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# Morpho-environmental characterization of the genus *Dianthus* (Caryophyllaceae) in the Iberian Peninsula: *D. pungens* group

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The morphology of several taxa of the *Dianthus pungens* group (*D. gredensis*, *D. langeanus*, *D. pungens* subsp. *brachyanthus* and *D. pungens* subsp. *hispanicus*) was characterized. In order to correlate the morphological variability with environmental parameters, an altitudinal and bioclimatic approach was applied. The data provided evidence of apparent correlations between the morphological variability within this taxonomic group and the altitudinal-climatic distribution. As the correlations detected here do not allow to establish significant relationships between the environmental variables considered, a complementary analysis (e.g. a geological approach) is needed. An analytical primer is proposed to pursue the morphological characterization of this genus. Two opposite tendencies were obtained: *D. gredensis*–*D. langeanus* and *D. pungens* subsp. *hispanicus*. *Dianthus pungens* subsp. *brachyanthus* is recognized as an intermediate taxon between the two tendencies, at morphological, altitudinal and climatic level. One new subspecific combination is proposed, and some old combinations are applied again in order to establish the taxonomic group *Dianthus pungens* (*D. pungens* subsp. *brachyanthus* (Boiss.) Bernal, Fernández Casas, G. López, Laínz & Muñoz Garmendia, *D. pungens* subsp. *gredensis* (Pau *ex* Caballero) A. Crespí, C.P. Fernandes, A. Castro, Bernardos & Amich, *comb. nova*, *D. pungens* subsp. *hispanicus* (Asso) O. Bolòs & Vigo, *D. pungens* subsp. *langeanus* (Willk.) O. Bolòs & Vigo.

Key words: altitude, bioclimatic regions, Caryophyllaceae, *Dianthus*, environmental characterization, Iberian Peninsula, morphology, taxonomy

# Introduction

Despite comprising several taxonomically critical and complex species (Bernal *et al*. 1990), the genus *Dianthus* (Caryophyllaceae) has been one of the least analysed taxon in the Iberian flora. It includes several diploid and polyploid closely related taxa distributed throughout most of Europe and also in northern Africa (Willkom & Lange 1878, Merino 1906, Tutin 1964, Franco 1971, Laínz 1985a, 1985b, 1986a, 1986b, 1987a, 1987b, Gallego 1987, Bernal 1988, 1989, 1990, Sampaio 1988, Bolós & Vigo 1990, Tutin & Walters 1993). The main consequence that derives from this complexity is the high number of endemic taxa reported for the Iberian Peninsula. According to Bernal *et al*. (1990), 68% of the *Dianthus* taxa in the Iberian Peninsula is endemic, which corresponds to about 8% of the European taxa (Tutin & Walters 1993). Among the endemic taxa, *D. gredensis*, *D. langeanus*, *D. pungens* subsp. *brachyanthus* and *D. pungens* subsp. *hispanicus* exhibit very similar patterns of morphological variation. Owing to this similarity, this group of taxa will be henceforth referred to as *D. pungens* group. It is worth noting that *D. pungens* subsp. *brachyanthus* is the most abundant taxon of the Iberian Peninsula.

Raven (1974) and Kaplan (2001) proposed the application of numerical methodologies to morphological characterizations, suggesting the possibility of using several types of parameters and analytical matrices that provide information regarding the phenotypic plasticity of the individuals (Bradshaw 1972, Sultan 1987). In the present contribution, which may be depicted as a first approach to the characterization of *Dianthus* in the Iberian Peninsula, the correlation between the morphological variability of the specimens and the altitudinal and bioclimatic parameters are examined. For this study, the taxa included in the *D. pungens* group were selected. The main goal of the present work is to determine the morphological and environmental correlations among these taxa. This analytical method will also be employed to characterize the other species and subspecies of the genus *Dianthus* in the Iberian Peninsula.

# Material and methods

## Taxonomic sampling and information sources

For scoring and measurements of vegetative morphological characters, 283 specimens from the Iberian herbaria AVE, BC, BCF, BRESA (= Escola Superior Agrária de Bragança, not in Holmgren *et al*. 1990), COI, FCO, HVR, JACA, LISE, LISU, LEB, MA, MAF, PO, SALA, SANT and SEV, were analysed. The specimens analysed were identified as follows: *Dianthus algetanus* subsp. *algetanus*, *D. algetanus* subsp. *turolensis*, *D. costae*, *D. gredensis*, *D. hispanicus*, *D. langeanus*, *D. pungens*, *D. pungens* subsp. *brachyanthus*, *D. pungens* subsp. *hispanicus*, *D. subacaulis* subsp. *brachyanthus*, and *D. turolensis*.

## Data analysis

Four vegetative and twenty-eight floral quantitative characters (Operational Taxonomic Units, OTUs; Camin & Sokal 1965) were measured (Fig. 1). According to Hill (1980) and Thiébaut (2000), the selection of the morphological characters depends on the quality of information they may offer. Here, the selection was based on the morphological descriptions of the taxa considered (Willkom & Lange 1880, Rozeira 1944, Tutin 1964, Franco 1971, Coutinho 1974, Gallego 1987, Sampaio 1988, Bolòs & Vigo 1990, Bernal *et al*. 1990, Tutin & Walters 1993, Crespí 1999). For the purpose of excluding artificiality of the analysis (Lubischew 1963) the combined morphological parameters were not considered in this work. The OTUs measured were:

Fsl1/2 = minimum and maximum length of calyx,
Fsdl1/2 = minimum and maximum length of calyx teeth,
Fsda1/2 = minimum and maximum width of calyx teeth,
Fsad1/2 = minimum and maximum width of calyx appendix (on the basis of the calyx teeth),
Fsab1/2 = minimum and maximum width of calyx,

Fge = maximum length of style Ful1/2, minimum and maximum length of the corolla nail,
Flac = maximum length of corolla teeth,
H = presence/absence of hairs in corolla throat,
Fel1/2 = minimum and maximum length of epicalyx,
Fsa1/2 = minimum and maximum length of the appendix of the calyx teeth,
Fbia1/2 = minimum and maximum length of the epicalyx teeth,
Ifl maximum length of inflorescence,
Fn1/2 = minimum and maximum number of flowers in inflorescence,
Lbif1/2 = minimum and maximum length of the basal bract of inflorescences,
Sl1/2 = minimum and maximum length of vegetative steams,
LlM = maximum length of leaves,
LwM = maximum width of leaves.

The altitudinal survey allowed us to correlate the morphological variability of the taxa with their altitudinal distribution. This correlation was established per classes of equidistance. In the present case five classes were selected: $0 > x \leq 450$ m, $450 > x \leq 950$ m, $950 > x \leq 1550$ m, $1550 > x \leq 1950$ m and $x > 1950$ m.

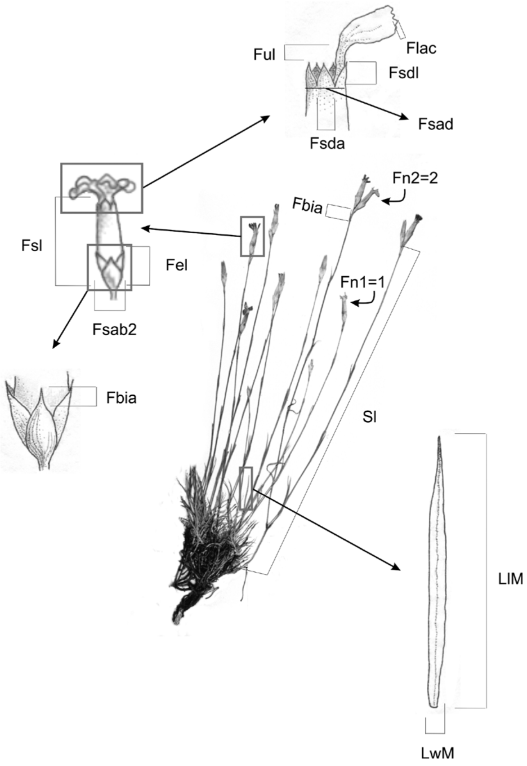

**Fig. 1.** The morphological characters analysed.

To perform a bioclimatic characterization, 200 and 61 Iberian termopluviometric stations were chosen (Instituto Nacional de Metereologia 1961–1990, Montero Burgos & González Rebollar 1983, Carballeira *et al.* 1983). The reported average values of the temperature per month ($T$), precipitation per month ($P$) and evapotranspiration per month (ETP) for each station for a period of 15 years were inspected. The annual period chosen for the climatic characterization was included only in the physiological activity period (PAP, Montero Burgos & González Rebollar 1983). The monthly climatic parameters involving average temperatures lower than 7.5 °C were excluded, as any physiological activity is adequate only above this value. Hence, PAP may be considered as the Potential Bioclimatic Intensity (PBI) corresponding to the most stable vegetative period. The parameters deduced here for the PAP are the following: (a) determination of the intervals for which the average temperature increases (warming period) and decreases (cooling period) month after month, on the basis of the highest average temperature per month; (b) determination of the sum of the average temperatures per month (ST1 and ST2, for the warming and cooling periods, respectively) and the sum of the average precipitations per month (SP); (c) according to Montero Burgos and González Rebollar (1983), the real evapotranspiration per month (ETR) may be calculated by means of the formula:

$$\mathrm{ETR} = \mathrm{ETP} \times 0.2 \qquad (1)$$

where ETP is the potential evapotranspiration per month. To calculate the most approximate value of the bioclimatic intensity (BI) for the warming and cooling periods, based on the accessible humidity, we employed the following expression:

$$\mathrm{BI} = P - \mathrm{ETR} \qquad (2)$$

The climatic variables indicated above were employed to construct a matrix for the 261 termopluviometric stations. In order to organize all the information, we adopted the biogeographical approach of Rivas-Martínez (1987a, 1987b), which considers a total of 11 biogeographical provinces (plus one additional province for the Balearic Islands) in the Iberian Peninsula (Fig. 2): P1, Pyrenean; P2, Atlantic; P3, Orocantabric; P4, Aragonese; P5, Catalan-Valencian; P7, Castilian-Maestracensean-Manchean; P8, Murcian-Almeriensian; P9, Carpetan-Iberian-Leonese; P10, Lusitan-Extremadurean; P11, Gaditan-Onubensean-Algarvian; and P12, Betic. The matrix, elaborated based on the climatic variables previously described, is classified according to this biogeographical characterization of the Iberian Peninsula, in order to describe the climatic differences between the Rivas-Martínez´s provinces. Elaboration of bioclimatic groups is the aim of this analysis.

### Species classification

The methodology involved a multivariate analysis supported by a basic matrix and performed on the standardised data values. To avoid the risk of overemphasizing the dominant morphological variables in the basic matrix (Ludwig & Reynolds 1988), the standardised matrix was employed for the statistical approach, in the context of a numerical phenetic methodology. To equalize phenotypic variances (Sokal & Sneath 1973, Duncan & Baum 1981), a principal component analysis (PCA) and a cluster analysis of populations of *D. brachyanthus*, *D. gredensis*, *D. hispanicus*, and *D. langeanus* were carried out. Firstly, these were represented by the mean values of the characters examined. Secondly, an R type of PCA (Sneath & Sokal 1973, Krzanowski 1990, Hair *et al.* 1995), based on a correlation matrix, was employed. UPGMA (Unweighted Pair-Group Method using Arithmetic Averages) and City-block clustering methods were used to check the hierarchical structure in the data set (Crespí 1999, Crespí *et al.* 2003, Bernardos *et al.* 2004, 2005). To assess the separation of population groups resulting from PCA and cluster analyses, a canonical discriminant analysis (CDA; Klecka 1980, Krzanowski 1990) was carried out. Individuals were characterized by means of OTUs and morphological tendencies were described through the results obtained from the PCA and cluster analyses. The total canonical structure expressing the correlation of morphological characters with the canonical axes was computed to identify the characters that contributed strongly to group separation. CDA was very useful in this respect, as it allowed us to determine the capacity of discrimination per species or per environmental factor (altitudinal class or bioclimatic region), through the $F$ value for statistical significance of the $R^2$ (Rao's approximation) and Wilk's lambda and $p$, for the first two eigenvalues (with more than 90% of the variance data, as recommended in the literature; *see* Gotelli & Ellison 2004). Means, standard deviations, and percentiles were calculated for all characters. In the description of the taxa, 5% and 95% percentiles have been given for character value ranges, with 1% and 99% included in brackets. Boxplots with boxes defined as interquartile ranges, whiskers as 10% and 90%, and asterisks as extreme values were also computed. The multivariate analysis was performed using Statistica AX V. 7.0 and the SPSS v. 12.0 software packages for Windows.

In order to characterize the morpho-physical variation (altitude and climatic variables, in this case), the standardized morphological matrix was classified per altitudinal and bioclimatic classes.

## Results

While *Dianthus gredensis* and *D. langeanus* have narrower distributions and are located in the north-western and the central-western Iberian Peninsula, *D. hispanicus* occurs in the east and *D. brachyanthus* is a characteristic high-altitude taxon, appearing between the occidental taxa (*D. gredensis* and *D. langeanus*) and the oriental taxon (*D. hispanicus*) (Bernal *et al.* 1990). Sampling of the taxa covering the geographic area of the Iberian Peninsula allows to deduce the occurrence behaviour for these taxa.

The climatic parameters used for the eleven biogeographical provinces of the Iberian Peninsula give rise to four apparent groups (Fig. 2): a temperate and humid group (G1: P2, or Atlantic

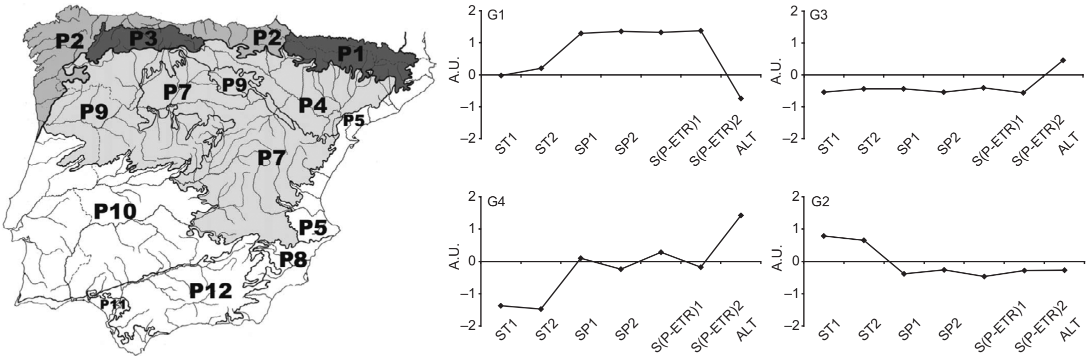

**Fig. 2.** Climatic variability of the four groups of provinces for the Iberian Peninsula (ST1 = sum of the average temperatures per month in period 1; ST2 = sum of the average temperatures per month in period 2; SP1 = sum of the average precipitations per month in period 1; SP2 = sum of the average precipitations per month in period 2; S(P-ETR)1 = sum of the differences between P1 and the real evapotranspiration per month in period 1; S(P-ETR)2 = sum of the differences between P2 and the real evapotranspiration per month in period 2; ALT = average altitude of the thermopluviometric stations. The units for each parameter are standardized, in order to compare them.

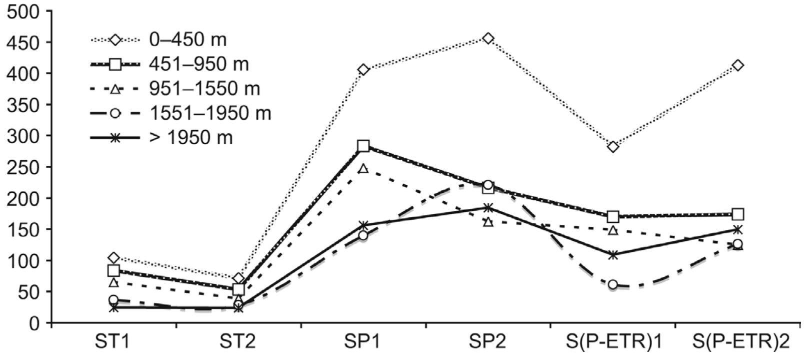

**Fig. 3.** Climatic variability for the thermopluviometric stations grouped per altitudinal classes. The classes $x \leq 450$, $1550 > x \leq 1950$ and $x > 1950$ m register lower temperatures in the second half of the year, and higher rainfalls during the first half. In the other two classes the precipitation is higher in the first half of the year. In this case the standardized matrix has not been used in order to show more significantly the thermopluviometric differences per class.

group), a warm and dry group (G2: P5, P8, P10, P11, P12), a cool and also dry group (G3: P4, P7, P9) and an extremely cool and moderately humid group (G4: P1, P3, or Oromediterranean/orotemperate group). G2 and G3 could be also considered Ibero-Mediterranean groups. These four groups will be considered as the bioclimatic classes, in order to characterize the morphological variation per class. The variation of the climatic parameters per altitudinal classes shows the highest values of temperature and precipitation along the whole year in the case of the minimum altitudinal class. In contrast, the lowest values are observed for the two maximum altitudinal classes. Nevertheless, the intermediate class ($950 > x \leq 1950$) is very irregular: cooler and with accumulation of the precipitation during the second half of the year (Fig. 3).

The distances for mean values of the characters analysed per taxon, from the standardized morphological matrix are shown in Fig. 4. The major distance is observed for *D. hispanicus*, whereas the other taxa are clearly closer.

The PCA confirms the results obtained by the cluster analysis. Three distinct groups of populations corresponding to *D. hispanicus*, *D. brachyanthus* and *D. langeanus*–*D. gredensis* can be seen in Fig. 5a. On the basis of the analysis of correlation groups, *D. hispanicus* was already separated along the first axis, while *D. brachyanthus* was partially separated from *D. langeanus*–*D. gredensis* along the first axis

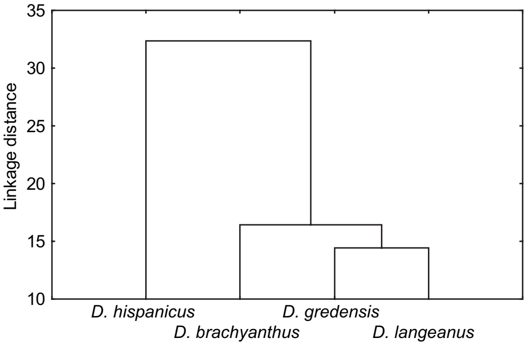

**Fig. 4.** Tree representation derived from the UPGA-City block cluster analysis for the average morphologic variables per taxon analysed.

and overlaps with these two last taxa along the second and third axes.

Canonical discriminant analysis confirms the results previously obtained by the cluster analyses and PCA. Individuals of the four taxa are clearly separated along the two canonical axes (Fig. 5b). While only one character (Fsl2, maximum length of calyx) contributed mostly to the separation of OTUs along the first axis, several other characters were more important for the separation along the second axis (the Fbia1 is the first of these complementary characters). These characters were also decisive to distinguish the taxa by the CDA (Table 1).

According to the methodological process, the morphological approach is started with the application of PCA and CDA to the four taxa. The PCA for the first three factors explains to 67% of the total variability of the correlation matrix for the specimens analysed (Fig. 5a). In accordance with these results, *D. langeanus* and *D. gredensis* are more correlated, unlike *D. hispanicus*. *Dianthus brachyanthus* is placed in an intermediate situation among these extreme correlations. This pattern is more clearly observed in the CDA data (Fig. 5b), in which we can observe that Fsl2 is the most discriminate OTU (Table 1) (corresponding to 83% of variation among groups).

The variation of the average values of Fsl2 and Fsbia1 per taxa reveals the differences between *D. langeanus*–*D. gredensis* and *D. hispanicus* (Table 1). However, the *F* value for Fsl2 is evidently distanced from the one for Fsbia1. In fact, Fig. 4 shows an intermediate morphological pattern for *D. brachyanthus*, if the Fsl2 variable is considered. The similarity analysis of the average values per OTU for each taxon leads to the same results (Fig. 6). This univariate examination of the most discriminant morphological characters provides evidence that: (1) *D. langeanus* and *D. gredensis* have shorter calyx (Fsl2) than *D. hispanicus*; (2) the shortest appendix bracts are in *D. langeanus* and *D. brachyanthus*,

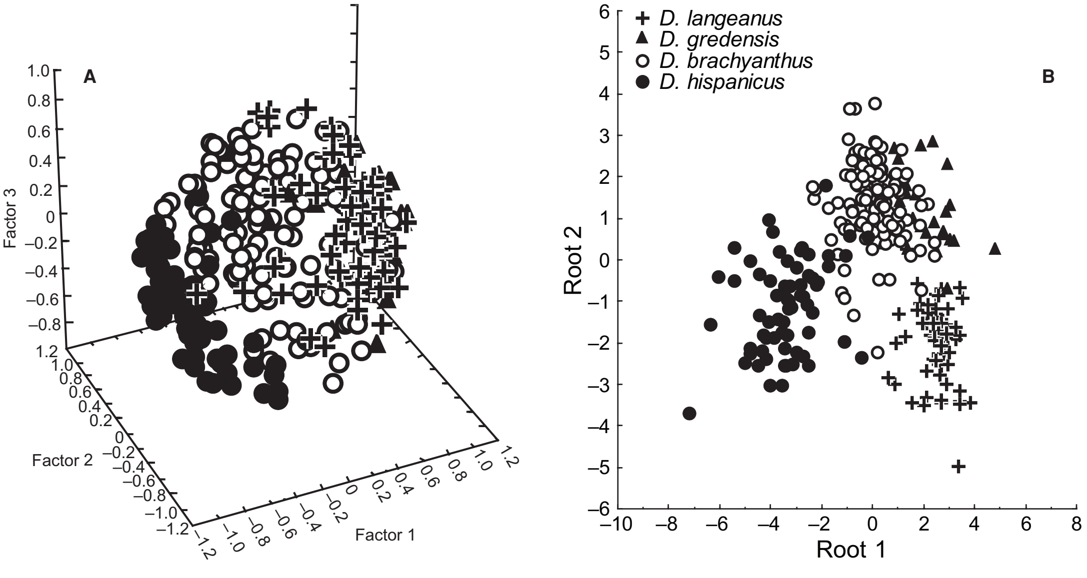

**Fig. 5.** First three PCA factors of the Pearson correlation matrix, (**a**) with the correlation areas per taxon, (**b**) CDA for the morphologic matrix classified per taxon.

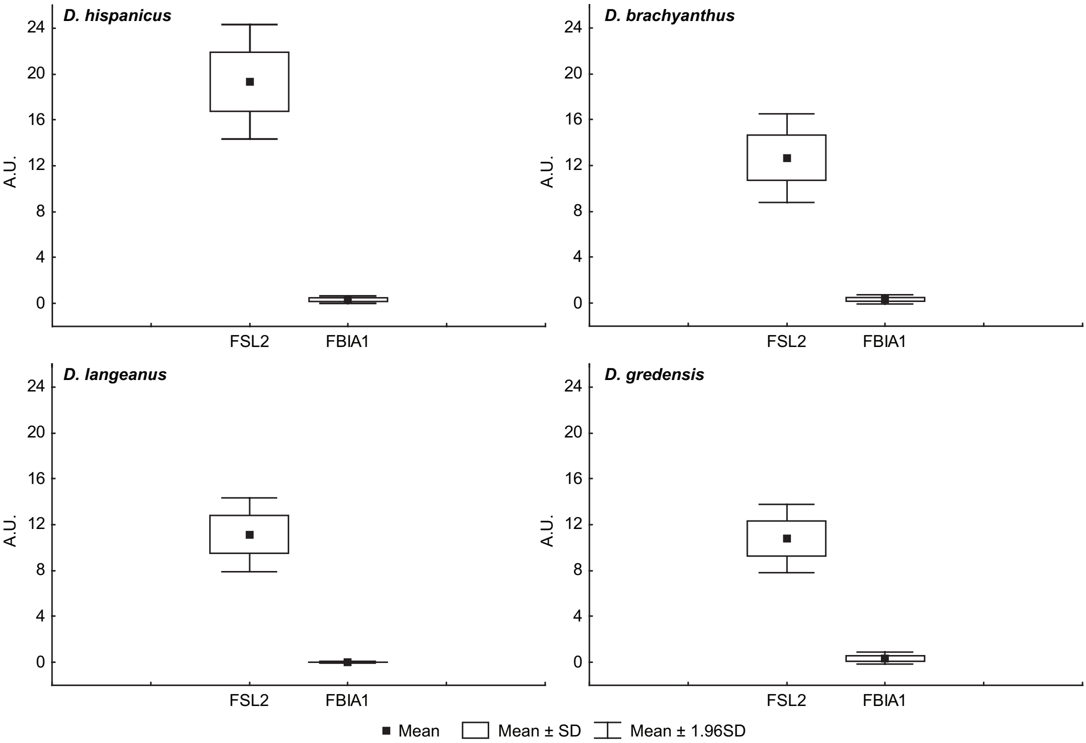

**Fig. 6.** Box-plot representations of the mean, standard deviation and 90% percentiles. The intermediate pattern of *Dianthus brachyanthus*, between *D. langeanus*–*D. gredensis* and *D. hispanicus*, is clearly evidenced for Fsl2.

**Table 1.** Summary of the numerical results retrieved from CDA for the individuals classified per taxon. Fsl2 and Fbia1 are the most discriminant variables, on the basis of the highest *F* and the reduced *p* obtained.

| | *F* | df 1 | df 2 | *p* | Wilks' lambda |
|---|---|---|---|---|---|
| Fsl2 | 229.5095 | 3 | 270 | 0.000000 | 0.281682 |
| Fbia1 | 122.3373 | 6 | 538 | 0.000000 | 0.178885 |
| Fsab2 | 94.7942 | 9 | 652 | 0.000000 | 0.130649 |
| Fsa2 | 77.1636 | 12 | 707 | 0.000000 | 0.109106 |
| Fsdl1 | 66.3479 | 15 | 735 | 0.000000 | 0.094040 |
| Fn2 | 58.5034 | 18 | 750 | 0.000001 | 0.083663 |
| LIM | 52.5536 | 21 | 759 | 0.000010 | 0.075873 |
| Sl2 | 48.2735 | 24 | 763 | 0.000009 | 0.068704 |
| Fsad2 | 44.9041 | 27 | 766 | 0.000019 | 0.062561 |
| Flac | 42.2753 | 30 | 767 | 0.000020 | 0.056983 |
| LwM | 39.9297 | 33 | 767 | 0.000094 | 0.052521 |
| Fbia2 | 37.8328 | 36 | 766 | 0.000303 | 0.048853 |
| Ful1 | 35.7799 | 39 | 765 | 0.002327 | 0.046193 |
| Fsad1 | 33.8629 | 42 | 763 | 0.007842 | 0.044112 |
| Lbif1 | 32.4627 | 45 | 761 | 0.001302 | 0.041492 |
| Fsab1 | 31.0223 | 48 | 759 | 0.007644 | 0.039600 |
| IfL | 29.5797 | 51 | 757 | 0.031730 | 0.038250 |
| Fel1 | 28.3142 | 54 | 755 | 0.029011 | 0.036913 |
| Fsl1 | 27.3730 | 57 | 752 | 0.005918 | 0.035134 |
| Fsda1 | 26.1943 | 60 | 750 | 0.116621 | 0.034319 |
| Fsda2 | 25.0593 | 63 | 747 | 0.215248 | 0.033713 |
| Fel2 | 24.0287 | 66 | 744 | 0.215518 | 0.033115 |
| Fge | 23.0850 | 69 | 742 | 0.223216 | 0.032536 |
| Sl1 | 22.1651 | 72 | 739 | 0.375260 | 0.032130 |

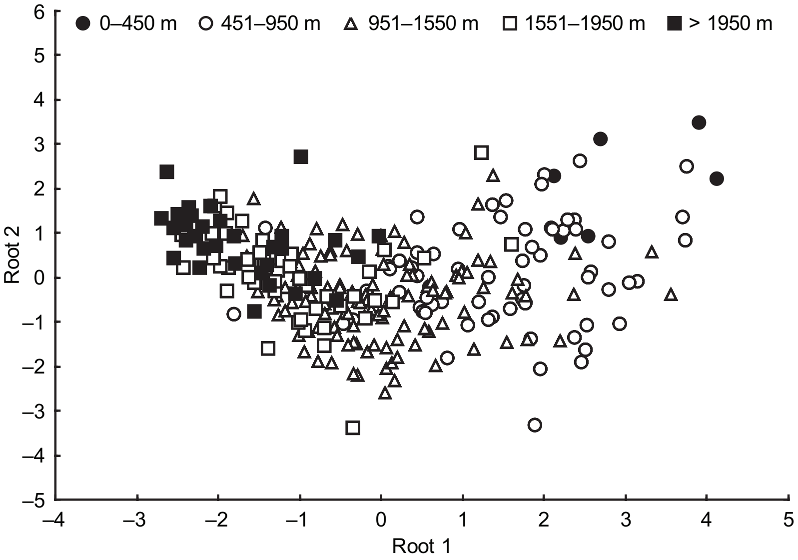

**Fig. 7.** Discriminant functions 1 and 2 with all individuals grouped in altitudinal classes.

while in *D. hispanicus* the bracts are the longest of the four taxa; in *D. gredensis* the bracts span the widest length range (Fig. 6). A summary of the morphological characters for identification of the four taxa is presented in Table 2.

An apparent differentiation exists along the first canonical axis (corresponding to 75% of variation among groups, eigenvalues not shown) between the populations belonging to the highest altitude range with respect to those of the lowest altitude range (Fig. 7). This differentiation is particularly manifested in three characters: the highest length of calyx (Fsl2), the longest stem (Sl2), and widest leaf (LwM) (Table 3). Significant variation among the five altitudinal classes was also observed for characters Fsl2 and Sl2, but not for LwM (Fig. 8). Finally, the percentage of taxa per altitudinal class evidences the extreme tendencies between *D. hispanicus* and *D. gredensis*. The former taxon is the only one in the first class ($x \leq 450$ m). In addition, it is the most abundant taxon of the second class ($450 > x \leq 950$ m).

**Table 3.** Summary of the numerical results retrieved from CDA for the individuals classified per altitudinal classes. Fsl2, Sl2 and LwM are the most discriminant variables, on the basis of the highest *F* and the reduced *p* obtained.

| | *F* | df 1 | df 2 | *p* | Wilks' lambda |
|---|---|---|---|---|---|
| Fsl2 | 38.06060 | 4 | 269 | 0.000000 | 0.638587 |
| Sl2 | 24.37868 | 8 | 536 | 0.000000 | 0.537601 |
| LwM | 19.86793 | 12 | 707 | 0.000000 | 0.463423 |
| LlM | 16.57716 | 16 | 813 | 0.000053 | 0.422177 |
| Fge | 14.02445 | 20 | 880 | 0.005265 | 0.399413 |
| Fel1 | 12.28922 | 24 | 922 | 0.009751 | 0.379812 |
| Ful1 | 11.05588 | 28 | 950 | 0.011335 | 0.361578 |
| IfL | 9.94356 | 32 | 968 | 0.085901 | 0.350532 |
| Ful2 | 9.01987 | 36 | 980 | 0.172677 | 0.342103 |
| Fbia2 | 8.27278 | 40 | 988 | 0.198980 | 0.334325 |
| Fel2 | 7.66255 | 44 | 993 | 0.203295 | 0.326767 |
| Fsda2 | 7.14750 | 48 | 996 | 0.227234 | 0.319722 |
| Fn1 | 6.68984 | 52 | 997 | 0.313647 | 0.313886 |
| Fsl1 | 6.30183 | 56 | 998 | 0.298271 | 0.307964 |
| Fsad1 | 5.97740 | 60 | 998 | 0.249523 | 0.301547 |
| Flac | 5.68089 | 64 | 997 | 0.311386 | 0.295955 |
| Lbif1 | 5.41592 | 68 | 995 | 0.332074 | 0.290656 |

**Table 2.** Summary of statistic data for the morphologic parameters per taxon.

| | *D.langeanus* | | | | *D.gredensis* | | | | *D.brachyanthus* | | | | *D.hispanicus* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | Percentile 10 | Percentile 90 | S.D. | Mean | Percentile 10 | Percentile 90 | S.D. | Mean | Percentile 10 | Percentile 90 | S.D. | Mean | Percentile 10 | Percentile 90 | S.D. |
| FSDL1 | 2.25 | 1.80 | 2.70 | 0.44 | 1.69 | 1.20 | 2.20 | 0.41 | 2.16 | 1.60 | 2.75 | 0.47 | 3.36 | 2.50 | 4.30 | 0.60 |
| FSDL2 | 2.83 | 2.40 | 3.40 | 0.43 | 2.50 | 2.00 | 3.30 | 0.53 | 3.00 | 2.30 | 3.70 | 0.60 | 4.43 | 3.50 | 5.40 | 0.87 |
| FSDA1 | 1.24 | 1.00 | 1.50 | 0.21 | 1.23 | 1.00 | 1.50 | 0.23 | 1.39 | 1.10 | 1.70 | 0.26 | 1.59 | 1.40 | 1.90 | 0.21 |
| FSDA2 | 1.70 | 1.40 | 2.00 | 0.28 | 1.79 | 1.50 | 2.10 | 0.29 | 1.98 | 1.50 | 2.50 | 0.36 | 2.21 | 1.70 | 2.80 | 0.49 |
| FSL1 | 9.48 | 7.60 | 11.90 | 1.53 | 8.49 | 6.50 | 10.10 | 1.44 | 10.62 | 8.60 | 12.65 | 1.88 | 16.37 | 13.40 | 19.00 | 2.24 |
| FSL2 | 11.15 | 9.50 | 13.40 | 1.64 | 10.79 | 8.70 | 12.50 | 1.51 | 12.68 | 10.50 | 15.50 | 1.97 | 19.31 | 16.50 | 22.40 | 2.56 |
| FSAD1 | 2.56 | 2.10 | 3.00 | 0.38 | 2.19 | 1.60 | 2.90 | 0.56 | 2.76 | 2.20 | 3.40 | 0.51 | 3.16 | 2.50 | 3.70 | 0.45 |
| FSAD2 | 3.30 | 2.60 | 3.90 | 0.45 | 3.73 | 2.90 | 4.60 | 0.63 | 3.85 | 3.00 | 4.70 | 0.69 | 4.40 | 3.50 | 5.50 | 0.77 |
| FSAB1 | 2.78 | 2.40 | 3.30 | 0.41 | 2.61 | 1.90 | 3.30 | 0.50 | 3.45 | 2.75 | 4.20 | 0.57 | 4.23 | 3.50 | 5.00 | 0.56 |
| FSAB2 | 3.50 | 3.00 | 3.90 | 0.38 | 3.82 | 3.40 | 4.50 | 0.48 | 4.44 | 3.70 | 5.10 | 0.55 | 5.29 | 4.60 | 6.10 | 0.57 |
| SL1 | 56.98 | 11.80 | 105.80 | 38.42 | 44.21 | 6.20 | 125.90 | 60.34 | 83.76 | 10.55 | 165.65 | 64.34 | 136.61 | 72.20 | 204.30 | 56.01 |
| SL2 | 138.00 | 84.40 | 187.40 | 41.63 | 118.45 | 34.00 | 277.90 | 90.55 | 172.76 | 86.10 | 269.50 | 70.04 | 244.89 | 166.70 | 321.40 | 59.18 |
| LLM | 17.30 | 11.60 | 23.00 | 4.45 | 20.68 | 10.80 | 37.20 | 10.30 | 27.25 | 13.70 | 45.65 | 14.78 | 59.33 | 27.60 | 87.30 | 22.61 |
| LWM | 1.06 | 0.80 | 1.40 | 0.24 | 1.52 | 1.20 | 1.90 | 0.35 | 1.66 | 1.20 | 2.25 | 0.44 | 1.56 | 1.10 | 2.10 | 0.41 |
| FN1 | 1.25 | 1.00 | 2.00 | 0.67 | 1.54 | 1.00 | 3.00 | 1.50 | 1.10 | 1.00 | 1.00 | 0.35 | 1.12 | 1.00 | 1.00 | 0.41 |
| FN2 | 3.80 | 2.00 | 7.00 | 2.12 | 4.33 | 1.00 | 9.00 | 3.67 | 2.58 | 1.00 | 4.00 | 1.55 | 3.33 | 2.00 | 6.00 | 1.45 |
| FUL1 | 0.14 | 0.00 | 0.50 | 0.28 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.07 |
| FUL2 | 0.79 | 0.00 | 1.60 | 0.58 | 0.29 | 0.00 | 0.70 | 0.35 | 0.26 | 0.00 | 0.90 | 0.46 | 0.86 | 0.00 | 2.60 | 1.07 |
| IFL | 52.42 | 6.80 | 116.40 | 48.09 | 53.93 | 0.00 | 155.00 | 76.05 | 36.60 | 0.00 | 90.40 | 44.66 | 86.95 | 28.00 | 162.10 | 56.79 |
| LBIF1 | 4.49 | 3.20 | 5.60 | 1.65 | 6.12 | 3.30 | 9.80 | 3.44 | 5.73 | 4.10 | 7.45 | 1.48 | 7.22 | 5.60 | 8.70 | 1.46 |
| LBIF2 | 8.93 | 5.40 | 15.40 | 3.87 | 12.27 | 6.90 | 20.30 | 5.03 | 10.06 | 6.90 | 13.65 | 3.71 | 15.48 | 8.30 | 23.70 | 7.77 |
| FEL1 | 4.22 | 3.50 | 5.40 | 0.72 | 4.13 | 3.00 | 5.60 | 1.08 | 5.09 | 3.90 | 6.30 | 0.94 | 6.87 | 5.40 | 8.40 | 1.02 |
| FEL2 | 5.25 | 4.50 | 6.30 | 0.78 | 5.51 | 4.30 | 7.40 | 1.23 | 6.31 | 4.90 | 7.70 | 1.06 | 8.73 | 7.40 | 10.40 | 1.28 |
| H | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| FBIA1 | 0.02 | 0.00 | 0.10 | 0.04 | 0.34 | 0.00 | 0.70 | 0.26 | 0.34 | 0.20 | 0.50 | 0.19 | 0.31 | 0.10 | 0.50 | 0.16 |
| FBIA2 | 0.19 | 0.10 | 0.30 | 0.12 | 1.27 | 0.50 | 1.60 | 2.12 | 0.69 | 0.40 | 1.20 | 0.34 | 0.65 | 0.40 | 1.20 | 0.35 |
| FGE | 7.29 | 4.20 | 9.70 | 2.30 | 5.86 | 4.50 | 7.20 | 1.29 | 7.53 | 5.25 | 10.40 | 2.47 | 12.90 | 8.20 | 17.90 | 3.31 |
| FSA1 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.10 | 0.05 | 0.03 | 0.00 | 0.10 | 0.07 | 0.04 | 0.00 | 0.20 | 0.07 |
| FSA2 | 0.03 | 0.00 | 0.10 | 0.06 | 0.15 | 0.00 | 0.30 | 0.14 | 0.25 | 0.10 | 0.40 | 0.13 | 0.28 | 0.20 | 0.40 | 0.11 |
| FLAC | 0.25 | 0.10 | 0.40 | 0.13 | 0.14 | 0.10 | 0.20 | 0.06 | 0.34 | 0.20 | 0.55 | 0.18 | 0.35 | 0.20 | 0.50 | 0.19 |

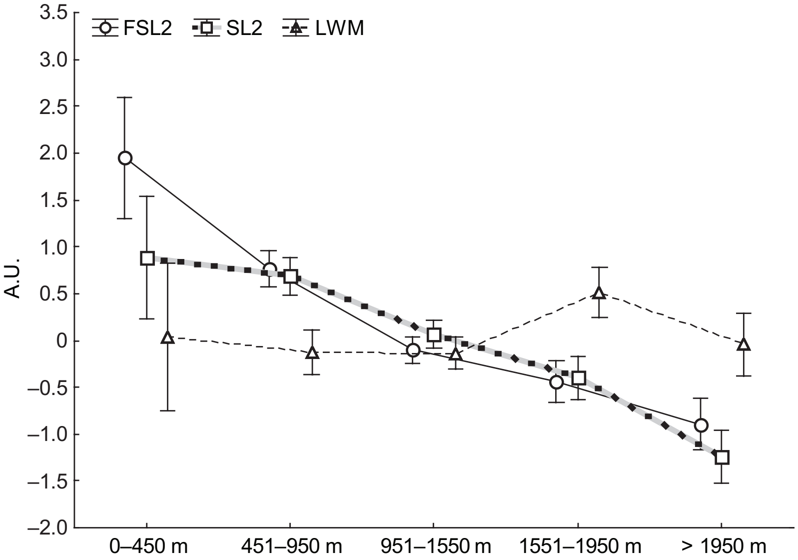

**Fig. 8.** Representation of the average variation for the most discriminant parameters, obtained from CDA per altitudinal classes (Fsl2, Sl2 and LwM).

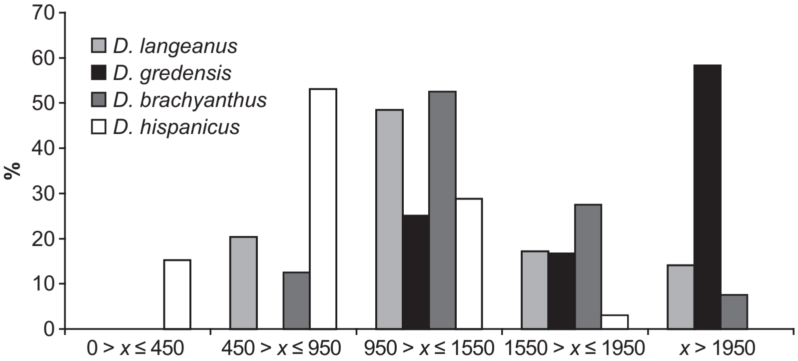

**Fig. 9.** Histogram of the percentages of each taxon per altitudinal class.

*Dianthus gredensis* is characteristic of the highest class ($x > 1950$ m). *Dianthus langeanus* and *D. brachyanthus* appear mostly in the intermediate class ($950 > x \leq 1450$ m) (Fig. 9).

An apparent differentiation is present along the first canonical axis (corresponding to 57% of variation among groups, eigenvalues not shown) between populations belonging to groups between G1 and G4 (Fig. 10). Essentially two characters contribute to the separation along the first axis: (1) the maximum calyx lenght (Fsl2); and (2) longest corolla teeth (Flac) (Table 4). Univariate examination of the average morphological characters for the four groups indicates similar behaviour for Fsl2 and Flac in the groups G2 and G3 (Iberian-Mediterranean groups), in contrast with G1 and G4 (Atlantic and Oromediterranean/orotemperate groups) (Fig. 11). The four taxa are present in group 3 (Fig. 12). Groups 1 and 2 display, however, opposite behaviour: in the former group *D. langeanus* and *D. brachyanthus* are the only taxa present, while *D. brachyanthus* and *D. hispanicus* are the only taxa in the group 2. *Dianthus brachyanthus* appears in all the groups (Fig. 12).

The combined altitudinal and bioclimatic analysis per taxon allows to confirm the preference of *D. gredensis* for G3. *Dianthus langeanus* and *D. brachyanthus* occur more frequently between 950 and 1550 m. Nevertheless, while *D. brachyanthus* appears in all the bioclimatic groups, *D. langeanus* does not occur in G2. The intermediate pattern of *D. brachyanthus* is confirmed again (Fig. 13).

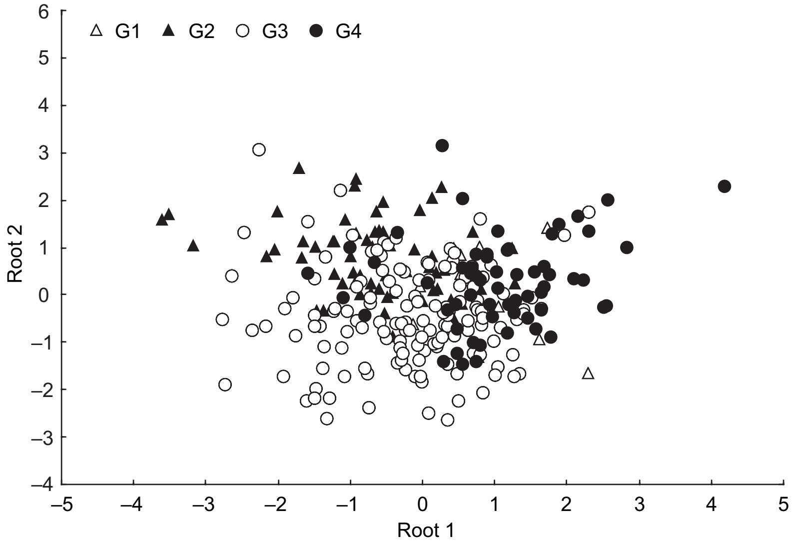

**Fig. 10.** Discriminant functions 1 and 2 with all individuals grouped in bioclimatic group.

## Discussion

The investigation carried out has demonstrated the continuous complexity of the morphological variation in the *Dianthus pungens* group. From the occurrence of the taxa analysed three different distributions have been drawn: an occidental distribution (*D. langeanus* and *D. gredensis*), an oriental distribution (*D. hispanicus*) and an intermediate one between the previous two (*D. brachyanthus*). The recognition of *D. langeanus*, *D. gredensis*, *D. brachyanthus* and *D. hispanicus* as distinct taxa is supported by the congruent results derived from the morphometric analyses. Although these taxa are clearly differentiated in their geographical distribution, we detected significant overlapping in their morphological traits. We must emphasize that just two morphological characters were sufficient to discriminate values that allow to distinguish the taxa morphologically.

According to the morphological approach, we can confirm a common morphologic group for the taxa analysed. This morphological characterization leads us to conclude that the mor-

**Table 4.** Summary of the numerical results retrieved from CDA for the individuals classified per bioclimatic group. Lwm, Flac and Fsda1 are the most discriminant variables, according to the highest *F* and the reduced *p* obtained.

| | *F* | df 1 | df 2 | *p* | Wilks' lambda |
|---|---|---|---|---|---|
| Fsl2 | 19.43163 | 3 | 269 | 0.000000 | 0.821889 |
| Flac | 14.19487 | 6 | 536 | 0.000007 | 0.744577 |
| Fn2 | 11.35274 | 9 | 650 | 0.001053 | 0.700937 |
| Fdl2 | 10.05138 | 12 | 704 | 0.000778 | 0.658121 |
| LwM | 8.88998 | 15 | 732 | 0.008931 | 0.630011 |
| Fbia1 | 8.08439 | 18 | 747 | 0.012181 | 0.604536 |
| Fsda1 | 7.49437 | 21 | 756 | 0.014664 | 0.580888 |
| FSad2 | 6.98893 | 24 | 760 | 0.027319 | 0.560982 |
| Lbif2 | 6.51505 | 27 | 763 | 0.063114 | 0.545552 |
| IfL | 6.31625 | 30 | 764 | 0.008928 | 0.521811 |
| Ful2 | 5.85545 | 33 | 764 | 0.303086 | 0.514543 |
| Fsdl1 | 5.46582 | 36 | 763 | 0.325416 | 0.507693 |
| Fsl1 | 5.18629 | 39 | 762 | 0.171557 | 0.497924 |
| Ful1 | 4.90871 | 42 | 760 | 0.292069 | 0.490735 |
| Fel2 | 4.64889 | 45 | 758 | 0.384992 | 0.484924 |

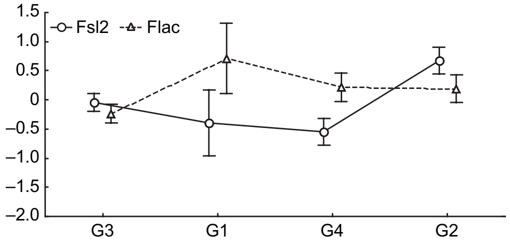

**Fig. 11.** Representation of the average variation for the most discriminant parameters, obtained by the CDA per bioclimatic group (Fsda, Lwm and Flac).

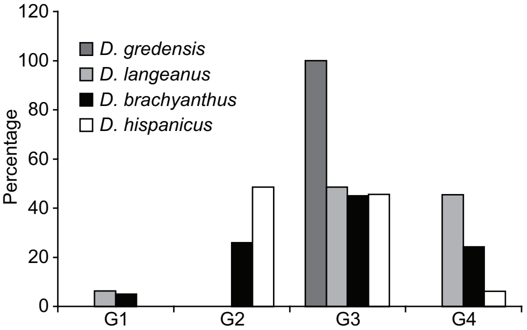

**Fig. 12.** Histogram of the percentages of each taxon per bioclimatic group.

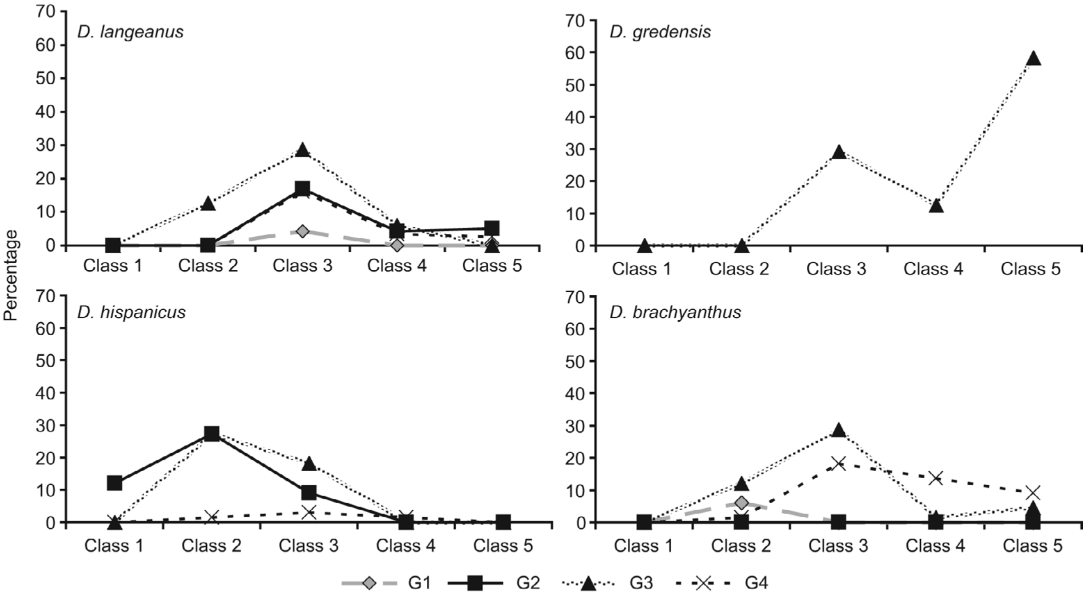

**Fig. 13.** Linear representation of the percentages of taxa per bioclimatic group and altitudinal class. *D. gredensis–D. langeanus* are present at high altitude, in contrast with *D. hispanicus*, which is more characteristic of lower altitudinal classes. *D. brachyanthus* maintains its more significant representation at intermediate altitudinal classes.

phological variability of *D. brachyanthus* is decisive, as a nexus between the morphological variation from the west and the east of the Iberian Peninsula. This group, designed as *D. pungens* group, is characterized by two opposite morphological tendencies: one of them shows the existence of smaller calyx, smaller stems and narrower leaves; the other one develops longer calyx, longer stems and wider leaves. The former tendency is distributed throughout the Occidental side of the Iberian Peninsula and never below 500 m of altitude. The latter tendency is manifested in the Oriental side of the Iberian Peninsula and never above 2000 m. The nexus between these two extreme tendencies is ensured by *D. brachyanthus*. This taxon is distributed all over the Iberian Peninsula, being present in the Occidental and Oriental sides. Anyway, this taxon has no occurrence below 500 m. Therefore, its morphological characteristics are adapted to the mountainous systems.

The environmental approach employed, which relies on the altitudinal and bioclimatic differentiations, confirmed the progressive behaviour of the floristic and vegetative characters from *D. gredensis–D. langeanus* to *D. hispanicus* through *D. brachyanthus*. The altitudinal survey provided more significant morphological discriminations than the bioclimatic approach. In terms of altitudinal intervals of distribution, *D. hispanicus* shows a significant occurrence for lowest altitudinal ranges (up to 950 m), unlike the other taxa, in particular *D. gredensis*, which is thrives only above 500 m. In terms of the morphological variation, the higher the altitude, the shorter the individuals. Small calyx and small stems are the morphological tendencies for higher altitudes. The climatic characterization indicated that the temperature is apparently the most relevant variable that permits to distinguish the morphological tendencies. According to this environmental factor, group G3 is the only one containing the four taxa. In this climatic group, as the sum of the average temperatures and precipitations (ST1, ST2, SP1 and SP2) are negative, co-existence of this taxonomic group becomes possible. In fact, in terms of morphological variation, group G3 displays the lowest values for the most discriminant morphological characters (Fsl2 and Flac). This climatic factor determines the continental and cool climatic conditions that enable the occurrence of all the taxa. In contrast, the morphological variation within group G3 is not significant. This morphological group occurs in most of the middle north of the Iberian Peninsula, at higher altitudes on the west side and wider altitudinal intervals on the east side. The adaptation to this characteristic distribution implies continuous morphological variation. Consequently, the average values of the morphological variables must be closer than those with a very characteristic morphology. Smaller calyx and corolla-teeth, as well as narrower leaves and smaller stems are clearly more adapted to higher altitudes and Atlantic or oromediterranean/orotemperate conditions (G1 and G4). In contrast with the variations detected for G2 and G3, G1 and G4 showed significant differences for the most discriminant morphological parameters (Fsl2 and Flac).

In conclusion, the *D. pungens* group represents a very complex set of morphological variations, correlated with altitudinal variations and with climatic preferences for the Ibero-Mediterranean region. From an eco-genetic point of view, this morphological behaviour could be considered an ecotype example of morphological variation. In fact, habitat-correlation morphologies are here detected (Ehrlich *et al*. 1974). However, an overlapping of individuals is not common. So, isolation-by-distance, or other different type of population structures, could be pointed out as the most important genetic cause for distinguishing these morphological patterns (Moritz 1996). Because of these exclusive occurrences between the taxa, the subspecies rank could be the most appropriate here. Consequently, and in taxonomic terms, we consider more appropriate the establishment of the species *Dianthus pungens* to distinguish the morphological continuity detected for the specimens here analysed.

Based on the results reported here, one new combination is proposed for the taxa analysed.

***Dianthus pungens*** subsp. ***brachyanthus*** (Boiss.) Bernal, Fernández Casas, G. López, Laínz & Muñoz Garmendia

SYNONYMS: *D. brachyanthus* Boiss., *D. subacaulis* subsp. *brachyanthus* (Boiss.) P. Fourn., *D. subacaulis* subsp. *cantabricus* (Font Quer) Laínz, *D. pungens* L. subsp. *pungens*.

***Dianthus pungens*** subsp. ***gredensis*** (Pau *ex* Caballero) A. Crespí, C.P. Fernandes, A. Castro, Bernardos & Amich, *comb. nova*

BASIONYM: *Dianthus gredensis* Pau *ex* Caballero, Anales Jard. Bot. Madrid 5: 512, 521. 1945.

***Dianthus pungens*** subsp. ***hispanicus*** (Asso) O. Bolòs & Vigo

*D. hispanicus* Asso, *D. costae* Willk, *D. algetanus* Graells *ex* F.N. Williams susbp. *algetanus*, *D. algetanus* susbp. *turolensis* (Pau) Bernal, Laínz & Muñoz Garmendia, *D. turolensis* Pau).

***Dianthus pungens*** subsp. ***langeanus*** (Willk.) O. Bolòs & Vigo

*D. langeanus* Willk.

## Key to taxa:

1. Calyx > 11 mm; calyx teeth more than 2 times as long as wide ................................ *D. pungens* subsp. *hispanicus*
1. Calyx < 11 mm; calyx teeth at least as wide as long ... 2
2. Calyx teeth and epicalyx scales obtuse, subobtuse or acute ............................... *D. pungens* subsp. *langeanus*
2. Calyx teeth and epicalyx scales acuminate or apiculate . .................................................................................... 3

3. Calyx ventricose, > 3.5 mm wide .................................. ................................... *D. pungens* subsp. *brachyanthus*
3. Calyx not ventricose, < 3.5 mm wide ............................. .......................................... *D. pungens* subsp. *gredensis*

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