

A taxonomic revision of the *Campanula lusitanica* complex (Campanulaceae) in the Western Mediterranean region

by

Jara Cano-Maqueda & Salvador Talavera

Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, E-41080 Sevilla, Spain. Corresponding author: stalavera@us.es

Abstract

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The systematics of the annual species of the *Campanula lusitanica* complex in the Western Mediterranean is reviewed using ITS sequences, karyology and morphology of all species of the complex. The information provided by these three sources is consistent, and the species are reorganized into two groups with the rank of section: *Campanula* sect. *Rapunculus* Boiss. and *Campanula* sect. *Decumbentes*, the latter described as new in this work. These sections comprise two well-defined subclades in the phylogenetic analyses. Sect. *Rapunculus* is composed, in the W Mediterranean region, by *C. lusitanica* L. and *C. matritensis* A. DC., both with $2n = 18$ chromosomes, and *C. cabezudo* Cano-Maqueda & Talavera, *C. specularioides* Coss., *C. transtaganana* R. Fern., and *C. broussonetiana* Schult., all with $2n = 20$ chromosomes. In the Iberian Peninsula, Sect. *Decumbentes* comprises two endemic species, *C. decumbens* A. DC. with $2n = 32$ chromosomes and *C. dieckii* Lange with $2n = 28$ chromosomes. In *C. decumbens* a new subspecies is described: *C. decumbens* subsp. *baetica* Cano-Maqueda & Talavera, which occurs in the Guadalquivir valley. In the formal systematic part we provide a key to identify these annual species of the Western Mediterranean, with a description and typification, photographs of flowers and fruits, distribution maps, and comments on the habitat for each taxon.

Keywords: phylogeny, rDNA ITS, karyology, systematic, typification.

Introduction

The genus *Campanula* comprises about 420 species distributed mainly in temperate regions of the Northern Hemisphere (Lammers, 2007a, b). They are usually perennial herbs, although some are shrubby, and

Resumen

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En este trabajo se revisa la sistemática de las especies anuales del complejo *Campanula lusitanica* en el occidente del Mediterráneo usando secuencias ITS, cariólogía y análisis de los caracteres morfológicos de todas las especies del complejo. La información proporcionada por estas tres fuentes de caracteres es congruente, y las distintas especies se reorganizan en dos grupos principales con categoría de sección, que se corresponden con los dos subclados bien definidos: *Campanula* sect. *Rapunculus* Boiss. y *Campanula* sect. *Decumbentes*, descrita como nueva en este trabajo. En el Mediterráneo occidental, la sect. *Rapunculus* está formada por las siguientes especies anuales: *C. lusitanica* L. y *C. matritensis* A. DC., con $2n = 18$ cromosomas, y *C. cabezudo* Cano-Maqueda & Talavera, *C. specularioides* Coss., *C. transtaganana* R. Fern. y *C. broussonetiana* Schult., con $2n = 20$ cromosomas. En la Península Ibérica la sect. *Decumbentes* está representada por *C. decumbens* A. DC., con $2n = 32$ cromosomas, y *C. dieckii* Lange, con $2n = 28$ cromosomas, ambas endémicas de la Península Ibérica; de *C. decumbens* se describe una subespecie nueva: *C. decumbens* subsp. *baetica* Cano-Maqueda & Talavera, taxon del valle del Guadalquivir muy bien diferenciado morfológicamente de la subsp. *decumbens*. En la parte sistemática se proporciona una clave para la identificación de estas especies anuales del oeste del Mediterráneo, así como una descripción y tipificación, fotografías de las flores y frutos, mapas de distribución, y aspectos de la ecología para cada uno de los táxones.

Palabras clave: filogenia, secuencias ITS, cariólogía, sistemática, tipificación.

there are also some annual herbs, the latter mainly in the Mediterranean. This genus has a high morphological complexity that is reflected in the different classifications that have been proposed.

Based mainly on the morphology of the calyx, A. de

Candolle (1830, 1838) divided the genus *Campanula* into two sections: sect. *Medium* A. DC., with calycine appendages, and sect. *Eucodon* A. DC., without them. This classification was followed by most nineteenth century authors (e.g. Endlicher, 1838; Willkomm, 1868; Bentham & Hooker, 1876; Rouy, 1908). In contrast, Boissier (1875) divided the genus into two sections based on fruit dehiscence: sect. *Medium* A. DC., with capsules opening by basal pores or valves, and sect. *Rapunculus* Boiss., with apical or middle position pores or valves. This classification was followed with some modifications by Fedorov (1957, 1976).

Perhaps the taxonomic treatment with most insight was that by Damboldt (1976) during the preparation of the Flora of Turkey. He divided the genus *Campanula* into six subgenera: *Campanula*, *Megalocalyx* Damboldt, *Sicyocodon* (Feer) Damboldt, *Roucela* (Dumort.) Damboldt, *Brachycodonia* (Fedorov) Damboldt and *Rapunculus* (Boiss.) Kharadze. The subgenus *Campanula* includes plants with 3 or 5 stigmas, with or without calycine appendages, and with the capsules opening by basal or middle position pores, or indehiscent. This is the most complex subgenus, with 12-15 recognized sections and it contains most of the species of the genus. According to Sáez & Aldasoro (2003), subgenera *Megalocalyx* and *Sicyocodon* are annual herbs with flowers with calycine appendages and with capsules opening by basal valves; the two subgenera differ in the size of style: very long (exceeding 35 mm) in the subgen. *Sicyocodon*, and short (less than 15 mm) in the subgen. *Megalocalyx*. The around 15 species of these two subgenera are distributed in the Mediterranean Basin, SW Asia and Macaronesia. The subgenus *Roucela* comprises annual plants, with flowers without calycine appendages and capsules opening by basal valves; it consists of 5 species distributed throughout the E Mediterranean and SW Asia, with the exception of *C. erinus* L. which has a wider distribution. The subgenus *Brachycodonia* comprises only *C. fastigiata* Dufour, an annual plant with axillary inconspicuous flowers, without calycine appendages, and with capsules opening by three apical valves; *C. fastigiata* occurs on gypsum soils in Spain, N Africa, C Asia and Transcaucasia.

The subgenus *Rapunculus* includes annual and perennial plants, without calycine appendages, with a large campanulate or infundibuliform corolla, and with capsules opening by apical or middle position pores. Damboldt (1976, 1978) divided this subgenus in three sections: *Pterophyllum* Damboldt, *Alaria* Damboldt and *Rapunculus*. Sect. *Pterophyllum* includes three species: *C. primulifolia* Brot. (Iberian Peninsula), *C. alata* Desf. (Algeria and Morocco), and

C. peregrina L. (E Mediterranean, including Cyprus, Lebanon and SW Turkey and S Anatolia); they are hispid perennial plants with large infundibuliform flowers, arranged in spikes or panicles, with capsules opening by three pores of middle position, and with winged seeds.

Sect. *Alaria* contains a single species, *C. pterocaula* Hausskn., endemic to N and C Anatolia (Turkey); it is a biennial glabrous plant, with winged stems, large flowers arranged in spiciform inflorescences, and capsules opening by apical pores.

Sect. *Rapunculus* contains around 50 species distributed mainly in the Mediterranean region; it comprises perennial, biennial or annual plants, glabrous or tomentose, with wingless stems, the inflorescence a panicle, or sometimes spiciform, the capsules opening by apical or middle position pores, and wingless seeds.

Recent molecular phylogenies (Eddie & al., 2003; Park & al., 2006; Roquet & al., 2008, 2009; Cellinese & al., 2009; Borsch & al., 2009; Haberle & al., 2009; Stefanović & Lakušić, 2009) have revealed that the genus *Campanula* is paraphyletic. Studies by Roquet & al. (2008) using ITS sequences, show that *Campanula* sect. *Pterophyllum* together with the genera *Musschia* Dumort. and *Gadellia* Schulkina form a clade (*Musschia* clade) that is sister to the *Campanula* core.

The *Campanula* core consists of two subclades: one formed by the subgenera *Campanula*, *Megalocalyx* and *Roucela*, together with other genera of Campanulaceae; and a second subclade comprising subgenus *Rapunculus* (sections *Rapunculus* and *Alaria*) and subgenus *Brachycodonia*, again with some other genera of Campanulaceae.

The annual species of sect. *Rapunculus* sensu Damboldt have two centers of diversity: the Iberian Peninsula and W Morocco, and the E Mediterranean (Greece and Turkey). The annual species of the Iberian Peninsula (which include many species names, viz. *C. lusitanica* L., *C. broussonetiana* Schult., *C. transtagana* R. Fern., *C. matritensis* A. DC., *C. decumbens* A. DC., *C. specularioides* Coss. *C. cabezudo* Cano-Maqueda & Talavera and *C. diekii* Lange) have received diverse treatments in recent taxonomic studies, i.e. as varieties of *Campanula patula* L. (Pau, 1921; Cuatrecasas, 1929), as subspecies or varieties of *C. lusitanica* L. (Pau, 1924; Sáez & Aldasoro, 2001), or as varieties of *C. decumbens* A. DC. (López-González, 1979-1980). In all cases most taxa have been relegated to infraspecific status.

However, our detailed morpho-geographical analysis of the exsiccata available for this group (which we call the *Campanula lusitanica* complex) lead us to con-

clude that not only are many of the species described by various authors valid, but that several new taxa can be recognised. Moreover, our analyses (Cano-Maque-da & al., 2008 and the present study) based on combined analysis of ITS sequences and *trnT-L* using samples from most of the annual species of the Western Mediterranean area not only support recognition of these species, but have also revealed that the annual species of sect. *Rapunculus* sensu Damboldt comprise a polyphyletic assemblage.

In this study we present a formal taxonomic revision of the *Campanula lusitanica* complex from the Iberian Peninsula and Morocco, based on our studies of exsiccata, karyological parameters, and molecular markers. And using information provided by the nrDNA ITS for a large number of *Campanula* species and allied taxa we have also attempted to place the species of *Campanula* sect. *Rapunculus* sensu Damboldt within the context of the ongoing molecular systematics of the genus *Campanula*.

Materials and methods

Molecular Phylogeny

Fresh material and herbarium vouchers of seven samples of the *Campanula lusitanica* complex (four of *C. lusitanica* s.str., one of *C. decumbens*, one of *C. sparsa* Friv., and one sample of *C. ramosissima* Sibth. & Sm.), two samples of *C. primulifolia* and one of *Walbenbergia bederacea* L., were sequenced for this molecular survey. Additionally, 100 sequences were taken from GenBank (Eddie & al., 2003; Susanna & al., 2006; Roquet & al., 2008, 2009; Cano-Maque-da & al., 2008; Park & al., 2006). The list of taxa, with locality, herbarium vouchers or collector's numbers, authorities and GenBank accession numbers is shown in the Appendix I.

Genomic DNA was extracted from silica-gel-dried leaves collected in the field and from herbarium material using the DNeasy Plant Mini Kit (Qiagen) following the protocols provided by the manufacturer.

Amplification of the ribosomal ITS region (ITS1-5.8S-ITS2) was performed in 25 μ L reaction volume with 22.5 μ L Thermo-Start ReddyMix Master Mix, 0.5 μ L of each primer, 1 μ L of DMSO (100%) and 0.5 μ L of DNA. Forward ITS5 and reverse ITS4 primers (White & al., 1990) were used in the amplification and sequencing processes. The polymerase chain reaction (PCR) sequence profile was one cycle of 1 min at 96 °C, followed by 35 amplification cycles of 10 s denaturing step at 96 °C, 5 s annealing at 50 °C, and 3 min elongation step at 60 °C, plus an ending cycle of 8 min at 72 °C.

Amplified products were purified using the QIAquick PCR Purification Kit (Qiagen) according to

the manufacturers protocols. Purified products were sequenced in both directions. The sequence PCR profile was of a time of incubation of 15 min at 37 °C and 15 min at 80 °C.

The direct and reverse sequences of each sample were compared and corrected using the program Geneious 4.8.3, obtaining the respective consensus sequence. Sequences were aligned using the algorithm of the program ClustalX, and then adjusted manually using the options of the program Se-AL v. 1.0 alpha 1 (Rambaud, 1996). Gap indels were coded as binary characters by their presence/absence (0/1 matrix). Only those gaps that were unambiguous and potentially informative (Torrecilla & Catalán, 2002) were added to their correspondent sequence matrix and used for parsimony-based analysis.

Phylogenetic analyses

The phylogenetic analyses were based on parsimony and Bayesian inference searches, which were respectively conducted with PAUP* v. 4.0 beta 10 (Swofford, 2002) and MRBAY ES v. 3.0 (Huelsenbeck & Ronquist, 2002) using *Galactites tomentosa* Moench. (Compositae) to root the trees.

In the parsimony analysis, the data matrix was subjected to two heuristic searches (first search: closest, TBR, MULTIPARS ON; second search: random-order-entry of 10,000 replicates, TBR, MULTIPARS OFF, saving no more than 10 trees of score > 10 per replicate) aimed at finding different putative islands of most-parsimonious trees. Bootstrap support for the best trees found under the parsimony criterion was estimated by heuristic search with 1,000 bootstrap replicates (Felsenstein, 1985) using the TBR and MULTIPARS OFF strategy proposed by DeBry and Olmstead (2000) to reduce the tree-search effort in bootstrap resampling analysis. Initial MaxTrees setting was 300,000 with an auto-increase of 100. Previous to the Bayesian inference search, 24 models of nucleotide substitution were tested for which the optimal model GTR + G + I. The Bayesian analysis was performed through 1,100,000 generations using the Markov chain Monte Carlo (MCMC), sampling trees every 100 generations and burn-in all sampled point from generations previous to convergence to a stable likelihood value (Huelsenbeck & Ronquist, 2002; Leaché & Reeder, 2002). From each search, a 50% majority-rule consensus tree that showed de posterior-probability values of branches was constructed.

Karyological study

Plants or seeds of each taxon of the *Campanula lusitanica* complex sensu Cano-Maque-da & al. (2008),

were collected from natural populations (Table 1) and cultivated in the greenhouses of the University of Seville. Chromosomes were observed from meristematic cells of root tips or meiosis in the anthers of flower buds. The root tips were treated with 8-hidroxi-quinoleine 0,002M for three hours and a half at 4 ° C. Subsequently, roots and flower buds were fixed with Carnoy solution (3:1 ethanol 96%: glacial acetic acid) for a minimum of 24 hours. Staining of chromosomes was performed with-alcoholic-hydrochloric carmine (Snow, 1963). The images were taken with a Leica DC 300 inserted in a Zeiss Axiophot microscope with Plan-apochromatic objective 63/1.4 and an increase of 1.25. Levan & al. (1964) were followed for the morphological terminology and Stebbins (1938) for size terminology of the chromosomes.

Systematic Treatment

A morpho-geographical analysis of herbarium specimens of all relevant taxa associated with the *C. lusitanica* complex was performed, based on the following Herbaria: C, COI, FCO, G, HVR, LISE, LISU, MA, MGC, P, SALA, SALAF, SEV, W. All recognized species and most heterotypic synonyms have been typified. The initials of the provinces of Spain and Portugal which are cited in the description of each taxon follow those used in “Flora iberica”.

Results and discussion

Molecular Phylogeny

The ITS region comprised 726 aligned nucleotide positions of which 469 were variable and 368 were

parsimony informative. The first heuristic search found 101,914,528 equally parsimonious trees that were 2,480 steps long, with a consistency index of 0.353, excluding uninformative characters, and a retention index of 0.748. The second search did not find any other island of most-parsimonious trees, and trees from the first search were used to compute the strict consensus tree. The Bayesian analysis sampled 7,639 trees, which reached a stable likelihood value after burn-in 1,500 trees. The 50% majority-rule consensus tree of all sampled trees showed a topology totally concordant with that recovered from the parsimony analysis. The Bayesian tree was better resolved than the parsimony-based tree, so only the Bayesian tree with both bootstrap and posterior probability support values for branches is shown in Fig. 1.

Topology within the ITS tree is consistent with results obtained in previous phylogenetic studies of the genus *Campanula* and allies (Eddie & al., 2003; Park & al., 2006; Roquet & al., 2008, 2009; Cellinese & al., 2009; Haberle & al., 2009; Stefanović & Lakušić, 2009). These show that the genus is paraphyletic and divided into two major clades, the ‘*Campanula* s.str.’ clade and the ‘*Rapunculus*’ clade, plus two small clades: the ‘*Musschia*’ clade (99% bootstrap support, BS; 100% posterior probability support, PPS), that includes *Musschia* Dumort., *Gadellia* Schulkina, *Campanula peregrina* and *Campanula primulifolia*; and the ‘*Platycodon*’ clade (79%BS; 100%PPS), that includes *Codonopsis* Wall., *Cyananthus* Wall., *Canarina* L. and *Leptocodon* Hook. The genus *Jasione* L. is sister to *Campanula* s. l. The ‘*Campanula* s. str.’ clade has good support (72%BS; 100%PPS) although it

Table 1. Chromosome numbers for annual species of the *Campanula lusitanica* complex in the W Mediterranean area. Origin of material, gametic (*n*) or somatic (*2n*) chromosome number of and authors who have studied the different annual species in this complex.

Taxa	Studied material	<i>n</i>	<i>2n</i>	Authors
<i>C. lusitanica</i>	Rivadavia (Orense, Spain)		18	In this work
	Serra de Lousã (Beira Litoral, Portugal)	9	18	Fernandes (1962)
<i>C. matritensis</i>	Hervás (Cáceres, Spain)		18	Fernández et al. (2001) (as <i>C. lusitanica</i>)
	Hinojos (Huelva, Spain)		18	In this work
	Coimbra (Beira Litoral)	9		Larsen (1954) (as <i>C. loefingii</i>)
<i>C. cabezudoii</i>	Venta de Zafarraya (Granada, Spain)		20	In this work
<i>C. specularioides</i>	Ubrique (Cádiz, Spain)	10		García-Martín & Silvestre (1985)
	Benaocaz (Cádiz, Spain)	10		Gallego (1986)
	Montejaque (Málaga, Spain)		20	In this work
<i>C. transtagana</i>	Valverde (Huelva, Spain)		20	In this work
	Vila Velha de Rodão (Beira Baixa, Portugal)	10	20	Fernandes (1962)
	Don Benito (Badajoz, Spain)	10		Gallego (1986) (as <i>C. lusitanica</i> subsp. <i>transtagana</i>)
<i>C. broussonetiana</i>	Jbel Tazzeke (Taza, Morocco)		20	In this work
<i>C. decumbens</i>	Benaoján (Málaga, Spain)	16		In this work
	Villamartín (Cádiz, Spain)	16		In this work
<i>C. dieckii</i>	Alfarnate (Málaga, Spain)		28	In this work

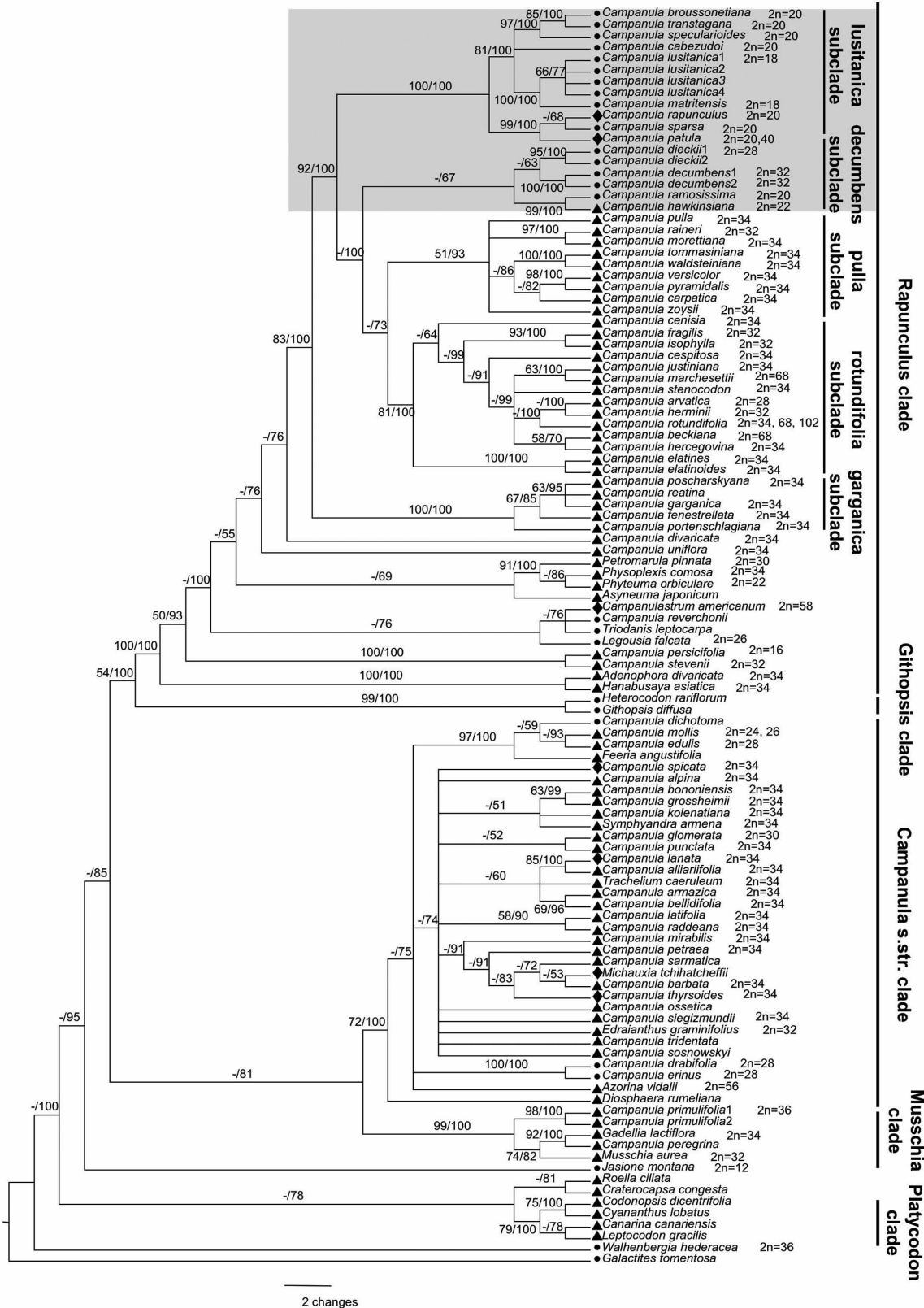


Fig. 1. Bayesian 50% MR consensus tree topology of Campanulaceae ITS. Bootstrap and posterior probability values are indicated on corresponding branches. Symbols indicate the habit of the species: ●, annual; ◆, biennial; ▲, perennial. The two sections that are the focus of this article are marked in gray. The chromosome numbers shown for the species that are not are specified in the text, derive from indices of plant chromosome number (Castroviejo, S. & Valdés-Bermejo, E. (eds.). 1991. *Archivos de Flora iberica I: números cromosómicos de plantas vasculares ibéricas*. CSIC. Madrid; *Index to plant chromosome numbers. Monographs in Systematic Botany from the Missouri Botanical Garden* [www.tropicos.org]; Moore, D.M. 1982. *Flora Europaea. Checklist and chromosome index*. Cambridge University press).

showed little internal resolution. This clade includes species of *Campanula* subgenera *Campanula* and *Roucela* and the genera *Diosphaera* Buser, *Azorina* Watson, *Edraianthus* A. DC., *Michauxia* L'Hér., *Trachelium* L., *Symphyantha* A. DC., and *Feeria* Buser. The two genera *Heterocodon* Nutt. and *Githopsis* Nutt. form a small clade, (the 'Githopsis' clade, 99%BS; 100%PPS) that appears between the 'Campanula s. str.' and 'Rapunculus' clades.

The 'Rapunculus' clade forms a monophyletic and strongly supported group (100%BS; 100%PPS), and as with the 'Campanula s. str.' clade, it includes taxa treated as separate genera [*Hanabusaya* Nakai, *Adenophora* Fisch., *Legousia* Durande, *Triodanis* Rafin., *Campanulastrum* Small, *Asyneuma* Griseb. & Schenk, *Phyteuma* L., *Physoplexis* (Endl.) Schur., *Petromarula* R. Hedw.] in addition to many species of *Campanula*. It comprises five principal well-resolved subclades: one subclade (100%BS; 100%PPS) corresponds to the 'garganica' subclade of Park & al. (2006); two subclades, 'rotundifolia' and 'pulla' subclade (81%BS; 100%PPS and 51%BS; 93%PPS) include the isophyllous and heterophyllous species of Park & al. (2006); And the other two subclades both include elements of the *Campanula lusitanica* complex of Cano-Maqueda & al. (2008) which we have called the 'decumbens' subclade and the 'lusitanica' subclade.

The 'decumbens' subclade (67%PPS) is formed by *C. ramosissima* and *C. hawkinsiana* Hauskn. & Heldr., that are sister to *C. decumbens* and *C. dieckii* Lange. The 'lusitanica' subclade (100%BS; 100%PPS) corresponds to the 'lusitanica' lineage of Cano-Maqueda & al. (2008). In this subclade, *C. patula*, *C. sparsa* and *C. rapunculus* L. are sister to *C. matritensis* A. DC., *C. lusitanica* s. s., *C. cabezudoii* Cano-Maqueda & Talavera, *C. specularioides* Coss., *C. transtagana* R. Fern. and *C. broussonetiana* Schult. The four samples of *C. lusitanica* s.str. (from three different populations, see Appendix I) collapse into a moderately supported subclade (66%BS; 77%PPS) and they appear as sister to *C. matritensis* in a well supported clade (100%BS; 100%PPS). Moreover, *C. lusitanica* s.str. presents morphological differences with *C. matritensis*, and it has a more restricted geographical distribution than the latter (see systematic treatment), so we have treated these two as separate species.

Karyological study

All species of 'lusitanica' subclade have $2n = 20$ or $n = 10$ chromosomes, except *C. matritensis* and *C. lusitanica* with $2n = 18$ or $n = 9$. The taxa of 'decumbens' subclade, *C. decumbens* and *C. dieckii*, have $2n$

$= 32$ or $n = 16$ and $2n = 28$ chromosomes, respectively (Table 1). All species studied have small or moderately small chromosomes (1.2-4.1 μm), with the centromere located in the middle or submid region (Fig. 2). In *C. specularioides*, one pair of chromosomes with the centromere in the submiddle region has a satellite on the short arm. Chromosomes form bivalents in the meiotic metaphase.

The basic number found in annual species of the 'lusitanica' subclade in the W Mediterranean, $x = 10$, coincides with that found in other species of this subclade: *C. rapunculus*, *C. patula* and *C. sparsa* (Larsen, 1956; Contandriopoulos, 1966). The basic number $x = 9$ found in *C. lusitanica* and *C. matritensis* can be considered as aneuploid of $x = 10$. The base number $n = 10$ is extremely rare in Campanulaceae, and has only been previously reported for *C. ramosissima* (Podlech & Damboldt, 1964). The chromosome number found in *C. dieckii*, $2n = 28$, has been previously found in the subgenus *Roucela* sensu Damboldt, in *C. erinus* (Gallego, 1986) and *C. drabifolia* Sibth. & Sm. (Contandriopoulos, 1964a), and in *C. edulis* Forssk. (according to Goldblatt & Johnson, 1990), all species of 'Campanula s. str.' clade, and also in *C. arvatica* Lag. (Podlech & Damboldt, 1964), a species of 'Rapunculus' clade (Fig. 1). The chromosome number found in *C. decumbens*, $2n = 32$, is also found in some species of the 'Rapunculus' clade, [*C. raineri* Perpentini (Podlech & Damboldt, 1964), *C. fragilis* Cyr. (Damboldt, 1965), *C. isophylla* Moertti (Merxmüller & Damboldt, 1962), *C. herminii* Hoffmans. & Link (Damboldt & Podlech, 1964), and *C. stevenii* Bieb. (according to Goldblatt, 1985), and *Edraianthus graminifolius* (L.) A. DC. (Contandriopoulos, 1964b), a taxon of the 'Campanula s. str.' clade, and *Musschia aurea* Dumort. (according to Goldblatt & Johnson, 1994), a taxon of 'Musschia' clade]. Since $2n = 34$ is the most frequent number in Campanulaceae, it seems likely that $2n = 32$ is an aneuploid of $2n = 34$ (see Fig. 1).

Systematic treatment

After reviewing all specimens we found that the different species can be separated in two groups on basis on the morphology of the style and stigma: one formed by *C. decumbens* and *C. dieckii*, with the style glabrous and with three stigmas with arms straight and erect or erect-patent; and another formed by all other species, with the style hairy in the upper half, and a trifid stigma, with the stigmatic arms curved or circinate. These two groups are consistent with the molecular results and karyology, so that they are probably natural, and the most appropriate taxonomic treatment is to recognise them as sections. The second

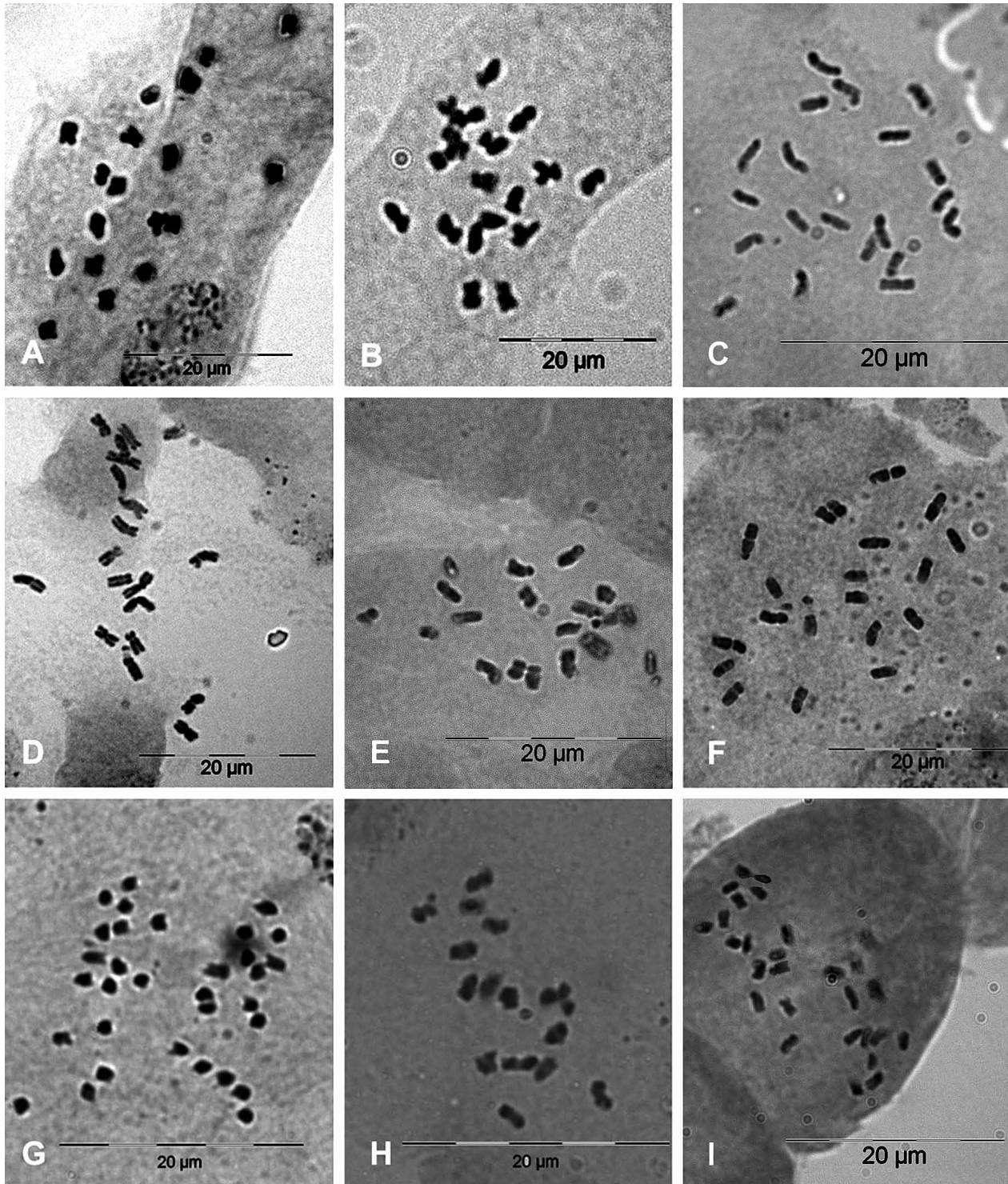


Fig. 2. Karyology of *Campanula* species. A-F and I, mitotic metaphase; G, meiotic anaphase I; H, meiotic metaphase I. **A**, *C. lusitanica*, $2n = 18$ (Rivadavia, Orense, Spain, SEV 218947); **B**, *C. matritensis*, $2n = 18$ (Hinojos, Huelva, Spain, SEV 216214); **C**, *C. cabezudoj*, $2n = 20$ (Venta de Zafarraya, Granada, Spain, SEV 218873); **D**, *C. specularioides*, $2n = 20$ (Montejaque, Málaga, Spain, SEV 216210); **E**, *C. transtagana*, $2n = 20$ (Valverde del Camino, Huelva, Spain, SEV 216212); **F**, *C. broussonetiana*, $2n = 20$ (Jbel Tazzeke, Taza, Morocco, SEV 216476); **G**, *C. decumbens*, $n = 16$ (Benaoján, Málaga, Spain, SEV 218875); **H**, *C. decumbens*, $n = 16$ (Villamartín, Cádiz, Spain, SEV 256653); **I**, *C. dieckii*, $2n = 28$ (Alfarnate, Málaga, Spain, SEV 256652). The scale bar = 20 μm .

group, which includes *Campanula rapunculus* L., would constitute the sect. *Rapunculus*. The first group would establish a new section, sect. *Decumbentes* which is formally described below. Within these sections, the most significant characters are: the shape of the corolla (campanulate or infundibuliform), middle cauline leaves (petiolate or sessile), capsule morphology (obpyramidal, subglobose or subovoid), and ovary indumentum (setose, glabrous or papillose).

We used this combination of characters to create a key for the identification of all annual species of the *C. lusitanica* complex in the Western Mediterranean.

KEY TO THE SPECIES

1. Style 2.1-4(4.8) mm, glabrous, with three stigmas; stigmas straight, erect or erect-patent 2
1. Style (4.5)5-14 mm, hairy in the upper half, with one trifold stigma; stigmatic branches curved or circinate, patent 3
2. Stems glabrous or with few antrorse hairs, often scabrid near the flowers; upper cauline leaves cuneate or shortly petiolate; corolla 12-21 mm **7. C. decumbens**
2. Stems densely pubescent with setose hairs, sometimes glabrescent towards the apex; upper cauline leaves sessile, subauriculate; corolla (6.6)8-13.7 mm **8. C. dieckii**
3. Corolla infundibuliform, with three purple nerves in each lobe; middle cauline leaves petiolate; plant decumbent 4
3. Corolla campanulate, without purple nerves in the lobes; middle cauline leaves sessile or petiolate; plant erect or decumbent 5
4. Capsule 2-3 × 3-4.5 mm, subspherical, generally glabrous, dehiscent by 3 pores of middle position, with 10 subwinged nerves; stems and leaves glabrous or glabrescent; calyx-teeth oblanceolate **4. C. specularioides**
4. Capsule 2.1-5.9 × 2.2-5 mm, ovoid or subspherical, usually densely hairy, dehiscent by three apical pores, with 10 ± acute but non-winged nerves; stems and leaves pubescent; calyx-teeth lanceolate or linear **3. C. cabezudo**
5. Middle cauline leaves petiolate and elliptic or sessile and cuneate 6
5. Middle cauline leaves sessile, ovate-lanceolate or lanceolate 7
6. Upper half of the stem and leaves with short hairs 0.1-0.3 mm; middle cauline leaves with petiole 0.2-4.5 mm **5. C. transtagana**
6. Upper half of the stem and leaves with long hairs, the longest 0.4-2 mm, or rarely glabrous; middle cauline leaves sessile and cuneate or with petiole up to 2 mm and rounded at the base **6. C. broussonetiana**
7. Middle cauline leaves ovate-lanceolate, subauriculate, densely patent-hairy, with long hairs up to 0.8-1.1 mm; capsule subovoid, with 10 subwinged acute nerves **1. C. lusitanica**
7. Middle cauline leaves lanceolate, glabrous or with sparse hairs 0.1-0.5 mm; capsule obpyramidal, with 10 very wide nerves, like flat ribs **2. C. matritensis**

A. Sect. *Rapunculus* Boiss., Fl. Orient. 3: 895. 1875

Campanula subgen. *Rapunculus* (Boiss.) Kharadze in Zametki Sist. Geogr. Rast. Tiflis 28: 100. 1970

Type: *C. rapunculus* L.

Annual or biennial plants. Lower leaves oblanceolate or spatulate, petiolate. Without calycine appendages. Corolla campanulate or infundibuliform. Stamens with white or blue anthers. Style with numerous pollen collecting hairs on the upper half, with a trifold stigma; stigmatic arms curved or circinate, patent, white or blue, with numerous pollen collecting hairs on the abaxial surface glabrous, and receptive on the adaxial surface. Capsule subspherical, ovoid or obpyramidal, dehiscent by three apical or middle position pores. $x = 9, 10$ (see karyology).

Observations: This section includes: *Campanula rapunculus* and *C. patula* of the Mediterranean region; *C. lusitanica*, *C. matritensis*, *C. cabezudo*, *C. specularioides*, *C. transtagana* and *C. broussonetiana* from the W Mediterranean; and *C. sparsa* and possibly *C. spatulata* Sibth. & Sm. of the E Mediterranean. The section is monophyletic (see *lusitanica* clade in Fig. 1).

Experimental manual crosses showed that all annual species of the W Mediterranean had hybridization barriers at different levels: (1)- fruits were not produced, (2)- seeds do not germinate, (3)- germinated seeds formed chlorotic seedlings which did not survive and (4)- no chlorotic seedlings survived after the cotyledon state but they did not complete their development (Cano-Maqueda unpublished studies).

1. *Campanula lusitanica* L. in Loebl., Iter Hispan.: 111, 126. 1758

Campanula loeflingii Brot., Phytogr. Lusitan. Select. Fasc. I: 20. 1800, nom. superfl. *C. patula* var. *lusitanica* (L.) Pau in Bol. Soc. Iber. Ci. Nat. 20: 181. 1921. Ind. loc.: "Habitat in Lusitania ad Porto in collibus & muris". Type: Portugal. Porto, June 1917, *Mário de Castro s.n.* [Sennen, Pl. Espagne n.º 3305] (neotype, here designated, G 104248!, Fig. 3; see observations).

C. duriaei Boiss., Voy. Bot. Espagne 2: 402. 1839. Ind. loc.: "Hab. in Hispaniâ circâ Olyssiponem (L. Et Hoffm.), Hispaniâ septentr. In Asturiis (Durieu)". Type: Spain. Asturias, Cangas de Tineo, 25 July 1835, *Durieu s.n.* [Plant. Select. Hispano-Lusit. Sect. 1ª n.º 280] (lectotype, here designated, G 104093!; see observations).

C. loeflingii var. *occidentalis* Lange in Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1861: 107, 108. 1862. Ind. loc.: "In Gallecia frequent!". Type: Spain. Galicia [not found in the Lange herbarium (C)].

C. lusitanica var. *puberula* C. Vicioso in Anales Jard. Bot. Madrid 6: 78. 1946. Ind. loc.: "Hab. Ribadela-go (Zamora)". Type: Spain. Zamora, Ribadela-ga,

19 July 1945, *C. Vicioso s.n.* (lectotype, here designated, MA 121525!; see observations).

Illustrations: Fig. 4 A, B.

Herb 16-50 cm, annual, erect, branched from the base, rarely in the upper half, densely pubescent, not brittle. Stems angled, branched or simple, densely pubescent, rarely glabrescent in the uppermost portion, with short and long hairs, the longest 0.5-1.5 mm. Leaves somewhat coriaceous, entire, crenulate or toothed; middle cauline leaves 5-30 × 3.1-10.9 mm, sessile, ovate-lanceolate, subauriculate, entire or toothed, densely pubescent, ± long hairs, the longest 0.8-1.1 mm; upper cauline leaves 4-14.5 × 0.5-4.4 mm, sessile, lanceolate, truncate or somewhat auriculate, pubescent, with hairs up to 0.9 mm. Inflorescence paniculate, highly branched, lax or dense and spiciform. Flowers pedicellate or subsessile; pedicel (3)7-16 mm, glabrous or with hairs 0.1-0.2 mm. Calyx-teeth 3.7-9(17.3) × 0.4-0.6(1.3) mm, linear, recurved in the female phase flower. Corolla (8.2)10-18.9 mm, campanulate, with tube longer or shorter than lobes; tube 3.5-9.7 mm, blue at the apex, white at the base; lobes 3.7-9.2 × 2.2-6.1 mm, elliptic-lanceolate, not re-

flexed in the female phase flower, blue. Stamens with enlarged base of 0.6-1 × 0.4-0.5 mm; filaments 0.2-0.5 mm; anthers (1.5)3-5 mm, whitish. Ovary papillose or with setose hairs of 0.1-0.2 mm; style 7.5-11.8 mm, hairy in the upper half; stigma trifid, with stigmatic branches of 0.3-1.2(2.8) mm, patent, circinate, white. Capsule (2.4)4-6 × (2.5)3-4 mm, subovoid, longer than wide, papillose, rarely with some setose hairs 0.1-0.2 mm, with 10 subwinged and acute nerves, dehiscent by three apical pores. Seeds 0.3-0.5 × 0.2-0.3 mm, ellipsoid, shining, yellowish to brown. $2n = 18$; $n = 9$.

Habitat, phenology and distribution: Wet grasslands on generally acid substrates, sometimes draining and river banks; 15-1800 m. (V)VI-VIII. •Endemic to the NW of the Iberian Peninsula, common in Galicia and N Portugal, and also occurring in S Portugal, Monchique (Fig. 5). **Portugal:** Ag BA BL DL Mi TM. **Spain:** C Le Lu O Or Po Sa Za.

Observations: López-González (in litere) has commented apropos the type of *Campanula lusitanica*: “Al parecer, Linneo no conoció nunca *Campanula lusitanica*, porque dicha planta no figura en la lista de materiales de Loeffling enviados a Linneo en 1752 (Spanish list), pero en una carta de Loeffling a Linneo, fechada el 7.VII.1751 y escrita en Oporto, le indicó que «*Campanula caule angulato, ramoso, vago, calice corollae tubulosae aequali*», la que Linneo denominaría *C. lusitanica*, habita aquí [Porto] en los caminos y en las tapias. Tampoco figura esta planta ni como *Campanula lusitanica* ni como «*Campanula caule angulato...*» en la lista del herbario de Loeffling que redactó un capellán sueco, probablemente porque en esta lista solo figuraban las plantas identificadas, y «*Campanula caule anguloso...*» aún no tenía nombre. Es en el herbario de Loeffling donde se podría encontrar la planta como *Campanula sp.*, pero este herbario lo perdió Casimiro Gómez Ortega, que al parecer, según cuenta en una carta, lo prestó a un botánico francés y éste no lo devolvió”.

Since it was impossible to find the type material of *C. lusitanica* in the different Linnean herbaria, the election of a neotype has been proposed. The plants in question have long and patent cauline hairs, and so do not correspond to the plant described by Loeffling, who indicates “*Caulis ... leviter hispida pilis pallidis, brevissimis*”. The shape of the cauline leaves, ovate-oblong or ovate-lanceolate, are however like those of the plants described by Loeffling, who indicates “*Folia caulina & subramorum ovato-oblonga, subglabra, sessilia, subserrata, alterna; ramorum superiora ovato-lanceolata, vix serrata*” and the whitish colour at the base of the corolla tube is also consistent with the description of Loeffling: “*Cor. caeruleis, tubulo infimo*

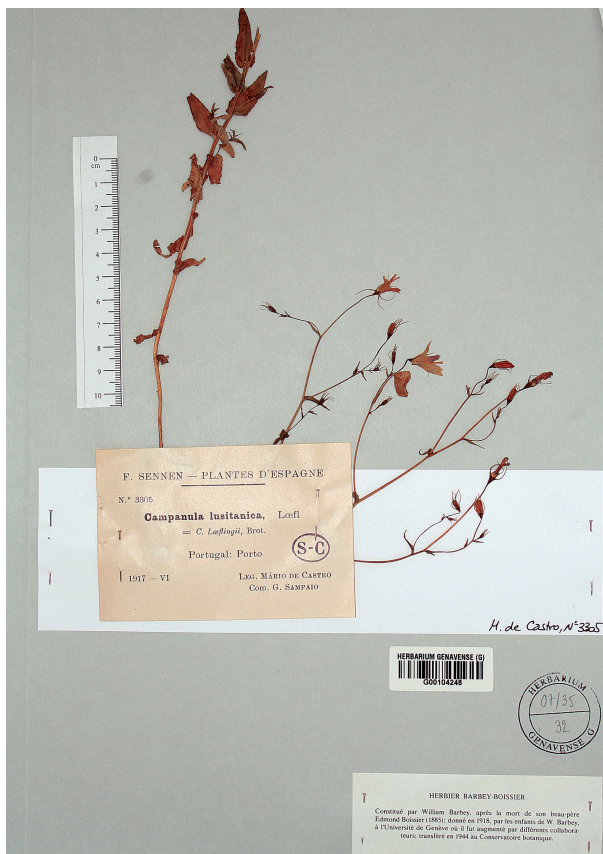


Fig. 3. Neotype of *Campanula lusitanica* (G 104248).

brevisimo albo”. In accordance with these characteristics, we have chosen the plants from Porto as neotype of *Campanula lusitanica*.

Brotero (1800: 20-21) gave a new name, *C. loeflingii*, to the plant collected in Porto by Loeffling, but

this name is illegitimate, since Linneus had named it as *C. lusitanica* in the work of Loeffling. Brotero (1804: 287) subsequently not only described the Loeffling plant, but also included characters from another species later described by Alphonse De Candolle

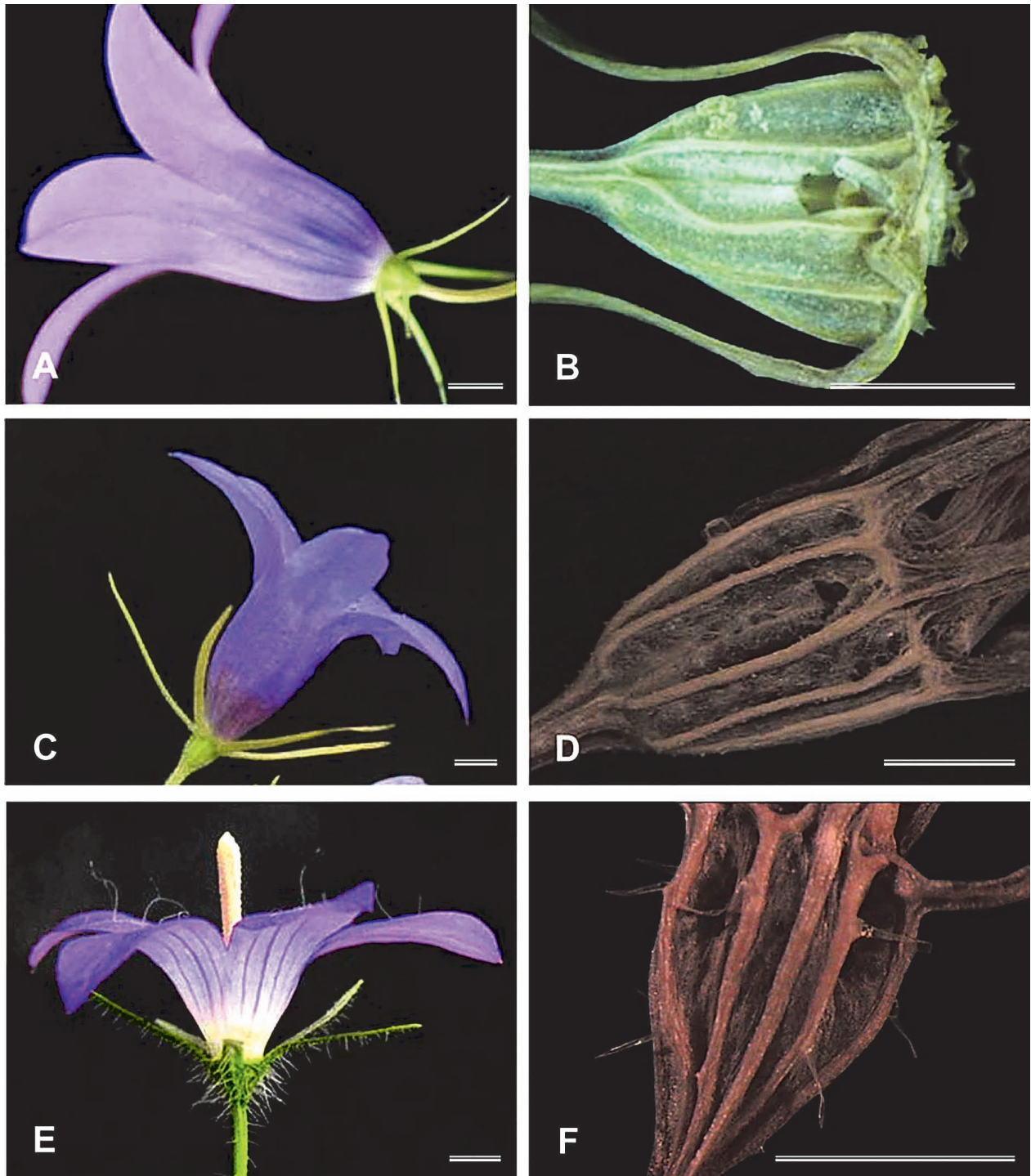


Fig. 4. Flowers and fruits of *Campanula* species. **A, B,** *C. lusitanica* (Rivadavia, Orense, Spain, SEV 218947); **C, D,** *C. matritensis* (Hinojos, Huelva, Spain, SEV 261264); **E, F,** *C. cabezudoii* (Venta de Zafarraya, Granada, Spain, SEV 218873). The scale bar = 3 mm.

(1830) as *C. matritensis*. Indeed, the illustration that appears in his “Phytographia Lusitaniae Selector” (Brotero, 1816, tab. 18) corresponds more closely to *C. matritensis* than to *C. lusitanica*. Hoffmannsegg & Link (1820-1824: 14) also provided a brief description of *C. loeflingii*, but like Brotero, they could be referring to both *C. lusitanica* and *C. matritensis*.

Boissier (1839) described *C. duriaei* based on the characters of plants collected by Durieu in Cangas de Tineo (Asturias) distributed as the Exiccata No 280 in 1835. In the herbarium at Geneva there are three sheets of this collection (G 104093, G 104120 y G 104116). The first (G 104093) consists of 4 complete plants mounted on two sheets, and comes from the Boissier Herbarium. One of the sheets contains two plants of 30 cm and 22 cm respectively, and a Boissier handwritten label indicating “C. Duriaei/284”. We have chosen as lectotype the 30 cm plant because it is the closest to the description; the other plant, of 22 cm, is an isolectotype. The other sheet also contains two plants without any annotation by Boissier; they are also likely isolectotypes. The other two sheets (G

104120 and G 104116) are from the herbarium of Moïse-Etienne Moricand which were incorporated into the herbarium of the Conservatoire et Jardín Botanique de Genève in 1908; the plants contained in them, which were not seen by Boissier, are not part of the type material. Boissier was the first author to clearly describe the characteristic hairs of the Asturian plants: “Toute la plante est d’une consistance délicate et couverte de poils long et étalés, tandis que la *C. loeflingii* est u glabre ou hérissée de poils rudes et courts”. Boissier’s concept of *C. loeflingii* was very wide, since he included in this species most of the taxa of this group which had been collected by him in southern Spain or that he had seen in the Fouche or De Candolle herbaria. We identify Fouche herbarium plants as *C. decumbens* subsp. *baetica* Cano-Maqueda & Talavera and those in the De Candolle herbarium as *C. broussonetiana*, and the plants that he collected in Southern Spain as *C. matritensis* and *C. dieckii* (see these species below).

The type material of *C. lusitanica* var. *puberula* consists of three plants mounted on the same sheet. We

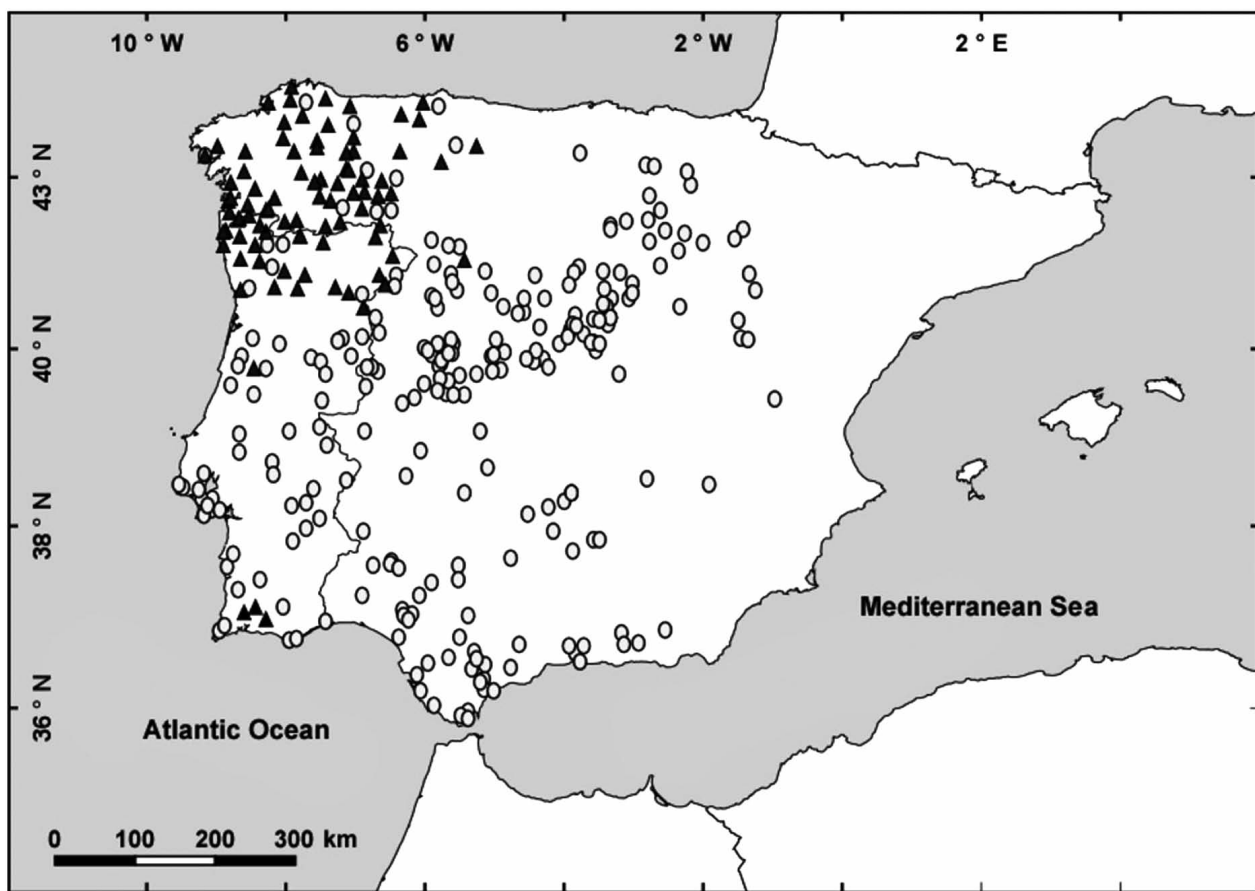


Fig. 5. Distribution map of *Campanula lusitanica* (▲) and *C. matritensis* (○).

have chosen as lectotype the larger specimen mounted on the left, and the other two plants are isolectotypes

Campanula lusitanica is very similar in the indumentum and the branching to *C. broussonetiana*, but *C. lusitanica* has $2n = 18$ chromosomes, as does *C. matritensis*, while *C. broussonetiana* has $2n = 20$ chromosomes, as do almost all species of sect. *Rapunculus*. The ITS phylogenetic tree shows that *C. lusitanica* and *C. matritensis* are sister species (see Fig. 1).

Selected specimens

PORTUGAL. **Algarve:** Serra de Monchique, entre Monchique e Alferce, Rouxinel, 27-VI-1978, *M. Beliz* (MA 270314); ibidem, de Pesos a Monchique, 24-VII-2009, *S. & M. Talavera* (SEV 248712). **Beira Alta:** Figueira de Castelo Rodrigo, Escalhão, 26-V-1996, *M. Santos & M. Sequeira* (HVR 8048). Serra da Estrela, without date, *Romariz* (LISU 2054); ibidem, Garganta de Loriga, VIII-1912, *A.A. Silva Martins* (LISU 36386). Vizeu, Santa Comba Dão, Pinheiro de Azer, arredores da ponte sobre a barragem, 20-VI-1982, *A. Marques* (MA 377387). **Beira Litoral:** Coimbra, Penacova, Oliveira do Mondego, 13-V-1982, *A. Marques* (MA 391392). **Douro Litoral:** entre Oliveira y San Joao de Madeira, dirección Oporto, 24-VI-1986, *J.A. Devesa & al.* (SEV 161720). Porto, Castelo prox. Souto de Lafões, 27-V-1940, *recolector ilegible* (LISU 36362). **Minho:** Ancora, VI-1886, *A.R. da Cunha* (LISU 36367). Areosa, VI-1886, *A.R. da Cunha* (LISU 36404). Barcelos, VI-1886, *A.R. da Cunha* (LISU 36368). Caldas do Gerez, IX-1882, *M.L. Enriques* (COI). Caminha, Retorta, VI-1885, *A.R. da Cunha* (LISU 36379). Celorico de Basto, VI-1884, *A.R. da Cunha* (LISU 36380). Entre Ponte de Barca y Vila Verde, 27-VI-1982, *M.J. Gallego & al.* (SEV 161716). Fafe, Lameira, 7-VIII-1977, *M. Beliz* (MA 270317). Gondarem, VI-1885, *A.R. da Cunha* (LISU 36377). Melgaço, VI-1894, *A. Moller* (COI). Monção, Lavandeira, VI-1885, *A.R. da Cunha* (COI, LISU 36407). Ponte de Lima, VII-1894, *M. Rodr. Maraes* (COI). Povoia de Lanhoso, VI-1920, *J. Sampaio* (MA 121499). Senhora da Peneda, Serra do Soajo, VII-1890, *A. Moller* (COI). Serra Amarela, Mata do Cabril, Carvalhal do Sono, 8-VIII-1977, *M. Beliz & J. Guerrero* (MA 270316). Serra da Peneda, 880m, VI-1956, *R. Bentos* (LISE 48610). Serra do Gerez, 2-VII-1948, *Romariz* (LISU 922). Soajo, Serra do Soajo, VI-1890, *A. Moller* (COI). Vanlença, Oliviar de Santa Barbara, VI-1885, *A.R. da Cunha* (LISU 36403). Veiga de Chaves, V-1910, *F. Mendez & al.* (LISU 36389). Veiga de Ganfei, VI-1885, *A.R. da Cunha* (LISU 36392). Vila Nova da Cerveira, VI-1885, *A.R. da Cunha* (LISU 36402). **Trás-os-Montes:** arredores de Bragança, VI-1882, *P.F.M. Var* (COI). Bragança, 1877, *Pereira Coutinho* (LISU 36358). Entre Montalegre e Chaves, Sapiões, VI-1910, *R. Palbinha & al.* (LISU 36385). Estação do Pocinho, VI-1915, *Mendes & Palbinha* (LISU 36387). Mogadouro, a montante da pte. de Ramondes, na margem dta. do rio Sabor., 18-V-1997, *A. Castro & Tjarda De Koe* (HVR 9475). Montalegre, 21-VII-1959, *M. da Silva* (G 104096). Montinho, Seixas, VI-1885, *A.R. da Cunha* (LISU 36401). Santa Marta de Penaguião, Veiga, Aldeia do Bertelo, 25-VI-1993, *A. Coelho Costa & A.L. Crespi, A* (HVR 10177). Vila Nova de Foz Côam, margem do Douro (esquerda) a jusante da Foz do Sabor, frente à Ilha, 30-IV-1995, *M. Sequeira* (HVR 5937). Vila Real Coêdo, 10-VII-1981, *A. Além* (HVR 3902, SANT 39046). Vimioso, VI-1888, *G. Mariz* (COI).

SPAIN. **Asturias:** Cangas de Tineo, 2-VI-1864, *E. Bourgeau*, in *E. Bourgeau*, Pl. d'Espagne 1864: n° 2657 (G 104119, G 104118, MA 121552, MA 152778). Cornelianá, 16-VIII-1868, *E. Boissier* (G 104109). Pravia, without date, *La Gasca* (MA 121844). Taramundi, VII-1979, *T.E. Diaz* (MGC 14104). Asturias, VII-VIII-

1878, *E. Boissier* (G 104121, G 104117). **La Coruña:** Aranga, 30-VI-1967, *J. Dalda* (SALA 35816). Cariño, Landoi, 4-VIII-1994, *X. Soñora* (SANT 31851). Carnota, 1-VI-1996, *R.I. Louzán* (FCO 24813, MA 581374, SANT 35758). Cuenca del río Deo, 1966-1968, *J. Dalda* (SANT 55699). Ferrol, 27-VI-1994, *X. Soñora* (SANT 29263). Mazaricos, 25-VI-1995, *R.I. Louzán* (SANT 35746). Santiago de Compostela, Pontepedriña, VI-1995, *Rodríguez-Hergueta* (SANT 42394). Sobrado, 24-VII-1882, *J. Lange* (G 104115). Somozas, 17-VII-1994, *X. Soñora* (SANT 31883). **León:** La Baña, Sierra de Cabrera, camino del Lago, 10-VII-1981, *Lansac & Nieto* (MA 317215, MA 317216, MA 317216). Palacios del Sil, Salentinos, 27-VIII-1996, *Martín-Blanco* (MA 597090). Ponferrada, Villanueva de Valdueza, VIII-1995, *Rodríguez-Hergueta* (SANT 42467). Riocastrillo de Ordás, 22-VI-1997, *C. J. Martín-Blanco* (MA 612392). Sobrado, Castropetre, 30-V-1990, *J. Amigo & J. Giménez* (SANT 26556). Valle del Bierzo, VI-1905, *M. Gandoger* (G 104142). **Lugo:** alrededores de la ciudad, 26-VI-1987, *E. Carreira* (MA 513456). Becerreá, El Cruzal, 18-VII-1989, *S. Castroviejo & al.* (MA 471686). Cabreira-Fonsagrada, VII-1957, *E. Carreira* (MA 204700). Cervantes, Correal, entre El Portelo y Piedrafita, 28-VI-1994, *M. A. Carrasco & al.* (MA 543383). Chantada, 18-VI-1988, *M. Buján* (SANT 25112). Entre Esperante y Carbedo, 5-VII-1979, *J. Amigo & al.* (SANT 16230). Ferreiravella, 19-VI-1980, *J. Amigo & al.* (SANT 16229). Meiraos, 16-VII-1981, *J. Amigo & al.* (SANT 16226). Monforte, 18-V-1991, *J. Amigo & M. Romero* (SANT 25426). O Saviñao, Mourelas, 14-VII-1992, *J. Amigo & M. Romero* (SANT 22471, MA 517178). Palas de Rey, 16-VI-1951, *Seijas* (SANT 6124). Piornedo, 23-VII-1952, *Bellot & Casaseca* (SANT 6783). Quiroga, Hermida, San Victorio, 18-VI-1988, *M. Buján & M. I. Romero* (MA 546783, SANT 25107). Riberas de Lea, 25-VII-1956, *E. Carreira* (MA 201352). Sierra del Caurel, Seoane, 28-VII-1992, *E. Blanco* (MA 564613). Tardad, Villalba, 30-VII-1951, *M. Orosa* (G 104101). Vilamelle, 6-VI-1990, *M.I. Romero* (MA 546757, SANT 26231). **Orense:** Carballeda, 10-VII-1984, *S. Ortiz* (SANT 16523). Chandreja de Queija, pr. Paradaseca, 24-VII-1974, *S.I. Laínz* (MA 345998). Corraínzas, 12-VIII-2000, *J. De Jesús & al.* (SANT 46020). Entre Sobradelo y Casayo, 15-VI-1958, *Bellot & Casaseca* (SANT 9940). Leboreiro, 13-VII-1958, *F. Bellot & B. Casaseca* (MA 180705). Lobios, 9-VII-1993, *I. Pulgar* (SANT 56572). Río Lonia, 15-VII-2000, *A.R. Romero & al.* (SANT 45644). Río Sil, 15-VI-1958, *Bellot & Casaseca* (SANT 10066). Rivadavia, carretera a la Franqueirán, 24-VIII-2007, *R. Pino* (SEV 218947). Rubiá, Pardellán, Río Sil, 29-VI-1994, *M.A. Carrasco & al.* (MA 542966, SALA 115638). Serra do Invernadeiro, inter Rocín et Suenzenza, 11-VII-1973, *S. Castroviejo* (MA 219730, MA 196712). Verín, 7-VI-1988, *M. Buján & M. I. Romero* (SANT 25110, SANT 25108). **Pontevedra:** Albeos, 14-VI-1988, *M. Buján* (SANT 25113). Cangas de Morrazo, 6-VIII-2007, *S. Castroviejo* (SEV 218948). Crecente, 24-V-1998, *J. Amigo & al.* (SANT 39787). Cuntis, 9-VI-2007, *J. García Devesa* (SANT 57381). Ermelo, Bueu, 15-VII-1970, *S. Castroviejo* (MA 196710). Meañó, 16-III-1988, *M. Buján & M.I. Romero* (SANT 25109). Porteliña, 16-VIII-1983, *S. Siwestre* (SEV 161714). Prado, 15-VII-1947, *Vieiter* (SANT 213). Salvaterra de Miño, 24-V-1998, *J. Amigo & al.* (SANT 39806). **Salamanca:** Aldeavilla, 22-IV-1977, *F. Amich* (SALA 15518). La Fregeneda, 30-IV-1977, *F. Amich* (SALA 15519). **Zamora:** Montelarreina, 31-V-1987, *R. García Ríos* (SALA 54045). Ribadelago, 14-VI-1987, *A. Roa & P. García* (MA 510330).

2. *Campanula matritensis* A. DC., Monogr. Campan.: 332. 1830

C. lusitanica subsp. *matritensis* (A. DC.) Franco, Nova Fl. Portugal: 2, 569. 1984. *C. patula* var. *matritensis* (A. DC.) Pau in Bol. Soc. Iber. Ci. Nat.: 20, 181.

1921. *C. loeflingii* var. *matritensis* (A. DC.) Lange in Vidensk. Meddel Dansk Naturhist. Foren. Kjøbenhavn 1861: 108. 1862. Ind. loc.: "Habitat in Hispania circa Matritum (Lagasc!)". Type: Spain. Madrid, 1806, *Lagasca s.n.* (lectotype, here designated, G 138402! (G-DC.), Fig. 6; see observations).

Illustrations. Gallego (1987: 564, as *C. lusitanica*); Brotero (1816, tab 18, as *C. loeflingii*); Hoffmannsegg & Link (1820, tab. 82, as *C. loeflingii*); Sáez & Aldasoro (2001: 130, fig. 39b-h, as *C. lusitanica* subsp. *lusitanica*); Fig. 4 C, D.

Herb (6)10-55 cm, annual, erect, branched at the base or in the upper half, often laxly pubescent, not brittle. Stems angled, little branched, laxly pubescent in the lower half with setose hairs 0.1-0.3(0.5) mm. Leaves not coriaceous, crenate, dentate or entire; middle cauline leaves 4.5-27 × 0.9-9.2 mm, sessile, lanceolate, entire or toothed, glabrous or laxly pubescent, with hairs 0.1-0.5 mm; upper cauline leaves 2-22 × 4.5-5.8 mm, sessile, lanceolate, glabrous or with some hairs of 0.1-0.4 mm. Inflorescence laxly paniculate. Flowers pedicellate; pedicel 3.5-123 mm, glabrous or with some hairs of 0.1-0.2 mm. Calyx-teeth (2.2)4-15 × 0.3-1(1.3) mm, linear, filiform. Corolla (8.8)11-26 mm, campanulate, with the tube much longer or much shorter than the lobes; tube (4.2)7-15.3 mm, bluish; lobes (5.5)6-16 × 2-7 mm, ovate, blue. Stamens with enlarged base of 0.6-1 × 0.3-0.7 mm; filaments 0.4-0.6 mm; anthers (2)3-5 mm, white, rarely bluish. Ovary glabrous, papillose or with scattered hairs of 0.1-0.2 mm; style 5-14 mm, hairy in the upper half; stigma trifid, with stigmatic branches of 1-2(3.1) mm, patent, circinate at the end of the female phase of the flower, white. Capsule (2.5)4-9.2 × 2-5 mm, obpyramidal, much longer than wide, glabrous, papillose or with some setose hairs less than 0.1 mm, with 10 very wide nerves like flat ribs, dehiscing by three apical pores. Seeds 0.4-0.6 × 0.2-0.3 mm, ovoid, shining, yellowish to brown. $2n = 18$; $n = 9$.

Habitat, phenology and distribution: Pine, cork oak and holm oak woodlands or their shrubby secondary communities, often on sandy substrates, but also on clay; 0-2200 m. V-VI(VII). • Endemic to the Iberian Peninsula. Distributed almost throughout the entire peninsula, but rare in limestone areas of C, E and N of Spain, and absent in NE of Spain (Fig. 5). **Portugal:** AAl Ag BA BAl BB BL E Mi R TM. **Spain:** Ab Al Av Ba Bu C Ca Cc Co CR Cu Gr Gu H J Le Lo Lu M Ma O S Sa Se Sg So Te To Va Vi Z Za.

Observations: This species is very variable in size, flower size, indumentum and shape of the calyx, and

indumentum and size of the capsules. The plants that live in very shady banks are usually delicate, have small flowers and, in general, asymmetric capsules due to lack of fertilization in one or two of the three locules, probably caused by deficient pollination. In contrast, plants living in sunny and humid areas are vigorous, highly branched, with large flowers and perfectly symmetrical obpyramidal capsules, with all locules full of seeds, denoting a very efficient fertilization. On shallow soils, in montane areas, plants are very small, slightly branched, with small flowers and sometimes with ± ovoid and malformed capsules due to a deficient pollination, and these may be confused with *C. transtagana* or even with *C. lusitanica*.

The three plants of type material of *C. matritensis* (Fig. 6), about 15 cm, attached to the label, have sessile cauline linear-lanceolate leaves, and obconical capsules. These agree with the characters described by



Fig. 6. Lectotype of *Campanula matritensis* (plant located in the lower left corner) (G 138402, indicated by the arrow). The lectotype is the plant of the center, the other two plants are isotypes. The other two plants with their respective labels are not material type.

Alphonse De Candolle (1830). That these three plants include the type material is further indicated by an Alphonse De Candolle label at the bottom of the sheet with “*Campanula matritensis* Alph. DC.”. Of these three plants, the largest, located in the middle, is chosen as lectotype of *Campanula matritensis* A. DC. The other two plants are isolectotypes. In the same sheet there are other two plants which are not type materials (see Fig. 6). One [Herb. Prodr. (G-DC)G 138459] indicates “*Campanula/ex hispania/m’ Guillemin 1827*” and the plant, branched and young, is identified as *C. matritensis*; the other [Herb. Prodr. (G-DC)G 138462] indicates “*C. pulla herb Lag./prope la Venta del Gorro in nov. Castell./1827 [1827? manuscript Lagasca?]/Londres 1828 [manuscript Lagasca]*”. Coupled with this label there is another, probably handwritten by A. De Candolle, with the following inscription: “*C. matritensis?/differt ab omnibus affinibus lobis/calycinis marginem extus revolutis.*”. Stitched to both labels there is a very small plant with a single flower, which we identify as *C. dieckii* Lange.

Selected specimens

PORTUGAL. **Algarve:** Broussailles à Monchique, 14-VI-1853, E. Bourgeau, in E. Bourgeau, Pl. d’Espagne et de Portugal, 1853; n° 1943 (G 104070, G 104125, G 104140). Cabo de San Vicente, Chodet (G 104147). Castro Marim, Terras da Ordem, 24-IV-1975, M. Sequeira & al. (HVR 4734). Entre Corte-Figueira y Mù, VI/VII-1885, J. Daveau (LISU 36408). Faro, Santo Antonio do Alto, V-1889, J. Brandeiro (G 104123). Olhão, Quinta de Marim, 24-V-1986, A. Moura (MA 430492). Entre Santa Catharina e Sagres, V-1906, F. Mendes & Palhinha (LISU 36391). Serra da Picota, VII-1891, J. Brandeiro (COI). Serra de Monchique, Ribeira da Perna Negra, 30-V-1979, M. Beliz & J. Guerrero (MA 270313). **Alto Alentejo:** Elvas, próximo da estrada Elvas-Badajoz, 1-I-1900, A. Forque (LISE 31816). Évora, V-1891, A. Moller (COI). Évora Monte, entre Estremoz y Évora, 28-V-1996, S. Castroviejo & al. (MA 588831). Gavião, 26-VI-1952, P. Silva, F. Fontes & B. Rainha (G 104102). Margem do rio Alirilungo, afluente de Xevora, V-1922, Fernandes (LISU 36417). Marvão, Serra de San Mamede, 16-V-1978, J.A. Devesa & J. Pastor (SEV 39778). Montargil, V-1883, G. Corteisção (COI). Mora, arredores nas arelas do leito da Ribeira da Raia, 13-V-1953, Bento Rainha (LISE 51183). Portalegre, Serra de Penha, VI-1882, A.R. da Cunha (LISU 36400). Portel, 15-V-1969, P. Silva & al. (LISE 93823). Povoá e Meadas, VI-1882, A.R. da Cunha (LISU 36370). Redondo, V-1892, D. Pita Simões (LISU 36361, LISU 36366). Reguengos, Berrocal, IV-1908, F. Mendes & Palhinha (LISU 36411). Serra d’Ossa, V-1891, A. Moller (COI). **Baixo Alentejo:** Cazevel, V-1888, A. Moller (COI). Cuba, entre Cuba e Vila de Frades, 4-V-1962, M. Silva (LISE 76879). Entre Garvão e Panóias, VI/VII-1885, J. Daveau (LISU 36393). Odemira, V-1915, F. Gomez & R. Machado (LISU 36415). Santiago de Cacém, 14-V-1958, B. Rainha, M. Silva & A.N. Teles (LISE 64924). Margem do rio Chança, VI-1913, F. Mendes, H. Navel & Palhinha (LISU 36414). Serra do Caldeirão, 12-V-1905, M. Gandoger (G 104143). Sines, a 1 Km a norte de porto Covo, 21-V-1982, F. Catarino & al. (LISU 145357). Tarrão, 29-V-1952, F. Fontes & al. (LISE 41814). **Beira Alta:** Águeda, perto de Escalhão, 26-V-1996, M. Santos & M. Sequeira (HVR 7845). Barca d’Alva, margen do Douro, VI-1915, F. Mendes & Palhinha (LISU 36416). Castelo Mendo, Moita do Carvalho, VII-1884, A.R. da Cunha (LISU 36399). Covilhã, VI/VII-1881, A.R. da Cunha (LISU

36395). Entre Guarda y Valhelhas, 16-VII-1983, S. Castroviejo & al. (MA 248455). Figueira de Castelo Rodrigo, Barca D’Alva, 28-IV-1943, J. Castro & A. Rozeira (MA 514273). Sabugal, 14-VI-1976, I. Melo & al. (LISU 69654). Serra da Estrela, VII-1887, A. Moller (MA 121501). Serra da Lapa e Mata da Vide, VI-1890, M. Ferreira (COI). Vale do Zêzere, 3-VIII-1949, C. Romariz (LISU 2053). Vouzela, 27-V-1940, Palhinha (LISU 36363). Sabugal, à saída da vila, na estrada Castelo Branco (Miradouro), 14-VI-1976, I. Melo, & al. (SEV 121226). **Beira Baixa:** Alcaide, Barroca do Chorão, VI-1882, A.R. da Cunha (LISU 36369). Castelo Branco, VI-1881, A.R. da Cunha (LISU 36398). Covilhã, nos latudes da estrada prose da ribeira da Carapineira, 23-VI-1946, B. Rainha (G 104146, LISE 21736, MA 121494). Monfortinho, prox. das termas, 14-VI-1948, B. Rainha (LISE 22693, MA 152780). Tavanca do Mondego, 31-V-1990, Z. Díaz & al. (SEV 161692). **Beira Litoral:** Arganil, Moita, V-1895, M. Ferreira (COI). Cantanhede, VI-1888, C.M. Ferreira (COI). Choupal prope Conimbricam, VI-1878, A. Moller (G 104124, G 104122). Coimbra, 6-VIII-1883, A. Moller (G 104139). Guardinha, arred. do Lourçal, VI-1897, J.A. Vaz Serra (COI). Meco, 16-IV-1995, A. Crespi & M. Sequeira (HVR 4604). Taboa, V-1883, A. Costa Carvalho (COI). **Estremadura:** Alfeite, V-1906, J. dos Santos (LISU 36384). Alrededores de Lisboa, Serra de Monsanto, VI-1884, A.R. da Cunha, in Flora Lusitanica (Soc. Brot. 7°. Anno) n° 910 (LISU 36360). Arredores de Setúbal, V-1906, F. Gomez (LISU 36409). Lagoa de Albufeira, V-1882, J. Daveau (LISU 36371). Moita, Arganil, V-1895, M. Ferreira (COI). Praia das Maças, V-1930, F. Matos (LISU 36364). S. Simão, Piedade, VIII/IX-1848, J. Daveau (LISU 36396). Sacavém, 1952, Duarte de Castro (LISE 40720). Seixal, V-1881, A.R. da Cunha (LISU 36397). Serra da Arrabida, Colina de Santa Margarida, 18-V-1942, C. Fontes & al. (LISE 15267, MA 121496). Serra de Montejunto, 31-I-1947, Romariz & Mendes (LISU 56937). Sesimbra, Alfirim, 2-VI-1971, M. Beliz & J. Guerreiro (MA 270318). Vila Nogueira, 25-V-1978, J.A. Devesa & al. (SEV 39777). **Minho:** Gerez, VII-1889, F. Loureiro (COI). Valença, Olivar de Sta. Barbara, VI-1885, A.R. da Cunha (COI). **Ribatejo:** Almeirim, 22-V-1952, P. Silva & M. Silva (LISE 41804). **Trás-os-Montes:** arred. de Miranda do Douro, Iffanes, VI-1888, J. de Mariz (COI). Arredores de Bragança, 16-VI-1941, A. Carneiro (COD). Arredores de Moncorvo, Concelho de Mogadouro, Urrós, 20-V-1997, J. Hernández & E. Rico (SALA 90849). Avelanoso, arred. de Vimioso, VI-1888, J. de Mariz (COI). Lígares, V-1884, J. de Mariz (COD). Valença, Olival de Santa Barbara, VI-1885, A.R. da Cunha (COI). Vila Real, Coêdo, 10-VII-1981, A. Além (COI).

SPAIN. **Álava:** Bernedo, Urturi, 1-VII-1987, J.A. Alejandro (MA 423674). **Albacete:** San Pedro, 11-VI-1984, J.M. Herranz (MA 318970). **Almería:** Abrucena, Las Rozas, 17-VI-1988, B. Valdés & al. (G 104090). **Ávila:** Arévalo, 20-VI-1971, J. Gómez (MA 432025). Castronuevo, 19-VI-1984, Barrera & al. (MA 314814, SALA 34644). Hoyocasero, Cueva del Moragato, 15-VI-1985, M. Luceño & P. Vargas (MA 407310). Hoyos del Espino, Las Chorreras, 9-VII-1988, Aizpuru & al. (MA 451362). Piedralaves, La Adrada, 22-VI-1982, F. de Diego Calonge (MA 538909, MA 538611). Poyales del Hoyo, 30-VI-1917, J. Cuesta (MA 121528). Ramacastañas, Cerro de las Cuevas del Águila, 30-V-1987, Vargas (MA 655999). Sierra de Ojos Albos, Los Regajales, 3-VII-1984, A.R. Burgaz & al. (MA 389677). Sotillo de la Adrada, 15-VI-1973, G. López & E. Valdés Bermejo (MA 430972). Valle de Iruelas, 12-VI-1956, C. Vicioso (MA 170174). Venta del Obispo, 20-VI-1945, A. Caballero (MA 121586). Villanueva de Gómez, 19-VI-2003, M. Ladero (SALA 108263). Valle de Amblés, Villatoro, 12-VII-1974, Ladero & Fuertes (SALAF 23155). **Badajoz:** Campanario, V-1911, V. Lagares (MA 121534). Castuera, 14-IV-2001, P. Escobar García (MA 707044). El Berrocal, 25-V-2001, P. Escobar García (MA 707042). El Toril, V-1951, Moreno Márquez (SEV 5005). Mérida, embalse de Proserpina, 16-IV-1994, F. Amich & al. (MA 717798). Oliva de la Frontera, 23-IV-1994, F. Amich & al. (MA 717195). Sierra del Palenque, 7-V-2000, P. Escobar

- García* (MA 766400). Talarrubias, 19-V-2001, *P. Escobar García* (MA 707043). Valdecaballeros, 17-III-1977, *M. Figueroa & al.* (MA 269851). **Burgos:** Aranda de Duero, V-1942, *A. Caballero* (MA 121572, MA 121526). Cardañajimeno, 21-VI-1914, *C. Pau* (MA 121533). Ciruelos de Cervera, pie del Alto de la Cabeza, 11-VII-1979, *Pons Sorolla & Susanna* (G 104082, MA 413025). De Quintanar de la Sierra a Neila, 1-VII-1925, *M. Losa* (MA 433608). La Revilla, camino de Ahedo, 17-VII-1979, *Muñoz Garmendia & al.* (G 104085, MA 414202). Miranda de Ebro, 15-VI-1912, *H. Elías* (MA 433606). Santa Gadea del Cid, 11-VII-1915, *H. Elías*, in *F. Sennen*, *Plantes D'Espagne*, n° 2447 (MA 121573). Tejada, Pico Valdosa, 3-VII-1979, *J. Fernández Casas & al.* (G 104084). **Cáceres:** Baños de Montemayor, 15-IV-1944, *A. Caballero* (MA 121543). Barrado, 19-V-1988, *A. Amor* (SALAF 16729, SALAF 23633). Cañaveral, cerro de Cabezarrubias, 14-V-1988, *Ladero & Santos* (SALAF 16506). Casatejada, Las Cabezas, Sexta Suerte, Arroyo de Fresno, 7-V-1983, *Ruiz Téllez* (SALAF 6774). En las bajadas de Puerto Viejo, hacia Valverde del Fresno, 23-V-1982, *A. Valdés Franzi* (SALAF 12190). Guadalupe, 16-VI-1948, *A. Caballero* (MA 121539). Hervás, 12-X-1987, *R. González* (SALA 101150). Jaraíz de la Vera, Las Costeras, 19-V-1988, *A. Amor* (SALAF 16703). La Bazagona, 1-V-1983, *Ruiz Téllez* (SALAF 6775). Losar de la Vera, Valle del Tiétar, 20-III-1980, *Meana & al.* (MA 393441, SANT 18476). Mirabel, 4-V-1980, *D. Belmonte* (MA 344687). Montánchez, Sierra de Montánchez, carretera a Cerro Moro, 20-VI-1998, *S. Castroviejo* (MA 613395). Navalморal de la Mata, 25-V-1984, *Ruiz Téllez* (SALAF 10761, MA 680829). Plasencia, 19-V-1988, *Ladero & al.* (SALAF 16507). Puerto de Hoyos, 17-VII-1978, *A. Valdés Franzi* (SALAF 12191). Puerto de Santa Clara, San Martín de Trevejo, 28-VI-1983, *M. Ladero & A. Valdés* (SALA 114203, SALAF 12192). Santiago de Alcántara, 26-IV-1994, *F. Amich & al.* (MA 718573). Sierra de San Pedro, 17-V-1909, *M. Gandoger* (G 104144). Torrecillas de la Tiesa, 22-V-1999, *L. Medina* (MA 624469). Valle del Jerte, 18-VI-1975, *Carrasco & Castroviejo* (SALA 25804). **Cádiz:** Algodonales, Sierra de Lijar, 11-VII-1980, *A. Aparicio & al.* (SEV 57983). Aprox. 5 km al E de Vejter de la Frontera, entre los pinos a lo largo de la carretera, 28-IV-1975, *S. Holmdahl* (MGC 50213). Bornos, 28-IV-1978, *B. Molesworth Allen* (SEV 53284). Chiclana de la Frontera, 22-V-1982, *A. Charpin & C. Defferrand* (G 104083, MA 243115). Grazalema, Puerto de las Palomas, 10-VI-1993, *A. Aparicio & al.* (MA 526987). Jeréz de la Frontera, 17-V-1985, *A. Asensi & J. Cuenca* (MA 570487). Los Barrios, Barranco del Arroyo de Valdeinfierno, 28-V-1978, *J. Fernández Casas* (G 104086, MA 226312, SALA 22564). Puerto de Santa María, Chiclana, et pr. Grazalema, V-1895, Porta & Rigo, *Iter IV Hisp.* 1895: 321 (G 104107). Sierra de Palma, 19-VII-1887, *E. Reverchon*, in *E. Reverchon*, *Plantes de L'Andalousie*, 1887: n° 17 (MA 121509). Tarifa, Sierra de Saladavieja, El Carrascal, 22-VII-1980, *J. Arroyo & J.M. Gil* (SEV 64621). Ubrique, 30-V-1972, *S. Holmdahl* (MGC 50212). **Cantabria:** Valderredible, páramo de la Lora, 2-IX-1983, *E. Oriente* (MA 683841, MA 599290). **Ciudad Real:** Argamasilla de Calatrava, finca La Laguna de las Carboneras, 13-V-2001, *M. Bellet & al.* (MA 711976). Cabezarrubias del Puerto, 22-V-1998, *R. García Ríos* (MA 711940). Casas del Río, Navalagruña, 1-VI-2001, *S. Castroviejo & M. A. Carrasco* (MA 692324). Sierra de Alhambra, 30-IV-1933, *González Albo* (MA 121583). Sierra Madrona, 29-V-1950, *S. Rivas Goday & J. Borja* (SALA 376). Sierra Morena, Venta de Cárdenas, 30-IV-1933, *J. Cuatrecasas* (MA 121520). **Córdoba:** Belalcázar, finca de Pedroche, 8-VII-1976, *J.A. Devesa* (SEV 33720). Cardaña, finca de Yegüerizo (UH-83), 30-V-1976, *J.A. Devesa* (SEV 33723). Torrecampo, ribazos del río Guadadora, 16-V-1976, *J.A. Devesa* (SEV 33388). Trassierra, 14-V-1982, *J. Arroyo* (SEV 87091). Villaviciosa de Córdoba, Tres puentes, V-1920, *C. Pau* (MA 121518). **Cuenca:** Ródenos de Cañete, 9-VI-1971, *E. Valdés Bermejo & al.* (MA 431991). Talayuelas, 18-VI-1979, *G. Mateo* (MA 256531). **Granada:** Cañar, Bco. río Chico, 20-VII-1979, *J. Molero Mesa* (MA 432023). Capileira, 3-VII-1948, *Viéuter* (SANT 211). In arenosis Regn. Granat. a littore, 1837, *E. Boissier* (G 104111). Jatar, Sierra Almijara, supra Jatar, 11-VI-1983, *B. Cabezu-do & J.M. Nieto* (MGC 41527). Puerto de la Ragua, cruce con la carretera a la Alpujarra, 19-VI-1988, *B. Valdés & al.* (G 104089). Sierra Nevada, 21-VII-1879, *Huter & al.* *Extinere hispanico* 1879: 234 (G 104137); ibidem, Cañar, 28-VII-1930, *C. Vicioso* (MA 121558). **Guadalajara:** Campillejo, VII-1973, *Demetrio* (FCO 4103). Cantalojas, Valle del Lillas, 20-VI-1985, *Burgos & Cardiel* (MA 487000). Checa, 25-VI-1997, *L.M. Ferrero & L. Medina* (MA 595634). El Pedregal, VII-1894, *J. Benedicto* (MA 121566). La Fuensaviñán, 26-V-1994, *J. Castillo & al.* (MA 543882). Prado Redondo, Monte del Condado (MA 153134). Valverde de los Arroyos, 13-VII-1998, *F. Lamata* (MA 615546). Guadalajara, VI-1994 (MA 546347). **Huelva:** Almonte, 28-IV-1943, *C. Vicioso* (MA 121510); ibidem, 12-V-2006, *A. Quintanar* (MA 772195). Ayamonte, 5-V-1902 (MA 121515). Calañas, 28-IV-1921, *Gros* (MA 121513). Chucena, Cerro de las Palomas, 19-IV-2001, *B. Cabezu-do & al.* (MGC 48566). Higuera de la Sierra, 24-V-1988, *E. Bayón & E. Villanueva* (MA 438689). Hinojos, 26-V-2004, *J. Cano-Maqueda & al.* (SEV 216214). La Barra de Huelva, 22-IV-1943, *C. Vicioso* (MA 121512). Sierra de Aracena, Aracena, 15-V-1979, *J. Rivera* (SEV 48340). **Jaén:** Andújar, El Abogado, 11-V-1985, *E. Cano* (MA 716641). Baños de la Encina, mina Matababras, 23-IV-1988, *C. Fernández & al.* (FCO 21720, G 104155, MA 553899, MGC 38654, SALA 59048, SANT 29973). Guarromán, camino hacia la mina de los Dolores, 5-V-1966, *S. Silvestre* (SEV 19712). Sierra Morena, Arroyo de Oruga, 7-VI-1923, *Fernández & al.* (MA 121519). **La Rioja:** Ezcaray, barranco Reoyo, pr. Urdanta, 16-VII-1998, *Gracia-Baquero & al.* (SALA 100212). Ocón, 27-VII-1930 (MA 121531). San Millán de la Cogolla, 16-VII-1981, *S. Castroviejo & Fernández Quirós* (MA 433427). Sierra de la Demanda, de Anguiano a Tabladas, 26-VII-1995, *L. Loidi & A. Berastegui*, in *Lambinon*, *Pl. Europe Occid.-Bas. Méd.*, 1997: n° 17459 (G 104092, MA 589694). **León:** Castroquilame, 12-V-1973, *Andrés & Carbó* (SEV 16643). La Gotera, 8-VII-1944, *Rojas* (MA 121550). Ponferrada, 10-VII-1933, *W. Rothmaler*, in *W. Rothmaler*, *Plantae Hispaniae Boreali-Occidentalis*, n° 128 (MA 121551); ibidem, carretera de San Esteban de Valdeusa a San Pedro de Montes, 21-VI-1981, *Alamillo & Nieto* (MA 317259). Trabadelo, San Fiz do Seo, valle del río Barjas, 18-VII-1998, *Martin-Blanco* (MA 641637). **Lugo:** Tardad, Villalba, 30-VII-1951, *M. Orosa* (G 104101). Villardíaz-Fonsagrada, 22-VII-1953, *E. Carreira* (G 104197). **Madrid:** Madrid, VI-1841, *Reuter* (G 104130, G 104131). Buitrago, 1-VI-1918, *C. Vicioso* (MA 121559). Collines à la base de la Sierra de Gredos, 8-VII-1863, *E. Bourgeau*, in *E. Bourgeau*, *Pl. d'Espagne et de Portugal*, 1863: n° 2442 (G 104127, G 104132, MA 721360, MA 121530, MA 121529, MA 152777). Casa de campo pres Madrid, 7-VI-1854, *E. Bourgeau* (G 104128, G 104145, MA 720519). Chamartín, 17-V, *Isern* (MA 153136). Chinchón, cerros de Butarrón, VI-1919, *C. Vicioso* (MA 121576). El Escorial, VI-1914, *C. Vicioso* (MA 121577). El Pardo, 4-VI-1936, *M. Martínez & A. Rodríguez* (MA 432685). Guadalupe de la Sierra, 29-VI-1983, *F. Gómez Manzaneque* (MA 450150). Hoyo de Manzanares, VI-1998, *A. Izuzquiza & al.* (MA 615516). La Pedriza, V-1932 (MA 432723). Miraflores, 25-VI-1945, *L.C. & A.R.* (MA 201400). Monte del Pardo, 20-V-1917, *C. Vicioso* (MA 121578). Montejo de la Sierra, 2-VII-1954, *A. Rodríguez* (G 104103). Navacerrada, VI-1915, *C. Vicioso & Beltrán* (MA 121580). Puerto de la Cruz Verde, 22-VI-1973, *Rivas-Martínez & Costa* (MA 432036). Robledo de Chavela, 19-VI-1988, *M. Costa Tenorio & H. Sainz Ollero*, in *J. Lambinon*, *Pl. Europe Occ.-Bas. Méd.* 1993: n° 15575 (G 104153, MA 532060, SALA 88527). San Martín de Valdeiglesias, Rozas de Puerto Real, 6-VI-1992, *P. Vargas* (MA 515427). Sierra de Guadarrama, 4-VII-1968, *O. Polunin* (MGC 5003). Sierra de la Cabrera, 4-VII-1993, *A. Izuzquiza & al.* (MA 529567). Torrelaguna, V-1912, *C. Vicioso* (MA 121582). **Málaga:** Benaolán, Sierra del Palo, 27-V-2007, *J. Cano-Maqueda* (SEV 218872). Benarrabá, carril de los Pepes, 29-V-2004, *O. Gavira*

(MGC 60964). Casares, Monte del Duque, 20-V-1988, *B. Cabezudo & A.V. Pérez-Latorre* (MGC 35466). Estepona, 16-V-1919, *E. Gros* (MA 121506). Gaucín, VI-1916, *E. Gros* (MA 121508). Gobantes, garganta de El Gaitán, 11-VI-1930, *C. Vicioso* (MA 121486). Los Villares, 12-V-1988, *B. Cabezudo & al.* (MGC 24576). Ronda, 07-VI-1889, *E. Reverchon*, in *E. Reverchon*, *Plantes de L'Andalousie 1889*: n° 17 (G 104260). Sedella, Los Picaricos, 30-V-2003, *B. Cabezudo & al.* (MGC 60070). Sierra Bermeja, 18-V-1919, *E. Gros* (MA 121507). Sierra Tejada, 26-VI-1982, *J.M. Nieto* (MGC 18110). Tolox, Castañar de los Hornillos, 13-VI-1932, *L. Ceballos* (MA 121505). Torrox, VI-1909, *Domingo* (G 104138). **Orense**: Lovios, 6-VI-1993, *I. Pulgar* (FCO 21431, MA 551003). Serra do Invernadeiro, entre Rocín y Suacenza, 11-VII-1973, *S. Castroviejo* (G 104080). **Salamanca**: Cantalapiebra, 25-V-1987, *X. Giráldez & Aragón* (SALA 46173). Ciudad Rodrigo, 4/6-VII-1932, *C. Pau* (MA 121549). Embalse del río Águeda, 6-VI-1976, *E. Rico* (SALA 9431). Entre Fuentes de Béjar y Navas de Béjar, 21-VI-1978, *J.A. Devesa & J. Pastor* (SEV 39776). Entre La Alberca y Sotoserrano, 20-VII-1972, *Fernández Díez* (SALA 5451). Guijuelo, 7-VI-1987, *E. Rico & J. Serradilla* (MA 476539, SALA 46836). Hurdes, 5-VII-1946, *A. Caballero* (MA 121547). Ledesma, 19-V-1976, *J. Sánchez* (SALA 17419). Linares de Riofrío, VII-1980, *J. L. Fernández Alonso* (MA 519040). Masueco, laderas del río Uces, 16-VI-1976, *F. Amich* (SALA 15517). Monleras, 22-X-1976, *J. Sánchez* (SALA 17428). Montemayor del Río, 3-VII-1983, *A. Guillén* (SALA 36167). Navacarros, 15-VII-1983, *F. Amich & F. Herrero* (SALA 34909, SALA 34910). Pelabravo, 2-VI-1990, *A. Pastor* (SALA 57034). Peñamecer, 23-V-1976, *J. Sánchez* (MA 219749, SALA 17427). Puerto Seguro, 9-V-1976, *E. Rico* (SALA 9432). San Esteban de la Sierra, 20-VI-1971, *Fernández Díez* (SALA 5595). Topas, 9-VI-1967, *B. Casaseca* (SALA 375). Valdelageve, 28-IV-1996, *J. Barrios Pérez* (SALA 121888, SALA 121889). **Segovia**: Aguilafuente, Cotarra de Juriñas, 6-VI-2002, *M. Pérez Valero* (MA 756780). Entre Riaza y Ayllón, cruce de la carretera hacia Pajares del Fresno, 28-V-1992, *A. Izuzquiza* (MA 508024). Fresno de la Fuente, 20-VI-1985, *A. Izuzquiza* (MA 348898). Fuentidueña, 15-VI-1983, *T. Romero* (SALA 40297). Lastras de Cuéllar, Molino Ladrón, 24-V-1998, *P. Bariego Hernández & A. Gastón González* (MA 754632). Ochando, 19-VI-2002, *M. Sanz Elorza* (MA 687112). Puerto de los Cotos, 5-VII-1989, *A. Charpin & P.A. Loizeau* (G 104151). Riofrío de Riaza, 7-IX-1975, *F.J. Fernández Casas* (MA 347715). Sigüero, 1-VII-1983, *T. Romero* (MA 567697). Torrecilla del Pinar, 12-VII-1984, *T. Romero* (SALA 40298). **Sevilla**: al S de Villamanrique de la Condensa, 7-V-1988, *E. Bayón & al.* (MA 438338). Aznalcázar, 20-IV-2003, *Z. Díaz* (MA 707168). Castilblanco de los Arroyos, Los Melonares, 1-VI-2006, *J. Cano-Maqueda & al.* (SEV 218870). Constantina, Hermita Virgen de Robledo, 1-VI-2006, *J. Cano-Maqueda & al.* (SEV 218869). Dehesa de Covarrubias, 6-IV-2001, *B. Cabezudo & al.* (MGC 48568). Gerena, 3-V-2001, *B. Cabezudo & al.* (MGC 48568). Paradas, 5-V-1933, *C. Vicioso* (MA 121517). **Soria**: Berlanga de Duero, 18-VI-1977, *A. Segura Zubizarreta* (G 104087, MA 226315, SALAF 437, SEV 74840). Canredondo, 22-VI-1990, *A. Segura Zubizarreta* (MA 581101). Cañón del río Lobos, 30-VI-1983, *A. Buades* (MA 504440). Carbonera de Frentes, 2-VII-1989, *A. Charpin* (G 104152). Herrera de Soria, 30-VI-1983, *A. Buades* (MA 504408). Molinos de Duero, 21-VIII-1987, *G. Mateo* (MA 383713). Quintana Redonda, 30-VI-1974, *A. Segura Zubizarreta* (SEV 41098). Tozalmoreno, 6-VII-1935, *C. Vicioso* (MA 121527). **Teruel**: Orihuela del Tremedal, 18-VI-1907, *C. Pau* (MA 433607). Segura de los Baños, VII-1894, *J. Benedicto* (MA 121566b). **Toledo**: Almorox, El Pinar, 3-VII-1982, *M. Luceño* (MA 430416). Nacimiento del río Estena, 19-VI-1986, *J. Assens & al.* (MA 430409). **Valladolid**: Castronuño, Sendero de los Ladrones, 22-V-1988, *G. Balbás* (SALAF 23342). Pedrajas de San Esteban, 7-VII-1975, *F.J. Fernández Díez* (FCO 4601, SALA 7575). **Zamora**: Aspariegos, La Salgada, 10-V-1990, *R. García Ríos* (SALA 54046). Corrales, 15-VI-1951, *Casaseca* (SANT

5565). Cubo del Vino, 19-VI-1981, *X. Giráldez* (SALA 31612). Escober, Los Linares, 15-VII-1996, *P. Bariego Hernández* (MA 651736). Lago de Sanabria, 25-VIII-1953, *A. Rodríguez* (MA 201347). San Cebrían de Castro, El Barrucal, 28-V-1990, *R. García Ríos* (SALA 54048). Villaseco del Pan, La Era del Campo, 30-IV-1988, *R. García Ríos* (SALA 54047). **Zaragoza**: Atea, 29-V-1909, *C. Vicioso* (MA 121565). Calatayud, VI-1987, *C. Vicioso* (MA 121560). Moncayo, 19-VII-1893, *C. Vicioso* (MA 121560). Belmonte, 4-V-1931, *Gros*, in *F. Sennen*, *Plantes d'Espagne 1932*: n° 8206 (G 104149, MA 121514).

3. *Campanula cabezudo* Cano-Maqueda & Talavera in Acta Bot. Malacitana 32: 254. 2007

C. decumbens var. *pseudospecularioides* G. López in Bol. Soc. Brot. ser. 2, 53: 301 (1979-1980) [syn. subst.]. Ind. loc.: "Habitat locis umbrosis, inter rupes calcareas, loco dicto Boquete de Zafarraya, Sierra Tejada (Málaga-Granada), ubi cum *P. Cubas* et *J.M. Moreno*, die 28-VI-1976, legi. Holotype: MA 210975, Fig. 7; Isotype: MA 210994".

Illustrations: Gallego (1987: 564, as *C. decumbens*);



Fig. 7. Holotype of *Campanula cabezudo* (MA 210975).

Sáez & Aldasoro (2001: 130, fig. 39a, as *C. lusitanica* subsp. *lusitanica*); Fig. 4 E, F.

Herb 8-30(45) cm, annual, decumbent, branched from the base, pubescent, not brittle. Stems slightly angled, branched, pubescent, sometimes glabrescent at the apex, with setose hairs of 0.1-1.4 mm. Leaves subcoriaceous, entire or toothed, petiolate; middle cauline leaves 6.2-18.2 × (2.9)5-9 mm, petiolate, elliptical, ± pubescent, with hairs to 1.1 mm, with petioles up to 2 mm; upper cauline leaves 4.5-14.5 × 1.3-3.9 mm, oblanceolate, ± hairy, with hairs up to 1.2 mm, with petioles of *c.* 0.5 mm. Inflorescence laxly paniculate. Flowers pedicellate; pedicel (9.8)20-68 mm, glabrous or setose, with hairs of 0.1-0.7(1.5) mm. Calyx-teeth (4)5-11 × 0.4-1.2 mm, lanceolate or linear. Corolla (7.3)8-16 mm, infundibuliform, with the tube shorter than the lobes; tube 3.1-6.9 mm, white; lobes (3.6)5-10.3 × 3.1-6.2 mm, elliptic, blue, with three purple nerves. Stamens with enlarged base of 0.6-1 × 0.5-0.7 mm, deltoid; filaments 0.4-0.5 mm; anthers (2.5)3-6.4 mm, whitish. Ovary densely hispid, with setose hairs 0.2-1.8 mm; style (5)7-12.3 mm, hairy in the

upper half; stigma trifid, with stigmatic branches 1-1.7 mm, patent, arched, white. Capsule 2.1-5.9 × 2.2-5 mm, subspherical or ovoid, generally wider than long, densely hairy, with papillose hairs up to 1.5 mm, with 10 nerves ± acute but not winged, dehiscing by three apical pores. Seeds 0.5-0.6 × 0.2-0.3 mm, ovoid, shining, yellowish to brown. $2n = 20$.

Habitat, phenology and distribution: Fissures of calcareous rocks; 400-1600 m. VI-VII. •Endemic to the Sierra Subbética from Seville to Jaén, and the Penibética, where it is very frequent, especially in the Sierra de Loja and Tejada (Fig. 8). **Spain:** Ca Co Gr J Ma Se.

Observations: Sáez & Aldasoro (2001) comment with reference to *C. decumbens* var. *pseudospecularioides* G. López: “existen formas intermedias entre esta subespecie [which they refer to *C. specularioides*] y *C. decumbens* [which they refer to *C. dieckii*], que han recibido reconocimiento taxonómico”. It is very likely that they are referring to *C. cabezudo*. In fact, the vegetative characters of decumbent habit and the presence of petiolate middle leaves of the stem,

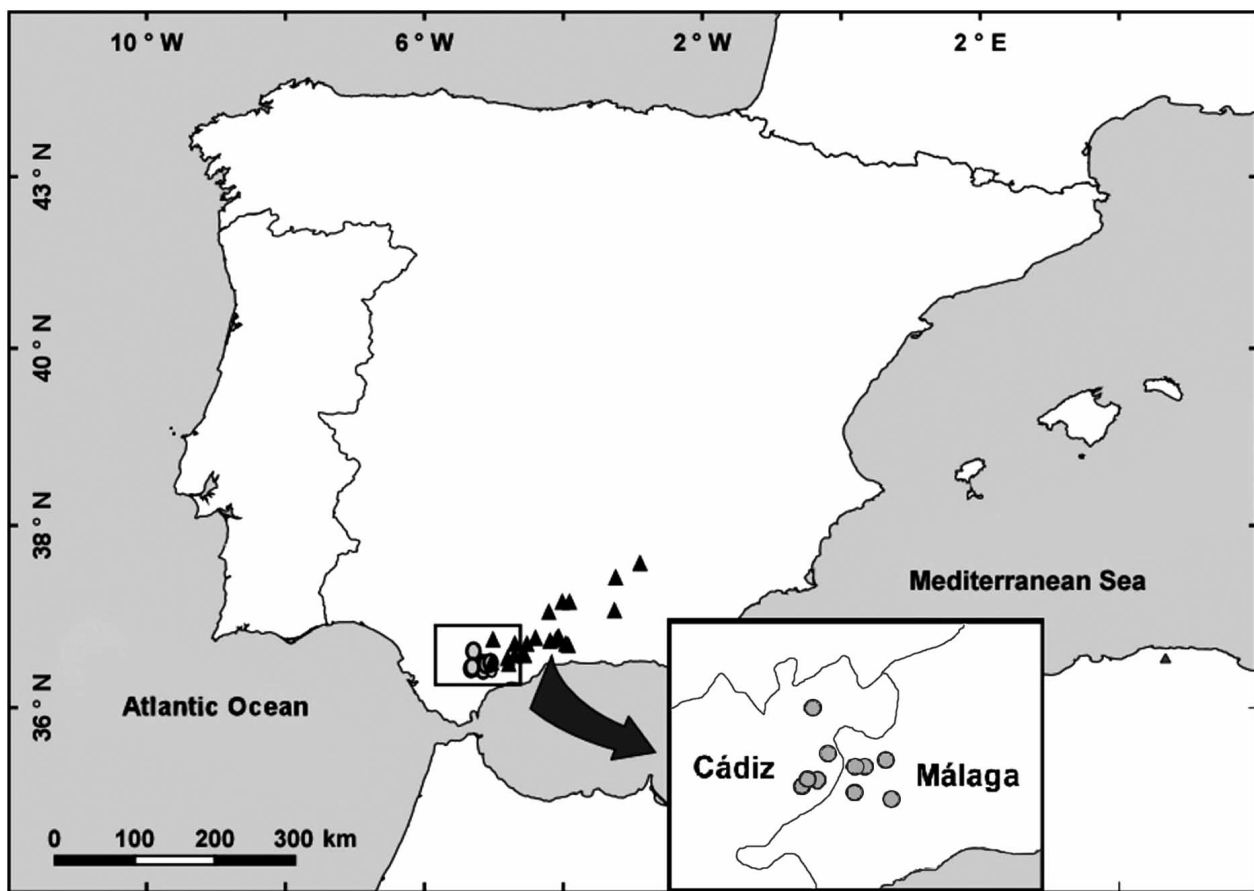


Fig. 8. Distribution map of *Campanula cabezudo* (▲) and *C. specularioides* (○).

are similar in *C. cabezudo* and *C. decumbens*, but *C. cabezudo* has hairy style in the upper half and a single trifold stigma with curved and patent stigmatic lobes, while *C. decumbens* has a glabrous style and three straight and erect-patent stigmas. Moreover, in the topology of the ITS analysis, *C. cabezudo* and *C. decumbens* are in two different clades (Fig. 1) and they have different chromosomes number (Table 1, Fig. 2).

Selected specimens

SPAIN. Cádiz: Grazalema, Puerto de las Palomas, El Pinar, 5-VII-1984, *A. Aparicio* (SEV 161693). **Córdoba:** Almedinilla, Sierra de Albayate, 7-VI-1980, *J. Muñoz* (MA 749306). Priego de Córdoba, Sierra Horconera, 4-VII-1980, *J. Muñoz & R. Tormo* (MA 749309). Rute, Sierra de Rute, Pico Las Cruces, 26-VI-1978, *J. Muñoz* (MA 749308, SEV 161894). **Granada:** entre Venta de Zafarraya y Zafarraya, Sierra Gorda, VI-2007, *Cano-Maqueda & al.* (SEV 218873). Sierra Harana, cercanías de la Cueva del Agua, 16-VI-1982, *Casares & al.* (MA 432054). Sierra Tejada, 7-VII-1935, *M. Laza* (MA 121470). **Jaén:** Mágina, 3-VII-1925, *J. Cuatrecasas* (MA 121522). Sierra de Cazorla, El Tranco, 30-VI-1988, *S. Talavera & al.* (G 104061, SEV 161662). **Málaga:** Alfarnate, Sierra de la Torca, 7-VI-2006, *B. Cabezudo & al.* (MGC 63804). Álora, Sierra de Huma, 26-VI-1986, *B. Cabezudo & R. Suan* (MGC 36711). Antequera, 14-VI-1930, *C. Vicioso* (MA 121488). De Ronda a El Burgo, 18-VI-1972, *L. Bernardi* (G 104157). Los Alazores, Puerto de los Alazores, Sierra de Alhama, Tres Mogotes, 5-VII-1973, *B. Cabezudo & B. Valdés* (SEV 161891). Puerto del Viento, 29-VI-1849, *E. Bourgeau* in Bourgeau, Pl. Espagne 1849: n° 320 (G 104256). Sierra Prieta, 07-VI-1879, *Hunter, Porta & Rigo* in Iter. Hisp. 1879: n° 232 (G 104184). Ronda-Sierra de las Nieves, entrando al Sabinar, Monte de la Peineta, 19-VI-1974, *S. Talavera & B. Valdés* (SEV 161889). Sierra de Peñarrubia, 12-VI-1930, *C. Vicioso* (MA 121487). Valle de Abdajalís, cortado del Cuervo, 15-VI-1973, *S. Talavera & B. Valdés* (SEV 161888). Villanueva del Rosario, Sierra Camorolos, 5-VII-1973, *B. Cabezudo & B. Valdés* (SEV 161887). Yunquera, P. N. Sierra de las Nieves, entre el Puerto Bellina y el cruce del camino con la Cañada de los Hornillos, 18-VI-1998, *B. Cabezudo & al.* (MGC 46750). **Sevilla:** Algámitas, Sierra del Tablón, 5-VII-1978, *B. Cabezudo & E. Ruiz de Clavijo* (SALA 13425, SEV 31778).

4. *Campanula specularioides* Coss., Notes Pl. Crit.: 41. 1849

C. lusitanica subsp. *specularioides* (Coss.) Aldasoro & L. Sáez in Anales. Jard. Bot. Madrid 59: 173. 2001. Ind. loc.: "In fissuris rupium regionis montanae regni Granatensis, loco dicto Cortijo blanco prope Ronda, a Bourgeau inventa". Type: Spain. Málaga, Ronda, Cortijo Blanco, 20 June 1849, *Bourgeau s.n.* [Pl. D'Espagne, 1849] (lectotype, here designated, P 185468!, Fig. 9; see observations).

Illustrations: Gallego (1987: 565); Sáez & Aldasoro (2001: 130, fig. 39i-m, as *C. lusitanica* subsp. *specularioides*); Fig. 10 A, B.

Herb 6-26 cm, annual, decumbent, branched from the base, glabrous or glabrescent, very brittle. Stems

angled, branched, glabrous, rarely with setiform hairs to 1.2 mm. Leaves fleshy, entire or toothed, petiolate; middle cauline leaves 7.5-13.4 × 4.5-20 mm, broadly elliptical, glabrous or glabrescent, with hairs 0.1-0.2 mm, and petiole 1-6.4(14) mm; upper cauline leaves 3.5-14.5 × (1)1.9-6.4 mm, elliptic, glabrous, with petiole 0.4-1.7 mm. Inflorescence laxly paniculate. Flowers pedicellate; pedicel (5.7)7-35 mm, glabrous or setose hairs 0.1-0.8 mm. Calyx-teeth (1.7)3-7.6 × 0.7-1.5 mm, oblanceolate. Corolla (6.6)8-10(14) mm, broadly infundibuliform, with the tube shorter than lobes; tube 2.6-4.9 mm, whitish; lobes 4.1-7.5(10.3) × 2.2-5.4 mm, elliptical, pinkish or bluish, with three purple nerves. Stamens with enlarged base of 0.5-1 × 0.2-0.5 mm, deltoid; filaments 0.6-0.8 mm; anthers 2.1-3.2 mm, blue or whitish. Ovary glabrous, rarely densely hairy; style (4.7)6-7.3(8.5) mm, hairy in the upper half; trifold stigma, with stigmatic branches 0.6-1(1.4) mm, patent, curved, white or blue. Capsule 2-3 × 3-4.5 mm, subspherical, wider than long, with 10 sub-winged, glabrous nerves, rarely with setose hairs up to 1.5 mm, dehiscing by three pores of middle position.

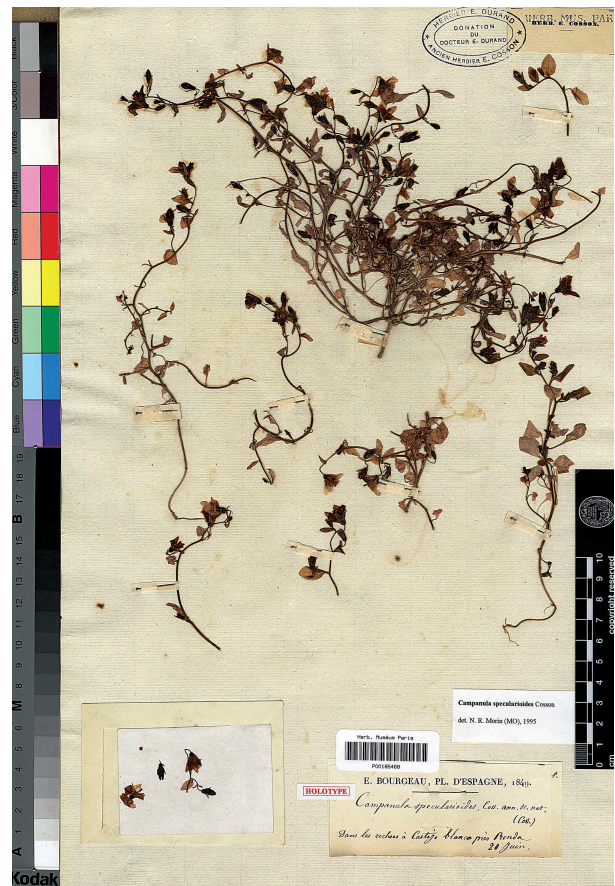


Fig. 9. Lectotype of *Campanula specularioides* (P 185468, herb. Cosson).

Seeds 0.5-0.7 × 0.2-0.3 mm, ovoid, shining, yellowish to brown. $2n = 20$; $n = 10$.

Habitat, phenology and distribution: In crevices in walls or limestone rocks; 500-1650 m. V-VI(VII). •En-

demio to Sierra de Grazalema and Serranía de Ronda (Fig. 8). **Spain:** Ca Ma.

Observations: Despite its narrow distribution, this species is markedly variable in the colour of anthers

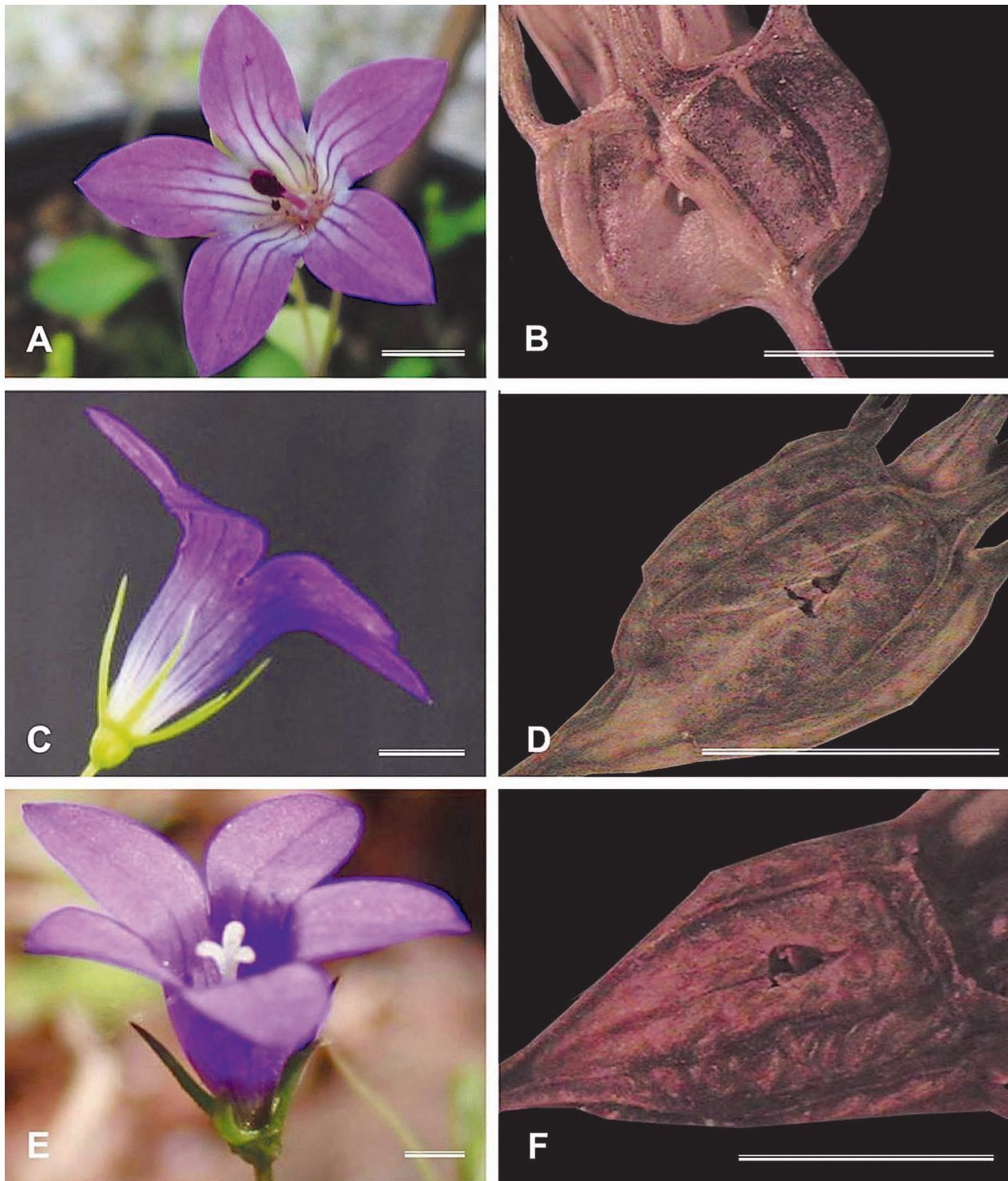


Fig. 10. Flowers and fruits of *Campanula* species. **A, B, C.** *specularioides* (Montejaque, Málaga, Spain, SEV 218871); **C, D.** *transtaganana* (Valverde del Camino, Huelva, Spain, SEV 216212); **E, F.** *broussonetiana* (Jbel Tazzeke, Taza, Morocco, SEV 216476). The scale bar = 3 mm.

and stigmas, and in the indumentum of calyx and capsule. since both can be very hairy or completely glabrous, even in the same population, although more commonly all plants of a population have glabrous calyx, and likewise the capsule. Within populations there are plants with white anthers and stigmas, and others with blue anthers and stigmas, or even plants with white anthers and blue stigma or vice versa. All these colour morphs, which certainly have a genetic basis, seem to be interfertile so this trait has little taxonomic value. Based on the middle position of the pores in the capsule, this species was included by Fedorov (1976) in the sect. *Campanula*. The phylogenetic tree of nr DNA ITS shows that *C. transtagana* and *C. broussonetiana* are sister species of *C. specularioides* (see Fig. 1).

The type material of *C. specularioides* consists of three complete plants and several fragments. The largest of the three plants, placed at the top of the sheet was chosen as lectotype, since it is consistent with the description of E. Cosson (see Fig. 9). In the general herbarium of the “Conservatoire et Jardin Botanique de Genève” there is a sheet (G 104263) with several plants of the same collection of E. Bourgeau, that are also possible type materials.

Selected specimens

SPAIN. **Cádiz:** Benaocaz, Km 16-17 a Ubrique, 22-VI-1984, A. Aparicio & J. G. Rowe (MA 490917, SEV 161738). Entre Benaocaz y Ubrique, 13-VII-1978, J. Devesa & al. (MA 465708, MA 111772, SEV 103546). Entre Ubrique y Grazalema, 13-VI-1970, E.F. Galiano & B. Valdés (SEV 108955). Entre Villaluenga del Rosario y Benahocaz, 26-VI-1988, Fernández Díez & Mochales (SALA 47474, MA 476540). Grazalema, 21-VI-1890, E. Reverchon, in E. Reverchon, *Plantes de L' Andalousie*, 1890: n° 331 (G 104191). Idem, 9-VII-2003, J. Cano-Maqueda (SEV 216211). Cerro de San Cristóbal, V-1961, J. Borja (MA 177095, SEV 5016). Manga de Villaluenga, 22-VI-1983, A. Aparicio & J.G. Rowe (SEV 161737). Sierra de la Silla, 21-VI-1983, A. Aparicio & S. Silvestre (G 104188, MA 490918, SEV 161731). Sierra de Zafalgar, Puerto de la Miera, 28-VI-1984, A. Aparicio & al. (SEV 161726). Sierra del Caillo, Navazo Alto, 30-VI-1983, A. Aparicio (SEV 161730). Sierra del Endrinal, Pozo de las Presillas, 12-VII-1984, A. Aparicio & S. Silvestre (SEV 161736). Ubrique, 26-VI-1925, P. Fonti Quer & E. Gros (MA 702195, MGC 53268, SALA 114797). Villaluenga del Rosario, 24-VI-1973, A. Asensi & B. Díez (MGC 81). **Málaga:** Benaoján, 17-VI-2007, J. Cano-Maqueda (SEV 218871). Cartajima, Cancha Almola, 12-VI-2004, O. Gavira (MGC 60974, MGC 60975). De Ronda a Montejaque et circa Cueva de la Pileta, 17/18-VI-1972, L. Bernardi (G 104194, MA 269887). Jimera de Líbar, Alto del Conio, 4-VII-2004, O. Gavira (MGC 60868). Montejaque, 8-VI-2005, J. Cano-Maqueda (SEV 216210). Serranía de Ronda, 23-VII-1888, E. Reverchon, in E. Reverchon, *Plantes de L' Andalousie*, 1889: n° 331 (G 104264, G 104185, G 104186, G 104187, G 104192, G 104193, LISU 50130, MA 121476, MA 121477).

5. *Campanula transtagana* R. Fern. in Bot. Soc. Brot. ser. 2, 36: 121-126. 1962

C. lusitanica subsp. *transtagana* (R. Fern.) Fedorov in Bot. J. Linn. Soc. 67: 281. 1973. Ind. loc.: “Habitat in Lusitania, regione Transtagana, ad marginem sinistram fluminis Tagis pr. pagum dictum Vila Velha de Ródão, ubi super declives solo argilloso et sicco inter sepes copiosa, 21-VI-1959, A. Fernandes, J. Matos & A. Sarmiento 2923 (COI, holotype)”, (Fig. 11; see observations).

C. loeflingii var. *filiformis* Lange in Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1861: 108. 1862. Ind. loc.: “La Carolina (Sierra Morena) 10 Mai.”. Type : not found in the Lange herbarium (C).

Illustrations: Fig. 10 C, D.

Herb 6-45 cm, annual, decumbent or erect, branched from the base, rarely in the upper half, very laxly pubescent, not brittle. Stems angled, branched, glabrescent, with hairs 0.1-0.2, commonly very laxly located in the stem angles. Leaves not coriaceous, crenate, entire or toothed, petiolate; middle cauline leaves (4.6)9-20(30) × 2.2-8(13.2) mm, elliptic, laxly pubescent, with hairs 0.1-0.3 mm scattered over the limb and margin of the leaf, and with petiole 0.2-4.5



Fig. 11. Holotype of *Campanula transtagana* (COI).

mm; upper cauline leaves (3)5-11(15) × 0.6-3.4 mm, elliptic, laxly pubescent, with hairs 0.1-0.3 mm scattered over the limb and leaf margin, and with petiole 0.2-0.3 mm. Inflorescence laxly paniculate. Flowers pedicellate; pedicel 9.6-64 mm, glabrous or with some hairs of *c.* 0.5 mm. Calyx-teeth (2.9)3.5-16.6 × 0.3-0.7 mm, linear. Corolla (6.5)8-12(14) mm, campanulate, with the tube greater or equal, rarely shorter, than the lobes; tube (2.9)3.7-7 mm, light blue with a white base; lobes 3.6-7 × 2.2-3.5 mm, elliptic, bluish. Stamens with enlarged base of 0.5-1 × 0.3-0.6 mm; filaments 0.2-0.6 mm; anthers 1.6-2.7 mm, whitish. Ovary glabrous, rarely with setose hairs 0.1-0.2 mm; style 4.5-6.4 mm, hairy in the upper half; stigma trifid, with estigmatic branches 0.6-1.2 mm, patent, curved, white. Capsule 2-4.4 × 1.5-3 mm, subovoid or subspherical, longer than wide, glabra, rarely with some setose hairs of 0.1-0.2 mm, with 10 angled nerves, but not winged, dehiscent by three pores of middle or subapical position. Seeds 0.4-0.6 × 0.1-0.2 mm, ovoid, shining, yellowish to brown. $2n = 20$; $n = 10$.

Habitat, phenology and distribution: Wet grasslands on sandy or slate-rich substrates; 50-800 m. V-VI (VII). • Endemic to SW Iberian Peninsula, from the River Tajo to the Guadiana, Sierra de Guadalupe and almost all Sierra Morena (Fig. 12). **Portugal:** AAL Ag BAI BB. **Spain:** Ba Cc Co H J Se.

Observations: *C. transtagana* is rare in Portugal and in Sierra de Guadalupe but very common throughout the Sierra Morena, especially in shady slopes and valley bottoms, where it normally co-habits with *C. matritensis*. The profuse branching, small corollas with white background tube and petiolate leaves of the stem, clearly differentiate it from *C. matritensis*.

The holotype of *C. transtagana* consists of five cultivated plants that are very branched from the base, between 20 and 35 cm, and placed on three sheets in Coimbra herbarium.

Selected specimens

PORTUGAL. Algarve: Serra da Picota, VII-1891, *J. Brandeiro* (COI). **Alto Alentejo:** Redondo, V-1892, *A. Fernandes & al.* (COI). Idem, VI-1893, *A. Fernandes & al.* (COI). Riveira da Sapatoa, a 5 km de Montoito e a 16 de Reguengos de Monsaraz, 10-VI-1962, *A. Fernandes & al.* (COI). **Baixo Alentejo:** Concelho de Moura, margens do rio Guadiana, 2-IV-1999, *P. Bringe & T. Rego*, in *Exsiccata Flora Iberomacaronésica Selecta*, centuria IV: n° 340: (FCO 25015, MA 632684, SALA 99329, SANT 42025). Entre Eiras Altas e Cláudia, 11-VI-1962, *M. da Silva* (LISE 76991, MA 199926). Margem da ribeira de Chança, prox. Vila Verde de Ficalho, 11-VI-1962, *A. Fernandes & al.* (COI). **Beira Baixa:** Encosta da margem esquerda do Tejo, entre a estrada e o rio Tejo, 8-VI-1962, *A. Fernandes & al.* (COI). Salvaterra do Extremo, 14-VI-2005, *A. Charpin* (G 104159).

SPAIN. Badajoz: Don Benito, La Zafrilla, 28-VI-1985, *M.J. Gallego* (SEV161715). Magacela, El Berrocal, 25-V-2001, *P. Esco-*

bar García (MA 707042). Oliva de la Frontera, riberas del río Ardilla, 23-IV-1994 *VI itinera Mediterranea n° 557* (MA 717195). **Cáceres:** Guadalupe, 31-V-1958, *E. Guinea* (MA 432639). **Córdoba:** Alcolea, margen derecha del Guadalquivir, 21-V-1987, *Z. Díaz & C. López* (SEV 130952). Cardeña, 24-VI-2005, *J. Cano-Maqueda & al.* (SEV 216480). Entre Azuel y el río de las Yeguas, 28-V-1982, *J. Devesa & García* (SEV 161896). Entre Montoro y Adamuz, proximidades a Montoro, 4-V-1982, *M.J. Díez & I. Fernández* (SEV 161898). Río Zújar, cruce con la carretera Los Blázquez-Peraleda de Zaucejo, 6-VI-1979, *J.M. Muñoz & E. Ruiz de Clavijo* (SEV 161897). Trassierra, derecha del Guadiato, Cerro del Trigo, pantano de la Breña, 16-VI-1978, *J.A. Varela* (SEV 161900). Villafranca, central eléctrica, río Guadalquivir, 21-V-1987, *Z. Díaz & C. López* (SEV 130876). **Huelva:** Alosno, 26-V-1942, *C. Vicioso* (MA 121571). Aracena, entre la Cefiña y la N433, 23-V-2005, *J. Cano-Maqueda & al.* (SEV 216213). Corterrangel, 18-VI-1978, *J. Rivera* (SEV 48336). Entre Aroche y Las Cantinas, 6-VI-1979, *J. Rivera & B. Cabezudo* (MGC 8832, SEV 48900). Escacena del Campo, Reserva de la Pata del Caballo, arroyo del Chacho, 31-V-2001, *B. Cabezudo & al.* (MGC 48565). Higuera de la Sierra, 400 m, 24-V-1988, *E. Bayón & E. Villanueva* (MA 438691). Linares de la Sierra, 22-VI-1942, *C. Vicioso* (MA 121570). Río Múrtiga, 8-VI-1984, *F.J. García & al.* (G 104154). Valverde del Camino, El Manzanito, 23-V-2005, *J. Cano-Maqueda* (SEV 216212). **Jaén:** Andújar, Arroyo de los Santos, 22-VII-1992, *J.M. Mancebo* (MA 651609). Baños de la Encina, Charca de la Enea, 29-VII-1992, *J.M. Mancebo & J.R. Molina* (MA 651610). Despeñaperros, 1-VII-1975, *J. Fernández Casas & al.* (MA 412612). **Sevilla:** Castilblanco de los Arroyos, 1-VI-2006, *J. Cano-Maqueda & al.* (SEV 232786). El Castillo de las Guardas, V-1914, *C. Vicioso* (MA 121569). El Garrobo, junto a la carretera, 15-V-1982, *J.M. Rodríguez & al.* (SEV 161950). Entre el Ronquillo y Almadén de la Plata, 22-VI-1976, *E.F. Galiano* (SEV 161899). Guillena, Arroyo Herrero, without date, *C. Fernández & J.A. Fariña* (SEV 109874).

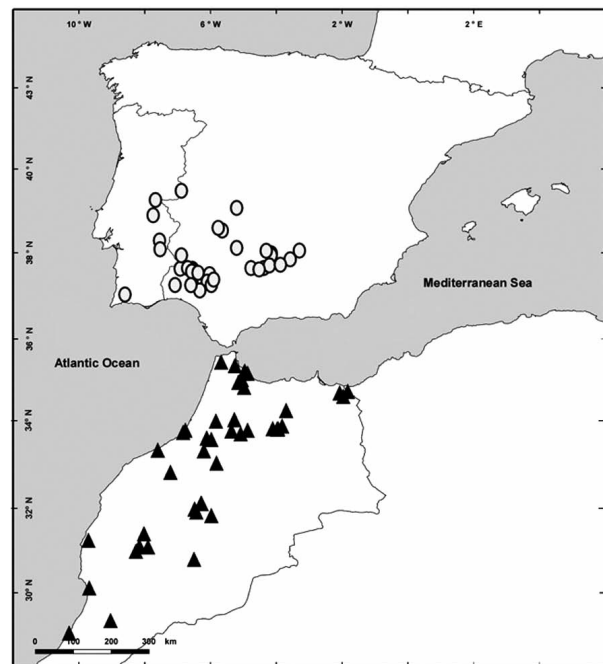


Fig. 12. Distribution map of *Campanula transtagana* (○) and *C. broussonetiana* (▲).

6. *Campanula broussonetiana* Schult. in Roem. & Schult., Syst. Veg. 5: 104. 1819-1820

C. lusitanica var. *broussonetiana* (Schult.) Pau in Mem. Real Soc. Esp. Hist. Nat. 12: 356. 1924. Ind. loc.: "In Mogador. Broussonet". Type: Morocco. Safi, Mogador, *Broussonet s.n.* (lectotype: here designated, W 03798!; see observations).

C. loeflingii var. *maura* Murb., Contr. Fl. Maroc. 2: 50. 1923. Ind. loc.: "Pentes herbeuses entre Amismiz et Oucheffine; Ighen Draa près Demnat. 900-1000 m.- J'ai vu la même plante des environs de Casablanca (leg. Mellerio)". Type: not studied.

C. lusitanica f. *pallidiflora* Maire in Jahand. et Maire, Cat. Pl. Maroc: 735. 1934. Ind. loc.: "Mont Tazzeka (Humbert et Maire)". Type: not studied.

C. lusitanica f. *tenuis* Caball. in Trab. Mus. Ci. Nat. Madrid, Ser. Bot. 30: 5. 1935. Ind. loc.: "Legi basi montis Tamarrut dicto, 6-VII-1934". Type: Morocco. Agadir, Tamarrut, 6 July 1934, *Caballero s.n.* (lectotype, here designated, MA 121492!; see observations).

C. vincaeflora Pau in Bol. Soc. Esp. Hist. Nat. 21: 278. 1921, nom. illeg., non Vent. 1804. Ind. loc.: "Tiguissar, 26-IV[1921]". Type: Morocco. Tittáguen, Tiguissar (Gomara), 26 April 1921, *Vidal López s.n.* (lectotype, here designated, MA 121493!; see observations).

Illustrations: Fig. 10 E, F.

Herb 6-45 cm, annual, erect or decumbent, branched from the base, pubescent, not brittle. Stems angled, branched, pubescent, rarely glabrous at the apex, with long hairs up to 0.4-2 mm. Leaves scarcely coriaceous, crenulated, entire or toothed; middle cauline leaves 8-37 × (4)6-15.5 mm, broadly elliptical or obovate, sessile and cuneate or with petiole up to 2 mm and rounded at the base, entire or toothed, ± pubescent, with hairs up to 1.2 mm; upper cauline leaves (4.2)6-13.5 × 1-7.6 mm, elliptical or lanceolate, generally entire, sessile, cuneate, pubescent, with hairs up to 0.4 mm or rarely glabrous, without a differentiated petiole. Inflorescence laxly paniculate. Flowers pedicellate; pedicel 7-67 mm, glabrous or with hairs 0.2-1.2 mm. Calyx-teeth (3.6)5.2-13.5 × (0.4)0.7-2(2.7) mm, oblanceolate, rarely linear. Corolla (7.2)8.8-17 mm, campanulate, with the tube usually shorter or equal in length to the lobes, rarely longer than lobes; tube 4.1-8.3 mm, with the base whitish and the apex light blue; lobes (2.4)3.5-8 × 2.1-5.2 mm, elliptic-lanceolate, bluish. Stamens with enlarged base of 0.6-0.7 × 0.4-0.6 mm; filaments 0.6-0.7 mm; anthers 2.1-4 mm, bluish or white. Ovary glabrous, rarely with hairs 0.1-0.8 mm; style 5-8.2 mm, hairy; stigma trifid, with

stigmatic branches of 1-2 mm, patent, curved, white or blue. Capsule 3-6.6 × 2-4.1 mm, subovoid, longer than wide, glabrous, rarely with setose hairs, with 10 nerves ± angled but not winged, dehiscent by three subapical pores. Seeds 0.4-0.6 × 0.2-0.3 mm, ellipsoid, shining, yellowish to brown. $2n = 20$.

Habitat, phenology and distribution: Shady hollows and the understory of cork woodlands, on limestone, or slate-rich or sandy substrates, from sea level to high mountains; 0-2000 m. IV-VII(VIII). •Endemic to W and N Morocco, along most of the Atlantic coastlands from Sidi Ifni to the Mamora forests; also the Rif, Middle Atlas and Great Atlas (Fig. 12).

Observations: This species has the same color morphs for anthers and stigmas as those found in *C. specularioides*, and similar, the morphs seem to be interfertile. Alphonse De Candolle (1830) synonymized this species with *C. loeflingii* Brot., possibly influenced by the illustration 18 of the "Phytographia Lusitaniae Selector" (Brotero, 1816) under this name. Certainly, *C. lusitanica* and *C. broussonetiana* are very similar morphologically. Both have long hairy indumentum that is straight and patent on the stem, and wide leaves, but in *C. broussonetiana* the middle cauline leaves are attenuate at the base or petiolate and in *C. lusitanica* are sessile and subauriculate. The molecular phylogeny has shown that *C. broussonetiana* is more closely related to *C. transtagana* than any other species of sect. *Rapunculus* (see Fig. 1).

The sheet of type material of *C. broussonetiana* (W03798) contains a complete highly branched plant with many flowers. Schultes (1819-1820: 104) already indicated that the type material was in the Willdenow herbarium under the name *Campanula ramosissima*. In the herbarium of the Prodrômus of De Candolle there are two sheets (G 138472 and G 138271-G 138478), one (G 138472) with a complete plant of c. 30 cm and the other (G 138271, G 138478) with three smaller plants (15-22 cm), all belonging to the expedition by Broussonet in 1804, collected at Mogador (Essaouira, Morocco). This last sheet contains two labels. In one (G 138478), handwritten by A. De Candolle, is indicated "Voyage de Broussonet 1804" at the base of two of the plants, and in the other (G 138271), with orthography of Broussonet, is written: "*Campanula/Mogador*" and also, with orthography of Alphonse De Candolle, "*Campanula loeflingii* Brot./ *Broussonetiana* Roem. Et Sch./ A. DC.". These materials were probably not studied by Schultes, and therefore they can not be considered type material (Fig. 13).

The sheet of type material of *C. lusitanica* f. *tenuis* contains two complete plants with flowers in postan-

thesis and two single flowered small stems. The larger sized plant (c. 20 cm) is chosen as lectotype. The sheet also contains three determinavit labels, one handwritten by C. Pau, which reproduces all the information of the name, the diagnosis and the protological description from Caballero; the second label was identified as *C. lusitanica* by Yvonne Nyman in 1987 and the third label by Juan José Aldasoro and Llorenç Sáez who identified the specimen as *C. broussonetiana*.

The type material of *C. vincaeflora* consists of a single whole plant in flower that we have chosen as lectotype. The sheet contains some other stems and a label printed with the original description.

Selected specimens

MOROCCO. **Agadir:** Col du Kerdous (Anti-Atlas), 26-V-1980, *A. Charpin & al.* (G 104179, MA 227542). Ida Ouehembal, Sud-ouest du Maroc, 1875, *Mardochee* (G 104254, G 104168, G 104255). O. Querat, Sous, 29-IV-1923, *E. Jahandiez*, in *E. Jahandiez*. Plantes Marocaines, 1923: n° 211 (G 104173). 3 Km Sidi Ifni, 16-IV-1989, *F. Jacquemoud* (G 104160). **Beni Mellal:** entre le

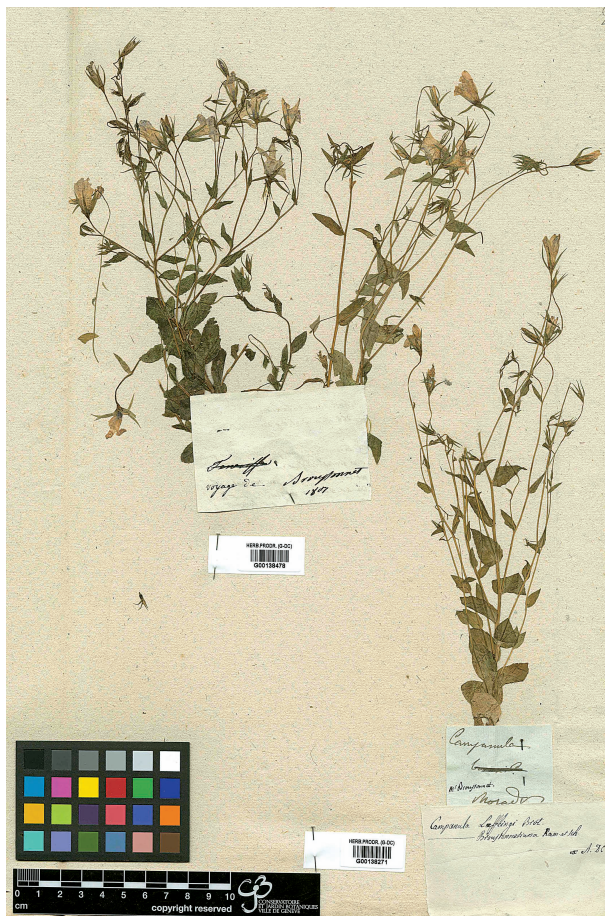


Fig. 13. Materials of *Campanula broussonetiana*. Collected by Broussonet in Mogador (Essaouira, Morocco) during his campaign in Morocco in 1805. The type material of this collection is located in Willdenow herbarium (B).

Col du Tizi Mlil et Beni Mellal, 5-VI-1980, *A. Charpin & al.* (G 104180, MA 243114). Entre Oulad M' Barek y Ouauouzarhte, cerca de Beni Mellal, 12-VI-1982, *J. Fernández Casas & al.* (MA 633188, MA 430482). Gran Atlas, entre Afouer y Bin-el-Ouidane, 9-VII-1996, *S. Cirujano & al.* (MA 625034). Subida al Jbel Tassemit, 23-IV-2003, *S. Talavera & al.* (SEV 216216). **Dar el Beïda:** Sidi Abd-Er-Rahman, 1886, *Ibrabim* (G 104250). **El Jadida:** 20 Km NE Benahmed an der Strase nach El-Khatouat (1419), 6-V-1989, *D. Podlech* (G 104182). **Er Ribat:** Arbaa-Sehoul, en la carretera hacia Romani, 2-V-2007, *S. Talavera & al.* (SEV 224279). **Fes:** subida a Jbel. Zalagh, al NE de Fes, 16-V-2006, *S. Talavera & al.* (SEV 217539, SEV 217537, SEV 217536, SEV 217535, SEV 217534). Bab Zitouna, collado del Jbel Zalagh, en la ruta de Fes a Ouezzane, 10-V-1994, *A. Achbal & al.* (SEV 161661). Jbel Zalagh, al NE de Fes, 17-V-2006, *S. Talavera & al.* (SEV 216499). **Kenitra:** entre Sidi-Slimane y Khemisset, en saladares, 9-IV-1983, *J.A. Devesa & al.* (SEV 161658). Forêt de la Mamora, entre Khemisset y Tiflet, a la izquierda en dirección a Máaziz, 25-V-2006, *S. Talavera & al.* (SEV 234710). Mamora, Dar Salem, sables, 29-IV-1924, *E. Jahandiez*, in *E. Jahandiez*, Plantes Marocaines, 1924: n° 211 (G 104174, MA 121503). Montes de Zaïan, entre Tiddas y Jbel Bouchchene, 24-V-2006, *S. Talavera & al.* (SEV 234709). Salé, 25-IV-1888, *Grant* (G 104251). **Marrakech:** cerca de Toufliht, entre Marrakech y Taddert, 14-VI-1982, *J. Fernández Casas & al.* (MA 430483). De Marrakech a Oukaimeden, Ogaionar, a 53 km de Marrakech, 1-VI-2007, *S. Talavera & al.* (SEV 223071). Gran Atlas, V-1871, *Hooker* (LISUG 50012). Krifla, 16/18-IV-1887, *Grant* (G 104167). Medna Ben Abou, 11-IV-1921, *G. Wibagek* (G 104175). Tabgourt, 20-VII-1884, *Ibrabim* (G 104259). Sidi-Ouamin, 12-VI-1889, *Ibrabim* (G 104252). **Meknés:** Atlas Medio, entre Oulmés y Aguelmous, 24-V-2006, *S. Talavera & al.* (SEV 234711). Entre Meknés et Fes, 2 Km avant le croisement à Ain Taoujdate, 15-V-1989, *B. Valdés & al.* (SEV 161657). Zerhoun, c. 25 Km due NE of Meknés road from Moulay Idriss to Nzaia-des-Beni-Ammar, 5-VI-1994, *S.L. Jury, M. Ait Lafkih & B. Tabiri* (SEV 161660). **Oudjda:** Berkane, Refuge Zegzel, 23-V-1928, *A. Faure* (G 104165). Env. de Martimprey-du-Kiss, Pelouses et broussailles, 14-V-1930, *A. Faure* (G 104177, G 104166, MA 121481). Montes des Beni-Snassèn, Djbel Fourhal, près de Taforalt, 23-V-1994, *J. Lambinon & G. Van Den Sande* (MA 562384). **Safi:** environs de Mogador, 1867, *B. Balansa* (G 104253). Falaises da Cap Safi, 17-IV-1924, in *E. Jahandiez*, Pl. Maroc. 1924: n° 82 (MA 121482). Mogador, 1804, *Broussonet* (G 138271, G 138472, G 138478). **Tandja:** Chaouia, 25-IV-1935, *Gattefossé* (G 104163). **Taza:** c. 32 Km from Taza on minor road near Bab-Bou-Idir, 6-VII-1993, *S.L. Jury & al.* (SEV 161656). 11 Km from Taza on minor road below Ras-El-Ma, 4-VII-1993, *M. Ait Lafkih & al.* (MA 577072, SEV 161659). Entre Bab-Azhar y Bab-Bou-Idir, 17-VI-2003, *S. Talavera & al.* (SEV 216476, SEV 216478). Entre Sidi-Abdallah-des-Rhiata y Bab-Azhar, 17-VI-2003, *S. Talavera & al.* (SEV 216475). **Tittáguen:** Armautah, lower part of Jbel Bouhalla, 3-VII-1993, *J.A. Mejías & S. Silvestre* (SEV 139107). Bou-Ahmed, pista entre Souk-el-Had e Imazerdane, 29-IV-1995, *M.A. Mateos & al.* (SEV 139102). C. Iaarguit (Beni Hosmar), 26-V-1930, *Font Quer*, in *Font Quer*, iter maroc. 1930: n° 637 (G 104162, MA 121489). Entre Bou-Ahmed y Targha, 3-V-1996, *M.A. Mateos & al.* (SEV 155222). Kaa Asras, Imarsboutene, 5-V-1996, *M.A. Mateos & al.* (SEV 155672). Oued-el-Kannar, 7-VI-1930, *Font Quer* (SEV 139142). Oued Laou, 9-IV-1995, *A.J. Caruz & al.* (SEV 139100). SE of Chefchaouen, E of Bab Taza, on road from Cherafat to Bab Berred, Matrasse Lakhmasse, 28-V-2002, *M. Ait Lafkih & al.* (MA 698258). Sok-el-Jemis (Beni Selman), pr. Tiguisas, 7-VI-1930, *Font Quer*, in *Font Quer*, Iter Maroc., 1930: n° 638 (G 104164, MA 121484). Talembote, 1 Km vor dem Ort in Flussbett des Oued Talembote, zw. Tamarix u. Oleander, 7-VII-1971, *M. Ditttrich* (G 104178, G 104172). Targha, 7-IV-1995, *A.J. Caruz & al.* (SEV

139141); ibidem, valle en la ladera W del Djebel Azenti, 8-IV-1995, A.J. Caruz & al. (SEV 154716). Tarsif, próximo a Oued-Laou, 30-IV-1995, M.A. Mateos & al. (SEV 139101). Tétouan, entre Chechaouen y Talembote, 31-V-1981, (MA 236533). Xauen, 14-V-1921, Font Quer, in Font Quer, iter maroc., 1928: n° 391 (G 104161, MA 121483, MA 121502, MA 121491).

B. Sect. *Decumbentes* Cano-Maqueda & Talavera, Sect. nov.

Type (here designated): *Campanula decumbens* A. DC.

Plantae annuae vel perennes. Sinus calycis exappendiculati. Corolla infundibuliformis. Antherae albae. Stylus glaber. Stigma tripartitum erectum vel erectopatens rectum album, in pagina abaxiali multos pilos pollen collectores exhibet, pagina adaxiali glabra in qua pollen germinat. Capsula obpyramidali vel ovata 5-angulari, poris tribus versus apicem vel subapicem sitis debiscente.

Annual or perennial plants. Without calycine appendages. Corolla infundibuliform. Anthers white. Style glabrous with a tripartite stigma. Stigma erect or erect-patent, straight, white, with numerous pollen collecting hairs on the abaxial surface, glabrous and receptive in the adaxial side. Capsule obpyramidal or ovoid, dehiscing by three apical or middle position pores.

Observations: This section consists of two species from the Iberian Peninsula (*C. decumbens* and *C. dieckii*), and two species from the Eastern Mediterranean (*C. ramosissima* and *C. hawkinsiana*). In the topology of the ITS tree (Fig. 1), this section forms a moderately supported clade (67% PPS), where *C. decumbens* appears as sister of *C. dieckii* (63% PPS), and *C. ramosissima* and *C. hawkinsiana* join into a well-supported subclade (99% BS; 100% PPS). This section thus includes both annual (*C. decumbens*, *C. dieckii*, *C. ramosissima*) and perennial (*C. hawkinsiana*) taxa, and also shows great variability in chromosome number: with $2n = 32$ in *C. decumbens* (in this work), $2n = 28$ in *C. dieckii* (in this work), $2n = 20$ in *C. ramosissima* (Damboldt & Podlech, 1964) and $2n = 22$ in *C. hawkinsiana* (Contandriopoulos, 1964a). The morphological characters that define this section (glabrous style with three straight, erect or erect-patent stigmas) are very rare in the Campanulaceae, and only co-occur in *Campanula* sect. *Pterophyllum* Damboldt.

7. *Campanula decumbens* A. DC., Monogr. Campan.: 334. 1830

C. patula var. *decumbens* (A. DC.) Cuatrec. in Trab. Mus. Ci. Nat. Barcelona 12: 441. 1929. Ind. loc.:

“Habitat in Hispaniâ propè Aranjuez ... [description]. Specimina numerosa apud dominum Delessert, in herbario Ventenatii vidi. Circâ Aranjuez in Hispania lecta fuerunt”. Type: Spain. Madrid. Aranjuez, 1827, *Delessert s.n.* [lectotype, here designated, G 138256! (G-DC), Fig. 14; see observations].

Herb 8(14)-38 cm, annual, decumbent or erect, branched in the upper half or from the base, glabrescent. Stems angled, branched only in the inflorescence, glabrous or with a few antrorse hairs 0.1-0.3(1.4) mm long, often scabrid near the flowers. Leaves not coriaceous, entire, toothed or crenulate; middle cauline leaves 9(13)-28 × 4.7-10 mm, elliptic or lanceolate, petiolate or sessile, toothed or entire, glabrous or with some hairs 0.1-0.2 mm scattered on the underside nerves, and petioles up to 7-12 mm; upper cauline leaves 3(5)-15 × (0.5)2.5-8 mm, elliptic or lanceolate, cuneate or shortly petiolate, glabrous or glabrescent, with some hairs 0.1-0.3 long on the



Fig. 14. Lectotype and islectotype of *Campanula decumbens* (G 138256). The lectotype is the plant located in the center, on the right, the only one with a flower in anthesis. The other plants are islectotypes.

nerves of the underside, and petioles up to 2 mm. Inflorescence laxely paniculate. Flowers pedicellate; pedicel (10.5)40-60(206) mm, glabrous or with some setose hairs near the ovary. Calyx-teeth (6)8-15 × 0.8-1.6 mm, lanceolate or closely oblanceolate, with the apex obtuse or acute, entire. Corolla 12-21 mm, infundibuliform, with the tube shorter than the lobes; tube 3-8 mm, light blue, with white base; lobes (7)9-10(14) × 5-8.1 mm, broadly triangular or elliptical, blue, with three darker nerves. Stamens with enlarged base of 0.7-1.5 × 0.5-1.5 mm; filaments *c.* 1 mm; anthers 1.6-3(3.8) mm, whitish. Ovary glabrous or papillose, rarely hairy; style (3)3.5-4(4.8) mm, glabrous, with 3 stigmas; stigmas (2)2.3-5(5.5) × 0.35-0.4 mm, erect-patent at anthesis, ± straight, flat in the adaxial side, convex and with numerous pollen collecting hairs on the abaxial side. Capsule (2.2)3-8 × 2.4-4(5.7) mm, ovoid or obpyramidal, longer than wide, glabrous or papillose, with 10 thick nerves, dehiscing by three apical or middle position pores. Seeds 0.4-0.7 × 0.2-0.3 mm, ovoid or ellipsoid, shining, brown-yellowish. $2n = 32$.

Habitat, phenology and distribution: Grassland and wet meadows, on basic substrates (limestone and dolomite); 10-1250 m. VI-VII(VIII). •Endemic to the S of Spain, in the Guadalquivir valley, Sierra de Grazalema and Serranía de Ronda, cited only once from Aranjuez. **Spain:** Ca M? Ma, Se.

Observations: The identity of *C. decumbens* has been discussed by various authors (Pau, 1896; Cuatrecasas, 1929; Caballero, 1942; Fedorov, 1976; López-González, 1979-1980); but in fact most authors do not treat with the decumbent plant from Aranjuez described by Alphonse De Candolle. These authors looked for this species near Aranjuez, but they only found an upright and very hairy plant with crenate leaves. This upright plant is the species described by Lange (1893) as *C. dieckii* and later by Pau (1896) as *C. semisphaerica*. Only Fedorov (1976) indicated that *C. decumbens* A. DC. is indeed decumbent. From the type he thought it endemic to Aranjuez, and that it might be better treated as subspecies or variety of *C. patula* L., as proposed by Cuatrecasas (1929).

The type material of *Campanula decumbens* (G 138256) contains two complete plants of 20 and 25 cm and two stems, all with flower buds and only one plant with an open flower. This flowering plant is chosen as lectotype. The other materials are isoelectotypes (see Fig. 14). In the general herbarium at Geneva there is another sheet (G 104141), also from the Ventenat herbarium, containing an incomplete plant of 20 cm with two flowers. The label indicates "*Campanula/affinis vincaeflorae/ Aranjuez près Madrid*". The

plant contained in this sheet may also form part of type material.

The type material has petiolate middle leaves of the stem, and a small and infundibuliform corolla, in which it resembles *C. cabezudo* [described by López-González (1979-1980) as *C. decumbens* var. *pseudospecularioides*]. But the style with three ± straight stigmas is similar to that of *C. dieckii* and so, it is clear that *C. decumbens* A. DC. belongs to sect. *Decumbentes*. Cano-Maqueda & al. (2008) indicated that this species, apparently only known only from the Delessert type materials, could be extinct. However, several populations have been located in Sierra de Grazalema and Serranía de Ronda, with the same characters as the type material of *C. decumbens* A. DC. Plants from two of these populations were cultivated in the greenhouses of the University of Seville. They retained the decumbent habit, are self-incompatible (Cano-Maqueda & al., unpublished data) and the meiotic number of chromosomes is $n = 16$.

Due to this discovery that *C. decumbens* occurs on diverse localities on alkaline substrates in the Serranía de Ronda and surrounding areas, it is likely that the material studied by Alphonse de Candolle came from the Southern Betic Cordillera and not from Aranjuez as stated in the sheet of the type.

Subsequently, a number of exsiccata by previous collectors in this area and also from the Guadalquivir valley and Cádiz coastland were also identified as *C. decumbens*. However, the Guadalquivir valley plants are morphologically rather different from those of the Sierras Béticas, although the molecular phylogeny has shown that both groups of plants do not present any changes in the nucleotide sequence (Fig. 1). They also have the same chromosome number ($n = 16$; Table 1 and Fig. 2H). However, since in addition to the morphological differences, the populations present a different ecology and distribution, we have considered it most appropriate to treat these two groups of populations as two subspecies.

KEY TO THE SUBSPECIES

1. Middle cauline leaves petiolate; capsule (2.2)3-4(4.4) × 2.4-4 mm, ovoid **a. *C. decumbens* subsp. *decumbens***
1. Middle cauline leaves sessile; capsule 4-8 × 3-5.7 mm, obpyramidal **b. *C. decumbens* subsp. *baetica***

a. *Campanula decumbens* A. DC. subsp. *decumbens*

Illustrations: De Candolle (1830, tab. 12 fig. A); Fig. 15 A, B.

Herb 20-36 cm, decumbent. Middle cauline leaves petiolate. Calyx-teeth (6)8-10 × 0.8-1.1 mm, lanceolate, with the apex obtuse. Corolla 12-14 mm; tube 3-

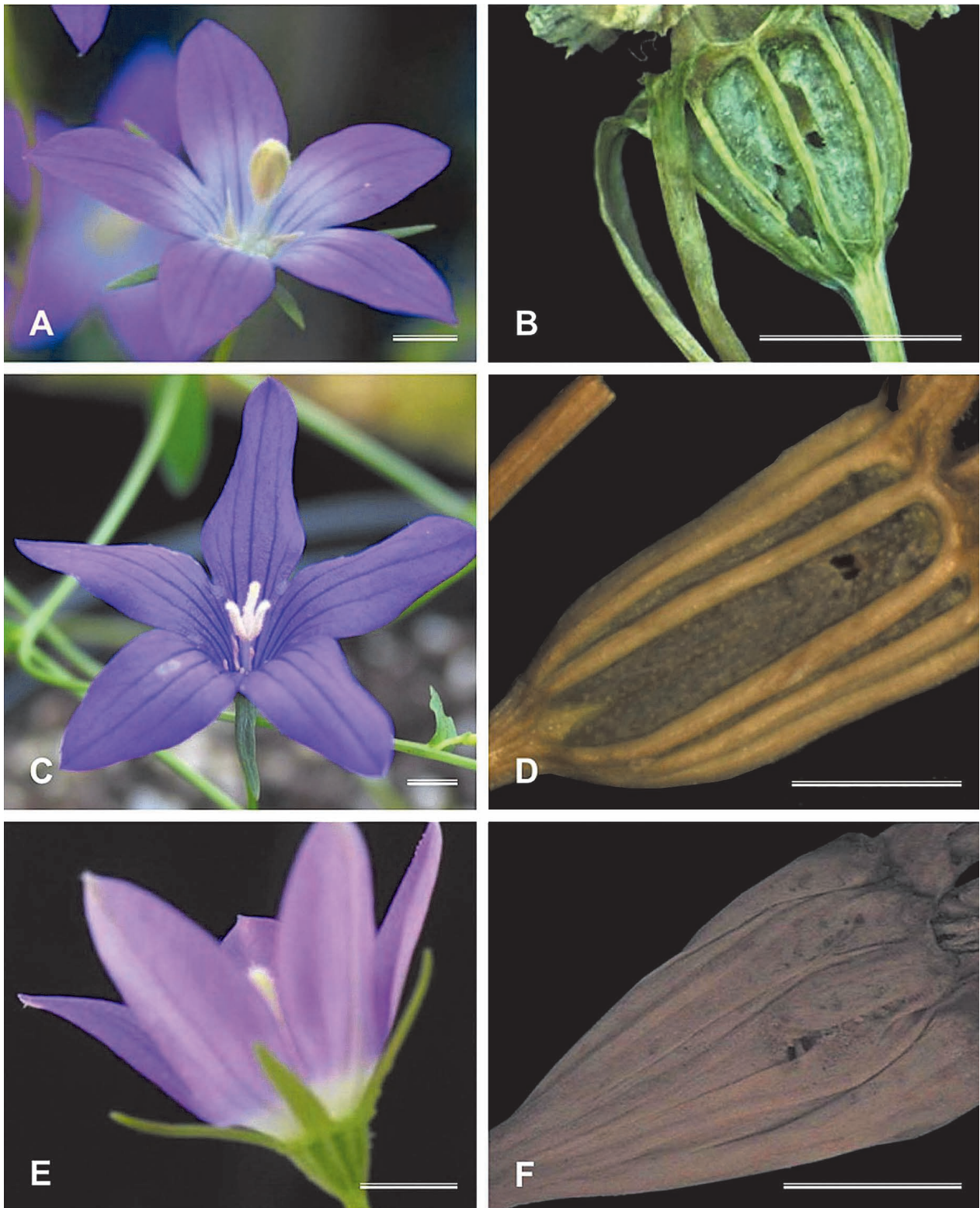


Fig. 15. Flowers and fruits of *Campanula* species. **A, B,** *C. decumbens* subsp. *decumbens* (Benaoján, Málaga, Spain, SEV 218875); **C, D,** *C. decumbens* subsp. *baetica* (Villamartín, Cádiz, Spain, SEV 256653); **E, F,** *C. dieckii* (Alfarnate, Málaga, Spain, SEV 256652). The scale bar = 3 mm.

4 mm; lobes 9-10 × 5-6 mm, broadly triangular. Stigmas 2-3.2 mm. Capsule (2.2)3-4(4.4) × 2.4-4 mm, ovoid. $2n = 32$.

Habitat, phenology and distribution: Wet meadows, on basic substrates (limestone and dolomite); (480) 1000-1250 m. VI-VII(VIII). • Endemic to the Sierra de Grazalema and Serranía de Ronda (Fig. 16). **Spain:** Ca M? Ma.

Selected specimens

SPAIN. **Cádiz:** Benaocaz, Manga de Villaluenga, 22-VI-1984, A. Aparicio & S. Silvestre (SEV 161834). Grazalema, 11-VI-1890, E. Reverchon, in E. Reverchon, *Plantes de l'Andalousie*, 1889: n° 17 (G 104066). Sierra del Endrinal, 10-VII-1925, Font i Quer & E. Gros (G 104158, MA 702573, MGC 53045); ibidem, 29-VI-1849, P. Font i Quer & E. Gros (SALA 114817). **Málaga:** Benaoján, Carretera hacia Ronda, 15-V-1988, D. Montilla (MGC 40574); ibidem, Sierra del Palo, 17-VI-2007, J. Cano-Maqueda (SEV 218875); ibidem, 6-VI-2001, M. Becerra & al. (MGC 52844, MGC 51636); ibidem, Puerto España, 25-V-2002, M. Becerra & F. Sánchez (MGC 51972). Ronda, 18-VI-1889, E. Reverchon, in E. Reverchon, *Plantes de l'Andalousie*, 1889 n° 17 (G 104072).

b. *Campanula decumbens* subsp. *baetica* Cano-Maqueda & Talavera, **subsp. nov.**

A Campanula decumbens subsp. decumbens foliis caulinis sessilibus non petiolatibus, caule erecto non decumbente, capsula obpyramidali non ovata differt. A Campanula dieckii foliis glabrescentibus integris vel serratis, calyce, corolla stigmatibusque majoribus differt.

This subspecies differs from *Campanula decumbens* subsp. *decumbens* in its non-petiolate, sessile cauline leaves, erect rather than decumbent stems, and obpyramidal capsule, not ovoid. It differs of *Campanula dieckii* by its entire or toothed and glabrescent leaves, and by the larger size of the calyx, corolla and stigmas.

Type: Spain. Sevilla. El Coronil, bujeos, June 1990, Aparicio & Silvestre s.n. (holotype: SEV 217838!, Fig. 17; isotype: SEV 238167!).

Illustrations: Boissier (1839, tab. 120a, as *C. erioides*); Fig. 15 C and D.

Herb (8)14-38 cm, erect. Middle cauline leaves sessile. Calyx-teeth (8)8.5-15 × 1-1.6 mm, closely oblanceolate, with the apex acute. Corolla (12)14.5-

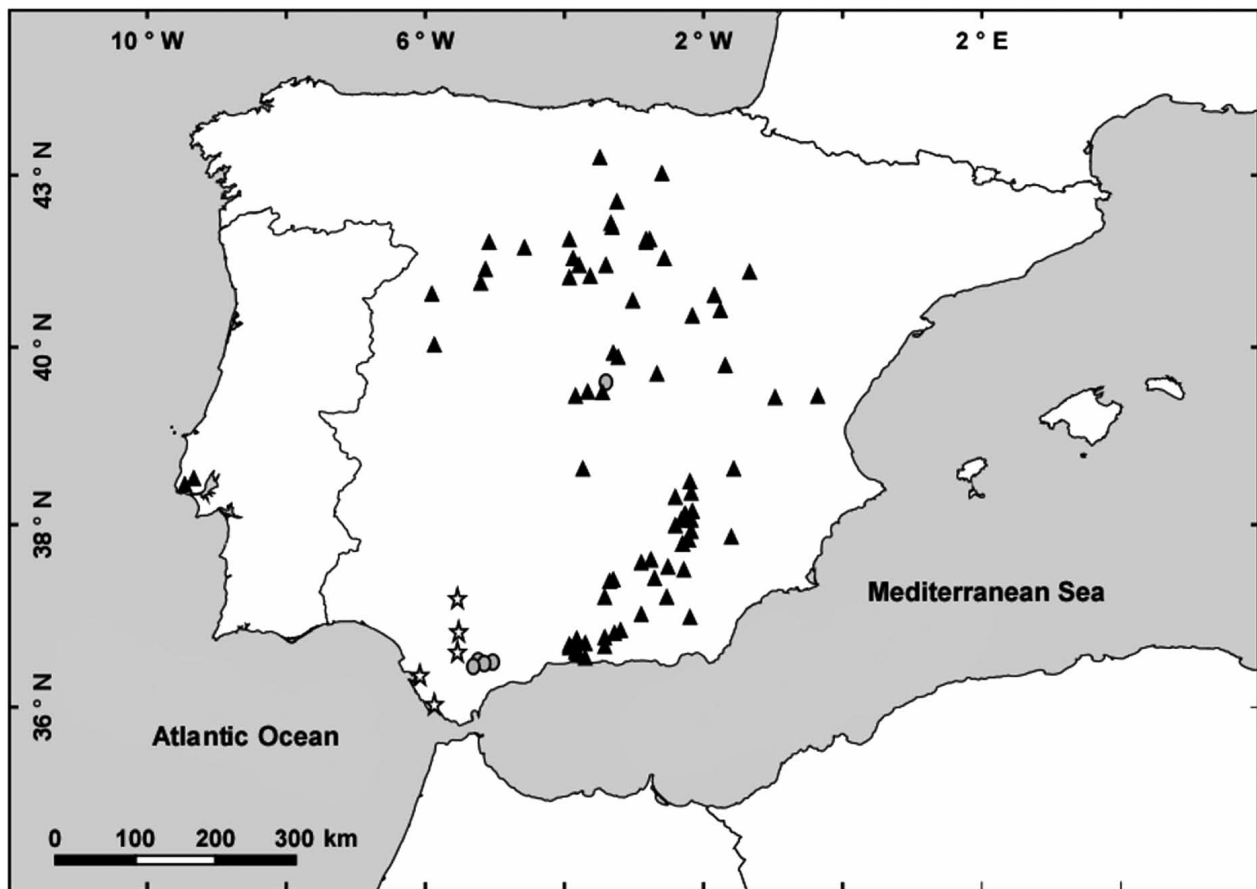


Fig. 16. Distribution map of *Campanula decumbens* subsp. *decumbens* (○), *C. decumbens* subsp. *baetica* (☆) and *C. dieckii* (▲).



Fig. 17. Holotype of *Campanula decumbens* subsp. *baetica* Cano-Maqueda & Talavera (SEV 217838).

21 mm; tube (3.4)4-8 mm; lobes 7-14 × 5-8 mm, elliptical. Stigmas (4)4.3-5.5 mm. Capsule 4-8 × 3-5.7 mm, obpyramidal. $n = 16$.

Habitat, phenology and distribution: Grasslands on basic substrates, usually very clay soils; 10-200 m; (V)VI-VIII. • Endemic to the S of Spain, in the Guadalquivir valley (Fig. 16). **Spain:** Ca Se.

Selected specimens

SPAIN. **Cádiz:** Cádiz, without date, *Chaubert* (G 104126). Cerca de Villamartín, 31-V-1969, *E.F. Galiano & al.* (SEV 161833); ibidem, en la carretera a El Bosque, 17-VI-2009, *S. Talavera & al.* (SEV 248711). Vejer de la Frontera, Caños de Meca, 15-V-1959, *D.M.C. Brinton-Lee* (SEV 81177). Villamartín, 8-V-2010, *J. Cano-Maqueda* (SEV 256653). **Sevilla:** Carmona, *J.M. Triguero* (SEV-histórico 1077).

8. *Campanula dieckii* Lange in Overs. Kongel. Danske Vidensk. Selsk. Forh. Medlemmers Arbejder 1893: 195. 1893

Ind. loc.: “Ciudad Encantada mellem Uña og Val-

decabras i Provinsen Cuenca, 1.juni 1892 blomstrende (Dieck!).” Type: Spain. Cuenca, Uña, 1 June 1892, *Dieck s.n.* (lectotype, here designated, C, herb. J. Lange, Fig. 18; see observations).

C. matritensis var. *nevadensis* A. DC. in DC., Prodr. 7(1): 481. 1838. Ind. loc.: “in editoribus Sierrae-Nevadae. (Boiss.!)”. Type: Spain. Granada, Sierra Nevada, 1838, *Boissier s.n.* (lectotype, here designated, G138396!; see observations).

C. semisphaerica Pau, Not. Bot. Fl. Españ. fasc. 6: 76. 1896. Ind. loc.: “Sacañet, á 1100 m de alt. en compañía de la *C. dichotoma*; 8 julio 1895”. Type: Spain. Castellón, Sacañet, 8 July 1895, *Pau s.n.* (lectotype, here designated, MA121465!; see observations).

C. argutidens Porta et Rigo, Iter. Hisp. III: n.º 309 (1891), in sched., nom. nud.

C. specularioides var. *argutidens* Porta et Rigo, Iter. Hisp. III: n.º 309 (1891), in sched., nom. nud.

Illustrations: Sáez & Aldasoro (2001: 132, fig. 40, as *C. decumbens*); Fig. 15 E, F.

Herb (3)8-20(30) cm, annual, erect, usually branched in upper half, often densely pubescent, at least in the lower half. Stem angled, little branched, densely pubescent, with ± antrorse setose hairs, 0.1-0.7 mm, sometimes glabrescent at the apex. Leaves somewhat fleshy, crenate, lobed or pedate, sometimes the uppermost subentire; middle cauline leaves (4)7-18 × 3-9(14) mm, ± elliptical, sessile, subauriculate, densely pubescent, with hairs 0.1-0.7 mm; upper cauline leaves 3-13.5 × 0.5-2.5(7.7) mm, ± lanceolate, sessile, subauriculate, glabrous or more often with scattered hairs 0.1-0.6 mm. Inflorescence paniculate, lax. Flowers pedicellate; pedicel (11.9)19-90(155) mm, glabrous or papillose on top. Calyx-teeth (2.3) 3-10.5 × 0.7-1.5 mm, lanceolate, obtuse, with thickened margins. Corolla (6.6)8-13.7 mm, infundibuliform, with the tube much shorter than the lobes; tube (1.5)3-4.5 mm, light blue with white base; lobes 7-12.3 × (3)4.5-5.5(7.6) mm, ovate-lanceolate, blue, with three purple nerves. Stamens with enlarged base of 1.1-1.9 × 1.5-1.9 mm; filaments 0.6-0.7 mm; anthers 2.1-3(3.8) mm, whitish. Ovary glabrous, papillose or densely hairy, with setose hairs of (0.2)0.7-2.2 mm; style 2.1-4(4.7) mm, glabrous, with three stigmas; stigmas (2.1)2.5-4 mm, erect-patent at anthesis, ± straight. Capsule (3.5)4.9-9(11.5) × 3.5-6.5 mm, obpyramidal, longer than wide, from papillose to densely hairy, with setose hairs of 0.3-1 mm, with 10 very wide nerves like flat ribs, dehiscing by three middle position pores. Seeds 0.5-0.8 × 0.2-0.3 mm, ovoid, shining, yellowish to brown. $2n = 28$.

Habitat, phenology and distribution: Wet meadows and kermes oak woodlands on basic substrates (gypsum, limestone and dolomite); 600-2300 m. VI-VII(VIII). • Endemic to the Iberian Peninsula, C, E and SE Spain, where it is frequent, and rare in CW Portugal, Serra do Sintra (Fig. 16). **Portugal:** E. **Spain:** Ab Al Bu Cs CR Cu Gr Gu J Lo M Ma Mu Sa Sg So To Va Z Za.

Observations: This species has been confused with *C. decumbens* by several authors. Cuatrecasas (1929) commented: “Las diferencias que separan a la planta de De Candolle [*C. decumbens*] de la de Loeffling [*C. lusitanica*] son mínimas. La primera son simplemente formas de tallos menos ramificados y lacínias calicinales más anchas que en la última, la cual, en general, también difiere por su mayor estrechez de la corola. Estos caracteres están, sin embargo, sujetos a variaciones, lo mismo que la vestidura del tubo de los cálices entre unos muy hispídeos y otros muy lampiños”. However, in this comment Cuatrecasas is referring to three different species from the Sierra de Má-

gina (Jaen): *C. matritensis* with a glabrous ovary, and *C. cabezudo* and *C. dieckii*, both with very hairy, almost hispid ovary.

We have seen material of this species from two collections from Sintra (Estremadura, Portugal). One collected by F. Fernandes in V-1914 (G 104249, 104150; LISU 36374; MA 121500), distributed in exiccata by F. Sennen (in F. Sennen Pl. Esp. n.º 6006), and another by W. Rothmaler on 13-V-1938 (G 104148; LISE 4368). Since this plant has not been collected again at this locality, the presence of this species as a native in Portugal may be considered doubtful. However, this kind of disjunction is not uncommon in other species of the Iberian Peninsula, i.e., *Silene distichia* Willd., a common species in the Eastern half of Spain and rare in the W Portugal (Talavera, 1990).

The type material of *Campanula dieckii* is composed by 7 whole plants at anthesis of 10-20 cm with sessile, elliptic, crenate cauline leaves, infundibuliform corolla, glabrous style, straight stigma and densely setose ovary. The sheet also contains two flowers in an envelope. The first plant, in the upper left corner of the sheet is chosen as lectotype, because it is the one that best fits the description of the author. The other six plants are isoelectotypes (see Fig. 18). In the Geneva herbarium there is a sheet (G104244) with three plants that are also isoelectotypes.

The sheet of type material of *C. matritensis* var. *nevadensis* contains 6 plants in flower. We have chosen as lectotype the plant placed at the top right, about 10 cm, very hairy, with crenate leaves and two flowers in anthesis. The remaining plants are isoelectotypes.

The type material of *C. semisphaerica* consists of two very small plants, each with one flower open. The plant on the right is the lectotype. On the sheet there is a typed label by Ginés López-González dated 13-11-1979 indicating the material contained on the sheet as holotype. Pau's indication “genuine” may be understood that this material was chosen as type by the author of the binomial.

Selected specimens

PORTUGAL. Estremadura: Sintra, V-1914, F. Fernandes, in F. Sennen, Plantes D'Espagne, 1926, n.º 6006 (G 104150, G 104249, LISU 36374, MA 121500, MA 474598); ibidem, 13-V-1938, W. Rothmaler, in W. Rothmaler, Flora Lusitanica n.º 13133 (G 104148, LISE 4368).

SPAIN. Albacete: Alcaraz, La Molata, 24-V-1993, B. Casaseca & M.A. Carrasco (MA 531238). Alrededores de Santa Elena de Ruidera, 24-V-1933, González Albo (MA 121567). El Balletero, 28-VI-1935, González Albo (MA 432730). El Cascajal, 24-V-1933, González Albo (MA 121480, MA 121479). Pontegruelos, 28-VI-1935, González Albo (MA 432731). Tús, vertiente SE del Calar del Mundo, 29-V-1987, E. Villanueva & al. (MA 393151). Villaverde



Fig. 18. Lectotype (in the upper left corner) and isoelectotypes (the rest of plants) of *Campanula dieckii* (C., herb. Lange).

- de Guadalimar, 18-VI-1969, P.E. Gibbs (SEV 161752). **Almería:** Bacaes, 4-VI-1929, E. Gros (MA 433604). De Bacaes a la Venta de Lleiva, 5-VI-1929, E. Gros (MA 433605). **Burgos:** Ciruelos de Cervera. Pie del Alto de la Cabeza, 11-VII-1979, Pons Sorolla & Susanna (MA 413025). Hortezuelos, 17-VI-1982, M.A. Carrasco & M. Velayos (MA 312710, SALA 32983). Huidobro, 5-VII-1987, Galán Cela & A. Martín (MA 639955). Tejada. Pico Valdosa, 3-VII-1979, J. Fernández Casas & al. (MA 413017). **Ciudad Real:** La Molata, 2-VI-1934, González Albo (MA 201345). **Cuenca:** Barajas de Melo, valle del río Calvache, pr. Urbanización Valderíos, 580 m, 30-V-1998, V.J. Arán & M.J. Tobá (MA 614852, MA 620787). Pinar de Beteta, 8-VII-1932, A. Caballero (MA 121464). Talayuelas, 1100m, 18-VI-1979, G. Mateo (MA 256531). **Granada:** Alhama de Granada, Barranco del Malinfierno, 17-VI-2004, B. Cabezudo & al. (MGC 59291). Arenas del Rey, El Cenacho, 3-VI-2004, B. Cabezudo & al. (MGC 59289). Ascenso a Sierra Nevada, falla del Purche, 8-V-1966, S. Silvestre (SEV 19702). Guadix, 11-VI-1921, E. Gros (MA 31778). Sierra de Albuñuelas, 15-VI-1976, A. Asensi & P. Díez (MGC 3617). Sierra de Baza, ascenso a Santa Bárbara, 21-VI-1988, S. Talavera & al. (G 104091). Sierra de Castri, VI-1903, E. Reverchon, in E. Reverchon, *Plantes d'Espagne* 1903: n° 1209 (G 104074, MA 121523). Sierra de Cázulas, 23-VI-1976, Ladero & al. (MA 204705, SALA 8787). Sierra de Guillimona, Cuerda de los Mirabetes, 23-VI-1988, S. Talavera & al. (G 104059). Huéscar, Sierra de la Sagra, cara sur, 14-VI-1995, B. Cabezudo & al. (MGC 39893). Padul, 4-VI-1980, M. Ladero & al. (SALA 92232). Sierra del Pinar, without date, Reverchon (G 104076). Sierra Nevada, Trevenque, VI-1973, J. Fernández-Casas (G 104078, SEV 19866). **Guadalajara:** Codes, 21-VI-1988, M.A. Carrasco & M. Velayos (MA 711892). Sacacorbo, 9-VI-1973, A. Segura Zubizarreta (G 104064, MA 269833). Tamajón, alrededores de la ermita de los Enebrales, 4-VII-1978, M.A. Rivas & C. Soriano (MA 385718). Torremocha del Pinar, 19-VI-1995, M.A. Martín Ballesteros (SALA 59846). **Jaén:** between Tobos and Vites, bed of river Zumeta, 25-VI-1988, S. Talavera & al. (G 104058). Cambil, Sierra de Mágina, Matabegí, 15-VI-1995, B. Cabezudo & al. (MGC 39707). Cazorla, alrededores de la C. F. Fuente del Oso, 31-V-1976, F. Muñoz Garmendia & C. Soriano (MA 454856). La Iruela, barranco de Guadahornillos, 16-VI-1976, F. Muñoz Garmendia & C. Soriano (MA 454825). Las Altarillas, 16-VI-1941, E. Guinea (MA 432654). Orcera, 6-VI-1980, C. Soriano (MA 592112). Pozo Alcón, pico de Cabañas, 20-VI-1975, F. Muñoz Garmendia & C. Soriano (MA 454823). Santiago de la Espada, cabecera del arroyo del Membrillo, 5-VI-1975, F. Muñoz Garmendia & C. Soriano (MA 454816). Segura de la Sierra, 17-VI-1850, E. Bourgeau, in E. Bourgeau, *Pl. d'Espagne*, 1850: n° 992 (G 104100). Sierra del Pozo, VI-1905, E. Reverchon, in E. Reverchon, *Plantes d'Espagne* 1905: n° 1209 (G 104134). Sierra Mágina, entre el Cortijo de los Prados y Cerro Carceles, 11-VI-1987, E. Villanueva & al. (MA 401189). Siles, VI-1850, M. Blanco (G 104113). **Madrid:** Algodor, 31-V-1925, A. Caballero & González Guerrero (MA 432742, MA 432744). Aranjuez, V-1897, C. Pau (MA 121457). Idem, 25-V-1919, C. Vicioso (MA 121459). Arganda, IV-1932, C. Pau (MA 432687). Piul de Rivas, V-1915, C. Vicioso (MA 121456). Venta del Gorro, 1802, Lagasca (G 138462). **Málaga:** Alcaucín. Sierra Tejada, loma de las Víboras, 7-VI-2002, D. Navas & al. (MGC 52239). Alfarnate, 30-III-2007, (SEV256652). Canillas de Albaída, Los Horcajos, puerto de la Orza, 5-VI-1919, E. Gros (MA 121468). Castillo de Frigiliana, VI-1919, E. Gros (MA 121467). Cómpea, Navachica, 22-VI-2004, B. Cabezudo & al. (MGC 59293). Sedella, 14-VI-1994, A. Aparicio & al. (MA 543877). Sierra Tejada, V-1914, E. Gros (MA 121471). **Murcia:** Sierra de Moratalla, Revolucionadores, 15-VII-1974, A. Charpín & J. Fernández Casas (G 104079). **Salamanca:** Ledesma, 19-V-1976, J. Sánchez (MA 219750). Molinillo, 1859, Sainz (MA 153143). **Segovia:** Cedillo de la Torre, 5-VI-1985, A.R. Burgaz & A. Izuzquiza (MA 306519). Fuentidueña, 24-VI-1983, T. Romero (SALA 41198). Lastras de Cuéllar, Molino Ladrón, 840 m, 24-V-1998, P. Bariego Hernández & A. Gastón González (MA 754470). Villaseca, 12-VI-1983, T. Romero (SALA 41951). **Soria:** Andaluz, 26-VI-1975, A. Segura Zubizarreta (FCO 7873, SEV 69199). Cañón del río Lobos, 17-VI-1982, A. Buades (MA 502178). Herrera de Soria, 30-VI-1983, A. Buades (MA 504408). Ucero, cuesta de la Galiana, 28-V-1983, A. Buades (MA 504043). **Toledo:** Toledo, 22-V-1897, C. Pau (MA 121458). **Valladolid:** Castronuño, 20-VI-1984, F.J. González & C. J. Valle (SALAF 7361). Encinas de Esgueva, 7-VII-1983, J.L. Fernández Alonso (MA 517691). Rábano, 15-VI-1983, T. Romero (SALA 411197). Urueña, 20-VI-1980, Fernández Díez (SALA 22002). Valladolid, 17-VI-1906, Senen (MA 121463). **Zamora:** Castrillo de la Guareña, 30-V-1983, X. Giráldez (SALA 31601). **Zaragoza:** Calatayud, 15-VI-1910, C. Vicioso (G 104095, MA 121462). Cerros de Andrés, VI-1898, C. Vicioso (MA 121460).

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Appendix 1

Species, origin of plant material, voucher, collector or reference and ITS GenBank accession no.

Adenophora divaricata Franch. & Sav.; cultivated in Royal Botanic Gardens Edinburgh; Eddie & al. (2003); AY 322005 & AY 331418. **Asyneuma japonicum** (Miq.) Briq.; Korea; Kim & al. (1999); AF 183437 & AF 183443. **Azorina vidalii** (Wats.) Feer.; cultivated in University of Edinburgh; Eddie & al. (2003); AY 322007 & AY 331420. **Campanula alliarifolia** Willd.; cultivated in Royal Botanic Garden, Kew; Eddie & al. (2003); AY 322008 & AY 331421. **C. alpina** Jacq.; Austria, Niedere Tauern; Park & al. (2006); DQ 304573. **C. armazica** Kharadze; Caucasus; Eddie & al. (2003); AY 322009 & AY 331422. **C. arvatica** Lag.; cultivated in University of Edinburgh; Eddie & al. (2003); AY 322010 & AY 331423. **C. barbata** L.; Italy; Eddie & al. (2003); AY 32211 & AY 331424. **C. beckiana** Hayek; Austria, Northeastern Alps; Park & al. (2006); DQ 304619. **C. bellidifolia** Adams; Caucasus; Eddie & al. (2003); AY 322012 & AY 331425. **C. bononiensis** L.; Austria, Leithagebirge; Park & al. (2006); DQ 304571. **C. brossonnetiana** Schult.; Morocco, Tazzeke (Middle Atlas); Cano-Maqueda & al. (2008); FM 212711. **C. cabezudo** Cano-Maqueda & Talavera; Spain, Málaga, Junquera; Cano-Maqueda & al. (2008); FM 212727. **C. carpatica** Jacq.; USA, Illinois; Eddie & al. (2003); AY 322013 & AY 331426. **C. cenisia** L.; Austria, Lechtaler Alps; Park & al. (2006); DQ 304622. **C. cespitosa** Scop.; Austria, Northeastern Alps; Park & al. (2006); DQ 304621. **C. decumbens** A. DC. subsp.

- 322035 & AY 331448. *C. raineri* Perpent; Italy, Alpi Bergamaschi; Park & al. (2006); DQ 304604. *C. ramosissima* Sibth. & Sm.; Greece, Lakonia; SALA 135597; Aedo & al.; HQ 407548. *C. rapunculus* L.; Spain, Huelva, Hinojos; Cano-Maqueda & al. (2008); FM 212738. *C. reatina* Lucchese; Italy, Turano Valley; Park & al. (2006); DQ 304599. *C. reverchonii* A. Gray; USA, Texas; Eddie & al. (2003); AY 322036 & AY 331449. *C. rotundifolia* L.; Spain, Cádiz, Grazalema; Cano-Maqueda & al. (2008); FM 212736. *C. sarmatica* Ker-Gawl.; Caucasus; Eddie & al. (2003); AY 322038 & AY 331451. *C. siegismundii* Fed.; Caucasus; Eddie & al. (2003); AY 322039 & AY 331452. *C. sosnowskyi* Charadze; Caucasus; Eddie & al. (2003); AY 322040 & AY 331453. *C. sparsa* Friv.; Greece, Grevená, Palaiokastros; SALA 135596; Aedo & al.; HQ 407549. *C. specularioides* Coss.; Spain, Cádiz, Grazalema; Cano-Maqueda & al. (2008); FM 212705. *C. spicata* L.; Italy, Southern Alps; Park & al. (2006); DQ 304574. *C. stenocodon* Boiss. & Reuter; Italy, Alpi Cozie; Park & al. (2006); DQ 304620. *C. steveni* Bieb.; Caucasus; Eddie & al. (2003); AY 322041 & AY 331454. *C. thyrsoides* L.; cultivated in University of Edinburgh; Eddie & al. (2003); AY 322042 & AY 331455. *C. tommasiana* Koch; Croatia, Učka; Park & al. (2006); DQ 304611. *C. transtagana* R. Fern.; Spain, Córdoba, Azuel (Sierra Morena); Cano-Maqueda & al. (2008); FM 212721. *C. tridentata* Schreb.; Caucasus; Eddie & al. (2003); AY 322043 & AY 331456. *C. uniflora* L.; Norway, Sor-Trondelag; Park & al. (2006); DQ 304588. *C. versicolor* Andrews; Greece, Ionian Islands, Kefallinía; Park & al. (2006); DQ 304607; *C. waldsteiniana* Schultes; Croatia, Velebit Mtns.; Park & al. (2006); DQ 304610. *C. zoyzii* Wulfen; Slovenia, Kamniške Alps; Park & al. (2006); DQ 304603. *Campanulastrum americanum* (L.) Small.; Eddie & al. (2003); AY 322044 & AY 331457. *Canarina canariensis* (L.) Vatke; Spain, Canary Islands; Eddie & al. (2003); AY 322045 & AY 331458. *Codonopsis dicentrifolia* W. W. Sm.; Nepal; Eddie & al. (2003); AY 322046 & AY 331459. *Craterocapsa congesta* Hilliard & B.L. Burtt; Lesotho; Eddie & al. (2003); AY 322049 & AY 331462. *Cynanthus lobatus* Wall. ex Benth; Eddie & al. (2003); AY 322050 & AY 331463. *Diosphaera rumeliana* (Hampe) Bornm.; cultivated in University of Edinburgh; Eddie & al. (2003); AY 322051 & AY 331464. *Edraianthus graminifolius* (L.) A. DC.; cultivated in Royal Botanic Gardens Edinburgh; Eddie & al. (2003); AY 322052 & AY 331465. *Feeria angustifolia* (Schousb.) Buser; Morocco; Eddie & al. (2003); AY 322054 & AY 331467. *Gadellia lactiflora* (M. Bieb.) Schulkina; cultivated in Royal Botanic Gardens Edinburgh; Eddie & al. (2003); AY 322055 & AY 331468. *Galactites tomentosa* Moench.; Sussana & al. (2006); AY 826285. *Githopsis diffusa* A. Gray; Eddie & al. (2003); AY 322056 & AY 331469. *Hanabusaya asiatica* Nakai; South Korea; Eddie & al. (2003); AY 322057 & AY 331470. *Heterocodon rariflorum* Nutt.; USA, California; Eddie & al. (2003); AY 322058 & AY 331471. *Jasione montana* L.; Spain; Eddie & al. (2003); AY 322062 & AY 331475. *Legousia falcata* (Ten.) Fritsch; cultivated in Royal Botanic Gardens Edinburgh and University of Texas; Eddie & al. (2003); AY 322064 & AY 331477. *Leptocodon gracilis* Lem.; Nepal; Eddie & al. (2003); AY 322066 & AY 331479. *Michauxia tchihatcheffii* Fisch. & C.A. Mey.; cultivated in Royal Botanic Gardens Edinburgh; Eddie & al. (2003); AY 322068 & AY 331480. *Muschia aurea* Dumort.; cultivated in Royal Botanic Gardens Edinburgh and University of Texas; Eddie & al. (2003); AY 322067 & AY 331481. *Petromarula pinnata* (L.) A. DC.; Greece; Eddie & al. (2003); AY 322069 & AY 331482. *Physoplexis comosa* (L.) Schur; cultivated in Royal Botanic Gardens Edinburgh; Eddie & al. (2003); AY 322070 & AY 331483. *Phyteuma orbiculare* L.; Eddie & al. (2003); AY 322071 & AY 331484. *Roella ciliata* L.; Eddie & al. (2003); AY 322074 & AY 331487. *Symphandra armena* (Stev.) A. DC.; cultivated in Royal Botanic Gardens Edinburgh; Eddie & al. (2003); AY 322075 & AY 331488. *Trachelium caeruleum* L.; cultivated in University of Edinburgh; Eddie & al. (2003); AY 322078 & AY 331491. *Triodanis leptocarpa* (Nutt.) Nieuwl.; USA, Texas; Eddie & al. (2003); AY 322079 & AY 331492. *Wahlenbergia hederacea* L.; Portugal, Sierra de Monchique, Talavera & al.; HQ 407556.

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