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Combining traditional morphometrics and molecular markers in cryptic taxa: towards an updated integrative taxonomic treatment for *Veronica* subgenus *Pentasepalae* (Plantaginaceae *sensu* APG II) in the western Mediterranean

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The aim of this study was to quantify the phenotypic differences amongst the taxa included in *Veronica* subgenus *Pentasepalae*, represented in the western Mediterranean area. In combination with previously obtained data on genotypic differences, this enabled the recognition of eight taxonomic units. The delimitation of the boundaries among species and subspecies was mainly based on molecular data, whereas the best characters to discriminate taxa were selected after an accurate study of herbarium material and living populations. Such a selection was also supported by a detailed morphometric study of 30 quantitative leaf traits in 88 populations. Several morphological characters, including the length of the trichomes, length of the petiole and leaf division, were found to be robust, and could be useful in the identification of the taxa involved. As a conclusion, a key to the taxa is proposed, as well as a complete nomenclatural treatment for the group, which includes the typification of several names. © 2009 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2009, **159**, 68–87.

ADDITIONAL KEYWORDS: leaf traits – multivariate analysis – nomenclature – Scrophulariaceae – taxonomy – typification.

INTRODUCTION

The determination of species boundaries in morphologically similar populations that are, to some extent, reproductively isolated represents a common problem for systematic biologists. We met this problem whilst working on the western Mediterranean representatives of *Veronica* subgenus *Pentasepalae* (Benth.) M.M.Mart.Ort., Albach & M.A.Fisch. According to Albach *et al*. (2004b), the subgenus is monophyletic and comprises perennial species, usually woody at the base and with prostrate to erect stems, sometimes caespitose; leaves sessile or sometimes short-petiolate, entire to pinnatisect; inflorescences axillary, racemose; calyx quinque- or quadripartite, the fifth sepal usually being significantly smaller; corolla rotate, white to violet or dark blue (sometimes with whitish veins and throat); capsules broadly ovoid to cordate, compressed laterally, usually emarginate. Further phylogenetically relevant characters refer to seeds (flat and with a reticulate-verrucate coat) (Muñoz-Centeno *et al*., 2006) and base chromosome number $x = 8$.

The subgenus includes *c.* 70–75 species and 16 subsections, two (sometimes grouped in one *Veronica* subsection *Pentasepalae* Benth.) represented in the western Mediterranean: *Veronica* subsection *Austriacae* (E.Wulff) Stroh, comprising taxa also distributed in central and eastern Europe and south-west Asia, and

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Veronica subsection *Hispano-Africanae* (Riek) Stroh, restricted to the Iberian Peninsula and North Africa (Riek, 1935).

Several taxonomic treatments have been proposed for the group (for a short review, see Martínez-Ortega *et al*., 2004), but some points, mainly with regard to taxonomic boundaries and the accurate selection of the morphological traits supporting the successive classifications, remain controversial. In a previous study (Martínez-Ortega *et al*., 2004), we used a molecular fingerprinting method [amplified fragment length polymorphism (AFLP)], combined with karyological studies, to address the questions of taxon delimitation and genetic diversity in this group. An association between leaf morphology and ploidy in natural populations was glimpsed at that time, in accordance with conclusions based on AFLP data, revealing a taxonomic structure organized into eight units, namely: *V. rosea*, *V. tenuifolia*, *V. javalambrensis* and *V. fontqueri*, traditionally included in *Veronica* subsection *Hispano-Africanae*; *V. aragonensis*, which is closely related to the latter subsection but, until now, has never been formally included within it; and *V. scheereri*, *V. orsiniana* and *V. sennenii* from *Veronica* subsection *Austriacae*. *Veronica* ×*gundisalvii* Sennen, a taxon presumably of hybrid origin (Martínez-Ortega *et al*., 2004), is considered to be related to *Veronica* subsection *Austriacae*, but its taxonomic position requires further study; unfortunately, it could not be included in the present study because of a lack of appropriate herbarium material. Based on the previously mentioned association, we decided to further examine leaf variation within this group and initiated a morphometric study of some quantitative leaf traits.

The role of traditional morphometrics in herbarium taxonomy has recently been discussed by several authors, such as Henderson (2006), and several recent studies have combined molecular and morphological data (for example, Shipunov, Fay & Chase, 2005; Kučera, Lihová & Marhold, 2006, among others). However, to our knowledge, no study using morphometric methods has been performed in *Veronica*, except that of Brandt (1961), who attempted to find differences between *V. prostrata* and *V. scheereri* (both from *Veronica* subgenus *Pentasepalae*) using the quantitative analysis of several characters.

Looking for characters to support taxon delimitation within *Veronica* subgenus *Pentasepalae* is not an easy task, mainly because homoplasy is generally widespread in *Veronica* and leaf morphology, in particular, seems to be affected by parallel syndromes in the subgenus (Albach, Martínez-Ortega & Chase, 2004a). In addition, hybridization also occurs in this subgenus and this may represent an important source of homology. Many of the most complicated taxa are polyploids, some of which are believed to be the result of hybridization events, whereas others may have originated recently through autopolyploidization events (Lehmann, 1937; Martínez-Ortega *et al*., 2004). As a consequence, the taxonomy of the group is highly complicated; the borders between species or infraspecific taxa are unclear, and there are considerable difficulties in the determination of individual plants.

Henderson (2006) detected hybrid zones between species of palms, and it seems that such hybrid zones between species are also common in *Veronica* subgenus *Pentasepalae* if the taxonomic hypotheses are based exclusively on morphological data. However, in the case of this subgenus, we have the advantage of having at our disposal a solid and well-supported taxonomic hypothesis at a fine level of detail (individuals and populations), based on genetic data, karyology, overall morphology and phytogeographical considerations (Martínez-Ortega, 1999; Martínez-Ortega *et al*., 2004).

In this situation, we were interested in improving the morphological knowledge of *Veronica* subgenus *Pentasepalae* in order to gain an acceptable and updated taxonomic treatment, integrating morphological and molecular data. We also aimed to search for the most discriminant traits related to leaf morphology using a detailed traditional morphometric study, with a view to checking to what extent these characters are relevant in the taxonomy of the subgenus, and in order to improve traditional keys by using additional characters, which may help in the identification of the taxa involved.

MATERIAL AND METHODS

This revision is based on the study of herbarium specimens from the following herbaria (herbarium acronyms according to Holmgren, Holmgren & Barnett, 1990): B, BM, BC, BCF, BIO, COA, COI, E, FCO, G, GDA/GDAC, JACA, K, LINN, MA, MGC, MPU, PR, PRC, RNG, SALA/SALAF, SESTAO, SEV, VAB, VIT, W and WU. Furthermore, microfiche, photographs of type specimens and other data have been examined from the following additional herbaria: ANG, BP, C, CGE, CL, CLF, FI, G-DC, GE, GRM, H, L, LAU, LISU, LIV, MANCH, MARSSJ, MW, NAP, NEU, NY, OXF, P, PAD, PH, RAB, RO, S-Linnaeus, SLBI, SOM, TL, TO, TR, UPS. A complete list of the material studied can be found at Martínez-Ortega (1999).

Occasionally, we encountered problems in locating or obtaining loans of type material; in such cases, the information provided was deduced from careful reading of the protologues. Where doubts persist regarding the original type material, we have used the symbol '?' before the full citation of the name to indicate that it is a dubious synonym. The specimens cited in the synonymy were always examined by us, unless explicitly indicated. Synonyms are ordered chronologically. Homotypic synonyms are preceded by the symbol '≡' and heterotypic ones by '='.

For the morphometric study, we measured specimens from the following herbaria only: B, BC, BCF, BM, E, FCO, G, GDA, GDAC, JACA, K, MA, MAF, MGC, RNG, SALA, SEST, VAB and VIT. Overall, 255 individuals from 88 populations (Table 1) collected in the western Mediterranean area were measured (Fig. 1). Details about these plant materials are given in the Appendix (ordered according to the initial determination), where the abbreviation assigned to each population for the morphometric study is indicated. Initial determinations were made following a key by Martínez-Ortega (1999), which is mostly in accordance with the taxonomic hypothesis proposed by Martínez-Ortega *et al.* (2004). Accordingly, the

Table 1. Number of individuals and populations included in the morphometric study

Operational taxonomic unit (OTU)	Number of individuals	Number of populations
Veronica aragonensis (ARA)	21	7
V. orsiniana (ORS)	51	17
V. rosea (ROS)	40	14
V. scheereri (SCH)	23	8
V. sennenii (SEN)	41	15
V. tenuifolia ssp. *fontqueri* (FON)	14	5
V. tenuifolia ssp. *javalambrensis* (JAV)	36	12
V. tenuifolia ssp. *tenuifolia* (TEN)	23	8
Uncertain determinations	6	2
Total	255	88

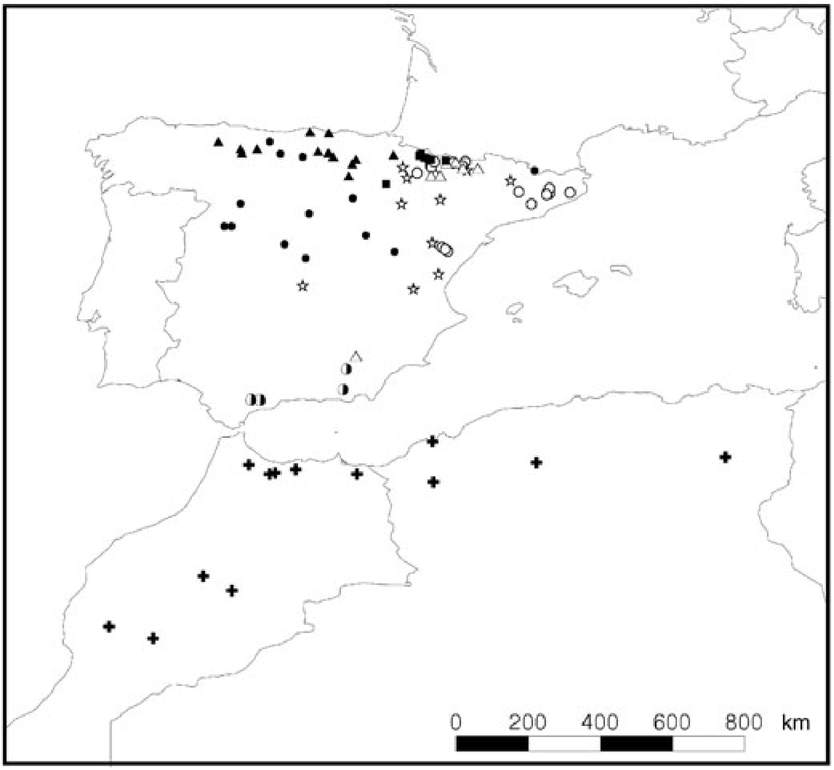

Figure 1. Populations sampled for the morphometric study according to the initial determinations: ○, *Veronica orsiniana*; ■, *V. scheereri*; ▲, *V. sennenii*; +, *V. rosea*; ◑, *V. fontqueri*; ☆, *V. tenuifolia*; ●, *V. javalambrensis*; △, *V. aragonensis*.

materials used for the quantitative analysis belong to the operational taxonomic units (OTUs) named (Table 1): *V. rosea* (ROS; 14 populations), *V. scheereri* (SCH; 8), *V. orsiniana* (ORS; 17), *V. sennenii* (SEN; 15), *V. aragonensis* (ARA; 7), *V. tenuifolia* (TEN; 8), *V. javalambrensis* (JAV; 12) and *V. fontqueri* (FON; 5), plus two additional populations (JAVC and TENC) which we were unable to ascribe *a priori* with certainty to any taxon, both being morphologically intermediate between *V. tenuifolia* and *V. javalambrensis* (in our opinion, they are not putative hybrids, but transitional forms). The population named JAVC was tentatively assigned by locality to *V. javalambrensis*, whereas TENC was assigned to *V. tenuifolia*. Only well-developed plants without missing values were considered. We attempted to use individuals collected in the same area to enable comparison of molecular (AFLP) and morphometric data, but this was not always possible; finally, about 30% of the populations included in the morphometric analysis were coincident with those used for AFLP analysis.

Thirty quantitative characters (Table 2) were selected. Except for cases in which the available herbarium material was not sufficient, each character was measured in three specimens (individuals) from each collection (populations). Each measurement was taken from either a leaf situated in the central segment of the stem (medium leaf) (Fig. 2) or from one on the apical shoot (Fig. 3). Characters related to the indumentum were only measured in the medium leaves. One measurement was made for each variable in the 255 individuals studied, except for hair length, for which we attempted to measure five trichomes per leaf. We initially intended to calculate the density of trichomes referred to 1 cm^2 but, because of the morphology of the leaves (for example, pinnatisect with very narrow segments), we were forced to estimate the 'density' of trichomes by counting the number of hairs present on a 1 cm long linear transect at the leaf margin.

Some characters were taken into consideration as ratios (LLM/MLWM, LLM/WMPM, LLM/DBMWM,

Table 2. Characters measured and abbreviations

Abbreviation	Morphological character
LT	Length of trichomes (medium leaf)
DI	Density of indumentum (medium leaf)
LLM	Length (medium leaf)
MLWM	Maximum width (medium leaf)
WMPM	Width in the middle part (medium leaf)
DBMWM	Distance between the leaf base and the maximum width line (medium leaf)
PLM	Length of petiole (medium leaf)
FTLM	Length of the first tooth/segment (medium leaf)
FTWM	Width of the first tooth/segment (medium leaf)
LFFM	Length of the first division/segment (medium leaf; pinnatisect leaf)
STLM	Length of the second tooth/segment (medium leaf)
STWM	Width of the second tooth/segment (medium leaf)
LFSM	Length of the first tooth of the second segment (medium leaf; pinnatisect leaf)
DLAUM	Distance between the leaf apex and the uppermost teeth/segment (medium leaf)
TLWM	Width of entire terminal part (medium leaf)
NTM	Number of teeth per hemilimb (medium leaf)
LLS	Length (leaf of the apical shoot)
MLWS	Maximum width (leaf of the apical shoot)
WMPS	Width in the middle part (leaf of the apical shoot)
DBMWS	Distance between the leaf base and the maximum width line (leaf of the apical shoot)
PLS	Petiole length (leaf of the apical shoot)
FTLS	Length of the first tooth/segment (leaf of the apical shoot)
FTWS	Width of the first tooth/segment (leaf of the apical shoot)
LFFS	Length of the first division/segment (leaf of the apical shoot; pinnatisect leaf)
STLS	Length of the second tooth/segment (leaf of the apical shoot)
STWS	Width of the second tooth/segment (leaf of the apical shoot)
LFSS	Length of the first tooth of the second segment (leaf of the apical shoot; pinnatisect leaf)
DLAUS	Distance between the leaf apex and the uppermost teeth/segment (leaf of the apical shoot)
TLWS	Width of entire terminal part (leaf of the apical shoot)
NTS	Number of teeth per hemilimb (leaf of the apical shoot)

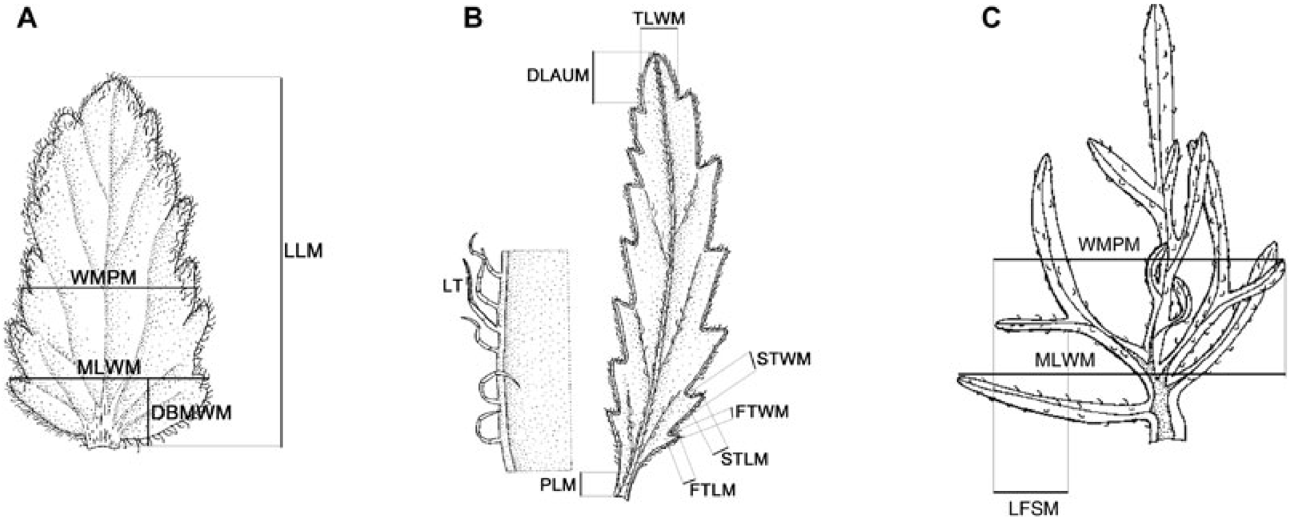

Figure 2. Characters measured in the medium leaves, represented by those of *Veronica orsiniana* (A), *V. sennenii* (B) and *V. tenuifolia* ssp. *tenuifolia* (C). Drawn by J. Castillo. See Table 2 for abbreviations.

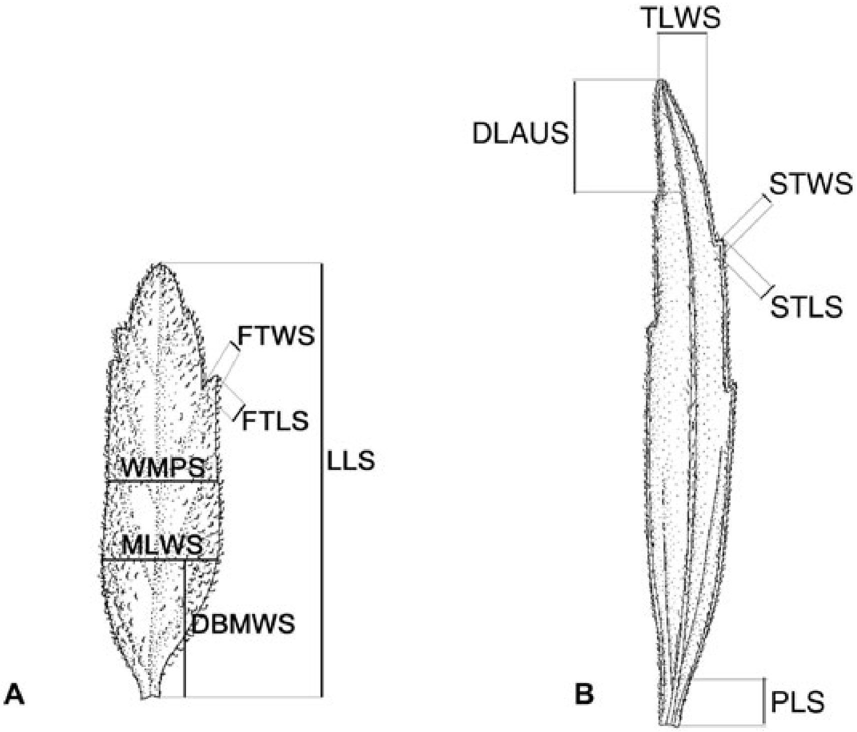

Figure 3. Characters measured in the leaf of the apical shoot, represented by those of *Veronica orsiniana* (A) and *V. sennenii* (B). Drawn by J. Castillo. See Table 2 for abbreviations.

FTLM/FTWM, STLM/STWM, DLAUM/TLWM, LLM/DLAUM, LLS/MLWS, LLS/WMPS, LLS/DBMWS, FTLS/FTWS, STLS/STWS, DLAUS/TLWS and LLS/DLAUS; see Table 2 for abbreviations) to avoid the size effect.

Characters were examined under a stereoscopic microscope (Nikon SMZ-U) and parameters were measured with a digital calliper or simply with a ruler. Other characters, such as trichome length, were recorded with a video camera (Sony DXC-930P-3CCD) connected to the stereoscopic microscope to transfer the image to a computer. In this case, the software Image-Pro Plus version 1.0 for image analysis was used.

Cluster analysis using the hierarchical unweighted pair-group method with arithmetic averages (UPGMA) (Everitt, 1986) was performed based on populations characterized by average values and taking populations as OTUs. A Euclidean coefficient was used to compute the secondary distance matrix after standardization of the characters in the primary matrix. Principal component analysis (PCA; (Sneath & Sokal, 1973) was then performed, also based on populations. We used quantitative data in UPGMA and PCA analyses with no *a priori* knowledge of the population groupings and the resulting ordination in taxonomic units, as revealed by morphological (presented here) and AFLP data (Martínez-Ortega *et al.*, 2004), as a basis for the inferential methods. Several canonical discriminant analyses (DAs) (Legendre & Legendre, 1998) were carried out in order to determine whether there was sufficient information in quantitative leaf characters to enable the separation of different previously recognized taxonomic units (i.e. species, subsections). This method maximizes the among-group variation relative to the within-group variation. The analyses were also conducted to search for the best linear combination of variables in order to discriminate taxa. The technique requires an *a priori* assignment of OTUs to groups, such that it allows the assessment of whether the previously recognized taxa are statistically definable entities.

The ordination methods based on quantitative leaf traits revealed a structure divided into a different number of units than that revealed by the AFLP data. Accordingly, we performed two DAs, each based on the number of groups revealed by either morphological (using exclusively the measured leaf characters) or genetic data. With the latter, our aim was to look for the best linear combination of quantitative leaf traits to discriminate the eight taxa considered in the taxonomic hypothesis of Martínez-Ortega *et al*. (2004).

In order to show the variability of the most important quantitative characters within each species in a clear and readily comparable way, graphical tests (box-plot with the indication of median values) illustrating the variation in parameters were applied.

Numerical analyses were carried out using SPSS 12.0 (descriptive statistics, box-plot graphics, Pearson correlation and DA) and NTSYSpc 2.0 (UPGMA cluster analysis and PCA).

RESULTS

The values obtained for the basic statistical parameters are shown in Table 3. The standard deviation was high for most traits and, although our data allowed an overall separation of taxonomic units, the values at the extremes of the ranges of variation overlapped in many OTUs.

Pearson correlation coefficients obtained from the original matrix of descriptors showed that some of the primary characters were very highly correlated (> 0.95). Therefore, the variables WMPM, WMPS, LLM/WMPM, LLS/WMPS and FTLS were excluded from the analysis.

The splits in the cluster suggested by UPGMA of all populations (Fig. 4) revealed some structure in the variation of the quantitative leaf characters studied, especially for the case of samples that, according to our initial determinations, were determined as *V. aragonensis*. The remaining populations were grouped into less coherent clusters, more or less corresponding to the groups of populations initially determined as *V. sennenii*, *V. tenuifolia*, *V. javalambrensis* and *V. orsiniana*, with mainly *V. rosea*, but also *V. scheereri* and *V. fontqueri*, being the most frequently overlapping taxonomic units.

The results of PCA for all populations are shown in Fig. 5 and Table 4. An ordination diagram representing the first three axes of PCA allowed the separation of three main groups. Again, most samples determined as *V. aragonensis* and *V. tenuifolia* were clearly separated from the remaining samples along the first and second components, which accounted for 67.89% and 15.65%, respectively, of the total variation among populations. *Veronica tenuifolia* formed a group looser than that corresponding to *V. aragonensis*. The remaining samples were not clearly separated in PCA.

Our results show that there is no single character allowing a clear discrimination of the taxonomic units, according to initial determinations, at the same time, although some structure was detected in our data. As both UPGMA and PCA revealed a similar structure in three groups, only partially consistent with the structure of genetic variation in the eight taxonomic units as revealed by AFLP data, we first performed a canonical DA based on the three morphological groups (Fig. 6) and, second, another DA (Fig. 7) for the eight groups based on the structure of the genetic variation.

The first DA (Fig. 6) shows that the three morphologically defined groups are separated along the first canonical axis, the STLM/STWM ratio being the most discriminant character. In addition, PLS and the previously mentioned ratio were the variables most highly correlated with the second canonical axis, which enabled the separation of *V. tenuifolia* plus *V. aragonensis*, on one side, and the remaining taxa studied on the other.

In the second DA (Fig. 7), the populations corresponding to the traditionally recognized *Veronica* subsection *Austriacae* were separated along the first

Table 3. Averages and standard deviations for quantitative leaf characters (see Table 2 for abbreviations) in the western Mediterranean representatives of *Veronica* subgenus *Pentasepalae*

Character	ARA	ORS	ROS	SCH	SEN	FONT	JAV	TEN
LT	–	0.95 (0.17)	0.20 (0.16)	0.40 (0.13)	0.49 (0.14)	0.44 (0.11)	0.11 (0.05)	0.23 (0.07)
DI	–	95.79 (16.53)	28.15 (19.69)	59.79 (32.10)	54.09 (13.85)	58.66 (22.46)	19.74 (2.69)	24.46 (17.09)
LLM	10.04 (2.17)	18.86 (3.72)	8.61 (9.23)	13.07 (4.00)	20.90 (5.19)	12.13 (1.75)	4.55 (4.08)	10.62 (2.68)
MLWM	5.45 (0.67)	8.87 (2.14)	4.00 (4.49)	4.10 (0.98)	6.92 (2.29)	4.32 (0.51)	2.44 (1.99)	8.95 (2.32)
WMPM	4.95 (0.85)	7.67 (1.84)	3.38 (4.14)	3.77 (0.96)	5.82 (1.53)	3.58 (0.31)	2.00 (1.95)	6.74 (1.55)
LLM/MLWM	1.83 (0.25)	2.14 (0.65)	1.19 (0.95)	3.47 (1.42)	3.14 (0.73)	2.81 (0.28)	0.54 (0.36)	1.24 (0.39)
LLM/WMPM	2.03 (0.26)	2.55 (0.63)	1.44 (1.13)	3.82 (1.89)	3.62 (0.89)	3.38 (0.41)	0.70 (0.38)	1.65 (0.57)
DBMWM	5.76 (0.88)	6.15 (1.69)	3.74 (2.60)	6.83 (2.61)	7.40 (3.16)	6.77 (2.16)	2.05 (0.62)	4.10 (1.37)
LLM/DBMWM	1.74 (0.24)	3.25 (0.95)	1.27 (1.07)	1.98 (0.39)	3.05 (0.81)	1.88 (0.36)	0.71 (0.36)	2.71 (0.71)
PLM	2.00 (0.53)	0.02 (0.08)	0.19 (0.15)	0.34 (0.30)	0.15 (0.27)	0.18 (0.26)	0.23 (0.07)	0.40 (0.28)
FTLM	0.53 (0.18)	1.11 (0.36)	0.75 (0.69)	0.52 (0.23)	0.93 (0.41)	1.09 (0.38)	1.06 (0.92)	4.86 (2.11)
FTWM	0.88 (0.22)	0.82 (0.15)	0.36 (0.31)	0.63 (0.30)	0.71 (0.17)	0.71 (0.07)	0.16 (0.14)	0.51 (0.08)
FTLM/FTWM	0.63 (0.22)	1.35 (0.41)	1.19 (1.49)	0.89 (0.34)	1.33 (0.52)	1.52 (0.46)	1.91 (1.69)	9.44 (3.77)
STLM	0.41 (0.22)	1.28 (0.50)	0.73 (0.63)	0.52 (0.17)	0.92 (0.33)	1.15 (0.16)	0.69 (0.56)	5.22 (1.27)
STWM	0.77 (0.37)	1.00 (0.28)	0.43 (0.39)	0.59 (0.16)	0.85 (0.29)	0.86 (0.14)	0.21 (0.17)	0.53 (0.08)
STLM/STWM	0.46 (0.25)	1.29 (0.38)	0.95 (1.20)	0.89 (0.23)	1.13 (0.42)	1.33 (0.10)	1.38 (1.37)	9.95 (2.83)
DLAUM	2.12 (0.52)	2.21 (0.89)	1.55 (1.02)	2.27 (1.27)	3.61 (1.36)	2.83 (0.60)	1.06 (0.48)	3.39 (1.55)
TLWM	3.36 (0.44)	2.46 (0.44)	1.15 (1.08)	1.78 (0.37)	2.76 (0.76)	1.88 (0.29)	0.51 (0.49)	0.71 (0.17)
DLAUM/TLWM	0.62 (0.09)	0.89 (0.28)	0.67 (0.46)	1.35 (1.06)	1.30 (0.25)	1.50 (0.23)	1.08 (1.28)	4.94 (2.56)
LLM/DLAUM	4.79 (0.63)	9.25 (2.51)	3.39 (3.02)	6.65 (2.55)	6.18 (1.56)	4.43 (1.08)	1.88 (1.02)	3.62 (1.53)
NTM	2.12 (0.55)	8.36 (1.35)	2.73 (3.02)	4.84 (1.60)	6.37 (1.13)	3.57 (1.08)	1.50 (1.35)	3.82 (0.41)
LFFM	–	–	–	–	–	–	–	0.60 (0.14)
LFSM	–	–	–	–	–	–	–	1.14 (0.77)
LLS	8.10 (1.41)	12.63 (3.94)	8.27 (7.18)	12.03 (4.53)	17.51 (5.08)	11.99 (1.82)	4.92 (2.78)	9.35 (5.57)
MLWS	3.69 (0.53)	3.22 (1.22)	2.33 (2.00)	2.27 (1.19)	2.67 (1.42)	3.05 (1.01)	2.49 (1.77)	4.34 (4.46)
WMPS	3.47 (0.47)	2.74 (1.07)	1.90 (1.85)	1.92 (0.80)	2.33 (1.09)	2.16 (0.78)	2.19 (1.61)	3.50 (3.94)
LLS/MLWS	220 (0.25)	3.98 (1.49)	2.79 (1.65)	6.43 (3.48)	7.30 (2.86)	4.31 (1.54)	1.61 (0.07)	2.14 (1.65)
LLS/WMPS	2.33 (0.24)	4.69 (1.71)	3.33 (1.98)	7.54 (4.77)	8.19 (2.93)	5.92 (1.51)	1.85 (0.30)	2.75 (2.07)
DBMWS	4.31 (0.80)	6.74 (2.30)	4.45 (3.00)	6.56 (2.66)	9.48 (3.33)	6.93 (1.77)	2.45 (0.62)	3.62 (2.58)
LLS/DBMWS	1.90 (0.29)	1.86 (0.67)	0.97 (0.72)	1.88 (0.36)	1.95 (0.50)	1.79 (0.29)	0.84 (0.61)	2.21 (1.50)
PLS	1.40 (0.28)	0.01 (0.04)	0.11 (0.17)	0.18 (0.25)	–	–	0.26 (0.31)	0.82 (0.60)
FTLS	0.50 (0.28)	0.65 (0.35)	0.67 (0.93)	0.25 (0.18)	0.27 (0.29)	1.04 (0.45)	1.32 (1.12)	2.91 (2.59)
FTWS	0.75 (0.21)	0.52 (0.17)	0.28 (0.19)	0.29 (0.22)	0.28 (0.26)	0.58 (0.09)	0.18 (0.08)	0.39 (0.25)
FTLS/FTWS	0.66 (0.26)	1.21 (0.65)	1.24 (1.48)	0.84 (0.82)	0.63 (0.53)	1.86 (1.04)	2.73 (2.56)	6.24 (5.68)
STLS	0.26 (0.21)	0.60 (0.30)	0.58 (0.70)	0.14 (0.17)	0.23 (0.32)	0.95 (0.58)	1.38 (1.28)	2.65 (2.85)
STWS	0.50 (0.41)	0.55 (0.21)	0.33 (0.20)	0.19 (0.22)	0.25 (0.31)	0.57 (0.34)	0.28 (0.07)	0.38 (0.31)
STLS/STWS	0.48 (0.34)	1.00 (0.50)	0.87 (0.81)	0.35 (0.40)	0.55 (0.54)	1.37 (0.86)	2.41 (2.72)	5.02 (2.55)
DLAUS	2.43 (0.76)	2.50 (2.29)	2.65 (1.96)	2.11 (2.05)	2.40 (1.88)	3.60 (0.83)	1.78 (0.88)	4.38 (2.56)
TLWS	2.65 (0.40)	1.61 (0.62)	1.01 (0.72)	1.20 (0.75)	1.29 (1.02)	1.40 (0.28)	0.97 (0.85)	1.16 (1.92)
DLAUS/TLWS	0.90 (0.16)	1.40 (0.89)	1.29 (0.70)	1.36 (1.20)	1.29 (1.07)	2.60 (0.57)	1.77 (1.96)	5.49 (4.03)
LLS/DLAUS	3.45 (0.52)	6.29 (2.78)	3.09 (1.82)	4.20 (3.99)	3.39 (2.90)	3.48 (0.96)	1.26 (0.48)	1.67 (1.01)
NTS	1.79 (0.52)	3.88 (2.31)	2.49 (2.35)	1.38 (1.21)	2.05 (2.59)	2.73 (1.14)	1.63 (0.64)	2.00 (1.39)
LFFS	–	–	–	–	–	–	–	0.06 (0.17)
LFSS	–	–	–	–	–	–	–	0.05 (0.14)

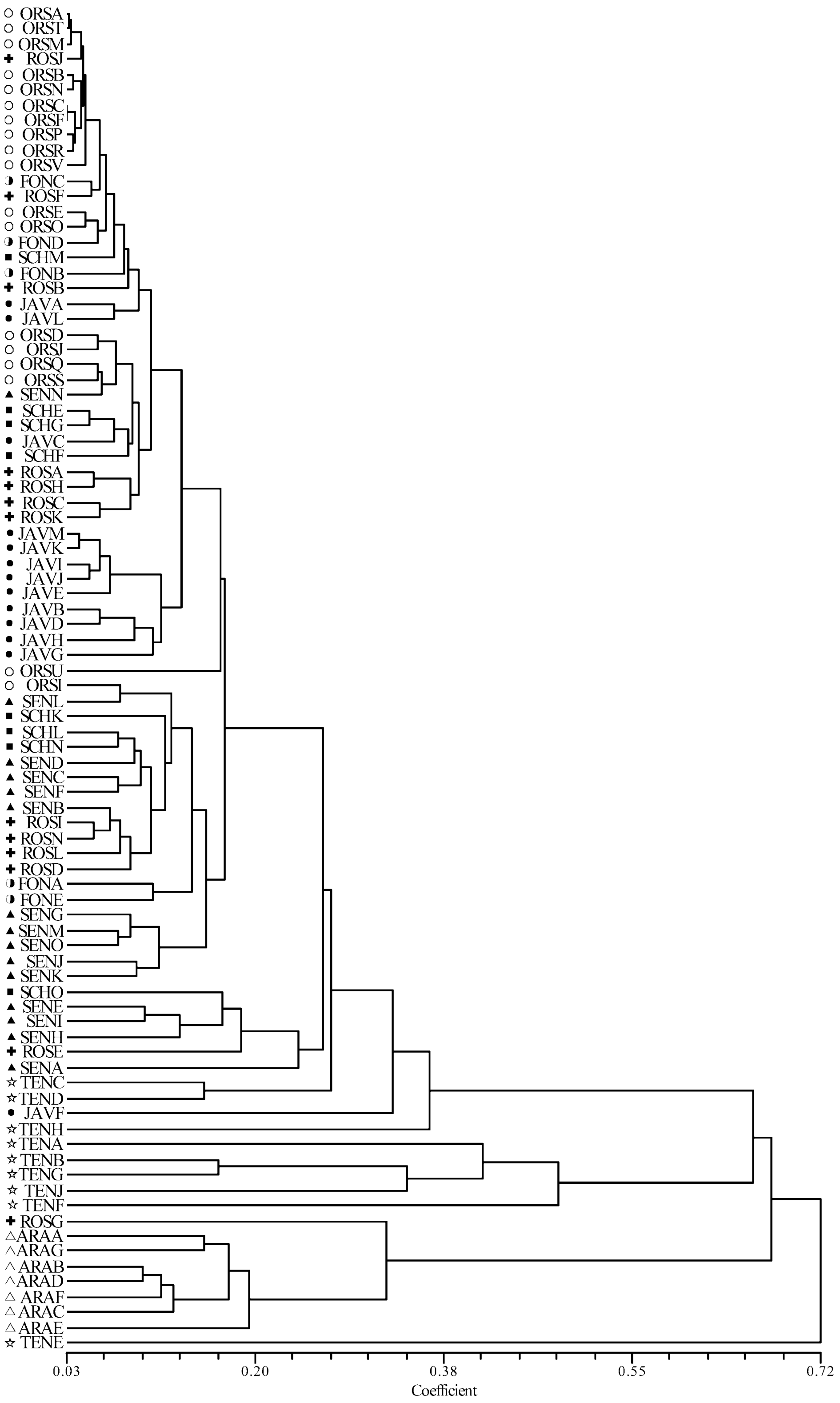

Figure 4. Cluster analysis (unweighted pair-group method with arithmetic averages, UPGMA) of 88 populations of the western Mediterranean representatives of *Veronica* subgenus *Pentasepalae* based on 30 quantitative leaf traits: ○, *V. orsiniana*; ■, *V. scheereri*; ▲, *V. sennenii*; +, *V. rosea*; ◑, *V. fontqueri*; ☆, *V. tenuifolia*; ●, *V. javalambrensis*; △, *V. aragonensis*.

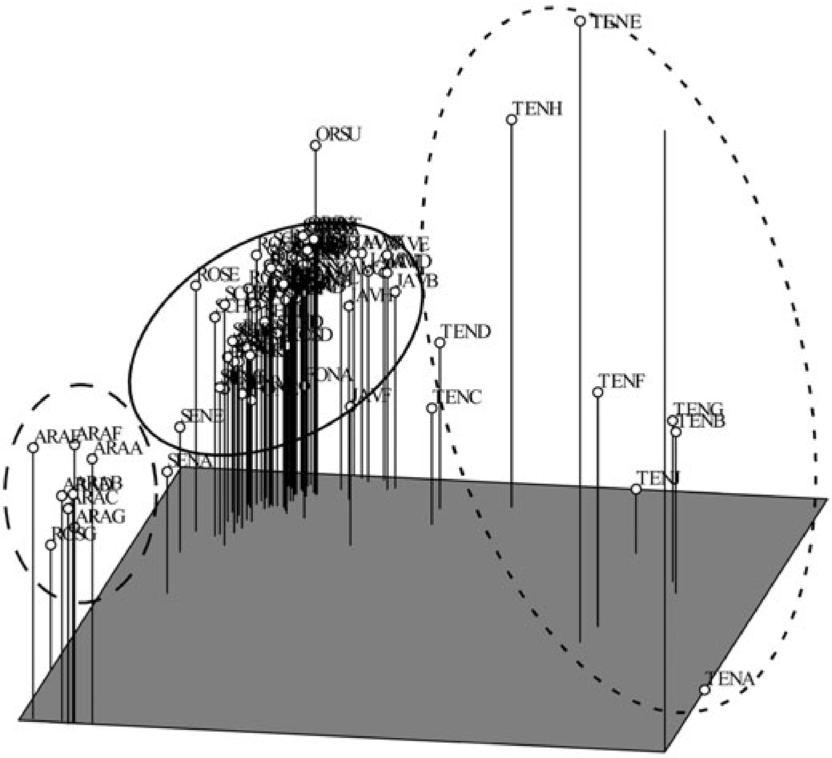

Figure 5. Principal component analysis (representation of the first three axes) of 88 populations of the western Mediterranean representatives of *Veronica* subgenus *Pentasepalae* based on 30 quantitative leaf traits: ◌, *Veronica tenuifolia* subsp. *tenuifolia*; ◌, *V. aragonensis*; ○, remaining populations.

Table 4. Principal component analysis. Eigenvalues and percentages of the data variance accounted for by each axis

Axis	Eigenvalue	Percentage	Percentage (cumulative)
1	497.49	67.89	67.89
2	114.72	15.65	83.54
3	39.36	5.37	88.91
4	23.44	3.19	92.11
5	12.62	1.72	93.83
6	10.05	1.37	95.20
7	7.02	0.95	96.16
8	6.17	0.84	97.00
9	5.19	0.70	97.70

canonical axis from those included in *Veronica* subsection *Hispano-Africanae*, NTM being the most discriminant character. The variability of this character can be seen in Fig. 8, which shows that *V. orsiniana*, *V. scheereri* and *V. sennenii* (from *Veronica* subsection *Austriacae*) are characterized by more than four teeth per hemilimb, whereas the remaining taxa, all from *Veronica* subsection *Hispano-Africanae*, have less than four teeth or segments. The most discriminant characters along the second canonical axis, which allowed the clear differentiation of *V. aragonensis* from the remaining taxa studied, were the STLM/STWM ratio together with STLM and PLM.

Some characters, such as LLS/MLWS (Fig. 8), contributed to the distinction between *V. sennenii* and the remaining taxa, whereas LLM helped to distinguish between *V. orsiniana* and *V. sennenii*, on the one hand, and the rest of the taxonomic units on the other (Fig. 8).

Further DAs were performed (graphical results not shown) within the subsections in order to look for the most discriminant characters, which may help in the elaboration of partial identification keys, although it should be noted that many of these characters are only useful taken as averages. The variability of such traits is shown in the graphical tests (box plots for median comparisons; Fig. 9). Within the western Mediterranean endemic *Veronica* subsection *Hispano-Africanae*, LT clearly separated *V. aragonensis* from the remaining taxa and may also help in the identification of *V. javalambrensis*, LLM/MLWM characterized *V. tenuifolia* as a separate unit within the subsection, and STLM/STWM was useful for distinguishing *V. tenuifolia* and *V. javalambrensis*. With

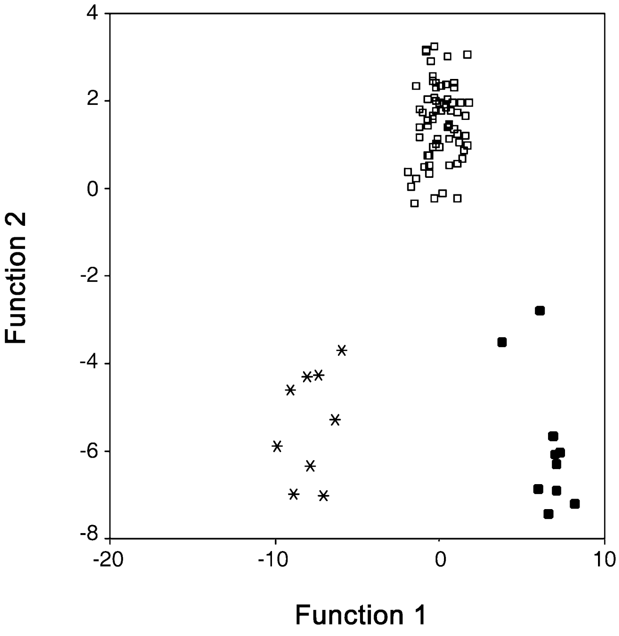

Figure 6. Canonical discriminant analysis of the western Mediterranean representatives of *Veronica* subgenus *Pentasepalae* for the three morphological groups based on the structure of the variation of 30 quantitative leaf traits: ■, *V. tenuifolia* ssp. *tenuifolia*; ⚹, *V. aragonensis*; □, remaining populations.

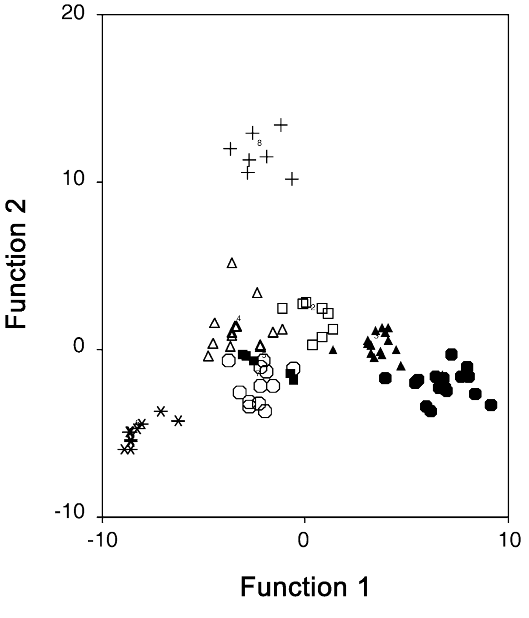

Figure 7. Canonical discriminant analysis of the western Mediterranean representatives of *Veronica* subgenus *Pentasepalae* for the eight groups based on the structure of genetic variation and on 30 quantitative leaf traits: ●, *V. orsiniana*; □, *V. scheereri*; ▲, *V. sennenii*; ■, *V. tenuifolia* ssp. *fontqueri*; △, *V. rosea*; ⚹, *V. tenuifolia* ssp. *tenuifolia*; ○, *V. tenuifolia* ssp. *javalambrensis*; +, *V. aragonensis*.

regard to the western Mediterranean representatives of *Veronica* subsection *Austriacae*, again LT was one of the most discriminant quantitative leaf characters, seemingly guaranteeing the identification of *V. orsiniana* ($LT > 0.7$) from *V. sennenii* (LT between 0.4 and 0.6) and *V. scheereri* ($LT < 0.4$); PLS was also very useful as, in the populations studied, the leaves of the apical shoot in *V. scheereri* showed a short petiole, whereas the remaining taxa had sessile medium leaves.

DISCUSSION

TAXONOMIC CONSIDERATIONS

As is usual in the case of cryptic taxa, those addressed in this study lack many of the evident morphological characters that make them clearly diagnosable morphological units. Nevertheless, it is completely without doubt that they are genetically (Martínez-Ortega *et al.*, 2004) and morphologically recognizable entities.

The relationships suggested by the phenograms (UPGMA and neighbor joining) and parsimony analyses of the AFLP data generally support the taxonomic hypotheses and relationships among the taxa as initially proposed by Martínez-Ortega (1999), thus indicating that differences in the general external morphology are correlated with an overall differentiation of the genomes. Such results provide good support for the monophyly of each of the eight cohesive genetic units (i.e. taxa), and also lead to the conclusion that there is no detectable current gene flow among them.

In this study, we have also demonstrated that there are sufficient phenotypic differences to allow the separation of the eight taxonomic units revealed by molecular data. These taxa can mostly be identified by the morphological characters used in the ‘Key for the taxa’. Although there is not sufficient information about quantitative leaf characters alone to enable the separation of the entire set of populations studied, as initially expected, leaf traits may help in the identification and taxonomic discrimination in some specific cases, although their direct use in identification keys is complicated, mainly because, in most cases, the values corresponding to the character states must be taken as averages.

In addition, we found support in the morphometric leaf traits studied for the subsections *Hispano-Africanae* and *Austriacae*, with *V. aragonensis* closer to the first subsection, although slightly aside. Correspondingly, the genetic analyses revealed three distinct groups of populations: (1) *V. aragonensis*; (2) *V. tenuifolia*, *V. javalambrensis* and *V. fontqueri* (at that time called ‘*V. tenuifolia* complex’) plus *V. rosea*; and

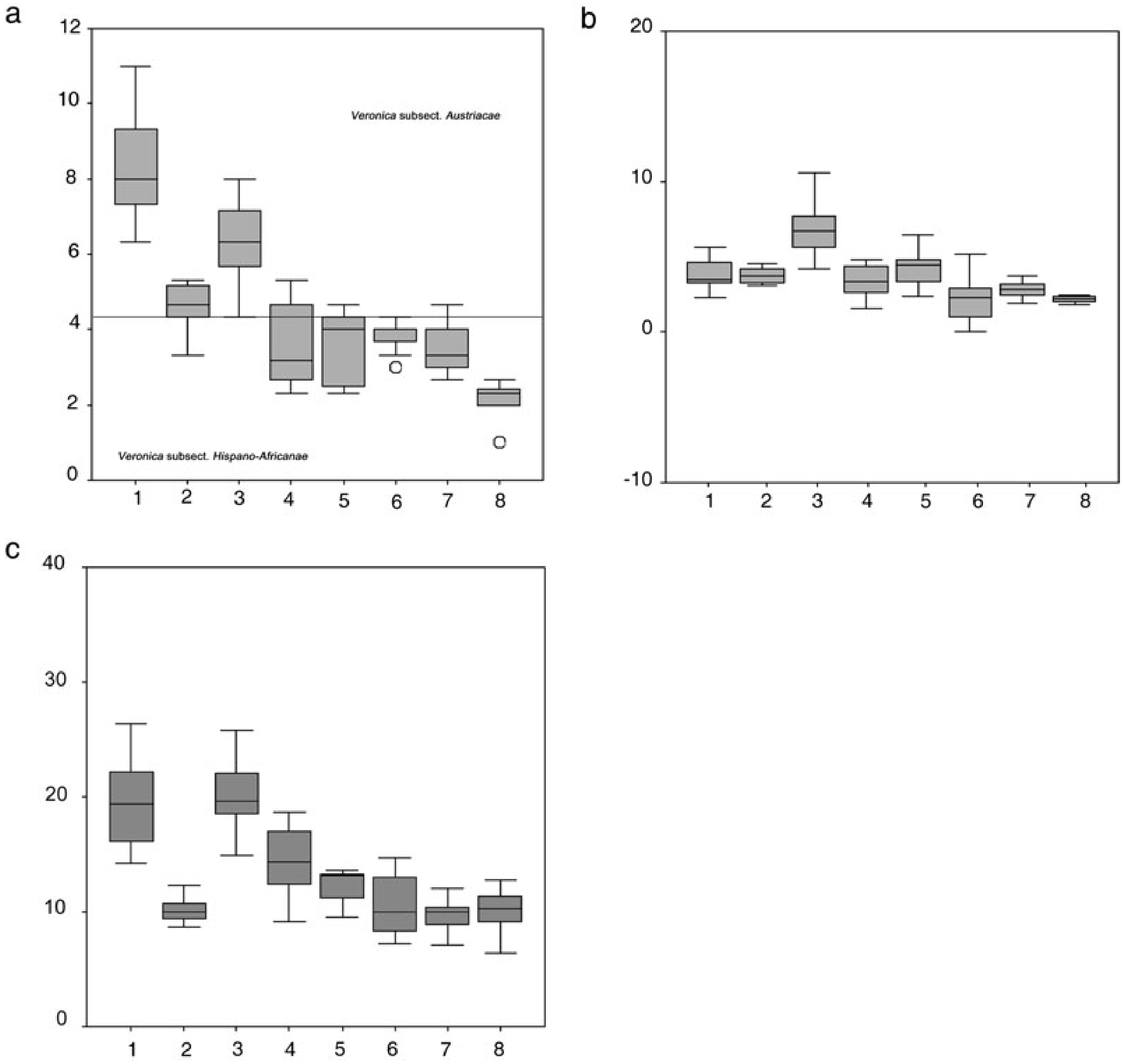

Figure 8. Box-plot of number of teeth per hemilimb of the medium leaf (NTM) (A), length/maximum width ratio of the leaf of the apical shoot (LLS/MLWS) (B) and length of the medium leaf in millimetres (LLM) (C) corresponding to the taxa: 1, *V. orsiniana*; 2, *V. scheereri*; 3, *V. sennenii*; 4, *V. tenuifolia* ssp. *fontqueri*; 5, *V. rosea*; 6, *V. tenuifolia* ssp. *tenuifolia*; 7, *V. tenuifolia* ssp. *javalambrensis*; 8, *V. aragonensis*.

(3) *V. orsiniana*, *V. sennenii* and *V. scheereri* ('*V. orsiniana* complex').

Historically, the affinities of *V. aragonensis* have been controversial (Römpp, 1928; Stroh, 1942; Montserrat, 1956, 1968) and, according to its morphology and as our analyses also confirm, the species is distinct. It exhibits a relatively long petiole in the (usually glabrous) medium leaves, and the length of the second tooth of such leaves is shorter than in the remaining taxa studied. Nevertheless, the genetic distance between *V. aragonensis* and the remaining taxa is small, and this species endemic to Spain seems to be closely related to the North African *V. rosea* from a phylogenetic point of view.

The genetic distances among *V. tenuifolia*, *V. javalambrensis* and *V. fontqueri* are smaller than those among the remaining taxa (Martínez-Ortega *et al.*, 2004), and this is one of the main reasons why we decide to rank them at subspecies level. Within this *V. tenuifolia* complex, the molecular data provide support for a closer relationship between *V. tenuifolia* and *V. javalambrensis*, whereas, phenotypically, the leaves of

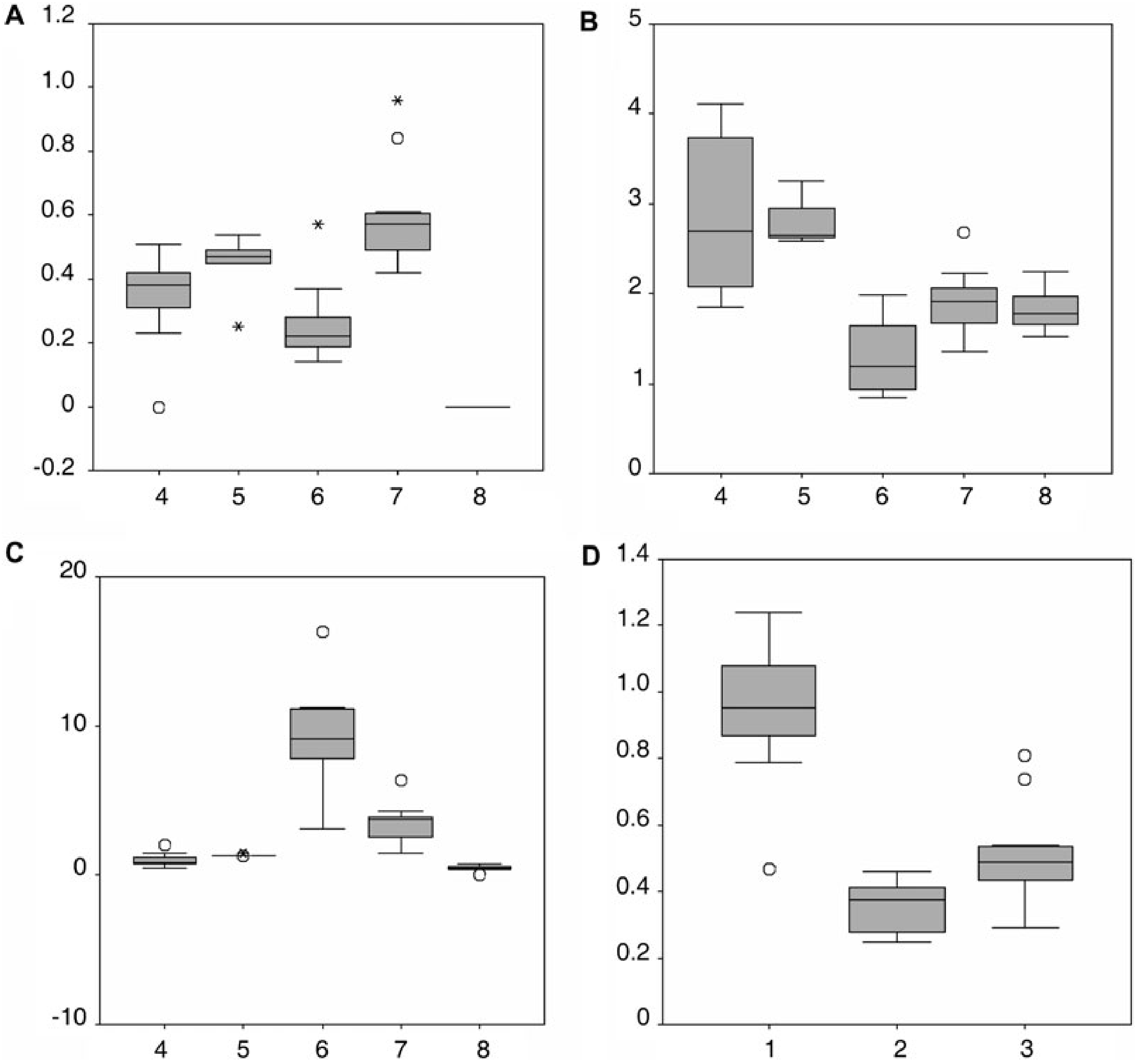

Figure 9. Box-plot of length of the trichomes of the medium leaf (LT) (A), length/maximum width ratio of the medium leaf (LLM/MLWM) (B) and length/width ratio of the second tooth/segment of the medium leaf (STLM/STWM) (C) corresponding to the taxa: 4, *Veronica rosea*; 5, *V. tenuifolia* ssp. *fontqueri*; 6, *V. tenuifolia* ssp. *tenuifolia*; 7, *V. tenuifolia* ssp. *javalambrensis*; 8, *V. aragonensis*. (D) Box-plot of the length of the trichomes of the medium leaf (LT) corresponding to the taxa: 1, *V. orsiniana*; 2, *V. scheereri*; 3, *V. sennenii*.

the latter show a greater similarity to those of *V. fontqueri*. One of the main purposes of our work was to attempt to quantify the phenotypic differences among these three taxa, because a gradation in some characters traditionally used to determine material belonging to the '*V. tenuifolia* complex' has been reported previously (Martínez-Ortega, 1999). We found some quantitative leaf characters that, taken as averages, help to distinguish among these taxonomic units. The most useful characters for this purpose are the LLM/MLWM and STLM/STWM ratios, which indirectly reflect the degree of division of the leaf blade. Although these characters are undoubtedly useful for this aim, some specific samples, such as JAVC and TENC, cannot be assigned with certainty to *V. tenuifolia* or *V. javalambrensis* exclusively on the basis of the quantitative leaf traits studied, which is not surprising given the cryptic nature of these taxa.

Veronica rosea shows a high polymorphism which, throughout history, has led to different taxonomic treatments (for example, Lange, 1870; Willkomm, 1893; Walters & Webb, 1972; Martínez-Ortega, 1999). For example, *V. rosea* has frequently been identified with *V. fontqueri*, because, as shown here, the leaves of both taxa are morphologically similar, although this correspondence is not supported by either genetic or phylogeographical data. We failed to find any morphological trait useful for the unequivocal identification of *V. rosea* when compared with *V. fontqueri*, other than the average length of the trichomes (LT) covering the medium leaves. Although this length mostly helps to distinguish these taxa, we are not convinced that it allows an unequivocal determination of the material, and so we were forced to use geographical distribution as additional information in our 'Key to the taxa'. Nevertheless, in this study, we demonstrate that the average LT is the best character to differentiate among the taxa included within *Veronica* subsection *Hispano-Africanae* (Fig. 9A), and have detected a gradation in this length: LT shows minimum values in *V. tenuifolia*, is increased in *V. rosea*, is even higher in *V. fontqueri* and the maximum length is found in *V. javalambrensis*.

Within the '*V. orsiniana* complex', polyploidy seems to have played an important role as a mechanism for speciation (Martínez-Ortega *et al.*, 2004). AFLP analysis revealed that *V. sennenii* is probably an autopolyploid (octoploid), and there is a close correspondence between *V. sennenii* and *V. scheereri* (tetraploid) with regard to both allele composition and allele frequency. Nevertheless, from a morphological point of view, *V. orsiniana* (diploid) shows a higher overall similarity with the octoploid than does *V. scheereri*. We found several quantitative leaf characters allowing a clear differentiation between *V. sennenii* and *V. scheereri* (i.e. LT, LLM, LLS/MLWS, NTM), apart from the indumentum of the sepals, which always allows an easy separation of both entities, as the former has pilose sepals, whereas the latter has a glabrous calyx. *Veronica orsiniana*, in turn, also has a pilose calyx but, according to our morphometric results, may easily and most unequivocally be distinguished from *V. sennenii* by LT of the medium leaves ($LT < 0.7$ mm; $LT > 0.7$ mm in *V. orsiniana*).

As we have attempted to demonstrate, there are phenotypes that seem to correspond well with genotypes, and this observation helps in the definition of the taxonomic boundaries among taxa within the western Mediterranean representatives of *Veronica* subgenus *Pentasepalae*. Based on the available morphological and genetic information, we have attempted to address the problem of ranking the taxa and to establish a formal classification. To this end, we used criteria such as morphological and karyological distinctiveness, as well as phylogeographical divergence, together with genetic cohesion of the taxonomic units, the apparent absence of or non-significant gene flow among them and further relevant information [for example, length of the branches in the phenograms leading to each of the taxa, analysis of molecular variance (AMOVA) applied to taxonomic groups, distribution of the AFLP bands, etc.], to propose the formal taxonomic treatment presented here. We recognize a total of six species: *V. orsiniana* diploid ($2n = 16$), south-west Europe; *V. scheereri* tetraploid ($2n = 32$), west and central-west Europe; *V. sennenii* octoploid ($2n = 64$), endemic to north Spain; *V. aragonensis* tetraploid ($2n = 32$), restricted to the Spanish Pyrenees with a disjunct isolated locality in Sierra de la Sagra (south Spain); *V. tenuifolia* diploid ($2n = 16$), endemic to Spain; and *V. rosea* diploid ($2n = 16$), North Africa (Morocco and Algeria). Three subspecies have been subordinated under *V. tenuifolia*: ssp. *tenuifolia*, from the north-east Iberian Peninsula; ssp. *fontqueri*, restricted to Sierra de Baza, Sierra de Las Nieves and Sierra de Gador in south Spain; and ssp. *javalambrensis*, from north and central Spain.

In our case, it was only possible to perform morphometric measurements on exactly the same plants as used for AFLP analysis in 30% of the populations. Nevertheless, we are convinced, as demonstrated by previous authors (for example, Shipunov *et al.*, 2005), of the advantages of using combined techniques in the case of taxonomically complex groups of species. As a conclusion to this study, we propose a taxonomic treatment in which the delimitation of the boundaries among species and subspecies is mainly based on molecular data, whereas the best characters to be used in the key were selected after an accurate study of herbarium material as well as living populations. Such selection was also supported by a detailed morphometric study. A full description of the taxa will appear in *Flora iberica* (Martínez-Ortega, Sánchez-Agudo & Rico, in press). We now offer a complete nomenclatural checklist for the group and make some typifications.

NOMENCLATURE OF *VERONICA* SUBGENUS *PENTASEPALAE*

1. *Veronica orsiniana* Ten., *Fl. Neapol. Prodr.* App. 5: 4, 1826.

Ind. loc.: 'In Aprutii montibus, circa montem de'fiori, collegit claris. Orsinius'.

Lectotype: NAP (Martínez-Ortega & Rico, 2001: 546).

≡ *V. teucrium* ssp. *orsiniana* (Ten.) Watzl in *Abh. K.K. Zool.-Bot. Ges. Wien* 5(5): 43, 1910.

= *V. catalaunica* var. *latifolia* Sennen, in sched., nom. nud. [mss., BM].

= *V. catalaunica* var. *monticola* Sennen, in sched., nom. nud. [mss., BM].

= *V. teucrium* var. *barcinonensis* Sennen, in sched., nom. nud. [mss., BM and MA 112457]; ≡ *V. barcinonensis* Sennen ex A.Sales & Font Quer in Cavanillesia 8: 161, 1936, nom. inval., pro syn. [Art. 34.1(c); Vienna I.C.B.N.].

= *V. teucrium* var. *normalis* Gren. in Gren. & Godr., *Fl. France* 2: 587, 1853, p.p. [excl. syn. *V. teucrium* L.].

= *V. teucrium* var. *pyrenaica* Willk. in *Linnaea* 30: 120, 1859–1860; ≡ *V. austriaca* var. *dentata* sensu Willk. in *Flora* 35: 262, 1852, non W.D.J.Koch, *Syn. Fl. Germ. Helv.*: 526, 1837. *Ind. loc.*: 'In glareosis Pyrenaeorum cum praecedente atque in monte Pena de Oroël ad alt. 5000′. Junio c. flor' [sec. Willk. in *Flora* 35: 262, 1852, sub *V. austriaca* var. *dentata*]. *Lectotype* (selected here): 'Peña de Oroël in Aragonia', 22.vi.1850, *Willkomm*, COI-Willkomm.

= *V. prostrata* var. *filicaulis* Halácsy in *Verh. K.K. Zool.-Bot. Ges. Wien* 38: 761, 1888; ≡ *V. filicaulis* Halácsy in *Verh. K.K. Zool.-Bot. Ges. Wien* 38: 761, 1888, nom. inval., pro syn. [Art. 34.1(c); Vienna I.C.B.N.].

= *V. teucrium* f. *borderi* Watzl in *Abh. K.K. Zool.-Bot. Ges. Wien* 5(5): 47, 1910; ≡ *V. teucrium* var. *borderi* A.Kern. in sched., nom. nud. [mss., WU-Kerner 34316].

= *V. teucrium* var. *catalaunica* Sennen & Pau ex Watzl in *Abh. K.K. Zool.-Bot. Ges. Wien* 5(5): 48, 1910 [16.vii.1910]; ≡ *V. teucrium* var. *catalaunica* Sennen & Pau ex Pau in *Bull. Inst. Catalana Hist. Nat.* 7: 28, 1910 [iii–iv.1910], nom. nud.; ≡ *V. catalaunica* Sennen & Pau ex Watzl in *Abh. K.K. Zool.-Bot. Ges. Wien* 5(5): 48, 1910 [16.vii.1910], nom. inval., pro syn. [Art. 34.1(c); Vienna I.C.B.N.]. *Ind. loc.*: 'Catalonien: Fortiá et Cabanas'. *Lectotype* (selected here): 'Catalogne, Fortià et Cabanas, pelouses', v–vi.1907, W; *isolectotypes* (see Martínez-Ortega, 1999 for further details on specimens): BC 831933, BC 45083, BM, MA 425319, RNG, WU.

= *V. verdagueri* var. *angustifolia* Sennen, *Pl. Espagne* 1918, n° 3491, 1918–1919, in sched., nom. nud. [BC-Sennen 832061, MA 112625, RNG and W].

= *V. verdagueri* var. *latifolia* Sennen, *Pl. Espagne* 1918, n° 3491, 1918–1919, in sched., nom. nud. [BC-Sennen 832061, MA 112625, RNG and W].

= *V. verdagueri* Sennen in *Bol. Soc. Ibér. Ci. Nat.* 29: 84, 1930; ≡ *V. verdagueri* Sennen in *Bull. Soc. Bot. France* 68: 406, 1921, nom. nud., pro hybrid.; ≡ *V. orsiniana* var. *verdagueri* (Sennen) M.M.Mart.Ort. & E.Rico in *Anales Jard. Bot. Madrid* 57: 478, 2000. *Lectotype*: MA 112625 (*isolectotypes* BC-Sennen 832061; RNG) (Martínez-Ortega & Rico, 2000: 478).

= ?*V. latifolia* var. *dubia* Chaix ex Lapeyr., *Hist. Pl. Pyrénées*: 9, 1813; ≡ ?*V. chaixii* Lapeyr., *Suppl. Hist. Pl. Pyrénées*: 6, 1818; ≡ ?*V. austriaca var. dubia* (Chaix ex Lapeyr.) O.Bolòs & Vigo in *Collect. Bot. (Barcelona)* 14: 98, 1983.

= ?*V. brevicaulis* Tausch in *Syll. Pl. Nov.*: 247, 1828.

= ?*V. praetutiana* Moretti in *Bibliot. Ital. Giorn. Lett.* 72: 213, 1833.

= ?*V. fuchsii* Bubani, *Fl. Pyren.* 1: 291, 1897.

– *V. teucrium* auct. hisp., non L., *Sp. Pl.* ed. 2: 16, 1762.

– *V. teucrium* var. *pyrenaica* sensu Willk., *Suppl. Prodr. Fl. Hispan.*: 182, 1893, p.p., non Willk. in Linnaea 30: 120, 1859–1860.

– *V. austriaca* ssp. *vahlii* sensu Walters & D.A.Webb in Tutin & al. (eds.), *Fl. Eur.* 3: 245, 1972, p.p., non (Gaudin) D.A.Webb in *Bot. J. Linn. Soc.* 65: 267, 1972 [*V. teucrium* ssp. *vahlii* Gaudin, *Fl. Helv*. 1: 22, 1828, basionym].

– *V. austriaca* ssp. *teucrium* sensu O.Bolòs & Vigo, *Fl. Països Catalans* 3: 451, 1996, non (L.) D.A.Webb in *Bot. J. Linn. Soc.* 65: 267, 1972 [*V. teucrium* L., Sp. Pl. ed. 2: 16, 1762, basionym].

– *V. austriaca var. dubia* sensu O.Bolòs & Vigo, *Fl. Països Catalans* 3: 452, 1996, non (Chaix ex Lapeyr.) O.Bolòs & Vigo in *Collect. Bot. (Barcelona)* 14: 98, 1983 [*V. latifolia* var. *dubia* Chaix ex Lapeyr., *Hist. Pl. Pyrénées*: 9, 1813, basionym].

– *V. austriaca var. teucrium* sensu O.Bolòs & Vigo, *Fl. Països Catalans* 3: 452, 1996, non (L.) O.Bolòs & Vigo in *Collect. Bot. (Barcelona)* 14: 98, 1983 [*V. teucrium* L., *Sp. Pl.* ed. 2: 16, 1762, basionym].

2. *Veronica scheereri* (J.-P.Brandt) Holub in *Folia Geobot. Phytotax*. 8: 177, 1973.

Ind. loc.: 'In graminibus siccis, declivitatibus et collibus apricis Europae occidentalis habitat. Typus in herbario neocomensi'.

≡ *V. prostrata* ssp. *scheereri* J.-P.Brandt in *Bull. Soc. Neuchâteloise Sci. Nat.* 84: 80, 1961, [basionym].

– *V. prostrata* auct. hisp., non L., *Sp. Pl.* ed. 2: 17, 1762.

3. *Veronica sennenii* (Pau) M.M.Mart.Ort. & E.Rico in *Anales Jard. Bot. Madrid* 57: 477, 2000.

Ind. loc.: 'Obarenes (Sennen et Elias)'.

Lectotype: BC-Sennen 829724 (*isolectotype* BC-Sennen 829723) (Martínez-Ortega & Rico, 2000: 477).

≡ *V. prostrata* var. *sennenii* Pau in *Bol. Soc. Aragonesa Ci. Nat.* 6: 28, 1907, [basionym]; ≡ *V. teucrium* var. *sennenii* (Pau) Pau in *Bull. Inst. Catalana Hist. Nat.* 7(2): 29, 1910 [iii–iv.1910] ['senneni']; ≡ *V. teucrium* var. *sennenii* (Pau) Watzl in *Abh. K.K. Zool.-Bot. Ges. Wien* 5(5): 47, 1910 [16.vii.1910], comb. superfl.; ≡ *V. sennenii* Pau ex Watzl in *Abh. K.K. Zool.-Bot. Ges. Wien* 5(5): 47, 1910 [16.vii.1910], nom. inval., pro syn. [Art. 34.1(c); Vienna I.C.B.N.]; ≡ *V. sennenii* Pau ex Uribe-Ech. in Aizpuru & al. (eds.), *Claves Fl. País Vasco*: 470, 1999, nom. inval.

= *V. chermezonis* Sennen & Leroy in Sennen, *Pl. Espagne* 1925, n.° 5629, 1925–1926, in sched., nom. nud. [BC 45087, BC 831965, BM, MA 164362 and W].

– *V. teucrium* auct. hisp., non L., *Sp. Pl.* ed. 2: 16, 1762.

– *V. austriaca* ssp. *vahlii* sensu Walters & D.A.Webb in Tutin & al. (eds.), *Fl. Eur.* 3: 245, 1972, p.p., non (Gaudin) D.A. Webb in *Bot. J. Linn. Soc*. 65: 267, 1972 [*V. teucrium* ssp. *vahlii* Gaudin, *Fl. Helv*. 1: 22, 1828, basionym].

4. *Veronica aragonensis* Stroh in *Beih. Bot. Centralbl.*, Abt. 2, 61: 398, 1942.
Ind. loc.: 'Detexi et legi a la Peña Montañesa; vertice dicto Astiviella, die 15. Jul. 1845; legi quoque in summitate montis La Sierra de Guara, die 18. Jun. 1850'.
Lectotype: GE (*isolectotype* WU) (Martínez-Ortega & Rico, 2001: 543).

≡ *V. humifusa* Bubani, *Fl. Pyren*. 1: 294, 1897, nom. illeg., [syn. subst.], non Dicks. in *Trans. Linn. Soc. London* 2: 288, 1794 [Art. 53.1; Vienna I.C.B.N.].

= *V. repens* var. *macrocarpa* Porta in *Atti Imp. Regia Accad. Rovereto* ser. 2, 9: 156, 1892 [checked in Veg. Itin. Iber.: 53, 1892].

5. *Veronica tenuifolia* Asso, *Syn. Stirp. Aragon.*: 2, tab. 1 fig. 1, 1779.
Ind. loc.: 'Nascitur circà Hijar, Alcañiz'.
Lectotype: Illustration in Asso, *Syn. Stirp. Aragon.*, tab. 1 fig. 1, 1779 (Martínez-Ortega & Rico, 2001: 548). *Epitype*: BC 47405 (*isoepitype* W).

≡ *V. austriaca var. tenuifolia* (Asso) Vahl, *Enum. Pl.* 1: 73, 1804; ≡ *V. austriaca var. assoana* Boiss., *Diagn. Pl. Orient.* ser. 2, 3: 168, 1856, nom. illeg. [Arts. 52.1 and 52.2; Vienna I.C.B.N.]; ≡ *V. assoana* Boiss. ex Willk. in *Linnaea* 30: 120, 1859–1860, nom. illeg. [Arts. 52.1 and 52.2; Vienna I.C.B.N.]; ≡ *V. austriaca* ssp. *tenuifolia* (Asso) O.Bolòs & Vigo in *Collect. Bot. (Barcelona)* 14: 98, 1983.

5a. *Veronica tenuifolia* ssp. *tenuifolia*

= *V. laciniata* Cav., *Observ. Hist. Nat.* 2: 323, 1797, nom. nud., non Moench., *Methodus*: 435, 1794, nom. illeg.

= *V. hispanica* Pourr. ex Lange in Willk. & Lange, *Prodr. Fl. Hispan*. 2: 601, 1870, nom. inval., pro syn. [Art. 34.1(c); Vienna I.C.B.N.].

= *V. tenuifolia* var. *cadevallii* Pau in *Actas Soc. Esp. Hist. Nat*. 25: 127, 1896 ['cadevalli'].

= *V. tenuifolia* var. *oscensis* D.Gómez in *Folia Bot. Misc*. 3: 57, 1982.

– *V. austriaca* var. *pinnatifida* auct. hisp., non W.D.J. Koch, *Syn. Fl. Germ. Helv.*: 526, 1837.

– *V. multifida* auct. hisp., non L., *Sp. Pl.*: 13, 1753.

– *V. austriaca* var. *bipinnatifida* sensu Kunze in *Flora* 29: 638, 1846, non W.D.J.Koch, *Syn. Fl. Germ. Helv*.: 526, 1837.

5b. *Veronica tenuifolia* ssp. *fontqueri* (Pau) M.M. Mart.Ort. & E.Rico in *Anales Jard. Bot. Madrid* 57: 477, 2000.
Ind. loc.: 'Sierra de Gador: 1900 metros de altura'.
Lectotype: MA 112416 (*isolectotype* BCF 45080) (Martínez-Ortega & Rico, 2000: 478).

≡ *V. fontqueri* Pau in *Bull. Inst. Catalana Hist. Nat.* 22: 33, 1922 ['fontquerii'] [basionym].

– *V. rosea* auct., non Desf., *Fl. Atlant*. 1: 13, 1798.

– *V. teucrium* var. *pyrenaica* sensu Willk., *Suppl. Prodr. Fl. Hispan.*: 182, 1893, p.p., non Willk. in *Linnaea* 30: 120, 1859–1860.

– *V. austriaca* var. *polymorpha* sensu Sagredo in *Anales Jard. Bot. Madrid* 32(2): 314, 1975, non (Willd.) Sagredo in *Anales Jard. Bot. Madrid* 32(2): 314, 1975, comb. inval. [*V. polymorpha* Willd., *Enum. Pl. Suppl*. 2, 1814, basionym].

5c. *Veronica tenuifolia* ssp. *javalambrensis* (Pau) Molero & J.Pujadas in *Folia Bot. Misc*. 2: 46, 1981.
Ind. loc.: 'Hab. in altioribus montis Javalambre ad 2.000 m alt.- 10 Jul.'.
Lectotype: MA 112496 (Izco, Molina & Fernández González, 1984: 178).

≡ *V. javalambrensis* Pau, *Not. Bot. Fl. Españ.* 1: 22, 1887 [basionym]; ≡ *V. teucrium* ssp. *javalambrensis* (Pau) Rivas Goday & Borja in *Anales Inst. Bot. Cavanilles* 19: 447, 1961.

= *V. assoana* f. *glabrescens* Gand., in sched., nom. nud [PRC].

= *V. assoana* f. *hirta* Gand., in sched., nom. nud [PRC].

= *V. assoana* var. *salmantica* Lacaita, in sched., nom. nud. [BM].

= *V. tenuifolia* f. *latisecta* Ceballos, in sched., nom. nud. [G].

= *V. commutata* Willk. in *Oesterr. Bot. Z.* 41: 82, 1891, nom. illeg., non Seidl in Bercht., *Oekon.-Techn. Fl. Böhm*. 1: 31, 1836 [Art. 53.1; Vienna I.C.B.N.].

6. *Veronica rosea* Desf., *Fl. Atlant.* 1: 13, 1798.
Ind. loc.: 'Habitat in Atlante prope Tlemsen'.
Lectotype: P-Desf. (Martínez-Ortega & Rico, 2001: 547).

≡ *V. atlantica* Pers., *Syn. Pl.* 1: 12, 1805, nom. illeg. [Arts. 52.1 and 52.2; Vienna I.C.B.N.]; ≡ *V. rosea* var. *typica* Maire in *Mém. Soc. Sci. Nat. Maroc* 7: 198, 1924, nom. inval. [Art. 24.3; Vienna I.C.B.N.].

= *V. austriaca* var. *maroccana* Pau & Font Quer in Font Quer, *Iter Marocc.* 1927, n° 579, 1928; ≡ *V. rosea* var. *maroccana* (Pau & Font Quer) Maire in Jahand. & Maire, *Cat. Pl. Maroc* 3: 687, 1934. *Ind. loc.*: 'Hab. in cistetis supra emporium Sok-et-Tnin (Beni Hadifa), 1200 m. alt., nec non (spec. fruct.) pr. El Ferrah, 1200 m. alt., solo siliceo; fl. 26 majii fruct. 29 junii'. *Lectotype* (selected here): 'In cistetis supra emporium Sok-et-Tnin (Beni Hadifa)', 1200 m, *Font Quer*, MA 112523; *isolectotypes*: BM, G, GDA 027834, MA 112522, MPU-Maire.

= *V. chartonii* Litard. & Maire in *Mém. Soc. Sci. Nat. Maroc* 26: 31, 1930. *Ind. loc.*: 'Hab. inter lapides calcareos labentes in editis alpinis Atlantis Majoris: in ditionis Glaoua monte Anremer, supra lacum, ad alt. 3200–3600 m, junio et julio florens. – Typus in Herb. Univers. Algeriensis, in Herb. Inst. Imp. Scient. Rabatensis, et in Herb. R. de Litardière'. *Lectotype* (selected here): 'In Atlantis majoris prope Anremer', 3200–3500 m, 27.vii.1926, *Litardière & Maire*, MPU-Maire; *isolectotype*: RAB (material not seen, revised by the curator of the herbarium RAB).

= *V. cuneifolia* ssp. *atlantica* Ball in *J. Bot.* 13: 174, 1875; ≡ *V. cuneifolia* var. *atlantica* (Ball) Ball in *J. Linn. Soc., Bot.* 16: 599, 1878; ≡ *V. rosea* var. *atlantica* (Ball) Murb. in *Acta Univ. Lund.* ser. 2, 19(1): 46, 1923 [checked in Murb., *Contr. Fl. Maroc* 2: 46, 1923]; ≡ *V. rosea* var. *atlantica* (Ball) Maire in *Mém. Soc. Sci. Nat. Maroc* 7: 198, 1924, comb. superfl.; ≡ *V. rosea* subvar. *eriocarpa* Maire in *Bull. Soc. Hist. Nat. Afrique N.* 20: 31, 1929, nom. inval. [Art. 26.2; Vienna I.C.B.N]; ≡ *V. rosea* ssp. *atlantica* (Ball) I.Soriano in *Lagascalia* 18: 299, 1996, comb. inval. [Arts. 33.4 and 33.7(a); Vienna I.C.B.N.].

= *V. rosea* var. *glabrescens* Emb. & Maire in *Bull. Soc. Hist. Nat. Afrique N.* 28: 372, 1937. *Ind. loc.*: 'Grand Atlas oriental: rochers calcaires des gorges de Ksiret, de l'Akka-n-Ouyad, de Bab-n-Ouyad, 1950–2300 m'. *Lectotype* (selected here): 'In rupibus calcareis Atlantis Majoris Orientalis, [three illegible words], in faucibus Ksiret', 1950 m, 19.vi.1936, *Maire*, MPU-Maire; *isolectotype*: MPU-Maire.

= *V. rosea* var. *lacera* Alleiz. in *Bull. Soc. Hist. Nat. Afrique N.* 12: 126, 1921.

= *V. rosea* var. *leiocarpa* Maire in *Mém. Soc. Sci. Nat. Maroc* 7: 198, 1924; ≡ *V. rosea* subvar. *leiocarpa* (Maire) Maire in *Bull. Soc. Hist. Nat. Afrique N.* 20: 31, 1929. *Ind. loc.*: 'Elle se retrouve dans les montagnes du Sud Oranais (Dj. Mzi) et dans le Moyen Atlas'. *Lectotype* (selected here): 'Sud Oranais, Djebel Mzi', vi.1889, *J.A. Battandier*, MPU-Maire.

= *V. rosea* var. *macrantha* Pau ex I.Soriano in *Lagascalia* 18: 300, 1996; ≡ *V. rosea* var. *macrantha* Pau in Font Quer, *Iter Marocc.* 1930, n° 603, 1932, in sched., nom. nud. [BM, BC 45039, MA 112414, GDA 27287, G, B]; ≡ *V. rosea* var. *macrantha* Pau ex Sistané & J.M.Monts. in *Treb. Inst. Bot. Barcelona* 12: 136, 1988, nom. nud. *Holotype*: 'In saxosis calc. montis Lexhab (Gomara)', 1750 m, *Font Quer*, BC 45039 (Soriano, 1996: 300).

= *V. rosea* var. *pallida* Maire in *Bull. Soc. Hist. Nat. Afrique N.* 20: 30, 1929. *Ind. loc.*: 'Hab. in pascuis lapidosis calcareis ad radices Atlantis Majoris prope oppidum Midelt, ad alt. 1500 m, maio florens (Emberger et Maire, 1927)'. *Lectotype* (selected here): 'Grand Atlas, Midelt, rocailles calcaires', 1500 m, 8.v.1927, *R. Maire*, MPU-Maire.

= *V. rosea* var. *virgata* Emb. & Maire in *Mém. Soc. Sci. Nat. Maroc* 21–22: 44, 1929; ≡ *V. rosea* ssp. *virgata* (Emb. & Maire) Dobignard & D.Jord. in *Saussurea* 18: 93, 1987.

= *V. rosea* f. *ciliatisepala* Maire, in sched., nom. nud. [RAB 32336].

= *V. rosea* subvar. *atrichocarpa* Maire in *Bull. Soc. Hist. Nat. Afrique N.* 20: 31, 1929.

= *V. rosea* subvar. *trichocarpa* Maire in *Bull. Soc. Hist. Nat. Afrique N.* 20: 31, 1929.

KEY TO THE TAXA

As already stated, in many cases, the taxa involved in this study lack evident morphological characters that make them clearly diagnosable units; therefore, the elaboration of identification keys is difficult. Nevertheless, we have worked on this and offer a key for the taxa, mainly based on general morphology, but also including the quantitative leaf characters studied by us.

For the most conflicting taxa, only the measurements of some variables considered as averages are suitable for use in the key. These include the length of the trichomes (LT) and the number of teeth per hemilimb of the medium leaf (NTM) (Figs 9a, 8a), which are used as averages directly in the following key, as no other morphological character seems to guarantee the correct determination of the taxa involved. As we are fully aware of the problems derived from the use of such traits in determination keys, we have added geographical information as an additional aid for correct identification.

One of the main problems encountered whilst trying to elaborate this key was finding characters that would help in the unequivocal determination of the extremely polymorphic *V. rosea*, on the one hand (indeed, many subspecies and varieties, as can be seen in the nomenclatural treatment, have been subordinated to this taxon), and *V. orsiniana* plus *V. sennenii*, on the other. These three species are clearly isolated from both the geographical and genetic point of view and, traditionally, have even been included in different subsections; however, we were unable to recognize traits to use in our key other than the problematic NTM value taken as an average. We revised *c*. 125 herbarium specimens (populations) and were also unable to find a pattern of variation that could be explained in any way (for further details, see Martínez-Ortega, 1999), as even intrapopulational variability is extremely high. Furthermore, genetic, morphological and karyological studies are required in this respect, aimed not only at explaining the reason for this high polymorphism, but also to improve, if possible, the quality of the key at this point.

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1. Leaves – at least those situated at the central part of the stem (from here onwards, medium leaves) – pinnatifid to pinnatisect …… 2
1a. Medium leaves subentire to crenate, serrate or, at the most, pinnatilobate …… 4
2. Medium leaves pinnatisect to bipinnatisect; internodes usually longer than leaves; lower bracts entire to five(seven)-lobed; calyx with five sepals – less frequently four sepals – usually, at least after drying, revolute, and those belonging to the basal flowers of the inflorescence commonly two- to three-lobed …… *V. tenuifolia* ssp. *tenuifolia*
2a. Medium leaves usually pinnatifid to pinnatipartite; internodes usually shorter than leaves; lower bracts entire or, at the most, with one to three lobes or teeth; calyx with four sepals – very rarely five sepals – never revolute, and those belonging to the basal flowers of the inflorescence almost always entire …… 3
3. Stem with hairs of variable length (0.15–)0.25–0.5(–0.7) mm; medium leaves ovate, oval or obovate, pinnatifid or pinnatipartite; capsule usually longer than wide; average value of the length/maximum width ratio of medium leaf < 2.5 …… *V. tenuifolia* ssp. *javalambrensis*
3a. Stem with short hairs < 0.25 mm; medium leaves narrowly ovate to ovate, entire to pinnatipartite; capsule usually wider than long; average value of the length/maximum width ratio of medium leaf ≥ 2.5 …… *V. tenuifolia* ssp. *fontqueri*
4. Inflorescence and capsule with abundant glandular hairs; axillary racemes, often pseudo-terminal; stems flexuous, herbaceous on the aerial portion, woody and branched at the base, and with this basal part more or less buried by rocks; racemes with 3–8(–12) flowers …… *V. aragonensis*
4a. Inflorescence and capsule without glandular hairs; axillary racemes; stems not flexuous, woody or sublignous at the base; racemes usually with more than ten flowers …… 5
5. Sepals glabrous or subglabrous …… 6
5a. Sepals pilose …… 8
6. Stems (2–)5–15(–25) cm; non-flowering stems procumbent – rarely ascendant – usually forming a dense mat from which arise ascending flowering branches; calyx almost always with five glabrous sepals or, rarely, those of the lower flowers with one to two short hairs; leaves of the apical shoot almost always petiolate …… *V. scheereri*
6a. Stems (5–)7–20(–40) cm; non-flowering and flowering stems ascendant to erect; calyx with four(five) subglabrous sepals, rarely glabrous; leaves of the apical shoot usually without a petiole …… 7
7. Average length of the trichomes of the medium leaves (LT) usually > 0.45 mm; capsule usually wider than long; south Spain …… *V. tenuifolia* ssp. *fontqueri*
7a. Average length of the trichomes of the medium leaves (LT) usually < 0.45 mm; capsule slightly longer than wide, slightly wider than long or almost as long as wide; north-west Africa …… *V. rosea*
8. Average number of teeth per hemilimb in medium leaf (NTM) < 5; north-west Africa …… *V. rosea*
8a. Average number of teeth per hemilimb in medium leaf (NTM) usually > 5; south-west Europe …… 9
9. Leaves of the apical shoot oval to ovate, sometimes narrowly oval, crenate or dentate, rarely subentire; medium leaves usually oval, ovate, widely oval or widely ovate, usually (6–)12–25(–40) mm long; stems (3–)10–25(–45) cm, usually decumbent to ascendant; average length of the trichomes (LT) > 0.7 mm …… *V. orsiniana*
9a. Leaves of the apical shoot linear or narrowly oval to lanceolate, entire or subentire; medium leaves usually lanceolate, narrowly oval, oval or oblanceolate, rarely ovate, usually (8–)25–50(–70) mm long; stems (8–)15–25(–35) cm, usually ascendant to erect; average length of the trichomes (LT) < 0.7 mm …… *V. sennenii*

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APPENDIX

VERONICA ORSINIANA

SPAIN: Huesca, Loarre, Sierra de Loarre, repetidor, XM99, 13.vi.1999, *M. Martínez Ortega & L. Delgado MO664* (SALA), ORSM; Barcelona, Malla, alto de Closcar, 31TDG3537, 9.v.1999, *L. Delgado, M. Martínez Ortega, E. Rico & J. A. Sánchez Agudo LD143* (SALA), ORSQ; Zaragoza, Luesia, Sierra de Luesia, collado en la subida al Puy Moné, XM6597, 11.vi.1999, *M. Martínez Ortega & L. Delgado MO653* (SALA), ORSP; Huesca, de Torla a Bujaruelo, puente de Los Navarros, 10.vii.1997, *M. Martínez Ortega & L. Delgado MO287* (SALA93482), ORSO; Huesca, Sobrarbe, valle de Chisagüés, solana, 31TBH6927, 20.vi.1996, *M. Martínez Ortega & Martín Ballesteros MO138* (SALA93492), ORSN; Teruel, Cantavieja, cerca del Cuarto Pelado hacia Cantavieja, 30TYK1489, 12.vii.1993, *Mercadal* (VAB944259), ORSD; Castellón, Villafranca, La Moleta, 30TYK2678, 8.vi.1991, *Fabregat & López* (VAB947095), ORSE; Barcelona, Carretera de Vic a Villadrau, km 2, en las cercanías del Can Pau Moliner, 31TDG4733, 10.v.1999, *L. Delgado, M. Martínez Ortega, E. Rico & J. A. Sánchez Agudo MO575* (SALA), ORSC; Huesca, Puértolas, Castillo Mayor, 2.viii.1999, *M. Martínez Ortega & L. Delgado MO759* (SALA), ORSA; Castellón, Villafranca, pr. Puebla del Ballestar, 30TYK28, 19.vi.1993, *Fabregat & Lopez* (VAB933759), ORSJ; Teruel, Iglesuela del Cid, rambla de las Truchas, 30TYK28, 19.vi.1993, *Fabregat & López* (VAB932949), ORSI; Barcelona, Santa Cecilia de Voltregá, km 3 de la carretera a Manlleu, hacia el Mas Gallissans, 31TDG3449, 10.v.1999, *L. Delgado, M. Martínez Ortega, E. Rico & J. A. Sánchez Agudo MO574* (SALA), ORSF; Barcelona, Montserrat, ermita de San Miguel, 11.v.1999, *L. Delgado, M. Martínez Ortega, E. Rico & J. A. Sánchez Agudo LD156* (SALA), ORSU; Barcelona, Tona, santuario de la Virgen de Lourdes, 31TDG3533, 10.v.1999, *L. Delgado, M. Martínez Ortega, E. Rico & J. A. Sánchez Agudo MO566* (SALA), ORST; Lérida, El Miracle, carretera Cardona-El Miracle, en las cercanías del monasterio, 31TCG7741, 12.v.1999, *L. Delgado, M. Martínez Ortega, E. Rico & J. A. Sánchez Agudo MO585* (SALA), ORSS; Gerona, Riudellots de la Selva, en los taludes de la carretera del polígono industrial, 11.v.1999, *L. Delgado, M. Martínez Ortega, E. Rico & J. A. Sánchez Agudo LD153* (SALA), ORSR; Huesca, Borau, Punta d'a Roda, km 6, 8.vii.1997, *M. Martínez Ortega & L. Delgado MO273* (SALA93483), ORSB.

VERONICA SCHEERERI

SPAIN: Huesca, Aragüés, Puerto Cucurasuelo, *M. Martínez Ortega & L. Delgado MO766* (SALA), SCHF; Huesca, Aragüés del Puerto, Collado de Mesola, 7.vii.1997, *M. Martínez Ortega & L. Delgado MO268* (SALA93472), SCHG; Huesca, Aragüés del Puerto, llanos de Lizara, 7.vii.1997, *M. Martínez Ortega & L. Delgado MO265* (SALA93470), SCHE; Huesca, Hoz de Jaca, subida al Mandilar, 10.vii.1997, *M. Martínez Ortega & L. Delgado MO285* (SALA93471), SCHO; Huesca, Hecho, Alanos, La Renclusa, ascenso a Alanos, 30TXN8143, 2.ix.1971, *Montserrat & Villar* (JACA680871), SCHM; Huesca, Ansó, Paso del Onso, 15.vi.1999, *M. Martínez Ortega & L. Delgado MO768* (SALA), SCHN; Navarra, Isaba, Belagua, 30TXN7656, 2.vi.1971, *Villar* (JACA10062571), SCHL; Navarra, Belagua, Roncal, 30TXN7757, *Montserrat* (JACA71965), SCHK.

VERONICA SENNENII

SPAIN: Álava, Pipaón, 30TWN3018, 3.v.1997, *M. Martínez Ortega MO245*, (SALA93478), SENG; Cantabria, Laredo, El Puntal, 30TVP6309, 26.iv.1999, *M. Martínez Ortega MO565* (SALA93475), SENH; Cantabria, Castro Urdiales, Oriñón, 30TVP7405, 26.iv.1999, *M. Martínez Ortega MO563* (SALA93477), SENI; Álava, Salinas de Añana, pista de Sobrón al Collado de La Rastrilla, 30TVN9036, 23.vi.1996, *Martínez Ortega & Martín Ballesteros MO151* (SALA93495), SENE; Álava, Valdegobía, Villamardones, 30TVN8046, 2.v.1997, *M. Martínez Ortega MO242* (SALA93479), SENJ; Álava, Valdegobía, Lalastra, 30TVN8346, 21.vi.1991, *P. M. Uribe-Echebarría* (SALA93485), SENK; Álava, Arlucena, 30TWN3732, 17.vi.1984, *Martínez & Morante* (SALA93487), SENL; Burgos, Junta de Trasloma, Colina, VN6465, 27.v.1991, *Patino & Valencia* (SEST386-91), SENM; Álava, Salinas de Añana, pista de Sobrón al collado de La Rastrilla, 30TVN9036, 2.v.1997, *M. Martínez Ortega MO239* (SALA93480), SENF; La Rioja, Pedroso, Sierra de Camero Nuevo, 30TWM2781, 23.vi.1991, *M. L. Gil de Zúñiga & J. A. Alejandre* (MA532538), SENO; Navarra, Sierra de Aralar, umbría de Aldaón, 30TWN7962, 18.vi.1999, *M. Martínez Ortega, L. Delgado & I. Aizpuru MO682* (SALA), SENA; León, Valdelugueros, Las Majadas, poco antes del cruce a Valdeteja, 30TUN0355, 7.vi.2001, *L. Delgado & E. Rico LD775* (SALA), SENB; León, Riaño, poco antes de llegar a Carende en dirección a Riaño, 30TUN3456, 7.vi.2001, *L. Delgado & E. Rico LD776* (SALA), SENC; León, Valdepiélago, Valdorria, peña Valdorria, 30TUN0251, 7.vi.2001, *L. Delgado & E. Rico LD774* (SALA), SEND; Asturias, calizas próximas al embalse de Valdemurrio, Sierra del Aramo, 15.vii.1973, *Navarro Andrés* (FCO04428), SENN.

VERONICA ARAGONENSIS

SPAIN: Huesca, Bisaurri, Montaneta de Gabas, ladera oriental del Monte Baciero, 31TBH9204, 4.vii.1988, *J. A. Sesé & P. Montserrat* (JACA0665787), ARAD; Huesca, Ordesa, sobre las clavijas de Soaso, 31TBH5527, 15.vii.1971, *P. Montserrat* (JACA473871), ARAC; Huesca, La Estiva, 31TBH7506, umbría de La Estiva, 22.vii.1979, *P. Montserrat* (JACA256379), ARAB; Huesca, Yésero-Gavín, solana de Tendeñera, 30TYN2628, 7.viii.1979, *L. Villar* (JACA349179), ARAA; Huesca, Guara, cumbres, vi.1947 (BCF41230), ARAE; Granada, Huéscar, Sierra de la Sagra, 2.vii.1983, *Negrillo* (GDA18086), ARAF; Huesca, Arguis, Bentué de Rasal, 30TYM0790, 12.v.1974, *P. Montserrat* (JACA52774), ARAG.

VERONICA TENUIFOLIA

SPAIN: Castellón, Forcall, vi.1980, *Mansanet & Mateo* (VAB80719), TEND; Huesca, Mediano, 31TBG6989, 29.iv.1957, *P. Montserrat* (JACA9857), TENE; Lérida, Organya, 31TCG6173, 4.v.1971, *P. Montserrat* (JACA77571), TENF; Valencia, Requena, Pico Tejo, 20.vi.1984, *J. B. Peris & G. Stübing* (SALA33052), TENG; Navarra, Cáseda, XM3094, 7.vi.1998, *M. Martínez Ortega MO363* (SALA95040), TENB; Barcelona, La Panadella, 1 km on road to Santa Coloma de Queralt, 16.v.1971, *V.H. Heywood* (RNG), TENH; Zaragoza, Bardenas Reales, junto Tres Mugas, 30TXM3283, 16.v.1980, *D. Gómez & Aseginolaza* (JACA0061188), TENA; Lérida, prope Almacelles in Catalonia occid, 9.v.1926, *Font Quer* (BC113724), TENJ.

VERONICA FONTQUERI

SPAIN: Granada, Sierra de Baza, subiendo al Calar de Santa Bárbara, WG13, 9.vi.1983, *Torres, Blanca & Morales* (GDAC26404), FONC; Granada, Sierra de Baza, puerto de los Tejos, WG13, 19.vii.1974, *Fernández Casas* (MA389465), FONB; Almería, Fondón, Sierra de Gádor, Llanos de Boliches, WF1885, 11.vi.1998, *M. Martínez Ortega MO369* (SALA95041), FONA; Málaga, Yunquera, Sierra de Las Nieves, Peñón de los Enamorados, 4.vii.1991, *Cabezudo, Nieto, Pérez & Vera* (MGC36827), FONE; Málaga, Ronda, Sierra de las Nieves, Los Quejigales, puerto de los Pilones, 9.vi.1998, *Cabezudo & M. Martínez Ortega MO364* (MGC46659), FOND.

VERONICA JAVALAMBRENSIS

SPAIN: Guadalajara, de Buenafuente a Huertahernando, 30TWL6419, 20.vi.1986, *Alejandre & al.* (VIT37034), JAVD; Burgos, Sargentes de la Lora, 30TVN2634, 6.vi.1985, *B. Fernández de Betoño & J. A. Alejandre* (MA339646), JAVH; Salamanca, Almenara de Tormes, 4.v.1978, *J. Sánchez* (SALA17631), JAVM; Palencia, Cervera de Pisuerga, Peña de Santa Lucía, 30TUN6552, 30.v.1990, *J. A. Alejandre* (MA532710), JAVL; Cantabria, Camaleño, Sierra Mediana, 30TUN5671, 12.vii.1996, *M. Martínez Ortega MO194* (SALA93456), JAVA; Salamanca, La Mata de la Armuña, entre Castellanos de Villiquera y Aldeaseca de la Armuña, 30TTL7446, 14.v.1996, *M. Martínez Ortega MO112* (SALA93463), JAVJ; Madrid, Cabrizos de Chozas, 18.v.1952, *Rivas & Fernández Galiano* (SALA1411), JAVI; Teruel, Sierra de Tramacastilla, les pelouses, sur le trias, *Reverchon* (B), JAVG; Cuenca, Sierra de Valdeminguete, eastern slopes of Mogorrita, *Brummitt, Gibbs & Ratter* (E), JAVF; Zamora, Abezames, 11.vi.1990, *Casaseca, Rico & Giráldez* (SALA49322), JAVE; Soria, Villaciervos, Sierra de Cabrejas, 30TWM2127, 11.vi.1988, *M. L. Gil Zúñiga & J. A. Alejandre* (MA468044), JAVK; Segovia, Navares de las Cuevas, Sierra de Pradales, Peñacuerno, 30TVL3990, 7.vi.1996, *M. Martínez Ortega MO121* (SALA93468), JAVB.

VERONICA ROSEA

MOROCCO: Lalla-Aziza, 5.vi.1884, *Ibrahim* (BM), ROSF; Beni Mellal, below summit of Irhil Ouaougoulzate, 5.vii.1966, *Harley 627* (BM), ROSG; El Ferrah, in cistetis supra emporium Sok-et-Tnin (Beni Hadifa), *Font Quer* (GDA027834), ROSI; Ouarzazate, à proximité di Tizi n'Melloul (Jab. Siroua), 30°47′N, 7°36′W, 31.v.1980, *A. Charpin, J. Fernández Casas, F. Jacquemoud & J. Jeanmonod MAR410* (G), ROSJ; Rif, *Sennen* (MA429804), ROSK; Ketama-El Hoceima, 26.v.1972, *Alexander & Kupicha* (E), ROSL; Ouarzazate, Tizi n'Ouaro, 31°58′N, 5°38′W, 1.vi.1985, *C. Blanché, J. Fernández Casas, J. Molero, J. M. Montserrat & A. Romo N = 20* (MA302831), ROSN; env. de Benkane, massif des Beni Snassene, Djebel Tamcojoutan. NE du refuge Zegzal, 20.iv.1928, *Wilczek, Briquet, Dutoit & Emberger* (K), ROSM; Lexhab (Gomara), 22.vii.1929, *Font Quer* (BM), ROSA; Beni Snassene, in cacumine montis Tamedjout ditionis Zegzel, 20.iv.1928, *Wilczek, Briquet, Dutoit & Emberger* (G), ROSD. ALGERIA: Djurdjura, between Tizi-N'Kouilal pass and Tikjda, 21.vii.1975, *Davis* (BM), ROSH; env. de Bossuet, pelouses et broussailles, 17 et 29.vi.1930, *Faure* (BM), ROSE; Wilaya Batna, massif de l'Aurès, SE-Hänge des Dj. Chelia, NW von Bouhamama 6/40 E–35/18N, 7.vi.1984, *Podlech* (G), ROSC; prov. d'Oran, Montagne de Gharrouban, au sud de Lalla-Maghrnia, ouest de la prov. d'Oran, 21.v.1856, *E. Bourgeau* (G), ROSB.

Uncertain initial determinations: Lérida, Puigcerda-Martinet, 31TCG9390, 6.vii.1986, *P. Montserrat & G. Montserrat* (JACA463686), JAVC; Toledo, Montes de Toledo, Sierras del Rebollarejo, 10.vi.1977, *Velasco* (MAF108794), TENC.