:
	1, 1/5 population
	2, 2/5 population
	3, 3/5 population
	4, 4/5 population
	5, 5/5 population

Table 2. *Continued*

Code	Character
tuf	Hypanthial tube shape (Fig. 2C): 1, abruptly widened at middle (Fig. 2C: 1) 2, gradually widened from base to upper part (Fig. 2C: 2–4)
teouf	Presence of elliptic to oblong outer tepals in the population: 1, 3/4 population 2, < 3/4 population
teinf	Presence of elliptic to oblong inner tepals in the population: 1, 3/4 population 2, < 3/4 population
teinap	Apex inner tepal: 1, mucronate or mucronulate 2, not mucronate or mucronulate
corcol	Corona colour: 1, yellow 2, orange to brown–orange
corcon	Corona upper outline (Fig. 2E): 1, circular 2, circular or triangular 3, triangular
corlob	Corona lobulation type (Fig. 2D): 1, 6 emarginate lobes (Fig. 2D: 1) 2, 6 entire lobes (Fig. 2D: 2) 3, 3 emarginate lobes (Fig. 2D: 3) 4, 3 smoothly emarginate lobes (Fig. 2D: 4) 5, 3 entire lobes (Fig. 2D: 5) 6, less than three lobes, or lobulations not reaching the corona base (Fig. 2D: 6–7) 7, corona entire, without deep lobulations (Fig. 2D: 8)
cordiv	Corona diversity as number of types of corona lobulation in the population

coefficient, and high significance for Bartlett's sphericity test ($\chi^2 = 1670.8$, $P < 0.0001$), indicating that the analysis was adequate. Five components reached eigenvalues greater than unity (Table 3), and the first four components explained 75.71% of the variance. The orthogonal Quartimax rotation method, appropriate for a large number of components, was applied.

In Table 4, eigenvector values for the first four principal components are shown. The first component, accounting for 36.99% of the total variation, is determined by many characters, most of them absolute, except for the relative *styl/filupl* (see Table 2 for character abbreviations). Thus, this component appears to reveal a general measure of size. The second component (15.19% of the total variation) is represented, although not exclusively, by *tul*, *filupl*, *styl*, and *teoul/tul* (Table 4). The distribution of OTUs in the two-dimensional plot (Fig. 3A) shows the proximity amongst populations 1–16, belonging to *N. serotinus* yellow morphotype, with negative values for component 1 (i.e. small size in all characters). Populations 41 and 42, identified as *N. elegans*, show the highest positive values for the first component (i.e. large size in many characters), but also the lowest negative values for the second component (see Fig. 3A), with tepals shorter in relation to the tube than other populations. The rest of the populations, identified as *N. serotinus* orange morphotype, appear midway between the other two groups for the first component. Population 40 from Greece, with a hypanthial tube, long filaments, and a style longer than in the other populations, separates in component 2. In Figure 3B, where the third component (11.80% of the total variation) is represented, several relative characters, such as *teoul/w*, *filupl/lol*, *tuw/tul*, and *spl/spshl*, are important for separating populations 33 and 35–40, which shows narrower tepals and tube, and a greater difference between the length of the longer and shorter filaments than other populations. In Figure 3C, the fourth component (10.39%) is represented. Characters such as *teoul*, *teoul/tul*, *ovl/w*, and *spl/spshl* distinguish populations 10–16 from others with the yellow morphotype, showing longer tepals, ovaries, and spathe sheathing parts.
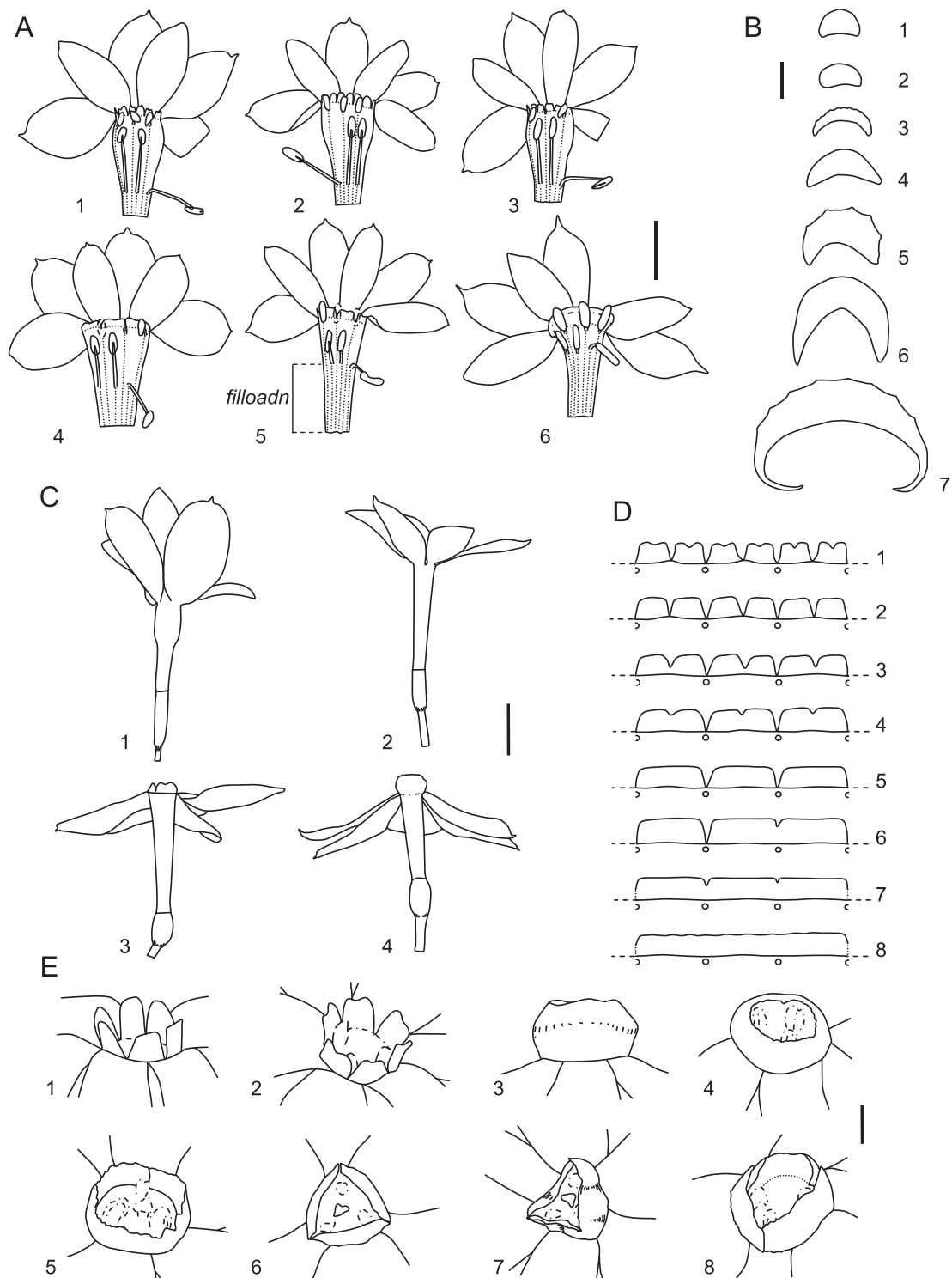
Figure 2. Variability in some morphological characters of *Narcissus serotinus s.l.* A, Longitudinal section of flower showing the variable position of the adnation point of the lower filaments (1, population 15; 2, population 2; 3, population 16; 4, population 19; 5, population 40; 6, population 42); scale bar, 1 cm. B, Leaf section outline states (1–2, subcylindrical or semi-cylindrical; 3–6, semi-cylindrical and canaliculate; 7, flat and canaliculate); scale bar, 1 mm. C, Hypanthial tube shape (1, population 14; 2, population 38; 3, population 28; 4, population 42); scale bar, 7 mm. D, Corona lobulation types (1–8 show states described in Table 2). E, Outline and lobulation of corona (1–2, population 12; 3–4, population 42; 5, population 27; 6, population 28; 7, population 20; 8, population 17); scale bar, 1.5 mm.

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Table 3. Eigenvalues, percentages, and cumulative variance for the first 13 principal components in the principal component analysis. Rotation method by Quartimax

Component	Initial eigenvalues			Eigenvalues after rotation		
	Eigenvalue	Variance (%)	Cumulative variance	Eigenvalue	Variance (%)	Cumulative variance
1	11.044	39.443	39.250	10.538	36.995	36.995
2	3.968	14.173	53.616	4.004	15.194	52.189
3	3.783	13.509	67.125	3.239	11.801	63.990
4	2.403	8.581	75.706	2.953	10.398	74.388
5	1.332	4.757	80.463	1.326	4.901	79.289
6	0.919	3.281	83.744	1.195	4.284	83.573
7	0.683	2.440	86.184	0.877	3.132	86.184
8	0.662	2.363	88.547			
9	0.572	2.043	90.590			
10	0.497	1.774	92.363			
11	0.482	1.720	94.083			
12	0.321	1.148	95.231			
13	0.318	1.135	96.366			

Table 4. Eigenvector values on the first four principal component (PC) axes in the principal component analysis (Quartimax rotation)

	PC1	PC2	PC3	PC4
bul	0.888	−0.281	0.112	−0.058
bul/w	−0.398	−0.013	0.559	−0.477
scl	0.678	−0.090	−0.116	−0.224
scw	0.817	0.193	−0.097	−0.152
ssinl	0.595	−0.032	−0.277	0.043
ssinw	0.918	−0.294	−0.056	−0.048
spl	0.782	0.244	−0.162	0.114
spw	0.631	−0.319	−0.099	0.184
spl/spshl	−0.032	−0.146	−0.359	−0.700
pedl	0.939	0.084	0.034	0.036
teoul	0.558	−0.082	0.111	0.709
teoul/w	0.203	−0.156	0.840	0.046
teoutip	0.705	0.044	0.109	−0.173
teoul/inl	0.433	0.151	0.156	−0.005
teoul/tul	0.362	−0.698	0.066	0.523
tul	0.238	0.944	0.057	0.093
tuw/tul	0.008	−0.360	−0.827	−0.121
corh	0.675	0.075	0.339	0.138
cordia	0.588	0.351	−0.508	0.008
filupl	0.282	0.942	0.022	0.035
filupl/lol	0.250	−0.022	0.672	0.244
filloadn	0.830	0.362	0.207	−0.205
antupl	0.728	0.297	0.315	0.319
antupex	0.759	0.239	0.412	0.235
styl	0.490	0.830	−0.004	0.123
styl/filupl	0.710	0.005	−0.048	0.288
ovw	0.790	0.227	−0.235	−0.248
ovl/w	−0.207	0.063	0.072	0.915

CATPCA, applied to 14 categorical characters, generated three dimensions with Cronbach α values of 0.931, 0.731, and 0.147 for the first, second, and third dimensions, respectively (Table 5). Eigenvectors for the categorical characters are also indicated in Table 5. The first dimension accounts for 52.62% of the total variation and is determined by the number of scape sheaths, spathe colour and transparency, hypanthial tube shape, corona outline and colour, and, secondarily, by the inner tepal tip length. The second dimension (22.31% of the total variation) is mainly represented by the leaf section, coexistence of leaf and scape, and the number of flowers per inflorescence, which is also represented in the first component, and, secondly, by the outline and lobulation of the corona.

The ordination of populations in the two-dimensional plot for the first and second dimensions (74.93% of the total variation) clearly distinguishes three groups of populations (Fig. 4A). In the scatter diagram for the character states (Fig. 4B), populations 1–16, identified as the yellow morphotype, show most of the states codified as 1: one leaf sheath, cylindrical to semicylindrical leaf section and not canaliculate (Fig. 2B: 1–2), leaf not coexisting with scape, pale and clear spathe, very rarely more than one flower per inflorescence, hypanthial tube abruptly widened at the middle (Fig. 2C: 1), inner tepals not mucronate, and yellow, circular corona with six lobes (Fig. 2D: 1–2; Fig. 2E: 1–2). All of these characters are very homogeneous in the 16 populations.

The remaining character states are presented in the other two groups, separated by the first and second dimensions. Populations 17–40 are characterized by having one or two leaf sheaths, occasionally scape and
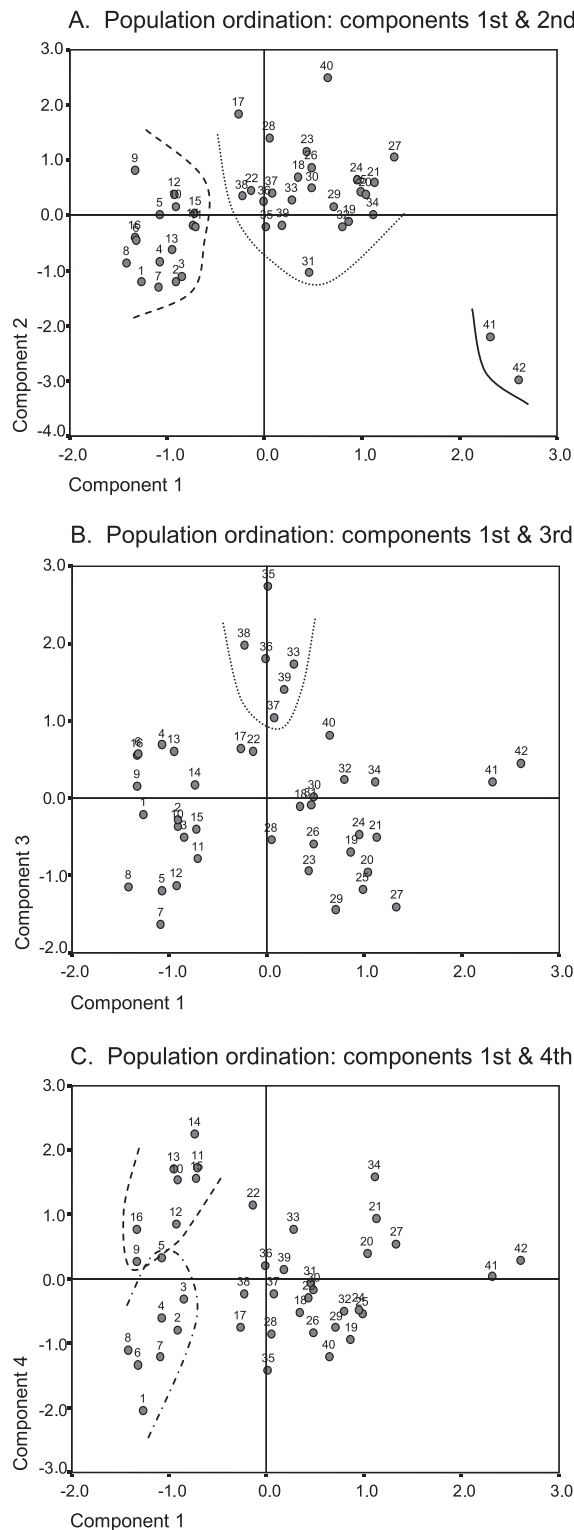
A. Population ordination: components 1st & 2nd

B. Population ordination: components 1st & 3rd

C. Population ordination: components 1st & 4th

Figure 3. Population ordination based on the first four principal components derived from the principal component analysis applied to 28 quantitative characters. A, First and second components. B, First and third components. C, First and fourth components. Operational taxonomic unit (OTU) numbers according to Table 1.

leaves, semicylindrical and caniculate leaves (Fig. 2B: 3–6), brown to dark brown and opaque spathes, 1–2(–3) flowers per inflorescence, a narrowly obconical tube (Fig. 2C: 2–3), inner tepals mucronate or not, orange to brown–orange corona, which presents variable lobulation (Fig. 2D: 3–7; Fig. 2E: 5–8), frequently three-lobed, very rarely six-lobed, and rarely entire corona, and variable shape for the outer and inner tepals. As shown in Figures 4A, B, populations 41 and 42 of *N. elegans* share several characters which differentiate them from the orange morphotype: two or three scape sheaths, leaf section flat and canaliculate (Fig. 2B: 7), scape with leaves, always two or more than two flowers per inflorescence, and conical entire corona (Fig. 2D: 8; Fig. 2E: 3–4). Other characters, such as a dark brown and opaque spathe, narrowly obconical tube (Fig. 2C: 4), and brown–orange corona, are shared with populations 17–40.

The third dimension (8.27% of the total variation) is mainly represented by the shape of the outer tepal, a character important for distinguishing between populations 1 and 2, located in the Guadiana river valley, from the other populations identified as the yellow morphotype, by their ovate tepal shape. The Moroccan population (population 16) can be differentiated by the lack of mucronate inner tepals. Populations 36 and 40 agree in frequently having only one flower per inflorescence and elliptic to oblong tepals, characters nevertheless not exclusive to them.

CLUSTER ANALYSIS

The UPGMA cluster applied to Gower's similarity coefficient matrix, obtained from 37 characters, is shown in Figure 5. The cophenetic correlation coefficient, as revealed by the Mantel test, is 0.946 (Mantel t, 27.715; $P < 0.0001$), indicating a very good fit to the similarity matrix (Rohlf, 1990). Two groups can be recognized at a similarity level of 0.56. One group, comprising populations 1–16, shows a high intrahomogeneity, and corresponds to the yellow morphotype. Nevertheless, within this group, two clear groups of populations (1–8, except for 5, and 9–16) can be separated at a similarity level of 0.83, each largely correlated with a different geographical area, regions II and I, respectively (Table 1). Population 5 does not group with the other populations from the same geographical region because of its longer filaments and larger *ovl/w* ratio. The Moroccan population 16 appears in the second group, but in a remarkably distant position. Two groups can be recognized at a similarity level of 0.65, one formed by populations 41 and 42 and identified as *N. elegans*. The other group comprises 24 populations (17–40) and corresponds to the orange morphotype. This group is heterogeneous, with segregation into new groups at a similarity level of

Table 5. Eigenvalues and eigenvector values on the three principal dimensions in the categorical principal component analysis (CATPCA)

	Vector				Centroid			
	Dimension				Dimension			
	1	2	3	Total	1	2	1	Mean
lsec	0.430	0.551	0.003	0.984	0.885	0.913	0.007	0.601
scsh	0.693	0.043	0.044	0.780	0.695	0.834	0.077	0.535
l&sc	0.430	0.551	0.003	0.984	0.885	0.913	0.007	0.601
spcol	0.831	0.094	0.004	0.928	0.831	0.094	0.004	0.309
sptr	0.680	0.041	0.000	0.721	0.680	0.041	0.000	0.240
n°fl	0.284	0.696	0.003	0.983	0.648	0.845	0.092	0.529
tuf	0.866	0.104	0.001	0.970	0.866	0.104	0.001	0.323
teouf	0.001	0.003	0.841	0.845	0.001	0.003	0.841	0.282
teinf	0.251	0.000	0.117	0.368	0.251	0.000	0.117	0.123
teinap	0.545	0.025	0.114	0.684	0.545	0.025	0.114	0.228
corcol	0.776	0.064	0.006	0.846	0.776	0.064	0.006	0.282
corcon	0.384	0.413	0.021	0.818	0.384	0.415	0.087	0.295
corlob	0.913	0.070	0.000	0.983	0.980	0.973	0.110	0.688
cordiv	0.283	0.469	0.003	0.754	0.306	0.507	0.010	0.274
Cronbach α	0.931	0.731	0.147	0.987				
Eigenvalue	7.367	3.123	1.158	11.648				
Cumulative variance (%)	52.622	22.307	8.273	83.201				

0.74. Population 40, from Greece, is the most distant. A group with populations 22 and 33–39 can be separated at a similarity level of 0.75. With the exception of 22, this group corresponds to populations located in the south-east Iberian Peninsula. Populations 33–35, from Jaén province (Table 1) situated in the eastern extreme of the Guadalquivir river valley, separate from populations 36–39 located in the south-east Iberian Peninsula. The remaining populations occupy the lowest and western part of the Guadalquivir river valley (geographical region I).

WELLS' DISTANCE DIAGRAM

Wells' distance diagram for 37 categorical and quantitative continuous characters shows a clear separation between *N. elegans* and the orange and yellow morphotypes of *N. serotinus* (Fig. 6), corroborating the results from the other multivariate analyses. As expected, populations of the orange morphotype are situated between the yellow morphotype and *N. elegans*, all falling inside the semicircular area traced according to the distance value between the two reference points obtained from the yellow morphotype of *N. serotinus* and *N. elegans*. They also fall inside the semicircle bounding the populations of these two taxa. Thus, the orange morphotype not only is intermediate in distance from each reference taxon, but also has

intermediate quantitative and qualitative character values between those of the reference taxa, which could be explained by the hybrid nature, according to Wells (1980).

COMPARISONS OF MORPHOTYPES

The mean values, standard deviations, and variation ranges for all quantitative characters are indicated for the yellow (populations 1–16) and orange (populations 17–40) morphs, as defined and corroborated by the three multivariate analyses (Table 6). The highest values for *t*, in excess of six, are reached for characters related to length or width measurements, such as *bul*, *scw*, *ssinw*, *spl*, *pedl*, *teoutip*, *filloadn*, *antupex*, *styl*, and *ovw*. The yellow morphotype shows the smallest values for these characters. Nevertheless, the outer tepal length, initially very different between the two morphs, shows very low *t*-values. Relative characters do not reach high *t*-values, and six of these (*bul/w*, *spl/spshl*, *teoul/w*, *teoul/tul*, *tuw/tul*, and *ovl/w*) are the lowest of all the 28 characters. The highest values for the relative characters *teoul/inl* and *styl/filupl* are reached in the orange morphotype. The most discriminating quantitative character between the two morphs is the adnation point of short filaments to the hypanthial tube (*filloadn*). This is near to the base in the yellow morphotype (Fig. 2A: 1–3), but towards the
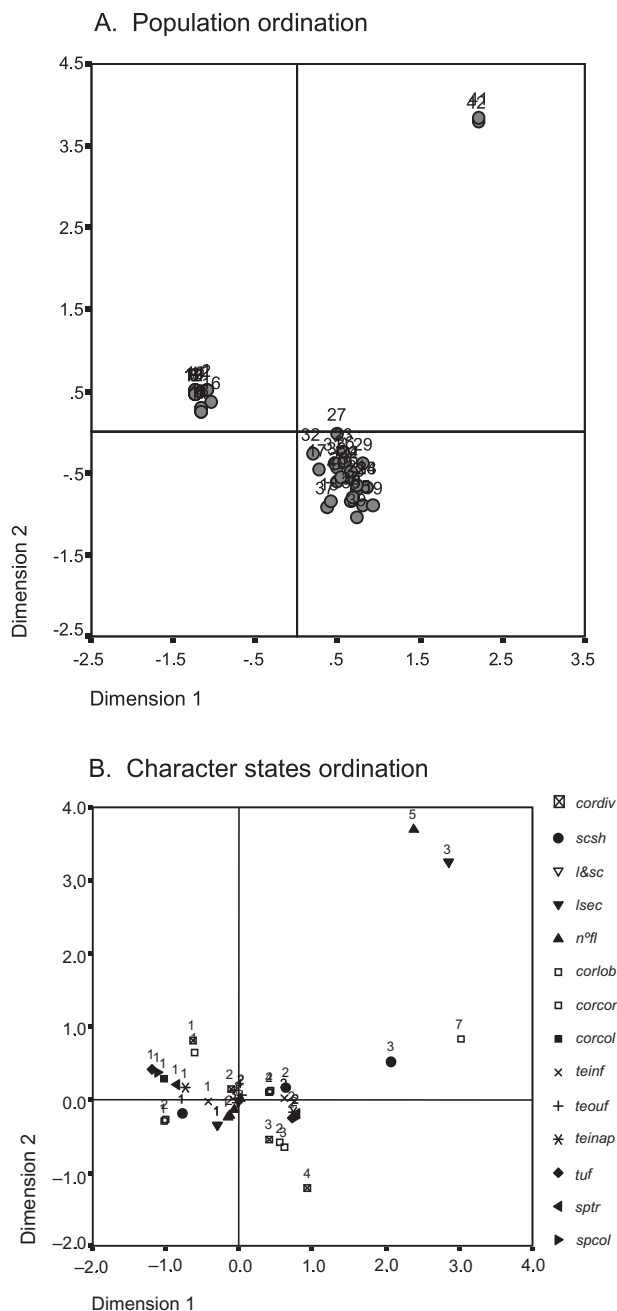
A. Population ordination

B. Character states ordination

Figure 4. Categorical principal component analysis (CAT-PCA) applied to 14 categorical characters. A, Population ordination based on the first and second dimensions. Operational taxonomic unit (OTU) numbers according to Table 1. B, Scatter diagrams for the character states based on the first two components. Character state numbers according to Table 2.

middle in the orange morphotype (Fig. 2A: 4–5). Clear discontinuities between the two morphs can be observed in the histogram of the ratio between the adnation point and the length of the lower filaments (Fig. 7).

A comparison between the two morphs in terms of qualitative characters is given in Table 7, where *N. elegans* is also included. The orange morphotype of *N. serotinus* is intermediate between the yellow morphotype and *N. elegans* for many characters.

DISCUSSION

MORPHOLOGICAL INTERMORPH VARIABILITY

The ordination and classification multivariate analyses, in addition to Wells' distance diagram, confirm the clear distinction of three taxa, taking into account morphological characters. There are clear discontinuities in many of the quantitative and categorical characters.

Ten absolute quantitative characters (*bul*, *scw*, *ssinw*, *spl*, *pedl*, *teoutip*, *filloadn*, *antupex*, *styl*, and *ovw*) differentiate the yellow morphotype from the orange morphotype, as defined by the multivariate analyses. Four (*bul*, *scw*, *pedl*, and *filloadn*) do not overlap in their variation range. Intramorph geographical variation is not found in these ten characters, but is better revealed by the relative (i.e. expressed as ratio) characters, which are less differentiating at the intermorph level. The ten quantitative characters combined with the ten categorical distinctive characters (*scsh*, *lsec*, *l&sc*, *sptr*, *spcol*, *nºfl*, *tuf*, *teinap*, *corcol*, *corcon*, *corlob*) constitute a total of 20 characters to distinguish between the two morphotypes.

Some of the quantitative characters observed in the two populations of *N. elegans* studied are useful for distinguishing it from *N. serotinus s.l.* These include the longer flower pedicel, upper and lower stamen filaments and style, tube shorter than tepals, upper anthers more exerted, less difference between the two whorls of stamens, shorter filaments adnate almost up to the apex of the tube, and higher and wider corona. These characters constitute differences in the presentation of anthers and stigmas to visiting insects, and therefore may have possible reproductive and biological consequences. Categorical characters, such as flat leaves always present with the scape, a larger number of flowers per inflorescence, and a conical and entire corona, clearly differentiate *N. elegans* from the other morphotypes. Other characters not evaluated, such as tepals tending to reflex before anthesis and fragrance (Z. Díaz Lifante and C. Andrés Camacho, pers. observ.), are exclusive to *N. elegans*.

Both quantitative and categorical characters, evaluated by PCA and CATPCA, respectively, discriminate clearly between the three taxa. Quantitative characters approximate the orange morphotype to *N. elegans*, whereas categorical characters approximate the orange morphotype to the yellow morphotype. According to Wells' distance diagram based predominantly on quantitative characters, the orange
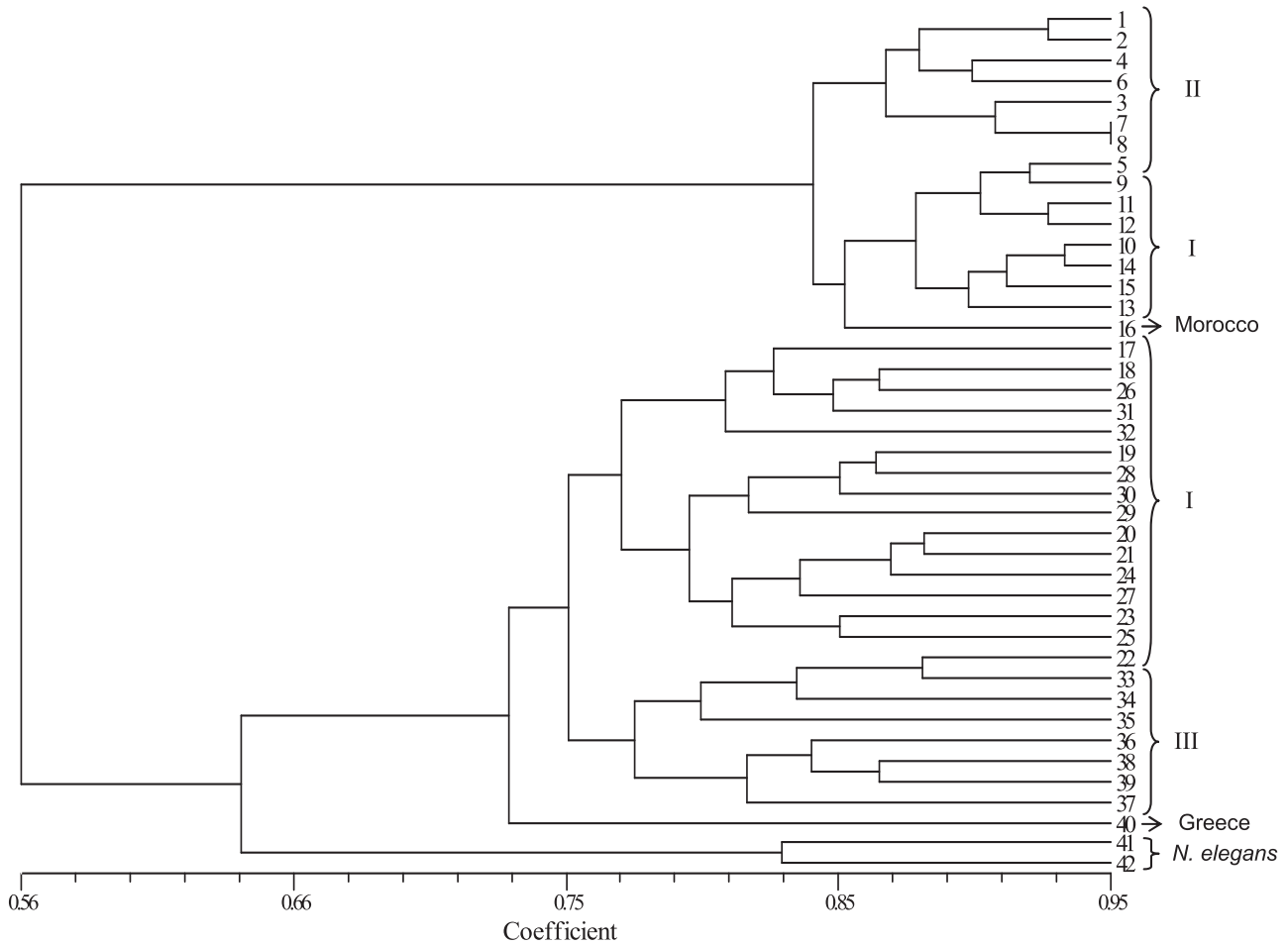
Figure 5. Phenogram obtained after cluster analysis (unweighted arithmetic average clustering method, UPGMA) applied to the Gower similarity coefficient matrix obtained from 37 quantitative and qualitative characters. Operational taxonomic unit (OTU) numbers according to Table 1.
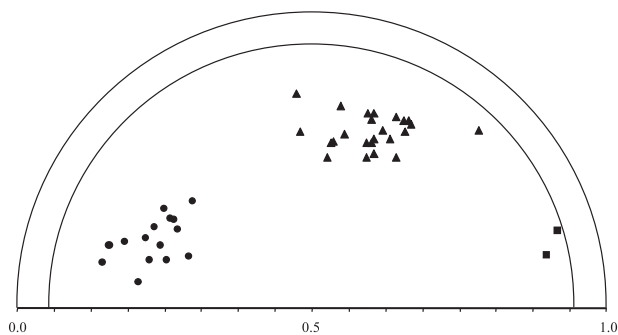

Figure 6. Wells' distance diagram for quantitative and qualitative characters based on the Gower similarity matrix obtained from 37 quantitative and qualitative characters for populations 1–16 (circles: *N. serotinus* yellow morph), 17–40 (triangles: *Narcissus serotinus* orange morph), and 41–42 (squares: *N. elegans*).
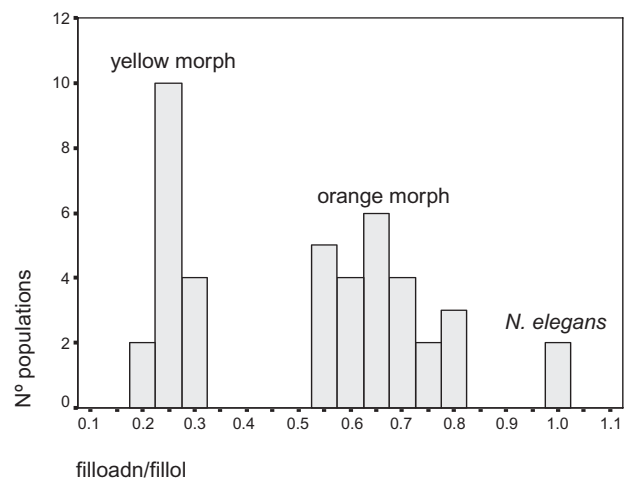

Figure 7. Histogram of the ratio between the adnation point and the length of the lower filament in *Narcissus serotinus s.l.* and *N. elegans*.

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Table 6. Mean values of quantitative characters for yellow (populations 1–16) and orange (populations 17–40) morphotypes in *Narcissus serotinus* L. *s.l.*, and Student's *t*-statistic values. Measurements are indicated in millimetres

	Yellow morphotype				Orange morphotype				Student's *t*
	Mean	SD	Minimum	Maximum	Mean	SD	Minimum	Maximum	
bul	12.70	0.785	10.84	14.32	18.70	2.327	14.80	24.28	−11.668
bul/w	1.18	0.125	1.00	1.51	1.16	0.142	0.94	1.60	0.305
scl	13.91	3.724	5.96	23.73	18.86	4.595	10.96	30.10	−3.590
scw	1.18	0.195	0.53	1.39	1.86	0.357	1.39	2.53	−7.725
ssinl	4.16	1.400	1.22	6.44	5.63	2.237	2.87	11.37	−2.338
ssinw	1.83	0.229	1.40	2.48	3.09	0.563	2.16	4.01	−9.776
spl	20.32	2.009	16.04	23.45	27.06	3.545	20.28	34.29	−7.645
spw	4.49	0.490	3.58	5.27	5.13	0.736	3.78	6.68	−0.305
spl/spshl	2.35	0.506	1.59	3.22	2.31	0.337	1.90	2.95	0.281
pedl	9.12	1.639	6.39	12.07	17.64	3.001	12.63	22.74	−11.561
teoul	13.94	1.431	11.92	16.20	14.67	1.072	12.58	17.09	−1.835
teoul/w	1.94	0.192	1.57	2.33	2.05	0.219	1.77	2.48	−1.668
teoutip	0.73	0.072	0.63	0.89	0.99	0.173	0.70	1.33	−6.408
teoul/inl	1.03	0.014	1.00	1.05	1.06	0.024	1.01	1.10	−4.421
teoul/tul	0.93	0.070	0.82	1.04	0.90	0.084	0.75	1.05	1.118
tul	15.05	0.795	13.75	16.42	16.37	0.815	14.80	18.81	−5.082
tuw/tul	0.23	0.019	0.20	0.26	0.21	0.024	0.17	0.25	1.887
corh	1.08	0.129	0.87	1.37	1.37	0.224	1.03	1.84	−5.161
cordia	2.36	0.171	2.02	2.66	2.65	0.319	2.10	3.23	−3.748
filupl	14.13	0.824	12.86	15.45	15.62	0.850	14.07	18.37	−2.436
filupl/lol	1.32	0.029	1.27	1.37	1.35	0.057	1.23	1.44	−2.436
filoadn	2.96	0.282	2.52	3.47	7.82	1.118	5.96	11.19	−20.381
antupl	2.32	0.402	1.81	3.14	3.16	0.437	2.54	3.87	−6.129
antupex	1.07	0.326	0.59	1.69	1.83	0.292	1.22	2.30	−7.678
styl	13.30	0.957	11.83	14.54	15.18	0.870	13.36	17.42	−6.420
styl/filupl	0.94	0.022	0.91	0.99	0.97	0.026	0.91	1.01	−3.770
ovw	1.80	0.165	1.57	2.10	2.27	0.221	1.72	2.66	−7.308
ovl/w	2.89	0.550	1.93	3.67	2.65	0.339	2.11	3.34	1.553

morphotype is closer to *N. elegans*. In the yellow morphotype, categorical characters are very homogeneous, being represented usually by one or two states exclusive for this morph. Nevertheless, in the orange morphotype, many of the characters are variable and several states are present within them. This morphotype shares the states presented in the yellow morphotype or *N. elegans* (*scsh*, *n°fl*, circular shape of corona, *teouf*, *teinf*, and *teinap*). The orange morphotype shares the states presented in *N. elegans* for *spcol*, *sptr*, *corcol*, and *tuf*, whereas it shares the absence of leaves with the scape, only presented occasionally, with the yellow morphotype. The semicylindrical and canaliculate leaf section, in spite of its intermediate trait between the yellow morphotype and *N. elegans*, is overall more similar to the yellow morph, with narrow and rushy leaves. Exclusive states for the corona lobulation are found in the orange morphotype, although they represent intermediate traits between the other two taxa. Only the

triangular outline of the corona is observed in populations of the orange morphotype, although it is also shown as circular. Fernandes (1951) described the tube of *N. serotinus* as triquetrous.

The use of absolute or relative quantitative characters provides additional information. Relative characters may indicate the existence of gaps in the correlation between characters, whereas dimensional differences in absolute characters may reflect an increase in ploidy level. In this study, absolute characters were more useful for distinguishing between morphs, whereas relative characters were more useful for distinguishing between populations within a morphotype. As a consequence, the increased size observed in many of the characters is important in the differentiation between morphs, but the ratio between characters is maintained. Interestingly, the size of the flower, one of the characters which initially attracted our attention, constitutes an exception to this trend. The difference in size probably implies the existence of

Table 7. Qualitative characters for *Narcissus serotinus* yellow and orange morphotypes and *N. elegans*

Character	Yellow morphotype	Orange morphotype	*N. elegans*
Leaf section	Cylindrical to semicylindrical, narrow	Semicylindrical, canaliculate, narrow	Flat and canaliculate, wide
Number of leaf sheaths in base of scape	One leaf sheath	One to two leaf sheaths	Two to more than two leaf sheaths
Leaf and scape in the same sheath	Rarely	Sometimes	Always
Spathe colour	Whitish to pale brown	Brown to dark brown	Brown to dark brown
Spathe transparency	Transparent	Opaque, rarely transparent	Opaque
No. flowers/inflorescence	Rarely more than one	1–3(–4)	2–7
Hypanthial tube shape	Abruptly widened at middle	Gradually widened from base to apex	Gradually widened from base to apex
Outer tepal shape	Variable	Variable	Variable
Inner tepal shape	Usually elliptic to oblong	Variable	Variable
Apex inner tepal	Mucronate or mucronulate	Mucronate or not mucronate	Not mucronate or mucronulate
Corona colour	Yellow	Orange to brown–orange, rarely yellow	Orange to brown–orange
Corona upper outline	Circular	Frequently triangular, rarely circular	Circular, rarely subtriangular
Corona lobulation	Six emarginate to entire lobes	Three emarginate to entire lobes, sometimes < 3 lobes or lobulations not reaching the corona base	Corona entire, without deep lobulations
Intrapopulational corona diversity	Low	High	Low

a polyploidy process in the evolution of *N. serotinus*. Diploid and hexaploid levels have been found (Fernandes, 1942, 1943, 1966, 1967, 1968), and an assignment of the ploidy level for each morphotype of *N. serotinus* is now being carried out (Z. Díaz Lifante and C. Andrés Camacho, unpubl. data). However, it seems that chromosome rearrangements and geographical isolation could have produced gaps in the correlation patterns. Nevertheless, the ploidy level does not satisfactorily explain the largest size of some of the structures of *N. elegans*, for which a tetraploid level has been indicated (Fernandes, 1942, 1943, 1967), in relation to the other taxa.

A characteristic geographical distribution can be added to the morphological discontinuities found between the three taxa studied. The yellow morphotype has a more restricted area of distribution: from central-west Iberian Peninsula, throughout the western part of Sierra Morena, extending to the lower part of the Guadalquivir river valley, and through the Gibraltar Strait towards the Atlantic coast of Morocco. *N. elegans* coexists with the yellow morphotype in northern Morocco, extending towards the eastern Mediterranean by the littoral border and islands, and reaching as far as Italy in the north of its distribution area. Very recently Ramírez López (2007) has located *N. elegans* in the Iberian Peninsula (Sierra de Cama-

rolos, Málaga province) for the first time. The orange morphotype shows the widest distribution area: littoral Mediterranean and islands from northern Morocco to Israel, advancing inland to the western Iberian Peninsula through the Guadalquivir river valley, where it makes contact with the yellow morphotype.

Only one morphotype was found in the populations sampled from the region in which the distribution areas for the two morphotypes overlap. More rarely, one to four plants of the orange morphotype were found in some of the populations with the yellow morphotype (9, 11, 12, and 13). Nevertheless, both morphotypes cohabited the location in which populations 14 and 22 were collected. In the western Sierra Morena and Guadiana river valley, only plants showing the yellow morphotype were found. Although more studies must be carried out, this may exclude the autopolyploidization process in the origin of the orange morphotype.

MORPHOLOGICAL INTRAMORPH VARIABILITY

Categorical characters clearly distinguish between morphs, whereas quantitative characters reveal some intramorph differentiation, as shown by clustering and PCA. This differentiation has a good geographical

structure, grouping populations in both morphotypes of *N. serotinus s.l.* Two groups of populations can be distinguished in the yellow morphotype. One group comprises populations 1–8 from region II [mountains of northern Guadalquivir river valley (Sierra Morena), Guadiana river valley, and south-east Portugal]. The other group comprises populations 9–15 in the lower lands of the Guadalquivir river valley, mainly on the right margin of the river (region I). These groups can be differentiated by the size of the flower characters (tepals, tube, stamens, style), the ratio between the ovary length and width, and the sheathing part of the spathe. The most distant population (16), located in Morocco, is nearer to populations 9–15 than populations 1–8.

In the orange morphotype, the populations from the lower and western part of the Guadalquivir river valley (region I) are clearly separated from the remaining populations from the upper and eastern Guadalquivir river valley and coastal areas in the south-east Iberian Peninsula. The narrower bulb, spathe, tepals, tube, corona, and ovary, shorter scape sheath, and larger differences between the upper and shorter filaments are features of the latter populations. This distinction is mainly a result of quantitative relative characters.

The geographical structure of the morphological intramorph variability may be correlated with the geological history of the regions considered in this study. Region II belongs to the Palaeozoic Iberian Massif, whereas the Guadalquivir river valley (region I) is geologically very recent (Pliocene). The early connection of this valley with the Mediterranean and the Betic corridor, subsequently closed in the Messinian stage (Alonso Zarza *et al.*, 2002; Duggen *et al.*, 2003), probably allowed communication between the eastern Iberian coastal areas and north of the present Guadalquivir river valley. Thus, low morphological homogeneity has been found in this region, with the orange morphotype populations from Jaén province, in the upper part of the Guadalquivir river valley, distant from those populations in the lower part, and nearer to the south-eastern Iberian Peninsula populations. This may indicate that *N. serotinus s.l.* in the Guadalquivir river valley has not had a monophyletic and independent evolutionary history. Moreover, the land-bridge connections between south-west Spain and north-west Africa (Thompson, 2005) could explain the present differentiation of this complex.

TAXONOMY

When combining the morphological differences, lack of overlap in the values for several characters, the unique combination of characters, and the geographi-

cal distribution, there is little doubt that the three entities within *Narcissus*, separated by multivariate analyses in this study, are different morphological species. These findings support those made for the genus *Narcissus* by Webb (1978). The intermediate appearance of the orange morphotype between the other two taxa suggests that an ancient hybridization must have occurred, as this morphotype diversified later and is morpho-geographically distinct from the other taxa. More populations from different regions (Morocco, eastern Mediterranean) must be studied to confirm the geographical intramorph variation pattern observed in this study, allowing the establishment of infraspecific taxa.

In his monograph of the genus *Narcissus*, Gay (1858) recognized that the group with rudimentary corona and late flowering was very natural, and gave it a section rank, section *Autumnales* J. Gay, comprising three species: *N. serotinus* L., *N. elegans* (Haw.) Spach, and *N. viridiflorus* Schousb. Although this section is not recognized at the present time, the monographic work of Gay is of great interest because of the exhaustive gathering of information showing the morphological variability of these species, and the taxonomic interpretation of the diverse names given by different authors to them. Many of these names, forgotten or misunderstood, must be reconsidered if a new entity is to be recognized in *N. serotinus*.

In *Species Plantarum* (Linneo, 1753: 290), *N. serotinus* is described as 'Narcissus spatha uniflora, nectario brevissimo sexpartito', and indicated for 'Hispania'. Barra & López González (1984) selected the sheet 412.14 A from the Linnean Herbarium as the type of the species ('Hispania in Estramadura prope Badajoz Loefl.'), which was collected by Loefling in October 1751. This sheet contains two one-flowered and leafless scapes, with a translucid spathe of 17–20 mm in length. The description of the typus material fits well with that of the yellow morphotype as defined in this study. The locality indicated in the description of the type, the Spanish Extremadura, is the area in which only the yellow morphotype exists. This morphotype also corresponds with the icons included by Clusio (1576: 252) for *N. autumnalis minor*, with leafless and one-flowered scapes, and subclavate tube, with reference to plants from the Tajo river valley ('ad Anam flumen in Turdulis'), taken into account by Linneo (1753). In the second edition of *Species Plantarum*, Linneo (1762) extended the geographical area of the species to Italy and 'Barbaria', thus comprising both morphs, yellow and orange.

The wide geographical distribution and morphological variability described in this study has also been described by previous authors. For example, in relation to the synanthous character of the plant, Roemer (1847: 232) and Gay (1858) pointed out that the

species are not always histeranthous. Although frequently only one or, rarely, two flowers per scape are indicated in plants from the Iberian Peninsula in standard floras on the Mediterranean region (Parlatore, 1858; Fiori, 1923; von Hayek, 1932; Maire, 1958; Bonafé, 1977; Guinochet & Vilmorn, 1978; Davis, 1984; Bolós *et al*., 2000), some authors include up to three or four flowers (Webb, 1980; Valdés, 1987; Blanchard, 1990). Other authors, such as Gay (1858), Parlatore (1858: 158), Maire (1958), and Valdés & Müller-Doblies (1984), described the corona as six-lobed, three-lobed, or, rarely, subentire, and yellow to orange-brownish. No reference is made to stamen arrangement or tube shape.

A century before Linnaeus, Parkinson (1629) distinguished two autumnal species of *Narcissus* in Spain, *N. autumnalis minor albus*, which seemed to him to be the homonymous species of Clusio (1576), and *N. albus autumnalis medio obsoletus*, which is distinguished in having 'two or three leaues at the moft, and very narrow, fo that fome doe reckon it among the Rufh Daffodills, . . . , betweene thefe leaues commeth vp the ftalke, bearing vfually two flowers and no more at the toppe, . . . the cup is fmall and round, . . . , of a yellow colour at the bottome, but toward the edge of a dunne or fullen colour'. On page 89 (fig. 4), he included an icon for this last species, in which a scape with two leaves and two flowers has an apparently entire and triangular corona, and narrowly obconic tube. This pre-Linnean taxon was renamed as *Hermione obsoleta* by Haworth (1819: 147), who recognized he had not seen it and accepted it in the faith of Parkinson. Later, Steudel (1841: 182) and Spach (1846) established the *N. obsoletus* combination.

Gay (1858: 80), who commented on the low quality of Parkinson's woodcut icon (Parkinson, 1629), recognized it as *N. serotinus* L., rejected Parkinson's species, and relegated it and later names based on it [*Hermione obsoleta* Haw. and *N. obsoletus* (Haw.) Spach] as synonyms of the first species. In contrast, he described *N. elegans* β *intermedius* (Typus: 'Habitat c. Tingidem, Novembri florens', Salzmann, *Pl. tingit. Exsicc. 1825*), with one leaf, a two-flowered scape, and conical entire corona, as typical *N. elegans*, from which he distinguished *N. serotinus* based on the oblong-elliptic and more obtuse tepals, the outer ones mucronate, and recognized it as 'inter ambos quasi intermedius'. He relegated *H. obsoleta sensu* Herb. to synonymy under *N. elegans* β *intermedius*, based on the reference of Herbert (1837: 328) to material from 'Tangiers'. Later, Herbert (1847: table 22) regarded the dry specimen from 'Tangiers' in Mr Bentham's herbarium, represented as figure 3 in his work, as *N. medio obsoletus* Parkinson. It is our opinion that the two-flowered plant with wide tepals represented in this figure agrees with *N. elegans* var. *intermedius* Gay.

Maire (1958) later considered *N. elegans* var. *intermedius* as a distinct species, naming it *N. obsoletus* (Haw.) Spach and describing it with a hybrid nature between *N. elegans* and *N. serotinus*. He described it according to Gay (1858), but added one to two synanthous flat and canaliculate leaves and a two- to four-flowered scape. When this synonym is established, two taxa are joined, one described from Moroccan plants and the other from Spanish plants, already both considered to be different by Gay (1858). Since that time, *N. obsoletus* has been used to refer to northern Moroccan plants by several authors (Talavera *et al*., 1995; Fernández Casas, 1997).

Taking into account the above information and the published descriptions of the different taxa, the two populations of *N. elegans* from northern Morocco examined in this study correspond to the species by having synanthous, flat, and canaliculate leaves, entire, conical, and orange-brownish corona, and tepals tending to reflect after anthesis. Nevertheless, their oblong-elliptic, and not lanceolate and narrow tepals as typical taxa, fit better with var. *intermedius* Gay.

We designate *N. obsoletus* (Haw.) Steud. to the orange morphotype of *N. serotinus* in this study. The morphological variability of the populations agrees with the description and figure of Parkinson (1629), and with its interpretation by Haworth (1819). Unfortunately, the herbarium and type specimens listed by this author are unknown (Stafleu & Cowan, 1983). The triangular outline and colour of the corona, the narrowly obconical tube, and more than one flower per inflorescence fit well with the material studied. Nevertheless, one comment must be made about the two leaves appearing with the scape in Parkinson's icon, giving synanthous character to this taxon: this character is infrequent in the populations studied, but, in culture conditions, scapes with one or two long leaves are frequently seen. Likewise, the plant from which Parkinson's icon was inspired was probably cultivated. The icon leaves also appear wider than as they are described ('very narrow'), but, as previously mentioned, the woodcut was of low quality. The location of this taxon ('Hispania') excludes the consideration of plants from north Africa in the typification process, where other taxa with probable hybrid origin could have been taken into account. This agrees with Gay (1858), who recognized this variability in *N. serotinus* L., but disagrees with Maire (1958), who, in spite of recognizing this variability, used *N. obsoletus* (Haw.) Spach to designate the taxon subordinated to *N. elegans*.

According to the opinion maintained here, *N. serotinus* var. *major* Pérez-Lara corresponds to *N. obsoletus* (Haw.) Steud., distinguishing it from the variety typically by a greater bulb size (18–25 mm in

diameter) and robust scape with two to four, rarely one, flowers. Also, *N. deficiens* Herb., described from Greece ('Ex Leucade, prope castellum Alexandri') by Herbert (1847: table 22, fig. 1), agrees with the variability shown for *N. obsoletus* (Haw.) Steud. in this study, including the obliterated, but brown corona, and the synanthous or sometimes hysteranthous leaves. The flower section included in Herbert's figure 1 (Herbert, 1847) shows a similar stamen disposal to the population from Greece examined in this study (see Fig. 2A: 6). The taxonomic treatment is included in the Appendix.

This study suggests that *N. obsoletus* (Haw.) Steud. is clearly intermediate between *N. serotinus* L. and *N. elegans* (Haw.) Spach. It is most likely that these taxa have taken part in its origin. Thus, the region in which both taxa coexist is the centre of origin and dispersal of the genus *Narcissus* (southern Spain, northern Morocco, and Gibraltar Strait, at present submerged), as shown by Fernandes (1966). Previous studies, regarding *N. serotinus s.l.* and *N. elegans* as the same species (Fiori, 1923), within the same section (Gay, 1858), or similar from a karyological perspective (Fernandes, 1951), highlight the relationships of both taxa. Nevertheless, besides an ancient hybridization, other evolutionary processes (geographical divergence, new hybridization processes, chromosome rearrangements) (Fernandes, 1951) occurring in the genus *Narcissus* must be operating on the constitution of *N. obsoletus* (Haw.) Steud., as it occurs at present. Studies based on other characters (not morphological), for example, karyological, molecular, and reproductive, are necessary to confirm this hypothesis. Likewise, more populations from northern Morocco and the eastern Mediterranean must be studied, with careful consideration given to mixed populations in which more than one taxon may be present.

ACKNOWLEDGEMENTS

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APPENDIX

TAXONOMIC TREATMENT OF *N. SEROTINUS* L. *S.L.* IN THE IBERIAN PENINSULA TAXA

Key for the three taxa treated

1. Leaves (2–)3–6 mm width, flat and canaliculate, always present with the flower scape. Corona entire and conical. Shorter stamen filaments adnate up to 1 mm from the insertion point of the anthers ....*N. elegans*
1. Leaves (0.7–)1–2(–3) mm width, cylindrical to subcylindrical or semicylindrical and canaliculate, never or occasionally present with the flower scape. Corona deeply lobed, very rarely entire. Shorter stamen filaments adnate more than 1 mm below the insertion point of the anthers 2
2. Hypanthial tube abruptly widened towards middle. Shorter stamen filaments adnate lower than one-third of length. Corona yellow, with circular outline and six entire or emarginate lobes reaching the base of the corona. One or, very rarely, two flowers per inflorescence..*N. serotinus*
2. Hypanthial tube narrowly obconical, gradually widening from the base to apex. Shorter stamen filaments adnate higher than one-third of length. Corona orange or orange-brownish, with triangular or circular outline and three entire or emarginate lobes reaching the base of the corona, sometimes corona with one to two incisions reaching the base and, more rarely, corona entire. 1–3(–4) flowers per inflorescence..*N. obsoletus*

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1. Narcissus serotinus L., Sp. Pl. 290 (1753)

= *Hermione serotina* Haw., *Monogr. Narcissin*. 13, n. 53 (1831).

Description: Perennial. Bulb 9–18 × 5–19(–21) mm, ovoid-globose, covered by dark brown, shiny scales. Leaves 1 on nonflowering bulbs; absent on flowering bulbs. Leaf sheaths 1(–2), scarious; inner sheath 1.3–10(–12) cm longer than the outer sheath; outer sheath 0.7–4.5 cm. Leaf blade 10–14 cm × 0.7–1.3 mm, green, filiform, subcylindrical to semicylindrical, not canaliculate, obtuse. Scape 7–26(–35) cm × 0.6–2 mm, cylindrical or subcylindrical, with one flower, very rarely two. Spathe 10–33 × 1.4–6.3 mm, lanceolate, acuminate, scarious, whitish to pale brown, transparent, with sheathing part 3–22 mm long. Flower pedicels 4–19 mm. Flowers erect to erect-patent, scented. Tepals patent or sometimes patent-recurved, white; outer tepals 7.5–18(–21) × 3.2–12.8 mm, oblong-elliptic, sometimes oblong-lanceolate, oblong-ovate, obovate, or oblong-spatulate, obtuse, mucronate with tip 0.2–1.5(–1.8) mm long, or nonmucronate; inner tepals 7–20(–22) × (2–)3.5–9(–10.5) mm, oblong-elliptic, sometimes oblong-lanceolate, oblong-ovate, or obovate, obtuse, sometimes emarginate, mucronulate or nonmucronulate. Corona (0.2–)0.4–2 mm in height, with circular outline, yellow, with six entire or emarginate lobes. Hypanthial tube 10.5–18.6(–19.5) × 2–5.5 mm, subclavate, abruptly widened in the middle part, green with yellow stripes in the upper part. Androecium with two different whorls of stamens. Longer stamens with filaments 10–18(–19) mm, almost totally adnate up to the distal part of hypanthial tube, with anthers 1.1–4.4 mm, usually semi-exert. Shorter stamens with filaments 7–14(–15) mm, adnate lower than one-third of its length, free at 1–5.9 mm from hypanthial tube base, and

anthers 1.4–5.1 mm, included into the tube. Style (6–)8–18 mm, stigma usually situated between the two whorls of anthers, sometimes exerted up to 1(–1.6) mm. Ovary (2–)2.4–11 × 3.4–6.6 mm, oblongoid or obovoid. Capsule 7–16 × 3.5–5.5 mm, obovoid, oblongoid, or ellipsoid, green, dull. Seeds 2–3 mm, ovoid, sharp, and shiny black. Fl. IX–XI.

Ind. Loc.: 'Habitat in Hispania' (Linnaeus, 1753: 290).

Type: 'Hispania in Estramadura prope Badajoz Loefl.' [Lectotype: sheet 412.14 A, K Linnean Herbarium, chosen by Barra & López González (1984: 357)].

Distribution: South-west Iberian Peninsula and north-west Morocco.

Habitats: Moist biotopes, such as meadows, pastures, marshes, along streams, and cleared forests (*Pinus pinea, Quercus suber*), on grassy or rocky slopes, in well-developed sandy or clay soils, but also in soils poorly developed on slates.

2. Narcissus obsoletus (Haw.) Steud., Nomencl. Bot., ed. 2, 2: 182 (1841)

≡ *Hermione obsoleta* Haw., *Suppl. Pl. Succ.*: 146 (1819).

≡ *Narcissus obsoletus* (Haw.) Spach, *Hist. Nat. Vég.* 452 (1846).

= *Narcissus serotinus* var. *major* Pérez Lara, *Anales Soc. Esp. Hist. Nat.* 15, 2: 446 (1886).

= *Narcissus deficiens* Herb., *Edward's Bot. Reg.* 33, table 22, fig. 1 (1847).

– *Narcissus serotinus sensu* auct.

Description: Perennial. Bulb 12–26.5(–30) × 7–26 (–29) mm, ovoid-globose, covered by dark brown, shiny

scales. Leaves 1(–2) on nonflowering bulbs; absent or more rarely 1(–2) leaves on flowering bulbs. Leaf sheaths 1–2(–3), scarious; inner sheath 1.7–11 (–13) cm longer than or sometimes as long as the outer sheath; outer sheath 0.8–11 cm. Leaf blade 4–20 (–27) cm × 0.7–2(–3) mm, green, slightly glaucous, filiform, semicylindrical to canaliculate, obtuse. Scape 7–38 cm × 0.9–3.3(–3.6) mm, subcylindrical, with 1–3(–4) flowers. Spathe 12–50 × 2–11 mm, lanceolate, acuminate, scarious, brown to dark brown, opaque, with sheathing part 3–29 mm long. Flower pedicels 5–40 mm. Flowers erect to patent, scented. Tepals, patent or sometimes patent-recurved, white; outer tepals 9.5–21(–23) × 4.2–11 mm, usually oblong-elliptic, sometimes oblong-lanceolate, oblong-ovate, obovate, or oblong-spatulate, obtuse, mucronate, with tip 0.4–2.6 mm long; inner tepals 9.5–20 × 3–9(–10.5) mm, usually oblong-elliptic, sometimes oblong-lanceolate, oblong-ovate, or obovate, obtuse, sometimes emarginate, mucronulate or nonmucronulate. Corona 0.5–2.3(–2.5) mm in height, with circular to triangular outline, orange, brownish-orange, or greenish-orange, usually with three entire or emarginate lobes, sometimes with only one to two incisions, and more rarely entire. Hypanthial tube 12–20 × 2.3–5.3 mm, narrowly obconic, progressively widening from base to apex, green, sometimes with orange stripes in the upper part. Androecium with two different whorls of stamens. Longer stamens with filaments 11–19 mm, almost totally adnate up to the distal part of hypanthial tube, with anthers 1.5–5.5 mm, usually semi-exert. Shorter stamens with filaments 8.3–15 mm, adnate higher than one-third of its length, free at 3.2–12 mm from hypanthial tube base, and anthers 2–5(–6) mm, included within the tube. Style 10.5–20 mm, stigma usually situated between the two whorls of anthers, sometimes exerted up to 1.8 (–2.5) mm. Ovary 3–12.5 × 1.5–3.6 mm, ellipsoid-oblongoid. Capsule (7–)9–20(–23) × 4–7(–9) mm, ellipsoid, oblongoid, or slightly obovoid, green, dull. Seeds 2–3 mm, ovoid, sharp, and shiny black. Fl. IX–XI.

Ind. Loc.: 'naturall of Spain' (Parkinson, 1629: 90).

Type: Figure 4, page 89 *Paradisus terrestris*, Parkinson, (1629), lectotypus, designated here.

Distribution: Mediterranean coasts, from northern Morocco and southern Spain to Israel, penetrating inland to south-west Spain and north-west Morocco (Fig. 1A).

Habitats: Moist biotopes, such as meadows, pastures, marshes, along streams, and seashores, on grassy or rocky slopes, in well-developed clay soils, but also in scarcely developed chalky or loamy soils.