

## Taxonomy of *Veronica* L. subsect. *Veronica* (Plantaginaceae) in the western Mediterranean

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*Veronica* subsect. *Veronica* in the western Mediterranean area is revised taxonomically in light of new karyological, palynological, and further diagnostic morphological features. The data confirm that the subsection comprises only two species and a hybrid taxon. Many previously recognized species are reduced to synonyms. An updated taxonomic treatment is supplied, including detailed descriptions of the taxa involved, as well as a list of synonyms, types of name, selected representative specimens, and a distribution map. © 2007 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2007, 155, 65–81.

ADDITIONAL KEYWORDS: chromosome numbers – palynology – Scrophulariaceae – seed morphology – typification – *Veronica officinalis*.

### INTRODUCTION

*Veronica* L. is the largest genus of the *Plantaginaceae sensu* Angiosperm Phylogeny Group (1998, 2003), having been formerly placed in Scrophulariaceae, with approximately 450 species. It is distributed mainly in the temperate regions of the northern hemisphere and Australasia (Albach *et al.*, 2004a).

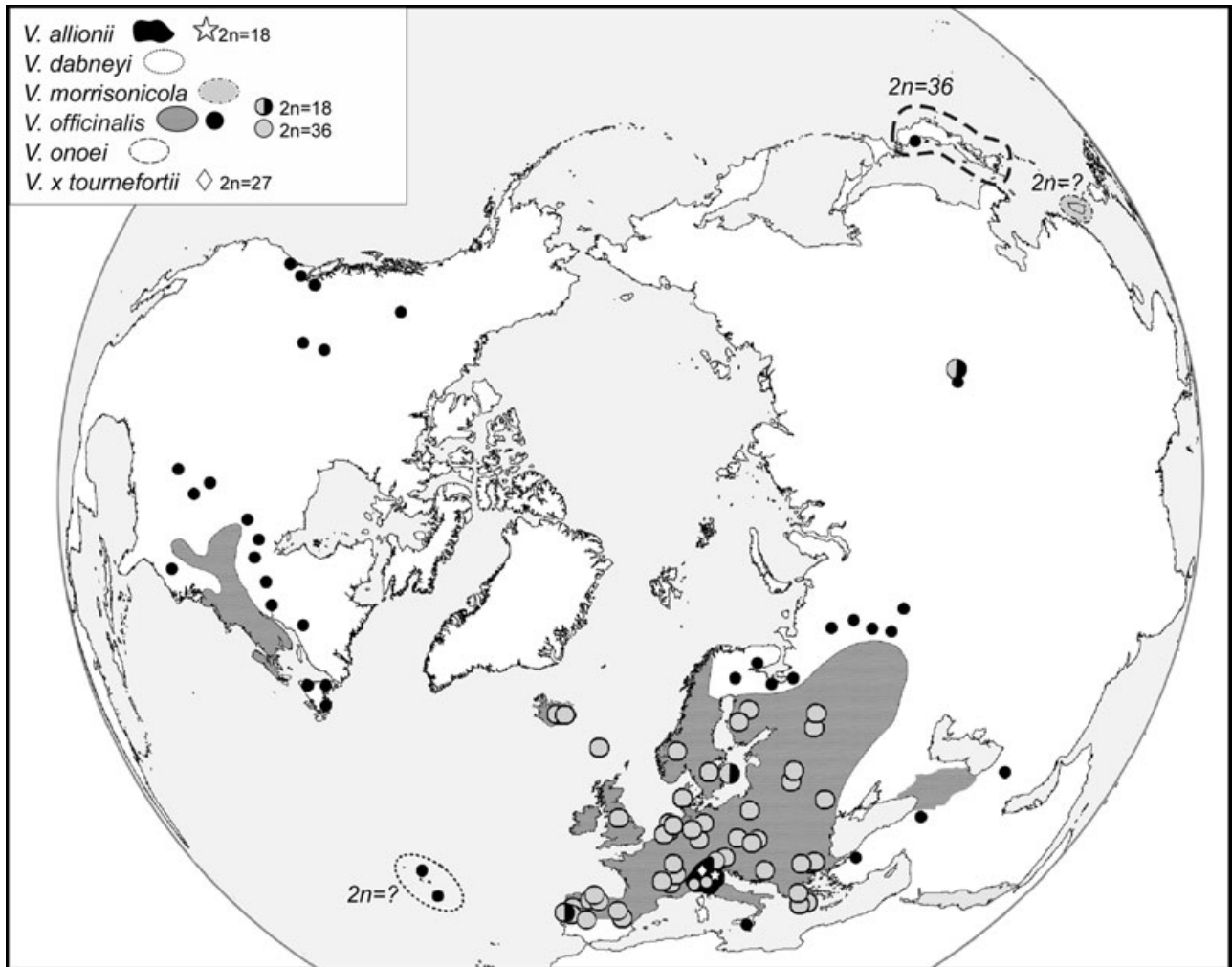
The taxonomic history of *Veronica* clearly illustrates the difficulties arising in the recognition of natural (monophyletic) groups within the genus based only on morphological traits, due to the fact that many of the traditionally used taxonomic characters are evolutionary labile and therefore not suitable for taxonomy (Albach *et al.*, 2004b). In recent years, evidence from DNA sequence data from three (nuclear and plastid) DNA regions (e.g. Garnock-Jones, 1993; Wagstaff & Garnock-Jones, 1998; Albach & Chase, 2001; Wagstaff *et al.*, 2002; Albach *et al.*, 2004b; Albach, Martínez-Ortega & Chase, 2004), combined with karyological (e.g. Albach *et al.*, in press), phytochemical (e.g. Taskova, Peev & Handjieva, 2002; Taskova, Albach & Grayer, 2004; Albach *et al.*, 2005;

Jensen *et al.*, 2005), and morphological evidence (e.g. Muñoz-Centeno *et al.*, 2006), as well as biogeographical considerations has allowed an infratribal and infrageneric rearrangement for the tribe Veroniceae and for the genus *Veronica* (Albach *et al.*, 2004a) to be proposed that is consistent with current knowledge of the evolutionary history of the group.

Here we use the supraspecific classification of Albach *et al.* (2004a) and the species arrangement and monophyletic sections currently accepted by Albach, Martínez-Ortega & Fischer [provisionally proposed in part in Albach *et al.* (in press)]. According to these authors, *V.* subgen. *Veronica* L. includes 45 species distributed in four monophyletic sections: *V.* sect. *Glandulosae* nom. prov., *V.* sect. *Scutellatae* G. Don, *V.* sect. *Montanae* (Boriss.) Assejeva, and *V.* sect. *Veronica*. Within the latter, six subsections have been recognized: *V.* subsect. *Alpinae* Benth., *V.* subsect. *Gouani* (Römpf) Stroh, *V.* subsect. *Urticifoliae* Boriss. ex Elenevsky, *V.* subsect. *Veronica*, *V.* subsect. *Aphyllae* (Römpf) Stroh, and *V.* subsect. *Carpathicae* Elenevsky.

*Veronica officinalis* L. (Europe, Anatolia, Caucasus, Transcaucasia, northern Iran, Azores, and introduced in North America) and *V. allionii* Vill. (south-west Alps), the subject of the present study, are placed

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**Figure 1.** ★☆ Distribution and chromosome counts in *Veronica allionii*. ○ Distribution of *V. dabneyi*. ● Distribution of *V. morrisonicola*. ●● Distribution of *V. officinalis*. ●○ Diploid and tetraploid counts in *V. officinalis*. ○ Distribution of *V. onoei*. ◇ Chromosome counts *V. x tournefortii* [adapted from Meusel *et al.* (1978)].

within *V.* subsect. *Veronica*. The remaining three species included in this section – *V. onoei* Franch. & Sav., *V. morrisonicola* Hayata, and *V. dabneyi* Hochst. ex Seub. – are distributed, respectively, in Japan, Taiwan, and the Azores, and hence outside the area included in this study (Fig. 1).

The plants included in *V.* subsect. *Veronica* are characterized within the genus by the following characters: they are perennial herbs; decumbent to ascendent stems, usually with a terminal vegetative shoot, internodes evident, although not always longer than leaves; inflorescences in axillary racemes; bracts clearly different from the leaves; flowers with more or less erect pedicels; calyx with four or five sepals, usually shorter than capsule; corolla longer than calyx, with a short broader than long tube; not many (usually <20) elliptic, ovate or

obovate seeds (see Seed morphology section). Regarding phytochemistry, the species often contain mussaenoside, whereas this compound is usually not present in the remaining sections (Taskova *et al.*, 2004; Albach *et al.*, 2005). The chromosome base number is  $x = 9$  (rarely 7).

The taxonomic problems of this subsection have been studied by several authors. The extreme morphological variability of *V. officinalis* L. in Europe was analysed in some detail by Böcher (1944), Bocquet, Favarger & Zürcher (1967), Walters & Webb (1972), Stepanov (1997), Martínez-Ortega (1999), and Alonso *et al.* (2003), among others.

Böcher (1944) studied the variation in leaf size in *V. officinalis* in relation to certain environmental factors and concluded that four intergrading morphological races could be distinguished (*microphylla*, *genuine*,

**Table 1.** Seed characters of *Veronica allioni* and *V. officinalis* based on material studied and measurements (in mm) obtained by Kulpa (1968) (Kulpa's results are given in the lower line, our results are in the upper one)

Taxa	L x	L Sn	L M–m	W x	W Sn	W M–m	N
<i>V. allioni</i>	0.51	0.07	0.62–0.40	0.35	0.07	0.47–0.22	25
	0.73		0.95–0.60	0.64		0.79–0.52	
<i>V. officinalis</i>	1.19	0.20	1.64–0.80	0.92	0.14	1.21–0.33	130
	1.01		1.22–0.81	0.78		0.91–0.64	

L x, mean of seed length; L Sn, standard deviation of seed length; L M–m, maximum and minimum values of length; W x, mean of seed width; W Sn, standard deviation of seed width; W M–m, maximum and minimum values of width; N, number of samples.

*media*, and *macrophylla*), although he did not propose a formal taxonomic rank for them.

Bocquet *et al.* (1967) reported the coexistence in the Alps of *V. officinalis*, *V. allionii*, and a sterile triploid hybrid ( $V. \times \textit{tournefortii}$  F. W. Schmidt  $\equiv V. \textit{allionii} \times V. \textit{officinalis}$ ), which exhibits intermediate morphology between both parental species, produces only aborted pollen grains, and always shows anomalous meiosis processes.

According to Walters & Webb (1972), Stepanov (1994, 1997), and Martínez-Ortega (1999), among other authors, several morphological variants and two chromosomal races (two ploidy levels –  $2x$  and  $4x$  – based on  $x = 9$  have been found) can be distinguished within *V. officinalis*, but none of these variants merits taxonomic recognition. Only Alonso *et al.* (2003) recently treated a morphological variant with small, glabrous leaves and a deeply obcordate capsule occurring in the Cordillera Cantábrica, but also scattered in north-west and north-central Europe (Walters & Webb, 1972; Martínez-Ortega, 1999) at species level (*V. vadiniensis* [*vadiniense*] R. Alonso, Lence, López Pach., Puente & Penas). However, almost a century ago, Sampaio (1906) described the same morphological variation in plants collected in the Portuguese Serra da Estrêla and gave them the name *V. carquejana* Samp. Martínez-Ortega (1999) had already made detailed studies of the morphological and karyological variation of such variants in several mountains of the Iberian Peninsula where they occur (several populations in the Cordillera Cantábrica, the Sistema Ibérico, and the Sistema Central; see specimens marked with an asterisk under 'Selected specimens seen of *V. officinalis*'), and concluded that the variants cannot be regarded taxonomic rank.

Here we revise the taxonomy and nomenclature of *V.* subsect. *Veronica* in the western Mediterranean area in light of the unpublished results of Martínez-Ortega (1999) and many additional data derived from recent investigations.

## MATERIAL AND METHODS

This revision is based on the study of herbarium specimens from the following herbaria [abbreviations 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, MPU, MW, NAP, NEU, NY, OXF, P, PAD, PH, RAB, RO, S-Linn, SLBI, SOM, TL, TO, TR, UPS.

All the species were studied in the field and several populations were cultivated in order to observe carefully the variability of some characters.

Macromorphological observations of mature seeds were carried out under a stereoscopic microscopy. Several parameters were measured (Table 1) from 130 and 25 seeds of *V. officinalis* and *V. allionii*, respectively. For scanning electron microscopy, dry seeds were either directly mounted on to stubs using double-sided adhesive tape or soaked in a 1 : 1 solution of chloroform and methanol for 48 h, dehydrated through an ethanol series (70, 90, and 100%) and finally treated with xylene for 3 days with a view to detecting and removing wax deposits. Samples were coated with gold-palladium in a BALZER SCD004 ion-sputter and then observed with standard techniques using a DSM 940 (ZEISS) microscope.

Pollen morphology was examined in acetolysed pollen with a Nikon Optiphot-2 light microscope. Thirty measurements per population were taken for all parameters in four geographically separated populations of *V. officinalis* and one of *V. allionii* using a Sony 3 CCD DCX-930P video-camera connected to the light microscope to transfer the image to a computer. We used the Image-Pro Plus program version 1.0 for image analysis. The following parameters were mea-

**Table 2.** Measurements (in  $\mu\text{m}$ ) and exine characteristics of pollen grains

Taxa	P	E	P/E	Exine
<i>V. allioni</i>	22.8 $\pm$ 1.17 (20.8–25.5)	21.3 $\pm$ 1.60 (16.7–23.8)	0.93	1.4–1.6
<i>V. officinalis</i>	30.4 $\pm$ 2.06 (26.6–35.1)	27.5 $\pm$ 1.76 (22.9–31.2)	1.10	1.7–2.2

P, length of polar axis (mean value  $\pm$  standard deviation, minimum and maximum values); E, length of equatorial diameter (mean value  $\pm$  standard deviation, minimum and maximum values); P/E, P/E ratio; Exine, equatorial exine thickness in meridional optical sections.

sured (Table 2): polar axis (P), equatorial diameter (E), P/E ratio, and equatorial exine thickness in meridional optic sections (Exine). For scanning electron microscopy, acetolysed grains were coated under a high vacuum with a film of gold-palladium (using BALZER SCD 004 ion-sputter) and examined with a JEOL, JSM-T330A microscope. The structure of the grains was studied on randomly cracked examples after ultrasonic treatment.

Chromosome counts from five populations (in two of them, two counts were made on individuals from two subpopulations, i.e. SALA 110616 and SALA 110615; SALA 93399 and SALA 110614) are assembled in Table 3 and previous counts for *V. officinalis* and *V. allionii* are shown in Table 4. Chromosome counts were carried out almost entirely on young floral buds where division processes were observed in cells from different tissues of the gynoecium, usually in mitotic metaphase, although in one subpopulation (SALA 110616) the haploid number ( $n$ ) was obtained from meiosis in starting anaphase I of the embryo sac of the mother cell. The material was always fixed in absolute ethanol : glacial acetic acid at a proportion of 3 : 1. The fixed material was stored at 4 °C until staining with 2% acetic orcein. It was mounted by squashing in 45% acetic acid. From each population at least five counts were made, from which schemes were drawn and photographs were taken. Sometimes, video-printer images were taken using a Nikon Optiphot-2 light microscope connected to a video-camera (Sony 3 CCD DXC 930 P). Schemes and negatives are deposited at the Department of Botany of the University of Salamanca.

A complete list of the material studied can be found in Martínez-Ortega (1999). We examined *c.* 450 herbarium sheets and give citations for selected representative specimens corresponding to each taxon in the Taxonomy section. We have used the following abbreviations after voucher citation: POM, material used to obtain pollen for studies under light microscopy; PSEM, material used to obtain pollen scanning electron micrographs; SE, material used to obtain scanning electron micrographs of seeds; CR, material used for chromosome counts.

**Table 3.** Material studied and chromosome numbers found

$n$	$2n$	Localities, collectors	Voucher
9	18	PORTUGAL. Beira Alta: Guarda, Sabugueiro, Serra da Estrêla, Lagoa Comprida. <i>L. Delgado, L. M. Muñoz-Centeno &amp; M. Martínez-Ortega</i> MO1753	SALA 110616
	36	PORTUGAL. Beira Alta: Guarda, Sabugueiro, Serra da Estrêla, Lagoa Comprida. <i>L. Delgado &amp; M. Martínez-Ortega</i> LD 926	SALA 110615
	36	SPAIN. Cantabria: Hermandad de Campoo de Suso, Pico Tres Mares. <i>M. Martínez-Ortega</i> MO 180	SALA 93399
	36	SPAIN. Cantabria: Hermandad de Campoo de Suso, Pico Tres Mares. <i>E. Rico</i> ER 7872	SALA 110614
	36	SPAIN. Cantabria: Vega de Liébana, Peña Llesba. <i>M. Martínez-Ortega</i> MO 189	SALA 93397
	36	SPAIN. La Rioja: Canales de la Sierra, Las Tres Cruces. <i>M. Martínez-Ortega</i> MO 163	SALA 93393
	36	SPAIN. Salamanca: Candelario, río Barquillo. <i>L. Delgado &amp; M. Santos Vicente</i> LD 923	SALA 110617

We occasionally had problems in locating or obtaining loans of type material; in such cases, the information provided is based on the opinions of other authors or deduced from careful reading of protologues. Where no reliable opinion was obtainable or doubts persisted regarding the original type



**Table 4.** Previous counts in *Veronica allionii*, *V. officinalis*, and *V. × tournefortii*

<i>n</i>	<i>2n</i>	Reference	Country of origin
<i>V. allionii</i>			
9	18	Bocquet <i>et al.</i> (1967)	France, Italy
<i>V. officinalis</i>			
	34	Afanasiyeva & Meshkova (1961)	Russia
	18	Böcher (1944)	Sweden
	36	Böcher (1944)	Germany, Faroe Islands, Iceland, Norway
18	36	Bocquet <i>et al.</i> (1967)	France, Italy
	32, 34	in Bolkhovskikh <i>et al.</i> (1969)	Holland
	32, 34, 36	in Bolkhovskikh <i>et al.</i> (1969)	
	32–37	in Bolkhovskikh <i>et al.</i> (1969)	Germany
	34, 36	in Bolkhovskikh <i>et al.</i> (1969)	France
	36	in Bolkhovskikh <i>et al.</i> (1969)	Poland, Ukraine
	36	Dzhus & Dmitrieva (2001)	Belarus
	36	Fernandes <i>et al.</i> (1977)	Portugal
18		Fischer (1969)	Austria
	<i>c.</i> 36	Fischer (1973)	Austria
	36	in Goldblatt & Johnson (1994)	Bulgaria, Belarus
	36	in Goldblatt & Johnson (1996)	UK
	18	in Goldblatt & Johnson (1998)	Russia
	34	in Goldblatt (1988)	Italy
	36	in Goldblatt (1988)	Finland
18		in Goldblatt & Johnson (1991)	
18		in Goldblatt & Johnson (1991)	Crete
	36	in Goldblatt & Johnson (2003)	Sweden
	36	in Goldblatt (1981)	Slovakia
	36	in Goldblatt (1984)	Greece, Yugoslavia
	36	Löve & Kjellqvist (1974)	Spain
	36	Löve & Löve (1956)	Iceland
	36	Löve & Löve (1982)	Italy
	36	Váchová (1974)	Slovakia
	34	in Moore (1974)	France
	34, 36	in Moore (1973)	France, Holland
	36	in Moore (1974)	Czech Republic-Slovakia
	36	in Moore (1977)	Holland
	36	Peev (1975)	Bulgaria
	36	Sokolovskaja (1972)	Russia
18	<i>c.</i> 36	Sorsa (1962)	Finland
	36	Strid & Franzen (1981)	Greece
	32, 36	Tischler (1934)	Germany
	36	Van Loon & De Jong (1978)	Portugal
	36	Van Loon & Van Setten (1982)	Bulgaria
<i>V. × tournefortii</i>			
	27	Bocquet <i>et al.</i> (1967)	Italy

material, we use the symbol ‘?’ after 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. Homotypic synonyms are preceded by the symbol ‘≡’ and

heterotypic ones by ‘≠’. We have aimed to offer a complete list of synonyms (at the specific, subspecific or varietal rank only; they are names mostly with their types in western and central Europe), that have been ordered chronologically.

## RESULTS AND DISCUSSION

## TAXONOMIC CHARACTERS

The variation in the structural characters not included in this section is described under the corresponding descriptions of the taxa in the Taxonomy section.

*Seed morphology*

The macro- and micromorphological characters of the seed are of essential systematic importance within *Veronica* (Riek-Häussermann, 1943; Thieret, 1955; Yamazaki, 1957; Kulpa, 1968; Juan, Fernández & Pastor, 1994; Martínez-Ortega & Rico, 2001; Muñoz-Centeno *et al.*, 2006). The general shape of the seed has been traditionally used in *Veronica* as a first-order taxonomic character and it has traditionally been used – together with the position of the inflorescence, among other characters – to support the infrageneric classification of the genus. Several authors, such as Elisens & Spencer (1983), Barthlott (1984), and recently Martínez-Ortega & Rico (2001) and Muñoz-Centeno *et al.* (2006), have emphasized the phylogenetic and systematic value of the structural characters of the seed coat due to its low phenetic variation.

The main data on seed size according to Kulpa (1968) and Martínez-Ortega & Rico (2001) corresponding to *V. allioni* and *V. officinalis* are shown in Table 1. The size of seeds within *V.* subsect. *Veronica* from the western Mediterranean region ranges between 0.4 and 1.6 mm in length and 0.2 and 1.2 mm in width. They are elliptic, ovate or obovate in outline (Fig. 2), dorsiventrally flattened and smooth under stereoscopic microscopy, with a funicular attachment, usually terminal (Fig. 3), and their colour varies from brown to yellow.

In the seeds of many *Veronica*, a special ventral structure appears, which was called ‘endosperm plateau’ by Meunier (1897) and Thieret (1955) and ‘Endospermopodium’ by Riek-Häussermann (1943). This structure looks like a shallow depression (Fig. 3) in *V. allioni* and *V. officinalis*. The raphial line is usually evident, although its clearness varies even within a single plant.

Several patterns of seed coat sculpture have been described by Martínez-Ortega & Rico (2001) and Muñoz-Centeno *et al.* (2006) based on differences in outer cell morphology under scanning electron microscopy. In the most recent investigations, up to eight main sculpturing patterns have been recognized within the whole genus (*V.* subgen. *Pseudoveronica* from the southern hemisphere and *Synthyris* from North America were excluded), each of them divided in some cases into subtypes. *V. officinalis* (Figs 4, 5; see notes to *V. officinalis* in the Taxonomy section)

and *V. allioni* (Fig. 6) share a flat seed with a smooth testa, with a typically reticulate seed coat surface, which is characterized by shallow to medium depth radial walls and by tangential walls that are commonly smooth. In this case, the testa does not show rings superimposed over the basal reticulum, which are common in other species of the subgenus (Martínez-Ortega & Rico, 2001; Muñoz-Centeno *et al.*, 2006). Within the subsection, the ultrastructure of the testa is known only in *V. onoei* and coincides with the previously described type.

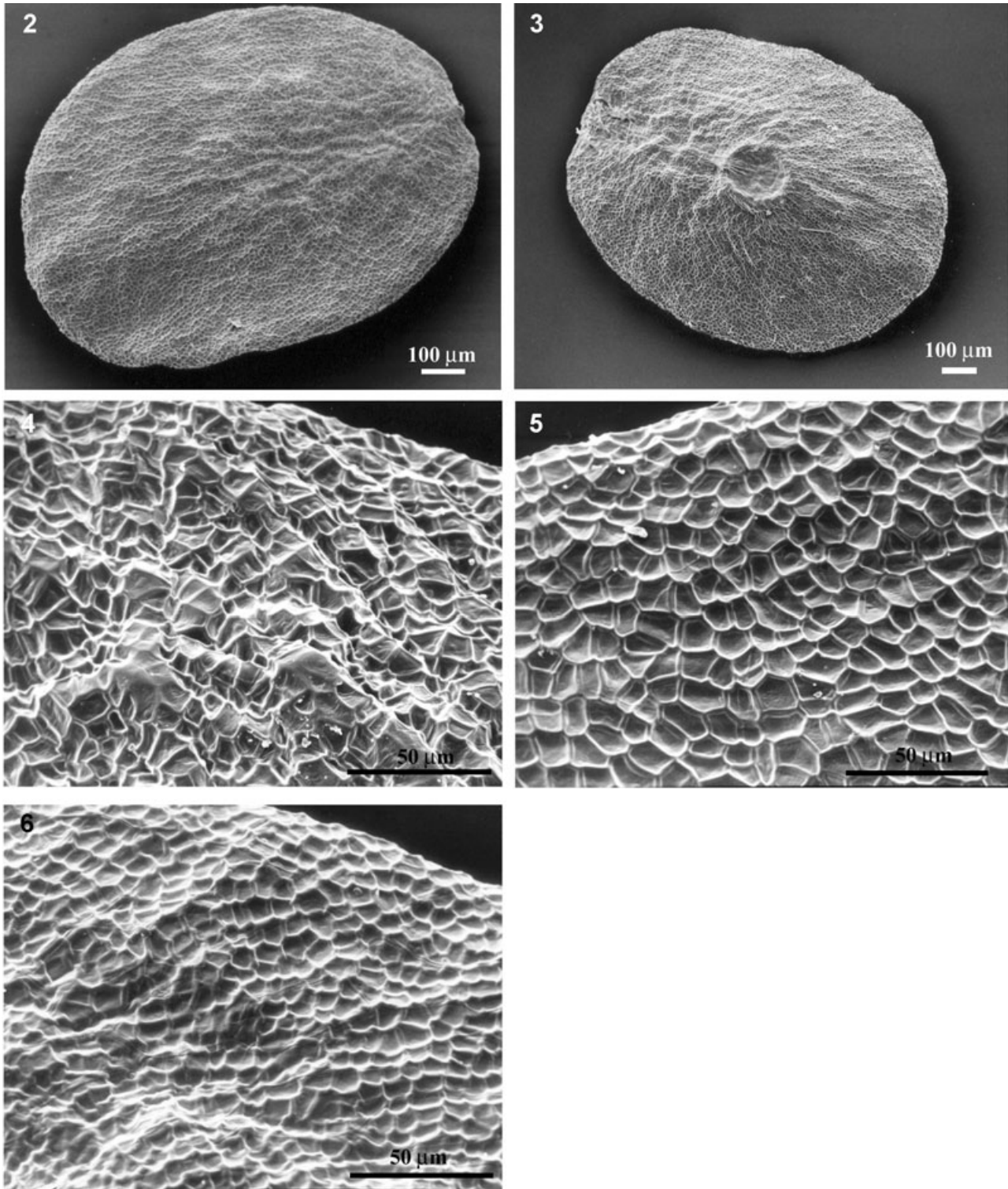
As far as is known, except for average sizes (Table 1), seed characters are generally uniform within *V.* subsect. *Veronica*. The ornamentation type of the seed coat is a unique feature shared by three of the four sections included in *V.* subgen. *Veronica* (i.e. *V.* sect. *Scutellatae*, *V.* sect. *Montanae*, and *V.* sect. *Veronica*), which further supports the monophyly of subgenus *Veronica*. Only the African endemic *V.* sect. *Glandulosae* – the fourth member of *V.* subgen. *Veronica*, sister to the rest of the subgenus – shows a different ornamentation (Muñoz-Centeno *et al.*, 2006).

*Palynology*

Pollen offers a variety of characters that have been used for taxonomic purposes in *Veronica*. Their interest as taxonomic tools has been discussed by many authors (e.g. Hong & Nilsson, 1983; Hong, 1984; Fernández, Juan & Pastor, 1997; Martínez-Ortega, Sánchez-Sánchez & Rico, 2000). Albach *et al.* (2004b) mapped the pollen types identified by earlier authors on the available DNA sequence-based phylogenetic hypothesis and showed that both data sets matched with little conflict.

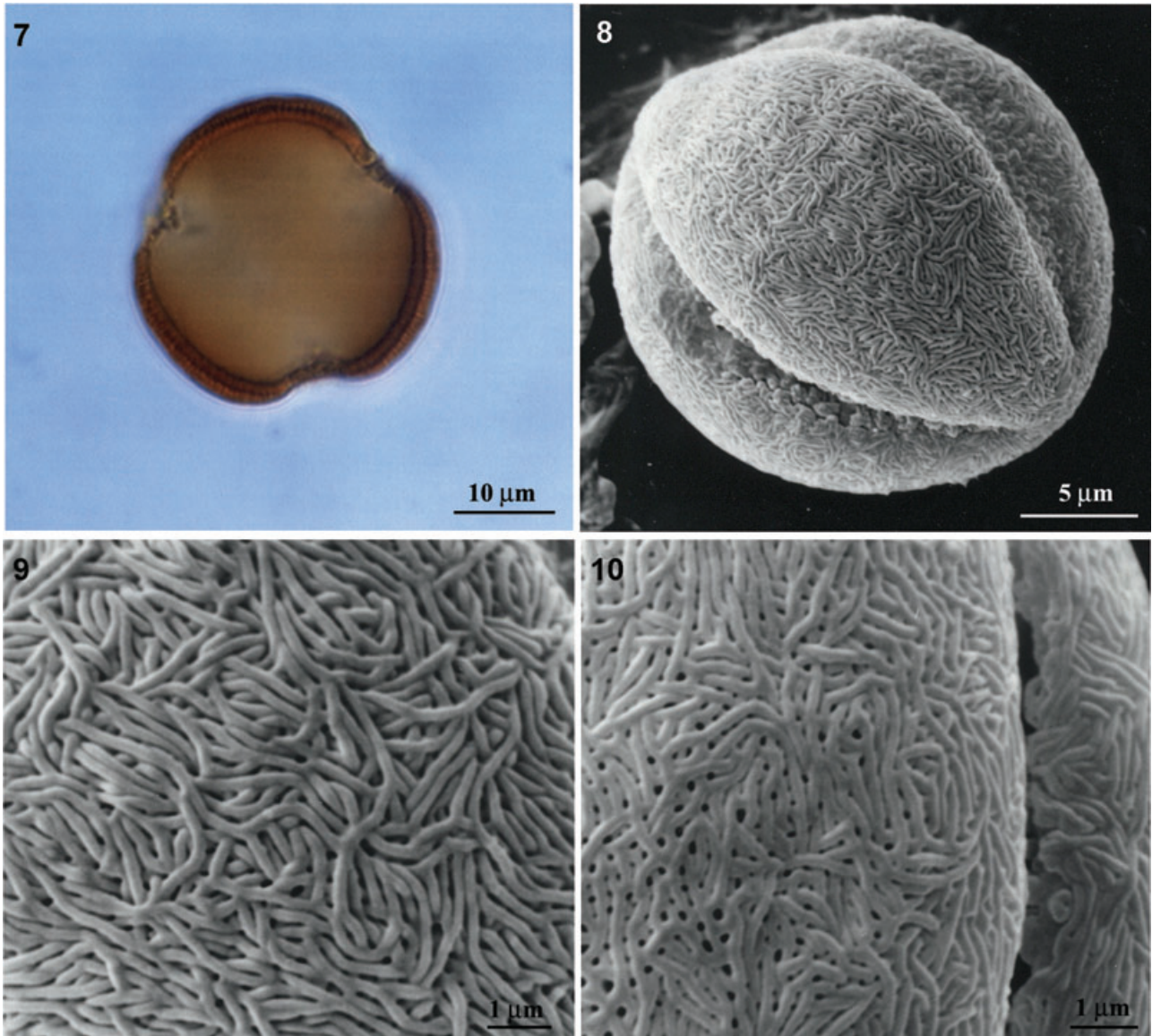
Pollen grains in *V.* subsect. *Veronica* belong within Hong's (1984) *Veronica*-type. They are isopolar, radially symmetric, have three-order symmetry (Fig. 7) (rarely four order), and are oblate-spheroidal or prolate-spheroidal (Fig. 8). They are circular to elliptic in outline in the meridional optical section and circular-trilobulate (sometimes tetralobulate) in the equatorial optical section. The apertural system, tectum, and infratectum types essentially correspond to the general type described in Martínez-Ortega *et al.* (2000).

Quantitative results obtained for the P, E, P/E ratios, and exine thickness have been published in Martínez-Ortega *et al.* (2000), although we have coalesced the main data corresponding to *V. allioni* and *V. officinalis* in Table 2. Those authors demonstrated that the size of the pollen grain in one taxon is directly influenced by the ploidy level of each taxon within every natural group or subsection. Within the group studied, the pollen grain of *V. allioni* – a diploid species – is always smaller than the tetraploid samples studied of *V. officinalis*.



**Figures 2–6.** Scanning electron micrographs of seeds. Fig. 2. General shape, dorsal face. Fig. 3. General shape, ventral face. Fig. 4. Seed coat pattern in *Veronica officinalis* (SALA 93408): typically reticulate. Fig. 5. Seed coat pattern in *V. officinalis* (SALA 93403)\*: typically reticulate. Fig. 6. Seed coat pattern in *V. allionii* (France, Lautaret, B): typically reticulate.





**Figures 7–10.** Light and scanning electron micrographs of pollen grains. Fig. 7. Optical cross-section of a typical tricolpate pollen grain in *Veronica officinalis* (SALA 93410), polar view. Fig. 8. Equatorial view of pollen grain in *V. officinalis* (SALA 93410). Fig. 9. Ornamentation of the exine in *V. officinalis* L. (SALA 93410): typically striate-reticulate. Fig. 10. Ornamentation of the exine in *V. allionii* Vill. (G 826341): typically striate-reticulate.

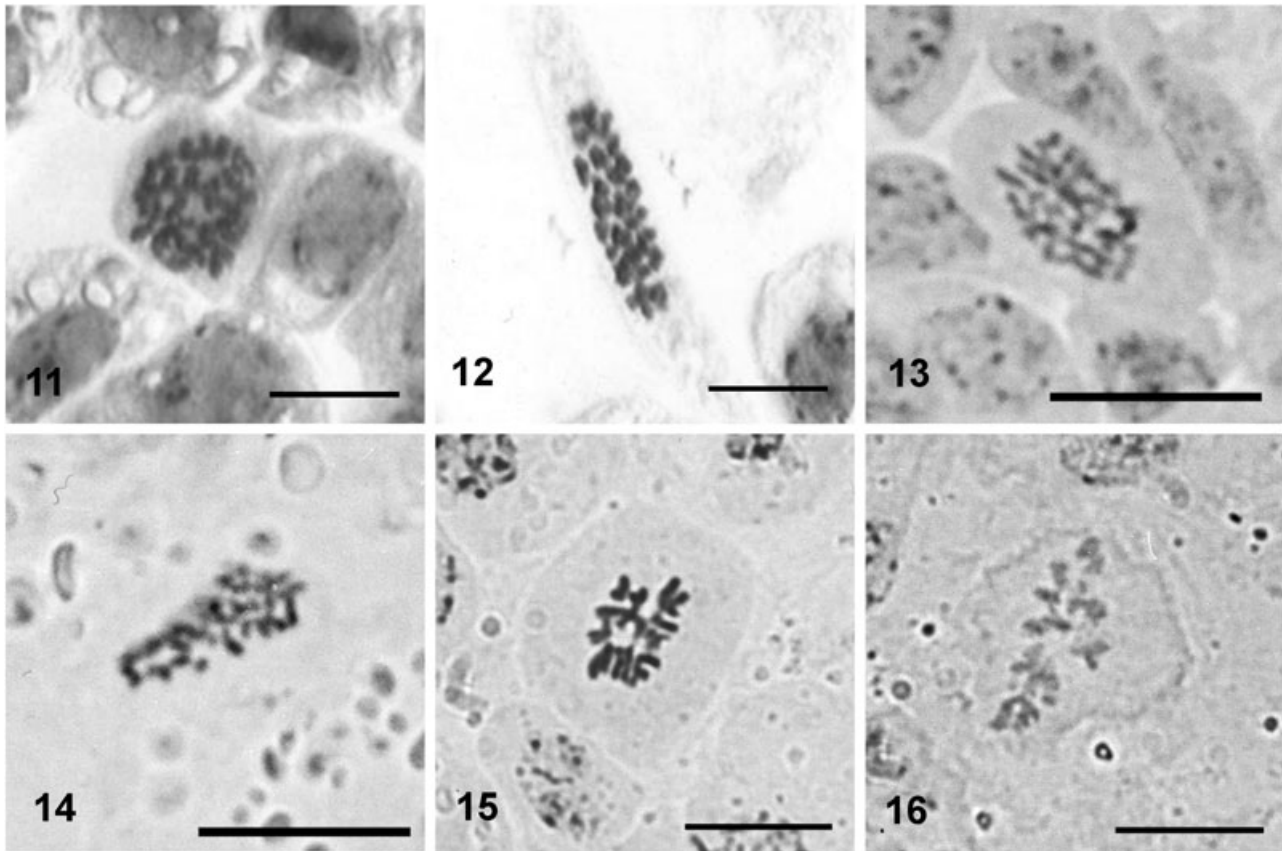
Regarding ornamentation of the exine, both species show a sculptural pattern that is frequent within the genus: a typically striate-reticulate, microreticulate pattern (Figs 9, 10).

Concerning the remaining representatives of the subsection, *V. onoei*, *V. morrisonicola*, and *V. dabneyi*, to our knowledge no additional information on the pollen is available.

Although the size of pollen seems to be useful for distinguishing between diploid and tetraploid

samples within the taxa of *V.* subsect. *Veronica* studied, as far as is known the remaining palynological characters are quite uniform within the subsection. Regarding exine ornamentation, almost no variation is found within *V.* subgen. *Veronica*: most species show a striate-reticulate microreticulate testa or slight variations in such a pattern and *V. bellidoides* L. – showing a rugulate-reticulate testa – represents the main deviation (Martínez-Ortega *et al.*, 2000).





**Figures 11–16.** *Veronica officinalis*. Fig. 11. Mitotic metaphase,  $2n = 36$  (SALA 93393)\*. Fig. 12. Mitotic metaphase,  $2n = 36$  (SALA 93399)\*. Fig. 13. Mitotic metaphase,  $2n = 36$  (SALA 110614)\*. Fig. 14. Mitotic metaphase,  $2n = 36$  (SALA 110615)\*. Fig. 15. Mitotic metaphase,  $2n = 18$ . Fig. 16. Starting anaphase I in embryo sac mother cell,  $n = 9$ . (SALA 110616)\*.

### Karyology

Chromosome numbers are available for many species of *Veronica* and chromosome counts have been reported for more than 2600 populations (Albach, Schönswetter & Tribsch, 2006). Albach *et al.* (2004b) inferred some trends regarding karyological evolution in the tribe Veroniceae. According to those authors, although no answer can be given to the issue concerning the ancestral number of chromosomes in the ancestor of Veroniceae, it seems that in *Veronica* such a number was probably  $x = 9$ , the usual base chromosome number within *V.* subgen. *Veronica*.

The results obtained for the five populations (seven counts; Figs 11–16) studied here (all of them collected in mountains of the northern Iberian Peninsula) are offered in Table 3. Here, the tetraploid level ( $2n = 4x = 36$ ) was found six times for *V. officinalis*. This chromosome number and ploidy level are in accordance with those reported by Fernandes, Queirós & Santos (1977), Van Loon & De Jong (1978), and Löve & Kjellqvist (1974) for *V. officinalis*

in the Iberian Peninsula. Thus, the diploid level ( $2n = 2x = 18$ ) was found in the remaining subpopulation (SALA 110616) collected in the Portuguese Serra da Estrêla (Fig. 15). This level is reported for *V. officinalis* in the Iberian Peninsula for the first time. Additionally, the species involved in our study have a rather uniform karyotype and the chromosomes are usually small (*c.*  $1.5 \mu\text{m}$ ). Most of them are clearly metacentric and some are reduced to points.

The most common chromosome number in *V. officinalis* is  $2n = 36$  ( $n = 18$ ). From a total of *c.* 60 counts known to us from the literature (Table 4), only two exceptional diploid  $2n = 18$  ( $n = 9$ ) populations have been reported (Fig. 1): one from the Swedish island of Gotland by Böcher (1944) and the other from Siberia (Buryatia Republic) by Stepanov (1994). Other numbers (see Table 4) are considered miscounts. No correlation has been found among ploidy level, morphology, ecology or geographical distribution in *V. officinalis*.

For *V. allionii*, only the diploid level ( $2n = 2x = 18$ ) has been reported. Regarding the remaining species in *V.* subsect. *Veronica*, we only know that *V. onoei* is a tetraploid ( $2n = 4x = 36$ ) (Bolkhovskikh *et al.*, 1969), and the chromosome numbers of *V. dabneyi* and *V. morrisonicola* remain unknown.

According to Bocquet *et al.* (1967), an ancestral widely distributed diploid taxon would have possibly been the origin of both *V. allionii* and the infrequent diploids within *V. officinalis*. The latter diploids would have been displaced to peripheral scattered localities (north and south-west Europe and Asia) by the dominant tetraploid *V. officinalis* (probably originated through autopolypoidy during glaciations). *V. allionii* would represent a schizoendemic taxon (Favarger & Contandriopoulos, 1961) restricted to high stations in the Alps. The tetraploid *V. officinalis* would have sometimes entered into contact with *V. allionii* after glaciations in sympatric areas of the Alps, originating the triploid hybrid *V. × tournefortii* ( $2n = 3x = 27$ ). Although the diploid counts in *V. officinalis* could support Bocquet's hypothesis, in our opinion further investigation is needed, including additional chromosome counts, as well as molecular markers.

In all cases, chromosome numbers within *V.* sect. *Veronica* are based on  $x = 9$ , except  $x = 7$  in *V. baumgartenii* Roem. & Schult. from *V.* subsect. *Carpathicae sensu* Albach *et al.* (in press), mostly considered closely related to *V. aphylla* L., a relationship not seen in DNA sequence analyses.

#### TAXONOMIC TREATMENT OF VERONICA SUBSECT.

##### VERONICA IN THE WESTERN MEDITERRANEAN

*Veronica officinalis* L., *Sp. Pl.* 11. 1753.

= *V. officinalis* var. *dorotheae* Sennen, nom. inval. [nom. nud. et in sched., MA 425327!].

= *V. officinalis* var. *major* Sennen, *Pl. Espagne*, n°3490, nom. inval. [nom. nud. et in sched., MA 112556!].

= *V. officinalis* var. *uniracemosa* Zubía, nom. inval. [nom. nud. et in sched. MA 152074!].

= *V. mas* Garsault, *Descr. Vertus Pl.* 4: 357, pl. 616. 1767, nom. inval. [Appendix VI I.C.B.N. Vienna (Opera utique opressa)].

= *V. repens* Gilib., *Fl. Lit. Inch.* 1: 108. 1782, nom. inval. [Appendix VI I.C.B.N. Vienna (Opera utique opressa)].

= *V. spadana* Lej., *Fl. Spa* 1: 22. 1811 (? no authentic material located) ≡ *V. officinalis* var. *spadana* (Lej.) Dumort., *Fl. Belg.* 36. 1827 (? no authentic material located).

= *V. hirsuta* Hopkirk, *Fl. Glott.* 9. 1813 (? no authentic material located); ≡ *V. setigera* D. Don, *Mem. Wern. Hist. Nat. Soc.* 3: 297. 1821 (? no authentic material located).

= *V. acutiflora* Lapeyr. ex Roem. & Schult., *Syst. Veg.* 1: 112. 1817 (? no authentic material located).

= *V. officinalis* var. *acutifolia* Lapeyr., *Suppl. Hist. Pl. Pyren.* 4. 1818 (? no authentic material located).

= *V. officinalis* var. *latifolia* Lapeyr., *Suppl. Hist. Pl. Pyren.* 5. 1818 (? no authentic material located).

= *V. muelleriana* Vest. ex Schult., *Mant.* 1 [2, 3] 1: 107. 1822 [‘mülleriana’] (? no authentic material located).

= *V. officinalis* var. *multicaulis* Wallr., *Sched. Crit.* 1: 22. 1822 (? no authentic material located).

= *V. officinalis* var. *sylvestris* Wallr., *Sched. Crit.* 1: 22. 1822 (? no authentic material located).

= *V. officinalis* var. *caespitosa* Wallr., *Sched. Crit.* 1: 23. 1822 (? no authentic material located).

= *V. monstrosa* Opiz ex Schult., *Mant.* 1, *Add.* 2: 229. 1822 (? no authentic material located).

= *V. plena* Opiz ex Schult., *Mant.* 1, *Add.* 2: 229. 1822 (? no authentic material located).

= *V.* [unranked] *guentheri* Opiz, *Naturalientausch:* 111. 1825, nom. nud. [‘güntheri’] (? no authentic material located).

= *V.* [unranked] *lanceolata* Opiz, *Naturalientausch:* 111. 1825, nom. nud. (? no authentic material located).

= *V. officinalis* var. *vulgaris* Opiz, *Naturalientausch:* 111. 1825 (? no authentic material located).

= *V. officinalis* var. *albiflora* G. Don, *Gen. Hist.* 4: 571. 1838 (? no authentic material located).

= *V. officinalis* var. *variegata* G. Don, *Gen. Hist.* 4: 571. 1838 (? no authentic material located).

= *V. officinalis* var. *luxurians* Walp., *Repert. Bot. Syst.* 3: 34. 1844 (? no authentic material located).

= *V. officinalis* var. *pusilla* Walp., *Repert. Bot. Syst.* 3: 34. 1844 (? no authentic material located).

= *V. officinalis* var. *minor* Benth. in DC., *Prodr.* 10: 472. 1846 (? no authentic material located).

= *V. officinalis* var. *erecta* Rabenh., *Bot. Centralbl.* 1846: 192. 1846 (? no authentic material located).

= *V. officinalis* var. *subrotunda* Peterm., *Anal. Pfl.-Schlüss.* 318. 1846 (? no authentic material located).

= *V. depressa* Schur, *Enum. Pl. Transsilv.* 495. 1866, nom. inval. (pro syn., art. 34.1 I.C.B.N. Vienna).

= *V. officinalis* var. *subarctica* Schur, *Enum. Pl. Transsilv.* 495. 1866.

= *V. subarctica* Schur, *Enum. Pl. Transsilv.* 495. 1866, nom. inval. (pro syn., art. 34.1 I.C.B.N. Vienna).

= *V. officinalis* var. *glabrescens* Bolle, *Verh. Bot. Vereins Prov. Brandenburg* 7: 25. 1867.

= *V. officinalis* var. *decolorans* Lange, *Bot. Tidsskr., ser.* 3, 2: 233. 1878 (? no authentic material located).

= *V. officinalis* var. *alpestris* Celak., *Prodr. Fl. Bohem.* 4. 1881 (? no authentic material located); ≡ *V. officinalis* ssp. *alpestris* (Celak.) Holub, *Folia Geobot. Phytotax.* 5: 439. 1970 (? no authentic material located).

= *V. talenceana* Gand., *Fl. Eur.* 18: 203. 1889, nom. inval. [Appendix VI I.C.B.N. Vienna (Opera utique opressa)].

= *V. talenceana* Gand., *Fl. Eur.* 18: 203. 1889, nom. inval. [Appendix VI I.C.B.N. Vienna (Opera utique opressa)].

- = *V. officinalis* var. *cyanea* Richen, *Öst. Bot. Z.* 47: 248. 1897 (? no authentic material located).  
 = *V. officinalis* var. *glabrescens* Merino, *Fl. Galicia* 2: 108. 1906, nom. illeg., non Bolle, *Verh. Bot. Vereins Prov. Brandenburg* 7: 25. 1867.  
 = *V. carquejana* Samp., *Ann. Sci. Nat. (Oporto)* 10: 47. 1906, basionym; ≡ *V. officinalis* var. *carquejana* (Samp.) Cout., *Fl. Portugal* ed. 2: 663. 1939.  
 = *V. officinalis* var. *montaniformis* Murr, *Jahresbericht des Landesmuseumsvereins für Vorarlberg* 50: 27. 1914 (? no authentic material located).  
 = *V. vadiniensis* R. Alonso, Lence, López Pach., Puente & Penas, *Bot. J. Linn. Soc.* 141: 119. 2003 ['vadiniense'].  
 – *V. tournefortii* auct. non F. W. Schmidt, *Fl. Boëm.* 1: 7. 1793.  
 – *V. officinalis* var. *tournefortii* auct. non Rchb., *Icon. Fl. Germ. Helv.* 20: 49. 1862.

#### Types

*V. officinalis* L., *Sp. Pl.* 11. 1753. *Lectotype* (designated by D. Sutton in Jarvis *et al.*, 1993: 98): Herb. Clifford 8, *Veronica* 4 (BM)!

*V. carquejana* Samp., *Ann. Sci. Nat. (Oporto)* 10: 47. 1906; ≡ *V. officinalis* var. *carquejana* (Samp.) Cout., *Fl. Portugal* ed. 2: 663. 1939. *Lectotype* (designated here): Portugal, Serra da Estrêlla, Lagoa Comprida, 09.ix.1884, *J. Tavares* (PO 6971!) (Fig. 17).

*V. vadiniensis* R. Alonso, Lence, López Pach., Puente & Penas, *Bot. J. Linn. Soc.* 141: 119. 2003. *Holotype*: Spain, León: Subida al Pico Murcia, proximidades de Las Peñas Zahurdias (30TUN5361), 1940 m, pastizal en pizarras, 29.viii.1997, *R. Alonso* (LEB 68182) (photo!).

#### Description

Perennial herb, with subliguous and frequently branched base. Stems decumbent to ascendent; 10–40 (–50) cm; usually with dense indumentum of long eglandular hairs 0.8–1.2 mm, rarely a little hairy or glabrous. Leaf lamina (8–) 20–35 (–50) mm × (3–) 10–20 (–30) mm; ovate, ovate-oblong, ovate or obovate; attenuate to cuneate or obtuse at the base; dentate, denticulate or serrulate margin; indumentum of variable density with hairs similar to those described for the stem although shorter 0.5–0.8 (–1) mm, rarely subglabrous; sometimes slightly coriaceous; petioles (1–) 2–5 (–6) mm long. Inflorescence one to four (to eight) axilar racemes, ten to 35 (–40) flowers; peduncles 2–6 cm long, indumentum as described for stem, plus additional short, incurvate and appressed eglandular hairs; inflorescence axis with indumentum as described for peduncles, and frequently with additional (0.2–) 0.4–0.5 mm glandular hairs, sometimes only eglandular indumentum. Bracts (1.5–) 3–4 (–5) mm, usually longer than

pedicels; linear-lanceolate or narrowly ovate; indumentum as described for caulinar leaves, occasionally with sparse glandular trichomes to the base; erect pedicels (0.5–) 1–2 (–3) mm long. Calyx with four (rare five) sepals, 2–3.5 (–4) mm long, lanceolate-linear to narrowly oval-oblong; with glandular trichomes that usually predominate over eglandular ones, exceptionally some eglandular hairs on the midrib and margin. Corolla 6–8 mm in diameter, pale blue-lilac to pale pink, with darker veins, rarely white with pink veins. Style 2.5–3.5 (–4) mm long. Capsule 3–5 × 4–5 mm; laterally compressed; triangulate-obdeltate to obcordate; frequently cuneate at the base, sometimes rounded base; usually truncate at the apex, without sinus or not very evident, rarely clearly emarginated; commonly glandulose-pubescent, rarely glabrous. Seeds 0.8–1.7 × 0.3–1.3 mm; *c.* 15–20 per capsule; elliptic, ovate or obovate, brown to yellow.

#### Habitat

In forests, meadows, pastures, scrubs, etc. mainly on siliceous substrates, although it also grows on limestone; 100–2400 m.

#### Phenology

Flowering (April) June–July (August).

#### Distribution

Circumboreal taxon; almost throughout Europe, Anatolia, Caucasus, Transcaucasia, north Iran and also in the Azores and North America.

#### Notes

Sampaio (1906) recognized, at the species level, the individuals showing a combination of characters used recently by Alonso *et al.* (2003) to describe their *V. vadiniensis* (i.e. plant small; leaves crowded, subcoriaceous, glabrous or with some scarce eglandular hairs; inflorescence dense; calyx with four or five sepals, capsule broader than long, obcordate, deeply notched and glabrous or with scarce indumentum). Coutinho (1939) accepted only a varietal level for such specimens. Walters & Webb (1972) emphasized the need for further investigation into variants that had already been reported from north-west and north-central Europe.

In this situation, we stress the careful study of the variation in *V. officinalis* through the mountains of the western Mediterranean (Martínez-Ortega, 1999; present study) and have checked that – regarding the set of previously mentioned morphological characters – such 'mountain variants' intergrade along the altitudinal gradient in the Iberian mountains, but also along the latitudinal gradient in Europe. Additionally, many of those characters, i.e. plant/leaf size, leaf





Figure 17. Type material of *Veronica caquejana* Samp.

shape and pilosity, show a clinal variation connected with continentality, environmental humidity, and shade (sun exposure), as demonstrated by Böcher (1944).

The variations in other characters relevant for the taxonomy of *Veronica* do not seem to support a taxonomical recognition for such variants. The pollen grains are not different in size, shape or exine ornamentation. We counted chromosomes in six individuals showing the morphology of the 'mountain variants' and observed that five of them were tetraploid and one was a diploid, so both ploidy levels are found within that morphological variant. Regarding seeds, no difference in size, colour, or seed coat ultrastructure (Figs 4, 5) was found. Consequently, from our point of view, only at the most a varietal rank would be acceptable, in this case *V. officinalis* var. *carquejana* (Samp.) Cout. being the priority combination.

#### *Selected specimens*

ALBANIA: In pratis ad Cafa? m. Sosit, distr. Scutari?, 25.vii.1987, *Baldacci* (BM); Above Mskopolë, vii.1933, *Alston & Sandwith* (BM); AUSTRIA: Kärnten, Mühlen hinter dem Hörfeld, 26.viii.1981, *Barnieske, Noster & Dircher* (B); Flor. Salisburg., 13.ix.1978, *Toepffer* (B). BULGARIA: Mte. Vitosa, 3.viii.1980, *Kuzmanov* (K). SPAIN: Álava, Elvillar, 17.v.1982, *Uribe-Etxebarria* (VIT 37097); Asturias, Puerto de Leitariegos, 30.vii.1978, *Casaseca, Fdez. Díez, Amich, Rico & Sánchez* (SALA 21318); Asturias, Covadonga, 16.viii.1952, *Guinea* (K)\*; Ávila, Tormellas, 2.vii.1995, *Martín Ballesteros* (SALA 93415); Barcelona, Massif du Tibidabo, 18.vii.1918, *Joseph, Lucien & Sennen* (MA 112556); Burgos, de Rábanos de Villamudria a Haedillo, 24.vii.1995, *Martínez-Ortega MO 94* (SALA 93408) (SE); Burgos, Pineda de la Sierra, 10.vi.1995, *Martínez-Ortega MO 42* (SALA 93417) (SE); Burgos, Valmala, 19.viii.1995, *Martínez-Ortega MO 106* (SALA 93410) (PSEM, POM); Cáceres, La Malena, 22.v.1982, *Valdés Franzi* (SALAF 12374); Cantabria, Hermandad de Campoo de Suso, 11.vii.1996, *Martínez-Ortega MO 180* (SALA 93399) (CR)\*; Cantabria, La Vega de Liébana, 12.vii.1996, *Martínez-Ortega MO 189* (SALA 93397) (CR)\*; Cantabria, Montes de Soba, Cordillera Cantábrica (no date), *Salcedo* (MA 112555)\*; Cantabria, La Vega de Liébana, Puerto de San Glorio, 23.viii.1995, *Martínez-Ortega MO 108* (SALA 93403) (SE)\*; Cantabria, Hermandad de Campoo de Suso, Pico Tres Mares, 1.viii.2004, *Rico ER 7872* (SALA 110614)\* (CR); Castellón, Vistabella, 21.vi.1986, *Fabregat* (VAB 885868); La Coruña, Sigüeiro, 25.vi.1966, *Álvarez* (SALA 3422); Cuenca, Talayuelas, 20.vii.1976, *Mateo* (VAB 904366); Girona, Cerdagne, 18.vii.1922, *Sennen* (BC 8320024); Guadalajara Cantalojas, Parque Natural del Hayedo de Tejada Negra, 2.vii.1995, *Martínez-Ortega MO 70* (SALA 93439); Guipúzcoa, Sierra de Aitzgorri, 2.vii.1977, *Uribe-Etxebarria* (VIT 37106); Huelva, Ortigosa, 6.vii.1905, *Caroli Pau herbarium hispanicum* (MA 112552); Huesca, Subida a la Peña Montañesa, 9.viii.1996, *Martínez-Ortega MO 221*, *Muñoz Centeno & González Rivera* (SALA 93386); Jaén, Nava del Espino, 27.vii.1985, *Valle et al.* (COI); León, Maraña, 13.vii.1996, *Martínez-Ortega MO 197* (SALA 93395)\*; León, Boca de Huérgano, 12.vii.1996, *Martínez-Ortega MO 196* (SALA 93396)\*; León, Puerto de San Glorio, 10.viii.1988, *Mateo* (VAB883776)\*; Lérida, Bossost, 8.vii.1992, *Aedo CA 3121 et al.* (MA 511725); Lugo, Cervantes, 26.viii.1992, *Navarro CN 972 & Monasterio-Huelin* (MA 530781); Madrid, Miraflores de la Sierra, 29.ix.1988, *Izuzquiza 1688AI, Corregidor, Dorda, Jiménez, López, Ruiz & Villanueva* (MA 452035); Navarra, subida al puerto de Larrau, 13.vii.1994, *Martínez-Ortega MO 9* (SALA 93437) (POM); Orense, Serra do Invernadeiro, 21.vii.1973, *Castroviejo* (SALA 6985); Palencia, Velilla de Río Carrión, 10.vii.1996, *Martínez-Ortega MO 178* (SALA 93400)\*; Palencia, De Cardaño de Arriba a la laguna de las Lomas, 11.vii.1995, *Rico CC 84* (SALA 93446)\*; Palencia, Brañosera, 11.vii.1996, *Martínez-Ortega MO 187* (SALA 93398)\*; Palencia, Vidrieros, 6.viii.1994, *Martínez-Ortega MO 33* (SALA 93402)\*; Palencia, Vidrieros, 6.viii.1994, *Martínez-Ortega MO 32* SALA 93401\*; Palencia, Brañosera, 11.viii.1994, *Martínez-Ortega MO 36* (SALA 93406)\*; Pontevedra, Forcarei, 29.v.1994, *Amigo & Romero* (FCO 21476); La Rioja, Canales de la Sierra, 3.vii.1996, *Martínez-Ortega MO 162* (SALA 93391)\*; La Rioja, Canales de la Sierra, 3.vii.1996, *Martínez-Ortega MO 160* (SALA 93392)\*; La Rioja, Canales de la Sierra, 3.vii.1996, *Martínez-Ortega MO 163* (SALA 93393) (CR)\*; La Rioja, Canales de la Sierra, 23.vii.1995, *Martínez-Ortega MO 90* (SALA 93405)\*; La Rioja, Canales de la Sierra, 21.viii.1995, *Martínez-Ortega MO 109* (SALA 93404)\*; Salamanca, Entre Navacarros y Candelario, 5.vii.1994, *Martínez-Ortega MO 53* (SALA 93432); Salamanca, Candelario, 10.vii.2004, *Delgado LD 923 & Santos Vicente* (SALA 110617); Segovia, Riofrío de Rianza, 1.vii.1995, *Martínez-Ortega MO 66* (SALA 93441); Soria, Montenegro de Cameros, 24.vii.1994, *Martínez-Ortega MO 27* (SALA 93430); Tarragona, Tortosa, 18.vi.1992, *Mateo 6383* (VAB 922165); Teruel, Valdelinares, 12.vii.1973, *Montserrat & Vilar* (JACA 349373); Vizcaya, Saibi, 18.vii.1991, *Ataucha* (COA 16278); Zamora, San Martín de Castañeda, 11.vii.1979, *Ladero, Cantó del Águila & Sánchez Mata* (MA 240495); Zaragoza, Tarazona, 17.vi.1994, *Mercadal, Benito & Martínez* (VAB960025); FRANCE: Corsica, Ghisoni, de la Bocca de Verde al monte Grosso, 21.vii.1998, *Martínez-Ortega MO 453* (SALA 95204); Faux-la-Montagne, dép. de la Creuse,



19.vi.1977, *Lugagne 7669* (MA 303806); FINLAND: Varsinais-Suomi (Ab), Korppoo, 12.vii.1962, *Kärenlampi* (SALA 1418) (POM); GREECE: Macedonia or prov. Dhrama, 22.viii.1978, *Greuter* (B); Nom. Kastorias, Vitsi, *Farsakoglou*, 9.vii.1981, *Franzén, Papanicolau & Strid* (B); HUNGARY: Hungaria borealis, in sabulosis prope vicum Valkó, 9.v.1970, *Vasak* (PR); Hungaria borealis, montes Bükk, 4.ix.1970, *Vasak* (PR); ICELAND: Pingvallir, 13.vii.1931, *Meinertzhagen & Clay* (BM); ITALY: Bolzano, Alpes Dolomitas, 20.vii.1990, *Giráldez et al. AI 2209* (MA 487622) (POM); Aosta-Tal, Gressoney, 19.ix.1983, *Hempel & Royle* (B); PORTUGAL: Arganil, Benfeita, 18.vii.1982, *Marques* (MA 398541); Beira Alta, Guarda, 15.vii.2004, *Delgado LD 926 & Martínez-Ortega* (SALA 110615) (CR); Beira Alta, Guarda, 12.vi.2004, *Delgado, Muñoz-Centeno & Martínez-Ortega MO 1753* (SALA 110616) (CR); UNITED KINGDOM: Surrey, Epsom Common, 5.vii.1929, *Britton* (RNG); SWITZERLAND: Flor, Helvet., vii.1887, *Beyer* (B); Vaud, La Dôle, 27.vii.1969, *Quenat* (G).

*Veronica allionii* Vill., *Prosp. Hist. Pl. Dauphiné*: 20. 1779, nom. cons. prop. (Martínez-Ortega, Herrero & Muñoz-Centeno, 2006 and see here notes to *V. allionii*).

≡ *V. pyrenaica* All., *Fl. Pedem.* 1: 73, tab. 46, fig. 3. 1785, nom. illeg.; ≡ *V. allionii* var. *allionii* Vill., *Hist. Pl. Dauphiné* 2: 8. 1787.

#### Type

*V. allionii* Vill., *Prosp. Hist. Pl. Dauphiné*: 20. 1779, nom. cons. prop. *Neotype* (selected by Bocquet *et al. Bauhinia* 3: 238. 1967; see also Martínez-Ortega *et al.*, 2006): France, Mt. Cenis, *Villars* (GRM) (photo!), typ. cons. prop.

#### Description

Perennial herb, with subligneous (sometimes ligneous) and frequently branched base. Stems decumbent to ascendent, usually rooting in its creeping part; 5–15 (–30) cm; glabrous or subglabrous. Leaf lamina (7–) 8–15 (–20) × (3–) 5–10 (–13) mm; subcoriaceous; frequently folded on both sides along the midrib; elliptic or ovate-elliptic to suborbiculate; slightly attenuate at the base; entire denticulate or crenulate margin; glabrous or subglabrous, except for some short (< 0.1–) 0.1–0.2 (–0.3) mm, incurvate, antrorse and appressed eglandular hairs; petioles short 2–3 mm long. Inflorescence one to three (to six) axilar racemes, 30–60 flowers; peduncles 2.5–3 cm long, puberulous, eglandular hairs as described for leaf margin, plus scattered glandular ones 0.1–0.3 mm; inflorescence axis with indumentum as described for peduncles, but frequently with glandular hairs not so

sparsely arranged. Bracts 3–4 mm, usually longer than pedicels; linear-lanceolate or narrowly elliptic; indumentum as described for inflorescence axis, clearly glandular; erect pedicels (0.5–) 1–1.5 (–2) mm long. Calyx with five (sometimes four and exceptionally six) subequal sepals, 2–3 (–4) mm long, lanceolate to narrowly elliptic; indumentum as described for inflorescence axis. Corolla 7–9 (–12) mm in diameter, intense blue to violet. Style 3–6 mm long. Capsule (1.5–) 2–3 (–4) × (1–) 1.5–2.5 (–3.5) mm; laterally compressed; obovate, obcordate or suborbiculate; notched; with very short eglandular and glandular hairs. Seeds 0.4–1 × 0.2–0.8 mm; *c.* 12–18 (–20) per capsule; elliptic, ovate or obovate, brown to yellow.

#### Habitat

In subalpine and alpine dry rocky pastures; 1500–2900 m.

#### Phenology

Flowering July–August (September).

#### Distribution

Endemic to south-western Alps.

#### Notes

The nomenclatural treatment here proposed is valid provided that the proposal in Martínez-Ortega *et al.* (2006) is accepted.

#### Selected specimens

FRANCE: Dauphiné, Le Lautaret, 14.vii.1929, *Theel* (B); Col de Malrif, Delphinatus, viii.1860, *Cosson* (BM); Col de Vars, hautes Alpes, 10.viii.1841, *Grenier* (K); Flora delphinensis, prairies sur Lautaret, vii.1886, *Krummel* (K); Savoie, Val de la Sassièrre, 29.vii.1911, *Groves* (BM); Mont Guillaume Embrun; Iter alpinum delphinense, vii.1829, *Sieber* (K); Belvedere, Cirque du Mt. Viso, 25.vii.1966, *Weibel* (G); Galibier, Lautaret, 22.vii.1989, *Aeschmann & Palese 4745* (G) (PSEM) (POM); Hautes Alpes, vii.1939, *D'alleizette* (PR); San Matino de Lantosca, Maritime Alp., 24.vii.1880, *Packe* (K); Monte Bego, maritime Alps, 22.viii.1882, *Lacaita* (BM); Lautaret, Hautes Alpes, 17.vii.1897, *Bernoulli* (B); Lac d'Allos, basses Alpes, 6.viii.1964, *Gavelle* (MA 182267); De la Grave à Peyro d'Amont, 13.viii.1863, *Borel* (K); Lautaret, prairies de l'Hospice, 14.vii.1869, *Reverchon* (K) (SE); Gondran, hautes Alpes, 27.viii.1882, *Lannes* (PR); Briançon, hautes Alpes, 12.vii.1925, *Alleizette* (BM); Mt. Cenis, vii.1907, *Bruneau* (MA 112580); Le Brune, hautes Alpes, 5.viii.1975, *Geissler* (G); ITALY: Salice d'Ulacio, Italian Alps, viii.1949, *Galiano* (MA 182275); Madonna de la Finestra Alpes Maritim, 13.vii.1889, *Bernoulli* (B); Val Casterino di Tenda, vii.1897, *Bicknell* (B, PR, BM); Pimont., Lago Tre Colpas,



17.vii.1931, *Fiedler* (B); Flor. Pedem., Alpes Maritim, vii.1884, *Beyer* (B); Fl. Pedem. Alpes Cottiae, 26.vii.1894, *Beyer* (B); Fl. Pedem., Alp. Cottiae, 24.vii.1892, *Beyer* (B, BM); Alpes de Salse, vii.1863, *Rostan* (B, K); Cuneo, Crissolo, 18.viii.1921, *Mattirolo* (K); Liguria, Alp. Maritim., 22.vii.1905, *Biekneli* & *Pollini* (PR).

*Veronica* × *tournefortii* F. W. Schmidt, *Fl. Boëm.* 1: 7. 1793, pro sp. [*V. allionii* × *V. officinalis*].  
 = *V. allionii* var. *tournefortii* Vill., *Hist. Pl. Dauphiné* 2: 9. 1787, nom inval. (art. 26.2 I.C.B.N. Vienna); = *V. allionii* var. *vestita* Gren. & Godr., *Fl. France* 2 (2): 591, 1852; = *V. officinalis* var. *tournefortii* (F. W. Schmidt) Dumort., *Fl. Belg.* 36. 1815.  
 = *V. dubia* DC. in Lam. & DC., *Fl. Franc.* Ed. 3, 3: 462. 1805 (? no authentic material seen).

#### Type

*V.* × *tournefortii* F. W. Schmidt, *Fl. Boëm.* 1: 7, tab. 15. 1793. *Neotype* (selected by Bocquet *et al.* *Bauhinia* 3: 238. 1967): a sheet annotated *Veronica tournefortii* var. *Ver. allionii* Vill. *Fl. Delph.* 2: 8 Dedit Villars (G; Ventenat's collections) (not seen).

#### Notes

Unfortunately, we have not been able to study material belonging to this taxon ourselves and therefore we cannot give a detailed description. According to Bocquet *et al.* (1967), the morphology of these plants is intermediate between that of the parental species. They are perennial herbs with radican and pubescent stems, covered with hairs shorter and more sparsely arranged than in *V. officinalis*; leaves slightly smaller than in *V. officinalis*, subcoriaceous, ovate-oblong, shallowly dentate, with hairs scattered on both faces; inflorescence, 25–30 flowers; pedicels, bracts and sepals with glandular hairs; flowers blue or violet, but not so intensely coloured as in *V. allionii*; corolla size intermediate between that of the parental species; usually the capsule is not developed. The hybrid grows in clearings of larch forests in the French Maritime Alps and Italian continental Alps.

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